Biol Invasions (2011) 13:1869–1880
DOI 10.1007/s10530-011-0006-y

ORIGINAL PAPER

Estimating human-mediated dispersal of seeds within an Australian protected area

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Received: 8 December 2010 / Accepted: 19 April 2011 / Published online: 13 May 2011

Abstract Dispersal is critical step in plant invasions but there is limited information about human-mediated long distance seed dispersal, including in protected areas. Seed dispersal by hikers was quantified for five invasive species (the native *Acaena novae-zelandiae,* and the non-native weeds *Rumex acetosella Anthoxanthum odoratum, Dactylis glomerata* and *Festuca rubra)* in part of Australia's Kosciuszko National Park. The proportion of seeds remaining attached to trousers and socks was quantified for replicated short (150 m) and long (5,000 m) distance walks. Functions were fitted for each dataset, and parameters compared among species and between trousers and socks. Dispersal data were combined with attachment rates and the number of people undertaking walks to estimate the total number of weed seeds that might be dispersed. The power exponential function gave the best fit for the majority of datasets, indicating that detachment probability decreased with distance. Seeds of all five species were more tightly attached to socks than trousers, with some seeds still present on socks at 5,000 m. *Anthoxanthum* and *Acaena* seeds were more tightly attached to clothing than the other species. Theoretically 1.9 million seeds could be dispersed on socks or 2.4 million seeds on trousers through a season but the actual numbers are likely to be much lower because of limited weed seed at the start of the walks. Because of differences in attachment and detachment rates, seeds from *Acaena* were more likely to be dispersed longer distances. Long distance human-mediated seed dispersal is potentially a major cause of spread of invasive weeds into protected areas that favours some invasive species over others.

Keywords Human mediated dispersal · Long-distance dispersal · Non-native species · Invasions · Recreation ecology · Weeds

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Introduction

Protected areas are one of the major mechanisms for conservation worldwide (Worboys et al. 2005). Nature-based tourism is not only popular, but it is also one of the few human activities permitted in many protected areas (Newsome et al. 2002; Worboys et al. 2005). However, a wide range of negative environmental impacts on soils, vegetation, animals and water from tourism activities in protected areas has been documented (Liddle 1997; Pickering and

Hill 2007a; Monz et al. 2010). Impacts on plants from common activities such as hiking include the reduced diversity, cover and biomass of sensitive species and, in some cases, an increase in the diversity and cover of more tolerant species including weeds (Liddle 1997; Hill and Pickering 2007a; Hill and Pickering 2009).

Weeds, here referring to undesirable species that are not native to the region, are a major threat to biodiversity, including that in protected areas, as they have many impacts, including altering fire regimes and hydrology, and directly replacing native species (Manchester and Bullock 2000; Williams and West 2000; Weber 2003). Although the association between tourism infrastructure, such as roads and tracks, and the presence of weeds is well documented (Spellerberg 1998; Pickering and Hill 2007b; Pickering et al. 2007) and greater tourism use of a protected area is associated with greater diversity of weeds (Usher 1988), there is limited research on the contribution of tourists to the dispersal of weed seeds into, and within, protected areas (Pickering and Mount 2010). It is likely that tourists could act as unintentional dispersal agents of weeds. Certainly, human clothing and transport can act as seed dispersal vectors and seeds from over 750 species has been collected from vectors associated with tourist activity: clothing and equipment (228 species), horses (fur 42, dung 216 species) and vehicles (505 species) (Pickering and Mount 2010).

Despite its importance, and the large number of species which can be transported, there are few experimental studies of human-mediated seed dispersal (HMD), by tourists or more generally. There are only three experimental studies of HMD which have examined attachment rates (Fallinski 1972; Mount and Pickering 2009; Wichmann et al. 2009) and three that examined dispersal (Bullock and Primack 1977; Lee and Chown 2009; Wichmann et al. 2009) on clothing. These studies have shown that species differ in their attachment rates, and in plant traits that affect attachment, such as seed/fruit morphology, seed weight, height of infructescences and the number of seeds produced. Attachment rates also vary among items of clothing and with type of material, with some species attaching at higher rates to socks, while others attach at higher rates to trousers (Mount and Pickering 2009). Seeds were less likely to be dispersed by clothing with Velcro, than that without (Lee and Chown 2009). Studies of seed detachment from the clothing of walkers found that seeds can be transported long distances: >2.4 km (Bullock and Primack 1977) and >5 km (Wichmann et al. 2009).

Quantifying dispersal of seeds by any vector requires information on attachment, detachment and the behaviour of the vector (Nathan et al. 2008; Will and Tackenberg 2008). For unintended HMD on clothing, including that by tourists in protected areas, all these factors can be measured and hence spatial dispersal patterns can be calculated. Comparison of dispersal patterns for different plant species on different types of clothing and for different behaviours can indicate the role of HMD in causing long distance dispersal, including that of invasive species. While there are many recent examples of modelling and experimental studies of long distance dispersal by wind (Nathan et al. 2002; Soons and Bullock 2008) and for a limited selection of animal vectors (Mouissie et al. 2005; Manzano and Malo 2006; Pablos and Peco 2007; Will and Tackenberg 2008), studies of HMD on clothing are rare.

We used an experimental approach to examine unintended tourist-mediated long distance seed dispersal on clothing within a protected area in Australia. First we measured detachment rates of seeds from four non-native weed and one native species on two types of clothing (socks and trousers) at distances up to 5,000 m. Then using values for attachment rates in the field, and data on visitor numbers and behaviour, we calculated potential seed dispersal patterns within a specific landscape, i.e. continental Australia's highest mountain, Mt Kosciuszko.

Methods

Study system

Mt Kosciuszko alpine area ($\sim$100 km^{2,} S36 27.3540 E148 15.8090) in the southern section of Kosciuszko National Park (6,900 km^2), New South Wales, is of high conservation importance. It is an UNESCO biosphere reserve as it contains examples of glacial and periglacial features including block streams and erratics, while the largest of the four glacial lakes, Blue Lake, is a RAMSAR wetland (Costin et al. 2000, Fig. 1). There are 33 rare and 21 endemic species among a total of 212 native vascular plant species in the small area around Mt Kosciuszko

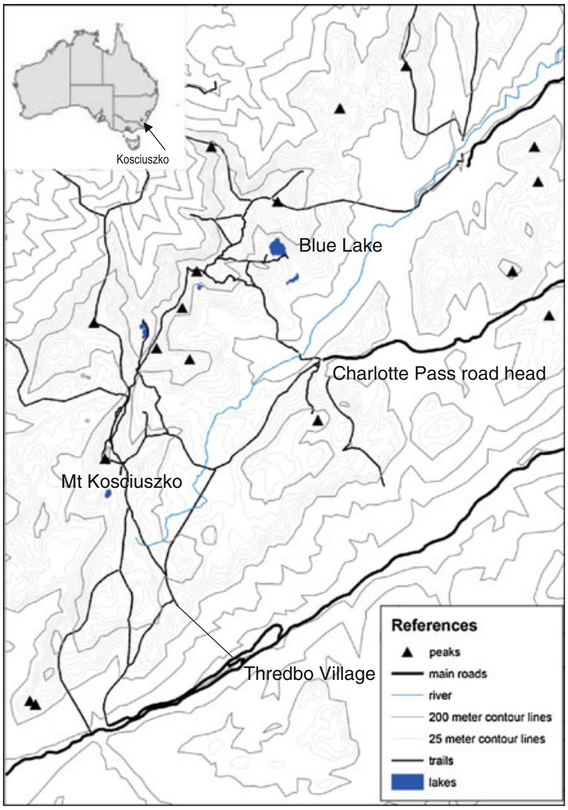

Fig. 1 Kosciuszko alpine area, in Kosciuszko National Park, in south-eastern Australia

(Fig. 1, Costin et al. 2000). Eleven species of non-native weeds are also found in the alpine area with 66 in the surrounding subalpine area (Bear et al. 2006; Pickering et al. 2007). The distribution of weeds is strongly associated with visitor infrastructure, including roadsides in the subalpine area, and trailsides in the alpine area (Johnston and Pickering 2001; Pickering and Hill 2007a, b).

The Park receives around three million visits a year, mostly in winter at ski resorts. In summer, walking in the Mt Kosciuszko alpine area is popular (Johnston and Growcock 2005). Nearly all of the 102,500 people who access the alpine area do so from the top of a chairlift in the Thredbo Village (67.5%), or the road head at Charlotte Pass (32.5%, Johnston and Growcock 2005, Fig. 1). At Thredbo Village visitors generally use car parks and access the chairlift either on paths or over mown lawns (Pickering, pers. obs.). In contrast, at Charlotte Pass visitors park on the roadside, then walk to the start of the trails at the road head (Pickering, pers. obs.). At least 18 species of weed and 16 natives grow on this roadside, with seed from 13 of them attaching to clothing in previous experiments (Mount and Pickering 2009). Although these roadsides are sometimes mown and/or sprayed, this usually occurs late in the season, with weed seeds present on plants growing on these flat roadsides often from mid January till mid March (Pickering, author obs.). Therefore seeds from roadside weeds are prone to be dispersed along short and long walks in the alpine area.

Species

Human-mediated dispersal of seeds was assessed for four invasive, non-native species (weeds) that originate from Europe (*Rumex acetosella* L. synonym *Acetosella vulgaris* Fourr, *Anthoxanthum odoratu* L., *Dactylis glomerat* L., *Festuca rubra* L.) and one species native to Australia (*Acaena novae-zelandiae* Kirk), which is invasive elsewhere, such as the USA. We subsequently refer to each species by its genus only. These species vary in traits that are likely to affect the probability of attachment (Sorensen 1986; Mouissie et al. 2005) and hence affect unintended HMD (Table 1). In Australia they occur in many protected areas, including Kosciuszko National Park where they can be found growing along roadsides and, less commonly, in the natural vegetation (Johnston and Pickering 2001, Bear et al. 2006). These species can be found seeding along the roadsides in the high subalpine zone of the Park from mid January till mid-March, with peak seeding in February (Pickering, author. obs.). Mature seeds of each species were collected at the peak time of seeding from plants on roadsides in Kosciuszko National Park and then stored loosely in envelopes in dry dark conditions.

Detachment of seeds on short and long walks

Dispersal distances of seeds for short (150 m) and long (>5 km) walks were assessed using a standardised experimental method. The short walks simulated what occurs when visitors arrive at car parks or road heads with weedy verges and then undertake short walks to viewing platforms, toilets, sitting areas and educational signs. For example, of the 33,650 visitors per year estimated to access the Kosciuszko alpine area from Charlottes Pass, 15,500 go sightseeing and/or undertake a short 5 min walk to a viewing platform (Johnston and Growcock 2005). The 5 km longer walk is equivalent to a walk of at least 1 h along a

Table 1 Characteristics of the five species used to examine dispersal distances

Species	Family	Common name	Native to	Growth form	Life form	Structures on seed	Max. height inflorescence (cm)	Inv.
Acaena novae-zelandiae	Rosaceae	Bidgee-widgee	Australia	H	P	Hair/spines/barbs	20	Yes
Rumex acetosella	Polygonaceae	Sheep's sorrel	Europe	H	P	None	50	Yes
Anthoxanthum odoratum	Poaceae	Sweet vernal grass	Europe	G	P	Awns	20	Yes
Dactylis glomerata	Poaceae	Cocks foot	Europe	G	P	Hairs	140	Yes
Festuca rubra	Poaceae	Red fescue	Europe	G	P	Awn	50	

H herb, *G* graminoid, *P* perennial, *Inv.* considered an environmentally invasive species internationally in Weber (2003)

track, with around 16,750 people who arrive at Charlotte Pass during the snow free period starting walks greater than 5 km.

A person with bare legs was assigned a clean sock (cotton/nylon blend sport sock extending to mid-calf) randomly to one leg and a trouser leg (100% drill cotton) to the other. They then put on shoes. Seeds were attached to a marked rectangular area ($\sim$18 cm by 14 cm, around 12–30 cm above the ground), on the outside of the sock and lower trouser leg using a gentle dabbing motion with the seed held loosely in the hand to reflect a walker brushing up against a plant. Seeds were found to readily attach to this area on socks and trousers in a separate experiment examining attachment rates of seeds to clothing on the same roadsides (Mount and Pickering 2009). Once a minimum number of seeds (>10 per item of clothing) was attached, the number of seeds in the marked areas was counted. The person then walked a fixed distance, stopped, and the numbers of seeds remaining recorded. This process was repeated for 12 distances for the short walk (0, 2, 5, 7, 10, 15, 20, 30, 50, 70, 100, and 150 m) and ten distances for the long walk (0, 5, 150, 300, 500, 1,000, 2,000, 3,000, and 5,000 m). There were ten replicate walks for each species for the short and the long distances, except for *Anthoxanthum*, where only seven replicate walks were conducted for the 5,000 m walks due to a shortage of seeds. Walks were conducted during dry still conditions using hardened wide (>1 m) paths similar to those in the Park.

Modelling seed detachment

Functions were fitted to the seed detachment data for each species. Wichmann et al. (2009) using four forms of an exponential function to describe dispersal of seeds in soil attached to the soles of walking boots, and Bullock et al. (in press) tested these functions on data for seed detachment from a variety of mammals. These functions deal with the probability of detachment of an individual seed. A simple exponential function (Eq. 1) assumes seeds detach from the vector at a constant rate (as the vectors in this study moved at constant speed, time and distance are equivalent), and Wichmann et al. (2009) proposed some simple modifications of this basic equation to allow detachment rate to change with time/distance. The simple exponential function with a constant detachment rate represents the proportion of seeds left on the vector, *lov*, at distance *d* as

$$lov = a\exp(-bd), \quad (1)$$

where *a* (the intercept) and *b* (the rate of detachment) are fitted. Forms of a double exponential function can allow either a decrease in detachment rate with distance

$$lov = a\exp(\exp(-bd)), \quad (2)$$

or an increasing rate of seed detachment with distance

$$lov = a\exp(-\exp(bd)). \quad (3)$$

An alternative formulation is the power exponential function

$$lov = a\exp\left(-d^{b}\right), \quad (4)$$

which allows detachment rate either to increase ($b > 1$) or decrease ($b < 1$) with distance. To test the fit of these formulations, we compared them with the inverse power model

$$lov = ad^{-b}, \quad (5)$$

which, although it does not have the mechanistic basis of the exponential family described above, is a widely-used and flexible two-parameter dispersal function (Bullock et al. 2006). Note that a and b are different parameters in each equation. Bullock et al. (in press) explore these functions in more detail and show their associated dispersal kernels.

These five alternative functions were fitted to the *lov* data for each species on trousers and socks for the short and long walk experiments using least-squares nonlinear regression in the R package (R Development Core Team 2008). As all models comprised two parameters, a and b, we used the residual sum of squares as a simple measure of goodness of fit of the models to the data.

Comparing detachment rates

Differences in the long-walk detachment rates among species and between trouser and sock vectors were analysed by fitting the power exponential model (the best-fitting function, see "Results") to paired datasets. For the power exponential, $a = lov(0)$ (Bullock et al. in press). Because 100% of seeds are attached at a distance of 0 m, all datasets would be expected to have $a = 1$. The value of b determines how the rate of seed detachment changes with distance (Bullock et al. in press),

$$r(d) = bd^{b-1} - (b-1)/d. \quad (6)$$

Therefore, a was fixed at a value of 1 for these comparisons and differences in the value of b were calculated. This was done by fitting b_1—the value of b for the first dataset—and b_{diff}, where the value of b for the second dataset $b_2 = b_1 + b_{diff}$. The 95% confidence intervals of b_{diff} were examined to determine whether this parameter value was significantly different from zero. All pairwise combinations of species were analysed for the trouser data, and again for the sock data. In addition, the trouser and sock data were compared for each species.

Estimating human mediated seed dispersal in the Kosciuszko alpine area

The potential for walkers to disperse seeds in the Kosciuszko alpine area was estimated by multiplying the number of seeds attached per type of clothing by the percentage of seeds dispersed per clothing item at particular distances (5, 150, 500 and 5,000 m) and the number of people walking to that distance during the 60 day period when the plants were likely to be seeding. Estimates of the number of seeds attached to socks and trousers at the start of walks were taken from Mount and Pickering (2009, unpublished data). For *Acaena*, *Rumex*, *Dactylis* and *Festuca*, it was the average number of seeds of each species attaching per sock and per trouser leg over 20 replicate 100 m walks through subalpine roadside vegetation along at Charlotte Pass in early February 2008 (Mount and Pickering 2009). For *Anthoxanthum* no seeds attached to socks or trouser legs over the 100 m walks. Therefore, the average number of seeds on a sock from 25 min walks on the same general area of roadside conducted in the following year (2009) was used (Pickering and Mount unpublished data).

The estimated numbers of people walking to each distance from Charlotte Pass were taken from data of visitation in 2000 (Johnston and Growcock 2005). A total of 9,145 people went walking for at least 150 m during the 60 days between 15 January and 14 March when roadside plants are likely to be seeding. This estimate of walker numbers was combined with the attachment rates from Mount and Pickering (2009) (multiplied by two to give a per person value) to estimate the total number of seeds that may be attached to visitors at the start of the walks, assuming that they all got out of their car, walked 100 m through the roadside vegetation to the start of the alpine walks. These values, combined with the proportion of seeds detached at different distances from the short walks, provide estimates of the number of seeds dispersed by 5 m and by 150 m along trails in the alpine area. The number of seeds dispersed in the first 500 m was estimated for all people walking the Lower Snowy River walk (~1 km return, 380 people), and for the first 500 m of the half day walks (4,552 people). The estimated total number of seeds dispersed in the alpine area was calculated as the total number of seeds dispersed by people on a 300 m return walk (Snow Gum walk or sightseeing) plus those on the a 1,000 m return walk (Lower Snow River walk), plus the number seed dispersed by people taking longer walks (>half day walks).

Results

Dispersal of seeds

All five species have seeds that could be dispersed unintentionally by humans over long distances. Although between 20 and 70% of seeds were dispersed from clothing in the first five metres, some seeds from all species were still attached to socks at 5,000 m (Fig. 2).

Seed retention for the five species on socks and trousers and on long and short walks showed the same general pattern (Fig. 2, Table 2). The simple exponential (Eq. 1), power exponential (Eq. 4) and inverse power (Eq. 5) functions always gave significant fits to the data (Table 2). The power exponential provided the best fit in the majority of data sets (14 out of 20), and while the inverse power had the best fit for the remaining datasets, the power exponential gave only a slightly worse fit in these cases (Table 2). The b parameter for the power exponential function was always <1, which indicated increasing seed retention probabilities at greater distances for all species. The double exponential functions (Eqs. 2, 3) gave variable fits, sometimes better than the simple exponential, but never as good as the power exponential.

Differences among species and clothing items in seed detachment

There were significant differences in seed detachment between sock and trousers and among the five species (Tables 3 and 4; Fig. 2). *Acaena* and *Anthoxanthum* seeds were more tightly attached to clothing than the other species, as indicated by significantly lower fitted values of b for the power exponential model. On trousers, *Dactylis* and *Rumex* seeds were more tightly attached than *Festuca* seeds, while on socks the species order changed slightly—*Rumex* > *Festuca* > *Dactylis*. Within 5 m of starting a walk, nearly half of the *Dactylis* and *Festuca* seeds had already fallen off socks, while less than 30% of the *Anthoxanthum* and *Acaena* seeds had detached by the same

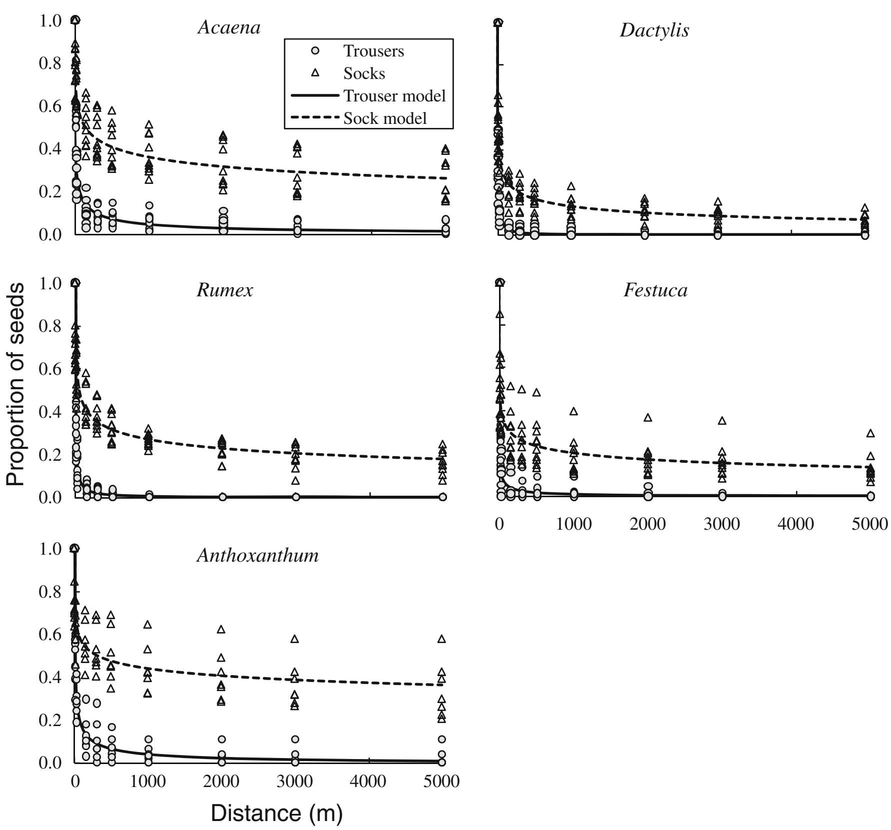

Fig. 2 The proportion of seeds retained on experimental trouser legs and socks at distances along replicated long walks, for five invasive plants. The *fitted curves* represent the power exponential function (Eq. 4), which generally fitted best to the data (Table 2)

Table 2 The fits of five alternative seed dispersal function to each species for short (150 m) and longer (5,000 m) walks when seed attached to socks or trousers

Model equation/type	*Acaena*		*Dactylis*		*Rumex*		*Festuca*		*Anthoxanthum*	
	Sock	Trouser	Sock	Trouser	Sock	Trouser	Sock	Trouser	Sock	Trouser
Short walk—to 150 m										
Residual sum of squares										
Simple exponential	1.085	1.608	1.358	1.291	2.54	1.424	1.338	1.484	1.625	1.328
Double exponential—decreasing rate	0.985	1.36	0.972	1.784	2.025	1.547	0.790	1.65	1.4	1.696
Power exponential	**0.831**	**1.082**	0.939	**1.042**	1.916	**1.113**	0.765	**1.213**	1.16	**1.251**
Double exponential—increasing rate	1.147	1.924	1.48	1.461	2.646	1.656	1.497	1.636	1.722	1.429
Inverse power	0.844	1.149	**0.931**	1.094	**1.864**	1.181	**0.717**	1.214	**1.144**	1.330
A for Power exponential	2.528	2.411	2.025	0.197	2.363	2.002	2.041	1.669	2.317	1.542
B for Power exponential	0.099	0.199	0.150	0.269	0.128	0.229	0.166	0.256	0.1254	0.260
Longer walk—to 5 km										
Residual sum of squares										
Simple exponential	1.59	0.698	0.818	0.215	1.018	0.192	1.38	0.254	0.872	0.394
Double exponential—decreasing rate	0.908	NA	0.502	NA	0.522	NA	0.993	0.387	0.791	0.744
Power exponential	**0.800**	0.490	**0.299**	0.204	**0.414**	**0.173**	**0.915**	**0.230**	**0.675**	**0.269**
Double exponential—increasing rate	NA	0.761	NA	0.215	NA	0.193	NA	0.267	NA	0.447
Inverse Power	0.840	**0.476**	0.300	**0.198**	0.476	0.178	0.917	0.231	0.691	0.277
A for Power exponential	2.504	1.909	1.757	1.656	2.283	1.28	1.657	0.846	2.216	1.854
B for Power exponential	0.095	0.193	0.137	0.288	0.110	0.255	0.109	0.224	0.070	0.193

Values in bold are for the model with the smallest residual sum of squares for that dataset

Table 3 Comparison of the parameter estimates for *b* from power models of the dispersal data between pairs of species on tourers and socks

	Acaena	*Dactylis*	*Rumex*	*Festuca*
Trousers				
Dactylis	*Dactylis*			
Rumex	*Rumex*	–		
Festuca	*Festuca*	*Festuca*	*Festuca*	
Anthoxanthum	–	*Dactylis*	*Rumex*	*Festuca*
Socks				
Dactylis	*Dactylis*			
Rumex	–	*Dactylis*		
Festuca	*Festuca*	*Dactylis*	*Festuca*	
Anthoxanthum	–	*Dactylis*	*Rumex*	*Festuca*

The entry for each pair gives the species with the higher *b* parameter and hence the faster seed detachment rate. – indicates no significant differences in *b* at $P < 0.05$

distance. By 5,000 m, at least 25% seeds of *Acaena* and 34% of *Anthoxanthum* were still attached to socks, while for the other three the figure was between 16 and 8% of seeds (Tables 3 and 4).

Seed of all five species detached from trousers faster than from socks (Fig. 2), with all within-species comparisons showing a significantly higher value of *b* for the trouser curves. Differences were apparent after just 5 m, with around 34% more *Anthoxanthum* seeds on socks than on trousers at 5 m. For the other species, values were more similar, with around a 15% difference for *Acaena* and *Dactylis*. By 5,000 m the difference in how tightly seeds were attached meant that for *Rumex*, *Dactylis* and *Festuca* there was no, or only one, seed left on only a few trouser legs, while there were an average of three seeds for *Acaena*, and two seeds per trouser leg for *Anthoxanthum*.

Estimating human mediated seed dispersal in the Kosciuszko alpine area

By combining attachment rates per species with distance-dependent detachment rates, estimates of the amount of seeds that could be transported per person were calculated. The simulated number of seeds that could be carried into the Kosciuszko alpine area on

Table 4 Simulated number of seed dispersed per item of clothing at different distance (5, 150 and 5,000 m) by people walking in the Kosciuszko alpine area

Species	*Acaena*		*Rumex*		*Anthoxanthum*		*Dactylis*		*Festuca*	
Item	Trou.	Sock	Trou.	Sock	Trou.	Sock	Trou.	Sock	Trou.	Sock
Seed attached at start										
Av. # seed per item	126	77.6	0.15	0.3	0	0.052	0.1	0.7	14.5	63.9
Min–Max	0–2,518	0–1,549	0–3	0–2	0	0–2	0–2	0–4	0–272	2–230
Total seed (9,145 people)	2,304,540	1,419,304	2,744	5,487	0	951	1,829	12,803	265,205	1,168,731
Dispersed in first 5 m										
Av. % seed	50%	24%	72%	32%	52%	28%	66%	49%	80%	49%
Min–Max % seed	19–75%	11–38%	56–83%	20–41%	43–71%	16–36%	50–85%	34–65%	64–100%	15–68%
Av. # seed per item	64.5	18.6	0.11	0.10	0	0.015	0.07	0.34	11.6	31.3
Min–Max # seed per item	0–1,889	0–589	0–2.5	0–0.82		0–0.72	0–1.7	0–2.6	0–272	156
Total seed (9,145 people)	1,152,270	340,633	1,975	1,756	0	266	1,207	6,273	212,164	572,678
Dispersed in first 150 m										
% seed per item	89%	49%	96%	58%	87%	44%	97%	78%	96%	72%
Min–Max % seed	78–97%	34–64%	92–100%	42–66%	70–97%	29–59%	94–100%	70–89%	87–100%	49–83%
Av. # seed per item	112.14	38	0.14	0.17	0	0.015	0.097	0.34	13.9	46
Min–Max # seed per item	0–2,442	991	3	1.3		0–1.2	0–2	0–3.6	0–272	1–191
Just short walks (4,212 people)	944,667	352,863	1,336	1,615	0	212	900	5,067	129,178	426,954
Dispersed in first 500 m										
% seed per item	93%	59%	99%	68%	93%	50%	99%	83%	98%	75%
Av. # seed per item	116.7	46.0	0.15	0.20	0.00	0.03	0.10	0.58	14.3	48.0
Just moderate walks (380 people)	88,722	34,937	113	154	0	20	75	444	10,833	36,510
Dispersed in first 5,000 m										
% seed per item	97%	75%	100%	84%	98%	66%	99.6%	92%	100%	87%
Min–Max % seed	93–100%	60–85%		75–92%	89–100%	42–79%	98–100%	87–97%		71–93%
Av. # seed per item	122	58.2	0.13	0.3	0	0.03	0.1	0.64	14.5	55.3
Min–Max # seed per item	0–2,518	0–1,317	0–3	0–1.8		0–1.6	0–2	0–3.9	0–272	1.4–214
Just long walks (4,552 people)	1,111,314	529,853	1,366	2,294	0	312	907	5,863	132,008	503,792
Total dispersed in alpine*	2,144,703	917,653	2,814	4,063	0	544	1,882	11,374	272,018	967,256

Trou. trouser leg. For details see the "Methods". % seed dispersal values at each distance are from the long distance walk. *Sum of seed dispersed by those just going on short walks (150 m, 4,212 people), those just on moderate walks (500 m, 380 people) and those just on long walks (5 km, 4,552 people) tourists' clothing was highly variable both within and among species (Table 4). It is also likely to vary between 15 January and 14 March, the period when weeds growing on the roadsides are likely to have mature seed. The number of seeds from all five species that could be dispersed varied from zero to 2,795 per trouser and from zero to 1,538 per uncovered sock, with nearly all the seeds from *Acaena*. Considering only the non-native weeds, the respective numbers are 277 per trouser leg, and 221 per uncovered sock. The average amount of seeds dispersed by a person going for a 5,000 m walk was calculated as 122 and 58.2 *Acaena* seeds, and 14.5 and 55.3 *Festuca* seeds per trouser leg and sock respectively, with less than one seed per clothing item for the other species.

Although these numbers are small, an estimate of the total amount of seed that could be introduced and then dispersed on socks and trousers is much larger. The number of seeds that could be carried into the alpine area on uncovered socks is 2.6 million of which most is *Acaena* (1.4 million) and *Festuca rubra* (1.2 million) assuming a constant attachment rate between 15 January and 14 March when weeds are likely to have mature seed. This value was calculated by multiplying the number of tourists entering the alpine area from Charlottes Pass during this time period (9,145 people) by the number of seeds per person on uncovered socks (average number of seeds attached per uncovered sock at the start of a walk for a given species multiplied by two) (Table 4). For the three other species, the number of seeds were orders of magnitude lower, partly due to fewer plants/seeds of these species found on roadsides, and also because seeds appear to be less likely to attach to clothing (Mount and Pickering 2009). The estimates of the total number of seeds on socks and trousers assume that the attachment rates for each species were constant over the whole period.

Not all the seed on tourists would be dispersed, and most would be dispersed close to the start of the walks. For example, the number of people walking to 5 m was 9,145, which combined with the average attachment and dispersal rates gives a total of 921,607 seeds dispersed within 5 m of the start of the walks for socks and 1,367,616 for trousers per season. Similarly, the 336,000 *Aceana* seeds estimated to be dispersed from socks in the first 5 m, is calculated by multiplying the number of seeds attached to socks at the start of the walk (1.4 million) by the average number of seeds dispersed by 5 m, e.g. 24%. The average number of seeds in total that could be dispersed in the alpine area if the attachment rate of seeds did not vary between 15 January and 14 March would be 1,901,327 for uncovered socks, and 2,421,198 for trousers per season (Table 4). This is calculated by combining the number of seeds dispersed by those undertaking walks of only 150 m, those walking just 500 m and those walking over 5 km.

Discussion

This study shows that humans have the potential to disperse large amounts of seeds over large distances. It also shows that the type of clothing worn affects the amount of seeds dispersed. The combination of data on seed collection (attachment) with data on dispersal (detachment) allowed estimates of the amount of seeds potentially dispersed by humans in a particular landscape during the hiking season. In doing so, the study has demonstrated the potential for tourists visiting an area of high conservation value to unintentionally spread seeds from a variety of weeds at long distances.

This study doubles (from five to ten) the number of species with quantified values of HMD by clothing (compare Wichmann et al. 2009; Lee and Chown 2009) and, to our knowledge, it is one of only six experimental studies examining seed dispersal on clothing (Fallinski 1972; Bullock and Primack 1977; Mount and Pickering 2009; Wichmann et al. 2009; Lee and Chown 2009). This reflects the very limited data on attachment and dispersal rates for human-mediated seed dispersal particularly in comparison to recent research into epizoochory which has examined large number of plant species (Mouissie et al. 2005; Pablos and Peco 2007; Will and Tackenberg 2008).

Differences among species in attachment rates to clothing, combined with differences in the detachment rates, demonstrate that clothing acts as a selective dispersal vector. Clothing facilitates longer dispersal distances of species such as *Acaena*—for which the long spine on the seed contributes to its high attachment rate and slow detachment—over others such as *Dactylis* whose pointed glumes and a short awn explain its lower attachment rates and faster seed detachment. *Rumex* also had low attachment rate and fast detachment, resulting in a few short distance dispersal events, and very little long distance dispersal. Attachment rates may not correlate with dispersal distances. For example, *Festuca* had a moderate attachment rate, but a reasonably fast detachment, while *Anthoxanthum* had very slow detachment rates, but low attachment rates and so dispersal is limited.

All of the species examined are non-native weeds in some regions of the world and all but *Festuca* have also been classed as internationally invasive environmental weeds (Weber 2003; Pickering and Mount 2010). Four species are environmental weeds in Australia, with *Dactylis* and *Festuca* also considered invasive in Australia. The differences found here in HMD on clothing among the five species may have large effects on how far and how fast the five species could invade new habitats. These differences highlight the fact that data on relative rates of unintended HMD, including that by tourists, is an important gap in current research into plant invasions. Such HMD could contribute to biotic homogenisation by increasing the capacity of species that benefit from human activities to expand their range (McKinney and Lockwood 1999). *Acaena* and *Festuca*, for example, appear from this study to be more likely to be dispersed unintentionally by humans, while *Rumex* had a low potential for dispersal, despite being the most common of the five species on roadsides in Kosciuszko National Park (Pickering and Hill 2007b). All the species have been recorded in other studies of unintended HMD on clothing and by vehicles (Pickering and Mount 2010).

Variation among clothing items in their potential to collect seed has been examined experimentally (Mount and Pickering 2009). The current study demonstrates that there are also differences in how far seeds are likely to be dispersed, with seeds more tightly attaching to socks than trousers. This is unsurprising, given the differences in material (socks were ribbed wool/nylon blend sports sock, while trousers were drill cotton), but demonstrates that seeds will attach to and be dispersed on even material with a low roughness (nap).

Modelling distance-dependent seed detachment for different species on different types of clothing can help to increase our understanding of the dispersal process and evaluates the possibility of a general model for this type of dispersal. Wichmann et al. (2009) found the power exponential model provided the best fit to their data on *Brassica* seed transported on boots, and Bullock et al. (in press) also found that data from studies of seed retention on a variety of mammals over long time periods were best fitted by this function. The power exponential also described best the majority of our datasets. For the remaining datasets here, the best fitting model was the inverse power model, which has been used in earlier studies of dispersal kernels (e.g. Willson 1993; Manzano and Malo 2006). However, in these datasets, the power exponential model gave the second best fit. While the inverse power model provides a good fit to the data, it is lacking a mechanistic justification (Bullock et al. in press). The most important advantage of the exponential power model is its mechanistic derivation: all parameters have a clear biological meaning and the model equation increases our understanding of the dispersal process. In this case, as also found by Wichmann et al. (2009) and Bullock et al. (in press), seed detachment became less likely with distance. This suggests that seeds vary in the extent to which they are stuck to the vector. Those travelling long distances were probably deeply entangled in the fibres of the materials. This raises the question whether such seeds would ever detach in a reasonable timeframe, which would allow them to germinate and establish. However, seeds were still detaching at the longest distances—which suggests seeds were not becoming irreversibly stuck—as demonstrated by the fact that the ratio of seeds still attached at 5,000 m to the number at 3,000 m was significantly less than one for both the sock (Wilcoxon test, $N = 47$, $P < 0.001$) and trouser data (excluding samples where seeds at 3,000 m = 0; Wilcoxon test, $N = 16$, $P < 0.05$).

It was possible to simulate the amount of seed dispersed into an ecosystem of high conservation value, the Kosciuszko alpine area. The measured attachment and distance-dependent detachment rates indicated that large amounts of seeds could be dispersed by visitors, with most of it falling within the first few metres of the road head. Therefore the starts of walking tracks are likely to receive not only more seeds than areas further along tracks, but they are also likely to be more disturbed by trampling. The high cover of weeds on the tracks in this alpine area shows that the seeds of many weed species have already been transported into the area and have established populations which will facilitate further spread (Pickering and Hill 2007a). For conservation reserves, such as Kosciuszko National Park where activities such as walking are seen as a relatively low impact, this study indicates that such activities can have important long-term indirect impacts on the environment(Pickering and Hill 2007b; Pickering et al. 2007).

Limitations on the estimation of seed dispersed

This study considers seed dispersal but not the following processes. Secondary predation, seed death, germination and establishment of new plants also play a role in the spread of species and of weeds in particular (Jongejans et al. 2008). However, the dispersal processes form a fundamental part of species spread, with propagule pressure being increasingly recognised as a critical step in plant invasions (Puth and Post 2005; Colautti et al. 2006; Lee and Chown 2009).

Estimation of the number of seeds carried into the alpine area on clothing and then dispersed within that area was based on a number of assumptions. It was assumed that visitors' socks or trousers were seed-free when they first arrived, which may under-estimate dispersal. A second assumption was that the estimate of attachment rates used would be similar to attachment rates on tourists and constant between the 15 January and 14 March. The width of the verge, the density of vegetation, and the potential distances visitors may walk along the verge are all variable, and hence would increase variability in the actual number of seeds dispersed. The number of seed on plants will vary naturally during a season, and for the weeds growing on the roadside at the start of the alpine walks, attachment rates are likely to decline over time as seed is continuously removed by tourists walking past. Preliminary data from brushing down the shoes of visitors at the Charlotte Pass road head show that of the 51 people tested, 14 did not have any seed with a total of 321 seeds collected from the remaining 37 visitors. Therefore the attachment rates used here for socks may be higher than those from real visitors.

Third, we assumed that all visitors either wore uncovered sports socks, or cotton drill trousers, but we did not include dispersal via other items of clothing such as shoes and laces which can collect and disperse large amounts of seed (Clifford 1956; Mount and Pickering 2009; Wichmann et al. 2009). The total amount of *Acaena* seed which could be introduced into the alpine area from hiking boots, cotton laces and cotton drill trousers would be 389 per visitor, while if they did not wear trousers the value would be 328 seeds (Mount and Pickering 2009). Data on the proportion of visitors wearing uncovered socks vs trousers, or what sort of material the clothing was made of was unavailable. Fourth, our calculations apply to the propagule pressure (amount of seeds available) at the time of our experiments while seed availability may vary within and among years.

Modelling using more detailed information on seed densities and visitor clothing and behaviour would allow more accurate estimates of seed dispersal. Directly collecting seeds from clothing when visitors enter and leave a reserve can also help quantify how much, and what type, of seeds are dispersed. Preliminary research however, found that the high variability in attachment and detachment rates made it difficult to relate seeds collected on clothing prior to walking with that on socks at the end of a walk, and hence measure what may be dispersed (Mount and Pickering 2009). What is clear is that long distance, unintended HMD by tourists in protected areas does occur and can involve large numbers of seeds and long distances.

Acknowledgments Funding from the International Centre for Ecotourism and the Sustainable Tourism Cooperative Research Centre at Griffith University to Pickering and Mount, and funding from NERC grant NE/B503141/1 to Bullock and Wichmann are acknowledged. We thank the two anonymous reviewers and the handling editor for their valuable comments on this paper.

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