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## Habitat Selection and Movement Patterns in Sandhills Rodents

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**ABSTRACT** — Using fluorescent pigments, we were able to gather accurate information about the use of habitat and movement patterns of small nocturnal rodents. Use of habitat is strongly affected by the patchiness of vegetation of the sandhills. *Microtus ochrogaster* occupies the dense grass, *Dipodomys ordii* occupies the open sandy area, and *Perognathus hispidus* and *P. flavescens* occupy a mixed grass-forb zone. Advantages of the fluorescent method over more traditional methods of determining habitat use are presented. There are significant differences in the trails of species at the fine 10-cm scale, but these differences disappear at a larger 3-m scale. The significance of this difference is discussed in the context of the foraging strategy of the rodents and optimal pathways.

There is a great deal of information contained in the pathway an animal makes as it moves through the environment. A path can document preference of macro- and microhabitat, use of the vertical habitat, diet, home range, and foraging strategy. As useful as pathway information might be to ecologists, it has been difficult to gather such data for nocturnal mammals. This study explores the use of fluorescent pigment and ultra-violet light, a technique that produces an extremely accurate picture of movement (Lemen and Freeman 1985), in a community of rodents in the sandhills of central Nebraska.

We investigated the habitat preferences of each species, summer and winter habitat use, and the estimated use of habitats as produced by the fluorescent pigment method versus the more conventional method of trapping. Differential use of habitats by rodents has been proposed as one of the mechanisms allowing their coexistence (Rosenzweig and Winakur 1969, Brown 1975, Price 1978, Lemen and Rosenzweig 1978, M'Closkey 1976, Grant 1972). This differential use is of particular interest because the vegetation of the sandhills is a mosaic of radically different habitats with sharp transitions from one habitat (grass) to another (open). It may be the combination of habitat types that allows the coexistence of such diverse rodents as the prairie vole, *Microtus ochrogaster*, a grassland species, and Ord's kangaroo rat, *Dipodomys ordii*, an open ground species. We wanted to see whether or not the rodents showed a similar sharp pattern of use of preferred habitat. While the grassland of the floristically interesting sandhills is one of the largest relatively undisturbed grasslands in North America and supports a diverse community of rodents, little work has been directed at how the rodents are using this habitat (Baumann 1982).

Vegetation of the study area, Arapaho Prairie, Arthur County, NE, has been described by Keeler et al. (1980). Valley floors between stabilized dunes are characterized by dense stands of grass. However, disturbance is a regular feature of these habitats. Disturbances occur when the grass cover is opened up by animals

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such as the plains pocket gopher (*Geomys bursarius*) or by erosion due to wind and rain that exposes the sandy soil. Vegetation of the disturbed sites varies with the age of the site and the degree of disturbance. At one extreme there is no vegetation, just open sand. In general, disturbed areas are characterized by having higher proportions of open ground, annuals, and forbs than grassland areas. The grassland areas and the disturbed areas form a mosaic of habitats in sandhills.

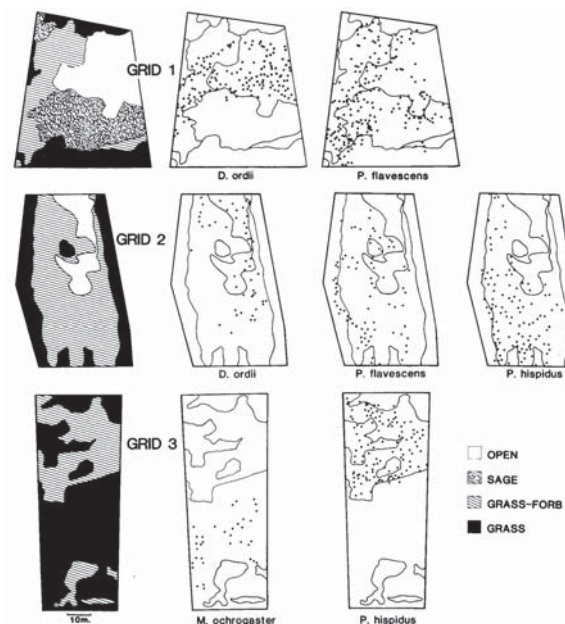
Pathways for a variety of organisms have been described (Siniff and Jessen 1969, Kleerekoper et al. 1970, Cody 1971, Levin et al. 1971, Smith 1974), but little is known about the paths taken by nocturnal rodents. Here we describe the basic characteristics of these trails. The description centers on two points, distribution of angles of turns and correlation of successive turns. I

A second level of inquiry about pathways has been pursued by Cody (1971, 1974) and Pyke (1978a) who used methods of optimal foraging theory to predict the characteristics of paths taken by animals. Their approach to this problem was to assume that to maximize its rate of energy intake a species should adopt pathways that will minimize searching areas that have been recently visited. Pyke (1978a) noted that an important assumption of his model was that the forager could not detect its prey at large distances. Pyke concluded that such long distance sensory detection of food was probably often the case, and that his model might have limited applicability. However, he noted that seed-gathering rodents might be one of the systems that would conform to the assumptions of his model. Using the fluorescent pigment method we were able to collect the necessary data to test the predictions of the model developed by Pyke (1978a).

Our analysis of pathways indicates that different scales of measurement along a trail appear to measure different biological properties of trails. At a small scale the changes in direction reflect course corrections and at a larger scale they reflect the course itself. We quantified movement at a fine 10-cm scale and at a gross 3-m scale to investigate this problem.

#### MATERIALS AND METHODS

We set out grids of Sherman live traps in three areas: near a large, active blowout; in an older blowout where vegetation had stabilized the sand; and in climax valley vegetation. In each area we mapped the amount of land occupied by grass, sage, grass-forb, and open (Fig. 1). The grass habitat is dominated by prairie sandreed (*Calamovilfa longifolia*), needle and thread (*Stipa comata*), blue grama (*Bouteloua gracilis*), and sedges (*Carex sp.*). The areas of sage are formed by large clones of white sage (*Artemisia ludovicana*). In grass-forb areas sunflower (*Helianthus petiolaris*), stickleaf (*Mentzelia nuda*), and ragweed (*Ambrosia psilostachya*) are common forbs along with a variety of grasses such as western wheatgrass (*Agropyron smithii*) and sand dropseed (*Sporobolus cryptandrus*). The open area has the highest proportion of bare ground. This habitat is found in such places as the lip of active blowouts. Large clumps of sand muhly (*Muhlenbergia pungens*), 1-2 m in diameter, are often the most obvious vegetation of this habitat. Between these clumps of grass (typically 1 m or more) is bare sand or at most a scattering of low growing annuals. We quantified the different habitats using 0.1-m<sup>2</sup> Daubemire plots (Table 1).



**Figure 1.** Maps of the three grids showing the different habitats and the distribution of selected species on each grid. Dots represent flags placed at 3-m intervals along a fluorescent trail.

**Table 1.** Estimates of the percent makeup of the different vegetative types based on 0.1-m<sup>2</sup> sampling quadrats.

Habitat	n	Coverage (%)		
		Grass	Forbs	Open
Grass	12	81.5	1.0	17.5
Sage	12	23.8	47.5	28.8
Grass-forb	12	37.5	21.2	39.8
Open	22	18.8	10.4	70.4

n = number of quadrats

Coverage = average of the sample

All three grids were trapped in July and August of 1983. The minimum number of animals caught on each grid and the sample size of species captured and dusted on each grid are reported in Table 2. Because the number of distinguishable fluorescent colors was limited, not all species were followed in detail on each grid. In February of 1984 we returned to the sandhills for the winter trapping period. Because of snow accumulation on Grid II, only Grids I and III could be trapped. Minimum numbers and sample sizes for the winter trapping are shown in parentheses in Table 2.

Table 2. Minimum number of animals present on the grids summer and winter, and sample sizes for all grids during the summer sampling period. Parentheses represent all winter data.

Species	Grid 1		Grid 2		Grid 3	
	Minimum on grid S (W)	Sample size n dusted	Minimum on grid S	Sample size n dusted	Minimum on grid S (W)	Sample size n dusted
<i>Perognathus flavescens</i>	7 (0)	12 30	6	7 12	5 (0)	
<i>P. hispidus</i>	2 (0)		2	2 8	2 (0)	3 12
<i>D. ordii</i>	7 (3)	6(3) 18(9)	2	2 4	0 (0)	
<i>Peromyscus maniculatus</i>	2 (3)	1(6) 3(16)	0		0 (6)	0(7) 0(13)
<i>O. leucogaster</i>	7 (2)	5 6			0 (0)	
<i>M. ochrogaster</i>	2 (0)	3 3	2	2 2	3 (1)	3(1) 9(2)

S = minimum number of animals present on grid in summer (Flowerdew 1976)

(W) = winter data

n = number of different individuals dusted

dusted = number of times individuals were dusted and released on grid

Following the method of Lemen and Freeman (1983), animals were trapped and dusted with fluorescent paint pigment. The next night we followed the trails left by the rodents with an ultraviolet light and planted a marker flag every 3m. During the day we mapped the positions of the flags using a plane table and alidade, equipment typically used to map geological sites.

Besides quantifying habitat use we also quantified movement of individual rodents in several ways. While trailing the animal we made general notes on behaviors such as climbing, feeding, and sand bathing. For a sample of rodents we recorded direction of movement on a fine scale of every 10 cm, and, finally, we recorded larger scale movement at the 3-m flag interval for all the rodents. This procedure yielded a detailed record of movements on both a small and large scale for analysis and comparison with other species.

## RESULTS

### Habitat Selection

Use of habitat by different species is shown in Fig. 1. The species of rodents captured on the three grids include the plains pocket mouse, *Perognathus flavescens*; hispid pocket mouse, *P. hispidus*; Ord's kangaroo rat, *Dipodomys ordii*; deer mouse, *Peromyscus maniculatus*; northern grasshopper mouse, *Onychomys leucogaster*; western harvest mouse, *Reithrodontomys megalotis*; and prairie vole, *Microtus ochrogaster*. For each rodent we calculated an average electivity index for all habitat types for all grids (Fig. 2) using the method described in Chesson (1983). Preference of *M. ochrogaster* for the sage and open habitats could not be calculated during the winter because those habitat types were only present on Grid I, and the movements of *M. ochrogaster* were not quantified on that grid. To compare the use of habitats of each species, we performed a contingency table analysis on each grid for the absolute amount of activity by each rodent in each vegetational area. Only one comparison (*P. maniculatus* and *O. leucogaster* on Grid I) is nonsignificant at the 0.05 level. Further, a goodness of fit analysis indicates that no species used the habitat in proportion to the total area of those habitats on the grids.

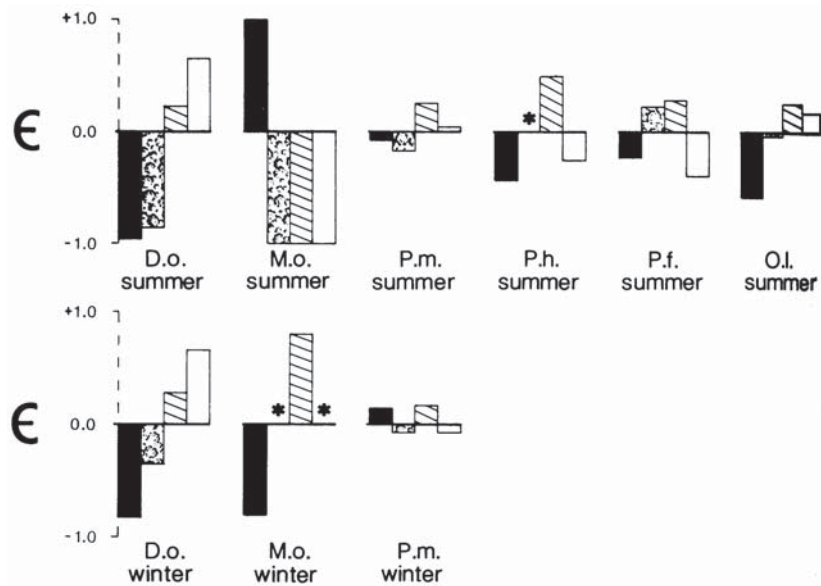
### Summer-Winter Comparison

Habitat preferences of *D. ordii*, *P. maniculatus*, and *M. ochrogaster* were determined for both the summer and winter (Fig. 2). Comparison of these seasonal preferences was made for each species using a Chi-square contingency table. No significant difference is found for *P. maniculatus* ( $X^2 = 2.51$ ,  $P < 0.25$ , summer  $n = 75$ , winter  $n = 143$ ). Significant shifts are found for both *D. ordii* ( $X^2 = 11.78$ ,  $P < 0.01$ , summer  $n = 159$ , winter  $n = 103$ ) and *M. ochrogaster* ( $X^2 = 32.41$ ,  $P < 0.01$ , summer  $n = 35$ , winter  $n = 12$ ; Fig. 2).

### Comparison of Trapping and Fluorescent Methods

A difficulty in comparing the results from the pigment method and the trapping method was the small sample size of data from the trapping study. The two largest data sets for the trapping results were from *Perognathus flavescens*





**Figure 2.** Electivity indices for habitat use averaged over all grids. At zero the rodent is using the habitat exactly as he finds it, above zero he is using it more, and below zero less. The habitats are grass, grass-forb, sage, and open (key to shading is same as Fig. 1) and the initials of the genus and species are indicated. The asterisk indicates that the electivity index could not be calculated for that habitat.

(40 capture points) and *D. ordii* (19 captures) from Grid I. To compare the two methods we determined in which vegetational type each trap was placed, and, using the number of captures at each trap, we calculated the number of captures in each vegetational type. These numbers were compared to the expected numbers of captures if the rodents were using the vegetational areas in proportions predicted by the fluorescent method. Results from contingency table analyses indicate there is no statistical difference (*P. flavescens*, d.f. = 3,  $X^2 = 0.10$ ,  $P > 0.10$ ; *D. ordii* d.f. = 2,  $X^2 = 2.31$ ,  $P > 0.10$ ).

#### Vertical Movement Patterns

While trailing the rodents we noted little vertical habitat use. In all the tracking done, *M. ochrogaster*, *O. leucogaster*, *R. megalotis*, and *Peromyscus maniculatus* never left the surface, but the heteromyids did occasionally forage in plants above the ground. Three times the same *Perognathus flavescens* climbed the fruiting stalk of *Carex* (sedge that is about 23 cm high) to eat the flowering head. One *P. hispidus* climbed 13 *Helianthus petiolaris* (all about 1 m high) to get at the fruiting heads at the top. Finally, to our surprise we followed the trail of a single *D. ordii*, a highly bipedal animal, nearly a meter into a *Helianthus* where the animal cut off a fruiting head and returned to the ground to eat it. But, given the hundreds of meters that we trailed this species, these forays into the vertical appear relatively unimportant.

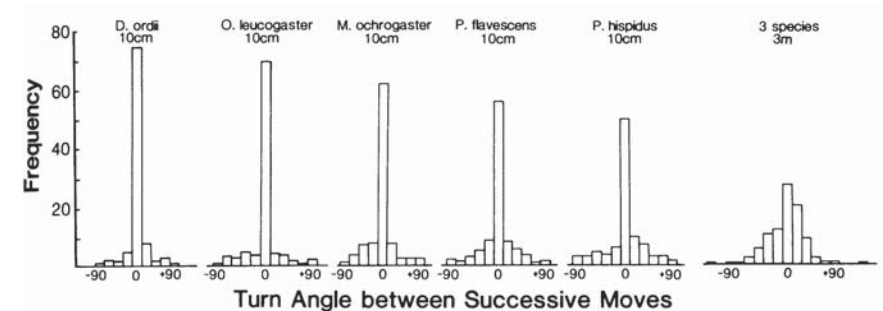
*Reithrodontomys megalotis*, often considered a good climber and a likely rodent that climbs to gather food, was not trapped during the summer. During February of 1984 we did capture and mark *R. megalotis*, but we found no indication that this animal had ever left the ground.

#### Analysis of path angles

The angle rodents turned every 10 cm is summarized in a series of histograms (Fig. 3). Analysis with a Chi-square contingency table indicates that there are significant differences among species in turning behavior (Table 3). In addition to the turning distributions we analyzed the correlation of sequence of turns along the path. With a stepwise multiple regression we related the angle of movement for a particular 10-cm segment of path with angles of movement from previous turns (all straight ahead moves are eliminated from the analysis). In general there is a negative relationship between the present turn a rodent takes and the turns it has just made.

A similar analysis was performed using data generated for a 3-m interval of movement. On this larger scale there were adequate data for comparison of three species, *P. flavescens*, *P. hispidus*, and *D. ordii*. We found no difference in the turning distribution of these rodents at the 3-m level, nor was there a negative correlation between successive moves at the 3-m level.

Simulations were run under two basic sets of assumptions to create artificial trails with which to analyze and compare real trails. The most radical simulation assumed a uniform distribution of turn angles and no correlation between successive turns. The other simulation used the same unimodal distribution found in real trails but assumed no correlation between successive turns by choosing turn angles at random from this distribution. Two characteristics of all trails were calculated, the  $R_n$  value (straight line distance traveled from start of trail after  $n$  moves) used by Kareira and Shigesada (1983), and the rate a trail recrosses itself. In our computer simulations we generated both  $R_n$  and its confidence limits for both the 10-cm and 3-m scale (Fig. 4). In each graph the  $R_n$  values generated assuming a uniform distribution of turns are labeled C. The  $R_n$  curves labeled B are created by a simulation that used the unimodal distribution of



**Figure 3.** Distribution of turn angles by species at the 10-cm scale. At the 3-m scale the distributions have been lumped for species because there was no statistical difference in their behavior.

**Table 3.** Results of Chi-square contingency tests comparing the histograms of turning at the 10-cm scale.

	<i>P. f.</i>	<i>P. h.</i>	<i>D. o.</i>	<i>O. l.</i>	<i>M. o.</i>
n =	878	328	418	369	179
<i>P. flavescens</i>					
<i>P. hispidus</i>	4.08				
<i>D. ordii</i>	44.32**	51.56**			
<i>O. leucogaster</i>	23.87**	26.10**	13.11**		
<i>M. ochrogaster</i>	2.34	6.88*	10.85**	6.43*	

The contingency table was performed by separating the data into three categories, straight, right and left turns.

n = number of turns

\* =  $P < 0.05$

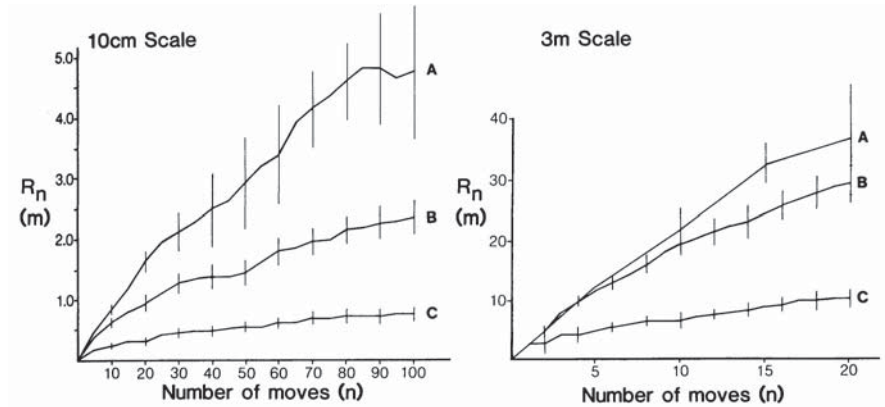
\*\* =  $P < 0.01$

turns, but makes no assumption of correlations between successive turns. At the 10-cm scale the unimodal distribution of turns from the trails of *P. flavescens* (Fig. 4) are used because we have the most data for that species at the 10-cm scale (an average of 89 angles quantified for 10 different individuals). At the 3-m level the distribution of turn angles used is from the summation of turns from *P. flavescens*, *P. hispidus*, and *D. ordii* (Fig. 4). Both simulations were run 100 times each to obtain estimates of the mean and standard error of  $R_n$ . Plotted in Fig. 4 as vertical bars are the 93% confidence limits of the mean of  $R_n$ .

Also plotted in Fig. 4 are the  $R_n$  values for real trails of *P. flavescens*, labeled A, at the 10-cm scale and for the summed heteromyid data at the 3-m scale. At the 10-cm scale there are dramatic, statistically significant differences between the uniform distribution simulation and the unimodal distribution ( $R_n$  changes by a factor of about 3.0) and also a significant difference between the unimodal curve simulation and real data (factor of 2.3). At the 3-m level there is a significant difference between the uniform and unimodal curve simulations (factor of 2.9), but little difference in the simulation assuming a unimodal distribution of turns and the real trails (factor of 1.2 and an overlap in confidence limits).

Another way to compare the simulated trails and the real trails was to contrast the number of times a trail crosses itself. Using the *P. flavescens* data at the 10-cm scale we found real trails crossed themselves an average of 0.2 times for the 10 trails we measured (average length = 8.9 m, or 89 10-cm segments). We simulated 11 trails that were 8.9 m in length using the assumptions of no correlation between successive turns and a real unimodal distribution of turn angles. We found the average number of crossings was 1.70. When there is no correlation and a uniform distribution of turns, the number of crossings averaged 26.09.

To test the model developed by Pyke (1978a) only two factors need to be



**Figure 4.** The relationship between  $R_n$  (the straight line distance traveled from a starting point after n moves) and n (the number of moves or the number of 10-cm or 3-m lengths along a trail) for the two simulated data sets and real data. The  $R_n$  curve labeled (A) is based on real data (*P. flavescens* at the 10-cm scale and a summation of species at the 3-m scale). The (B) curve was generated from the simulation assuming an unimodal distribution of turns and the (C) curves from the simulation assuming a uniform distribution of turn angles.

known, home range size and directionality of movement. In his model, turns were restricted to straight ahead, 90° to the right or left, and 180° reverse. To convert our data to this system we divided the turn angles into four categories also (i.e. the straight ahead category becomes any turns within 43° of straight ahead). Pyke calculated directionality as the proportion of turns in the straight ahead category minus the proportion of reverses. Using this method we calculated directionality for *D. ordii* (0.77), *P. hispidus* (0.80), and *P. flavescens* (0.77).

Although home ranges were not calculated, they might reasonably be placed between 0.23 and 0.80 ha. Pyke offered estimates of directionality for home ranges as a function of the scale at which the turn angles are measured (his Fig. 3). Based on this figure, the possible home range sizes just mentioned and the movement scale of 3 m, Pyke's model predicts directionality should be from about 0.76 to 0.80. This result is very close to the values actually observed here.

## DISCUSSION

### Habitat Use

The fluorescent pigment method for trailing small mammals produces an accurate picture of habitat use. Movement of rodents in the sandhills is often correlated with the sharp transitions found in the mosaic of vegetational types (Fig. 1). Further, there are strong differences among species in their use of habitat. All species studied have statistically significant differences in their habitat preference except *Peromyscus maniculatus* and *O. leucogaster* on grid one.

The three largest species, *M. ochrogaster*, *Perognathus hispidus*, and *D. ordii*, are the most specialized in their preferences and have nearly non-overlapping distributions. During the summer months, *M. ochrogaster* is almost entirely in

the grass, a habitat that, based on area, is avoided by all other species studied in this community. *Dipodomys ordii*, on the other hand, shows a preference for the open habitat and rarely entered the grass or sage habitat. *Perognathus hispidus* prefers the grass-forb habitat and is found only rarely in the open and grass areas. The pattern we find is a transition from *D. ordii* to *P. hispidus* to *M. ochrogaster* as the habitat changes from open to grass. These findings are in general agreement with studies done in other areas on these same or similar species of rodents. Several studies have determined that *Dipodomys* prefers the open habitat and *Perognathus* prefers areas of denser vegetation (Lemen and Rosenzweig 1978, Brown 1973, Price 1978), and *Microtus* is a species of the grassland (Getz 1961).

The remaining species, *P. flavescens*, *P. maniculatus*, and *O. leucogaster*, are more generalized in their preferences of habitats. All three of these species are found in the grass-forb habitat more often than expected by the area of that habitat.

Both *P. hispidus* and *P. flavescens*, species that concentrate their activity in the grass-forb and sage habitats, are inactive in the winter months. We wondered if during the inactivity of *Perognathus* there was any alteration of habitat use of *D. ordii* and *M. ochrogaster*. Data collected in February indicate that the foraging pattern of *D. ordii* is unchanged from the summer. Interestingly, the single *Microtus* captured during the winter was using both grass and grass-forb habitats. In the summer *Microtus* never set foot outside the grass habitat.

We also compare the pigment and trapping methods. The results are similar, but the fluorescent method gives the habitat preferences with relatively few captures. Further, the fluorescent tracking method gives additional information about the climbing and feeding habits as well as a detailed record of the trail the rodent took. These data are difficult to obtain by other methods.

#### Analysis of Pathways

The distributions of turn angles are in general agreement with the observation from several studies that animals tend to have a uni-modal distribution of turns with the peak centered at the straight ahead direction (Kleerekoper et al. 1970, Smith 1974, Siniff and Jessen 1969; however, see the latter for information on the snowshoe hare).

We also find a significant negative correlation between sequential changes in directions in the paths of all species. Rodents tend to correct their movements to compensate for previous turns. This compensation may help explain why the rodents rarely cross their own trails. The negative correlation between sequential turns has also been documented in other studies on widely different animals (Smith 1974 for European thrushes, Pyke 1978b for bumblebees). I

Both the uni-modal curve and the negative correlation between successive turns have been explained as adaptations to reduce the chance of revisiting areas just searched (Pyke 1978a, Zimmerman 1982), but little is known about the magnitude of their effects in real data. To quantify these effects, we investigated the number of times a trail crosses itself and  $R_n$  (straight line distance traveled from a starting point after  $n$  moves), two indices of how much a traveler is likely to re-search areas. The movement of *P. flavescens* indicates that at the 10-cm

scale the uni-modal distribution of turns has a strong effect on  $R_n$  and the number of times a trail crosses itself. This is true even though *P. flavescens* has one of the lowest percentages of straight ahead moves at the 10-cm level. We also find that the distribution of turns has a large impact on  $R_n$  and trail crossings at the 3-m scale.

The negative correlation between successive turns can also affect  $R_n$  and the recrossing rate. Inspection of Table 4 shows that for *P. flavescens* the negative correlation between successive turns explains only about 6% of the total variance in turn angles at the 10-cm scale. This low percentage is typical of all the species studied here. At first glance such low  $r^2$  values might suggest that negative correlations would have relatively little effect on the characteristics of the pathways. However, our simulations indicate that even this small negative relationship has a strong influence on trail recrossing and  $R_n$  (Fig. 4). At the 3-m scale there is not a significant negative relationship between successive turns. Our analysis indicates that there is little difference between real data and simulated data using the same distribution of turns (Fig. 4). Therefore, at the 3-m scale, but not the 10-cm scale, trails of these rodents are similar to the first order Markovian chain discussed by Kareira and Shigesada (1983) or Pyke (1978a). This difference at the 10-cm and 3-m level is paradoxical because it indicates that on the small scale, course corrections occur, while at the larger scale the trail is nearly a random walk.

Pyke (1978a), using methods of optimal foraging theory, recognized that the scale by which movements are measured is of critical importance in generating predictions of movement. However, his concern about scale was from a strictly geometrical point of view. The biological problems of the scale of movements have not been considered. It is our contention that the movements of rodents on a 10-cm scale and the 3-m scale reflect basically different phenomena. Although we have no hard evidence on exactly what the 10-cm and 3-m scales represent, we speculate that at the 10-cm scale the trail reflects search strategies,

**Table 4.** Results of a stepwise multiple regression with the present turn as the dependent variable.

Species	variable	F	P	R <sup>2</sup>	Slope	d.f.
<i>P. flavescens</i>	turn1	21.06	0.0001	0.062	-0.25	1, 320
<i>P. hispidus</i>	turn1	18.17	0.0001	0.107	-0.33	1, 149
<i>M. ochrogaster</i>	turn1	5.35	0.025	0.092	-0.30	1, 53
<i>O. leucogaster</i>	turn2	5.74	0.018	0.048	-0.21	1, 115
<i>D. ordii</i>	turn2	7.69	0.007	0.076	-0.28	1, 93

turn1 = independent variable, the angle of the last turn preceding present turn

turn2 = independent variable, the angle of the second to the last turn before the present turn

In all cases only one independent variable was significant at the 0.05 level. All relationships between the independent and dependent variables are negative.

foraging speed, or how different rodents treat obstacles. It may be that the small side-to-side motions reflect the speed of a rodent more than anything else. Bowers (1982) found that *Dipodomys* moves quickly over long distances, while *Perognathus* moves more slowly. His conclusions were that *Dipodomys* travels at high speeds between large clumps of seeds, and *Perognathus* ambles along foraging for scattered seeds all along the way (also see Thompson 1982). It seems likely that a fast-moving rodent would leave a straight trail, first because of the extra speed and second because of the inference that the animal may not be actively foraging, but is traveling from one seed concentration to another. At the 3-m scale the picture obtained is more how a rodent is using space in the sense of Pyke (1978a) and Cody (1971).

Pyke (1978a) suggested that rodents might be excellent candidates to test his model of movement and use of home range. Our investigation supports this conclusion. Rodent trails at the 3-m scale approximate the correlated random walks specified in his model. To determine the prediction of the model only two things need be known, scale at which movement is to be measured and size of home range. Our results indicate that Pyke's model does accurately predict the directionality of rodents at the 3-m scale. Another conclusion we can draw from the model is that if the species under study have home ranges that are approximately the same size (true for these heteromyids), then the movement patterns of the species should be similar. We obtain exactly this result in our study. At the 3-m level there is no difference in behavior in *D. ordii*, *P. flavescens*, and *P. hispidus*. The dissimilarity of movements at the 10-cm level has little effect on the results at the 3-m level. *Perognathus hispidus* and *Dipodomys ordii* are opposite extremes in behavior at the 10-cm level, but show no difference at the 3-m level. This correspondence supports the idea that movement patterns at the 3-m scale have converged in these species to minimize re-searching areas just visited.

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