



RESEARCH ARTICLE

# Agonistic behavioural asymmetry in two species of montane lizard that exhibit elevational replacement

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## Abstract

**Context** In montane systems, closely related species tend to segregate spatially along elevational gradients. The role of biotic interactions, relative to species physiological requirements, in maintaining these distribution patterns is an important question in spatial ecology. Theory suggests that the role of interspecific competition can be significant in the maintenance of elevation replacement distributions. Despite this, there has been limited work investigating factors beyond thermophysiology in determining ranges in temperate montane species.

**Objectives and methods** We investigated agonistic (i.e. aggressive) behaviour in response to a simulated intruder (conspecific versus heterospecific 3D printed

models) in two sister species of temperate montane lizard, *Liopholis guthega* and *L. montana*, from south-eastern Australia. The two species have similar thermal tolerances at an area of distributional overlap between 1600 and 1700 m above sea level, above which *L. montana* is replaced by the high elevation specialist *L. guthega*.

**Results** We found that response to intruder stimuli differed between the two species, with the high elevation *L. guthega* actively biting both conspecific and heterospecific models, whereas the lower elevation *L. montana*, never attacked either model type. Our findings provide evidence of asymmetric agonistic response in the two montane reptile species.

**Conclusions** These findings have important implications for understanding how biological interactions and behaviour, in addition to thermo-physiological data, might mediate landscape scale distribution

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patterns both now and as environments change in the future. More broadly, our results are not consistent with the widespread idea that low elevation species will inevitably ‘push’ higher elevation species out, as global warming erodes species’ thermal envelopes.

**Keywords** Australia · Alpine zone · Behaviour · Climate change · Reptile · Skink

## Introduction

The mechanisms that determine and maintain species distributions have long been a source of interest to ecologists (McArthur 1972; Diamond 1973; Terborgh and Weske 1975; Gifford and Kozak 2012). The idea that biotic interactions act together with abiotic constraints to impose limits on the distribution of organisms is pervasive in the literature (Cadena and Loiselle 2007; Chock et al. 2018). Interspecific competition plays a crucial role in this context, because competitive interactions between species have the potential to constrain a species to a limited range (the realised niche) of the full set of conditions to which they are physiologically suited (the fundamental niche) (Cadena and Loiselle 2007). Consideration of species’ competitive behaviour is therefore crucial for our understanding of how species are distributed across space and time. This is increasingly important under regimes of widespread environmental change, where behavioural differences may benefit one species over another and influence patterns of distribution (Duckworth et al. 2015).

Montane systems offer valuable opportunities to study species distributions and the mechanisms that affect them (Graham et al. 2014; Barve and Dhondt 2017). In many montane-dwelling species, there is a common pattern in which closely related taxa replace each other along an elevational gradient (Barve and Dhondt 2017). Behavioural interference, a form of interspecific competition, has been postulated as a critical mechanism in maintaining elevational partitioning (Gifford and Kozak 2012; Pasch et al. 2013; Freeman et al. 2016; Barve and Dhondt 2017). However, direct tests of differences between competing species in competitive ability are rare, which is surprising given that climate-induced changes in the environment have the potential to disrupt community

composition, leading to a higher frequency of inter-specific interactions. Importantly, the role of inter-specific competition in mediating elevational boundaries is unlikely to be uniform across species. Interspecific aggression is predicted to be most common between species that are closely related and ecologically similar (Freeman and Miller 2018; Martin et al. 2017). In these comparisons, there is often a strong tendency for aggression to be asymmetrical, with larger species often prevailing if there is a size difference (Martin et al. 2017). Moreover, in direct combat, one species is consistently the aggressor (Pasch et al. 2013; Martin et al. 2017). As a consequence, the more aggressive species are generally behaviourally dominant in the environment (Freeman 2016; Duckworth et al. 2017). Such asymmetry in competitive ability between species is common and can have important ecological implications. For example, Grether et al. (2017) implicated behavioural asymmetry in species’ range expansions and the displacement of congeners under environmental change. Duckworth et al. (2015) showed that aggressive asymmetries drive successional replacement in two species of bluebirds that compete for nest cavities in newly created habitat post fire.

Studies have implicated competitive interference in the maintenance of elevational replacement distributions across a number of tropical systems (Cadena and Loiselle 2007; Pasch et al. 2013; Barve and Dhondt 2017). In contrast, few studies have focussed on the role that interspecific interference plays in mediating elevation replacement of species inhabiting temperate montane environments (Freeman and Montgomery 2015). Temperate montane systems contain highly endemic and range restricted species (Caldwell et al. 2015). Given the rapid loss of biodiversity and anthropogenic induced distribution shifts (Grether et al. 2017), studies of this type are increasingly necessary. Anthropogenic climate warming has the potential to erode thermal niches, leaving highland species exposed to incursion from lowland species, resulting in novel secondary contact among species that may not have interacted in recent evolutionary time (Krosby et al. 2015; Grether et al. 2017).

For the studies that have examined asymmetrical aggression in closely related montane species, the majority have been on birds (Freeman et al. 2016; Barve and Dhondt 2017) and, to a lesser extent, mammals and amphibians (Gifford and Kozak 2012;

Pasch et al. 2013). Such behavioural patterns have rarely been examined directly in reptiles, despite the pervasiveness of elevational replacement distributions in this group (Fischer and Lindenmayer 2005; Kryštufek et al. 2008), and the vulnerability of this group to multiple effects of climate warming (Sinervo et al. 2010). Indeed, studies that examine patterns of diversity and endemism in montane reptiles (Sinervo et al. 2010; Caldwell et al. 2015) have largely focused on understanding distribution patterns driven by thermophysiology, and rarely incorporate data on other mechanisms, such as biological interactions (Strangas et al. 2019).

In this study we investigate agonistic behaviour in response to a simulated intruder in two sister species of temperate montane lizards, *Liopholis guthega* and *L. montana*, that replace each other along an elevation gradient in south-eastern Australia. The high elevation *L. guthega* is an Endangered species (IUCN Red List, Nationally, and in New South Wales; Clemann et al. 2018b; Chapple et al. 2019) with a highly restricted range in two mountain regions between 1600 and 2170 m above sea level (a.s.l.) (Atkins et al. 2018). *Liopholis montana*, by contrast, is distributed more widely from 900 to 1700 m a.s.l., but is listed as Near Threatened (IUCN Red List, Clemann et al. 2018a). Within subalpine environments, a zone of replacement has been identified between 1600 and 1700 m a.s.l. (Fig. 1), at Kosciuszko National Park, New South Wales (NSW) (Senior et al. 2019). Although these species are broadly sympatric in this transition zone (1600–1700 m), they have never been found in syntopy (author's observations). *Liopholis guthega* exclusively inhabits the alpine zone (above the tree line) and exhibits a higher tolerance to cold temperatures compared to *L. montana* (Senior et al. 2019). Maximum temperature tolerances of the two species are statistically similar (Senior et al. 2019). The two species occur in broadly similar habitats, forming colonies in close association with rock habitat, including outcrops and rocky ranges (Donnellan et al. 2002; Sato et al. 2014; Michael and Lindenmayer 2018; Senior et al. 2019). The species are morphologically similar but for scale pattern and colour (Fig. 1), and share an omnivorous diet including seasonal fruits (Donnellan et al. 2002; Atkins et al. 2018, author's observations). Many closely related skink species that occur in these habitats form stable social groups centred around extensive burrow

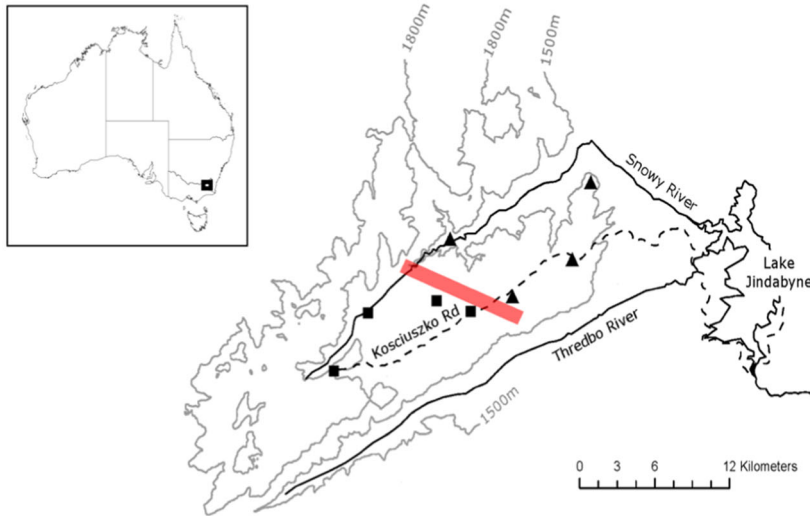
systems, beneath boulders, slabs and in rock crevices (Chapple 2003; Michael and Lindenmayer 2018). This includes the study species' closest relative *L. whitii*, that inhabits lower elevations below 1400 m in the same region (Donnellan et al. 2002). We expect the study species to exhibit similar social systems to *L. whitii* (Chapple 2003) and to compete for shelter resources within a colony. Aggression and its effect in mediating resource partitioning of shelter use has been demonstrated within colonies of *L. whitii* (While et al. 2009a, b; McEvoy et al. 2013, 2015), and when occurring in sympatry with larger and smaller lizard species (Langkilde and Shine 2004).

We predict that competition between the two *Liopholis* study species over finite rock habitat is likely within the subalpine zone, especially given their similarities in size and diet. Additionally, the upper and lower thermal limits of *L. guthega* and *L. montana* are comparable where they overlap in distribution at 1600–1700 m, suggesting that non-thermophysiological factors could be important in shaping the distribution patterns of these species (Senior et al. 2019). Understanding the implications of competitive interactions between the two species will be important under global warming, with subalpine habitat projected to track upwards (Atkins et al. 2018). *Liopholis guthega* has very little capacity to move up in elevation in response to encroachment from *L. montana* as the species has been recorded at 2170 m and Australia's tallest peak (Mt Kosciuszko) is 2228 m high.

## Materials and methods

### Animal collection and husbandry

*Liopholis guthega* (n = 18) and *L. montana* (n = 16) were collected from Kosciuszko National Park, NSW, during January and February 2018, respectively. Surveys of herpetofauna in the study area identified a pattern of elevational replacement in this genus that does not match that of other co-occurring lizards (our unpublished data). A similar sized but unrelated skink, *Eulamprus tympanum* co-occurs in wetter microhabitat with both *Liopholis* species, suggesting the mechanisms restricting *Liopholis* distribution are genus specific (our unpublished data). *Liopholis guthega* were collected from one colony (1840 m



**Fig. 1** Study species (a) *Liopholis guthega* and (b) *L. montana*. Map details distribution of each species (■—*L. guthega*, ▲—*L. montana*) and zone of replacement (red bar) between 1600 and 1700 m above sea level in Kosciuszko National Park, New South Wales, Australia. Photo of *L. guthega* by George Madani and *L. montana* by Lachlan Hall

a.s.l.), while *L. montana* were collected from three adjacent smaller colonies (within ~ 5 km of the *L. guthega* site, but lower elevation [1340–1660 m]) to ensure adequate sample size. For both species, we collected males and females, with all females being gravid at the time of the study. The use of both males and females in our study allowed us to capitalise on the number of animals that were captured, which was particularly important given the rarity and conservation status of the two lizard species. All individuals were caught by hand, or with the aid of a noose pole. On day of capture, skinks were held in cloth bags in the field, before transfer to a nearby research facility located within the National Park.

On arrival at the research facility, sex was determined via cloacal examination and eversion of the hemipenes of males, and females were palpated to confirm reproductive status. Snout-vent length (SVL) was measured to the nearest 1 mm using a clear plastic ruler. Incidence of toe loss was recorded as toe injury is a suggested measure of aggression within lizard colonies (Vervust et al. 2009). Skinks were housed in individual plastic enclosures (60 × 40 × 35 cm) lined with paper towel, with a flat granite rock for basking and a plastic hide for shelter. Ambient daytime temperatures ranged from 15 to 25 °C. Skinks were provided with a heat source in the form of a 40 W incandescent light bulb suspended from the roof of the enclosure at one end, providing a thermal gradient of 22–40 °C for a 12 h period (07:00–19:00 h) that allowed for behavioural thermoregulation. Lizards were fed every second day on a diet of mealworm dusted with calcium and vitamin supplements (Vetafarm, Multical dust) except during behavioural trials. Water was available ad libitum.

#### Use of 3D models to test behaviour of focal lizards

The conservation status of our focal species and the potential for inadvertent disease transmission between animals and populations precluded us from studying

competitive interactions using live stimulus animals in dyadic encounters (c.f. Melville 2002; Langkilde and Shine 2004, 2005). Instead, we capitalised on 3D printed models to test the behavioural responses of our focal individuals. Such models have a significant advantage over live stimuli by allowing us to explicitly control for confounding factors that might otherwise arise due to differences in stimulus phenotype and behaviour. Indeed, artificial models have been used to study aggressive behaviour in a range of taxa (Lehtonen et al. 2015a, b; Yewers et al. 2016; Fan et al. 2018), including *Liopholis* skinks (While et al. 2009a, b). Lizard models were printed based on a 3D scan of museum wet specimens of the two species (Online Appendix). Models were painted with colours matched as closely as possible to previously collected field spectral measures of each species (Figs S1, S2) within 300–700 nm, the approximate visual range of most diurnal lizards (Teasedale et al. 2013). The two species are not sexually size dimorphic (Atkins et al. 2018; our own unpublished data), so the model dimensions reflected the mean size of each species (i.e. for sexes combined) in the collection region (*L. guthega*: n = 33, SVL = 96 mm, head width = 15 mm, head length = 13 mm; *L. montana*: n = 22, SVL = 96 mm, head width = 13 mm, head length = 12 mm).

#### Behavioural trials

Trials were performed following a laboratory acclimation period of five days. We know from studies on closely related *L. whitii* that within-individual consistency in aggressive behaviour is common (While et al. 2009a, b; McEvoy et al. 2013). Each focal lizard was tested over two days in their own housing enclosure by subjecting them to six trials, three per day. On any given day, trials commenced at 0900, with each trial separated by a two hour break. Prior to the commencement of the first trial on each day, focal lizards were given the opportunity to bask for 2 hours, resulting in a body temperature of approximately 33 °C (i.e. the preferred body temperature of *L. guthega* when thermoregulating in the lab: 32.1–33.2 °C; Atkins, unpublished data). Each trial involved presenting the focal lizard with either a single conspecific or a single heterospecific model, with the order of presentation randomised. A different stimulus model was used in each trial, meaning that, over the

course of the two days, each focal lizard saw three different conspecific and three different heterospecific models. We found that lizards continued to remain highly responsive to the models throughout the two day period, suggesting no issues with habituation.

At the beginning of each trial, the model was introduced into the enclosure and moved towards the focal lizard by sliding it into view on the end of a 1.5 m dowel rod. This initial approach was followed by a brief pause to line up the model to within 1 cm of the focal lizard, prior to initiating physical contact between the model and the focal lizard. This physical contact, designed to simulate an aggressive interaction, took the form of a gentle tap by the model on the snout of the focal animal (While et al. 2009a, b). The snout touch was performed on all lizards that did not immediately flee when approached by the model. This included lizards that responded to the approaching model by remaining stationary, by presenting their body laterally to the model (a typical threat display) or by biting. In some instances, the focal lizard, when approached by the model (and before the snout touch could be initiated) fled into or on top of the shelter at the opposite end of its enclosure. If the lizard returned to the model within three seconds, a snout touch was performed. If the lizard did not return, the trial was ended. The process of approaching and touching the snout of the focal lizard was repeated up to 10 separate times within each trial or until the lizard fled to the shelter and did not return (whichever came first). The behavioural responses scored during the trials included latency to flee, number of lateral displays, and number of bites (Table 1). All trials were filmed and observations were made by the same observer (A.F.S) on recordings to increase accuracy. It was not possible to score the behaviours blind to treatment, as each species (and model) has a distinctive colour pattern.

It is important to also note that we recorded whether the lizard was basking on the rock at the commencement of each trial (occupancy = yes or no). In this respect, we found that lizards that were not basking at the commencement of the trial (41.95%) ran to the basking resource following initial approach by the model, whereas others retreated away from the basking resource in response to the model. If the lizard was not basking and retreated immediately, this was classed as a retreat and the trial was ended. If the lizard was not basking at the commencement of the

trial but moved to take up position on the basking resource the trial was allowed to continue.

### Statistical analysis

We removed five focal lizards (four *L. guthega* and one *L. montana*) from the dataset as these lizards fled into the shelter as the trial commenced, for all six repeats. The fleeing occurred before the model was adjacent to the focal lizard, and we could not deduce whether the response was to the models or to another stimulus. Hence, the total number of focal *L. guthega* and *L. montana* used in the analyses were 14 and 15, respectively. Data were run through principal component analysis (PCA) with varimax rotation to test the relationships between behaviours prior to analysis of effects. The three behaviours loaded strongly onto a principal component in PCA (Table 2), explaining 60% of the variation. A second principal component explains a further 27% and separates bites from lateral presentations and latency to flee. Pearson's correlations support this, revealing that latency to flee and lateral presentations are highly correlated ( $r = 0.57$ ,  $p < 0.001$ ), whereas bites and lateral presentations ( $r = 0.21$ ,  $P = 0.05$ ) and bites and latency to flee ( $r = 0.37$ ,  $P = 0.003$ ) are less so.

Lizard body size has been demonstrated to be an important factor in determining the outcome of aggressive interactions in some lizards (Umbers et al. 2012). Thus, using the measured SVL of focal lizards, we created a categorical variable 'body size'. Focal lizards were categorised as either larger or smaller than the simulated intruder to test whether size in relation to intruder had an effect of focal lizard behaviour (SVL = 96 mm). We then assessed the effect of species (*L. guthega*, *L. montana*), model type (conspecific, heterospecific), trial order, sex (male or female), body size (SVL < > 96 mm), and occupancy (yes or no) on latency to flee and the number of lateral presentations, using generalised mixed models. We applied these models using the 'glmmPQL' function of the packages 'nlme' and 'MASS' in R 3.5.1 software (R Development Core Team 2018), with a negative binomial error distribution as appropriate for over-dispersed count data (Zuur et al. 2013). To account for any effects related to the use of individual lizards in multiple replicates, 'lizard identification number' was added as a random factor. Targeted two-way interactions were included for variables, as well

**Table 1** Ethogram of the agonistic behaviours most commonly observed in *Liopholis* intruder response

Behaviour	Description
Latency to flee	Number of times taken for the focal lizard to be approached and touched on the head by the model before retreating to shelter or opposite end of its enclosure
Bite	Lizard lunges towards the model and grasps model with jaws (lunges were always accompanied by a bite)
Lateral presentation	Lizard moves its head to face away from the model, moving parallel to the model in a lateral-orientation

**Table 2** Component loadings of behaviours observed on two orthogonally rotated principal components (PC1, PC2)

	PC1	PC2
latency to flee	0.65	0.14
Lateral presentation	0.59	0.52
bites	0.47	– 0.26
% of variance explained	59.38	26.91
Total variance explained	86.29	

as three-way interaction between model type, species and sex. We proceeded with step-wise refits of the model, each time without its highest order interaction term, using  $p = 0.05$  as the cut-off point. To test effect of species on number of bites, we used a Fisher's exact test to account for lack of bites by *L. montana*. We then examined the effect of variables on biting behaviour in *L. guthega* using generalised mixed models with lizard identification number as a random factor.

## Results

The only predictor variable that had a significant effect on the latency to flee was lizard occupancy (Table 3; Fig. 2). Specifically, focal skinks occupying the basking rock at the commencement of a trial were less likely to flee immediately following an interaction with the intruder models. Latency to flee was not affected by species, model type, sex or body size (Table 3). For the lateral presentation response, there was a significant effect of model type, sex and species (Table 3; Fig. 3). The lateral presentation response was stronger towards heterospecific models compared to conspecific models, *L. montana* exhibited the lateral presentation response more than *L. guthega*, and males of either species were more likely to exhibit lateral

presentation than females. A bite response was never elicited in *L. montana*, whereas bites to models of either heterospecific or conspecific were exhibited in 50% of *L. guthega* individuals ( $p < 0.01$ ) (Fig. 4). There was no effect of model type, sex or body size on bite response in *L. guthega* (Table 3; Fig. 4). Order of trials had a significant effect on latency to flee, and *L. guthega* biting response, with some evidence of escalation of response to intruders over time (Online Appendix: Table S1).

## Discussion

We found evidence for asymmetry in agonistic response to intruders in two lizard species that overlap in distribution in temperate south-eastern Australia. Both *Liopholis* species displayed a similar latency to flee, but exhibited different responses towards intruders. In particular, while the higher elevation species (*L. guthega*) actively bit both conspecific and heterospecific models, the mid-elevation species (*L. montana*) did not. Instead, *L. montana* only exhibited lateral presentation behaviour, but did not bite the model. We found that males of both species were more likely to engage in this behaviour than females, and more so in response to heterospecific compared to conspecific models.

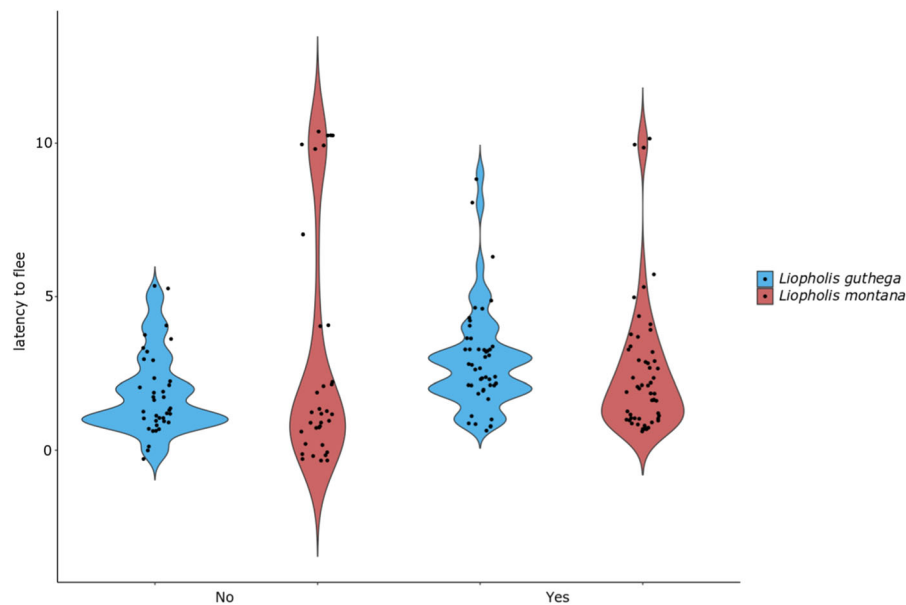
## Distribution

The behavioural differences identified in montane *Liopholis* may have implications for interspecific interactions between the two species, in part explaining the lack of syntopy in similar habitats in the subalpine region where they both occur in broad sympatry. This behavioural asymmetry may also have implications for distribution patterns in the future, as

**Table 3** Results of the generalised mixed model to determine effect of species, sex, body size (< or > 96 mm), model type (heterospecific or conspecific) and occupancy (yes or no) on latency to flee, number of taps and lateral presentation response in *Liopholis guthega* and *L. montana*, and bite response in *L. guthega*

	Coefficient	SE	t	df	P value
Latency to flee					
Intercept	0.05	0.25	0.20	132	0.84
Species ( <i>L. montana</i> )	0.69	0.35	1.95	26	0.06
Sex (M)	0.25	0.24	1.03	26	0.31
Body size (small)	− 0.28	0.25	− 1.12	26	0.27
Model type (heterospecific)	− 0.06	0.15	− 0.44	132	0.66
Occupancy (yes)	0.29	0.11	2.58	132	<b>0.01</b>
Lateral presentations					
Intercept	− 2.17	0.49	− 4.43	137	<0.001
Species ( <i>L. montana</i> )	0.75	0.33	2.25	26	<b>0.03</b>
Sex (M)	0.91	0.30	2.99	26	<b>&lt;0.01</b>
Body size (small)	− 0.49	0.33	− 1.46	26	0.16
Model type (heterospecific)	0.69	0.28	2.47	137	<b>&lt;0.05</b>
Occupancy (yes)	0.44	0.28	1.58	137	0.11
Bites - <i>Liopholis guthega</i> only					
Intercept	− 4.41	1.06	− 4.15	62	<0.001
Sex (M)	− 0.30	1.42	− 0.21	12	0.84
Body size (small)	1.41	1.41	1.00	12	0.34
Model type (heterospecific)	− 0.74	0.54	− 1.38	62	0.17
Occupancy (yes)	− 0.60	0.36	− 1.67	62	0.10

Significant values (< 0.05) are in bold

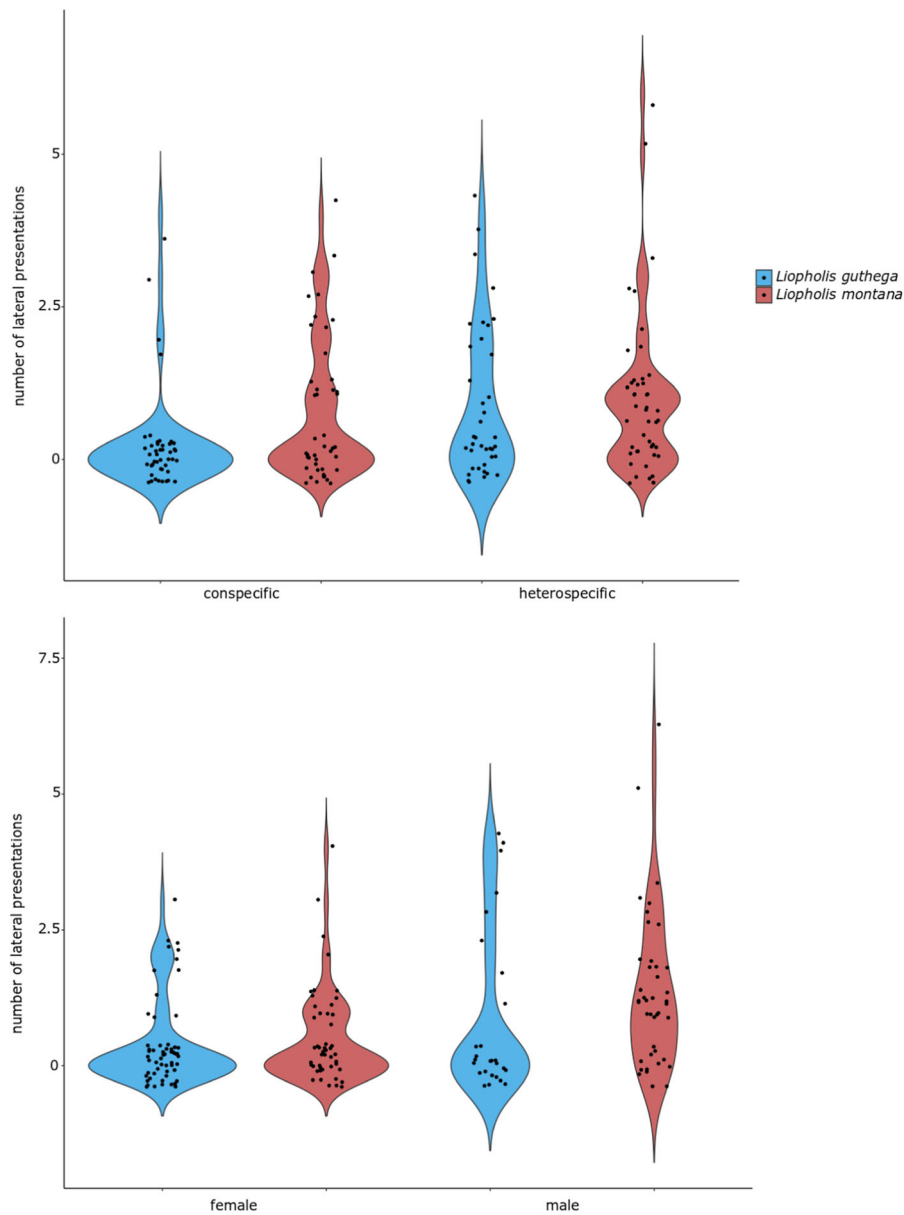


**Fig. 2** Violin plot of the latency to flee for *L. guthega* (n = 14) and *L. montana* (n = 15), by occupancy (whether the focal lizard began trial in contact with basking resource (no/yes). Each point represents a response to a simulated intruder

contact between the two species increases with high elevation habitat predicted to contract in response to climate warming (Atkins et al. 2018). At their highest

elevational distribution, *L. guthega* are tolerant to very cold temperatures (Senior et al. 2019). It is plausible that *L. montana* is excluded from high alpine

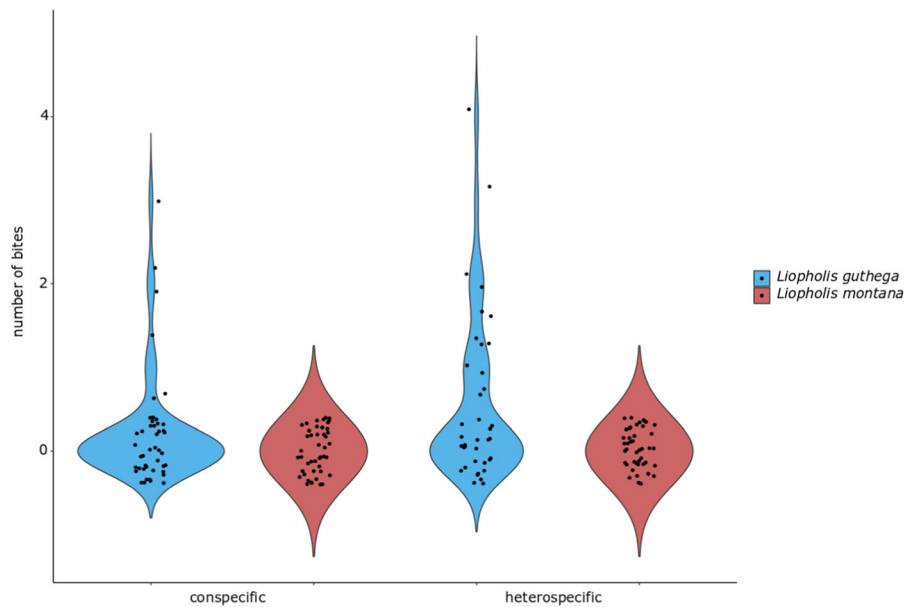




**Fig. 3** Violin plot of the lateral presentation response for *L. guthega* ( $n = 14$ ) and *L. montana* ( $n = 15$ ), by model type (conspecific and heterospecific), and focal lizard sex. Each point represents a response to a simulated intruder

elevations by an inability to retain function at cold alpine temperatures, in contrast to *L. guthega* (Senior et al. 2019). Gene flow from warmer environments to higher populations of *L. montana* could impede adaptation to colder temperatures experienced at the species' highest elevational extent (Strangas et al. 2019). As climate changes frees this species from thermophysiological constraints, its ability to colonise higher alpine elevations may be impeded by the

presence of a more aggressive congener, *L. guthega*. Distribution patterns where lowland species are excluded by a more aggressive alpine species have been identified in salamanders, small mammals and birds (Gifford and Kozak 2012; Pasch et al. 2013; Freeman et al. 2016). In our system, both species are of conservation concern, and their persistence will likely be mediated by the outcome of interspecific interactions.



**Fig. 4** Violin plot of the bite response for individual *L. guthega* (n = 14) and *L. montana* (n = 15), by model type (conspecific and heterospecific). Each point represents a response to a simulated intruder

If *L. guthega* is indeed the superior competitor, then what is preventing this species from encroaching on *L. montana* dominated habitat and in colonising lower elevations? At the core of its elevational range, birthing in *L. guthega* currently coincides with peak availability of an important food resource (*Acrothamnus montanus* berries), a plant species that does not occur below the alpine zone (1800–1900 m) (Atkins et al. 2018). *Liopholis guthega* could have a competitive disadvantage at lower elevations where this plant does not occur. Under worst-case climate scenarios, the entire Australian alpine zone will be replaced by subalpine vegetation by 2050, reducing *A. montanus* habitat above the treeline (Green et al. 1992; Hennessy et al. 2003; Pickering 2007). The persistence of *L. guthega* populations in the future will likely in part be mediated by the species' ability to adapt to changing vegetation, and competition from lowland species. We suggest that future work examining the microhabitat requirements of the two species and how these change along the altitudinal gradient, is required to fully understand where and why *L. guthega* replaces *L. montana*, allowing greater scope to hypothesise about the two species persistence under climate warming.

#### Behavioural asymmetry

Asymmetry in aggressive behaviour has been recorded in another Australian montane lizard system where species exist in both allopatry and sympatry (Melville 2002). Specifically, when examining the role of competition in habitat occupation and character displacement in *Carinascincus* species, Melville (2002) found that the larger *C. greeni* was consistently more aggressive and behaviourally dominant when paired with smaller *C. microlepidotus*. Furthermore, in that study, it was suggested that this behavioural difference has likely played a role in maintaining distributions of the less dominant species. Specifically, *C. microlepidotus* shifted its habitat to less thermally optimal heathlands and body size was significantly smaller than *C. greeni* when in sympatry (Melville 2002).

In another montane lizard assemblage, body size was consistently important in determining a resident's ability to defend territory from heterospecific competitors, with larger species almost always excluding smaller species (Langkilde and Shine 2004). In the current study on *Liopholis*, both species are similarly sized at maturity. Thus, prior to the collection of behavioural data there was no clear predictable fore-runner for agonistic encounters. Considering the similarity in size, we suggest *L. guthega* may be the

dominant aggressor in any interactions between the two, given their tendency to bite intruders. Fighting is costly, and the behaviour of *L. montana*, though less overtly aggressive, is a form of territory defence, and may be an effective strategy to intimidate the intruder, whilst avoiding injury from physical contact. In situations where the intruder is another lizard and not a model that continues to encroach repeatedly regardless of focal lizard behaviour, we suggest that bites are more likely to quickly induce fleeing in an intruder than lateral presentations. Intruder size compared resident lizard size may also be important in such interactions, whereas in the current study we found no difference in behaviours exhibited by focal lizards that were larger than the intruder and those that were smaller.

The observed behavioural asymmetry suggest that behavioural interference may be important in restricting the upper elevational limit of *L. montana* at the subalpine zone where *L. guthega* replaces *L. montana*, before the species' reaches its thermophysiological limits in the alpine zone (Senior et al. 2019). That said, the behavioural differences we report should be interpreted with some degree of caution given the modest sample sizes, which, unfortunately, were constrained by the conservation status of both of our two lizard species (Clemann et al. 2018a, b; Chapple et al. 2019). Nevertheless, the behavioural asymmetries reported are consistent with those observed previously in two similar sized salamander species in the Appalachian Highlands (Gifford and Kozak, 2012). When examining the factors that underlie the elevational replacement distribution of the species, Gifford and Kozak (2012) found that competition with high elevation *Plethodon jordani* prevented low elevation species, *P. teyahalee*, from expanding its range to include higher elevation habitats.

What is responsible for the asymmetries in behaviour response? One suggestion is that it is linked to contrasting population density and the resulting heightened intraspecific aggression in *L. guthega*. Intruder recognition and territorial response are most important in situations where a failure to react appropriately to a threat can have negative consequences, such as injury and loss of shelter or basking resources (Langkilde and Shine 2007). Such consequences are more likely in high density lizard populations (Langkilde and Shine 2007). In areas where lizard densities are low, territorial competition

is expected to be less common (Langkilde and Shine 2004). In the study region, *L. guthega* occurs in high density populations compared to *L. montana*. This may be due to high elevation *L. guthega* being relatively free from competition in colder environments, as lizard species richness decreases with elevation (Fischer and Lindenmayer 2005; our unpublished data). In the sampled population, 33.3% of *L. guthega* individuals collected were missing one or more toes, compared to 14.3% for *L. montana*. Toe injury has been used as a measure of intraspecific aggression in lizards (Vervust et al. 2009). We suggest that higher lizard densities may promote increased selection for agonistic responses such as biting seen in *L. guthega*, and that this could have flow on effects for heterospecific interactions.

### Residency effects

A number of factors have been found to play a role in predicting outcomes of agonistic interactions between lizards. The residency effect—which describes the tendency for territory holders to win conflicts with intruders—is commonly demonstrated (Titone et al. 2017). This pattern is generally thought to be driven by higher levels of aggressive behaviour (such as biting) in residents (Titone et al. 2017), or an increased likelihood of resident lizards initiating fights (Umbers et al. 2012). Our study found that focal lizards of either species were less likely to immediately retreat from the intruder when occupying the basking resource at commencement of trial. Lizards that were not occupying the basking rock at commencement of the trial were often induced to occupy the basking resource once the intrusion began; however, these lizards relinquished the resource more quickly than lizards that had been basking on the rock from the outset.

### Conclusion

Our study found asymmetry in agonistic behaviour in two species of lizard that exhibit elevational replacement. The high elevation endemic *L. guthega* was more likely to attack and bite models, and would likely have a competitive advantage over the more passive *L. montana*. If the high elevation species *L. guthega* is a superior competitor compared to lowland species *L. montana*, then this is a pattern replicated in other

montane taxa including mammals and birds (Gifford and Kozak 2012; Pasch et al. 2013; Barve and Dhondt 2017). To our knowledge, this is the first time such a behavioural pattern has been identified in montane reptiles. High impact climate change scenarios (+ 2.9 °C) in Australia predict the alpine zone will be replaced by subalpine habitat by 2050 (Green et al. 1992; Pickering 2007), reducing the core habitat of *L. guthega* above the tree line, whilst expanding that of lower elevation species *L. montana* (Atkins et al. 2018). This will likely lead to distribution shifts, and increased competition between the two species. We suggest asymmetry in aggressive behaviour will play a role in determination and maintenance of future species distributions in this group. As well as the level of intraspecific competition, the outcome will depend also on the underlying habitat and thermal requirements of each species that will mediate their persistence under ongoing environmental change.

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**Data availability** Data will be deposited on Figshare upon acceptance of the manuscript.

#### Compliance with ethical standards

**Ethical approval** Research was conducted in accordance with appropriate collection and research permits (New South Wales: SL101798) and was approved by the Monash University animal welfare committee (BSCI/2016/24).

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