Observational and metabarcoding approaches reveal the ecology, natural history and conservation status of *Scolopendra abnormis*, a threatened centipede endemic to Mauritius.

Running head: Ecology and conservation of *Scolopendra abnormis*

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Abstract

The Serpent Island centipede, *Scolopendra abnormis*, is a threatened centipede species found on only two small islands in the Indian Ocean: Round Island, located 22.5 km north-east of Mauritius, and Serpent Island, 4 km north-west of Round Island. Current understanding of its ecology is based on limited direct observations from 30 years ago. Round Island has since undergone significant habitat restoration. Hyperabundant non-native ants are also present, which may impact centipede nesting behaviour, ecology and survival. Recent methodological advances, such as high-throughput sequencing of dietary DNA, can extend our understanding of invertebrate ecology and provide data complementary to direct observation. Using a combination of dietary metabarcoding and observational approaches, we provide new insights into the ecology and natural history of this threatened invertebrate predator. *Scolopendra abnormis* nest most consistently in the root network found beneath endemic *Pandanus vandermeeschii* trees. They are also found in areas with good soil cover, herbaceous growth, and areas of bare rock slab. Only four of 43 centipedes in this study were found near an ant foraging trail, which may have significant implications for *S. abnormis* nesting habits. These centipedes primarily consume insect prey (particularly taxa within Lepidoptera, Hymenoptera, Diptera), irrespective of centipede body size. A quarter of centipedes also consumed endemic lizards. We also found marked differences in diet composition between wet and dry seasons arising from the changing availability of prey. We provide additional natural history observations and conclude by suggesting conservation actions that would help better understand and safeguard *S. abnormis* populations.

1. Introduction

Scolopendrid centipedes (Myriapoda: Chilopoda: Scolopendridae) are some of the largest and most distinctive of all terrestrial invertebrate predators. Island-dwelling *Scolopendra* may be top predators in their respective communities (McCormick & Polis 1982, Halpin et al. 2021), though little is known of the ecology of most species (Shear & Peck 1992). Conserving such species can be challenging because they may suffer a high risk of extinction before their ecology or principal threats have been identified and studied.

The Serpent Island centipede, *Scolopendra abnormis* Lewis and Daszak 1996 (Figure 1), is a threatened endemic species found on two small islands located north-east of Mauritius: Round Island (219 ha) and Serpent Island (32 ha; Pearce-Kelly 1996; Lewis et al. 2010). It is the only scolopendrid listed on the IUCN Red List (Vu, D2: Pearce-Kelly 1996) with only two other centipedes listed, both also endemic to islands: *Seychellonema gerlachi* (Gerlach 2014), a scutigerid from the Seychelles, and *Nothogeophilus turki* (Macadam 2022), a geophilid from the Isles of Scilly. Unfortunately, extinction of scolopendrid centipedes from islands has occurred before, including two species from Galapagos (Shear & Peck 1992). *Scolopendra abnormis* is locally abundant and previous behavioural observations offer useful insights into its natural history (Lewis & Daszak 1996, Lewis et al. 2010), though little is known about its diet, nesting habits, or breeding behaviour. Round Island has undergone significant habitat restoration in the almost 30 years since *S. abnormis* was last studied. Much of the island is now covered in dense herbaceous cover and young trees after suffering severe habitat destruction by now-eradicated invasive herbivores. Non-native ants are abundant across Round Island (Tercel 2023), which have been shown to threaten invertebrate communities globally (Tercel et al. 2023) through predation, stinging/spraying, and competition. It is not known whether these may be affecting *S. abnormis*.

New molecular tools can be used to learn about target species rapidly and in unprecedented detail. For example, population genetics can be used to ascertain historical population dynamics (Bruford & Wayne 1993, Thomas et al. 2022), and dietary metabarcoding can reveal the key food resources threatened species require (Tercel et al. 2022, Moorhouse-Gann et al. 2022, Stenhouse et al. 2023). Very few studies exist that examine the diet of centipedes at all, fewer still using DNA metabarcoding (we found only two in our literature search: Eitzinger et al. 2018, Bortolin et al. 2018), and these do not assess the diets of species of high conservation concern, nor of any scolopendrids. Here, we present results from a combination of dietary metabarcoding and observational approaches to enhance our basic knowledge of the biology of *S. abnormis.* We present new insights into the ecology of *S. abnormis* from its Round Island population that provide possible next steps for the conservation of this species. Though we aimed to reveal more about the natural history of *S. abnormis* generally, we also wanted to answer the following questions:

1) What habitats do centipedes nest in most commonly and do non-native ants affect their nesting behaviour?
2) What are the key prey groups for centipedes, do centipedes consume vertebrate prey on Round Island, and does centipede body size affect diet?
3) Does centipede diet vary seasonally on Round Island?

2. Methods

2.1 Study site

Round Island (Figure 2) is a 219 ha basaltic cone that reaches 280 m above sea level and represents the last remnant of native lowland palm forest within the Mascarenes (Cheke & Hume 2008). The island suffered severe habitat destruction and soil erosion, leaving bare rock slab over much of the island, because of introduced goats *Capra aegagrus hircus* Linn., 1758, and rabbits *Oryctolagus cuniculus* Linn., 1758, which were eradicated in 1979 and 1986, respectively. Native habitat has been recovering since non-native vertebrate herbivores were eradicated (Merton 1987, Cheke & Hume 2008) and is primarily dominated by the blue latan palm, *Latania loddigesii* Mart. (1838) and, to a lesser extent, the screwpine *Pandanus vandermeeschii* Balf.f. Habitat restoration intensified in 2002 and there have been extensive efforts to restore the lost hardwood forests and to enhance the natural regeneration of the palm habitat (Jones 2008). Round Island has never suffered from invasion by non-native predatory mammals, such as rats, and therefore hosts many endemic species extirpated from other islands and mainland Mauritius (Cheke & Hume 2008).

Broad dry and wet seasons exist in Mauritius (Senapathi et al. 2009). The dry season begins in May, with low rainfall, mean air temperature of ~20.5 °C and stronger winds. The driest months are September and October. The wet season begins in December, with much more frequent rainfall, a mean air temperature of ~24.5 °C and minimal wind. The wettest months are January and February (Senapathi et al. 2009).

2.2 Centipede collection and sample processing

Centipedes were collected and observed by searching in soil, within and under rocks, and in leaf litter between August 2019 and March 2020. An effort was made to search for centipedes in all major habitat types across Round Island. This species is strictly nocturnal (Lewis et al. 2010) and surveys were therefore conducted during the day to locate nesting centipedes. Centipedes were collected using forceps and transferred into sterile collection tubes and subsequently frozen. To determine the most frequent nesting substrate, we conducted a habitat survey assessing the substrate type in a 4 m^2 quadrat centred around the location in which a centipede was found. This was done by approximating percentage cover of the following substrate types over the quadrat: bedrock, loose stones/rocks, herbaceous plant cover, soil, tree trunks, and leaf litter. We also noted all tree species within 2 m of a quadrat to determine if centipedes were associated to the root networks of any trees, whether the area was densely covered in herbaceous vegetation, or whether the area was largely without significant plant growth.

Invasive ants are some of the most abundant invertebrates on Round Island (Tercel 2023). We wanted to determine whether these species affected the nesting behaviour of *S. abnormis*, given that both groups nest in the soil and invasive ants have been shown to reduce soil arthropod diversity substantially (Tercel et al. 2023). We therefore recorded the presence-absence of ant nests and foraging trails, and ant species identity if present, in a 5 m radius around the point a centipede was found.

Centipedes were killed by freezing at -20 °C and stored in 100 % ethanol until transfer to -20 °C storage at Cardiff University. A total of 43 centipedes were taken forward for dietary metabarcoding, 27 from the dry season and 16 from the wet season. To remove the gut, centipedes were dissected in fresh 100 % ethanol using sterile equipment. Guts were placed separately in 1.5 mL microcentrifuge tubes and homogenised in 180 µL of lysis buffer using a Qiagen TissueLyser (Qiagen, Manchester, UK) with sterile steel beads at 60 Hz for 30 seconds. To determine if centipede size influences dietary composition, we measured centipede head width and body length during dissections using electronic callipers with a precision of 0.01 mm. These measurements may not exactly represent the dimensions of living centipedes due to centipedes changing size in ethanol; all samples were treated the same.

2.3 Dietary metabarcoding

High-throughput sequencing methods broadly followed Tercel et al. (2022): DNA extraction followed DNeasy Blood & Tissue Kit manufacturer recommendations, but with a lysis time of approximately 14 hours to increase penetration of chitinous tissue. We used one negative control per seven samples, which comprised molecular grade water treated identically to samples. Polymerase chain reactions (PCR) were used to amplify dietary DNA using invertebrate primers BerenF-LuthienR (Cuff et al. 2021) and AntExF-AntExR (Tercel 2023; Table S1 and see the Appendices of Tercel 2023 for full primer validation). These amplify 314bp and 214bp fragments of the mitochondrial COI gene, respectively, and broadly amplify the DNA of terrestrial invertebrates found on Round Island (Tercel 2023). Beren-Luthien also amplify the DNA of several vertebrate species on Round Island, such as the skinks, geckos, and seabirds. We used two primer pairs for centipede dietary DNA amplification, which mitigates the problems associated with using a single primer pair (Tercel et al. 2021, Cuff et al. 2023). Primers were uniquely labelled using 8bp molecular identification tags (MID-tags) to identify samples bioinformatically. PCR products were analysed for fragment sizes and concentrations via QIAxcel, and subsequently pooled for equimolarity and cleaned: each pool was cleaned using SPRIselect beads (Beckman Coulter, Brea, USA), with a left-side size selection using a 1:1 ratio. Libraries were prepared for Illumina sequencing using NEXTflex™ Rapid DNA-Seq Kit following the manufacturer's instructions (Bioo Scientific Corp, Austin, TX, United States). To confirm fragment size and correct ligation of adapters, libraries were run on an Agilent 4200 TapeStation with D1000 ScreenTape (Agilent Technologies, Waldbronn). PCR products from each primer pair were sequenced separately using an Illumina MiSeq as part of a larger project. BerenF-LuthienR amplicons were sequenced on a V3 cartridge using 2 x 300 bp reads, and AntExF-AntExR with a V2 cartridge using 2 x 250 bp reads. The Illumina sequencing runs generated an average read depth of 8,151 and 12,993 per sample for AntEx and Beren-Luthien primer pairs, respectively.

Bioinformatics and data cleaning followed Tercel (2023): FastP (Chen et al. 2018) was used to check the quality of reads, discard poor quality reads (< Q30, < 125bp long or too many unqualified bases, denoted by "N"), trim reads to a minimum length specific to each primer pair (AntEx: 214bp, Beren-Luthien: 314bp) and merge read pairs from MiSeq files (R1 and R2). Read pairs were assigned to samples and demultiplexed using Mothur v1.39.5 (Schloss et al. 2009), after which MID-tag and primer ends were removed. Unoise3 (Edgar 2010) was used to remove replicates, denoise the sequences, and group identical sequences into zero-radius operational taxonomic units (zOTUs, which are clustered without % identity to avoid multiple species being nested within an OTU). These zOTUs are analogous to species-level identifications but may not be assigned a full binomial species name (e.g., family- or genus-level taxonomy may be assigned if the species has not been barcoded). BLASTn with an up-to-date BLAST database downloaded from GenBank was used to directly assign taxonomic identities to each zOTU (Camacho et al. 2009). The Round Island system has not received much entomological study, and thus morphological identification resources are not easily accessible for most groups. Many of Round Island's invertebrates have therefore also never been barcoded. In these cases, different species of the same family or genus are given higher-level taxonomic information and then numbered (e.g., Noctuidae species 1, species 2, species 3; Braconidae species 1, species 2, etc.,). Data were cleaned for statistical analysis broadly following the same methods as Tercel *et al*. (2022), whereby we removed the maximum read count found in blanks and negative controls for each taxon from all samples. After data clean-up, 43 centipede samples were taken forward for statistical analysis. Since it is impossible with the data generated to ascertain how many prey of each species were consumed by an individual centipede, any number of sequencing reads after data-cleaning within a centipede gut DNA sample was considered a single detection (i.e., frequency of occurrence).

2.4 Statistical analyses

All statistical analyses were conducted in R version 4.3.1 (R Core Team 2023). We wanted to test whether centipede dietary richness was significantly different between seasons. Data were not normally distributed (Shapiro-Wilk: W = 0.77, p-value = <0.001), thus we used the non-parametric Mann-Whitney U test to assess this. As well as richness, we tested whether diet composition varied between seasons using R package 'mvabund' (Wang et al. 2012). Multivariate generalised linear models (MGLMs) were run using the "manyglm" function with a Monte Carlo resampling method and "binomial" error family. Similarly, we tested whether body length, head width, or overall body size (length multiplied by width) affected dietary composition using the 'manyglm' function and used the "p.uni = adjusted" command in the "anova.manyglm" function to test whether consumption of any specific dietary taxa varied with body size, including any vertebrate prey. Variation in the diet was visualised using non-metric multidimensional scaling analysis (NMDS) using the "metaMDS" function in the "vegan" R package (Oksanen et al. 2019) with Jaccard distance and was plotted using "ggplot2" (Wickham 2016). We used simple linear regression to determine the relationship between body length and head width.

3. Results and discussion

3.1 Nesting habits

The average (mean ± SE) substrate of a 4 m^2 quadrat where centipedes were found consisted of 37.8 % (± 3.33) bedrock, 3 % (± 0.48) loose rock, 10.6 % (± 2.27) herbaceous cover, 15.2 % (± 1.7) soil, 7.2 % (± 1.29) tree trunk, and 26.1 % (± 2.67) leaf litter. Centipedes were almost exclusively found under or between slabs of rock or beneath thick leaf litter (>4 cm depth) within these quadrats. Individuals were most reliably found in the root networks, rocks, and leaf litter beneath *Pandanus* trees (58 %), though some were found near *Latania* palms (16 %). The remaining centipedes were found either in areas of dense herbaceous cover (7 %) or without significant plant growth (19 %). Our surveys update previous observations that this centipede does not nest in areas with thick plant growth, good soil cover, or rocks embedded in soil (Lewis et al. 2010). Since the last surveys in 1996, soil, vegetation, and tree cover on Round Island have increased with habitat regeneration. Indeed, the majority of centipedes were found in quadrats with significant soil accumulation and several individuals were found nesting directly within soil underneath rocks surrounded by herbaceous plants. Grazing damage by goats and rabbits left much of the island an expanse of exposed rock (North et al. 1994, Bullock et al. 2002) that may have restricted centipede nest sites to rocky stacks and crevices (Lewis et al. 2010). However, before habitat destruction took place on Round Island, centipedes probably nested primarily in the forest root network and rocks embedded in the soils of the forest floor beneath thick leaf litter.

Our ant surveys also show that centipedes tend to nest in areas of low ant activity. Of the 43 centipedes collected, only four were near an ant foraging trail and none were within 5 m of ant nests. In contrast, a separate study randomly generated 69 quadrats over Round Island and found ants in all quadrats (Tercel 2023), including in quadrats generated in *Pandanus* thicket habitat, i.e., where centipedes are most reliably found nesting. Whilst the discrepancy in the occurrence of ants could be down to simple differences in habitat preferences, non-native ants have been shown to reduce the diversity of soil-dwelling invertebrate communities substantially (Tercel et al. 2023) through predation and competition, as well as indirect effects. Centipedes on Round Island may be vulnerable to attack by non-native ants whilst nesting during the day and may therefore avoid nesting in areas where ants are particularly abundant.

3.2 Diet richness and drivers of diet composition

A total of 432 prey detections from 63 prey taxa were found across the 43 centipede individuals. The mean number of prey taxa per centipede was 10.04 (± 7.27 SD). Centipedes were found to be consuming a broad range of prey, though primarily consumed taxa within Lepidoptera, Hymenoptera and Diptera (Figure 3). Approximately 25 % of centipedes consumed Bojer's skink, *Gongylomorphus bojerii* (Desjardins, 1831), a critically endangered diurnal skink endemic to Mauritius (Cole & Payne 2022) that is abundant on Round Island (Cole et al. 2018). Young adult and juvenile Bojer's skinks could be easily overpowered by centipedes, especially during the night when skinks are inactive and centipedes are typically hunting. Notably, we did not detect consumption of Durrell's night gecko, *Nactus durrellorum* Arnold and Jones, 1994, a similarly sized but nocturnal small lizard which may be capable of escaping *S. abnormis* at night. Previous diet observations suggest that *S. abnormis* consumes invertebrates they can overpower, such as the abundant cockroaches on Round Island (Lewis et al. 2010), as well as carcasses they can scavenge (Lewis & Daszak 1996, Pearce-Kelly 1996, Lewis et al. 2010), including the carcasses of seabirds on Serpent Island. Our dietary analysis corroborates this, though we did not find evidence of seabird consumption despite the PCR primers used being able to amplify them. Carrion DNA may be more degraded, limiting its detection, although it is usually detectable for relatively long periods (Neidel et al. 2022). The density and overall biomass per unit area of seabirds on Round Island is much lower than on Serpent Island and centipedes may therefore scavenge seabird tissue far less often on Round Island. The high occurrence rate of Lepidoptera is unsurprising given the diverse and highly abundant moth assemblage of Round Island (Tercel and Cole, unpubl. data), though this had not been observed previously (Lewis et al. 2010). Several species of moth are found primarily on expanses of rock slab, where centipedes are often seen at night.

A Mann-Whitney U test showed that centipedes had significantly higher diet richness in the dry season compared to the wet season ($W = 360.5$, $p < 0.001$; mean: dry = 15.88, wet = 6.59). The MGLMs demonstrate that dietary composition also differed between seasons (LRT: 13.36, $df = 1$, $p < 0.001$; Figure 4, stress value = 0.17), probably arising from large seasonal changes in vegetation and the abundance of potential prey species on Round Island (Tercel 2023). Dietary composition appears to be more consistent between centipedes in the dry season whilst also being more diverse in absolute terms (Figure 4). Centipede individuals in the dry season have considerably more consistent diets than those in the wet season, i.e., they share a greater number of dietary species, whilst they also consume more species in total. Seasonal changes to diet have also been shown for other consumers on Round

Island (Zuël 2009, Tercel et al. 2022, Moorhouse-Gann et al. 2022, Tercel 2023). Two non-exclusive reasons could explain the markedly higher dietary diversity of *S. abnormis* in the dry season. The first is that the diversity of potential invertebrate prey on Round Island is higher in the dry season (Tercel 2023). The second is that low humidity during the dry season may drive centipedes to consume more prey to obtain hydration, as many invertebrate predators obtain significant hydration directly from their food.

Scolopendra centipedes are generally thought to be able to consume anything they can overpower (McCormick & Polis 1982, Halpin et al. 2021), and this is likely to be true for *S. abnormis*. However, our MGLMs investigating the relationship between body size and diet composition show that they are unrelated (body length: LRT = 9.58, res.df = 41, p = 0.64; head width: LRT = 7.6, res.df = 40, p = 0.68; body size: LRT = 7.65, res.df = 39, p = 0.68). Despite this, we also tested whether larger centipedes were more likely to consume Bojer's skinks. Simple linear regression showed the expected morphological relationship between centipede head width and body length (R^2 = 0.89, df = 41, p = <0.001; head width = 11.479 * body length + 5.882; Figure 5), but we found no relationship between centipede body size and predation of Bojer's skinks from our univariate mvabund analysis (Dev = 0.123, res.df = 39, p = 0.99). Scolopendrid centipedes have been seen consuming vertebrates in other island systems (McCormick & Polis 1982, Halpin et al. 2021), and approximately 25 % of *S. abnormis* centipedes were found to have consumed skinks. Bojer's skinks may therefore represent an important source of nutrition for *S. abnormis* given that they are presumably amongst the largest food items available to centipedes based on our dietary analysis.

3.3 Additional observations

Our surveys revealed that the mating season of *S. abnormis* takes place in the wet season. Females nurse clutches of 25-40 eggs in their nests (Supplementary Figure S1) from at least late-February to late-March, though the breeding season may extend from December through to April. Some centipedes appeared to be nursing their eggs in nests resting on heavily water-logged soil beneath rocks. No females tending eggs have been seen in the dry season.

Multiple adult centipedes were sometimes found in a single nest site showing no aggression to one another. A lack of aggression was observed in a previous study that experimentally induced meeting reactions (Lewis & Daszak 1996, Lewis et al. 2010). This could be an adaptation to a previously much higher density of centipedes on Round Island before habitat loss, though cannibalism has been shown from populations of *S. abnormis* on Serpent Island where, due to almost no vegetation, resource availability is presumed to be far more limited (Nik Cole, pers. obvs.).

3.4 Conservation of Scolopendra abnormis

The population of *S. abnormis* on Round Island appears healthy: they are readily found over much of the island, are commonly seen at night in multiple habitats, and can obtain nutrition from many prey species. However, *S. abnormis* is found only on two small islands, and is therefore listed as Vulnerable, D2: a "restricted distribution" and "susceptible population", on the IUCN Red List (Pearce-Kelly 1996). The principal threat to *S. abnormis* therefore comes from the potential introduction of invasive mammalian predators to these islands (Lewis et al. 2010). Our study suggests that invasive ants may be causing a problem for centipedes whilst nesting. Centipedes nest in areas with relatively low ant presence, despite a generally high abundance of ants over Round Island. Ants might restrict *S. abnormis* to certain areas and limit the population by evicting them from potential nest sites, which may be particularly problematic for females nursing eggs. Establishing ant suppression plots on Round Island would allow this to be tested experimentally, as well as examining the wider effects of non-native ants on the invertebrate community, which may have important ramifications for centipede diet.

A captive breeding program for *S. abnormis* could be implemented, which would safeguard their future and genetic diversity in the event of invasions by other non-native species or the population expansion of invasive ants on Round Island. Captive populations could also be used to translocate centipedes to islands that were thought to host the species previously. Gunner's Quoin, for example, may have hosted *S. abnormis* in the past before rats invaded. However, the island is similarly invaded by ants and hosts several species found nowhere else. It is possible the centipedes may even pose a risk to some of these endemic species. Increasing the number of sites of occupancy would help safeguard *S. abnormis* in the event of environmental incidents or further biological invasions, but translocation events would need to be carefully planned to maximise their conservation value to the wider ecosystem.

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Conflict of interest statement

The authors have no conflicts of interest to declare.

Data availability

Data are available as supplementary files.

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Figure 1. The Serpent Island centipede, *Scolopendra abnormis*, photographed on Round Island, 2023. This individual was approximately 90 mm in length. Photograph by MPTGT.

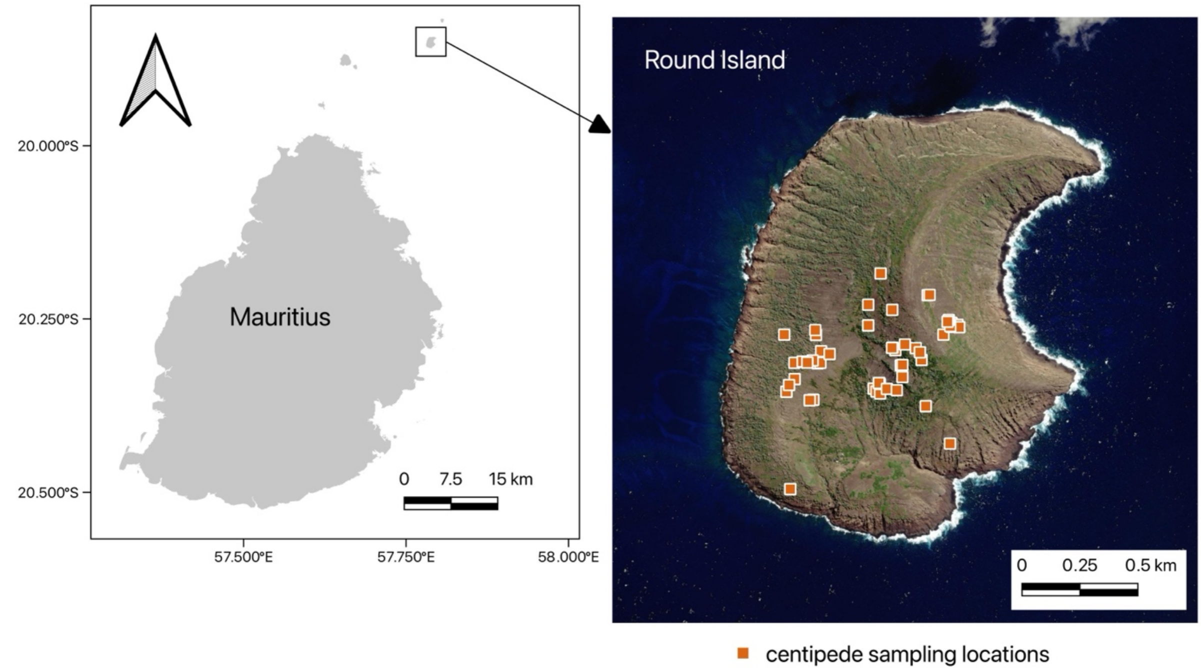

Figure 2. The position of Round Island in the Mauritian archipelago and centipede sampling sites across Round Island (basemap: Google © 2021).

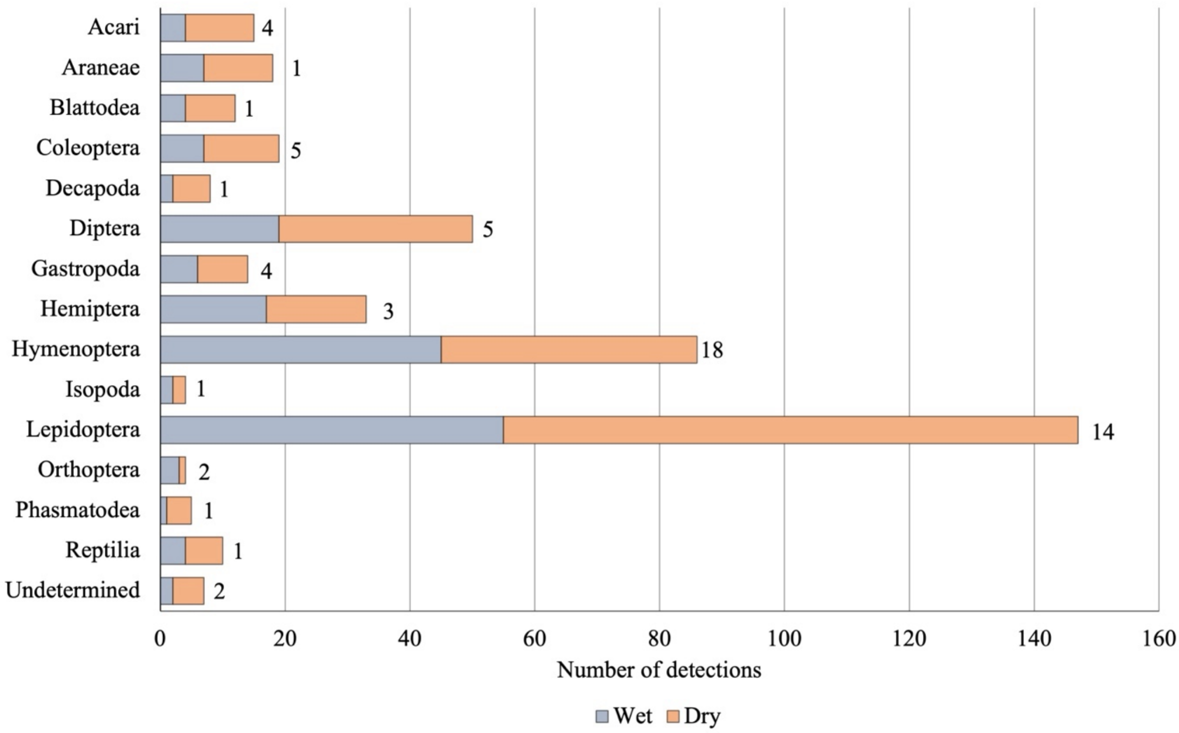

Figure 3. *Scolopendra abnormis* diet (n = 43) represented as number of prey detections for different animal groups. Stacked bars show the number of detections for a given group in wet (blue-grey) and dry (orange) seasons. Numbers to the right of the bars denote the number of species-level prey taxa within each group.

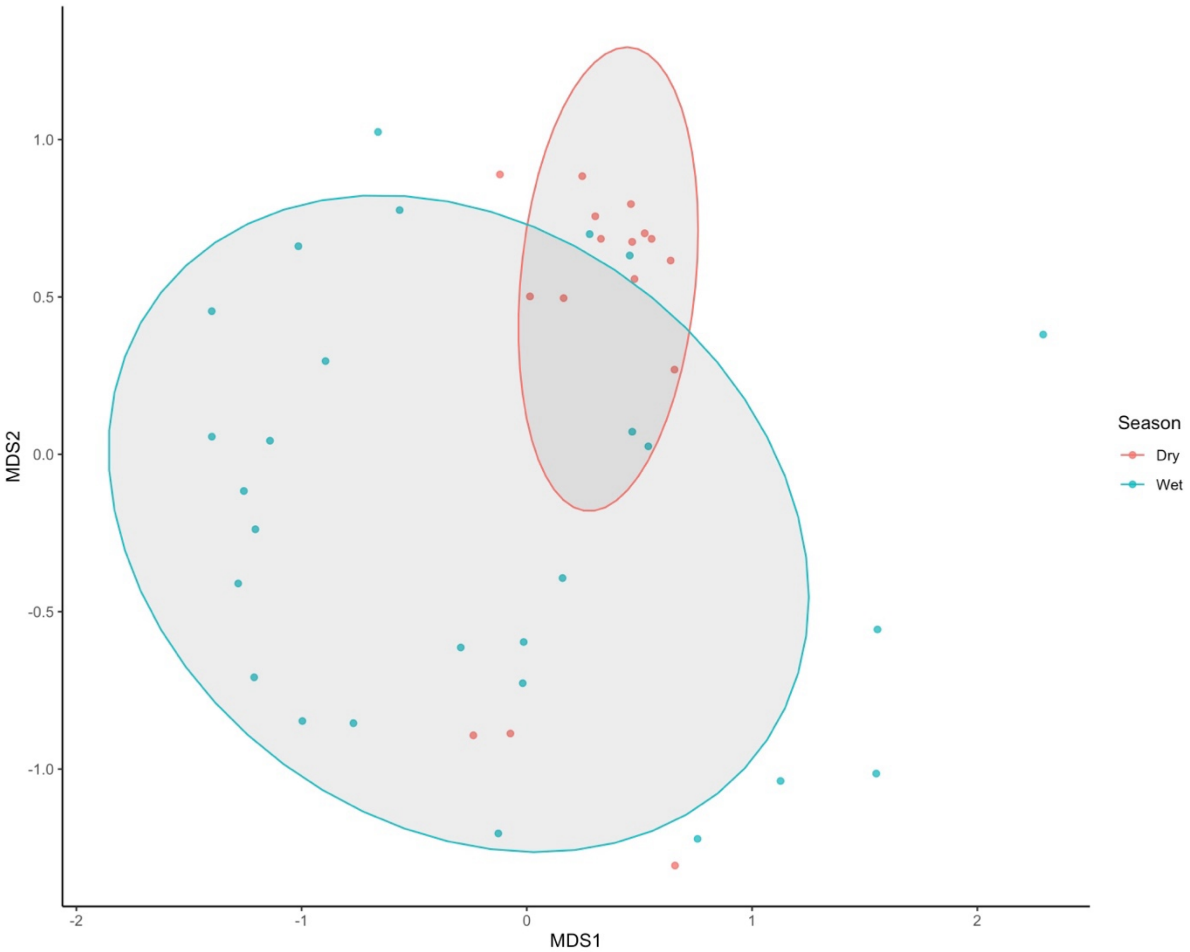

Figure 4. Centipede diet composition visualised using non-metric multidimensional scaling. Each point represents the dietary composition of a centipede individual. Colours denote the season that samples were collected in. Ellipses are 80% data circles. Stress value = 0.17.

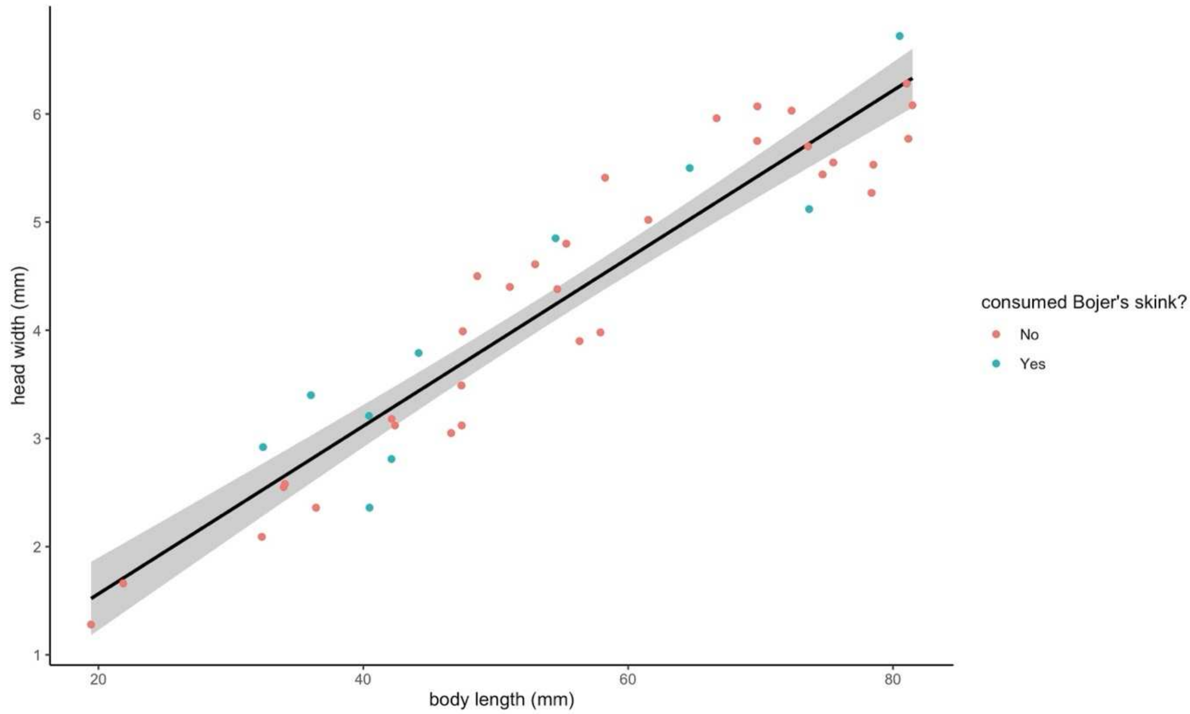

Figure 5. The relationship between centipede body length and head width. Each point represents an individual centipede; dark line is the line of best fit, grey shading denotes 95% error margins. Centipedes found to have consumed Bojer’s skink are represented by light blue points.