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RESEARCH

Trail cameras enhance understanding of lizard behaviour in a remote alpine environment

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Abstract: The number and type of threats that a species is exposed to is often influenced by their activity patterns. For ectotherms, environmental conditions are likely to strongly influence activity, given that external heat is needed to reach body temperatures that promote physiological functions, including locomotion. As a result, one might expect ectotherms to avoid cold environments, such as the alpine zone, known for large temperature variations and prolonged winters. However, many endemic lizards, including diurnal skinks (*Oligosoma* spp.), inhabit the alpine zone across Aotearoa, New Zealand. We used trail cameras to monitor the surface activity of skinks (likely to be predominantly McCann's skinks, *Oligosoma maccanni*) in the alpine zone of the southern South Island (c. 44°S; 1150 to 1600 m a.s.l.) from spring until autumn. We asked: (1) under which environmental conditions do skinks emerge? (2) which temperatures and other weather variables promote the highest levels of surface activity? and (3) what sort and duration of activity are typical? We observed more skink activity when temperatures at basking locations were warm, with 95% of skink observations occurring when temperatures recorded at copper models were between 13.2 and 43.2°C; these patterns follow trends observed in McCann's skinks at lower elevation and in species of alpine skinks in Australia. Furthermore, skinks were most active when conditions were dry and sunny, with observations in mid-summer peaking in the late afternoon. When visible, skinks were very mobile, only remaining in the same position for 1–3 min. Our study increases understanding of a generalist skink in an alpine environment. During summer, activity of skinks is highly dependent on warm sunny conditions, and our study highlights trail cameras as an effective tool for monitoring behaviour (including potential predator exposure) in this remote environment.

Keywords: activity period, alpine, heliothermic, lizard, thermoregulation, trail camera

Introduction

Understanding how a species is active within its environment is a crucial aspect of conservation management. The period in which an animal is active dictates the temporal niche that a species fills and thus influences the environmental and ecological conditions to which active individuals will be exposed (Mech et al. 1966; Terezow et al. 2008). Activity periods also influence the interaction of species by allowing individuals to use the same space at either the same or different times (Kronfeld-Schor & Dayan 2003). As a result, activity periods dictate the sorts of threats that a species experiences, whether from predators (Holomuzki 1986) or anthropogenic factors (Thiers et al. 2014). Finally, understanding how a species' activity relates to environmental conditions (i.e. temperature and other weather variables) can help inform us when monitoring should take place and how climate change might affect a species' activity (Tirado et al. 2018). How a species reacts to local weather conditions is especially important to understand when studying ectotherms because the ability of ectotherms to be active is strongly influenced by temperature and other weather conditions in their environment (Angilletta

2009). However, monitoring ectotherms such as lizards within their microhabitats is complicated as many species are small, cryptic, and easily disturbed.

Alpine regions are a challenging habitat in which to monitor wildlife activity as these areas are often remote and rugged. Alpine climates exhibit large daily temperature swings, high thermal radiation, and prolonged periods of snow cover (Billings & Mooney 1968; Martin 2001). Ectotherms, including lizards, that reside in the alpine zone have multiple adaptations to survive periods of cold weather. These can include morphological adaptations such as increased melanin in the skin, allowing these species to warm up more quickly (Hegna et al. 2013) and behavioural adaptations such as postural adjustments when basking to increase exposure to the sun (Sømme 1989). Increasingly, species that reside in the alpine zone are facing several anthropogenic threats. Most notable are those created by rising temperatures as a result of anthropogenic climate change. These include a loss of habitat as warm temperatures shrink the alpine region, as well as an increase in competition as the elevational range of introduced pests and native species increases with rising temperatures (Gilman et al. 2010). Alpine zones have also become a popular

location for recreational activities, including tramping and skiing, which has led to an increase in habitat modification (Sato et al. 2014). As a result, it is imperative that we better understand the ecology of species that reside in the alpine zone.

With recent advances in technology, trail cameras or camera traps have become an important tool for monitoring animals in remote habitats over prolonged periods. To date, studies employing trail cameras have predominantly involved mammals, especially large-bodied species, and have included studies of movements (Kays et al. 2009), behavioural interactions (Lazenby et al. 2015; Allen et al. 2016), and the success of management interventions (Foster & Humphrey 1995; Donaldson 2007). For example, numerous studies in New Zealand have employed camera traps to monitor the presence of introduced mammalian predators, including cats, stoats, and hedgehogs (Glen et al. 2013; Glen et al. 2016). More recently, trail cameras have become prevalent in the study of small ectotherms using time-lapse settings in which cameras are programmed to take photos at scheduled intervals throughout both day and night (Pagnucco et al. 2011; Bogisch 2014; Johnston 2014; Gibson et al. 2015). This method allows camera traps to monitor small lizards that are too small and similar in temperature to their surroundings to trigger a trail camera's sensor reliably. Time-lapse technology generates hundreds of thousands of photos, and often very few of those photos contain the target species (Hobbs & Brehme 2017). Additionally, time-lapse images are often reviewed manually, which creates the possibility of input errors as reviewers process large numbers of photos (Swanson et al. 2015). Nonetheless, this equipment allows researchers to monitor species in remote habitats including the alpine zone.

We used trail cameras, combined with temperature dataloggers placed in likely lizard microhabitats, to remotely monitor the activity and basking behaviour of diurnal skinks in an alpine region of the southern South Island. At our site, c. 95% of skinks are believed to be McCann's skink (*Oligosoma maccanni*), with the remainder being Canterbury grass skink (*Oligosoma* aff. *polychroma* Clade 4) and Lakes skink (*Oligosoma* aff. *chloronoton* 'West Otago') (C Knox, Southern Scales, pers. comm.). McCann's skinks are found in the lower half of the South Island, from Canterbury to Southland, at elevations that span from sea-level to at least 1500 m (O'Neill et al. 2008). This species lives in open, dry grasslands or scree and is especially common in alpine grasslands (Hare & Cree, 2016). McCann's skinks are relatively well-understood at lower elevations with multiple studies exploring their thermal ecology and reproduction (for overviews see: Cree & Hare 2016; Hare & Cree, 2016; Cree et al. 2020), effectiveness of monitoring tools (Wiedemer et al. 2007; Jones & Bell 2010), and how the species is influenced by introduced predators (Wilson et al., 2017). For the alpine regions of New Zealand, there are few studies on skinks, and none from the alpine regions of western and central Otago (c. 44° S, c. 1150–1800 m a.s.l.; Knox et al. 2019). The available studies focus on phylogeography (Liggins et al. 2008) or descriptions of newly recognised species (Patterson & Bell 2009). Although McCann's skink is not threatened (Hitchmough et al. 2021), our study provides a unique opportunity to understand how a generalist species of lizard adjusts its activity to the thermal conditions common to alpine areas.

This study aimed to identify the environmental conditions that permit diurnal skinks (hereafter considered to be mainly, if not solely, McCann's skinks) to be visible outside their retreats in an alpine environment. We addressed several questions: (1) Which environmental conditions allow these alpine skinks to be present on the surface? (2) When skinks are detected out of their retreats by trail cameras, for how long can they be inferred to be active, and are they actively moving throughout the site or sedentary at basking locations? (3) When skinks have emerged, which combination of temperature and other weather variables promotes the highest levels of surface activity?

Methods

Field site

Camera monitoring took place in a location within the Queenstown Lakes District. Due to the high potential for the illegal collection of lizards, we avoid making reference to the specific location and instead refer to it as QL-A, following Knox et al. (2019) and Bertoia et al. (2021). The site is composed of exposed rock on the steep upper slopes of a mountain at elevations from 1150 to 1650 m a.s.l. The habitat mainly consists of scree slopes, with some rocky bluffs and aggregations of loose surface rocks. The dominant vegetation is narrow-leaved snow tussock (*Chionochloa rigida*), and other species of shrubs and grass such as inaka (*Dracophyllum rosmarinifolium*), and common speargrass (*Aciphylla squarrosa*) are also present (Knox et al. 2019). Snow can be experienced at any time of the year, but it usually only settles between April–October.

Emergence behaviour in relation to weather conditions recorded via trail cameras

During the austral late spring to early autumn, we monitored emergence using KeepGuard KG -780EB (ScoutGuard, USA) and Reconyx HC 500 Hyperfire cameras (Reconyx Inc. Holmen). Trail cameras were placed at locations where we had previously found lizards (locations ranged from 1300 to 1550 m a.s.l). Monitoring took place during daylight hours (c. 07:00–20:00 but adjusted across the season) across four sessions: 28 November 2018–25 December 2018, 20–28 January 2019, 20 February–7 March 2019, and 15–28 March 2019. We combined all monitoring periods for analysis. Cameras were deployed as described in further detail by Bertoia et al. (2021), a study in which the footage was analysed for a separate and primarily nocturnal species of lizard.

To analyse our photos, we used Timelapse 2 (Greenberg & Godin 2015), a programme that simplifies the data collection from a large number of images. We recorded counts of skinks visible on the surface (i.e. any part of the skink was visible in the photo) and quantified observations of local weather conditions, including fine (1 - sunny or partially cloudy days), rain (2 - any sign of rain on the rocks) or snow (3 - presence of snow); wind level (0 - vegetation not moving; 1 - vegetation moving slightly; or 2 - vegetation moving noticeably in the wind, as judged from consecutive photos). We chose to use visible weather conditions collected by our cameras as there is no geographically relevant weather station for our study site, and weather data is difficult to accurately interpolate across large distances in alpine regions (Case et al. 2016). We used the position of skinks in multiple consecutive photographs to infer the duration of time that individuals were active. Once an individual left the frame for more than 10 min, we considered the next sighting as an independent observation. There may have been small numbers of species other than McCann's skinks in the photos, such as juvenile Lakes skinks or Canterbury grass skinks. However, due to their size and

colour similarity, we could not identify all lizards to the species level. McCann's skink is by far the most common species at our field site (C Knox, Southern Scales, pers. comm.), and as a result, we treat all observations of skinks as this species. In addition to skinks, we were able to identify orange-spotted geckos (*Mokopirirakau* 'Roy's Peak') residing in the same habitat (for more information see Bertoia et al. 2021).

Temperatures of likely microhabitat for lizards

While the cameras were recording, we used Thermochron iButton data loggers (model DS1922L, resolution $\pm$ 0.5°C; Maxim Integrated, San Jose, CA, USA) to record hourly, daytime, ambient temperature in potential basking microhabitat (as reported by Bertoia et al. 2021). Each of five iButtons was placed into a copper model that consisted of a hollow copper pipe (110 mm length, 24 mm width, 11 mm height), painted brown (Café Royale, Resene, Wellington, New Zealand). These copper models have been shown to correspond closely to the body temperature during heating and cooling for similar-sized korero geckos (*Woodworthia* 'Otago/ Southland') (Penniket & Cree 2015). They resemble slightly narrower models that have been calibrated against McCann's skinks (Hare et al. 2009) and that in laboratory trials performed similarly with the wider models used in the present study, which had the advantage of accommodating an internal iButton (AC, unpubl. obs.). We sealed the copper models with the data loggers inside and glued them (facing north-south) to potential basking positions (i.e. flat surface rocks) that were within 10 cm of a retreat that contained at least one gecko found on a previous survey (Bertoia et al. 2021). Copper models were not in the frame of the trail cameras but are used to illustrate the potential body temperatures of lizards had they remained motionless and equilibrated in basking positions, such as the positions recorded by our cameras. Copper models were secured with "THE ONE", an all-surface adhesive (Selleys, New Zealand). From here on, this microhabitat is referred to as the 'copper model' position.

Statistical analysis

We first looked at general trends in the trail camera footage to discern which conditions allowed skinks to be active. Due to the large number of zeros in our dataset, we truncated the data to include photos only when skinks were present (i.e. 1930 photos from the total data set of 210 802 photos). We then summed the number of skink observations in each hour per camera (note, these are sightings rather than the total number of different individuals). Using these data, we ran a generalised additive mixed model (GAMM) within the package MGCV (Wood 2011) to better understand which environmental factors influence surface activity. The model contained sightings of skinks per camera per hour as the response variable, with combined mean temperatures recorded by copper models, and hours from sunrise (time of sunrise was adjusted for changes in daylight hours across the season), as smoothed predictor variables. Season was included as a continuous predictor variable (with 1 for spring, 2 for summer and 3 for autumn), whereas wind levels and weather conditions were included as categorical predictor variables. Lastly, we included camera location as a random effect to account for the multiple photos taken from the same position. There were no interaction terms included between variables within the model as we were only interested in the factor main effects.

Results

During the monitoring period, 85.6% of all daytime photos (n = 210,802) were sunny, 13.6% had evidence of rain on the rocks, and 0.8% had snow present. Only a small percentage (7.5%) of photos had no wind (no vegetation movement), whereas 79.3% were taken in light wind (slight movement in vegetation) and 13.2% were taken in windy conditions (vegetation noticeably moving). Skinks were observed in rainy and sunny conditions and at all levels of wind strength, but we saw no skink activity when snow was present. The total average copper model temperature during the daytime monitoring period was 24.4 $\pm$ 0.2°C with a mean range of -5.4–58.0°C, although skinks were active on the surface only when copper model temperatures ranged from 12.8–51.0°C, a range available at copper models for 77% of daylight hours.

Our model showed that temperatures at the copper model, hours from sunrise, month in which the photo was taken all significantly influenced observations of skinks, while weather did not. Higher counts of skinks were observed when copper-model temperatures were between 12.8°C and 30.0°C, and observations decreased markedly as temperatures surpassed 30.0°C ($F_{4.17,5.25}$ = 57.32, P = < 0.001; Fig 1a). The relationship between hours from sunrise and counts of skinks per camera per hour is significant; counts of skinks peaked in the mid to late afternoon ($F_{4.88,5.99}$= 49.20, P = < 0.001; Fig 1b). Observations of skinks decreased slightly as the seasons changed from spring to autumn (χ^2 = 6.39, P = 0.01; Fig 1c).

The mean activity period was 3 $\pm$ 0.29 (SE) minutes (maximum 63 minutes). Skinks visible on the surface were very mobile. They were often only in the frame for 1–2 photos in a row, and even then, individuals changed positions between frames (Fig. 2). Skinks were constantly moving and repositioning themselves and were almost always in direct sunlight. Lastly, we saw no interactions between lizards of any kind, nor any photos of either birds or mammals (including potential predators) on daytime photos. The maximum number of skinks seen in a single image was two (n = 19 images).

Discussion

Our study provides new information on the thermal behaviour of diurnal skinks in an alpine environment. When examining surface activity when skinks (presumed McCann's skinks) were present, skinks were more active when copper models at basking locations were between 12.8°C and 30.0°C. Observations of skinks peaked 10 hours after sunrise and were higher in spring and early summer than in autumn (we did not examine activity in winter). When skinks were on the surface, they were constantly moving and repositioning themselves and were almost always in direct sunlight. Skinks remained in the frame for only short periods of time (mean 3 minutes).

A limitation of this study is that we could not identify every skink to the species level conclusively. Canterbury grass skink, McCann's skink, and juvenile Lakes skink are all present at QL-A, of similar size and colour, and the photos generated by our trail cameras do not have high enough resolution to distinguish these species. Fortunately, McCann's skink is extremely common at QL-A, whereas the Canterbury grass skink and Lakes skink are relatively rare (C Knox, Southern Scales, pers. comm.). Although a few observations may be of a different species, they are likely to be inconsequential as the vast majority of observations are likely to be of McCann's skink.
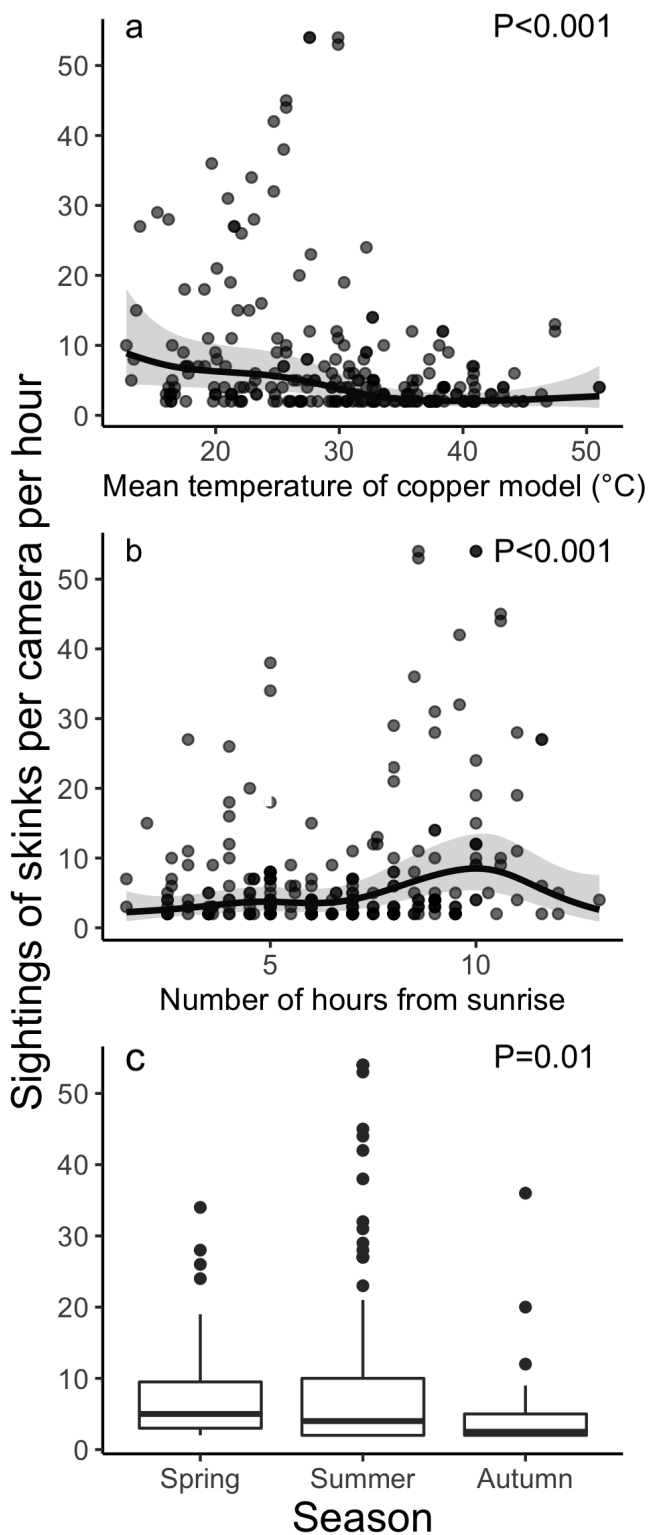
Figure 1. Significant relationships from the GAM with sightings of skinks (primarily McCann's skinks) per camera per hour as the predictor variable. (a) represents the relationship between skink sightings and mean temperatures recorded in the copper-model microhabitat ($P < 0.001$). (b) represents the relationship between sightings of skinks and the number of hours from sunrise ($P < 0.001$). (c) represents the relationship between sighting of skinks per hour with the season in which the photos were taken ($P = 0.01$). Spring represents observations from only November; summer contains observations from December–February, while autumn has observations from March. The grey shading represents the 95% confidence interval of the model.

Activity of skinks in relation to copper model temperatures at QL-A is consistent with what is known of the thermal ecology of McCann's skink at lower elevation in Otago. For example, McCann's skinks at the mid-elevation subalpine habitat of Macraes in eastern Otago (c. 700m a.s.l) select a mean body temperature of 28.9°C on a thermal gradient when in early pregnancy; field body temperatures of emerged skinks range between 5 and 35°C (Hare et al. 2009; Cree et al. 2021) with mean values of 22.9°C for pregnant and 21.5°C for non-pregnant skinks (Hare et al. 2009). In a laboratory study, the voluntary thermal maximum (initiation of escape behaviour) for McCann's skinks ranged between means of 35.0 ± 0.3°C and 36.0 ± 0.4°C for pregnant and postpartum females, males and neonates, whereas critical thermal maximum (loss of righting response, with probable risk within minutes of heat death) was between 40.4 ± 0.2°C and 41.7 ± 0.1°C (Virens & Cree 2019). We assume that temperatures of our copper models at QL-A would resemble body temperatures if skinks remained basking and motionless at the same location, based on calibration data for similar-sized and painted models in a previous study (Hare et al. 2009; note, however, that copper models heat to higher extremes than air temperature). Given this assumption, our observation of greatest skink emergence when copper models were between 12.8°C and 30.0°C, with little emergence at higher temperatures (when rapid movements of skinks would have made equilibration unlikely) corresponds well with the known thermal limits for McCann's skinks at Macraes. Our comparisons suggest that the alpine population may share a similar thermal preference to McCann's skink at the sub-alpine Macraes site.

The copper-model temperatures at which skinks were active at QL-A are also similar to body temperatures for alpine skinks overseas. The spotted snow skink *Carinascincus ocellatus* in Tasmania at c. 1050 m a.s.l. is active with body temperatures of 18.2–34.2°C (air temperatures of 10.3–26.6°C) and has a preferred temperature between 28–31°C (Yuni et al. 2015, 2019). In another example, the Guthega skink (*Liopholis guthega*), a high-alpine specialist found at 1860 m has a critical thermal minimum of c. 1°C, and a critical thermal maximum of c. 40°C. Senior et al. (2019) found that sprint speed was slow around 15°C and found no individuals outside of retreats when surface temperatures were below 15°C, similar to the absence of emerged McCann's skinks at QL-A when copper-model temperatures were below 12.8°C. This suggests that thermal constraints limit activity in alpine regions for both alpine specialists and more generalist species of skinks, including McCann's skink which is also found at much lower elevations than QL-A.

Surface activity of skinks

Skink activity at QL-A was heavily influenced by surface temperature in that skinks were more active when temperatures in likely basking areas were warm (12.8–30.0°C) and during seasons that are associated with warmer temperatures. Higher activity levels during warmer conditions is not surprising as McCann's skinks are heliothermic ectotherms that rely on warmth from their environment to reach high body temperatures promoting several biophysical processes, including digestion and locomotor ability (Angilletta 2009; Hare et al. 2016). The mobile surface activity and short basking sessions of skinks appeared thermoregulatory in nature, with individuals shuttling between hot basking positions and nearby cooler retreats; such behaviour would enable them to stay close to their preferred body temperature, a behaviour common in other New Zealand

Figure 2. Examples of skink basking behaviour on 30 November 2019 at 1510 m a.s.l in the Queenstown Lakes District of southern New Zealand. A photo was taken every minute, starting from photo one at 11:00 and finishing with photo four at 11:03. The same individual (probably a McCann's skink) was in a different position for each of the first three photos and was no longer in the frame on the fourth photo. These photos illustrate the mobile basking behaviour that we frequently observed during this study.

lizards (Gibson et al. 2015). As a result, vegetation cover and surface retreats likely play a critical role in thermoregulatory behaviour for these skinks allowing them to escape extreme heat, to avoid overheating, or acting as a refuge from sub-zero surface temperatures (Bertoia et al. 2021). These microhabitats are likely vital as QL-A offers limited time to access preferred body temperatures as overnight lows in summer reach below 0°C, and microhabitat temperatures in exposed locations often surpass the voluntary thermal maximum during the day.

Skink observations were lowest in the early morning (2–7 hours after sunrise) and peaked in the late afternoon. This pattern may also be temperature-driven, in that overnight lows that fall near or below 0°C make early morning surface activity less productive. For example, McCann's skinks have a greatly reduced ability to swallow and digest prey at temperatures around 12°C, and individuals often stop eating altogether at 5°C (Besson & Cree 2011). Skinks may be active in the late afternoon as the habitat has had time to warm up, allowing skinks to reach higher body temperatures while avoiding extremely hot mid-day temperatures that exceed the likely voluntary thermal maximum. Melville and Swain (1997) saw

similar behaviour in the skink *Carinascincus microlepidotus*, an alpine specialist in Tasmania; that species was often not visible at mid-day but "basked" on warm rocks into the evening, likely supplementing its temperature gain through thigmothermy (heat conduction via direct contact with a warm substrate). A similar benefit from thigmothermy could explain the increase in late-afternoon activity in McCann's skink at QL-A.

Monitoring and management

Our observations can inform monitoring in terms of identifying the ideal conditions in which to observe alpine populations of McCann's skinks; these recommendations are likely applicable to other skink species in the alpine zone. Our results suggest that fewer individuals are active in the early morning (2–7 hours after sunrise). As a result, searches during this time may be less effective. However, skinks on the surface in the morning are likely to be cold and slow, making them easier to catch or photograph. To increase observations of skinks, monitoring efforts using trail cameras should focus on the mid to late afternoon. Our study further highlights the use of remote monitoring tools to passively monitor the behaviour of

small lizards in a remote habitat. Future research could use trail camera photos to analyse microhabitat preferences of alpine skinks. This would inform researchers and managers of what habitat is higher priority to survey and manage.

There are many advantages of monitoring a habitat remotely. Remote monitoring tools may require only an initial set-up and final removal, depending on battery life or the length of the study, thus limiting the number of trips required to monitor a field site over a summer season. This reduces field-related costs (i.e. fuel, vehicle rental, salaries for field staff, health and safety risks of working in alpine regions) and reduces the carbon emissions associated with travel. Remote monitoring can also be less disruptive when compared to other methods, including rock turning, that can destroy microhabitats that lizards depend on (Pike et al. 2010). Lastly, dataloggers and trail cameras can monitor a habitat continuously, for prolonged periods, which provides unique insights into daily or seasonal cycles (Steen 2017) and makes them less influenced by short-term temperature or weather variables, a common pitfall of more snapshot methods such as manual searches (Lettink & Monks 2016). Drawbacks of trail cameras include that they are expensive and cannot always be used to identify individuals, especially if the target species is small. Trail cameras can also have technical difficulties leading to data loss, and processing of images can be time-consuming (Pagnucco et al. 2011). It took us roughly 120 hours to process the 210 802 photos that we collected in our field season. This was a fairly large time commitment considering a reasonable amount of effort was put into obtaining the photos as well.

Going forward, camera technology will only improve. Recent studies have utilised machine learning to sort or classify photographs (Yousif et al. 2019) or even identify species from trail camera photos (Hoye et al. 2020; Pegoraro et al. 2020). Higher megapixel trail cameras will provide better quality photos which may allow for identification to the species level. New trail cameras, like the Bushnell Core DS (Bushnell Outdoor Products, Overland Park, Kansas, USA), have a 31-megapixel camera, ten times higher than the cameras we used in this study. Lastly, our understanding of the influence of introduced predators on alpine lizards is limited; however, stoats, cats and possums likely predate on skinks in alpine regions and have been detected at high elevations like that of QL-A (O'Donnell et al. 2017; Foster et al. 2021). Although we did not see any interactions between pest mammals and skinks at QL-A, trail cameras allow researchers to monitor pests and their target species simultaneously. As alpine regions warm, further invasion of introduced mammalian pests into the alpine zone is a significant concern (Christie 2014). The better we can understand alpine species and their environment, the better we will be able to manage them as their potential threats begin to rise.

Our study contributes to a more nuanced understanding of lizards in a high elevation scree, rock, and tussock-covered habitat. We observed that alpine populations of skinks (likely to be primarily McCann's skinks) are more active in warm, dry conditions in the mid to late afternoon and that, in general, activity of skinks in this alpine population follows similar trends to those observed in lower-elevation populations of McCann's skinks in New Zealand and other alpine skinks in Australia. We have also shown the value of trail cameras and dataloggers for monitoring the behaviour of lizards and the environment in which they live. These devices allow the collection of basking observations that would not be possible by other forms of monitoring and over extended periods in which temperature and seasonal trends can be explored. In light of projected changes to our environment due to anthropogenic climate change, it may become difficult to justify frequent field trips using fossil-fuelled transport to remote locations (Christie 2014; Climate Change Commission 2021). Therefore, we suggest that more studies use remote-monitoring tools, including trail cameras, to monitor activity or behaviour in remote hard-to-reach environments.

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Data and code availability

The data from this article are openly available at https://doi.org/10.6084/m9.figshare.19953944.v1. There is no code available for this article.

Authors contributions

AC and JM conceptualised this study; AB, AC, and JM developed the methods and investigation, and AB and JM undertook the analysis. AB wrote the original manuscript draft, and all three authors contributed to review and editing.

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