

Consistent temporal variation in the diet of an endangered alpine lizard across two south-eastern Australian sky-islands

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Abstract A species' diet and feeding strategy directly affect fitness and environmental interactions. Understanding spatial and temporal variation in diets can identify key resources, inform trophic relationships, and assist in managing threatened species. The nationally endangered Guthega skink, *Liopholis guthega*, is restricted to two isolated Australian alpine plateaux, the Bogong High Plains (BHP) in Victoria and Kosciuszko National Park (KNP) in New South Wales. We compared this species' foraging ecology over the summer period between these 'sky-islands' separated by ~100 km of lowland valleys. Scat composition did not differ between the two lizard populations, despite differences in the invertebrate assemblages present. However, *L. guthega* diet varied temporally over summer at both locations. Invertebrates, predominantly Hymenoptera and Coleoptera, were the dominant food group in early summer (78% volume (V), 100% frequency occurrence (F)) and mid-summer (80% V, 100% F). A significant dietary shift occurred in late summer, when lizards consumed predominantly plant material (63% V, 95.5% F), consisting primarily of seasonally abundant berries from the snow beard heath, *Acrothamnus montanus*. In contrast to similar-sized Egerniinae species, it appears *L. guthega* is capable of opportunistically shifting its diet towards plant material in response to temporal variation in resource availability. Furthermore, the prevalence of intact seeds in scats indicates *L. guthega* may play a significant role in seed dispersal. Understanding these trophic interactions will assist conservation management of *L. guthega*, allowing conditions for an already established captive colony to mimic the temporally variable diets present *in situ*, as well as informing revegetation initiatives aimed at maintaining and expanding wild populations.

Key words: alpine ecology, endangered species, foraging ecology, mutualism, trophic interaction.

INTRODUCTION

Feeding and food selection are key ecological processes affecting an animal's fitness and environmental interactions (Duffield & Bull 1998). Extensive diversification in foraging modes has occurred in squamate reptiles, reflecting morphological (Stayton 2006), behavioural (Meyers & Herrel 2005) and biological adaptations (Vitt *et al.* 2003; Mackie *et al.* 2004) that contribute to niche partitioning and ecosystem function (Huey & Pianka 1981; Carretero *et al.* 2006; Luiselli 2008). This has resulted in diverse diets that range from insectivory (Meyers *et al.* 2006) to carnivory (Jessop *et al.* 2010),

omnivory (Herrel *et al.* 2004) and herbivory (Espinoza *et al.* 2004), each of which can vary ontogenetically (Duffield & Bull 1998), between sexes (Perry 1996), sites (Barden & Shine 1994), and seasons (Fenner *et al.* 2007).

Diet may vary spatially or temporally with changes in food abundance (van Wyk 2000; Oonincx *et al.* 2015). Importantly, while a generalist diet may be adopted by species with broad geographic distributions (Rocha & Anjos 2007) that are subject to greater climatic and resource variability (van Wyk 2000), species with restricted distributions and habitats may have reduced foraging opportunities, resulting in dietary specialisation (van Wyk 2000; Meyers & Herrel 2005). Information on diet and feeding strategies is therefore essential when trying to understand and manage threatened species in

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vulnerable ecosystems (Duffield & Bull 1998; Hart *et al.* 2003).

Dietary analyses have contributed greatly to our understanding of the Australasian skink subfamily Egerniinae (Duffield & Bull 1998; Chapple 2003; Arena & Wooller 2004; Clemann *et al.* 2004; Pavey *et al.* 2010), which includes some of Australia's most threatened lizard species (Gardner *et al.* 2008). Egerniinae exhibits striking variation in life history, body size (ranging from 70 to 350 mm snout-vent length (SVL)) and habitat (Chapple 2003; Fenner *et al.* 2012). Diversity within this group extends to feeding strategies, which encompass diurnal, crepuscular and nocturnal feeders (Gardner *et al.* 2008) whose diets vary from primarily insectivorous (Hickman 1960) and omnivorous (Clemann *et al.* 2004), to highly herbivorous (Arena & Wooller 2004).

Within Egerniinae, dietary patterns and body size are closely linked, with the degree of herbivory increasing with lizard size (Brown 1991; Chapple 2003; Pavey *et al.* 2010), a common feature of lizards globally (Fialho *et al.* 2000; Cooper & Vitt 2002). However, Egerniinae are considered generalist predators (Greer 1989), and invertebrates are opportunistically eaten (Chapple 2003), particularly by smaller species (75–95 mm SVL) (Duffield & Bull 1998; Chapple 2003; Clemann *et al.* 2004; Fenner *et al.* 2007; Pavey *et al.* 2010). For example, the similarly sized *Liopholis whitii* and *Liopholis slateri* are basically insectivorous, with Formicidae contributing the main element of their diet (>95% frequency of occurrence in scats), while vegetation accounts for as little as 8.4% of volume ingested (Brown 1991). The medium sized (100–130 mm SVL) *Lissolepis coventryi*, *Egernia saxatilis* and *Liopholis striolata* are more omnivorous, ingesting 26.7%, 28.6% and 39.7% of vegetative components (Chapple 2003), respectively, while the larger (190–250 mm SVL) *Egernia kingii* and *Egernia cunninghami* are far more herbivorous, with around 90% of their diet coming from plant sources (Chapple 2003; Arena & Wooller 2004). The diet of some species in this group vary seasonally with changes in resource availability (Duffield & Bull 1998; Fenner *et al.* 2007), highlighting the importance of dietary studies across temporal scales.

The Guthega skink (*Liopholis guthega*, Egerniinae) is a medium-sized (~100 mm SVL), viviparous, cool-climate specialist lizard endemic to the Australian Alps (Atkins *et al.* 2015). It is found above 1600 m in two geographically isolated locations: Kosciuszko National Park (KNP) in New South Wales, and the Bogong High Plains (BHP) in Victoria (Donnellan *et al.* 2002). Within these locations, *L. guthega* exists in small, discreet colonies, forming burrows in family groups (Atkins *et al.* 2015). This restricted distribution means that *L. guthega* is threatened by activities

related to alpine tourism and the recession of alpine habitat associated with climate change (Hughes 2003; Monasterio *et al.* 2009). It is listed as Endangered under Australian Federal legislation (the *Environmental Protection and Biodiversity Conservation Act* 1999), and field-based conservation efforts are augmented by a captive program. However, a lack of information regarding key elements of *L. guthega* ecology, including its diet, hamper effective conservation management of the species in the wild and in captivity (Atkins *et al.* 2015).

This study aimed to document the diet of *L. guthega* over the summer active season to determine trophic interactions within the alpine ecosystem that will inform habitat restoration for the conservation of wild populations and assist captive management of this species. With approximately 100 km of lowland valleys separating the two populations, this also presented an opportunity to investigate geographical variation in invertebrate composition and how that influences *L. guthega* feeding strategies.

METHODS

Study sites

Fieldwork was undertaken between December 2015 and February 2016 at the BHP (36.87°S 147.28°E) in the Alpine National Park in Victoria's north-east, and KNP (36 04' 20°S 148 20' 55°E) in the south-east of New South Wales (Fig. 1). The study area ranges between approximately 1650–1850 m above sea level. Three *Liopholis guthega* colonies at each locality were randomly selected from 33 colonies identified during extensive prior surveys and each contained >30 resident lizards (Z. Atkins unpub. data, 2017). Simultaneous invertebrate surveys and *L. guthega* scat collections were conducted monthly throughout summer at each site.

Scat analysis

Liopholis guthega were captured via noosing and their scats were collected at each of the three sites at both locations for three consecutive days per month. Scats were collected from both sexes and all size classes (male $n = 46$, female $n = 63$, juvenile $n = 11$) when the lizards defecated during handling and were stored at room temperature in 70% ethanol in 2 mL microcentrifuge tubes until processing. Unlike some Egerniinae species, no differences were observed between sexes or between adults and juveniles (e.g. Duffield & Bull 1998), so were subsequently grouped. SVL and mass were recorded for each lizard and they were tagged with a Trovan nano passive integrated transponder (PIT) tag (Microchips Australia Pty Ltd, Keysborough, Australia) for recapture identification. This ensured the same skins were not sampled more than once during the 3-day sampling period. Fifty-seven scats were collected in Victoria and 69 in New South Wales. Each scat was later

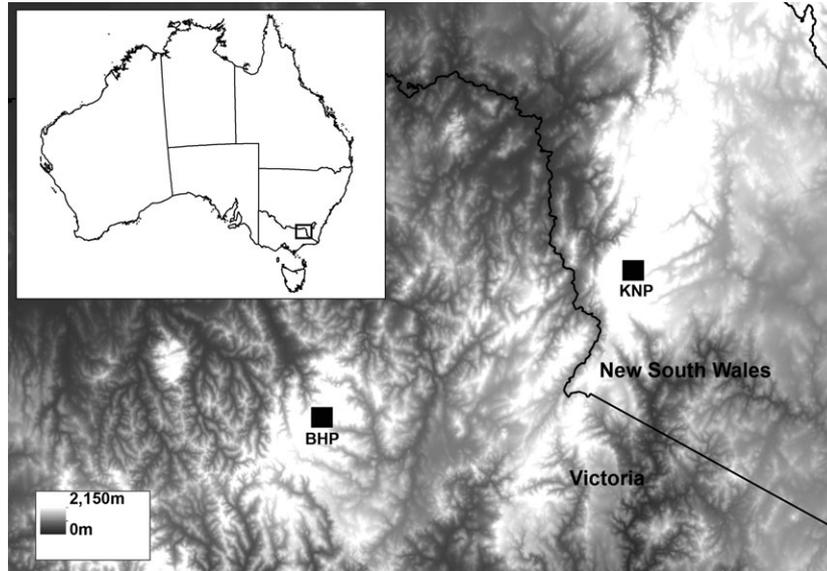


Fig. 1. The allopatic distribution of *Liopholis guthega* to the two sky-islands; the Bogong High Plains (BHP) in Victoria and Kosciuszko National Park (KNP) in New South Wales.

placed in a petri dish with 70% ethanol, and teased apart with fine forceps. Arthropod cuticle could easily be distinguished from plant material. With the aid of a binocular dissecting microscope a visual estimate was made of the relative proportions (% volume) of plant and animal material. To help identify arthropod material, comparison was made between the chewed fragments of cuticle and whole invertebrate specimens obtained from pitfall trapping in the same areas. Invertebrate remains in the scats were identified to Order, except Hymenoptera, which were identified to family and genus where possible. Leaves, flowers, seeds and fruits of angiosperm plants were identified using plant cuttings obtained from the sites, a microhistological vegetation reference library (Green *et al.* 2013) and in alpine flora reference books (Costin *et al.* 2000). The relatively short lists of plant species at each study site made matches to species level possible. The proportion of insect larvae and other soft bodied forms such as earthworms and flatworms may have been underestimated, as their cuticle is generally more easily digested than that of adult arthropods, and therefore more readily overlooked. The results are expressed in (i) frequency of occurrence (%) of each dietary component (F); and (ii) volume (%) (V) of dietary items within scats.

Invertebrate abundance

During the three consecutive days of scat collection per month, relative invertebrate abundance was measured at each of the three sites per location. Two 40 m transects, consisting of 10 pitfall traps (250 mL plastic vials) spaced 4 m apart, were placed parallel at a distance of 20 m. The placement of pitfall lines was determined randomly. Traps were filled with 70 mm of propylene glycol and buried in the ground with the rim at surface level. Trapped invertebrates were identified using an entomology field guide

(Naumann *et al.* 1991) to order, or genus where possible, and counted.

Statistical analysis

At each site, scat composition and relative invertebrate abundance (% based on counts) were compared separately per month over the summer period to quantify changes in invertebrate assemblages and *L. guthega* feeding patterns at a local scale. Relative abundances were used because pitfall traps are biased toward catching active, terrestrial invertebrates and underrepresent species in the soil and herbaceous layers (Kaufmann 2001).

Community assemblage of invertebrates in pitfall traps

To determine whether there was a difference in the community assemblage of invertebrates in pitfall traps through time, we first log transformed the invertebrate taxa counts and calculated Bray-Curtis similarity between each trap. We fitted a three way PERMANOVA (Anderson 2001) with 10 000 permutations to the similarity matrix, fitting month (Dec, Jan, Feb) and State (NSW, VIC) as fixed factors, with sites a random effect nested within each State, and individual traps as random replicates within sites. To elucidate which levels of significant factors had different invertebrate communities, we performed follow up pairwise PERMANOVAs on significant fixed factor terms in the overall model.

To establish which invertebrate taxa were associated with the different localities and dates, we first used the Bray-Curtis similarity matrix to create a two-dimensional non-metric MDS of the traps in invertebrate community ordination space. Principal axis correlations (Faith and

Norris 1989) were then used to determine invertebrate species that were correlated with that space. Whilst all traps are used in the ordination ($n = 360$), for brevity and to aid interpretation we only present the ordination centroids for each State and month ($n = 18$) and invertebrate groups that have a significant rank correlation ($\alpha = 0.05$; $n = 18$ independent centroid data points) with the space.

Community assemblage of invertebrates in scats

To determine the community assemblage in scats through time, the same statistical protocols were performed as above, except individual lizards within each site were the replicates rather than the traps.

Comparison of invertebrates in diet and traps

We calculated the average abundances of taxa in traps, or dietary items in scats, for each site in each month. We log-transformed the data and calculated Bray-Curtis Similarity matrices for each data set. A Mantel test was performed to determine whether there was concordance in site similarities between the scat and trap data sets. The analysis was repeated using presence/absence data and Jaccard similarity in both data sets, which has a straightforward interpretation (e.g. Green *et al.* 2014), as it simply represents the proportion of shared taxa between any pair of samples. All multivariate analyses were performed using E-primer V6 (Clarke & Gorley 2005).

Table 1. Summary of the dietary items (Frequency of occurrence (F) (%) and volume (V) (%)) in *Liopholis guthega* scats collected from the Bogong High Plains, Victoria and Kosciuszko National Park, New South Wales over a 3 month period (December–February) in 2015/16.

| Higher classification | Class | Order | Subfamily | Month | Genus | Victoria | | | | | |
|-----------------------|-----------|-------------|----------------|-------------|----------|------------------|-------|------------------|-------|------------------|-------|
| | | | | | | Dec ($n = 21$) | | Jan ($n = 18$) | | Feb ($n = 18$) | |
| | | | | | | F (%) | V (%) | F (%) | V (%) | F (%) | V (%) |
| Arthropoda | Insecta | Coleoptera | | | | 0.66 | 19 | 0.71 | 36.4 | 0.5 | 5.72 |
| | | Orthoptera | | | | 0.14 | 10 | 0.16 | 4.5 | 0.13 | 0.5 |
| | | Lepidoptera | | | | 0.05 | 0.47 | 0.09 | 2.27 | 0 | 0 |
| | | Hymenoptera | | | | 0.95 | 35.9 | 1 | 34 | 1 | 19.6 |
| | | Iridomyrmex | Dolichoderinae | | | 0.95 | 34.8 | 1 | 30 | 1 | 16.7 |
| | | | Amblyoponinae | Amblyopone | | 0 | 0 | 0.11 | 0.55 | 0.11 | 0.61 |
| | | | Myrmicinae | Pheidole | | 0.14 | 0.14 | 0.16 | 0.38 | 0.05 | 0.05 |
| | | | Monomorium | | | 0 | 0 | 0 | 0 | 0 | 0 |
| | | | | Myrmeciinae | Myrmecia | 0 | 0 | 0.22 | 2.5 | 0.11 | 1.66 |
| | | | | Ponerinae | | 0 | 0.04 | 0.04 | 0 | 0 | 0 |
| | | | | Non ants | | 0.04 | 0.95 | 0.05 | 0.55 | 0.11 | 0.61 |
| | | | | Hemiptera | | 0 | 0.47 | 6.71 | 0.38 | 2.16 | 0.44 |
| | | | | Diptera | | 0.04 | 0.24 | 0.14 | 0.16 | 0 | 0 |
| | | | | Blattodea | | 0.19 | 2.43 | 0.05 | 0.55 | 0.05 | 0.55 |
| | | | Diplopoda | | | 0.09 | 0.47 | 0.09 | 0.11 | 0.05 | 0.05 |
| Arachnida | Araneae | | | 0.09 | 1.19 | 0.16 | 1.44 | 0 | 0 | | |
| | Acarina | | | 0 | 0 | 0 | 0.05 | 0 | 0 | | |
| | Opiliones | | | 0 | 0 | 0 | 0 | 0.05 | 0.44 | | |
| Planta | | | | | 0.57 | 20.3 | 0.83 | 15.6 | 0.94 | 63.3 | |
| Lizard scale | | | | | 0.14 | 1.9 | 0 | 0 | 0.05 | 5.44 | |
| Unid. insect | | | | | 0.09 | 1.8 | 0.05 | 2.77 | 0 | 0 | |

Temporal change in diet over summer

We calculated the proportion of vegetation (leaf + fruit + flower + seed) in each scat, and fitted a mixed model using the Mixed procedure in SAS (SAS Institute Inc., 2013) to compare proportions between localities and months. We included sites as a random and repeated effect nested within each state. Residual plots were inspected to confirm that assumptions of normality and homogeneity of variance were met by the analysis. Significant effects were followed up using comparisons of least squares means and Tukey's HSD adjustment for type 1 error.

We performed a linear regression to examine the relationship between percentage volume of plant material and SVL within Egerniinae. In addition, we plotted mean *L. guthega* plant intake early/mid-summer and late summer to highlight temporal change.

RESULTS

Scat analysis

The diet of *Liopholis guthega* included both invertebrate and plant material. Invertebrates consisted of 11 orders of insects (9) and arachnids (2), while plant material consisted of leaves, flowers, seeds and fruit (Table 1). Invertebrates were the dominant food group in *L. guthega* scats at both localities in early

summer (Dec) (78% V) and mid-summer (Jan) (80% V, Fig. 2; Table 1). Hymenoptera (particularly *Iridomyrmex*) were present in almost all scats (>95% F in Victoria and >88% in New South Wales, Table 1) and Coleoptera were present in greater than 66% of scats during this period. The prevalence of hymenopterans in scats translated to greater than 34% of the scat volume in Victoria and 17% in New South Wales. The volume of coleopterans in scats in December exceeded 18% and 31% in January at both localities (Table 1). In contrast, plant material in February dominated the diet in both locations, and occurred in almost all scats (>94% F), contributing 63% of the total scat volume (Fig. 2; Table 1).

Community assemblage of invertebrates in scats

There was a significant difference in the composition of scats collected in each month (Pseudo $F = 10.9$, $df = 2$, 42, $P < 0.0001$), but not between localities (Pseudo $F = 1.9$, $df = 1$, 4.6, $P = 0.07$). The non-significant location effect may have been obscured by the significant variation in scat composition between sites within each locality (Pseudo $F = 2.1$, $df = 4$, 89, $P < 0.01$). In Victoria, the scats from one of the sites had a significantly different composition to either of the other two sites (both $P < 0.005$). In New South Wales, there was no statistically significant difference between the sites

(both $P > 0.25$). There was a tendency for sites in both locations to have scats with higher abundances of fruits in February, and more Coleoptera, Hymenoptera and flowers in December (Fig. 3).

Similarity matrices

There was no significant relationship between the trap and scat similarity matrices calculated using Bray Curtis ($R = 0.008$, $P = 0.43$, 9999 permutations) or Jaccard similarity ($R = 0.24$, $P = 0.08$, 9999 permutations).

Community assemblage of invertebrates in pitfall traps

Invertebrates from 20 orders were captured in traps (Table 2). Eleven of these orders were also identified in lizard scats (Table 1). Using Bray-Curtis similarities, there were significant differences in invertebrate communities collected in traps between locations and between dates; however, the differences were dependent on their interaction (Pseudo $F_{\text{state} \times \text{date}} = 7.8$, $df = 2$, 8, $P < 0.0001$). While there was no significant difference between New South Wales and Victorian invertebrate communities in any month (all pairwise PERMANOVA Pseudo F , $P > 0.10$), the similarity of ant

Table 1. Continued

| Higher classification | New South Wales | | | | | |
|-----------------------|------------------|-------|------------------|-------|------------------|-------|
| | Dec ($n = 17$) | | Jan ($n = 17$) | | Feb ($n = 35$) | |
| | F (%) | V (%) | F (%) | V (%) | F (%) | V (%) |
| Arthropoda | 0.7 | 18.6 | 1 | 31.4 | 0.4 | 2.94 |
| | 0.29 | 20.7 | 0.29 | 12.6 | 0.31 | 7.46 |
| | 0.12 | 3.17 | 0.29 | 3.17 | 0.08 | 2.6 |
| | 1 | 13.8 | 0.88 | 20.3 | 0.88 | 10.4 |
| | 1 | 6.64 | 0.82 | 10.9 | 0.71 | 4.62 |
| | 0 | 0 | 0.05 | 0.05 | 0.26 | 1.37 |
| | 0.35 | 0.58 | 0.35 | 0.82 | 0.2 | 1.43 |
| | 0 | 0 | 0 | 0 | 0.02 | 0.14 |
| | 0.41 | 6 | 0.05 | 0.29 | 0.23 | 2.6 |
| | 0 | 0 | 0 | 0 | 0 | 0 |
| | 0.24 | 0.53 | 0.59 | 8.28 | 0.17 | 0 |
| | 4.38 | 0.47 | 7.17 | 0.29 | 2.29 | 0.68 |
| | 0.12 | 0.88 | 0 | 0 | 0.28 | 2.28 |
| | 0.05 | 0.29 | 0 | 0 | 0 | 0 |
| | 0.12 | 0.12 | 0.17 | 0.65 | 0 | 0 |
| | 0.47 | 11.9 | 0.35 | 4.65 | 0 | 0 |
| | 0 | 0 | 0 | 0 | 0.12 | 0.23 |
| | 0 | 0 | 0 | 0 | 0.51 | 3.26 |
| Planta | 0.64 | 22.7 | 0.88 | 24.2 | 0.23 | 3.66 |
| Lizard scale | 0.05 | 1.47 | 0.05 | 1.65 | 0.97 | 62.8 |
| Unid. insect | 0 | 0 | 0 | 0 | 0.17 | 3.97 |

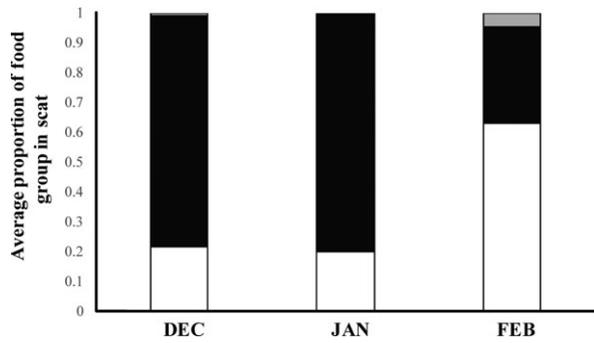


Fig. 2. Average proportion of invertebrate (black), plant (diagonal bars) and other (grey) food groups (% volume) in scats of *L. guthega* collected from the Bogong High Plains, Victoria, and Kosciuszko National Park, New South Wales, over the months of December (DEC), January (JAN) and February (FEB), 2016.

communities between the States varied significantly between 41.8% in December, 34.9% in January and 31.8% in February. Furthermore, all pairs of months had significantly different ant communities in both States (all pairwise pseudo $F < 0.05$). However, in Victoria the least similar ant communities in the traps were those between December and February, whereas this pair of months had the most similar ant communities in New South Wales.

The ordination of samples based on Bray-Curtis similarity of invertebrates showed a clear difference in communities between the States, with Victorian samples distinctly aligned with higher abundances of *Iridomyrmex* and *Pheidole* species (Fig. 4; Table 1). New South Wales samples tended to have more Acarina and Diptera (Fig. 4; Table 1). These spatial differences were not always consistent over the study period, and February tended to have a stronger association with *Iridomyrmex* spp. in Victoria, and Diptera in New South Wales (Fig. 4; Table 1). In both states, Acarina were far more abundant in January, and Hemiptera increased in abundance from December to January to February (Fig. 4; Table 1).

Temporal change in diet over summer

There was a significant difference in the proportion of vegetation in the diet of *L. guthega* between sampling months ($F = 41.70$, $df = 2, 4$, $P < 0.005$), but no differences between States ($F = 0.42$, $df = 1, 6$, $P = 0.54$) or their interaction ($F = 0.16$, $df = 2, 4$, $P = 0.86$). Vegetation made up an average of 63% of scats collected in February, significantly greater (Tukeys adjusted P -values both < 0.005) than December (21%) or January

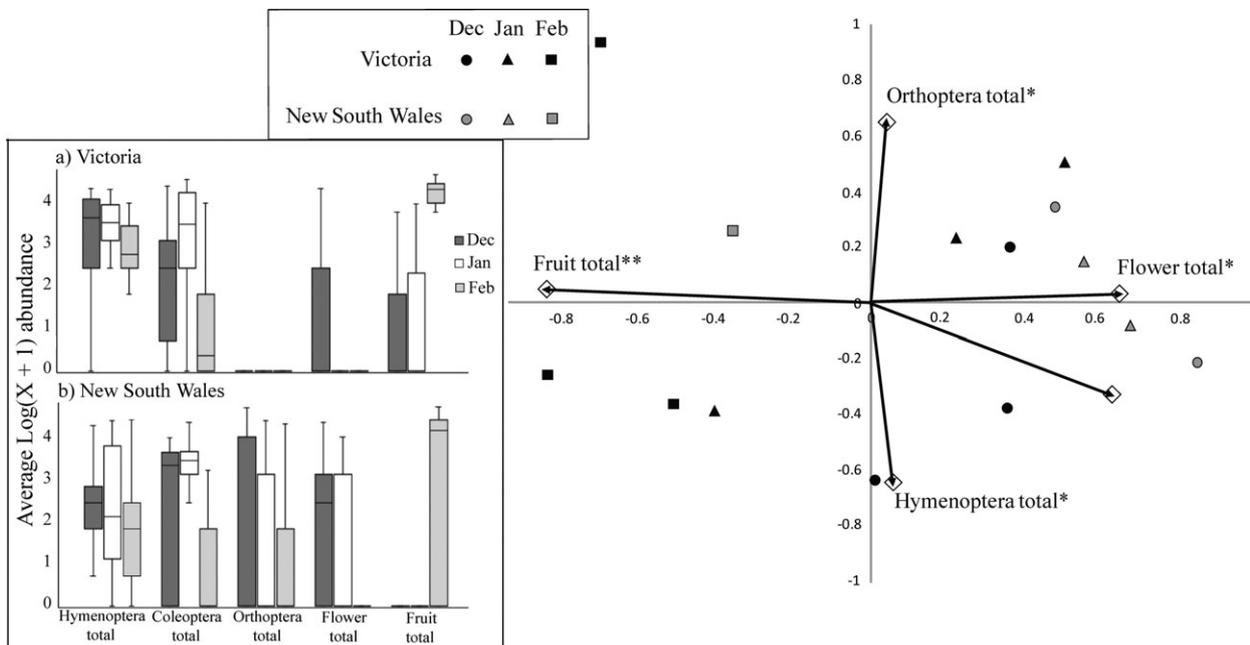


Fig. 3. Non-metric multidimensional scaling ordination based on Bray-Curtis similarity of dietary composition determined by scats from the Bogong High Plains, Victoria, and Kosciuszko National Park, New South Wales, over the months of December to February, 2016 (Stress = 0.22). Only the ordination axis centroid scores for replicate scats within each site are displayed. Invertebrate taxa that are significantly correlated (Spearman's R_s , $n = 14$) with the ordination space are included. * $P < 0.05$, ** $P < 0.01$

Table 2. Summary of the mean counts of invertebrate orders recorded in pitfall traps ($n = 60$) from three sites on the Bogong High Plains, Victoria and three sites at Kosciuszko National Park, New South Wales, over a 3 month period (December–February) in 2015/16

| Invertebrate order | Victoria | | | New South Wales | | |
|--------------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| | Dec ($n = 3$) | Jan ($n = 3$) | Feb ($n = 3$) | Dec ($n = 3$) | Jan ($n = 3$) | Feb ($n = 3$) |
| Hymenoptera | 1590.3 ± 469.2 | 2875.6 ± 711.8 | 1841 ± 264.3 | 264.6 ± 42.4 | 225.6 ± 73.4 | 224.3 ± 63 |
| Iridomyrmex | 1529 ± 453.9 | 2751 ± 693 | 1785.6 ± 260 | 224.3 ± 23.8 | 201.6 ± 73.7 | 196 ± 71.6 |
| Pheidole | 33.6 ± 12.5 | 74 ± 13.5 | 34.6 ± 8.9 | 9 ± 4.5 | 5.6 ± 1.9 | 7.3 ± 3.5 |
| Myrmecia | 3.6 ± 1.5 | 12.6 ± 5.7 | 2.6 ± 1 | 6.3 ± 3.1 | 0.6 ± 0.3 | 2.3 ± 1.5 |
| Prolasius | 4.6 ± 2.1 | 1.3 ± 1 | 1.6 ± 1.4 | 17 ± 12.3 | 6.6 ± 5 | 4.3 ± 3.5 |
| Hypoponera | 2 ± 0.8 | 2 ± 1.2 | 0.6 ± 0.5 | 0 | 0 | 0 |
| Amblyopone | 0 | 0 | 0.3 ± 0.3 | 0.6 ± 0.3 | 0.6 ± 0.5 | 2.6 ± 1.4 |
| Monomorium | 0 | 0 | 0 | 0 | 0 | 0.3 ± 0.3 |
| Anonychomyrma | 8 ± 6.5 | 0 | 0 | 0 | 0 | 0 |
| Non-ant | 9.3 ± 2.2 | 34.6 ± 6.1 | 15.3 ± 2.3 | 7.3 ± 1.7 | 10.3 ± 2.8 | 11.3 ± 3 |
| Coleoptera | 41 ± 15.1 | 46 ± 4 | 13.6 ± 3.1 | 20.6 ± 2.8 | 9 ± 2.5 | 1.3 ± 0.3 |
| Hemiptera | 18 ± 6.8 | 67.6 ± 26.2 | 104.3 ± 33.8 | 15 ± 3.1 | 23.6 ± 13.2 | 29.3 ± 9.2 |
| Diptera | 55 ± 18.4 | 79.3 ± 9.5 | 24 ± 6.1 | 214 ± 56.1 | 23.6 ± 5.5 | 51.3 ± 15.6 |
| Orthoptera | 2.6 ± 0.9 | 13.6 ± 4.8 | 12.3 ± 5.3 | 30.3 ± 17.5 | 9.3 ± 5.2 | 4.3 ± 1.2 |
| Blattodea | 1 ± 0.5 | 1 ± 0 | 0.3 ± 0.3 | 2.3 ± 0.3 | 0.3 ± 0.3 | 0.6 ± 0.3 |
| Lepidoptera | 4 ± 0.9 | 3.3 ± 1.2 | 1.3 ± 0.7 | 12.6 ± 3.3 | 5 ± 2 | 11 ± 2.9 |
| Acarina | 10.3 ± 4.8 | 65 ± 2 | 8.6 ± 3.1 | 17 ± 3.7 | 462.3 ± 45.6 | 7 ± 1.2 |
| Araneae | 38.6 ± 5.8 | 36 ± 2.5 | 10 ± 2 | 47.3 ± 15.8 | 29.6 ± 9.5 | 29.6 ± 5.9 |
| Opiliones | 3 ± 2 | 0.3 ± 0.3 | 0 | 5.3 ± 2.7 | 3.3 ± 1.5 | 1.6 ± 0.9 |
| Diplopoda | 2.3 ± 0.7 | 1.3 ± 1 | 2.3 ± 1.2 | 17.6 ± 11.9 | 1.3 ± 1 | 0.6 ± 0.5 |
| Chilopoda | 1.6 ± 0.9 | 3.6 ± 1.4 | 0 ± 0 | 0 ± 0 | 0.3 ± 0.3 | 0 |
| Isopoda | 1.3 ± 0.5 | 1.6 ± 0.7 | 0 ± 0 | 1 ± 0.8 | 0 | 0 |
| Amphipoda | 2 ± 0.5 | 11 ± 8.6 | 3.3 ± 2.3 | 24.3 ± 9.5 | 15 ± 1.6 | 0.6 ± 0.5 |
| Turbellaria | 0.6 ± 0.5 | 1.6 ± 0.9 | 0 ± 0 | 3.3 ± 1.2 | 0.3 ± 0.3 | 0 ± 0 |
| Oligochaeta | 0.3 ± 0.3 | 0.6 ± 0.3 | 0 ± 0 | 2.6 ± 1.7 | 0.3 ± 0 | 0.3 ± 0 |
| Neuroptera | 0 | 0 | 0 | 1 ± 0.5 | 0 | 0 |
| Psocoptera | 0 | 0 | 0 | 0 | 0 | 0.6 ± 0.3 |
| Dermaptera | 0 | 0 | 0 | 0 | 0.3 ± 0.3 | 0 |
| Pseudoscorpionida | 0 | 0 | 0 | 0 | 0 | 0.3 ± 0.3 |

(20%), which did not differ from each other ($P = 0.69$) (Fig. 5).

The vegetative components making up the total plant material per month within scats also varied temporally. Non-fruit vegetation (leaves, flowers and seeds) comprised 18% and 14% of the scat volume in early (Dec) and mid-summer (Jan), respectively, while fruit during this period only accounted for 3% and 6%, respectively (Fig. 5). However, in late summer (Feb) fruit made up 54% of the *L. guthega* scat volume, while non-fruit vegetation made up only 9% (Fig. 5). This was largely due to consumption of berries from the Snow Beard-heath, *Acrothamnus montanus* (Table 1, Appendix S1), an alpine plant of conservation concern.

DISCUSSION

This study documents, for the first time, the diet of the *Liopholis guthega*, a highly threatened and

geographically restricted alpine reptile. Scat analysis revealed that *L. guthega* has a flexible, yet selective, feeding strategy that is subject to marked temporal variation coinciding with resource availability. The shift from a diet based predominantly on invertebrates to a diet dominated by vegetation was consistent across the range of this species over the summer period, despite location differences in invertebrate assemblages. The high proportion of vegetation in the diet of *L. guthega* in late summer contrasts with similarly sized members of the Egerniinae subfamily, highlighting the importance of temporal considerations in dietary analyses. The extremely high incidence of *Acrothamnus montanus* berries in the scats of *L. guthega* coincides with their availability late in summer, suggesting *L. guthega* opportunistically exploits a seasonally abundant resource. The high prevalence of intact seeds from *A. montanus* in the scats of *L. guthega* suggests that these lizards may play a role in seed dispersal and germination, and might indicate an important mutualism between two species of conservation concern.

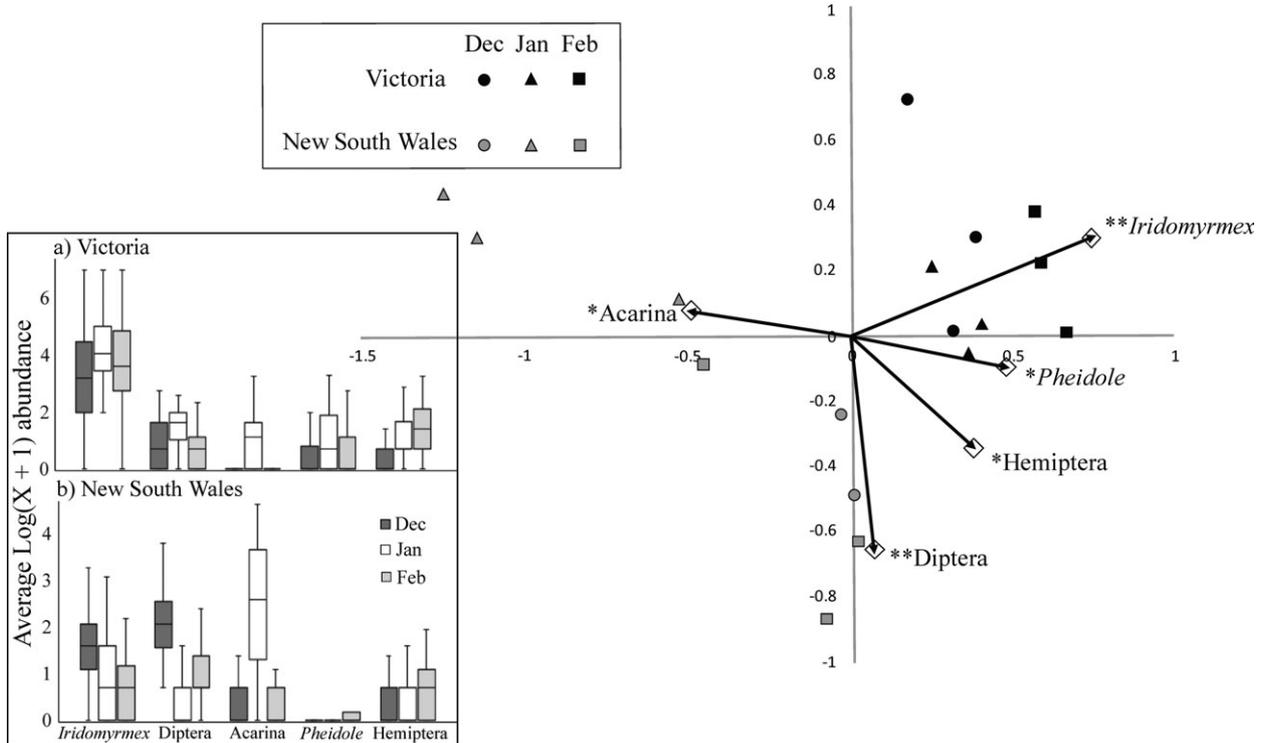


Fig. 4. Non-metric multidimensional scaling ordination based on Bray-Curtis similarity of invertebrate communities collected in pitfall traps from the Bogong High Plains, Victoria, and Kosciuszko National Park, New South Wales, over the months of December to February, 2016 (Stress = 0.26). Only the ordination axis average scores for each set of 20 pitfall traps are displayed. Invertebrate taxa that are significantly correlated (Spearman's R_s , $n = 18$) within the ordination space are included. * $P < 0.05$, ** $P < 0.01$.

Seasonal fluctuation in *Liopholis guthega* scat composition

Significant temporal variation is evident in the diet of *L. guthega* over the summer period, which is consistent between two sky islands separated by considerable distance, despite locality differences in the community composition of invertebrates. Formicidae was the main dietary element of the closely related, lower elevation species, *Liopholis whitii* (Brown 1983, 1991). As in this study, Formicidae were extremely abundant at the field sites of Brown (1991), suggesting that both lizards exploit an abundant resource. A significant inverse relationship between SVL and percentage of ants by volume in the diet of Egerniinae species has been reported (Pavey *et al.* 2010); ants were the major prey item for the similarly sized congeneric arid zone lizards *Liopholis slateri* (Pavey *et al.* 2010) and *Liopholis inornata* (Pianka & Giles 1982), contributing 35% and 35.2% of scat volume, respectively. This level of consumption is considered to represent dietary specialisation on ants and, until our study, *L. slateri* and *L. inornata* were the only two species within Egerniinae known to have a diet dominated by ants (Pavey *et al.* 2010). Given the smaller size of Victorian *L. guthega* compared to their New

South Wales counterparts (Z. Atkins, unpublished data, 2017), the trend for greater Hymenopteran intake in Victorian versus New South Wales *L. guthega* is consistent with the inverse SVL relationship. The high prevalence of Hymenopteran and Coleopteran orders in scats in both early and mid-summer, despite an array of other invertebrate orders present throughout *L. guthega* habitat, suggests that *L. guthega* may be more of a dietary specialist than the generalist invertebrate predator *L. whitii* (Chapple 2003). Moreover, while dietary selection could not be accurately quantified, the consistency of the food groups across both populations of *L. guthega* indicates that prey selection likely takes place in this species.

Spatial variation in invertebrate abundance

The invertebrate community assemblage differed between the Bogong High Plains in Victoria and Kosciuszko National Park in New South Wales, largely driven by differences in ant communities, most notably *Iridomyrmex* spp., with species from this genus being more abundant on the Bogong High Plains. The Dolichoderine ant genus *Iridomyrmex* is virtually ubiquitous throughout Australia, and

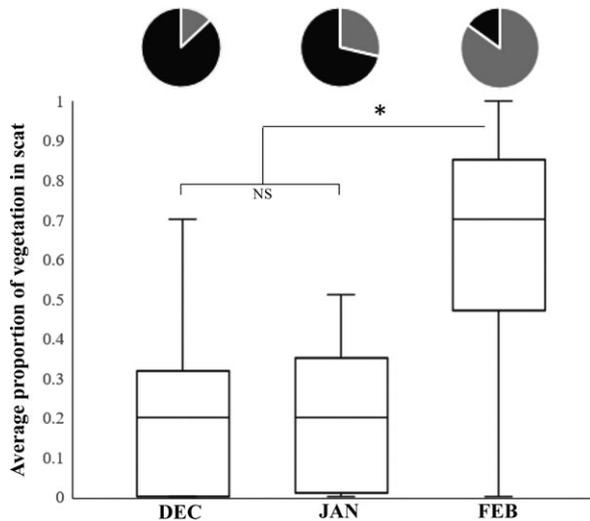


Fig. 5. Box plot of the average proportion of vegetative material in scats of *L. guthega* collected from the Bogong High Plains, Victoria, and Kosciuszko National Park, New South Wales, over the months of December to February, 2016. The proportion of fruit (black) and non-fruit (grey) vegetation within scats is also shown in pie charts. The lower quartile (Q1), median and upper quartile (Q3), representing the central 50% of the data for a particular month is shown, along with minimum and maximum values (whiskers). (*) denotes significance, NS, not significant. * $P < 0.05$

consists of abundant, highly active and aggressive species that exert a major competitive influence on other ants (Andersen 1995). Mcdougall (2007) noted the increased numerical dominance of the Dolichoderine species with increased elevation in alpine areas of Australia, with his study recording only a single species of this genus at the highest elevation site sampled. In addition, a single species of *Iridomyrmex* contributed 30% of the invertebrates trapped in tall alpine herbfield in the area of our study (Green & Osborne 2012). This sharp decline in ant species richness from mid to high elevations occurs globally (Samson *et al.* 1997; McCain & Grytnes 2010).

Our sites in Kosciuszko National Park were approximately 150–200 m higher than those on the Bogong High Plains. These elevational differences may contribute to the observed differences between localities in relative ant abundances. In addition, the sites at the Bogong High Plains have differing land use and fire histories, having burned more extensively during the 2003 alpine wildfire (Atkins *et al.* 2015) and having been subject to greater grazing pressure (Wahren *et al.* 2001). *Iridomyrmex* spp. favour more open (Hoffmann & Andersen 2003) and fire disturbed environments (Gibb & Hochuli 2003).

The dominance of *Iridomyrmex* within the Australian alpine environment and its subsequent prevalence in the diet of *L. guthega*, may be more a

product of their availability than their palatability. The energy content of invertebrates varies both within and among species (Pavey *et al.* 2009). Hymenoptera, and more specifically Formicidae, have one of the lowest energy contents (kJ g^{-1} dry mass) of all of the insect orders (Bell 1990). The seemingly high importance of ants in the diet of *L. guthega* early to mid-summer may be due to the fact that comparatively more ants need to be ingested to yield the same energetic output provided by other invertebrate orders (Bell 1990).

Additional differences in invertebrate assemblages were evident between our Victorian and New South Wales sites; Dipteran and Acarina orders were more abundant in Kosciuszko National Park. Dipterans are the most common invertebrates in heath communities in the Snowy mountains, contributing 24% of invertebrates caught in pitfall traps, while Acarina species made up 14% of invertebrates in tall alpine herbfields studied by Green and Osborne (2012). The much higher prevalence of these groups in pitfall traps compared to *L. guthega* scats suggests that they are not a favoured food source, or are largely inaccessible to foraging *L. guthega* due to their small size and soil-dwelling (Acarina) or largely arboreal (Diptera) habits.

Variation in invertebrate communities between these two alpine locations (Endo *et al.* 2015) has been attributed to past climatic oscillations and the modern isolation of taxa to discrete sky islands (Hewitt 2000; Chapple *et al.* 2005). The consistency of invertebrates in *L. guthega* scats across both locations, despite these differences in invertebrate community assemblage, is indicative of a selective diet.

Temporal shift to vegetation by *Liopholis guthega*

The average proportion of vegetation in the diet of *L. guthega* during early and mid-summer is consistent with the literature on Australian scincid diets, and adds support to the relationship between diet and body size within Egerniinae (Chapple 2003). The percentage of plant material in the diet of a hypothetical *L. guthega* (with a SVL of 100 mm) should be 16.4% (Fig. 6); we recorded plant volume of around 20% in early and mid-summer, which closely fits with the trend line (Fig. 6). However, a striking temporal dietary shift occurs during February, when it becomes dominated by vegetation (>60%). This is a stark contrast to the body size-plant intake relationship, and based on the regression equation, would predict a SVL of 179 mm – close to double that of *L. guthega*. However, we note that the studies contributing to the regression analysis collected data at variable times over their

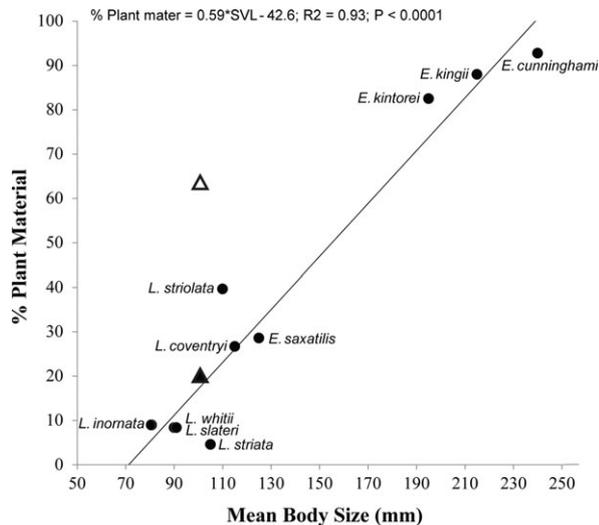


Fig. 6. Percentage of plant material in the diet of Egerniinae species, incorporating studies compiled by Chapple (2003) that estimated per cent volume of vegetation. Additional source data: *Liopholis slateri* (Pavey *et al.* 2010). Body size is based on the median snout-vent length reported in Chapple (2003). The percentage of plant material identified in diet of *L. guthega* in early and mid-summer (black triangle) and late summer (white triangle) were not included in the regression analysis, but added to show position relative to past studies on Egerniinae.

subject species' active period, and did not make month by month comparisons (Pianka & Giles 1982; Brown 1983, 1991; Arena 1986; Richards 1990; Chapple 2003; Clemann *et al.* 2004; Pavey *et al.* 2010). The grouping of scats in this manner may have obscured seasonal diet variation, and highlights the importance of temporal sampling when attempting to understand diet.

However, temporal variation in the diet of species related to *L. guthega* has been documented in larger species. Duffield and Bull (1998) identified increasing intake of plant material and diminishing invertebrate consumption from mid-late summer in *Egernia stokesii*. Fenner *et al.* (2007) documented seasonal trends in the diet of *Tiliqua adelaidensis* from spring to summer, with significantly more plant material in scats late (38.2%) compared to early (16.2%) in the season; the increased importance of vegetation in the diet of these lizards later in the season was unexpected, given it coincided with the drying of vegetation. The authors of these studies speculated that temporal change may have reflected reduced invertebrate activity or a behavioural change in adults to avoid intraspecific competition with insectivorous young (Duffield & Bull 1998; Fenner *et al.* 2007). However, we observed neither of these factors, and our results suggest that if vegetation was classified more specifically into vegetative parts in previous studies, dietary shifts based on increased fruit

availability may have been evident (Valido & Olesen 2007).

Frugivorous response to seasonally abundant resource

The pronounced shift in the diet of *L. guthega* from early to late summer was driven by increased intake of fruit. Of the 63% total vegetation in scats in late summer, fruit made up 54% of the total volume, of which, 53% were berries from the Snow Beard-heath, *A. montanus* (Appendix S1). The presence of this fruit in the scats of *L. guthega* coincided with the seasonal fruiting and peak availability of this alpine species. During the study period, *A. montanus* flowering was first observed within Kosciuszko National Park in mid-spring (7 October 2015) and continued until mid-summer (18 January 2016), with cessation of flowering signalling the commencement of fruiting (K. Green, pers obs, 2016). Therefore, the peak availability of ripe *A. montanus* fruits was in late summer at both locations, suggesting that *L. guthega* alters its diet in response to an increase in resource availability.

Dietary plasticity in response to fruit availability has been documented in other lizard species from across the globe (Olesen & Valido 2003; Wotton *et al.* 2016). Striking similarities to *L. guthega*'s seasonally frugivorous diet are evident in the endemic Canary Islands lizard, *Gallotia galloti* (Rodríguez *et al.* 2008). This species became more frugivorous in response to availability of ripe fruit during summer compared with other seasons, with fruit accounting for precisely the same scat volume as it did for *L. guthega* (63%; Rodríguez *et al.* 2008). Similarly, the diet of the South American lizard, *Tropidurus torquatus* varied temporally; ripe fruits were only available during the wet season, coinciding with the increased consumption of this food type (Fialho *et al.* 2000).

The occurrence of *A. montanus* fruit in greater than 77% of *L. guthega* scats during its fruiting period indicates the importance of this food source for this lizard. Four additional fleshy fruiting plant species (*Tasmannia xerophila*, *Dianella tasmanica*, *Podocarpus lawrencei* and *Melicactus dentatus*) were identified within *L. guthega* sites during this study (Z. Atkins unpub. data, 2017), but were not eaten by the lizards during this period in late summer, while at least a further five fruiting species are present in the sub-alpine and alpine region of mainland Australia (Duncan 1994; Costin *et al.* 2000). Selection of particular plant species by other lizards (Rocha 2000; Wotton *et al.* 2016) and *L. guthega* suggests that these species are not generalist herbivores during this period, but rather feed selectively on the more nutritional and easily assimilated fruit components (Fialho *et al.* 2000; Chapple 2003; Valido & Olesen 2007).

The seasonal prevalence of fruit in the diet of many lizards suggests that they act as vectors for seed dispersal (Valido & Olesen 2007; Rodríguez *et al.* 2008; Wotton *et al.* 2016). Less than 10% of seeds ingested by New Zealand lizards were visibly damaged (Wotton *et al.* 2016), while large proportions of viable seed following lizard ingestion and excretion has been documented (Valido *et al.* 2003; Rodríguez-Pérez *et al.* 2005). Gut passage of seeds by the lizard *G. galloii* was found to significantly increase the germination rate of the plant *Withania aristata* (Valido & Nogales 1994). Conversely, ingestion and excretion of fruit by the New Zealand gecko, *Woodworthia maculata*, had no effect on the percentage of *Piper excelsum* seeds that successfully germinated compared with seeds simultaneously obtained directly from plants (Wotton *et al.* 2016). While neutral effects on germination rates following seed passage through reptile guts has been confirmed by the meta-analysis of 39 species (Traveset & Verdú 2002), the majority of studies lack quantitative analysis on the importance of lizards as plant mutualists (Valido & Olesen 2007).

The extent of seed dispersal is a product of lizard abundance and dispersal capacity, the availability of accessible fruits and the degree of frugivory (Wotton *et al.* 2016). Lizards can be important dispersers of seeds in island environments as a result of high population densities, along with increased endemism and the evolution of associated symbiotic relationships (Cooper & Vitt 2002; Olesen & Valido 2003; Wotton *et al.* 2016). However, lizards may also play an important role in seed dispersal in mainland systems where fruit consumption rates can be seasonally high despite low population densities of lizards (Young *et al.* 2012; Wotton *et al.* 2016). The high prevalence of intact *A. montanus* seeds in *L. guthega* scats suggests that these lizards may disperse (and perhaps contribute to the germination of) these seeds (Olesen & Valido 2003; Rodríguez *et al.* 2008).

Conservation implications

Liopholis guthega's restricted distribution in Australia's highest environments (Atkins *et al.* 2015) means that this species is threatened by alpine tourism (Pickering & Hill 2007) and climate change (Hughes 2003), both of which have the potential to disturb and fragment habitat (Sato *et al.* 2014), alter community composition and ecosystem processes (Pickering 2007), and ultimately generate a cascade of trophic changes (Tylianakis *et al.* 2008; Sentis *et al.* 2015).

The significant interactions identified between *L. guthega* and alpine vegetation can inform

conservation management (Fenner *et al.* 2007). Our study suggests that revegetation initiatives within the distribution of *L. guthega* should promote heterogeneity of native alpine flora to maximise invertebrate diversity (Schaffers *et al.* 2008). Furthermore, revegetation efforts should focus on establishing and maintaining populations of *A. montanus*. This plant is an integral component of *L. guthega* diet and is listed as threatened over a considerable proportion of its range; its presence at *L. guthega* colonies is likely to be an important factor in the persistence of these lizards. In addition, this study allows us to mimic natural temporal variation in the diet of captive *L. guthega*; such information has been integral to the success of other threatened vertebrate species programs (Oftedal & Allen 1996; Gibson 2007). Ultimately, revealing crucial trophic interactions between species equips conservation managers with knowledge to mitigate threatening processes, which may be pronounced in alpine regions, facilitating the maintenance of biodiversity and ecosystem function.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Summary of the vegetative components identified in *Liopholis guthega* scats collected from the Bogong High Plains, Victoria and Kosciuszko National Park, New South Wales over a 3 month period (December–February) in 2015/16.