

# ACTIVITY, MOVEMENT AND HOME RANGE OF VIRGINIA OPOSSUM (*DIDELPHIS VIRGINIANA*) IN FLORIDA

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## ABSTRACT

The activity and spatial organization of the Virginia opossum (*Didelphis virginiana*), a solitary didelphid marsupial, were studied in north-central Florida. Opossums were strictly nocturnal, and the activity level peaked between 2000 h and 0200 h. Activity was influenced by temperature. Below 8°C, duration of nightly activity decreased strongly with decreasing temperature. Above 8°C, activity tended to decrease with increasing temperature. Average nightly activity did not differ among months from August to December or between males and females. Opossums lived in well defined and at least seasonally stable home ranges with moderate to extensive home range overlap. Females tended to more exclusive space use and greater stability of home ranges than males. Males often shifted home ranges at the end of mating seasons. Three different measures of home range size were presented. Average values for males and females were 141.6 ha and 64.4 ha, respectively (corrected minimum convex polygon). Individual home range sizes of males were influenced by habitat, being larger in presumably poorer habitats, and by body size. Average distances moved per hour were 234 m in males and 178 m in females. Nightly movements of males and females averaged 1835 m and 1465 m, respectively (maximums 4665 m and 3973 m). Distances traveled were associated with temperature, home range size or body size. Very limited data from other regions suggest greater space use by opossums in the studied population.

## RESUMEN

En el centro-norte de Florida, se estudió la actividad y organización espacial de la comadreja de Virginia (*Didelphis virginiana*), el cual es un marsupial didélfido solitario. Las comadreas fueron estrictamente nocturnas y el nivel de actividad llegó a su máximo entre las 2000 hr y las 0200 hr. La actividad estuvo influenciada por la temperatura. Bajo los 8 ° C, la duración de la actividad nocturna disminuyó fuertemente con una disminución de la temperatura. Sobre 8 ° C, la actividad tendió a decrecer a medida que la temperatura aumentaba. El promedio de actividad nocturna no difirió entre meses, entre agosto y diciembre, ni entre hembras y machos. Las comadreas habitaron ámbitos de hogar bien definidos y estables al menos estacionalmente con

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moderada a extensa sobreposición de ámbitos de hogar. Las hembras tendieron a ser más exclusivistas en el uso de espacio y a presentar una mayor estabilidad en los ámbitos de hogar comparado con los machos. Los machos frecuentemente cambiaron de ámbito de hogar al término de la temporada de montas. Se presentaron tres diferentes medidas de tamaño de ámbito de hogar. Los valores promedio para machos y hembras fueron 141.6 ha y 64.4 ha, respectivamente (polígono convexo mínimo corregido). El tamaño de los ámbitos de hogar individuales de los machos estuvo influenciado por el hábitat, siendo más grandes en hábitats supuestamente más pobres, siendo además influenciados por el tamaño corporal. Las distancias promedio recorridas por hora fueron 234 m en machos y 178 m en hembras. Los movimientos nocturnos de machos y hembras promediaron 1835 m y 1465 m, respectivamente (máximos: 4665 m y 3973 m). Las distancias recorridas fueron asociadas con la temperatura, tamaño de ámbito de hogar o tamaño corporal. Datos muy limitados de otras regiones sugieren que esta población de comadrejas utiliza un mayor espacio.

## INTRODUCTION

The spatial distribution of an animal population is ultimately shaped by environmental factors, such as the quality and distribution of resources in space and time, intraspecific competition, and predation pressure (Clutton-Brock and Harvey 1978; Davies and Houston 1984; Wrangham and Rubenstein 1986). The spatial distribution, on the other hand, influences the social organization including the mating system, which in turn affects morphological, behavioral and other traits such as sexual size dimorphism (Clutton-Brock and Harvey 1978; Rubenstein and Wrangham, 1986; Ryser 1992).

The spatial organization of the Virginia opossum has been subject to uncertainty. In his review, Gardner (1982) termed opossums solitary wanderers that rarely remain in any area and do not maintain separate home ranges. More recent studies (Gillette 1980; Allen et al. 1985; Seidensticker et al. 1987), however, suggested that opossums live in well defined and at least seasonally stable home ranges.

Here I present results on space use and home range size of opossums in north-central Florida. The opossum is a nocturnal, solitary, omnivorous marsupial about the size of a house cat, ranging over most of the eastern United States and south to Costa Rica, and showing a wide range of ecological tolerance (Gardner 1982). In Florida, opossums have two breeding seasons of about four weeks each in January/February and May, respectively (Ryser 1992; Sunquist and Eisenberg 1993). The young are born after a 13-day gestation, weaned at the age of about 100 days (Reynolds 1952; Wright 1989), and are sexually mature by the end of the year. The data were collected during a two-year radio-tracking study as an essential basis for understanding the opossum mating system and male mating strategies (Ryser 1990, 1992). Additionally, I collected quantitative data on activity and movements to investigate geographical and sex differences in these parameters as well as individual and environmental factors influencing activity and movement. Despite the opossum's abundance in many parts of its range, reliable, quantitative data on activity, movement, and home range size are rare. Gillette (1980) and Allen et al. (1985) presented data on home range size and Allen et al. (1985) and Seidensticker et al. (1987) on nightly movements. Activity has been studied in captivity by McManus (1971) and in the field by Seidensticker et al.

(1987). So far there has been no study of an opossum population in Florida, an environment that differs, particularly in temperature regime, markedly from that of other studied populations in Wisconsin or Virginia. Moreover, few attempts have been made to identify the factors that could account for the often considerable individual variation in space use and activity (Seidensticker et al. 1987; Kissell and Kennedy 1992).

## ACKNOWLEDGEMENTS

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## STUDY SITE AND METHODS

The study was conducted at the Katharine Ordway Preserve of the University of Florida, located 40 km east of Gainesville in Putnam County, north-central Florida. The 37 km<sup>2</sup> tract consists of a mosaic of habitat types (see Franz and Hall 1991 for details): Permanent and temporary lakes and ponds, freshwater marshes, swamp forests, mesic hardwood hammocks, sand live oak hammocks, sand hill high pine forests (tree cover dominated by *Pinus palustris* and *Quercus* sp., ground cover dominated by wiregrass *Aristida stricta*), and grass-dominated areas derived from former agricultural lands (old fields, pastures, and orange groves). Maximum elevation is 55 m above sea level.

The climate is characterized by hot, humid summers and cool, mild winters with freezing occurring at least on a few days or nights. Mean daily maximum and minimum temperatures are 26.7°C and 14.0°C, respectively, varying from 19.3/5.9°C in January to 32.5/21.7°C in July and August. Mean annual rainfall is 133 cm, with 60% falling in the summer months May to September (data for Gainesville, from the National Oceanic and Atmospheric Administration).

Information on the spatial organization of opossums and its dynamics was gathered by trapping and radio-tracking opossums mostly in an approximately 8-km<sup>2</sup> core study area in the center of the preserve from January 1986 to February 1988. Opossums were trapped in Tomahawk live-traps baited with fish and dry dog food. In 1986 and early 1987, during the weeks prior to the breeding seasons, I attempted to trap all opossums in the study area, resulting in 1028 trap-nights. From March 1987 to February 1988, D. Wright and myself conducted four trapping sessions with 140 trap sites covering most of the preserve. During each trapping session in March/April, July/August, October/November and December-February we ran the trap lines for 6 to 8 days. Opossums were measured, ear-tagged at their first capture, and pouch young

were toe-clipped for permanent identification. Adult animals in the study area were fitted with radio-collars (Cedar Creek Bioelectronics, Bethel MN), weighing about 35 g. In 1987, radio-tagged individuals included subadults trapped in October/November, weighing at least about 1 kg. Data were collected by radio-tracking opossums at night during breeding seasons (see Ryser 1992), by nightly interval-tracking (see below), and by regularly locating opossums in their dens during the day at all seasons. A total of 113 opossums (70 males and 43 females) was radio-tagged in the course of the study.

I studied the activity and movements by locating 28 different radio-tagged males and females at 1-hour intervals, usually on four consecutive nights per month from August to December (non-breeding season, except for four opossum-nights of data from January), yielding 147 opossum-nights of data. While still inactive, the animals were checked about every 15 to 30 minutes to allow a reasonably exact determination of the onset of activity. Activity was detected by the changing strength of the radio signal caused by the animal's movements. Similarly, the end of activity was determined by a lack of movement and was verified an hour later as well as on the next day, when the actual den sites were checked. Nightly movements were plotted on a map (scale 1:6666), and distances traveled were measured as the sum of straight-line distances between consecutive locations. Two measures were calculated: Mean distance moved per hour and total distance traveled per night. Factors influencing these two variables were investigated by means of partial correlation analyses. Variables examined included nightly minimum temperature (obtained from a weather station in the preserve), home range size, body size (head and body, millimeters), and age (months). Age was known based on marking of the animals as pouch young or juveniles/subadults or was estimated based on tooth wear and appearance. The short life-span of opossums and seasonal births facilitated age determination (Sunquist and Eisenberg 1993). The level of significance was set at 0.05 divided by the number of examined factors (Bonferroni correction), thus 0.01.

Data for determining home ranges consisted of all available location points of radio-tagged opossums, that is daytime locations (animals inactive) and nighttime locations (animals active) of all seasons, except for male locations during the breeding seasons. Most data were collected in the period just before and during breeding seasons and on the nights when animals were located hourly. Tracking periods from the time of radio-tagging until individuals died, were lost, or transmitters were removed, and thus the time frame for estimation of home ranges of individual opossums averaged 118 days in males and 133 days in females. Sizes and shapes of home ranges containing at least 20 location points were calculated using the computer program McPAAL, version 1.2 (M. Stuwe, National Zoological Park, Front Royal VA 22630). I calculated three different measures of home range size based on the minimum convex polygon and the harmonic mean model (Dixon and Chapman 1980): (1) the minimum convex polygon (MCP), (2) the MCP with inaccessible areas (lakes >1 ha, wet prairie) subtracted (MCPcorr), and (3) the harmonic mean 95% isopleths (HM95). A grid of 15x15 cells was chosen for the harmonic mean calculations.

If opossums clearly shifted their area of activity and did not return to the previously used area, the new location points were excluded or two separate home ranges were calculated if data were sufficient. For the calculation of average home range sizes, the data set was restricted to values based on at least 40 location points in order to reduce the effect of sample size on home range size. Factors associated with home range size (MCPcorr) were investigated by a partial correlation analysis. Examined variables included age, body size, tracking period (days), number of location points (N), and the percentage of total home range size comprised of sandhill and of old fields and pastures. These are areas of presumably low productivity with regard to food abundance. Studies on population densities and habitat use of rodents (Brand 1987; Jones 1989), and an analysis of habitat use of opossums showing that these two habitats were used significantly less than expected based on their area (Ryser 1990), supported this notion.

Means were compared for significant differences using student's *t*-test (two-tailed). The level of significance was set at 0.05.

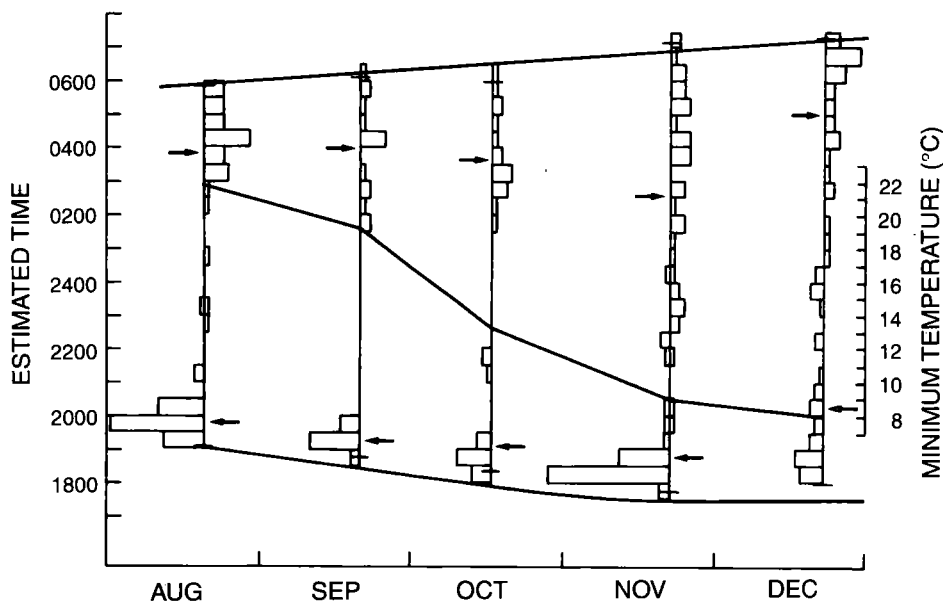


Figure 1. Distribution (half-hour-intervals), means (arrows), and extremes (1) of the individual onset and end of nightly activity from August to December. The lower and upper bordering lines represent the time of sunset and sunrise. Average nightly minimum temperatures of each month are connected by straight lines. Minimum temperatures varied from 21-22°C in August, 19-20°C in September, 12-14°C in October, 1-16°C in November, and 0-15°C in December. Samples sizes for the five months are 35, 16, 17, 43, and 32, respectively. Data from males and females were pooled.

## RESULTS

### Activity and Movement

Opossums were strictly nocturnal (Figs. 1, 2). Figure 1 shows the distribution of the onset and end of nightly activity from August to December in relation to sunset and sunrise and minimum nightly temperatures. Usually opossums emerged about one hour after sunset and were active for a varying period of time before reentering a den. However, some animals became active only later at night. Leaving the den late was more common in cool nights. Minimum temperature at nights when opossums emerged from dens after 2200 h averaged 8.0°C ( $n=12$ ) compared to 13.2°C of all considered nights. The time activity ended varied more strongly than the time of the onset of activity. The scatter increased in November and December as average nightly temperatures declined and the variation in temperature increased. Average nightly activity ( $\pm$  S.D.) from August to December was 8.01 h ( $\pm$  1.67), 8.81 h ( $\pm$  1.47), 8.54 h ( $\pm$  1.24), 7.85 h ( $\pm$  3.13) and 8.22 h ( $\pm$  3.66) and did not differ significantly among months (Kruskal-Wallis test,  $df=4$ ,  $H=4.28$ ,  $p=0.37$ ).

Maximum activity is reached between 2000 h and 0200 h (Fig. 2), when on average up to 97.4% of the monitored animals were active (cold nights excluded).

Individual nightly activity varied greatly in duration and tended to be slightly, but not significantly longer in females than in males (Table 1,  $t_{145}=0.97$ , ns). Activity was neither correlated with home range size ( $r=0.01$ ,  $n=147$ ) nor with age ( $r=-0.03$ ) or body size ( $r=-0.04$ ), but was clearly influenced by temperature (Fig. 3). Activity increased linearly with temperature up to about 8°C ( $y=2.561+0.828x$ ,  $n=33$ ,  $r^2=0.571$ ,  $p<0.0001$ ). Above this threshold activity was less temperature-dependent, but tended to decrease with increasing temperature ( $y=11.053-0.136x$ ,  $n=114$ ,  $r^2=0.129$ ,  $p<0.0001$ ). Based on the former equation, activity is predicted to cease altogether at nightly minimum temperatures of -3°C. Nightly inactivity was recorded in only one case (minimum temperature 0°C), but several additional cases occurred during the mating season in January at nightly lows of -7° to +6°C.

Distances moved per hour and per night varied widely, but were significantly greater in males than in females ( $t_{140}=3.90$  and 2.53, respectively,  $p<0.01$  and  $<0.05$ , Table 1). Maximum recorded movements within an hour reached 950 m in males and 790 m in females. Maximum distance traveled per night was nearly 4 km in females and 4.7 km in males. A partial correlation analysis showed that distance moved per hour in males was positively associated with home range size and minimum nightly temperature, whereas in females only body size exerted a significant positive effect (Table 2). Distance traveled per night is a function of the duration of activity and of average distances moved per hour and is therefore influenced by the same factors that influence activity and average hourly movement (Table 2). Thus males with large home ranges tended to move farther than males with small home ranges and

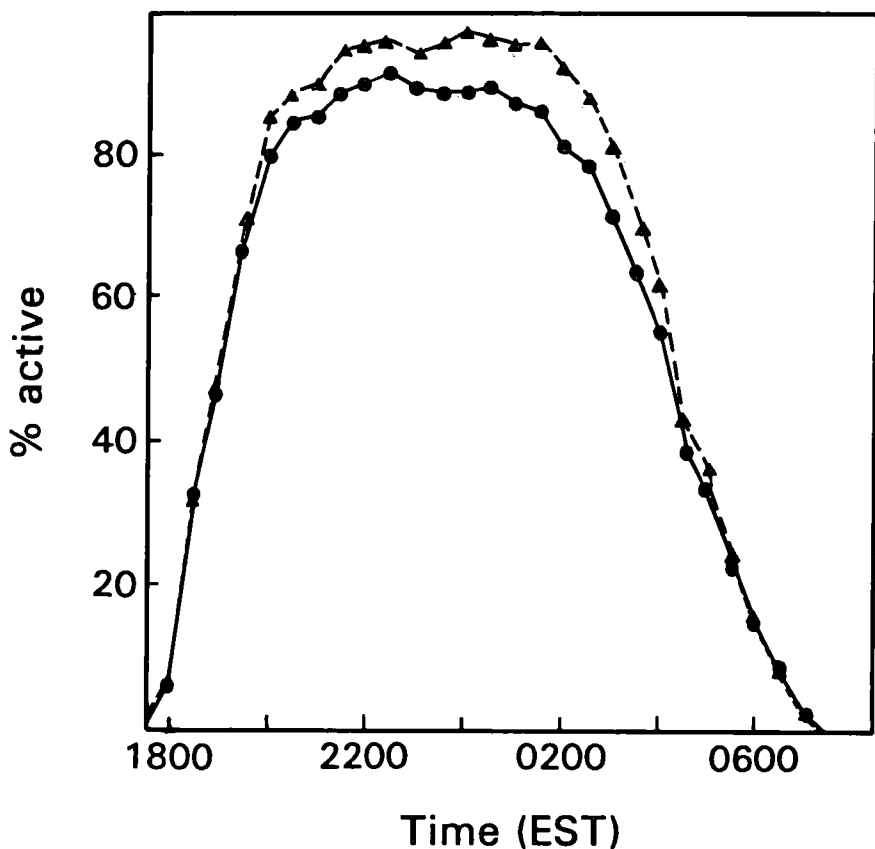


Figure 2. Percentage of opossums active as a function of the time of night. ● = all nights included, ▲ = only nights with a minimum temperature  $>8^{\circ}\text{C}$  included.

movements decreased with decreasing temperatures. In females, low temperature negatively affected nightly movements, certainly through its effect on activity.

Nightly foraging movements of opossums, as revealed by radio-tracking at 1-hour intervals, were usually erratic and unpredictable. However, nightly routes also included loops and, rarely, straight-line movements. Opossums sometimes moved at a fairly regular speed during the night while others remained within a small area for several hours. During a 4-day-period of interval-tracking, individuals with medium to large home ranges often stayed within a certain but, compared with other months, changing part of their home range, suggesting that opossums may exploit different parts of their home range at different times.

Table 1. Duration of activity and distances traveled per hour and per night of opossums radio-tracked at 1-hour intervals. All: all nights, >8°C: nights with minimum temperatures of more than 8°C, N=number of opossum-nights.

	Activity (h)		Distance (m) traveled			
			per hour		per night	
	all	>8°C	all	>8°C	all	>8°C
<b>Males</b>						
Mean	7.86	8.56	234	243	1835	2015
S.D.	2.72	1.91	84.1	81.5	880.8	768.4
Range	0.83-12.0		83-466		100-4665	
N	89	69	88	69	88	69
<b>Females</b>						
Mean	8.31	9.33	178*	177	1465*	1630
S.D.	2.77	1.56	81.0	76.5	787.6	745.4
Range	0-13.0		60-439		100-3973	
N	58	45	54	43	54	43

\* One case of inactivity excluded.

### Spatial Organization

Female opossums lived in fairly well separated and fairly stable home ranges. As an example of spatial organization, Figure 4 shows female distribution in mid- winter 1987/88. During this period and the second breeding season (April/May) 1987, for which the data are considered the most complete, 0 to 100% and an average of 43% of the area of individual female ranges (MCPcorr, n=28) was overlapped by one or more other female home ranges. On one hand, this figure would be increased by untagged females living in ranges adjacent to the study area. On the other hand, it overestimates the actual degree of overlapping use, because the convex polygons do not take into account spatial or temporal differences in the extent various parts of the home range are used. Neighboring females often seemed to exploit overlapping areas during different periods of time, sometimes caused by slight home range shifts, or less intensively than exclusively used areas. In one case of complete home range overlap, the individuals were a mother and daughter, and two other cases of complete overlap involved suspected close relatives. In areas with a presumably greater food abundance,



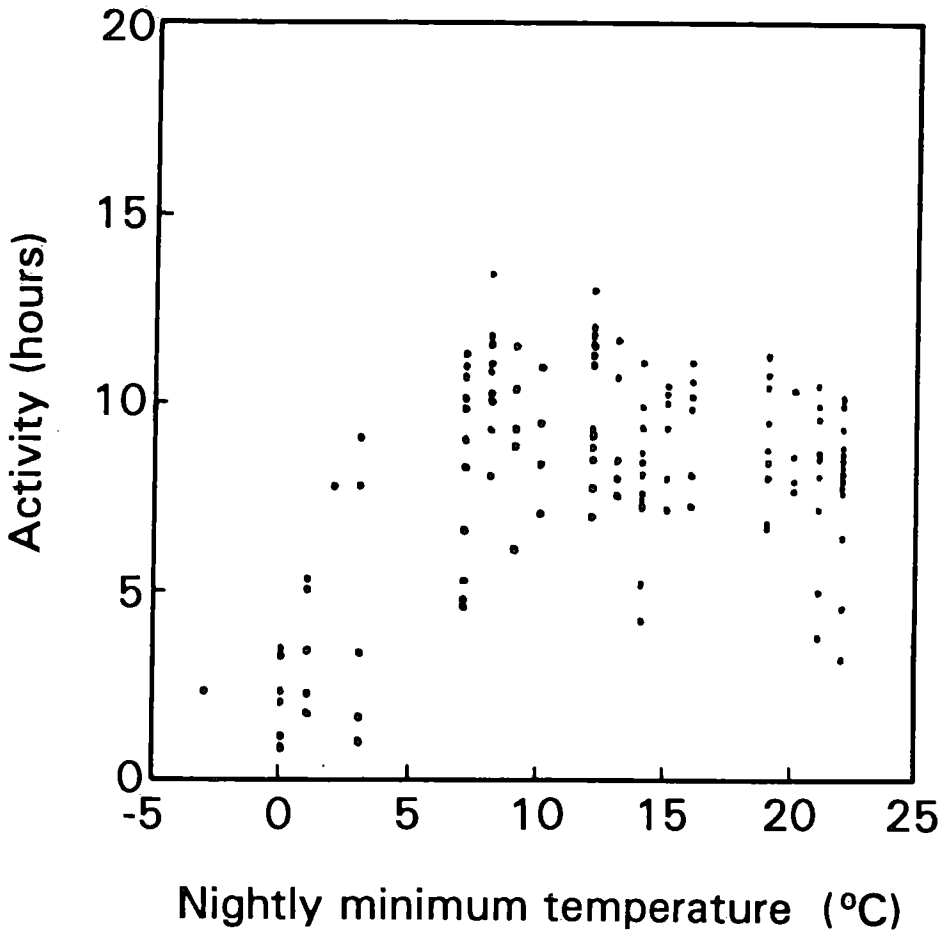


Figure 3. Duration of activity as a function of nightly minimum temperatures.

such as along lakes and in mesic forests, density and home range overlap was apparently greater than in less productive areas.

Most females stayed in a well defined area until death. Of 19 females tracked for a period of more than three months, only two clearly shifted their home range about 500-1000 m, and a third continuously expanded her range as she grew older. None of the radio-tagged females dispersed, but two were lost without being retrapped, so were possible dispersers. One female was apparently trapped and radio-tagged during a dispersal movement. She disappeared the next day, but one of her small young was trapped 4.7 km away. One marked female from outside the study area dispersed 2.8

Table 2. Partial correlation between mean distance traveled per hour, distance traveled per night or home range size and various potentially influencing factors (see method for definitions). Level of significance is set at 0.01 (Bonferroni correction).

		Males	Females
		(n=88)*	(n=55)
Distance/hour	Min.temp.	r=0.27*	r=0.24
	Range size	r=0.47**	r=-0.18
	Body size	r=0.03	r=0.36*
	Age	r=0.01	r=0.13
Distance/night	Min.temp.	r=0.38**	r=0.55**
	Range size	r=0.44**	r=-0.18
	Body size	r=0.01	r=0.27
	Age	r=-0.11	r=0.11
		(n=33)*	(n=33)
Home range size	Habitat	r=0.40*	r=0.31
	Body size	r=0.40*	r=-0.11
	Age	r=0.14	r=0.26
	Track period	r=-0.18	r=0.32
	N of locations	r=0.57**	r=0.30

\* p<0.01  
 \*\* p<0.001

km. Both dispersal movements occurred when females were carrying young in their pouch. Vacancies caused by death were rapidly filled by immigrants (unmarked females) or young. Female young were philopatric and usually established a home range close to or even within that of their mother. During their first breeding season in January, female young of 1987 were trapped or located an average of 752 m (maximum 1950 m, n=12) from their mother. During the study period, female young were in three cases known to have established a home range within their mother's range. In one case the young female took over her mother's range when the mother died after weaning of her young.

Male home ranges showed greater overlap than female home ranges, because male ranges were considerably larger at similar male population density (Fig. 5). In summer 1987, for which the most reliable data from the non-breeding season are available, 0% to 100% or an average of 63% (n=12) of the area of male home ranges was overlapped by other male ranges. It was not unusual to find three or four males exploiting the same area. In no case were adult males exploiting the same area known to be related to each other or to females living within their ranges.

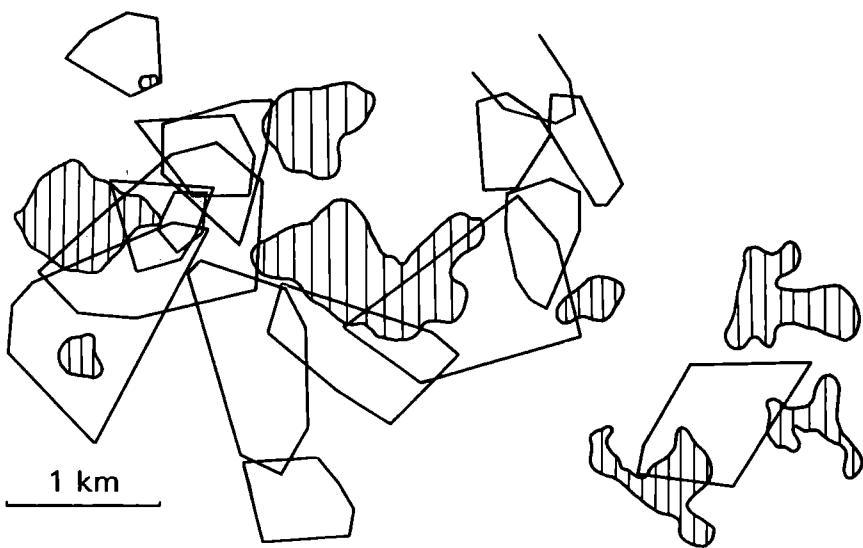


Figure 4. Distribution of female home ranges (minimum convex polygons) in the study area in winter 1987/88. Hatched areas are lakes.

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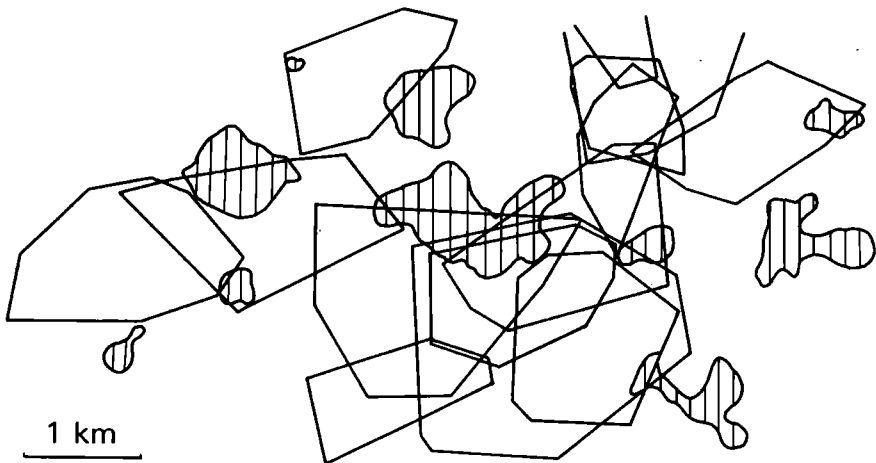


Figure 5. Distribution of male home ranges in the study area in summer 1987.

Table 3. Means, standard deviations, and extremes of male and female home range sizes (ha). MCP=minimum convex polygon, MCPcorr=MCP with unusable area subtracted, HM95=harmonic mean 95% isopleth. The data include home range calculations based on more than 40 location points.

	Number of location points	Tracking period (days)	MCP	MCPcorr	HM95
Males (n=23)					
Mean	90.0	142.6	155.9	141.6	170.6
S.D.	46.1	69.8	113.1	103.1	90.9
Range	46-217	34-275	33.7-564.1	31.1-520.4	41.7-433.3
Females (n=23)					
Mean	113.9	161.8	73.1	64.4	86.0
S.D.	70.3	112.7	45.8	40.7	46.7
Range	43-285	54-400	8.1-195.2	8.1-186.6	14.6-220.5

Male spatial structure was less stable than that of females, mainly because of range expansion during breeding seasons, frequent shifting of home ranges at the end of breeding seasons, and because of natal dispersal. During mating seasons, males expanded their home range considerably (see Ryser 1992). After breeding seasons, males retreated again to a smaller range. But only 11 of 19 males for which sufficient data from breeding and non-breeding seasons are available, retreated to the same area as before. Eight males established home ranges in another part of the expanded breeding range, up to 3.8 km away from the previous home range. Among opossums trapped in July 1987, two males were caught 2.8 and 4.6 km, respectively, away from their original site of capture during the breeding season in April/May. One male was apparently trapped and radio-tagged during a dispersal movement at the end of the breeding season. He had moved 5.3 km when his collar was removed after 5 days. Between mating seasons, male home ranges were fairly stable. Of 21 adult males tracked for more than two months during non-breeding seasons, only two clearly shifted or expanded their home range. Four males were lost during non-breeding seasons (July, August) and could possibly have dispersed, although a failure of the transmitters is more likely.

Male young generally dispersed before or during their first breeding season (see Wright 1989). Contrary to other males, young males that were recorded dispersing during the breeding season did not expand home ranges prior to dispersal and thus did not seem to participate in mate searching. Their ranges averaged only 67.5 ha (n=6, compare with data below).

## Home Range

Home ranges varied greatly in size, ranging from 8 to 564 ha (Table 3). Male home ranges were on average about twice the size of female home ranges (MCP:  $t_{44}=3.25$ ,  $p<0.01$ ), irrespective of the method of calculation. HM95 tended to yield greater values than convex polygons (MCP): Means differed by 10 to 15% ( $t_{44}=0.31$  and 0.53 in males and females, respectively, both ns), and in 82% of all cases individual HM95 were larger than the corresponding MCP. Factors influencing individual home range size were examined by means of a partial correlation analysis (Table 2). In males, home range size tended to be positively influenced by habitat (see method for definition), body size, and number of locations. In females, none of the examined factors exhibited a coefficient significantly different from zero.

## DISCUSSION

### Activity

Opossums were strictly nocturnal and, outside mating seasons, none was found active before sunset or after sunrise. Most opossums left their dens at dusk and stayed active for a varying period of time before reentering a den, usually well before dawn. Consequently, the portion of active animals increased rapidly after dusk and reached its highest level from 2000 h to 0200 h before gradually declining to zero. McManus (1971) studied activity patterns in outdoor cages and found a similar curve in spring and summer. However, the increase in activity was slower, and no more than 85% were active at any time. In the present study, average nightly duration of activity ranged from 7.85 to 9.33 hours, depending on season, sample, and sex. Seidensticker et al. (1987) recorded average values of 8.23 to 10.95 hours, depending on season and sex, but with no significant differences among the groups.

Activity of opossums showed a temperature-dependence in two directions. At nightly lows below about 8°C, activity decreased linearly with decreasing temperature, whereas above this threshold, activity tended to decrease with increasing temperature. Decreased activity at low temperatures has been reported before in several studies. Gillette (1980) reported that activity of opossums in Wisconsin decreased rapidly as temperatures dropped below freezing, and that opossums did not leave their dens at temperatures below -15°C. Fitch and Sandidge (1953) and Fitch and Shirer (1970) found that opossums in Kansas stayed in dens for several days during extremely cold weather and that they sometimes foraged during the daytime after such cold periods. With activity starting to decrease already at 8°C and, as predicted by the regression, ceasing altogether at -3°C, opossums in Florida seem to react more sensitively to cold temperatures than opossums in areas with harsher climates.

Decreasing foraging activity at low temperatures is likely to be the consequence of increased energy expenditure and, at the same time, decreased foraging success, particularly concerning invertebrates and ectotherm vertebrates, leading to a negative energy balance at some low temperature. Increasing energetic costs already at moderately cold temperatures are suggested by the fact that opossums are not well adapted to the cold. Their pelage is sparse and has relatively poor insulative properties (Scholander et al. 1950 cited in McManus 1971; Hsu et al. 1988). Opossums start showing behavioral thermoregulation (e.g. shivering) already at around 10°C (McManus 1969; Dills 1972), and they are unable to maintain average body temperatures below 3°C (McManus 1969). In north-central Florida, the generally mild winter temperatures certainly do not seriously limit the opossum's energy intake, but the favorable conditions may allow the animals to reduce activity already at less cold temperatures compared to opossums in more northern parts of their range with longer lasting freezing temperatures.

The decrease of activity with increasing temperatures above 8°C is most likely related to other factors associated with temperature. However, average duration of nightly activity did not differ among months, excluding the possibility that decreasing activity at higher temperatures was a seasonal effect. Perhaps it was greater food abundance at higher temperatures which allowed opossums to reduce activity in warm nights.

The time of the onset of nightly activity did not show much individual variation, as most animals left their dens within about an hour. However, a few individuals started activity distinctly later at night, and the onset of activity shifted seasonally according to the time of sunset. Due to varying individual duration of activity, the temporal distribution of the end of activity varied to a much greater degree than did the distribution of the onset. In November and December, apparently as a consequence of the much greater variation in nightly temperatures, including low values close to freezing, the patterns of activity clearly deviated from that in August to October. However, despite similar temperature regime, opossums behaved differently in the two months. In November, the pattern of the onset of activity corresponded to that of the earlier months, but increased individual variation in the duration of activity led to a great scatter in the time activity ended. Average nightly activity, however, was only slightly lower than in the previous months, because the long nights allowed opossums in mild nights to stay active for up to 13 hours. In December, on the other hand, increased individual variation in activity was expressed primarily as variation in the onset of activity.

Other factors beside temperature that may be responsible for the individual variation in nightly activity may include the physical condition of the animals, previous and current weather conditions, and foraging success. Opossums seemed to stay active longer than expected following periods of cold nights. Individual differences also seemed to exist, as it was often the same animal that stayed active the longest, and as opossums sometimes left and entered dens in the same order on each of the four nights of consecutive tracking.

## Spatial Organization

The opossum is not necessarily nomadic, as suggested by Hunsaker (1977), Gardner (1982), and others. Under stable environmental conditions, the opossum's spatial organization is characterized by fairly even spacing among individuals and at least seasonal stability of the spatial structure. There are sexual differences, however, with females having smaller home ranges and tending to more exclusive use and greater stability of home ranges than males. The impression of earlier capture-recapture studies of an unstable spatial structure may have been, among others, the result of the males' expansion of home ranges during, and frequent shifting of home ranges after mating seasons (Ryser 1992), which could cause males to be trapped several kilometers from their usual area of activity.

The data from this study suggest that opossums have a highly flexible strategy of space use. On one hand, females exploit much of their home range exclusively, which allows the exploitation of predictable resources with minimal competition. On the other hand, mutual tolerance allows the opossum, as an omnivorous, opportunistic feeder, to jointly exploit high quality areas or clumped food supplies, such as fruiting trees, amphibian breeding ponds, or animal carcasses. In May 1987, an amphibian breeding pond was visited by four opossums almost every night. At close distance, however, overt aggressive behavior prevailed. Opossums also frequently shifted foraging areas within home ranges after days or weeks, probably to react to temporal and spatial changes in the distribution and abundance of food. Although I could not compare seasonal home ranges due to a lack of adequate data, there seemed to be no obvious shifts of home range related to particular seasons. Except for cases of aggression at common feeding places, there was no evidence for physical interactions among neighbouring individuals, suggesting that exclusive areas in female ranges were maintained by mutual avoidance. A similar spatial system was found by Charles-Dominique (1983) in several South American didelphids and by Sunquist et al. (1987) in *Didelphis marsupialis*.

Female reproductive success in polygynous mammals such as the opossum is usually limited by access to adequate resources, such as food and shelter (Trivers 1972). Male reproductive success, on the other hand, is largely limited by access to mates (Ryser 1992). Male spatial distribution is therefore expected to be influenced not only by ecological factors, but also by the mating system and the distribution of females. The sexual difference in space use, which has also been observed in many other mammals (Harestad and Bunnell 1979), therefore, most likely is related to a great degree to the male's reproductive strategy, which includes covering numerous female home ranges during mating seasons (Ryser 1992). The notion that sex hormones influence greater space use in males is supported by the fact that a male castrated prior to maturity exhibited a home range size (MCP 68.6 ha) typical of a female. Some of the sexual difference in home range sizes, however, is also expected

to be due to the larger body size of male opossums (means 2.73 vs. 2.08 kg) and consequently greater energetic needs (Harestad and Bunnell 1979; Reiss 1988).

### Home Range and Movement

The minimum convex polygon has often been criticized for its sample-size bias, sensitivity to extreme locations, linear borders, and because it may include large unused areas (Jennrich and Turner 1969; Dixon and Chapman 1980). In the present study, however, unused areas consisted mostly of lakes and wet prairie which could easily be excluded (resulting in MCPcorr). Extreme locations were very rare and did not represent a serious bias. The harmonic mean isopleths, on the other hand, are related to the intensity of use and can define home ranges of any shape while being largely insensitive to extreme locations (Dixon and Chapman 1980). However, although the limits of the 95% isopleths roughly followed the distribution of data points, the model was not able to closely delimit the areas of activity, and it could include large unused areas while excluding particular location points. This makes the method difficult to use in quantitative studies of habitat use (Ryser 1990). HM95 were also in most cases larger than convex polygons, the difference being considerable in cases with clumped location points. The same effect was also observed by Spencer and Barrett (1984). Additionally, a closer examination of the results showed that HM95 were only slightly less sensitive to varying samples sizes than were MCPs (Ryser 1990).

Therefore, I consider the corrected minimum convex polygon the most reliable home range size estimate. With average values of 64.4 and 141.6 ha for females and males, respectively, they are larger than values reported by Gillette (1980) from Wisconsin (females: 51 ha,  $n=9$ ; males: 108 ha,  $n=5$ ) and by Allen et al. (1985) from Georgia (females: 22 ha,  $n=5$ ; males: 78 ha,  $n=2$ ). However, these were based on 95% convex polygons and a modified minimum area method, respectively, so possibly underestimated home range sizes compared to this study. Sunquist and Eisenberg (1993) found a similar mean home range size (58.7 ha,  $n=18$ ) for female opossums on the Ordway preserve. Values based on earlier capture-recapture studies (see Gardner 1982) can not be considered comparable to those of radio-tracking studies. Quantitative data on nightly movements of opossums are equally rare. Allen et al. (1985) and Sunquist et al. (1987, for *D. marsupialis*), both using 2-hour tracking-intervals, reported values of 1278 (males) and 1026 m (females), and 1376 (males) and 1025 m (females), respectively. Seidensticker et al. (1987) reported values of 1137 to 1550 m depending on sex and season. The opossums in Florida thus tended to travel farther in search of food, which corresponds to the possibly larger home range sizes and may reflect a lower overall food density in the study area. The notion that differences in space use are correlated with habitat productivity is supported by the finding that the proportion of sandhills and former agricultural lands, areas of



presumably low food abundance, was positively associated with male and slightly positively associated with female home range sizes, suggesting that home ranges are larger in poor habitats where opossums are expected to range more widely to satisfy their metabolic needs. Additionally, a quantitative study of habitat use showed that opossums avoided sandhills and former agricultural lands compared to the proportion of these habitats (Ryser 1990). Kissell and Kennedy (1992) in Tennessee, on the other hand, did not find a correlation between habitat parameters and the number of opossums trapped.

The positive relationship of body size with home range size in males may also be the result of increasing energetic needs of large individuals. The same explanation may hold for the influence of body size on movements in females. The correlation between home range size and movement in males may be related to the habitat. As was shown, large home ranges tended to be associated with a greater portion of presumably poor habitat in the range, which could force these opossums to travel farther to compensate for the lower food density. In the future, field experiments involving the feeding of selected individuals might help elucidate the relationships between temporal and spatial food availability, energetic needs and home range size, movements, or activity.

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