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Short Communication

The relative importance of different seed dispersal modes in dry Mongolian rangelands

C. Bläß[a,*], K. Ronnenberg[a], O. Tackenberg[b], I. Hensen[a], K. Wesche[c]

[a] Institute of Biology – Geobotany and Botanical Garden, Martin-Luther-University Halle-Wittenberg, Am Kirchtor 1, 06108 Halle, Germany
[b] Institute of Ecology, Evolution & Diversity, Goethe University Frankfurt, Siesmayerstraße 70, 60323 Frankfurt am Main, Germany
[c] Senckenberg Museum of Natural History Görlitz, PO Box 300 154 , 02806 Görlitz, Germany

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A B S T R A C T

Nomadic livestock husbandry is the main form of land use in Mongolia. Grazing impact on plant productivity has frequently been studied, but effects on dispersal modes are largely unknown. We assessed the relative importance of zoochorous dispersal for several species but focused on the dominant fodder grasses *Agropyron cristatum* and *Stipa krylovii*. We searched for seeds in the fur of goats and sheep, but also experimentally attached diaspores and monitored retention. Endozoochory was tested by incubating faecal samples under standardised conditions. Lab experiments on zoochory, anemochory and hydrochory supplemented the field studies.

Seed retention in sheep fur was consistently good, and seeds stayed in the fur for hours or even days. Endozoochory proved to be of minor importance, while hydrochory is possible but depends on rarely occurring surface floods. Modelling potential dispersal distances showed that anemochory over larger distances is hardly possible. Thus, long-distance dispersal largely depends on epizoochory, as herds of sheep and goats cover up to 15 km per day and conduct long-range migrations in years of drought.

In terms of seed retention potential, goats are relatively poor vectors, which is of concern due to their relative and absolute share of Mongolian livestock herds having dramatically increased in recent years.

1. Introduction

Studies from various regions of the world underline the general importance of zoochorous dispersal (Bonn and Poschlod, 1998; Cain et al., 2000) and this has also been discussed for drylands (van Oudtshoorn and van Rooyen, 1999). Livestock have played an important role in dispersal in cultural landscapes, but transhumant and nomadic livelihoods are rapidly disappearing in most regions including parts of Central Asia (Brogaard and Zhao, 2002; Foggin, 2008; Scholz, 1999). Mongolia is unique in offering still relatively intact pastures and nomadic systems, where even long-distance migrations are still conducted in times of fodder shortage (Sneath, 1998).

Animal husbandry has a long tradition in Mongolia, and the impact of nomads has persisted for 2300 years or more (Müller, 1999). About half of the population still live in the traditional nomadic way and, following the political transition of the early 1990s, increasing unemployment has forced even more families to return to nomadism as a main source of income (Janzen, 2005; Müller, 1999). As a result, livestock stocking rates had risen to 33 million by the end of the 20th century. As a consequence of droughts in 2001–2002, herd numbers fell to pre-1990s levels; with the exception of goats, which have more than doubled their 1990s numbers (Janzen, 2005). Goats have thus increased in both relative and absolute importance, and livestock remains one of the most important factors influencing the Mongolian rangelands unequivocally affecting the growth and reproduction of steppes and their plants.

Efficiency of seed dispersal has hardly been studied in Mongolia or other parts of Central Asia although it is fundamental for gene flow and the long term survival of plant species. Studies from northern Chinese drylands provide evidence of pronounced genetic structuring, even among widespread steppe grasses such as *Stipa krylovii* and *Stipa grandis*. G_{ST}/φ_{ST}-values for these species, which represent a measure of fragmentation between populations, are considerably higher than global averages for wind-pollinated species (Dan et al., 2006; Zhao et al., 2006). Authors interpreted

* Corresponding author. Tel.: +49 (0) 345 5526215; fax: +49 (0) 345 5527228.
E-mail addresses: christine.blaess@botanik.uni-halle.de (C. Bläß), katrin.ronnenberg@botanik.uni-halle.de (K. Ronnenberg), tackenberg@bio.uni-frankfurt.de (O. Tackenberg), isabell.hensen@botanik.uni-halle.de (I. Hensen), karsten.wesche@senckenberg.de (K. Wesche).

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apparently reduced gene flow in *S. grandis* and *S. krylovii* as a consequence of land use changes, because genetic structuring was most pronounced in regions where grazing had intensified in the preceding decades (Zhao et al., 2008). Livestock impact may have resulted in almost complete grazing of inflorescences and/or high seedling mortality. Alternatively, quality and/or quantity of dispersal vectors may also have changed. This seems reasonable with respect to the pronounced increase in goat numbers, which have much shorter home ranges than other animals such as camels, which were previously more widespread. Goats, unlike sheep and camels, roam relatively far, but their fur is much shorter and diaspores become easily dislodged, rendering long-distance diaspore transport at best limited (Tackenberg et al., 2006; Will et al., 2007).

As dispersal is notoriously difficult to measure directly (Fischer et al., 1996; Römermann et al., 2005; Tackenberg et al., 2006), we combined field and lab studies to assess the potential importance of the currently most abundant vectors for zoochorous dispersal in dry steppes of Central Mongolia, i.e. sheep and goats. Data were compared with the potential for anemochory as the presumably second most important dispersal vector. Hydrochory was also included because, due to the low vegetation cover and low water retention capacity in the dry Mongolian steppes, sheet flows occur and episodic water flows may well extent over several kilometres (pers. observations). Potential dispersal agents and their efficiency were assessed for the locally most abundant steppe species *S. krylovii* and *Agropyron cristatum* and for other associated species in order to put the results into a broader context. Specifically, we addressed the following questions:

- How long do seeds remain attached to the fur of locally bred livestock like sheep and goats? Are there differences between plant species, animal vectors and body parts of vectors?
- Are any seeds detectable in the fur and in the faeces of free-ranging livestock, and which species are common?
- Is anemochorous dispersal a possible important alternative to zoochory? Are seeds able to float and thus be transported by hydrochory?

2. Materials and methods

2.1. Study area and study species

Most of the field experiments and sampling of seeds for the lab experiments were performed in the Gobi Gurvan Saykhan National Park in southern Mongolia in 2005 and 2006. However, in the main study year (2006), conditions were unusually dry and grazing impact was so intense that hardly any seeds ripened in the natural vegetation. One of our field experiments (collection of seeds from free roaming animals, see below) was therefore carried out in Central Mongolia (steppes north of Ulaan Baatar, N 48°15.43; E 106°33.23). Not only is the climate moister and the vegetation denser there, but the focus species are common as well.

The Gobi Gurvan Saykhan National Park was designated in the 1990s, however, in spite of its protection status, virtually all suitable sites are grazed by domestic livestock. In the study area (43°36.95′ N, 103°46.45′ E, 2300 m asl.), goats and sheep by far outnumber other livestock species and, together with horses, account for the larger part of the grazing pressure exerted by larger mammals; other livestock species and wild ungulates are of minor importance (Retzer et al., 2006). Animals are raised in semi-nomadic animal husbandry as the major form of land use in the Gobi, which has continued for centuries, if not millennia (Miehe et al., 2007).

Outside the few oases, the most productive pastures are found in and around the mountain ranges between 2300 and 2900 m asl. Mean annual precipitation is between 100 and 150 mm on the piedmont regions, and up to 200 mm in the summit regions. Rains are largely concentrated in the short, warm season, and are sufficient to support sparse but continuous vegetation. The interannual variability of precipitation is high (coefficient of variation > 30%, stations Bayandalay, 1570 m asl, and Dalanzadgad, 1470 m asl, National Meteorological Service Mongolia). Surface floods are rare but possible events, during which water flows up to several kilometres through the steppe (pers obs.), and storms occur regularly in spring and summer.

This study was performed in montane desert steppes, which form the most important pastures and cover some 20% of the park area (Wehrden von et al., 2006). Most of the dominant species are grasses such as *A. cristatum* and several *Stipa* species (*S. krylovii*, *Stipa glareosa*, *Stipa gobica)*; also abundant, but less important as fodder, are the onion *Allium polyrrhizum* and the dwarf shrub *Artemisia frigida* (Wesche et al., 2005). Shrubs (*Artemisia santolinifolia*, *Caragana leucophloea*) are restricted to disturbed sites or erosion gullies while trees are rare and occur only at sites with permanent water surplus. Annual species are common on heavily disturbed sites but are unimportant in terms of overall cover and biomass production.

Studies on zoochory concentrated on the two most abundant Poaceae, namely *A. cristatum* and *S. krylovii*. *A. cristatum* has small awned caryopses (Fig. 1a, hereafter also called seeds) with a mean weight of 3.3 mg. Germination is highest at incubation temperatures of 20/10 °C and there is no dormancy. *S. krylovii* has diaspores with a small hook and a long awn (Fig. 1b) and an average weight of 3.0 mg. Germination is also highest at 20/10 °C, and populations from the Gobi show no sign of dormancy (Ronnenberg et al., 2008). At that incubation temperature, effects of stratification are also limited for accessions from moister northern Mongolia (Ronnenberg et al., 2008). Comparative assessments of the potential for anemochorous and hydrochorous dispersal included up to eleven additional species (Table 1): *A. frigida* (Asteraceae, dispersal units

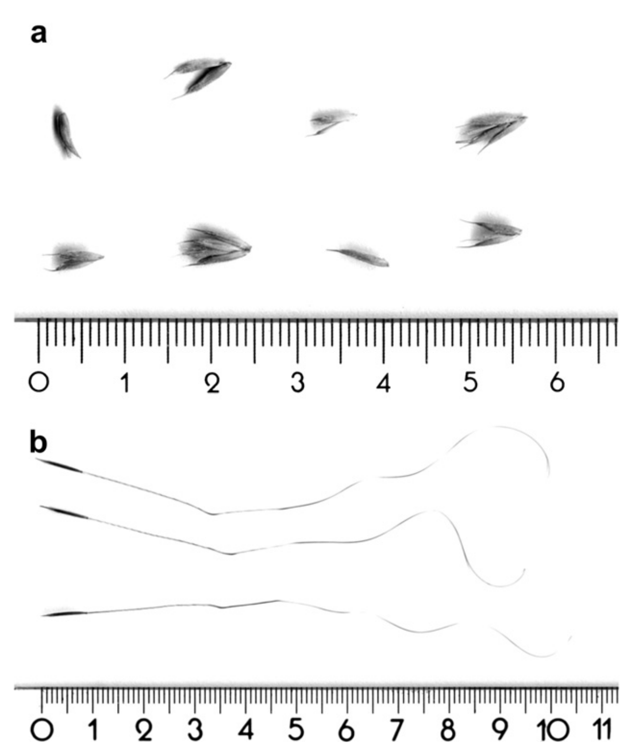

Fig. 1. Seeds (caryopses) of (a) *Agropyron cristatum* and (b) *Stipa krylovii*.

Table 1
Species used in the different experiments.

Experiment	Used species
Experimental epizoochory in the field	*Agropyron cristatum* and *Stipa krylovii*
Experimental epizoochory in the lab	*Agropyron cristatum*, *Stipa krylovii*, *Artemisia frigida*, *Ulmus pumila*, *Eurotia ceratoides*, *Salsola collina*, *Chenopodium vulvaria* and *Axyris hybrida*
Anemochory	*Agropyron cristatum*, *Stipa krylovii*, *Artemisia frigida*, *Ulmus pumila*, *Eurotia ceratoides*, *Salsola collina*, *Chenopodium vulvaria*, *Axyris hybrida*, *Caragana leucophloea*, *Galitzkya potaninii* and *Potentilla ikonnikovii*
Hydrochory	*Agropyron cristatum*, *Stipa krylovii*, *Artemisia frigida*, *Ulmus pumila*, *Eurotia ceratoides*, *Salsola collina*, *Chenopodium vulvaria* and *Axyris hybrida*

with no appendages), *Ulmus pumila* (Ulmaceae, winged), *Eurotia ceratoides* (Chenopodiaceae, with long hairs), *Salsola collina* (Chenopodiaceae, no appendages), *Chenopodium vulvaria* (Chenopodiaceae, no appendages), *Axyris hybrida* (Chenopodiaceae, no appendages), *C. leucophloea* (Fabaceae, no appendages), *Galitzkya potaninii* (Brassicaceae, winged) and *Potentilla ikonnikovii* (Rosaceae, no appendages, elaiosom small). Seeds were mostly collected in 2005 (in 2006, hardly any seeds were available due to drought) at the peak of maturation of the dominant herbs and grasses, and samples were pooled from at least three populations with a total of >1000 plants.

2.2. Methods

To assess the potential of the dominant grass species *A. cristatum* and *S. krylovii* for epizoochorous dispersal, 10 dyed seeds were placed in the fur on the legs, flank and belly of 6 goats and 6 sheep (360 caryopses per species). Animals were kept on their typical pastures; falling seeds were monitored over the following 8.5 h (after 0.1, 15, 45 and 90 min as well as after every hour from then on). In addition, the fur of three randomly chosen goats and three sheep was searched for the accumulation of seeds of any plant species in the steppes north of Ulaan Baatar (see above), again concentrating on the legs, flank and belly.

Lab studies were conducted over a larger range of taxa from the local vegetation to allow for comparisons (Table 1). The adhesive potential of the seeds was tested in the lab, for which we put 50 dry seeds of each plant species in sheep's and chamois' fur and observed retention over the following 24 h (Tackenberg et al., 2006). In order to estimate the importance of endozoochory, we collected half a litre of each goat and sheep's dung from an area of 40 m^2 (though we do not know how many animals produced the collected dung) north of Ulaan Bataar at the peak of maturation of the dominant herbs and grasses, where climatic conditions allowed for seed formation. After a 2 month storage period (dry and dark at room temperature), pellets were crumbled onto permanently moist sand (0.5 cm layer) in a greenhouse and monitored for 12 weeks (20 °C/10 °C, 12 h/12 h light/dark), ensuring that conditions were moister than those of the dry Mongolian environment. Emerging seedlings were counted and identified as far as possible.

To put data on zoochorous dispersal into perspective, we estimated the potential for anemochory by measuring the falling velocity of diaspores in a total of eleven species (Table 1) following Askew et al. (1997) and feeding the data into a model for wind dispersal (Tackenberg, 2003). The model was parameterized with high resolution wind velocity data for a central European high-altitude grassland as no suitable wind data of high temporal resolution were available from southern Mongolian desert steppes. As a further standard parameter, potential for hydrochorous dispersal was also tested in the lab based on the floating potential of the diaspores. Fifty seeds were put into a beaker of water ($n=2$, because standard deviation is normally low in this experiment) which was then placed on a rotary shaker (100 rotations per minute) and the rate at which seeds sank was monitored over the following week (after 5 min, 1, 2, 6 and 24 h as well as after one week; in accordance with Römermann and Tackenberg, 2005).

Data were analyzed with a *t*-test and general linear models. Where appropriate, hierarchical ANOVAs/repeated measure models were chosen in order to test against the appropriate error terms. Percentage data were generally arcsine-transformed; other figures were rank-transformed where necessary to increase normality and homogeneity of variances, as suggested by graphical inspection of data distribution. Statistical tests were performed with SPSS 12 (SPSSInc., 2003).

3. Results

3.1. Zoochory – field studies

Retention time of seeds in the field significantly differed between the plant species *A. cristatum* and *S. krylovii*, between animal species and also body parts (Fig. 2). The ANOVA for the main

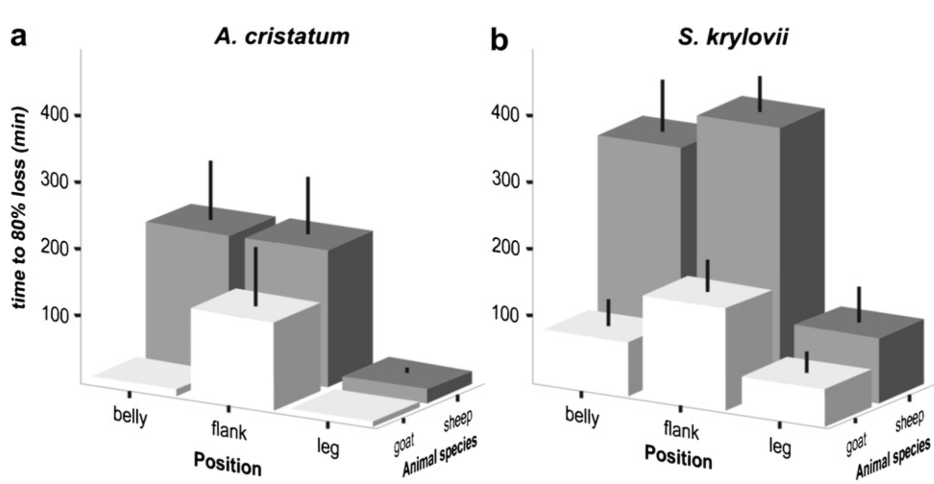

Fig. 2. Means and 1 standard error for elapsed time until 80% of applied seeds had fallen from fur of both sheep and goat. Plant species were a) *Agropyron cristatum* and b) *Stipa krylovii*. Seeds were applied to the three body parts: lower abdomen/belly, flank and leg ($n=6$).

Table 2
Hierarchical ANOVA for the seed retention experiment (a: main effect for animal species; b: residual effects). Plant species (*A. cristatum*, *S. krylovii*) and body parts (leg, flank, belly) were nested in animal species.

Factors	df	Type III sum of squares	Mean sum of squares	F	p
a)					
animal species	1	332,792.00	332,792.00	6.16	0.032
error	10	540,312.00	54,031.00		
b)					
plant species	1	141,778.00	141,778.00	10.72	0.0019
body part	2	376,709.00	188,355.00	14.24	<.0001
animal * body part	2	121,847.00	60,923.00	4.61	0.0146
animal * plant	1	31,878.00	31,878.00	2.41	0.1269
plant * body part	2	5814.58	2907.29	0.22	0.8035
animal * plant * body part	2	15,152.00	7576.04	0.57	0.5676
individual animal	10	540,312.00	54,031.00	4.08	0.0004
error: MS	50	661,351.00	13,227.00		

effect (Table 2a) indicated differences among animal species ($p = 0.032$) with seeds remaining attached to sheep much longer than to goats.

The ANOVA-table for the residual effects (Table 2b) shows significant differences between the two plant species ($p = 0.002$) and the three body parts ($p < 0.001$). Seeds remained longest at the flanks and were most easily lost from the legs. Most interaction terms were not significant, with the exception of the ANIMAL SPECIES * BODY PART interaction ($p = 0.015$).

A total of 97 diaspores were found in the fur of 3 goats and 3 sheep in Central Mongolia, 96 of which were from *S. krylovii*; both species were equally abundant and at similar stages of fruiting at the site. Again, animal species differed, with 86 seeds being found in sheep and only 11 in goat fur. The corresponding split-plot-ANOVA (Table 3) confirms the observed differences between the plant ($p = 0.019$) and the animal species ($p = 0.044$).

3.2. Zoochory – lab studies

The results in the lab support the field data: retention time depends on the type of fur and seed morphology (Table 4). Seeds of *S. krylovii* have longer retention times than others (Fig. 3), including *A. cristatum* and *A. frigida*, *U. pumila* or *A. hybrida*. Moreover, seeds were much more readily lost from Chamois' than from sheep's fur.

Only 8 seedlings emerged from the dung incubated in the greenhouse, with 6 coming from sheep's dung. Three of these seedlings could be identified as *Potentilla bifurca*, with the others being dicotyledonous plants. On the goat's dung there was one seedling of *Stipa* spec. and one dicotyledonous plant. Due to the low overall numbers, the *t*-test did not infer any difference between animal species ($p = 0.329$).

Table 3
Split-plot-ANOVA for the number of seeds found in two animal species (a: main effect), plants species were nested in animal (b).

Factors	df	Type III sum of squares	Mean sum of squares	F	p
a)					
animal species	1	0.6837	0.6837	8.3711	0.0444
error	4	0.3267	0.0817		
b)					
animal species * individual	4	0.3267	0.0817	0.5196	0.7292
plant	1	2.2677	2.2677	14.4263	0.0191
animal * plant	1	0.4265	0.4265	2.7132	0.1749
animal * plant * individual (error term)	4	0.6288	0.1572		

Table 4
Split-plot-ANOVA to distinguish the influences of fur type (main effect) and plant species (nested).

Factors	df	Type III sum of squares	Mean sum of squares	F	p
a)					
animal	1	52.8076	52.8076	72.1181	<0.0001
error	8	5.8579	0.7322		
b)					
animal * individual	8	5.8579	0.7322	4.6351	0.0002
plant	7	18.0200	2.5743	16.2953	<0.0001
animal * plant	7	10.2188	1.4598	9.2408	<0.0001
animal * plant * individual (error)	56	8.8467	0.1580		

3.3. Anemo- and hydrozoochory – lab studies

The terminal velocities of the focus species were 2.18 ± 0.57 m/s for *A. cristatum* (culm height 23 cm) and 2.55 m/s ± 0.27 for *S. krylovii* (culm height 46 cm). Running the PAPPUS model over 100,000 permutations showed that probabilities of dispersal over distances >1 m are lower than 0.1% for both species. Maximum modelled dispersal distance was 2.32 m in *A. cristatum* and 2.33 m in *S. krylovii*. None of the other herbaceous species included for comparison showed considerably larger values; the only exception was *U. pumila*, where seeds were dispersed over distances >100 m. This species, however, is a tree with winged fruits.

The test for hydrochorous dispersal shows that all species' seeds are at least partly able to float for several hours or even days (Table 5). The majority of seeds of *A. cristatum* floated for well over 24 h. If one assumes an average flow velocity of 1 m/s, diaspores can be moved up to 7 km per day. Even for *S. krylovii*, more than 50% of the seeds floated for longer than one day. We refrained from performing a statistical test because of the small number of replicates.

4. Discussion

Our experiments show that epizoochory has a large potential for dispersal and, consequently, genetic exchange between populations of our two focus species, *S. krylovii and A. cristatum*. In contrast, endozoochory appears to be rare, while anemochory and hydrochory are even less likely to contribute to dispersal over greater distances. The experiments on epizoochory show clear differences between the tested plants, animals and body parts. *S. krylovii*, with its long awn, was found in the fur more often than *A. cristatum*; and sheep are better vectors than goats.

It is widely known that diaspore morphology is the first major predictor of dispersal efficiency (see e.g. Couvreur et al., 2005; Fischer et al., 1996; Shmida and Ellner, 1983). Kiviniemi (1996) demonstrated that seeds of species with awns, hooks etc. are more prevalent in grazers' fur, and *Stipa* spp. are well known in Mongolia (and elsewhere) to stick to animals' fur and hooves and to even drill themselves deep into animal skin by hygroscopic awn movement (Jigjidsuren and Johnson, 2003). Our lab data support these observations and show the relatively high adhesion potential of *S. krylovii* as well as of very small diaspores without any appendages such as *A. frigida*. Tackenberg et al. (2006) verified that diaspore morphology is of minor importance for retention capacity of seeds up to 10 mg, above which weight seed morphology not only influences retention time, but the probability by which seeds become lodged in the fur in the first place (Will et al., 2007).

Our results also support the general notion that fur structure is another factor determining dispersal (Couvreur et al., 2004). We detected at least twice as many seeds in curly sheep fur than in straight goat or chamois fur. This is of an order of magnitude

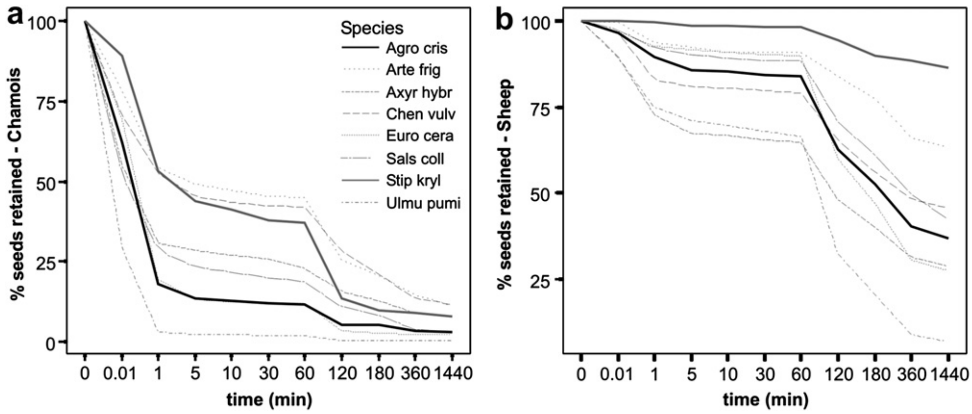

Fig. 3. Retention capacity of a) Chamois' and b) sheep's fur (*Agropyron cristatum*, *Artemisia frigida*, *Axyris hybrida*, *Chenopodium vulvaria*, *Eurotia ceratoides*, *Salsola collina*, *Stipa krylovii*, *Ulmus pumila*).

described in other studies (Liddle and Elgar, 1984; Shmida and Ellner, 1983). Differences between body parts are partly related: diaspores remained longer in the fur at the flank than on that of the belly or legs of the animals. This is probably due to differences in the length and denseness of the fur as well as differences in grooming intensity between body parts (Sorensen, 1986). Seeds on the head (Kiviniemi, 1996; Roché et al., 1992) or shoulder (Milton et al., 1990) usually remain attached much longer because the animals can hardly reach them. Moreover, they are less likely to be brushed off by taller vegetation.

In any case, our data demonstrate a pronounced potential for zoochorous dispersal. According to personal interviews ($n = 3$), goats and sheep are always kept in mixed herds, and few of them ever roam more than 5 km from their nightly base close to herders' yurts in any one day (Table 6). If the family moves camp from one place to another, this distance increases to up to 15 km per day. Fernandez-Gimenez (2000) found that the Gobi's nomads sometimes move to the Khangai region in summer and return south in the autumn. This means that the livestock covers up to 300 km twice a year. It has also been shown that seed retention times can amount to several months (Fischer et al., 1996; Shmida and Ellner, 1983) and Fischer et al. (1996) describe that one sheep is able to retain more than 8500 diaspores over the course of one summer. The spatial scale that can potentially be covered by epizoochoric dispersal can be estimated by combining data on retention times with data on animal movements. Table 6 shows that on an ordinary day $\geq$25% of all seeds in sheep fur may be transported for c. 1.5 km, and this figure may increase to 2.3 km during long-distance movements. During such events, >5% of all seeds may be transported 12 km or more.

Compared to epizoochory, the potential for endozoochory seems limited. *Stipa* spp. and *A. cristatum* are preferentially grazed by domestic livestock and the locally most common small mammal, the Mongolian Pika (*Ochotona pallasi*) (Bläß et al., 2008; Jigjidsuren and Johnson, 2003). Livestock density is comparatively high in our study region at 0.3–1.0 Mongolian Sheep Units (MSU: 1 MSU is equivalent to 1 kg of biomass uptake per ha per day, (Retzer et al., 2006), so the potential for endozoochorous dispersal may also be high. However, only 8 seedlings emerged in the greenhouse from the collected dung sample. This is already low, and the natural rate of germination and establishment in the field is probably even lower due to competition, grazing or unfavourable abiotic factors, such as a lack of precipitation. We know from further studies (Ronnenberg et al., 2008) that seed germination *in situ* and germination from soil samples is also relatively low for the focus species. The present data may thus point to a limited importance of endozoochoric dispersal, although ruderal herbs (*P. bifurca*) seem to benefit more than the important grasses.

Mouissie et al. (2005) did not find any seedlings emerging from sheep dung over a two year period. They hypothesise that dung pellets dry out too fast or have to be broken up before germination is possible. Numbers of seedlings in dung also change over the year as a consequence of plant phenology. However, we collected dung at the peak of maturation of the dominant herbs and grasses. Diaspores in the faeces may also need more time for germination than 3 months. Dung germination tests lasting three years (Malo, 2000) showed that after one year, 47.7% of seeds had germinated. We did not test for this aspect, but our own screenings (Wesche et al., 2006) show that seeds of most species germinate quickly, i.e. within 2–6 weeks with no apparent sign of dormancy being present. Germination was also not affected by dry storage over 2 months. We also believe that endozoochory is of limited importance in our large-seeded focus species due to the fact that seeds have to survive three critical stages during endozoochory; namely mastication, the impact of digesting enzymes and the low pH in the stomach and intestines (Gardener et al., 1993). It is noted that Mongolian nomads use dried dung as their main fuel source. Moreover, with faeces often being deposited at night time near herders' camps (Stumpp et al., 2005), any resultant vegetation is heavily influenced by trampling and the chances of establishment are poor. Taken together, the potential for endozoochorous dispersal in Mongolia seems to be rather limited. However, single events can be expected because of the huge numbers of livestock.

Anemochory is often said to be the dispersal mode with the widest dispersal potential (Fridriksson, 1975; Willson, 1993). Howe and Smallwood (1982) pointed out that the number of species dispersed by wind increases with increasing habitat aridity. Detailed data for Central Asia are unfortunately not available; however, at least the herbaceous species analyzed in our study did

Table 5
Average number of still floating seeds (in %) observed over one week ($n = 2$, 50 seeds each).

time (h)	0	0.01	0.083	1	2	6	24	72	168
Stipa krylovii	100	82	82	71	66	57	56	10	2
Agropyron cristatum	100	100	100	99	98	96	95	63	26
Eurotia ceratoides	100	100	100	100	100	100	100	99	90
Ulmus pumila	100	100	100	100	100	100	99	26	6
Artemisia frigida	100	89	33	15	15	6	6	5	5
Salsola collina	100	99	93	76	66	35	34	16	9
Chenopodium vulvaria	100	97	95	80	77	74	74	74	56
Axyris hybrida	100	76	75	75	75	75	75	75	75

Table 6
Estimated distances livestock cover on a normal day and while moving to another region; compared to data for seed retention time (belly) given in Fig. 1.

time (min)	0	15	45	90	150	210	270	330	390	450	510
Distance in km (normal)	0	0.25	0.75	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5
Distance in km (move)	0	0.375	1.125	2.25	3.75	5.25	6.75	8.25	9.75	11.25	12.75
Estimated % seeds retained											
Sheep											
Stipa krylovii	100.0	71.7	66.7	58.3	51.7	43.3	28.3	18.3	16.7	15.0	11.7
Agropyron cristatum	100.0	46.7	33.3	25.0	15.0	13.3	11.7	10.0	10.0	8.3	6.7
Goat											
Stipa krylovii	100.0	45.0	25.0	11.7	6.7	5.0	1.7	0.0	0.0	0.0	0.0
Agropyron cristatum	100.0	3.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

not seem to be preferentially wind-dispersed. Our results are tentative though as factors such as wind speed, vertical turbulence and air humidity influence anemochorous dispersal (Bonn and Poschlod, 1998; Kerner, 1871). We measured wind speeds of up to 12 m/s during windy days at our study site (near the soil surface), and velocities in evening hours were almost always >3 m/s. However, detailed measurements with high temporal resolution, which would be needed to improve parameterization of the PAPPUS model, are not available for the study region. The species analyzed for our study are characterized by a low seed release height and a relatively high falling velocity. Under grazing, inflorescences tend to be smaller, which reduces wind dispersal potential and further supports the view that the potential for anemochorous dispersal is limited.

All species tested here show a high or very high floating capacity. However, any potential for secondary dispersal of already sunken seeds is difficult to model (Staniforth and Cavers, 1976). Being a dryland habitat, our study area offers limited options for hydrochory because heavy rains are rare. Despite this, in July 2006, we experienced two single events which yielded 36 mm and 20 mm of rainwater in a single day. Sheet flows covered the pediments, and runlets and fast-flowing streams formed in the gullies. The water flowed approx. 5 km downstream, which could represent a realistic dispersal distance be it by floating or by additional washing down of seeds lying on the surface.

5. Conclusions

Taken together, zoochorous – and especially epizoochorous – long-distance dispersal seems to be much more effective for our focus species than dispersal via wind or water. This is not surprising considering that grazing by wild ungulates has persisted in the region over evolutionary time scales. Intense grazing impact in the course of human land use has also been present over extended periods of time and will also have led to the effective extinction of species that are not adapted to animal activity. The available evidence for reduced gene flow in Central Asian *Stipa* species (Dan et al., 2006; Zhao et al., 2006) may still be related to changes in herd composition. Compared to the traditional dominant animal of the Gobi, namely the Bactrian camel with its long fur and large migration distances, goats certainly represent more inferior vectors. Even compared to other small livestock, retention times are less than half that of sheep. No study has yet addressed this issue, which has possible ramifications on seed, and thereby genetic, exchange. As such, it represents a potential direction for further research.

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