Investigating Epizoochorous Adaptations to Mammalian Furs

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A thesis submitted in partial fulfillment of the Honours Thesis (05.4111/6) Course
Department of Biology, The University of Winnipeg 2004

Abstract

The method of seed dispersal by which a diaspore (a seed or fruit) is transported on the exterior surface of an animal, is known as epizoochory. To search for adaptations by the diaspores to specific fur types, I selected eight species of plants with adhesive diaspores, and twelve species of mammals. Fifteen characteristics of diaspore morphology and six characteristics of the fur were measured for clustering purposes. Five fur types and eight diaspore types were selected from cluster analyses as representative types. An experimental study investigated a neglected aspect, the attachment phase, where the diaspores detached from the stem of the plant, and became attached to the mammalian fur. Brushing the plants along the furs and measuring the adhesive qualities of the diaspores accomplished this. Bison fur was well suited to adherence and retention by an array of diaspore types, which could indicate the role of the bison as a generalist disperser. This generalist trait was observed in the alien species (*Arctium minus* and *Lappula echinata*), which would benefit their invasive life style. Diaspores with wide hook spans were picked up and held more tightly by long haired mammals, with dense undercoats. Epizoochory is believed to have been responsible for the introduction of numerous alien species to new locations, and the knowledge gained from this study may better our understanding of this largely unexplored seed dispersal syndrome.

Acknowledgements

I would like to thank the Arklie family for support and technical assistance. The project was made possible by the University of Winnipeg Department of Biology. Supervisor Dr. Richard J. Staniforth was more patient and helpful than could ever have been asked from a supervisor. Thanks also goes out to committee members Dr. Jacques Tardif and Dr. Richard Westwood for their advice and assistance in numerous aspects of the project especially in statistics and experimental design. Additional thanks are extended to Janice Klapecki for the loan of the mammal skins, and Dr. Ric Moodie, the projects course coordinator, whose support and encouragement was greatly appreciated.

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Introduction

Effective dispersal by plants is accomplished by the placement of propagules in habitats which are favourable for their survival, growth, and reproduction (Stamp, 1989). This process may be accomplished by a number of different methods, or dispersal syndromes. Ridley (1930) described three major types of diaspore dispersal, i.e. anemochory, hydrochory and zoochory (dispersal by wind, water, and animals, respectively). Zoochory (animal mediated dispersal) can be divided into several types including: frugivory, and adhesive dispersal (Ridley, 1930). The adhesive dispersal of a diaspore (the disseminating unit, usually a fruit or seed) on the surface of an animal, including humans, is known as epizoochory. This syndrome is a little known and studied syndrome of seed dispersal (Sorenson, 1986). The diaspores remain attached to the surface of the animal until actively removed, passively fall off, or when the animal dies (Fenner, 1985). This method of seed dispersal is thought to be responsible for numerous introductions of alien species throughout the world, by the movement of livestock and humans (Vibrans, 1989).

Diaspore dispersal in general consists of three stages: intake/attachment, transportation, and deposition (Staniforth and Cavers, 1977). Early studies of epizoochory (Agnew and Flux, 1970; Bullock and Primack, 1977) focused mainly on the retention times (transport phase) of the diaspores on the dispersal vector. The importance of the attachment stage was either ignored, or misrepresented by unnatural experiments. Fischer et al, (1996) for example dropped individual diaspores onto a substrate from a standardized height to represent the adherence phase of epizoochory. This method and others (i.e. Bullock and Primack, 1977) may have given biased results because it is likely that any diaspore would adhere successfully under certain unnatural conditions.

Stebbins (1972) stated that large amounts of evolutionary modification have occurred in the structures of diaspores of different species and genera. He also suggested that plants that dispersed

adhesively, could possibly achieve “directed” or “targeted” dispersal. This is possible because mammals tend to seek out similar habitats, which they find favourable. The transportation of diaspores to habitats similar to those of the parent plants would be favourable to the offspring.

Sorensen (1986) was more skeptical. She stated that there was no evidence showing that adhesively dispersed diaspores achieved “directed” dispersal. Rather, she was convinced that many diaspores are knocked off of the dispersal vector while traveling through dense brush. Such dense vegetation may not be suitable for seedling establishment due to low light levels and competition by other seedlings.

Sorensen (1986) and Stebbins (1972) agreed that diaspores dispersed by epizoochory have the potential to disperse longer distances than those dispersed by ingestion, wind, or water. This is because adhesive dispersal is mainly limited by the amount of time it takes for the disperser to notice the diaspores and remove them, or until the diaspore falls off, or the disperser dies. Wind and water dispersal relies on an inconsistent and unpredictable force, while the dispersal distance of a diaspore ingested by a bird or mammal relies on the gut passage time of the disperser. Janzen (1984) however, has shown that the gut-passage time may be short (e.g. seven minutes for some birds), but the passage rate has been documented as long as the three years in some elephants. It is clear that there is no consensus in the literature which dispersal syndrome has the greatest potential for long distance dispersal.

The notion that some diaspores may have an affinity to a specific substrate was speculated by Fenner (1985), but surprisingly his idea was never pursued. Information on this subject would shed light on many attributes of plants that show the epizoochorous syndrome, such as aggressiveness of colonization and population establishment. This research will shed some light on this issue and show the occurrence of specialized strategies between specific plants and substrates. The presence of

specialized strategies might explain why many epizoochorous species are commonly found in their "typical habitats" of disturbed areas and trial edges (Hawthorn and Hayne, 1978).

It was hypothesized that diaspores of certain species would become attached more readily to some substrates (or substrate types), than others. This would be reflected in a greater tendency to adhere to, and retain a more durable attachment to that substrate. This greater affinity for a specific substrate may then be correlated with diaspore and substrate characteristics, which may reveal adaptations of a diaspore to specific substrate types

Methods

The selection of burr-bearing plant species (plants which clearly show an epizoochorous dispersal strategy, i.e. the possession of diaspores with hooks, barbs, or spines) was made to include a diversity of diaspore morphologies, such as diaspore size and shape, height of diaspore presentation, hook/barb length, and origin (i.e. native or introduced). The study species were: *Anemone canadensis* L. (Canada anemone), *Arctium minus* (Hill) Bernh. (common burdock), *Bidens vulgata* Greene (beggars ticks), *Geum aleppicum* (Ait.) Fern. (yellow avens), *Glycyrrhiza lepidota* (Nutt.) Pursh (licorice root), *Lappula echinata* Gilib. (stickseed), *Sanicula marilandica* L. (black snakeroot) and *Xanthium strumarium* L. (cocklebur) (Scoggan, 1978). Intact shoots with ripe diaspores were collected from the vicinity of Anola, Oakbank, and Winnipeg, Manitoba between August and October, 2003. Plant height and the distance the diaspores were held away from the main stem of the plants were recorded at the time of collection. The plants were then stored in paper bags and allowed to dry.

The furs studied belonged to: *Peromyscus maniculatus* (Arch.) Naturgesch (deer mouse), *Tamias minimus* Bachman (least chipmunk), *Spermophilus richardsonii* Sabine (Richardson's ground squirrel), *Lepus americanus* Erxleben. (snowshoe hare), *Procyon lotor* L. (raccoon), *Cervus elaphus* L (elk), *Odocoileus virginianus* (Georg.) Thiere. (white tail deer), *Ursus americanus* Pallas (black bear), *Canis lupus* L (gray wolf), *Mephitis mephitis* Schreber (skunk), *Vulpes vulpes* L. (red fox), *Bos bison* L. (American bison) (Smithsonian Institute, 2004). An article of human clothing (cotton pants) was included in the list of substrates. The number of types of furs (substrates) to be used in the experiment was then reduced to six, as many showed similar characteristics. This selection was based on the results of a cluster analysis on pelt characteristics that was performed prior to experimentation. All furs were loaned from the Department of Natural History, The Manitoba Museum, 190 Rupert Avenue, Winnipeg MB, courtesy of Janice Klapecki, collections manager.

Preliminary Diaspore and Substrate Analyses

Analyses of diaspore and substrate characteristics were performed prior to experimentation. This allowed the determination of the level of similarity amongst the diaspores and amongst the substrates.

Diaspore Analysis

Fifteen characteristics were measured for each of the diaspores and their hooking mechanisms (Fig.1, Table 1). These measurements were made on five randomly selected diaspores from each plant species. A mean value for each characteristic was then generated for each species of plant.

Figure 1. Measures on individual hooks (Gorb and Gorb, 2002)

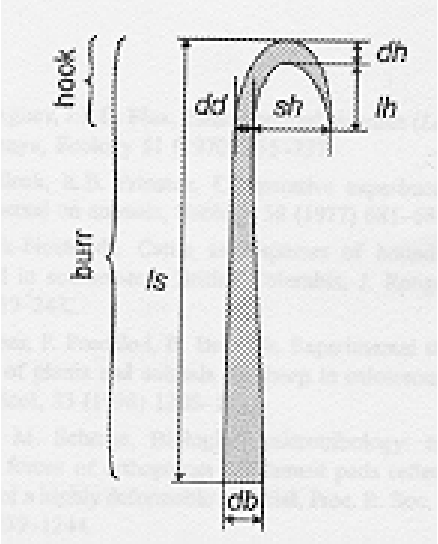

Table 1. Variables measured in the analysis of diaspore characteristics

Hook Characteristics	**Diaspore Characteristics**
Quantity of hooks per diaspore	Weight (grams)
ls - Length of hook (mm)	Length (cm)
db - Basal diameter of hook (mm)	Width (cm)
dd – Distal diameter of hook (mm)	Shape (scale 1-4)
dh – Diameter of hook (apex of "bend") (mm)	Height above ground level (cm)
lh – Length of hook ("bend" part) (mm)	Distance from main stem (cm)
sh – Hook span (mm)	Number of seeds per diaspore
hp – Presence of absence of bristles	

Substrate Analysis

Six characteristics were used to describe the substrates (Table 2). Five points on each mammalian pelt (one pelt per mammal species) were randomly determined, and at each point the characteristics in Table 2 were measure and a mean value for each characteristic was generated. Pile was a measurement from the skin of the animal to the top of the "hair level," giving a "depth" of fur measurement. The height of the animal was taken as the distance from mid leg to the top of the back. Hair densities were determined by placing a 1 cm^2 wire frame on the random points and counting the number of hairs in the frame.

Experimental design

Table 3 shows the plants and substrates that were tested experimentally, i.e. each plant species was tested against each substrate. Two experiments were designed to mimic a mammal's encounter with a burr-bearing plant. First, the efficiency by which diaspores became attached to the animal was examined (Experiment 1), and second, the strength of that attachment was measured (Experiment 2). Each treatment combination (plant species /substrate) was replicated four times (i.e. $n = 4$) in each experiment.

Experiment 1. The attachment phase of epizoochory - diaspore adhesion.

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 potential dispersal vector and a burr-bearing plant.

Table 2. Variables measured for the substrate analysis

Hair Characteristics	Substrate Characteristics
Guard-hair length (cm)	Guard-hair density (hairs/cm^2)
Undercoat hair length (cm)	Undercoat hair density (hairs/cm^2)
Height of animal (cm)	Pile (cm)

Table 3. Burr-bearing plant species and substrates investigated in Experiments 1 and 2

Plant Species	Substrates
Anemone canadensis (Canada anemone)	*Peromyscus maniculatus* (Deer mouse)
Arctium minus (Common burdock)	*Procyon lotor* (Raccoon)
Bidens vulgata (Beggars ticks)	*Odocoileus virginianus* (White tailed deer)
Geum aleppicum (Yellow avens)	*Ursus americanus* (Black bear)
Glycyrrhiza lepidota (Wild licorice)	*Bos bison* (American bison)
Lappula echinata (Stickseed)	Cotton pants
Sanicula marilandica (Black snakeroot)	
Xanthium strumarium (Cocklebur)	

The diaspores were left on the stems in order to best mimic a natural encounter. Plant stems possessing more than ten diaspores each were randomly chosen from the sample. For each plant-substrate combination, a plant stem with a known number of diaspores was brushed along a pelt in the direction of the hair follicles. It was then passed in the opposite direction (i.e. against the hair follicles). This process was repeated so that four passes were made for each stem of each plant species and substrate type. After each pass, the stem was rotated 180° degrees (rotated a total of 4 times), to ensure an equal opportunity for all the diaspores to disperse onto the substrate. All plant species-substrate trials were randomly arranged to acknowledge potential bias through "experimental" experience. A different plant stem was used for each plant-substrate replication. The number of diaspores which adhered to the substrate was counted after each of four passes and a percentage adherence value calculated.

The experimental substrate area was 25 cm × 10 cm for each fur/clothing type. The briskets (lower front portions) of the mammalian substrates, and the lower portions of the pant legs were designated areas for diaspore exposure. The mouse pelt substrate required a different methodology due to its relatively small size. In this case, both sides and the back of the pelt were considered as the experimental surface. The furs were vertically fixed to the shaking device to prevent the loss of diaspores prior to agitation (Experiment 2) and to eliminate the transportation of substrates with attached diaspores to the shaking apparatus.

Experiment 2. The transportation phase of epizoochory – diaspore retention.

The ability of burrs to be transported on (i.e. retained by) pelts of animals or clothing was tested using a shaker table. To do this, each substrate from the proceeding experiment with its attached diaspores (from Experiment #1) was fixed by means of straps to an aluminum frame mounted on the shaker table and agitated for 180 seconds at 2.63 oscillations per second. Agitation was stopped after

5, 15, 30 60, and 180 seconds (cumulative) to count the diaspores that still remained attached and those that had become detached. The mean percentages of seeds adhering to each substrate per time from these data were then calculated.

Statistical Analysis

The preliminary diaspore and substrate analysis was accomplished through the k-means clustering procedure upon the means of characteristics for the diaspores and substrates. The resulting clusters were preset to five clusters for both plant diaspores and substrates. A sixth group (cotton pants) was added later as it possessed few of the characteristics that had been observed in the mammalian furs. Therefore, the human clothing was not part of the analysis experienced by the rest of the substrates.

Non-parametric statistics were employed in the analyses of the adherence and retention data due to the lack of normal distributions, and also because the sample size was small. Various methods of standardization were attempted without success. Non-parametric statistics included; the Kruskal-Wallis test for significance (adherence and retention percentages), and the Mann-Whitney U-test (to check significant differences between two samples). The latter was used like a pos-hoc test equivalent (Sheskin, 1997). The acceptable level of significance for the Kruskal-Wallis and the Mann-Whitney U-test was set at $\alpha = 0.05$. Spearman's correlation coefficients (r_s) were determined in order to examine associations between fur type and plant species. These correlations were two-tailed tests and utilized both $\alpha = 0.05$ and $\alpha = 0.01$ levels of significance.

Results

Diaspore and Substrate Analysis

Table 4 shows the mean values of the measured diaspore characteristics relative to the largest value. The resulting clusters were strongly influenced by the length of hook (*ls*), and the hook span (s*h*). The members of Cluster 1 (*Anemone canadensis* cluster) contained long hooks and medium hook spans, while representatives of Cluster 2 (*Bidens vulgata* cluster) had shorter hooks, with moderate hook span*s*. Cluster 3 (*Lappula echinata* cluster) contained plant species with short hooks, and short hook spans. The sole member of Cluster 4 (*Arctium minus* cluster) had long hooks and medium hook span*s*. Finally, Cluster 5 (*Xanthium strumarium* cluster) had medium hooks lengths, and large hook spans. Table 5 shows the final cluster centers for each of the five groupings of diaspores.

The mean values of the measured substrate characteristics are shown in Table 6a. The final cluster center locations for the k-mean cluster analysis on the substrates are also located in Table 6b. Cluster 1 (bison cluster) contained mammals with long guard hairs, and dense undercoat*s*. The bison is the lone member of this cluster. Cluster 2 (bear cluster) had the longest hair length*s*, and the most dense undercoat hair counts, these criteria were met by the black bear. Cluster 3 (deer cluster) were animals with moderated hair lengths and low undercoat densities, and was comprised of elk and deer. Cluster 4 (mouse cluster) containing the mouse, chipmunk, and ground squirrel, shared the traits of very short hair measurements and thin undercoats. Cluster 5 (raccoon cluster) was composed of the fox, skunk, raccoon, hare, and wolf. These five mammals had moderate hair lengths and moderate undercoat densities. Finally, cluster 6 was comprised solely of the cotton pants. This category was added as representative of human clothing. Cotton pants were not included in the cluster analysis because human clothing did not possess many of the characteristics recorded for the other substrates.

Table 4a. Mean values and standard deviations of diaspore characteristics ($n = 5$)

Species	Weight (grams)	Length (cm)	Width (cm)	Shape (scale 1-4)	Height off ground(cm)	Distance from main stem(cm)	Seed Number (#/diaspore)	Quantity of hooks (# hooks/diaspore)
Anemone canadensis	0.004 (±0.001)	7.340 (±1.050)	3.160 (±0.763)	2.000 (±0)	27.300 (±4.817)	2.600 (±0.418)	1.000 (±0)	1.000 (±0)
Bidens vulgata	0.004 (±0.001)	9.420 (±1.397)	3.480 (±0.402)	4.000 (±0)	70.200 (±3.033)	7.900 (±2.509)	1.000 (±0)	2.000 (±0)
Lappula echinata	0.004 (±0.001)	2.520 (±0.148)	1.720 (±0.192)	2.000 (±0)	63.150 (±8.695)	25.060 (±6.301)	4.000 (±0)	115.200 (±28.899)
Arctium minus	0.431 (±0.089)	14.540 (±0.953)	14.840 (±0.907)	1.000 (±0)	91.400 (±10.784)	67.200 (±8.228)	37.600 (±3.781)	168.600 (±25.589)
Glycrrhiza lepidota	0.085 (±0.026)	17.620 (±4.704)	7.040 (±0.336)	3.000 (±0)	44.200 (±19.32)	9.200 (±3.033)	4.000 (±1.224)	111.000 (±33.444)
Xanthium strumarium	0.221 (±0.036)	19.600 (±0.943)	7.240 (±0.404)	3.000 (±0)	32.000 (±3.391)	23.200 (±1.924)	2.000 (±0)	110.200 (±14.481)
Geum aleppicum	0.003 (±0.002)	9.360 (±0.586)	1.400 (±0.200)	4.000 (±0)	58.000 (±5.395)	7.600 (±1.816)	1.000 (±0)	1.000 (±0)
Sanicula marilandica	0.017 (±0.002)	5.280 (±0.217)	4.080 (±0.517)	2.000 (±0)	41.800 (±3.563)	4.860 (±0.336)	2.000 (±0)	59.800 (±9.705)

Table 4b. Mean values and standard deviations of diaspore characteristics relative to the largest value ($n = 5$)

Species	ls (µ)	db (µ)	dd (µ)	dh (µ)	lh (µ)	sh (µ)	hp (present/absent)
Anemone canadensis	2548.343 (±1202.928)	558.789 (±215.832)	110.625 (±84.581)	105.626 (±89.290)	285.011 (±173.621)	171.680 (±126.621)	1.000 (±0)
Bidens vulgata	4077.681 (±121.429)	537.075 (±91.797)	168.689 (±40.776)	55.902 (±12.054)	113.058 (±39.377)	136.355 (±43.859)	0.000 (±0)
Lappula echinata	776.620 (±126.92)	129.839 (±47.208)	52.580 (±9.706)	27.657 (±9.038)	52.401 (±22.041)	38.404 (±12.338)	0.000 (±0)
Arctium minus	4898.463 (±452.336)	349.032 (±63.372)	183.246 (±27.307)	107.465 (±17.380)	198.933 (±58.076)	171.218 (±42.999)	0.000 (±0)
Glycrrhiza lepidota	2957.854 (±345.220)	538.643 (±341.059)	136.120 (±24.774)	108.188 (±25.021)	136.125 (±3.409)	172.145 (±97.658)	0.000 (±0)
Xanthium strumarium	2071.736 (±371.076)	332.160 (±79.509)	139.001 (±23.219)	94.226 (±20.537)	295.594 (±104.519)	363.934 (±59.279)	1.000 (±0)
Geum aleppicum	4905.377 (±180)	369.280 (±34.596)	88.795 (±15.450)	78.597 (±18.298)	162.762 (±32.019)	121.930 (±13.499)	1.000 (±0)
Sanicula marilandica	1782.675 (±331.442)	241.362 (±62.433)	99.026 (±8.331)	80.323 (±10.579)	158.304 (±32.247)	63.680 (±45.747)	0.000 (±0)

Table 5. Final cluster centers for diaspore k-means cluster groupings showing relative distances

	Clusters				
Variable	***Anemone canadensis* Cluster**	***Bidens vulgata* Cluster**	***Lappula echinata* Cluster**	***Arctium minus* Cluster**	***Xanthium strumarium* Cluster**
Weight	0.01	0.10	0.02	1.00	0.51
Length	0.43	0.69	0.02	0.74	1.00
Width	0.15	0.35	0.02	1.00	0.49
Shape	0.75	0.88	0.05	0.25	0.75
Height off ground	0.47	0.63	0.57	1.00	0.35
Distance from stem	0.08	0.13	0.22	1.00	0.35
Number of seeds	0.03	0.07	0.08	1.00	0.05
Hook number	0.01	0.34	0.52	1.00	0.65
ls	0.76	0.72	0.26	1.00	0.42
db	0.83	0.96	0.33	0.63	0.59
dd	0.54	0.83	0.41	1.00	0.76
dh	0.85	0.76	0.50	0.99	0.87
lh	0.76	0.42	0.36	0.67	1.00
sh	0.40	0.42	0.14	0.47	1.00
hp	1.00	0.00	0.00	0.00	1.00

Table 6. Mean and standard deviations of substrate characteristics ($n = 5$)

Mammal	**Guard-Hair Length (cm)**	**Undercoat Hair Length (cm)**	**Guard-Hair Density (hairs/cm^2)**	**Undercoat Density (hairs/cm^2)**	**Pile (cm)**	**Height $n = 1$ (cm)**
American Bison	5.00 (±0.935)	2.70 (±0.447)	103.00 (±8.366)	218.00 (±21.679)	2.40 (±0.707)	115.00
Black Bear	9.52 (±0.823)	5.90 (±0.367)	133.00 (±8.366)	223.00 (±19.875)	6.08 (±0.884)	75.00
White-Tailed Deer	4.30 (±0.464)	0.96 (±0.288)	181.00 (±6.519)	13.00 (±7.583)	3.38 (±0.432)	80.00
Elk	5.98 (±1.146)	0.76 (±0.206)	125.40 (±17.511)	61.00 (±13.565)	2.00 (±0.787)	95.00
Red Fox	5.38 (±1.672)	2.48 (±0.672)	86.80 (±10.010)	159.00 (±60.183)	3.62 (±1.139)	7.50
Skunk	2.11 (±0.432)	1.15 (±0.130)	80.80 (±7.572)	124.40 (±10.299)	1.17 (±0.114)	7.00
Raccoon	5.10 (±0.489)	2.76 (±0.336)	59.00 (±19.209)	145.20 (±41.294)	1.80 (±0.339)	6.00
Snowshoe Hare	3.48 (±0.396)	1.16 (±0.462)	106.00 (±5.477)	191.00 (±18.166)	0.80 (±0.158)	3.75
Deer Mouse	0.80 (±0.071)	0.00 (±0)	146.00 (±16.733)	0.00 (±0)	0.22 (±0.130)	2.13
Wolf	3.37 (±2.141)	1.51 (±0.638)	95.72 (±24.489)	123.92 (±10.839)	1.52 (±0.952)	35.00
Chipmunk	0.94 (±0.253)	0.54 (±0.088)	69.00 (±12.980)	97.00 (±18.695)	0.52 (±0.094)	2.25
Ground Squirrel	0.99 (±0.152)	0.58 (±0.144)	81.80 (±14.704)	59.80 (±11.032)	0.33 (±0.118)	6.00

Table 7. Final cluster centers for substrate k-means cluster groupings showing relative distances

	Cluster				
Variable	**Bison Cluster**	**Bear Cluster**	**Deer Cluster**	**Mouse Cluster**	**Raccoon Cluster**
Guard-Hair Length	0.53	1.00	0.54	0.09	0.41
Undercoat Length	0.46	1.00	0.15	0.06	0.31
Guard-Hair Density	0.57	0.73	0.85	0.55	0.48
Undercoat Density	0.98	1.00	0.17	0.23	0.67
Pile	0.39	1.00	0.45	0.06	0.29
Height	1.00	0.65	0.76	0.03	0.10

Mean diaspore adherence and retention

Mean percentages of diaspores adhering to the substrates were calculated from the adherence data (Experiment 1). Table 7 shows these mean values with their standard deviations. The highest percentage of diaspores adhering to a substrate was seen in the adherence of *L. echinata* on bison fur. A mean of 82.15% of the diaspores adhered to the substrate, off of the stem. The lowest adherence percentages were observed in the *X. strumarium* on mouse fur trials. Only 1.19% of the diaspores adhered to the mouse fur. The percentage of seeds retained by the substrates after agitation (Experiment 2) is reported in Table 8. The largest mean percent retention of diaspores was observed in the bison's complete retention of *A. minus* (100% mean retention). The smallest percent of diaspores retained by a substrate was 0% retention, and was achieved by the following pairs: *A. canadensis* on mouse and bison fur, *A. minus* of mouse fur, *G. lepidota* on mouse fur, *S. marilandica* on deer fur, and finally *X. strumarium* on mouse fur.

Diaspore and substrate correlations

Table 9 shows the Spearman correlation coefficients for the adherence percentages of the plant species, with the 5 characteristics of the substrates. Those values that were significant have their corresponding level of significance shown ($p<0.05$ and $p<0.01$; see Table 9). Particular attention was given to the correlation coefficients of the two substrate characteristics which were considered important for the clustering of the substrates (guard-hair length and under-coat density). The most important features of this series of correlations are those correlations of the plant species adherences to the density of undercoat hairs.

Table 8. Mean percent adherence and standard deviation of diaspores on six substrates ($n = 4$)

	Anemone canadensis	*Arctium minus*	*Bidens vulgata*	*Geum aleppicum*	*Glycyrrhiza lepidota*	*Lappula echinata*	*Sanicula marilandica*	*Xanthium strumarium*	Kruskal-Wallis p-value
Raccoon	19.2995^{A} (±13.4295)	74.1247^{B} (±19.7624)	24.0551^{A} (±13.1940)	36.9898^{AB} (±28.5126)	16.4322^{A} (±5.3091)	69.5608^{B} (±30.8787)	17.9825^{A} (±11.8760)	29.9271^{A} (±22.3878)	0.009
Bear	12.0245^{A} (±6.8152)	27.0735^{A} (±29.4549)	22.7617^{A} (±19.9392)	20.5204^{A} (±6.1195)	14.6784^{A} (±9.1437)	23.3517^{A} (±17.6701)	23.9354^{A} (±19.9002)	20.6735^{A} (±11.8199)	0.948
Mouse	25.3559^{A} (±12.3662)	14.1667^{A} (±18.9297)	16.4773^{A} (±16.8860)	15.1264^{A} (±9.4420)	5.2350^{A} (±7.2555)	9.3750^{A} (±11.9678)	1.92308^{A} (±3.8462)	1.19048^{A} (±2.3810)	0.057
Bison	24.4745^{A} (±15.0685)	64.3304^{BC} (±15.9055)	34.0063^{AB} (±18.2487)	46.4781^{ABC} (±34.5218)	29.3276^{AB} (±22.4265)	82.1496^{C} (±16.1644)	33.7843^{AB} (±10.3780)	33.1753^{AB} (±11.5015)	0.030
Deer	8.1755^{A} (±5.6272)	37.9486^{B} (±14.5798)	15.2533^{A} (±8.2858)	30.4786^{AB} (±22.7887)	10.5103^{A} (±4.7878)	76.3971^{C} (±16.9475)	9.96504^{A} (±14.5165)	17.8260^{AB} (±12.8038)	0.009
Pants	16.4861^{AB} (±10.7736)	48.5417^{BC} (±35.8648)	43.4724^{BC} (±16.1890)	32.4696^{BC} (±10.6843)	4.3507^{A} (±4.2076)	68.2195^{C} (±26.7129)	18.4295^{B} (±6.3347)	13.6809^{AB} (±7.0822)	0.002

Substrate adherence percentages followed by a different letter in the neighboring columns are significantly different, Mann-Whitney-U test ($p<0.05$)

Table 9. Mean percent retention and standard deviation of plant diaspores after agitation ($n = 4$)

	Anemone canadensis	*Arctium minus*	*Bidens vulgata*	*Geum aleppicum*	*Glycyrrhiza lepidota*	*Lappula echinata*	*Sanicula marilandica*	*Xanthium strumarium*	Kruskal-Wallis p-value
Raccoon	35.4167^{A} (±41.0369)	4.1667^{AB} (±8.33333)	80.0595^{B} (±21.8947)	67.4978^{B} (±14.3228)	59.1667^{B} (±33.3750)	76.5901^{B} (±21.7163)	87.5000^{B} (±25.0000)	52.5000^{B} (±27.6720)	0.042
Bear	16.6667^{A} (±33.3333)	75.0000^{AB} (±50.0000)	91.6667^{B} (±16.6667)	82.3813^{AB} (±19.0452)	90.6250^{B} (±18.7500)	91.3961^{B} (±12.8933)	50.0000^{AB} (±43.0331)	75.0000^{AB} (±28.8675)	0.012
Mouse	0.0000^{A} (±0.0000)	0.0000^{A} (±0.0000)	17.5000^{A} (±23.6291)	87.3016^{B} (±14.8902)	0.0000^{A} (±0.0000)	33.3333^{A} (±47.1405)	25.0000^{A} (±50.0000)	0.0000^{A} (±0.0000)	0.011
Bison	0.0000^{A} (±0.0000)	100.0000^{C} (±0.0000)	79.1667^{BC} (±15.9571)	94.0385^{BC} (±9.5330)	93.7500^{BC} (±12.5000)	75.0379^{B} (±15.5972)	95.0000^{BC} (±10.0000)	88.8889^{BC} (±15.7135)	0.008
Deer	31.2500^{AB} (±47.3242)	58.8889^{B} (±43.2620)	35.0000^{AB} (±27.4199)	58.8175^{B} (±34.7171)	85.4167^{B} (±17.1796)	53.3654^{B} (±12.0424)	0.0000^{A} (±0.0000)	64.8810^{B} (±25.4495)	0.042
Pants	25.0000^{A} (±50.0000)	75.0000^{A} (±50.0000)	31.9478^{A} (±18.8887)	32.0742^{A} (±22.2526)	8.3333^{A} (±16.6667)	68.9583^{A} (±30.1645)	25.0000^{A} (±50.0000)	37.5000^{A} (±47.8714)	0.246

Substrate retention percentages followed by a different letter in the neighboring columns are significantly different, Mann-Whitney-U test ($p<0.05$)

Table 10. Spearman correlation coefficient values (r_s) for percent adherences and substrate characteristics ($n = 6$)

Plant Species	Hair Characteristic				
	Guard-hair length	Undercoat hair length	Guard-hair density	Undercoat hair density	Pile
Anemone canadensis	-0.200	-0.290	-0.200	-0.232	-0.543
Lappula echinata	0.143	0.203	-0.086	0.319	0.257
Bidens vulgata	-0.143	-0.029	-0.943**	0.029	-0.486
Arctium minus	0.200	0.290	-0.657	0.232	-0.143
Glycyrrhiza lepidota	0.771	0.754	-0.029	0.812*	0.543
Xanthium strumarium	0.714	0.754	-0.257	0.812*	0.486
Geum aleppicum	0.143	0.232	-0.600	0.290	-0.086
Sanicula marilandica	0.429	0.522	-0.486	0.696	0.314

* Correlation is significant at the 0.05 level (2-tailed)
** Correlation is significant at the 0.01 level (2-tailed)

Table 10 contains the results of a series of correlations between the retention percentages of diaspores by the substrates and the 5 substrate characteristics. Particular attention was again given to the characteristics, which played a significant role in the clustering of the substrates (guard-hair length and undercoat density). The change in correlations from the adherence data to the retention data was noted. In the adherence data, only 3 significant correlations were found, while in the retention data 4 significant correlations were found. This observation may have implications on the various roles which adherence and retention play in diaspore dispersal.

Another series of correlations were performed on the adherence and retention data and the 15 measured characteristics of the diaspores. Table 11 shows the correlations with the adherence data, while Table 12 shows the correlations with the detachment data.

Variables of particular interest were the hook length, and hook span of the diaspores, as these variables were responsible for the segregation of the plant diaspores into their respective groupings. There were no significant correlations between adherences and hook length, and only one significant correlation between percent adherence and hook spans of the diaspores (pants; r_s= -0.738). Surprisingly, only human clothing was found to be significantly correlated with hook span in the adherence data (r_s =-0.738). The retention data however showed a significant correlation with human clothing and hook span again (r_s =-0.762), but also with mouse fur and hook span (r_s =-0.862).

Upon completion of the Spearman correlations, it was noticed that the raccoon and mouse fur were not significantly correlated between any characteristics of the diaspores with respect to their adherence data. In the retention data however, raccoon fur was only correlated (r_s =-0.762) with one variable (dh- diameter of hook, see Figure 1). Mouse fur was significantly correlated with hook diameter (r_s =-0.710) and hook span (r_s =-0.862).

Table 11. Spearman correlation coefficient values (r_s) for percent retention and substrate characteristics ($n = 6$)

Plant Species	Hair Characteristic				
	Guard-hair length	Undercoat hair length	Guard-hair density	Undercoat hair density	Pile
Anemone canadensis	0.435	0.485	-0.029	0.221	0.319
Lappula echinata	0.371	0.493	-0.543	0.551	0.257
Bidens vulgata	0.943**	0.986**	-0.143	0.928**	0.714
Arctium minus	0.493	0.559	0.058	0.765	0.725
Glycyrrhiza lepidota	0.486	0.522	0.200	0.696	0.714
Xanthium strumarium	0.657	0.696	0.086	0.870*	0.771
Geum aleppicum	0.600	0.522	0.200	0.696	0.486
Sanicula marilandica	0.086	-0.029	-0.029	-0.029	-0.257

* Correlation is significant at the 0.05 level (2-tailed)
** Correlation is significant at the 0.01 level (2-tailed)

Table 12. Spearman correlation coefficients (r_s) for percent adherence and diaspore characteristics ($n = 8$)

	Raccoon	Bear	Mouse	Deer	Bison	Pants
Weight	0.024	0.390	-0.586	0.049	-0.122	-0.224
Length	-0.071	-0.190	-0.286	0.000	-0.333	-0.524
Width	-0.048	0.357	-0.500	-0.048	-0.190	-0.286
Shape	-0.247	-0.469	0.111	-0.074	-0.148	-0.272
Height	0.595	0.619	0.214	0.690	**0.610***	**0.762***
Dist. Stem	0.643	0.524	-0.357	**0.810***	0.595	0.405
Seed No.	0.284	0.531	-0.519	0.469	0.358	0.185
Hook No.	0.371	0.599	-0.503	0.563	0.443	0.287
ls	0.214	-0.143	0.500	0.119	0.095	0.048
db	-0.452	**-0.739***	0.619	-0.571	-0.643	-0.476
dd	0.048	0.190	0.048	-0.071	-0.167	-0.119
dh	-0.333	-0.262	-0.143	-0.361	-0.571	-0.619
lh	-0.071	-0.238	-0.071	-0.238	-0.452	-0.452
sh	-0.286	-0.500	-0.143	-0.333	-0.690	**-0.738***
hp	-0.056	-0.620	-0.169	-0.169	-0.394	-0.394

* Correlation is significant at the 0.05 level (2-tailed)

** Correlation is significant at the 0.01 level (2-tailed)

Table 13. Spearman correlation coefficients (r_s) for percent retention and diaspore characteristics ($n = 8$)

	Raccoon	Bear	Mouse	Deer	Bison	Pants
Weight	-0.439	0.049	-0.572	0.561	0.366	0.000
Length	-0.476	0.214	-0.685	0.667	0.310	-0.524
Width	-0.405	0.095	-0.583	0.500	0.381	-0.071
Shape	0.383	0.148	0.197	-0.037	-0.062	-0.432
Height	0.048	**0.952****	0.140	0.333	0.405	0.643
Dist. Stem	-0.286	0.619	-0.330	**0.786***	0.262	0.452
Seed No.	-0.334	0.272	-0.276	0.692	0.358	0.371
Hook No.	-0.252	0.371	-0.287	0.695	0.263	0.455
ls	-0.381	0.619	-0.165	0.238	0.548	-0.214
db	-0.476	-0.095	-0.507	0.024	-0.190	**-0.762***
dd	-0.429	0.318	-0.647	0.357	0.238	-0.143
dh	**-0.762***	-0.190	**-0.710***	0.476	0.310	-0.571
lh	-0.571	-0.333	-0.482	0.024	0.167	-0.405
sh	-0.643	-0.214	**-0.862****	0.476	-0.048	**-0.762***
hp	-0.282	-0.394	-0.180	-0.169	-0.169	-0.507

* Correlation is significant at the 0.05 level (2-tailed)

** Correlation is significant at the 0.01 level (2-tailed)

Discussion

Van der Pijl's (1969) definition of epizoochory (once known as exozoochory) is that it is one of several classes of animal dispersal, or zoochory, in which the diaspores are accidentally carried on the outside of the animal. Epizoochorous diaspores usually possess hooks, spines or some form of stickiness. The hooks of diaspores may have been derived from wings, or even protective spines (Dansereau and Lemms 1957). There are many examples in which the division between the wing of an anemochore (wind dispersed diaspore), or a protective spine, is not distinct from the hooking mechanism of an epizoochore (Dansereau and Lemms 1957, van der Pijl 1969). This blurred distinction is exemplified by several taxa in the present study, i.e. *Arctium minus* and *Xanthium strumarium*. Similarly, the diaspores of *Anemone canadensis* are partially winged, thus making the achenes both functional anemochores and epizoochores.

It is difficult to enumerate Manitoban taxa that can be described as truly epizoochorous, because of the ambiguity of the function of elongated and persistent stigmas (i.e. many *Carex* spp), or the function of long awns in many grasses (i.e. *Stipa* spp.). All taxa in the present study possess hooked diaspores that are undeniably used in epizoochory, even so the morphology, number, size and placement of the hooks on the fruit or infructescence is extremely variable. This study attempted to answer the question of whether different diaspore morphologies in common Manitoba plant species are specifically adapted to specific types of fur, and thus to specific kinds of mammals found in the habitats of the plants.

Epizoochorous Diaspore Syndromes

The first objective of this study was to determine whether certain epizoochorous characteristics tended to be associated with each other. If so, these clusters of characteristics may represent epizoochorous syndromes, each of which is specifically adapted to particular fur or substrate type. Five clusters, i.e. groupings of plant species, with similar epizoochorous features are shown in Table 13 and are described as follows: The "Canada anemone group"; taxa which possess long hooks with medium hook spans, i.e. *Anemone canadensis* and *Geum aleppicum.* Both of these species have long single hooks that are derived from very long persistent styles. Curiously both genera also possess members which are anemochorous, i.e. *A. cylindrical*, *G. triflorum*. The "Beggar's ticks group"; taxa which possess short hooks with small hook spans, i.e. *Bidens vulgata* and *Glycyrrhiza lepidota.* This grouping of species was unexpected because their diaspores appeared to be morphologically different, except for comparable hook length and hook span measurements. The diaspores of *B. vulgata* usually possess a pair of terminal hooks from the tip of each achene, whereas that of *G. lepidota* is a modified pod, which is covered with hooks. The hook lengths in this grouping were approximately 40% of that of the longest hooked species, *Geum aleppicum*. The "Stickseed group", taxa which possess short hooks with short hook spans i.e. *Lappula echinata* and *Sanicula marilandica.* These two species are also similar in size and shape, but differ in that *S. marilandica* is a native species, while *L. echinata* originally from Europe. The "Burdock group", possesses infructescences (not fruits) having long hooks with medium hook spans, i.e. *Arctium minus*. There is some controversy whether this is an example of epizoochory or, an example of

autochory (self-dispersal). Van der Pijl (1969) believes that the diaspores are not passively released from the parent plant, and says that the diaspore hooks onto a substrate and is only released by the spring-back movement of the parent plant. His contention is that release energy is not limited to internal tension of the diaspore but the plant itself provides energy for the action. My studies support the argument of Ridley (1930) that the diaspores are epizoochorous, i.e. they are released without such a spring-back mechanism. The fifth syndrome, the "Cocklebur group" possesses diaspores with medium hooks lengths and large hook spans, i.e. *Xanthium strumarium*. Van der Pijl (1969) described this diaspore as a "hooked involucrum" (making it similar to the diaspore of *Arctium minus*) "derived from the female inflorescence and characteristic of weedy pioneers of most Compositae".

Epizoochorous substrate syndromes

Six syndromes of substrate types were identified and are summarized in Table 14. The "Bison group"; these mammals possess long guard hairs and dense undercoats, i.e. bison (*Bos bison*). No other large extant native mammal appears to fit into this syndrome, however extinct Pleistocene camels, horses, other bison species, and perhaps even mammoths may have had similar fur characteristics. The "Black bear group" had the longest hair lengths and the most dense undercoat hair counts, i.e. the Black bear (*Ursus americanus*). This was the sole member of this cluster from this study; however, it is likely that the Grizzly bear (*Ursus horribilus* L) and perhaps Musk Ox (*Ovibos moschatus* Zimm.) would also fall into this group. Extinct bears or other large mammals may also fall into this category. The "Deer group" had moderate hair lengths and low undercoat fur densities, i.e. elk (*Cervus elaphus*) and white-tailed deer (*Odocoileus*

Table 14. Five epizoochorous diaspore syndromes identified in this study

"Canada anemone group"	"Beggars ticks group"	"Stickseed group"	"Burdock group"	"Cocklebur group"
Anemone canadensis (Canada anemone)	*Bidens vulgata* (Beggars ticks)	*Lappula echinata* (Stickseed)	*Arctium minus* (Burdock)	*Xanthium strumarium* (Cocklebur)
Geum aleppicum (Yellow avens)	*Glycyrrhiza lepidota* (Wild licorice)	*Sanicula marilandica* (Black snakeroot)		

Table 15. Six epizoochorous substrate syndromes identified in this study

Bison group	Black bear group	White-tailed Deer group	Mouse group	Raccoon group	Clothing group
Bos bison (American Bison)	*Ursus americanus* (Black bear)	*Odocoileus virginianus* (White-tailed Deer)	*Peromyscus maniculatus* (Deer mouse)	*Vulpes vulpes* (Red Fox)	Cotton Pants
		Cervus elaphus (Elk)	*Tamias minimus* (Least Chipmunk)	*Mephitis mephitis* (Striped skunk)	
			Spermophilus richardsonii (Richardson's Ground squirrel)	*Procyon lotor* (Raccoon)	
				Lepus americanus (Snowshoe hare)	
				Canis lupus (Grey Wolf)	

virginianus). Other deer species and perhaps pronghorn antelopes (*Antilocapra Americana* Ord) are likely to fit into this grouping. The "Mouse group" was characterized as having very short hair measurements and thin undercoats, i.e. deer mouse (*Peromyscus maniculatus*), least chipmunk (*Tamias minimus*) and Richardson's ground squirrel (*Spermophilus richardsonii*). These study species would likely represent other small rodents of the same genera, and hence this is quite a large group of species. The "Raccoon group" had moderate hair lengths and moderate densities of undercoats, i.e. red fox (*Vulpes vulpes*), striped skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*), snowshoe hare (*Lepus americanus*) and grey wolf (*Canis lupus*). Relatives of the snowshoe hare, i.e. Eastern cottontail (*Sylvilagus floridanus* Allen) and other species of hare or Jack rabbits (*Lepus* spp) would fall into this category. The sixth group, the "clothing group" was composed of cotton pants. It did not possess many measurable characteristics that were common to the other substrates. A study by Carlquist and Pauly (1985) showed that strand length was of great importance to attachment of diaspores to artificial substrates. They found that velvet; with a very low strand length had nearly no diaspores adhering it. The synthetic wool on the other hand (75% acetate and 25% nylon) accommodated numerous diaspores (Carlquist and Pauly, 1985). The increased affinity for diaspores was attributed to the longer strands, which were markedly curly, and gave a larger pile (3 mm) to the synthetic wool. Therefore cotton pants in this study behaved similarly to the velvet in the study by Carlquist and Pauly (1985), in regards to adhering and retaining diaspores.

It would be not unreasonable to expect domesticated mammals to also play a role in epizoochoric seed dispersal. Indeed, Janzen and Martin (1982) showed how

domesticated horses dispersed seeds on their legs in some Neotropical habitats. Thus, assuming that other such domesticated mammals, in other habitats could achieve the same result is not unreasonable. These mammals are mostly those with short guard hairs, and relatively thin undercoat densities (i.e. goats, horses, cattle). Domestic mammals are large, and much care must be taken to place them into one of the above substrate syndrome groupings. Other smaller domesticated mammals such as dogs and cats can be placed into a number of different substrate syndrome categories. Almost all substrate syndromes may have domestic representatives because of fur variation amongst so many breeds of domestic pets.

Correlations between diaspore and fur characteristics

I hypothesized that the characteristics of certain diaspores would make them more susceptible to dispersal by certain groups of animals. To test this, specific diaspore and substrate characteristics were examined for significant correlations in both the adherence and retention data (Tables 9 through 12).

The height of the diaspore presentation above the ground was associated with the size of the animal species for bison fur and pants in the adherence data, and only bears fur in the retention data. Diaspores of taller plants (i.e. *A. minus* and *G. lepidota***)** adhered better to these large animals (bison and pants); on the other hand, no association between shorter plants and smaller mammals was observed. Retention of diaspores by furs after their initial adherence was shown in only one association between bear fur and diaspore presentation height. This suggested that diaspore retention may be more tolerant of a wider range of diaspore presentation types than the process of adherence. These findings supported those of Fischer *et al*. (1996). They determined that the height of

diaspore presentation was "…of prime importance for the attachment of diaspores…" (Fischer *et al*, 1996).

Correlations between other diaspore characteristics and adherence data provided other noteworthy findings. First, the deer fur had significantly positive correlations between adherence percentages and the distance the diaspore was presented away from the main stem. This correlation was repeated for the same variable in the retention data for the deer fur. This suggests that that diaspores presented further away from the main stem (i.e. *A. minus*) adhere to and are held more tightly than those closer to the main stem of the plant (i.e. *S. marilandica*).

Human clothing displayed a different trend as a substrate with respect to dispersal of plant diaspores. In the adherence data, there were two negative correlations, one with the hooks basal diameter, and the other with hook span. The retention data however had a positive correlation with plant height, and hook span continued to be negatively correlated. This may indicate that diaspores with thin basal portions of their hooks and small hook spans (i.e. *L. echinata* and *B. vulgata*) adhere best to pants, while tall plant diaspores with short hook spans (i.e. *B. vulgata*) are better retained by the plants. That being said, diaspores of *Bidens vulgata* adhered best to pants (44% adherence) but only 32% were later retained. Vibrans (1999) found that farmers clothing was the principal long-distance dispersal vector for three species of *Bidens* (*B. odorata*, *B. ferulifolia*, and *B. ballsii*) in rural Mexico. The diaspores of *Bidens spp* may not have evolved to disperse on human clothing, but appear to be equipped sufficiently to take advantage of human movement for dispersal.

There were no other meaningful correlations between the adherence/retention data and individual diaspore characteristics that would suggest the presence of dispersal strategies.

Correlations between the substrates and diaspore characteristics provided evidence that diaspore retention was more flexible than adhesion with respect to the diaspore characteristics. Correlation analyses for adherence and retention data with respect to the plant species and the substrate characteristics revealed that undercoat density were of particular importance to *X. strumarium*. Diaspores of *G. lepidota* and *X. strumarium* showed significantly positive correlations between undercoat density and adherence. However, only *X. strumarium* preserves this correlation in the retention data. The importance for a thick undercoat density for *X. strumarium* may be found in the fact that *X. strumarium* had the largest hook spans of all the study species. An increased density may be sufficient to "fill up" this extra space. This statement is supported by the relatively high adherence and retention values shown b bison and black bear fur for the diaspores of *X. strumarium*.

An ecologically interesting relationship exists between the significant correlations of adherence and retention for the diaspores of *B. vulgata* with respect to substrate characteristics. The adherence data and density of guard hairs showed a strong negative correlation. However, that correlation was lost in the retention data. In place of that relationship were three correlations with guard hair length, undercoat length, and undercoat density. This suggested that diaspores of *B. vulgata* adheres best to furs with thick, dense guard hair, but is best retained by substrates with long guard hairs and long, thick undercoat hair. The explanation for this may be found in the morphology of the

fruits of *B. vulgata*. These are flat, but have two long spines with apical hooks. A fur type with low guard hair density would allow penetration of these hooked spines with minimal resistance. Then in the retention of *B. vulgata*, a thick undercoat would supply a suitable medium for dispersal, while the long guard and undercoat hairs press against the flat surfaces of the diaspore, thus stabilizing the propagule.

Every significant correlation between guard-hair length, or undercoat density, and adherence or retention was positive, regardless of plant species. This indicated that longer guard hairs and denser undercoats were more suitable for dispersal of diaspores in this sample of local Manitoban plant species.

Specialist and generalist dispersers and diaspores

There were no indications of any obvious special substrate-diaspore type relationship in this study. A specialist disperser would have displayed a high affinity ("faithfulness") to a particular substrate, either in the adhesion, retention, or both stages of dispersal. No such trend was observed in this study.

Bison fur showed the highest levels of both adherence and retention for most of the plant diaspores (see Table 7 and 8). In fact, when bison fur was not the first best adhering substrate (i.e. had the highest percent adherence of diaspores for that species compared to the other substrates), it was the second best. This result may be indicative of bison being a generalist dispersal agent. This brings to question the importance and effect that the extirpation of bison may have had on populations of adhesively dispersed plants. This question deserves further investigation.

Native vs. nonnative plant species

The two non-native plant species (*A. minus* and *L. echinata*) had higher average adherence percentages than the native species. This is likely an example of the "invasiveness" of these two taxa. Successful adherence to a wide variety of substrates means that there are more prospective dispersal vectors and a corresponding high potential for colonization and invasion.

Conclusions

1) Groupings of similar fur substrates and groupings of similar plant diaspores were achieved by k-means cluster analysis**.** Plant species principally became grouped according to the lengths and spans of the hooks on their diaspores. The groupings of fur substrates were determined largely on the basis of guard-hair length and the density of the undercoat fur.

2) Correlation coefficients were carried out between adherence and retention of diaspores with the substrate and diaspore characteristics. These correlations revealed that undercoat densities of the substrates were positively correlated with the adherence and retention data in some plant species.

3) The hook span on a diaspore played a substantial role in the adherence and retention of that diaspore according to correlations between hook span and attachment/retention data on various substrates.

4) There was no evidence to suggest a special relationship between any particular fur type or mammal species. However the role of generalist disperser may be granted to the American bison, as it was very accepting to nearly all of the plant diaspores in this study, and was also quite efficient at retaining those diaspores.

5) The diaspores of non-native plant species in this study (*A. minus* and *L. echinata*) had very different diaspore characteristics relative to each other. Despite this, they were both effective at adherence on a variety of fur types. This generalist diaspore attribute would be advantageous to their invasive life style.

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Appendix A. Information regarding the pelts loaned from the Manitoba Museum for the purpose of the experimentation described in the present study

Mammal Species	**Museum Call Number**	**Location of Capture**	**Date of Capture**	**Sex**	**Notes**
Cervis canadensis	4732	Riding Mountain park, MB	1971	female	n/a
Spermophilus richardsoni	19850507	Souris, MB	unknown	female	n/a
Tamia miniums	21492	Skidmore Lake, MB	June 18, 1999	female	non-breeding
Ursus americanus	2063	Marchand, MB	Nov. 27, 1971	female	n/a
Procyon lotor	15774	Winnipeg, MB	June 21, 1982	female	n/a
Lepus americanus	1284	Duck Mountain, MB	March 20, 1971	female	large ovary
Peromiscus maniculatus	12837	White-mouth river, MB	June 30, 1980	female	n/a
Mephitis mephitis	no data	no data	no data	no data	no data
Vlupes vulpes	15773	Glenlea, MB	Dec. 17, 1983	female	n/a
Canis lupus	409	Whiteshell Park, MB	February 1983	female	n/a
Bos bison	4735	Riding Mountain park, MB	1971	female	n/a
Odocoileus virginianus	no data	no data	no data	no data	no data