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Changes in seed dispersal processes and the potential for between-patch connectivity for an arid land daisy

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Abstract. Dispersal is a major and critical process in population biology that has been particularly challenging to study. Animals can have major roles in seed dispersal even in species that do not appear specifically adapted to animal-aided dispersal. This can occur by two processes: direct movement of diaspores by animals and modification of landscape characteristics by animals in ways that greatly influence dispersal. We exploited the production of large, persistent dispersal structures (seed heads, henceforth) by *Erodiohyllum elderi* (Asteraceae), a daisy from arid Australia, to further understand secondary dispersal. Seed head dispersal on and off animal tracks in eight *E. elderi* patches was monitored for 9.5 months by periodically recording the location of marked seed heads. Sites were located inside a reserve that excludes sheep but not kangaroos, and in a nearby area with both kangaroos and sheep. The distance moved and likelihood of seed head movement was higher in areas with sheep, and especially along animal tracks. There was clear evidence that seed heads were channeled down animal tracks during large rainfall events. Seed head dispersal away from patches occurred to a limited extent via their physical contact with sheep and potentially via wind dispersal. Thus, the advantages of this study system allowed us to demonstrate the two postulated effects of herbivores on dispersal via direct movement of seed heads, and two distinct indirect effects through landscape modification by herbivores from the creation of animal tracks and the denudation of vegetation.

Key words: aboveground seed bank; Asteraceae; *Erodiohyllum elderi*; Koonamore daisy; Koonamore Station, South Australia; patchy distribution; population dynamics; secondary dispersal; xeric vegetation.

INTRODUCTION

Dispersal is a major and critical process in population biology that has been particularly challenging to study across all ecosystems. Two aspects of seed dispersal ecology are of particular relevance for plant species in arid and semiarid landscapes. Firstly, dispersal affects the long-term persistence of patchily distributed species with patchily distributed resources in a highly temporally variable environment. Dispersal over even small distances reduces the chance of subsequent density-dependent interactions by moving seeds away from the immediate vicinity of parent plants (Howe and Small-

wood 1982) but retaining them in a favorable area (Schupp 1995). Longer-distance dispersal involves risk, as few propagules typically reach sites suitable for germination and growth (Venable and Lawlor 1980). However, long-distance dispersal is required for populations to expand into new areas (Howe and Miriti 2004), and between-patch movement allows the persistence of subdivided populations when local populations are subject to extinction, in line with metapopulation theory (Hanski and Gilpin 1991, Cain et al. 2000). Secondly, the introduction of large herbivores throughout arid regions of the world has had a dramatic influence on ecological processes, including dispersal (Peters et al. 2006).

Animals can affect seed dispersal even for seeds that do not appear specifically adapted to animal dispersal. This can occur by either direct movement of diaspores by animals, or changes in the landscape produced by animals in ways that influence dispersal. There is ample circumstantial evidence of changes to seed dispersal processes resulting from the introduction of large grazing herbivores into arid regions (Peters et al. 2006). However, because of the intrinsic difficulty in studying dispersal, there has not been much direct experimental research of dispersal itself (e.g., Venable et al. 2008). Comparing dispersal in nearby sites with

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original and modified herbivore communities, e.g., where rangelands adjacent to protected areas can be studied (Emmerson et al. 2010), can provide this information.

The introduction of herbivores to arid and semiarid regions typically results in degraded vegetation and microbiotic layer and the disruption of fundamental ecological processes (Peters et al. 2006). In Australia, for example, the consequences of introduced sheep on vegetation are well documented (Stafford-Smith and Morton 1990). Sheep browse vegetation heavily near watering points (Landsberg et al. 1997) and their hooves damage the delicate soil crust (Friedel et al. 1993), which can lead to erosion and interferes with seedling establishment and vegetation recovery (Stafford-Smith and Morton 1990). Vegetation traps seeds and litter and reduces the intensity of wind near the ground, and thus potentially has a large influence on seed dispersal. Reduced vegetation cover, along with soil surface compaction, also results in higher water run-off, which impacts resource accumulation and redistribution (Ludwig et al. 1994, Ludwig and Tongway 1995) and can affect seed redistribution by water flow. Although introduced herbivores clearly modify ecological processes, their potential impacts on seed transport and deposition have not been adequately assessed (Tremont 1994).

Here we examine seed dispersal of the arid-land Asteraceae, *Erodiohyllum elderi* in adjacent sites, one affected by introduced vertebrate herbivores and the other subject mainly to grazing by native herbivores. This species is ideal for such studies because of its production of hard, roughly spherical capitula (seed heads; Black 1986) that can be monitored for long periods (Emmerson et al. 2010). The lack of obvious dispersal-promoting structures makes it typical of other xeric species. Further, because of the patchy distribution of *E. elderi* and the high temporal variability in its environment, we expected that some long-distance dispersal is required to allow the recolonization of patches when local extinction occurs. Here, we assessed the evidence for long-distance or between-patch dispersal to determine under what conditions dispersal between local populations is likely to occur. Specifically, we asked the following questions. How are seed head dispersal patterns affected by the presence of introduced herbivores? Is dispersal enhanced by animal tracks, and do they result in dispersal either predominantly toward or away from the patches? Does secondary seed head dispersal along animal tracks enhance connectivity between patches? Finally, we incorporate results from this and a previous experiment (Emmerson et al. 2010) to explain patch contraction and expansion by linking dispersal outcomes to the fluctuating environment, the state of the vegetation, and soil condition.

METHODS

Erodiohyllum elderi (Koonamore Daisy) is a short-lived perennial growing in low-lying areas in semiarid

and arid areas of southern Australia. It grows in distinct “patches” of up to several thousand plants spread over several hundred square meters. The patches are separated by hundreds to thousands of meters. The hard, 20 mm high woody capitula weighs up to 2.5 g, and holds up to 120 viable seeds, forming an above ground seed bank (Black 1986). Seeds are released over two decades in response to rainfall and seed head decay (L. Emmerson, unpublished data), which is longer than the time frame over which dispersal was recorded here. Seeds germinate rapidly in the presence of water after their release. Primary dispersal of *E. elderi* is limited, as the intact seed heads drop to the ground below the parent plant. As with many other xeric species, *E. elderi* seed heads lack obvious dispersal-promoting structures.

Site description

The study was conducted at Koonamore Station (32°07' S, 139°22' E), located in the mid-east of South Australia. The site receives an average annual rainfall of 215 mm, concentrated in winter as small rainfall events, with large, unpredictable rainfall events during summer. The daily maximum temperature averages 32°C in summer (December–February) and 15°C in winter (June–August). The gently undulating topography includes clay pans bordered by small sandy dunes, with a chenopod shrubland dominated by *Atriplex vesicaria* (bladder saltbush), *Maireana sedifolia* (pearl bluebush), and *M. pyramidata* (black bluebush) and a scattered overstory mainly of *Acacia aneura* (mulga) and *Myoporum platycarpum* (sandalwood). Annual plant species are often prominent in the low-lying areas after rains promote germination and growth (Osborn 1925).

An area of ~390 ha, hereafter referred to as the Reserve, was fenced to exclude sheep in 1925 (Osborn 1925), and a successful rabbit eradication program was started in the 1970s.

Grazers create well-defined tracks through the repeated use of particular routes that can persist for many years, especially where grazing is intense (Friedel et al. 1993). Outside the Reserve, the tracks are predominantly made by sheep and can extend for many kilometers. These tracks are 0.3 m wide and up to 0.2 m deep, although they are generally shallower. There are fewer tracks inside the Reserve, and these are made by kangaroos and, to a far lesser extent, emus. They are usually the same width as sheep tracks, but shallower (0.01–0.05 m) and less well defined. Although track presence suggests frequent use, sheep and kangaroo movement is not restricted to the tracks. Although sheep may browse *E. elderi* foliage when other forage is scarce, it is not a large component of their diet (Cunningham et al. 1992). There is no evidence that kangaroos graze the foliage. By using the Koonamore Vegetation Reserve, we were able to examine dispersal in a location where the vegetation and soil crust layer has been recovering over seven decades from the earliest impacts of grazing after European settlement.

Seed head dispersal on animal tracks

Intact seed heads were collected from the ground and sprayed with paint that fluoresced at night under a UV lamp to monitor their dispersal. The paint does not affect seed head dispersal (Emmerson et al. 2010). Seed head dispersal was monitored on and off animal tracks in eight *E. elderi* patches located within 10 km of each other. Four patches were inside the Reserve (R patches: R1, R3, R4, and R5) and another four were outside the Reserve (O patches: O1, O2, O5, and O6) with sheep and kangaroos present. The patches ranged from 50 m to over 500 m across. Where possible, three well-defined and recently used tracks (i.e., with signs of fresh dung and hoof or footprints) were selected crossing each patch. In two of the inside-Reserve sites, there were only two animal tracks. Along each track, seed head release sites (0.2 × 0.2 m areas) were located for convenience on the inside, at the edge, and beyond the boundaries of the patch, both on and off animal tracks. The off-track release site was immediately adjacent to the on-track release site but off the animal track; release site pairs were within 1 m of each other. There were up to 18 release sites in each patch in which we placed 20 seed heads, painted with a unique color combination for each release site.

The distance and direction that seed heads moved was monitored over 9.5 months. We located the painted seed heads at night with a portable UV lamp under which they glowed and were obvious for up to tens of meters away. We searched for seed heads on our approach to each release site, then for up to several hundred meters away from each release site, and then on the way to the next release site. The location of each seed head was marked and the direction and net distance that each seed head had moved was measured the following day, as well as the number of seed heads remaining within each release site. Seed heads were released on 7 March 1995 and their movement was measured on 9 June 1995, 6 September 1995, and 31 December 1995 (3, 6, and 9.5 months, respectively, after deployment). Frequent dispersal measurement allowed us to maximize the number of seed heads followed through time.

Covariates for seed head dispersal

We noted soil type (clay or sand) at each release site and measured the elevational change at 5-m intervals in each direction along the animal track in relation to each release site. Elevation change was slight: on the order of 10-m change along 250-m transects; the maximum topographical gradient was 0.084 and was typically less than 0.03. Clay release sites always had slopes less than 0.025. Daily precipitation was recorded at the nearby Koonamore Station Homestead (an Australian Bureau of Meteorology site). The number of rain days and total precipitation between seed head dispersal measurement occasions were compared to determine their effects on dispersal. Rainfall monitored in *E. elderi* patches located

within 10 km of each other had previously displayed little difference between patches (Emmerson et al. 2010).

Methods for estimating survival of seeds through animal digestive systems

We assessed the possibility of *E. elderi* seed dispersal by animals via ingestion and defecation. To determine this, the readily germinable seed bank in dung was examined. Dung from sheep, rabbits, kangaroos, and emus in two outside-Reserve patches (O1 and O3) was collected on 3 February 1995. Dung was divided into 25-g aliquots, mixed thoroughly with 500 g of potting mix after being loosely crumbled, placed in containers in a glasshouse, and watered when necessary. There were 6, 9, 13, and 18 replicates for emu, rabbit, kangaroo, and sheep dung, respectively. Seedling emergence was monitored for two months; *E. elderi* seedling emergence generally occurs within the first week. Although flowers or seed heads were not fed to animals, we had seen sheep eating daisy flowers in the field, and the emergence of *E. elderi* seedlings would clearly indicate that they can survive ingestion.

DATA ANALYSIS

The effectiveness of pairing of the average distance moved and the proportion of seed heads that moved per quadrat for the on- and off-track release sites was tested with the Pearson correlation coefficient to determine whether spatial dependence occurs between on- and off-track pairs. Because on-off track pairing within each patch was ineffective, the pairs were treated independently.

Data were analyzed with two steps: firstly, the proportion of the seed heads that moved, and secondly the distance that moving seed heads moved. This approach is common for zero-inflated data (Martin et al. 2005). The proportion moved required generalized linear mixed-effects models (GLMM) with a binomial error structure, while linear mixed-effects models (LME) were used for the distance moved. Models were fitted in R (version 2.10.0; R Development Core Team 2009) using the “glmer” function in the *lme4* library (Bates and Maechler 2009), which is useful for unbalanced data (Pinheiro and Bates 2000), and “lme” in the *nlme* library (Pinheiro et al. 2009). Variance components for LME models were estimated with restricted maximum likelihood (REML) when comparing models with different random effects components, and with maximum likelihood (ML) for models with similar random effects components but different fixed-effects structures (Crawley 2002).

Because of the large number of potential factors that could be included in the full models, we separated the analyses according to soil type (C, clay; S, sand), which was previously found to be important (Emmerson et al. 2010) and had different topographical gradients. Full models for each soil type included the explanatory variables: topographical gradient at each release site (0–

0.084), herbivore identity (K, kangaroos inside the Reserve; K + S, kangaroos and sheep outside the Reserve), and position in relation to animal tracks (on or off). Interaction terms between each pair of main-effects terms were also included. Random effects included patch, track within patch, and, for distance moved, release site within track within patch (one-, two-, or three-level components).

To determine the most suitable random components structure, the full model was compared with simpler models by systematically removing each random effects term and choosing the model with the smallest Akaike's information criterion (AIC) value (Akaike 1974). Comparing GLMM and GLM for the proportion of seed heads that moved was only possible once the AIC value had been rescaled. After the random components had been specified, systematic deletion of the fixed-effects terms was assessed using this model as a starting point, with significance determined by the change in model deviance compared against the χ^2 distribution for GLM models, the likelihood ratio test for LME models, and AIC for GLMM models until a final model was established.

Data were examined to determine whether seed heads moved predominantly toward or away from each patch. This could only be assessed for seed heads released at the edge or outside the patch. Wilcoxon rank sum tests were used to determine whether the median distances moved were in a particular direction (away from patch, median distance moved > 0 ; toward patch, median distance < 0). Although seed heads from the same release site may exhibit spatial dependence, this analysis reflects the direction that seed heads typically move for seed heads aggregated over a scale typical in the field. Effectiveness of pairing and Wilcoxon sum rank tests were assessed with GraphPad PRISM (version 3.02, GraphPad Software).

Statistical analyses are presented for dispersal after three months (9 June 1995) and 9.5 months (31 December 1995).

RESULTS

We relocated 96% of seed heads after three months and 88% after 9.5 months. Most seed head loss occurred from release sites in sandy areas, and raking these areas uncovered many of them buried in the sand; the results from the buried seed heads were excluded from analyses. Although we saw no evidence that granivores collected the remaining seed heads, ants collected seeds after seed release, as evidenced by seedling emergence around ant mound openings. An initial dispersal burst occurred during the first three months when 63 mm of rainfall fell over two days (30 April and 1 May 1995) (Fig. 1). Seed heads were more likely to disperse and move farther outside the Reserve where there were sheep and kangaroos, especially on animal tracks (Figs. 1 and 2c, g; herbivore identity was important for proportion of seed heads dispersing and distance moved. In all cases, P

< 0.03 ; Tables 1 and 2). Seed head movement was largely episodic. After three months, those that had not moved were most likely to move, but only short distances, resulting in the mean dispersal distance leveling off after three months (Fig. 1). Although initial dispersal was largely driven by rainfall, the 34.8 mm of rain over two consecutive days in October did not result in substantial movement (Fig. 1) and seed heads were trapped in debris on the ground or stuck in the hardened mud at this stage.

Seed heads moved farther and were more likely to move when on animal tracks (Fig. 2b, f; position was considered important for both soil types for proportion dispersing and distance moved after 9.5 months; Tables 1 and 2). Dispersal was reduced inside the Reserve (Fig. 2; herbivore identity was important for proportion dispersing and distance moved; Tables 1 and 2). After 9.5 months, seed heads dispersed farther on clay than on sandy soil (Fig. 2). Model predictions show that the proportions of seed heads moving were similar for the clay and sandy soil types for the on-track positions both inside and outside the Reserve, as well as the off-track inside-Reserve positions (Fig. 3a). More seed heads dispersed on clay than on sandy soils in the off-track positions outside the Reserve. In contrast, seed heads on clay soils moved farther irrespective of being on or off tracks or inside vs. outside the Reserve (Fig. 3b). There was no effect of steepness of slope on the proportion of seed heads moving or the distance moved (Tables 1 and 2).

Analyses of the proportion of seed heads moving did not include random effects ($AIC_{\min} = 147$ and 65, respectively, for clay and sand GLM after 9.5 months; Table 1), but dispersal distances required seed head movement within a release site as a random term (three-level random effects models had minimal AIC values; Table 2). Seed heads released in the same release site often moved different distances (e.g., Patch O3, track 1, release site 2 on-track dispersal varied from 0.69 m to 38 m). In some cases, seed heads moved along the track or downhill together, whereas in others, a few seed heads were scattered around the release site and the rest had not moved. This was the result of distinctly different dispersal processes: movement through sheet water flow after heavy rainfall and the scattering of seed heads by sheep or wind. Water flow moved seed heads downhill where they aggregated with seeds, twigs, and pieces of vegetation and dung. Unfortunately we did not consistently record the most likely dispersal vector.

The dispersal kernels showed a large proportion of seed heads moving small distances away from the release sites, with fewer seed heads moving > 2.5 m away from the release site (Fig. 4). There was little difference between dispersal kernels inside the Reserve and the off-track outside-Reserve position, with $> 60\%$ of seed heads not moving and maximum movement of 10 m (Fig. 4a, b). The outside-Reserve on-track dispersal

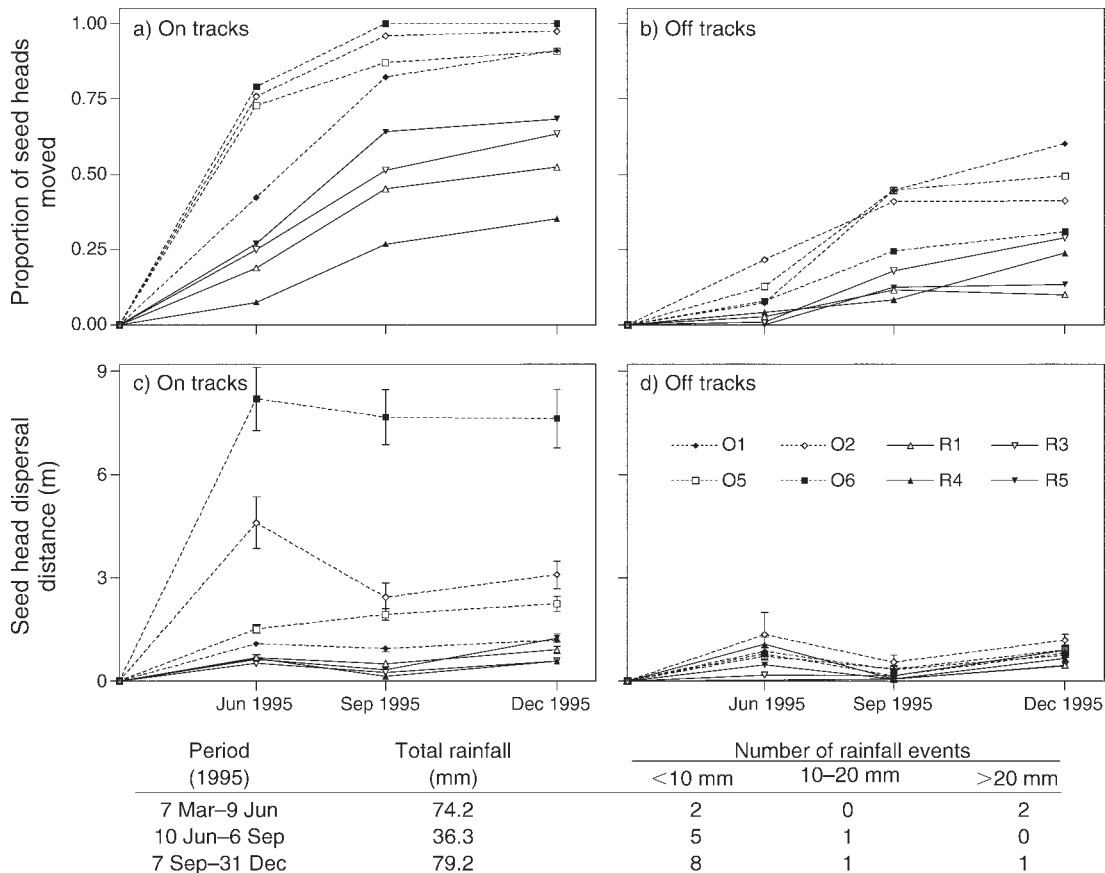


FIG. 1. Seed head dispersal of *Erodiohyllum elderi* (Koonamore daisy, Asteraceae) in South Australia over 9.5 months. Mean proportion of seed heads that moved from each release site for (a) on track positions and (b) off track positions for each patch through time, as well as distance (mean \pm SE) moved by seed heads for (c) on track positions and (d) off track positions in each of eight patches. Solid lines represent four patches (R) inside the Koonamore Vegetation Reserve, and dashed lines are four patches (O) outside the Reserve. Statistical analyses account for spatial dependence for seed heads from the same release site. Cumulative rainfall and the number of events between dispersal measurements are presented.

kernel extended to 38 m, with a lower proportion of seed heads moving <1 m from the release site (Fig. 4c).

Seed heads moved predominantly toward the patch when they were released on animal tracks (Wilcoxon sum rank test: on-track inside Reserve: $W = -5665$, $P = 0.011$, $n = 264$; on-track outside Reserve: $W = -34600$, $P < 0.0001$, $n = 542$ for 9.5 months). Seed heads did not move in any particular direction when deployed off tracks outside the Reserve (off-track outside Reserve: $W = -89$, $P = 0.487$, $n = 277$ for 9.5 months), but moved away from the patch inside the Reserve (Wilcoxon sum rank test: off-track in Reserve: $W = 1371$, $P = 0.003$, $n = 91$), although this movement was negligible (<1.75 m away).

Maximum dispersal distances were recorded on animal tracks (on-track outside Reserve: 38 m toward patch, 19 m away from patch) and this was farther than inside the Reserve (on-track inside Reserve: 6.64 m toward patch, 3.3 m away from patch). Off-track maximum distances outside the Reserve (off-track outside Reserve: 6.05 m toward patch, 6.9 m away from

patch) were greater than inside the Reserve (off-track inside Reserve: 3.97 m toward patch, 1.75 m away from patch).

No *E. elderi* seedlings emerged from any type of dung.

DISCUSSION

Our results from this and previous research (Emmerson et al. 2010) show compelling evidence that introducing sheep to the Australian arid lands has had a notable impact on seed dispersal processes. *Erodiohyllum elderi* seed head dispersal was greater in the area outside a reserve where sheep graze vegetation and their hooves damage the soil surface crust (Osborn 1925). We attribute this directly to the physical interaction from sheep trampling and inadvertently kicking seed heads, and indirectly to their effect on the vegetation and soil and the consequent effect that this has on seed dispersal processes. Although we expected limited dispersal inside the reserve where dense vegetation and fallen branches trap windblown and water-washed material (Friedel et al. 1990, Ludwig et

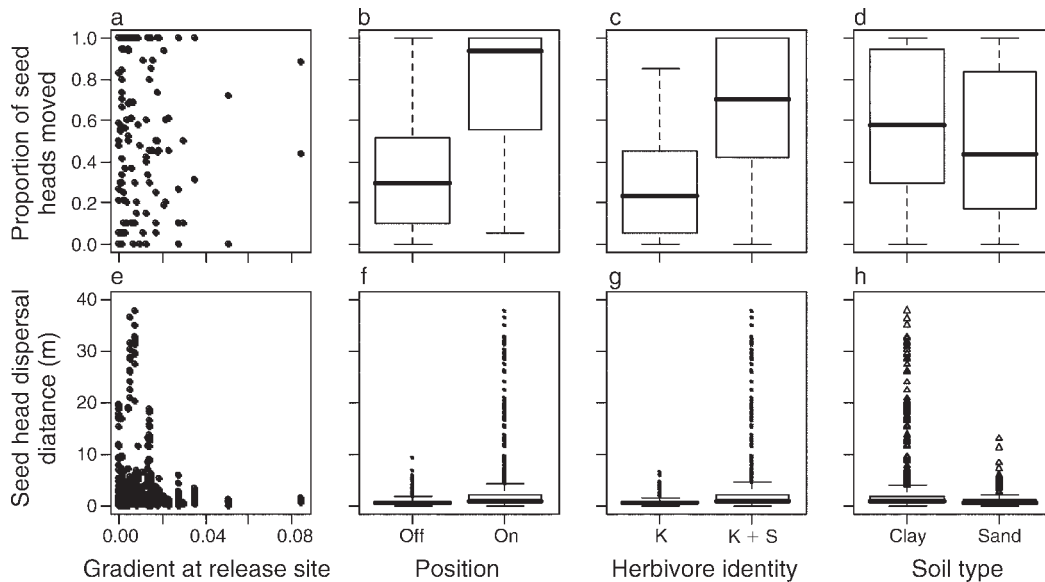


FIG. 2. (a–d) Proportions of seed heads that had moved after 9.5 months for each release site as a function of (a) topographical gradient (ratio of change in elevation with horizontal distance) at each release site, (b) position in relation to track (on or off), (c) herbivore identity (K, kangaroos inside the Reserve; K + S, kangaroos and sheep outside the Reserve), and (d) soil type (clay or sand). (e–g) Seed head dispersal distances in relation to (e) topographical gradient, (f) position in relation to track, (g) herbivore identity, and (h) soil type. Statistical analyses take into account spatial dependence of seed head movement from the same release site. Boxes show the 25th, 50th, and 75th percentiles, and whiskers extend to maximum and minimum values.

al. 1994), we anticipated that seed head dispersal via water flow would be similar on animal tracks, irrespective of location, for any particular rainfall event. We interpret the increased seed head dispersal

distances along animal tracks in areas with introduced herbivores as a consequence of increased water run-off where there is reduced vegetation (Stafford-Smith and Pickup 1990, Ludwig et al. 1994, Ludwig and Tongway

TABLE 1. Model results of variables affecting the proportion of *Erodioophyllum elderi* seed heads moving from each release site (analyzed separately for clay vs. sandy soil) after 3 and 9.5 months.

Model and variable (s)	Initial (3 months)			Final (9.5 months)		
	AIC	Δ Dev	P	AIC	Δ Dev	P
a) Clay soil						
Two-level GLMM	193			151		
One-level GLMM	194			149		
GLM (no random effects)	201			147		
Herbivore identity \times position	194				-6.61	0.01
Herbivore identity \times gradient	191				-0.87	0.35
Gradient \times position	190				-0.83	0.36
Position (on or off tracks)	not tested			not tested		
Herbivore identity	not tested			not tested		
Gradient at release site	188.9				-0.96	0.37
b) Sandy soil						
Two-level GLMM	66			69		
One-level GLMM	65			67		
GLM (no random effects)	63			65		
Herbivore identity \times position		-0.23	0.63		-0.33	0.57
Herbivore identity \times gradient		-0.63	0.43		-0.62	0.43
Gradient \times position		-0.01	0.91		-0.28	0.60
Position (on or off tracks)		-122.7	<0.001		-58.4	<0.001
Herbivore identity		-44.6	<0.001		-13.25	<0.001
Gradient at release site		-0.001	-0.001		-0.008	0.93

Notes: Inclusion of random effects is examined by comparing AIC values. The model with the smallest AIC (boldface) was used in deletion tests to examine fixed effects. Change in deviance from the minimal AIC model on removal of a given explanatory variable is tested against the χ^2 distribution for GLM models and by using AIC for GLMM models. Each explanatory variable is associated with 1 df. For clay soil, initial and final models include position, herbivore identity, and the interaction term between the two. For sandy soil, initial and final models include position and herbivore identity.

TABLE 2. Model results of variables affecting the distance moved by *Erodiohyllum elderi* seed heads from each release site (analyzed separately for clay vs. sandy soil) after 3 and 9.5 months.

Model and variables	Initial (3 months)			Final (9.5 months)		
	AIC	<i>L</i> ratio	<i>P</i>	AIC	<i>L</i> ratio	<i>P</i>
a) Clay soil						
Three-level LME	1178			2503		
Two-level LME	1365			2662		
One-level LME	1380			2713		
LM (no random effects)	1448			2748		
Herbivore identity × position		4.17	0.04		4.62	0.03
Herbivore identity × gradient		0.56	0.46		0.32	0.57
Gradient × position		0.43	0.51		0.18	0.68
Position (on or off tracks)	not tested			not tested		
Herbivore identity	not tested			not tested		
Gradient at release site		0.766	0.38		2.64	0.10
b) Sandy soil						
Three-level LME	358			751		
Two-level LME	357			771		
One-level LME	365			771		
LM (no random effects)	363			769		
Herbivore identity × position		0.37	0.54		5.50	0.02
Herbivore identity × gradient		2.16	0.14		0.37	0.55
Gradient × position		3.10	0.38		3.04	0.08
Position (on or off tracks)		0.87	0.35	not tested		
Herbivore identity		2.99	0.08	not tested		
Gradient at release site		2.69	0.10		0.01	0.91

Notes: Inclusion of random effects is examined by comparing AIC values. The model with the smallest AIC (boldface) was used in deletion tests to examine fixed effects. Change in deviance on removal of a given explanatory variable is tested using likelihood (*L*) ratio tests. For clay soil, initial and final models include position, herbivore identity, and the interaction term between the two. For sandy soil, no terms were included in the initial model, and the final model includes position, herbivore identity, and the interaction term between the two.

1995), creating a larger effective water flow along the tracks and hence enhanced seed head dispersal. We propose that areas with more vegetation and therefore higher water infiltration (Tongway and Ludwig 1994) would have reduced seed head dispersal, and vice versa for areas with soil compaction and reduced vegetation cover from the effects of grazing.

Although animal tracks channeled water that transported seed heads and other debris downhill, trampling by sheep scattered *E. elderi* seed heads around release sites and enabled their movement uphill. This resulted in maximum away-from-patch dispersal distances of ~19 m. Although we were unable to measure the effects here, strong winds and convectional whirlwinds that trans-

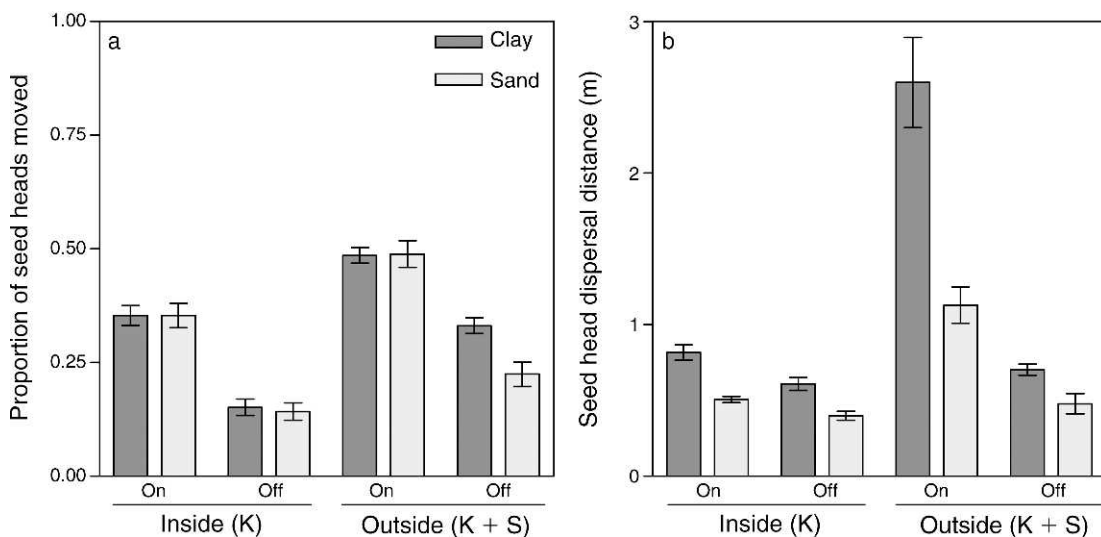


FIG. 3. Model predictions for (a) the proportion of seed heads that moved from each quadrat and (b) seed head dispersal distances after 9.5 months. Separate models were used for clay and sand soil types. Values indicate mean \pm SE.

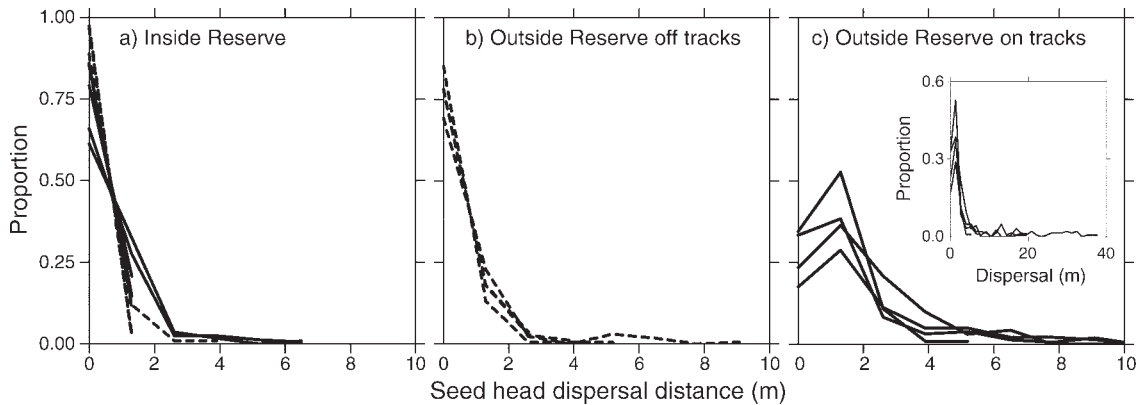


FIG. 4. *E. elderi* seed head dispersal kernels after 9.5 months (a) inside the Reserve for on and off track positions, (b) outside the Reserve for the off track position, and (c) outside the Reserve for the on track position. The insert shows a full dispersal kernel for outside Reserve on track movement. Dashed lines indicate off track positions and solid lines indicate on track positions.

ports dust and litter debris (Ludwig and Tongway 1995) could also enable uphill seed dispersal, especially where reduced vegetation cover causes increased wind strength on the ground's surface. Although long-distance seed dispersal by large herbivores is reported through either seed ingestion or attachment to animal fur (Myers et al. 2004, Ramos et al. 2006, Russo et al. 2006, Vittoz and Engler 2007), we found no evidence of this for *E. elderi*. There was also no evidence of granivores taking seed heads. The most prominent effect of introduced herbivores on *E. elderi* seed head dispersal was an indirect one, through the effects of grazing on vegetation and soil cover rather than their direct interaction with seed heads.

Dispersal by water flow was evident from the accumulation of debris and seed heads in water-washed lines and rill lines immediately after heavy rainfall. These patterns were particularly noticeable in degraded areas, as previously noted in other arid ecosystems (Guterman 1994, Ludwig et al. 1994). Seed heads dispersed readily with water flow along an unimpeded path, when on clay soil rather than sand, or when on animal tracks. Most importantly, the dispersal potential of a seed depends in part on its dispersal history. If seed heads are already in a locally low-lying region or a "sink," then dispersal will be limited by the mechanisms reported here. Downhill seed head dispersal to low-lying areas promotes the patchy distribution of this species but can also lead to seed head loss when seed heads accumulate in areas that are unfavorable for germination and subsequent growth. Likewise, dispersal away from a patch into areas that are unsuitable for seed germination and seedling growth is ineffective unless subsequent dispersal transports seeds to more suitable locations.

We found no compelling evidence of *E. elderi* seed exchange between patches at a rate relevant to the requirements of metapopulation theory (Hanski and Gilpin 1991, Cain et al. 2000), even with the enhanced dispersal from the effects of sheep. In this case,

propagule exchange between patches requires seed heads to move up the gentle slope beyond a patch toward and into a neighboring patch. The ability of seeds to move between patches depends on the inter-patch distance and seed longevity in relation to the time frame over which they disperse. With an expected seed head longevity of two decades (L. Emmerson, *unpublished data*), seed head dispersal between patches via the mechanisms reported here, particularly trampling or kicking by sheep (<19 m away from a patch over 9.5 months), could only occur between patches separated by less than several hundred meters.

It is likely that the indirect effects of grazing on the distance and direction of seed head movement through reduced vegetation cover is similar to, but generally an exacerbation of, the effects of extended drought. Populations of short-lived species can potentially expand through short-distance dispersal during extensive favorable conditions, followed by their coalescence when conditions become unfavorable (Morton 1990). For some species, this expansion during favorable periods could extend their range into usually unsuitable areas, or could at least establish "bridge" populations that may then allow further incursions and replenishment of patches that suffered local extinction in the previous period between extraordinary pulses.

We propose that the interplay among rainfall, the condition and type of soil, and the amount of vegetation present as a result of grazing or drought determines the dispersal potential of seeds in arid lands, in addition to the specific adaptations of the seed for dispersal. The vegetation in Australia's interior responds with various time lags to highly variable rainfall, ranging from lush to drought-stricken and barren over the years (Morton 1990). Soil condition and the amount and structure of vegetation, in turn, are a complex result of previous grazing and rainfall history, with reduced vegetation expected with intense grazing (Landsberg et al. 1997). Additionally, irregular and dramatic roving storm cells that can deposit more than the average annual rainfall in

a single event (Friedel et al. 1990) act as pulses in this process. For example, if a large rainfall event were to occur when the vegetation is lush, seed dispersal would be more limited than with a similar rainfall event over a landscape barren from drought or overgrazing. Under the last scenario, seeds that had previously dispersed away from the patch would be redistributed toward the lowest area within a patch, resulting in deposition in a location that is suitable for germination and plant growth because it is where water and resources accumulate (Tongway and Ludwig 1994). In contrast, an extraordinary deluge of rain (>80 mm over a few hours) is likely to trigger seed dispersal irrespective of the amount of standing biomass or soil condition. Long-distance dispersal, i.e., between patches or colonization of new areas, may occur when water overflows from one patch into another, transporting seeds and other debris over long distances (Ludwig et al. 1994) and allowing connectivity between otherwise demographically isolated patches. However, large rainfall events that cause widespread flooding are rare and may only occur every few centuries; one such deluge was recorded at Koonamore in 1939, when 140 mm fell over two days, causing massive flooding.

Although these scenarios mainly concern the dynamics of populations with an aboveground seed bank (a common, albeit not dominant, strategy), we propose that extreme rainfall events also shape the distribution of other arid-land species (e.g., Friedman and Stein 1980, Gutterman 1994, Gutterman and Ginott 1994, Vittoz and Engler 2007, Venable et al. 2008). This could apply, for example, to several Chenopodiaceae species with large propagules that are moved by wind and water and are only slowly incorporated into the soil seed bank after weeks or months (J. M. Facelli, *personal observation*). Seed dispersal potential therefore depends on seed longevity, specific adaptations for dispersal, the interaction between the seed and its environment (including the direct and indirect effects of introduced and native herbivores), and the occurrence of potentially rare ecosystem-shaping dispersal processes. Because such dispersal events are rare, short-lived arid-land species need a strategy that allows persistence in the most favorable patches during periods between seed redistribution events. This highlights the importance of the trade-off between dispersal and dormancy that allows seeds to escape unfavorable conditions in either space or time (Venable et al. 2008). For many arid-land species with limited dispersal, including *E. elderi*, this is achieved with a long-term, persistent seed bank with specific dormancy-breaking requirements (Venable and Lawlor 1980, Ellner 1985, Venable et al. 2008).

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