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The Evolution of a Response to Smoke within the Arthropoda

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The Evolution of Arthropods Response to the Presence of Smoke

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Albert Meier Digitally signed by Albert Meier Date: 2024.07.11 16:25:23 -05'00'

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Abstract

Many animals have a survival instinct to flee in response to fire, but do they respond to smoke alone? Many arthropods respond to fire or smoke by moving in the opposite direction (a negative taxis) to obtain shelter. At the species level, taxa that have adapted a behavioral response to fire increase their fitness. This response behavior has been observed in many terrestrial arthropods. Still, the behavior is currently unknown for marine, aquatic, or cave arthropods, which are atypically exposed to smoke or fire. This project assesses how often behavioral adaptation to smoke avoidance may have evolved within Arthropoda. Twenty-two different orders within Arthropoda were used to assess how many times a behavioral response to smoke may have evolved. The data collected was the total amount of time that an individual moved during the control and experimental trials, measured in seconds. Pairwise t-tests were performed on orders and selected families to assess which taxa had a response to smoke. The insect orders that significantly responded to smoke in the experimental trials and included members of the Coleoptera, Lepidoptera, Orthoptera, Plecoptera, Archaeognatha, and Hemiptera. Based on these results, the behavioral trait of responding to smoke seen in an increase in movement is polyphyletic within Arthropoda; six different evolutionary hypotheses were proposed from these results. The most parsimonious hypothesis outside of the Insecta involves two gains of a behavioral adaptation to smoke - in both the Araneae and Opiliones – and is based on earlier studies. In this study, two hypotheses within the Insecta for the evolution of a behavioral response to smoke are equally parsimonious. The first involves one gain in the common ancestor of all insects with a loss in the Paleoptera (old winged insects), while the second involves two separate gains of a response in both the apterygotes (wingless insects) and neopterans (new winged insects).

Acknowledgments

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I would next like to thank my advisor, Dr. Albert Meier, for his continued support throughout this project, guidance for the last six years, and for bringing me up in the world of conservation, ecology, and biology.

To the other members of my committee: Thank you, Dr. Keith Philips, for your continued guidance and knowledge of the world of arthropods, especially the taxa within Insecta, and for assistance in collecting and identifying arthropods collected. Thank you, Dr. Doug McElroy, for providing me with guidance and direction in the statistics to use in analyzing the data in this project.

Thank you to Elizabeth Strasko, Marley Askren, Mahamad Miya, Jerica Eaton, Jack Merloa-Lapson, Julia Brzezicki, and the other graduate students for their assistance in collecting identifying arthropods. Additionally thank you for sitting through hours of practice presentations, and for their overall general support in getting through graduate school.

Lastly, many thanks and appreciation to my family and friends, who offered constant support and encouragement. Special thanks to my girlfriend, Paige, and her son, Boudin Pierre, for listening to all of my problems and frustrations when things weren't operating as planned in this project and for encouraging me to keep working on this project when I would rather be a bum. Thanks to my parents, John and Pamela, and siblings, John and Mallory, for always checking my progress and encouraging me to finish this project. Thanks to everyone for helping me grow as a biologist and person throughout this process.

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Introduction

Landscape fires, including wild and anthropogenic fires, occur globally and almost exclusively in vegetated areas (Fried et al., 2004; Roberts & Wooster, 2021). Many systems benefit from landscape fires ecologically, but not all organisms within a system are well suited to the presence of fire. Studies of biomes with plant and animal species adapted to fire, and which may be dependent upon this environmental event for their long-term survival, demonstrate that fire plays an important role in shaping the ecology and evolution of species (Bond et al., 2005; Keane, 2008; Pausas, 2018). Periodic wildfire maintains the integrity and species composition of many ecosystems, particularly those that include taxa adapted to fire (Savage et al., 2000; Pausas, 2004). At the system level, fire disturbance enhances heterogeneity by creating new niches and potentially enhancing the evolutionary process. At the species level, taxa that have adapted a behavioral response to fire since their goal is to increase their fitness (Pausas & Keeley, 2019).

Evolutionary history of arthropods

Arthropods are the most diverse phylum in the animal kingdom. Arthropoda branched off from a common ancestor around 575 million years ago (Figure 1) (Misof et al 2014; Budd & Tecford 2009; Regier et al. 2010). Terrestrial arthropods began to colonize and evolve on land around 450 million years ago when terrestrial ecosystems originated (Misof et al. 2014; Aria 2022). Members of this phylum are found in every continent and almost every ecosystem on Earth. Arthropods are found in various ecosystems, including some that frequently experience fires and others that do not. The habitats where arthropods can be found include terrestrial ecosystems - caves, forests, deserts, grasslands, tundra, fossorial habitats - and aquatic ecosystems including marine and fresh water, both lentic and lotic habitats (Howarth, 1983;

Lancaster & Downes, 2013; Short, 2017). The diversity of arthropods and the ecosystems in which they are found have facilitated the evolution of a diversity of behaviors, life cycles, and life histories (Foottit & Adler, 2009; Hill et al., 2016; Román-Palacios et al., 2022).

Plants and arthropods co-evolved together on land, and since both clades contain the most described macroorganism diversity, their interactions with each other are very important (Figure 2) (Regier et al., 2010). Importantly, plants are the most common type of biofuel that feeds landscape fires. The earliest signs of fire are charred remains of vegetation 440 mya (Glasspool et al., 2004), shortly after the class Insecta evolved 450 mya (Misof et al. 2014). Hence, most of the terrestrial arthropod taxa have been exposed to fire and its emissions (light, smoke, sound, and heat) during their evolution.

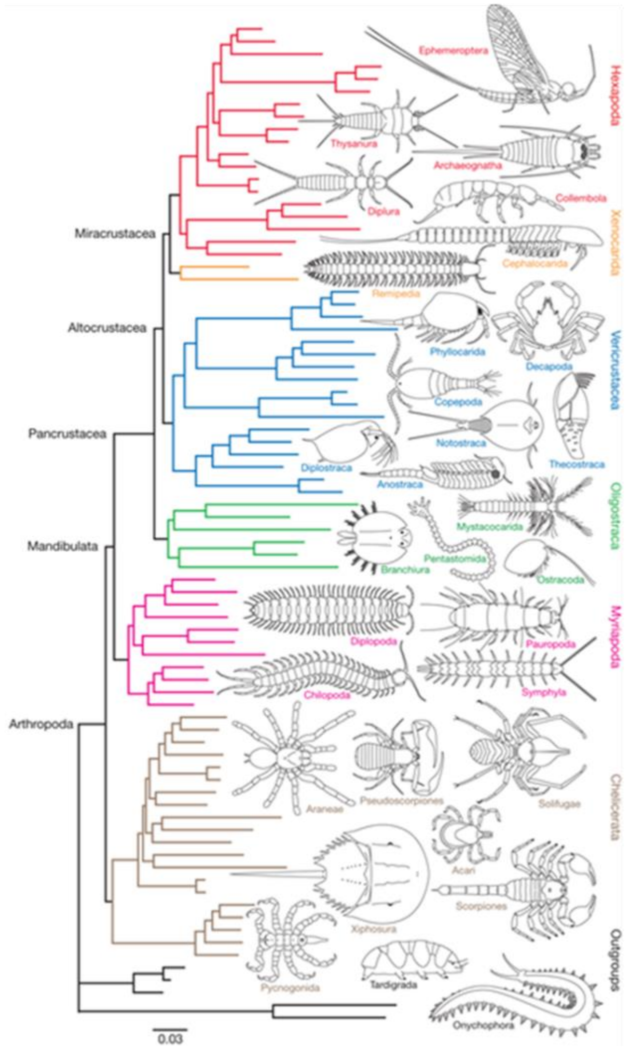


Figure 1. Phylogenetic tree of Arthropoda and its subphyla, represented in different colors (Regier et al. 2010)

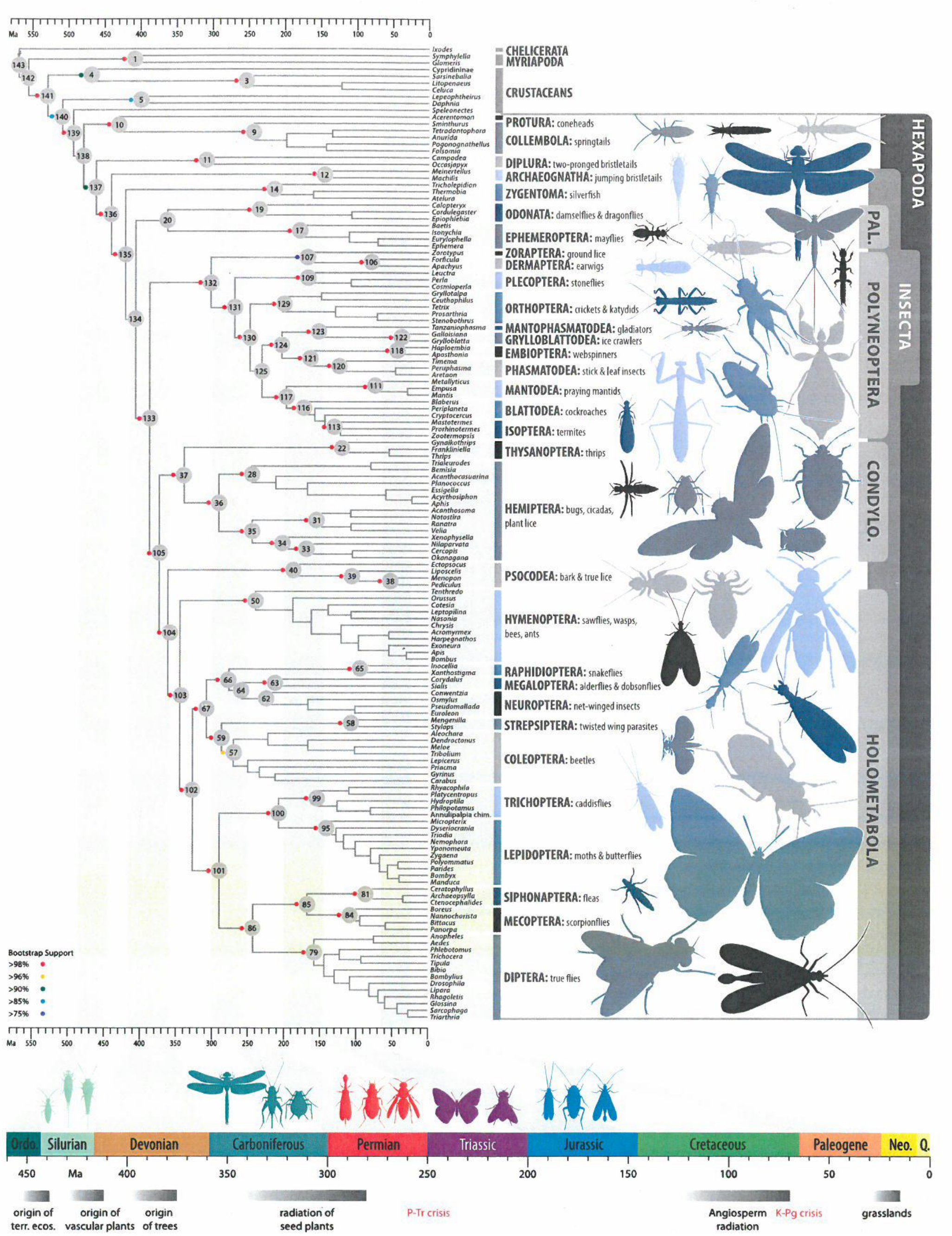


Figure 2. Phylogenetic tree illustrating how arthropods evolved along with the origins of terrestrial ecosystems and plants (Misof et al. 2014).

Fire events altered due to anthropogenic disturbance

Anthropogenic activity has altered natural fire regimes in severity, frequency, scale, and intensity (Syphard et al., 2007). Three primary mechanisms are now altering fire regimes: fire suppression, the consequences of climate change, and increased anthropogenic ignitions (Keeley & Fothermeham, 2003). Fire suppression and climate change create fire regimes that increase severity, intensity, and scale due to increased biofuel but fire suppression decrease frequency, while climate change increases frequency (Komarek, 1974). These types of fires lead to a higher mortality rate of plants and animals in the area affected by the fire and smoke (Liu, 2022; Jain, 2024). Increased anthropogenic ignitions reduce severity and intensity, but fire frequency increases and the scale can vary. This has had a detrimental effect on some habitats where fires occur with far greater frequency than that to which species are adapted. These three mechanisms alter fire regimes and affect the diversity of organisms found in an area. Further, pollutants like smoke and ash in the air are cues for mobile organisms to change their behavior so that they can survive (Robert, 2021).

One example of how fire regimes have been altered are the Canadian fires of 2023. This massive set of fires was caused by fire suppression in the area for over one hundred years and the climate crisis increasing the air temperature and temporal changes in the precipitation patterns (Jain et al., 2024). The severity of these fires was very high, and it will take a long time for this area to recover. The intensity of that fire season was extreme with numerous crown fires. The scale of the area that was burned was 7.8 million hectares, and smoke emissions traveled hundreds to thousands of kilometers downwind (MacCarthy et al., 2024).

Arthropod ecology with fire and smoke

The first records of arthropods having a behavioral response to fire were seen in agricultural areas where fires were started in order to reduce pest species (e.g., locusts, grasshoppers, and flies) and to reduce wildlife impacts on agricultural productivity (Branson, 2006; Polito, 2013; Evans, 2013). These targeted insects exhibit a flee response (negative taxis) in the presence of fire (Evans, 2013) and leave the agricultural areas before any negative impacts.

The lack of separation of the response to heat versus smoke in insects was discussed in a review paper on the effect of landscape fire smoke exposure (Liu et al., 2022). These authors noted that previous research focused primarily on chemosensory response rather than the behavioral response, and that the few taxa studied had different responses to smoke. For example, potter wasp *Eumenes curvata L.* (Hymenoptera: Vespidae) were attracted to smoke while the honeybee *Apis mellifera capensis* Escholtz (Hymenoptera: Apidae) either fled or flew to their nest (Brues, 1950; Tribe et. al., 2017; Newtons, 2000). Also noted was that honeybees temporarily suppress aggressive behavior when exposed to smoke (Harrison et al., 2019). The flight performance of the painted lady butterfly (*Vanessa cardui L.*) when exposed to smoke was negatively impacted (Liu et al., 2020). Two Diptera taxa were shown to have a behavioral response to smoke. *Hypocerides nearcticus* Peterson (Diptera: Phoridae) responded positively to smoke (positive fumotaxis), while *Anopheles gambiae* Coggeshall (Diptera: Culicidae) responded negatively (negative taxis) (Klocke et al., 2011; Milberg et al., 2015; Gibbins, 1933; Bockarie et al., 1944; Biran et al., 2007 However, these studies did not distinguish between the effects of smoke versus heat. These insects may have been attracted to heat via infrared sensors, light via photoreceptors, or smoke via chemoreceptors (Herrmann 1998, Foottit 2009, Evans 2010).

Dell et al. (2017) conducted a study to assess if arthropods had a response to fire with a focus on noise created by burning vegetation, although it is unclear how they could separate the effect of heat and/or smoke from fire noise. Regardless, they found more non-flying arthropods collected in the burned sticky traps on tree trunks compared to unburned areas.

Lee et al. (2016) distinguished the effects of smoke on a pitcher plant moth (*Exyra semicrocea* Guenée). The moths displayed negative taxis by leaving the trumpet of the pitcher plant when smoke was puffed inside (Lee et al., 2016). Trials on the effect of smoke on spiders noted a response of either dropping off the web or moving away from the smoke (Bell and Meier, unpublished).

The main questions of this project are when arthropods evolved a response to smoke and how many times it evolved. Further hypotheses tested are if a response to smoke was either gained or lost during transitions to various environments, including from the sea to land, land to fresh water and from above-ground to cave ecosystems. Lastly, this study will also assess if arthropods in environments that lack fires, such as caves, have retained a behavioral response to smoke detection.

Methods

Taxa tested

The trials used 299 individuals from 22 orders and 59 families within the Arthropoda. The following arthropod taxa were tested: 81 individuals of Coleoptera (beetles), 25 individuals of Lepidoptera (butterflies and moths), 27 individuals of Orthoptera (grasshoppers, katydids, and crickets), nine individuals of Plecoptera (stoneflies), nine individuals of Archaeognatha (jumping bristle tails), 16 individuals of Hemiptera (true bugs), 10 individuals of Mantodea (mantids), 10 individuals of Opiliones (harvestmen), 23 individuals of Decapoda (hermit crabs), 13 individuals of Isopoda (pill bugs and sowbugs), three individuals of Araneae (spiders), 14 individuals of Scorpiones (scorpions), four individuals of Hymenoptera (bees, ants and wasp), six individuals of Diptera (true flies), 12 individuals of Xiphosura (horseshoe crabs), six individuals of Trichoptera (caddisflies), two individuals of Mecoptera (scorpionflies), 10 individuals of Odonata (damselflies and dragonflies), twelve individuals of Polydesmida (millipedes), two individuals of Scolopendromorpha (centipedes), five individuals of Ephemeroptera (mayflies). Sample sizes range from 81 in Coleoptera to 2 in Scolopendromorpha and Mecoptera with a mean sample size of 14.2 ± 3.0.

Collection of Arthropods

Arthropod specimens were collected from April 21st to October 4th, 2023 in southcentral Kentucky, at the WKU Green River Preserve (GRP, Hart Co.), Barren River Lake (Barren Co.), Drakes Creek (Warren Co.), Friendship Cave (Warren Co.), and in several locations in Bowling Green. Arthropods were collected via sweep netting, at a blacklight, and via hand collecting. Specimens were collected exclusively on private property or public lands and hence this study required no permit. Specimens were tested for their response to smoke within 48 hours of collection.

Twelve marine hermit crabs (*Clibanarius vittatus* Bosc) and 12 horseshoe crabs (*Limulus polyphemus* Harriot) were purchased from Gulf Shore Specimens (Panacea, Florida) These arthropods were kept in a saltwater tank at 75 degrees Fahrenheit and a salinity level of 28 parts per thousand (ppt). Horseshoe crabs were fed frozen brine shrimp every two days, and the marine hermit crabs every day. Twelve terrestrial hermit crabs (*Coenobita clypeatus* Fabricius) from Backwater Reptiles (Rockland, California). Two Caribbean hermit crabs were kept in each 10-gallon terrarium (total of six terraria) with six inches of a 50/50 mixture of loose coconut fiber substrate and sand. They were fed raisins and dried omnivore mix (Thrive®) every two days, and a petri dish full of water was supplied.

Behavioral trials

Arthropod behavioral responses were tested in a plastic arenas (both a control and a test arena) made of Tupperware® containers (35 cm x 25 cm in size) with three created openings. One opening had a 30 cm long PVC® pipe that could be connected to a bee hive smoker (Honey Keeper Hive Smoker®) (Figure 3). The pipe length prevented heat from entering the smoke trial arena, as Lee et al. (2016) recorded a maximum temperature increase of only 0.1 °C using a shorter pipe length of 10 cm. The other two openings, on the cover and opposite side, had a fine mesh screen to prevent pressure buildup in the arena (Figure 4).

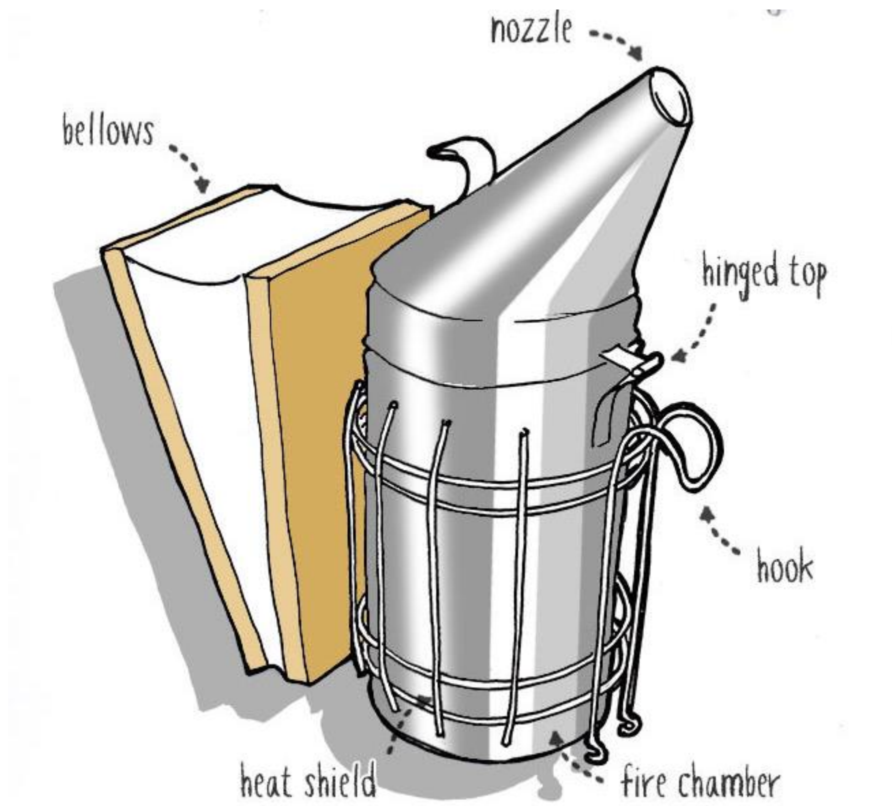
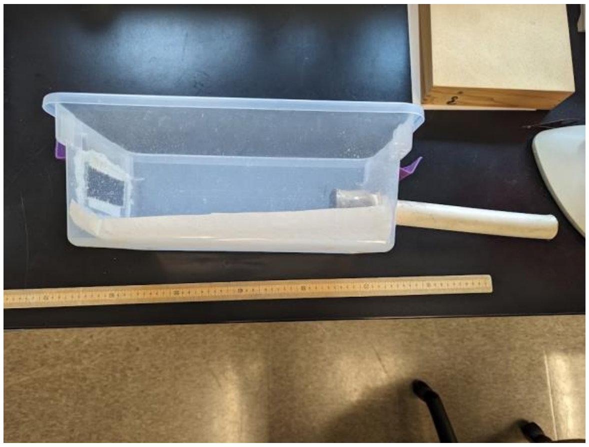


Figure 3. Bee hive smoker used in this study. The image is from https://beekeepinginsider.com/how-to-use-a-bee-smoker/



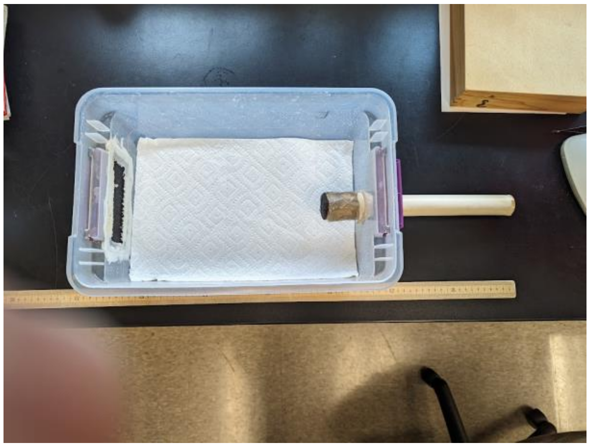


Figure 4. Top and side views of the trial arenas.

The control arena received air from the smoker without any fuel burning inside the fire chamber. The experimental arena received smoke from the smoker with burning fuel. One gentle puff of air (control arena) or smoke (experimental test arena) was introduced every 3 seconds for 30 seconds total. Each specimen was first tested in the control chamber and then the experimental chamber. After the control trial, the individual arthropod tested was moved to the experimental trial and then given 10 minutes to acclimate before smoke was introduced. Each specimen was used only once for each of the trials. These tests were conducted in a laboratory under a fume hood. Individuals were euthanized after the trials for identification at a later time.

Data Collection and Analysis

The qualitative data was an insect identification number as individuals were later identified to at least genus, with a majority to species, after the trials were run. For each individual, response to either the control or smoke treatment was quantified as the amount of time spent moving during the duration of the 30-second trial, measured in seconds. Pairwise t-tests were used to determine the extent of differences in response between the control and smoke trials. A total of two pairwise t-tests were conducted: One at the order and family level. For each family of tests, a sequential Bonferroni correction was used to determine significance. The families included in the family-level t-test were selected if they are found in unique environments (i.e., aquatic or cave habitats); to the purpose here was to see if the environment they are adapted to (that is at least potentially protected from fire) has an effect on their response to smoke compared to the other taxa tested . Additional families were not tested since coverage within each order was generally sparse for adequate statistical testing. Figures 5-10 were created using the phylogenies of Giribet & Edgecombe 2019, Bracken et al. 2010 and Tihelka et. al. 2021.

Results

Only six of the 22 orders of Arthropoda tested showed a significant response to smoke; these included Coleoptera, Lepidoptera, Orthoptera, Plecoptera, Archaeognatha, and Hemiptera (Table 1). These orders all had significantly longer periods of movement during the experimental trial compared to the control trial, indicating a flee response (behavioral adaptation) to the smoke. All the orders that showed a response are members of the Insecta. One order, Archaeognatha, is an Aperygota (subclass), a group of wingless insects. The others are all members of the Neoptera (a subclass known as the "new" winged insects) that have the ability to fold their wings. Notably, neither of the two Paleoptera orders that cannot fold their wings (a subclass known as the "old" winged insects) nor any of the non-insect arthropod orders tested showed a significant time difference between trials, suggesting that these groups do not have a response to smoke.

Table 1. Results of pairwise t-tests of the response to smoke for each order tested within Arthropoda. Asterisks indicate a significant difference between control and smoke trials based on sequential Bonferroni-adjusted criteria. Ephemeroptera had no movement in either of the trials.

Order	Habitat	Sample size	Control Time (s) with SE	Experimental Time (s) with SE	Mean Difference with SE	t-value	p-value for t-test	p-value for Significance
Coleoptera	Terrestrial & Aquatic	81	8.2 ± 1.3	21.2 ± 1.3	12.96 ± 1.65	7.837	*<0.001*	0.002

Lepidoptera	Terrestrial	25	0.2 ± 0.2	19.7 ± 2.2	19.48 ± 2.19	8.913	*<0.001*	0.002
Orthoptera	Terrestrial	27	5.8 ± 2.1	19.3 ± 2.0	13.52 ± 2.27	5.962	*<0.001*	0.002
Plecoptera	Aquatic	9	1.9 ± 1.4	24.0 ± 2.7	22.11 ± 2.59	8.538	*<0.001*	0.002
Archaeognatha	Terrestrial	9	10.2 ± 3.9	26.6 ± 1.7	16.33 ± 3.17	5.151	*<0.001*	0.003
*Hemiptera	Terrestrial	16	5.8 ± 2.4	19.2 ± 3.43	13.38 ± 3.76	3.554	*0.003*	0.003
Mantodea	Terrestrial	10	15.1 ± 4.5	29.0 ± 0.9	13.90 ± 4.21	3.302	0.009	0.004
Opiliones	Terrestrial	10	10.8 ± 4.5	26.2 ± 3.0	15.40 ± 5.68	2.711	0.023	0.004
Decapoda	Terrestrial & Marine	23	9.2 ± 2.9	3.2 ± 1.9	5.96 ± 1.86	2.206	0.038	0.004
Isopoda	Terrestrial	13	23.0 ± 2.9	17.4 ± 3.2	-5.62 ± 2.70	2.080	0.059	0.005
Araneae	Terrestrial	3	13.3 ± 4.8	29.3 ± 0.6	16.00 ± 4.51	3.548	0.071	0.005
Scorpiones	Terrestrial	14	0.3 ± 0.2	2.9 ± 1.5	2.64 ± 1.40	1.881	0.082	0.006
Hymenoptera	Terrestrial	4	13.5 ± 7.8	28.3 ± 1.8	14.75 ± 6.93	2.130	0.123	0.006
Diptera	Terrestrial	6	0.2 ± 0.2	9.8 ± 6.2	9.66 ± 6.11	-1.581	0.174	0.007
Xiphosura	Marine	12	6.9 ± 3.7	2.5 ± 2.5	-4.42 ± 3.50	-1.262	0.232	0.008
Trichoptera	Aquatic	6	13.2 ± 6.1	20.7 ± 3.4	7.50 ± 5.95	1.260	0.263	0.016
Mecoptera	Terrestrial	2	22.0 ± 6.0	25.5 ± 3.5	3.50 ± 2.50	1.400	0.394	0.013
Odonata	Aquatic	10	3.7 ± 2.7	4.5 ± 2.9	0.80 ± 1.69	0.474	0.656	0.017
Polydesmida	Terrestrial	12	24.8 ± 3.5	25.7 ± 2.7	0.91 ± 2.90	0.313	0.760	0.025
Scolopendromorpha	Terrestrial	2	15.0 ± 15.0	14.0 ± 14.0	-1.00 ± 29.00	0.034	0.978	0.05
Ephemeroptera	Aquatic	5	0 ± 0	0 ± 0	0 ± 0	N/A	N/A	N/A

The families included in the family-level t-test were selected if they are found in unique environments that lack fire (i.e., aquatic or cave environments) or had aquatic immature stages (Table 2). Hydrophilidae and Gyrinidae are aquatic families within Coleoptera. One Carabidae tested (Trechinae: Trechini: *Neaphaenops* sp.) is a cave-dwelling taxon of Coleoptera. Rhaphidophoridae is a cave-dwelling family within the Orthoptera. Diogenidae is a marine family of hermit crabs within Decapoda crustaceans while the Coenobitidae is a terrestrial family of the same group. The Hemiptera family Cicadidae develops in a fossorial below-ground habitat as a nymph and emerges as an above-ground flying adult. Only two of these seven families tested, the Hydrophilidae and Rhaphidophoridae, showed a significant difference in response to smoke between control and smoke trials; both families are members of the Neoptera and showed an increase in movement during the experimental trials, suggesting a negative reaction to the smoke.

Table 2. Pairwise t-test of each family in a unique habitat collected within Arthropoda. The names with asterisks next to them and in yellow have a significant difference between the trials. The significant p-value was found using the sequential Bonferroni correction. Coenobititdae had no movement in either of the trials.

Family	Habitat	Sample size	Control Mean Time (s) with SE	Experimental Mean Time (s) with SE	Mean Difference with SE	t-value	p-value	p-value for Significance
Hydrophilidae	Aquatic	5	1.0 ± 1.0	27.0 ± 1.9	26.00 ± 3.67	15.820	*<0.001*	0.008
Rhaphidophoridae	Cave	11	0 ± 0	16.2 ± 11.7	16.18 ± 11.70	4.600	*<0.001*	0.010
Diogenidae	Marine	12	17.6 ± 4.3	6.2 ± 11.8	-11.42 ± 16.35	2.420	0.0341	0.013
Carabidae	Cave	10	14.2 ± 4.2	23.7 ± 9.4	9.50 ± 15.56	1.889	0.096	0.017
Cicadidae	Terrestrial	4	5.3 ± 5.3	11.8 ± 14.6	6.50 ± 8.19	1.588	0.211	0.026
Gyrinidae	Aquatic	5	15.0 ± 6.7	21.0 ± 12.5	6.00 ± 23.02	0.582	0.591	0.050
Coenobitidae	Terrestrial	11	0 ± 0	0 ± 0	0 ± 0	NA	NA	N/A

Outside of Insecta

Figures 5 and 6 show the phylogenetic relationship of the major lineages of the Arthropoda tested in this study; significant responses to smoke are mapped onto these phylogenies. These data do not support a behavioral adaptation to detect smoke outside of Insecta either due to a lack of response or due to a small sample size which affected the ability to attain significance (Figure 5). The second hypothesis has one gain (at a minimum) of a behavioral adaptation for the Insecta while the gains of this response in the Araneae and Opiliones are based on previously published data (Dell et al. 2017 and Bell & Meier, unpublished, Figure 6).

Within Insecta

The phylogenetic trees (Figures 7, 8, 9, and 10) show the relationship between the different taxa at the order level within Insecta included in this study. Four different hypotheses can be drawn from the results of the pairwise t-test (Table 1) within Insecta. The first hypothesis is that there are six gains in the adaptation to smoke within Insecta in the groups as follows: Archeognatha, Plecoptera, Orthoptera, Hemiptera, Coleoptera, and Lepidoptera (Figure 7). The second hypothesis and equally parsimonious is that there was only one gain within Insecta and five losses in the Paleoptera (Odonata and Ephemeroptera), the common ancestor of Phasmatodea + Mantodea, Hymenoptera, the common ancestor of the Diptera + Mecoptera, and Trichoptera (Figure 8). The third and fourth hypotheses are what might be considered as the holistic picture of how a smoke behavioral adaptation evolved within the Insecta, and are also equally parsimonious. The third hypothesis is a gain of smoke avoidance evolving separately in both the Archeognatha and Neoptera (Figure 9). The fourth hypothesis has one gain of a behavioral adaptation to smoke at the base Insecta and a loss in the Paleoptera (Odonata and Ephemeroptera) (Figure 10).

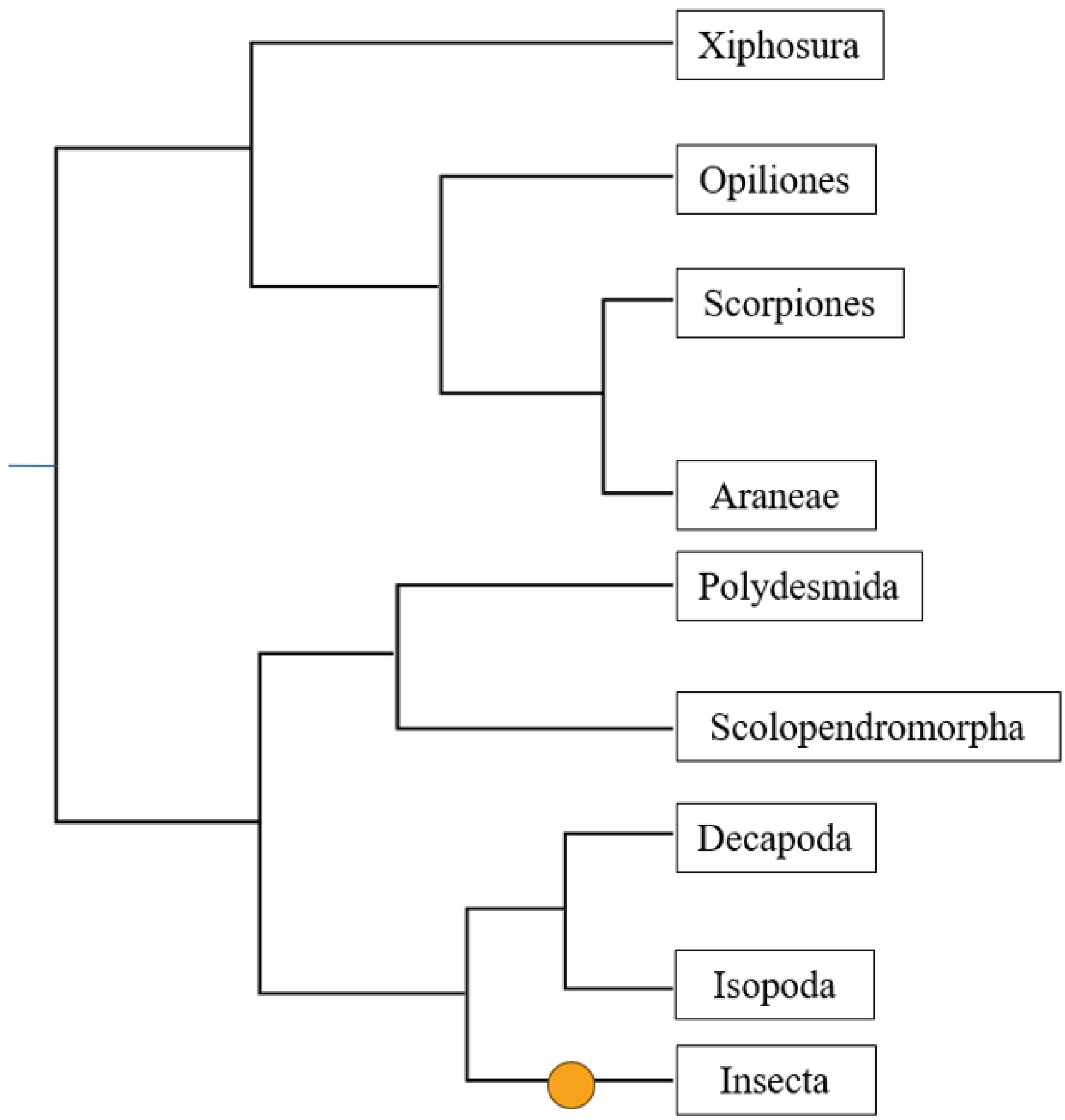


Figure 5. The first hypothesis in the Arthropoda: no gains of a behavioral adaptation to smoke outside of the Insecta. Evolution of an adaptation gain is indicated by an orange circle. The figure was created using the phylogenies of Giribet & Edgecombe, 2019, and Bracken et al., 2010.

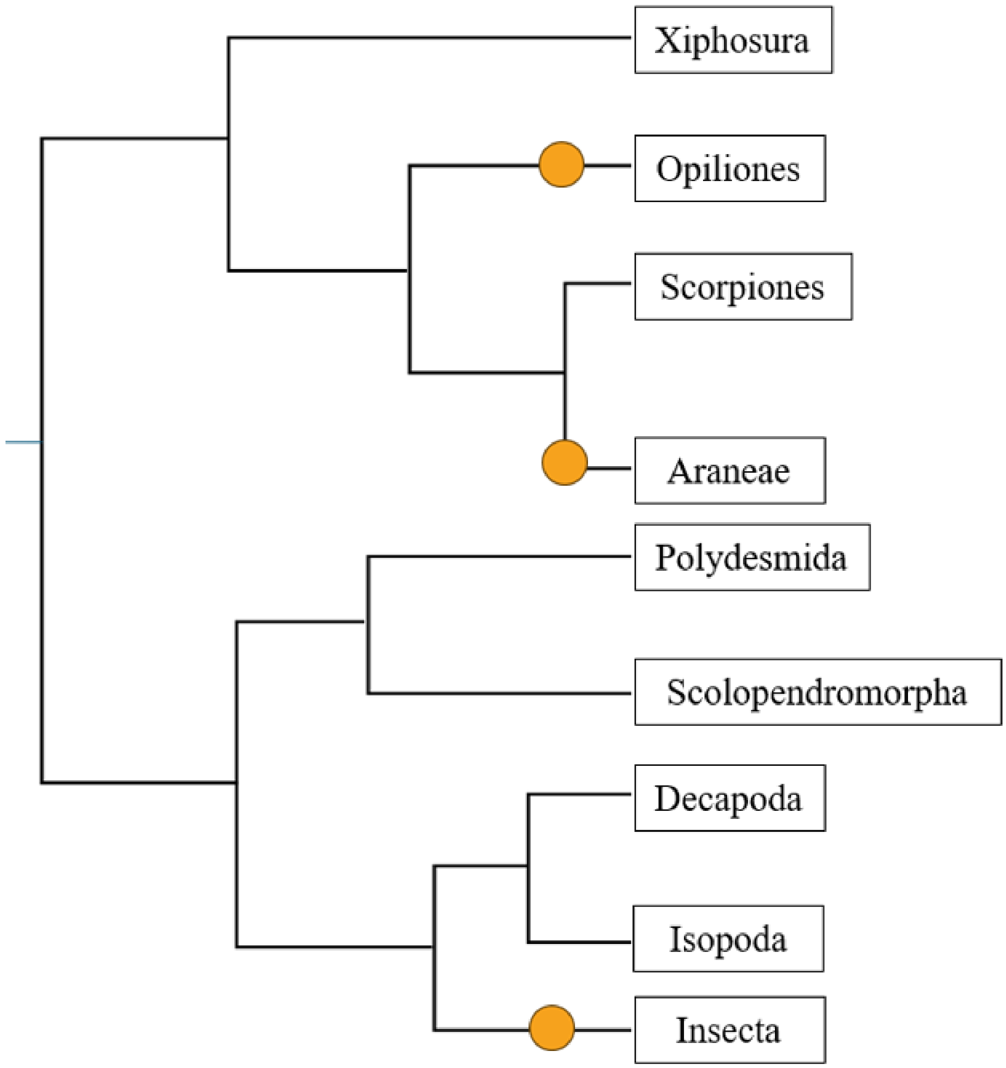


Figure 6. The second hypothesis in the Arthropoda: one gain of behavioral adaptation to smoke based on this study within Insecta and two adaptations to smoke within Araneae and Opiliones based on previously published data (Dell et al. 2017, Bell & Meier, unpublished). Evolution of an adaptation gain is indicated by an orange circle. The figure was created using the phylogenies of Giribet & Edgecombe, 2019, and Bracken et al., 2010.

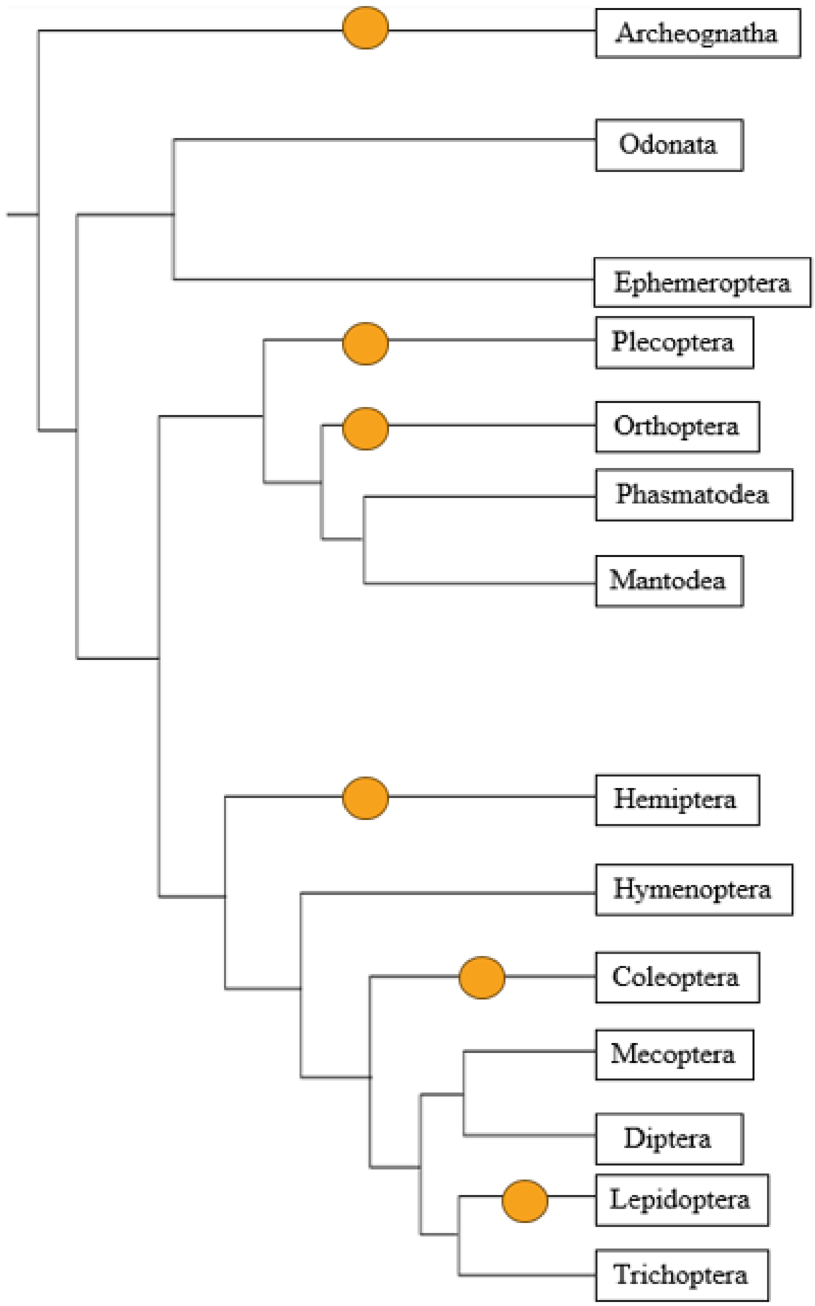


Figure 7. The phylogenetic tree above displays the first hypothesis within Insecta, which is that six gains of an adaptation to smoke occur within Insecta: Archeognatha, Plecoptera, Orthoptera, Hemiptera, Coleoptera, and Lepidoptera. Evolution of an adaptation gain is indicated by an orange circle. The figure was created using the phylogeny of Tihelka et. al., 2021.

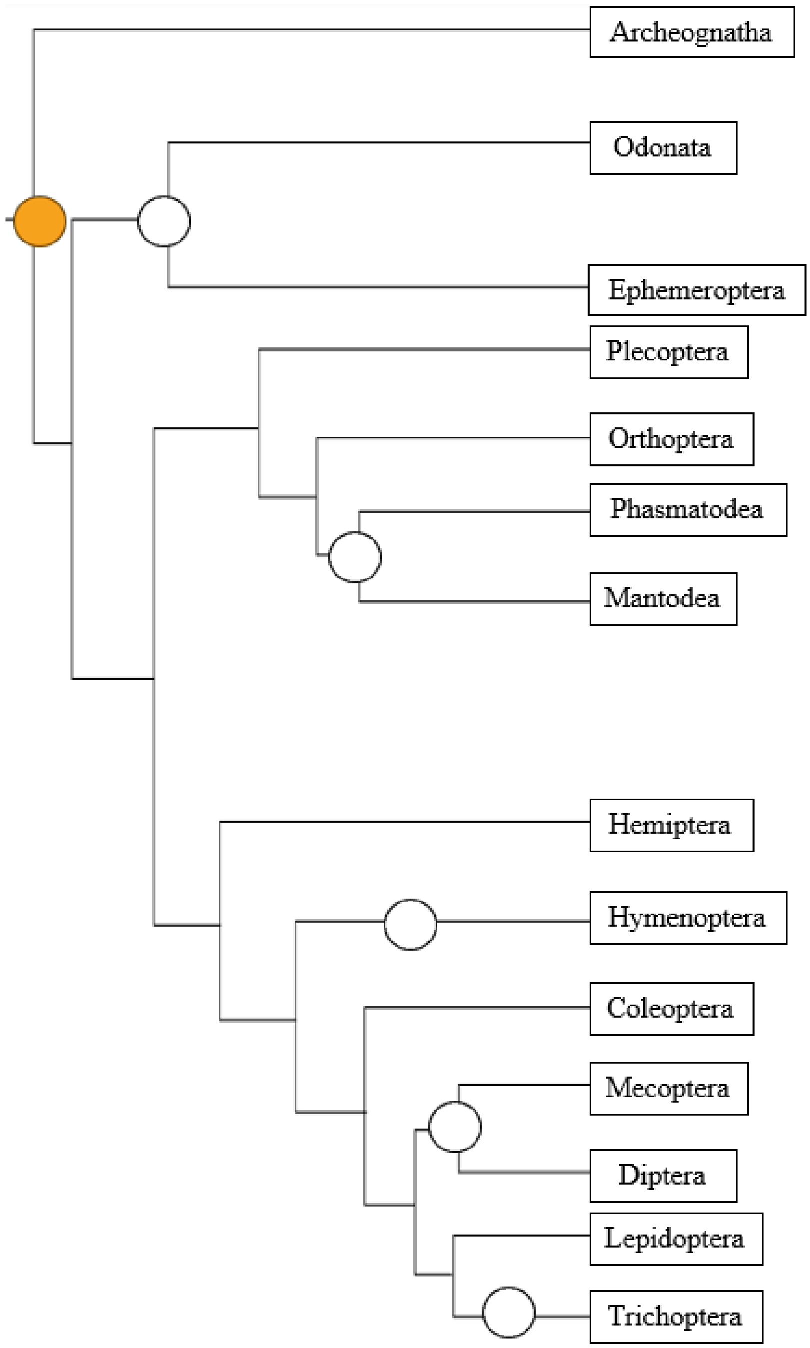


Figure 8. The phylogenetic tree above displays the second hypothesis within Insecta: one gain within Insecta (orange circle) and five losses (white circle) for the Paleoptera (Odonata and Ephemeroptera), the common ancestor of Phasmatodea + Mantodea, Hymenoptera, the common ancestor of the Diptera + Mecoptera, and Trichoptera. Note that two independent gains in the Diptera and Lepidoptera are equally parsimonious. Evolution of an adaptation gain is indicated by an orange circle. The figure was created using the phylogeny of Tihelka et. al., 2021.

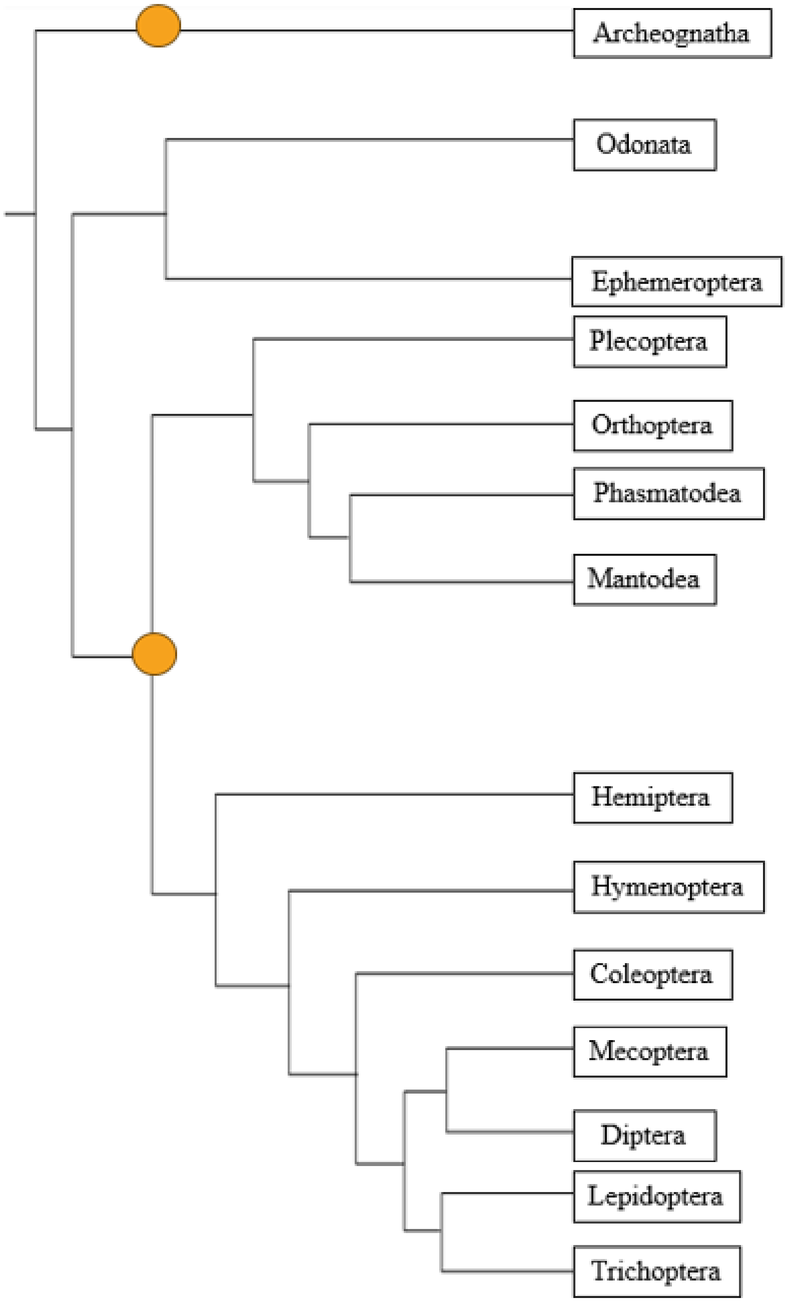


Figure 9. The phylogenetic tree above displays the third hypothesis within Insecta: two gains of an adaptation to smoke avoidance in the Archeognatha and Neoptera indicated by an orange circle. The figure was created using the phylogeny of Tihelka et. al., 2021.

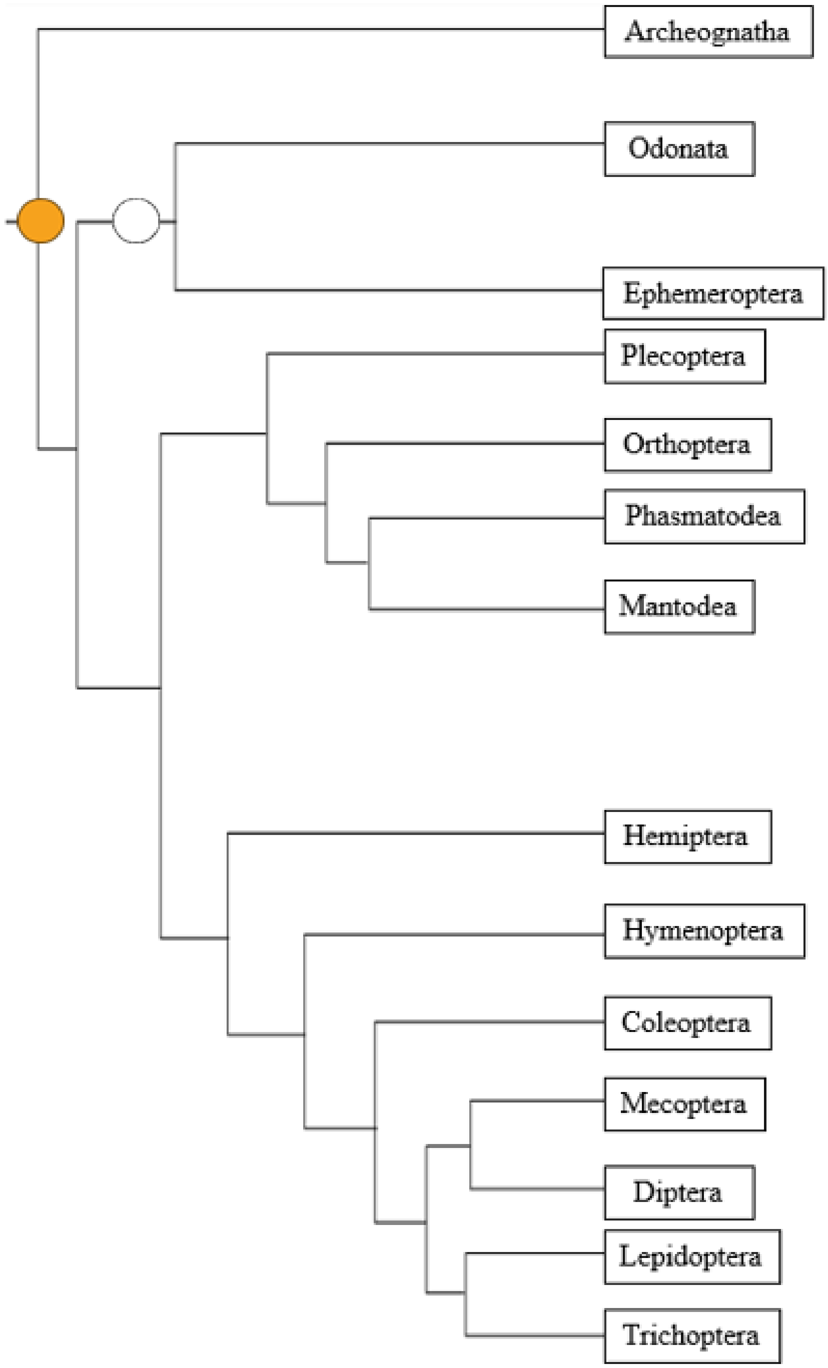


Figure 10. The phylogenetic tree above displays the fourth hypothesis with one gain of an adaptation to smoke within Insecta, with the loss of this trait in the Paleoptera (Odonata and Ephemeroptera). The adaptation gain indicated by the orange circle and a loss with the white circle. The figure was created using the phylogeny of Tihelka et. al., 2021.

Discussion

Behavioral response trait to smoke

This study suggests that the evolution of the ability to detect and avoid smoke in the arthropods only evolved within the Insecta. The literature on the behavioral response to fire, at least in the insects, also supports this premise and that it is a negative taxis (Kral et al., 2017; Liu et al., 2022). Before this study, there has been no previously published research to show that any terrestrial Arthropoda outside of the Insecta have evolved a behavioral adaptation to detect smoke and/or fire to increase their survival (i.e., fitness). If a population does not evolve a behavioral adaptation to this type of disturbance, fire could cause extirpation and, in extreme cases, extinction of a species.

Effects of Habitat

Assessing the responses of the different taxa with respect to the environments in which they live (and relative to a phylogeny) can suggest how and why arthropods groups may have evolved a response to smoke. In this study, all of the arthropods that had a behavioral response to smoke are within the Insecta. The order level pairwise t-test (Table 1) showed that the neopteran Plecoptera with flying adults (and aquatic nymphs) do have a significant response to smoke. The taxa that did respond were various Neoptera that have flying adults and one Aperygota that is primitively wingless. In contrast, the Paleoptera (Odonata and Ephemeroptera) that similarly have flying adults but aquatic nymphs did not have a response to smoke. Notably, the the neopteran Plecoptera or stoneflies also have flying adults and aquatic nymphs but did respond significantly to smoke. While six orders had a response to smoke, some that were tested did not, but this may be due solely to small sample sizes (see below). Most of the arthropod taxa outside of Insecta that are either terrestrial and/or marine such as horseshoe and hermit crabs and those with terrestrial taxa like Isopoda did not have a response to smoke. Therefore, the results indicate that some environments such as marine may play a role in determining if a taxon has a response while others, and importantly where fire can occur, have evolved this ability due to natural selection.

Response to Smoke Outside of Insecta

The phylogenetic trees shown in Figures 5 and 6 depict the accepted relationships among different taxa at the order (and class level for the insects) within the Arthropoda and show that the behavioral adaptation to smoke likely evolved in both the Araneae and Opiliones and certainly the Insecta (Figure 5 and 6) based on this study and previously published data by Dell et al. (2017) on Opiliones and on the Araneae (Bell & Meier., unpublished). Neither of these two non-insect orders in this study showed a significant difference in the control compared to the experimental trials, but notably the Araneae had a small sample size and the Opiliones had a high amount of movement during the control trials.

Response to Smoke Within Insecta

The evolutionary trees shown in Figures 7, 8, 9, and 10 depict four different hypotheses for the evolution of a response to smoke within the Insecta. The first hypothesis suggests that there have been six gains of response to smoke within Insecta: in the Archeognatha, Plecoptera, Orthoptera, Hemiptera, Coleoptera, and Lepidoptera (Figure 7). The second equally parsimonious hypothesis is that there was one gain at the base of the Insecta and five convergent losses in the Paleoptera (Odonata and Ephemeroptera), the common ancestor of Phasmatodea + Mantodea, the Hymenoptera, the common ancestor of the Diptera + Mecoptera, and the Trichoptera (Figure 8). Though data from this study support both hypotheses, the second with numerous losses of a response is less likely to be true due to literature on the behavioral response to smoke that indicates more widespread behavior of this type. For example, the Hymenoptera and Diptera have already been shown to have a response to smoke (Klocke et al., 2011; Milberg et al., 2015; Gibbins, 1933; Bockarie et al., 1944; Biran et al., 2007 Brues, 1950; Tribe et. al., 2017; Newtons, 2000, Harrison et al., 2017). There are also insect orders that had a high mean amount of movement in the experimental trials (Mantodea, Hymenoptera, Diptera, Mecoptera, and Trichoptera) which affected the significance, and with further testing with larger sample sizes and/or a different experimental setup (to reduce possible effects of disturbance such as movement of the observer outside the arena) may actually have a response to smoke. This study also did not include several of the orders within Insecta, so it is quite possible (or even likely) that more orders within Insecta actually do have a behavioral adaptation to smoke.

The data from this study and from previous studies made it possible to create two additional hypotheses of a behavioral adaptation to smoke within Insecta that are equally parsimonious. A third hypothesis shows only two gains of an adaptation to smoke (Figure 9) occuring in Archeognatha and Neoptera. A fourth hypothesis shows that there is one gain of an adaptation to smoke within Insecta and one loss at Paleoptera (Figure 10). Both hypotheses have all orders within the Insecta with a behavioral response to smoke except the paleopterans. Both of these hypotheses are equally parsimonious.

Limitation of the Study

The trial chambers used in this study likely affected the behavior, as there was no ability for the tested arthropod to move in a directed manner; hence the response appeared as a kinesis, or overall increase or decrease in an organism's movement, instead of a directional taxis. . Therefore, this study cannot determine if the behavioral response to smoke is fumokinesis or fumotaxis. Arthropods' behavioral response to smoke should be investigated further to determine (1) if the taxa that had no response in this study truly do not react to the presence of smoke and (2) if the arthropods that have a behavioral adaptation display a fumotaxis or fumokinesis. It would obviously be adaptive only if the response was a fumotaxis. At least one group of crustaceans, the woodlice, have actually been found to have a kinesis behavior with the effects of a higher temperatures and lower humidities (Cloudsley-Thompson, 1956). This may be an adaptation in that the increased movement increases the likelihood of escaping the unfavorable conditions.

One other issue in this study was that the lack of a significant response to smoke in some cases was due to small sample sizes. In particular, the orders Araneae, Hymenoptera, Mecoptera, and Scolopendromorpha were close to significant based on sequential Bonferroni criteria and, for at least the Hymenoptera and Diptera, a response has been found in other studies (Brues, 1950; Newtons, 2000; Tribe et. al., 2017; Harrison et al., 2019). Another issue was the insects that had a high amount of movement in the control trials. This may have resulted from being disturbed in various ways, such as movement of the observer, and may have affected the trials. One last issue are that some insects are very sensitive to temperature and humidity such as the carabid cave beetles (Apostolopoulos and Philips 2022). These trials occurred in a laboratory setting and may have caused individuals to move in an attempt to find a preferred temperature and humidity environment, independent of the presence of smoke and similar to the effects found with the woodlice.

Appendix

Only one individual of Phasmatodea was tested. Regardless, this individual did not move in a fleeing motion during the experimental trial, but had the most unique response in this study.This insect displayed its cryptic behavior of swaying back and forth during the smoke trial, which is considered anti-predatory (Feerer, 2012).

All trials were recorded with a SONY® video camera recorder CCD-TR910 Hi8 camera. These videos were used to measure the individual's start and end points in the trial for the distance data. The distance data was not used in the analysis of the behavior due to experimental design error.

This Appendix, part i, contains the models, ANOVA, and estimated marginal means of distance and time variables at the order and family level. This data was not used to produce the different hypotheses of how many times arthropods have developed a behavioral adaptation to smoke. Appendix, part ii, contains plots of the time and distance of the different orders and families comparing differences in trails.

Models and ANOVA of distance and time variables at the order and family level

Table 1. 1. The four different models have time as the independent variable.

Null Time model = Response.1 ~ 1 + (1|Ind)

Time interaction model 1 = (Time ~ Type of Trial*Order+(1|ID))
Time model 2 = (Time ~ Type of Trial + Order+(1|ID))
Time interaction model 3 = (Time ~ Type of Trial*Family+(1|ID))
Time model 4 = (Time ~ Type of Trial + Family+(1|ID))

Table 1. 2. The four different models have distance as the independent variable.

Null Distance model = Distance ~ 1 + (1|Ind)
Distance interaction model 1 = (Distance ~ Type of Trial*Order+(1|ID))
Distance model 2 = (Distance ~ Type of Trial + Order+(1|ID))
Distance interaction model 3 = (Distance ~ Type of Trial*Family+(1|ID))

Distance model 4 = (Distance ~ Type of Trial + Family+(1|ID))

Table 1. 3. The results of how many individuals in each order of Arthropoda were used to test distance difference. It also shows the mean time of movement for control and experimental trials. Lastly, this table shows the mean difference between each order's control and experimental trials.

Order	**Number of Individuals**	**Mean Difference**	**Mean Time for Control (Seconds)**	**Mean Time for Experimental (Seconds)**
Araneae	3	-89.6	196	106.4
Archaeognatha	9	118.93	62.4	181.33
Coleoptera	74	54.8432	52.865	107.708
Diptera	6	11.2	1.2	12.4
Ephemeroptera	5	0	0	0

Hemiptera	16	0.6	55.05	55.65
Hymenoptera	4	84.6	40.2	124.8
Isopoda	11	-55.854	164.945	109.091
Lepidoptera	23	97.67	43.826	141.496
Mantodea	10	80.16	111.36	191.52
Mecoptera	2	72	169.2	241.2
Odonata	10	11.76	12.96	24.72
Opiliones	10	76.08	83.28	159.36
Orthoptera	27	83.289	25.244	108.533
Phasmatodea	1	0	0	0
Plecoptera	9	107.4	14.4	121.8
Polydesmida	11	-54.98182	180.436	125.455
Scolopendromorpha	2	-56.6	122.4	178.8
Scorpiones	14	55.886	18.171	74.057
Trichoptera	6	-10	142.8	132.8
Xiphosura	12	-43.8	54.2	10.4

Table 1. 4. Results of comparing the different models, with an interaction or not, and using different quantitative variables and taxon levels. The results that have asterisks next to the model's name are chosen.

Models	**npar**	**AIC**	**BIC**	**Log likely hood**	**Deviance**	**Chi-squared**	**Degrees of Freedom**	**P value**
Null Time	**3**	**4828.9**	**4842.1**	**-2411.5**	**4822.9**			
Order Time	**25**	**4647**	**4757**	**-2298.5**	**4597**	**225.96**	**22**	**<0.00001**
***Order Time Interaction ***	**46**	**4576.6**	**4779**	**-2242.3**	**4484.6**	**112.36**	**21**	**<0.00001**
Models	**npar**	**AIC**	**BIC**	**Log likely hood**	**Deviance**	**Chi-squared**	**Degrees of Freedom**	**P value**
Null Time	**3**	**4828.9**	**4842.1**	**-2411.5**	**4822.9**			
Family Time	**71**	**4623.1**	**4935.5**	**-2240.6**	**4481.1**	**341.83**	**68**	**<0.00001**
***Family Time Interaction ***	**138**	**4561.5**	**5168.7**	**-2142.7**	**4285.5**	**195.64**	**67**	**<0.00001**

Table 1. 5. Results of comparing the different models, with an interaction or not, and using different quantitative variables and taxon levels. The results that have asterisks next to the model's name were chosen.

Models	npar	AIC	BIC	Log likely hood	Deviance	Chi-squared	Degrees of Freedom	P value
Null Distance	3	6481.4	6494.2	-3237.7	6475.4			
Order Distance	24	6431.2	6533.8	-3191.6	6383.2	92.208	21	<0.00001
*Order Distance Interaction *	44	6429.4	6617.4	-3170.7	6383.4	41.838	20	0.002903
Models	npar	AIC	BIC	Log likely hood	Deviance	Chi-squared	Degrees of Freedom	P value
Null Distance	3	6481.4	6494.2	-3237.7	6475.4			
Family Distance	66	6454.7	6736.8	-3161.4	6322.7	152.67	63	<0.00001
*Family Distance Interaction *	127	6473.6	7016.3	-3109.8	6219.6	103.12	61	0.00061

Table 1. 6. Two-way ANOVA for each model selected

			ANOVA			
Order Time	Sum squared	Mean squared	Num DF	Den DF	F value	P value
Type of trial	3308.85	3308.5	1	277	39.95	<0.0001
Order	12821.6	610.6	21	277	7.37	<0.0001
Type:Order	10307.1	490.8	21	277	5.93	<0.0001
Family Time	Sum squared	Mean squared	Num DF	Den DF	F value	P value
Type of trial	7579.5	7579.5	1	240	98.78	<0.0001
Family	22377.5	385.8	58	240	5.03	<0.0001
Type:Family	14830.2	255.7	58	240	3.33	<0.0001
Order Distance	Sum squared	Mean squared	Num DF	Den DF	F value	P value
Type of Trial	52754	52754	1	236.2	6.64	0.0106
Order	553602	27680	20	241.6	3.48	<0.0001
Type:Order	323122	16156	20	238.6	2.03	0.0068
Family Distance	Sum squared	Mean squared	Num DF	Den DF	F value	P value
Type of Trial	97352	97352	1	203.3	13.12	0.0004

Family	875162	15912	55	207.1	2.14	<0.0001
Type:Family	709101	12893	55	204	1.74	0.0031

Table 1. 7. Estimated marginal means for specified factors: the control and experimental means of movement time for each order. The asterisk next to the order name indicated a significant difference between control and experimental trial movement time means. Kenward-roger method to find the degrees of freedom and P value adjustment of 22 test.

Order	Difference	SE	DF	T ratio	p-value
Araneae	16	7.43	277	2.153	0.5064
Archaeognatha	16.33	4.29	277	3.807	0.0038
Coleoptera	12.951	1.43	277	9.057	<0.0001
Decapoda	-5.957	2.68	277	-2.22	0.4498
Diptera	9.667	5.25	277	1.84	0.7741
Ephemeroptera	0	5.76	277	0	1
Hemiptera	13.375	3.22	277	4.157	0.0009
Hymenoptera	14.75	6.43	277	2.292	0.3910
Isopoda	-5.615	3.57	277	-1.573	0.9303
Lepidoptera	19.48	2.57	277	7.568	<0.0001
Mantodea	13.9	4.07	277	3.146	0.0159

Mecoptera	3.5	9.10	277	0.385	1
Odonata	0.8	4.07	277	0.197	1
Opiliones	15.4	4.07	277	3.784	0.0041
Orthoptera	13.519	2.48	277	5.454	<0.0001
Phasmatodea	0	12.87	277	0	1
Plecoptera	22.11	4.29	277	5.154	<0.0001
Polydesmida	0.909	3.88	277	0.234	1
Scolopendromorpha	-1	9.10	277	-0.11	1
Scorpiones	2.643	3.44	277	0.768	1
Trichoptera	7.5	5.25	277	1.428	0.9726
Xiphosura	-4.417	3.72	277	1.189	0.9968

Table 1. 8. Estimated marginal means for specified factors: the control and experimental means of the difference in distance for each order. The asterisk next to the order name indicated a significant difference between the control and experimental trial difference in distance means. The Kenward-Roger method was used to find the degrees of freedom and P value adjustment of 22 tests.

Order	Difference	SE	DF	T ratio	p-value
Araneae	-89.6	72.8	237	-1.231	0.9933
Archaeognatha	118.93	42	237	2.83	0.1008
Coleoptera	54.28	14.7	243	3.755	0.0045
Diptera	11.2	51.5	237	0.218	1
Ephemeroptera	0	56.4	237	0	1
Hemiptera	0.6	31.5	237	0.019	1
Hymenoptera	84.6	63	237	1.319	0.9829
Isopoda	-50.18	37.8	270	1.328	0.9851

Lepidoptera	95.27	26.2	252	3.635	0.0070
Mantodea	80.16	39.9	237	2.011	0.6155
Mecoptera	72	89.1	237	0..808	1
Odonata	11.76	39.9	237	0.295	1
Opiliones	76.08	39.9	237	1.908	0.7032
Orthoptera	83.29	24.3	237	3.433	0.0147
Phasmatodea	0	126.1	237	0	1
Plecoptera	107.4	44.6	237	2.41	0.2946
Polydesmida	-63.34	41.7	277	1.518	0.9426
Scolopendromorpha	56.4	89.1	237	0.633	1
Scorpiones	55.89	33.7	237	1.659	0.8798
Trichoptera	2.51	54.5	258	0.046	1
Xiphosura	-43.8	36.4	237	1.203	0.9952

Table 1. 9. Estimated marginal means for specified factors: each family's control and experimental means of movement time. The asterisk next to the family name indicated a significant difference between control and experimental trial movement time means. Kenward-Roger method was used to find the degrees of freedom and P value adjustment of the 59 test.

Family	Difference	SE	DF	p-value
Acanloniidae	13.25	6.19	240	0.8498
Acrididae	11.33	4.13	240	0.3130
Agelenidae	20	12.39	240	0.998
Alateridae	6.75	6.19	240	1
Aeshnidae	0	12.39	240	1
Anthribidae	30	12.39	240	0.6027
Apidae	3	8.76	240	1
Armadillidiidae	-3.167	5.06	240	1
Asilidae	0	12.39	240	1

Calopterygidae	3.5	8.76	240	1
Carabidae	0	12.39	240	1
Cerambycidae	11.8	5.54	240	0.8562
Cicadidae	6.5	5.54	240	1
Coenagrionidae	2.167	5.06	240	1
Coenobitidae	0	3.74	240	1
Diogenidae	-11.413	3.58	240	0.0891
Elateridae	-2	5.54	240	1
Emphemeridae	0	5.54	240	1
Erebidae	25.778	4.13	240	<0.0001
Gryllidae	23	8.76	240	0.4103
Gyrinidae	6	5.54	240	1
Hesperiidae	26	8.72	240	0.1742
Hydrophilidae	26	5.54	240	0.0003
Lampyridae	9.1	3.92	240	0.6974
Leiobunidae	15.4	3.92	240	0.0065
Libellulidae	2	12.39	240	1
Limulidae	-4.417	3.56	240	1
Lucanidae	7.8	5.54	240	0.9999
Lycaenidae	0.33	7.15	240	1
Machilidae	16.33	4.11	240	0.0059
Mantidae	13.9	3.92	240	0.0270
Noctuidae	18.25	6.19	240	0.1851
Nymphalidae	14.5	6.19	240	0.6805
Oniscidae	-7.714	4.68	240	0.9970
Panorpidae	3.5	8.72	240	1
Passalidae	16.5	8.72	240	0.9666
Pentatomidae	16.167	5.06	240	0.0879
Perlidae	22.11	4.13	240	<0.0001
Phasmidae	0	12.33	240	1
Pholcidae	21	12.39	240	0.9947
Phryganeidae	7.5	5.06	240	0.9997
Pieridae	30	12.39	240	0.6027
Pyrochroidae	0	12.39	240	1

Reduviidae	21.667	7.15	240	0.1461
Rhaphidophoridae	16.182	3.74	240	0.0013
Saltcidae	7	12.39	240	1
Scarabaeidae	19.455	2.64	240	<0.0001
Scoliidae	23	12.39	240	0.9747
Scolocrytopidae	-1	8.76	240	1
Spechidae	30	12.39	240	0.6027
Sphingidae	15	12.33	240	1
Staphylinidae	11.5	3.92	240	0.1426
Tabanidae	7.25	6.19	240	1
Tenebrionidae	11.5	6.19	240	0.9747
Tettigoniidae	7.8	5.54	240	0.9999
Tipulidae	29	12.39	240	0.6805
Tortricidae	26	12.39	240	0.8764
Vaejovidae	2.643	3.31	240	1
Xystodesmidae	0.909	3.74	240	1

Table 1. 10. Estimated marginal means for specified factors: the control and experimental means of the difference in distance for each family. The asterisk next to the family name indicated a significant difference between the control and experimental trial difference in distance means. The Kenward-Roger method was used to find the degrees of freedom and P value adjustment of 56 tests.

Family	Difference	SE	DF	p-value
Acanloniidae	-35.4	60.9	202	1
Acrididae	6.13	40.6	202	1
Agelenidae	-146.4	121.8	202	1
Alateridae	-0.6	60.9	202	1
Aeshnidae	0	121.8	202	1
Anthribidae	201.6	121.8	202	0.9955
Apidae	99.6	86.1	202	1
Armadillidiidae	-3.15	55.9	247	1
Asilidae	0	121.8	202	1

Calopterygidae	57.6	86.1	202	1
Carabidae	-64.8	121.8	202	1
Cerambycidae	91.61	58.6	224	0.9986
Cicadidae	26.4	60.9	202	1
Coenagrionidae	-1.2	49.7	202	1
Elateridae	4.8	60.9	202	1
Emphemeridae	0	54.5	202	1
Erebidae	142.13	40.6	202	0.0313
Gryllidae	74.4	86.1	202	1
Gyrinidae	-31.68	54.5	202	1
Hesperiidae	321.6	86.1	202	0.0136
Hydrophilidae	118.56	54.5	202	0.8065
Lampyridae	68.88	38.5	202	0.9835
Leiobunidae	76.08	38.5	202	0.9296
Libellulidae	9.6	121.8	202	1
Limulidae	-43.8	35.2	202	1
Lucanidae	16.8	54.5	202	1
Lycaenidae	0	91.9	337	1
Machilidae	118.93	40.6	202	0.1878
Mantidae	80.16	38.5	202	0.8736
Noctuidae	132.25	66.9	231	0.9303
Nymphalidae	-86.4	60.9	202	0.9998
Oniscidae	-84.98	48.4	217	0.9873
Panorpidae	72	86.1	202	1
Passalidae	73.2	86.1	202	1
Pentatomidae	-15.2	49.7	202	1
Perlidae	107.4	43.1	202	0.5161
Phasmidae	0	121.8	202	1
Pholcidae	-81.6	121.8	202	1
Phryganeidae	2.13	52.7	220	1
Pieridae	261.6	121.8	202	0.8283
Reduviidae	52	70.3	202	1
Rhaphidophoridae	121.75	36.8	202	0.0585
Saltcidae	-40.8	121.8	202	1

Scarabaeidae	105.74	28.9	213	0.0179
Scoliidae	7.2	121.8	202	1
Scolocrytopidae	56.4	86.1	202	1
Spechidae	132	121.8	202	1
Sphingidae	194.4	121.8	202	0.9978
Staphylinidae	16.8	38.5	202	1
Tabanidae	1.2	60.9	202	1
Tenebrionidae	40	66.9	231	1
Tettigoniidae	141.12	54.5	202	0.4272
Tipulidae	62.4	121.8	202	1
Tortricidae	-249.6	121.8	202	0.8929
Vaejovidae	55.89	32.6	202	0.9911
Xystodesmidae	-63.24	40.4	236	0.9986

Plots time and distance of the different orders and families comparing differences in trails

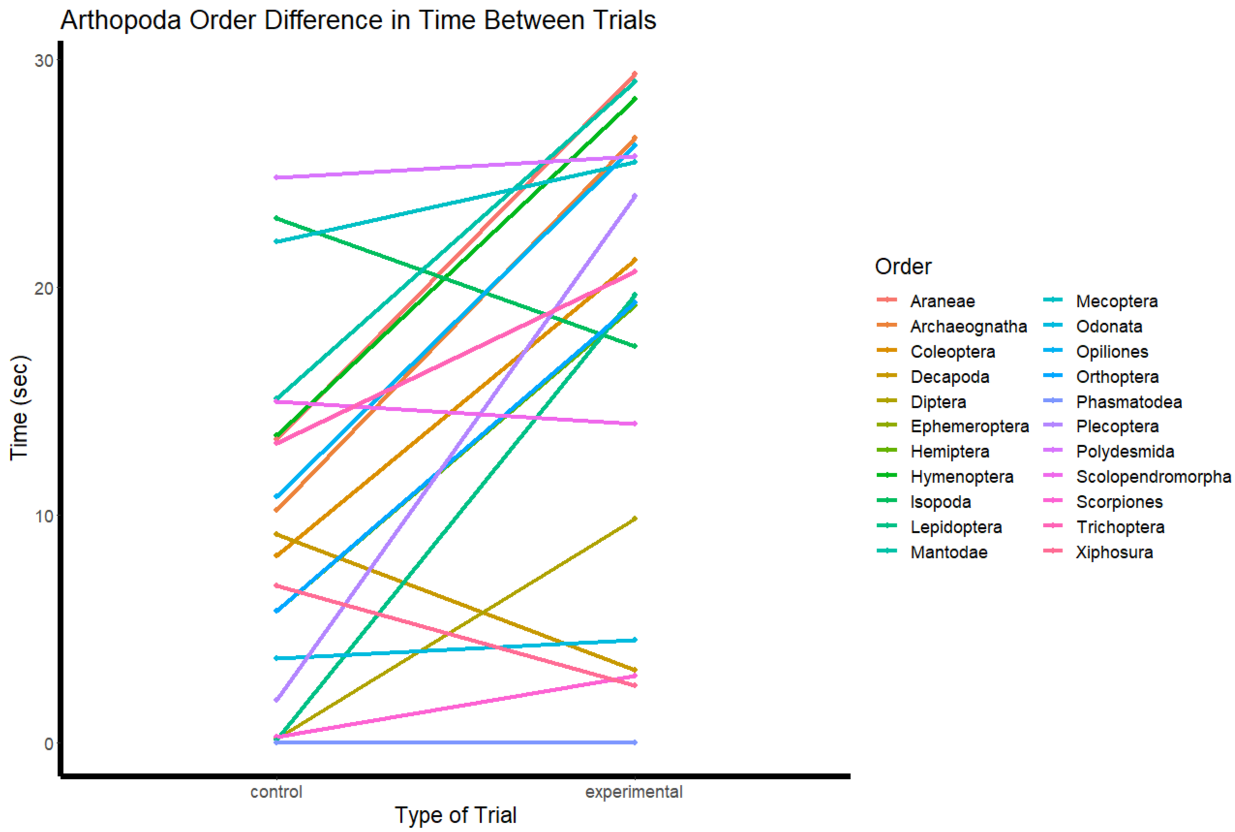


Figure 1. 1. Display the mean time spent moving during a trial at the order level. On the x-axis is the type of trial, the left category is the control data, and the right category is the experimental data. On the y-axis is the amount of time an individual spent moving. The legend shows the order assigned with each colored line.

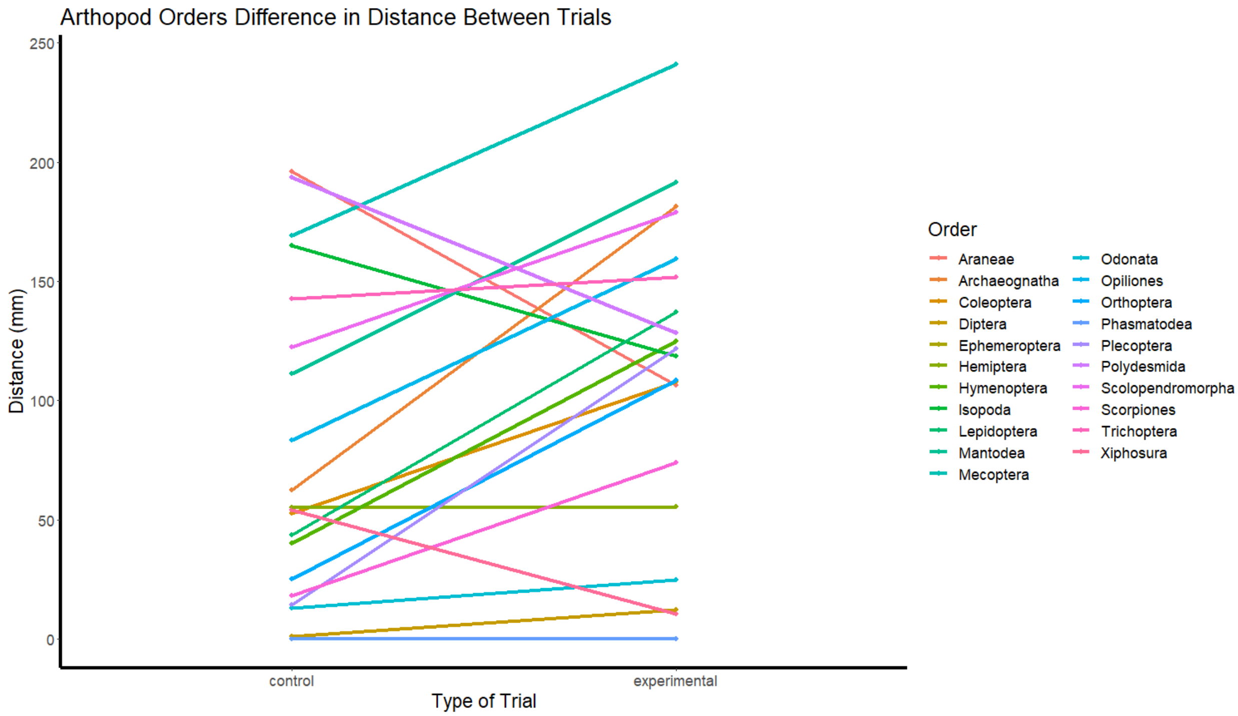


Figure 1. 2. Display the mean distance between an individual's start and end points during a trial at the order level. On the x-axis is the type of trial, the left category is the control data, and the right category is the experimental data. On the y-axis is the mean distance between each order's start and end points (in millimeters). The legend shows the order assigned to each colored line.

Figure 1. 3. Display of the mean time spent moving during a trial at the family level in the order Coleoptera. On the x-axis is the type of trial, the left category is the control data, and the right category is the experimental data. On the y-axis is the amount of time an individual spent moving of each family in Coleoptera. The legend shows the order assigned with each colored line.

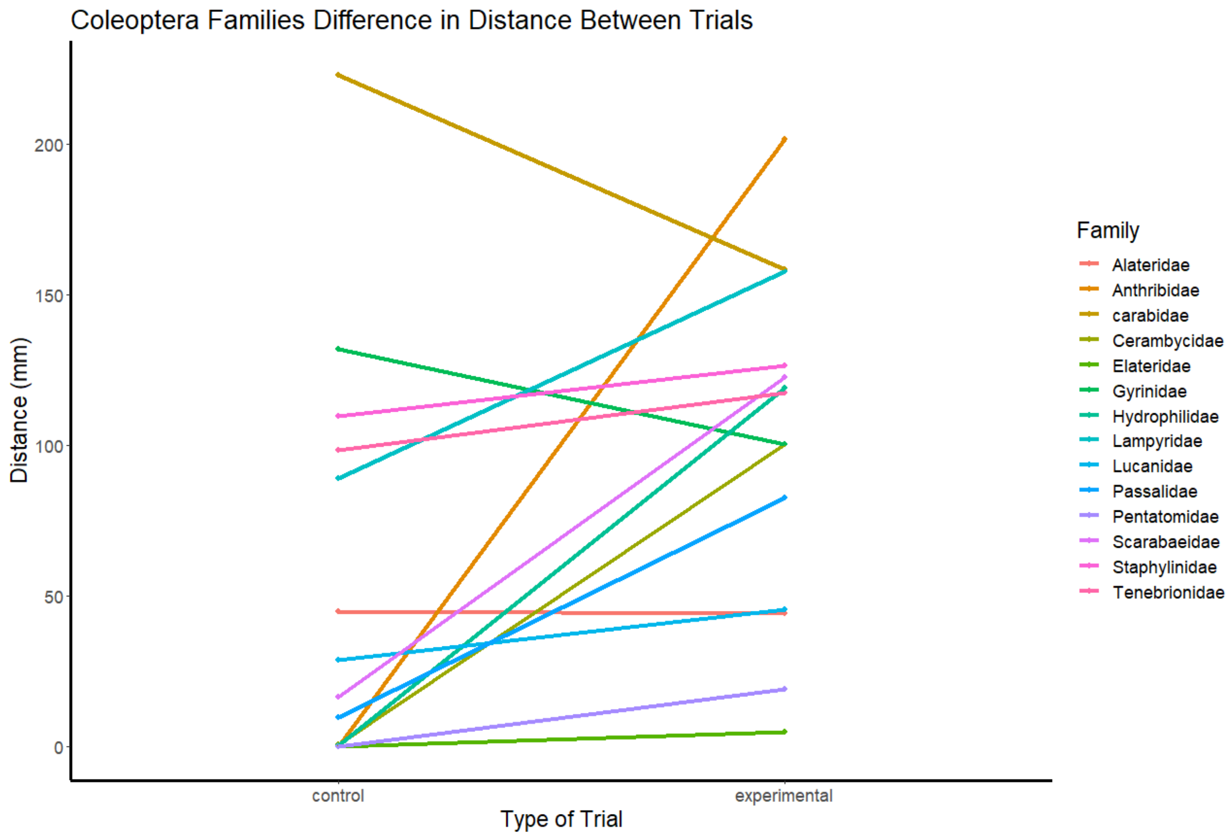


Figure 1. 4. Display the mean distance between an individual's start and end points during a trial at the family level in the order Coleoptera. On the x-axis is the type of trial, the left category is the control data, and the right category is the experimental data. On the y-axis is the mean distance between each family's start and end points (in millimeters) in Coleoptera. The legend shows the family assigned with each colored line.

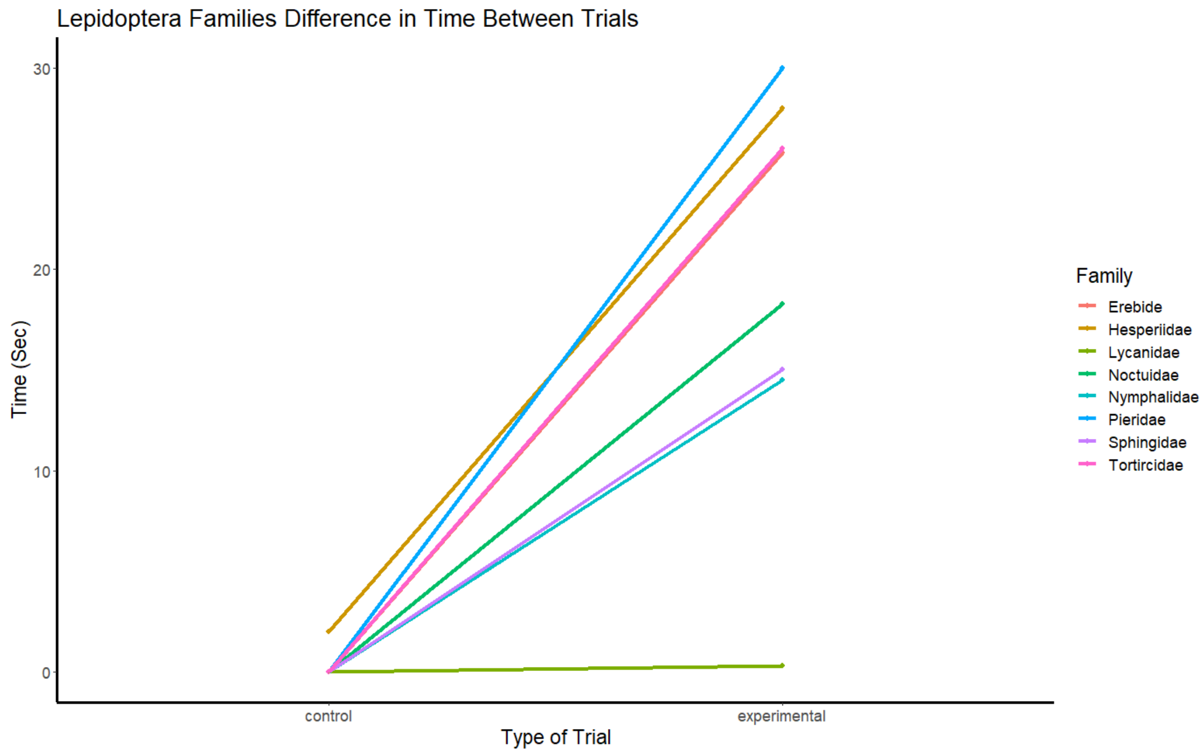


Figure 1. 5. Display of the mean time spent moving during a trial at the family level in the order Lepidoptera. On the x-axis is the type of trial, the left category is the control data, and the right category is the experimental data. On the y-axis is the amount of time an individual spent moving of each family in Lepidoptera. The legend shows the order assigned with each colored line.

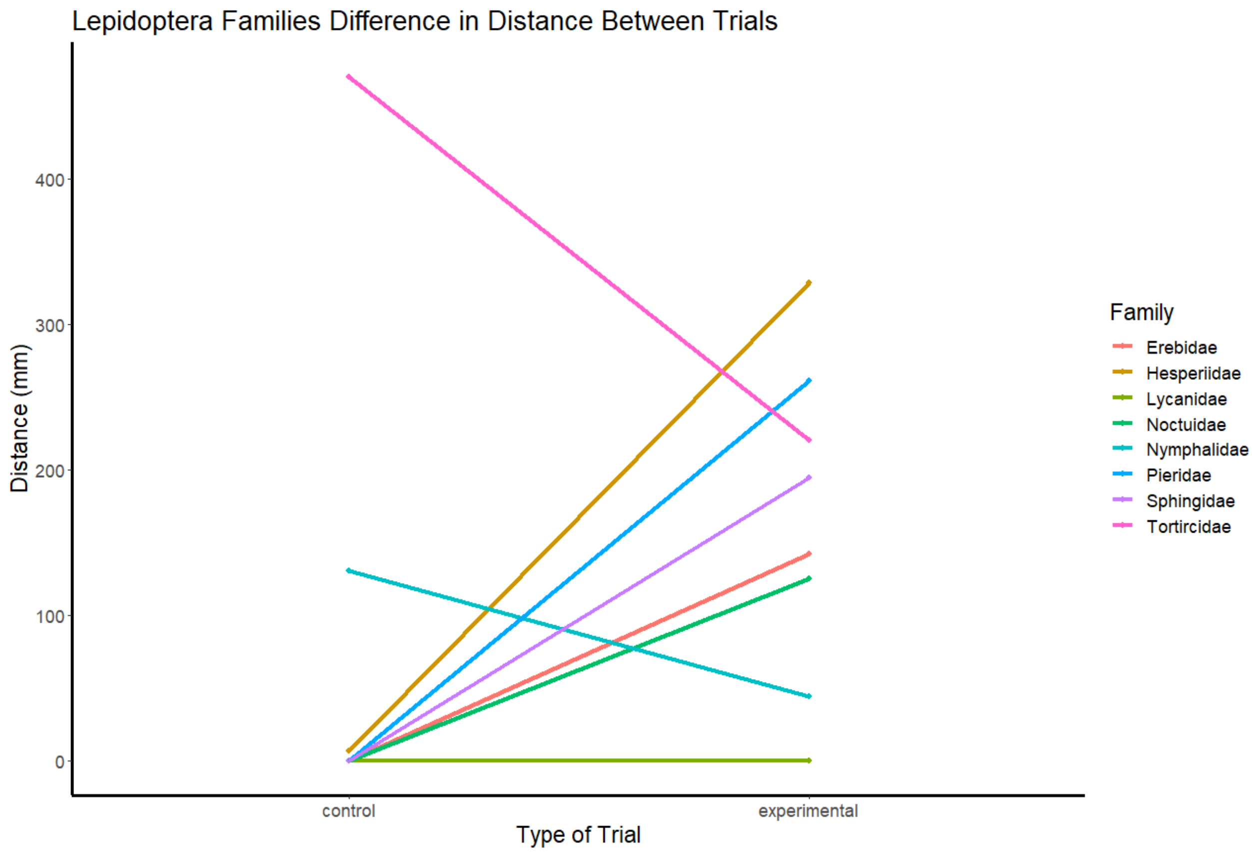


Figure 1. 6. Display the mean distance between an individual's start and end points during a trial at the family level in the order Lepidoptera. On the x-axis is the type of trial, the left category is the control data, and the right category is the experimental data. On the y-axis is the mean distance between the start and end points (in millimeters) of each family in Lepidoptera. The legend shows the family assigned with each colored line.

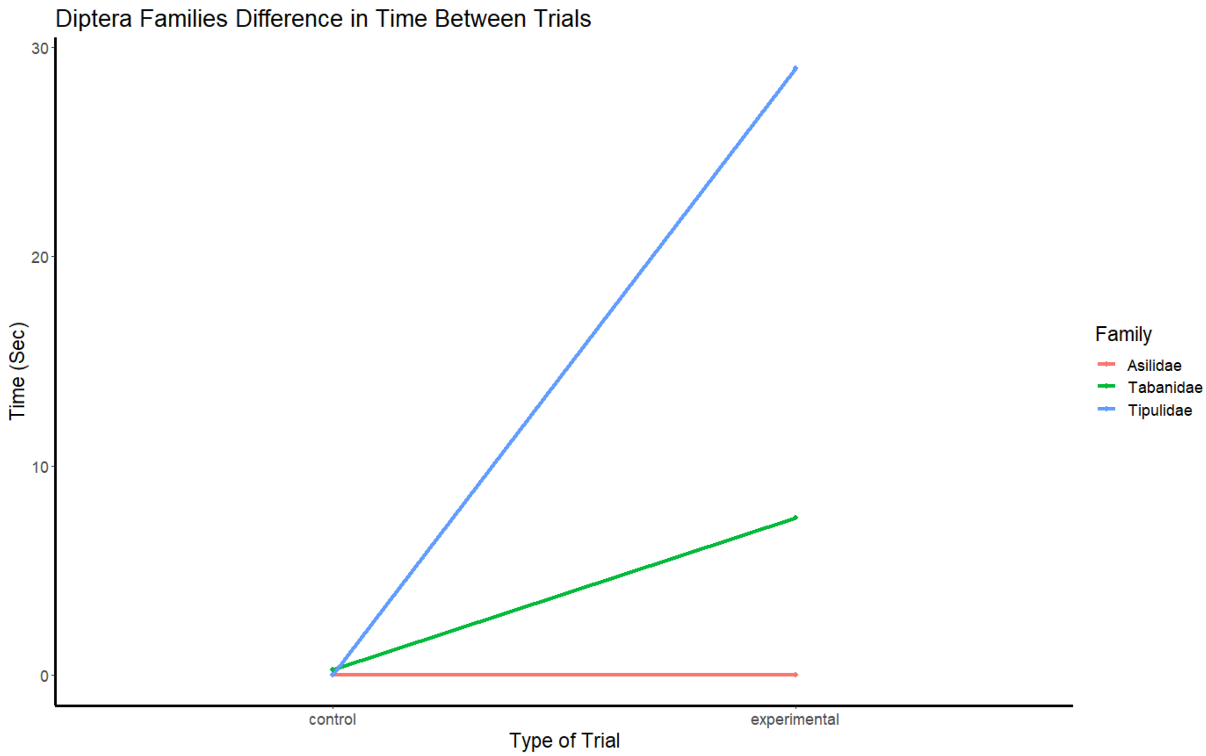


Figure 1. 7. Display the mean time spent moving during a trial at the family level in the order Diptera. On the x-axis is the type of trial, the left category is the control data, and the right category is the experimental data. On the y-axis is the time an individual spent moving of each family in Diptera. The legend shows the order assigned with each colored line.

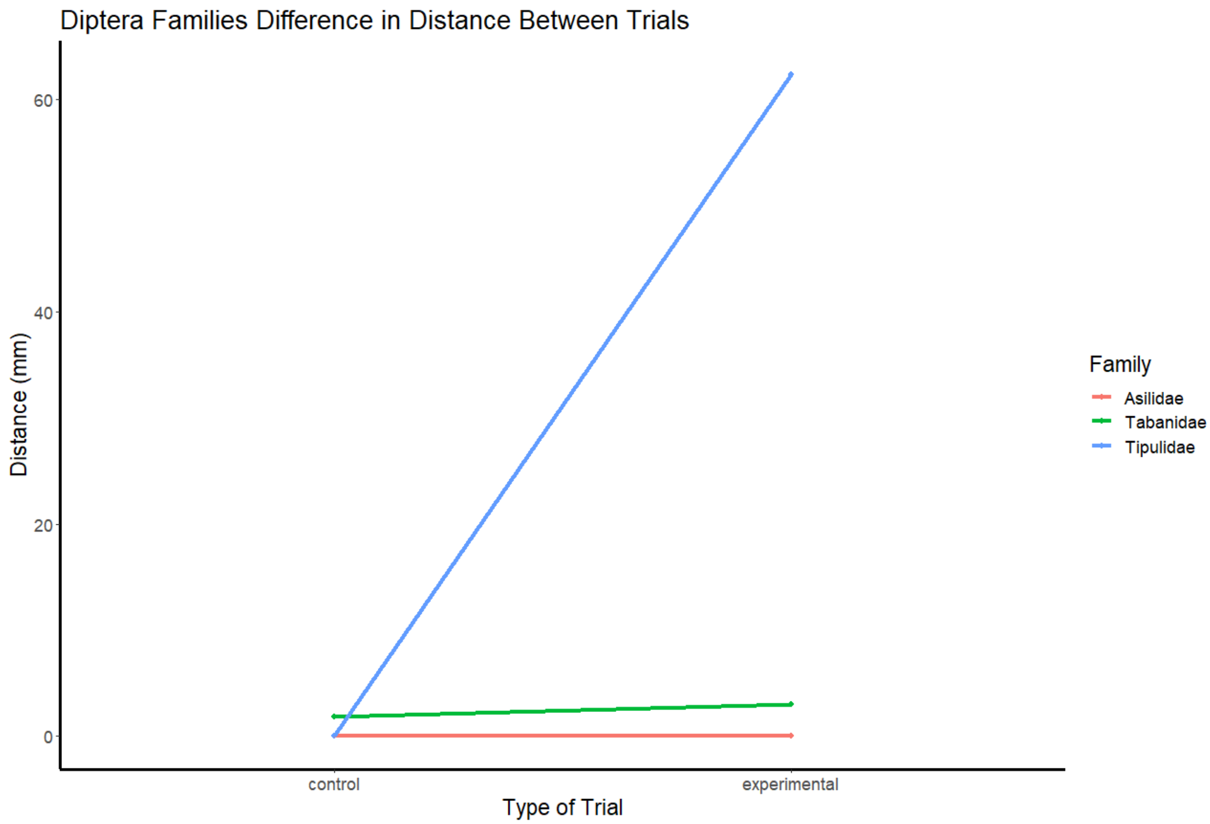


Figure 1. 8. Display the mean distance between an individual's start and end points during a trial at the family level in the order Diptera. On the x-axis is the type of trial, the left category is the control data, and the right category is the experimental data. On the y-axis is the mean distance between each family's start and end points (in millimeters) in Diptera. The legend shows the family assigned with each colored line.

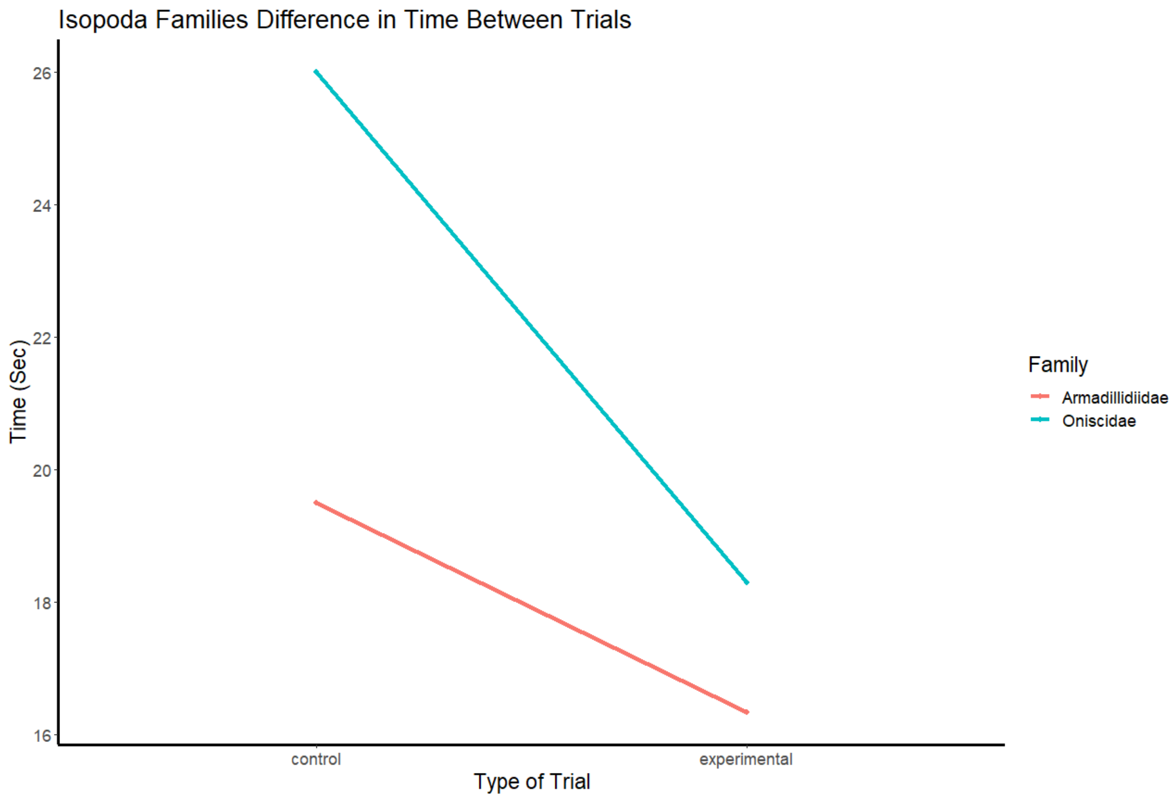


Figure 1. 9. Display of the mean time spent moving during a trial at the family level in the order Isopoda. On the x-axis is the type of trial, the left category is the control data, and the right category is the experimental data. On the y-axis is the time an individual spent moving of each family in Isopoda. The legend shows the order assigned with each colored line.

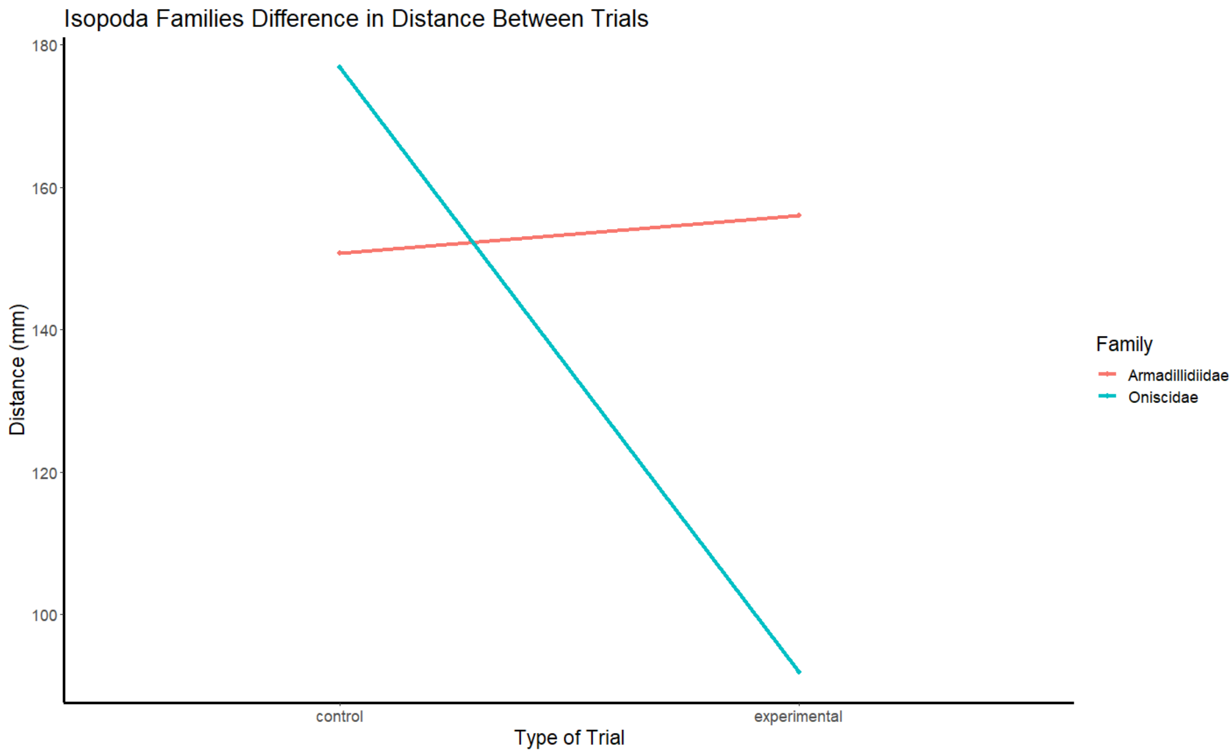


Figure 1. 10. Display the mean distance between an individual's start and end points during a trial at the family level in the order Isopoda. On the x-axis is the type of trial, the left category is the control data, and the right category is the experimental data. On the y-axis is the mean distance between each family's start and end points (in millimeters) in Isopoda. The legend shows the family assigned with each colored line.

Figure 1. 11. Display the mean time spent moving during a trial at the family level in the order Araneae. On the x-axis is the type of trial, the left category is the control data, and the right category is the experimental data. On the y-axis is the time an individual spent moving of each family in Araneae. The legend shows the order assigned with each colored line.

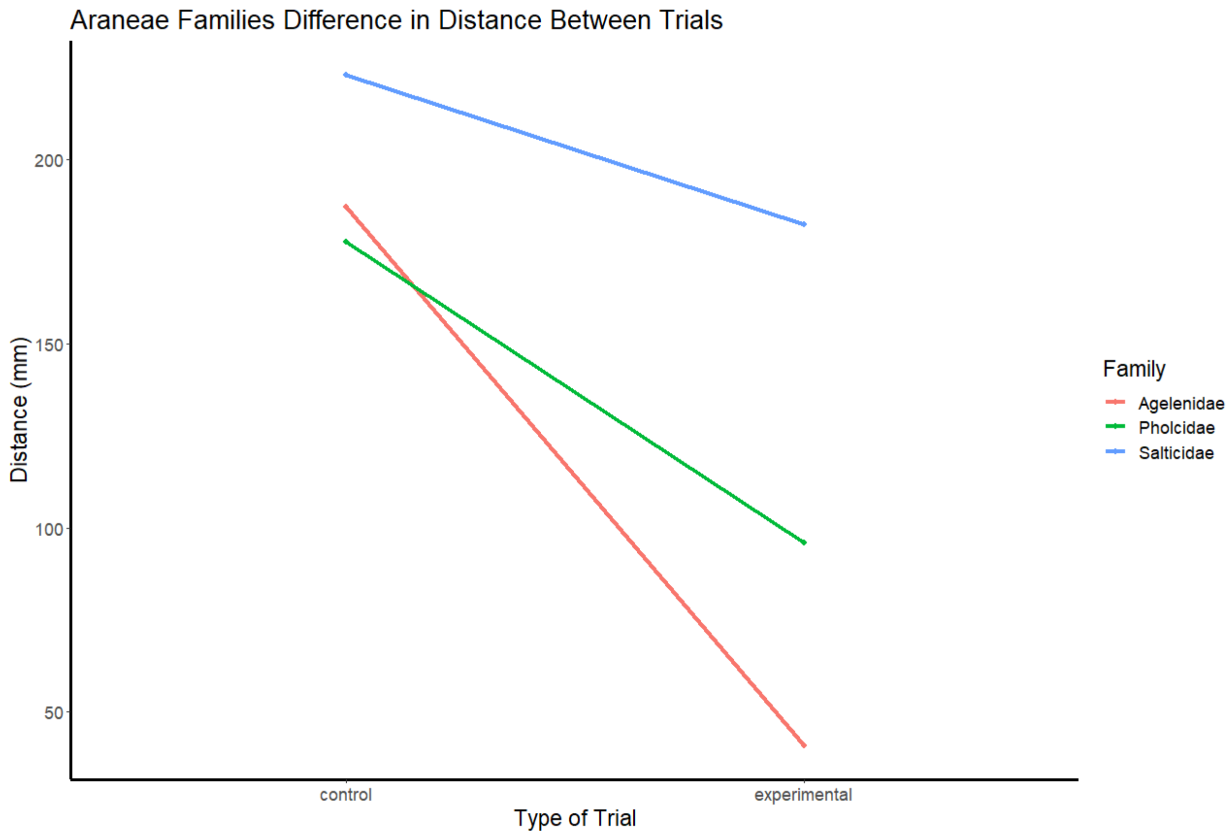


Figure 1. 12. Display the mean distance between an individual's start and end points during a trial at the family level in the order Araneae. On the x-axis is the type of trial, the left category is the control data, and the right category is the experimental data. On the y-axis is the mean distance between each family's start and end points (in millimeters) in Araneae. The legend shows the family assigned with each colored line.

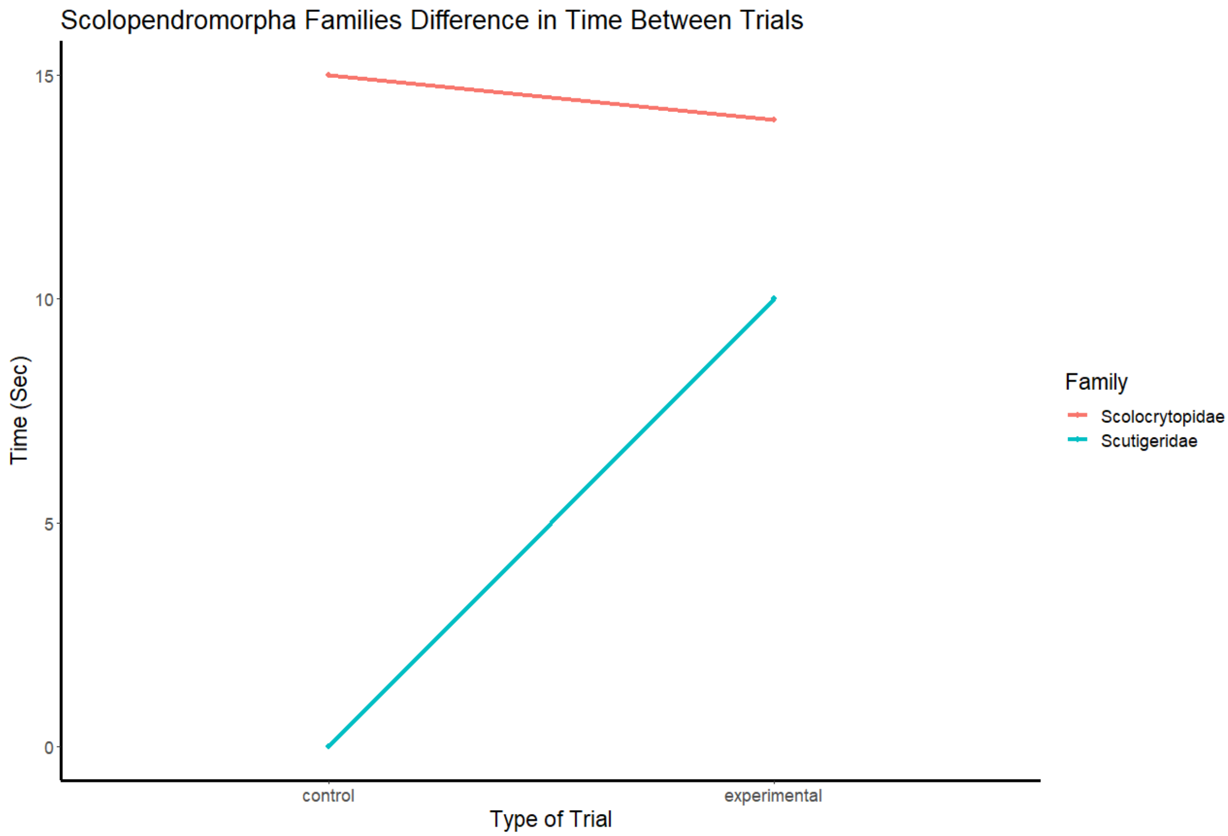


Figure 1. 13. Display of the mean time spent moving during a trial at the family level in the order Scolopendromorpha. On the x-axis is the type of trial, the left category is the control data, and the right category is the experimental data. On the y-axis is the amount of time an individual spent moving of each family in Scolopendromorpha. The legend shows the order assigned with each colored line.

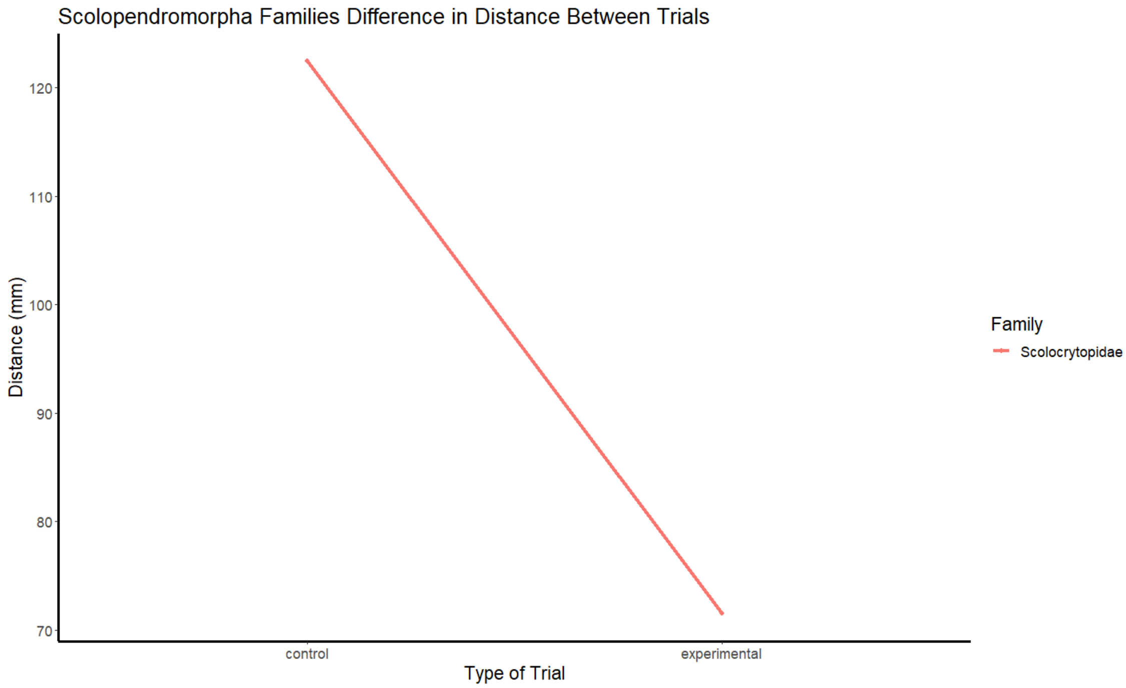


Figure 1. 14. Display the mean distance between an individual's start and end points during a trial at the family level in the order Scolopendromorpha. On the x-axis is the type of trial, the left category is the control data, and the right category is the experimental data. On the y-axis is the mean distance between each family's start and end points (in millimeters) in Scolopendromorpha. The legend shows the family assigned with each colored line.

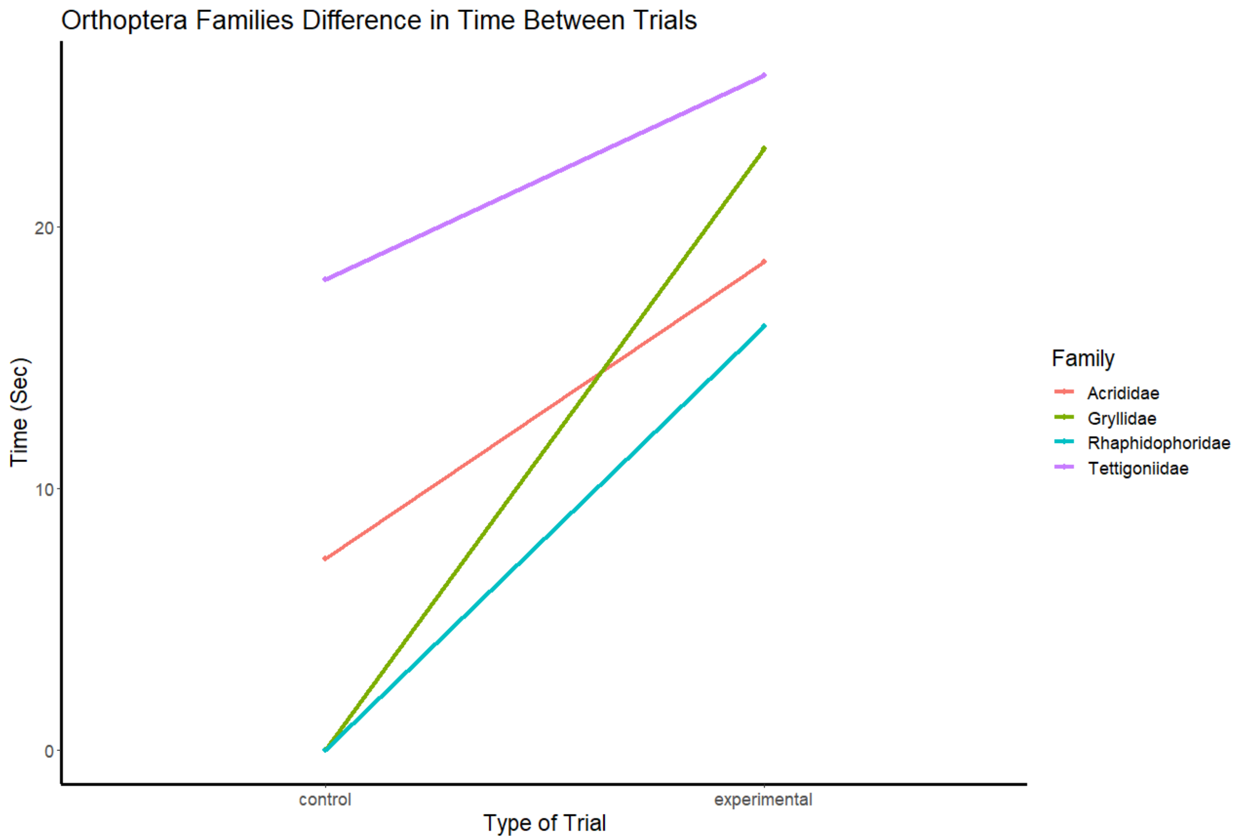


Figure 1. 15. Display of the mean time spent moving during a trial at the family level in the order Orthoptera. On the x-axis is the type of trial, the left category is the control data, and the right category is the experimental data. On the y-axis is the amount of time an individual spent moving of each family in Orthoptera. The legend shows the order assigned with each colored line.

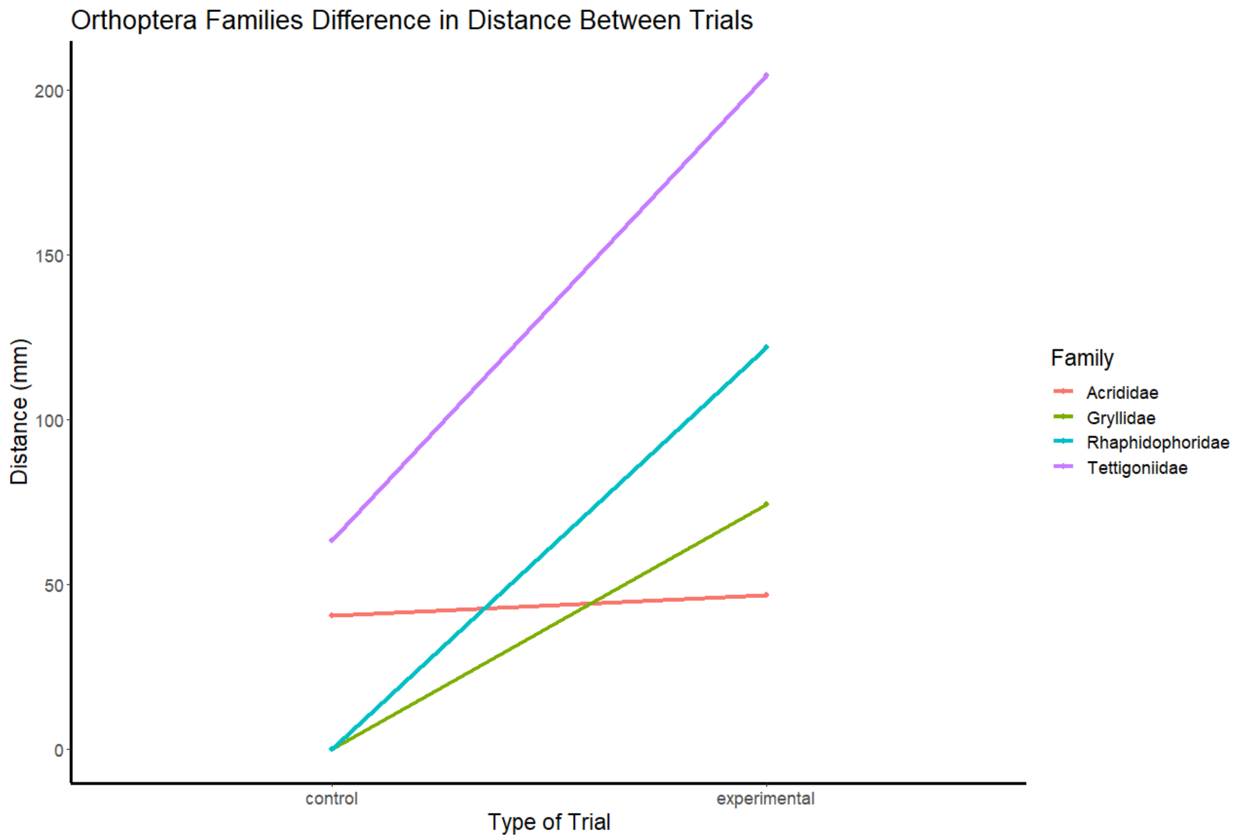


Figure 1. 16. Display the mean distance between an individual's start and end points during a trial at the family level in the order Orthoptera. On the x-axis is the type of trial, the left category is the control data, and the right category is the experimental data. On the y-axis is the mean distance between each family's start and end points (in millimeters) in Orthoptera. The legend shows the family assigned with each colored line.

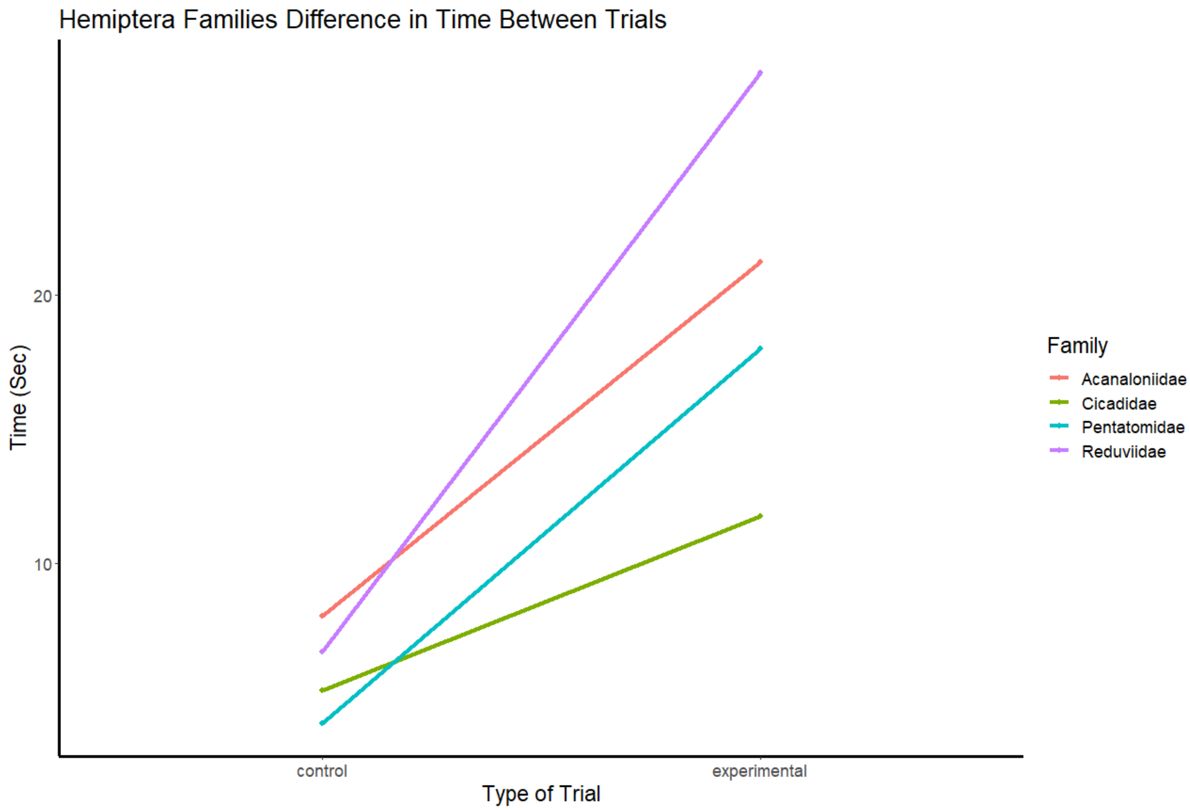


Figure 1. 17. Display the mean time spent moving during a trial at the family level in the order Hemiptera. On the x-axis is the type of trial, the left category is the control data, and the right category is the experimental data. On the y-axis is the amount of time an individual spent moving of each family in Hemiptera. The legend shows the order assigned with each colored line.

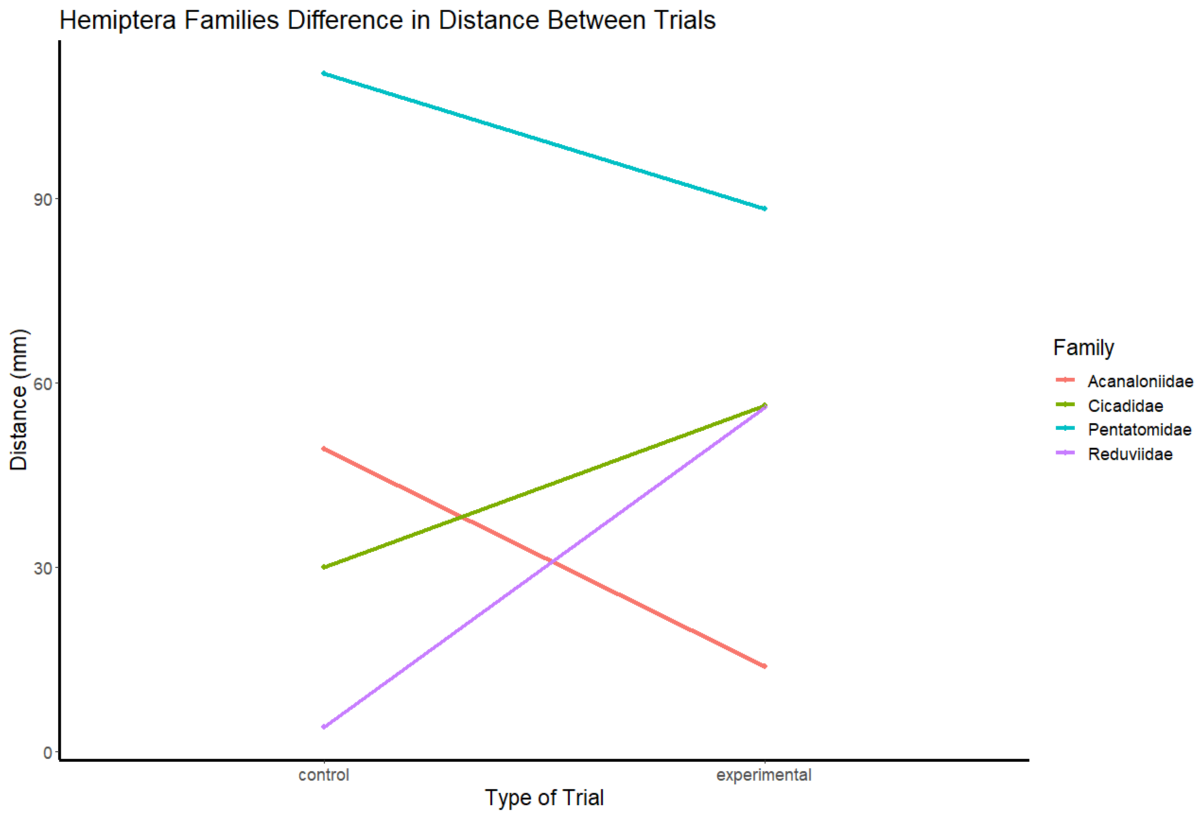


Figure 1. 18. Display the mean distance between an individual's start and end points during a trial at the family level in the order Hemiptera. On the x-axis is the type of trial, the left category is the control data, and the right category is the experimental data. On the y-axis is the mean distance between each family's start and end points (in millimeters) in Hemiptera. The legend shows the family assigned with each colored line.

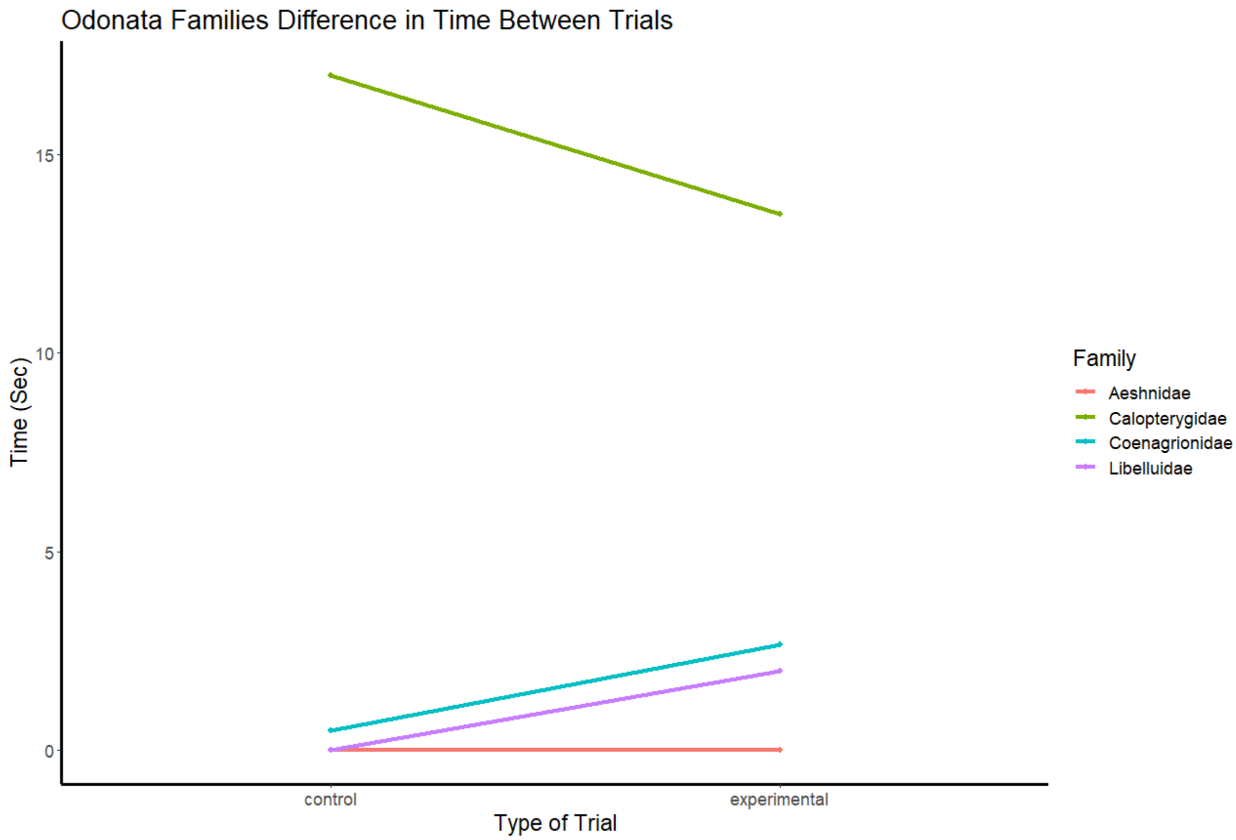


Figure 1. 19. Display the mean time spent moving during a trial at the family level in the order Odonata. On the x-axis is the type of trial, the left category is the control data, and the right category is the experimental data. On the y-axis is the amount of time an individual spent moving of each family in Odonata. The legend shows the order assigned with each colored line.

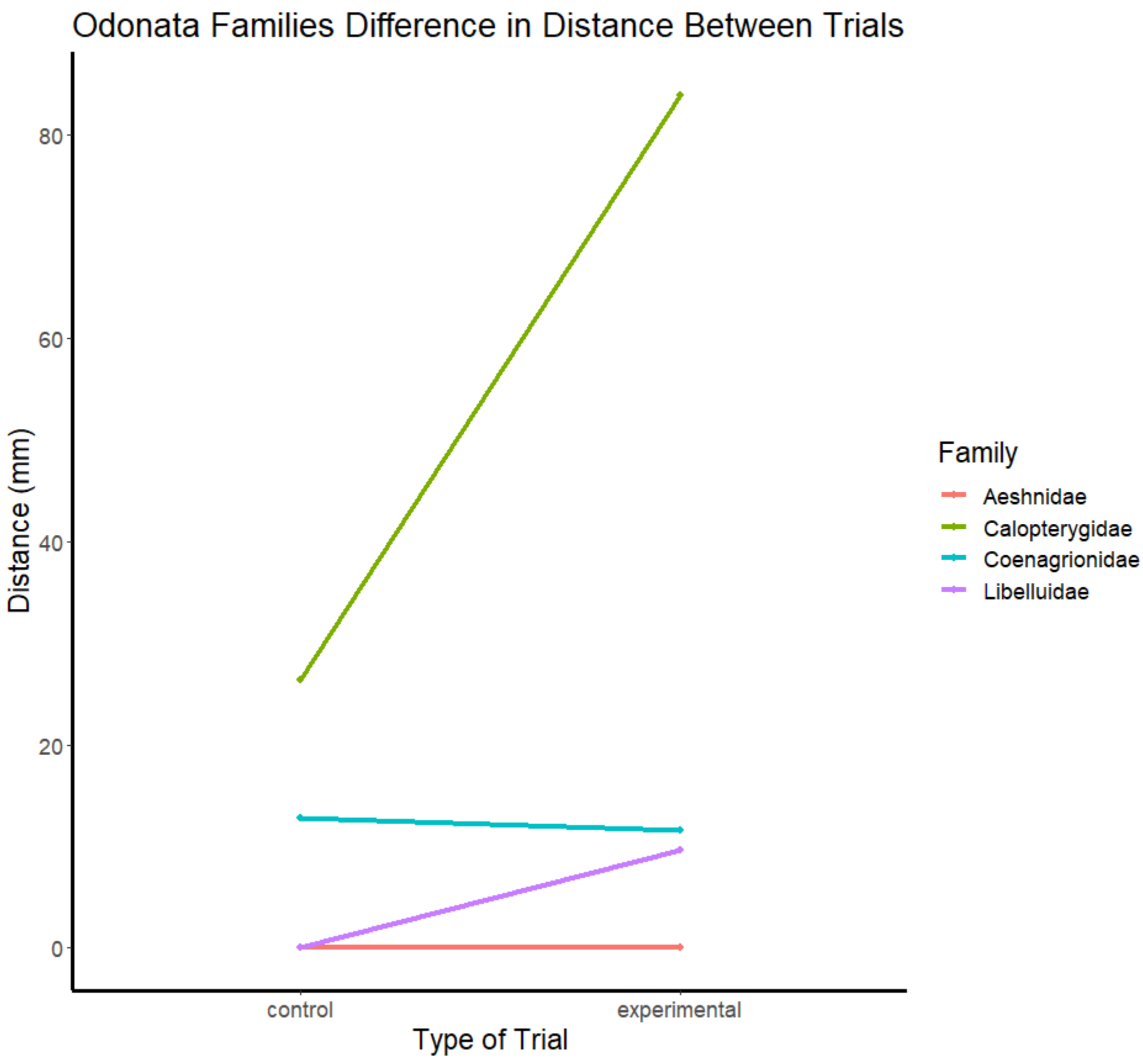


Figure 1. 20. Display the mean distance between an individual's start and end points during a trial at the family level in the order Odonata. On the x-axis is the type of trial, the left category is the control data, and the right category is the experimental data. On the y-axis is the mean distance between each family's start and end points (in millimeters) in Odonata. The legend shows the family assigned with each colored line.

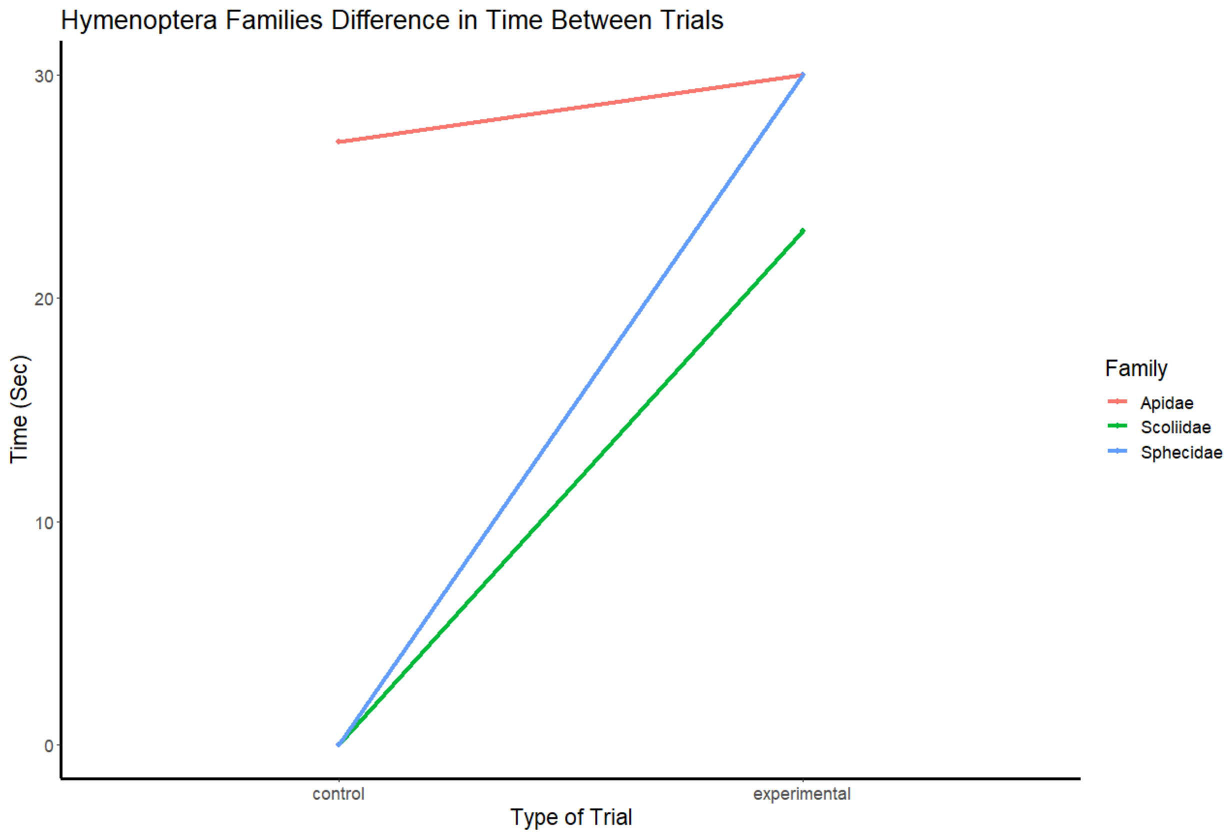


Figure 1. 21. Display of the mean time spent moving during a trial at the family level in the order Hymenoptera. On the x-axis is the type of trial, the left category is the control data, and the right category is the experimental data. On the y-axis is the time an individual spent moving of each family in Hymenoptera. The legend shows the order assigned with each colored line.

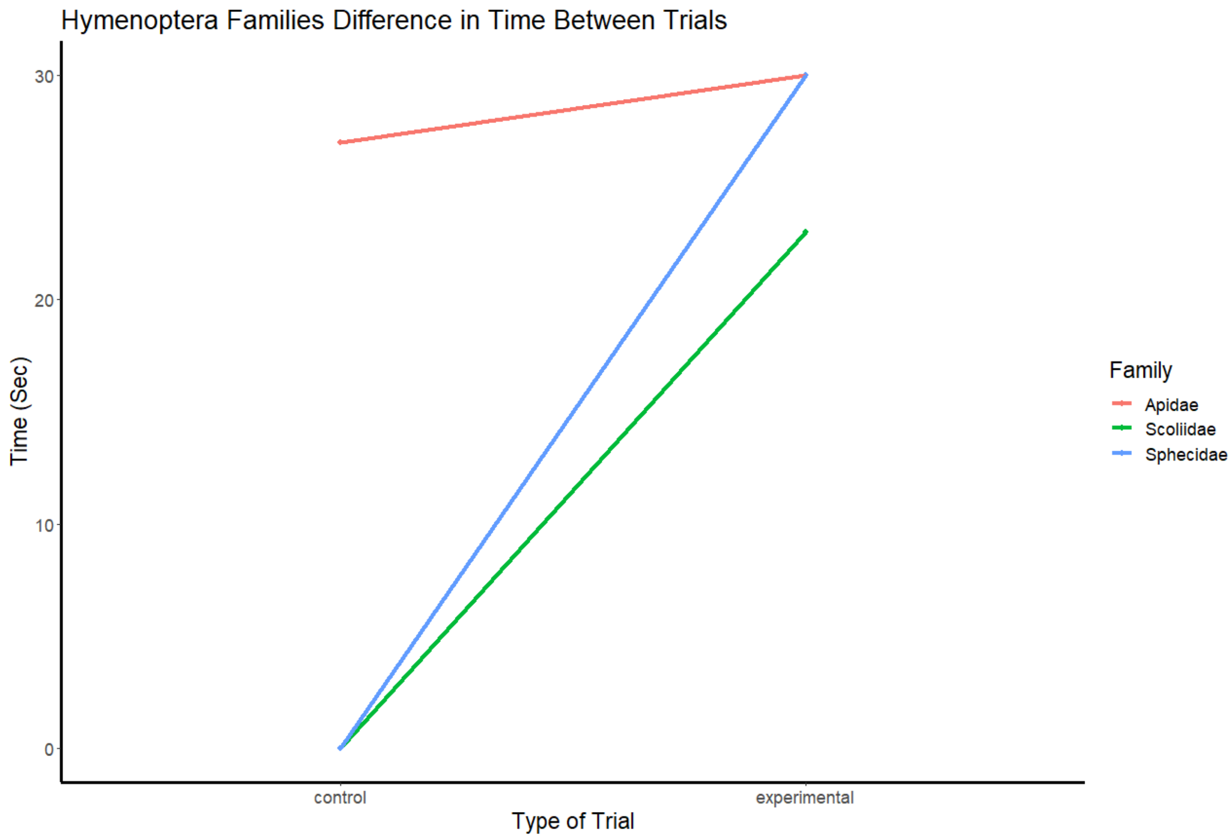


Figure 1. 22. Display the mean distance between an individual's start and end points during a trial at the family level in the order Hymenoptera. On the x-axis is the type of trial, the left category is the control data, and the right category is the experimental data. On the y-axis is the mean distance between each family's start and end points (in millimeters) in Hymenoptera. The legend shows the family assigned with each colored line.

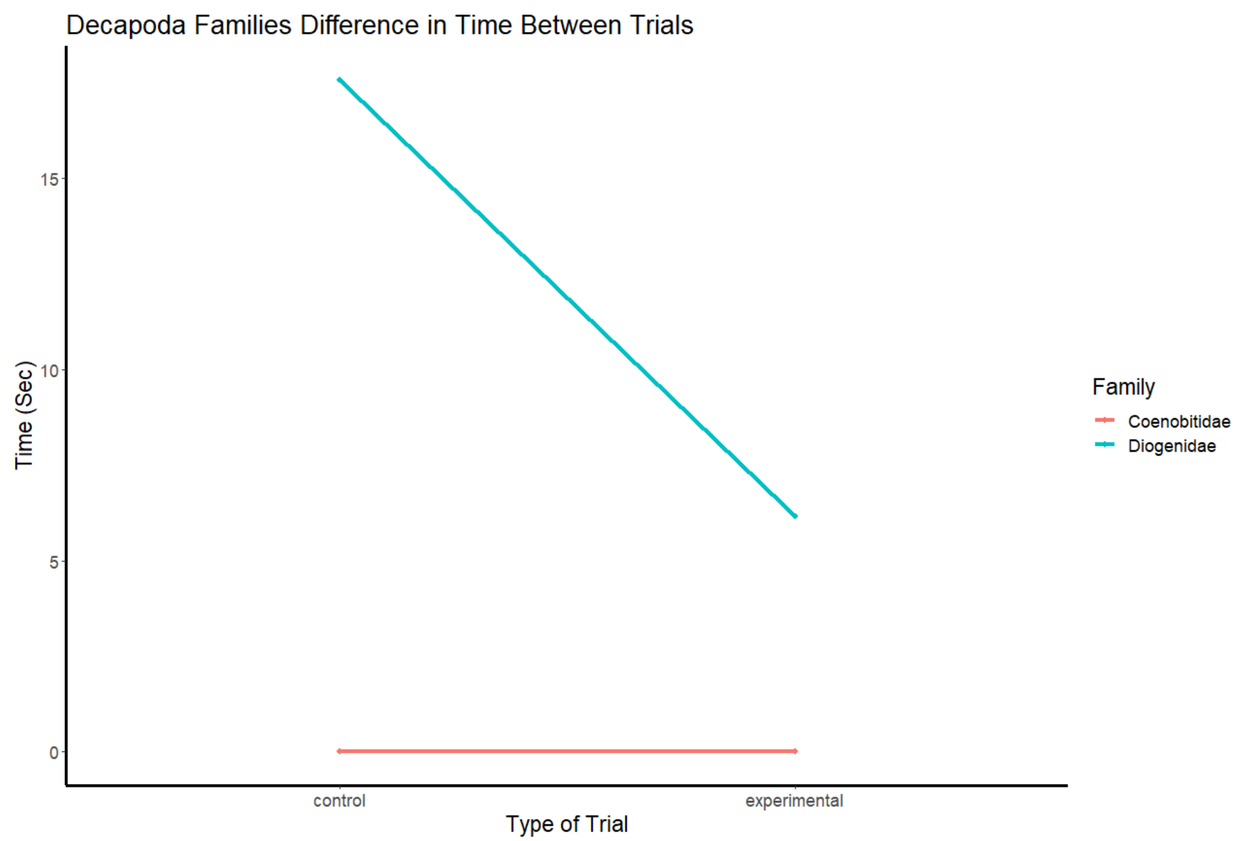


Figure 1. 23. Display of the mean time spent moving during a trial at the family level in the order Decapoda. On the x-axis is the type of trial, the left category is the control data, and the right category is the experimental data. On the y-axis is the amount of time an individual spent moving each family in Decapoda. The legend shows the order assigned with each colored line.

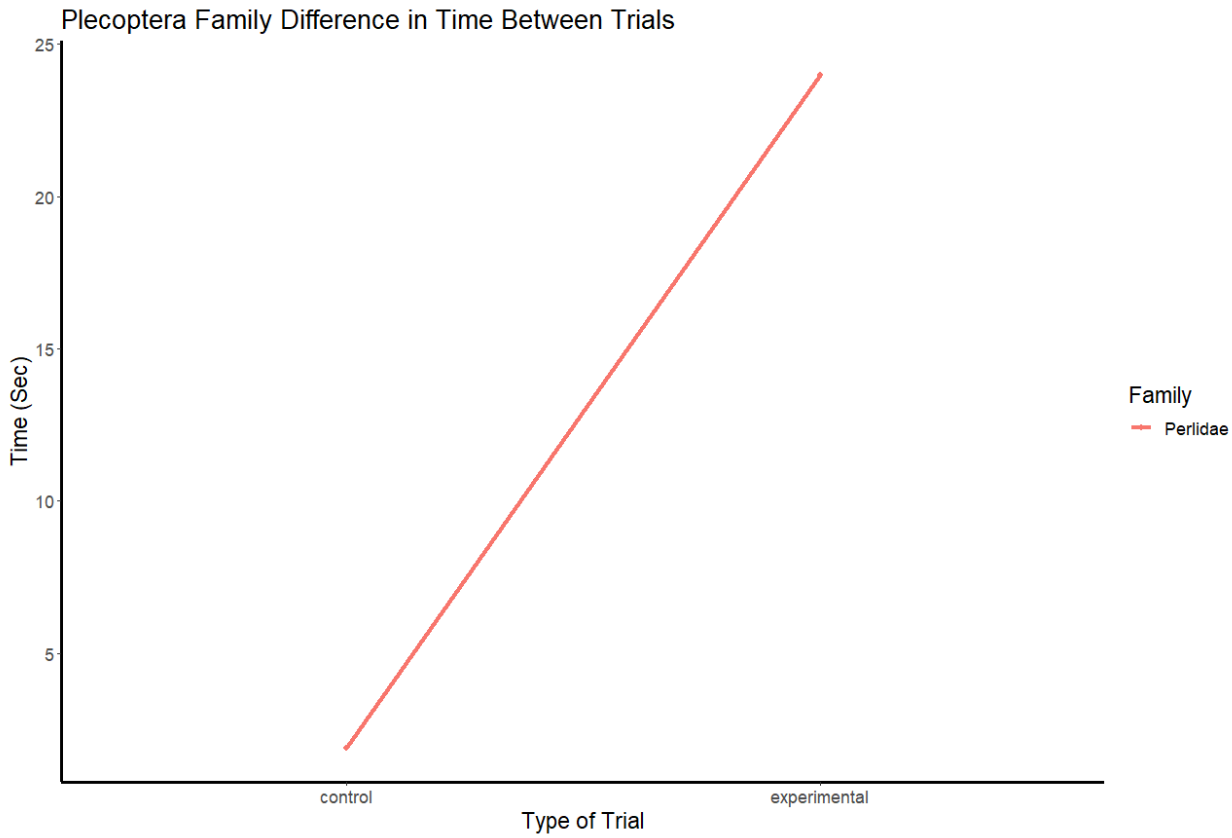


Figure 1. 24. Display of the mean time spent moving during a trial at the family level in the order Plecoptera. On the x-axis is the type of trial, the left column is the control data, and the right column is the experimental column. On the y-axis is the amount of time an individual spent moving of each family in Plecoptera. The legend shows the order assigned with each colored line.

Figure 1. 25. Display the mean distance between an individual's start and end points during a trial at the family level in the order Plecoptera. On the x-axis is the type of trial, the left column is the control data, and the right column is the experimental column. On the y-axis is the mean distance between each family's start and end points (in millimeters) in Plecoptera. The legend shows the family assigned with each colored line.

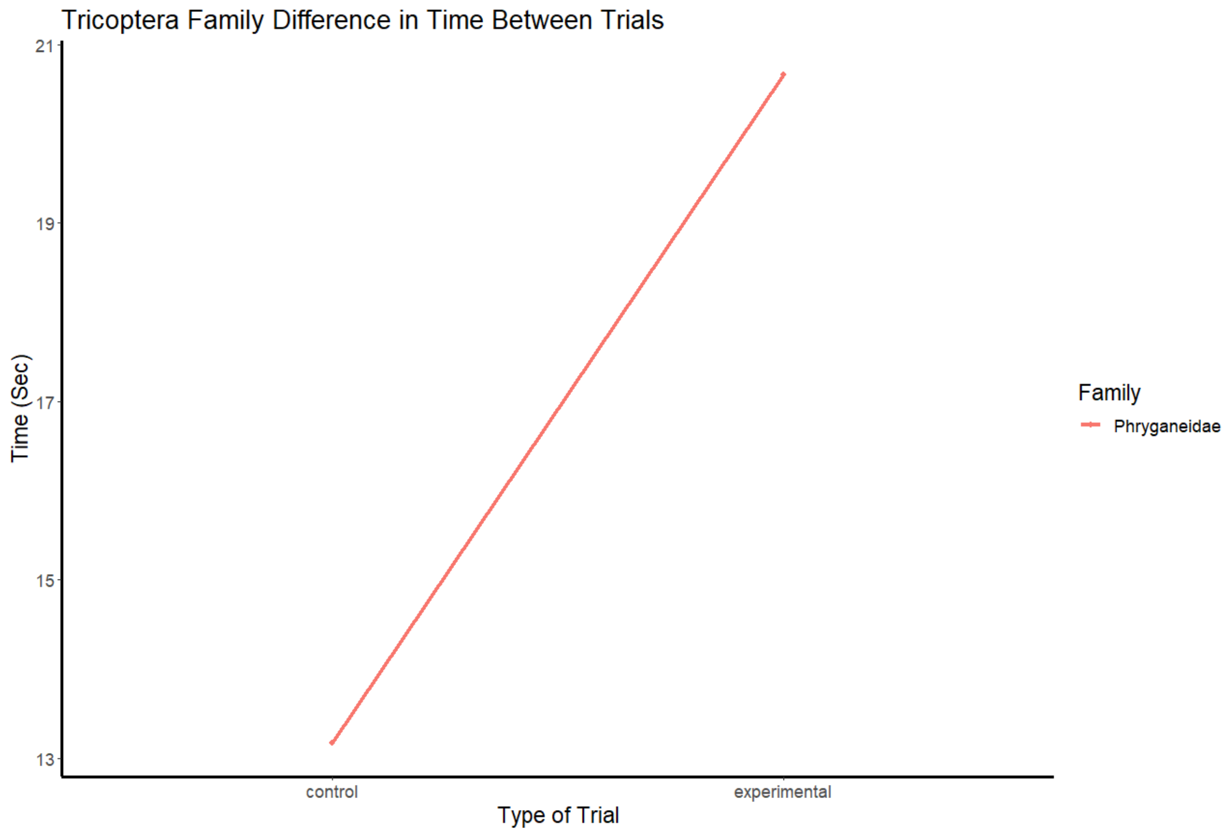


Figure 1. 26. Display of the mean time spent moving during a trial at the family level in the order Tricoptera. On the x-axis is the type of trial, the left column is the control data, and the right column is the experimental column. On the y-axis is the amount of time an individual spent moving of each family in Tricoptera. The legend shows the order assigned with each colored line.

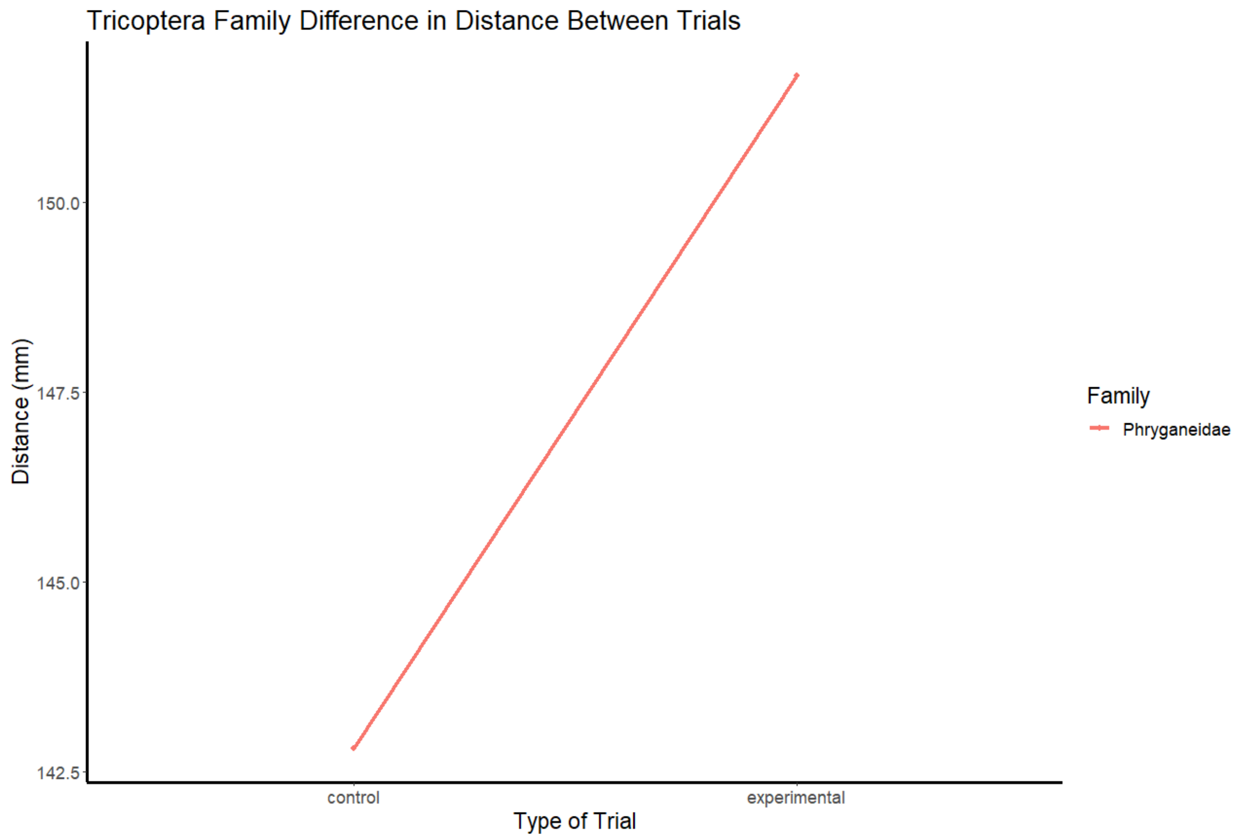


Figure 1. 27. Display the mean distance between an individual's start and end points during a trial at the family level in the order Tricoptera. On the x-axis is the type of trial, the left column is the control data, and the right column is the experimental column. On the y-axis is the mean distance between each family's start and end points (in millimeters) in Tricoptera. The legend shows the family assigned with each colored line.

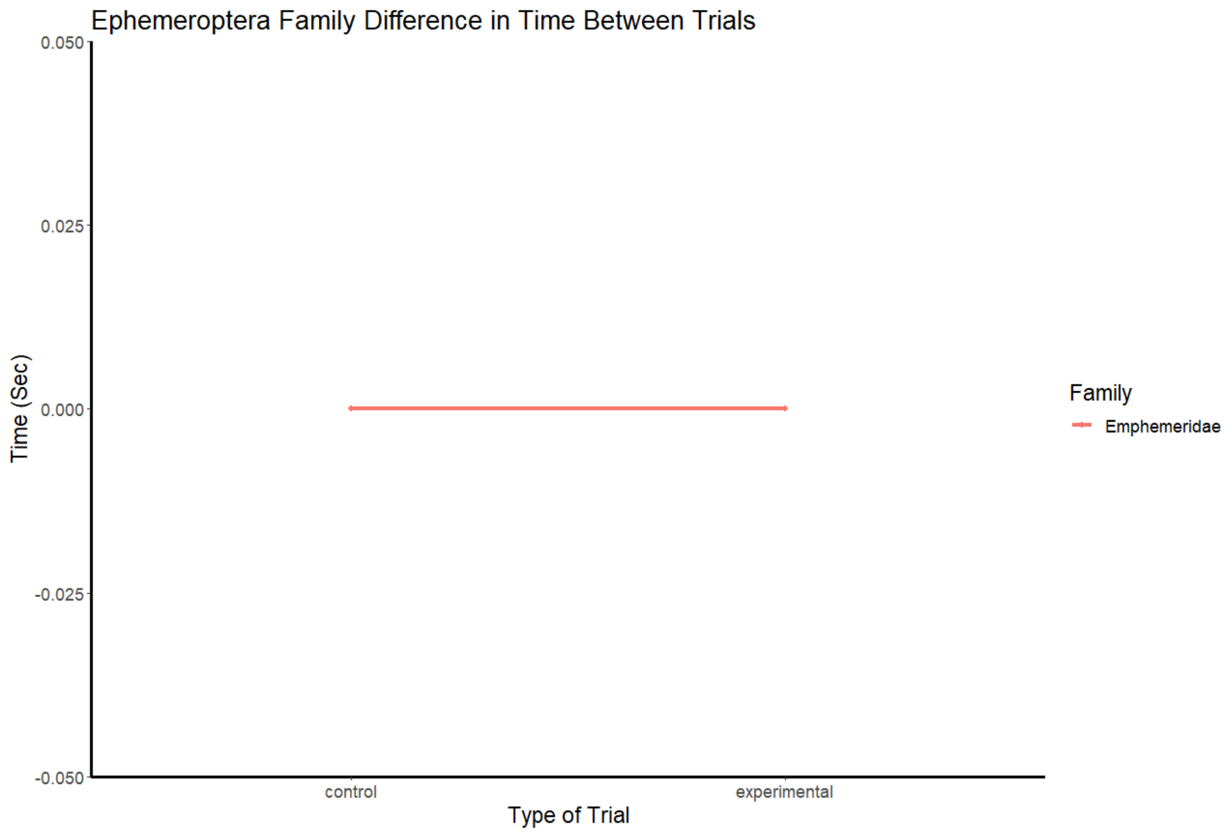


Figure 1. 28. Display of the mean time spent moving during a trial at the family level in the order Ephemeroptera. On the x-axis is the type of trial, the left column is the control data, and the right column is the experimental column. On the y-axis is the amount of time an individual spent moving of each family in Ephemeroptera. The legend shows the order assigned with each colored line.

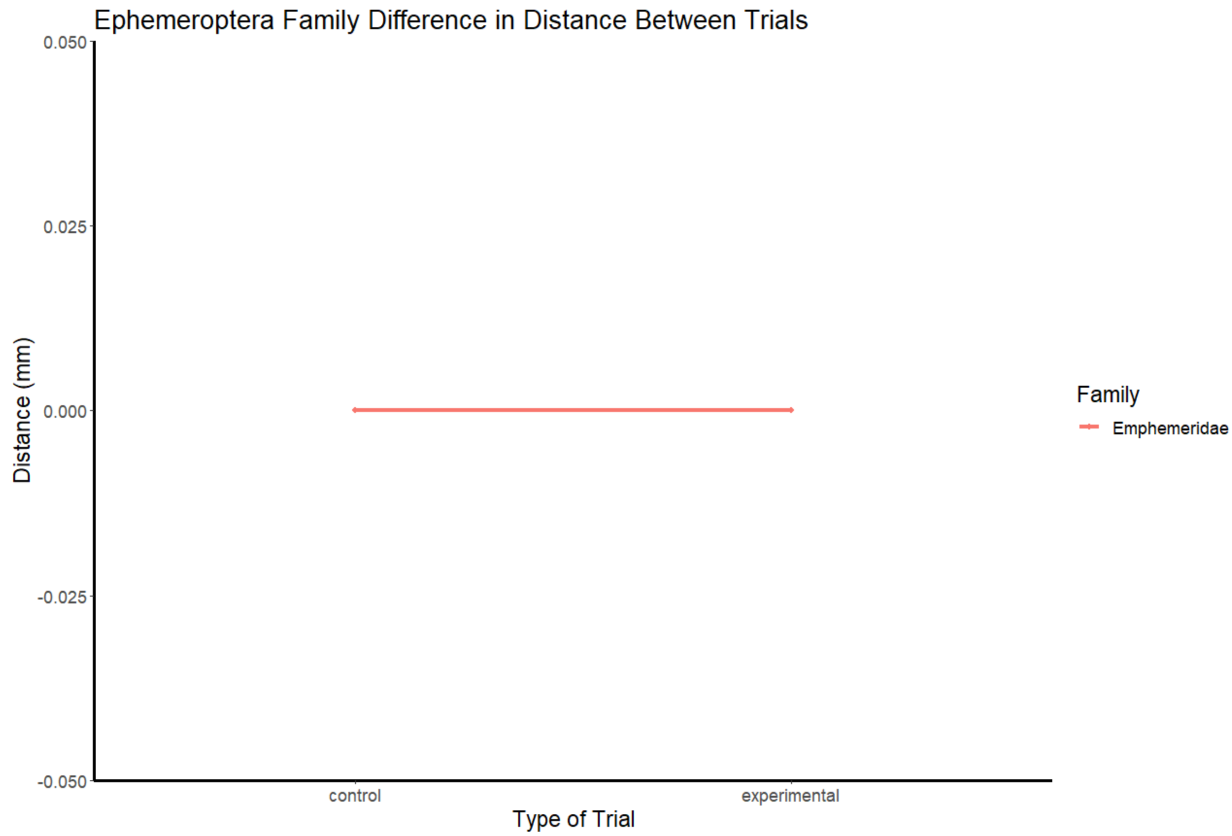


Figure 1. 29. Display the mean distance between an individual's start and end points during a trial at the family level in the order Ephemeroptera. On the x-axis is the type of trial, the left column is the control data, and the right column is the experimental column. On the y-axis is the mean distance between each family's start and end points (in millimeters) in Ephemeroptera. The legend shows the family assigned with the colored line.

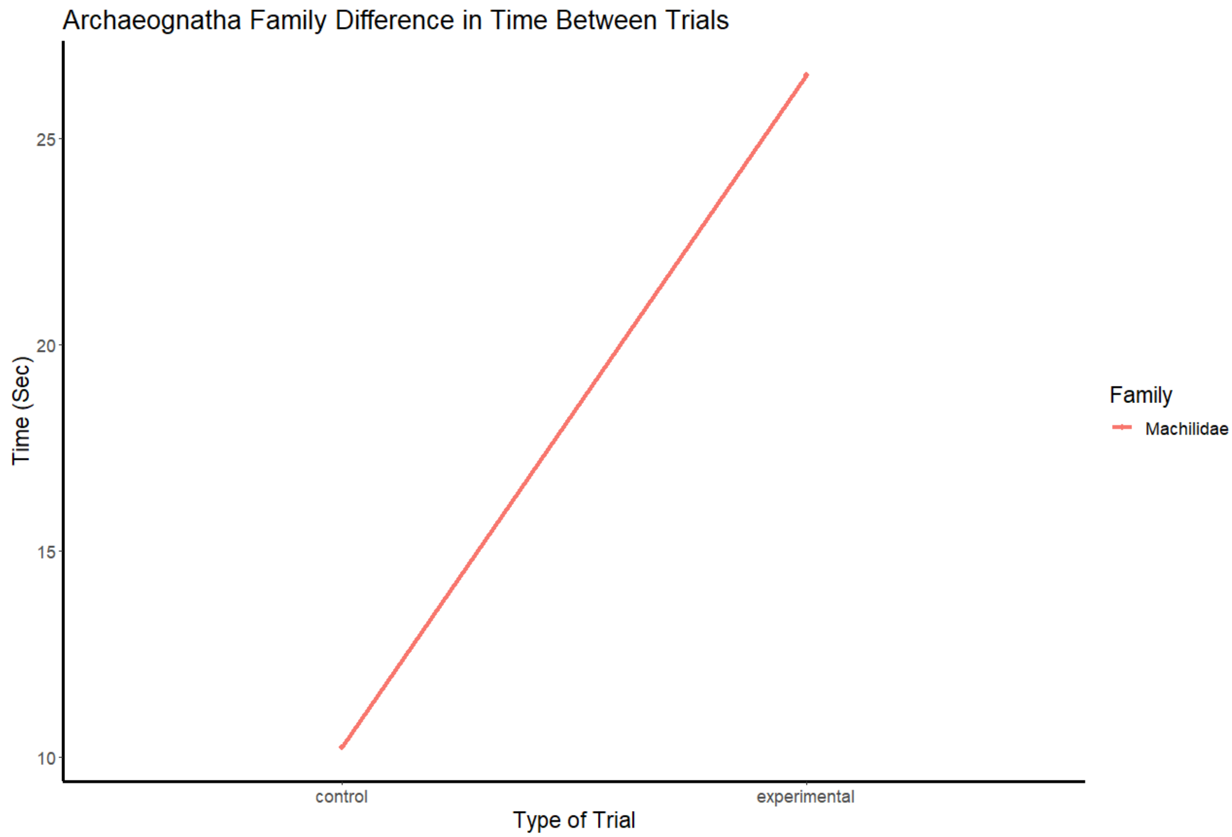


Figure 1. 30. Display of the mean time spent moving during a trial at the family level in the order Archaeognatha. On the x-axis is the type of trial, the left column is the control data, and the right column is the experimental column. On the y-axis is the amount of time an individual spent moving of each family in Archaeognatha. The legend shows the family assigned with the colored line.

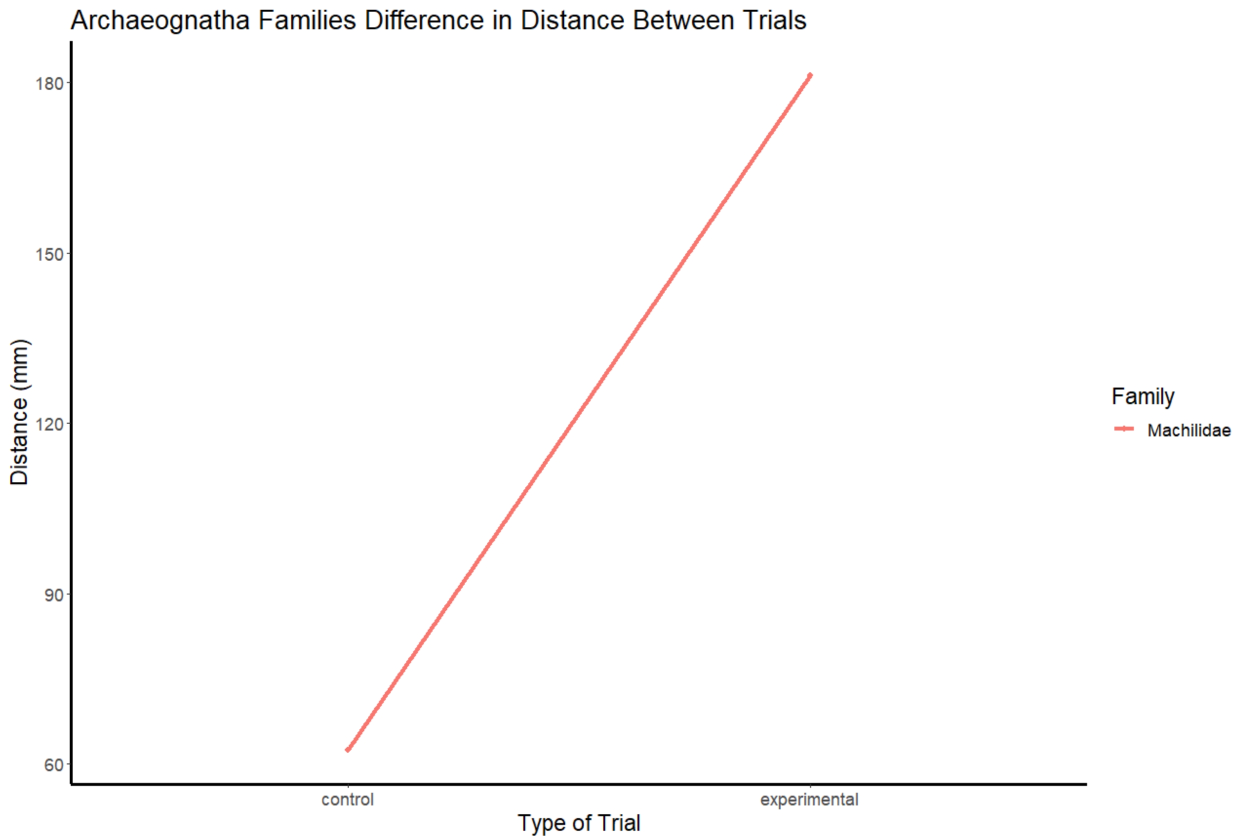


Figure 1. 31. Display the mean distance between an individual's start and end points during a trial at the family level in the order Archaeognatha. On the x-axis is the type of trial, the left column is the control data, and the right column is the experimental column. On the y-axis is the mean distance between each family's start and end points (in millimeters) in Archaeognatha. The legend shows the family assigned with the colored line.

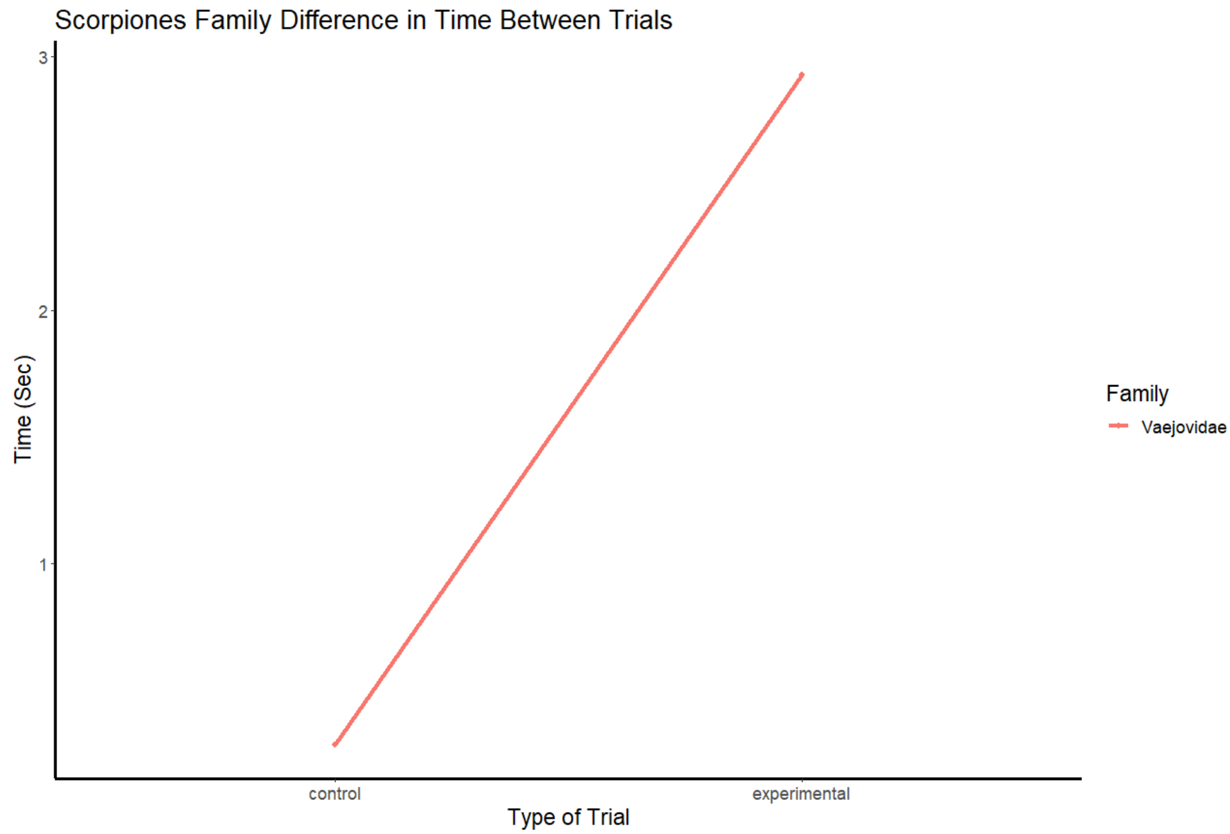


Figure 1. 32. Display of the mean time spent moving during a trial at the family level in the order Scorpiones. On the x-axis is the type of trial, the left column is the control data, and the right column is the experimental column. On the y-axis is the amount of time an individual spent moving of each family in Scorpiones. The legend shows the family assigned with the colored line.

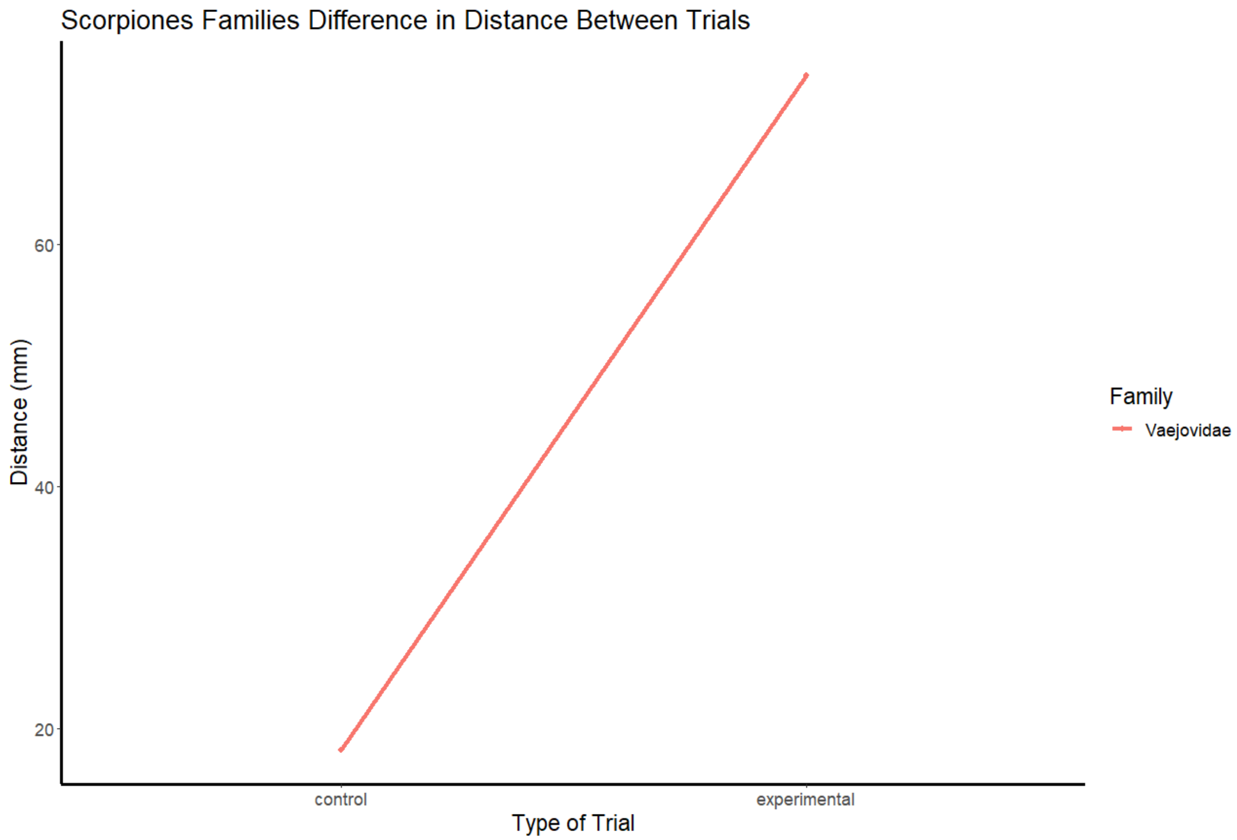


Figure 1. 33. Display the mean distance between an individual's start and end points during a trial at the family level in the order Scorpiones. On the x-axis is the type of trial, the left column is the control data, and the right column is the experimental column. On the y-axis is the mean distance between each family's start and end points (in millimeters) in Scorpiones. The legend shows the family assigned with the colored line.

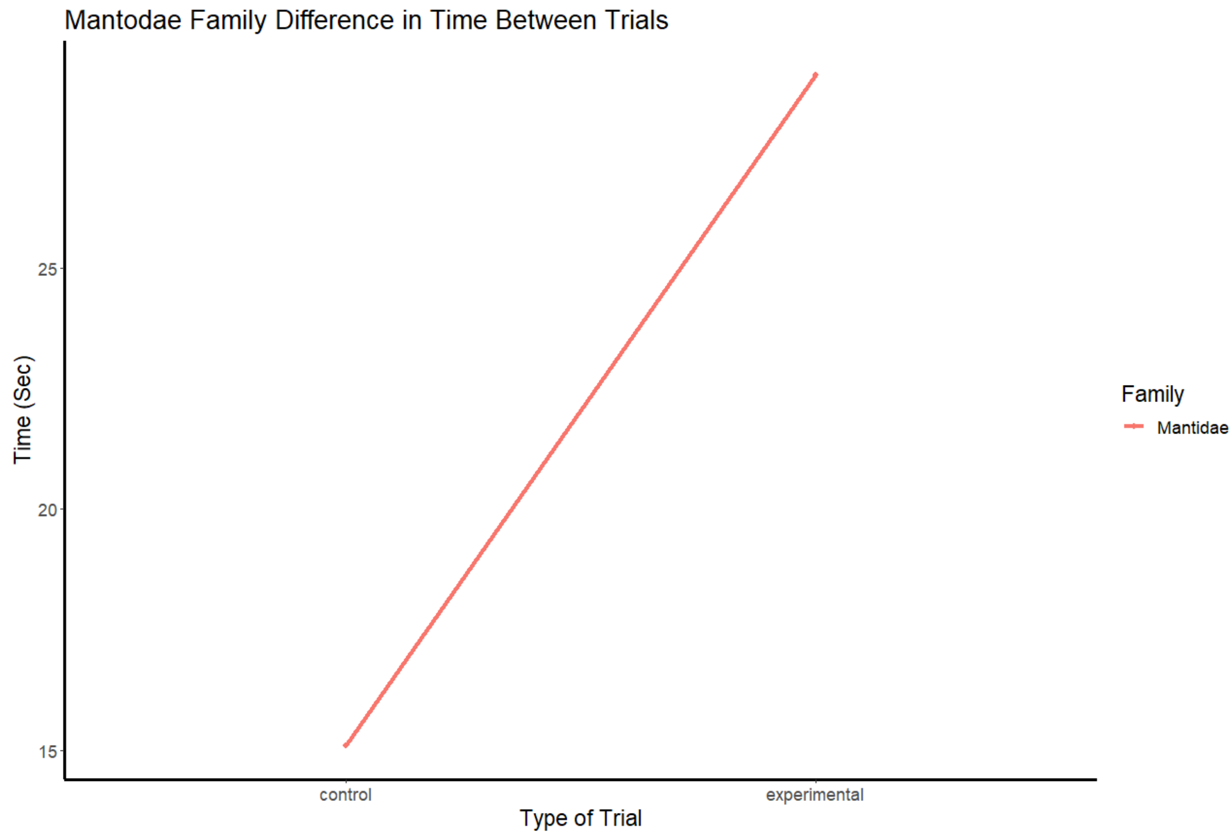


Figure 1. 34. Display of the mean time spent moving during a trial at the family level in the order Mantodea. On the x-axis is the type of trial, the left column is the control data, and the right column is the experimental column. On the y-axis is the amount of time an individual spent moving of each family in Mantodea. The legend shows the family assigned with the colored line.

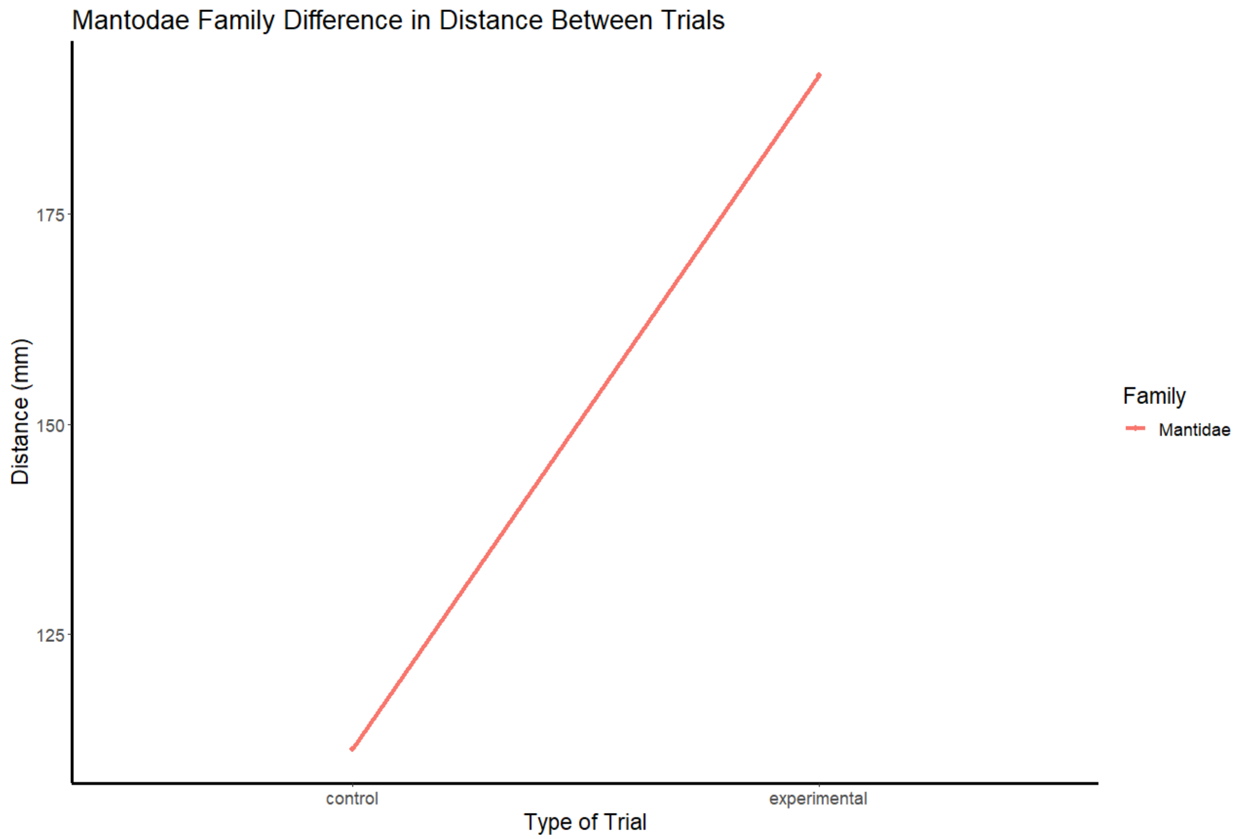


Figure 1. 35. Display the mean distance between an individual's start and end points during a trial at the family level in the order Mantodea. On the x-axis is the type of trial, the left column is the control data, and the right column is the experimental column. On the y-axis is the mean distance between each family's start and end points (in millimeters) in Mantodea. The legend shows the family assigned with the colored line.

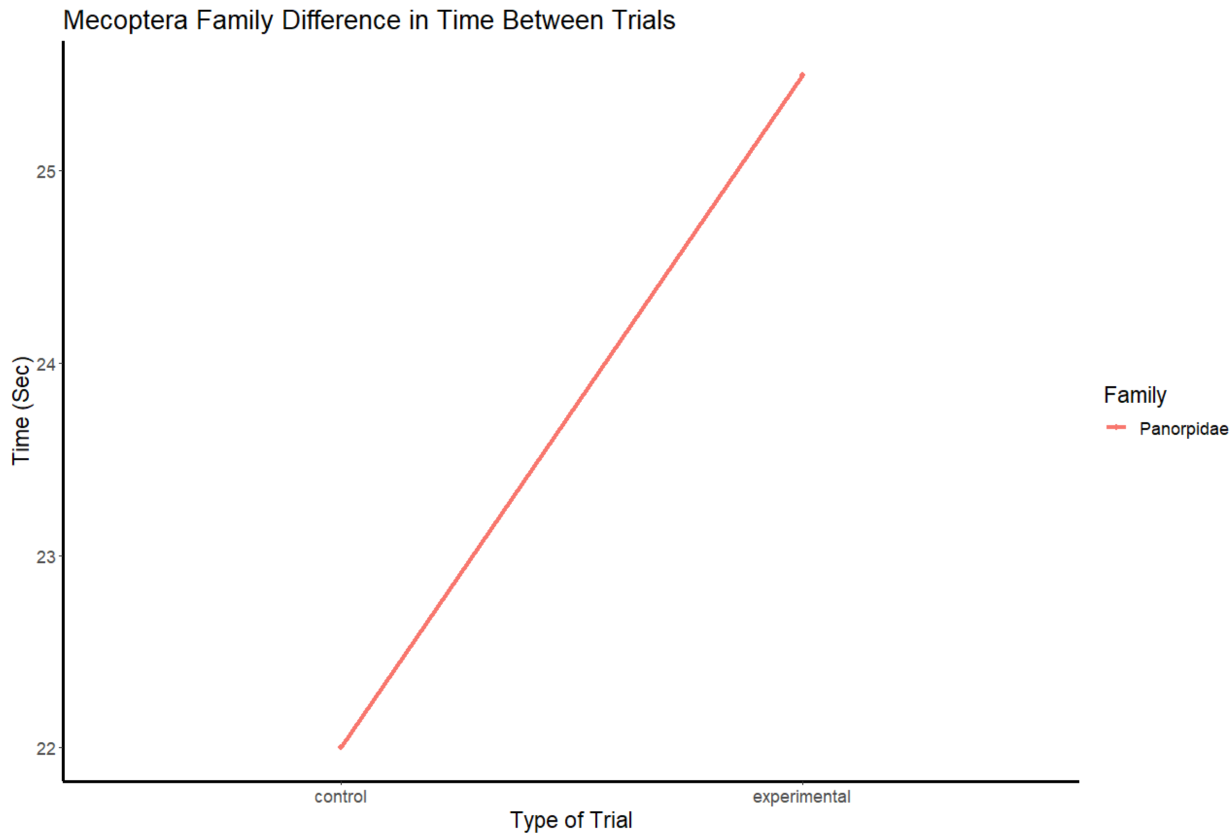


Figure 1. 36. Display of the mean time spent moving during a trial at the family level in the order Mecoptera. On the x-axis is the type of trial, the left column is the control data, and the right column is the experimental column. On the y-axis is the amount of time an individual spent moving of each family in Mecoptera. The legend shows the family assigned with the colored line.

Figure 1. 37. Display the mean distance between an individual's start and end points during a trial at the family level in the order Mecoptera. On the x-axis is the type of trial, the left column is the control data, and the right column is the experimental column. On the y-axis is the mean distance between each family's start and end points (in millimeters) in Mecoptera. The legend shows the family assigned with the colored line.

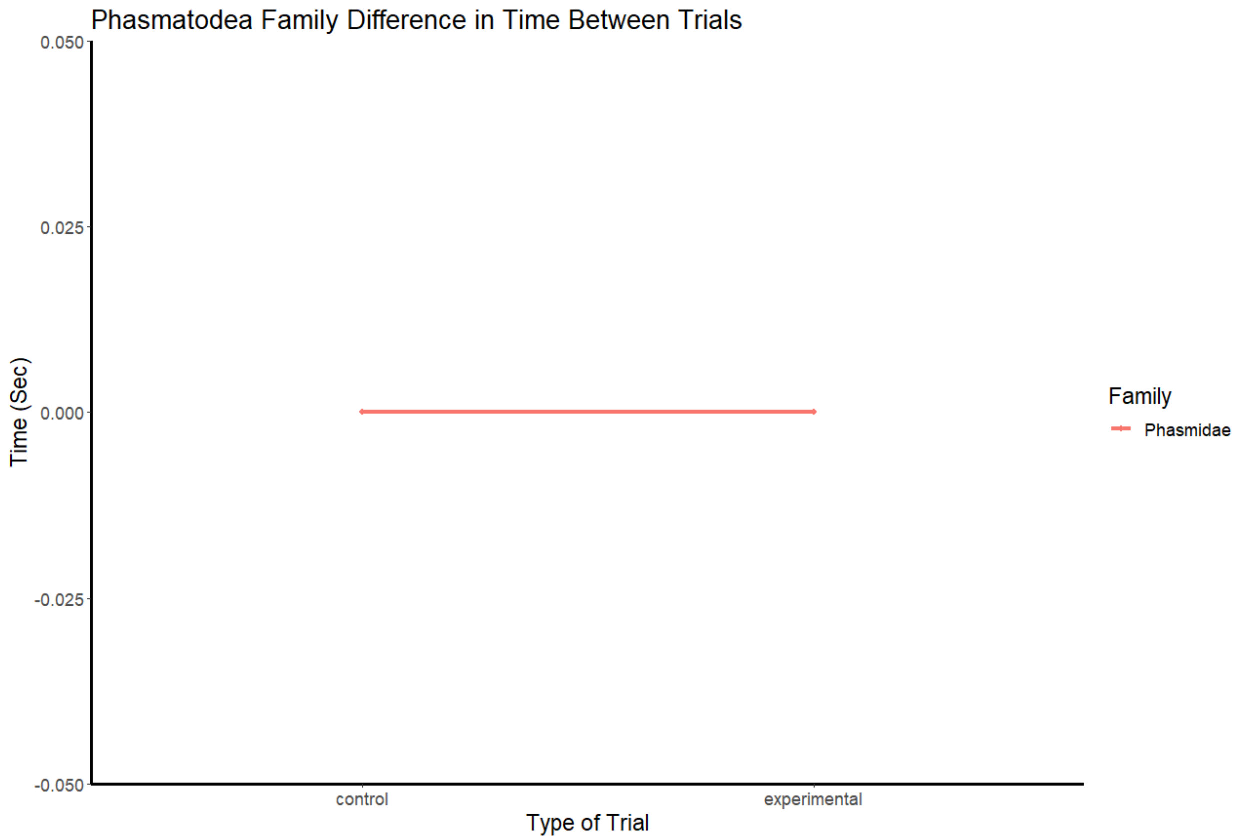


Figure 1. 38. Display of the mean time spent moving during a trial at the family level in the order Phasmatodea. On the x-axis is the type of trial, the left column is the control data, and the right column is the experimental column. On the y-axis is the amount of time an individual spent moving of each family in Phasmatodea. The legend shows the family assigned with the colored line.

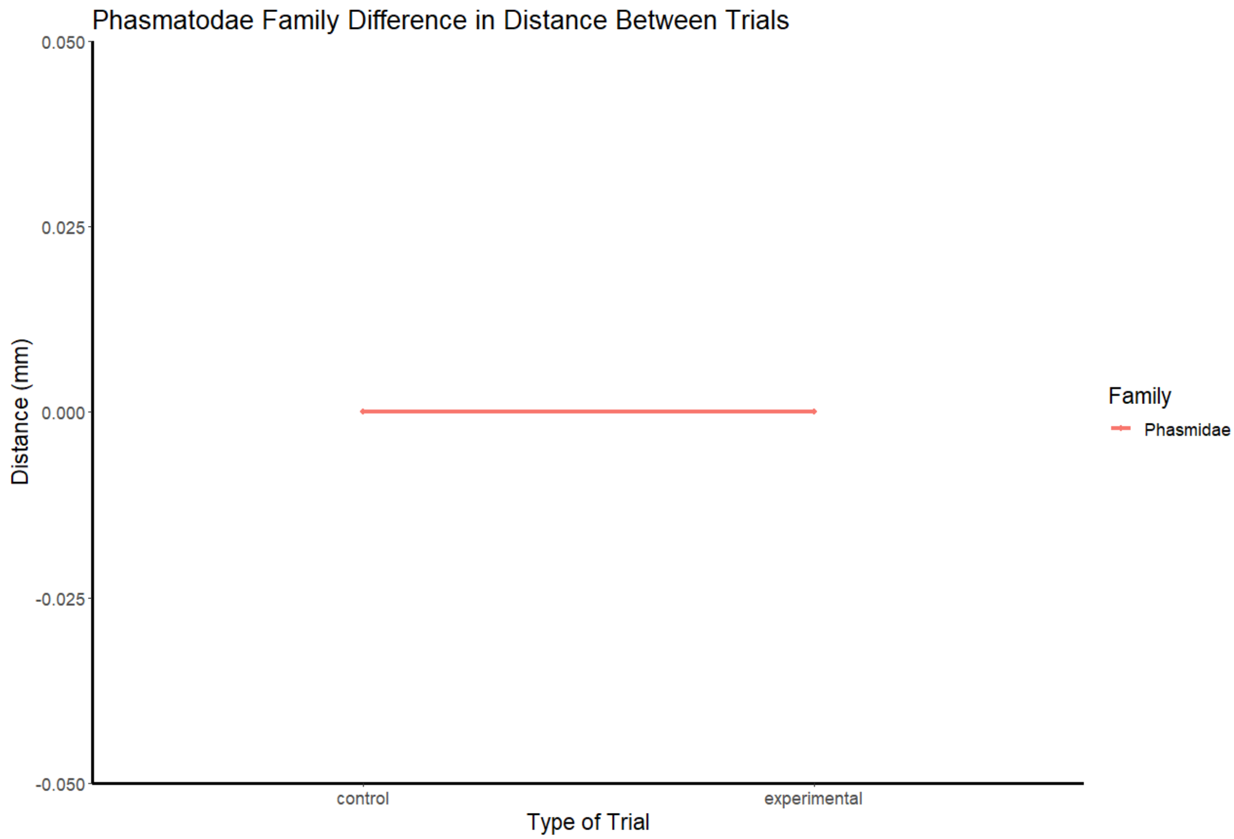


Figure 1. 39. Display the mean distance between an individual's start and end points during a trial at the family level in the order Phasmatodea. On the x-axis is the type of trial, the left column is the control data, and the right column is the experimental column. On the y-axis is the mean distance between each family's start and end points (in millimeters) in Phasmatodea. The legend shows the family assigned with the colored line.

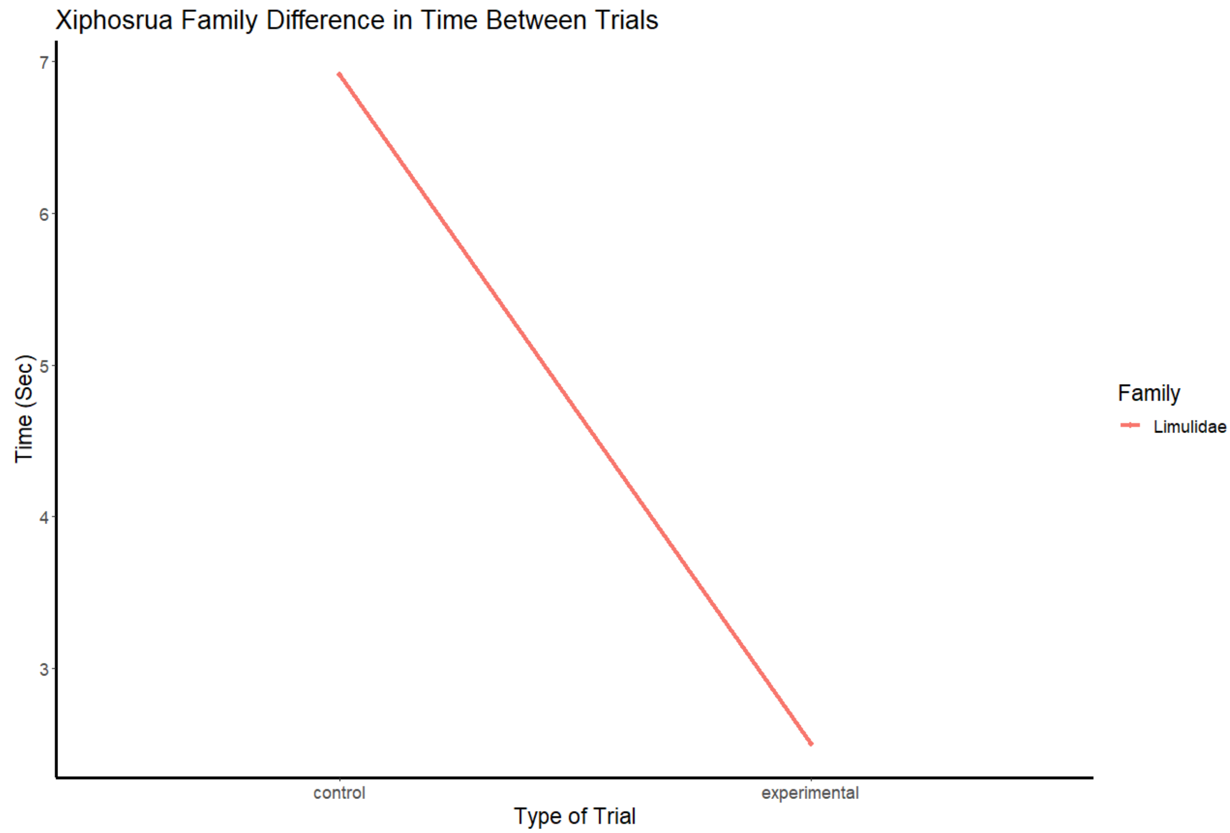


Figure 1. 40. Display of the mean time spent moving during a trial at the family level in the order Xiphosura. On the x-axis is the type of trial, the left column is the control data, and the right column is the experimental column. On the y-axis is the amount of time an individual spent moving of each family in Xiphosura. The legend shows the family assigned with the colored line.

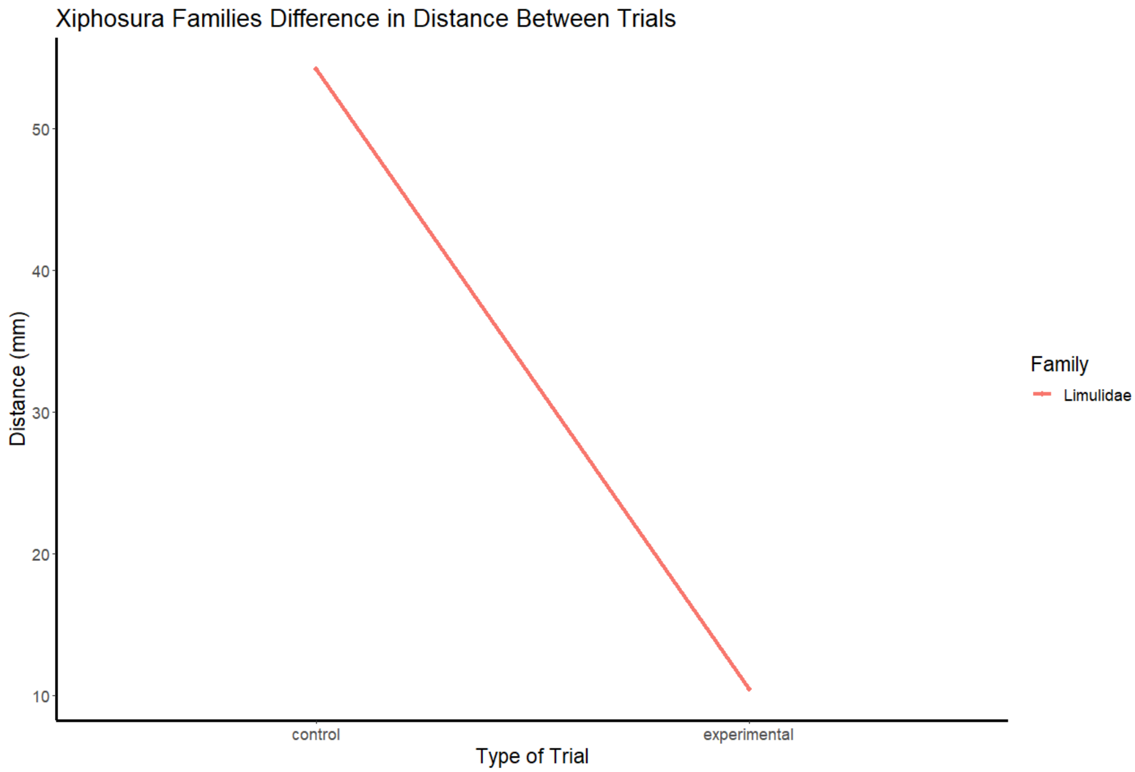


Figure 1. 41. Display the mean distance between an individual's start and end points during a trial at the family level in the order Xiphosura. On the x-axis is the type of trial, the left column is the control data, and the right column is the experimental column. On the y-axis is the mean distance between each family's start and end points (in millimeters) in Xiphosura. The legend shows the family assigned with the colored line.

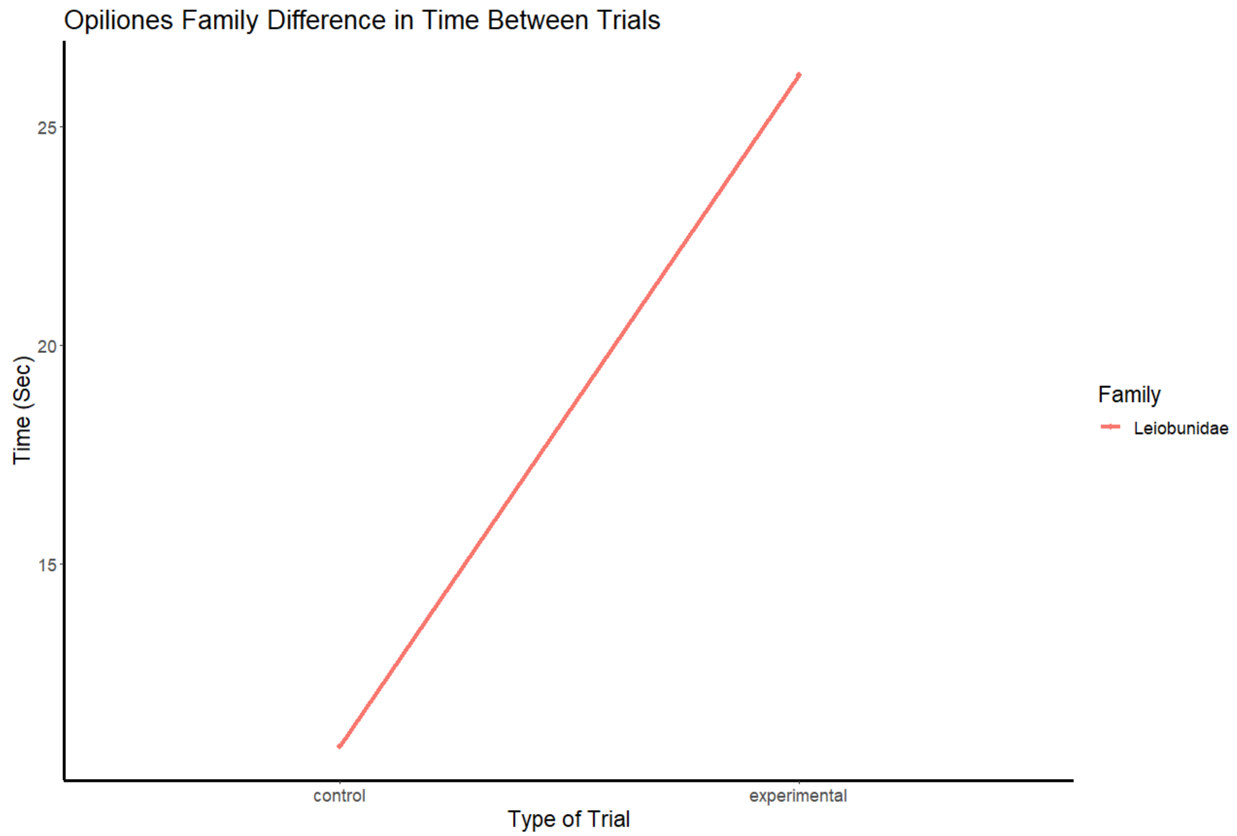


Figure 1. 42. Display the mean distance between an individual's start and end points during a trial at the family level in the order Opiliones. On the x-axis is the type of trial, the left column is the control data, and the right column is the experimental column. On the y-axis is the mean distance between each family's start and end points (in millimeters) in Opiliones. The legend shows the family assigned with the colored line.

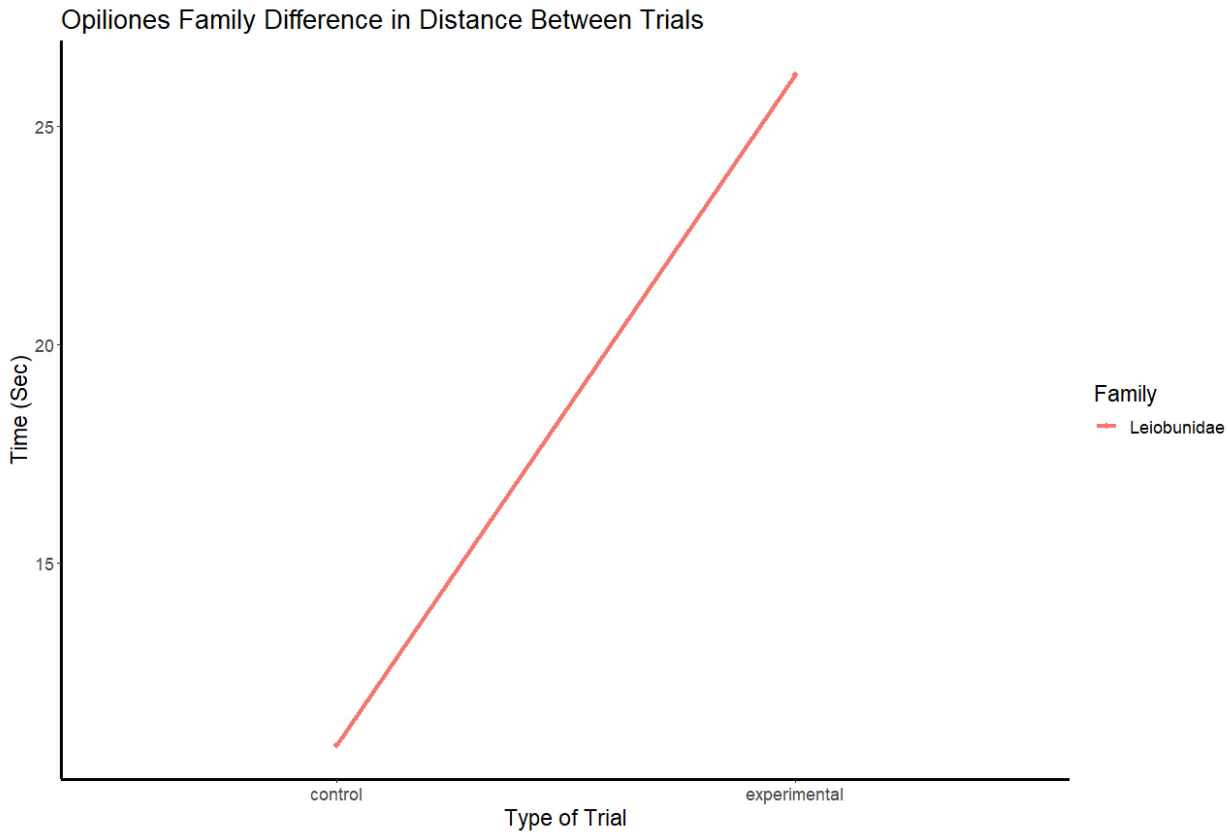


Figure 1. 43. Display the mean distance between an individual's start and end points during a trial at the family level in the order Opiliones. On the x-axis is the type of trial, the left column is the control data, and the right column is the experimental column. On the y-axis is the mean distance between each family's start and end points (in millimeters) in Opiliones. The legend shows the family assigned with the colored line.

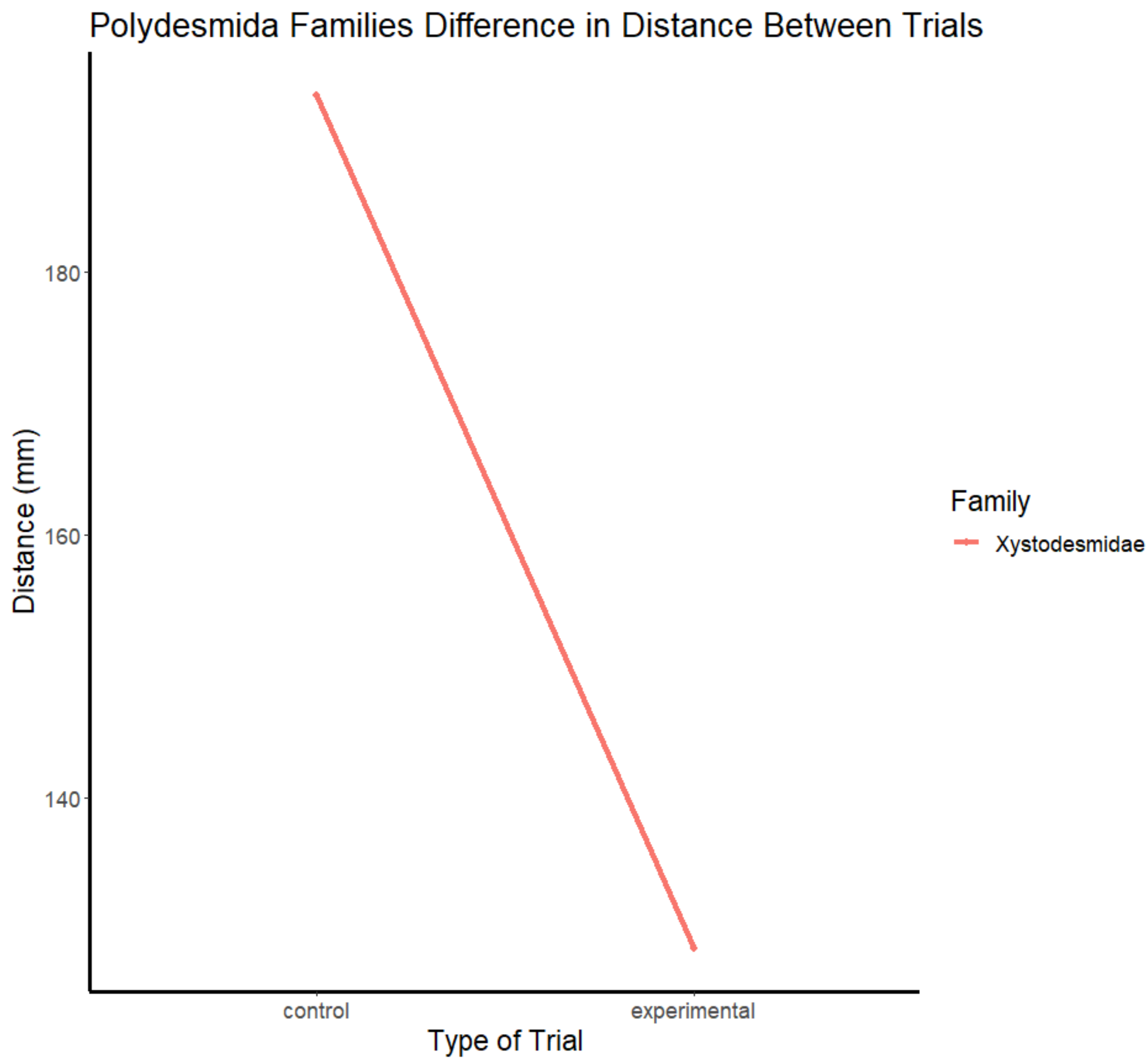


Figure 1. 44. Display the mean time spent moving during a trial at the family level in the order Polydesmida. On the x-axis is the type of trial, the left category is the control data, and the right category is the experimental data. On the y-axis is the amount of time an individual spent moving the family in Polydesmida. The legend shows the family assigned with the colored line.

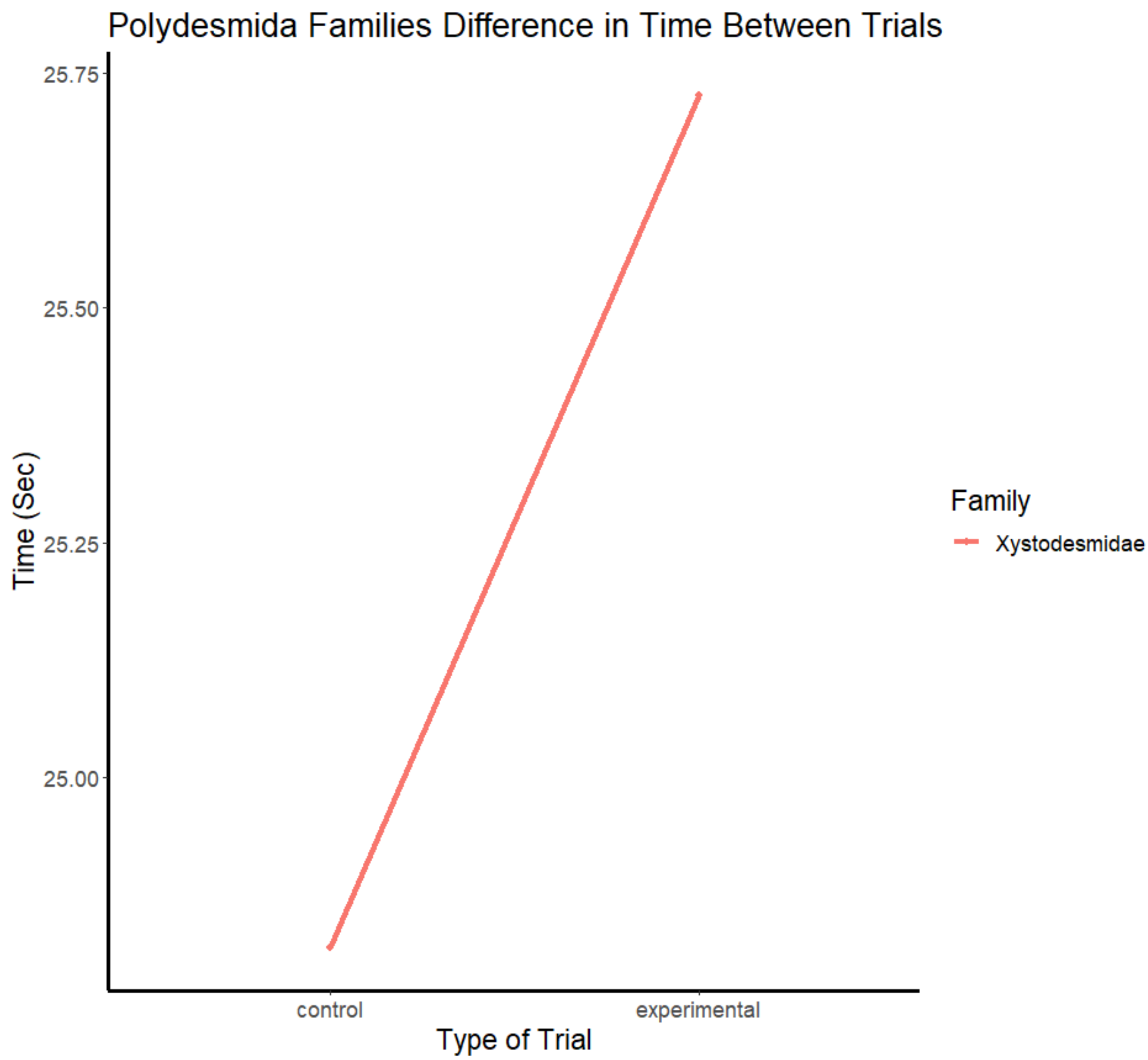


Figure 1. 45. Display the mean distance between an individual's start and end points during a trial at the family level in the order Polydesmida. On the x-axis is the type of trial, the left category is the control data, and the right category is the experimental data. On the y-axis is the mean distance between the family's start and end points (in millimeters) in Polydesmida. The legend shows the family assigned with the colored line.

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