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RESEARCH

Time-lapse cameras improve our understanding of invertebrate activity in the alpine zone

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Abstract: Understanding when a species is active in its' environment is essential when designing inventory and monitoring protocols, especially for ectotherms whose activity depends on local weather conditions. The New Zealand alpine zone hosts a diverse native assemblage of invertebrates that are poorly understood yet likely to face an increasing number of threats, particularly associated with climate change and the range expansion of introduced pests. Large-bodied flightless invertebrates are particularly vulnerable to introduced predators, like mice and stoats, which have decimated native species at lower elevations. Using trail cameras, we aimed to understand what conditions and times of the summer field season (spring–autumn) are optimal for monitoring large-bodied alpine invertebrates in the Homer and Gertrude valleys, Fiordland, New Zealand, from late austral spring to late autumn (2020/2021). Beetles (Coleoptera), wētā (Orthoptera), and spiders (Araneae) were the three most common taxonomic groups detected at our sites. The activity of all three groups was significantly influenced by mean hourly temperature. Ninety-five per cent of beetle observations occurred when temperatures ranged from 5.9–12.6°C, while 95% of wētā observations occurred when temperatures were between 6.0–12.6°C. Spiders were active across a broader range of temperatures, with 95% of observations occurring when ground temperatures were between 5.4–13.0°C. The activity of all three groups was also influenced by the time of year. Beetles were observed more often in late spring, wētā in early summer, and spiders in mid-summer. The activity of spiders and beetles, but not wētā, was negatively correlated with precipitation. These results suggest optimal monitoring periods for wētā, beetles, and spiders differ. Still, if the objective is to monitor a range of invertebrates simultaneously, we recommend that surveys occur in spring and mid-summer during nights when temperatures are higher than 5.4°C with little to no rain.

Keywords: activity, alpine, invertebrate, monitoring, trail camera

Introduction

Monitoring the abundance, distribution, or diversity of animals in an environment helps us understand how they respond to pressures, allows us to understand their population trends, and whether management practices have the desired outcomes (Gibbs 2000; McComb et al. 2010). To effectively monitor populations we need to understand their ecology to ensure our surveys have enough detectability to observe actual changes in relative abundance or distribution (Block et al. 2001; Spellerberg 2005). This is particularly important for invertebrates because they rely on ambient temperature to maintain body temperatures that promote essential functions like locomotion (Angilletta 2009). Consequently, invertebrate surveys must be planned around temperature and other weather conditions that facilitate high activity levels (Petford & Alexander 2021). Surveys also need to be scheduled around the phenology of the target species so that they occur when individuals are detectable (e.g. holometabolous insects are often detected when they have emerged as adults; Fountain et al. 2013; Schori et al. 2020). Surveys during high-activity periods will increase the number of detections allowing management practitioners to observe changes in the invertebrate community and confidently make decisions.

The alpine zone is defined as the area between the climatic treeline and permanent snow line, which is the lower limit of the nival zone (Burrows 1967; Mark et al. 2000). In New Zealand, this habitat contains a wide range of plant cover and terrain including tussock grasslands, shrubs and forbs, and rocky fields (Mark et al. 2000). The New Zealand alpine zone hosts a broad ground-dwelling invertebrate community consisting of but not limited to spiders (Malumbres-Olarte et al. 2013), grasshoppers (Koot et al. 2020), wētā (Leisnham et al. 2003), and cockroaches (Wharton et al. 2009). Many of these invertebrates can be found across a range of elevations (Watt 1980; Buckley et al. 2022), while others, like the adult alpine scree wētā (*Deinacrida connectens*), are generally restricted to areas above the treeline (Field 1980). Commonly, invertebrate activity in alpine regions is associated with warmer temperatures in the summer months. For example, Sinclair et al.

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(2001) found a significant reduction of several invertebrate groups, including lycosid spiders, Hemiptera, Coleoptera, and Diptera under surface rocks in the Rock and Pillar Range between January (summer) and June (winter). In another example, reproductive activity for grasshoppers (*Paprides nitidus* and *Sigaus australis*) has been observed more commonly on warm (15–35°C) summer days, and alpine grasshopper activity is generally associated with warmer summer periods where individuals can be found openly basking (Mason 1971; White 1974). For some alpine invertebrates, we have a strong understanding of what temperatures promote higher activity levels. For example, the mountain stone wētā (*Hemideina maori*), an especially well-studied alpine invertebrate, has been shown to prefer temperatures between 4.3–29.3°C with an overall median and mean of 13°C in a lab environment (Rock et al. 2002). However, our understanding of temperature and weather thresholds that promote activity of many other invertebrate groups is much more limited.

Alpine invertebrates have several adaptations that allow them to survive and remain active in cool conditions including, melanism, reduced or lack of wings, they can be larger, develop more slowly, and live longer (Mason 1971; Chinn & Chinn 2020). Though these adaptations have physiological benefits, they can also make alpine invertebrates especially vulnerable to threats like environmental change and introduced predators. Limited or lack of wings in alpine invertebrates limits their dispersal ability making them vulnerable to habitat loss and fragmentation driven by human development and climate change (Chinn & Chinn 2020; Carmelet-Rescan et al. 2021; Koot et al. 2022). The relatively large size of alpine invertebrates and lack of defence mechanisms make them ideal prey for introduced predators (Stringer & Hitchmough 2012). Rising temperatures in alpine areas may allow a wider range of species to enter the alpine zone, increasing predation (Rowe-Rowe et al. 1989; Watts et al. 2011) and competition for resources (O'Donnell et al. 2017; Macinnis-Ng et al. 2021; Buckley et al. 2022). A significant threat to native fauna in New Zealand is introduced mammalian predators (O'Donnell 1996; Dowding & Murphy 2001; Gibbs 2009). Below the tree line, from coastlines to forested habitats, mice (*Mus musculus*), rats (*Rattus rattus*, *R. norvegicus*, and *R. exulans*), stoats (*Mustela erminea*), cats (*Felis catus*), and possums (*Trichosurus vulpecula*) have already devastated native flora and fauna that have evolved without mammalian predators (Hare et al. 2019; Vergara et al. 2021). The alpine zone was considered relatively safe from introduced predators in the past, but there is increasing evidence that they utilise this habitat (O'Donnell et al. 2017; Foster et al. 2021a).

In the alpine zone, the most notable introduced predators are stoats and mice, although rats, cats, and possums are also present (O'Donnell et al. 2017). Large-bodied invertebrates (≥ 1 cm body length) are thought to be especially at risk of predation (Stringer 2005; Stringer et al. 2014). Below the treeline in low-elevation forests, introduced predators have decimated local populations of large-bodied invertebrates so that many can only exist in predator-free ecosanctuaries or on predator-free offshore islands (Sherley & Hayes 1993; Watts et al. 2008). There is a clear need to understand how invertebrates respond to the increasing number of biotic and abiotic threats in the alpine zone. However, we must first improve our understanding of how alpine invertebrates interact with their environment. This will inform sampling design, allowing us to better understand how invertebrates respond to threats like introduced predators.

Trail cameras have become a prominent monitoring tool that aids researchers in better understanding wildlife activity and behaviour across a wide range of habitats (Rosatte 2011; Blagdon & Johnson 2021; Surmacki & Podkowa 2022). Trail cameras can monitor animals in the wild for months, allowing researchers to make observations without the need for multiple and potentially costly field trips (Surmacki & Podkowa 2022). Trail cameras also provide time-coded information, which gives insight into temporal behaviour that can be especially helpful when monitoring elusive species or in environments that are difficult to access (Dillon & Kelly 2007; Li et al. 2018). Trail cameras have recently been used to monitor smaller organisms like lizards (Gibson et al. 2015; Bertoia et al. 2021, 2023) and invertebrates (Zaller et al. 2015; Collett & Fisher 2017). For invertebrates, common trapping tools (e.g. pitfall traps or pan traps) do not provide precise information on when an individual was caught; instead, researchers aggregate sampled individuals and their associated temperature and weather data over the sampling period (Collett & Fisher 2017). The timestamps from trail camera photos allow researchers to examine the interactions between invertebrate activity and weather variables like temperature or precipitation in more detail. Changes in invertebrate detection can be compared with fine-scale weather variables to better understand which conditions promote invertebrate activity. This fine-scale information can inform targeted searches and community surveys or be used to inform tools that predict how a species may respond to climate change.

In this study, we focus on large-bodied (≥ 1 cm body length), ground-dwelling alpine invertebrates likely to be vulnerable to predation by introduced mammalian predators. To better understand activity patterns of large-bodied alpine invertebrates, we used trail cameras to monitor invertebrates in the alpine zone from November 2020–May 2021. We aimed to understand how temperature and precipitation influence the detectability of alpine invertebrates on a finer scale to inform monitoring. We also sought to better understand how timing across the summer field season (spring–autumn) influences detection levels of alpine invertebrates. Lastly, we compare our findings with other studies investigating weather, season and invertebrate activity. At lower elevations in New Zealand, invertebrate activity is highest from late spring to summer when temperatures are warm (Sherley & Hayes 1993; Cartellieri & Lövei 2003). Within the late spring to summer period, activity peaks at different times for different invertebrates. For example, some beetles can be more active in spring (Anderson et al. 2004), while wētā can be more active in early summer (Van Wyngaarden 1995). There is little information on how invertebrates in New Zealand respond to precipitation beyond observations of wētā activity in wet and dry conditions (Watts & Thornburrow 2009). We provide specific recommendations on conditions that promote large-bodied alpine invertebrate activity to help optimise future surveys to better our understanding of invertebrates in the alpine zone.

Methods

Field site

This study occurred in the Homer and Gertrude valleys, Fiordland National Park, Aotearoa New Zealand. The field sites range from 810–920 m a.s.l and consist of three major habitat types: shrub fields, tussock grasslands, and rock fields. Shrub fields were dominated by woody shrubs (less than 1 m in height), including hebes (e.g. *Veronica hectorii*) and dracophyllum (*Dracophyllum rosmarinifolium*). The shrub habitat also contained a variety of other native plants, including mountain daisies (*Celmisia* spp.), mountain buttercup (*Ranunculus lyallii*), common spear grass (*Aciphylla squarrosa*), and various ferns and mosses (Fig. 1a). Tussock grasslands were 50–60% red tussock (*Chionochloa rubra*), narrow-leafed snow tussock (*C. rigida*), and fescue tussock (*Festuca novae-zelandiae*). The remaining vegetation consisted of mosses, dracophyllum, common speargrass, and mountain buttercup (Fig. 1b). Lastly, rock fields were 60–80% rock-covered, ranging from large boulders to a few centimetres in length. Rock fields were scattered with light vegetation, including mosses, ferns, and mountain buttercup (Fig. 1c).

Trail Cameras

We placed nine Reconyx HC 500 Hyperfire (Reconyx Inc., Holmen) cameras in the alpine habitat to monitor invertebrate activity. Three cameras were placed in the Homer Valley, one at each habitat type (shrub, rock and tussock at 961, 934, and 894 m a.s.l., respectively). We deployed the remaining six cameras in the Gertrude Valley, with two at each habitat type. Tussock sites were at 812 and 845 m a.s.l., rock sites were at 823 and 850 m a.s.l. and shrub sites were at 805 and 841 m a.s.l. All sites were at least 100 m away from each other (Fig. 2).

Cameras were mounted 60 cm off the ground on a 1 m black steel pole using a DSLR swivel mount to position the cameras with the lens facing the ground (Fig. 3). We also placed a 30 cm ruler in the field of view to provide scale for the invertebrates in the picture. We secured rulers in rocky habitats with an all-surface adhesive (THE ONE®, Selleys, New Zealand), and in tussock and shrub habitats, rulers were secured with wire. We programmed the cameras to take a picture every 15 min, which has been shown to adequately survey invertebrates without generating more photos than can be processed (Collett & Fisher 2017). Cameras ran continuously from 19 November 2020 (the earliest we could safely access the site due to potential avalanche risk) to 3 May 2021. In March, we replaced the batteries and memory cards, and all the equipment was removed at the end of the trial (May 2021). These cameras use an infrared illuminator for photos at night

Figure 1. Example habitat of (a) shrub fields, (b) rock fields, and (c) tussock grasslands in Homer and Gertrude Valley Fiordland, New Zealand.

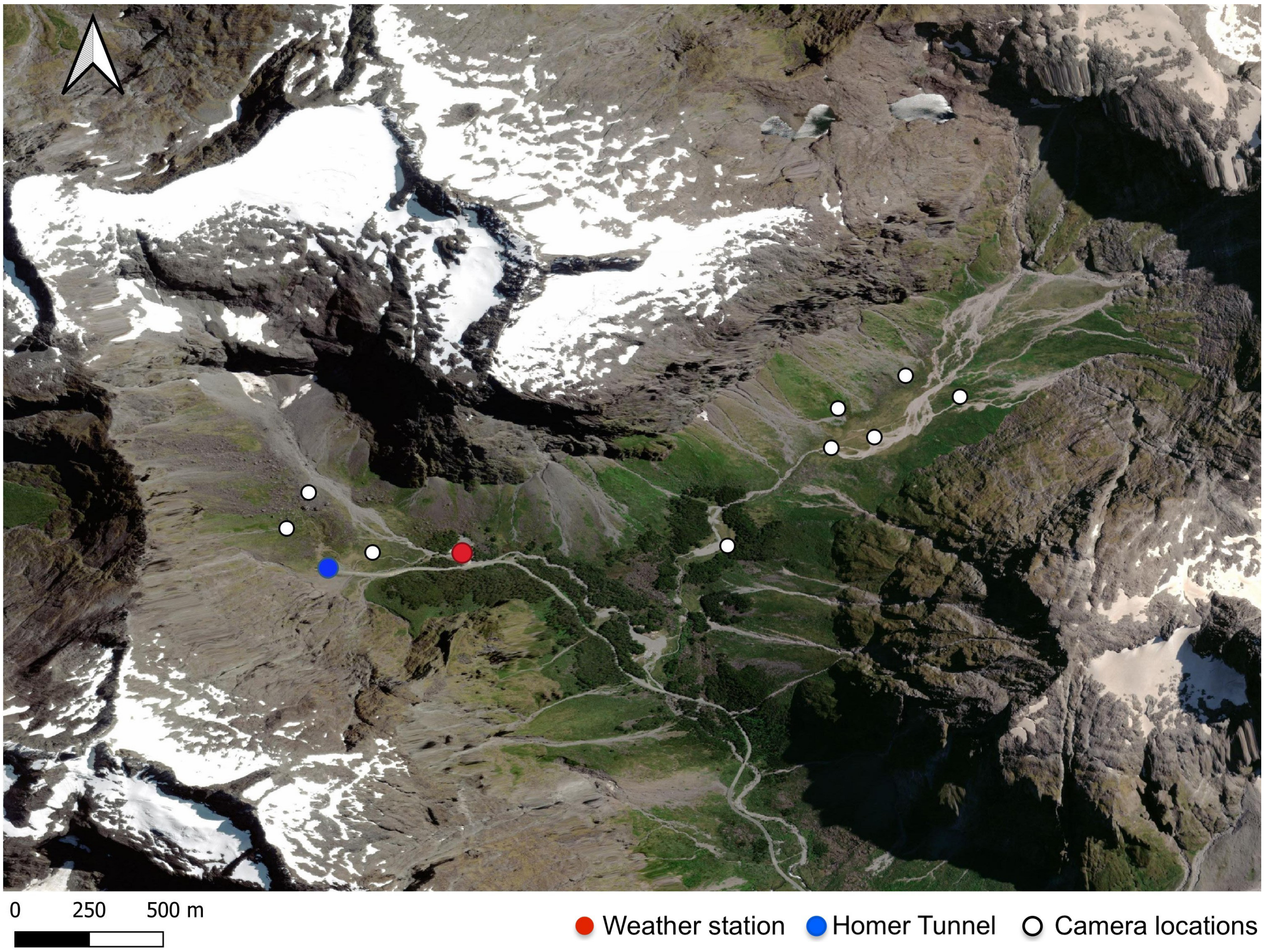

Figure 2. Map of our field site highlighting the location of the weather station and our trail cameras alongside nearby landmarks in the Homer and Gertrude Valley, Fiordland, New Zealand.

to limit the influence a flash may have on the wildlife being photographed.

We used Timelapse (Greenberg & Godin 2015), an image-analysis programme that streamlines the data collection from trail camera photos to generate data from the images. Timelapse requires the users to look through each picture and aids in quantifying images. Using Timelapse, we counted and identified all individual invertebrates that were 1 cm or larger in body length. Observations were split into three easily identifiable taxonomic groups, which consist of beetles (Coleoptera), wētā (Orthoptera), and spiders (Araneae). Hourly temperature and precipitation data were acquired from the Milford Road Alliance East Homer Road weather station. This station is in the Upper Hollyford Valley at the base of Mt Talbot, 500 m southeast of the eastern Homer Tunnel entrance (Latitude -44.764011, Longitude 167.995403, 870 m a.s.l., Fig. 2). This weather station is within 2 km of all field sites and 60 m of elevation. We intended to include relative humidity in our analysis, as it is an important factor for terrestrial invertebrate activity (McColl 1975), but our loggers malfunctioned, excluding this factor from our dataset.

Statistical analysis

All analysis was completed in R (R Core Team 2023). We summed the number of invertebrates visible in each image from each camera per hour (note that these are counts of all individuals in each image and not necessarily the total number of unique individuals). There were only 78 observations of diurnal invertebrate activity, so we truncated the data to include nocturnal activity only. Using these data, we ran a generalised additive mixed model with a zero inflated poisson distribution (GAMM) using the package mgcv (Wood 2017) to investigate which environmental factors influence activity of all large-bodied invertebrates. The model contained invertebrate detections per camera per hour as the response variable, with hourly temperature, hourly precipitation, and number of days from 19 November 2020 (the day the cameras were deployed) as smoothed predictor variables. We tested for concurvity, a generalisation of co-linearity for additive models (Wood 2017). Our highest concurvity measure across all variables from all models was 0.46, which is under commonly used thresholds of 0.8 (Leonardi et al. 2022) and 0.5 (Salazar et al. 2021). We also gave cameras a unique ID included as a random effect. We used additive models because they do not assume that the relationship between a dependent and independent variable is linear, thereby allowing the models to capture non-linear relationships that are readily interpreted by plotting fitted smoothed lines (Wood 2017; Larsen 2015). The relationship

Figure 3. Example camera set up in tussock habitat in Fiordland, New Zealand.

between weather variables or season and invertebrate activity was expected to be non-linear as activity increases and decreases following periods of preferred temperatures or invertebrate reproductive cycles. We then separately modelled each taxonomic group (beetles, wētā, and spiders). These models had the same structure as described above but counts per camera per hour were limited to the target invertebrate group.

Results

We took 119 484 photos in the Homer and Gertrude valleys during the monitoring period. Of these photos, 67 391 were taken during the day, with the remaining 52 093 taken at night (between sunrise and sunset). We detected substantially more invertebrates at night than during the day (2359 and 78; respectively). At night there were 1980 photos containing invertebrates with 2359 invertebrates ≥ 1 cm in length: 1452 beetles, 659 wētā, 234 spiders, and 14 other invertebrates (harvestmen, lepidopteran larvae, and unidentifiable taxa; Table 1). Photographs of wētā are likely all ground wētā (*Hemiandrus* spp.) based on the images, and they were the only kind of wētā caught in pitfall traps run at the exact locations (Bertoia et al. unpubl. data; Fig. 4). Spiders are likely wolf spiders based on the general shape of their body in the photographs and that they were the only group of spiders caught in the same traps (Bertoia et al. unpubl. data). Beetles were more challenging to identify as the community was wider, and it was impossible to identify every individual from the photographs. We saw individuals that were likely a mix of herbivorous and carnivorous species. Still, it is difficult to say which groups with high confidence (See Supplementary Material; for example, photographs where identification was difficult).

The average nightly temperature was 8.2°C with a minimum of −1.1°C and a maximum of 16.9°C. Invertebrates were detected as being active on the ground surface when temperatures ranged from 0.8–16.9°C, and these temperatures were available for 98% of nighttime hours during the monitoring period. Average nightly precipitation was 0.5 mm per hour, with a minimum of 0.0 mm and a maximum of 16.4 mm.

We found a significant relationship between temperature, precipitation, date (number of days from the start of monitoring) and invertebrate detections. Ninety-five per cent of invertebrate counts were observed when overnight temperatures ranged from 5.9–12.6°C, with a peak at c. 11°C ($\chi^2_{(4.45)} = 177.36$, $P < 0.001$; Fig. 5a). Invertebrate detections decreased with rising precipitation levels ($\chi^2_{(1.57)} = 36.29$, $P < 0.001$; Fig. 5b). We also observed more invertebrates in mid-November to late December (late austral spring to early austral summer), and observations declined as the summer progressed thereafter ($\chi^2_{(7.14)} = 332.07$, $P < 0.001$; Fig. 5c). The explained deviance of the model was 54.3%. A Pearson correlation coefficient was computed to assess the linear relationship between temperature and precipitation; However, we detected a significant negative relationship ($r(14905) = -0.02$ $p = 0.01$), and the correlation coefficient was minimal, suggesting a very weak relationship between the two variables.

When examining beetles, 95% of counts occurred when temperatures ranged from 5.9–12.6°C ($\chi^2_{(4.69)} = 77.65$, $P < 0.001$; Fig. 6a). Observations of beetles decreased slightly with increasing levels of precipitation ($\chi^2_{(2.10)} = 37.31$, $P < 0.001$; Fig. 7 a), and detections were highest in November (austral spring; $\chi^2_{(14.18)} = 390.92$, $P < 0.001$; Fig. 8a). The explained deviance of the model examining beetles only was 42.7%. We detected a significant relationship between wētā temperature and time of year, but not precipitation. Ninety-five per cent of wētā detections occurred at temperatures between 6.0–12.6°C ($\chi^2_{(3.17)} = 59.94$, $P < 0.001$; Fig. 6b) and were highest in mid-December (early austral summer; $\chi^2_{(8.97)} = 155.04$, $P < 0.001$; Fig. 8b). Wētā observations decreased slightly with rising precipitation levels, but the relationship was not significant ($\chi^2_{(1.95)} = 1.94$, $P = 0.57$; Fig. 7b). The explained deviance of the model containing only wētā observations was 46.1%. For

Table 1. Total number of invertebrates from the three most common invertebrate groups observed by trail cameras in the alpine zone of Fiordland. There were nine cameras: three in the Homer Valley and six in the Gertrude Valley.

Habitat type	Beetles	Wētā	Spiders	Total
Tussock grasslands	501	394	144	1039
Shrub fields	814	204	64	1082
Rock fields	137	61	26	224

Figure 4. Example photograph of three wētā (likely ground wētā taken in tussock habitat in Gertrude Valley.

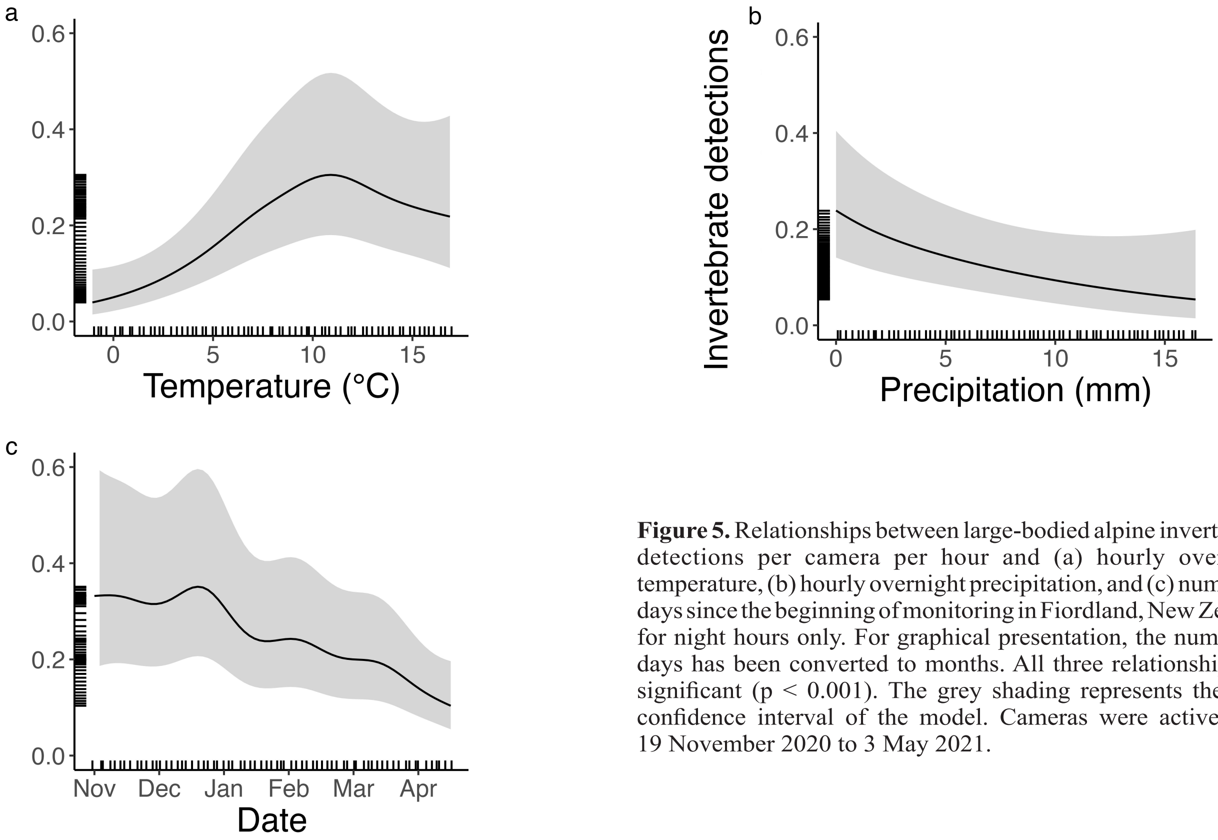

Figure 5. Relationships between large-bodied alpine invertebrate detections per camera per hour and (a) hourly overnight temperature, (b) hourly overnight precipitation, and (c) number of days since the beginning of monitoring in Fiordland, New Zealand for night hours only. For graphical presentation, the number of days has been converted to months. All three relationships are significant ($p < 0.001$). The grey shading represents the 95% confidence interval of the model. Cameras were active from 19 November 2020 to 3 May 2021.

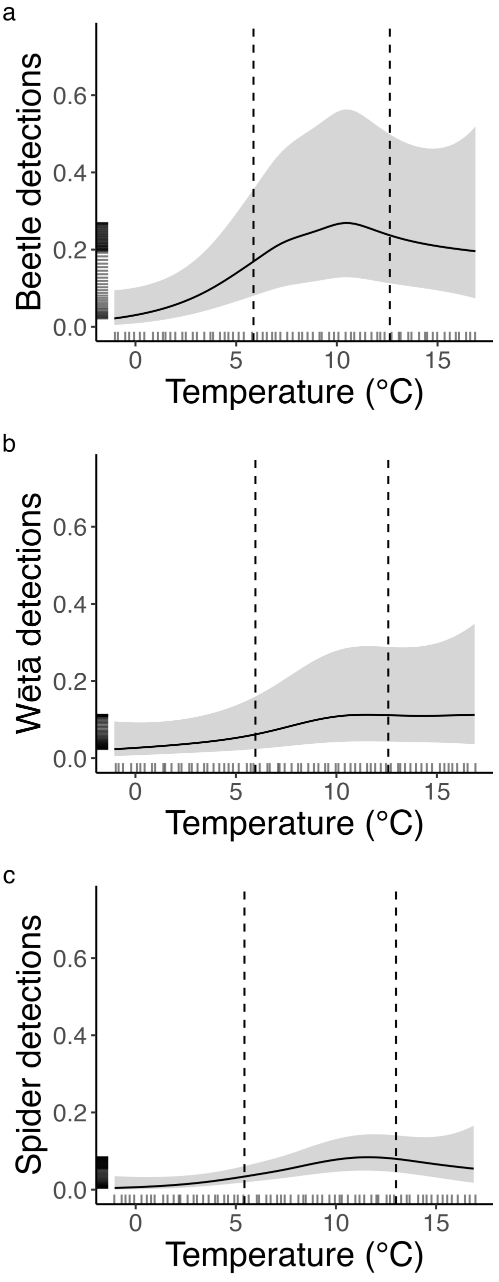

Figure 6. Relationships between large-bodied alpine invertebrate observations per camera per hour and hourly overnight temperature in Fiordland New Zealand for (a) beetles, (b) wētā and (c) spiders ($p < 0.001$ for all relationships). The grey shading represents the 95% confidence interval of the model. Vertical lines represent the lower and upper threshold containing 95% of all observations for each invertebrate group. Cameras were active from 19 November 2020 to 3 May 2021.

spiders, we found a significant relationship between spider detections and temperature, precipitation, and time of year. Ninety-five per cent of spider detections occurred between 5.4 and 13.0°C ($\chi^2_{(2.97)} = 23.94$, $P < 0.001$; Fig. 6c). Spiders had a negative relationship with precipitation ($\chi^2_{(1.00)} = 12.87$, $P < 0.001$, Fig. 7c) and were most detectable in February (the middle of the austral summer; $\chi^2_{(7.95)} = 90.76$, $P < 0.001$, Fig. 8c). The explained deviance of the model examining spider observations was 41.1%.

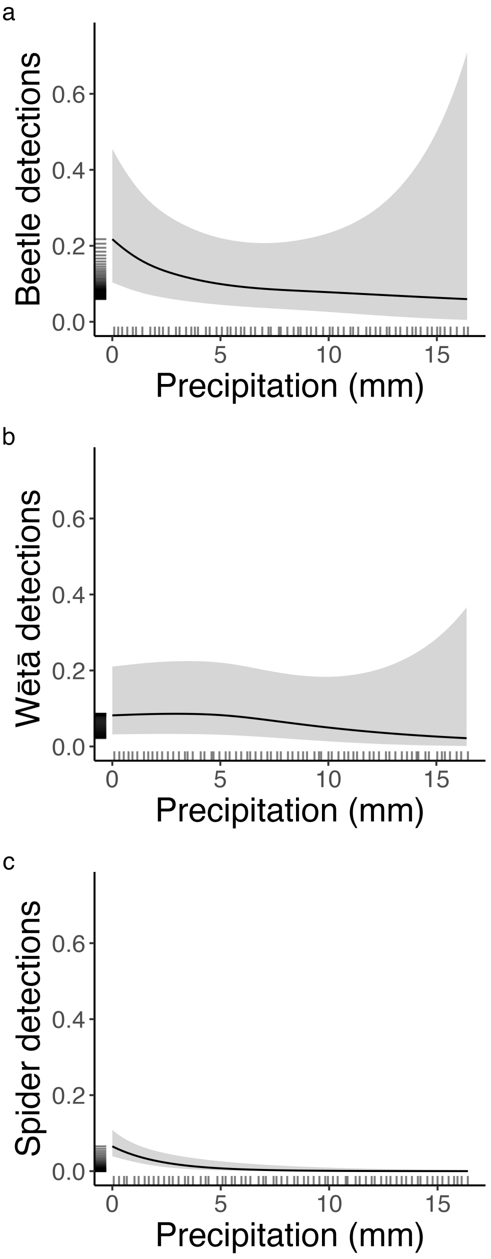

Figure 7. Relationships between large-bodied alpine invertebrate observations per camera per hour and hourly overnight precipitation in Fiordland New Zealand. Figures represent the relationship between precipitation and observations of (a) beetles ($p < 0.001$), (b) wētā ($p = 0.07$), and (c) spiders ($p < 0.001$). The grey shading represents the 95% confidence interval of the model. Cameras were active from 19 November 2020 to 3 May 2021.

Discussion

Monitoring is vital to understand the responses of wildlife to environmental change and to discern if management programmes have the desired outcomes. This study aimed to better understand the relationships between large ground-dwelling alpine invertebrates and environmental variables to help inform and optimise survey designs. Our trail camera monitoring trial allowed us to document relationships between

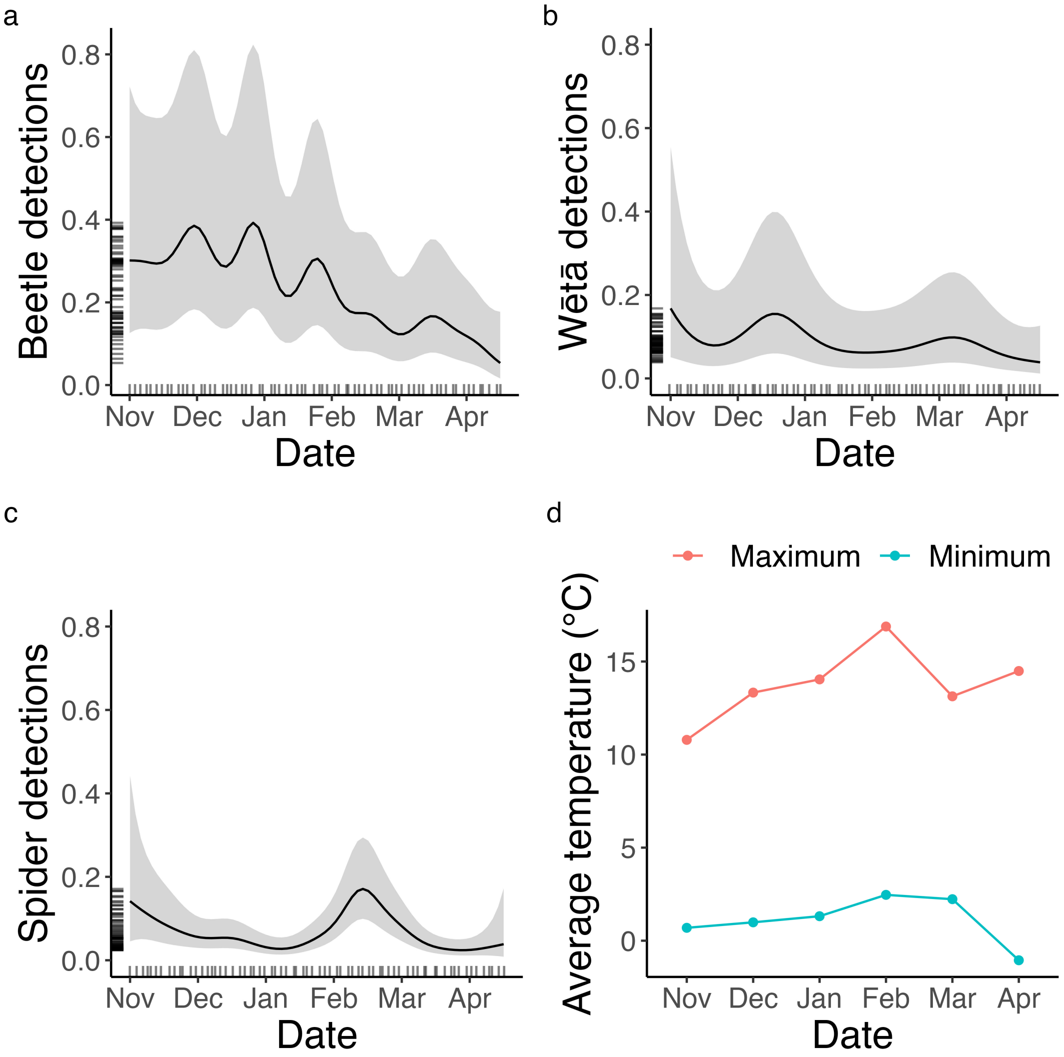

Figure 8. Relationships between large-bodied alpine invertebrate observations per camera per hour and days since the start of filming in Fiordland, New Zealand. For graphical representation, the number of days from the beginning of filming has been converted into months. Figures represent the relationship between time since the start of the season and observations of (a) beetles, (b) wētā, and (c) spiders ($p < 0.001$ for all relationships). The grey shading represents the 95% confidence interval of the model. Figure (d) displays the mean monthly maximum and minimum temperature for each month.

environmental variables and the activity of three abundant invertebrate groups (beetles, wētā, and spiders). These three invertebrate groups showed similar overall responses to daily temperature and precipitation. Invertebrate detections for all three groups increased as nighttime temperatures rose. At around 11°C, observations plateaued for wētā and decreased slightly for beetles and spiders, with 95% of all observations for all three groups falling roughly between 5.4 and 13.0°C. Activity for all three groups decreased with rising precipitation levels, but the effect was stronger for spiders than beetles and wētā. We also observed differences in seasonal activity patterns where beetles were more active in spring and early summer, wētā were more active in early summer, and spiders were more active in mid to late summer.

Alpine invertebrate activity and environmental conditions

On any given night, the most influential driver of invertebrate activity appears to be the weather, where higher levels of surface activity are linked to warmer temperatures. Logically, warm overnight temperatures promote activity as invertebrates rely on ambient heat from their environment to promote activities like foraging and reproduction (Terblanche et al. 2011; Everatt et al. 2013). Many invertebrates, like ground beetles, spiders, and harvestmen, limit their surface activity in cold temperatures in favour of sub-surface retreats that provide shelter from the extremes (Nitzu et al. 2014; Ledesma et al. 2020). However, some specialist invertebrates are active on the surface even in cool temperatures. In New Zealand, many alpine invertebrates are considered to be cold-adapted with adaptations like melanism, freeze avoidance proteins, and active thermoregulation that allow for activity in the cold alpine environment (Mason 1971; Forster 1975; Chinn & Chinn 2020). Although some invertebrate surveys can take place over multiple weeks or months, many surveys that target individual species or sample the community as a whole take place over shorter periods (1–14 days) and can be planned around ideal weather windows (Sinclair et al. 2001; Watts & Thornburrow 2009; Hoare et al. 2016). Most of our detections occurred when air temperatures were between 5.4 and 13.0°C for spiders and c. 6.0–12.6°C for beetles and wētā. We recommend 5.4°C as the lowest temperature during which surveys should occur. Below this, the chances of observing invertebrates are low, and surveys in these conditions would be inefficient and may underrepresent the large-bodied invertebrate community.

The threat of desiccation also is prominent in arid environments, so water availability is crucial for alpine invertebrate activity and survival (Sinclair 2000; King & Sinclair 2015). Consequently, higher annual precipitation is often associated with higher levels of abundance and activity for alpine and low-land invertebrates (Williams et al. 2014; Zajicek et al. 2021). Many alpine orthopterans are more abundant and active in areas with higher annual precipitation levels (Fielding & Brusven 1990; Illich & Zuna-Kratky 2022). At lower elevation meadows and farmland, spider abundance and diversity has been shown to increase with rising levels of annual precipitation (Dondale et al. 1972; Frampton et al. 2000). Additionally, higher levels of precipitation and soil moisture benefit the prey species of many spiders (e.g. detritivores), which increases spider activity and abundance (Chen & Wise 1999).

Though water availability is important for invertebrate survival, our results suggest that high amounts of rain on any given night can reduce activity for beetles and spiders. Rainfall events can disrupt invertebrates by impeding flight or reducing foraging efficiency (Peng et al. 1992; Drake 1994; Barnett & Facey 2016). In heavy rainfall events, arthropods may seek shelter or use submersion tolerance strategies as water pools in the environment, which reduces surface activity (Bonte et al. 2008). Rain events may particularly disrupt spiders. Spiders in the family Ctenidae sense chemical cues from their prey and other predators, which may be disrupted by rainfall resulting in decreased activity (Queiroz & Gasnier 2017). Wolf spiders (Lycosidae), a common family in our field sites (Bertoia et al. unpubl. data), also use chemical cues to catch prey and avoid predators, which could explain the negative relationship that we observed between spider occurrences and precipitation (Eiben & Persons 2007). These trends are especially interesting as Fiordland is a region often associated with extremely high levels of rainfall (Hendrikx 2005).

Season often influences invertebrate activity, which varies by invertebrate group. Overseas and in New Zealand, beetles are often active in spring, where warmer temperatures, high soil moisture, and the lack of dense vegetation can promote activity for herbivorous species (Anderson et al. 2004; Harry et al. 2011; Hiramatsu & Usio 2018). An increase in herbivorous beetle activity could drive the activity of carnivorous invertebrates, which could explain the two peaked distributions of beetle detections in November and December. Beetles are holometabolous insects, and trail cameras would only sample adults. The peaks and troughs of beetle detections observed during spring and early summer are likely driven by reproductive activity, the loss of adults, and the resurgence of new adults across multiple species (Anderson et al. 2004; Hutchison 2007; Harry et al. 2011). Conversely, wētā are hemimetabolous, relatively long-lived insects, allowing multiple instars to be observed across a summer season. The peak in wētā detections in late December and early January corresponds with reproductive timing for other ground wētā in New Zealand (Van Wyngaarden 1995). The relatively stable relationship afterwards could be caused by sampling different generations of wētā. *Hemiandrus* wētā from the fifth to eighth instar can all be active in the same habitat across the summer field season (November–April) and fall within our 1 cm size classification (Van Wyngaarden 1995). Lastly, spiders were detected in late summer when temperatures were the warmest. Spiders are key invertebrate predators. As a result, spider detections may be driven by the activity of prey species that is promoted by warm summer temperatures (Moeed & Meads 1985; Muff et al. 2007; McCulloch & Waters 2018).

Trail cameras as invertebrate monitoring tools

Trail cameras proved to be a valuable tool for gathering information on activity patterns of large-bodied alpine invertebrates that will be useful for designing and improving future monitoring methods. The main drawbacks of trail cameras for invertebrate surveys are the camera trigger mechanism and the quality of the photos. Reconyx cameras have a passive infrared sensor that uses a combination of motion and temperature to trigger the camera (Welbourne 2014). Invertebrates are often too small and similar in temperature to their environment to reliably trigger the sensor; as a result, a timelapse mode must be used to survey invertebrates (Hobbs & Brehme 2017). Timelapse cameras, like the ones used in this study, generate hundreds of thousands of photos and the vast majority contain no invertebrates. Sorting and generating data from many photos is time-consuming and there is a potential for human error (Pagnucco et al. 2011; Soininen et al. 2015; Potter et al. 2021). Additionally, the identification of invertebrates from trail camera images is challenging. Identification at the family level is possible if the invertebrate is clear in the frame. However, in many cases, the invertebrate was obscured by vegetation or rocks, leaving only a small portion of the individual visible on camera. Due to this limitation we identified individuals to the order level, as identifying it further was too subjective. To help identify invertebrates from photographs, researchers can supplement trail cameras with another collection method, like pitfall traps, to create a baseline understanding of what invertebrates are in the environment (Zaller et al. 2015). The beetle community at our site was the most diverse. For groups like beetles that span multiple feeding guilds, it may be challenging to interpret the ecological relevance of your data when there is a possibility that herbivores or key predators are not caught on camera. On the other hand, if you are studying a narrow community or large or easily identifiable invertebrates, trail cameras may be a useful tool (Ruczyński et al. 2020; Potter et al. 2021; Naqvi et al. 2022).

Invertebrate activity and conservation management

In New Zealand, introduced mammalian predators are a significant threat to native fauna, including large-bodied invertebrates (O'Donnell et al. 2017; McAulay et al. 2020). Unfortunately, our understanding of how predators specifically influence alpine invertebrates lags behind other alpine species, partly because of our lack of practical monitoring tools. Rock wrens, *Xenicus gilviventris* (a small native alpine passerine), provide an example of how targeted research on the influence of predators can inform management leading to better management outcomes. Tools that enable us to effectively monitor both rock wren and mammalian predators have shown that stoat predation on nests is a major cause of decline (Little et al. 2017; Weston et al. 2018), and controlling stoats with tools like aerial 1080 has positive outcomes for rock wrens (Weston et al. 2018; Rawlence 2019). More recently, low-cost monitoring tools have been developed to look at the effectiveness of this landscape predator control. This will allow managers to understand how rock wrens respond to management and make changes as necessary (Monks et al. 2021). In contrast, we are just at the initial stages of understanding which introduced predators might be important to manage to protect alpine invertebrates (O'Donnell et al. 2017; Buckley et al. 2022; Watts et al. 2022). Like rock wrens, there is a need for effective monitoring methods to see if current alpine predator control efforts benefit smaller organisms like invertebrates. Furthermore, future warming scenarios project a significant reduction in alpine habitat (Dirnböck et al. 2011; Parida et al. 2015; Barredo et al. 2020; Chinn & Chinn 2020; Koot et al. 2022). As temperatures increase, the elevational range of introduced pests, mammals, invertebrates, and plants is likely to rise, which will increase pressure on alpine invertebrates in the years to come (Christie et al. 2017; O'Donnell et al. 2017; Foster et al. 2021b; Macinnis-Ng et al. 2021). With additional threats looming, improving our understanding of how invertebrates respond to predation and management efforts will become more critical.

Fine-scale data generated by trail cameras has greatly improved our understanding of large-bodied invertebrate activity in the alpine zone. From the observations made in this study, we suggest that surveys aiming to quantify the large-bodied invertebrate community, whether they be targeted searchers or short-medium term sampling sessions that can target ideal weather conditions, should take place when the air temperature is no lower than 5.4°C with little to no precipitation. To sample the invertebrate community, sampling should occur at two periods, one in spring and the latter in mid-summer. If a study has more specific goals, or is interested in a particular group of invertebrates, researchers can target the period when their species of interest is expected to be the most active (i.e. monitor in late spring to early for beetles or summer periods for spiders). Furthermore, this study highlights the importance of understanding the thermal ecology and lifecycle of the target species when designing a monitoring programme and interpreting data. Although we have a good understanding of these factors for some alpine invertebrates, e.g. grasshoppers (Mason 1971; White 1974; Koot et al. 2020) and mountain stone wētā (Jamieson et al. 2000; Rock et al. 2002), there is still room to increase our understanding of the alpine invertebrate community. This study provides a starting point for improving our ability to sample alpine invertebrates. In time, more successful surveys will provide additional high-quality data to enhance our understanding of large-bodied alpine invertebrates.

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Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. Example photographs showing partially obscured beetles making it impossible to identify them to the family level with confidence.

The New Zealand Journal of Ecology provides supporting information supplied by the authors where this may assist readers. Such materials are peer-reviewed and copy-edited but any issues relating to this information (other than missing files) should be addressed to the authors.