

Homing Strategies of *Microtus pennsylvanicus* Following Displacement

Mara Irby  
BIOS 35503 01: Practicum in Environmental Biology II  
August 9, 2006

## Abstract

Homing behavior of *Microtus pennsylvanicus* was studied on the National Bison Range, western Montana, in July 2006. Meadow voles were displaced 35m perpendicular to a main trapping transect into a grassland prairie habitat similar to that of the capture location, into a dissimilar habitat (a riparian zone), or released at the point of capture (control). The initial orientation of 32 meadow voles used in this study were tracked using fluorescent powder until their trails could no longer be followed. Distance, displacement (straight-line distance), and angle toward home were taken for each trail. This study found significantly greater wandering ratios (distance/displacement) in female voles than in male voles, and in voles released into the dissimilar riparian habitat than in the similar prairie habitat. Distance traveled was significantly greater among the riparian released voles than among the control or prairie released voles likely a result of the tracking method being used. Soil moisture and cover data showed no orientation of the voles toward these characteristics. I conclude that *M. pennsylvanicus* adheres to either a random-memory strategy or a critical distance strategy when homing. Differences in wandering ratios are most likely due to differential familiarity with the two habitats, differential trail availability, or the level of agitation of the animals.

---

Key Words: homing, homing strategy, initial orientation, *Microtus pennsylvanicus*, meadow vole, small mammal, random-memory strategy, critical distance strategy, National Bison Range

## Introduction

Homing behavior has been observed in a variety of animal species, including invertebrates, fish, amphibians, reptiles, birds, and mammals. Homing behavior is “any movement undertaken to reach a spatially restricted area which is known to an animal,” often the animal’s home range (Papi 1992:1). This ability enables individuals to return to breeding sites, to migrate between summer and winter habitats, and to return from foraging, hunting, or other excursions. Homing is also important to the success of individuals displaced from their home range by natural disturbances such as flood, drought, storm, and fire (Linzey 2001). An animal’s home range, defined by Anderson (1982) as “the smallest area that accounts for a meaningful percentage of the animal’s space utilization,” is valuable to animals as a result of their great familiarity with the area

and their fitness for that specific habitat. An individual's knowledge of shelter/refuge locations, and food sources in and around the home range, the presence of potential mates and prey species, and the absence of competitive species that might exclude it, make home ranges and the ability to return to them important to the success of individuals.

Animals accomplish homing by either allothetic (external reference) or idiothetic (internal reference) means. Studies suggest that sight, hearing, taste, smell, information gathered en route, and possibly magnetism and the use of celestial bodies to be among the methods employed to inform the various homing strategies of different species (Linzey 2001; Papi 1992). Homing pigeons (*Columba livia*), for example, are known to use a combination of visual, olfactory, and magnetic cues, as well as the position of the sun to inform themselves for their position relative to home (Alerstam 1990). Fish, in contrast, use gradients of temperature, salinity, and chemicals as well as sun orientation, orientation to polarized light, and orientation to geomagnetic and geoelectric fields to direct themselves to and from their breeding sites (Linzey 2001). The information thus gathered is then used to inform the various homing strategies used by different species. Commonly discussed strategies include random or systematic search, genetically-based orientation, trail following, route-based orientation including route reversal, course reversal, and path integration, as well as pilotage and true navigation (Papi 1992). Individuals may use only one or a combination of these above strategies.

Homing studies usually address one or both of the two major aspects of homing: the nature of the motivation to return home and/or the means utilized to return (Griffo 1961). Due to the wide range of species that display homing behavior, a great variety of methods have been employed in their study. Common methods can be divided into three

categories: capture-mark-recapture, tracking, and displacement experiments. Capture-mark-recapture (CMR) is used to quantify homing success (the proportion of animals that return home following displacement) and homing speed. Animals are caught, marked as individuals, and released at a certain distance. Animals recaptured at the original site have homed. Tracking experiments vary greatly: common methods include simple visual observation, use of grids on soil (i.e. insects), thread trailing (i.e. tortoises, toads), and radio and ultrasonic transmitters (i.e. large mammals). Displacement experiments encompass any homing experiment in which animals are experimentally displaced from their home range, usually at varying distances, over obstacles, or into different habitats (Papi 1992). The above methods are often used in combination with one another in order to best examine the behavior and abilities of a species.

Small mammals are often used in homing studies because they are easy to handle, abundant, and have relatively small home ranges, making experimental displacement easier. In addition, there are inexpensive methods of observation and tracking available for their study. Griffo (1961) studied homing in the cotton mouse (*Peromyscus gossypinus*). Mice were displaced from their home range into adjacent natural and unnatural habitats. Homing success was found to be greater in the mice displaced into familiar habitat. No correlation was found between initial orientation and the direct route home. Laboratory isolation showed cotton mice learn and retain information about their environment for long periods of time. Griffo (1961) postulated that psychological factors were the principal source of motivation to home. Fislser (1962) studied homing in the California vole (*Microtus californicus*) and found homing success decreased with increasing displacement distance. Homing was successful only up to a distance six times

the diameter of the home range. Trapping around release points showed animals returned home when necessitated by intraspecific competition or conditions insufficient to support voles and possibly by innate or psychological factors. Homing was believed to occur by either navigation or simple random wandering. Robinson and Falls (1965) used CMR to study meadow voles (*Microtus pennsylvanicus*) displaced at various distances. In addition, they re-released captured mice and captured around the release sites. The study concluded that homing success decreases with increasing displacement distance. Homing became no more direct when an animal was displaced a second time to the same spot. Animals in unfamiliar terrain made no apparent attempt to orient home, but were instead recaptured around the release location. Robinson and Falls (1965) interpreted the results in support of homing by means of prior knowledge of the terrain and by random wandering. Fluharty et al. (1976) also gathered evidence suggesting the practice of sun-compass orientation in this species.

*Microtus pennsylvanicus* was selected for this study because of its abundance at the National Bison Range in western Montana. The species is commonly found in grassland habitats, showing a preference for areas of higher moisture, and may also be found in forested areas (Burt and Grossenheider 1976). *Microtus pennsylvanicus* feed on most available species of grasses, sedges, and herbaceous plants, with small portions of their diets occasionally made up of insects (Zimmerman 1965) and scavenged animal remains (Riewe 1973). Home range sizes of this species range from 405m<sup>2</sup> to 3,480m<sup>2</sup> for males and from 160m<sup>2</sup> to 3,115m<sup>2</sup> for females (Vleck 1969), most of the variation being a result of population densities and resource availability. The following environmental characteristics have been found to be significant in *M. pennsylvanicus*

habitat selection: relative ground cover of grasses and herbs (Getz 1970), soil moisture (Wrigley 1974), soil sodium levels (Autmann and Emlen 1965), soil pH and potassium levels (Krebs et al. 1971), and surface temperature and humidity (Getz 1971). Voles have short activity cycles, averaging about 4.8 hours, therefore these animals can be active at any time of day (Ambrose 1973). Ambrose (1973) found, at any time, 50 percent of the population or more to be active.

This study was an exploration of homing behavior in *Microtus pennsylvanicus*. The study involved the capture, displacement, and tracking (as far as methods allowed) of the species and the comparison of groups displaced into different locations to a control group released at the point of capture. The study looked specifically at the initial orientation and behavior of the species upon experimental displacement into habitat similar to that of the area where they were captured (grassland prairie) and a habitat type that differed markedly (riparian). Angular orientation toward home as well as movement directed toward specific environmental characteristics, possibly similar to the home range, are considered. I hypothesized that:

H<sub>1</sub>: *Microtus pennsylvanicus* initial orientation is random with respect to home (capture point).

H<sub>2</sub>: *M. pennsylvanicus* will orient toward high vegetative cover and toward soil moisture similar to that of the capture site upon experimental displacement.

H<sub>3</sub>: *M. pennsylvanicus* male and female initial orientation and trail characteristics do not differ significantly.

H<sub>4</sub>: Trail characteristics of *M. pennsylvanicus* released at the riparian location will differ significantly from those of the control and prairie locations (greater distance, smaller displacement, higher wandering ratio).

## Methods

Field portions of this study were conducted from July 6-18, 2006 at the National Bison Range in western Montana (Lake County). Sites were selected along Mission Creek in areas with riparian zones  $\geq 20\text{m}$  in width with an edge that abruptly transitions into grassland habitat for  $\geq 80\text{m}$ . Data were collected from three suitable sites (Figure 1). At each site 25 Sherman live-traps were placed along a transect 30m from the riparian-grassland edge running parallel to the tree line following the contours of the edge as to constantly maintain this 30m distance. Traps were placed an average of 2-5m apart. Trap placement was approximate because traps were placed along visible vole runs to increase trapping success.

Traps were set in the evenings (ca. 1800 MST) in order to decrease the likelihood of small mammal death due to high temperatures during late morning and afternoon hours. The traps were checked the following morning, starting at 0830 MST. All small mammals captured in the traps were weighed, sexed, and identified to species. Weights were taken using a cloth handling bag and Avinet (500g) spring scale. The homing experiment concerns only *Microtus pennsylvanicus*; therefore any other species were released upon capture. Voles captured in the Sherman traps were released at one of the following distances:

- (1) 0m (Control) - voles were released at the capture site,

(2) 35m grassland (experimental-Prairie) - voles were released 35m from capture point perpendicular to the transect in the grassland,

(3) 35m riparian (experimental-Riparian) - voles were released 35m from the capture point perpendicular to the transect in the riparian zone (the opposite direction as in case (2)).

(Note that voles in group 3 were released 5m into the riparian area because the transect is 30m from the riparian-grassland edge; Figure 2)

The displacement distance of 35m was selected based on several factors. The displacement distance needed to be greater than the maximum radius of the home range of the species, 33.3m (Vleck 1969), in order to induce homing behavior. It was also necessary that the voles be near enough to their home range that a large proportion would be capable of homing, because this study concerns initial orientation and homing strategy, not homing success. Robinson and Falls (1965) found that voles in their study, conducted in an abandoned farmland exhibiting typical early old field succession (similar to a grassland in structure and food availability to the sites used in this study), had a homing success of about 90% at a displacement of 60m. Given these parameters and site availability, 35 meters was selected as the displacement distance for this study.

Release locations were assigned based on the sex of the vole and a rotating schedule of release types (1<sup>st</sup>, capture site; 2<sup>nd</sup>, riparian; 3<sup>rd</sup>, grassland; 4<sup>th</sup>, capture site, etc.) in order to equally distribute males and females and overall individuals to the different locations without bias.

Experimentally-displaced voles were carried to their release locations in a dark cloth bag to prevent visual observation en route. Routes taken were more or less direct.

Voles were then scruffed and liberally dusted on their ventral side with fluorescent powder (DayGlo Color Corp., AX-11-5) using a cosmetic brush. All voles were released facing parallel to the main transect. Immediately upon release the area was vacated (by the researchers) for 3 minutes to allow the individual move and orient without unnatural influences. After 3 minutes, the release point was flagged and the trail of fluorescent powder left by the voles was followed. The trail was followed until the point at which two researchers searching constantly for 2 minutes found no additional points in the trail. This point, the End point, was also flagged. Flexible fluorescent flagging tape was laid down along the trail to acquire a *distance traveled* measurement for each path. The straight-line distance between the release point and the end point (i.e. *displacement*) and the angle created by the intersection of the lines from the capture point to the release point and from the end point to the release point was measured using a compass (Figure 3). Zero degrees was defined as the capture-release line.

At each of the three points, capture, release, and end (only capture and end for Control; Figure 3), data were gathered on the environmental characteristics of the site, soil moisture and grams of cover. Soil moisture was obtained by taking weights before and after drying (24 hours, American Scientific Products Constant Temperature Oven DK-42, 100°) a 30cm<sup>3</sup> sample from each point. Grams of cover was obtained through clipping 0.1 m<sup>2</sup> plots at each point. All aboveground plant material rooted in this area was clipped, dried 24 hours, and weighed.

After the completion of the tracking portion of this study, snap traps were set out along the main (trapping) transect to verify the vole species being used in this study. Vole species were distinguished by dental characteristics. The only vole species found

was *M. pennsylvanicus*, with five closed triangles on the first lower molar, three transverse loops and no triangles on the third lower molar, four closed triangles and a posterior loop on the second upper molar, and three closed triangles on the third upper molar (Hall and Cockrum 1953; Hall and Kelson 1959). A concurrent study also found *M. pennsylvanicus* to be the only vole species in the Mission Creek area (N. Williams, personal communication).

Statistical analysis was performed on Jumpin5.1 Statistical Software and Systat (for Fisher's LSD statistics). Regression analysis was used to look for relationships in trail length over time. ANOVAs were used to explore the distribution of the vole sex and mass among the release locations (Control, Riparian, Prairie). Chi square analysis was used to evaluate all angle data ( $H_{01}$ ). ANOVAs were used to compare environmental characteristics among release locations and among points ( $H_{02}$ ). Student's t-tests were used to compare males and females for all trail characteristics ( $H_{03}$ ). ANOVAs were used to compare trail and environmental characteristics among the release locations ( $H_{04}$ ).

## **Results**

A total of 32 meadow voles were captured and tracked in this study. The mean mass ( $\pm$ SD) of males and females was  $34.67 \pm 17.34$ g and  $27.12 \pm 10.77$ g respectively. A Student's t-test showed that the difference in mass was not significant ( $P=0.19$ ). An ANOVA of the number of male and female voles released at each location, showed no significant differences ( $P=0.15$ ). An ANOVA of the mass of voles released at each location, also showed no clear patterns ( $P=0.77$ ). A regression of average trail length and trapping day, found no significant trend ( $P=0.17$ ).

## **Orientation**

Chi-square analyses of angular data gathered from the two experimental locations found no significant deviation from randomness (Table 1). The average home range size of *Microtus pennsylvanicus*, 23.7m given by Vleck (1969), was used to define the range of angles considered to demonstrate orientation toward home. Subjects were displaced 35m from the capture point, therefore, if it is assumed that the capture point is in the center of the animal's home range, *homing* should be defined as any angle falling between 0 and 69 degrees (Figure 4). If the same principle is used, but the sexes are evaluated separately (due to differences in average home range size), homing in females is defined between 0 and 58 degrees (avg. home range radius=19.3m), and homing in males between 0 and 77 degrees (avg. home range radius=28.0m). Chi-square analysis was used to compare the proportions of angles within and without the defined *homing* range from all subjects combined, males and females separately, experimental locations separately, and sexes and locations separately to the proportions expected if every direction had an equal chance of being selected (Table 1). Further chi-square analysis was run (with the delineations as above) while excluding data from voles that traveled less than 5 meters, in order to reduce variability created by poorly tracked animals (Fritts et al. 1984; Table 1).

## **Environmental Characteristics**

### *Moisture*

The percent soil moisture in the soil was calculated for the capture points and end points of the Control and for the capture points, release points, and end points of the Riparian and Prairie locations. Comparison of capture point moisture of the three locations showed no significant differences (ANOVA:  $P=0.36$ ). Comparison of release

point moisture among the three locations revealed a nearly significantly greater percent moisture in the soils of the Riparian location than the Control and Prairie locations (ANOVA: F-ratio=3.2, df=2,26, P=0.057; Fisher's LSD: Riparian × Control, P=0.028; Riparian × Prairie, P=0.063; Figure 5). The change in percent moisture between the end and release points was calculated for each of the three locations to try to detect directed movement with respect to soil moisture; no significant differences were found in these values between the three locations (ANOVA: P=0.83).

### *Cover*

Grams of aboveground vegetative cover in a 0.1m<sup>2</sup> plot was calculated as an index of cover for the capture points and end points of the Control and for the capture points, release points, and end points of the Riparian and Prairie locations. Comparison of capture point cover of the three locations showed no significant differences (ANOVA: P=0.55). Comparison of release point cover among the three locations revealed a significantly lower cover index at the Riparian location than at the Control and Prairie locations (ANOVA: F-ratio=9.9, df=2,24, P=0.0007; Fisher's LSD: Riparian × Control, P=0.001; Riparian × Prairie, P=0.001; Figure 6). The change in the cover index between the end and release points was calculated for each of the three locations to try to detect directed movement with respect to cover; no significant differences were found in these values between the three locations (ANOVA: P=0.50).

### **Trail Characteristics**

The *distance* (length of trail) and *displacement* (straight-line distance from release point to end point) was measured for each vole in the study. These two trail descriptors were used to create a third descriptor, the *wandering ratio*, which is the

distance:displacement ratio. This ratio was devised to compare the amount of directional movement (displacement) compared to the amount of actual traveling (distance) and can be thought of as an index of decisive movement: numbers approaching 1 display very directional movement, moving in a straight line, suggesting travel in a particular or known direction. Large wandering ratio scores suggest a less directed (more wandering) searching pattern.

Student's t-tests were used to compare the trail characteristics of male and female voles; male voles showed a nearly significantly lower wandering ratio than female voles (distance,  $P=0.49$ ; displacement,  $P=0.31$ ; wandering ratio,  $t\text{-ratio}=2.156$ ,  $df=18.3$ ,  $P=0.0446$ ; Figure 7). Regression analysis found no trend between vole mass and any of the trail characteristics (distance,  $P=0.60$ , displacement,  $P=0.45$ , wandering ratio,  $P=0.82$ ). One-way ANOVAs comparing the trail characteristics of the three locations revealed significantly longer trails in the Riparian location than in the Control and Prairie locations (ANOVA:  $F\text{-ratio}=4.1$ ,  $df=2,29$ ,  $P=0.028$ ; Fisher's LSD:  $RIP \times CON$ ,  $P=0.082$ ;  $RIP \times PRA$ ,  $P=0.039$ ; Figure 8) and nearly significantly greater Wandering ratios in the Riparian than in the Prairie (ANOVA:  $F\text{-ratio}=3.6$ ,  $df=2,28$ ; Fisher's LSD:  $PRA \times RIP$ ,  $P=0.018$ ; Figure 9).

## Discussion

As was hypothesized, initial orientation was found to be random with respect to home (capture point;  $H_{01}$ ). *Microtus pennsylvanicus* did show any orientation to soil moisture or vegetative cover ( $H_{02}$ ), contrary to what was predicted. Male and female voles' initial orientation did not differ significantly, nor did their distance or displacements ( $H_{03}$ ). The wandering ratio, contrary to the hypothesis, was found to be

significantly different between males and females ( $H_{03}$ ). Trail characteristics of *M. pennsylvanicus* released at the riparian location differed from the control and prairie locations in distance and the wandering ratio, but not displacement ( $H_{04}$ ). Distance traveled was greater and the wandering ratio higher, at the riparian location.

### **Methods**

Alternating the assignment of experimental groups within male and female classes proved to be a successful method of evenly dispersing males and females into release locations (about equal numbers were assigned to each location). This method worked similarly well for mass, though it was not considered in the assignment of individuals to location groups, as mass also did not differ significantly among locations. Tracking skill did not change over time, because trail length did not change significantly over time.

### **Strategy**

Two possible homing strategies are supported by the findings of this study. The first, and most straight forward, is the *random-memory strategy* (Davis 1966; Joslin 1977; Wilson and Findley 1972; Furrer 1973). This strategy theorizes that animals have various landmarks stored in their long term, or reference, memory. This information is gathered during previous dispersals, migrations, and/or excursions from the home range. When animals are within their home range or life range, they home using these known landmarks to orient themselves. On the occasion that these animals are displaced into unfamiliar terrain, they select a course direction randomly, since no orienting landmarks are available. The animals then travel in a more or less straight trajectory, what is called an initial straight course (ISC), in the hopes that by chance alone they will encounter familiar territory on which they can orient. The second strategy, the *critical distance*

*strategy*, is based on the resemblance of experimental displacement homing trips to natural excursion return trips (Bovet 1984, 1987, 1990). This strategy is an evolutionary adaptation in which an animal travels from the release point in straight lines approximately the average length of an excursion for the species. If the animal's home range is not reached after this distance has been covered, the animal assumes a mistake in direction has been made, and the animal u-turns and returns to the release point. Here it sets out on another straight course in another direction repeating the pattern. During actual excursions this strategy is fairly successful; however, in the case of experimental displacements in which an individual is usually displaced a distance far greater than its average excursion length, the strategy is less effective (Bovet 1992).

### **Orientation**

Thorough analysis of initial orientation, measured in degrees between zero and 180, resulted in no significant deviation from an even distribution. Because no directional preference was shown in the data, voles in this study must have been selecting their initial orientation randomly. Other studies have similarly concluded that brush rabbits and other rodents' vanishing bearings (equivalent to End points) reveal a random initial orientation with reference to home. Moreover, this initial orientation is not related to the individual's eventual homing success (e.g. Griffio 1961; Sims and Wolfe 1976; Durup 1982). It has been found instead that rodents' initial orientation is usually toward familiar habitat and/or shelter, not toward home (e.g. Lehmann 1956; Gentry 1964; Jamon and Bovet 1987; Chapman 1971).

### **Environmental Character**

Analysis of percent moisture and grams of cover of the three release sites used in this study supported the assumption that the riparian site did indeed represent a different microclimate than the control and prairie sites. Percent moisture of the soil was significantly higher at riparian release and end points and grams of cover significantly lower than at all other points. All capture points in this study had significantly similar levels of moisture and cover, thus, all voles used in this study had home ranges in the same habitat type.

Most mammals' behavioral response to experimental displacement, Bovet (1992) explains, is to "stay for a few minutes or hours in the first sheltered location encountered, grooming, dozing and/or watching (Chapman 1971; Alho 1980; Jamon et al. 1986)...or engage for minutes or hours in an often frenzied, apparently aimless search, roaming close to and about the release site, with occasional breaks" (Müller 1965; Williams and Williams 1970; Lozan 1980; Mironov and Kozhevnikov 1982; Bovet 1984). If it is the case that the first objective of *M. pennsylvanicus* is to find shelter, as has been observed with other mammals, their initial orientation would not be indicative of homing. Due to this consideration, future studies may obtain more applicable data to the question of homing if they measure intermediate orientation, taken after the "pause point" where an animal finds shelter and recomposes, instead of initial orientation (taken from the point of release) as in this study (Bovet 1972, 1980). Initial orientation may not be a reliable predictor of homing (Bovet 1992). The "pause point" can be identified in different ways depending on the method being used to track the animal under study. Using fluorescent powder, as in this experiment, one can try to identify a point in the trail where there is a concentration of powder where it looks like the animal groomed itself. This point may be

difficult to precisely identify using the powder tracking method. It may also be challenging because if the animal has groomed itself at the pause point a great deal of the powder will have been removed before any tracking meaningful for data collection has begun. This method would be more successful in studies employing radio or ultrasonic transmitters where the pause point could be more easily identified as the point where a certain amount of time is spent by the animal before it re-embarks. This method would increase the efficacy of the use of the end point as the angular measurement in particular (zero now being the pause-capture line) would be more meaningful with respect to initial orientation because the data would not be confounded with error from the sometimes conflicting motivation to find shelter.

### **Trail Characteristics**

Trail length (*distance*) was significantly longer for among the Riparian location than for the Control and Prairie locations. The long length of trails left by voles released in the riparian zone could be an indication of the varying effectiveness of the fluorescent powder in different habitats. The riparian zone was moister than the other two locations, perhaps causing the powder to fall in larger clumps, thus making the trails easier to find. The trails may also have been easier to locate due to the darker colors of the flora in the riparian zone.

The wandering was significantly greater among females than among males. Female voles showed less directed movement than male voles. This could be due to the often larger home ranges of male *M. pennsylvanicus* (Vleck 1969). Having a larger home range means that male voles are familiar with more territory than female voles. Additionally, male voles often leave their natal range as they become an adult to establish

their own home range. This is not commonly seen in females. Therefore, this also would cause male microtines to be more likely to have a more wide ranging familiarity with the area than females; thus less wandering would be necessary in order for males to orient themselves.

Voles released in the riparian zone had significantly higher wandering ratios than those released into the prairie habitat, indicating that the riparian released voles followed less direct paths. It is likely that the voles used in this study were more familiar with the territory of the prairie displacement habitat than with the riparian territory, which made wandering in these areas more necessary. The prairie location is the same habitat type as the capture location where the voles were found. That is to say the voles used in this study probably had a greater familiarity with the area near the prairie habitat than with the area near the riparian habitat since it represents such a distinctly different microclimate, vegetation, etc. Greater knowledge of the areas surrounding, and in a few cases possibly including, the prairie location decreases the amount of wandering normally necessary before known terrain is encountered. Both of the homing strategies described above, the random-memory strategy or the critical distance strategy, are consistent with this postulate.

Another possible explanation for the higher wandering ratios at the riparian location as compared to the prairie location, is the ease of locating trails. Vole runs, paths used frequently by voles (Burt and Grossenheider 1976), seem to be more abundant in the prairie habitat than in the riparian zone. If this is the case, voles may be employing the same homing strategy in both habitats, and may be equally unfamiliar with both locations, but due to the greater abundance of vole runs in the prairie, the voles come

across paths more quickly, which they then follow until the next intersection of runs.

Random wandering along vole runs would produce more direct paths, smaller wandering ratios, than pure random wandering.

A third possible explanation for the different wandering ratios between the two displacement sites is the level of agitation of the subjects. In laboratory experiments, Southwick (1959) showed that introduction of adult mice to new, but physically similar environments, induced stressful responses in the animals. One can assume that the more different the new environment, the more stressful the experience. The high wandering ratios could be an indication of greater agitation in the riparian released individuals due to the greater difference of that habitat type from the habitat type of their home range. Griffo (1961) found that when artificially displaced from its home range the mouse, *Peromyscus gossypinus*, “become psychologically disturbed” and in many cases showed “physiological changes similar to those symptomatic of stress, resulting in a search for familiar territory.” Stress and the accompanied response to search for shelter and familiar territory, heightened especially in very unfamiliar sites, might explain the higher amount of wandering observed in the riparian releases.

## **Conclusion**

The conclusion of this study is that displaced *Microtus pennsylvanicus* follow either a random-memory homing strategy or a critical distance strategy. Differentiation between these two strategies was not possible given the design of this study. Initial orientation from the release point showed no significant orientation towards home or any other direction, however, voles released in the riparian zone ‘wandered’ more than control and prairie-released voles, likely due to lesser knowledge of the surrounding areas

and/or to the greater agitation of the voles. It is likely that the first concern of released individuals was to locate shelter. Future studies should consider focusing on intermediate orientation, taken after the pause point, which is more likely to reveal any homeward orientation in *M. pennsylvanicus* if it exists.

### **Acknowledgements**

I would like, first of all, to thank Lee Jones at the National Bison Range for allowing me to conduct my study on the range. I would like to acknowledge the help of James English in the development of this study, for his assistance in the field, his powers of estimation, and especially for his help in fine tuning the methods of this study making it final incantation possible. I would also like to thank the University of Notre Dame, UNDERC, and Gary Belovsky for making this program possible. I would additionally like to thank Nikki Williams, Aileen Kelly, Tommy Hayes, Ashley Braun, and Fern Lehman for their assistance in the field and Karen Francl for her editorial assistance. I would especially like to thank Patrick Wood because without him I wouldn't be here.

### **Literature Cited**

- Alho, C.J.R. 1980. Homing ability in the wild rodent *Proechimys roberti* determined by radio-telemetry. *Rev. Brasil. Biol.*, 40:91-4.
- Alterstam, T. 1990. *Bird Navigation*. New York: Cambridge University Press.
- Ambrose, H.W., III. 1973. An experimental study of some factors affecting the spatial and temporal activity of *Microtus pennsylvanicus*. *J. Mamm.*, 54:79-110.
- Anderson, D.J. 1982. The home range: a new nonparametric estimation technique. *Ecology*, 63:103-12.
- Aumann, G.D., and J.T. Emlen. 1965. Relation of population density to sodium availability and sodium selection by microtine rodents. *Nature*, 208:198-99.
- Bovet, J. 1984. Strategies of homing behavior in the red squirrel, *Tamiasciurus hudsonicus*. *Behav. Ecol. Sociobiol.*, 16:81-8.

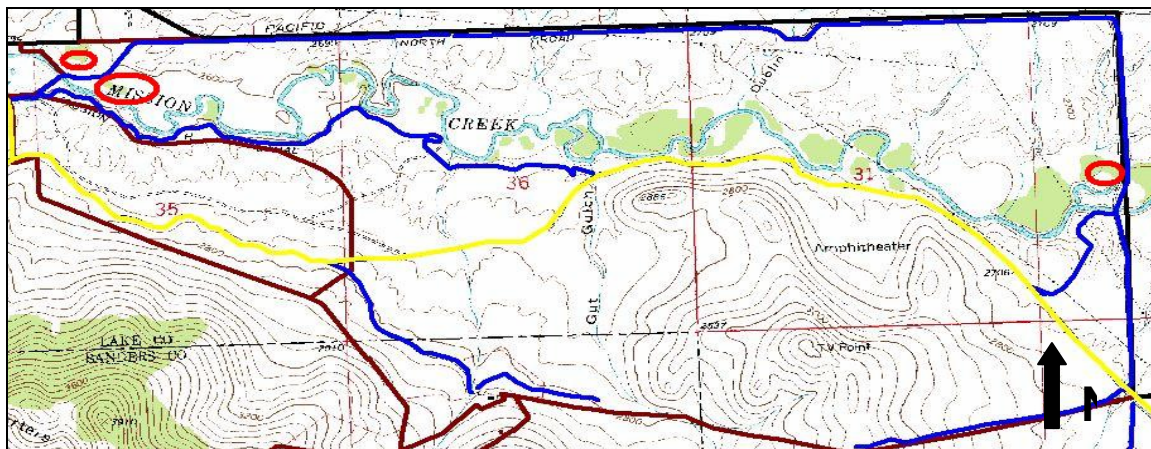
- 1987. Cognitive map size and homing behavior, in *Cognitive Processes and Spatial Orientation in Animal and Man*, Vol. 1 (eds P. Ellen and C. Blanc-Thinus), Nijhoff, Dordrecht, pp.252-65.
- 1990. Orientation strategies for long distance travel in terrestrial mammals, including humans. *Ethol. Ecol. Evol.*, 2:117-28.
- 1992. Mammals, in *Animal Homing*, (ed. F. Papi) London: Chapman and Hall pp.321-53.
- Burt, W.H., and R.P. Grossenheider. 1976. *A field guide to the mammals*. Boston: Houghton Mifflin.
- Chapman, J.A. 1971. Orientation and homing of the brush rabbit (*Sylvilagus bachmani*). *J. Mamm.*, 52:686-9.
- Davis, R. 1966. Homing performance and homing ability in bats. *Ecol. Monogr.*, 36:201-37.
- Durup, M. 1982. Etude du retour au gîte du mulot sylvestre (*Apodemus sylvaticus* L.). *Biol. Behav.*, 7:277-91.
- Fisler, G.F. 1962. Homing in the California vole, *Microtus californicus*. *Am. Midl. Nat.*, 68:357-68.
- Furrer, R.K. 1973. Homing of *Peromyscus maniculatus* in the channeled scablands of East-Central Washington. *J. Mamm.*, 54:466-82.
- Gentry, J.B. 1964. Homing in the old-field mouse. *J. Mamm.*, 45:276-83.
- Getz, L.L. 1970. Influence of vegetation on the local distribution of the meadow vole in southern Wisconsin. *Occas. Papers Biol. Sci. Ser.*, Univ. Connecticut, 1:213-41.
- 1971. Microclimate, vegetative cover, and local distribution of the meadow vole. *Trans. Illinois State Acad. Sci.*, 64:9-21.
- Griffo, J.V., Jr. 1961. A study of homing in the cotton mouse, *Peromyscus gossypinus*. *Am. Midl. Nat.*, 65:257-89.
- Hall, E.R., and E.L. Cockrun. 1953. A synopsis of North American microtine rodents. Univ. Kansas Publ., Mus. Nat. Hist., 5:373-498.
- Hall, E.R., and K.R. Kelson. 1959. *Mammals of North America*. Ronald Press, New York, 2:547-1083 + 79.

- Jamon, M., S. Benhamou, and J.P. Sauvé. 1986. Initial orientation and navigation in homing rodents, in *Orientation in Space* (ed. G. Beugnon), Privat, Toulouse, pp.45-55.
- Jamon, M. and P. Bovet. 1987. Possible use of environmental gradients in orientation by 'homing' wood mice. *Behav. Proc.*, 15:93-107.
- Joslin, J.K. 1977. Rodent long distance orientation ('homing'). *Adv. Ecol. Res.*, 10:63-89.
- Krebs, C.J., B. L. Keller, and J. H. Myers. 1971. *Microtus* population densities and soil nutrients in southern Indiana grassland. *Ecology*, 52:587-607.
- Lehmann, E. von. 1956. Heimfindeversuche mit kleinen Nagern. *Z. Tierpsychol.*, 13:485-91.
- Linzey, D. 2001. *Vertebrate Biology*. Boston: McGraw Hill.
- Lozan, A.M. 1980. Orientation of the wild boar toward positive stimuli at medium and great distances. *Vest. Sool.*, 1980:56-60.
- Mironov, A.D. and Kozhevnikov, V.S. 1982. Character of migrations of *Clethrionomys glareolus* within the home range and outside it. *Zool. Zh.*, 61:1413-18.
- Müller, B. 1965. Experimentelle Untersuchungen über das Heimfinden beim Jund. PhD Dissertation, University of Basle.
- Papi, F. 1992. General aspects, in *Animal Homing*, (ed. F. Papi) London: Chapman and Hall pp.1-15.
- Riewe, R.R. 1973. Food habits of insular meadow voles, *Microtus pennsylvanicus terraenovae* (Rodentia: Cricetidae), in Notre Dame Bay, Newfoundland. *Canadian Field-Nat.*, 87:5-13.
- Robinson, W.L., and J.B. Falls. 1965. A study of homing of meadow mice. *Am. Midl. Nat.*, 73:188-224.
- Sims, R.A. and Wolfe, J.L. 1976. Homing behavior of the house mouse (*Mus musculus* L.). *J. Miss. Acad. Sci.*, 21:89-96.
- Southwick, C.H. 1959. Eosinophil response of C57Br mice in behavioral disturbances. *Ecology*, 40:156-57.
- Van Vleck, D.B. 1969. Standardization of *Microtus* home range calculation. *J. Mamm.*, 50:69-80.
- Williams, N. Personal communication. July 2006.

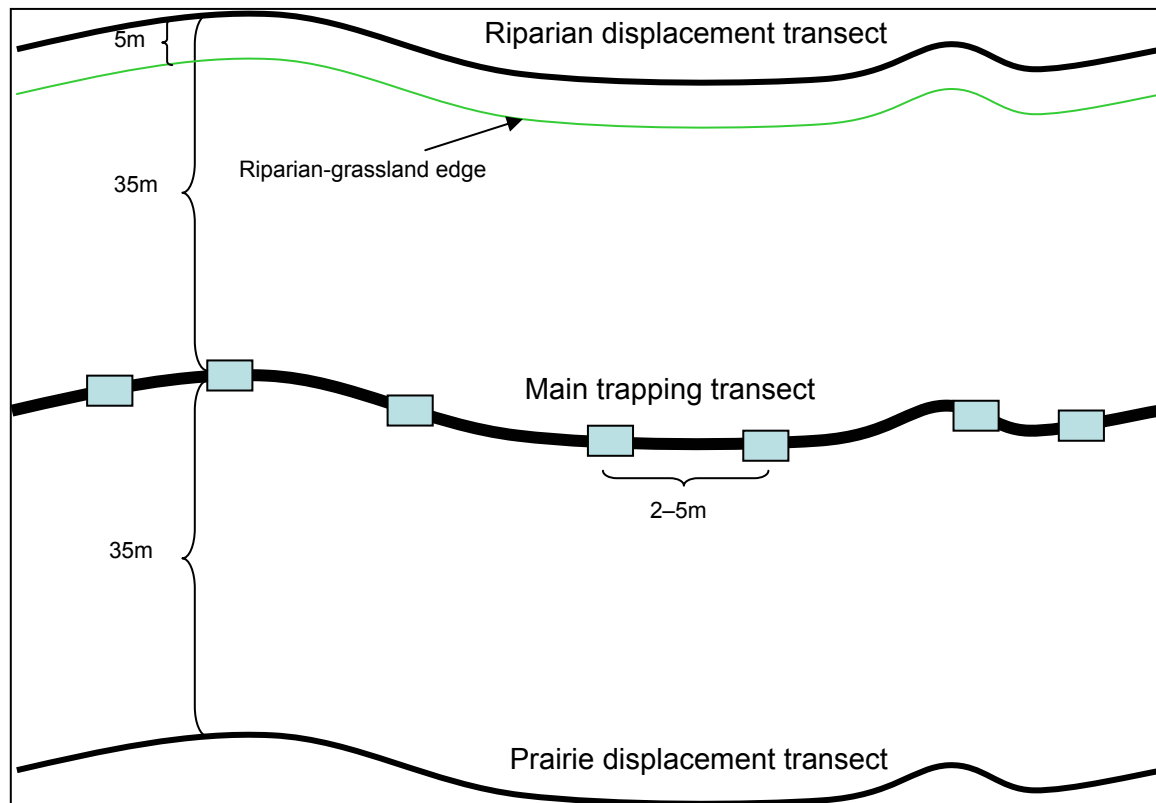
- Williams, T.C. and Williams, J.M. 1970. Radio tracking of homing and feeding flights of a neotropical bat, *Phyllostomus hastatus*, with evidence for visual orientation. *Anim. Behav.*, 14:468-73.
- Wilson, D.E. and J.S. Findley. 1972. Randomness in bat homing. *Am. Nat.*, 106:418-24.
- Wrigley, R.E. 1974. Mammals of the sandhills of southwestern Manitoba. *Canadian Field-Nat.*, 88:21-39.
- Zimmerman, E.G. 1965. A comparison of habitat and food of two species of *Microtus*. *J. Mamm.*, 46:605-12.

**Table 1.** P-values of Chi-square analysis. Proportion of angles falling within and without defined homing angle compared to proportions giving equal likelihood to every angle, the case if *M. pennsylvanicus* selects angular direction randomly with respect to home. Table shows p-values including and excluding voles that traveled less than 5m in total distance (Fritts et al. 1984).

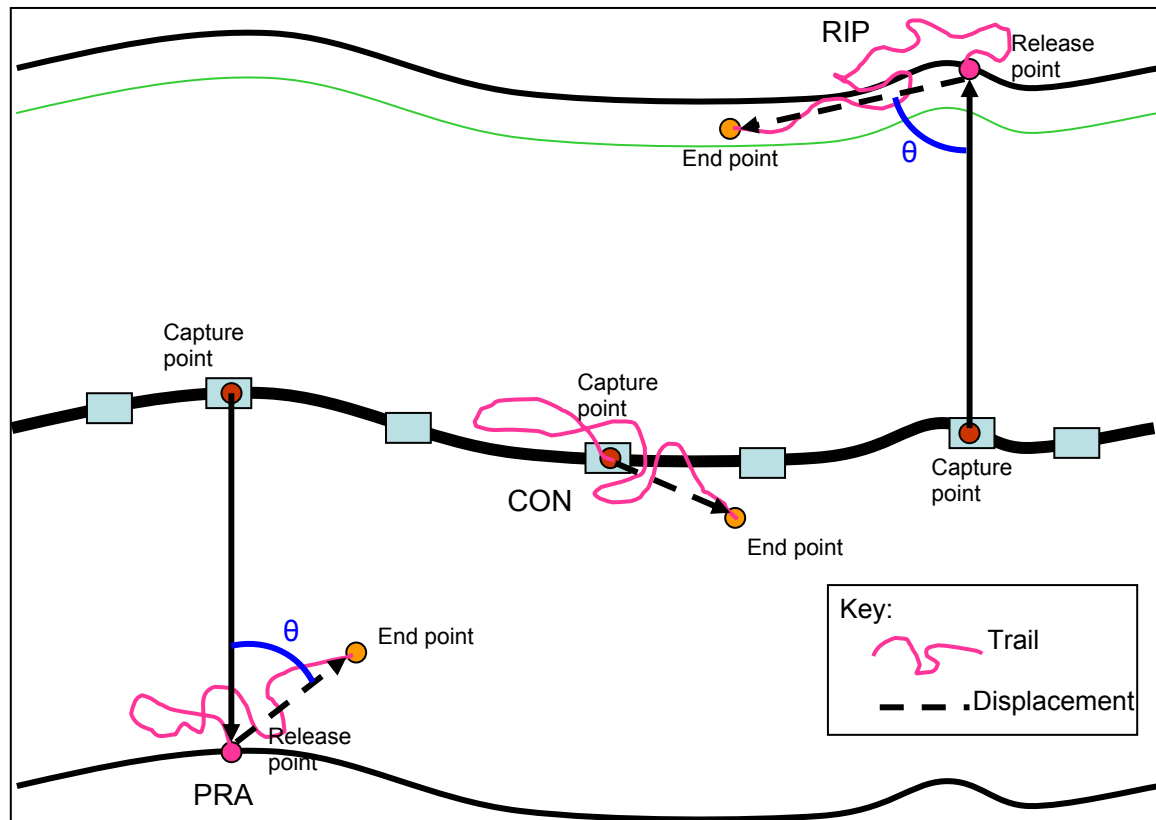
<u>Group (Homing Angle)</u>	<u>Including &lt; 5m</u>	<u>Excluding &lt; 5m</u>
All (69°)	0.71	0.76
♀ (58°)	0.63	0.97
♂ (77°)	0.45	0.71
Riparian (69°)	0.43	0.43
Prairie (69°)	0.17	0.58
Riparian ♀ (58°)	0.57	0.57
Riparian ♂ (77°)	0.45	0.45
Prairie ♀ (58°)	0.98	0.32
Prairie ♂ (77°)	0.13	0.20



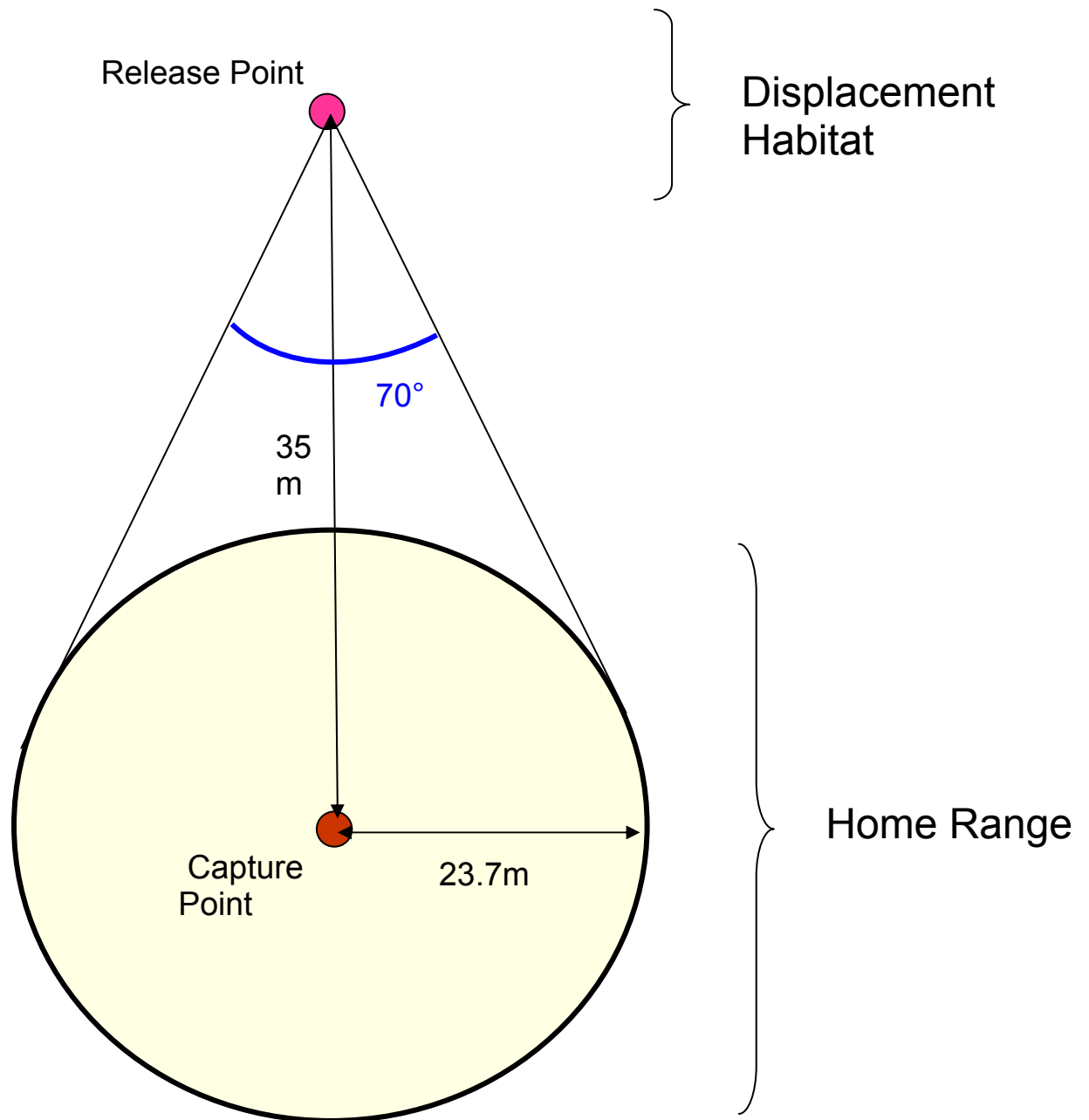
**Figure 1.** Map of trapping locations (circled in red) on the National Bison Range, Lake Co., MT. Yellow lines indicate the Bison Range tour road. Brown lines indicate fences.



**Figure 2.** Transect placement. Traps are set along the main trapping transect. Voles are released and tracked at their capture point on the main trapping transect, or perpendicular to it on either the riparian displacement transect, or the prairie displacement transect. Not to scale.

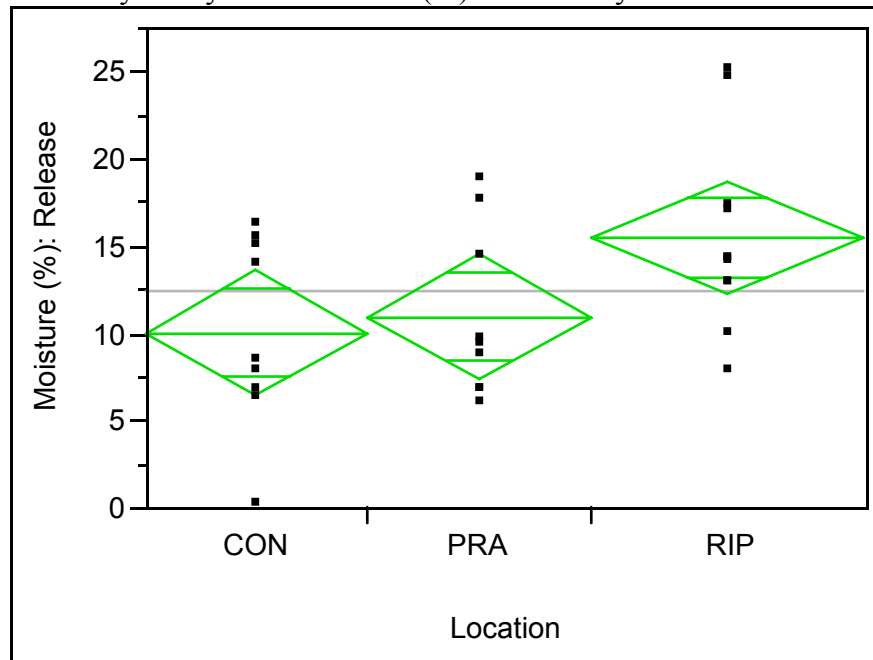


**Figure 3.** Position of points and illustration trail characteristics: distance, displacement, angle. Displacement locations prairie (PRA), control (CON), and riparian (RIP) shown. Trails shown are examples only. Not to scale.

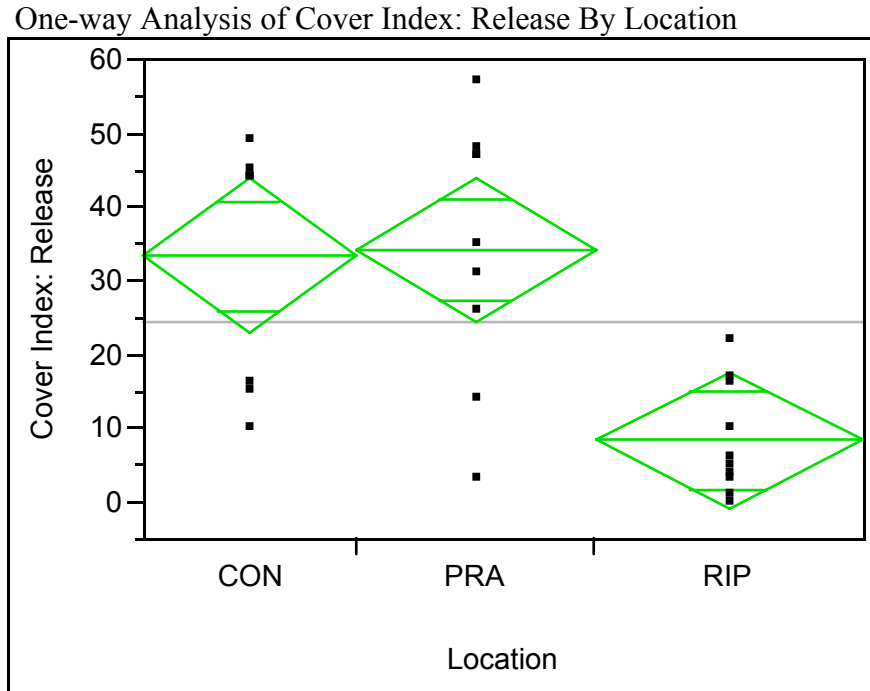


**Figure 4.** Derivation of homing angles for meadow voles on the National Bison Range, studied in July 2006. Derivation based on average meadow vole home range radii (23.7m) and 35m experimental displacement. Illustration for sexes pooled. Not to scale.

One-way Analysis of Moisture (%): Release By Location

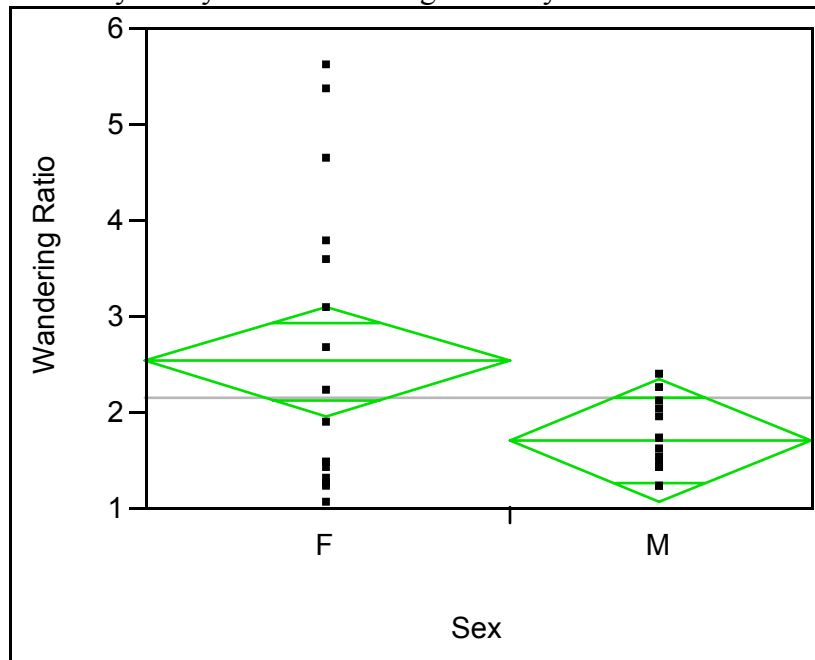


**Figure 5.** ANOVA of percent moisture at the Release points of each location (ANOVA: F-ratio=3.2, df=2,26, P=0.057) for meadow voles captured on the National Bison Range and displaced in July 2006. A post-hoc Fisher's LSD test indicated that moisture readings in riparian sites were greater than those in prairies (P=0.063) and control (P=0.028) sites. The control and prairie sites did not statistically differ (P=0.718). Diamonds indicate means (mid horizontal line) and 95% confidence intervals.

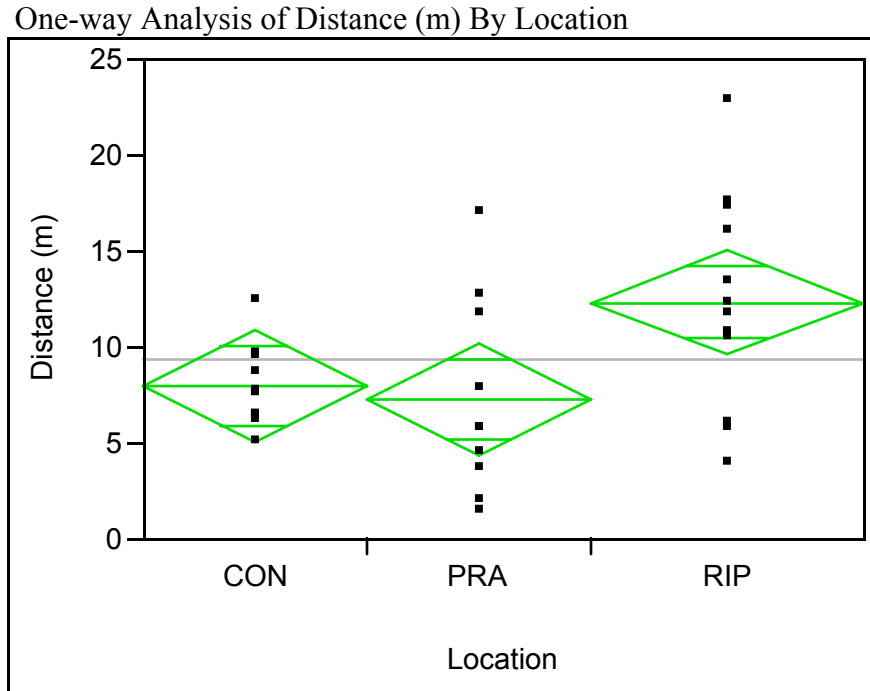


**Figure 6.** ANOVA of the cover index at the Release points of each location (ANOVA: F-ratio=9.9, df=2,24, P=0.0007) for meadow voles captured on the National Bison Range and displaced in July 2006. A post-hoc Fisher's LSD test indicated that cover readings in riparian sites were less than those in prairies (P=0.001) and control (P=0.001) sites. The control and prairie sites did not statistically differ (P=0.904). Diamonds indicate means (mid horizontal line) and 95% confidence intervals.

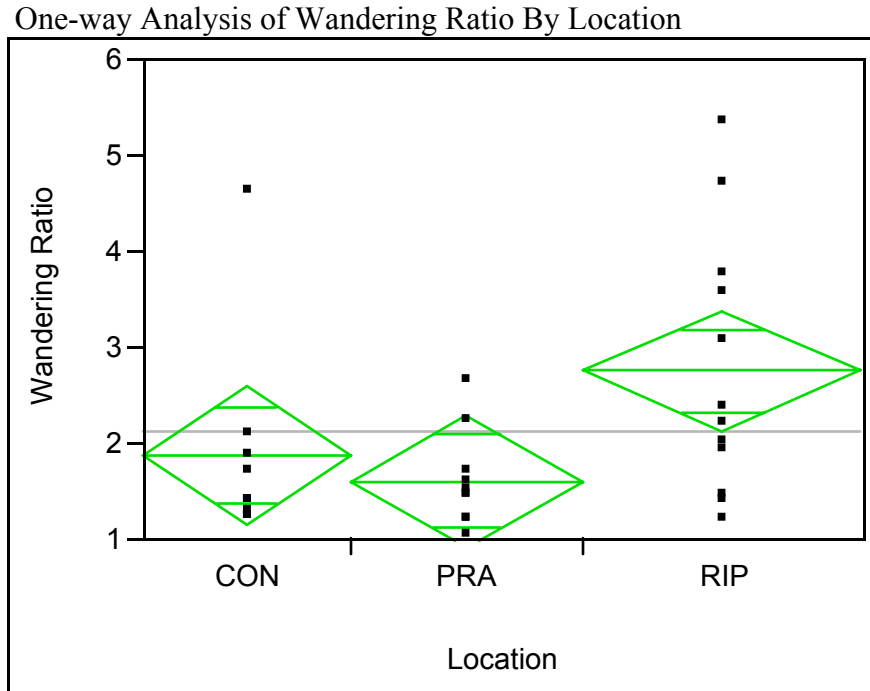
One-way Analysis of Wandering Ratio By Sex



**Figure 7.** Student's t-test of Wandering Ratio (distance/displacement) between female and male *M. pennsylvanicus* (Student's t-test: t-ratio=2.156, df=18.3, P=0.0446). Diamonds show means and 95% confidence intervals.



**Figure 8.** ANOVA comparing distance in meters of trails at each location (ANOVA: F-ratio=4.1,  $df=2,29$ ,  $P=0.028$ ) for meadow voles captured on the National Bison Range and displaced in July 2006. A post-hoc Fisher's LSD test indicated that distance was greater among riparian released meadow voles than those released in prairies ( $P=0.039$ ) and control ( $P=0.082$ ) sites. The control and prairie sites did not statistically differ ( $P=0.737$ ). Diamonds indicate means (mid horizontal line) and 95% confidence intervals.



**Figure 9.** ANOVA comparing wandering ratios of trails at each location (ANOVA: F-ratio=3.6,  $df=2,28$ ,  $P=0.0421$ ) for meadow voles captured on the National Bison Range and displaced in July 2006. A post-hoc Fisher's LSD test indicated that wandering ratios were greater among riparian released meadow voles than those released in prairies ( $P=0.018$ ) and control ( $P=0.070$ ) sites. The control and prairie sites did not statistically differ ( $P=0.591$ ). Diamonds indicate means (mid horizontal line) and 95% confidence intervals.