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A study of adhesive seed dispersal of three species under natural conditions

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SUMMARY

Seeds of three plant species, *Agrimonia eupatoria* L., *Geum rivale* L. and *Triglochin palustre* L., were tested for their ability to remain attached in fur of fallow deer and domestic cattle under natural conditions in the field. The plant species are relatively common in managed semi-natural pastures and all three species possess seed structures which enhance adhesive dispersal. The results indicate that seed morphology and the position of seeds on an animal's body influence the length of time that seeds are attached in fur. The relative adhesive seed dispersal ability of the plants (*A. eupatoria*> *G. rivale*>*T. palustre*) did not differ between the two investigated animal species. However, taking grooming behaviour into account, animal species may differ in dispersal efficiency. Seed morphological structures that increase the inherent capacity of adhesive dispersal may also be irritating to animals and initiate grooming. Potential dispersal distances were obtained for seeds on cattle, suggesting that adhesive seeds may disperse from tens of metres to a kilometre. The implications of the results of this study for plant dispersal in a fragmented landscape are discussed.

Key-words: diaspore morphology, epizoochory, half-time, plant–animal interaction, seed retention.

INTRODUCTION

Seed dispersal is of interest for the dynamics of local plant populations. Furthermore, small numbers of dispersing seeds may act as founders of new populations which may grow to significant proportions within a few generations (Silvertown 1987). The importance of empirical studies of seed dispersal has recently been stressed by several authors, both in a general ecological context (e.g. Venable & Brown 1993; Willson 1993), and for conservation of plants in fragmented landscapes (e.g. Verkaar 1990; Marshall & Hopkins 1990; Hansson *et al.* 1992). Thus, there is an increasing interest in research on whether 'ecological corridors' for dispersal minimize effects of isolation (Verkaar 1990), or more generally, how different dispersal attributes enable seeds to travel over long distances. There is evidence that the process of dispersal may affect patterns of species abundance and distribution (Hodgson & Grime 1990; Quinn *et al.* 1994), in which the ability to reach new sites suitable for establishment may be as important as the suitability of the sites (Overton 1994).

Transport of seeds on the outside of animals, adhesive dispersal, has been ascribed to many plant diaspores on the basis of morphological traits. Diaspores with hooks, spines and viscid outgrowths have been regarded as adaptations for attachment in fur (e.g. Sernander 1901; Ridley 1930; Van der Pijl 1972). In studies where morphological structures of diaspores have been used to assess the frequency of different dispersal modes, adhesive dispersal has been found less common than other modes of dispersal (Venable & Levin 1983; Willson *et al.* 1990). Sorensen (1986) concluded that less than 5% of the species in her survey of 10 regional floras had adaptations for external dispersal. Milton *et al.* (1990) recorded low frequencies of adhesive diaspores caught in the fleece of sheep in the plains of the arid south-western Karoo in South Africa, and suggested that it may indicate that the vegetation of this region evolved with little impact from herbivorous large mammals. In contrast, Agnew & Flux (1970) recorded high numbers of adhesive fruits in fur of hares in Kenya, but noted that there were great regional differences in the abundance of zoochorous plants.

Adhesive dispersal differs from other kinds of animal dispersal in that the dispersal agent does not receive any nutritional reward. The plants do not attract their dispersers by advertising, and it seems that dispersal may be even more successful if the animals are not aware of the fact that they are carrying the diaspores (Sorensen 1986). The plants bearing adhesive diaspores generally grow in the ground layer (Hughes *et al.* 1994), and tend to be more common in disturbed habitats (Ridley 1930; Sorensen 1986; Willson 1992). Willson *et al.* (1990) suggested that the low growth form of these species could be an ecological constraint on the abundance of this dispersal mode.

Our knowledge about the ecology of seed dispersal is increasing. Data about seed shadows (Willson 1993), dispersal spectra in relation to different vegetation types (Willson *et al.* 1990) and plant attributes (Hughes *et al.* 1994) have recently been reviewed. There are, however, still relatively few empirical studies of the dispersal capabilities of diaspores under natural conditions, especially when regarding the transport of adhesive diaspores (Falinski 1972; Schmida & Ellner 1983; Carlquist & Pauly 1985). There are even fewer studies in which dispersal distances of adhesive diaspores have been estimated (Bullock & Primack 1977; Liddle & Elgar 1984). Sorensen (1986) studied the retention of burdock burrs on snowshoe hare in laboratory, and she found that the retention of diaspores in fur largely depends on how noticeable the diaspores are for the animals. She suggested that non-irritating diaspores should be tolerated longer than irritating diaspores, and should therefore be dispersed longer distances.

In this study, fallow deer (*Dama dama*) and domestic cattle (*Bos taurus*) were used as seed dispersers in experiments made under natural conditions in the field. Three plant species with different morphological structures on their diaspores were used, *Agrimonia eupatoria*, *Geum rivale* and *Triglochin palustre*. Five questions were addressed: (i) Does diaspore morphology influence the length of retention of diaspores in fur? (ii) Does the location of the diaspores on an animal's body affect their retention? (iii) Are there behavioural differences between individual animals that could influence the retention of diaspores? (iv) Are there differences in retention of diaspores between different animal species? and (v) What are the potential dispersal distances of adhesive diaspores? The last question was only dealt with for diaspores in the fur of cattle.

METHODS

Study site and species

The studies were performed in pastures near Tovetorp Zoological Research Station situated in southern Sweden, about 100 km SSW of Stockholm. The adhesive ability of diaspores of three species were tested in the fur of two bottle-raised fallow deer hinds (*Dama dama*) and two heifers (*Bos taurus*). The plant species were *Agrimonia eupatoria* L., *Geum rivale* L. of the family Rosaceae and *Triglochin palustre* L. of the family Juncaginaceae. The latter species has a fruit (schizocarp) that splits into three one-seeded parts (mericarps). The separate fruitlets have been used in this study. *G. rivale* has achenes with hairy hooked styles. *A. eupatoria* has a receptacle enclosing two seeds. The receptacle has small hooked bristles at the edge. These morphological structures are, for convenience, called 'seeds' throughout this paper. *A. eupatoria* and *G. rivale* have seeds that are adhesive. The seeds of *T. palustre* can, due to the needle-like form of the seed, be inserted into the skin of the animals (Romell 1954), and can also attach to the fur. *G. rivale* is mainly found in meadows and deciduous woodland. *A. eupatoria* mainly grows in open grassland. Both *G. rivale* and *A. eupatoria* also occur along roadsides. *T. palustre* is mainly found in wet meadows. The pasture, where the study of fallow deer dispersal took place, is about 20 ha and the ground cover consists of grasses and herbs. The study on cattle was done in two pastures that are about 4 ha each. The plant species studied did not occur in the study pastures, but they are relatively common in managed semi-natural pastures in general. The three plant species are also subject to demographic studies in southern Sweden.

There were two rationales for the choice of animals. First, it is reasonable to assume that man and his grazing livestock are important for the dispersal of seeds in managed semi-natural grasslands. Secondly, the use of the two tame fallow deer hinds was due to practical reasons. The fur of fallow deer is comparable to the fur of other deer of the family Cervidae; for example, roe deer (*Capriolus capriolus*), which are very common in Sweden. Fallow deer were introduced to Europe in the Middle Ages and to Sweden during the sixteenth century, and were kept in parks and fences for hunting, but nowadays wild populations of fallow deer are quite common in southern Sweden.

Field experiments

The field work on fallow deer was done during September–November 1991. Field observations were made before the study to find out where seeds normally adhere on the deer. Seeds were also attached at different sites, e.g. breast, belly, flanks and legs, to find out the best positions to use for the experiment. The head and back positions were selected for the study. Seeds of the three species were attached by hand at both positions on the hinds. The two sites differ in their degree of exposure to the surrounding vegetation, and in the hinds' ability to directly remove seeds from them. Seeds have been observed on these two positions 'naturally'. During the study, there were no attempts to remove seeds from the head site, but seeds on the back site were located and removed by the hinds. In each observation series, 10 seeds each of *G. rivale* and *T. palustre*, and five seeds of *A. eupatoria* were placed on each position. *A. eupatoria* has a larger seed size and was rather irritating for the hinds and therefore only five seeds were used per observation series. The number of seeds per species were counted every fifteenth minute at the two sites until there were no seeds left (=one observation series). Thereafter, new seeds were attached by hand. The seeds of the three species were followed on the head and the back at the same time. By comparing the species at the same time, the seeds experienced the same conditions.

The field work on cattle was carried out during September–October 1994 and with a similar procedure to that used with the fallow deer. Seeds of the three species were attached at one position, namely on the flanks of the cattle. In each observation series

10 seeds each of *A. eupatoria* and *T. palustre* and 20 seeds of *G. rivale* were used. The number of seeds used per observation series of *T. palustre* were restricted by the supply of seeds. The number of seeds remaining in fur were recorded after 1, 5, and 10 and then every fifteenth minute until there were no seeds left. By quantifying the distance that the heifers moved during the studies, estimates on dispersal distances for the seeds were obtained. The position of the heifers were marked on a map every time seeds were counted in fur. The dispersal distances obtained are therefore somewhat underestimated.

Studies where seeds are actively attached at different sites in the fur can be rather irritating for the animals. It is therefore important to minimize the disturbance of the animals. The seeds were placed in a fairly homogeneous region of fur and during the studies there were no problems with approaching the animals and attaching the chosen seed number or counting the seeds at the sites.

Data analysis

The dataset from the study of dispersal on fallow deer consists of 158 observation series, divided into 12 subsets: three species, two positions (head and back) and two hinds. The number of replicates per species were 41 (head, 19; back, 22) for *A. eupatoria*, 72 (41; 31) for *G. rivale* and 45 (27; 18) for *T. palustre*. The data set from the study of dispersal on cattle consists of 180 observation series. The number of replicates per species were 60 and 30 per heifer, respectively. Each observation series was described by a seed depletion curve. The point of time when 50% of the seeds were shed, the 'half-time' ($t_{1/2}$), was calculated for all separate observation series by the formula: $(t{\cdot}\ln 2/(\ln a-\ln e)$, where a is the number of seeds at the beginning and e is the number of seeds at the end of the observation series, and t is the length of time of the series. These values of half-time were used in the statistical analyses where differences among the subsets were tested for. One-way ANOVA (Kruskal–Wallis test) was used to compare the three species together followed by Mann–Whitney *U*-tests in the pairwise comparisons between species.

For 13% of the observation series ($n=158$) in the study on fallow deers, all seeds had been shed after 15 min. For seven of these 21 series, there were data from measurements made after 5 min. With the help of these data, a curve was plotted for $t=0$, 5 and 15 min, and the point of time when only one seed remained was solved. This time t was then used in the equation above for $e=1$, and the obtained $t_{1/2}$ was used for the 21 series.

The real half-time value for each observation series could have been solved from the plotted seed depletion curve by hand. By using the formula above, estimations of the half-time values were obtained smoothly. All observation series were treated in the same manner, and therefore the results from the statistical tests are not affected by the method for calculating values of half-time. The seed distribution patterns commonly follow a negative exponential form, so the use of the half-time equation in this study reflects the general expectation of seed shadows, although some exceptions are found (Willson 1993).

RESULTS

Fallow deer

Figure 1a–c shows the depletion curves for the seeds of each species at the head and back positions. The depletion of seeds from the back is described for the individual hinds separately, because of differences found between the hinds (described below). The maximal time that any seed was attached ranges from 105 to 180 min at the two sites.

When comparing the hinds at the two positions for each species, there were significant differences in the back position for two species. *A. eupatoria* (Mann–Whitney *U*-test; $n=22$, $Z=2{\cdot}16$, $P=0{\cdot}03$) and *G. rivale* ($n=31$, $Z=2{\cdot}56$, $P=0{\cdot}01$). The seeds of *T. palustre* did not differ in retention between the hinds on the back site ($n=18$, $Z=1{\cdot}72$, $P=0{\cdot}08$). The median values for the half-time data of each of the three species, did not differ at the head position between the two hinds ($P=0{\cdot}16$–$0{\cdot}71$).

Comparisons between the head and back position for the three species were made separately on the two hinds, to illustrate the effect of both position and individual behaviour of the animal. Seeds of *A. eupatoria* were retained significantly longer at the head position compared to the back position on hind 1 (Mann–Whitney *U*-test; $n=23$, $Z=-3{\cdot}67$, $P=0{\cdot}0002$). *G. rivale* was also differently retained on only one animal, where seeds remained attached significantly longer on the back site compared to the head site of hind 2 ($n=28$, $Z=2{\cdot}39$, $P=0{\cdot}017$). The curves in Fig. 1 describe how seeds attached on the back of hind 2 were retained for longer than seeds placed on the back of hind 1. However, seeds of *T. palustre* exhibited significant differences in half-time between the head and back positions on both hinds (hind 1: $n=26$, $Z=2{\cdot}44$, $P=0{\cdot}014$; hind 2: $n=19$, $Z=3{\cdot}19$, $P=0{\cdot}001$).

The half-time data of the hinds were combined for the species comparison on the head and back position (Table 1); hence, retention of the three species on both hinds shared the same pattern. When comparing the three species together, there were significant differences on both the head site (Kruskal–Wallis test; $n=87$, $P<0{\cdot}001$) and the back site ($n=71$, $P=0{\cdot}015$). In the pairwise tests, there were significant differences between all species for half-time at the head position. The time after which 50% of the seeds were shed was significantly longer for *A. eupatoria* compared to the other two species. On the back site, *A. eupatoria* was retained a significantly shorter time compared to the other two species, which in turn did not differ in retention at this site.

Cattle

Figure 2 shows the depletion of seeds of the three species on the flank position of the heifers. The seeds of *A. eupatoria* were retained better than the other species. The maximal time that any seed remained attached ranged from 30 to 195 min for the three plant species.

The data for seed retention for the three species were analysed for the two heifers together (Table 2). This did not affect the outcome of the statistical tests, where the three species' half-time data were compared. There were significant differences in retention on the flank position, when comparing the three species together (Kruskal–Wallis test; $n=180$, $P<0{\cdot}001$). In the pairwise comparisons, *A. eupatoria* was retained significantly longer than *G. rivale*, which in turn was retained significantly longer than *T. palustre*.

On average, the heifers moved a distance of 4 m min^{-1} ($n=24$, SD ± 1 m) when grazing during the day. There were no significant differences in movement between the two heifers ($n=24$, $t=-0{\cdot}56$, $P=0{\cdot}58$). The time the cattle spent lying on the ground, resting and ruminating, is excluded from the above measurement. The dispersal distances of the seeds on cattle, based on these measurements of movement and maximal times that any seed was attached, vary from a few metres to a maximal

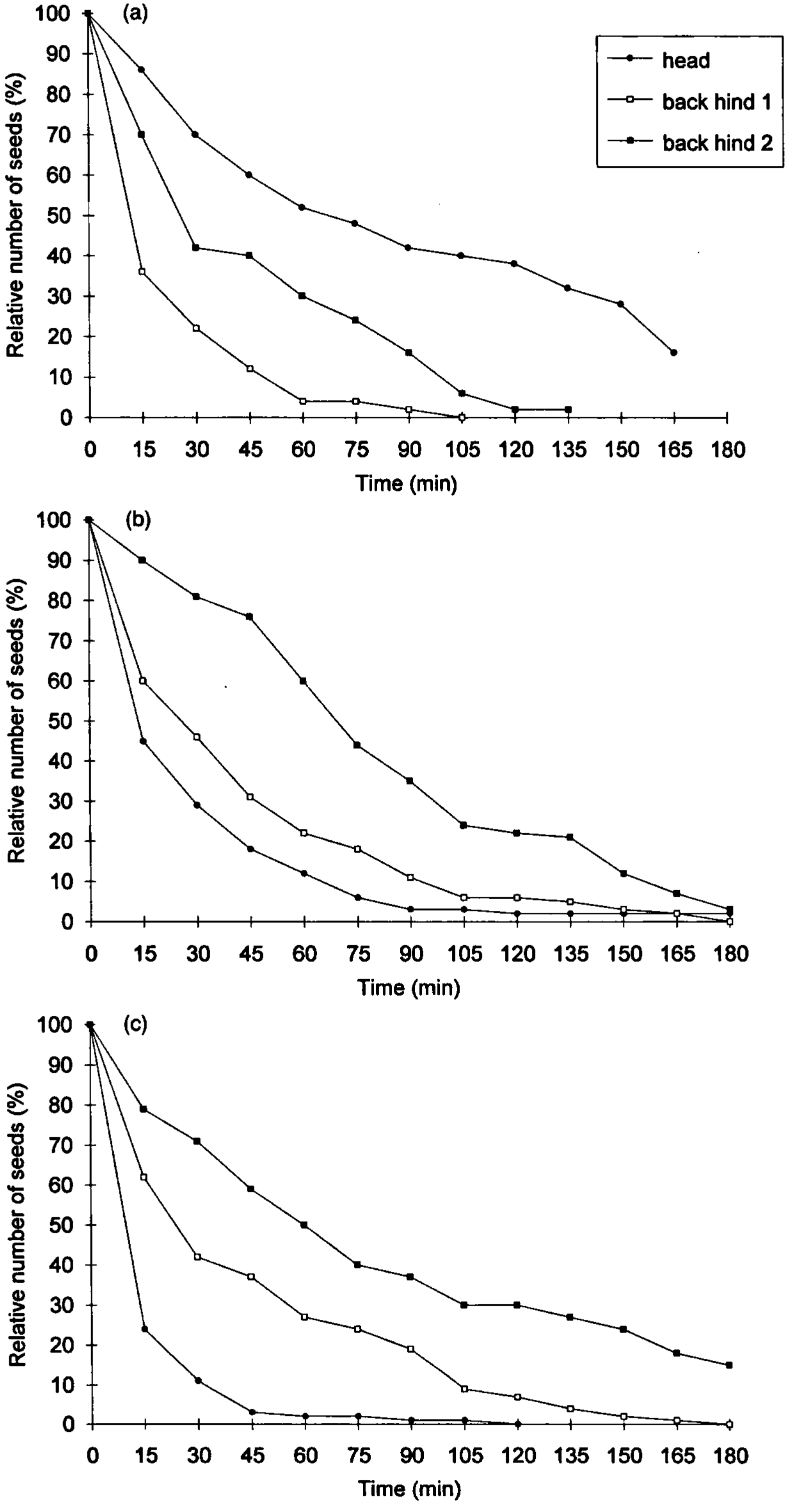
(a)
(b)
(c)
head
back hind 1
back hind 2
Relative number of seeds (%)
100
90
80
70
60
50
40
30
20
10
0
0
15
30
45
60
75
90
105
120
135
150
165
180
Time (min)

Table 1. Adhesive dispersal of *Agrimonia eupatoria*, *Geum rivale* and *Triglochin palustre* in fur of fallow deer hinds. The median values, ranges and sample sizes for the half-time data are presented for the three species on the head and the back position. The results from pairwise Mann–Whitney *U*-tests at the two positions are also presented. Values (within rows) that do not share a common letter are significantly different from each other at $P<0{\cdot}001$ at the head site and at $P<0{\cdot}05$ at the back site

Position	*A. eupatoria*	*G. rivale*	*T. palustre*
Head			
Median (min)	68·1^{a}	18·1^{b}	6·5^{c}
Range	493·1	195·2	39·1
n	19	41	27
Back			
Median (min)	19·4^{a}	40·6^{b}	35·3^{b}
Range	119·9	393·2	147·0
n	22	31	18

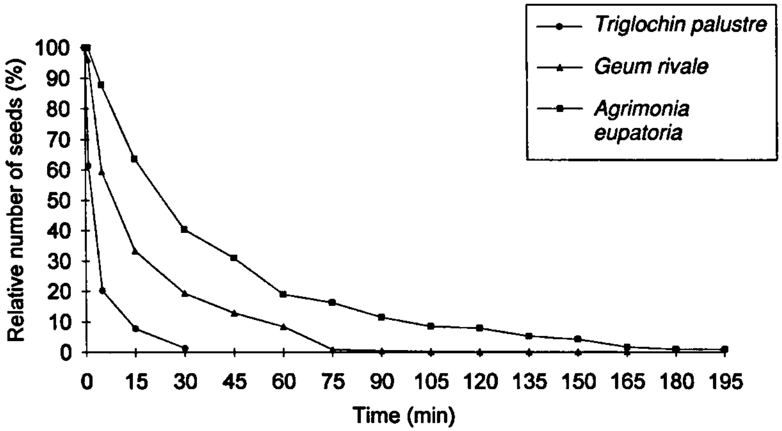

Fig. 2. Seed depletion curves for *Agrimonia eupatoria*, *Geum rivale* and *Triglochin palustre* in fur of domestic cattle, based on observation series made in the field. The depletion of seeds placed on the flank position of the heifers are described by plotting the relative mean values of seeds attached in fur towards time. The number of seeds used per observation series were 20 for *G. rivale* and 10 for the other two species.

distance of 120 ± 30 m for *T. palustre*, 700 ± 165 m for *G. rivale* and 780 ± 195 m for *A. eupatoria*. Based on the median values for the half-time data, seeds were dispersed on average 9 ± 2 m for *T. palustre*, 27 ± 7 m for *G. rivale* to 80 ± 20 m for *A. eupatoria*.

Fig. 1. Seed depletion curves for (a) *Agrimonia eupatoria*, (b) *Geum rivale* and (c) *Triglochin palustre* in fur of fallow deer hinds, based on observation series made in the field. The relative mean values of the number of seeds attached in fur are plotted every fifteenth minute for each species, to show the general pattern of how seeds are shed in time at the head and the back. The depletion of seeds from the back is shown for the two hinds separately. Five seeds of *A. eupatoria* and 10 seeds of the other two species were attached in the fur per observation series.

Table 2. Adhesive dispersal of *Agrimonia eupatoria*, *Geum rivale* and *Triglochin palustre* in fur of domestic cattle. The median values, ranges and sample sizes for the half-time data are presented for the retention of seeds of the three species on the flank position. The results from Mann–Whitney *U*-tests are shown, where the three species half-time data for retention of seeds in fur were compared. Values that do not share a common letter are significantly different from each other at $P<0{\cdot}0001$

Flank position	*A. eupatoria*	*G. rivale*	*T. palustre*
Median (min)	19·0^{a}	6·7^{b}	2·2^{c}
Range	153·5	45·0	22·1
n	60	60	60

DISCUSSION

This study demonstrates that retention of seeds in fur varies among plant species, between different positions on the animal, and between different individual animals. The relative adhesive seed dispersal ability of plants did not differ between the two animal species investigated, as far as the inherent capacity of seeds to attach in fur is concerned. Sorensen (1986) found that the size of the diaspore, diaspore number, and the location of diaspores on an animal's body, i.e. how noticeable the site is for the animal, influence the length of time that animals tolerate and retain diaspores. The results of this study provide further support to these suggestions.

The positions chosen in the present study of dispersal in fur differ concerning the animals' abilities to directly affect the seeds placed there. In the study of dispersal on fallow deer, the back position is more noticeable and accessible for the hinds than the head site. The two sites also reflect differences in relation to surrounding vegetation. The back site is a more sheltered position compared to the head site, which is more exposed during grazing. The rather large flank position of the cattle is quite accessible for grooming and it is also rather exposed to the surroundings, for instance when the cattle are lying down. The large size of the cattle also affects the retention of seeds in fur, because there is a greater possibility for the seeds to escape detection compared with smaller animals.

The half-time values for the seeds of *G. rivale* and *T. palustre* at the head and the back site on the fallow deer hinds reflect the different degrees of exposure to the surroundings at these two sites. *A. eupatoria* differed from the other two species by having a longer half-time for the seeds at the head site compared to the back site, where the seeds were removed by grooming. The grooming behaviour of the individual hinds, where hind 1 removed seeds earlier from the back site compared to hind 2, had a considerable effect on the results. For instance, this explains why *A. eupatoria* and *G. rivale* only displayed significant differences on one animal. It appears as if the seeds of *A. eupatoria*, due to the larger size and morphology, are more irritating for the hinds compared to the other two species.

The length of retention of seeds in fur may indicate the seeds' morphological adaptation for dispersal. The differences in adhesive capacity between the three plant species on cattle are congruent with the results from the head position of fallow deer. The seeds of *A. eupatoria* were retained longer compared to the other species, even though the flank position is within reach for the cattle. Therefore, one can argue that the seeds of *A. eupatoria* have better adhesive structures for dispersal compared to the other two species. The seeds of *A. eupatoria* can thus be dispersed a longer distance, but only if the seeds are inaccessible for the animal or if they escape detection. Accordingly, it seems that the seeds of *T. palustre*, which are bare and needle-like, are 'less adapted' for dispersal in fur compared to the other two species, which have hairy and hooked seeds. However, at the 'sheltered' back site on the hinds, the seeds of *T. palustre* were retained as well as the seeds of *G. rivale*. The retention of seeds on the back position of fallow deer differed from the results on cattle. This suggests that the inherent capacity of the seeds, i.e. the relative adhesive seed dispersal ability, of the three plant species to adhere to the fur of the two animal species is similar, but different animal species may still differ in efficiency as seed dispersal vectors because of differences in their behaviour.

In a survey by Willson (1993) for herbaceous species, it was found that adhesive characters of the diaspores enhance the dispersal distance, and that species without dispersal structures achieved only short-distance dispersal. However, some studies indicate that even diaspores without any clear adaptation for dispersal can be carried externally (e.g. Ridley 1930; Shmida & Ellner 1983; Carlquist & Pauly 1985), particularly small seeds (Falinski 1972; K. Kiviniemi & O. Eriksson, unpublished). The results from the study indicate the existence of a trade-off, where pronounced adhesive structures on seeds, which promote their attachment to fur, may actually reduce the probability of successful dispersal by increasing grooming behaviour, especially if the seeds are accessible and noticeable for the animals. Sorensen (1986) noted that seeds that are not detected by the animal may be transported until they drop, rot or the animal sheds its coat.

The dispersal of adhesive seeds depends to a great deal on the behaviour of the animals, such as the animals' pattern of movement and home range (Stiles 1992). There are no data about home range size for natural populations of fallow deer (Björn Birgersson, personal communication), but it is likely that they can move distances of up to 4–5 km day^{-1} when they are grazing. Due to their similar fur, it may be of interest to consider the home range size for other deer species, such as the common roe deer. Home range sizes of *c.* 20–30 ha have been reported for this species (Agneta Johansson, personal communication). In contrast, the movement of grazing cattle was estimated to be 1–2 km day^{-1} in this study, but they are of course restricted by the size of the fenced pastures.

The majority of the seeds on the flank position of the cattle were dispersed within 100 m, but some seeds could potentially be dispersed nearly 1 km. Accordingly, the potential exists for seeds to be dispersed long distances on cattle. Considering the mobility of the deer and the half-time values obtained for the three plant species, including the tails of the depletion curves, seeds could be dispersed from tens of metres to a few kilometres, but could also be carried for longer distances. The tail of the depletion curve should receive attention, because it determines the long-range dispersal of seeds (Willson 1992).

The actual movement of animals is likely to be a major limitation for seed dispersal. For conservation of semi-natural grasslands, it is therefore important that 'ecological corridors' with similar vegetation exist, facilitating the movement of wild animals in the landscape. For domestic animals, like cattle, it is of interest to move animals between pastures. The idea that the persistence of a species regionally depends on the colonization and extinction of subpopulations, has usually been applied in studies of species living in a landscape with fragmented habitat (Hanski & Gilpin 1991). One of the species in the study, *A. eupatoria*, has been chosen for metapopulation studies, in which the influence of dispersal on abundance and distribution will be investigated.

The results from this study suggest that the dispersal capacity of adhesive seeds is considerable, and comparable to other modes of dispersal, like wind and fleshy fruits (Hughes *et al.* 1994). There are many approaches to the study of adhesive dispersal, and one must agree with Shmida & Ellner (1983) that more studies under natural conditions are needed to evaluate the efficiency of this kind of seed dispersal.

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