A Radiotelemetric Study of Spatial Relationships in the Opossum

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ABSTRACT: Habits of 27 opossums were studied by attaching small radio transmitters and trailing them on the University of Kansas Natural History Reservation in 1966 and parts of 1965 and 1967. Activity is normally nocturnal and during the day each animal stays in a den. Most of the 88 dens located were in underground cavities of hilltop limestone outcrops; others were among tree roots in cutbanks of gullies; relatively few were in miscellaneous situations such as hollow trees, old buildings, or burrows away from rock outcrops. The average sojourn at a den is 2.2 days and each opossum uses many different dens but returns frequently to each of several favorite dens. An adult opossum forages from its den over an area with mean radius of 620 m but tends to stay much closer to its den. Extent of movement and frequency of shift were not closely correlated with season or temperature. A newly independent, young opossum tends to stay within a relatively small area at first, and to extend its range by gradual stages. Of nine young opossums that were trailed, three were preyed upon by the horned owl.

INTRODUCTION

Autecological studies over the past 20 years at the University of Kansas Natural History Reservation have involved many of the most common species of vertebrates living there. An early and relatively small-scale study involved the opossum (*Didelphis marsupialis*); from late 1949 to early 1952, 117 were live-trapped and marked by toe-clipping and 276 recaptures were recorded (Fitch and Sandidge, 1953). These records yielded information concerning habitat preferences, behavior, movements, food habits, and the composition and density of the population. Interest in the opossum on the area was revived in 1965 because of the development of small radio beacons which could be attached to free-ranging animals, making it possible to trail them in the field and to obtain types of information supplementing the data gained earlier. In our renewed study relatively few opossums (18 adults and nine young) were involved and attention was focused on detailed histories of individual animals. Effort was concentrated on studying spatial relationships and gathering information not readily obtainable from live-trapping. The opossums themselves were not often seen; but once equipped with a radio transmitter, each could be trailed and its location determined at any time of the day or night.

MATERIALS AND METHODS

The radio-tracking system developed for this study, as modified for the study of marmots, has already been described (Shirer and Downhower, 1968). Briefly, the system consisted of three basic com-

ponents: a transmitter attached to the animal to broadcast a beacon signal; two types of receivers to detect the signal and identify the animal from its radio frequency; and assorted types of antennas to pick up the signal and determine its bearing.

EQUIPMENT

The transmitters were crystal-controlled, self-pulsed transistor oscillators operating in a band from 26.5 to 26.65 MHz. They were constructed on rigid, circular collars formed from acrylic strips 4 mm thick and 13 mm wide. The collars were completed by wrapping with fiber-glass tape and dipping in epoxy or acrylic varnish. Their weight ranged from 25 to 35 g. Several of the opossums used early in our study were equipped with a harness of nylon webbing to hold the collar firmly in place. These harnesses were soon found to be both harmful and unnecessary. A collar that was barely large enough to slip over the animal's head remained in place and generally seemed to be ignored.

Four different combinations of receivers and antennas were used in locating animals in the field. A stationary receiver with a large rotating beam antenna at the Reservation headquarters served to indicate the approximate location of the animals within a 200- to 400-m range. Areas accessible by road were searched with automobiles equipped with whip antennas and portable receivers. Seven rotable Yagi antennas well spaced over parts of the area remote from the headquarters increased the range of our portable receiver and permitted searching of large areas inaccessible by road. These three methods were used in the early stages of search, but the small portable receiver with direction-finding loop antenna was always used for following clues and final trailing of the animal to its den.

PROCEDURES

Our study was made primarily on the University of Kansas Natural History Reservation. The opossums used were nearly all live-trapped in a small area near the Reservation headquarters, mostly at a garbage pit, at the buildings, or at the margin of a small pond. Usually the animal was released within a day or two after capture, equipped with a collar and radio transmitter; but sometimes several days elapsed before a transmitter was available.

Routinely, we attempted to locate each animal each day in its den. Occasionally extremes of weather or the pressure of other duties prevented us from attempting the daily search. Frequently it happened that extensive search proved unfruitful and for one or several days an animal was not found, though later relocated. When the search for any particular animal was unsuccessful, there was no immediate means of determining whether the transmitter had failed, because of breakage or run-down battery, or whether the animal had merely shifted to a new and unexpected location. Sometimes retrapped animals were found to be carrying damaged or run-down units that were

no longer transmitting. Lost animals were not discounted permanently until many hours had been spent in concentrated search. Nevertheless, occasionally such animals were rediscovered by chance after a lapse of weeks, still transmitting signals.

A relatively small part of our effort in the field was devoted to nighttime tracking of animals that had left their dens and were actually foraging. Usually it was difficult to locate such free-ranging animals with any degree of precision. Active opossums were shy and at night usually could not be approached closely enough to be seen. Instead, positions were determined approximately by triangulation with compass readings taken from two or three different points.

DENS OF THE OPOSSUM

TYPES OF DEN SITES

Inactive opossums spend their time in dens sheltered from the weather and from most natural enemies. An opossum in its den is usually in deep sleep and requires several seconds to become fully aroused at any disturbance. Den sites are mostly in two contrasting situations — hilltop limestone ledges or gullies. The combined Reservation and Rockefeller Experimental Tract, at the north edge of the Kaw River Valley, have peninsular flat hilltop areas extending across them, with a small escarpment exposing the Oread Limestone along the hilltop edges for a total length of 9 km. A lower layer of hard limestone outcrops on the slope about 6 m below the level of the hilltop. Along the edges of the cap rock and beneath loose slabs broken from it, and at the lower outcrop, natural cavities and those dug by animals provide secure shelter against digging enemies such as dogs and coyotes. In two small valleys and the lower slopes and hills around them are gullies with cutbanks having combined linear distances of approximately 9 km. The dens in the gullies usually had entrances among tangled tree roots where the roots were exposed by erosion. In many instances partly undermined trees tipped into the gullies, sometimes falling only part way until their tops were supported by adjacent trees. The small cavity remaining behind the mass of roots then provided a den fairly well sheltered against the weather and protected against predators.

Actual resting places of the animals were seen only on rare occasions. They were usually out of sight and out of reach. However, their depth and location could be estimated from the strength and variation of the signal as the receiver loop antennas were moved over the surface of the ground. Dens in the limestone outcrops were most often 0.6 to 1.2 m from the soil surface and were a meter or more in from the entrance. They were doubtless warmer and dryer than dens along the gullies.

Sixteen of the opossums studied were adults or large young which were trailed on many occasions. For the remaining 11 few records were available. Each of the 16 mentioned used one or more rock outcrop dens, but only eight used dens along gullies. Five used hollow trees,

but each of the remaining seven types of den sites was used by only one or two animals. The period spanned by an animal's use of a den for sleep or protection is considered a sojourn whether the animal emerged for a nightly foray and then returned, or, as often happened in severe weather, remained sleeping or resting during the night. In any case occupancy of the den was temporary. Table 1 shows that 88% of the sojourns and 86% of the "opossum-days" were in dens that were situated either at rock outcrops or at gullies.

Each animal on the average spent nearly 40% of the sojourns (regardless of length) at one favorite den. More than 20% were spent at the next most preferred den. The remaining one-third of the sojourns was distributed among several or many dens, no one of which was used with much consistency. One adult male used only four dens over the five-week period that he was trailed, and 89.7% of his records involved a favorite den. Another adult male, the one for which the most records were accumulated, was trailed over a five-month period and was recorded from a total of 19 dens.

The majority of sojourns at a den spanned only one day and most of the longer sojourns spanned only two or three days; but the 304 recorded sojourns included exceptionally long ones of 12, 19, 20, 22 and 26 days. On occasional days when no search was made, it was assumed that each animal used the same den as on the previous day. This may have resulted in a slight bias toward erroneously long average and maximum sojourns if such an animal made a one-day sojourn elsewhere and then returned.

COMMUNAL USE OF DENS

For the 16 opossums on which most of our records were based, a total of 88 dens were recorded. Of these, 59 were along limestone outcrops (24 at the hilltop and 35 on the upper slopes at the stratum 6 m below the hilltop), 13 were along cutbanks of gullies, and 16

TABLE 1.—Amount of use of different types of dens by 16 opossums on the study area

Type of den site	Number of animals	Number of sojourns	Number of days
Hillside limestone outcrop	14	146	281
Hilltop limestone outcrop	12	58	93
Gully	8	66	133
Old house	1	3	35
Hollow tree	5	14	17
Squirrel nest in tree	2	9	11
Burrow in soil	1	1	10
Brush pile	2	2	2
Hollow log	1	2	2
Under rock wall	1	1	1
Under wooden trough	1	2	2
TOTAL		304	587

were in miscellaneous situations including brush piles, hollow logs and stumps, and in the stick and leaf nests of tree squirrels.

All individuals using these dens were captured in the same general area and it was not surprising to find, as records accumulated, that their ranges overlapped to a large extent. Also, it soon developed that dens were communal property, not used exclusively or defended by any one opossum. Of 88 dens, 1 was used by 5 opossums, 2 were each used by 4, 4 were used by 3, and 17 were used by 2. The remaining 64 dens were each used by only one animal, insofar as we know, but these were mostly dens low on the scale of preference and used on only one occasion. Only 28% of 587 "opossum-days" were spent in these 64 dens.

From time to time radio signals indicated that two individuals were occupying the same den simultaneously. On some occasions it seemed that the animals must have been side by side or in actual contact, but in other instances the signals indicated the animals were a meter or more apart. No two animals were found to den together with any consistency, and it is doubtful whether social attraction was involved. Individuals equipped with transmitters at any one time comprised only a small part of the local population. Hence, it is probable that, unknown to us, simultaneous use of a favorite den by two or more animals in constantly changing combinations occurred frequently.

Some of the most frequented dens to which we trailed opossums—at the hilltop ledges—were known to have been in use at least 15 years earlier. The burrows had been used by other mammals in the same general size range, the red fox (*Vulpes vulpes*), raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), and woodchuck (*Marmota monax*), although the opossum was by far the most frequent occupant.

HOME RANGE AND MOVEMENTS

FORAGING RADIUS

A total of 90 records were obtained (Fig. 1), each representing a movement of an adult opossum between a den and a place where it was carrying on normal activities like prowling in search of food. These records show generally the extent of an individual's range. In some instances the records are based on capture in a live trap of an individual which had been trailed to a den on the previous day. The linear distance between the capture point and the den then constituted the known (minimum) foraging radius of that particular animal on that particular night. In other instances the record was based upon approximate location of an animal at a definite time in the course of its nocturnal activities, as determined by triangulation.

In some instances an animal was located at a den both the day before and the day after the recording of a nocturnal location during the period of activity. In 11 such instances the den used on the two successive days was the same, and in 18 instances it was different. However, in both cases the records were construed as representing

two separate movements: from the den to the triangulation point and from this point back to the den. Even if it be considered inadmissible to count the return movements on the grounds that this procedure gives undue weighting to certain individuals and certain locations, the trend of the records, based only on den-to-triangulation-point movements, is not appreciably changed from that of the larger series.

Opossums recorded at random in the course of their foraging would rarely have been near the den from which the foray began or at the outer limit of the home range; rather they would tend to be at intermediate distances. If the entire range were covered uniformly in the course of foraging, the records would tend to be uniformly distributed from the minimal to the maximal distance, and their average

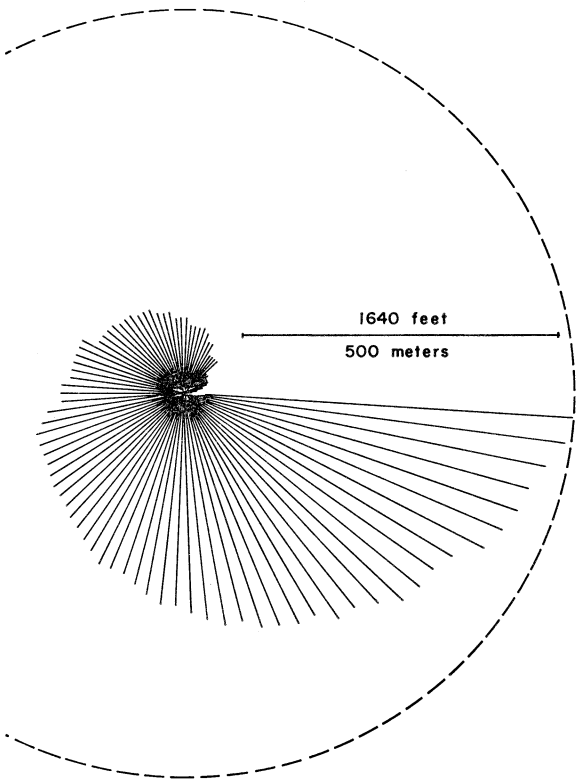

Fig. 1.—Diagram of 89 distances travelled by adult opossums between the dens and places where they were recorded foraging, arranged according to length. They tend to form a graduated series from 9 to 620 m, indicating a home range of about 620 m radius, with most activity limited to the inner parts. A relatively long movement of 681 m (not shown) may represent wandering beyond the home range boundary.

would represent a point about halfway from the center to the outer edge of the range.

Foraging opossums located soon after evening emergence would naturally be found nearer the den than those checked late at night when time had permitted them to wander to outlying parts of the home range. It might even be expected that distance from the den would tend to be proportional to elapsed foraging time, at least in the early part of the night. To test this idea 39 records of adult opossums which listed times of nocturnal activities at specific points were grouped according to numbers of hours elapsed since sunset, as follows: 2 hours—49 m (1 record); 3 hours—average 281 m (7 records, 49 to 586); 4 hours—average 257 m (13 records, 31 to 689); 5 or 6 hours—average 209 m (18 records, 15 to 526). It is concluded that since most of the records were several hours after nightfall, the animals involved had ample time to find their way to preferred foraging areas, and that distances recorded were not correlated with time elapsed since sunset.

Movements for immature opossums tended to be shorter than those for adults (Table 2). Figure 1 shows 89 records of distances travelled by adults between dens and places where the animals were foraging. These distances are distributed in a compact series from 9 m up to 620 m with only one gap (between 500 m and 537 m) greater than 25 m. A 90th record, not shown in Figure 1, is notably longer, 681 m, and perhaps represents a movement beyond the limits of a home range. Although circular shape could not be demonstrated

TABLE 2.—Movements of opossums according to age and sex

No. of individuals	Age or sex group	Average distance in meters between den and field point*	Average movement in meters from den to den
2	Newly independent young (June)		11 (3 to 25) in 3
4	Young in third month of independence (August)	23 (9 to 49) in 5	89 (9 to 245) in 10
5	Young in fifth month of independence (October)	158 (62 to 367) in 10	140 (128 to 147) in 5
3	Young in sixth month of independence (November)	196 (16 to 429) in 18	204 (83 to 429) in 13
8	Adult male	229 (31 to 588) in 40	305 (25 to 734) in 130
7	Adult female	155 (9 to 620) in 38	299 (31 to 636) in 93

* Range in parentheses

for any home range, the ranges for which most records were available tended toward a circular shape. Therefore, it seems reasonable to suppose that home ranges of the opossum, except where altered by the terrain, tend to approximate circles with a radius of about 600 m.

In an earlier study of the opossum (Fitch and Sandidge, 1953) it was postulated on the basis of tracking several individuals in the snow that the animal wanders over its range in a random and circuitous manner, using all parts of the area rather uniformly. However, the more detailed records of individual activities in the present study indicate otherwise. If the home range were a circular area around the den with a radius of 620 m, it would cover approximately 120 hectares. If such an area is divided into ten equal parts consisting of an inner circle of 12 hectares, and nine concentric bands around it (Fig. 2), the records of opossums are found to be unevenly distributed with respect to distance from the center. A high proportion falls within the inner areas while relatively few fall in the outer bands. The innermost 10% of the area has 51.1% of the records, and the records decrease to only 2.2% in the outermost band. The inner 5% of the area contains 30.0% of the total records, and the inner 2.5% contains 17.8%. From this distribution it is evident that the home range is not used uniformly, but the intensity of use is proportional to the distance from the den. More time is spent on the innermost 10% of the range than on the remaining 90%, and even on this relatively small area activity is so unevenly distributed that more than 66% of the records are on the inner half of it. Therefore, it seems that dens are chosen according to the available food supply, or else that food is usually so readily available that it can be found nearby whatever den is chosen.

On numerous occasions the opossums were live-trapped or recorded at night far outside the areas encompassed by their known dens. They apparently tend to distribute their activities in different directions from whichever dens they may be using, instead of moving toward a central area.

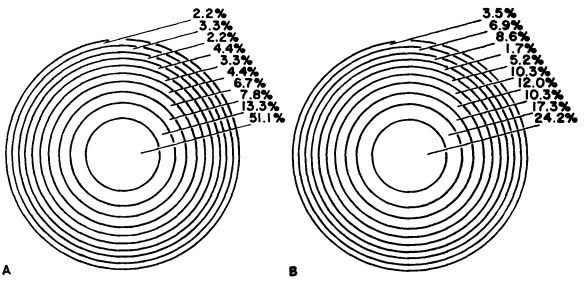

Fig. 2.—*A*. Hypothetical circular home range of an opossum divided into ten equal areas consisting of a central circle and nine concentric bands, showing relative amounts of activity in these different areas. *B*. Central one-fifth of the hypothetical home range, *A*, further subdivided so that each band represents 1/50th of the total home range area. Activity is most concentrated near the center.

COMPOUND NATURE OF THE HOME RANGE

The opossum, like many other animals, does not conform in its spatial relations with the classical concept of a home range. Even with a large amount of data concerning the movements of an individual, mapping a home range requires arbitrary decisions. A den may be occupied for only one day or a few consecutive days before the animal shifts to a second den and later to still others. It often returns to previously used dens but not in any predictable sequence, and it may at any time shift to a den beyond the area encompassed by the dens used previously. Its home range may be thought of as consisting of many overlapping segments, each having a den as its focal point. The area covered increases with time and the lifetime range is much greater than the area covered during the sojourn at one den. The home range might be mapped as the lifetime range, the range from one den, or the area covered in some arbitrary period such as a month. These three types of areas would differ greatly in size and none would correspond exactly with the usual idea of a home range. The opossum's home range is extremely fluid. The animal gradually becomes familiar with additional areas and tends to expand the scope of its activities, but also, it definitely abandons extensive areas that have been used. A male that has survived to maturity probably dies in a place remote from the area he occupied as a juvenile.

Each adult opossum occupied, on the average, a den for 2.2 days before shifting to another den; 220 such shifts were recorded with occupancy varying from one to 26 days. The distance of shift from den to den averaged 301 m and was not significantly different in males (306 m) and females (299 m). Because such a shift is less than half the radius of a typical home range, an opossum in its new den would still be using a home range that corresponded closely to the one previously used; but a crescent-shaped area of about one-fifth the original home range lying outside the 620 m radius of the new den might be abandoned and a corresponding area within the new radius added. Because the opossum's activities are relatively concentrated in the parts of the range nearest the den, the shift would result in exploitation of a somewhat different food source, with estimated overlap of less than 10% in time spent in foraging from the first den and from the second.

In making a second shift, six of 13 animals returned to the same den where they were originally recorded; the remaining seven each occupied a third den. In making a third shift, five of the 13 returned again to the second den, and in making a fourth shift eight of 13 returned to one of the first three dens used. In their sixth to tenth shifts these animals occupied their previously used dens in nearly half (26 of 53) of the recorded instances. Thus there is a strong tendency to shift back to one of a few favorite dens, but at any time the individual may move on to another den entirely outside the area it has previously exploited.

Hypothetical home ranges were plotted for each of the opossums for which sufficient records were available, using each den as a central

point with a 620 m radius. The limitations of our instruments probably resulted in some bias toward recording shorter movements. On many occasions we failed to locate an animal, and on such occasions the failure might have often been a result of the animal's wandering too far from its last used den to be readily located by random search. For eight adult males each recorded at from three to 19 dens the calculated compound home ranges varied from 177 to 401 hectares and averaged 257 hectares (Table 3). For five adult females each recorded at from five to 16 dens, calculated compound home ranges varied from 186 to 293 hectares and averaged 249 hectares. For the entire group of 13, home ranges averaged 254 hectares. Figures 3 and 4 show the trend toward increased size of home ranges for animals of this group, with lapse of time and use of additional dens.

CORRELATION WITH AGE AND SEX

Obviously many factors affect the movements of opossums. Two of the most obvious are age and sex of the individual. Immatures wander less widely than adults in their day-to-day activities, but occasionally they make dispersive movements into new areas. In June 1966 three young opossums, recently emerged from the mother's pouch (while she was in confinement), were equipped with transmitters and released at the Reservation headquarters. They were kept in individual compartments of a container for a few days before release and then, when they chose, were allowed to leave from the open container onto a screened porch and to the outside through an open door. Their

TABLE 3.—Histories of the 13 adult opossums from which the most records were obtained

Sex	Days	Moves	Non-moves	Total distance den to den in meters	Greatest den separation in meters	Area encompassed by dens in hectares	Area of potential range from known dens (hectares)
♀	52	7	20	2462	505	2.55	185
♀	37	12	11	3440	735	11.6	293
♀	170	27	19	11000	827	24.0	274
♀	239	35	36	9100	845	36.3	286
♀	35	8	18	1480	657	7.31	206
♂	90	29	54	3650	571	4.14	197
♂	126	25	54	909	1270	137.9	347
♂	38	7	4	2450	695	2.19	210
♂	96	6	10	1500	565	4.74	177
♂	7	5	1	1670	581	6.16	202
♂	11	2	1	837	633	6.40	199
♂	165	49	45	18450	1501	50.1	401
♂	52	8	34	1960	520	3.27	325

exploratory outward movements may be representative of the movements that occur in newly independent young in nature. Daytime dens used at first were: a small woodpile beside the building only 5 m from the container where the animals had been kept; a pail hanging on the outside wall of the porch 2 m above the ground (reached by climbing the screen); and a hollow in the base of a tree, at the edge of woodland 25 m from the porch, with an open area intervening. Because of their small collars and relatively weak radio signals, these young opossums were soon lost, but on 3 August one of them was relocated in a den approximately 611 m from the place of release.

On 1 August 1965 a young male opossum which had been detained in the laboratory for several weeks (from just before it left the female's pouch until some time after) was equipped with a transmitter and released. For several days it was not seen but was located once at night while foraging and several times in a hollow log which was its daytime retreat, always within 46 m of the point of release. Then on 9 August it was caught in a live trap. The transmitter had ceased to function. The animal had been seriously injured by tearing the skin of its right foreleg on a point of wire projecting from its collar, and it was brought back to the laboratory.

Circumstances prevented re-equipping and release of this opossum until 19 October. By then its injury was long since healed and it was approximately half grown (1193 g). On the day it was released the animal was detected after dark with the portable receiver and was located moving about actively near the release point. Attempting to approach this young opossum, we were led across a meadow, along a ravine, and up its farther bank, and into a field of tall weeds and brush. For a half hour we were led consistently in a southwesterly direction, but we finally abandoned the chase some 430 m from the

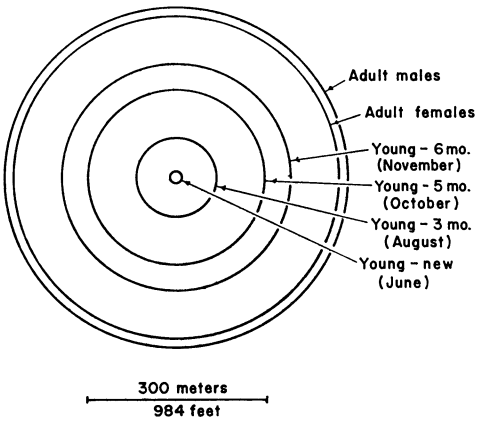

Fig. 3.—Relative sizes of areas used by adult opossums, and by young at various stages after becoming independent of the female, as indicated by the average combined movements for each group

starting point after having been led through thickets of thorns, nettle and poison ivy. While returning to the Reservation headquarters by a route that took us away from the last contact, we again detected the opossum's radio signal, and it soon became evident that the animal was retracing its course toward the starting point. Within 45 minutes it had returned to the release-point area. On many subsequent occasions, both day and night, it was found to be in this same general area. Part of the time it used the same hollow log where it had denned in July.

During the subsequent month this opossum was trailed and located frequently but insofar as known it never again wandered so far from the point of release. Obviously its trip to the weedy field was made as it fled to escape pursuit; the homing performance on that occasion seemed remarkable inasmuch as it was made with little or no hesitation, over a route that had been used while fleeing in fright, in almost total darkness and without obvious landmarks. Furthermore, the animal was young and inexperienced, and had little opportunity to become familiar with its home grounds in a brief period of freedom before being returned to the laboratory for another ten weeks of captivity. Homing ability associated with excellent memory and location-sense is thus indicated in the opossum.

Table 2 summarizes 365 measured movements of opossums from den to den or between a field point where trapped or located during a foraging period, and a den used immediately before or afterwards. For adult males and females extent of movements is about the same, and in these large series den-to-den movements are of about the same magnitude as movements between dens and field points. For immature

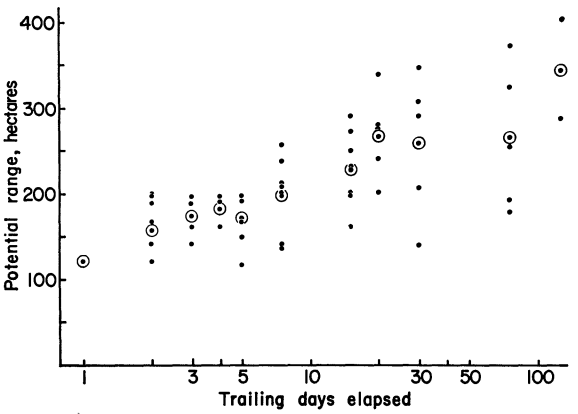

Fig. 4.—Trend of increase in area covered by adult opossums with time and occupancy of additional dens, from each of which the animals may range over a 620-meter radius. The area covered from a single den is calculated as about 120 hectares, but after 100 days many additional dens have been used, with combined areas around them totalling from 287 to 401 (average 344) hectares. Circled dots represent the average range.

animals the series are considerably smaller, but there is a definite trend toward much shorter movements, proportional to the age of the individual.

Figure 3 is based upon Table 2 and shows relative sizes of areas covered for young of different ages and for adult males and females. Seemingly, the adults cover areas several hundred times as large as those covered by the newly independent young. The young explore their surroundings thoroughly, and progressively extend their ranges, becoming well acquainted with new areas as these are incorporated. In the adults difference between the sexes in size of area covered is not statistically significant.

EFFECTS OF SEASON AND WEATHER

Opossums are influenced in their movements by the weather, both directly and indirectly. In the region of this study they undergo progressive loss of weight during the winter and early spring. By the time warm weather arrives in late spring they are more or less emaciated. Winter is obviously a time of severe stress, particularly in periods of cold weather. Most of the food sources that are readily available in the warmer half of the year, including insects, amphibians and reptiles, the young of birds and small mammals, and certain kinds of fruit, are either absent or difficult to find. Opossums are obliged to expend more energy in obtaining their food, and must rely to a large extent on carrion, and such small birds and mammals as they are able to catch. Having extensive areas of almost naked skin on their ears, tail and toes, opossums are ill adapted to withstand the cold. They suffer from exposure and their exposed parts are subject to freezing. Depending on the severity of the weather, they are forced to limit the time and distance of their forays, or else to forego periods of foraging altogether, with resultant deficits in energy. Some are in critical condition by the end of the winter.

Although opossums are ordinarily nocturnal in their activities, diurnal emergence and foraging occur in winter when there has been sudden warming following a period of bitter weather. Such daytime activities have been observed on many occasions over a period of 20 years, in January, February, and especially March. During the present investigation such incidents were observed four times in February and March, 1966. On 5 February an adult male was found outside in the late afternoon at an air temperature of 8.5 C after 20 days of continuously subfreezing temperature. Another adult male was found outside on both 7 and 9 March when air temperatures were 3.5 and 17.5 C, respectively. Three days with temperatures continuously below .5 C preceded 7 March, but 9 March was the warmest of three consecutive mild days. A third adult male was found outside in the daytime on 20 March when air temperature was 23.5 C, although this was the thirteenth consecutive spring-like day with maximum temperature above freezing.

It might be expected that through the influence of the weather and

the changes in quantity, quality and distribution of the food supply, opossums would be induced to alter radically their pattern of behavior toward use of dens, frequency of shifts, and distances of forays between, for example, winter and summer. However, our data do not indicate such alteration. Table 4 compares length of sojourn at dens in males and females at different times of year, but well-defined trends are lacking. For the purpose of the table the year is divided into five parts, unequal because in some times of the year our records were inadequate for a sample of one or both sexes. Seasonal trends that are consistent for both sexes are notably lacking in this set of data. It seems that at all times of year one-day sojourns are by far the most frequent, and that most other sojourns are short (two to seven days) with only occasional sojourns of ten days or longer.

In the region of our study, much of the opossum's breeding occurs in February, judging from the facts that births of litters are concentrated in the last week of February and the first week of March and that gestation requires approximately 13 days (Hartman, 1952:73). After their young become independent near the end of May, females may again become pregnant and have second litters.

TABLE 4.—Length of sojourns at dens of adult opossums at different times of year. Figures are per cent of records for the period

Period	Number of records	Length of sojourn: 1 day	2-4 days	5-7 days	8-10 days	more than 10 days
Jan-Feb	4 ♂♂ 27	44.4	22.2	14.8	7.4	11.1
	1 ♀ 11	63.6	9.1	18.2	9.1	....
	Both 38	50.0	18.4	15.8	7.9	7.9
Mar-Apr-May	4 ♂♂ 43	62.9	25.8	9.3	1.9	....
	3 ♀♀ 17	29.4	41.2	29.4	....	....
	Both 60	53.4	30.0	13.3	1.9	1.9
June-July-Aug-Sept-Oct	2 ♂♂ 14	57.1	14.3	7.1	14.3	7.1
	2 ♀♀ 39	66.6	25.6	5.1	2.6	....
	Both 53	64.1	22.6	5.7	5.7	1.9
November	4 ♂♂ 23	52.1	43.5	4.4	....	....
	5 ♀♀ 29	76.0	20.7	3.5	....	....
	Both 52	65.5	30.8	3.8	....	....
December	3 ♂♂ 52	73.2	23.1	1.9	1.9	....
	2 ♀♀ 20	80.0	20.0	....	....	....
	Both 72	75.0	22.2	1.4	1.4	....
Combined samples of males	159	61.4	26.0	6.4	4.8	2.5
Combined samples of females	116	63.9	24.1	9.5	1.7	.8
Combined samples of both sexes	275	62.4	25.1	8.0	2.6	1.9

It might be expected that males, impelled by sexual drive, would be inclined to shift frequently and to wander more widely in the breeding season than at other times, but instead the few records indicate relatively long sojourns. Nine February sojourns for males included four (44.4%) of one day each, and longer sojourns of 4, 5, 7, 8 and 26 days. A second period of concentrated breeding is in the latter half of May; but as only ten May sojourns were recorded, it cannot be stated whether males are unusually active then. Actually males are probably in full breeding condition and ready to mate throughout the late winter and spring. The concentrations of pregnancies are due to the fact that most females come into oestrus at about the same time in late winter, and again when their first litters become independent in late spring.

Figure 6 shows the ratios for opossums that stayed in the same den, already used, as compared to those that shifted to new dens, and how these ratios are correlated with changes in minimum temperature from the previous night. At temperatures that had increased to a level more than 10 C degrees warmer than the previous night the ratio of moves to non-moves was about 2 to 1. At temperatures that ranged from unchanging to an increase of 10 C degrees the ratio was near 1 to 1, but when minimum temperatures were falling the ratio was near 1 to 2. Hence, the frequency of shift in den is highly correlated with temperature change. When weather is bitterly cold, remaining far below freezing throughout the daily cycle, opossums have no opportunity to forage and remain in their dens without emerging for days at a time. Hence, a tendency toward longer sojourns in winter is to be expected. Nevertheless, one-day sojourns made up at least half the total at all times of year.

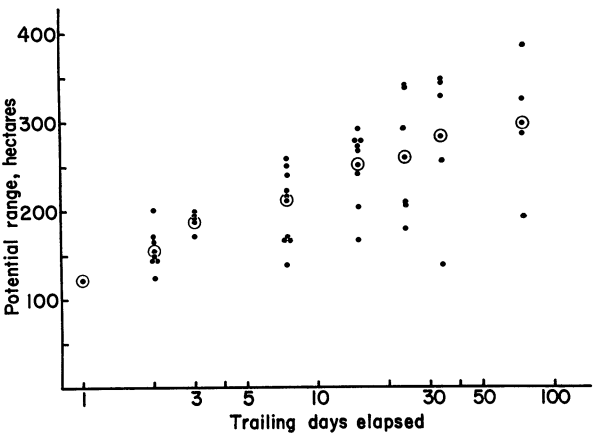

Fig. 5.—Trend of increase in area covered by adult opossums, with time, as in Figure 4, except that only those days on which an animal was actually found were included in the totalling. The trend of the averaged ranges shows less scatter.

MORTALITY

Reproductive potential is notably high in the opossum, but is correlated with a high rate of population turnover and short life expectancy. Our records terminated with the known death of eight of 27 animals equipped with transmitters, and an incidental outcome of the field work was determination of the cause of death in most of these instances.

Although our chief objective was to find out as much as possible regarding the normal ways of life, routines and activities of the animals, our own activities interfered to varying degrees. Live-trapping the animals, holding them in captivity, equipping them with collars (and with harnesses in some of those first studied), anesthetizing them and trailing them, all must have resulted in some deleterious effects and consequent handicapping of the individuals involved. The death of an adult male was attributable to these effects. His records extended over 3½ months. In the last month he was equipped with a new collar and transmitter. Later he was found dead in a den; in an effort to remove the collar he had thrust one foreleg beneath it, and had been unable to withdraw his leg. In other instances our interference with the animals' normal routines may have indirectly resulted in their deaths. An opossum was found lying dead a few meters from its last used den. It was half grown and appeared to be in excellent condition. It had been seen moving about in daylight less than two hours earlier and the cause of death was not apparent.

Another death occurred in an adult male trapped at the end of February 1966. He was unusually emaciated, blind in one eye, lethargic and uninterested in food during four days of captivity. Two days after release he was found dead, having moved only a short

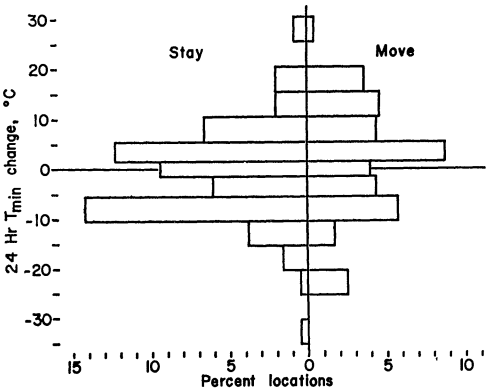

Fig. 6.—Correlation of relative amount of movement from den to den with change in minimum temperature (T_{min}) from the previous night. Data were used only when one or both nightly minima fell below 4 C. Animals tended to remain in dens when minimal temperatures were falling and to change dens when minimum temperatures were rising.

distance. Another male was released on 27 November 1965, disappeared after three days of trailing, and was found dead on 6 December. He had travelled a kilometer from his last recorded location. He was found to have extensive mechanical injuries; subcutaneous hemorrhage and penetration of the thoracic cavity suggested that the animal had been attacked by a dog or coyote. None of the carcass had been eaten. An adult female was found dead on a county road, a traffic casualty after 35 days of trailing.

Three other opossums were victims of the horned owl. All were members of the same litter, kept in captivity until judged ready for release, and all were approximately fox squirrel size. Deaths occurred on the nights of 29 October, 5 November, and 17 November 1965, one, seven, and nine days after the animals' releases. Perhaps the same horned owl was involved in all three instances. All these deaths occurred within a 330 m radius under somewhat similar circumstances. In each instance the plastic collar, bloody but still transmitting and intact, was found on the ground. The opossum was missing but telltale dropped feathers, down adhering to low vegetation, tufts of opossum fur, excreta of the owl, and a blood trail provided circumstantial evidence of the struggle and death of the captured opossum. The animals involved may have been somewhat handicapped by previous captivity and by their collars which were relatively heavier burdens than those carried by adult opossums. However, a fourth litter mate survived longer, and escaped predation. Such predation is probably normal and may be a major factor in the elimination of the annual crop of surplus young locally.

Acknowledgments.—Many persons helped us with different aspects of this study, both in the field and in the laboratory. Our sons, especially, rendered valuable assistance; Chester W. Fitch live-trapped most of the opossums used for trailing, and Hampton N. Shirer spent hundreds of hours in detailed analysis of field data and a search for correlations. We shared the field work in routine trailing of animals, but had help from several persons; Mr. David D. Pippitt was employed on our project throughout most of its course; Mr. Bruce Kurfman located animals on several occasions. Financial assistance was provided by NASA Interdisciplinary Grant NSG 298.

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