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EXPERIMENTAL STUDIES ON EPIZOOCHOROUS DISPERSAL IN  
CALIFORNIAN PLANTS

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ABSTRACT

Experiments studying degrees of adherence ability to various surfaces were undertaken with presumably epizoochorous diaspores of 14 native and eight introduced species from southern California. A commonly available laboratory shaker was modified so as to provide a standard means for dislodging diaspores from surfaces. Diaspores were dropped onto a cloth-covered board and percentages of dislodged diaspores recorded after inversion and then after intervals of shaking. Three fabrics were used: a velvet with short pile, an artificial wool with short curly strands, and a furlike fabric with straight strands. Attachment to the velvet was nil for most species, showing that a lower threshold for strand length necessary to promote attachment exists. On the artificial wool, some species tended toward brief attachment, some toward prolonged attachment, and some were intermediate. Results with the furlike fabric were similar, but a difference could be seen in that diaspores with hooklike devices adhered better to the artificial wool; a few species (notably grasses with bristly awns) showed better adherence on the furlike fabric. Diaspores were also tested on natural animal surfaces (one feather and four fur samples). Natural substrates proved comparable to artificial counterparts. Distinctive categories of diaspores are evident, based upon diaspore morphology and adherence capability. Nature of surface proves more important than weight or size of the diaspore in promoting adherence.

Key words: dispersal, epizoochory, plant dispersal, southern California flora, seed dispersal.

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INTRODUCTION

Earlier accounts of epizoochorous plants dealt with morphology of seeds and fruits. In recent years, various ways of observing interaction of diaspores of epizoochorous plants with surfaces have been undertaken in order to see if different animals are differently effective in dispersal. Falla (1960) and Merilee (1969) found that burlike fruits, such as *Acaena* (Rosaceae) and *Uncinia* (Cyperaceae) could be observed frequently on bird feathers in nature. Tomich, Wilson and Lamoureux (1968) reported that fruits of the grasses *Cenchrus echinatus* L., *Chloris inflata* Link, and *Setaria verticillata* (L.) Beauv. could be found abundantly on hair of rabbits on Manana Island, Hawaii. Much more moderate rates of epizoochory were reported by McClintock (1965) in England and Flux (1967) in New Zealand. One must note that Flux was working with a hare (*Lepus europeus* Pallas) not native to New Zealand (which lacks native terrestrial mammals), so that lack of plants adapted to epizoochory near ground level there may be expected. Agnew

and Flux (1970) recorded plant disseminules that adhered to hares (*Lepus capensis* L.) in Kenya, and found those of 17 plant species characteristically attached to fur of these animals in several localities. Biogeographically-inclined students of plant dispersal have regarded epizoochory as effective in achievement of long-distance dispersal (Ridley 1930; Carlquist 1967, 1983). However, experimental data showing adherence capabilities are needed to support these contentions.

The study by Bullock and Primack (1977) moved beyond observation of seed loads on animals into experimental work on epizoochory in a tropical area, Costa Rica. Bullock and Primack studied the height at which diaspores were shed by plants. They recorded degree of attachment to trousers, shirts, and a cloth-covered board; several habitats were compared. The studies involved three genera: *Achyranthes* (Amaranthaceae), *Bidens* (Asteraceae), and *Petiveria* (Phytolaccaceae). The relative adherence was expressed in terms of distance moved (in meters) by various disseminules in the habitats studied. Liddle and Elgar (1984) manually attached "burs" of the cocklebur (*Xanthium occidentale* Bertol., Asteraceae) to cattle, horses, and sheep. They recorded adherence times in terms of days. They also determined dispersal distances.

The present study has employed means different from those of the abovementioned investigations, and is therefore involved in different kinds of questions. We chose a selection of epizoochorous native and introduced angiosperm species from southern California (as defined by the flora of Munz 1974). All of these have mechanical devices for adherence, and species with viscid diaspores were not included. Thus, all species studied belong to the "BB" category (dry fruits bearing barbs, bristles, hooks, and like devices) of Carlquist (1967, 1983). A range of species was selected in order to test different epizoochorous disseminule designs as well as to see if relatively small interspecific differences in diaspore morphology have demonstrably different behavior. Some distinctively epizoochorous genera were not included, notably *Chorizanthe* (Polygonaceae), *Galium* (Rubiaceae), *Lappula* (Boraginaceae), and *Pectocarya* (Boraginaceae), but the present study does contain morphological equivalents to the diaspores of those genera. The following species shown in Table 1 are introduced: *Scandix pecten-veneris*, *Bidens pilosa*, *Xanthium spinosum*, *Bromus commutatus*, *B. diandrus*, *B. rubens*, and *Hordeum glaucum*. Some genera that may be epizoochorous at least in part were not included (e.g., *Cryptantha* of the Boraginaceae). However, one species not hitherto cited as epizoochorous, *Eriogonum fasciculatum*, was included because field work showed it attaches easily to some kinds of clothing. The species selected represented a probable range of adherence capability, based on the nature of diaspore surfaces.

Our study differs from that of Bullock and Primack (1977) in that we studied species of a temperate area. Our study employs a larger number of species in order to offer comparative data. An artificial, but uniform, method of measuring adherence was used, and three fabrics with a range of pile length and strand curvature were employed as surfaces. Natural surfaces from vertebrates were also used to demonstrate the comparability of fabrics with fur and feathers.

The questions we are addressing include the following:

- (1) Are some diaspores suited for particular textures (e.g., long or short pile, curved or straight strands)? For example, do some plant species evolve disseminules specifically better at attachment to curved hairs than straight hairs?

- (2) Do epizoochorous species differ in adherence ability? Do some species have diaspores adapted to adhere indefinitely, whereas other species have diaspores that tend to cling for shorter periods?
- (3) Are there correlations between diaspore morphology and the degree of adherence?
- (4) Are there correlations between diaspore morphology and texture of substrate to which adherence is maximal?
- (5) Are epizoochorous introduced weed species superior to indigenous species in adherence ability?
- (6) Are there any correlations between efficiency of epizoochorous dispersal and geographical range?
- (7) Are differences in diaspore weight and size differences within genera related to differences in dispersal ability?

By obtaining data based on the devices and species roster we employed, we believe we will contribute to design of subsequent experimental studies on epizoochory. The interest of epizoochory is furthered by the fact that such dispersal mechanisms may also be part of a mechanism for lodging of a diaspore in soil (Zohary 1959, 1960).

#### MATERIALS AND METHODS

A shaking machine to which could be attached various surfaces bearing diaspores was employed. The machine selected was a shaker commonly used for agitating solutions (the Dubnoff Metabolic Shaking Incubator available from Precision Scientific Co. of Chicago). This machine was selected because it offered a range of agitation intensity suited to dislodging diaspores from surfaces attached to it. The essential action of the shaker is a transverse movement. The shaker bears a metal tray. To this tray a plywood rectangle bearing a given fabric or animal skin sample could be attached. The plywood rectangle was the same length and width as the metal tray of the shaker. At the corners of the tray four wooden dowels were affixed. The plywood rectangle could then be attached to the dowels either with the diaspore-bearing face upwards or downwards, much like a tabletop.

For each experimental condition, the plywood rectangle was attached with its fabric- or skin-bearing surface upwards (the fabric or skin was affixed to the plywood with clips). Diaspores were dropped onto the fabric or skin from a height of 10 cm and the shaker was turned on for 10 sec. The purpose of this action was to allow diaspores to become engaged to a surface with minimal action—less force than would be involved when an animal brushes against a fruiting plant, in all likelihood. Although a very gentle way of inducing attachment of diaspores to a surface, this action did result in appreciable attachment. More forcible action resulted in such a high degree of adherence that gradations between species were not demonstrated. The action consisted of pressing a disseminule onto the surface of the substrate in a gentle manner that might simulate a chance contact between an animal and a diaspore-bearing plant. The method of dropping rather than manually placing diaspores onto a substrate was undertaken in all experiments except those reported in Table 8. We believe that the dropping technique is a useful experimental approach because it represents differences among species in adherence capability much more sensitively than does pressing diaspores against a surface (e.g., Table 8), in which case all epizoochorous species show high per-

Table 1. Characteristics of diaspores studied with respect to epizoochory.

| Species   | Diaspore type          | Weight | Length |
|---|------------------------|--------|--------|
| <b>Apiaceae</b>   |                        |        |        |
| <i>Eryngium aristulatum</i> Jeps.                                     | sharp-scaled fruit     | 1.7 mg | 2.5 mm |
| <i>E. armatum</i> (Wats.) C. & R.                                     | sharp-scaled fruit     | 1.1    | 3.0    |
| <i>Osmorhiza chilensis</i> H. & A.                                    | bristly mericarp       | 8.8    | 20.0   |
| <i>Sanicula graveolens</i> Poepp.                                     | hooked mericarp        | 4.1    | 5.0    |
| <i>S. hoffmannii</i> Munz   | hooked mericarp        | 3.0    | 5.0    |
| <i>Scandix pecten-veneris</i> L.                                      | bristly mericarp       | 20.8   | 85.0   |
| <b>Asteraceae</b>   |                        |        |        |
| <i>Ambrosia acanthicarpa</i> Hook.                                    | spinose head           | 8.1    | 10.0   |
| <i>A. chamissonis</i> var. <i>bipinnatisecta</i> (Less.) J. T. Howell | spinose head           | 13.3   | 10.0   |
| <i>A. chamissonis</i> Less. var. <i>chamissonis</i>                   | spinose head           | 11.5   | 10.0   |
| <i>A. dumosa</i> (Gray) Payne   | spinose head           | 4.6    | 8.0    |
| <i>Bidens frondosa</i> L.   | achene, barbed awns    | 2.6    | 10.0   |
| <i>B. laevis</i> (L.) BSP.  | achene, barbed awns    | 1.0    | 8.0    |
| <i>B. pilosa</i> L.   | achene, barbed awns    | 1.9    | 15.0   |
| <i>Xanthium spinosum</i> L.   | hooked head (bur)      | 46.5   | 13.0   |
| <i>X. strumarium</i> L.   | hooked head (bur)      | 167.0  | 35.0   |
| <b>Krameriaceae</b>   |                        |        |        |
| <i>Krameria parvifolia</i> Benth. var. <i>imparata</i> Macbr.         | glochidiate fruit      | 33.2   | 17.0   |
| <b>Lamiaceae</b>  |                        |        |        |
| <i>Salvia mellifera</i> Greene  | hooked calyx           | 2.6    | 8.0    |
| <b>Polygonaceae</b>   |                        |        |        |
| <i>Eriogonum fasciculatum</i> Benth.                                  | nutlet in calyx        | 1.2    | 4.0    |
| <b>Poaceae</b>  |                        |        |        |
| <i>Bromus commutatus</i> Schrad.                                      | bristly awned spikelet | 4.9    | 18.0   |
| <i>B. diandrus</i> Roth.  | bristly awned spikelet | 7.4    | 68.0   |
| <i>B. rubens</i> L.   | bristly awned spikelet | 4.5    | 40.0   |
| <i>Hordeum glaucum</i> Steud.   | awned spikelet trio    | 16.8   | 55.0   |

centages of attachment. In addition, chance contacts between animals and diaspore-bearing plants are not always forceful. Some contacts are gentle, dislodging a diaspore from the plant so that it falls onto the animal surface in a manner that may simulate the technique employed in the data of Tables 2–7. The distance of 10 cm above the substrate was used for dropping of the diaspore in those experiments because this can be considered a reasonable simulation of the distance a gently dislodged diaspore might fall before reaching an animal surface; the moderate height of the herbs studied makes the distance of 10 cm a more logical one than, say, 2 m (in which case a higher rate of attachment could doubtless have been achieved, but few of the herbs studied here are that tall). The reader must be cautioned that experimental methods for securing diaspore attachment in the experiments reported in this paper are simulations that may deviate from natural events in both degree and kind.

After the initial 10-sec agitation, the shaker was stopped and the plywood

Table 2. Affinity of diaspores to artificial fur (species listed in same order as in Table 1).

| Species                              | % dislodged during inversion | % dislodged at end of shaking interval in sec (times cumulative) |    |    |    | % not dislodged |
|--------------------------------------|------------------------------|--|----|----|----|-----------------|
|                                      |                              | 5  | 10 | 15 | 20 |                 |
| <i>Eryngium artistutatum</i>         | 43                           | 41   | 2  |    |    | 14              |
| <i>E. armatum</i>                    | 54                           | 43   | 1  | 0  | 1  |                 |
| <i>Osmorhiza chilensis</i>           | 27                           | 27   |    |    |    | 46              |
| <i>Sanicula graveolens</i>           | 44                           | 37   | 8  | 4  |    | 7               |
| <i>S. hoffmannii</i>                 | 43                           | 36   | 3  | 0  | 3  | 15              |
| <i>Scandix pecten-veneris</i>        | 66                           | 24   |    |    |    | 10              |
| <i>Ambrosia acanthicarpa</i>         | 90                           | 10   |    |    |    | 0               |
| <i>A. chamissonis bipinnatisecta</i> | 70                           | 26   | 1  | 3  |    | 0               |
| <i>A. c. chamissonis</i>             | 66                           | 29   | 2  |    |    | 3               |
| <i>A. dumosa</i>                     | 78                           | 19   |    |    |    | 3               |
| <i>Bidens frondosa</i>               | 34                           | 44   | 5  | 2  | 3  | 12              |
| <i>B. laevis</i>                     | 41                           | 47   | 2  |    |    | 10              |
| <i>B. pilosa</i>                     | 31                           | 36   | 5  | 1  |    | 27              |
| <i>Xanthium spinosum</i>             | 50                           | 36   | 6  | 0  | 2  | 6               |
| <i>X. strumarium</i>                 | 66                           | 26   | 4  | 4  |    | 0               |
| <i>Krameria parvifolia imparata</i>  | 37                           | 35   | 6  | 2  |    | 20              |
| <i>Salvia mellifera</i>              | 28                           | 55   | 5  |    |    | 12              |
| <i>Eriogonum fasciculatum</i>        | 23                           | 43   | 9  | 9  | 2  | 22              |
| <i>Bromus commutatus</i>             | 82                           | 9  | 2  | 1  | 2  | 4               |
| <i>B. diandrus</i>                   | 34                           | 19   |    |    |    | 47              |
| <i>B. rubens</i>                     | 23                           | 26   | 3  | 1  |    | 47              |
| <i>Hordeum glaucum</i>               | 11                           | 12   |    |    |    |                 |

rectangle inverted. At this point, some diaspores fell off into the metal tray of the shaker. The percentage dislodged was recorded ("% dislodged during inversion" column of Tables 2–8). The shaker was then turned on for the period recorded in the second column of Tables 2–7 (5 sec), and the number of diaspores dislodged during this interval was recorded. The experiments proceeded with further intervals of agitation as recorded in the tables (times shown are cumulative). Dislodging action decreased precipitously after a total shaking time of 15 sec or less, and thus there was no need to extend the total duration of shaking to more than 60 sec. The percentage recorded in the last column of Tables 2–8 shows not the percentage dislodged after shaking intervals had been completed, but rather the percentage still remaining attached.

Experiments involving manual placement of diaspores on substrates rather than dropping of diaspores are reported in Table 8 (note also wording below Table 8).

The fabrics employed can be described as follows. The velvet was 100% rayon, with straight pile 1.3 mm long. The artificial fur was 100% acrylic, with pile 13 mm long. The artificial wool was composed of 75% acetate and 25% nylon, and had a pile 3 mm long composed of markedly curly strands.

The animal skins bearing fur or feathers (cited in Tables 4–7) were made available by the Department of Biology of Pomona College. Specimens documenting the plant diaspores (species listed in Table 1) are located in the herbarium of the Rancho Santa Ana Botanic Garden. A listing of these specimens is available upon request. More detailed description of these diaspores may be found in Munz (1974) or other floristic or taxonomic works. The results of experiments reported

Table 3. Affinity of diaspores to artificial wool (species listed in same order as in Table 1).

| Species                              | % dislodged during inversion | % dislodged at end of shaking interval in sec (times cumulative) |    |    |    | % not dislodged |
|--------------------------------------|------------------------------|--|----|----|----|-----------------|
|                                      |                              | 5  | 10 | 15 | 20 |                 |
| <i>Eryngium aristulatum</i>          | 61                           | 20   | 4  |    |    | 15              |
| <i>E. armatum</i>                    | 87                           | 12   |    |    |    | 1               |
| <i>Osmorhiza chilensis</i>           | 44                           | 25   | 3  |    |    | 28              |
| <i>Sanicula graveolens</i>           | 31                           | 17   | 3  |    |    | 49              |
| <i>S. hoffmannii</i>                 | 59                           | 15   | 0  | 1  |    | 25              |
| <i>Scandix pecten-veneris</i>        | 81                           | 17   | 1  |    |    | 1               |
| <i>Ambrosia acanthicarpa</i>         | 67                           | 29   |    |    |    | 4               |
| <i>A. chamissonis bipinnatisecta</i> | 72                           | 18   | 2  | 1  |    | 7               |
| <i>A. c. chamissonis</i>             | 65                           | 22   |    |    |    | 13              |
| <i>A. dumosa</i>                     | 67                           | 23   | 1  | 1  |    | 8               |
| <i>Bidens frondosa</i>               | 47                           | 21   | 0  | 2  |    | 30              |
| <i>B. laevis</i>                     | 62                           | 12   | 1  |    |    | 25              |
| <i>B. pilosa</i>                     | 47                           | 22   | 0  | 1  |    | 30              |
| <i>Xanthium spinosum</i>             | 3                            |  |    |    |    | 97              |
| <i>X. strumarium</i>                 | 10                           | 8  |    |    |    | 82              |
| <i>Krameria parvifolia imparata</i>  | 10                           | 13   |    |    |    | 77              |
| <i>Salvia mellifera</i>              | 39                           | 38   | 3  |    |    | 20              |
| <i>Eriogonum fasciculatum</i>        | 60                           | 28   | 2  |    |    | 10              |
| <i>Bromus commutatus</i>             | 98                           | 2  |    |    |    | 0               |
| <i>B. diandrus</i>                   | 82                           | 7  |    |    |    | 11              |
| <i>B. rubens</i>                     | 78                           | 17   |    |    |    | 5               |
| <i>Hordeum glaucum</i>               | 77                           | 13   |    |    |    | 10              |

require no comment other than that included in the Conclusions section. Standard deviations were low except on the 0–5 sec interval of the experiments. This paper represents a modified version of a Senior Thesis, a graduation exercise at Pomona College, by the junior author. The general experimental design and construction of the text represent the work of the senior author; the details of experimental procedures and the collection of data are the work of the junior author.

#### DISCUSSION OF RESULTS; CONCLUSIONS

##### *Effect of Strand Length*

Velvet exhibited very low adherence for diaspores of all 22 plant species studied. When the same method as the one employed in Tables 2–7 was used, the majority of species showed no disseminule adherence to velvet. Those species that did show adherence showed it to only a limited extent: *Salvia mellifera*, 13%; *Krameria parvifolia imparata*, 10%; *Bidens laevis*, 6%; *Ambrosia dumosa* 3%; *Osmorhiza chilensis*, 3%; *Bidens frondosa*, 2%; *Sanicula hoffmannii*, 2%. The glochidiate nature of structures on the fruits of *Krameria*, and the fact that both the arms of the glochidia and the stalks which bear them radiate in all directions from the fruits may account for adherence of fruits of that species. A moderate degree of adherence was also observed for the fruiting calyces of *Salvia mellifera*, which bear not merely small hooks but numerous very short stiff hairs, the shortness of which may have permitted attachment to the velvet. The most significant result demonstrated by adherence to velvet, however, is that there is a lower threshold

Table 4. Affinity of diaspores to desert wood rat fur.

| Species                    | % dislodged during inversion | % dislodged at end of shaking interval in sec (times cumulative) |    |    |    | % not dislodged |
|----------------------------|------------------------------|--|----|----|----|-----------------|
|                            |                              | 5  | 10 | 15 | 20 |                 |
| <i>Bidens laevis</i>       | 52                           | 29   | 5  |    |    | 14              |
| <i>Osmorhiza chilensis</i> | 47                           | 45   | 4  |    |    | 4               |
| <i>Xanthium spinosum</i>   | 56                           | 29   | 2  |    |    | 13              |

in attachment capability based upon strand length of surface. The length of the velvet pile is insufficient for appreciable attachment. The present study did not determine the shortest strand length at which attachment begins to be appreciable; that remains an interesting goal for a future study.

#### *Slender Diaspores with Retrorse Trichomes*

This group is composed of *Bromus commutatus*, *B. diandrus*, *B. rubens*, *Hordeum glaucum*, *Osmorhiza chilensis*, and *Scandix pecten-veneris*. All these species except *Osmorhiza chilensis* have diaspores heavier at the peduncle end, with the bristles directed away from that end. This characteristic may account for the high adherence of these species on the artificial fur (Table 2). As the diaspores were dropped onto the artificial fur, the heavier end reached the substrate first, entering the pile. The retrorse nature of bristles enhanced diaspore attachment and hindered release from the pile. *Scandix pecten-veneris* and *Bromus commutatus* penetrate less efficiently, as reflected in their low adhesion rates. *Osmorhiza chilensis*, the only native North American species in this diaspore group, does not display this kind of adherence. However, *O. chilensis* has a high affinity for both the artificial fur and the artificial wool, whereas the remainder of this group have less than 12% of diaspores retained indefinitely by the artificial wool. *Osmorhiza chilensis* diaspores also show strong affinity to the natural substrates (Tables 4–7), which may account for the notable amphitropical disjunction in this species as well as the other disjunctions reported for the genus by Constance (1948).

The European grasses *Bromus diandrus*, *B. rubens*, and *Hordeum glaucum* were the only plants in this study to exhibit indefinite adherence of greater than 45% to artificial fur and indefinite adherence of less than 12% to artificial wool. This remarkable affinity for a straight-fibered fabric may relate to the weedy adaptations of these species. Weeds may be expected to excel at long-distance dispersal not only because of the high dispersion of suitable habitats, but also because capability for attachment to straight-haired animals would be advantageous; most potentially dispersing animals are straight-haired rather than woolly.

Table 5. Affinity of diaspores to Audubon cottontail fur.

| Species                    | % dislodged during inversion | % dislodged at end of shaking interval in sec (times cumulative) |    |    |    | % not dislodged |
|----------------------------|------------------------------|--|----|----|----|-----------------|
|                            |                              | 5  | 10 | 15 | 20 |                 |
| <i>Bidens laevis</i>       | 63                           | 22   | 5  | 0  |    | 8               |
| <i>Osmorhiza chilensis</i> | 63                           | 24   | 0  | 4  |    | 9               |
| <i>Xanthium spinosum</i>   | 55                           | 33   | 2  | 0  |    | 10              |



Table 6. Affinity of diaspores to bobcat fur.

| Species                    | % dislodged during inversion | % dislodged at end of shaking interval in sec (times cumulative) |    |    |    |    | % not dislodged |
|----------------------------|------------------------------|--|----|----|----|----|-----------------|
|                            |                              | 5  | 10 | 15 | 20 | 25 |                 |
| <i>Bidens laevis</i>       | 55                           | 19   | 3  | 0  | 3  |    | 22              |
| <i>Osmorhiza chilensis</i> | 48                           | 18   | 3  | 1  | 4  | 1  | 25              |
| <i>Xanthium spinosum</i>   | 27                           | 17   | 7  | 0  | 0  | 1  | 48              |

When spikes of the grasses were pressed into the textile substrates (Table 8), groups of spikelets disarticulated and the rigid awns helped guide the peduncle end of the spikelets toward the substrate. This end characteristically is the one that becomes attached to substrates, because the stiff trichomes are then oriented in a retrorse position which tends to prevent dislodging of the spikelets.

#### *Diaspores with Hooks*

This group is composed of *Salvia mellifera*, *Sanicula graveolens*, *S. hoffmannii*, *Xanthium spinosum*, and *X. strumarium*. These diaspores display adherence characteristics different from those of the preceding group. A much higher affinity for the artificial wool is evident. The hooks apparently are ideal for catching on the curled fiber strands of the artificial wool. *Salvia mellifera* is the only species in this group in which diaspores were not covered by hooklike devices equally on all surfaces. The fruiting calyces of *S. mellifera* bear hooklike aristae only at their tips. However, the fruits of *S. mellifera* are formed in radiating clusters ("glomerules"), with calyx tips pointing outwards, so that only the hooked portion of the calyx is displayed. Although there are also trichomes on the surfaces of the calyces of *S. mellifera*, the hooks are clearly the main adherence mechanism.

*Sanicula graveolens* diaspores have better adherence to substrates than do those of *S. hoffmannii*. Possibly correlated with this is the much wider range of *S. graveolens* (San Diego Co., California, to British Columbia) as compared to that of *S. hoffmannii* (limited coastal and island areas of southern California); Shan and Constance (1951) have, however, considered the possibility that *S. hoffmannii* is of hybrid origin, which might be a more important correlation. Diminution of hooks on fruits of *Sanicula* may be correlated with loss of dispersal in relation to narrowness of habitat, as evidenced by the near-absence of hooks on fruits of *S. tracyi* Shan & Constance; this is consistent with ideas expressed earlier (Carlquist 1966a, b) on loss of dispersibility.

Table 7. Affinity of diaspores for red-tailed hawk feathers.

| Species                    | % dislodged during inversion | % dislodged at end of shaking interval in sec (times cumulative) |    |    |    | % not dislodged |
|----------------------------|------------------------------|--|----|----|----|-----------------|
|                            |                              | 5  | 10 | 15 | 20 |                 |
| <i>Bidens laevis</i>       | 33                           | 59   | 5  |    |    | 3               |
| <i>Osmorhiza chilensis</i> | 44                           | 47   | 1  |    |    | 8               |
| <i>Xanthium spinosum</i>   | 51                           | 29   | 3  | 3  |    | 13              |

Table 8. Affinity of diaspores of *Hordeum glaucum* when spikes were pressed into substrate rather than dropped onto it.

| Substrate       | % dislodged during inversion | % not dislodged after 60 sec of shaking |
|-----------------|------------------------------|---|
| Artificial fur  | 63                           | 37                                      |
| Artificial wool | 58                           | 42                                      |

(Note: with use of the same procedure, 100% of diaspores of *Bidens laevis*, *Osmorhiza chilensis*, and *Xanthium spinosum* remained attached to both substrates after 60 sec of shaking.)

#### *Diaspores with Glochidia or Retrorsely Barbed Awns*

This group is composed of *Bidens frondosa*, *B. laevis*, *B. pilosa*, and *Krameria parvifolia* var. *imparata*. The adherence figures are greater for this group on the artificial wool than they are on the artificial fur (Tables 2, 3). Like the hooks of species in the category just above, the retrorse barbs or glochidia of this group appear optimally adapted for attachment to curly strands. The barbed awns plus upwardly-appressed trichomes of the achene body in *Bidens* prevent dislodging of *Bidens* fruits from a substrate no matter which end is inserted (Carlquist 1966a). The achenes of *Bidens*, however, are presented with awns outward; the achenes radiate from a head. Each achene is not radially symmetrical, but the head is. Each fruit of *Krameria* is radially symmetrical in its covering of glochidia. Because of these differences in diaspore symmetry, the figures in Tables 2 and 3 are lower for *Bidens* than they are for *Krameria*, a circumstance reminiscent of the difference mentioned above between diaspores of *Salvia mellifera* and those of *Sanicula*. The experimental condition of dropping diaspores onto a surface favors species with radial symmetry of hooklike or barblike devices, and thus *Krameria* ranks higher than *Bidens*. However, when fruits of *Bidens* were inserted awns first into a substrate, they adhered excellently (see legend below Table 8); 100% of the fruits remained lodged in all substrates.

#### *Diaspores with Straight Spines*

This group is composed of *Ambrosia acanthicarpa*, *A. chamissonis bipinnatisecta*, *A. c. chamissonis*, *Eryngium aristulatum*, and *E. armatum*. Although a higher adherence is indicated for the artificial fur than for the artificial wool, adherence rates are remarkably low. This seems a clear experimental demonstration of the difference between a category of diaspores dispersed in fur or feather and a category of diaspores dispersed by insertion into skin. This distinction was noted earlier (Carlquist 1983).

#### *Diaspores with No Obvious Attachment Mechanism*

This category is recognized for the purpose of discussing one species, *Eriogonum fasciculatum*. The fact that diaspores (minute nut surrounded by persistent calyx) do adhere to clothing and to the fabrics of the present study demonstrates that obvious morphological adaptations for epizoochory are not always present, although they have been used as indicators by Darwin (1859) and Pijl (1972). Over 19% of the diaspores of *E. fasciculatum* were retained indefinitely by the artificial wool; this figure includes a small percentage which adhered between 10 and 30

sec before dislodging, indicating an intermediate or short-range capability of dispersal. The adherence of *E. fasciculatum* calyces appears to result from catching of the ovate calyx lobes in curly strands of a substrate; in inland populations of *E. fasciculatum*, calyces bear upwardly-appressed trichomes which may aid in adherence, since the radiating nature of the calyx lobes forces the calyx, when dislodged, to enter a substrate by the pointed base of the calyx. Other species may have moderate capacity of epizoochory. *Cryptantha* was cited as a genus in which both epizoochory and anemochory may operate (Maddox and Carlquist 1985).

#### *Natural and Artificial Substrates Compared*

The natural fur and feather samples (Tables 4–7) revealed similar adherence values and standard deviations when compared to the textiles other than velvet (Tables 2, 3). Therefore, the textiles used in this study appear to be replicas of animal surfaces suitable for use under experimental conditions, where the uniformity of textiles is valuable. The textiles probably do not replicate the texture of skin, however, and therefore cannot demonstrate the epizoochorous nature of diaspores in which stout spiny excrescences (e.g., *Ambrosia*, *Eryngium*) suitable for penetration of skin are present.

#### *Effect of Diaspore Weight and Size*

Comparison of species for those genera where more than one species were studied (*Bidens*, *Bromus*, *Eryngium*, *Sanicula*, *Xanthium*) shows no consistent patterns based primarily upon size or weight; rather, the density and morphology of adherence devices seems of overriding importance.

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