Morphological and Ecological Relationships between Burrs and Furs

Author(s): Mason W. Kulbaba, Jacques C. Tardif, Richard J. Staniforth

Source: The American Midland Naturalist, 161(2):380-391.
Published By: University of Notre Dame
https://doi.org/10.1674/0003-0031-161.2.380
URL: http://www.bioone.org/doi/full/10.1674/0003-0031-161.2.380

Am. Midl. Nat. 161:380–391

Morphological and Ecological Relationships between Burrs and Furs

Abstract.—Epizoochory is the mode of seed dispersal where a diaspore (disseminating plant propagule) is disseminated on the external surface of an animal. While the structures that facilitate diaspore adherence are diverse, epizoochory is considered to be relatively rare (approximately 10% of angiosperms), but is commonly utilized by several invasive plant species. We experimentally sought species specific associations between the adherence and retention of eight common plant species' diaspores and five mammalian furs, plus human clothing. We sought relationships between both fur and diaspore characteristics in both the adherence and retention of diaspores. Diaspores of *Geum aleppicum* were the only ones interacting significantly better with one kind of substrate (mouse fur) than diaspores of all other plant species by being retained well in mouse fur. Alternatively, bison fur behaved as a ''generalist'' disperser, by consistently accommodating the adherence and retention of a wide range of diaspore morphologies. Finally, exotic plant species displayed a higher tendency than natives to adhere to a variety of mammal fur types, indicating a more flexible dispersal strategy for the invasive habit.

Introduction

Effective dispersal by plants is attained if propagules reach habitats favorable for survival, growth and reproduction (Stamp, 1989). Ridley (1930) recognized anemochory (dispersal by wind), hydrochory (dispersal by water) and zoochory (dispersal by animals) as the three primary dispersal syndromes. Van der Pijl (1969) further divided zoochory into two sub-syndromes: endozoochory (internal seed transportation) and epizoochory (external seed transportation). The *modus operandi* of an epizoochorous diaspore (adhesively disseminating propagule) is to remain attached to the surface of an animal by hooks, barbs or spines until it is actively removed, passively falls off or the dispersing animal dies (Fenner, 1985). However, diaspores lacking obvious adhesive characters (*e.g.*, hooks, spines, barbs) have also been shown to disperse long distances by epizoochory, particularly on the surface of wet or oily furs (Higgins *et al.*, 2003; Couvreur *et al.*, 2004b). Epizoochory has been recently examined as a means of potential long distance dispersal in domestic (Couvreur *et al.*, 2004a; Manzano and Malo, 2006; Tackenberg *et al.*, 2006) and wild animals (Laughlin, 2003). The local and intercontinental movement of livestock and humans has created ideal circumstances for long-range epizoochory that has been responsible for the introduction of invasive plant species to many parts of the world (Ridley, 1930; Vibrans, 1999).

Stebbins (1972) hypothesized that epizoochory is a ''directed'' or ''targeted'' dispersal strategy, because animals tend to visit certain habitats more frequently than others. Hence diaspores would be deposited non-randomly in specific suitable environments (for a discussion on the phases of dispersal *see* Staniforth and Cavers, 1977). This may explain the observation of epizoochorous taxa predictably occurring along trails and water edges (Hawthorn and Hayne, 1978). Sorensen (1986) was doubtful that epizoochory was a directed strategy, and suggested that many diaspores are knocked free of their vectors while traveling through dense brush, a habitat not necessarily conducive to the establishment of seedlings.

Diaspores show considerable morphological diversity (Stebbins, 1972) and those with hooks (burrs) are no exception. Burrs of epizoochorous plants vary with respect to their origins, dimensions, weights and presentation. In addition, hooking devices can vary in number, size, morphology and shape. For example, the burrs of *Geum aleppicum* Jacq. consist of achenes each with a single, long (1–2 cm) hook, and are presented collectively in dense clusters at the apex of the plant, whereas those of *Lappula echinata* Gilib. have many minute (< 1 mm long) terminally barbed prickles on the surfaces of each nutlet, and presented on long-reaching (30–40 cm) lateral stems.

Fenner (1985) proposed that certain diaspore morphologies may have affinities to specific substrates or substrate traits. Recently, some studies have explored the potential specificity of diaspores on domesticated animal fur (*e.g.*, Couvreur *et al.*, 2004b; Tackenberg *et al.*, 2006). Indeed, the large variation in diaspore morphology (including hooking structures) and presentation may be suggestive for selection of morphological attributes that best attach these diaspores to particular substrate types. Therefore, it may be possible to consider these characteristics as adaptive. Considerably more work is required to asses the factors that determine effective epizoochorous dispersal, as the results of these studies are inconclusive (Manzano and Malo, 2006). Early experimental studies in epizoochory (Agnew and Flux, 1970; Bullock and Primack, 1977) focused on the retention times of diaspores by their vectors, *i.e.*, the transport phase. Separate analysis of the attachment and detachment stages have been given limited attention (but *see* Castillo-Flores and Calvo-Irabien, 2003; Laughlin, 2003), or examined by experiments that were difficult to interpret (Fischer *et al.*, 1996; Bullock and Primack, 1977). Therefore, empirical studies that examine specific relationships between diaspore morphologies and fur characteristics are required to fully elucidate species specific epizoochoric relationships.

In this study, we experimentally sought species specific associations between the adherence and retention of eight common plant species' diaspores and five mammalian furs, plus human clothing. We hypothesized that diaspores of certain species (or diaspores with similar attributes like hook morphology) would adhere to and be retained longer by some substrates than others. More specifically, we expect that certain morphologies of hooking appendages will more strongly interact with certain fur traits than others. Such a strong association between diaspore and hair characteristics may result in greater potentials of dispersal (cf., Tackenberg *et al.*, 2006). For example, we expect many hooked diaspores to adhere to, and be retained longer by long and dense haired furs. If such associations do not exist, most diaspore and hook morphologies should display relatively constant adherence and retention rates among all substrate types.

MATERIALS AND METHODS

The burr-bearing plants species chosen for the current study were: Canada anemone (*Anemone canadensis* L.), lesser burdock (*Arctium minus* (Hill) Bernh.), common beggarticks (*Bidens frondosa* L.), yellow avens (*Geum aleppicum* Jacq.), wild licorice [*Glycyrrhiza lepidota* (Nutt.) Pursh], bluebur (*Lappula echinata* Gilib.), snakeroot (*Sanicula marilandica* L.) and cocklebur (*Xanthium strumarium* L.). Scientific and common names followed Scoggan (1978). Taxa were chosen because they: (1) show a wide diversity of diaspore and hooking morphologies; (2) are common throughout their range in Manitoba; and (3) represent both native and exotic elements of the flora (*A. minus* and *L. echinata* are introduced species).

Approximately thirty fruiting plants of each species were collected from rural Manitoba (Anola-Oakbank area) between August and October, 2003. Plant heights and the horizontal distance that the diaspores were held away from the main stem of the plants were recorded at the time of collection. The plants were stored in paper bags and allowed to dry. Fifteen morphological characters were measured for five randomly selected diaspores from each taxon. Diaspore characteristics were: height of diaspores above ground, distance of diaspore from main stem, diaspore weight, number of seeds per diaspore; length, width and shape of diaspore. The measurement of diaspore hook characteristics (Fig. 1) largely followed those of Gorb and Gorb (2002): number of hooks per diaspore, total hook length (*ls*), basal diameter of hook shaft (*db*), distal diameter of hook shaft (*dd*), diameter of the curve of the hook (*dh*), length of curve of the hook (*lh*), the size of hook span or opening (*sh*) and the presence or absence of bristles on the hook (*hp*). Five hooks from 5 diaspores (total of 25 hooks) of each species were measured to obtain mean values for the above measurements (Fig. 2). Digital images of the hooks were captured, and their measurements taken in the program WinSeedle Ver. 5.0a (Régent Instruments Inc., 2000).

Pelts of the following five mammal species were used in this study: deer mouse (*Peromyscus maniculatus* Wagner), northern raccoon (*Procyon lotor* L.), white-tailed deer (*Odocoileus virginianus* Zimmerman), American black bear (*Ursus americanus* Pallas), and American bison (*Bison bison* L.). Nomenclature is that of the Smithsonian Institute (2004). Single furs of each species were loaned from the Department of Natural History, The Manitoba Museum, Winnipeg, MB. These taxa exhibit diversity in habitat, size and fur morphology. Five hair characteristics were measured at five random points on each pelt: guard-hair length, length of undercoat hair, density of guard-hairs, density of undercoat hair and depth of pile. Pile was a measurement from the skin's surface to the top of the hair level. Hair densities were determined by counting the number of hairs in 1.0 cm^2 wire frames located at five random locations on each substrate. Measurements pertaining to the fur types are presented in Appendix A. Human clothing

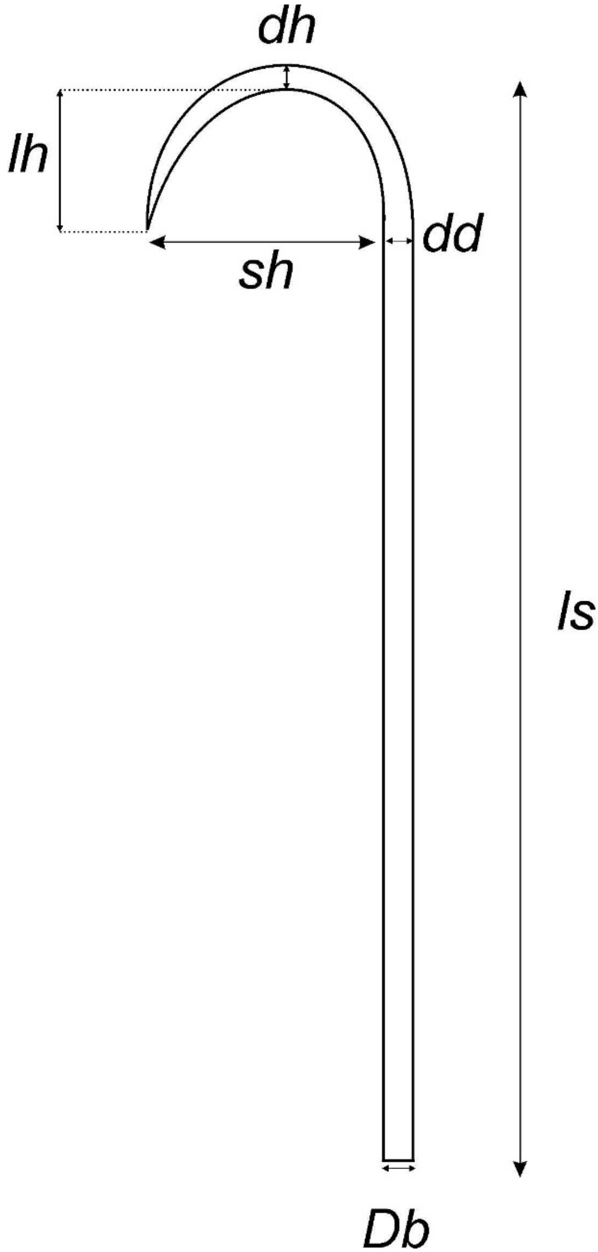
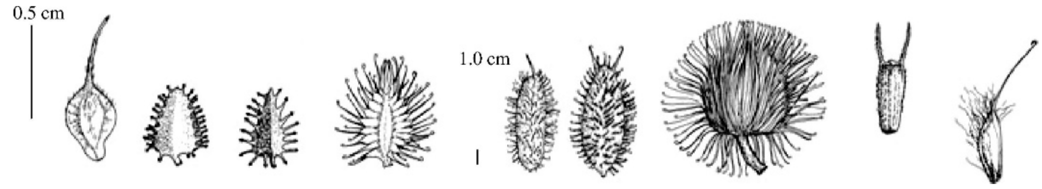


FIG. 1.—Illustration of a hook and respective measurements. *ls* is the length of hook, *db* is the proximal diameter of the hook, *dd* is the distal diameter of the hook, *dh*, is the diameter of the "bend" portion of the hook at its apex, *lh* is the length of the "bend" portion of the hook, and *sh* is the distance between the hook point and primary hook shaft. The presence or absence of bristles (*hp*) was also scored



Plant species	Diaspore measurements							Hook measurements (mm)					
	Plant height (cm)	Horiz. pres.◆ (cm)	Diaspore weight (mg)	No. seeds	Length (mm)	Width (mm)	No. hooks	Length (*ls*)	Basal diameter (*db*)	Distal diameter (*dd*)	Curve diameter (*dh*)	Curve length (*lh*)	Hook span (*sh*)
Anemone canadensis	27.3±4.8	2.6±0.4	4.0±0.01	1.0±0.0	7.3±1.1	3.2±0.8	1.0±0.8	2.5±1.2	0.6±0.20	0.1±0.8	0.1±0.90	0.3±0.2	0.2±0.1
Arctium minus	91.4±10.8	67.2±8.2	431.0±0.09	37.6±3.8	14.5±0.9	14.8±0.9	168.6±25.6	4.8±0.4	0.3±0.06	0.2±0.03	0.1±0.02	0.2±0.06	0.2±0.04
Bidens frondosa	70.2±3.0	7.9±2.5	4.0±0.01	1.0±0.0	9.4±1.4	3.5±0.4	2.0±0.0	4.1±0.1	0.5±0.09	0.2±0.04	0.06±0.01	0.1±0.04	0.1±0.04
Geum aleppicum	58.0±5.4	7.6±1.8	3.0±0.02	1.0±0.0	9.4±0.6	1.4±0.2	1.0±0.0	4.9±0.2	0.4±0.03	0.09±0.02	0.08±0.02	0.2±0.03	0.1±0.01
Glycyrrhiza lepidota	44.2±19.3	9.2±3.0	85.1±0.03	4.0±1.2	17.6±4.7	7.0±0.3	111.0±33.4	3.0±0.3	0.5±0.30	0.1±0.02	0.1±0.03	0.1±0.003	0.2±0.1
Lappula echinata	63.2±8.7	25.1±6.3	4.0±0.01	4.0±0.0	2.5±0.1	1.7±0.2	115.2±28.9	0.8±0.1	0.1±0.05	0.05±0.01	0.03±0.01	0.05±0.02	0.04±0.01
Sanicula marilandica	41.8±3.6	4.9±0.3	0.02±0.01	2.0±0.0	5.3±0.2	4.1±0.5	59.8±9.7	1.8±0.3	0.2±0.06	0.09±0.01	0.08±0.01	0.2±0.03	0.06±0.05
Xanthium strumarium	32.0±3.4	23.2±1.9	0.2±0.04	2.0±0.0	19.6±0.9	7.2±0.4	110.2±14.5	2.1±0.4	0.3±0.08	0.1±0.02	0.09±0.02	0.3±0.1	3.63±0.59

◆ Perpendicular distance of diaspore from the main stem

FIG. 2.—Diaspores of (from left): *Anemone canadensis*, internal view *of Lappula marilandica*, external view of *Lappula echinata*, *Sanicula marilandica*, *Glycyrrhiza lepidota*, *Xanthium strumarium*, *Arctium minus*, *Bidens frondosa* and *Geum aleppicum*. Measurement values are mean ± standard deviation, calculated for n = 5 for diaspore measurements, and n = 25 for hook measurements. Bristles (*hp*) were present on *Anemone canadensis*, *Geum aleppicum*, and *Xanthium strumarium*. Drawings by R. J. Staniforth

in the form of cotton pants was also examined as a potential dispersal substrate. However, pants possessed few characters of the mammalian fur, and are, therefore, not as well characterized as the mammal furs.

Diaspores from each plant species were tested against each substrate in two experiments that have been designed to mimic a mammal's encounter with a burr-bearing plant. The first experiment investigated the efficiency by which diaspores became attached to the animal (hereafter *adhesion*). The second experiment measured the durability and duration of that attachment (hereafter *retention*). Each treatment combination (plant species-substrate) was replicated four times in each experiment.

The adhesion experiment tested the ability of a diaspore to adhere to a substrate in a manner which would mimic a natural encounter between a dispersal vector and a burr-bearing plant. The diaspores were therefore left attached to the stems to best mimic a natural encounter. Stems with ten or more diaspores were randomly chosen from the collected samples. For each plant-substrate combination, a stem with a known number of diaspores was gently brushed along a pelt first in the direction of the hair follicles. The stem was then rotated 180° and passed in the opposite direction (*i.e.*, against the direction of the hair). This procedure was repeated for a total of four passes of each plant stem, on each substrate. The stems were rotated to ensure an equal opportunity for all its diaspores to contact the substrate. All plant species-substrate trials were randomly arranged and a different plant stem was used for each plant-substrate replication. The number of diaspores which had adhered to a substrate was counted after each of four passes, and a percent adherence value calculated. The experimental substrate area was 25 cm × 10 cm (250 cm^2) for each fur type. The briskets (lower front portions) of the pelts, and lower portions of the pant legs were the designated areas for diaspore contact. Both the sides and back of the Deer mouse was considered as an experimental surface because of this animal's small size.

The ability for burrs to be transported or retained on pelts of animals and clothing was tested using a shaker table. To do this, each substrate from the preceding experiment with its attached diaspores was vertically fixed by means of straps to a rectangular aluminum frame mounted on end to a shaker table, and agitated for 180 s at 2.63 oscillations per second. The mean percentage of seeds adhering to each substrate after agitation was then calculated.

STATISTICAL ANALYSIS

Non-parametric statistical tests were used to accommodate the lack of normality in our data, despite attempted transformations. Non-parametric statistics included the Kruskal-Wallis ($\alpha = 0.05$) test for overall significance in the relative adherence/retention of a plant's diaspores, among all six substrates. Upon finding a significant result by the Kruskal-Wallis test, individual contrasts of adherence/retention between pairs of substrates were tested by the Mann-Whitney U test. The Mann-Whitney U test was used as a post-hoc equivalent (Sheskin, 1997). Two-tailed Spearman's correlation coefficients (r_s) were also calculated to examine associations between fur and diaspore characters with respect to adherence and retention. The sequential Bonferroni correction was manually applied to tables of correlation coefficients, as described by Rice (1989). All statistical tests were performed in SAS Ver. 9.1 (SAS Institute, 2004).

RESULTS

Generally, less than 50% of the diaspores on a stem adhered to a substrate (Fig. 3). *Arctium minus* and *Lappula echinata* (the two exotic species) were the only two plant species that displayed greater than 50% adherence (on raccoon, bison and cotton pants). The diaspores of *L. echinata* provided the only example of greater than 50% adherence on the deer fur. The highest percentage of diaspores to adhere to any substrate was that of *L. echinata* on bison fur (82.2%), whereas the lowest adherence value was for diaspores of *Xanthium strumarium* on deer mouse hair (1.2%). All plants except *Anemone canadensis, Bidens frondosa* and *L. echinata* showed significant differences among their rates of diaspore adherence (Fig. 3).

The retention of diaspores after agitation varied among all substrates, but was usually greater than 50% (Fig. 3). Exceptions were *Anemone canadensis* (on all substrates), *Arctium minus* (on mouse and raccoon), *Bidens frondosa* and *Sanicula marilandica* (on deer, mouse and pants), *Geum aleppicum* (on pants), *Glycyrrhiza lepidota* and *Xanthium strumarium* (on mouse and pants) and *Lappula echinata* (on

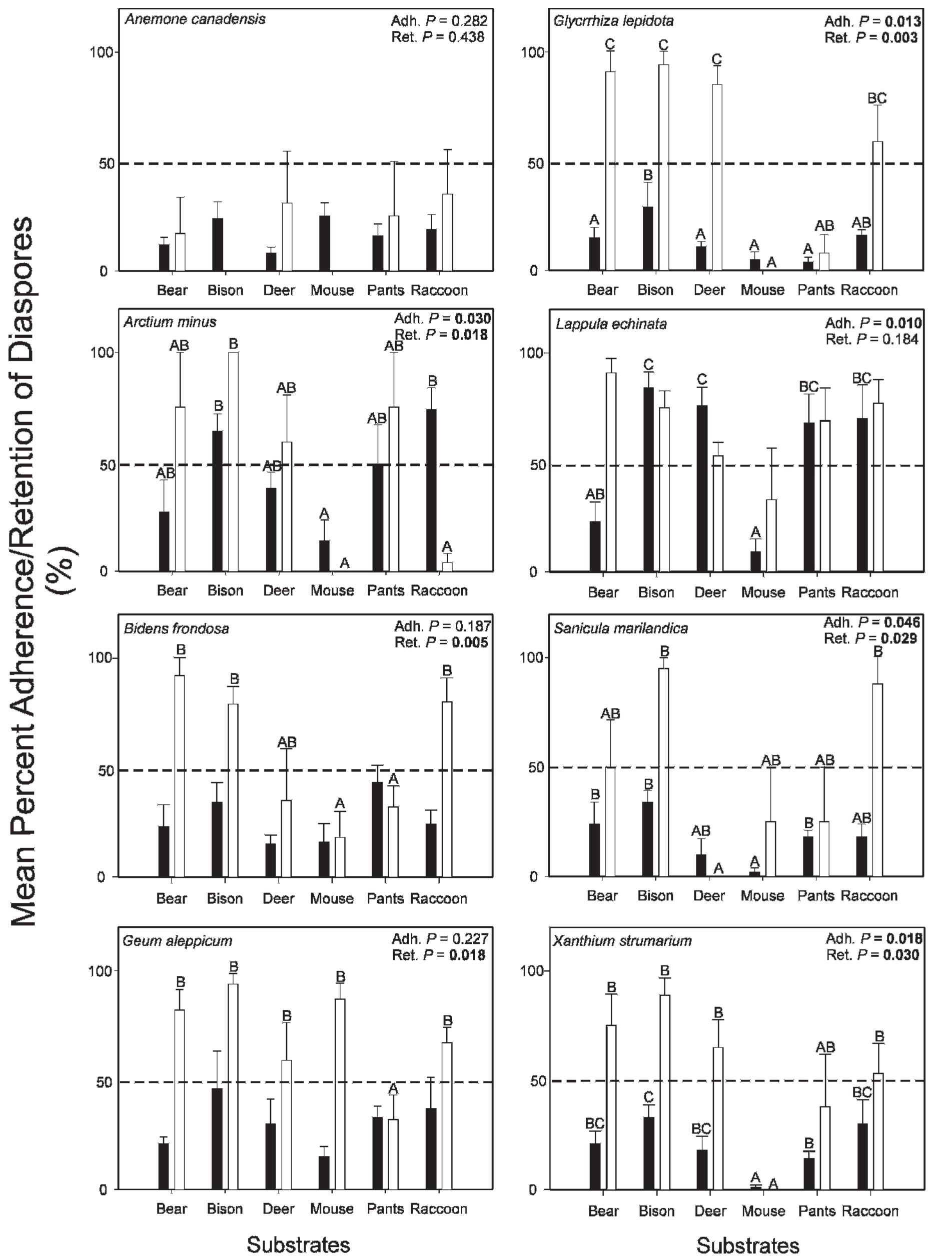


FIG. 3.—Mean proportions and standard errors of plant diaspore adherence (closed bar) and retention (open bar) to the six experimental substrates (n = 4 trials). Values in upper right corner of each panel represent Kruskall-Wallis P-values, with significant values in boldface. Adherence/retention values followed by values denoted by a different letter are signifieantly different as determined by Mann-Whitney U tests (α = 0.05)

mouse). Interestingly, cotton pants only retained high numbers of diaspores of the non-native *A. minus* and *L. echinata*. The highest mean percent retention (100%) of diaspores among all eight plant species was recorded for *A. minus* on bison fur. The lowest percentage of diaspore adherence (0%) was recorded for the following pairings of diaspores and furs: *A. canadensis* on raccoon and bison fur, *A. minus*, *G. lepidota* and *X. strumarium* on raccoon fur, and *S. marilandica* on deer fur (Fig. 3). Significant differences among the retention of diaspores were found among all plants except *A. canadensis* and *L. echinata*, as determined by the Kruskal-Wallis test (Fig. 3).

High rates of adherence and retention for any given pair of plant-animal species did not always coincide. For instance, 74.1% of diaspores from *Arctium minus* adhered to raccoon fur, but their retention was low (4.2%) (Fig. 3).

The horizontal distance of diaspore presentation from the plant's stem showed a significant positive correlation with adherence to deer fur (Table 1). The distal diameter (*db*) of hook appendages was negatively correlated with diaspore adherence to black bear fur. Bison fur and cotton pants both displayed positive correlations with the height of diaspore presentation. Finally, cotton pants showed a significant negative correlation with diaspore hook spans (left-hand side of Table 1).

Several significant correlations between diaspore characteristics and the substrates retention data were found (right-hand side of Table 1). The retention of diaspores by raccoon fur was negatively correlated with the diameter of the hooks curve (*dh*). Similarly, the retention of diaspores by mouse fur was negatively correlated with the diameter of hook curves (*dh*) and hook spans (*sh*). Retention of diaspores by black bear fur was positively correlated with the height of diaspore presentation, while retention by deer hair was correlated with the horizontal distance that the diaspore was presented away from the plants main stem. Finally, cotton pants were negatively correlated with both the basal diameter of diaspore hooks (*db*) and hook spans (*sh*) (right-hand side of Table 1).

Three plant species displayed significant correlations between the adherence/retention of their diaspores and the measured fur characteristics (left-hand side of Table 2). The adherence of *Bidens frondosa* was negatively correlated with the density of guard hairs. Adherence of *Glycyrrhiza lepidota* and *Xanthium strumarium* both positively correlated with the density of undercoat hairs (left-hand side of Table 2).

The retention of *Xanthium strumarium* diaspores was significantly correlated with the density of under-coat hair, but those of *Glycyrrhiza lepidota* were not (right-hand side of Table 2). Finally, the retention of *Bidens frondosa* diaspores significantly correlated with under-coat density, and also with guard-hair length and under-coat hair length (right-hand side of Table 2).

DISCUSSION

All taxa included in this study possessed hooked diaspores that are used in epizoochory, with the possible exception of the winged achenes of *Anemone canadensis* that may also function as an anemochore (wind dispersed diaspore). The morphology, number, size and placement of the diaspore appendages on fruits or infructescences were highly variable; the rate of adhesion and retention of the plant diaspores varied among substrates.

A specialist diaspore association would have displayed a high affinity (faithfulness) to a particular substrate that would be evident in either a particularly high adhesion and/or retention rate to that substrate. The only instance of a high proportion of diaspore adherence and/or retention was found in the retention of 85% of *Geum aleppicum* diaspores by mouse fur. The second highest retention of diaspores by mouse fur was 35% by *Lappula echinata*. While *Geum aleppicum* had a moderate proportion of diaspores adhering to the mouse fur, it is important to note that all plant species displayed a low adherence rate on this particular substrate. These results reflect those of Kiviniemi and Telenius (1998), who found a high retention of morphologically similar *G. rivale* diaspores to the fur of wood mice (*Apodemus flavicollis* Meldrior). Whereas *G. aleppicum* may not be specifically adapted to mouse dispersal, its epizoochoric strategy (*e.g.*, a single long, slender hook) appears suited for retention by the thin mouse fur. No other unique associations were observed with these plant and animal taxa in the present study.

In contrast to specialist dispersal associations, bison fur showed the highest rate of adherence and retention for diaspores of most plant species. In fact, it was always the first or second best substrate for

TABLE 1.—Spearman's ranked correlation (n = 8) of diaspore characters on adherence (left) and retention (right) rates. Only diaspore traits that displayed significant correlations are shown for space considerations. See materials and methods section for complete list of measured diaspore characters. Significant correlations are indicated in boldface

	Substrate adherence						Substrate retention					
Diaspore character	Raccoon	Bear	Mouse	Deer	Bison	Pants	Raccoon	Bear	Mouse	Deer	Bison	Pants
Height	0.595	0.619	0.214	0.690	**0.810***	**0.762***	0.048	**0.952****[B]	0.140	0.333	0.405	0.643
Horizontal pres.◆	0.643	0.524	−0.354	**0.810***	0.595	0.405	−0.286	0.619	−0.330	**0.786***	0.262	0.452
db	−0.452	**−0.739***	0.619	−0.571	−0.643	−0.476	−0.476	−0.095	−0.507	0.024	−0.190	**−0.762***
dh	−0.333	−0.262	−0.143	−0.361	−0.571	−0.619	**−0.762***	−0.190	**−0.710***	0.476	0.310	−0.571
sh	−0.286	−0.500	−0.143	−0.333	−0.690	**−0.738***	−0.643	−0.214	**−0.862****[B]	0.476	−0.048	**−0.762***

◆ Perpendicular distance of diaspore from the main stem where *db* is the proximal diameter of the hook, *dh*, is the diameter of the ''bend'' portion of the hook at its apex, *sh* is the distance between the hook point and the primary hook shaft

[B] Indicates correlations that remained significant after sequential Bonferroni correction

* $P < 0.05$

** $P < 0.01$

TABLE 2.—Spearman's ranked correlation (n = 6) of substrate characters on adherence (left) and retention (right) rates. Only substrate traits/plant species that displayed significant correlations are shown for space considerations. *See* materials and methods section for complete list of measured substrate traits. Significant correlations are indicated in boldface

	Hair characters adherence				Hair characters retention			
Plant species	Guard-hair length	Undercoat hair length	Guard-hair density	Undercoat hair density	Guard-hair length	Undercoat hair length	Guard-hair density	Undercoat hair density
Bidens frondosa	−0.143	−0.029	**−0.943**,B**	0.029	**0.943**,B**	**0.986**,B**	−0.143	**0.928**,B**
Glycyrrhiza lepidota	0.771	0.754	−0.029	**0.812***	0.486	0.522	0.200	0.696
Xanthium strumarium	0.714	0.754	−0.257	**0.812***	0.657	0.696	0.086	**0.870**B**

[B] Indicates correlations that remained significant after sequential Bonferroni correction

* $P < 0.05$

** $P < 0.01$

adherence, *i.e.*, had the highest percent adherence values for the diaspores. This result may imply that bison was a generalist dispersal vector, having the ability to accommodate a wide range of diaspore morphologies. In the island ecosystem of Santa Catalina Island, Constible *et al.* (2005) found diaspores of several plant species (including *Xanthium strumarium*) in clumps of bison hair samples, most of which were non-native plant species. If several plant species relied on adhesive dispersal via bison fur, it is unclear what effect the extirpation of bison may have had on plant populations that relied on bison vectors for adhesive dissemination. One possible result is the fragmentation of populations, as observed in *Bouteloua curtipendula* (Michx.) Torr. (Laughlin, 2003).

The current study suggests the density of undercoat hairs is important to epizoochoric dispersal. These findings are supported by those of Heinken *et al.* (2002), who found that the denser undercoats of wild boar (*Sus scrofa* L.) provided a better substrate for diaspores than the thin coats of roe deer (*Capreolus capreolus* L.). Similarly, Couvreur *et al.* (2004b) found a general trend among 66 plant species on seven different mammals indicating ''deep furs'' with long, coarse hairs are best for diaspore retention. Diaspores of *Glycyrrhiza lepidota* and *Xanthium strumarium* both showed significant positive correlations between undercoat density and adherence, however only *X. strumarium* preserved this correlation in its retention data. The importance for a thick undercoat density for *X. strumarium* may be reflective of *X. strumarium* possessing the largest hook spans of all the study species. An increased density may be sufficient to ''fill up'' the extra space in the hook span. This statement is supported by the relatively high adherence and retention values shown by bison and black bear fur (furs with high hair densities) for the diaspores of *X. strumarium* (Fig. 3). Laughlin (2003) found that the length and stiffness of animal hair was important for the adherence of *Bouteloua curtipendula* diaspores, while long haired animals like bison and elk (*Cervus canadensis* Erxleben) best retained the diaspores. Our study also found a positive association between the retention of diaspores (*Bidens frondosa*) and guard-hair length.

Vibrans (1999) inferred that the clothing of farmers in rural Mexico was the principal, long-distance dispersal vector for three species of *Bidens* (*B. odorata*, *B. ferulifolia* and *B. ballsii*). We found the diaspores of *Bidens frondosa* to be amply equipped to take advantage of human clothing, even though they could not have specifically evolved for such a means of dispersal. With respect to pant material as a substrate for dispersal, we found that diaspores with small hook spans showed the greatest adherence values, whereas their retention was greatest if their hooks had small basal diameters in addition to small hook spans. This explains why the diaspores of *Lappula echinata* were most likely to adhere to and be retained on pants, and those of *B. frondosa* were somewhat less so. Adhesive dispersal via human clothing, ''epianthropochory'' is likely common among plant species with well developed appendages. Indeed, Shmida and Ellner (1983) found a total of 25 different plant species adhering to socks after a series of standardized walks through Mediterranean chaparral.

Several studies have detected a negative effect of diaspore mass on retention potential (see Kiviniemi and Telenius, 1998; Römermann *et al.*, 2005; Tackenberg *et al.*, 2006). In contrast, Couvreur *et al.* (2005) found large heavy diaspores were retained longer by the long wavy hair of galloway cattle, and light-smaller diaspores were retained longer by the short fur of haflinger horses. Surprisingly, we found no association of diaspore mass with either adherence or retention. This may reflect the fact that all plant species examined in the present study, with the possible exception of *Anemone canadensis*, displayed obvious adhesive appendages. However, Tackenberg *et al.* (2006) found that the negative effects of mass could override the positive effects of adhesive appendages. Furthermore, Tackenberg *et al.* (2006) didn't find differences in retention rates (and thus dispersal potential) over several different diaspore morphologies, which contrasts with the present study. This lack of differences among retention rates may be due to the Tackenberg *et al.* (2006) only examining two different animal furs.

The two exotic plant species involved in this study (*Arctium minus*, *Lappula echinata*) were the only plant taxa to have an overall mean diaspore adherence greater than 50%, across all substrates. As well, these two taxa generally produced more equal adherence and retention values of diaspores, than did the native plant species. Successful adherence to a wide variety of fur and clothing substrates may increase the total number of potential dispersal vectors and therefore, a correspondingly higher potential for colonization and invasion (*see* Graae, 2002). In addition, *A. minus* and *L. echinata* produced the highest adherence and retention by human clothing. This may implicate human movement as a reliable means of invasive plant dispersal (*see* Vibrans, 1999). However, field trials incorporating factors not considered in the present study (*e.g.*, weather, animal behavior, variation in fur) are likely important (*see* Kiviniemi, 1996), and are required to assess the findings of the current study.

In conclusion we found: (1) a single specific relationship between *Geum aleppicum*'s diaspore morphology (a single longer slender and narrow hook) being best retained by the thin fur of deer mice, in contrast (2) bison fur (long and curly dense fur) behaved as a ''generalist'' dispersing substrate, by accommodating many diaspore and hook morphologies, (3) the density of undercoat hair is important to epizoochorous dispersal (adhesion and retention) and finally, (4) the two invasive plant species' diaspore morphology (spherical diaspores, with many small spanned hooks) displayed the highest adhesive percentages, with comparable retention values appropriate to the invasive habit.

Acknowledgments.—We would like to thank Dr. Bruce A. Ford, Dr. G. Eric E. Moodie, Miss L.S. Sawich and Dr. Anne C. Worley for insightful conversations, and suggestions at various stages of this study. We also thank J. Klapecki and the Manitoba Museum for loan of the animal furs. Finally, we thank two anonymous reviewers for a thorough and critical review of a previous version of this manuscript.

LITERATURE CITED

AGNEW, S. H. AND R. B. FLUX. 1970. Plant dispersal by hares (*Lepus capensis* L) in Kenya. *Ecology*, **51**:735–737.

BULLOCK, S. H. AND R. B. PRIMACK. 1977. Comparative experimental study of seed dispersal on animals. *Ecology*, **58**:681–686.

CASTILLO-FLORES, A. A. AND L. M. CALVO-IRABIEN. 2003. Animal dispersal of two secondary-vegetation herbs into the evergreen rain forest of south-eastern Mexico. *J. Trop. Ecol.*, **19**:271–278.

CONSTIBLE, J. M., R. A. SWEITZER, D. H. VAN VUREN, P. T. SCHUYLER AND D. A. KNAPP. 2005. Dispersal of non-native plants by introduced bison in an island ecosystem. *Bio. Inv.*, **7**:699–709.

COUVREUR, M., B. CHRISTIAEN, K. VERHEYEN AND M. HERMY. 2004a. Large herbivores as mobile links between isolated nature reserves through adhesive seed dispersal. *Appl. Veg. Sci.*, **7**:229–236.

———, B. VANDENBERGHE, K. VERHEYEN AND M. HERMY. 2004b. An experimental assessment of seed adhesivity on animal furs. *Seed Sci. Res.*, **14**:147–150.

———, K. VERHEYEN AND M. HERMY. 2005. Experimental assessment of plant seed retention times in fur of cattle and horse. *Flora*, **200**:136–147.

FENNER, M. 1985. Seed ecology. Chapman and Hall Ltd, New York, New York.

FISCHER, S. F., P. POSCHLOD AND B. BEINLICH. 1996. Experimental studies on the dispersal of plants and animals in calcareous grasslands. *J. Appl. Ecol.*, **33**:1206–1222.

GORB, E. AND S. GORB. 2002. Contact separation force of the fruit burrs in four plant species adapted to dispersal by mechanical interlocking. *Plant Physiol. Biochem.*, **40**:373–381.

GRAAE, B. J. 2002. The role of epizoochorous seed dispersal of forest plant species in a fragmented landscape. *Seed Sci. Res.*, **12**:113–121.

HAWTHORN, W. R. AND P. D. HAYNE. 1978. Seed production and predispersal seed predation in the biennial Composite species, *Arctium minus* (Hill) Bernh. and *A. lappa L. Oecologia*, **34**:283–295.

HEINKEN, T., H. HANSPACH, D. RAUDNITSCHKA AND F. SCHAUMANN. 2002. Dispersal of vascular plants by four species of wild mammals in a deciduous forest in NE Germany. *Phytocoenologia*, **32**:627–643.

HIGGINS, S. I., R. NATHAN AND M. L. CAIN. 2003. Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? *Ecology*, **84**:1945–1956.

KIVINIEMI, K. 1996. A study of adhesive seed dispersal of three species under natural conditions. *Acta Bot. Neerl.*, **45**:73–83.

——— AND A. TELENIUS. 1998. Experiments on adhesive dispersal by wood mouse: seed shadows and dispersal distances of 13 plant species from cultivated areas in southern Sweden. *Ecography*, **21**:108–116.

LAUGHLIN, D. C. 2003. Geographic distributions and dispersal mechanisms of *Bouteloua curtipendula* in the Appalachian Mountians. *Am. Midl. Nat.*, **149**:268–281.

MANZANO, P. AND J. E. MALO. 2006. Extreme long-distance seed dispersal via sheep. *Front. Eco. Env.*, **5**:244–248.

RÉGENT INSTRUMENTS. 2000. WinSeedle™ V. 5.0a Reference manual. Régent Instruments, Québec, Québec.

RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution*, **43**:223–225.

RIDLEY, H. N. 1930. The dispersal of plants throughout the world. Reeve & Company, Ashford, Kent, United Kingdom.

RÖMERMANN, C., O. TACKENBERG AND P. POSCHOLD. 2005. How to predict attachment potential of seeds to sheep and cattle coat from simple morphological seed traits. *Oikos*, **110**:219–230.

SAS INSTITUTE. 2004. SAS/STAT software. Rel. 9.1.2. SAS Institute, Cary, North Carolina.

SCOGGAN, H. 1978. The flora of Canada part 4, Dicotyledoneae (Loasaceae to Compositae). National Museum of Natural Sciences Publications in Botany, No. 7 (4). National museums of Canada, Ottawa.

SHESKIN, D. J. 1997. Handbook of parametric and nonparametric statistical procedures. CRC Press LLC, Boca Raton, Florida.

SHMIDA, A. AND S. ELLNER. 1983. Seed dispersal on pastoral grazers in open Mediterranean chaparral. *Israel. J. Bot.*, **32**:147–160.

SMITHSONIAN INSTITUTE. 2004. Mammal species of the world database: http://www.mnh.si.edu/mna/.

SORENSEN, A. E. 1986. Seed dispersal by adhesion. *Ann. Rev. Eco. Sys.*, **17**:443–463.

STAMP, N. E. 1989. Efficacy of explosive vs. hygroscopic seed dispersal by an annual grassland species. *Am. J. Bot.*, **17**:443–463.

STANIFORTH, R. J. AND P. B. CAVERS. 1977. The importance of cottontail rabbits to *Polygonum* spp. *J. Appl. Ecol.*, **14**:261–268.

STEBBINS, G. L. 1972. Adaptive radiation of reproductive characteristics in angiosperms, II: seeds and seedlings. *Ann. Rev. Ecol. Sys.*, **2**:237–260.

TACKENBERG, O., C. RÖMERMANN, K. THOMPSON AND P. POSCHOLD. 2006. What does diaspore morphology tell us about external animal dispersal? Evidence from standardized experiments measuring seed retention on animal-coats. *Basic Appl. Ecol.*, **7**:45–58.

VAN DER PIJL, L. 1969. Principles of dispersal in higher plants. Springer-Verlag, Berlin, Germany.

VIBRANS, H. 1999. Epianthropochory in Mexican weed communities. *Am. J. Bot.*, **86**:476–481.

MASON W. KULBABA[1], JACQUES C. TARDIF AND RICHARD J. STANIFORTH, Department of Biology, University of Winnipeg, 515 Portage Avenue, Manitoba, Canada R3B 2E9. *Submitted 8 August 2007; accepted 9 June 2008.*

APPENDIX A.—Measured characters on five experimental mammal skins. Each measurement is the average of five randomly sampled areas of the experimental region (see materials and methods for description). Values are means ± standard deviation

Mammal	Guard-hair length (cm)	Undercoat hair length (cm)	Guard-hair density (hairs/cm^2)	Undercoat hair density (hairs/cm^2)	Pile (cm)
American Bison	5.0±0.9	2.7±0.4	103.0±8.4	218.0±21.7	2.4±0.7
Black Bear	9.5±0.8	5.9±0.4	133.0±8.4	223.0±19.9	6.08±0.9
White-Tailed Deer	4.3±0.5	0.9±0.3	181.0±6.5	13.0±7.6	3.38±0.4
Raccoon	5.1±0.5	2.8±0.3	59.0±19.2	145.2±41.3	1.8±0.3
Deer Mouse	0.8±0.1	Nil	146.0±16.7	Nil	0.2±0.1

[1] Corresponding author present address: 501 Buller Building, University of Manitoba, Department of Biological Sciences, Winnipeg, Manitoba, R3T 2N2. E-mail: umkulbam@cc.umanitoba.ca