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Land use effects on “spring annual” herbs in rare non-forest ecosystems of New Zealand

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Abstract We examined trends over six consecutive spring seasons in three “spring annual” herbs, *Myosurus minimus* subsp. *novae-zelandiae* (Ranunculaceae), *Ceratocephala pungens* (Ranunculaceae), and *Myosotis pygmaea* var. *minutiflora* (Boraginaceae), in terms of their habitats and site land uses in several rare, non-forest ecosystems. On dry hillslopes, saline soils, and turfs of ephemeral wetlands (including coastal turfs), *Ceratocephala* and *Myosotis* declined where sites were managed for conservation by removal of mammalian herbivores. Some populations of *Myosurus* declined only marginally or remained stable despite high cover of ruderal and weedy, herbaceous exotic plants. Loss of monitored populations during the study was offset by discoveries of additional populations of all three taxa. Statistical models of population trends suggest that in some instances spring annual populations benefit from farm animal and rabbit (*Oryctolagus cuniculus*) disturbance of their habitats perhaps by 1) suppressing transitions to taller vegetation and retarding competition of invasive exotic plants and 2) maintaining nutrient supplementation from faeces lost with the extinction of ground-dwelling birds. Frequent seeds of all three taxa preserved in moa coprolites from several sites in Central Otago point

to 1) the herbs’ probable non-rarity in pre-human times and 2) dispersal mutualisms and mediation of community ground cover by extinct ratites.

Keywords annual plants; spring annuals; New Zealand; *Myosurus*; *Myosotis*; *Ceratocephala*; land use; herbivores

INTRODUCTION

New Zealand’s three spring annual herbs, *Ceratocephala pungens* (Ranunculaceae) (Garnock-Jones 1984) (hereafter referred to as *Ceratocephala*), *Myosotis pygmaea* var. *minutiflora* (Boraginaceae) (hereafter referred to as *Myosotis*), and *Myosurus minimus* subsp. *novae-zelandiae* (Ranunculaceae) (Garnock-Jones 1986) (hereafter referred to as *Myosurus*), occupy habitats vulnerable to land conversion or invasion by exotic plants (Walker 2000; Rogers et al. 2002). The “desert” or bare soil habitat of *Ceratocephala* and the turf and gravel habitats bordering water bodies of *Myosotis* and *Myosurus* are, today, non-forest habitats, although they may have survived as an interstitial component of zonal scrub or treeland in pre-human times. All habitats are assumed to experience summer soil-moisture deficits within their dryland climatic zone (Rogers et al. 2005) or on excessively well-drained soils within more mesic climates at montane elevations in eastern South Island or in coastal North Island.

The study by Rogers et al. (2002) inferred different individual responses by spring annual species to competition from exotic plants across their range of habitats. The clumped arrangement of *Ceratocephala* and its positive correlation with patches of bare soil suggested that it appeared to be rapidly out-competed by exotic species in the absence of grazing. *Myosurus* and *Myosotis* appeared to be slightly more tolerant of invasive exotic forbs and grasses than *Ceratocephala* in sparsely vegetated scabweed or degraded pasture, albeit dependent on continued grazing disturbance. The joint environmental stresses of a long and uninterrupted

period of water inundation in winter followed by prolonged summer soil aridity may be critical to buffer the habitat of *Myosurus* and the turfs of ephemeral wetlands as habitat for *Myosotis* against invasion of exotic grasses and forbs. Salt-tolerant *Plantago coronopus* is an aggressive competitor for *Myosurus* on seasonally damp salty soils in Central Otago. Overall, the genuine non-forest habitats of all three taxa appeared to have greater resistance to weeds than their shared habitat in scabweed or mat vegetation.

The protection status of spring annuals is improving with covenanting of private land and the creation of crown reserves by land purchase or through the Tenure Review of Crown Pastoral Leases of the South Island high country. Land use appropriate for maintaining and restoring the small-scale, genuine non-forest habitats of spring annuals following land protection may differ from that appropriate for restoring the matrix forest or scrub vegetation within the greater landscape. By monitoring plant and ground cover over six spring seasons across all types of spring annual habitat, we sought to understand population trends in relation to land use and disturbance regimes and competition with exotics in order to provide information for conservation management.

METHODS

Field sampling

We monitored vegetation in 65 permanently located 500 × 500 mm plots at sites which were selected on the basis of the presence of one or more of the three spring annual taxa. Each plot was designated as a target plot for one or more of the spring annual species. Nested within each plot were 25 subplots (100 × 100 mm) to allow analysis of spatial patterns at the spatial scale in which these species compete with other plants. In each subplot, the cover of each vascular plant species, all exotic grasses, all mosses, all lichens, and bare ground (which included soil and rock) was estimated in six cover-classes (1, <1%; 2, 1–5%; 3, 6–10%; 4, 11–25%; 5, 26–50%; 6, >50%). The numbers of *Ceratophylla* and *Myosotis* plants were also recorded, but the densely aggregated pattern of *Myosurus* prevented individual counting of plants. Most but not all plots were monitored annually, with a total of 312 plot measures over the six spring seasons between 1999 and 2004. Although monitoring was confined to the month of October,

we did not control for annual phenological variation.

We subjectively classified the habitats of the spring annual taxa at each plot as hillslope herbfield, turf community bordering a water body, saline soil, and beach gravel based on the predominant land-form-soil-vegetation association. We categorised land-use disturbances at each plot as sheep (*Ovis aries*), cattle (*Bos taurus*), pest (which includes rabbit (*Oryctolagus cuniculus cuniculus*), hare (*Lepus europaeus occidentalis*), and possum (*Trichosurus vulpecula*)), pedestrian traffic, and vehicles. We also recorded the elevation of each plot.

The numbers of populations of spring annual taxa discovered, additional to the summary in Rogers et al. (2002), were also recorded.

Data analysis

Data summaries

The subplot*year observations were summarised to the plot level for further analysis to avoid pseudo-replication and provide conservative tests of significance. We derived a number of variables relating to the spatial and temporal patterns of distribution and abundance of the species ("distribution" variables) and a number of variables relating to the vegetation, disturbance, or environmental characteristics of the plot ("habitat" variables) (Table 1). Variables that have no spatial or temporal context (e.g., cov) were calculated as the subplot and year means for each plot. Variables that had a temporal component (e.g., dcov) were calculated for each time step and then summarised across subplots and times steps. Variables that had a spatial context (e.g., lloyds) were calculated at the plot level, and then averaged across years. Plots that were not target plots for a particular species were excluded from the analyses for that species.

Analysis of patterns

Generalised Regression Analysis and Spatial Prediction (GRASP) (Lehmann et al. 2002) was used to model multivariate relationships between the three spring annual herbs and environmental factors (Table 1). The GRASP process defines patterns of a response variable in relation to multiple predictor variables. GRASP uses generalised additive models (GAMs), a modern, non-parametric method of multiple regression that allows combinations of continuous and categorical predictor variables in each model (Overton & Lehmann 2003). The overall model sums the partial contribution of each predictor

variable. The GRASP models are constructed by backwards stepwise selection, with significance tests for variable removal that vary with model family (Lehmann et al. 2002). The graphs of the GAMs show the partial contribution of each predictor variable that was included in the final model. For each response variable, the model produces:

- 1 Graphs of the modelled variable against each predictor variable.
- 2 Final GAM, with the curve of the partial contribution of each predictor variable to the overall model.
- 3 Model validation and cross-validation results, with the correlation between the observed and predicted being used to assess the model.
- 4 Estimates of the relative contributions of each predictor variable to the overall model.

We used Lloyd's index (Lloyd 1967) to test for spatial clumping in the occurrence of spring annuals. Lloyd's index provides a measure of the degree of

intraspecific competition compared with what they would experience if they were evenly or randomly distributed (Overton & Levin 2004).

RESULTS

Ceratocephala

Twelve plots at the six known sites of *Ceratocephala* in 1999 were used to monitor its trends, 11 on hillslope herbfields and 1 on saline soils. The species has very low mean cover of 0.15%, a low mean count of 0.21 plants per plot, and low occurrence of 0.08 (Table 2). The mean number of years since its last presence (prevrecent) is 2.00, showing it has an inconsistent annual and more frequently biennial presence at the subplot scale. There were no significant GRASP models chosen for the response variables of cover, count, and occurrence for *Ceratocephala*, perhaps due to the small sample size.

Table 1 Names of three spring annual herbs, and the distribution and predictor variables derived from subplot data as used in GRASP analysis and on Fig. 1 and Table 2. n.a., not applicable; no., number.

Taxon	Abbreviation	Unit	Definition
<i>Ceratocephala pungens</i>	cerpun		
<i>Myosotis pygmaea</i> var. <i>minutiflora</i>	myopmin		
<i>Myosurus minimus</i> subsp. <i>novae-zelandiae</i>	myomnov		
Distribution variables			
Mean cover	cov	%	mean percentage cover across all subplots and years
Change in cover	dcov	%	mean percentage change in cover from year to year
Mean abundance	cnt	no.	mean number of individuals per subplot
Change in abundance	dcnt	no.	mean change in abundance from year to year
Mean previous presence	prevcount	no.	mean number of years the species was present in its target plots
Mean number of years since last presence	prevrecent	no.	mean number of years since its last presence
Occurrence	occ	n.a.	the proportion of subplot*years that the taxon had positive abundance
Lloyd's index	lloyds	n.a.	the ratio between the observed local density perceived by each individual, relative to the mean local density across the plot
Habitat variables			
Altitude	altitude	m	mean altitude of plots
Total cover	coverTotal	%	mean cover of all vascular and non-vascular plants
Cover non-target	coverNT	%	cover of all non-targeted or non-spring annual taxa
Cover bare ground	coverBareGroundNT	%	cover of bare soil
Cover exotic	coverExoticNT	%	cover of all exotic plants
Cover native herbs	coverNativeHNT	%	cover of all non-targeted or non-spring annual native herbs
Cover native sub-shrubs	coverNsshruhNT	%	cover of all native sub-shrubs

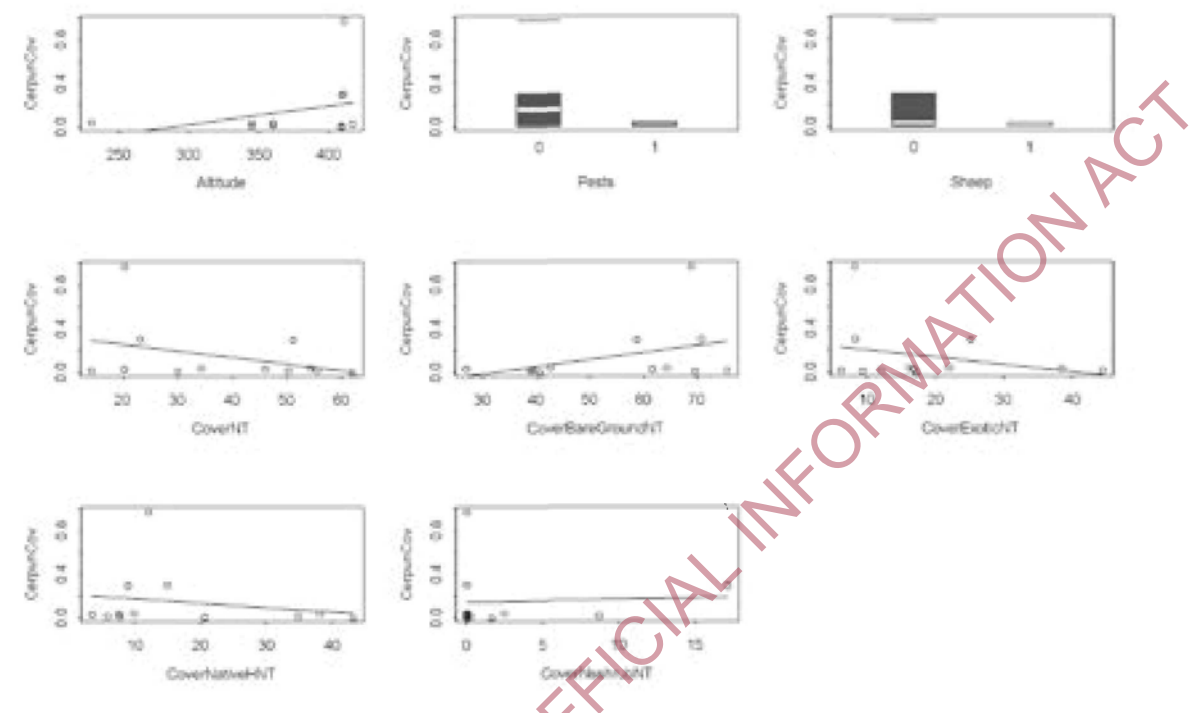


Fig. 1 GRASP plots of response in mean percentage cover of *Ceratocephala* in relation to habitat and bare ground predictor variables. See Table 1 for an explanation of predictor variable abbreviations and scale units.

Table 2 Summary statistics of distribution and habitat variables from GRASP models for spring annual herbs monitored over six spring seasons. See Table 1 for definition of variables.

	<i>Ceratocephala</i>	<i>Myosotis</i>	<i>Mysosurus</i>
Distribution variables			
Cov (%)	0.15	0.39	5.85
Dcov (%)	-0.01	-1.40	-0.34
Cnt (no.)	0.21	0.49	n.a.
Dcnt (no.)	0.03	-0.23	n.a.
Prevcount (no.)	0.28	0.78	1.6
Prevrecent (no.)	2.00	1.90	1.4
Oco	0.08	0.20	0.55
Lloyd's index	8.80	4.85	n.a.
Habitat variables			
Altitude (m)	372.2	371.2	474.5
CoverTotal (%)	39.61	44.90	51.93
CoverNT	38.46	44.20	45.88
CoverBareGroundNT	54.90	40.35	46.25
CoverExoticNT	18.68	23.37	32.62
CoverNativeHNT	17	20.32	13.10
CoverNsshubNT	2.52	0.51	0.15

Yet, both count and cover have a weak positive response with bare ground and negative response with several indices of increasing cover of native and exotic plants, suggesting avoidance of companionship with other plants (Fig. 1; plots for cover only shown). There were small changes only in count and cover throughout the five years and GRASP also failed to model these. *Ceratocephala* has a moderate Lloyd's index of about 9, suggesting that it experiences a 9-fold greater degree of intraspecific competition or spatial clumping than it would if evenly or randomly distributed (Table 2).

Myosotis

Thirty-seven plots at 14 sites were used to monitor trends in *Myosotis*. Plots spanned four habitat classes: 5 on beach gravels, 12 on hillslope herbfields, 3 on saline soils, and 17 on turfs bordering water bodies. This spring annual also has low and declining cover and count values of 0.39% and 0.49 individuals, respectively, but a greater occurrence than *Ceratocephala* of 0.2 (Table 2). The mean number of years prior to its previous presence was also high at 1.9.

The GRASP model for cover used just two predictor variables, accounting for 35% of the variation, showing higher cover on saline soils and decreasing cover with more bare ground (Table 3). The model for count (cnt) included just vehicles, with 23.6% of variance explained, indicating a strong incompatibility with vehicle disturbance.

The model for change in cover (dcov) used three variables for 52.5% variance explained (Table 3). This model indicates that the reduction in cover (the inverse of dcov) through the monitoring period increased in the turfs of water bodies, reduced where there was cattle disturbance, and was less with increasing cover of all competing plants. The

model for change in count also fitted three variables, which indicated that the loss in numbers (the inverse of cnt) is reduced where there is pedestrian traffic, reduced with cover of bare ground, and reduced with the cover of exotic plants.

Lloyd's index of 4.9 indicates a relatively low degree of spatial clumping.

Myosurus

Myosurus was monitored in 26 plots at 17 sites, with 11 plots on hillslope herbfields, 7 on saline soils, and 8 on turfs bordering water bodies. Overall, *Myosurus* showed much greater mean cover at 5.9% than the other spring annuals (Table 2). It may not, however, tolerate greater competition from other plants because the mean total cover (coverTotal) of all plants less the contribution from *Myosurus* is similar to that for *Myosotis* (Table 2). However, its habitats experienced greater competition from exotic plants than did the other two spring annuals, with mean exotic cover of 33%, along with lower cover of native herbs (Table 2). *Myosurus* showed the greatest consistency on subplots of all three taxa (prevcount and prevcent) (Table 2) and the highest occurrence in subplots of all three species at 55%. It experienced a small mean annual decline of 0.34% cover. It occurred at a higher mean altitude than the other two taxa.

The GRASP model for cover fitted six predictor variables and explained 59% of the variance (Table 3). The model suggests that the rate of decline of *Myosurus* reduces when there is disturbance by pests and sheep, increases as the combined cover of all plants and bare ground increases, yet it is favoured by the cover of exotic plants and native herbs.

Myosurus had no significant relationships with the change in cover variables.

Table 3 Predictor variables, and total variance explained in GRASP models of the various response variables for two spring annual taxa. Symbols / and \ indicate +ve and -ve fits for continuous variables, while + and - indicate +ve and -ve fits for categorical variables.

Taxon response variable	Predictor variables in GRASP model	Variance explained (%)
<i>Myosotis</i> cover	saline soils +, coverbaregroundNT \	34.7
count	Vehicles -	23.6
change in cover	turf of water body +, cattle -, coverNT \	52.5
change in count	pedestrian traffic -, coverbaregroundNT \, coverexoticNT \	26.6
<i>Myosurus</i> cover	Pests +, sheep +, coverNT \, coverbaregroundNT \, coverexoticNT /, covernativeHNT /	59.4

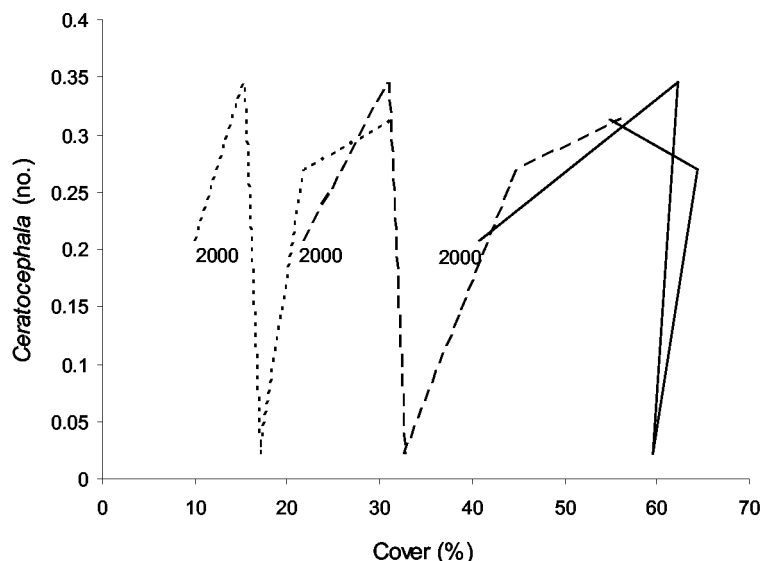


Fig. 2 Mean count of *Ceratocephala* on hillslope plots in relation to mean percent cover of bare ground (solid line), total plants (dashed line), and exotic plants (dotted line) at yearly intervals from 2000.

Habitat trends

Ceratocephala

The mean cover of all plants and all exotic plants increased throughout the study in the predominant hillslope habitat of *Ceratocephala*, the former from 22% to 56%, the latter from 10% to 32% (Fig. 2). The mean count of *Ceratocephala* was unusually low in 2002 compared with other years.

Myosotis

Although the number of *Myosotis* plants on beach gravels fluctuated widely, the cover of all plants and all exotics had consistently low cover there (Fig. 3A). The trend on hillslopes was for the cover of all plants and all exotics to substantially increase, whereas the numbers of *Myosotis* varied widely (Fig. 3B). On saline habitats, numbers of *Myosotis* declined throughout, yet bare ground increased from 25% to 61% cover (Fig. 3C). On turfs, again the numbers of *Myosotis* declined throughout but the cover of vegetation and bare ground fluctuated (Fig. 3D).

Myosurus

The mean cover of bare ground in the hillslope habitat of *Myosurus* first increased from low levels then declined during the last three years, whereas total plant and total exotic cover increased only marginally over the five years (Fig. 4A). The mean cover of *Myosurus* varied over the four years from 3.5% to 7.0%. Trends in its saline habitat show that

its decline in cover over the last three years occurred as the cover of all other vegetation also declined (Fig. 4B). In its turf habitat, *Myosurus* showed the greatest overall cover of all three habitat types. Further, its 2004 cover substantially declined there as it did on the other two habitat classes (Fig. 4C).

Number of populations/sites

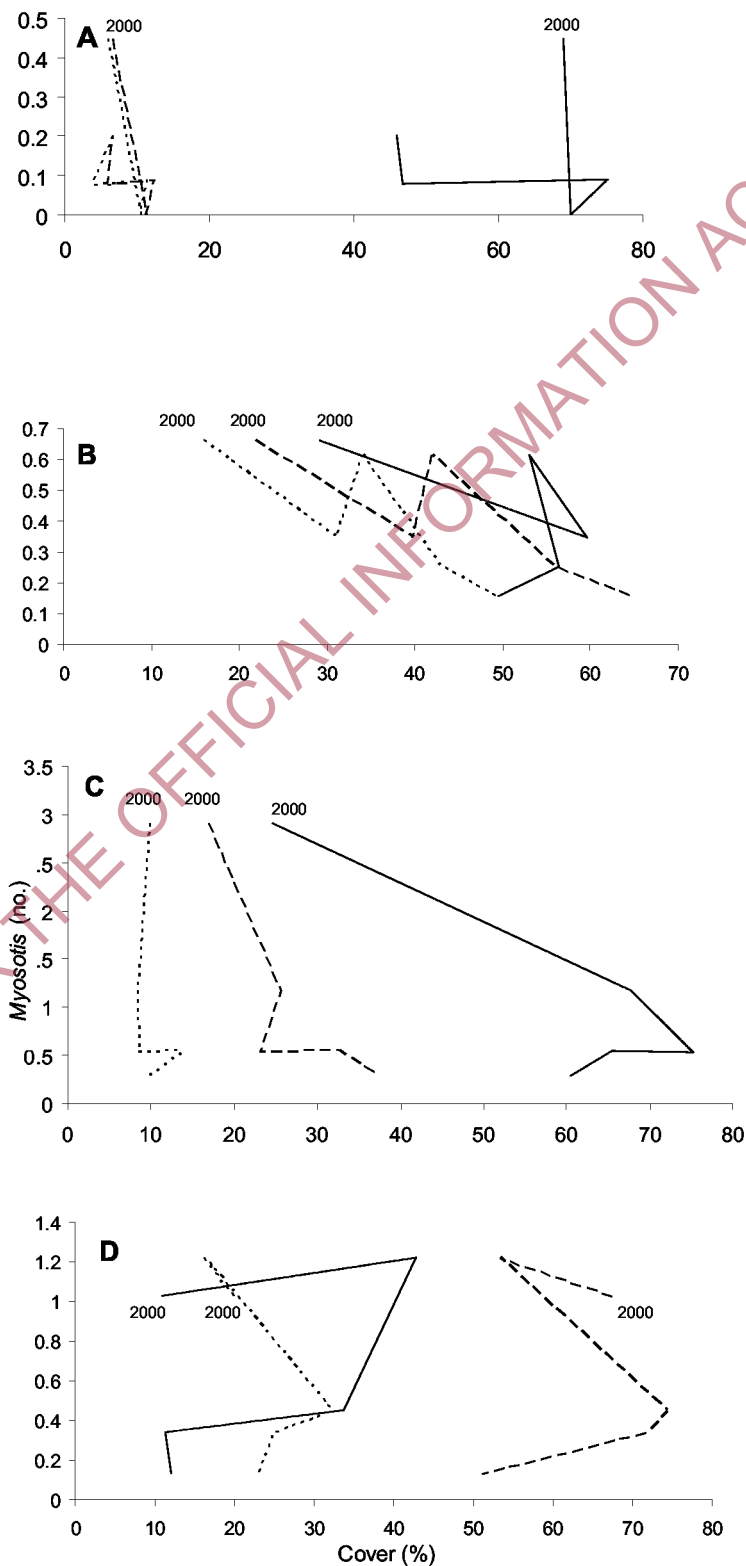
Ceratocephala

Plants appeared at all six monitored sites in Central Otago in 2000 and 2001. Thereafter, plants failed to reappear at two sites between 2002 and 2004. Accordingly, just four consistent populations are now known from Central Otago, with total numbers of known plants varying between 20 and 30 in 2003 and 2004. However, during the present study, eight new populations of *Ceratocephala* were discovered in the Mackenzie Basin, south Canterbury, four within a 10 ha area of stony terrace, and with total plant numbers there estimated between 3000 and 4000. This reaffirms a Canterbury presence for the species documented by herbarium vouchers from 1924 to 1954 (CHR 5257, CHR 90270, CHR 48142) (Garnock-Jones 1984; Rogers & Walker 2002).

Myosotis

Ten populations have been discovered since the summary of Rogers et al. (2002) (GMR pers. obs.; K. Lange & J. Barkla pers. comm., 2006). There are three new populations in Canterbury, at Bush Stream, a tributary of the upper Rangitata River, on

Fig. 3 Mean count of *Myosotis* on **A**, beach gravel; **B**, hillslope; **C**, saline; **D**, turf plots, in relation to mean percent cover of bare ground (solid line), total plants (dashed line), and exotic plants (dotted line) at yearly intervals from 2000.



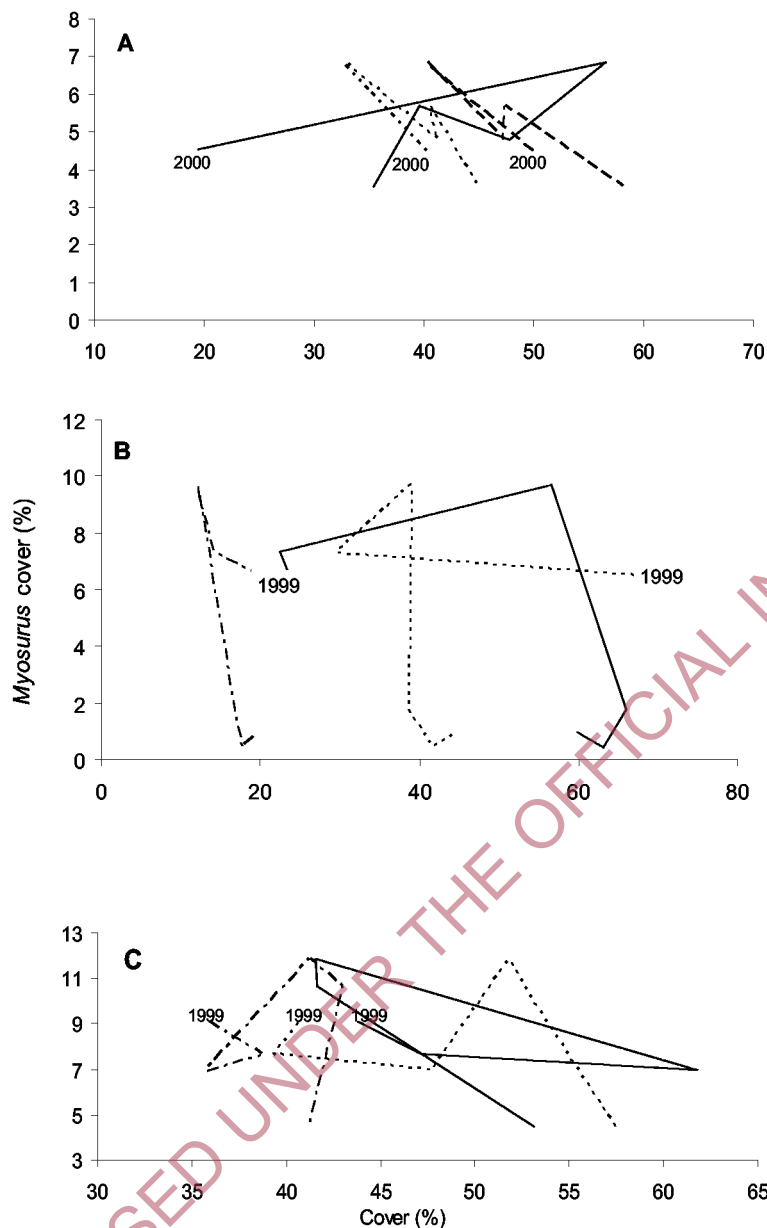


Fig. 4 Mean cover of *Myosurus* on A, hillslope; B, saline; C, turf plots, in relation to mean percent cover of bare ground (solid line), total plants (dashed line), and exotic plants (dotted line) at yearly intervals from 1999 or 2000.

Mesopotamia Station, at Seagull Lake, in the Clent Hills area of the Heron Basin, and on Simons Pass Station in the Mackenzie Basin. Seven new populations occur in Otago, three on mine tailings on the floor of the Nevis Basin, one on an access track at Bendigo, one on a broad spur crest at Alexandra, one in a snow-bank on the western Rock and Pillar Range, and one on a shingle terrace of the upper Cliff Burn on the Pisa Range.

Myosurus

The species may be extinct at 4 (24%) of the 17 monitored sites because it disappeared in the last three years' of monitoring. In plots and their environs at three of those sites occupying shallow, winter-wet, cut-off meanders on valley floors, it failed to appear after exotic plants increased rapidly and early in the monitoring period to cover the entire site. At the other site from which it appears to have gone, its

habitat was destroyed by a change in farming land-use. However, 12 additional populations to those documented in Rogers et al. (2002) have been discovered in both Central Otago and Canterbury: one on a rabbit-infested terrace near Luggate, one in a damp depression on the floor of the Nevis valley, one on a dry spur above Arrowtown, one on a wetland margin at Chatto Creek, one on a damp depression near Alexandra, one on a rabbit-degraded interfluvial crest near Alexandra, one in a damp depression of a basalt crater on Taieri Ridge near Middlemarch, five on damp depressions and “sheep camps” on the slopes of the western Rock and Pillar Range (J. Barkla pers. comm., 2005) and two on “sheep and rabbit camps” on the floor of the Mackenzie Basin (GMR pers. obs.).

DISCUSSION

Habitat trends

High inter-annual variability in population size occurs in many annual herbaceous and short-lived perennial plants. Accordingly, deriving demographic trends and a species conservation status can be problematic. Our results support this, although *Myosurus* showed less inter-annual variability than *Ceratocephala* and *Myosotis*. Combining numbers of plants with numbers and persistence of populations would strengthen a demographic assessment of conservation status.

From that standpoint, *Ceratocephala* in Otago has a precarious status. Its numbers fluctuated at low levels and the number of populations declined by a third, while the cover of competing vegetation, substantially exotics, consistently increased (Fig. 2). Five of the six study populations are on conservation land where exotic plants are increasing following herbivore control (see, e.g., Walker 2000). The weak negative GRASP correlations with variables for companion plants suggest that *Ceratocephala* declines with community competition. The five, recently discovered, abundant, Mackenzie Basin populations on stony river terraces or hillslopes are largely confined to patches of skeletal soils supporting scabweed vegetation heavily disturbed by sheep and rabbits. This observation suggests that herbivore disturbance aids perpetuation of *Ceratocephala* in its “desert” or bare soil habitat, perhaps by suppressing taller herbaceous plants, particularly exotics, providing nutrient supplements in faeces and urine and/or by scarifying the ground surface, thus aiding

establishment. However, this is not supported by the weak negative GRASP correlations with pest animals and sheep (Fig. 1).

The GRASP models for *Myosotis* show that its declining cover and count through the monitoring period are positively correlated with increasing cover of exotic plants, bare ground, and on the turfs of water bodies and negatively correlated with pedestrian traffic, cattle disturbance, and increasing cover of all plants (Table 3). These apparently contradictory influences producing similar trends can be explained by habitat-specific, divergent trends in its count on its saline, turf, and hillslope habitats. On saline soils, the species’ decline was correlated with increasing bare ground, perhaps stimulated by several recent, low-rainfall spring seasons (GMR pers. obs.) and/or removal of sheep and rabbits from all these sites. The sites with *Myosotis* on hillslopes and on turfs bordering water bodies (kettleholes and coastal turfs) mostly have had farm stock and rabbits removed by conservation intervention, resulting in increasing cover of exotic plants, greater vegetation stature, and reducing counts for *Myosotis*. Accordingly, vertebrate herbivory may benefit *Myosotis* within prostrate turf communities of mainly native herbs and grasses on exposed coastal headlands and around ephemeral tarns by suppressing compositional transitions to taller vegetation and retarding competition of invasive exotic plants.

Myosurus shows the least inter-annual variation of the three spring annuals. The GRASP models for cover have similar trends for apparently contradictory influences, such as a negative correlation with bare ground and the cover of all plants and a positive correlation with the cover of all natives and all exotics. It is also enhanced by the presence of sheep. An explanation for these contradictions again lies in habitat-specific, divergent trends. On its saline sites, the majority managed for conservation and no longer grazed by sheep, it declined to low levels in the last three years in concert with a substantial increase in bare ground, perhaps due to a loss of nutrient inputs in faeces. On turfs of water bodies, its cover fluctuated while the cover of all plants and exotics increased substantially. Almost all its monitored turf sites are grazed by sheep (but not cattle), a land use apparently maintaining the cover of *Myosurus* while enhancing the cover of all plants. Yet sheep grazing failed to prevent apparent extinction due to smothering by weeds on three wet depression habitats with seasonally dry mud floors. On its hillslope sites, all of which are sheep camps and are heavily grazed by sheep, no consistent trends in any cover classes

are apparent. We conclude that on the hillslope and turf sites of *Myosurus*, grazing by sheep is at least not detrimental to its maintenance in the face of invasive exotics, although extinction risk is high on wet depressions.

Patterns and dynamics of plant richness in semi-arid open vegetation depend on location within a fertility–disturbance matrix, with grazing favouring richness at higher fertility and diminishing richness at lower fertility (Proulx & Mazumder 1998; Osem et al. 2002; Wilson & Tilman 2002). In testing for vegetation community equilibrium in grazed semi-arid grassland in Central Otago, Walker & Wilson (2002) showed that some sites had directional change in composition over time while others appeared to fluctuate about an average equilibrium state. Although our study was not set against a theoretical disturbance–productivity framework, inter-habitat fertility differences may explain the observed divergent trends in the rarity component on the different habitat types under a grazing/non-grazing treatment. An extension to the present study will examine richness trends within a disturbance–productivity framework.

Loss of spring annual-ratite mutualisms

In pre-human times, avian disturbance would have included foliar clipping, trampling, ground scarification, and nutrient supplementation, particularly on grazing-favoured sites (Rogers et al. 2005). Herds of wild grazing animals maintain the vegetation in their concentration areas at very low statures, regulating such ecosystem processes as energy flow and nutrient cycling, thus contributing to species coexistence and the resulting species diversity of communities (McNaughton 1984). All hillslope sites of *Myosurus* are sheep camps, heavily grazed and littered with faeces. The newly discovered sites of abundant *Ceratocephala* in the Mackenzie Basin are heavily grazed and scarified by rabbits and, to a lesser extent, by sheep. Analysis of fossil seeds from samples of moa coprolites preserved in dry soils beneath rock overhangs from several riverine sites along a 41-km stretch of the Clutha River in Central Otago showed comparatively frequent occurrence and often abundant quantities of intact seeds of all three spring annual taxa (J. Wood unpubl. data, 2006). Fossil seeds of *Ceratocephala* are also numerous in dry soils beneath the same rock overhangs. This suggests that spring annual plants were not rare in Central Otago in pre-human times and that they may have had dispersal mutualisms

and ground cover mediation dependencies on ratites and perhaps other birds. Indeed, the seeds of *Ceratocephala* and *Myosurus* are adapted for epizoochoric dispersal (Rogers et al. 2002). Given that today's introduced mammalian herbivores do not consume spring annuals, we postulate a breakdown in the plant's long-distance dispersal biology with the extinction of ratites and other birds. Alternatively, short-distance dispersal may occur on the pelts of rabbits.

Ceratocephala spp., like other species of the closely related *Ranunculus* genus, produce and accumulate significant amounts of ranunculin, a potent poison, at least for mammals (Lagarde et al. 2003). A tortoise of the Russian steppe (*Testudo horsfieldi*) shows strong seasonal, forage dependency on *Ceratocephala falcatus* as part of an annual diet of plants which mostly show high toxicity to herbivorous mammals. A plant diet rich in elements potentially toxic to mammals is reported for other turtles, tortoises, and terrapins (Lagarde et al. 2003). Further, a sample of moa coprolites from the Dart River, Mt Aspiring National Park, showed abundant seeds of *Coriaria* sp. (J. Wood pers. comm., 2006), a genus toxic to cattle and sheep but not to birds (Connor 1977). Acid scarification increases the germination of seed of the Asian plant *Ceratocephala* [*Ranunculus*] *testiculatus* (Young et al. 1992), suggesting the prospect of enhanced germination from vertebrate ingestion. Intriguing shifts in forage preferences and plant–animal mutualisms probably have accompanied mammalian replacement of avifaunal herbivory in New Zealand.

Ecosystem management

Overall, the present study suggests that excluding all mammalian herbivores from many of the rare non-forest ecosystems occupied by spring annuals brings no benefit to these herbs and may increase their risk of smothering by taller competitors. Inferences on the benefits of mammalian disturbance to soil nutrient status from faeces containing exchangeable nitrogen need testing. The use of mammalian herbivores as substitutes for extinct birds in spring annual habitats may conflict with recommendations that these mammals be removed from the surrounding dryland hill-country to rebuild their depleted woody communities (Walker et al. 2003a,b). A mix of intensive spring annual habitat management and restoration of the matrix scrub within the greater landscape may be required for these ecosystem mosaics.

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