

Thermoregulatory behaviours and ecology of wolf spiders in the Australian alpine region

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Abstract

Research on temperature regulation in invertebrates has been limited, particularly in arachnids such as the alpine wolf spider *Tasmanicosa musgravei*. This study in Kosciuszko National Park, Australia, examined thermoregulatory activity in *T. musgravei* and whether this was influenced by temperature or spider size. The spatial distribution of this species and the relationship between burrow width and temperature/size were also explored. Sixteen spiders were filmed for at least one hour to determine frequency of thermoregulatory behaviours in relation to both temperature and size. Internal burrow and ground temperatures were also measured at different sites. This data indicated a significant difference in spider activity patterns with temperature (range 14–21°C) but not with body mass. Body mass was not significantly different between sites at different altitudes. Burrow dimensions were not affected by ground temperature but were significantly correlated with the size of the spider. This information may be useful in formulating management strategies for this species both currently and in response to changes in the environment.

Key Words: *Tasmanicosa*, Australian Alps, Lycosidae

Introduction

Temperature regulation is a vital process in animals as it allows them to maintain a steady internal environment necessary for normal body function (Atkin 2011). Endotherms (warm-blooded animals) have the ability to carry out physiological processes in order to regulate their internal temperature, such as alterations in evaporation, circulation and metabolism (Angilletta *et al.* 2010). Ectotherms (cold-blooded animals) lack this ability to generate heat through physiological processes and so their body temperature is heavily influenced by the external environment (Abram *et al.* 2016). In place of homeostatic control mechanisms, ectotherms are able to regulate their temperature through behavioural means, such as moving between areas with differing temperatures and changing body position to enable different levels of heat transfer (Atkin 2011). The behavioural thermoregulation of ectothermic vertebrates has been studied extensively, but there is a lack of literature regarding many arthropods, particularly regarding burrow-dwelling behaviours relevant to temperature regulation (Humphreys 1978).

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Lycosids, commonly known as wolf spiders, can be found globally and occupy a wide variety of different ecosystems including arid and alpine environments (Framenau and Baehr 2016; McKay 1974). Members of the subfamily Lycosinae are particularly diverse within Australia and largely occupy environments with harsher climates (Framenau and Baehr 2016). The capability of these wolf spiders to survive such conditions is likely due to their ability to construct burrows (Langlands and Framenau 2010). The use of burrows has several advantages including ameliorating temperature extremes and providing a gradient of environmental conditions that the spider can use for regulation (Humphreys 1973). Most of the activities of burrow-dwelling lycosids revolve around their burrow, including thermoregulatory behaviours essential for surviving certain environments (Humphreys 1978).

Mount Kosciuszko is an alpine environment reaching 2,228 m above sea level in New South Wales, Australia, where temperatures can range between -7°C and 29.5°C (Mason and Williams 2013). Both the flora and fauna of this region display adaptations that enable them to survive in the colder climate (Pickering and Green 2004). Lycosid spiders are included in this fauna and multiple species have been found to burrow in the tall alpine grasslands. *Tasmanicosa musgravei* (previously known as *Lycosa musgravei*) is the most frequently sighted, particularly in warmer months (Framenau and Baehr 2016; McKay 1974). *Tasmanicosa* species are common in eastern Australia and have a distinctive pattern on their carapace that has resulted in their common name, the union-jack wolf spider (Framenau and Baehr 2016). These species have been found to be inactive during the winter in cooler areas, resuming activity in warmer seasons (Humphreys 1973).

Previous research on *Tasmanicosa* species has demonstrated several key behaviours that function in thermoregulation. These include remaining at the bottom of the burrow in colder temperatures, sunning at the top of the burrow during warmer temperatures, and changes in orientation and position within the burrow (Humphreys 1973; Humphreys 1978). However, these same adaptations have not been explored in alpine species such as *T. musgravei*, and little work has been done regarding the ecology of this particular species.

Due to the ecological and social importance of national parks, including Kosciuszko, management strategies are vital to protecting and maintaining the balance between conservation and human activity (Wyborn 2009). Management strategies must be informed by ecological data to ensure that conservation in protected zones is effective, which is partially why scientific research is a large component of use in Kosciuszko National Park (Department of Environment and Conservation NSW 2006). The lack of research on alpine lycosid species in the national park suggests that it would be difficult to detect changes to the population size or behaviour in response to climate change and human activities. For this reason, further study on the behaviour and ecology of these species is essential for maintaining the integrity of the ecosystem in Kosciuszko National Park.

In this study, we aim to collect more information on the thermoregulatory behaviour of *T. musgravei*, primarily by observing if spider activity differs with body size and ambient temperature. It is predicted that larger spiders will be able to spend less time inside the burrow as they retain more heat due to their higher volume. It is also predicted that ambient temperature will have an effect on the amount of time spiders spend inside of the burrow. The spatial distribution will also be observed to determine if larger spiders are able to survive at colder microclimates. Larger spiders may be able to live at higher altitudes because of their lower surface area to volume ratio. However,

this effect may not be seen because of their small size when they are young. The third aim of this project is to determine whether the diameter of the burrow is correlated with temperature or with spider size. It is likely that the width of the burrow will increase depending on the size of the spider; however, it is possible that temperature may have an effect also. Humphreys (1973) reported an increase in *T. godeffroyi* burrow depth in response to colder temperatures suggesting that burrow dimensions can be affected by temperature. All of these aims will contribute to further knowledge about the behaviours and ecology of these spiders, particularly in relation to their adaptations towards colder environments.

Methods

Study sites

This research project was undertaken at three sites within Kosciuszko National Park, a nature reserve that protects a large section of the Australian alpine region. The three sites that samples were taken from included Perisher Valley (-36.404472°S, 148.413879°E) and two sites at different elevations within Charlotte Pass (-36.427891°S, 148.333679°E). The sites were all primarily alpine grassland and many burrows were found on an incline. Observations were also made near Diggers Creek (-35.381801°S, 148.651199°E) at 1,510 m though no recordings were taken there. The study was conducted 1–15 December 2018.

Specimen collection

Several different methods were used to collect specimens of *T. musgravei* including Humphreys' (1973) trapping method which involved inserting a cut section of hose, in which the inside had been coated in blackboard paint, into the entrance of the burrow. This allows the wolf spider to gain purchase on the inside of the burrow but not be able to get back into the burrow. A PVC pipe was placed around the burrow to trap the spiders from being able to get back into the burrow or escape to another area. This was used to catch approximately 3 to 4 of the 18 specimens collected. Other methods used to catch the spiders included luring them out of the burrow with a short stick or a piece of grass and capturing them in a specimen jar when they emerged, or digging out the burrow where a hole was dug parallel to the direction of the burrow (determined by inserting a rigid object into the burrow), and moving closer into the burrow until the spider could be seen and collected. These specimens were euthanised by freezing and then preserved in 70% ethanol.

Species identification

Generic status of specimens was first determined by comparing the carapace patterning of the spiders we were observing to references for *Tasmanicosa* and *Venatrix*. The patterning for *Tasmanicosa* species is quite distinct from that of *Venatrix*, and *Venatrix* species are considerably less abundant than *Tasmanicosa*. Due to the patterning and density, *Tasmanicosa* was determined as the genus over *Venatrix*. Following this, we used known distributions (Framenau and Bauer 2016) to determine which species overlapped within the Kosciuszko region. The distributions narrowed it down to two

possible species: *T. musgravei* and *T. godeffroyi*. However, *T. musgravei* is the most common alpine wolf spider species and of the 724 museum specimens for *T. godeffroyi* that were examined in the *Tasmanicosa* review (Framenau and Bauer 2016), none were found within the Kosciuszko region. Nevertheless, the morphology of the preserved specimens was observed under the microscope to determine the species using the taxonomic key provided in the Framenau and Bauer (2016) paper. Differences in the epigynum of the female spiders was indicative of *T. musgravei* over *T. godeffroyi* so the species was identified as *Tasmanicosa musgravei*.

Spider activity

Spider activity was measured by filming the entrance of an occupied burrow for approximately 1 hour with an iPhone. Recordings were only made on burrows demonstrated to contain spiders, which was determined by whether spiders could be seen at the entrance or within the burrow based on eye shine. Sixteen samples (videos) were taken over three different sites: Perisher Valley (1,720 m), Bottom of Charlotte Pass (1,778 m), Top of Charlotte Pass (1,835 m). The videos were recorded in the mornings or the afternoons when conditions were favourable – sunny – and the ambient temperature was also recorded. Following recording, the videos were analysed to determine the amount of time the spider spent performing each activity as a percentage of the total video time. Each activity was defined by where the spider was relative to its burrow: ‘inside’, inside the burrow with no part of the spider visible; ‘entrance’, visible inside the burrow or in contact with the entrance; and ‘outside’, outside of the burrow with no legs in contact with the entrance.

Burrow measurements

Burrow width was measured to the nearest 0.5 mm using calipers on the widest section of the burrow as they were often not perfectly round. Burrow temperature data was collected using both temperature probes and infrared thermometers to the nearest 0.1°C. The temperature probes were used to determine the temperature within the burrow and the ground temperature on the surface within 5 cm of the burrow. The probes were placed 10 cm inside the burrows with the receiver placed on the ground near the burrow to read ground temperature. They were left in the burrow until the temperature reading stabilised to get the most accurate recording. This was the primary method for obtaining the ground temperature at night recordings. In addition, infrared temperature readings of the ground temperature outside the burrows were taken using a temperature gun placed approximately 10–20 cm above the ground.

Body mass calculations

The head width of each of the preserved specimens was measured using calipers, and the spiders were weighed using a digital balance. These measurements were analysed using a linear regression and determined to be significantly correlated ($p < 0.0001$). The equation of the slope ($y = 0.4876x - 1.3017$) was later used to estimate the body size of the spiders in the video without the need to catch them.

To estimate the spider size from the videos, screenshots were taken of the video samples and entered into ImageJ. Because the burrow width was measured for each of the burrows sampled, this provided a scale for each of the images. Head width for each of the spiders was able to be estimated from this scale by digitally measuring the head width directly above the chelicerae. Body mass was then estimated from this head width by using the correlation curve developed from the preserved spiders.

Statistical analysis

JMP Analysis Software was used for regressions and analysis of variance (ANOVAs) of data for each of the aims. First, the dependent variables were tested for normal distribution by generating a histogram and a normal quantile plot and then using the Anderson-Darling test to analyse fit to a normal distribution. Upon doing this, the percentage of time inside burrow was found to be positively skewed and so the Johnson transformation tool was used to transform the data into a normal distribution. The first analysis was a one-way ANOVA comparing the percentage of time spent inside the burrow with the ambient temperature. In this analysis, the percentage of time a spider spent inside the burrow was used as the response variable and ambient temperature (3 levels – 14, 16 and 21°C) was the explanatory variable. Second, a linear regression was run between the time spent inside the burrow and the estimated body mass in which time spent inside acted as the response variable and estimated body mass was the explanatory variable. Next, another regression was carried out between the altitude of different sites compared with the estimated body mass to measure the effect body size has on the spatial distribution of *T. musgravei*. Here, the response variable was the estimated body mass and the explanatory variable was the altitude across the three different sampling sites. Another regression correlated ground temperatures and burrow width; in this case, ground temperature was used as the explanatory variable to determine if burrow width (response variable) was affected by temperature. Finally, another regression was performed to analyse the relationship between burrow width and estimated body size. This analysis used estimated body size as the response variable and burrow width as the explanatory variable to determine if there was a correlation between spider size and burrow width.

Results

General observations

Further qualitative observations were made on the life history of the wolf spiders recorded. Based on the patterning, distribution and physiology of the spiders observed, they all appeared to be of the species *Tasmanicosa musgravei* and the burrows seemed to be in reasonably close proximity to each other. Of the spiders that were captured, most appeared to be adult females or juveniles but adult males were also identified. It was observed in the field that spiders seemed to be larger at lower elevations based on burrow size and the spiders that were witnessed at the entrances of the burrows. *T. musgravei* was active throughout the day, mostly performing sunning behaviours but some were also witnessed leaving the burrow. It was observed in the field that spiders were present at the entrance of the burrow at night but were not seen outside of the burrow.

Reproductive behaviour was observed at the time of which the experiments were carried out (1–15 December 2018) as indicated by two specimens that had egg sacs, held in the spinnerets, and one sample that had spiderlings present inside the burrow at the time of filming. Feeding habits were also observed throughout recording, all were during the day and close to the burrows. The spiders were observed chasing ants, beetles and what appeared to be a millipede. An ant was the only prey item that was observed as being caught and eaten. Burrow maintenance was also observed in some of the videos where the spiders moved dirt out of the burrow by holding it in its palps and placing it outside of the burrow. Webbing around the entrance of the burrow was also observed in the recordings.

Spider activity

The head width, mass and percentage of time spent performing each activity (inside/at the entrance/outside of the burrow) were measured for all 16 spiders that were filmed (Table 1). From this information, the mean percentage of time spent engaged in each activity across all 16 specimens was calculated (Figure 1). This figure demonstrates that the spiders spent the greatest proportion of time at the entrance of the burrow ($81.53 \pm 5.00\%$), a much lower proportion of time inside the burrow ($14.34 \pm 5.13\%$) and the least proportion of time outside of the burrow ($4.14 \pm 2.33\%$). An ANOVA was performed to determine if the percentage of time spent inside the burrow differed depending on the ambient temperature. Spider activity was significantly related to ambient temperatures between 14°C and 21°C ($F_{(2,13)} = 3.999$, $p = 0.044$; Figure 2). A regression was also carried out to compare whether the amount of time spent inside the burrow was reduced in larger spiders. Body size was not related to the amount of time spent inside of the burrow ($F_{(1,14)} = 0.048$, $p = 0.831$; Figure 3).

Table 1: The estimated head width and body mass and the measured percentage of time spent at each activity (inside the burrow, at the entrance of the burrow and outside the burrow).

Specimen	Head width (mm)	Body mass (g)	Proportion of time spent at each activity (%)		
			Inside	At entrance	Outside
1	5.845	1.548	2.66	97.34	0.00
2	3.902	0.601	1.53	71.86	26.61
3	4.295	0.793	22.55	77.50	0.00
4	3.934	0.617	3.72	87.92	8.36
5	4.967	1.120	70.71	29.29	0.00
6	3.431	0.371	41.59	58.41	0.00
7	3.129	0.224	2.01	95.75	2.24
8	3.227	0.272	6.24	93.76	0.00
9	3.836	0.569	28.12	71.81	0.07
10	4.987	1.130	3.30	96.68	0.02
11	4.329	0.809	1.47	98.53	0.00
12	5.887	1.569	1.70	98.30	0.00
13	4.924	1.099	38.44	60.81	0.75
14	4.026	0.661	1.80	98.20	0.00
15	5.569	1.414	2.09	97.91	0.00
16	3.149	0.234	1.43	70.36	28.22

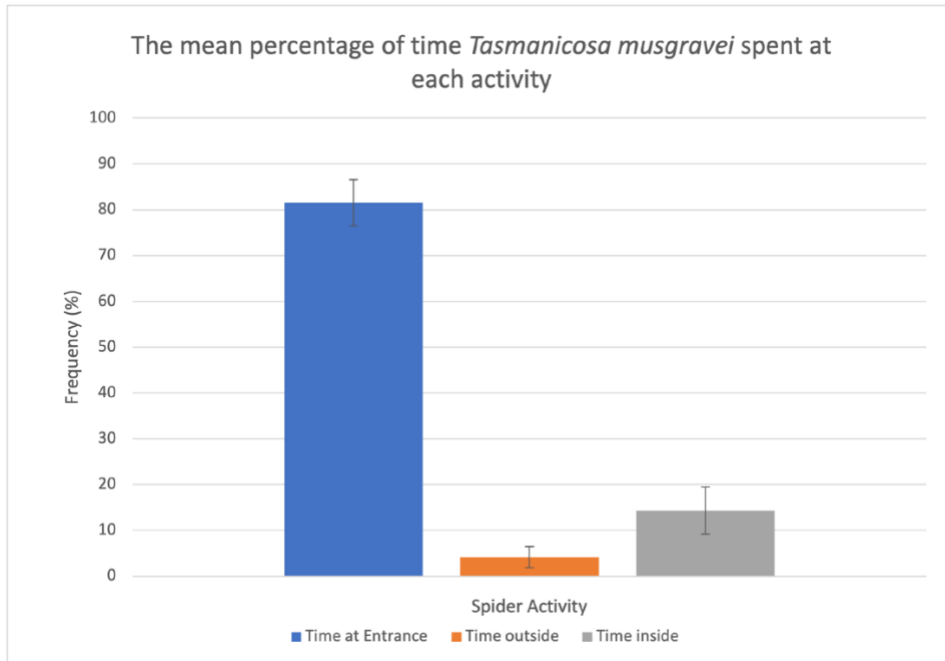


Figure 1: The mean proportion of time spent at each activity (inside/at the entrance/outside of the burrow) for all spider samples (n = 16).

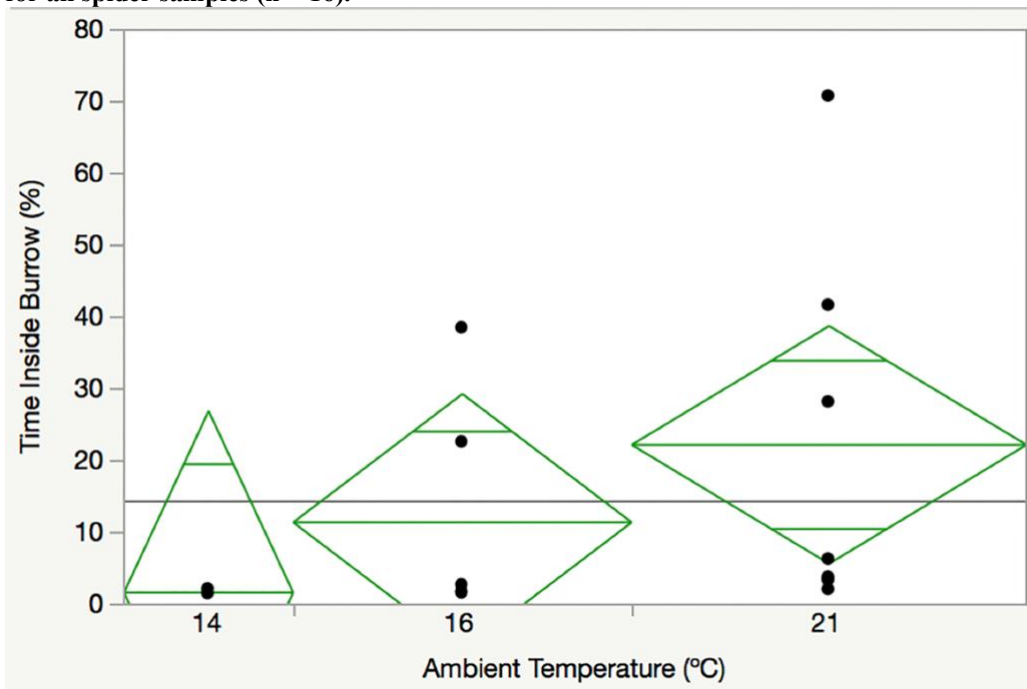


Figure 2: Comparison between the percentage of time spent inside of the burrow and the ambient air temperature for all samples ($n = 16$, $F_{(2,13)} = 3.999$, $p = 0.044$).

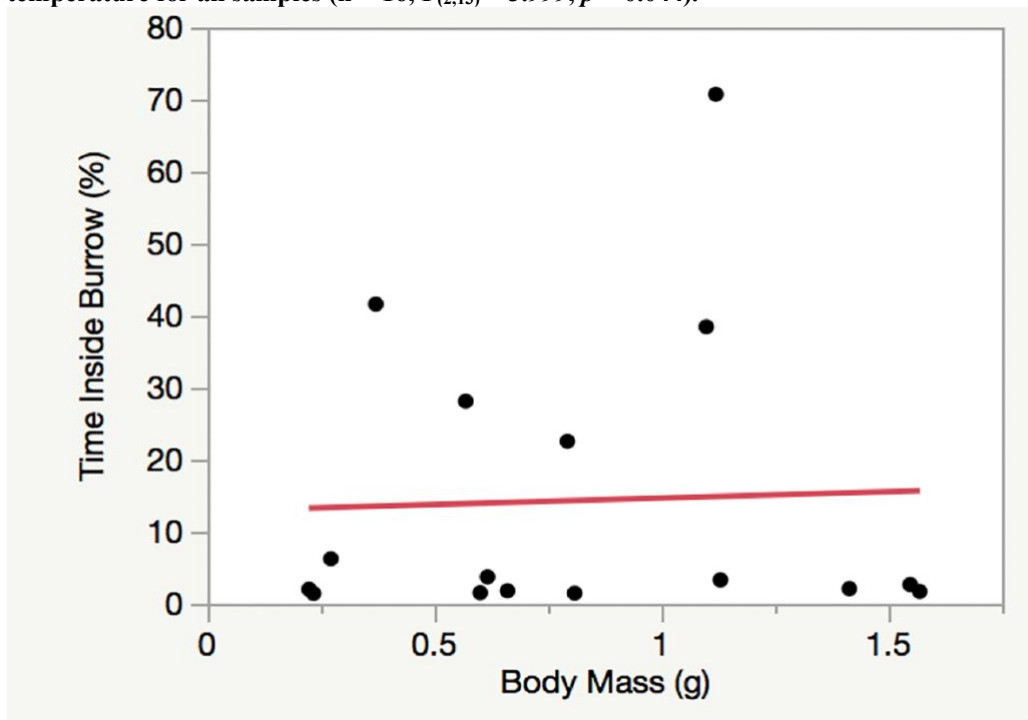


Figure 3: Regression between the percentage of time spent inside of the burrow and the estimated body mass of the spider for all samples ($n = 16$, $F_{(1,14)} = 0.048$, $p = 0.831$).

Spatial distribution

The body mass of the spiders calculated from the videos was compared with the altitude of the three sites that were sampled. There was a weak trend towards larger spiders inhabiting higher elevations but this result was not significant ($F_{(1, 14)} = 2.141$, $p = 0.166$, Figure 4).

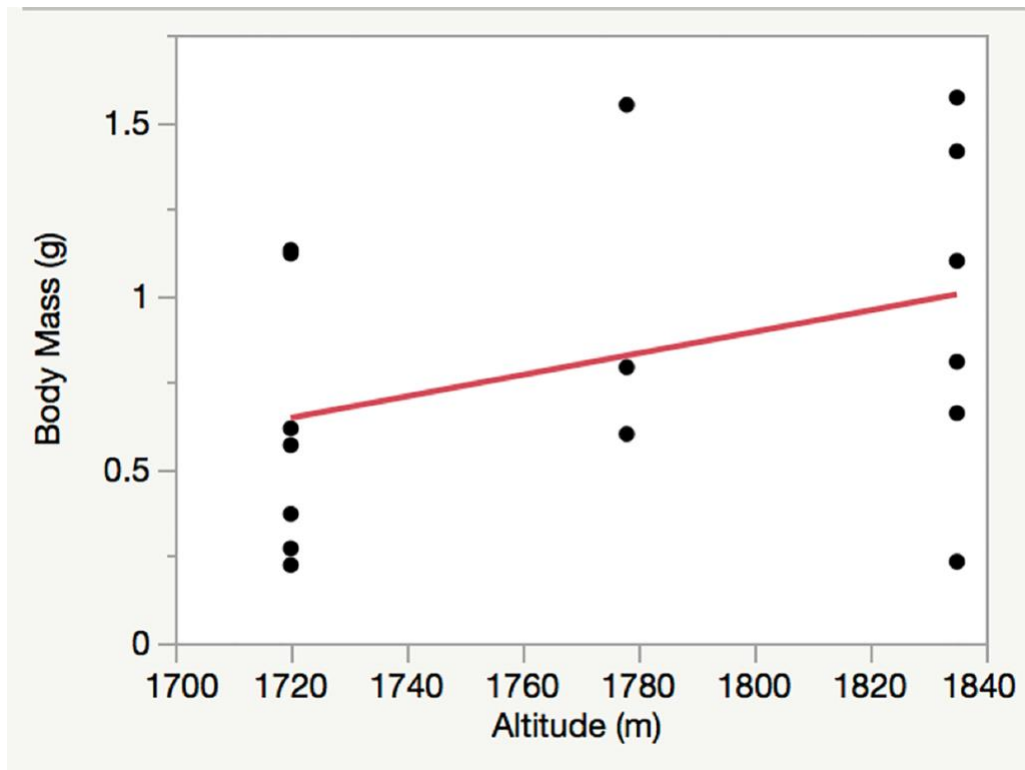


Figure 4: Correlation between the estimated body mass and the elevation of all samples ($n = 16$) at three different sampling sites: Persher Valley (1,720 m), Bottom of Charlotte Pass (1,780 m) and Top of Charlotte Pass (1,840 m) in Kosciuszko National Park ($F_{(1,14)} = 2.141, p = 0.166$).

Burrow dimensions

Burrow widths were compared with the ground temperature at night. The ANOVA that was performed demonstrated a weak trend towards smaller burrows at higher ground temperatures though this was not a significant relationship ($F_{(1,41)} = 2.892, p = 0.097$, Figure 5). The relationship between the width of the burrow and the estimated body mass of the spiders inhabiting them was also measured for the 16 specimens that were sampled (Figure 6). The ANOVA yielded a significant result ($F_{(1,14)} = 30.492, p < 0.0001$) suggesting that there is a strong relationship between the size of the spider and the width of the burrow.

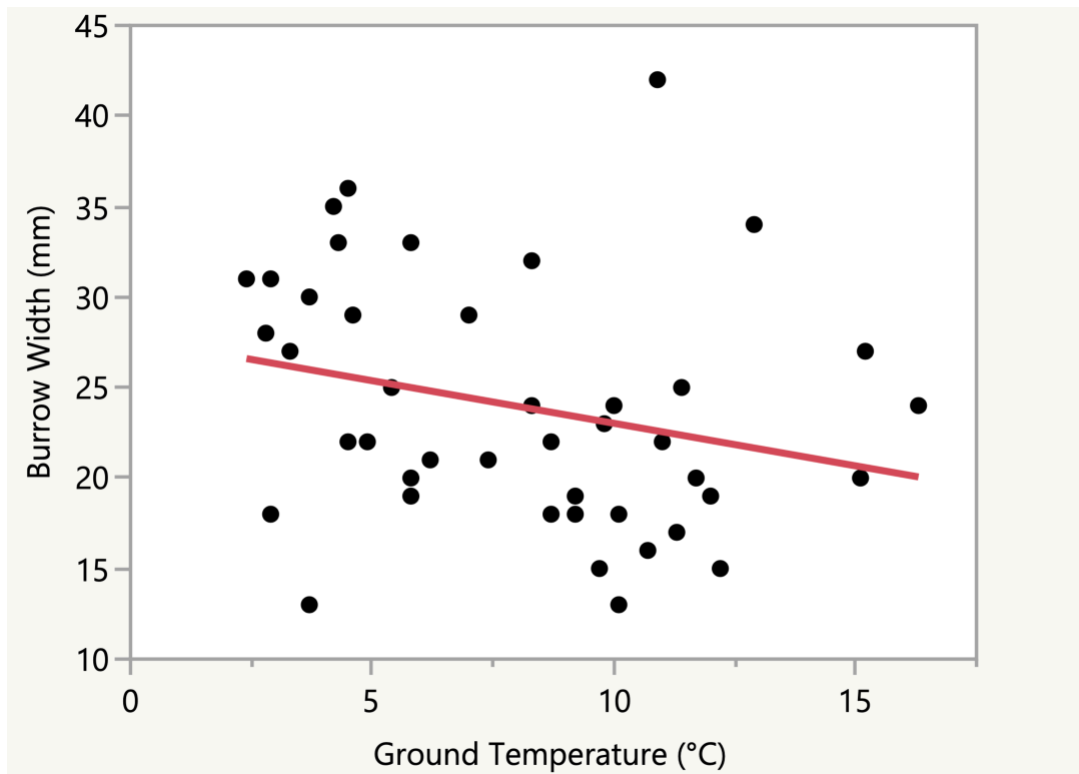


Figure 5: ANOVA comparing burrow width with ground temperature outside of the burrow at night ($n = 43$, $F_{(1,41)} = 2.892$, $p = 0.097$). Samples were taken near Diggers Creek and Charlotte Pass, Kosciuszko National Park.

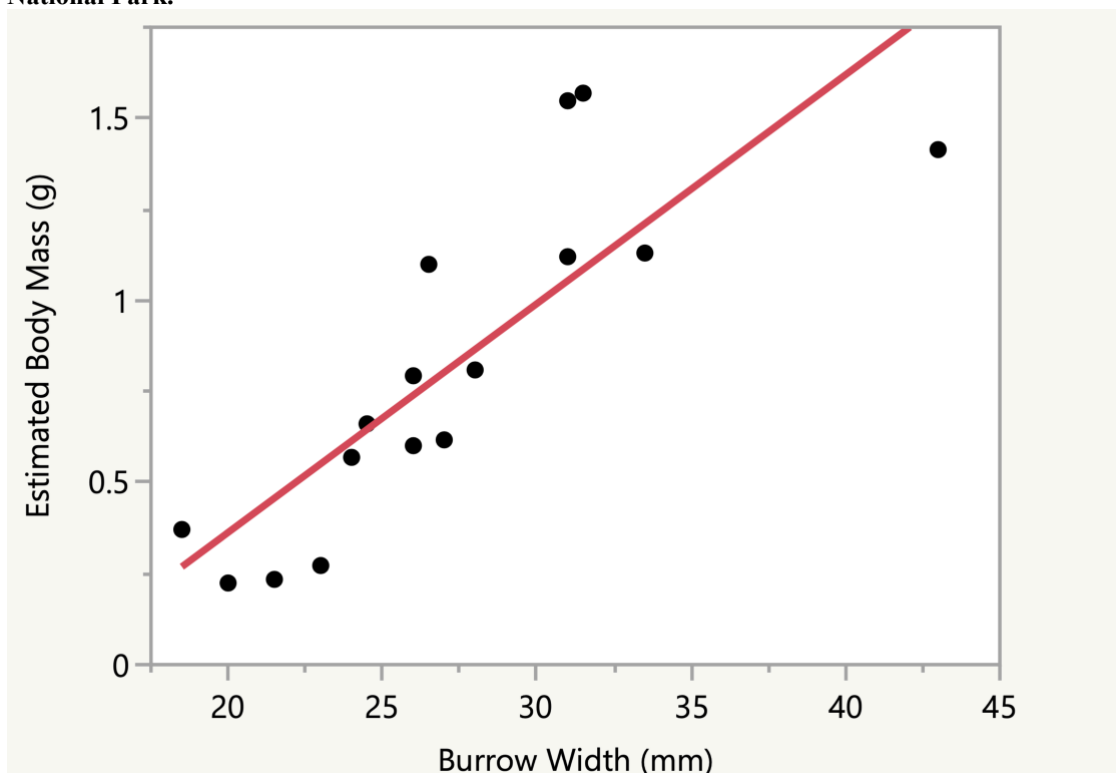


Figure 6: ANOVA showing a regression between the burrow width and the estimated body mass of all samples (n = 16, $F_{(1,14)} = 30.492$, $p < 0.0001$).

Discussion

This study aimed to gain more information on thermoregulation in *T. musgravei* by exploring the behaviour of this species in relation to its burrow. First, we wanted to observe if spider size has an effect on behaviour by looking at whether spider activity and spatial distribution differed with body mass. There was no significant result to suggest that size affected either of these variables. Second, we measured if spider behaviour changed with the ambient temperature as well as size. There was a significant correlation between the ambient temperature and the amount of time spiders spent inside of the burrow. Third, we also wanted to determine whether the size of the burrow is dependent on the size of the spider or on the ground temperature. There was no significant correlation between temperature and burrow width but there was a significant relationship between the burrow width and the spider size.

General observations

Along with the specific aims of this project, several observations on the ecology of the alpine wolf spiders in Kosciuszko National Park were noted. The specimens collected were identified to be *Tasmanicosa musgravei*, which appears to be the same species that was filmed. This is consistent with claims that *T. musgravei* is the most common species of alpine wolf spider in this area (Framenau and Baehr 2006). Adult females and juveniles were more common but adult males were also collected in this study. Spiders were active during the day but did not appear to leave their burrows at night. It is possible that the colder climate may influence the activity patterns of this species but further sampling at night would need to be performed to provide evidence for this. Reproduction had already begun at the time of the study as indicated by the presence of egg sacs and spiderlings in some of the samples. Maternal care of the egg sacs and spiderlings was as described by Humphreys (1978) in *Tasmanicosa (Geolycosa) godeffroyi*. Feeding was observed when prey items were in close proximity to the entrance of the burrow, similar to that observed by Humphreys (1978). It is possible that this species is opportunistic and feeds when prey is easily available. Burrowing behaviour, including the use of pedipalps for removal of debris and spinning silk around the edges of the burrow, seemed to be consistent with what has been seen in other wolf spider species (Suter *et al.* 2011). While these observations were not related to the aims of this project, this information builds upon our limited knowledge of *T. musgravei*.

Spider activity

The first aim of this project was to explore the behaviour of the spiders in relation to their burrows (inside/at the entrance/outside) and see if the frequency of each activity was dependent on temperature or body mass. The results showed that the spiders spent the majority of time at the entrance of the burrow, which is consistent with the sunning behaviours discussed by Humphreys (1978) of other spiders within the same genus. The time spent inside of the burrow did significantly differ between temperatures of 14°C and 21°C, with the time spent inside of the burrow increasing with higher temperatures. Humphreys (1978) reported that sunning behaviour in *T. godeffroyi* was

observed when conditions were suitable and that lycosids displayed both sun and shade seeking behaviour.

The greater length of time spent outside of the burrow at 14°C is consistent with previous studies showing that basking behaviours increased internal temperature significantly and served as a heating function in ectotherms when ambient temperatures were decreased (Abram *et al.* 2016; Dreisig 1984). Chai and Wilgers (2015) found that the likelihood of wolf spiders being inside the burrow increased when treated at 4.4°C. The increase in time spent inside the burrow at high ambient temperatures is likely due the internal temperature of the spiders reaching a point that is no longer suitable. This would be consistent with many burrowing arachnids that spend more time within the burrow when temperatures are high and limit surface activity to when ambient temperatures are cooler (Turner *et al.* 1993).

Spider activity did not significantly change when compared to body mass, suggesting that the ability to retain heat better may not effect amount of time spent inside of the burrow (at least between 14°C and 21°C). Ectotherms that are larger lose heat at a slower rate than those with a smaller body mass, but they also gain heat at a slower rate as seen previously in lizards (Zamora-Camacho *et al.* 2014). It is possible that changes in the proportion of time spent inside of the burrow were not observed because slower heating rates in larger lycosids would require them being exposed to the cold for longer periods. This could be explored further in future studies by measuring the cooling and heating rates of a wide range of spider sizes to confirm the effect of body mass. Such research may indicate whether the lower rate of heating negates changes in behaviour. This study could be expanded further by also measuring changes in behaviour over a wider difference of temperatures as in the study by Zamora-Camacho *et al.* (2004). This would likely be more informative on the optimal temperatures for *T. musgravei* as I predict that time inside the burrow would increase at lower ambient temperatures as well. Overall, the hypothesis that the time spent inside the burrow would decrease with larger body mass was not supported by the results collected. However, future studies as described above may be able to expand on the results observed in this project to gather more information about the factors that affect thermoregulatory behaviour in *T. musgravei*.

Spatial distribution

The second aim of this project was to investigate the spatial distribution of *T. musgravei* by comparing the body mass of the samples with the elevation at which they were sampled. There was a weak trend suggesting larger spiders were present at higher altitudes but this result was not significant. In addition to this, field observations of the spiders across the different altitudes suggested that spiders were generally larger at the lower sites. Bergmann's rule is an ecological hypothesis proposing that the size of animals will increase in colder climates, largely applied to endothermic species (Gohli and Voje 2016). Previous studies have demonstrated increased body size in ectothermic animals reared in lower temperatures, including those at higher elevations, which is consistent with Bergmann's rule (Partridge and Coyne 1997). However, other studies have suggested that the inverse is true with smaller ectotherms at colder temperatures/higher elevation (Mousseau 1997). Høye and Hammel (2010) found that carapace width (indicative of size) did differ between elevations for some species of arctic wolf spiders, but did not differ in others. The study by Zamora-Camacho *et al.* (2004) on a lizard that inhabited areas along an elevation gradient showed that there

was a significant increase in size as altitude increased. Both of these studies indicate effects on spatial distribution vary between ectotherms. While it appears from our study that body mass does not have an effect on spatial distribution, it would be beneficial to sample across a greater range of altitudes and have a larger sample size to gather further evidence for this similar to the study by Høye and Hammel (2010).

Burrow dimensions

The final aim of this project was to determine if the width of the burrow was affected by the climate or dependent on the body size of the spider inhabiting it. The first was tested by comparing the burrow width with the ground temperature at night (lower temperatures when not exposed to sunlight). There was no correlation found between the ground temperature and the width of the burrow. This suggests that burrow width is not affected by the microclimate. A study on fiddler crabs by Reaney and Backwell (2007) showed that narrower burrows had a significantly higher internal temperature than those with larger diameters. Because of this, it was predicted that the width of *T. musgravei* burrows may be reduced due to the temperature being colder at Kosciuszko National Park. However, it appears that burrow width is not correlated with temperature for this species of burrowing wolf spider. The fiddler crab's tropical environment may contribute to this difference; the burrow primarily being used to shield the crab from high temperatures throughout the day rather than to conserve heat obtained from sunning (Darnell *et al.* 2013). Perhaps a similar pattern would be observed in burrowing lycosids that live in warmer climates over alpine species like *T. musgravei*. Humphreys (1978) found that burrow depth increased over winter in *Tasmanicosa (Geolycosa) godeffroyi*, therefore a useful future direction of study may be to measure the depth of the burrows for *T. musgravei* to see if this is correlated with colder temperatures.

The burrow width was also compared to the estimated body mass of the wolf spiders inhabiting them to see if there is a correlation between spider size and burrow diameter. There was a significant positive correlation between body mass and burrow width suggesting that burrow width is dependent on the size of the spider. Carrel (2003) demonstrated similar results in his study comparing the burrow width and body mass of two species of temperate burrowing-dwelling lycosids. The formula for this regression is $y = 0.0628x - 0.8935$, which should of use in future studies to estimate the size of the spider based on the burrow width without the need to capture the spiders. This result for *T. musgravei* is important, as it will permit future researchers to survey spider size non-invasively.

Wolf spiders are often able to survive harsh environments due to their ability to create burrows, and this is demonstrated in *Tasmanicosa musgravei* (Langlands and Framenau 2010). The results of this project are informative about the thermoregulatory behaviours of *T. musgravei* and the correlation of these behaviours to variables such as temperature, size, spatial distribution and burrow dimension. Based on the effect temperature had on spider activity in this study, increasing temperatures may have a significant effect on current behaviour. In addition, climate change will result in reduced periods of snow fall, which may also have an effect on the ecology of this species, which typically close their burrows over winter (Humphreys 1978). Climate change is also predicted to cause a higher frequency of extreme weather conditions, which may result in changes to typical thermoregulatory behaviours. However, further research as suggested above is required in order to make conclusive statements about the ecology

of this species and how it may react to changes in the environment. This research is essential to preserve this species and the ecosystem within Kosciuszko National Park both now and in the future.

Conclusions

This project aimed to gain more knowledge on the thermoregulatory behaviours of alpine wolf spiders in Kosciuszko National Park. Spider activity seems to be affected by temperature regulation requirements as indicated by the large amount of time spent performing sunning behaviours (Figure 1). These behaviours did differ at temperatures between 14°C and 21°C, suggesting that spider activity outside of the burrow decreases in warmer temperatures (Figure 2). Size did not seem to play a role in changing thermoregulatory behaviours within this temperature range (Figure 3). Size also did not appear to have an effect on the spatial distribution of this species with there being no significant difference between elevations (Figure 4). Burrow dimensions were not correlated with the temperature suggesting that climate does not affect the diameter of the burrow whereas spider size was strongly correlated with burrow width (Figures 5, 6). Spider activity may change dramatically in response to climate change or other environmental disturbances as warmer temperatures seem to be a confounding variable. Increases in weather extremes may also have a significant effect on behaviour and activity levels. Gaining a further understanding of temperature regulation and ecology in *T. musgravei* will assist in managing populations now and in response to environmental change and human disturbance.

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References

- Abram P, Boivin G, Moiroux J, Brodeur J (2016) Behavioural effects of temperature on ectothermic animals: Unifying thermal physiology and behavioural plasticity. *Biological Reviews* **92**, 1859–1876. doi.org/10.1111/brv.12312
- Angilletta M, Cooper B, Schuler M, Boyles J (2010) The evolution of thermal physiology in endotherms. *Frontiers in Bioscience* **E2**, 861–881. doi.org/10.2741/e148
- Atkin J (2011) Homeostatic processes for thermoregulation. *Nature Education Knowledge* **3**, 7.
- Carrel J (2003) Ecology of two burrowing wolf spiders (Araneae: Lycosidae) syntopic in Florida Scrub: Burrow/body size relationships and habitat preferences. *Journal of the Kansas Entomological Society* **76**, 16–30.
- Chai Y, Wilgers D (2015) Effects of temperature and light levels on refuge use and activity in the wolf spider *Rabidosa punctulata*. *Transactions of the Kansas Academy of Science* **118**, 194–200. doi.org/10.1660/062.118.0302

Madeline Hanna: Temperature regulation in alpine wolf spiders

- Darnell M, Fowler K, Munguia P (2013) Sex-specific thermal constraints on fiddler crab behavior. *Behavioral Ecology* **24**, 997–1003. doi.org/10.1093/beheco/art006
- Department of Environment and Conservation NSW (2006) 'Plan of Management Kosciuszko National Park'. (Department of Environment and Conservation NSW: Sydney). Available at: www.environment.nsw.gov.au/-/media/OEH/Corporate-Site/Documents/Parks-reserves-and-protected-areas/Parks-plans-of-management/kosciuszko-national-park-plan-of-management-060335.pdf [Accessed 29 Nov. 2018].
- Dreisig H (1984) Control of body temperature in shuttling ectotherms. *Journal of Thermal Biology* **9**, 229–233. doi.org/10.1016/0306-4565(84)90001-9
- Framenau V, Baehr B (2016) Revision of the Australian Union-Jack wolf spiders, genus *Tasmanicosa* (Araneae, Lycosidae, Lycosinae). *Zootaxa* **4213**, 1. doi.org/10.11646/zootaxa.4213.1.1
- Gohli J, Voje K (2016) An interspecific assessment of Bergmann's rule in 22 mammalian families. *BMC Evolutionary Biology* **16**, 222. doi.org/10.1186/s12862-016-0778-x
- Høye T, Hammel J (2010) Climate change and altitudinal variation in sexual size dimorphism of arctic wolf spiders. *Climate Research* **41**, 259–265. doi.org/10.3354/cr00855
- Humphreys W (1973) The environment, biology and energetics of the wolf spider *Lycosa godeffroyi*. Phd thesis, The Australian National University.
- Humphreys W (1978) The thermal biology of *Geolycosa godeffroyi* and other burrow inhabiting Lycosidae (Araneae) in Australia. *Oecologia* **31**, 319–347. doi.org/10.1007/BF00346251
- Langlands P, Framenau V (2010) Systematic revision of Hoggicosa Roewer, 1960, the Australian 'bicolor' group of wolf spiders (Araneae: Lycosidae). *Zoological Journal of the Linnean Society* **158**, 83–123. doi.org/10.1111/j.1096-3642.2009.00545.x
- Mason R, Williams J (2013) 'Climate and weather of the Australian Alps'. [online] Australian Government, 1–7. Available at: theaustralianalps.files.wordpress.com/2013/11/climate.pdf [Accessed 12 Sep. 2019].
- McKay R (1974) The wolf spiders of Australia (Araneae: Lycosidae): 4, three new species from Mount Kosciusko, N.S.W. *Memoirs of the Queensland Museum* **17**, 27–36.
- Mousseau T (1997) Ectotherms follow the converse to Bergmann's rule. *Evolution* **51**, 630–632. doi.org/10.1111/j.1558-5646.1997.tb02453.x
- Partridge L, Coyne J (1997) Bergmann's rule in ectotherms: Is it adaptive?. *Evolution* **51**, 632–635. doi.org/10.1111/j.1558-5646.1997.tb02454.x
- Pickering C, Green K (2004) 'Potential Effects of Global Warming on the Biota of the Australian Alps: A Report for the Australian Greenhouse Office'. (Australian Greenhouse Office: Canberra).
- Reaney L, Backwell P (2007) Temporal constraints and female preference for burrow width in the fiddler crab, *Uca mjoebergi*. *Behavioral Ecology and Sociobiology* **61**, 1515–1521. doi.org/10.1007/s00265-007-0383-5

Madeline Hanna: Temperature regulation in alpine wolf spiders

- Suter R, Stratton G, Miller P (2011) Mechanics and energetics of excavation by burrowing wolf spiders, *Geolycosa* spp. *Journal of Insect Science* **11**, 1–15. doi.org/10.1673/031.011.0122
- Turner J, Henschel J, Lubin Y (1993) Thermal constraints on prey-capture behavior of a burrowing spider in a hot environment. *Behavioral Ecology and Sociobiology* **33**, 35–43. doi.org/10.1007/BF00164344
- Wyborn C (2009) Managing change or changing management: Climate change and human use in Kosciuszko National Park. *Australasian Journal of Environmental Management* **16**, 208–217. doi.org/10.1080/14486563.2009.9725236
- Zamora-Camacho F, Reguera S, Moreno-Rueda G (2014) Bergmann's Rule rules body size in an ectotherm: Heat conservation in a lizard along a 2200-metre elevational gradient. *Journal of Evolutionary Biology* **27**, 2820–2828. doi.org/10.1111/jeb.12546