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The impact of elevated aestivation temperatures on the behaviour of bogong moths (*Agrotis infusa*)

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ABSTRACT

Bogong moths are an iconic Australian insect. They migrate annually in spring from low elevation locations in southern Australia to the Australian Alps where they aestivate during summer. As summer ends they make their return journey to the breeding grounds where they mate, lay eggs, and die. Given the moth's extreme behaviour in seeking out cool alpine habitat and with the knowledge that average temperatures at their aestivation sites are rising because of climate change, we first asked whether increased temperatures affect bogong moth activity during aestivation. We found that moth behaviour patterns changed from showing peaks at dawn and dusk with supressed activity during the day at cooler temperatures to near-constant activity at all times of day at 15 °C. Second, we asked whether moth mass changes after aestivating at different temperatures for a week due to dehydration or consumption of body energy reserves. We found that moth wet mass loss increased with increasing temperature, but found no difference in dry mass among temperature and that it may be lost at around 15 °C. The impact of warming on the likelihood of individuals to complete their aestivation in the field should be investigated as a matter of priority to better understand the impact of climate change on the Australian alpine ecosystem.

1. Introduction

Aestivation is a period of behavioural dormancy often facilitated by a down-regulation of physiological processes, similar to hibernation, that occurs in summer rather than winter (Withers and Cooper 2010). Aestivation is characterised by whole-body metabolic depression, including inhibited digestion and muscular movements (Cowan et al., 2000) and paused growth and development (Masaki 2009), and this behaviour is most common in ectotherms including many insects (Dao et al., 2014; Young et al., 2011). The function of aestivation is to severely depress the organism's metabolic rate to enable dormancy and prolong survival when in an unfavourable summer environment, e.g. elevated temperature and reduced food and water resources, until conditions improve (Storey and Storey 2012). For example, the mosquito *Anopheles coluzzii* aestivates when there are no viable larval sites during the Sahelian dry summers (Dao et al., 2014), and several African

snail species aestivate during periods of drought (Rubaba et al., 2016).

As climate change drives hotter and drier conditions in many places, species' abilities to successfully aestivate are becoming increasingly uncertain. Elevated temperatures are likely to disrupt aestivation, particularly in ectotherms where changes in external temperature can directly impact body temperature and metabolism (Young et al., 2011). Increases in metabolism while aestivating may lead to the organism's energy reserves being depleted more rapidly than the rate at which environmental conditions become more favourable. Furthermore, increased temperatures and subsequently increased metabolic rate may have a compounding effect if organisms become more active while aestivating in warmer temperatures (Lorenz and Gä;de 2009).

The impact of climate change induced increases in temperature on aestivation have been observed in several species. Mech et al. (2018) found that elevated aestivation temperatures significantly increased the mortality rates of the hemlock woolly adelgid bug (*Adelges tsugae*). It was

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Table 1

Parameter estimates and test statistics for a generalised additive mixed model examining the effects of aestivation temperatures on bogong moth activity levels. Temperature (temp) was included as a fixed effect, and separate smooth terms were estimated for time (hour 0–23) at each temperature. Experimental box nested within experimental day were specified as random effects. Note that temperature waw treated as an ordered factor, such that reported statistics represent tests of differences in smooth terms from the reference level of 7.5 °C. Model $R^2 = 0.229$.

Parameter	β	SE	t	р
Intercept	-0.724	0.167	-4.342	< 0.001
temp. 10	0.2788	0.239	1.158	0.247
temp. 12.5	-0.342	0.229	-1.491	0.1367
temp. 15	-0.5221	0.246	-2.122	0.034
Smooth terms	Effective d.f.	Ref. d.f.	F	р
s(hour) * temp. 7.5	7.554	8	37.065	< 0.001
s(hour) * temp 10	5.471	8	7.6338	< 0.001
s(hour) * temp 12.5	3.382	8	2.464	< 0.001
s(hour) * temp 15	4.898	8	4.7546	< 0.001

suggested that this was perhaps due to increased heat-induced desiccation and elevated metabolic rates (Neven 2000; Sussky and Elkington 2015), though the elevated temperatures may have additionally led to disruption of the insect's bacterial endosymbionts due to heat shock (Dunbar et al., 2007). Elevated aestivation temperatures can also lead to species decline through habitat loss. In south-western Australia aestivating fish species *Galaxiella nigrostriata* and *Lepidogalaxias salamandroides* have been extirpated from 28% to 33% of their historical sites (Ogston et al., 2016). This is thought to be due to altered habitat quality and niche availability as a result of elevated water temperatures caused by global warming (Morrongiello et al., 2011; Ogston et al., 2016).

Aestivating organisms vary in their response to increased temperatures. Some species make no changes and simply pay the costs of temperature changes at the aestivation sites, perhaps because they are unable to move into more favourable environments. Such species may face an increased risk of mortality while dormant as a result of their energy reserves becoming exhausted before their habitat returns to favourable conditions. For example, when the frog Cyclorana alboguttata experienced elevated temperatures under laboratory conditions during aestivation, its metabolic rate significantly increased contributing to depleted fuel stores and subsequent muscle disuse atrophy (Young et al., 2011). Species that migrate to their aestivation sites may change the time of year or duration spent at the site (Turbill and Prior 2016), or potentially alter arrival and departure times to and from the aestivation sites. Other species may change the location of aestivation, for example several burrowing frog species can mitigate the effects of rising temperatures on their metabolic rate while aestivating by burrowing into cooler ground (Young et al., 2011).

Bogong moths (Agrotis infusa) are an iconic Australian insect famous for their annual return migration from the lowlands of southern Australia to the Australian Alps in summer 1000 km away (Warrant et al., 2016). They are of deep cultural value to First Nations Australians, important to alpine ecosystem functioning (Green et al., 2021), and a significant pest of wheat and barley (Common, 1954). Once triggered to begin their annual migration in spring, perhaps by the growing scarcity of edible larval food plants through spring and into summer (Common 1954; Warrant et al., 2016), bogong moths travel at night for several weeks, with individuals flying up to 1000 km on consecutive nights (Drake and Farrow 1985), to reach their alpine aestivation sites (Common 1954). Once there, they aggregate in small caves and crevices, commonly in granite boulder fields, between approximately 1200-2100 m elevation (Common 1954; Warrant et al., 2016) in astonishing densities of up to 17,000 per m^2 (Common 1954). Inside the caves and crevices, the moths pack very closely together, in a behaviour known as 'tiling', with each moth placing their head and upper body under the wings and abdomen of another moth. The tiling arrangement may decrease their rate of desiccation (Common 1954).

Bogong moths generally aestivate from October to March (Caley and Welvaert 2018) and during aestivation their behaviour is characterised by generally low activity levels and developmental delays, with the moths not sexually maturing until their return to their breeding grounds in autumn (Warrant et al., 2016; Common 1954). While aestivating, the moths typically do not attempt to mate or feed, though they have been observed ingesting water (Common 1954). Aside from their generally dormant nature while aestivating, many moths display daily periods of activity prior to dawn and after sunset including short flights around their boulders, vibrating their wings and crawling around the rocky outcrops or cave walls (Common, 1954; Warrant et al., 2016). This activity is thought to be triggered by changes in light intensity, which causes pigment migration in the moth's eyes (Vaduva 2016; Common, 1954), but its function is currently unclear (Karpovich et al., 2009).

Due to the shrinking availability of aestivation sites with the right temperature profile together with a crash in the number of moths arriving in the alps since 2019 (Green et al., 2021) - around 5% of the normal 4 billion expected – bogong moths are now listed by the IUCN as Endangered and currently being assessed for the national legislation, Environmental Protection and Biodiversity Conservation Act (1999). The Australian Alps are warming quickly with the distributions of many Australian mountain species expected to change in the next 25 years (Camac et al., 2020). The Murray murrumbidgee region which includes part of the Kosciuszko National Park has a projected increase in mean temperature of 0.62 °C between 2020-39 and 1.94 °C between 2060-79 (https://www.climatechange.environment.nsw.gov.au/projections

-map NSW Interactive climate change projections map 2014), whereas, under the best-case scenario, projected an increase for the Australian Alps are 0.6 °C by 2050, and under the worst-case scenario, an increase of 2.9 °C (Pickering 2007; Hennessy et al., 2003). There are also projections of reduced precipitation in the Australian Alps by 2090 (Clarke et al., 2019).

Bogong moth aestivation sites are warming and the potential impact of these rising temperatures is currently unknown. This study aims to determine how bogong moths respond to increased temperatures while aestivating. There are many important reasons to understand and attempt to mitigate consequences of climate change on bogong moth aestivation. They are of significant cultural importance to First Nations Australians from across Country, who gather to conduct moth hunts for ceremony and food (Warrant et al., 2016; Flood 1980, 1996). The moths' decline represents another fading opportunity for First Nations Australians to reconnect with Country. Elevated temperatures in the mountains may already have caused changes in the moth's arrival and departure times, with moths observed by Caley and Welvaert (2018) to be arriving and leaving nearly a full month earlier than the moths studied by Common in 1954, which arrived at the end of October. Changes in moth arrival times and distribution of aestivation sites may have important impacts on Australia's alpine ecosystem. For example, some species are largely dependent on moths as a main food source or host. These include the mountain pygmy possum (Burramys parvus) and the bogong obligate symbiont worms Amphimermis bogongae and Hexamermis cavicola (Common 1954; Green 2010a, 2010b; Welch 1963). Bogong moths are of high ecological importance in the mountains due to their key roles in nutrient and energy transport, particularly in transport of nitrogen and phosphorus (Green 2011).

To understand how bogong moths respond to elevated temperatures while aestivating, we tested two hypotheses. The first hypothesis was that there is a difference in activity level of moths at different temperatures, with the prediction that there would be a higher activity level in the warmer conditions than cooler conditions. The second hypothesis was that moths lose body mass at different rates in different temperatures, with the prediction that increased temperature leads to an increased rate of body mass loss.



Fig. 1. The activity of bogong moths over 24 h following aestivation at four different temperatures. Shown are raw data (left panels), denoting the number of moths moving at each timepoint (out of 10 moths total per box, see methods for full sample size & replicate details). And generalised additive mixed-model fits (±95% CIs, right panels) to these data. Red vertical lines indicate the experimental shift from day to night.

2. Materials and methods

2.1. Collection of moth specimens

The bogong moths included in this study were collected from Charlotte Pass in Kosciuszko National Park, New South Wales, Australia (-36.427891, 148.333679) at an elevation of 1882m under NSW NPWS Scientific Permit [SL100835, L. Broome] in early December 2019 using a light trap deployed for 24 h. The moths were kept together and stored at cool temperatures during transit to the site of experiments, Western Sydney University, Hawkesbury Campus (-33.603200, 150.760900, 19m elevation).

2.2. Marking and housing moths

240 moths were separated into 24 clear plastic boxes (15 cm \times 10 cm x 5 cm) of ten individuals each, and were initially stored in an incubator at 5 °C. CO₂ was used to make the moths temporarily inactive for weighing and labelling. Each moth was labelled by drawing a number on

a forewing using a metallic felt-tip marker with a number from 1 to 10, and weighed (g) prior to the experiment using a scale sensitive to three decimal places. Three small holes were made in the sides of each box with a soldering iron to allow airflow.

2.3. Temperature treatments

We kept moths in one of four different temperature treatments, each of which was representative of different climate scenarios at Charlotte Pass, the origin of the moths used in this study. The lowest temperature 7.5 °C was chosen to act as a historical comparison for the likely average temperature of aestivation sites around 50 years ago (Common, 1954). The temperature chosen to most closely represent current aestivating sites for bogong moths was 10 °C (Green, 2010). The two warmer incubators were set at 12.5 °C and 15 °C to represent the worst case temperature scenario in 50- and 100-years' time respectively (Pickering, 2007).

2.4 Artificial aestivation set up.

Four incubators were held at 7.5 $^\circ\text{C},$ 10 $^\circ\text{C},$ 12.5 $^\circ\text{C}$ and 15 $^\circ\text{C}$



Fig. 2. The effect(s) of aestivation temperature on (a) the change in wet mass (day 1 – day 8) and dry mass (b). All Tukey-adjusted pairwise contrasts of wet mass change (a) were statistically significant at $\alpha = 0.05$ (Table S1), while no measures of dry mass (b) differed between temperature levels (Table S2).

Table 2

Parameter estimates and test statistics for a generalised linear model examining the change in bogong moth wet mass between experimental day 1 (13th Dec) and 8 (20th Dec), across each of four aestivation temperatures. The difference in mass (day 1–8) was specified as a response with temperature as the single fixed effect, and we specified a Gaussian error distribution with identity link function. Model $R^2 = 0.224$.

Fixed Effects	β	SE	t	р
Intercept	0.023	0.001	17.375	< 0.001
temp. 10	0.008	0.002	4.530	< 0.001
temp. 12.5	0.015	0.002	7.592	< 0.001
temp 15	0.022	0.002	10.279	< 0.001

(Memmert IPP750, Panasonic MIR554). The lighting for each incubator was set up using a Jaycar LED aluminium light strip with a Jaycar LED Dimmer Switch and Jaycar Mains Timer with LCD display to simulate dawn/dusk timings for the time of year in Charlotte Pass (dawn: 05:42, dusk: 20:09). The camera traps monitored four moth boxes per incubator. To allow the night vision camera (Raspberry Pi Camera module 2

Table 3

Parameters estimates and test statistics for a generalised linear model examining the dry mass of moths between temperature treatments at the conclusion of the experiment. Model $R^2=0.038.$

Fixed effects	β	SE	t value	р
Intercept temp. 10 temp. 12.5 temp. 15	$0.064 \\ -0.001 \\ -0.007 \\ -0.005$	0.004 0.005 0.004 0.005	$18.175 \\ -0.236 \\ -1.516 \\ -1.043$	<0.001 0.814 0.134 0.300

noIR) to 'see' the moths in the dark we trained an infrared (IR) torch on the moth boxes for one shelf per incubator (Techview long range infrared spotlight with 50m model: qc-3654, 12V, power 6×3 W 18W max). This meant that in the boxes lit by the infrared light movement could be detected by the cameras at all times of day rather than the non-IR lit shelves whose activity could only be detected during daylight hours. Two out of the four boxes containing moths that were filmed in each incubator were illuminated by the IR LEDs. A tray of water was placed at the bottom of each incubator to provide a constant high relative humidity. The mean relative humidity measured by miniature temperature/humidity Thermocron iButton loggers ranged from 83.8 to 93.8% across the incubators for the duration of the experiment.

On the December 13, 2019 the 24 boxes of moths were divided equally among four incubators set at different temperatures (7.5 °C, 10 °C, 12.5 °C and 15 °C), with six boxes per incubator and two boxes per incubator shelf. On December 18, 2019 Raspberry Pi motion-capture camera traps (Raspberry Pi Foundation, 2012) were set up on two shelves per incubator to record moth activity levels (each camera recorded two boxes, with 16 boxes recorded in total) 24 h per day for the duration of the experiment. Each camera trap was constructed from a 'Raspberry Pi Camera Board V2', an infrared Raspberry Pi Camera Module 2 NoIR, a battery (Anker PowerCore + 10050mAh QC 2.0), an SD card (64 GB microSDXC) and a wireless adapter so that the videos could be accessed remotely. SD cards for each camera trap were formatted and the 'rasbian' operating system was installed in each of them. The method for setting up the Raspberry Pi camera traps by Whitehead and Lanfear can be followed at: https://github.com/ro blanf/raspberrytrap. Motion-software (PiKrellCam) was installed in each camera trap, which detects motion by the position and motion of objects in the frame (vectors). The camera provides the software with vectors, which are then filtered through vector density tests to ensure that the vector is a valid 'motion event'. The time limit of each motion capture video was 300 s.The camera traps recorded activity levels until the December 25, 2019.

2.4. Question 1: Is there a difference in moth activity over the day when aestivating at different temperatures?

The videos produced by the eight incubator camera traps were downloaded and viewed using VLC media player. One author (RL) screened 7312 videos in total. In each video the number of moths moving was scored. To ensure the scorer was unaware of the temperature treatments when viewing the videos, the file names originally containing the details of each trap including incubator temperature, time and date were anonymised, and the order of videos randomised, to avoid bias in the scoring. Half of the boxes analysed were recorded at both day and night using the infrared light, and the other half only during the day. Any videos that could not be scored with full confidence due, for example, to large numbers of moths gathering in one place were rescored independently by a different scorer. If there was a difference in the scores of these videos among the two scorers, the video was excluded from further analysis (n = 46 videos).

To examine the daily pattern of moth activity under different aestivation temperatures, we fit a generalised additive mixed-model with the proportion of moths moving as our response, temperature (7.5, 10, 12.5, 15) as a fixed effect, and individual smooth terms for time (0-23 h) using a penalised cubic regression spline to account for its circular nature at each level of temperature. We specified a binomial error distribution with logit link, and included the identity of each ''box' (containing n = 10 moths) nested within experimental day as random effects. For all statistical analyses we used R (v4.1.2; R Core Team, 2021) and the packages 'mgcv' (v1.8-40; Wood, 2017) for GAMs and 'emmeans' for post-hoc tests (v1.7.4-1; Russell 2022) (v1.1–23; Bates et al., 2015). We visually confirmed model assumptions by examining diagnostic plots using the 'performance' package (v0.9.0; Lüdecke, 2021).

2.5. Question 2: Is there a difference in moth mass after aestivating at different temperatures?

2.5.1. Wet mass

Moths were weighed twice during the experimental period; once in the 48 h prior to the installation of the cameras (11th/12th December) and again on the 20th December. The initial total mass of moths in each box was calculated and compared to ensure that there were no significant differences in total moth mass per box. During weighing all moths were taken out of their incubator, with behavioural data excluded from weighing days.

To test whether aestivation temperature influences moth wet mass we fit a generalised linear model with the change in each individual's mass from 11/12th December to the 20th December as the response, and aestivation temperature (7.5, 10, 12.5, 15) as a fixed effect. We specified a Gaussian error distribution with Identity link function and ran posthoc contrasts to examine all pairwise differences among temperature treatments.

2.5.2. Dry mass

Post-experiment the moths were frozen, and then later desiccated for 72 h in a Thermoline dehydrating oven at 70 °C. The moths from each box (n = 10) were placed into pouches made from baking paper for desiccation. To test whether aestivation temperature influences dry mass we fit a generalised linear model with dry moth mass as a response, and aestivation temperature (7.5, 10, 12.5, 15) as a fixed effect. We specified a Gaussian error distribution with identity link, and ran posthoc contrasts to examine all pairwise differences among temperature treatments.

3. Results

3.1. Question 1: Is there a difference in moth activity over the day when aestivating at different temperatures?

There was a total of 7312 videos recorded by the motion-activated camera traps and scored for moth activity. As cameras were trained on two boxes of moths each, each video was watched twice, once for each box, a total of 14,624 views. Videos were screened for the presence and absence of movement, and no movement was present in 9012 views with the motion sensing cameras which we cannot explain. These were scored as zero for movement, leaving a total 5612 boxes with moth activity. These boxes were scored for the number of moths moving.

Our generalised additive models identified strong patterns in moth activity over the 24 h day/night cycle, which varied between aestivation temperatures (Table 1). At 7.5 °C and 10 °C, peak moth activity was seen immediately pre-dawn (ca. 0500 h) and post-dusk (ca. 2100 h; Fig. 1), with minimal activity in daylight hours. These bimodal peaks in activity reduced fractionally at 12.5 °C, before being near-completely eliminated at 15 °C. Moth activity during daylight was markedly elevated at 15 °C relative to the activity during the daylight hours in the other three treatments, with only minimal increases to activity evident in the predawn and post-dusk hours that characterise their peak activity periods at 7.5–12.5 °C (Fig. 1).

3.2. Question 2: Is there a difference in moth mass after aestivating at different temperatures?

3.2.1. Wet mass

We identified a moderate to strong effect of aestivation temperature on the loss of wet mass (Fig. 2a). The greatest decline in mass was at 15 °C (0.045 \pm 0.019g), followed by 12.5 °C (0.038 \pm 0.170g), 10 °C (0.032 \pm 0.012g), and 7.5 °C (0.023 \pm 010g), respectively (Table 2, Table S1a and Table S1b).

3.2.2. Dry mass

We found no overall effect of aestivation temperature on the dry mass (Fig. 2b). This held true among all post-hoc pairwise contrasts between temperatures, which did not differ from one another (Table 3, Table S2a, Table S2b).

4. Discussion

The pattern of daily moth activity differed across the four temperatures. The pattern of peak activity at dawn and dusk with lower activity during the day was largely lost in the warmer temperatures which show similar activity levels around-the-clock. The normal pattern of bogong moth aestivation behaviour was disrupted at 12.5 °C and lost at 15 °C. Moths kept at 15 °C also had the greatest reduction in wet mass over experiment, but there was no difference in dry mass among temperature treatments at the end of the experiment. Moths seem to dehydrate more rapidly at 15 °C than at cooler temperatures. Overall, our results suggest that climate change-induced warming of bogong moth aestivation sites will cause changes in moth activity, potentially disrupting aesitvation behaviour and leading to dehydration during aestivation. The impact of changes in activity during aestivation on moth survival and reproduction in the lab and in the wild should be the focus of future investigations.

In our experiment, moths in cooler treatments showed peaks of activity at dawn and dusk which match field observations of moths flying out of their boulder fields in large numbers at dawn and dusk during aestivation (Common 1954; Warrant et al., 2016). This suggests that broadly, moths were behaving normally in our experimental enclosures. The more consistent around-the-clock activity levels in the warmer incubators suggest a switch point where moths no longer conduct their normal behaviour no longer showing activity peaks at dawn and dusk and supressed activity during the daylight hours. This is perhaps due to consistently raised metabolic rate caused by the higher temperatures (Clarke and Fraser 2004; Deutsch et al., 2018; Neven 2000), which makes greater amounts of energy available for movement (Lorenz and Gäde, 2009) perhaps to search for cooler locations or leave the mountains to breed. Wallace (2022) reported that increased daily maximum temperatures correlated with increased bogong moth counts in several mountain aestivation sites in the Australian Alps.

Increased metabolic rate may impact moth survival. Young et al. (2011) suggested that increases in metabolic rate during aestivation under elevated temperature conditions may impact survival in the frog *C. alboguttata* during aestivation, as a result of the greater energetic cost of physiological functions. This has also been observed in the aestivating insect hemlock woolly adelgrid bug (*A. tsugae*) where warmer forests have a higher rate of fatality among the adelgrids while they are dormant (Sussky and Elkington, 2015). If moth activity levels and metabolic rate are correlated with higher mortality rates during aestivation due to exhausting energy reserves before the environment becomes more favourable, it could reduce bogong moth abundance and subsequently alter the Australian alpine ecosystem.

Moth wet mass decreased more rapidly at the higher temperatures, but dry mass did not differ, suggesting that the loss of mass at the higher temperatures was caused by dehydration rather than loss of body fat. Bogong moths have been observed to ingest water on occasion during aestivation in the wild, and so putting a small water source within a box of moths may allow drinking. It is possible that over a longer time period fat reserves would be used up during movements and flight at higher temperatures faster than at cooler temperatures. Common (1954) reported decreases in fat content in both male and female bogong moths between December and January 1951–1952 and suggested that it may be partly as a result of moth metabolism during aestivation. Green (2011) measured the mean dry mass of 150 dead moths collected from the mountains as 0.155g, while our measurement of mean dry mass was 0.060g. This supports the idea that the much lower dry masses from this study may be from a combination of increased levels of desiccation and higher activity levels in the incubators than observed in nature, but these comparisons must be investigated.

Future directions could include studying the effects of different temperatures on bogong moth metabolic rate directly by closed-box respirometry where the moth's gaseous exchange can be directly measured. It would also be useful to accurately determine the critical thermal limits of bogong moths to further understand the implications of climate change (Figs. S2 and S3). Male and female moths could also be separated for the duration of temperature studies to determine whether they show different temperature preferences - Drosophila melanogaster for example, show different temperature preferences depending on sex (Rajpurohit and Schmidt 2016). Bogongs could be dissected to determine whether they were sexually mature while aestivating at different temperatures, as while studies by Common (1954) found that moths do not become sexually mature during their time in the mountains there were two instances of mating observed in the present study. Additionally, it would also be interesting to compare the effects of different temperatures on bogong moths both from aestivating sites in the mountains to moths from populations which seemingly do not make a yearly migration (Warrant et al., 2016). These moths are thought to remain in the milder areas of southern New South Wales and Australian Capital Territory over summer, and may show very different temperature preferences and summer activity levels.

In summary, the clear change in activity pattern, from peaks at dawn and dusk to consistent activity over 24 h we detected in the warmest temperature treatment, suggests that there is a temperature between 12.5 °C and 15 °C at which bogong moth aestivation behaviour is lost. Increased temperatures may affect the moth's survival and changes in bogong moth population densities which would have significant impacts on the Australian alpine ecosystem. These results may be of importance in aestivation studies for species worldwide because as higher temperatures may lead to increased metabolic rates and activity levels, particularly in dormant ectotherms (Young et al., 2011).

Data availability statement

Data from this research are available at: https://doi.org/10.6084/ m9.figshare.21384792.v2.

CRediT author statement

Lownds: Methodology, Investigation, Writing-original draft. Turnbill: Conceptualization, Resources. White: Software, Formal analysis, Validation. Umbers: Conceptualization, Writing- Review and editing, Supervision.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2023.103538.

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