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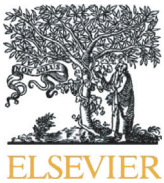
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Horse Activity is Associated with Degraded Subalpine Grassland Structure and Reduced Habitat for a Threatened Rodent

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Horse Activity is Associated with Degraded Subalpine Grassland Structure and Reduced Habitat for a Threatened Rodent

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ABSTRACT

Feral (wild) horses present significant challenges for landscape managers. A major effect of horses is trampling, which erodes soil and alters vegetation cover, which is often critical habitat for threatened animals. We examined the direct and indirect impacts of horses, kangaroos, and rabbits on the broad-toothed rat (*Mastacomys fuscus*), a threatened rodent in subalpine grasslands in Kosciuszko National Park, which contains a large wild horse population. Our objective was to examine the relationship between the activity of different herbivores and 1) structural attributes of the vegetation (cover and density of different plant groups) and 2) length of broad-toothed rat runways and the presence of scat along these runways as proxies of broad-toothed rat activity. We assessed herbivore activity and measured vegetation cover, structure, and richness and total length of runways used by broad-toothed rats as a measure of activity. We used structural equation modeling to test the hypothesis that horse activity would lead to reductions in rat habitat directly, by increasing disturbance, and indirectly, by altering vegetation structure. Quadrats showing no evidence of horse activity had longer broad-toothed rat runways, taller but fewer grasses, double the shrub cover, and lower plant richness than quadrats showing evidence of horse activity. Structural equation modeling showed that there were no significant direct associations between horse activity and rat activity. However, increasing horse activity was associated with an indirect negative effect on broad-toothed rat activity by suppressing the positive relationship between grass height and rat activity. There were no significant effects of rabbits on any environmental variables, and kangaroo grazing was associated with an increase in shrub cover only. Disturbance by horses likely alters vegetation structure, by reducing grass height, making it less suitable for broad-toothed rats, thereby reducing their populations. Horses should be restricted from accessing critical broad-toothed rat habitat.

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Introduction

Unmanaged feral or wild horses (*Equus caballus*), also known as brumbies or mustangs, present substantial challenges for landscape managers worldwide (Zalba and Cozzani, 2004; Nimmo and Miller, 2007; Boyd et al., 2017). Horse impacts span a wide range of terrestrial biomes including drylands (Symanski, 1994), riparian areas (Nimmo and Miller, 2007), wetlands (Turner, 1987) and alpine environments (Dyring, 1990). Feral horses, or “wild” horses, as they are referred to in some states of Australia, are regarded as pests because they threaten native wildlife by competing for food, water, and habitat of native species (Hall et al., 2016). One of the most pervasive impacts of horses is

trampling (Butler, 1995), which often results in detrimental and irreversible effects on soil structure, soil quality, and plant species composition (Hobbs, 1996; Augustine and McNaughton, 1998). Trampling leads to erosion either directly by hoof action, or indirectly, by removing plant cover through soil compaction (Beever and Herrick, 2006), reducing infiltration and soil stability, and increasing the risk of runoff and erosion (Aksakal et al., 2011). The direct and indirect effects of horses can be substantial.

The degree to which horses modify vegetation is related to complex interactions among soils, climate, landscape features, and the characteristics of the plant community (Hobbs, 1996). In drylands, the impacts of horse activity appear to be density dependent and mediated by abiotic conditions such as rainfall (Milchunas et al., 1988), whereas riparian areas are much more sensitive to year-round horse activity (Ostermann et al., 2008). Horse grazing has been shown to reduce the density and recruitment of shrubs in both riparian and dryland area (Davies et al., 2014). Horses often graze preferentially in riparian

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areas, reducing vegetation biomass, diversity, height, and cover and altering plant community composition (Ganskopp and Vavra, 1986; Davies et al., 2014; Zeigenfuss et al., 2014). Together these effects can lead to reduced riparian function by reducing the cover of deep-rooted plants and destroying streambanks as they congregate close to water (Turner, 2015).

Changes in the vertical structure of vegetation and shifts in plant functional group composition can have strong impacts on the suitability and availability of habitat for a variety of riparian wildlife species (Levin et al., 2002). For example, surveys by Boyd et al. (2017) of riparian vegetation within sagebrush steppe rangelands in northwestern Nevada showed that Brewer's blackbird (*Euphagus cyanocephalus*) nested almost exclusively in the tall sedges that occurred only in horse-free exclosures. These changes in vegetation structure and streambank quality have been shown to have cascading effects across multiple species, with reports of feral horse populations adversely affecting invertebrates (Ostermann-Kelm et al., 2009), small mammals (Beever and Brussard, 2004), birds (Zalba and Cozzani, 2004), and estuarine fauna (Levin et al., 2002).

Australia has one of the largest feral horse populations in the world. There are an estimated 6 000–8 000 horses distributed over ~3 450 km² of Australia's iconic Kosciuszko National Park (OEH, 2016), which contains a large proportion of Australia's alpine environments. The horse population at Kosciuszko National Park is estimated to be increasing by 6–17% annually (Cairns, 2014). The impacts of horses in Kosciuszko National Park exacerbate existing threats to alpine species, which are vulnerable to human-induced ecosystem changes, such as modified fire regimes and climate change. Alpine soils are particularly sensitive to compaction, highly erodible, and therefore more susceptible to trampling than soils from other Australian environments (Whinam and Comfort, 1996). For example, Dyring (1990) found that only 20–50 passes of an unshod horse create significant compaction on dry alpine soils. Within the park, soil and vegetation disturbance due to horse activity is concentrated in bogs and riparian areas associated with subalpine grasslands and heathlands (Dyring, 1990). These environments recover slowly from large herbivore damage during short summer growing seasons (Montague-Drake, 2005). These sites are also critical habitats for a number of threatened species including a number of alpine skinks (*Pseudemoia cryodroma*, *Cyclodomorphus praealtus*, *Eulamprus kosciuskoi*), the alpine spiny crayfish (*Euastacus crassus*), alpine tree frog (*Litoria verreauxii alpina*), and the broad-toothed rat (*Mastacomys fuscus mordicus*) (O'Brien et al., 2008).

Here we examine the direct effects of horse activity on vegetation structure in subalpine grasslands in Kosciuszko National Park and the direct and indirect effects on the broad-toothed rat, a threatened rodent. The broad-toothed rat is a nocturnal subniveal rodent that was once widespread across alpine and subalpine areas of eastern Australia (Green and Osborne, 2003; Woinarski et al., 2014). Broad-toothed rats are highly dependent on large, dense native grasses that offer critical shelter and foraging habitat and form a major component of their diet (Carron et al., 1990). These large tussock grasses occur as the dominant feature in the groundstorey of heathlands, grasslands, and occasionally woodlands and forests (Wallis et al., 1982; Green and Osborne, 2003). During summer, broad-toothed rats nest in burrows beneath the soil,

but during winter, they den communally in nests constructed of shredded grasses beneath the snow in dense undergrowth or under logs (Bubela and Happold, 1993). Winter survival of broad-toothed rats is critically dependent on tall grasses, which the rats use to create runways between tussocks so that they can continue to forage beneath deep snow packs. In summer these runways provide protection from predators. Given their strong dependency on grass structure, they are highly susceptible to processes that reduce native grass cover. A 10-yr study of broad-toothed rats in the Long Plain region of Kosciuszko National Park showed that their numbers declined only where horses were present and that habitat was primarily degraded by two mechanisms: grazing of tussocks and trampling of intertussock spaces (OEH, 2016). However, we still have a relatively poor understanding of the effects of horses and different herbivores such as kangaroos (*Macropus* spp.) and European rabbits (*Oryctolagus cuniculus*) on alpine systems, as well as how they might affect habitat for rats and other grassland-dependent vertebrates both directly, for example, by competing directly for food or by interrupting their daily activity, and indirectly, by removing grass cover and, therefore, altering critical habitat.

We used structural equation modeling to explore the direct and indirect effects of grazing on broad-toothed rats. We measured the total length of runways created by rats and the presence or absence of scats along these runways as proxies of broad-toothed rat occupancy and activity. We expected that increasing intensity of grazing by horses would be strongly associated with reductions in broad-toothed rats directly, by altering their behavior (e.g., foraging patterns (pathway 1, Fig. 1), and indirectly, by altering vegetation structure (pathway 3 via 2; Fig. 1). We therefore measured the structural components of the vegetation, including the cover of different vegetation components, grass butt (tussock grass base) density, grass height, and plant richness. Vegetation height and cover are critical to ensure broad-toothed rat survival over winter. Increased disturbance and reductions in plant height would therefore likely reduce the quality of broad-toothed rat habitat leading to reduced abundance. Our systems-based, a priori model (see Fig. 1) also included the activity of two other herbivores: kangaroos and European rabbits that co-occur throughout subalpine grasslands.

Methods

Study Area

This study was conducted in the Kiandra, Long Plain, Cooleman, and Tantangara regions of Kosciuszko National Park, in the Snowy Mountains of New South Wales in southeastern Australia (–35.6° to –35.9°, 148.5° to 148.7°). The area has an average elevation of 1 400 m above sea level and receives about 1 600 mm rainfall annually (BOM, 2017). The region has a mean annual temperature range of 6.1°C to 20.7°C in summer (January), and –4.7°C to 3.9°C in winter (July; BOM, 2017). Soils in the areas have weathered from granitic and sedimentary parent rock and consist of sandy alpine humus loam on gently sloping sites and peat lithosols in shallow valleys with impeded drainage.

Our sample areas were located close to drainage channels in open grassy plains and grassy woodland foothills of timbered ridges. We

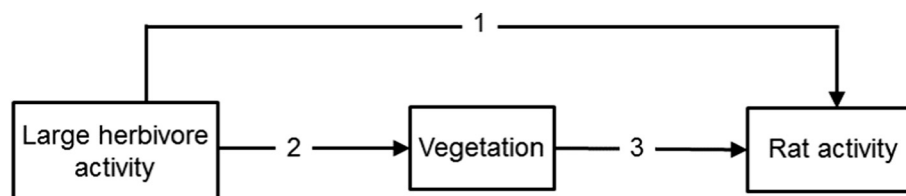


Figure 1. A priori model of the direct (pathway 1) and indirect (pathways 2 and 3) impacts of large herbivores (horse, kangaroo, rabbit, wombat) activity, via alterations to structural/compositional attributes of the vegetation (shrub, grass and sedge cover, grass height, grass density, plant richness) on our proxy of broad-toothed rat activity (runway length).



Figure 2. General view of the riparian area showing tracks created by horses and taller grasses in the foreground and grazing lawn and eroded bank close to the stream bed.

sampled along drainage lines and streams, most of which were perennial (Fig. 2), though two sites were on ephemeral streams emanating from natural springs. Most streams were deeply incised, of low sinuosity and low slope, with a width-to-depth ratio < 5 and channel material dominated by gravels and channels. Channels exhibited a wide range of condition states, from intact, high-condition, deeply incised channels to heavily eroded channel banks at sites where horses have created tracks to reach riparian vegetation. Snowfall in the area is highly variable among years, and therefore snowmelt has a variable impact on stream size and flow rates. The vegetation on these lower slopes and plains surrounding the channels was dominated by small-leaved shrubs, herbs, and tussock grasses, which have functional adaptations to survive a high number of frost days and snowfall (e.g., seasonal dormancy; Keith, 2004). Dominant species included snow grasses (*Poa* spp.), wallaby grasses (*Rhytidospermum* spp.), sedges (*Carex* spp.), and Sphagnum moss (*Sphagnum* spp.), which are typically found on level or gently sloping valley floors (Codd et al., 1998). In areas of high horse density (0.031 horses ha^{-1} ; Cairns 2014), large native tussock grasses were generally absent and often replaced with a high density and cover of exotic annual and perennial forbs such as *Potentilla recta* L., *Aphanes inexpectata* W. Lippert, *Poa compressa* L., *Bromus* spp., *Veronica arvensis* L., *Veronica anagallis-aquatica* L., *Lotus uliginosus* Schkuhr, *Lotus corniculatus* L., *Crepis capillaris* (L.) Wallr., *Symphytum officinale* L., *Achillea millefolium* L., *Hypericum perforatum* L., and *Medicago* spp.

Site Establishment and Animal Activity

We preselected 30 sites in lowland grasslands along natural drainage lines using topographic maps and local knowledge. Sites were located a minimum distance of 1 km apart, and each site consisted of a 200 m transect running parallel to, and 10 m away from, the channel, and following the contours of the drainage line. Within each site we placed five large square quadrats (25 m^2) equidistant along the transect (i.e., 0 m, 50 m, 100 m, 150 m, and 200 m).

To assess herbivore activity, we conducted a survey of kangaroo, deer, rabbit, and wombat pellets and horse manure within the five 25-m^2 quadrats. Manure and pellet counts have been used frequently in studies examining habitat use and estimating population densities for large ungulates (Seber, 1982; Dyring, 1990) and kangaroos (Eldridge

et al., 2016; Travers et al., 2017). During surveys in March 2017, we collected all horse manure visible on the soil surface and weighed it on site using spring balances. For rabbits, wombats, deer, and kangaroos, we counted individual pellets. Samples of rabbit, kangaroo, and wombat pellets and horse manure were collected from most sites, weighed, and oven-dried at 35°C for 72 h to determine a standard dry mass of dung in kilograms per hectare. Field-based weights were then adjusted accordingly to kilograms per hectare (kg ha^{-1}) dry weight. Deer (*Cervus* spp.), pig (*Sus scrofa*), and wombats (*Vombatus ursinus*) were also considered, but there were too few records to analyze their effects separately. Rodent activity was noted as either present or absent within each $5 \text{ m} \times 5 \text{ m}$ quadrat on the basis of the presence of scats. The presence of scats has been shown to be a useful method of assessing the presence of *Mastomys* spp. in field surveys (Happold, 1989; Wallis, 1992). In addition, we assessed the total length of runways, which are known to be constructed by broad-toothed rats, within one smaller 2.25 m^2 ($1.5 \text{ m} \times 1.5 \text{ m}$) quadrat centrally located within the large quadrat. Tunnels may also be used by other rodents such as bush rats (*Rattus fuscipes*), but broad-toothed rats construct these tunnels and unlike bush rats, they are critically important for survival of broad-toothed rats over winter (Green, 2002).

Vegetation Structure Assessment

In March 2017 we assessed vegetation structure within each of the 25-m^2 quadrats. We measured the maximum height (i.e., the tallest point) of groundstorey or midstorey plants (i.e., excluding trees) in each corner and the center of the 25 m^2 . We also counted the number of perennial grasses (generally *Poa labillardierei* var. *labillardierei* Steud., *Poa sieberiana* var. *sieberiana* Spreng., *Rhytidospermum* spp.) and measured the diameter at the base (i.e., grass butt diameter) and height of 10 random individual grasses within the quadrat or immediately around it where *Poa* spp. were present. We made visual assessments of the cover of shrubs, sedges, forbs, and grasses and used these to derive total ground cover. We also assessed the cover of biocrusts, bare soil, rock, and litter. In early summer, at the peak of the growing season, we counted the number of different plant species (plant richness) within the smaller 2.25-m^2 quadrats.

Statistical Analyses

We used *t*-tests to test for differences in total length of runways, shrub cover, sedge cover, grass height, grass density, grass cover, and total plant richness between quadrats showing evidence of horse activity (horse manure; $n = 82$) and those with no horse manure ($n = 68$). χ^2 goodness of fit tests were then used to see whether quadrats showing evidence of horse activity were likely to contain rodent pellets and whether quadrats with rat runways were more likely to show evidence of horse grazing. We then used structural equation modeling (SEM; Grace, 2006) to further clarify the direct and indirect effects of herbivore (horse, kangaroo, rabbit) activity (dung kg ha^{-1}) and vegetation structure on habitat for broad-toothed rats, using the length of runways as our proxy of broad-toothed rat abundance. It is critical to separate the direct and indirect effects of herbivore activity because this provides insights into the possible mechanisms underlying these changes. In our a priori model, therefore, we hypothesized that the activity of herbivores would have both direct effects on broad-toothed rats, for example, by interruption of rat activity, alteration of rat behaviors, trampling of rats or removal of food; Fig. 1 pathway 1) and indirect effects, mediated by changes in vegetation structure and composition. These indirect effects could include trampling-induced soil erosion in riparian areas, leading to changes in plant species composition, preference for particular plant species as food leading to changes in species composition, or removal or trampling of grasses that form critical habitat for rats over

winter (Fig. 1 pathway 3 via 2). The presence of scats was weakly, though significantly, correlated with tunnel length across the study (Pearson's $r = 0.35$, $P < 0.001$). We used in all of these analyses the length of tunnels used by broad-toothed rats, rather than presence or absence of scats, as our proxy for rat activity because these data were continuous and therefore provide more rigorous models. In our models, predictor (endogenous) variables were standardized (*z*-transformed) after examining their distribution and testing their normality. To test for the effects of herbivore activity, we compared our a priori model with the variance-covariance matrix of the data and derived an estimate an overall goodness of fit, using the χ^2 statistic. This estimates the likelihood of the observed data for a given a priori model structure. High probability values indicate that the models are highly plausible causal structures underlying the observed correlations. Models with low χ^2 , high goodness of fit index (GFI), high normal fit index (NFI), and low root mean square error of approximation (RMSEA < 0.05) are interpreted as showing the best fit to our data. We also used the Bollen-Stine bootstrap test to improve goodness of fit when variables were not normal. We performed these analyses using the AMOS 20 (IBM, Chicago, IL) software.

Results

Across the 150 quadrats the mass of horse manure ranged from 0 to 3 534 kg ha^{-1} (mean $\pm$ SE: 241.6 ± 37.9 ; median: 29.7). Kangaroo

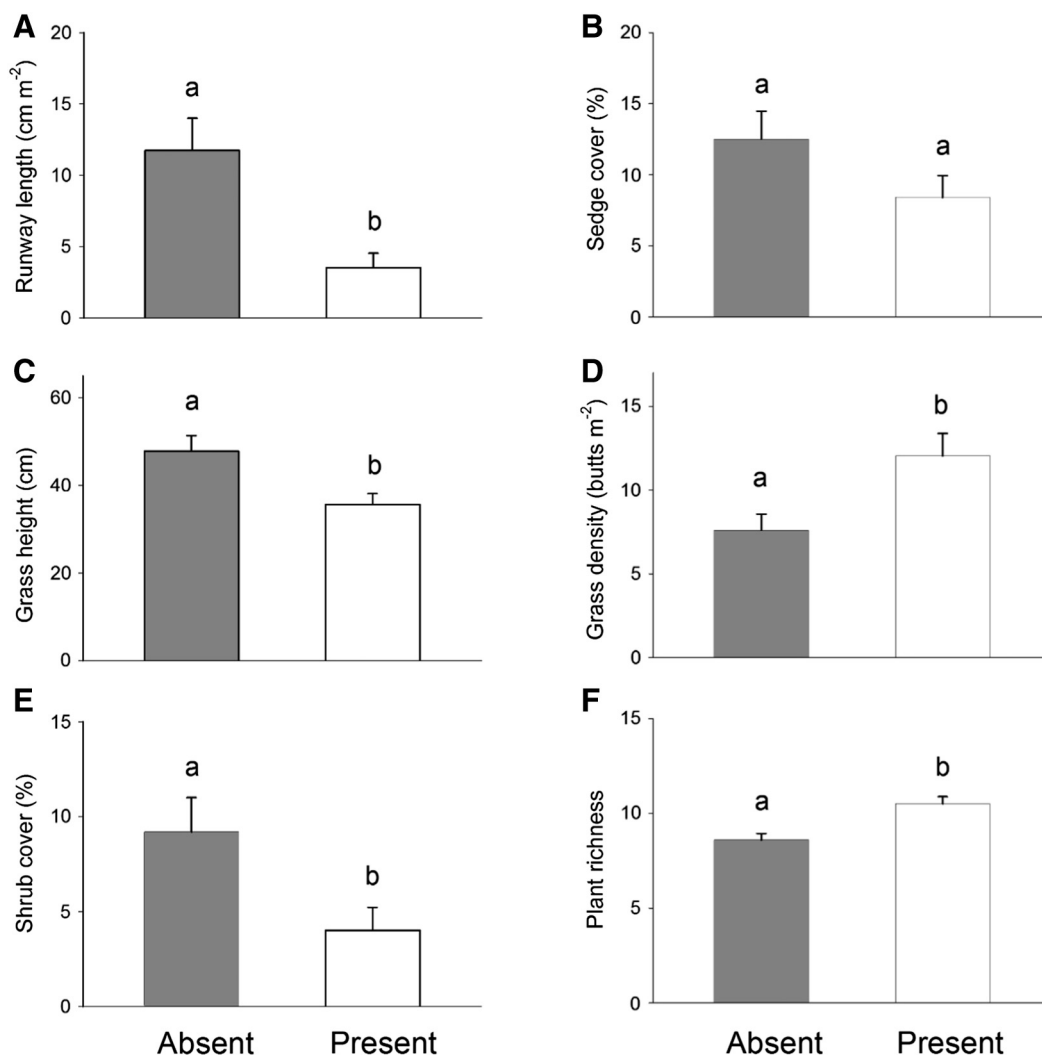


Figure 3. Mean ($\pm$ SE) values of runway length, sedge cover, grass height, grass butt density, shrub cover, and plant richness at sites where horses were absent ($n = 109$) or present ($n = 41$). Different superscripts indicate a significant difference in relation to the presence or absence of horses at $P < 0.05$.

dung ranged from 0 to 80 kg ha⁻¹ (8.7 ± 4.2 ; median: 0) and rabbit dung from 0 to 6.4 kg ha⁻¹ (6.3 ± 1.0 ; median: 0). We found no deer pellets in any quadrat and wombat pellets in only one quadrat. Quadrats with no evidence of horses were more likely to contain rodent pellets ($\chi^2 = 11.32$, DF = 1, $P = 0.001$). Similarly, of the quadrats that contained broad-toothed rat runways, more were likely to show no evidence of horse grazing ($\chi^2 = 9.59$, DF = 1, $P = 0.002$).

Quadrats with no evidence of horse activity (assessed as the absence of horse manure) had 3× the length of runways ($t = 3.31$, $P = 0.001$; Fig. 3a), taller grasses ($t = 2.80$, $P = 0.006$; Fig. 3c), twice the shrub cover ($t = 3.47$, $P = 0.015$; Fig. 3e), and 60% fewer grass butts ($t = -2.82$, $P = 0.005$; Fig. 3d) but supported 22% fewer species ($t = -3.78$, $P < 0.001$; Fig. 3f) than quadrats showing evidence of horse activity (i.e., some horse manure). There were no significant differences in sedge (Fig. 3b, $P = 0.10$) or grass cover ($P = 0.85$) between quadrats with and without horse activity.

Using the length of runways created by rats as our proxy of broad-toothed rat habitat, we found no direct association between horse activity and broad-toothed rat activity (Fig. 4). Our SEM also showed that increasing horse activity was associated with reduced shrub and sedge cover, reduced grass height, increased grass butt density, but no changes in grass cover (see Fig. 4). Apart from a greater shrub cover in areas with more kangaroo grazing, there were no effects of rabbits or kangaroos on any environmental variables. Increasing grass height was associated with an increase in our proxy of rat habitat (assessed as the length of runways) and reduced plant richness (see Fig. 4). However, we found that the negative association between horse activity and grass height suggests that horse grazing indirectly reduces broad-toothed rat habitat and therefore their activity.

Discussion

Our study shows clear evidence of an indirect negative association between horse activity and broad-toothed rat habitat by reducing grass height. This is not unexpected, as broad-toothed rats are highly dependent on large, tall tussock grasses for food and shelter, particularly over winter (Carron et al., 1990; Green and Osborne, 2003). However, the indirect associations between horses and broad-toothed rat habitat via associated changes in grass height has not, to our knowledge, been

previously tested. Like many large herbivores, horses tend to concentrate on the actively growing vegetation on grazing lawns (Menard et al., 2002), which are clearly poor rat habitat, so the preference of horses for short vegetation could be coincident with the preference of rats for taller grasses. In our study, however, horses still foraged in areas of tall grasses and grazed, defecated, and trampled on tall grasses as they traveled from uplands to riparian areas. This physical disturbance substantially reduces tussock height. The mechanism underlying the effect of horses on broad-toothed rat habitat likely relates to 1) vegetation destruction, whereby the vegetation is trampled along pathways that lead to riparian areas, and 2) direct reduction in grass size through herbivory and its associated processes. We also detected some evidence of a decline in the cover of sedges (*Carex gaudichaudiana* Kunth, *Carex inversa* R.Br.) in sites that were heavily grazed by horses, but the strength of the effect was weak. The shrub effect probably results from the fact that horses eat the actively growing tips of sedges and, therefore, have a greater effect on plant height than plant cover. Prober and Thiele (2007) showed that *Carex gaudichaudiana* was substantially smaller and had less cover in grazed riparian areas than sites that had been excluded from grazing with the use of fenced enclosures.

We also found two other effects of increasing horse activity. First, greater horse activity was associated with increased plant richness. However, sites that were more species rich tended to be dominated by more exotic plants, particularly rosette-forming annual forbs (e.g., *Hypochaeris* spp.), nitrogen-fixing annual forbs (e.g., *Medicago* spp.), and annual grasses (*Holcus lanatus* L.; Doherty et al., 2015). Second, increasing horse activity was associated with more, but shorter, grasses. Grasses make up a major component (77–89%) of horse diets (Scasta et al., 2016). Although we found no significant effect of grass density on broad-toothed rat habitat, lower levels of horse activity are likely associated with fewer but larger grass tussocks that are more suitable for subnival broad-toothed rat habitat.

Studies of broad-toothed rat habitat in Kosciusko National Park showed a significant negative relationship between the presence of rats and increasing impacts of feral horses (Schulz and Green 2018). Indeed, we found that runways, our proxy of rat activity, were more numerous and contained more scats at sites with fewer, but larger, *Poa* spp. grass tussocks. Tussocks at sites showing evidence of broad-toothed rat activity (assessed as the presence of fresh scats) were

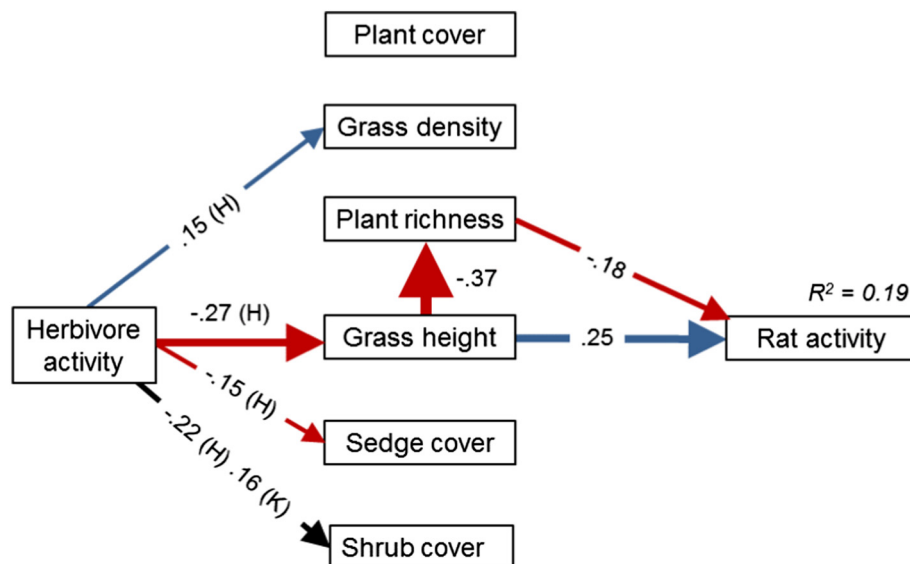


Figure 4. Structural equation model showing the direct and indirect effects of herbivore activity (horse, kangaroo, rabbit); grass density; grass cover; grass height; sedge cover; shrub cover; and plant richness on broad-toothed rat habitat (assessed as the total length of runways). Standardized path coefficients, adjacent to arrows, are analogous to partial correlation coefficients and indicative of the effect size and direction of the relationship. Positive relationships are in blue, negative in red, mixed in black. The width of arrows is proportional to the strength of the path coefficients. R^2 is the proportion of variance explained in broad-toothed rat habitat and plant richness. H indicates horse; K, kangaroo. $\chi^2 = 1.07$, DF = 1, Bollen-Stine bootstrapped $P = 0.301$, goodness of fit index = 0.999, normal fit index = 0.994, root mean square error of approximation = 0.022.

almost twice as tall (58.7 ± 4.5 cm; mean $\pm$ SE) as those where rats were absent (38.4 ± 2.2 cm). Tall vegetation allows broad-toothed rats to construct a complex of runways that enables them to remain active under a cover of deep winter snow. Reductions in this grass cover reduce the ability of broad-toothed rats to survive over winter (Green, 2006). These grasses may take many years to reach a size that is suitable for broad-toothed rat habitat following fires or heavy grazing by horses.

Our findings that horse grazing was associated with substantial change in vegetation structure within these grasslands also have substantial implications for other native grassland-dependent species. The evolutionary history of Australia did not include hard-hooved grazers such as horses. Consequently, their introduction and burgeoning population size have strong negative impacts on both native species and ecosystems that have not adapted to horse disturbance. For example, the alpine she-oak skink (*Cyclodomorphus praealtus*), an endangered species that inhabits treeless sub-alpine grasslands (Koumoundouros et al., 2009), is heavily dependent on tall tussock grasses for basking (Clemann, 2003). Other rodents such as the bush rat also use grass tussocks for shelter and movement. Given our finding that horse activity is strongly associated with lower grass height, it is likely that horse activity will also negatively affect other grassland-obligate species. Reductions in grass height and cover will reduce the connectivity between different riparian areas, further isolating already disjunct broad-toothed rat populations. We also found a negative effect of horse grazing on shrub cover, but few rat scats under shrubs and, therefore, no significant relationship between shrub cover and rat activity. Small shrubs could potentially provide a similar function to tussock grasses by creating subnival runways for rats, though unlike tall tussock grasses, they are more rigid and less likely to provide the snow-free patches required by rats. Further, our study site was essentially a grassland with low shrub cover (~5%), and therefore compared with tussock grasses, shrubs are less likely to be critical habitat for rats.

Other herbivores also have potentially damaging effects on alpine ecosystems. Rabbits and pigs have been identified as significant pests in subalpine grasslands (Wimbush and Forrester, 1988), and the spread of deer (*Cervus* spp.) is a serious emerging threat in many areas (OEHL, 2016). We recorded the presence of different herbivores (pig and deer) but found too few records of their activity to test their effects, likely because deer prefer more timbered sites (Keith and Pellow, 2005). However, neither kangaroos nor rabbits had any significant effects on grass height or the occurrence of runways in our study areas. Rather, the effects were limited to horses.

Implications

The severity of wild horse impacts is likely to depend on their density and distribution, which are influenced by landscape features. Within horse-accessible areas, management practices such as culling or removal will be required to control horse population densities to minimize their degradation of fragile riparian areas (Robertson et al., 2015). In the absence of human intervention, the primary controls on horse density are natural events such as wildfire, drought, and heavy snowfalls (Walter, 2002). Although horses have been shown to decline under extreme winters, an emerging threat to alpine ecosystems is climate change, which reduces the frequency of heavy snowfalls and allows horses to overwinter at higher altitudes, placing increasing stress on sensitive riparian areas and broad-toothed rat habitat (Robertson et al., 2015).

We found evidence that horses have an indirect negative effect on broad-toothed rat habitat by reducing grass height and, to a lesser extent, by altering plant species richness. As broad-toothed rat populations are already substantially isolated and disjunct at a national level (O'Brien et al., 2008), this is likely to lead to further segregation of populations and potential genetic inbreeding. Recovery will depend, however, on the management of all introduced herbivores, particularly

horses, in order to retain critical habitat and hydrological function provided by these riparian systems (Naiman et al., 1993).

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