

Feral horse impacts on threatened plants and animals in sub-alpine and montane environments in Victoria, Australia

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Summary Feral herbivores are a major driver of biodiversity loss globally and can alter the structure, composition and functioning of ecosystems. The direct impacts of feral herbivores on plant communities are well studied, but the direct and indirect effect they have on wildlife is not well understood. In Victoria (south-eastern Australia), a large feral Horse (*Equus caballus*) population coincides with highly sensitive and nationally endangered Alpine *Sphagnum* Bogs and Associated Fens communities, and several threatened animal species. We assessed the impact of feral horses on this ecological community and the Alpine Water Skink (*Eulamprus kosciuskoi*) and the Broad-toothed Rat (*Mastacomys fuscus*) at 20 sites with varying levels of horse disturbance. We used scat counts to determine an index of feral horse abundance and quantified impacts associated with their presence in the landscape. Active searches were used for Alpine Water Skink and scat and runway surveys for Broad-toothed Rat. We also measured the vegetation structure and the abundance of different vegetation types (life forms). Our results suggest that feral horses are associated with vegetation types and characteristics that negatively influence the presence or abundance of Alpine Water Skink and Broad-toothed Rat. Sites with high horse activity had more low-growing forbs, and the abundance of Alpine Water Skink was negatively related to this vegetation type. Grasses, sedges, rushes and shrubs were also less dense and lower in height in high horse activity sites, and Broad-toothed Rat was less likely to be present in areas with these habitat attributes. We recommend that feral horses are controlled to protect these threatened vertebrate species and their *Sphagnum* bog habitat.

Key words: biological invasion, habitat, *Eulamprus kosciuskoi*, feral herbivore, *Mastacomys fuscus*, *Sphagnum* bog.

Introduction

Biological invasion is a major driver of biodiversity loss globally and large, feral herbivores are a prominent group in this regard. These animals can significantly influence the structure, composition and functioning of ecosystems (e.g. Danell *et al.* 2006). One species, the Horse (*Equus caballus*), occurs as feral populations on all continents except Antarctica and occupies a wide range of ecosystems (Beever *et al.* 2008).

Through trampling, pugging, wallowing, herbivory and defecation, feral horses can negatively affect nutrient cycling, soil properties, hydrology, fire regimes and plant and animal communities (e.g. Beever & Brussard 2004; Wright *et al.* 2019). In plant communities across North America, New Zealand and Australia, selective grazing and trampling by feral horses has been

associated with altered vegetation cover, abundance, biomass, structure and richness (e.g. Rogers 1991; Prober & Thiele 2007; Beever *et al.* 2008). In contrast, the impacts of feral horses on wildlife are poorly understood. Feral horses can alter bird species richness and abundance (Zalba & Cozzani 2004) and fish and reptile communities, facilitating increased predation in some instances (Levin *et al.* 2002; Beever & Brussard 2004). Research quantifying the effects of feral horses on native Australian animals is lacking, a concerning knowledge gap considering many threatened species are likely being affected (e.g. Cleemann 2002).

In Australia's temperate, mountainous regions, horses represent a relatively recent (<200 years) and significant threat to ecosystems and native species (Tolsma & Shannon 2018). These regions host diverse and sensitive ecological communities already under

pressure from climate change, changing fire regimes, weed invasion and other exotic animals (e.g. Department of Environment, Water, Heritage and the Arts (DEWHA) 2009; Williams *et al.* 2008). The nationally endangered 'Sphagnum Bogs and Associated Fens' ecological community is particularly vulnerable to disturbance by horses (Tolsma & Shannon 2018; Wright *et al.* 2019). It has a restricted and fragmented geographic range and is dominated by vegetation highly susceptible to trampling (Whitnam *et al.* 2003; DEWHA 2009).

Empirical data on the responses of plant communities and native fauna to feral horses are required to inform and support evidence-based feral horse management. Our study therefore aimed to quantify the effects of feral horses on *Sphagnum* bog communities and two associated threatened animal species. Specifically, we examined the abundance and structure of

vegetation life forms, the presence and abundance of Alpine Water Skink (*Eulamprus kosciuskoi*), and the presence of Broad-toothed Rat (*Mastacomys fuscus*), relative to horse presence, activity and impact.

Methods

Study area

Our study was conducted in north-eastern Victoria, extending south of Cobberas in the Alpine National Park to Nunniong and Nunnet State Forests. The climate is cool and wet with annual, winter snowfalls at high elevations. Mean annual rainfall at the nearby weather station at Falls Creek is 1,274 mm and the mean annual minimum and maximum temperatures are 2.6 and 9.4°C, respectively (Bureau of Meteorology 2018).

We focused on nationally endangered 'Sphagnum Bogs and Associated Fens' ecological communities, henceforth termed *Sphagnum* bogs. Dominant plant species include Candle Heath (*Richea continentis*), Broad-leaf Flower-rush (*Carphe nivicola*), Alpine Baeckea (*Baeckea gunniana*), Alpine Bottlebrush (*Callistemon ptyoides*) and *Sphagnum* Moss (*Sphagnum cristatum* and *Sphagnum novozelandicum*) (Whinam *et al.* 2003; DEWHA 2009). This community is typified by slow-growing, treeless vegetation, soft *Sphagnum* moss and permanent water sources. These traits make it susceptible to damage from hard-hooved animals such as horses (e.g. Wahren *et al.* 2001; DEWHA 2009).

The study area contained approximately 2,500 feral horses in 2014, making it the largest feral horse population in Victoria (Cairns & Robertson 2015). This population is contiguous with feral horses in the Kosciuszko National Park, New South Wales (Cairns & Robertson 2015).

We used 20 of Wright *et al.*'s (2019) randomly selected *Sphagnum* bog sites (1100–1550 m ASL). Sites were required to meet certain criteria such as vehicle access and appropriate habitat attributes for the Alpine Water Skink and the Broad-toothed Rat (Appendix S1). The sites captured natural variation in horse

population density and horse impacts. They were 2,500 m² (100 × 25 m) and contained four evenly spaced 50 m² (25 × 2 m) transects (Fig. S1).

Study species

The Alpine Water Skink (*Eulamprus kosciuskoi*) is a live-bearing reptile found exclusively in montane, sub-alpine and alpine *Sphagnum* bogs along drainage lines (Meredith *et al.* 2003). The species is restricted to this geographically isolated habitat because of its highly specialised habitat requirements (Steane *et al.* 2005). Consequently, deterioration or reduction of this habitat by feral horse grazing and trampling is a significant threat and one reason for its listing under the *Flora and Fauna Guarantee Act 1988* (FFG Act) and critically endangered status in Victoria (Department of Environment, Land, Water and Planning (DELWP) 2018; Department of Sustainability and Environment (DSE) 2013; Meredith *et al.* 2003).

The Broad-toothed Rat (*Mastacomys fuscus*) is a small, herbivorous rodent, listed under Victoria's FFG Act (DELWP 2018) with a conservation status of endangered in Victoria (DSE 2013) and listed as vulnerable by the Commonwealth (Department of Environment and Energy 2018). The species mostly persists in small, disjunct populations in alpine and sub-alpine heathlands, grasslands and sedgeland across south-eastern Australia (Green & Osborne 2003). The Broad-toothed Rat requires abundant vegetation cover and specific plant species for food and shelter (Green & Osborne 2003; Hapold 2008; Menkhorst *et al.* 2008). Their populations have declined considerably since European settlement and research suggests that habitat destruction and modification, climate change and predation from feral predators are major threats to the species (e.g. Seebeck 1971; Green & Osborne 2003; Bilney *et al.* 2010).

Vegetation surveys

We surveyed vegetation structure at 1-m intervals using a structure pole along the length of two 50-m transects (Fig. S1). Vegetation was grouped by life form as either graminoid, moss, forb or shrub and recorded where it touched the pole.

Dominant life forms were also surveyed with line intercepts at 10-cm intervals and combined to calculate the abundance of dominant life forms (hereby termed abundance of life forms) along two transects (Fig. S1).

Fauna surveys

Feral horses

Scat pile counts were carried out across the four transects at each site to acquire an index of feral horse abundance (Fig. S1) (e.g. Neff 1968; Hone 2002). Scats were counted and removed in November 2017 and recounted exactly 50 days later by two observers. This duration was deemed suitable in other summer studies (e.g. Gibson & Kirkpatrick 1989) and by our own scat decomposition plots (Appendix S1). Scats and signs of other native and introduced herbivores (i.e. wallows of deer (*Dama dama* and *Rusa unicolor*)) were recorded to determine whether they could be contributing to the impacts we observed (Appendix S1).

Three indicators were used to assess herbivore impacts and vegetation condition, similar to the methods used by Wright *et al.* (2019). Across the entirety of each site, we recorded grazing disturbance, the degree of pugging (substrate damage by hooves) and the level of impact of defined animal tracks. These indicators were scored out of four where a higher number inferred greater damage.

Alpine Water Skink

To determine Alpine Water Skink abundance and occupancy, we conducted three 30-minute active searches through suitable habitat (*Sphagnum* moss adjacent to water and where bog transitioned with wet heath). All repeat surveys were carried out within approximately 45 days of each other from December 2017 to February 2018 between 9.00 am and 6.00 pm AEDT. This reduced the likelihood of large variations in temperature and subsequent skink activity. All active searches were completed by RC to eliminate observer bias. Temperature, sunlight intensity, sunlight cover, rainfall, wind, cloud cover and Julian date (Table S1) were recorded for

each survey as per Clemann (2002) and Steane *et al.* (2005).

Broad-toothed Rat

Time-constrained scat and runway surveys were used to determine the occupancy of Broad-toothed Rat. Within each site, four transects of 50 m² (25 × 10 m) were searched for five minutes for runways containing fresh (green coloured) scat (Appendix S1).

Other studies suggest that the total area of potential, continuous habitat may be important for both the Alpine Water Skink and the Broad-toothed Rat (e.g. Steane *et al.* 2005; Milner *et al.* 2015). We therefore used ArcGIS version 10.2.2 (ESRI Pty Ltd, Redlands, CA, USA) to measure the area (km²) of all *Sphagnum* bog and wet heathland vegetation that was continuous with the vegetation in each survey site (termed 'habitat area').

Statistical analyses

Feral horse abundance and impacts

The combined herbivore impacts correlated with horse scat counts ($R = 0.50$, $P = 0.024$, Fig. S2) and did not correlate with deer scats ($R = 0.06$, $P = 0.800$). It was therefore reasonable to assume that most of the measured herbivore impacts (hereby termed 'horse impacts') could be attributed to feral horses. We combined horse scat and horse impact to give each site an overall score of horse activity (Appendix S1, Table S2). Using this method, we had an even spread of low, medium and high sites (Table S2), we eliminated the issue of correlation between the impact scores and the scat count and we were able to simplify analysis.

Vegetation structure and abundance

We used nonmetric multidimensional scaling (NMDS) to identify patterns in the structure and abundance of the vegetation life forms with regard to environmental characteristics and horse activity group. Environmental characteristics (elevation, habitat area, horse scat count, pugging damage, grazing disturbance and level of

defined tracks) were fitted as vectors to the ordination diagram to identify those variables that displayed significant trends across the ordination. Analyses of similarities (ANOSIM) based on 9999 permutations was used to determine if there was a difference between the low, medium and high horse activity groups. One-way similarity percentages (SIMPER) with the Bray–Curtis similarity index was then used to determine which life forms and plant heights were most responsible for the differences and similarities between and within the horse activity groups (Clarke 1993). We used PRIMER (version 6.1.16) for these analyses (Clarke & Gorley 2006).

Pairwise correlation analysis revealed collinearity between the vegetation variables that were to be used in the fauna modelling analysis (vegetation structure and life form abundance variables). Principal component analysis was used to reduce multiple, colinear vegetation variables into fewer variables (axes). The same principal components for the abundance of life forms were used for both Alpine Water Skink and Broad-toothed Rat. For vegetation structure, we used different principal components based on the habitat requirements of each species. PCA analysis was performed using JMP 14.0.1 (JMP® 2018).

Alpine Water Skink detection, occupancy and abundance

We used N-mixture models to analyse Alpine Water Skink occupancy and abundance (MacKenzie *et al.* 2005; Fiske & Chandler 2011). The occupancy model was based on the presence or absence of skinks during each survey, whereas the abundance model used the number of skinks detected. The N-mixture model assumes that populations are closed to movement, recruitment and mortality between repeated surveys (Royle 2004). It is likely that Alpine Water Skink populations were closed during our study as they are restricted to geographically isolated habitats (Meredith *et al.* 2003).

For detectability, occupancy and abundance analysis, we modelled all additive combinations of the predictor variables (Appendix S1). We included the best

detection covariates in the occupancy and abundance analysis (Appendix S1). We analysed the life form abundance and vegetation structure principal components in two distinct sets of models as they were highly correlated with each other. Models were ranked according to Akaike's Information Criterion corrected for small samples (AICc) to determine which variables best explained the data. Models with the lowest AICc value and models with AICc values that were no more than 2 from the best model ($\Delta\text{AICc} < 2$) were considered to have equal support (Burnham & Anderson 2002). For the abundance models, we varied the 'tuning parameter' K to confirm model stability and identifiability, that is parameter estimates and AICc values did not change as K increased (Kéry 2017). We plotted the predicted values of the parameters that appeared in the best models to better understand their effects on Alpine Water Skink. If parameters appeared in more than one best model and the effect was similar, only the effect from the model with the lowest AICc was plotted. Analyses were undertaken in R version 3.5.1 (R Core Team 2018) using the unmarked and effects packages (Fox 2003; Fiske & Chandler 2011).

Broad-toothed Rat occupancy

To determine the influence of environmental factors on the occupancy of Broad-toothed Rat, a generalised linear mixed-effects model (GLMM) with a binomial distribution was fitted using the lme4 package (Bates *et al.* 2015). N-mixture modelling was not suitable as the long-lasting nature of the species' signs and scats did not meet the requirements for independent detections (Royle 2004). This mixed-effects model enabled the addition of an observation level random factor, which is a method of accounting for some types of overdispersion (Harrison 2014). As with Alpine Water Skink, we used two global models with the principal components for vegetation structure or abundance of life forms and habitat area and horse activity group. Models were compared by their AICc, ΔAICc and AICc weight values (Burnham & Anderson

2002; Quinn & Keough 2002). If the standard error estimates overlapped zero, the effect was considered to be associated with uncertainty (Burnham & Anderson 2002; Symonds & Moussalli 2011). Analyses were undertaken in R version 3.5.1 (R Core Team 2018) using the lme4 package (Bates *et al.* 2015) and MuMIn package (Barton 2018).

Results

Feral horse abundance and impacts

Horses were more active than deer in our study region. All sites except one had clear evidence of horse impacts and scat, seven sites (35%) had evidence of deer. Two sites contained deer wallows, one of which also had a relatively high deer pellet count (Table S2). However, eighteen sites (90%) had higher counts of feral horse scat than deer scat. Pig impacts and scat were not observed in any site.

Vegetation and feral horses

NMDS ordinations revealed some separation between sites of different horse activity for vegetation structure (Fig. 1a). This was supported by ANOSIM analysis (global $R = 0.25$, $P = 0.007$) (Fig. 1a). The strongest separation was between low and high horse activity sites which were 33.3% dissimilar to each other ($R = 0.57$, $P = 0.002$) (Table S4). Four vegetation variables contributed to more than 10% of the variation between low and high horse activity sites. Low horse activity sites had higher values for graminoid (20–40 cm and 40–70 cm) and shrub structure (40–70 cm and >70 cm).

The abundance of vegetation life forms differed slightly between sites according to horse activity (global $R = 0.135$, $P = 0.05$), with a small amount of separation evident on the ordination (Fig. 1b). Pairwise comparisons revealed this difference was between low and high horse activity sites only ($R = 0.35$, $P = 0.015$). Four variables explained more than 10% of the variation between low and high horse activity sites (Table S4). Low horse activity sites had a greater mean abundance of shrubs and moss, and lower

mean abundance of graminoids and forbs (Table S4).

Two principal component axes were used to combine variables for the abundance of dominant life forms. These principal component axes explained 70% of the variation in the abundances of life forms (Table 1a) and were used for both Alpine Water Skink and Broad-toothed Rat analyses. Life form PC1 described a gradient of increasing water, moss and bare ground and decreasing graminoids. Life form PC2 described increasing graminoids and decreasing shrubs. We also used two principal component axes to combine vegetation structure variables for moss and forb (used for Alpine Water Skink analysis) and shrub, graminoid and forb (used for Broad-toothed Rat analysis). For Alpine Water Skink, the two PCs accounted for 68% of the variation of the total variance matrix. Moss PC described a gradient of increased moss structure across all height increments. Forb PC described a gradient of increased forb structure from 0 to 20 cm, which were the heights at which the vast majority of forbs were measured (Table 1b). For Broad-toothed Rat, the PCs accounted for 60% of the variance of vegetation structure. Graminoid/shrub PC described a gradient of increased graminoid and shrub structure above 20 cm. Forb/shrub PC described a gradient of increased forb structure and decreased shrub structure 20–70 cm (Table 1c).

Alpine Water Skink and feral horses

Alpine Water Skinks were detected at 10 sites (50%) and had a high probability of detection (0.83). There were two best models for occupancy in both the life form and the vegetation structure model groups. Habitat area appeared in the best-supported models for both model groups (Table 2), followed by the null model. This suggests that there is uncertainty with these results. The probability that a site was occupied by Alpine Water Skink increased with increasing habitat area, although this relationship was weak (Fig. 2a).

Detectability analysis revealed that Julian date and wind, and Julian date on its own, were the most appropriate detection covariates for the abundance model (Table 2, Fig. S3). Taking detection probability into account, the null model was the best model of Alpine Water Skink abundance for the life form model group. The moss and forb PCs appeared in the best models for vegetation structure when Julian date only was included as a detection covariate. The forb PC alone was the best predictor variable when both Julian date and wind were included as detection covariates (Table 2). Alpine Water Skink abundance decreased in areas with more low-growing forbs (Forb PC, Table 1) (Fig. 2b), and increased in areas with more structurally complex moss (Moss PC, Table 1) (Fig. 2c).

Broad-toothed Rat and feral horses

Broad-toothed Rat scats and runways were recorded at 11 sites (55%) and detected in 30% of the transects. There was more than one best occupancy model and all of the vegetation PCs appeared in the best models (Table 2). The probability that a site was occupied by Broad-toothed Rat increased with denser and taller graminoids and shrubs above 20 cm (graminoid/shrub PC, Table 2) (Fig. 3a) and the abundance of moss, water (life form PC 1, Table 1) and shrubs (life form PC 2, Table 1) (Fig. 3b,c). Occurrence probability decreased with increasing forbs (forb/shrub PC, Table 1) (Fig. 3d) and abundance of graminoids (life form PC1 and 2, Table 1) (Fig. 3b,c,k). 95% confidence intervals of all parameters except graminoid/shrub PC overlapped zero suggesting substantial variability among sites (Fig. 3).

Discussion

Large-bodied, hard-hooved herbivores can substantially affect ecosystem structure, composition and condition (e.g. Danell *et al.* 2006). Feral horses are one such invasive herbivore that is altering Australian ecosystems (Tolsma & Shannon 2018). Our results suggest that feral horses could drive changes in vegetation that negatively influence the presence or

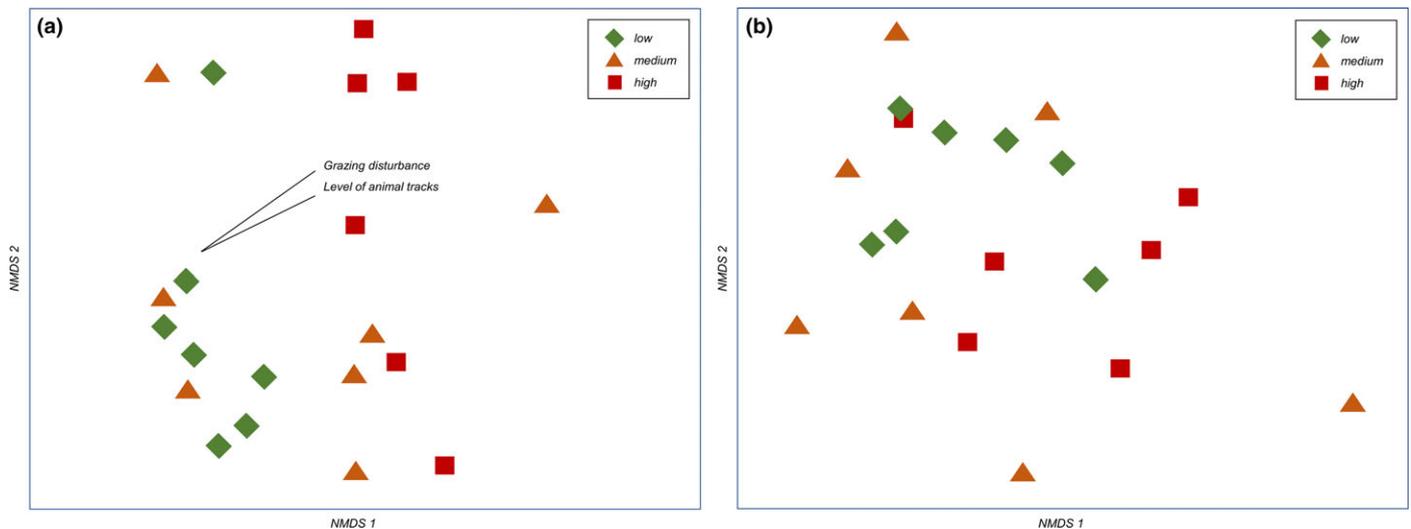


Figure 1. Ordination NMDS of bog sites in north eastern Victoria (Australia), based on (a) the structure of vegetation life forms (stress 0.12) and (b) the mean abundance of life forms including bare ground, leaf litter and water (stress 0.11) with different levels of horse activity (l = low, m = medium, h = high). Vectors of maximum correlation are included, representing grazing disturbance and level of impact of defined animal tracks ($R^2 = 0.50$).

Table 1. Principal components (unrotated) of (a) the abundance of dominant life forms (b) moss and forb structure at heights which are likely to influence Alpine Water Skink, and (c) graminoid, shrub and forb structure at heights which are likely to influence Broad-toothed Rat, in bogs across north-eastern Victoria (Australia)

(a). Life form abundance variables	PC1	PC2	(b). Vegetation structure variables – Alpine Water Skink	Moss PC	Forb PC	(c). Vegetation structure variables – Broad-toothed Rat	Graminoid/shrub PC	Forb/shrub PC
Water	0.57	0.15	Moss 0–10 cm	0.49	-0.15	Gram 20–40 cm	0.34	-0.13
Bare ground	0.33	0.18	Moss 10–20 cm	0.52	-0.10	Gram 40–70 cm	0.46	0.14
Moss	0.58	0.19	Moss 20–40 cm	0.50	-0.06	Gram > 70 cm	0.37	-0.04
Graminoid	-0.48	0.56	Moss 40–70 cm	0.42	-0.04	Shrub 20–40 cm	0.27	-0.45
Shrub	-0.02	-0.77	Forb 0–10 cm	-0.08	0.71	Shrub 40–70 cm	0.47	-0.27
			Forb 10–20 cm	0.20	0.68	Shrub >70 cm	0.43	-0.27
			Forb 20–40 cm	0.11	-0.01	Forb 20–40 cm	0.10	0.55
Eigen value	1.92	1.59	Eigen value	3.38	1.38	Eigen value	3.30	1.51
Variation (%)	38.41	31.70	Variation (%)	48.27	19.75	Variation (%)	41.23	18.89
Cumulative variation (%)	38.41	70.11	Cumulative variation (%)	48.27	68.01	Cumulative variation (%)	41.23	60.12

Values in bold represent factor loadings contributing most to each axis.

abundance of Alpine Water Skink and Broad-toothed Rat. Sites with high horse activity supported a greater abundance of forbs, a vegetation type that was negatively associated with Alpine Water Skink abundance. Graminoids and shrubs were less dense and lower in height in high horse activity sites, and Broad-toothed Rat was less likely to be present in areas with these habitat attributes. Our findings add to a growing body of research

indicating that feral horses alter *Sphagnum* bog communities and hence co-occurring, habitat-dependent species may also be indirectly adversely affected.

Impacts of feral horses on bog vegetation

At low horse activity sites, shrubs and moss were more abundant and shrubs and graminoids were denser and taller. Horse grazing and trampling are known

to reduce the overall height and density of palatable, small woody and soft moss species (e.g. Dyring 1990; Prober & Thiele 2007). The impact of horses on *Sphagnum* moss is particularly severe because of its soft life form and its association with water, a limiting resource for horses (Williams 2019), and with palatable species such as *Carex* spp. (Dyring 1990). Conversely, we found that sites with high horse activity were dominated by forbs

Table 2. A model selection summary for Alpine Water Skink detection, occupancy and abundance and Broad-toothed Rat occupancy in bogs across north-eastern Victoria (Australia) for two different global model groups – vegetation structure (structure) and abundance of dominant vegetation life forms (abundance)

Global model group	Species	Model type	Best detection model	Best occurrence/abundance model	AICc	Δ AICc	w_i	Rsq
N/A	Alpine Water Skink	Occupancy detection only	~ 1	N/A	69.02	0.00	0.71	0.00
Abundance	Alpine Water Skink	Occupancy + detection	~ 1	~ Habitat area	67.09	0.00	0.61	0.32
Abundance	Alpine Water Skink	Occupancy + detection	~ 1	~ 1	69.02	1.93	0.23	0.00
Structure	Alpine Water Skink	Occupancy + detection	~ 1	~ Habitat area	67.09	0.00	0.63	0.32
Structure	Alpine Water Skink	Occupancy + detection	~ 1	~ 1	69.02	1.93	0.17	0.00
N/A	Alpine Water Skink	Abundance detection only	~ Julian date + wind	N/A	277.59	0.00	0.46	0.87
N/A	Alpine Water Skink	Abundance detection only	~ Julian date	N/A	278.09	0.50	0.36	0.71
Abundance	Alpine Water Skink	Abundance + detection	~ Julian date	~ 1	278.09	0.00	1.00	0.00
Abundance	Alpine Water Skink	Abundance + detection	~ Julian date + wind	~ 1	277.59	0.00	1.00	0.00
Structure	Alpine Water Skink	Abundance + detection	~ Julian date	~ Forb PC	249.79	0.00	0.67	0.84
Structure	Alpine Water Skink	Abundance + detection	~ Julian date	~ Moss PC + forb PC	251.17	1.39	0.33	0.92
Structure	Alpine Water Skink	Abundance + detection	~ Julian date + wind	~ Forb PC	244.35	0.00	0.99	0.86
Abundance	Broad-toothed Rat	Occupancy	N/A	~ 1	62.71	0.00	0.28	0.40
Abundance	Broad-toothed Rat	Occupancy	N/A	Life form PC1	63.88	1.17	0.16	0.45
Abundance	Broad-toothed Rat	Occupancy	N/A	Life form PC2	64.32	1.61	0.13	0.44
Structure	Broad-toothed Rat	Occupancy	N/A	Graminoid/shrub PC	60.33	0.00	0.37	0.54
Structure	Broad-toothed Rat	Occupancy	N/A	Graminoid/shrub PC + forb/shrub PC	61.73	1.40	0.18	0.58

Models shown are those with delta AICc < 2.0. Akaike's Information Criterion corrected for small samples (AICc), Δ AICc, delta weights (w_i), likelihood-ratio based pseudo r -squared value (Rsq).

and graminoids to a greater extent than those with low horse activity. Other studies have recorded similar results in response to cattle, sheep and horse grazing and trampling (e.g. Gibson & Kirkpatrick 1989; Prober & Thiele 2007; Evju *et al.* 2009). Many forbs and graminoids are more resistant to, and better able to cope with, trampling compared with upright, woody species and may therefore increase in abundance in high horse activity areas (e.g. Dyring 1990 and references within). It is also possible that horses were acting as vectors for herbaceous weeds to enter the area (e.g. Beever *et al.* 2008; Ansong & Pickering 2013). Common weed species in this region include Ribgrass (*Plantago lanceolata*), White Clover (*Trifolium repens*) and Flatweed (*Hypochoeris radicata*) (Prober & Thiele 2007; Tolsma & Shannon 2018), all of which were recorded in our study sites.

Australian *Sphagnum* bogs also have a natural successional process whereby tall sedges, rushes, shrubs and *Sphagnum* moss colonise on top of and outcompete, grazing-resistant forbs (Wimbush & Costin 1979a,b; Wahren *et al.* 2001). This natural process is disrupted by large, introduced

herbivores that trample and damage bog and heathland vegetation and increase water channelling, creating favourable conditions for some forb species. This could explain why we detected more forbs and graminoids and less shrubs and moss in sites with high horse activity. A transformation of wet bogs into different, degraded ecosystem states has been observed elsewhere (e.g. Wimbush & Costin 1979a,b; Wahren *et al.* 2001; Tolsma & Shannon 2018).

We suggest that habitat selection by horses may also have contributed to our results. Sites dominated by herbaceous vegetation may be easier for horses to access and contain higher quality forbs and grasses for grazing (Duncan 1983; Dyring 1990). These sites may be preferred by horses and consequently have greater horse activity than shrubby sites. Similarly, *Sphagnum*-dominated areas may be selected because of their association with water and *Carex* spp. (Dyring 1990; Williams 2019). Hence, *Sphagnum*-dominated sites may be used to a greater extent, which leads to a reduction in the structure of *Sphagnum* moss from horse trampling until low horse activity sites (possibly

naturally shrubbier) and high horse activity sites (possibly naturally mossier) have similar amounts of *Sphagnum*. As our study is correlative, it is impossible to ascertain the extent to which habitat selection vs. habitat modification contribute to our results. However, the possibility of habitat modification by horses is supported by numerous previous studies (e.g. Prober & Thiele 2007; Beever *et al.* 2008).

Impacts of feral horses on Alpine Water Skink

The Alpine Water Skink was less abundant in areas with more forbs. These areas tended to have higher horse activity, an associated decrease in shrub and graminoid structure, and a lower abundance of moss. The Alpine Water Skink requires extensive live vegetation cover, particularly *Sphagnum* moss, for foraging, thermoregulation and protection from predators (Clemann 2002; Meredith *et al.* 2003; Steane *et al.* 2005). Areas with increased forbs likely represent unsuitable habitat for the species. We suggest that horses could indirectly, negatively impact Alpine Water Skink by driving vegetation change that compromises survival.

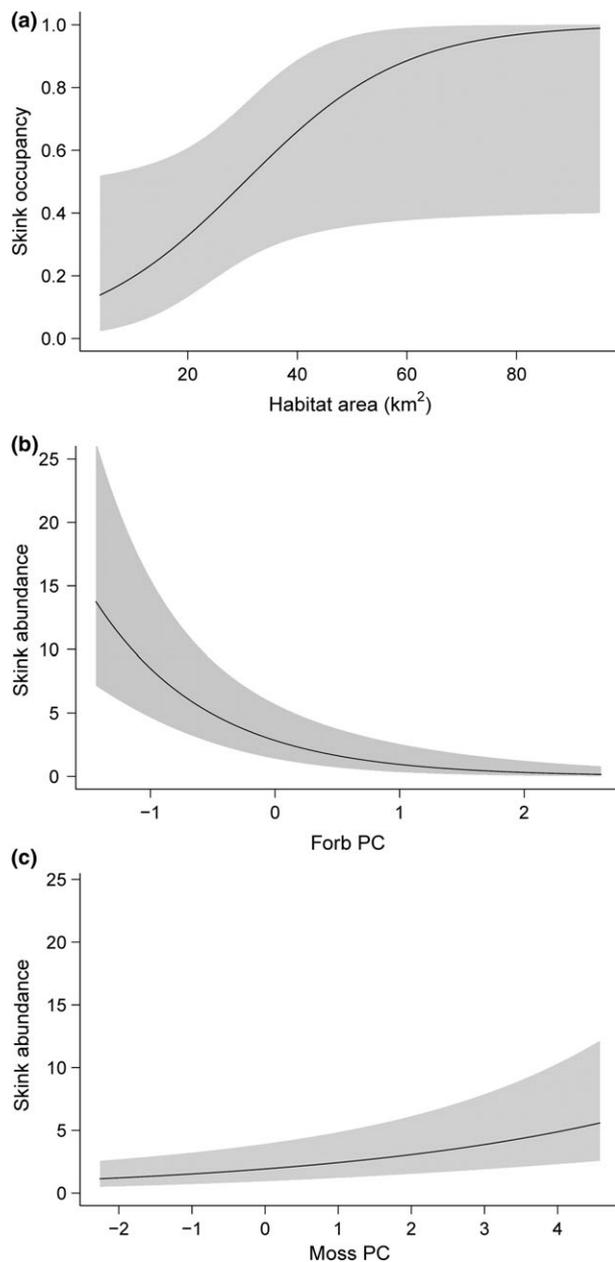


Figure 2. The influence of (a) suitable habitat area (km²) on the occupancy, (b) low-growing forb structure (forb PC) and (c) moss structure (moss PC) on the abundance, of Alpine Water Skink in bogs across north-eastern Victoria (Australia).

Monitoring the survival of individual skinks and populations through time, in horse affected and horse-free areas, is needed to test this hypothesis.

Previous research has suggested that Alpine Water Skink abundance is strongly positively associated with *Sphagnum* moss (Steane *et al.* 2005); however, we detected only a weak relationship between the species' abundance and this vegetation. It is possible that this reflects

our modest sample size (20 sites). However, we did observe some skinks in areas with very small amounts of *Sphagnum* moss and high horse impacts, such as on Native Cat Flat. Here, we found three adults and a juvenile around an isolated *Sphagnum* moss hummock less than 3 m² after the survey had finished. This suggests that Alpine Water Skink was persisting and breeding at the site. However, given the small area of suitable habitat, the

likelihood of these animals persisting in the long term may be low, particularly as horse trampling has the potential to completely drain bogs and cause a subsequent disappearance of suitable bog and wet heathland habitat (e.g. Wahren *et al.* 2001; DEWHA 2009). Alpine Water Skink populations may also become increasingly fragmented and isolated as suitable habitat is altered and damaged, particularly as the species has limited dispersal (Meredith *et al.* 2003; Steane *et al.* 2005). We detected a positive relationship between skink occupancy and area of *Sphagnum* bog and heathland habitat (suitable habitat area). This further supports the hypothesis that, although Alpine Water Skink may be somewhat resilient to habitat disturbance by feral horses, once suitable habitat (moss and shrub) is lost entirely and forbs become abundant, the species is likely to decline. Further examination of the role of moss in promoting lizard resilience to horse impacts is required, but this possible lag time between partial moss loss and local extinction of lizards offers a window of opportunity for ecosystem and Alpine Water Skink population recovery.

Impacts of feral horses on Broad-toothed Rat

Grazing can alter habitat suitability for small mammals by reducing vegetation cover and complexity (e.g. Eccard *et al.* 2000). In this study, Broad-toothed Rat was strongly positively associated with complex graminoid and shrub structure (above 20 cm). Thick vegetation reduces the exposure of these rodents to predation from foxes, cats, wild dogs (*Canis* spp.) and birds of prey (Green & Osborne 2003). Abundant heath and grass are also required for runways and grass nests, particularly in winter when they act as insulation from cold temperatures and snow, allowing Broad-toothed Rat to remain active and forage during this time (e.g. Green & Osborne 2003; Happold 2008; Menkhurst *et al.* 2008). Feral horses typically reduce vegetation cover and structure (e.g. Prober & Thiele 2007, and this study), lowering habitat suitability and resource availability and hence possibly affecting Broad-toothed Rat. This may also expose the species to greater predation

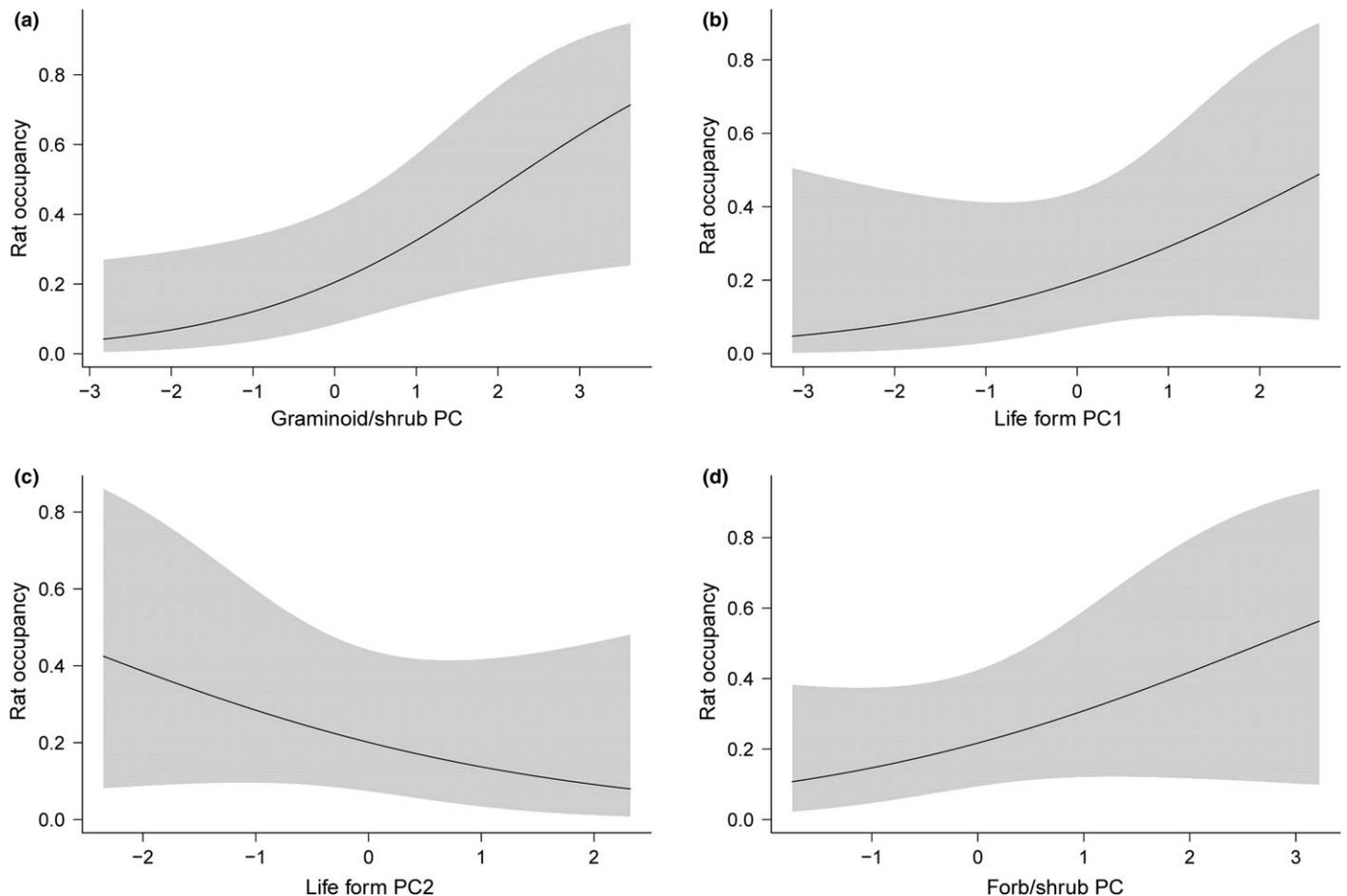


Figure 3. Environmental variables influencing the occupancy of Broad-toothed Rat in bogs across north-eastern Victoria (Australia).

(Green & Osborne 2003) and we recommend further studies on the possible interaction between habitat simplification and increased predation (Doherty *et al.* 2015) of Broad-toothed Rat resulting from horse grazing and trampling. Our findings are consistent with Schulz *et al.* (this volume), Belcher and Leslie (2011) and Green and Osborne (2003), who reported negative impacts of grazing and trampling on Broad-toothed Rat. The positive association we detected between Broad-toothed Rat occupancy and increased abundance of moss, water and shrubs also fits this explanation as these areas tended to have low horse activity and denser vegetation as a result. We suggest horses have the potential to indirectly, negatively impact Broad-toothed Rat by driving a change in vegetation structure and abundance.

Our findings suggest Alpine Water Skink and Broad-toothed Rat appear threatened to varying extents by the

impacts of horses on their habitat, and this is consistent with the global literature examining the ecological effects of feral herbivores on native wildlife. Ballinger and Congdon (1996) studied populations of the bunch grass lizard (*Sceloporus scalaris*) in south-eastern Arizona and found that cattle grazing reduced native grasses required to protect the lizard from predators and harsh winter conditions. This was associated with a subsequent decline in the bunch grass lizard population. Similarly, Eccard *et al.* (2000) evaluated the response of numerous small mammal species to livestock grazing and exclusion over a 10-year period in South Africa. They found that small mammal species responded in a variety of ways to livestock grazing, but that specialist, primarily herbivorous species were negatively affected.

We did not observe any direct effects of feral horses on Alpine Water Skink and Broad-toothed Rat and both species are

occurring in areas of relatively high horse abundance and impact compared with other alpine regions in Australia (Wright *et al.* 2019). However, we did not investigate the population dynamics or behaviour of either species or explore how their survival and persistence is being affected long term and at what scale. Such high horse numbers are a relatively recent phenomenon and our sample of twenty sites was modest compared to the geographic extent of feral horses in Australia's alpine and montane ecosystems. There was also substantial site-to-site variability, leading to variability and uncertainty in some of the patterns we observed. Our results, for example, can be compared with Schulz *et al.* (this edition), who used 180 sites and found unambiguous and strong negative effects of feral horses on Broad-toothed Rat and widespread declines of the species to the north of our study region.

Management implications and future research directions

Our results support a growing body of evidence demonstrating that feral horses are detrimental to threatened *Sphagnum* bog vegetation. As a result, co-occurring, habitat-dependent species such as the Broad-toothed Rat and the Alpine Water Skink are indirectly, negatively affected. While it is important to gather further information about the expected trajectory of bogs and native fauna exposed to already high or increasing feral horse numbers, the broad body of evidence in the literature provides a firm basis for taking management action now. In the absence of feral horse removal, bog habitat appears likely to further decline, posing an extinction risk to this ecosystem type and its associated native animals. Finally, it appears skinks and rodents have survived to varying extents in the presence of horses, meaning there is an opportunity to increase their numbers if the impacts of horses are reduced or removed.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Extended methods.

Figure S1. Survey methods used to determine the impacts of feral horses on vegetation and other animals in bogs across north eastern Victoria (Australia).

Figure S2. Scatterplot of the relationship between the combined herbivore impact score (grazing disturbance, degree of pugging and the level of impact of defined animal tracks) and horse scat counts ($R = 0.50$, $P = 0.024$) in bogs across north eastern Victoria (Australia).

Figure S3. The influence of a. Julian date and b. wind on the detection probability of Alpine Water Skink based on abundance data in bogs across north eastern Victoria (Australia).

Table S1. Survey covariates measured during Alpine Water Skink active searches in bogs across north eastern Victoria (Australia).

Table S2. Horse scat count, horse scat score, score for the combined indicators of horse impact (degree of pugging, level of impact of defined animal tracks and grazing disturbance), horse activity score, horse activity group, deer scat count and record of deer wallows in bogs across north eastern Victoria (Australia).

Table S3. The mean similarity (%) (SIMPER analysis) within low, medium and high horse activity groups for abundance of dominant life forms and vegetation structure in bogs across north eastern Victoria (Australia).

Table S4. The mean dissimilarity (%) (SIMPER analysis) between high and low horse activity sites for abundance of dominant life forms and vegetation structure in bogs across north eastern Victoria (Australia).