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ORIGINAL PAPER

The impact of cave lighting on the bioluminescent display of the Tasmanian glow-worm *Arachnocampa tasmaniensis*

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Abstract Bioluminescent larvae of the dipteran genus Arachnocampa are charismatic microfauna that can reach high densities in caves, where they attract many visitors. These focal populations are the subjects of conservation management because of their high natural and commercial value. Despite their tourism importance, little is known about their susceptibility and resilience to natural or human impacts. At Marakoopa Cave in northern Tasmania, guided tours take visitors through different chambers and terminate at a viewing platform where the cave lighting is extinguished and a glowing colony of *Arachnocampa tasmaniensis* (Diptera: Keroplatidae) larvae on the chamber ceiling is revealed. Research has shown that exposure to artificial light can cause larvae to douse or dim their bioluminescence; hence, the cave lighting associated with visitor access could reduce the intensity of the natural display. We used time-lapse digital photography to record light output over 10 days to determine whether cave lighting affects the intensity or rhythmicity of bioluminescence. Simultaneously, another colony in a different section of the cave, away from tourist activity, was photographed over 3 days. Both colonies showed high-amplitude 24 h cycling of bioluminescence intensity, with the peak occurring at 11.50 h at the unvisited site and 12.50 h at the main chamber, so the time of peak display did not appear to be substantially affected by light exposure. Intermittent light exposure experienced by larvae in the main chamber caused detectable reductions in bioluminescence intensity; however, recovery was rapid and the overall shape of the daily bioluminescence curve closely matched that of the unvisited colony. In conclusion, the artificial light exposure regime used in Marakoopa Cave does not have a substantial effect on the timing or quality of the bioluminescence display. The time-lapse photo- graphic monitoring method could be permanently implemented at focal tourism sites to provide information about daily, seasonal and annual fluctuations in the displays, the response to events such as drought and flood, and the population's ability to recover from adverse conditions.

Introduction

Aggregations of charismatic species in a restricted location can be subject to strong wildlife tourism demand. Examples include wildlife viewing at African waterholes, penguin breeding colonies, turtle roosting sites (Roe et al., 1997) and aggregations of glow-worms in caves. In protected areas, the managers' challenge is to conserve and even enhance these focal sub-populations while ensuring that the site retains its natural values. Tourism based upon viewing glow-worms—a group of nine species in the fly genus, *Arachnocampa* (Baker, 2010)—has developed at a number of caves in Australia and New Zealand. While glow-worms aren't restricted to caves, tourism has arisen there because some species, such as *A. tasmaniensis* and *A. luminosa*, can reach high population densities in some caves. Further, glow-worms can be conveniently viewed in deep caves during daylight hours as a component of tours that also feature the caves' geological formations.

The single most visited site is Waitomo Glowworm Cave, New Zealand, attracting 500,000 visitors per year (de Freitas, 2010) to view the endemic species *Arachnocampa luminosa* (Skuse). In Australia, major commercial glow-worm viewing occurs at three locations: Marakoopa Cave in Tasmania; Natural Bridge, Springbrook National Park in Queensland; and an artificial cave environment at Mount Tamborine, Queensland. At Natural Bridge, approximately 99,000 visitors per year attend at night to see the large colony of *Arachnocampa flava* (Harrison) larvae on the roof of a recess-like cave behind a waterfall (Wilson et al., 2004; Barnes et al., 2007). At Marakoopa Cave in Mole Creek Karst National Park, Tasmania, Australia, viewing of *Arachnocampa tasmaniensis* Ferguson is one of the attractions of guided tours taking place during the day, attracting approximately 30,000 visitors per year (Eberhard et al., 2004). At all sites, with the exception of Natural Bridge, all tours are guided: at Natural Bridge, the number of unguided visitors is exceeded by guided visitors (Barnes et al., 2007). Because of the tourism, commercial and educational values of these sites, the conservation focus is on ensuring the survival of the population rather than the species—none of the species that are subject to tourism are regarded as threatened—and keeping the display at its natural best. Historically, several different techniques have been used for sampling populations over time, including quadrat counts at Natural Bridge (Baker, 2002), film-based photography at Natural Bridge (Thornton, 2003), quadrat counts at Mystery Creek Cave (Driessen, 2010), and both photographic film and quadrats at Waitomo Glowworm Cave (Pugsley, 1980). These studies covered periods from less than one year to several years. All have revealed a strong seasonal pattern in the number glowing at any one site. High-frequency digital photographic imaging of cave larvae of *A. tasmaniensis* and *A. luminosa* over periods of several days revealed synchronised daily cycles of intensity (Merritt and Clarke, 2011).

Larvae use their bioluminescence to attract prey into their webs (Meyer-Rochow, 2007) so colonies are usually found where a stream enters or exits a cave as they primarily feed on flying insects with aquatic immature stages (Broadley and Stringer, 2001; Driessen, 2010). Known natural risks for these focal populations include flooding—winter floods were noticed to remove many larvae at Waitomo Glowworm Cave (Richards,

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1960)—predation by other cave invertebrates (Richards, 1960; Pugsley, 1984) and fungus disease (Pugsley, 1984). Human threats include disturbance through touching of larvae or their webs, harmful activities such as lighting of fires (Barnes et al., 2007), changes in water quality, and changes in cave microclimate. In 1979, the bioluminescence display at Waitomo Glowworm Cave decreased to the extent that the cave was temporarily closed to visitors (Pugsley, 1984). The decline was eventually traced to increased evaporation within the glow-worm chamber due to the installation of a vented door in another part of the cave. After remediation, the *Arachnocampa* larvae appear to have returned to their former numbers.

It is arguable whether intensely visited populations in caves are especially at risk of permanent loss. Populations appear to have a capacity to recover from crashes based on the Waitomo Glowworm Cave experience, and are able to colonise newly available habitats such as waterworks tunnels, abandoned railway tunnels and abandoned goldmines (Richards, 1960; Lee, 1976). It has been noted that caves in the Mole Creek karst have significant glow-worm populations despite extensive land clearing in the catchment, indicating that glow-worms may be a naturally resilient component of the cave fauna (Eberhard, 2000).

In tourist caves, where it is desirable to maintain high populations that are glowing brightly, the cave lighting itself could cause the larvae to reduce their light output as artificial light exposure causes *Arachnocampa* larvae to dim (Gatenby, 1959; Meyer-Rochow and Waldvogel, 1979; Baker, 2002). While the time course of dousing and recovery under controlled intensities and spectral compositions of light has not been determined, some characteristics of the dimming response are known. Exposure of cave-dwelling *A. luminosa* to white light at 800 lux for five minutes led to immediate dousing, with recovery after about one hour and exposure to colored lights indicated a relative insensitivity to red light (Meyer-Rochow and Waldvogel, 1979). *A. luminosa* in the twilight zone of Waitomo Glowworm cave did not glow when intensity was above 0.5 foot-candles, equivalent to approximately 5.4 lux (Richards, 1960). In forest-dwelling *A. luminosa* exposed to natural light cycles, approximately 1 foot candle (c. 10.5 lux) of daylight was reported as the threshold intensity at which larvae start or stop glowing dusk and dawn (Stringer, 1967).

In Tasmania, glow-worms have been a recognized feature of the cave fauna going back as far as the 1840's, although Marakoopa Cave is the only cave with capacity to accommodate viewing by large numbers of tourists (Clarke, 2001). Mystery Creek Cave and Exit Cave in the Ida Bay karst region have larger populations of glow-worms but are comparatively difficult to access (Driessen, 2010). In Marakoopa Cave, the viewing chamber is usually in complete darkness except when tourists or cave staff enter, usually between the hours of 9 am and 4 pm. After visitors arrive at a viewing platform, the path lighting is switched off, revealing the bioluminescent larvae on the chamber ceiling. While cave lighting has been in place for many years it is possible that it causes partial dimming of the display. The objectives of this study were to use time-lapse photography to (1) investigate the natural rhythmicity of *A. tasmaniensis* bioluminescence in Marakoopa Cave by photographically recording bioluminescence of a colony away from visitor activity, and (2) compare it to the rhythmicity and light output in the cave chamber that is subject to daily, intermittent artificial light exposure associated with tourist activity. A further consideration of the study is the utility of the time-lapse method as a monitoring tool.

Materials and Methods

Time-lapse camera equipment was set up in Marakoopa Cave, northern Tasmania (41° 35' 2" S; 146° 17' 2" E) between 21st February and 3rd March, 2011. One camera was located beyond the tourist section of the cave, focused on a colony of glow-worm larvae on a vertical wall above a stream-bed. These larvae experienced constant darkness. A second camera was set up in the main viewing chamber, focused on the ceiling above a series of cascades at the site where the glow-worm colony is most often viewed by tourists. The time-lapse imaging used Canon EOS 1000D digital SLR cameras (Canon Australia, Sydney, Australia), with 18-50 mm lens at maximum aperture, F3.5, and 30 second exposure at ISO equivalent 1600, as deployed in a previous study (Merritt and Clarke, 2011). The time-lapse interval was set at 10 minutes (PClix time-lapse controller, Visual Effects Inc. Ontario, Canada). The time (Australian Eastern Standard) at which each photograph was taken was recorded with the image. Recording at both sites was initiated 24 minutes apart and ran concurrently. The camera upstream of the main viewing chamber relying on battery power provided 75 hours of continuous recording using two 6-volt (V) lantern batteries connected in series, transformed to camera voltage using a Cercis Astro A635 DC-DC converter (Pennington, New Jersey, USA). The camera in the viewing chamber could operate indefinitely on 240 V mains voltage available at the recording site. For the purposes of this study it was operated continuously for 10 days.

The application ImageJ (U. S. National Institutes of Health, Bethesda, Maryland, USA, http://imagej.nih.gov/ij/, 1997-2011) was used to analyze bioluminescence. Images (2592 × 3888 pixels, 24-bit RGB, jpeg compressed) were converted to 8-bit greyscale using ImageJ. The intensity of the larvae within the field of view was calculated at each time point using the "integrated density" function and a minimum threshold value that highlighted contiguous pixels associated with bioluminescence but did not detect background chip noise due to long exposures. Because the two cameras were used at different lens focal lengths and distances from the subjects, the absolute units of light output are not comparable, rather the time-course of bioluminescence intensity changes or the number of larvae that are visibly bioluminescent are the bases of comparisons. The units for light output are arbitrary and not calibrated against standards. To count the number of glowing larvae, the ImageJ "analyze particles" function was used to count particles of a stipulated size range within the field of view after establishing a threshold value.

To calculate the time of day at which luminescence peaks occur, the time series of intensity values was smoothed using a Butterworth filter (low pass, six hours; high pass, 72 hours) using MatLab (Mathworks, Sydney, Australia) functions. The filter removes the high-frequency component of the signal due to larvae brightening or dimming between frames and preserves the 24-hour cycle present in the time series. The resulting smooth curve then allows calculation of the time of peak and trough using Matlab functions (Levine et al., 2002). The time of peak bioluminescence derived this way is termed the acrophase.

Cave Lighting

Lighting in the chamber comprises 11 track lights designed to illuminate the footpath with just enough light for visitors to safely negotiate the path and stairs. Six track lights are located between the cave entrance and the glow-worm chamber (approximately 50 meters) and five track lights along the next 10 meters of path and stairs connecting the glow-worm chamber to the viewing platform. Each light assembly (240V festoon type with 60W globe) stands on a pipe approximately 150mm high with plastic diffusers directing light to the footpath. The first set of six lights is turned off and the next set turned on when tours reach the switch point. A light meter with integrating sphere directed at the center of the

camera's view from the camera location registered 0.1 lux with the first light set on, 0.1 lux with first set off and second set on, and 0.3 lux with both sets on.

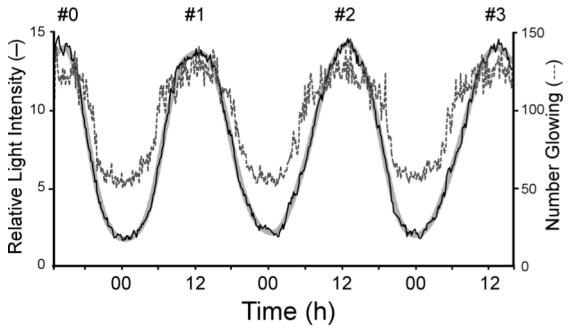

Fig 1 Relative bioluminescence intensity (black line) and number glowing (grey dashed line) of a cluster of *Arachnocampa tasmaniensis* larvae in an unvisited section of Marakoopa Cave over three consecutive days. The daily bioluminescence peaks are numbered 0-3, consecutively. The thick grey line is the smoothed line after application of a Butterworth filter used to calculate time of peak bioluminescence.

Results

Upstream, "unvisited" larval bioluminescence

Analysis of time-lapse recordings of bioluminescence of the approximately 130 larvae in the field of view over 75 hours showed a sinusoidal curve with 24 hour periodicity. The time at which peak intensity occurred was estimated at 12.30, 12.50 and 13.20 hours AEST respectively (peaks 1-3 in Figure 1), calculated to within ten minutes using a curve-smoothing algorithm. The minimum phase occurred at 0.30, 0.40 and 0.10 hours, respectively (Fig. 1). Counts of the number of larvae detectable in the field of view showed that the number of bioluminescing larvae varied between approximately 60 and 130. The curve showed similar times of peak and trough to the overall intensity curve (Fig. 1). Notably, the number glowing did not approach zero, indicating that individuals cycled their bioluminescence intensity even if they did not completely douse their bioluminescence.

Viewing Chamber Bioluminescence

The approximately 120 larvae visible to the camera in the main viewing chamber show a similar rhythm to the "unvisited" larvae. Figure 2 shows a linear plot of the unvisited larval colony's bioluminescence superimposed on the longer-term (244 hours) bioluminescence curve derived concurrently from the viewing chamber. The first three days of recording was simultaneous at both sites while recording at the viewing chamber continued for a further seven days. The viewing chamber record shows a number of breaks during the external daylight hours when the cave lighting was on during tour activity. The points of light associated with individuals were visible on the photographic images as blue dots however intensity measurements were unreliable due to the interference from artificial light. To create a smooth curve and estimate time of acrophase, the data gaps were filled with a linear series between the pre- and post-exposure values before applying the Butterworth filter. For full days one to ten (#1 to #10 in Fig. 2), the bioluminescence acrophase in the viewing chamber was calculated at 11.50, 11.50, 11.30, 12.20, 11.40, 12.00, 11.50, 11.20, 12.30, 12.00 hours, respectively, with a mode of 11.50 hours.

Comparing sites, the shape of the bioluminescence output curve was similar and consistent day-to-day. The peak in light intensity occurred at approximately the same time. The most noticeable difference between sites is that the upstream, unvisited site did not reach zero, whereas in the viewing chamber larval light output is close to zero at the minima. It is not known whether this is a real difference in larval output at the two sites. The greater subject-to-camera distance in the viewing chamber may result in low bioluminescence emissions becoming undetectable, producing the lower minimum readings in the viewing chamber.

To better display the effect of artificial light, the bioluminescence data from the viewing chamber plotted in time series in Figure 2 is re-plotted in a vertical series (Fig. 3). The lights-on periods occurring during tours and maintenance were quantified from the time-lapse images. On days one to nine, the lights were visible in the main chamber for totals of 200, 130, 150, 140, 150, 170, 130, 120 and 80 minutes, respectively. In total, 92 light exposure bouts were recorded. The duration of bouts varied from one to seven data points (10 – 70 minutes) with an estimated mean duration of 1.50 (± 0.10 SE) data points (15 minutes). Lights could have been turned on briefly at other times but would not be detected if occurring between photographs, taken at 10 minute intervals.

Alterations in the natural curve of bioluminescence due to light exposure during the upswing phase were defined using the criterion of a decreased light intensity immediately following light exposure compared to the pre-exposure level (examples in Fig. 3,

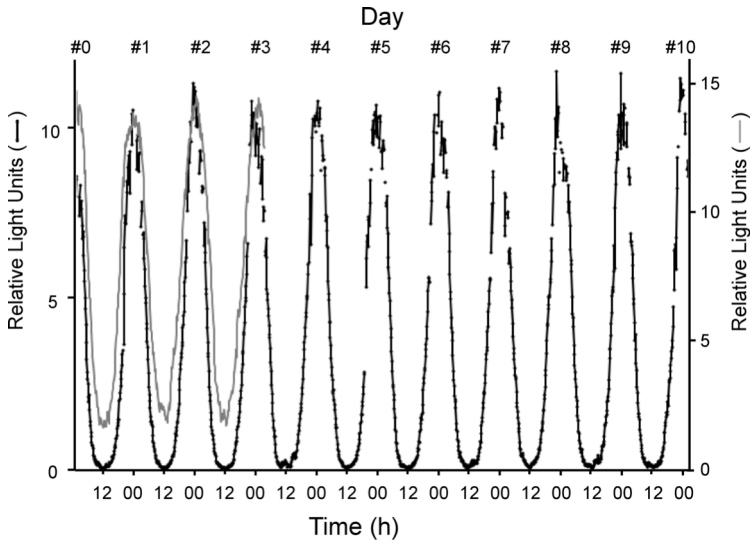

Fig. 2 Relative bioluminescence intensity (grey line) of *Arachnocampa tasmaniensis* larvae in the upstream, unvisited monitoring site compared with the intensity curve of the colony in the glow-worm viewing section of Marakoopa Cave (black line) over nine consecutive full days (#1 - #9) and part of an initial (#0) and final day (#10).

open arrows). On the downswing, the criterion for light-induced reduction is that, after exposure, the bioluminescence increases between subsequent sample points before continuing the downward trend (Fig. 3, grey arrows). Using these relaxed criteria, 57 of the 92 light exposure bouts caused an ensuing reduction in light output and 35 were neutral.

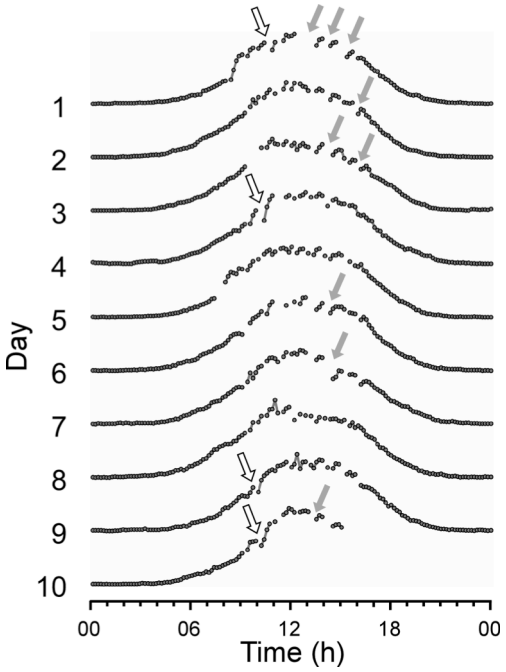

Fig. 3 Relative bioluminescence intensity (black line) of *Arachnocampa tasmaniensis* larvae in the glow-worm viewing section of Marakoopa Cave over nine consecutive days and part of a tenth (1-10). Gaps in the lines connecting data points indicate times when larvae were exposed to lighting during cave operations. Examples of decreased bioluminescence after light exposure in the upswing phase (open arrows) and downswing phase (filled arrows) of the bioluminescence cycle are indicated.

Discussion

The control colony of *A. tasmaniensis* in Marakoopa Cave monitored in this study shows the rhythmic periodicity consistently seen in other cave-inhabiting populations of the species: a sinusoidal bioluminescence pattern with peaks occurring in the afternoon (Merritt and Clarke, 2011). Comparing the period and phase of larvae in the viewing chamber to the colony in the unvisited upstream region, the time-course and characteristics of the bioluminescence output matched closely, with an approximate one hour difference in the time of acrophase between the two colonies. Therefore, we conclude that the period and phase of the viewing colony has not been substantially altered by chronic, intermittent light exposure that occurs during regular tourist visitation. An alternative and less parsimonious explanation is that light exposure in the viewing chamber has shifted the acrophase of that colony to coincidentally match the acrophase of the upstream, unvisited site.

Notably, the time of peak bioluminescence (acrophase) of *A. tasmaniensis* in Marakoopa Cave may have shifted slightly since November 2005, when bioluminescence recording over two days showed an acrophase at 14.14 hours (Merritt and Clarke, 2011). The present study of a nearby location in Marakoopa Cave—the upstream, unvisited site—in February, 2011 shows a modal peak phase at 12.50 hours, so some plasticity in the timing of the acrophase is reinforced by this study. At Mystery Creek Cave in southern Tasmania, the main colony in the inner reaches of the dark zone peaks at about 14.30 hours. A colony in Mystery Creek Cave changed its peak phase dramatically—by about 11 hours—between years (Merritt and Clarke, 2011) and, even within a single colony, two visually isolated subgroups separated by a rock overhang can cycle with different acrophases (Merritt, unpublished). It is possible that clusters are able to adjust their phase, either in competing for prey or in order to match changes in the time of availability of prey items.

We could not categorically determine the degree of dimming caused by artificial lighting in the viewing chamber: close-up, high frequency recording of the bioluminescence of individuals after exposure to tightly regulated intensities and durations of light is needed to determine this. Using specific criteria for a dimming response based on a lower than expected light intensity at the first time point after lights were turned off, more than half of the light exposures resulted in dimming. However, the larvae appeared to recover quickly, returning to the levels expected according to the undisturbed curve established at the control site. It is possible that the amplitude of the bioluminescence maximum, i.e. the maximum achievable level, is reduced due to the chronic light exposure during the day. This could be tested by recording the bioluminescence curve on a day when there are no visits to the cave.

Marakoopa Cave comes under the Mole Creek Karst National Park and Conservation Area Management Plan (Eberhard et al., 2004) that lists a number of threatening processes relevant to cave fauna of the region including hydrological impacts, where water quality can be compromised by land-use, land-slips and fire in the catchment area, atmospheric impacts, where the cave microclimate can be affected by alterations to the cave or presence of visitors, and direct visitor impacts such as installation of structures within caves, or vandalism and harmful behaviours. The management plan recommends that the glow-worm population in Marakoopa Cave be monitored because it is a prominent attraction and planning objectives include provision of opportunities for visitors to encounter wildlife along with minimization of harmful impacts on indigenous fauna. The photographic procedure employed in this study is not intrusive nor is it labor-intensive. It is relatively cheap to implement as it uses recreational or hobby equipment. At sites where mains voltage is available and with an appropriate air-tight enclosure to keep the equipment dry, a camera could operate for many months with occasional attendance to download images.

It is worth considering how monitoring outcomes can be integrated into both conservation and enhancement of the visitor experience at Marakoopa Cave and elsewhere. First, for conservation, a way of telling whether the population is at risk is needed. At least one year of monitoring is required to reveal the natural daily and seasonal cycles in glow-worm bioluminescence (Pugsley, 1984; Eberhard, 2000; Driessen, 2010) and the reaction to occasional flood in the catchment area. The focal population's resilience to catastrophic events may be inferred from observing the population's response to more regular occurrences that may result in reductions in the number glowing. Most importantly, monitoring provides a baseline that allows management to differentiate between long-term incremental degradation and an immediate response to environmental conditions. The availability of cave temperature data and stream levels within the cave are both likely to be important in interpreting the impact of seasonal changes, floods and drought. Implementation of monitoring in an unvisited part of the cave as done in this study would allow distinctions to be made between processes that are affecting the cave system as a whole and those affecting the visited population. The analysis of seasonal trends in the context of climatic data such

as rainfall, water-flow and temperature could allow inferences to be made about the ecology and physiology of *Arachnocampa* in the cave, leading to refinement of conservation and recovery plans and further research into the ecology and seasonality of prey items.

Outcomes from monitoring can also be used to enhance the visitor experience. First, the quality of the display should be predictable according to time of day, season and perhaps other environmental variables such as recent rainfall. This information can be integrated into the educational component of tours as the guides inform visitors about the biology of glow-worms. Further, given that caves such as Marakoopa Cave have been substantially modified to allow visitor access, the augmentation of prey availability in the visited part of the cave may be feasible through changed management practices, leading to increases in the larval population. Monitoring data can be used to analyse the outcomes of any such management trials.

Finally, a consideration in the long-term use of time-lapse monitoring is the need to be able to calibrate counts and intensity data between cameras, as discussed in a study using digital cameras to monitor synchronously flashing fireflies in Malaysia (Kirton et al., 2011).

Conclusions

The time-lapse photographic method reported here provides quantifiable estimates of the numbers of larvae glowing as well as the intensity of each larva at a much higher frequency than is practical using manual counts. *A. tasmaniensis* larvae in Marakoopa Cave show the high-amplitude daily cycle of bioluminescence intensity seen in other cave populations (Merritt and Clarke, 2011). The lighting regime used in Marakoopa Cave does not appear to have disturbed the natural rhythm of the resident *A. tasmaniensis* larvae because the daily-visited colony shows almost identical rhythmicity to an unvisited colony. Ongoing monitoring, perhaps combined with laboratory experimentation defining the dousing and entrainment of bioluminescence in response to artificial lighting, could clarify whether the natural oscillation is affected by cave lighting and whether the Marakoopa Cave glow-worm display could be improved by adjusting the in-cave illumination. Use of the time-lapse method described here has a number of potential applications: continuous monitoring would identify seasonal patterns and climatic impacts on the display; it would allow fine-tuning of cave lighting, visitation times, and other management decisions to optimise the glow-worm display, and could provide early warning of population reductions due to environmental change. While the population at Marakoopa Cave is not under any direct environmental threat, the focus of commercial tourism on cave-restricted populations at this and other sites of intense visitation means that ongoing monitoring is a prudent precautionary measure and has the potential to enhance the visitor experience.

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