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COYOTE MOVEMENT PATTERNS WITH EMPHASIS ON HOME RANGE CHARACTERISTICS

by

Stephen J. Hibler

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Wildlife Science

UTAH STATE UNIVERSITY
Logan, Utah

1977

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Stephen J. Hibler

Stephen J. Hibler

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ABSTRACT

Coyote Movement Patterns with Emphasis on
Home Range Characteristics

by

Stephen J. Hibler, Master of Science

Utah State University, 1977

Major Professor: Dr. Frederick F. Knowlton
Department: Wildlife Science

Standard radio telemetry techniques via triangulation were used to determine coyote locations and to construct maps of coyote movement patterns in Curlew Valley (Utah and Idaho). Home range sizes were determined by establishing corresponding boundaries drawn on the basis of location, density and relative number of visitations (contour method), and then tracing the boundaries with a compensating polar planimeter. Mean home range sizes were determined directly for only those animals with home range values that reached an asymptote when plotted against corresponding time periods. This asymptotic value was considered the best estimate of the actual home range size. Four adult females and one adult male were in this category, with mean values of 18.3 km^2 and 14.5 km^2 respectively. The asymptote was estimated for home ranges which did not stabilize (mean values of 20.2 and 17.8 km^2 for adult females and males respectively) using a home range estimator; validation of the estimator is discussed. Since no juvenile animal's home range appeared to reach an asymptote, no asymptotic estimates were made. Various methods of constructing home range boundaries, their

advantages and disadvantages, are listed. Standardization in the home range concept is necessary if meaningful comparisons are to be made between studies. Home ranges are dynamic, and must be considered in terms of specific time frames. Guidelines for adequate description of the home range are discussed with emphasis on quantity of data, time requirements and recognition of seasonal shifts in the home range. Map analysis suggested three general patterns with regard to home ranges; namely, animals with contiguous home range areas, those with disjunct home ranges, and wandering individuals. Fifty percent of the coyotes were trapped more than 0.5 km outside home range boundaries while an additional 42 percent were trapped on the periphery of the home range. Only 8 percent, all juveniles, were trapped within their home range. None of the 21 animals killed by hunters or trappers died well within their respective home ranges. Twenty-nine percent were killed on the periphery of their home ranges and 71 percent were killed an average of 11 km outside their home range boundaries. Several movement patterns other than home range were discernible, including brief excursions away from the home range (sallies), dispersals, and total area utilized. Mean dispersal distances for adult males, juvenile males and females respectively were 56, 9 and 54 km; no adult female was known to disperse. Juvenile females had the greatest tendency to disperse with 53 percent involved; juvenile males, 33 percent and adult males, 30 percent. Sallies were analyzed according to distance, duration and frequency, with adult females having the longest (4.9 km) and the greatest number of sallies (7.9 per month), and adult males spending the most time per sally (16.2 hours) as well as time per month (72.9 hours) in sally activity. The total area utilized by coyotes is

discussed in terms of size and measurement. Mean values for total areas utilized are 138 km^2 for adult females, 90 km^2 for adult males, 68 km^2 for juvenile males and 46 km^2 for juvenile females. Home range configuration is discussed in terms of importance and variability in form, with the majority of shapes being ameoboid in character. Linearity may be a function of the method used to establish home range boundaries and use of baseline data from fixed radio telemetry stations.

(125 pages)

INTRODUCTION

Coyotes (Canis latrans) are the most ubiquitous of the large North American predators. They are ecological and behavioral generalists and thus flourish in a variety of environments. The animals have adjusted to human activity and even responded opportunistically in some situations. Some responses, such as killing livestock, have placed the species in disfavor with some segments of the public; as a result, coyotes have been trapped, shot, and poisoned as pests. Recently, other segments of the public have voiced aesthetic and environmental concern over efforts to remove coyotes. There now is an intense controversy over how best to deal with the problem. A more scientific approach in coyote management presumably would be helpful.

Efficient management of any species necessitates detailed knowledge of the animals' natural history. One of the important concepts concerns the animals' movement in and use of space.

The movement of coyotes has been studied by tagging-recapture methods (Robinson and Cummings 1951, Robinson and Grand 1958, Hawthorn 1971), by tracking the animals in the snow (Ozoga and Harger 1966) and by using radio telemetry (Gipson 1972, Chesness 1974, Danner 1976). Although these studies have made a fine start, few generalizations can yet be made about the movements of coyotes. The information generally lacking is: (1) numerous relocations per animal; (2) relocations of many individuals living in a common habitat; and (3) studies of animals living in different types of environments. This study attempts to

supply some of this information on coyotes living in an arid area with a mixture of native and agricultural vegetative communities. The specific objective is to examine dispersion of coyote relocations using radio telemetry techniques.

METHODS

This study was conducted on an area of approximately 1800 km in southern Idaho and northern Utah (Figure 1). The major types of native vegetative cover in the study area were big sagebrush (Artemisia tridentata) on the valley floor and juniper (Juniperus osteosperma) on hillsides. About 25 percent of the area was modified for agricultural purposes. A more detailed description of the topography and vegetation of the study area is given by Clark (1972).

Coyotes were captured in September of 1972 and 1973 using steel-jawed traps (Clark 1972). A total of 150 traps were spaced at approximately 1.6 km intervals in three lines of 50 traps each. Tranquilizer tabs (Balser 1965) were wired to the jaws of each trap to reduce injury, prevent escape of poorly caught animals, and facilitate handling. Captured animals were confined in cages for 1 - 5 days to permit recovery from tranquilizer effects, after which they were released at their capture sites. Prior to release, each surviving coyote was marked with an ear tag and a radio transmitter (Kolz, et al. 1973) weighing approximately 346 g and containing reward information. Transmitters operated on one of 12 frequencies in the 164 MHz range, emitting signals at rates of 30, 60, 90, or 120 per minute. A whip antenna was attached to the side of each transmitter and was bent to approximate the curve of the collar around the neck. In addition, the

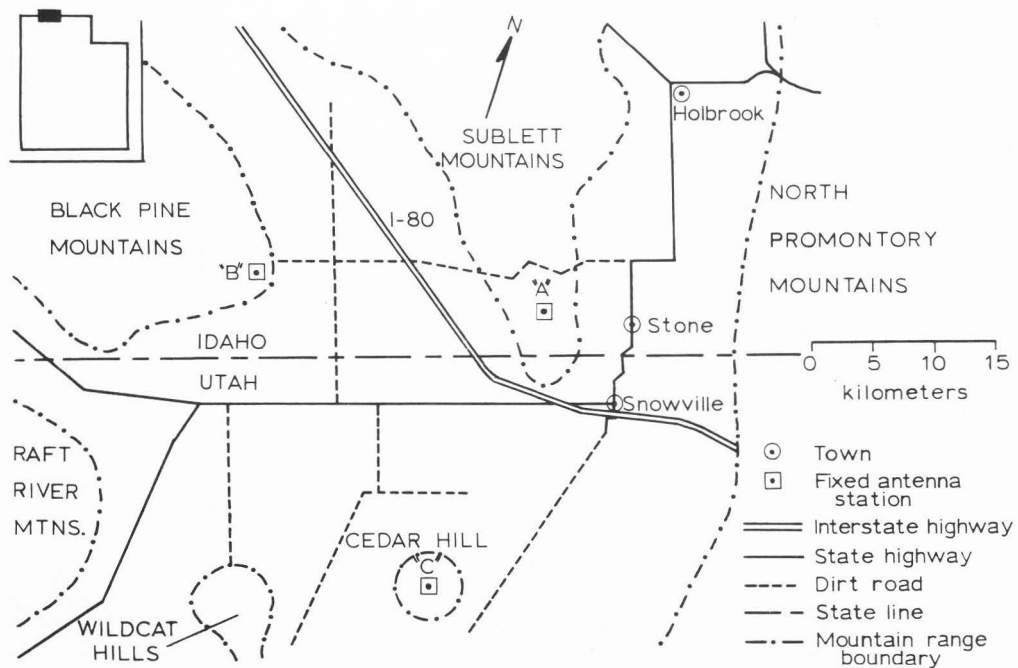


Figure 1. Map of Curlew Valley study area.

following information was recorded for each coyote: capture location, weight, general physical condition, sex, and age (classifying animals less than one year old as juveniles and all others as adults). Tooth wear, weight, and general appearance were used as criteria for estimating age at the time of capture; tooth sectioning and staining (Knudsen 1976) permitted a more accurate assessment of age in individuals that were subsequently recovered.

Instrumented coyotes were radio tracked from September 1972 through June 1974 to determine their movement patterns. Transmitted signals were received using standard radio telemetry techniques (Heezen and Tester 1967). A model LA12 AVM receiver and several types of antennas were used. Most location data were obtained using antennas mounted on three permanent shelters located approximately 300 m above the valley floor. Each shelter was equipped with two five-element yagis stacked horizontally and coupled out-of-phase with a sum-and-difference hybrid junction. The typical reception range was 30 - 40 km. Antenna orientation was established and maintained by a "beacon" transmitter. Baseline distances between shelters were 19.3 km from A to B and 19.7 km from A to C (Figure 1).

If a transmitter signal could not be detected at the permanent shelters, trucks equipped with similar antennas were used to locate the animals. The reception range of a truck's antenna was approximately 8 km. If the signal could not be detected by either of these means, a Cessna 182 aircraft equipped with two three-element yagis was used. The antennas were fastened to wing struts and were directed laterally to the fuselage with the elements oriented vertically. The reception range was approximately 80 km at an altitude 500 m above the ground.

When an instrumented coyote died in terrain accessible only by foot, a hand-held directional loop antenna was used to locate the animal. Hunters provided additional information on kill locations of instrumented coyotes that they shot.

The monitoring schedule used in this study consisted of two three-day sessions each month. During the months immediately following the trapping period, only one relocation per hour per animal was obtained. As the number of instrumented animals decreased, each animal was relocated every half-hour.

The accuracy and precision of the tracking system were determined by comparing radio location bearings with surveyor's transit bearings. Systematic (consistent) error was determined by calculating the mean difference between antenna-derived bearings and corresponding transit readings. The effect of this type error is demonstrated by the displacement of four squares by the amount of the mean consistent error from each antenna (Figure 2). Each corner of the square was then displaced by the mean systematic error from each shelter. The percent change in area was 1.4, 7.8, 0.4 and 3.3 for squares I, II, III and IV respectively. Since systematic error displaced the squares but did not appreciably change their size, this value was removed from all deviations. Resolution error remained but was small, averaging $1.1^{\circ} \pm 1.0^{\circ}$.

A map of the study area was drawn to a scale of 1 cm = 0.32 km. Duplicates of this map were used to record the movements of individual coyotes. Animal locations were plotted sequentially and dated. Circumscribed areas containing relocations were calculated using a compensating polar planimeter.

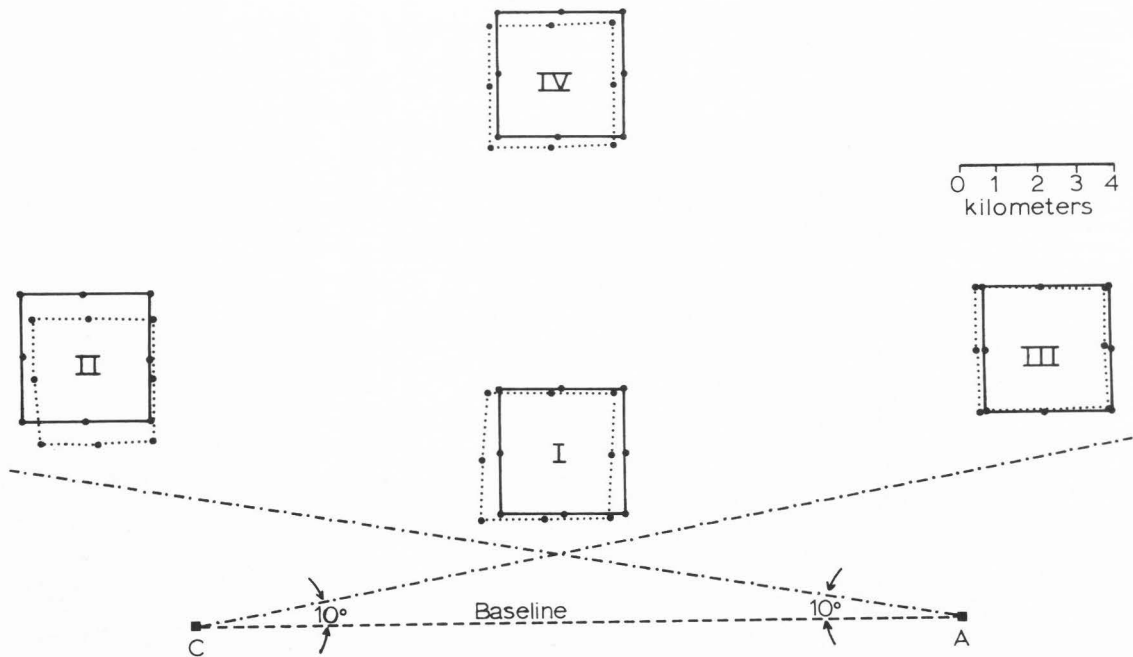


Figure 2. Displacement and distortion of shape and size of four 10.38 km^2 areas due to systematic errors. Relocations within ten degrees of the baseline were excluded in the analyses.

RESULTS

During the 2 years of fieldwork, 87 coyotes were instrumented with transmitters; 27 adult males, 12 adult females, 20 juvenile males and 28 juvenile females. A total of 5059 relocations was obtained, with 79 percent on 36 animals (averaging 111 per coyote). Maps depicting capture site, home ranges and mortality sites comprise the Appendix. Although only 36 coyotes were used in home range calculations, data from four additional coyotes provided information on other aspects of movement. Ninety-one percent of all locational data were obtained between September and March. Relatively few locations were acquired April through August due to loss of instrumented animals and transmitter malfunction or expiration.

Among the 51 coyotes excluded from home range calculations, 29 lacked sufficient data to warrant home range calculations; including 10 adult males (37 percent of all adult males instrumented), four adult females (33 percent), three juvenile males (15 percent) and 12 juvenile females (43 percent). Of the remaining 22 coyotes, seven died as a result of handling procedures, one carried a non-functional transmitter, another lost its transmitter, and 13 were never relocated after release (three adult males, six juvenile males and four juvenile females; adult females were not represented in this group).

Total Area Utilized

I determined the total area that a coyote was known to utilize by connecting the outermost relocations with straight lines (polygonal method) and tracing the resultant boundary with a compensating polar

planimeter. Mean values as assessed for adult males was 90.4 km; adult females, 137.9 km; juvenile males, 67.5 km; and juvenile females, 46.0 km (Tables 1, 2). None of these was significantly different ($p > .05$). The mean value for adults was twice that of juveniles (111.5 and 56.2 km², respectively), but differences were not significant at the 95 percent confidence level.

It is important to know when an area utilized by an animal is adequately sampled. Then its physical characteristics, particularly size, can be accurately described. In this study, size of total area utilized by individual coyotes was plotted as a function of the number of relocations and/or months under observation (Figures 3, 4). Asymptotes would be interpreted as possible maximum ranges.

From the graphs there is little evidence to suggest that total areas utilized by the monitored coyotes were approaching asymptotic values. These results are consistent with the idea that total areas utilized will not reach an asymptote (life range) until the animal ceases to explore new territory. Hence the only practical solution is to present existing or "known" values accompanied by the time intervals monitored.

Home Range Assessment and Related Observations

On all maps of coyote movements containing 50 or more relocations, I could distinguish areas of more intense use within the total area utilized. Such patterns were difficult to recognize on maps containing less than 50 relocations. I suggest that these areas of routine use are equivalent to home range and henceforth I will refer to these more intensely utilized areas as such.

Table 1. Calculations for total areas utilized and home ranges for individual adult coyotes in Curlew Valley, 1972--1974

Sex	Animal number	Number of months monitored	Number of locations	Total area utilized (km ²)	Home range size(km ²)	
					asymptotic	non-asymptotic
males						
	5110	6	96	61.5	--	11.8
	5050	5	50	54.5	--	3.8
	5079	2	14	16.8	--	6.3
	5040	3	20	--	--	2.8
	5082	2	43	97.4	--	5.8
	5083	10	323	73.2	14.5	--
	5089	5	77	72.2	--	4.7
	5053	5	65	21.8	--	10.8
	5113	5	110	427.6	--	5.6
	5064	3	31	21.0	--	4.3
	5060	3	16	58.5	--	11.2
	mean	4.5	76.8	90.4 (121.32)	14.5	6.7 (3.31) ^a 7.4 (3.92) ^b
females						
	5080	10	314	59.9	21.6	--
	5081	6	92	91.2	--	14.4
	5075	11	312	91.4	26.8	--
	5066	13	264	81.5	17.4	--
	5107	7	150	469.1	7.5	--
	5106	7	170	236.8	--	15.4
	5055	3	36	29.0	--	3.5
	5085	1	16	44.1	--	--
	mean	8.1 ^c	191.1 ^c	137.9 (148.20)	18.3 (8.18)	11.1 (6.60) 15.2 (7.93) ^b
adult mean		5.9 ^c	121.3 ^c	111.5 (132.00)	17.6 (7.29)	7.7 (4.38) 10.5 (6.83) ^b

^aParentetical values are standard deviations

^bIncludes asymptotic values

^cExcludes data from 5085

Table 2. Calculations for total areas utilized and home ranges for individual juvenile coyotes in Curlew Valley, 1972--1974

Sex	Animal number	Number of months monitored	Number locations	Total area utilized (km ²)	Home range size (km ²)	
					asymptotic	non-asymptotic
males						
	5112	5	163	73.3	--	6.1
	5043	10	207	69.9	--	11.6
	5120	4	152	32.0	--	9.9
	5099	4	159	181.7	--	9.1
	5002	5	121	45.7	--	19.1
	5090	4	43	33.2	--	4.0
	5105	2	45	13.4	--	5.9
	5041	4	30	91.0	--	2.5
	5118	6	171	67.3	--	21.0
	mean	4.9	121.2	67.5 (49.34)	--	9.9 (6.44) ^a
females						
	5100	6	227	32.5	--	15.5
	5086	6	42	35.6	--	4.1
	5088	1	24	8.7	--	2.5
	5070	4	56	18.2	--	6.1
	5010	6	103	95.1	--	9.2
	5042	8	51	100.4	--	15.8
	5123	4	161	45.1	--	10.5
	5098	3	39	12.6	--	2.3
	5067	1	31	85.7	--	--
	5008	2	31	26.3	--	8.1
	mean	4.4 ^b	81.6 ^b	46.0 (34.81)	--	8.2 (5.07)
juvenile mean		4.7 ^b	101.4 ^b	56.2 (42.53)	--	9.1 (5.69)
grand mean ^c		5.3 ^d	111.3 ^d	83.1 (99.59)	17.6 (7.29)	8.5 (5.14) ^e

^aParentetical values are standard deviations

^bExcludes data from 5067

^cValue is based on totals from adults (Table 3) and juveniles

^dExcludes data from 5085 (adult female) and 5067

^eIncludes asymptotic values from adults

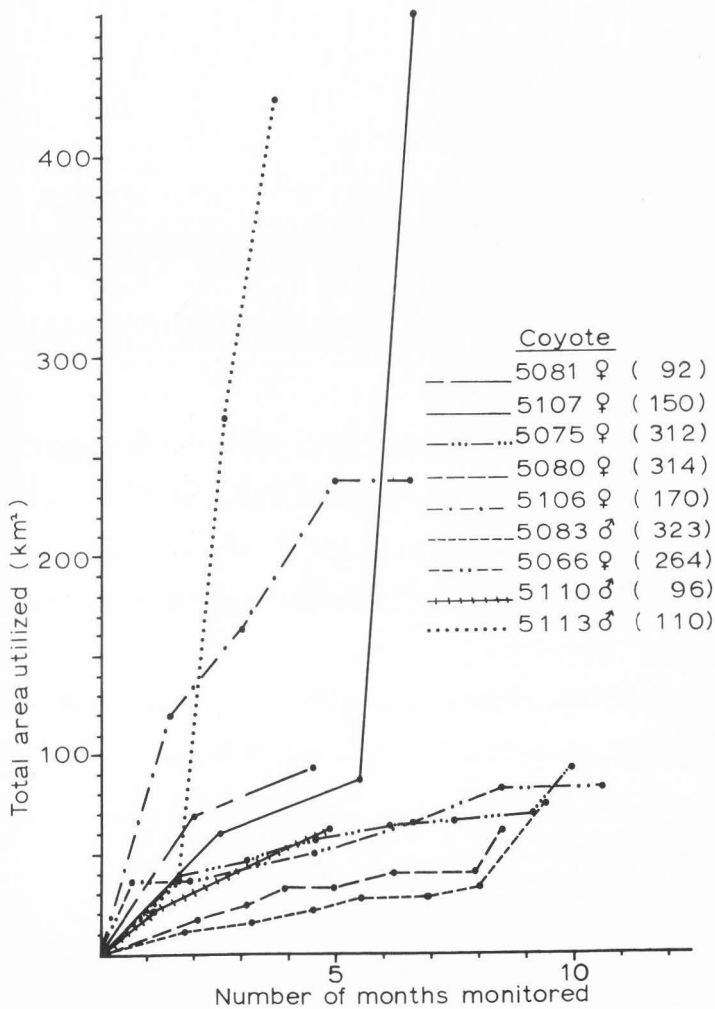


Figure 3. Size of the total area utilized by nine adult coyotes as a function of the number of months they were monitored, with each plot representing increments of 50 relocations. Numbers in parens represent total numbers of relocations.

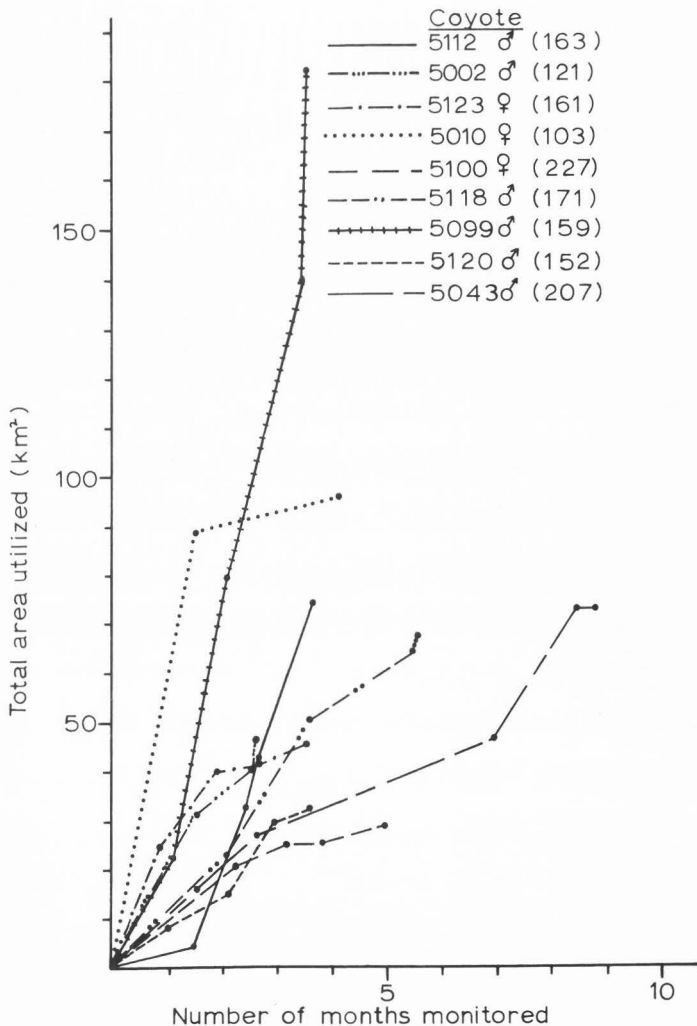


Figure 4. Size of the total area utilized by nine juvenile coyotes as a function of the number of months they were monitored, with each plot representing increments of 50 relocations. Numbers in parens represents total numbers of relocations.

Graphs depicting assessment of home range size as a function of time were also constructed to evaluate the adequacy with which these areas were sampled (Figures 5-8). Assessed home ranges for only five of the 36 animals appeared to reach an asymptote. All were adults; four females and one male. The mean home range size for the females was 18.3 km^2 , that for the male was 14.5 km^2 (Table 1). Three of the animals (Nos. 5075, 5080 and 5083) were radio-tracked June through March, while the other two (Nos. 5107 and 5066) were tracked September through March, and January through November respectively.

Since the home ranges depicted for the remaining 14 adult coyotes did not appear to reach asymptotic values, I assumed the animals' movements were inadequately sampled to include their entire home range. A positive correlation between amount of sampling and mean assessed home range size (Table 3) further indicated that ranges were inadequately sampled. Therefore most values in Tables 1 and 2 must be regarded as minimal. In a later section, values for these home ranges are extrapolated from an equation derived from a relationship between rate of accrual and ultimate size of assessed home ranges.

Even though three juveniles were monitored for nearly 5 or more months, none of the home range values determined for juvenile coyotes appeared to approach asymptotes (Figures 7, 8). Either longer periods of time are required (under this monitoring schedule) to assess home ranges of juveniles, or home ranges of coyotes in this age class continue to enlarge. Burt (1943) states, "...young adolescent animals often do a bit of wandering in search of a home region. During this time they do not have a home, nor, as I consider it a home range." In either case, home range estimates for this group should be accompanied

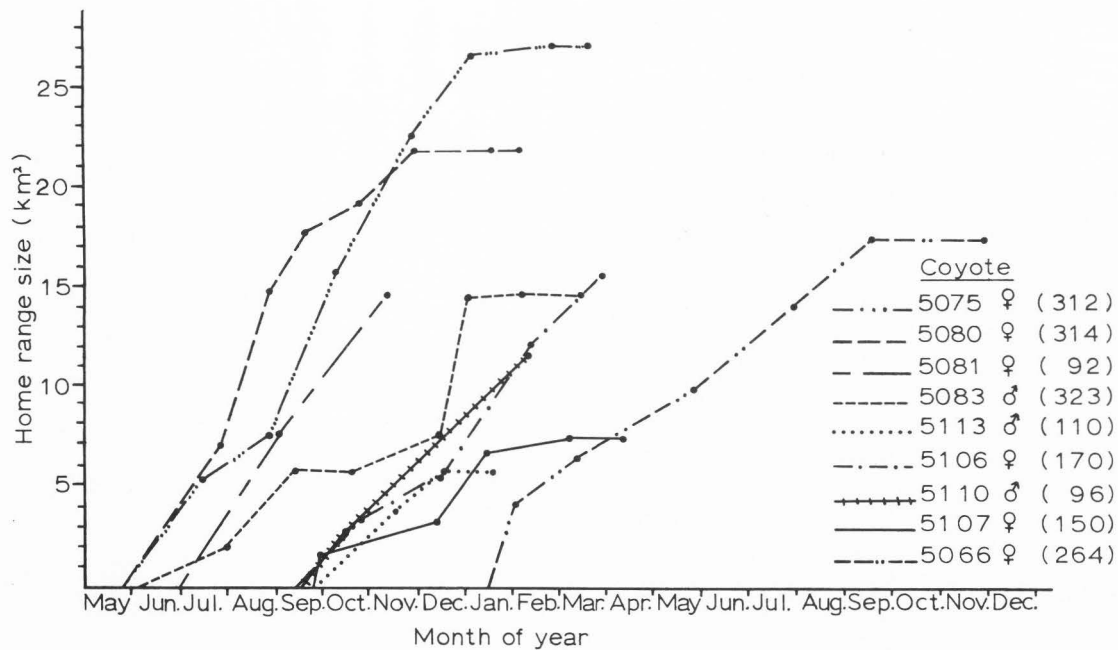


Figure 5. Assessed home range size of nine adult coyotes as a function of the months monitored, with each plot representing increments of 50 relocations (except animal 5107 where they represent increments of 35). Numbers in parens represent total numbers of relocations.

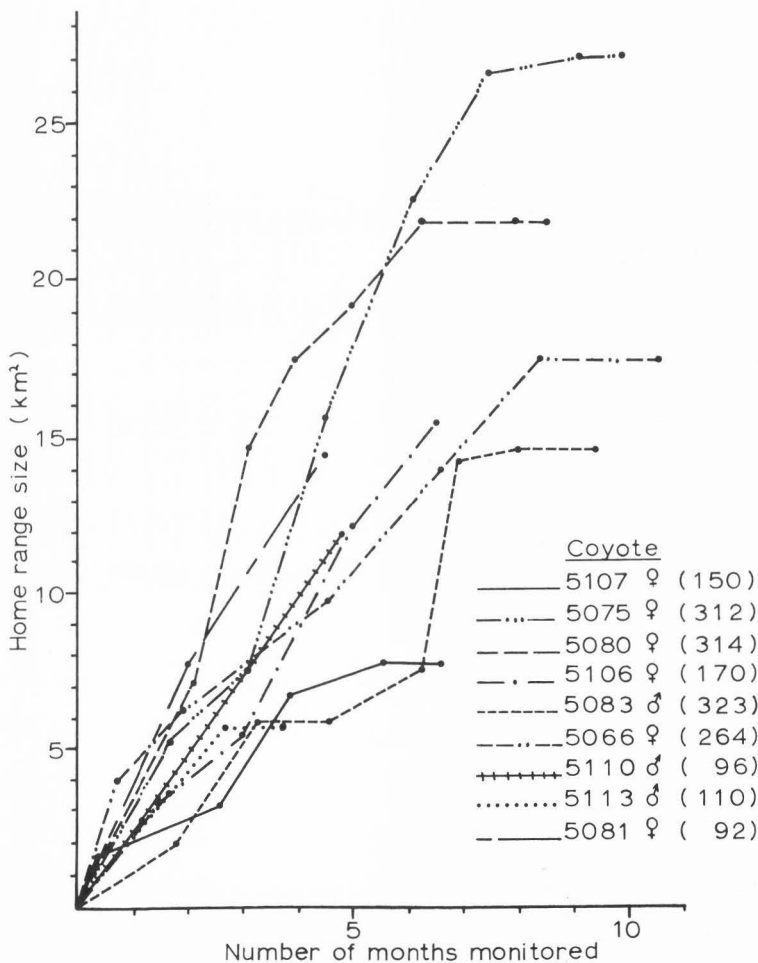


Figure 6. Assessed home range size of nine adult coyotes as a function of the number of months monitored with plots representing increments of 50 relocations (except animal 5107 where they represent increments of 35 relocations). Numbers in parens represent total numbers of relocations.

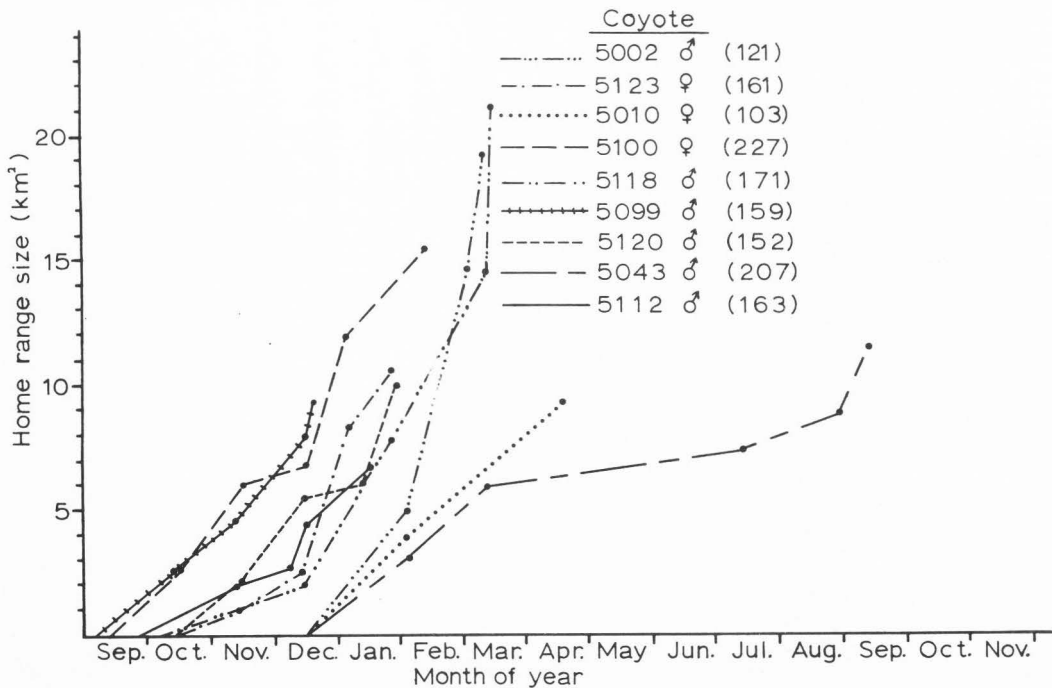


Figure 7. Assessed home range size of nine juvenile coyotes as a function of the months monitored, with each plot representing increments of 50 relocations. Numbers in parens represent total numbers of relocations.

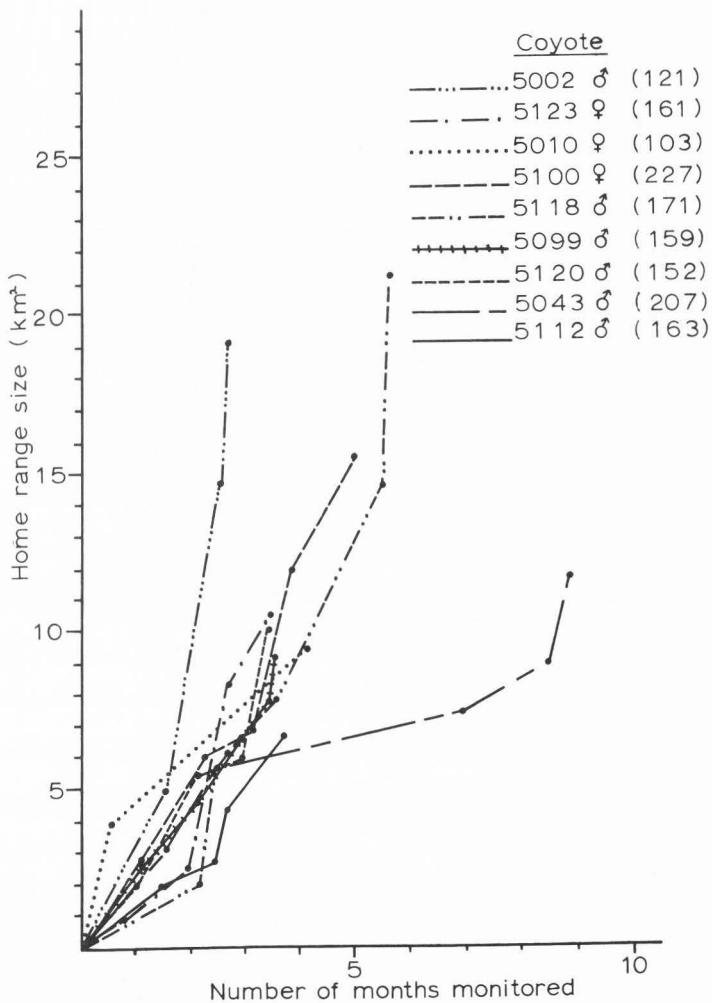


Figure 8. Assessed home range size of nine juvenile coyotes as a function of the number of months monitored, with plots representing increments of 50 relocations. Numbers in parens represent the total numbers of relocations.

Table 3. Number of relocations and home range size (km²) for coyotes in Curlew Valley

Age and sex classification	Asymptotic home ranges				Non-asymptotic home ranges			
	Sample size	Mean home range size	\bar{x} No. of relocations	\bar{x} No. of mos. monitored	Sample size	Mean home range size	\bar{x} No. of relocations	\bar{x} No. of mos. monitored
Adult males	1	14.5	323	10	10	6.7	76.8	4.5
Adult females	4	18.3	260	10.25	3	11.1	191.1	8.1
Juvenile males	--	--	--	--	9	9.9	121.2	4.9
Juvenile females	--	--	--	--	9	8.2	81.6	4.4

by the time interval during which they were monitored to permit meaningful comparisons with other studies (Table 2).

In Figure 5, curves representing assessed home range of adults became asymptotic between late November and mid-January regardless of the date monitoring was initiated. The superficial implication is that adult coyotes in Curlew Valley restricted their activities to more specific areas during the winter. Comparisons with breeding dates of coyotes in Curlew Valley may lend credence to this observation. Knudsen (1976) reported that adult female coyotes engaged in breeding activities from late January to early February. This would immediately succeed the apparent stabilization in areal use by adult coyotes.

However there are factors which may indicate that the onset of these asymptotes are artifacts of the monitoring schedule. The length of time required for curves to become asymptotic varied from 4 to 8 months, which is far longer than some other studies have indicated. Ables (1969) using a more intensive monitoring schedule found that red fox home ranges were adequately described within 5 - 16 days. Peters and Mech (1975) indicated that wolf packs required only 3 weeks to cover their territories. This information indicates that the asymptotes for the Curlew data may have occurred sooner under a more rigorous monitoring schedule. Another factor to consider is that the assessed home range for animal 5066 stabilized in September. Finally, the sample size of five is relatively small to be convincing.

Configuration of home range

Configurations of home range boundaries were classified according to suggested geometric shapes or were designated as ameiboid when

irregular. Home range shapes were circular, ellipsoid, triangular, rectangular, L-shaped, U-shaped, and mostly ameoid (Appendix). Home ranges that could be described by some geometric shape were rare and contained few locations.

Burt (1943) stated that "home ranges are rarely, if ever, in convenient geometric designs. Many home ranges probably are somewhat ameoid in outline..." Sanderson (1966) stated that "All areas used by individuals of a species are rarely encompassed by circles or by any other regular shapes..."

The actual shape of a given home range is the result of an animal's behavioral reaction to habitat characteristics, including prey distribution, vegetation type, topography of the land, man-made structures and presence of others of its kind. Saunders (1963) reported that the shape of home ranges was apparently influenced by topography. Since areas utilized by different coyotes vary in physical characteristics, the shapes of respective home ranges will also vary, and not necessarily correspond to any one particular form.

Use of the terms "circular," "elliptical," or "linear" to describe home range shape apparently originated from the use of small data sets derived from tagging-recapture and snow-tracking studies. Unfortunately actual home range shapes usually remain obscure. Linear shapes are logical interpretations resulting from the polygon and elliptical methods of enclosing relocation data, since point distributions are not circular in nature, and the process of connecting outlying points results in elongated figures.

When data are collected using radio telemetry techniques from fixed stations, linearity in home range configurations may also be, in

part, a function of baseline data. Nelson (1968), in studying distortion of observed home ranges, reported: "When several triangulated locations are used to delineate home range of an animal, these appear to have an increasingly elongate distribution as the baseline is approached."

Patterns of areal use

Coyotes were classified into three categories, based on the contiguity and relative use of the "home range" (Figure 9). The types are: (1) coyotes with relocations primarily contained within one contiguous area; (2) coyotes with relocations in two or more disjunct areas within a common time interval; and (3) wandering animals with proportionately small intensely utilized areas. The majority of coyotes (58 percent) concentrated activity in one area (Table 4). Twenty-two and 19 percent of the animals displayed disjunct and wandering patterns respectively.

Age and sex classifications were analyzed separately to determine whether any groups were more prone to particular categories (Table 4). Adult males may have a greater tendency to concentrate activity within a single area than adult females (64 to 57 percent respectively). Sample sizes are small, however, and most data were not collected during the denning season when females presumably are most sedentary. Juvenile males exhibited the greatest tendency to wander (33 percent) and juvenile females the least (11 percent). Juvenile females, although not as prone to wander, frequented separated areas more than their male counterparts (33 percent to 11 percent respectively). Adult females likewise occupied disjunct to areas more than adult

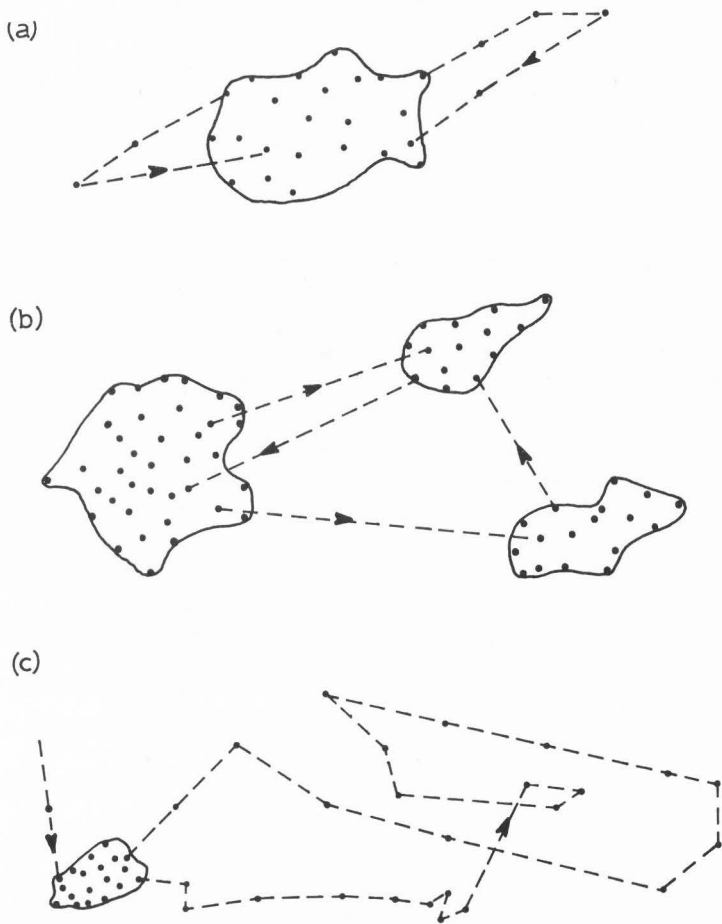


Figure 9. Diagrammatic representation of three patterns of areal use by coyotes based upon the nature and relative "importance" of home range, namely: (a) contiguous home range, (b) disjunct home range, and (c) wandering with relatively small and seldom used home range.

Table 4. Frequency of three types of areal use among Curlew Valley coyotes

Age and sex classification	Sample	Percent with contiguous home range	Percent with disjunct home range	Percent wanderers
Adult males	11	64	18	18
Adult females	7	57	29	14
Juvenile males	9	56	11	33
Juvenile females	9	56	33	11
Total	36	58	22	19

males (29 to 18 percent respectively). None of these comparisons were significantly different at the 95 percent confidence level.

Whether patterns in coyote relocations should be categorized into discrete types may be argued. The above classifications may be the result of an insufficient sampling of coyotes to detect transitional types. Perhaps a continuum of behavioral types exists. It can also be argued that disjunct patterns may not exist, but in reality, are biases in monitoring, with insufficient data to show the animal moving between areas. If additional relocations were obtained, the space between disjunct areas may become smaller or disappear altogether. Four of the five (80 percent) home ranges adequately described were contiguous, compared to 58 percent for all coyotes whose home ranges were described.

Other factors suggest that disjunct areas are not artifacts of the monitoring schedule. In situations where the disjunct areas are

separated as much as 15 or more kilometers, it is unlikely that a coyote could maintain intimate awareness of the vast area between. Also, some coyotes habitually moved directly from one area to another during monitoring sessions. These monitoring "observations" coincided with direct movements between disjunct areas plotted on maps. To a degree, it appeared that the animals may actually have been avoiding prolonged visits to the intervening area.

Niewold (n.d.:333) presents other evidence in support of the three types of patterns described here. From his study of red fox, maps 2 and 3 suggest contiguous schemes, while map 1 is similar to a disjunct home range. In map 4 the distribution of plots is more concentrated than for typical "wandering" coyotes in Curlew Valley and may represent a transitional type between disjunct and wandering types. However, without knowing the sequence of the relocations, interpretations are less certain.

Spatial relationships among coyotes

Home range maps for adult male and female coyotes suggest that mutual avoidance may occur within each group (Figures 10, 11) but such tendencies may not be as prevalent between sexes (Figure 12). Also three adult females (Numbers 5075, 5080 and 5081) appeared to shift home range boundaries upon the return of a fourth female (Number 5107), which had temporarily occupied another portion of her disjunct home range (Figure 13). No overlap in home ranges of juvenile coyotes were observed.

Gipson (1972) studying coyotes in Arkansas did not find evidence of mutually exclusive use of areas by any age and sex classification.

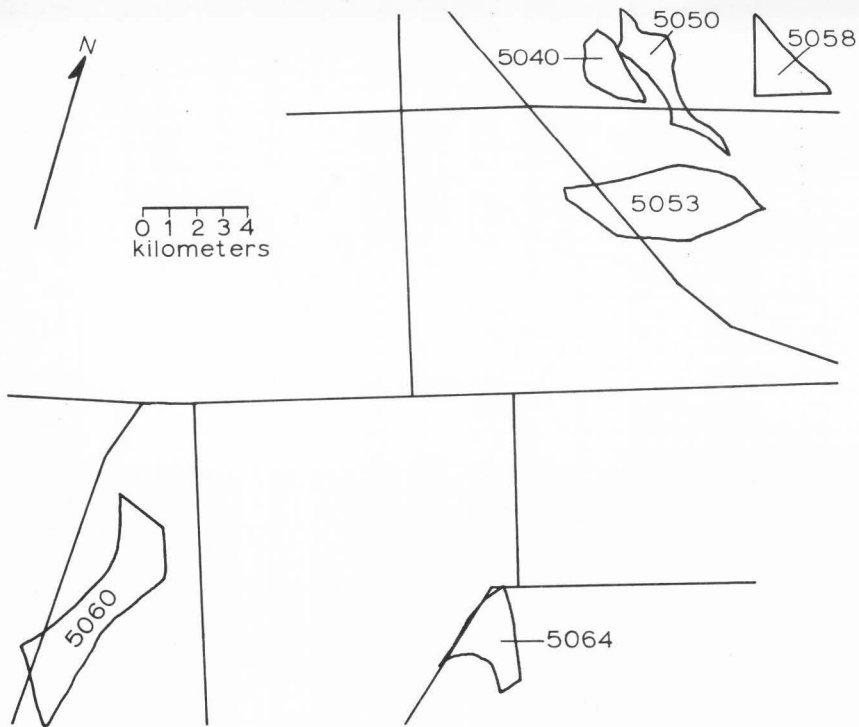


Figure 10. Spatial relationship of home ranges of adult male coyotes in Curlew Valley.

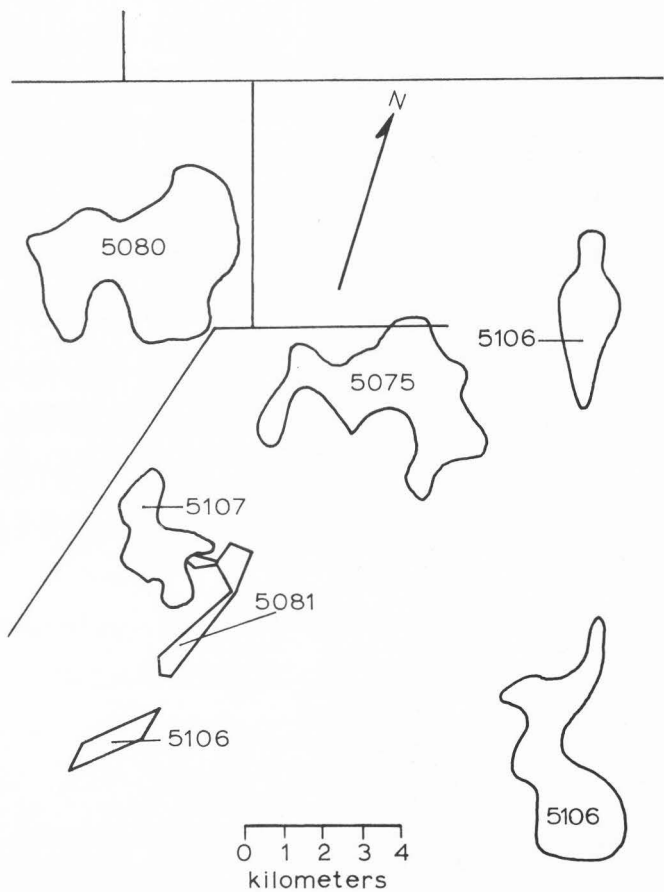


Figure 11. Spatial relationship of home ranges of adult female coyotes in Curlew Valley.

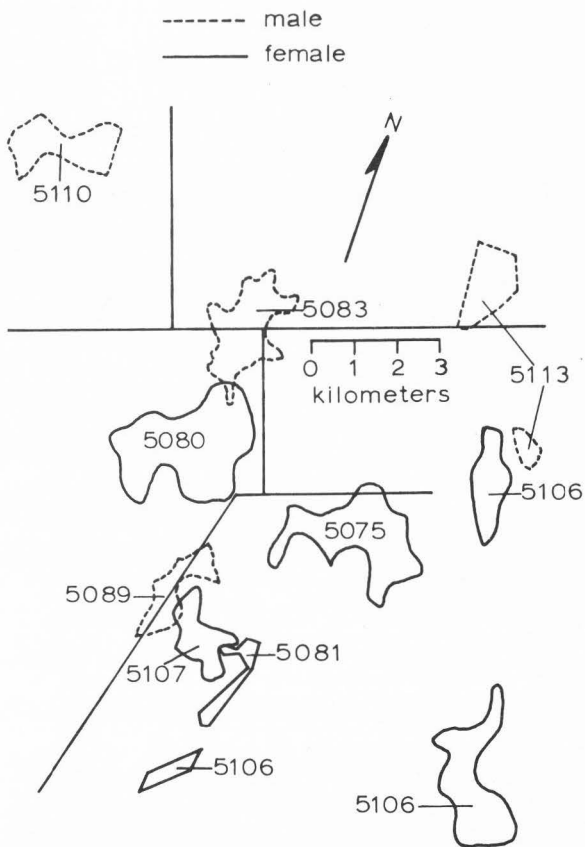


Figure 12. Spatial relationship between adult male and adult female coyotes in Curlew Valley.

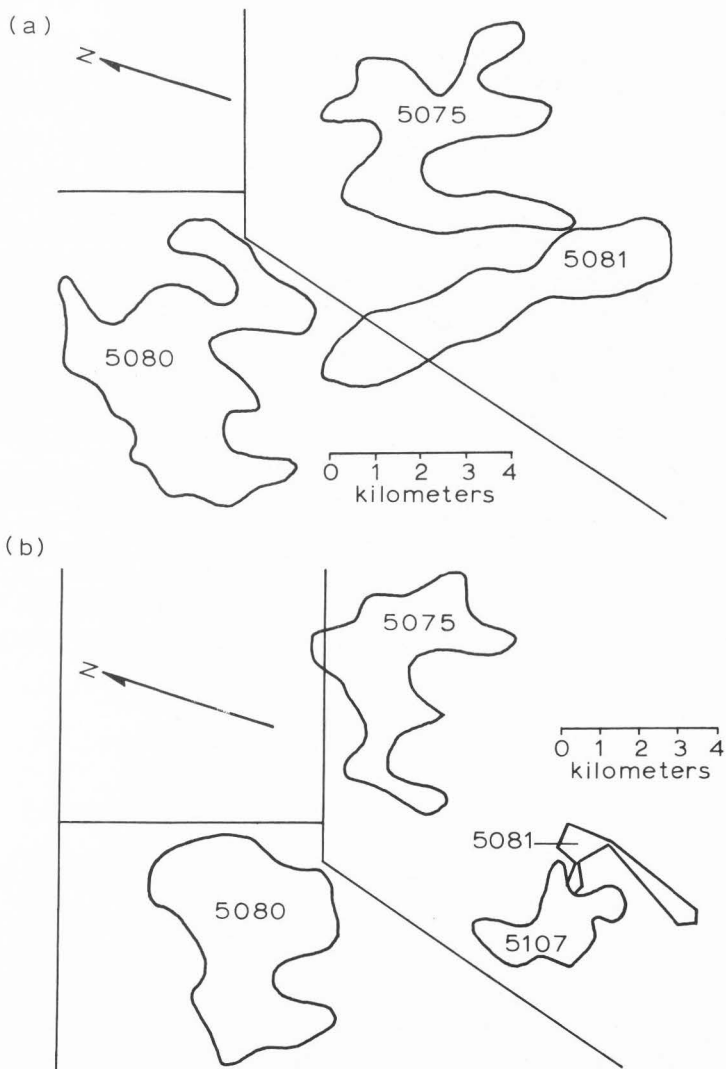


Figure 13. Spatial relationships between adult female coyotes (a) prior to, and (b) after appearance of coyote 5107.

However he enclosed locations with an ellipse, which may exaggerate the home range size as well as alter the actual shape, making it difficult, if not impossible, to detect mutual avoidance. Danner (1976) found evidence of associations among adult females (March 31), between an adult male and female (March 9 and 11) and loose associations with small groups involving pups and/or adults. However he suggests that this situation was compounded by an artificial feeding site created by a cattle carcass dump. Camenzind (1974) reported coyote groups feeding on elk carcasses in the Jackson Hole, Wyoming area. Danner suggests that territoriality between individual coyotes may be waived temporarily when large carcasses are available. Perhaps lone individuals cannot afford to fend off all conspecifics that would partake of this food source. Danner also states that the high coyote density may have reduced the influence of territoriality in his study.

Coyote density, type of food available, and mortality rate may have influenced the lack of home range overlap noted in this study. Coyote densities in Curlew Valley were low (Stoddart 1975 reported 0.19 to 0.54 coyotes per km²), perhaps allowing these animals the "luxury" of not sharing home ranges. Food sources were principally small items such as jackrabbits and mice (Clark 1972, Knudsen 1976, Hoffman pers. comm.), and generally not conducive to the formation of social contacts among coyotes. Jackrabbits concentrate in portions of the study area for brief periods in winter (Stoddart 1975), but overlap in coyote home ranges was not observed in these areas at that time. In addition, coyotes are removed from the population through hunting, trapping, and aerial gunning at rates that may preclude establishment of pack bonds. When coyotes do not travel in packs, mutual avoidance may be easier to

discern from telemetry data. The data are more difficult to interpret when coyotes travel in packs since overlap between individual coyote home ranges necessarily occur. This does not negate the possibility of mutual exclusion, since groups are known to be exclusive of other groups or individuals both among coyotes (Camenzind 1974) and wolves (Peters and Mech 1975).

Caution in interpreting the preceding evidence of exclusive use of areas is essential since the concurrent presence of non-instrumented coyotes is possible. The status of non-instrumented animals as to age, sex, and number is unknown, but their potential influence upon the home ranges of instrumented animals should not be ignored. In addition the behavior of animals toward each other where home ranges overlap is unknown; overlapping boundaries do not necessarily imply tolerance, or even awareness of the "intruder" by the "owner." Peters and Mech (1975) found that territories of wolf packs were exclusive of other packs, but that they overlapped approximately 2 km along the borders. Since Curlew Valley coyotes were not monitored continuously, estimated home range boundaries may be minimal figures, and overlap in home ranges may have been greater than depicted.

Relationship of capture sites to home range boundaries

Inspection of home range maps with regard to the capture locations of individual coyotes suggests that most coyotes were captured at the periphery or outside of their respective home ranges. To evaluate these possibilities, a peripheral zone 1.0 km wide was drawn around each home range boundary (0.5 km on either side). Each coyote was then categorized with regard to whether it had been captured (1) inside its

respective home range; (2) within the peripheral zone; or (3) outside the peripheral zone. Over 90 percent of the coyotes were trapped peripherally or outside their home range (Table 5, Figure 14).

No adults were trapped inside their respective home ranges, compared to 16.7 percent for juveniles. Seventy-three percent of adult males were trapped outside the home range compared to 43 percent for adult females. The trend is reversed for juveniles, with 56 percent of the females being trapped outside the home range compared to 22 percent for males.

Several factors may have biased these results. One involves a temporal discrepancy in which capture occurred one to several months prior to determination of home range boundaries. In the interim, coyotes may have shifted home ranges in response to the trapping experience.

Unequal exposure to traps in each "zone" constitutes a second bias. This differential results from disparities in: (1) numbers of traps within each zone; (2) area within each zone; and (3) the amount of time coyotes spent in each zone.

A third bias is associated with inadequately defined home ranges. The boundaries of these presumably encompassed areas greater than indicated by the data. If these home ranges were inadequately described, some capture locations may have been more centrally located. This is particularly true among adult males (Table 5) which had a high percentage of inadequately defined home ranges.

Among adult females, four had adequately described home ranges with none captured inside, three caught along the margins and one outside. Of the three with inadequate descriptions of the home range, two

Table 5. Capture sites of 36 coyotes with regard to respective home range boundaries

Age and sex classification	Sample size	Percent of coyotes captured with regard to location of home range boundary			Sample size	Mean distance of capture site out-home range boundary (km)	
		Inside	Peripheral	Outside		Mean	Range
Adult males ^a	11	0	27.3	72.7	8	3.9	0.6 -9.3
Adult females ^b	7	0	57.1	42.9	3	3.4	2.6 -4.5
Juvenile males	9	22.2	55.6	22.2	2	0.8	0.6 -1.0
Juvenile females	9	11.1	33.3	55.6	5	4.4	0.5 ^c -10.9
Adults	18	0	38.9	61.1	11	3.7	0.6 -9.3
Juveniles	18	16.7	44.4	38.9	7	3.4	0.5 ^c -10.9
Males	20	10.0	40.0	50.0	10	3.2	0.6 -9.3
Females	16	6.2	43.8	50.0	8	4.0	0.5 ^c -10.9
All coyotes	36	8.3	41.7	50.0	18	3.6	0.5 ^c -10.9

^aIncludes one adequately described coyote home range.

^bIncludes four adequately described coyote home ranges.

^cValue was greater than peripheral limits (0.5 km) prior to rounding off.

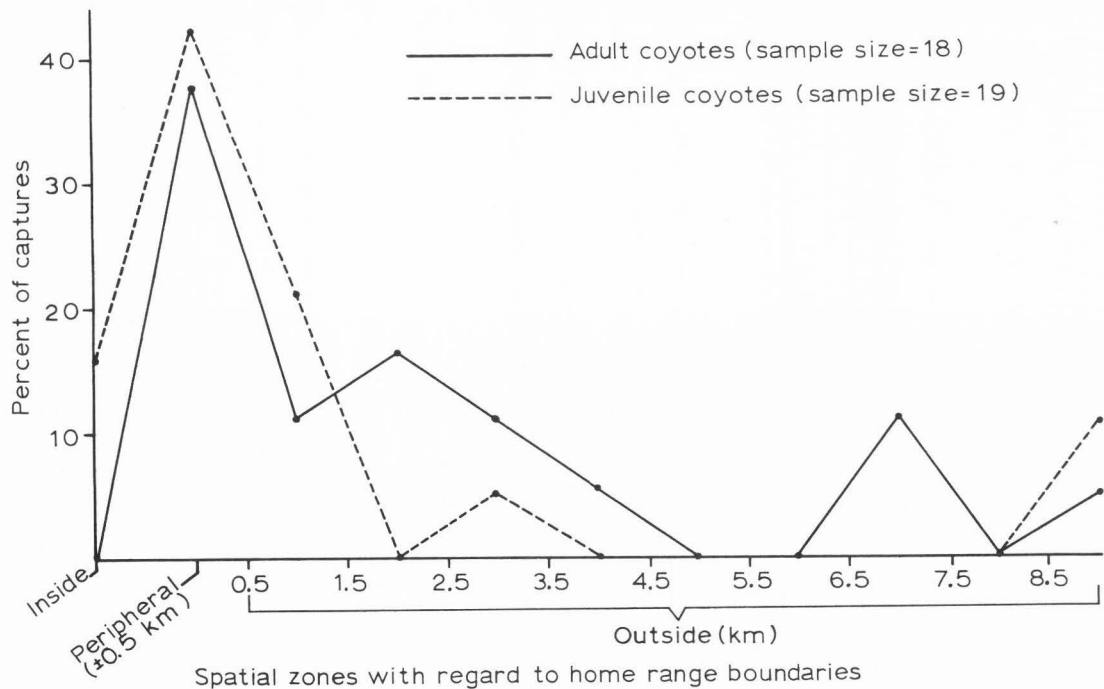


Figure 14. Relative distribution of coyote captures with respect to home range boundaries delineated later.

were 2.6 and 4.6 km outside the home range boundary and one was within the peripheral zone. If allowances for inadequate sampling are considered, the latter animal might have been designated as "inside," but that would be unlikely for the other two. The net result still suggests that a high percentage (85.7) of adult females were captured along the margin or outside the home range. Niewold (n.d.) reports that lactating female red foxes were often caught outside their home range.

Distance of capture from the home range was measured to determine if differences existed between the various age and sex classifications (Table 4). Adults and juveniles were quite similar with mean distances of 3.7 and 3.4 km respectively. Juvenile males, however, were captured closer (within 1.0 km) to the home range than other groups, but the differences were not significant ($p > .05$); 56 percent were caught along the margins and 22 percent were caught well within the home range.

Relationship of mortality sites to home range boundaries

Of the coyotes for which home ranges were delineated, 20 were killed by hunters and 1 was trapped. Kill sites of these animals were also categorized by whether the animals were killed within their home range, along the periphery, or well outside (Table 6). As previously mentioned, not all home ranges were adequately described; and peripheral limits are defined as 0.5 km either side of the line representing the home range boundary. In addition, mean distances outside home range boundaries were calculated where appropriate.

Mortality increased in zones more distant from home range interiors. None of the coyotes was killed within the home range;

Table 6. Mortality sites of 21 coyotes with regard to their respective home range boundaries

Age and sex classification	Sample size	Percent mortality with respect to home range boundary			Sample size	Mean distance outside home range boundary (km)	
		Inside	Peripheral ^a	Outside		Mean	Range
Adult males	7	0	14.3	85.7	6	6.0 ^b	1.0-13.3
Juvenile males	5	0	0	100.0	5	7.9	1.0-16.0
Adult females	2	0	50.0	50.0	1	24.0	--
Juvenile females	7	0	57.1	42.9	3	20.7	10.2-32.0
Adults	9	0	22.2	77.8	7	8.6	1.0-24.0
Juveniles	12	0	33.3	66.7	8	12.7	1.0-32.0
Males	12	0	8.3	91.7	11	6.9	1.0-16-0
Females	9	0	55.6	44.4	4	21.5	10.2-32.0
All coyotes	21	0	28.6	71.4	15	10.8	1.0-32.0

^a+ 0.5 km from the home range boundary.

^bVertical lines indicate non-significant differences ($p > .05$).

29 percent were killed in the peripheral zone (5 of the 6 were females), and 71 percent were killed outside (11 of the 15 were males). All juvenile males were killed outside their home ranges. Had all juvenile male home ranges been adequately described, it is doubtful that interpretations would have been changed since kills averaged 7.9 km from the home range. Relative distribution of mortality within zones was similar for adults and juveniles.

Considering only mortalities that occurred outside the home range, adult males were generally killed nearest to the boundary (6.0 km); with juvenile males 7.9 km outside; juvenile females, 20.7 km outside and the adult female, 24.0 km outside. Significant differences for these comparisons are indicated in Table 6. The most statistically significant difference ($p < .01$) is that between males (6.9 km) and females (21.5 km); the most conspicuous difference is between adult males and females, but there is little reliability in the comparison due to the small sample size for adult females.

Data from 28 additional coyotes were available but were excluded from Table 5 because the number of relocations (generally less than 50) was insufficient to differentiate between movements within and outside the home range, since home range boundaries were not identified. Of these 28, kill sites for 5 coyotes (all juvenile females) were obviously outside existing telemetric relocations, and the animals were quite probably killed outside their respective home ranges. However the number of coyotes killed within "peripheral" and "inside" zones is not known due to uncertainty of the location of home range boundaries.

Sallies

Excursions away from and returning to the home range, characteristically of short duration (hours to a few days), were classified as sallies. These linear movements were measured in a straight line from the nearest point of the home range from which the movement originated, to the furthest known location of the excursion (Figure 15a, b). Direct movements between disjunct segments of the home range were not considered to be sally activity (Figure 15c). Movements less than 1.6 km (1 mile) from the home range boundary were not considered sally activity. Excursions for coyotes with inadequately described home ranges could only be assessed with regard to delineated home range boundaries and therefore represent maximum values.

I analyzed length, duration and frequency of sallies and categorized results according to age and sex groupings (Table 7). On the average, adult females engaged in the longest sallies as well as the greatest number of sallies per unit of time. However adult males tended to engage in sallies for considerably longer periods of time than did other groups. Within each age group, males exhibited approximately two to three times the mean duration as their female counterparts. As a group, adults tended to spend more time per sally than did juveniles with mean values of 8.5 and 5.9 hours respectively. None of these differences were statistically significant ($p > .05$).

Although adult males spent the greatest amount of time per sally, they did not engage in as many sallies per month (4.5) as the other age and sex groups. Adult females were highest with 7.9 sallies per month.

The total time each sex and age group spent in sally activity per

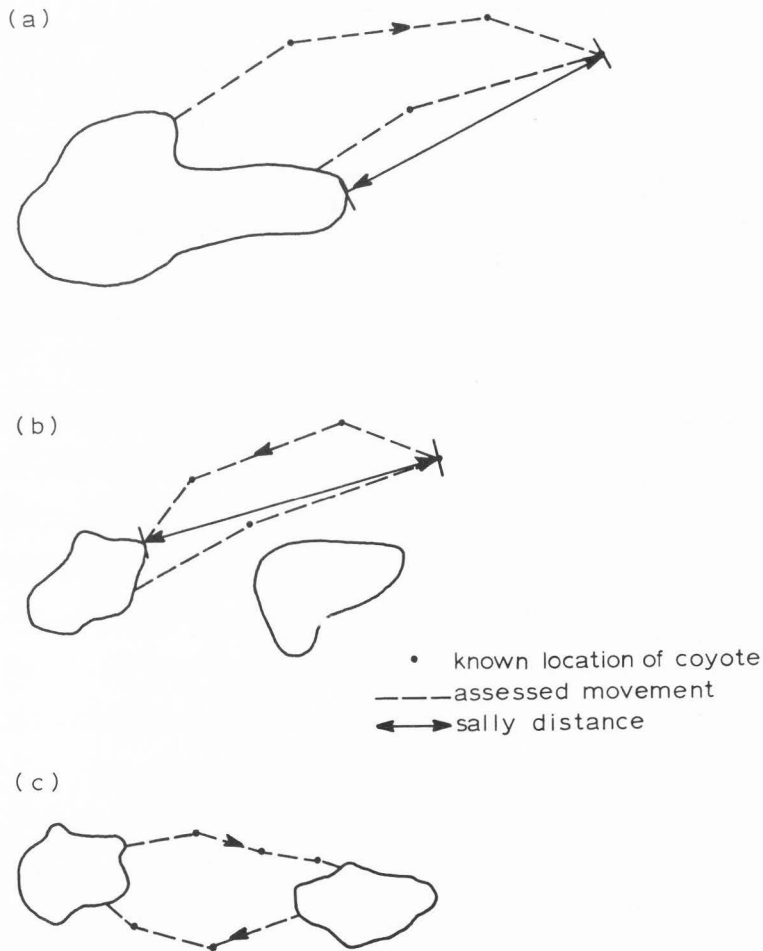


Figure 15. Method of measuring length of sally from (a) contiguous home range and (b) disjunct home range. Situation in (c) was not considered a sally.

Table 7. Distance, duration and number of sallies per temporal unit among Curlew Valley coyotes

Classification	Distance (km)			Duration (hrs.)		No. of sallies per month per animal ^a			Mean duration x mean number per month per coyote
	n ^b	Mean ± S.D.	Range	Mean ± S.D.	Range	n ^c	Mean ± S.D.	Range	
Adult males	21	4.6 ± 2.8	1.6--12.9	16.2 ± 44.7	0.5--204.5	11	4.5 ± 4.2	0.0--1.5	72.9
Adult females	44	4.9 ± 4.5	1.6--21.5	4.9 ± 6.8	0.5-- 33.5	7	7.9 ± 2.5	0.5--1.3	38.7
Juvenile males	29	3.9 ± 3.3	1.7--17.5	7.2 ± 12.2	0.5-- 60.0	9	6.4 ± 5.8	0.0--1.8	46.1
Juvenile females	18	3.3 ± 1.5	1.8-- 7.1	3.8 ± 6.1	0.5-- 24.0	9	5.3 ± 3.5	0.0--1.0	20.1
Adults	65	4.8 ± 4.0	1.6--21.5	8.5 ± 26.2	0.5--204.5	18	5.8 ± 3.9	0.0--1.5	49.3
Juveniles	47	3.7 ± 2.7	1.7--17.5	5.9 ± 10.4	0.5-- 60.0	18	5.9 ± 4.5	0.0--1.8	34.8
All coyotes	112	4.3 ± 3.5	1.6--21.5	7.4 ± 21.0	0.5--204.5	36	5.9 ± 4.2	0.0--1.8	43.7

^aMultiplied by 10 to compensate for 10 percent sample

^bNumber of sallies

^cNumber of animals

month was estimated from the product of mean duration and mean number of sallies per month per animal (Table 7). Adults spent more time than juveniles and males more than females within each age group. Hence adult males spent more time in sally activity than any other age or sex grouping. None of the above comparisons were significant ($p > .05$), however.

Dispersal

Dispersal comprises movements directed away from a previous area of occupation which ultimately ends in establishment of a different area of habitation. Dispersal distances were measured in a straight line from the boundaries of the home range areas from which they originated to the boundary of the succeeding home range areas. In some instances the "new" area did not include sufficient relocations to establish home range boundaries. In other situations final relocations were obtained while coyotes were still engaged in dispersal activity. In these cases, distances were measured from the boundary of the original home range to the furthest point along the dispersal route.

Requirements for onset, duration and cessation of dispersal were that animals had to be monitored during the respective stages of dispersal movement. For animals whose dispersal movements were not "tracked" as they occurred, only distance and direction were calculated.

A greater proportion of juvenile females (53 percent) dispersed than juvenile males (33 percent) or adult males (30 percent), but differences were not significant ($p > .05$). None of the adult females was known to disperse (Table 8).

Table 8. Dispersal parameters of radio-instrumented coyotes in Curlew Valley

Age and sex classification	Animal number	Onset ^a	Cessation ^a	Duration (days)	Direction	Dispersal distance (km)			Percent Dispersing
						Distance	Mean	S.D.	
Adult males	5040	1/13	--	--	North	72	56	13.9	30
	5084	--	--	--	East	48			
	5089	--	--	--	East	48			
Adult females	--	--	--	--	--	--	--	--	--
Adults combined							56	13.9	19
Juvenile males	5105	10/23	--	--	Southwest	7	9	2.1	33
	5041	1/1	1/23	27	South	10			
	5112	11/23	11/29	6	Northwest	11			
Juvenile females	5042	--	--	--	Northwest	29	54	92.3 ^b	53
	5063	--	--	--	West	16			
	5010	--	--	--	North	31			
	5088	9/21	--	--	Northeast	16			
	5003	11/29	--	--	Northwest	281			
	5062	11/21	12/2	11	West	8			
	5012	--	--	--	West	37			
5052	--	--	--	Southeast	13				
Juveniles combined						42 ^b	80.0 ^b	46	
All animals						53.2	83.0	34	

^aMonth/day^bLong dispersal of 281 km for juvenile female 5003 omitted.

Adult males, on the average, dispersed greater distances than did other age and sex groups, and adult coyotes dispersed further than juveniles. However, differences were not significant ($p > .05$). When juvenile female No. 5003, with an exceptionally long movement of 281 km, was omitted, the mean dispersal distance for adult males was significantly greater than juvenile males or females ($p < .01$). The difference between juvenile males and females was not significant, with or without No. 5003 ($p > .05$).

Juvenile coyotes dispersed between late September and late January, with durations of 6 to 27 days. Females generally initiated dispersal before males. Cessation of dispersal occurred between late November and late January. Only one adult coyote was detected during dispersal, and this involved the initial phase (onset) which occurred on January 13.

The coyotes observed tended to disperse in northerly and westerly directions (Table 8). Eight of the 14 animals dispersed within the northwest quadrant (within 270° to 360°).

Fate of Individuals

Human activities (essentially hunting) was the greatest known cause of mortality among all age and sex classes, with 70.0, 66.7, 63.6 and 20.0 percent noted for juvenile females, juvenile males, adult males and adult females respectively (Table 9). Adult females incurred significantly less hunting mortality than other groups ($p < .05$). In addition, a greater percent of adult females was known to be alive at termination of field work than other groups, but differences were not significant ($p > .05$).

Table 9. Percent mortality among age and sex classifications of coyotes as well as home range patterns

Fate	Age and sex classification				Home range patterns		
	Adult Males (n=21)	Adult Females (n=9)	Juvenile Males (n=12)	Juvenile Females (n=20)	Continguous (n=21)	Disjunct (n=8)	Wandering (n=7)
Man-induced (hunting, trapping, road kills, etc.)	66.7	22.2	66.7	70.0	52.4	62.5	71.4
Natural	0.0	0.0	0.0	5.0	4.8	0.0	0.0
Unknown	33.3	44.4	25.0	20.0	33.3	12.5	14.3
Viable at termination of monitoring	0.0	33.3	8.3	5.0	9.5	25.0	14.3

A greater percent of wanderers (71.4) are known to have been shot than coyotes with contiguous (52.4) and disjunct (55.6) home range areas (Table 9). Again, differences were not significant at the 95 percent confidence level.

DISCUSSION

Home Range and Its Measurement

It is apparent from the coyote movements observed that three distinct movement patterns can be distinguished, including home range, sallies, and dispersals. Previous studies have not always made these distinctions. Omission of these patterns may be partially related to problems associated with home range definitions and measurement, and frequently results in misleading interpretations.

Standardizing the home range concept

The term home range has been used to convey many different ideas with regard to animal movement, ranging from "core area" to "life range." While it may be expedient to redefine terms to fit the needs of particular data, it results in vague concepts which lack the conciseness necessary for meaningful comparisons. Comparisons between different patterns with similar labels are misleading because it is not known whether the differences are truly behavioral, or result from measuring different phenomena.

It may not be feasible, at this point, to formulate a standard definition for all species of animals because of differences in behavioral patterns. However, present knowledge of coyote behavior

suggests some general guidelines. As new information accumulates, the guidelines can be modified.

The proposed home range definition is based on the following historical development. Burt (1943) restricted "home range" by associating it with "normal activities of food gathering, mating, and caring for young." He excluded specific types of movements (migration, dispersal, or sallies) that were not regarded as normal, i.e., routine. Several other authors including Blair (1953), Brandt (1962), and Ables (1969), concurred that non-routine, atypical, or infrequently occurring activities should not be included within the home range. The maps depicting movements of coyotes in Curlew Valley (Appendix) indicate that sallies and dispersal indeed are different from areas of routine use.

Blair (1953) defined home range to include the area covered in normal daily activity, thereby restricting the implications of the term "normal." Shillito (1963) replaced the term "habitual" in place of "daily" to include routine movements which may not reoccur on a daily basis. His definition states that home range is "that area habitually traversed by the individual in its normal activities within a specified period of time."

Jewell (1966) rejected the use of the terms "habitual" and "daily," when referring to home ranges of larger animals. He altered Burt's definition, stating "home range is the area over which an animal normally travels in pursuit of its routine activities." I agree that the term "daily activities" places too much restriction on the definition, especially as it applies to larger animals. However it seems inconsistent to use the term "routine" and simultaneously

reject "habitual" since the terms seem synonymous. Habitual use does not imply any particular time interval, but carries the connotation of an activity that occurs frequently and regularly. The fact that an animal only travels over a certain route once every 3 weeks does not negate the fact that it is habitual, provided the animal does so on a regular basis.

Shillito (1963) modified the definition by adding a time constraint. A specified period of time allows one to recognize and delineate the dynamic properties of home ranges associated with changes in seasons, food, and cover. Burt also was aware that the home range was not static since he mentioned that "Often animals would move from one area to another, thereby abandoning the old home range and setting up a new one." Brown (1962) stated that "established homes" were not always permanent, "and that the area of activity also must not be considered to be fixed rigidly." Robinette (1966) found evidence that "deer which are seasonally migratory have home ranges on both summer and winter ranges." Altmann and Altmann (1970) found that as seasons changed, so did the size of home ranges of baboons.

With the preceding historical development in mind, I propose the following definition for home range: the area or volume that is habitually occupied or traversed by an animal in pursuit of routine activities, within a specified period of time. The specified time period can be determined by the behavior of the particular species under study, being left to the discretion of the researcher. Specific movement patterns including sallies, dispersal, homing, and migration are not generally considered routine and therefore are excluded from the concept.

The preceding definition may not necessarily apply to all species. It is intended to establish a standard concept offering the conciseness necessary for meaningful comparisons, yet allowing flexibility to include differences in behavioral characteristics of coyotes from various geographical regions. Whether the definition is applicable to other species is left to the discretion of other researchers.

Problems associated with measurement
of home range

There are at least five major problems associated with measurement of home range using telemetry data, namely: (1) deciding whether to delineate home ranges with "boundaries;" (2) establishing criteria for determining whether home range descriptions are adequate; (3) determining which peripheral locations to include within the home range; (4) selecting the method which most accurately delineates the home range; and (5) establishing criteria for excluding areas from the home range . . . which may result in isolating portions of the home range.

In reference to the first problem Hayne (1949), Harrison (1958), Dice and Clark (1953), Calhoun and Casby (1958), and Burg and Jorgensen (1973), and others suggest a method of describing home range by determining the probability of an animal being within a certain distance (activity radius) of the center of activity (geometric center). This does not delineate the home range with boundaries. When describing home range from tagging and recapture data, or where few locations are involved, this method may be useful. It has several shortcomings, however. Telemetry technology can provide sufficient relocations to distinguish different movement patterns. Most of these

patterns, including home range, appear to have well-defined limits. Tanaka (1963) criticized the probability concept stating "It is reasonable that the natural entity of home range should have a delimited area . . ." This is supported by the assumption that there is some limit to the area which animals can effectively utilize for routine activities, even though they may "wander" far beyond this functional concept. Peters and Mech (1975) speculated that the size of a wolf pack territory was limited by the frequency with which members could mark a given area.

Dice and Clark (1953) and Odum and Kuenzler (1955) interpreted the absence of platykurtosis in frequency distributions of activity radii to mean that no boundaries to range existed. However Ables (1969) found that actual spatial distribution of relocations for two of five red foxes which did not exhibit platykurtosis showed rather definite limits to the home range.

A second limitation is that zones or areas of probability do not suggest anything about the nature of the activity occurring at various locations; only the probability the animal may be found there. If types of activity are not differentiated, then it is not known whether the animal was involved in routine activities while at a particular location. In addition, using geometric centers of activity and activity radii may place the geometric center of activity in a location the animal may never have been, especially if disjunct and/or irregular areas were commonly used.

Assuming that home ranges have definite spatial limits, the remaining problems can be discussed. The second problem in home range measurement is defining minimum requirements for adequate description,

and involves the parameters of time, density of relocations, and seasonal shifts in home range.

To meet minimum requirements for the first parameter, animals should have sufficient time to cover their entire home ranges. Other authors suggest several methods which attempt to detect the point at which an adequate amount of data, collected over a sufficient period of time, produces stabilization in the size of the area circumscribed. Odum and Kuenzler (1955) accepted the point after which each additional observation yielded less than 1 percent increase in the asymptote. Brandt (1962) plotted maximum mean distance between successive captures as a function of the number of recaptures; the asymptote, which represented the greatest mean distance, was the point at which the animal had been captured at the limits of its range. Tester and Siniff (1965) determined the number of locations necessary to adequately describe the center of activity of the home range by plotting mean length of radii as a function of the number of locations. When the mean length stabilized (asymptote), the appropriate number of locations had been obtained. Altmann and Altmann (1970) accepted the point at which successive days of baboon troop progression yielded no significant increase in the areas covered. In my study, the assessed home range size was plotted as a function of the number of months monitored (Figures 5-8), with sampling adequacy assumed when the assessed home range appeared to stabilize.

The second parameter involves obtaining a sufficient density of points to differentiate specific movement patterns. Otherwise activities unrelated to home range will inadvertently be included, resulting in exaggerated sizes. Lack of discernable patterns encourages

connecting outlying locations (polygon method), since no internal figures exist.

Meeting the requirements of the first parameter does not guarantee the second, or vice versa. For example, if an animal requires four weeks to move throughout its entire home range, and 50 relocations were obtained at equal intervals throughout a 4-week period (requirements for time parameter) it is quite probable that the animal would be detected in all areas of its home range. However there may not be enough points to distinguish movements within the home range from sally activity. On the other hand 5,000 or more relocations obtained during the first week (requirements for density parameter) would leave some portions of the home range undetected. However, by taking a much smaller number of relocations (500) on the same animal over a period of 4 weeks using an appropriate schedule, a more accurate estimate of the home range is possible.

The Curlew Valley data suggest that a minimum of 6 months and approximately 150 locations were required for four of the five home ranges to stabilize. These minimum requirements are associated with the particular monitoring schedule used. More continuous monitoring schedules may greatly reduce the time required. Ables (1969) reported that home ranges of red foxes were adequately described within 5-16 days, and that he was able to obtain a mean of 285 relocations per animal (indicative of a more intensive monitoring schedule than used in this study). Niewold (n.d.) also suggested a period of one week was required to define the activity area for most foxes studies. Peters and Mech (1975) indicated that wolf packs required 3 weeks to cover most parts of their territories.

Differences in behavior between animals in different habitats may alter requirements. Ideally, each study should attempt to establish requirements for assessing adequacy of home range descriptions.

The third parameter involves identifying seasonal shifts in assessed home ranges. When an animal shifts all or a portion of its home range to another locality, the assessment of the previous home range must be terminated, and a new assessment initiated. Otherwise the resulting "asymptote" will reflect accumulated areas from two or more different home ranges. A method for detecting this phenomenon involves checking for absence of revisitations to all or some of the previous home range areas.

Caution must be exercised in assuming that any horizontal portion, or "plateau," of the curve representing expansion of assessed home range is a true asymptote. The home range of coyote No. 5083 (Figure 5) reveals that the assessed home range increased following a period of stabilization. Movements of all animals exhibiting such characteristics were analyzed to determine if all areas of the home range prior to the inflection point were visited afterwards. If they were not, it could be argued that the animal shifted its home range at the inflection point and the horizontal portion actually represented the previous home range.

The third problem involves determining which peripheral locations are part of the home range. Maps of animal movements with ample data suggest distinct differences in behavioral patterns, but the type of activity is still conjectural. Interpretation of these patterns may require simultaneous visual and telemetric observations on a few animals to assess their significance. Altmann and Altmann (1970) state

that "The most straightforward approach to the problem of preferential land use is to observe how the animals distribute their activities among the various portions of their range, and record what each portion provides the animals." Once interpretive problems are resolved, and the researcher knows which activities to include within the home range, it is a more objective process to include the appropriate activities within the home range boundary.

The fourth problem involves delineating boundaries around home range activity. Use of polygons and ellipses to circumscribe relocations may be an expedient way to describe data insufficient to reveal different behavioral patterns. However it seems dubious to call these areas home ranges since they essentially include all data points collected and potentially include sallies, dispersal, and migration as well as areas never utilized. The area circumscribed approximates the total area utilized more than home range. Consequently Odum and Kuenzler (1955) referred to the polygon method as describing the "maximum home range" since they believed that the resulting area would often be larger than the utilized home range. Burt indicated that connecting outlying points with straight lines gives a false impression of the area covered, and may indicate a larger range than actually used.

The polygon method may also overestimate the actual home ranges if the boundaries include extensive areas devoid of data points. Such areas may represent: (1) vegetation or terrain types unsuited to the animal's needs, either in terms of cover or food; (2) physiographic and man-made structures (lakes, fenced areas, and other inaccessible portions of the terrain) which prevent the animal from occupying these

areas; (3) areas defended by other coyotes; or (4) failure to monitor the animal when it was in these "vacant" areas, the void being an artifact of the monitoring schedule. Field inspection of these areas may be helpful in determining which of these hypotheses are correct.

If we assume the latter (4) as a possible explanation, there still is no positive reason to include these void areas (except when the void is smaller than the resolution of the telemetry system) since there are no relocations involved. Manville (1949) modified the inclusive boundary strip method by including only the area of the quadrants that animals were known to occupy.

Some researchers (Mohr and Stumpf 1966, Metzgar 1972) have attempted to correct the problem of overestimation by omitting an arbitrary percentage of the peripheral points equally from all sides of the range. However the number of points to exclude, leaving only the home range, is difficult to determine. Also the actual percentage of locations occurring within the home range may vary with the behavior of the individual; eg. wanderers would be expected to spend proportionately more time in nomadic activity as compared to coyotes which more consistently exhibit home range functions (Figure 9). Arbitrary exclusions do not consider individual differences in behavior. This method also assumes that all home range activity is conveniently located toward the center of the point distribution. This is not necessarily the case, as some home ranges may be situated at one edge of the point distribution. In addition, it does not eliminate the inclusion of areas devoid of locational data.

Following the contours suggested by the point distributions appears to be the best method for including locations representing home

range, as well as excluding areas devoid of points. Used in conjunction with ample data plotted chronologically, the method is substantially more accurate than the polygon method. The interpretation necessary for selecting points to include or exclude makes the process arbitrary. Additional behavioral cues would be advantageous.

The fifth problem of assessing home ranges is an extension of the fourth and involves the criteria to include disjunct concentrations of points (created by eliminating areas devoid of relocations) as part of the home range. Nearly all coyotes in this study with disjunct home range areas spent more time in one of the areas as compared to the others, sometimes making it difficult to determine whether the less-utilized areas were visited sufficiently to be considered part of the home range. The initial criterion, total number of locations occurring within the area, was later discarded in favor of the number of visitations by the animal to an area. In this study, one visit per 100 locations was arbitrarily required for a disjunct concentration of points to be considered as part of the home range.

The rationale is best explained by the following example. An animal may only be located in area A during 1 day, but during that day 30 different "fixes" established. The animal may never have been located there again. The same animal may be detected visiting area B on five different occasions, but located only sporadically on each occasion. If the animal was located an average of two times on each visit, only 10 locations from area B would have been established. It would seem logical that area B was used more frequently than area A, but using "total number of points" as a criterion results in a different conclusion.

A standard method in measurement of home range areas should be established, because as Odum and Kuenzler (1955) point out, "Very little confidence can be placed in the comparisons of measurements made by different investigators because of the great variation in procedures used . . ."

Comparisons with other studies of coyotes home range

Other studies of coyote home range use either polygons (Chesness 1974, Danner 1976) or ellipses (Gipson 1972 and Danner 1976) to create boundaries negating meaningful comparisons with Curlew Valley home range values presented here, since the latter were calculated with the contour method. It may be appropriate, however, to compare total areas utilized from this study with home ranges reported by other studies, since both use all reliable locations to calculate the animal's range. Similar to previous studies, I utilized polygons to calculate the total areas used by individual coyotes.

In this study the mean size for total areas utilized for all coyotes was 83 km^2 (Table 10). This compares favorably with the home ranges of $20\text{-}50 \text{ mi}^2$ ($52\text{-}130 \text{ km}^2$) reported by Ozogo and Harger (1966) for coyotes trailed in Michigan. Comparisons at the age and sex level cannot be made between these two studies.

Three studies (Knowlton et al 1972, Gipson 1972, and Chesness 1974) indicate that adult male coyotes have considerably larger ranges than adult females. The reverse is indicated for coyotes in Curlew Valley, with adult female ranges approximately $1\frac{1}{2}$ times larger than adult males.

Of the different age and sex classifications from the Curlew

Table 10. Comparison of total areas utilized (in km²) for coyotes in several studies

Study	Method ^a	Age and Sex Classifications						
		Adult Males	Adult Females	Juvenile Males	Juvenile Females	Adults	Juveniles	All Coyotes
This study, 1976 (Utah-Idaho)	polygon	90(17-428) ^b	138(29-469)	68(13-182)	46(9-100)	112(17-469)	56(9-182)	83(9-469)
Danner, 1976 (South-central Arizona)	polygon ellipse	53	55	6 ^c	7 ^c	54	7 ^c	32(1-81)
		74	76	9 ^c	10 ^c	76	10 ^c	45(1-109)
Chesness, 1974 (Minnesota)	polygon	68(11-233)	16(5-52)				5-8	
Gipson, 1972 (Arkansas)	ellipse	33(11-61)	13(10-17)		12(7-17)			
Knowlton et al, 1972 (South Texas)	empirical	26	8					
Ozoga and Harger, 1966 (Northern Michigan)	empirical							52-130

^a Method of enclosing area utilized

^b Mean with range in parentheses

^c Value is based on juveniles and yearlings

Valley study only adult males are reasonably similar to any of the other studies; Chesness (1974) reports a mean of 26.2 mi^2 (68 km^2) compared to 90 km^2 for this study. All other age and sex comparisons indicate that Curlew Valley coyotes have much larger ranges.

Possible factors influencing differences in observed values include seasons in which movements were assessed, inequalities in habitat, prey density and coyote density between study areas. For example, coyotes were much more abundant ($1.5\text{-}2.3 \text{ per km}^2$) in Texas⁵ than in Curlew Valley ($0.19\text{-}0.54 \text{ per km}^2$) during the periods in which these studies were conducted. With greater coyote densities, smaller ranges might be anticipated, assuming the degree of range overlap remained constant. Burt (1943) found that increased population densities may cause home ranges to shrink in size; Brandt (1962) found that home range sizes were inversely density dependent.

The period of time during which an animal is monitored, as well as the number of relocations, will also influence the size of the total area utilized. Since area accumulates as long as the animal explores new territory, it will continue to increase in size. Therefore comparisons of total areas utilized should be made over equivalent periods of time.

Comparisons with home ranges of other canids

Home ranges of other canids were compared to those of coyotes in Curlew Valley, and as with the intraspecific comparisons, values for

⁵Personal communication with Dr. Frederick Knowlton, Logan, Utah, June 1975.

total area utilized were used. Comparisons were made with red fox (Vulpes fulva), red wolf (Canis rufus) and timber wolf (Canis lupus) to determine whether relationships and trends exist between these species, especially in terms of animal size.

Arnold and Schofield (1956) reported that home ranges of red fox in Michigan was 1.4 mi^2 (3.6 km^2). In a less diverse farm habitat, a single fox had a home range of 2 mi^2 (5.2 km^2). Storm (1972) reported a mean home range size of 3.75 mi^2 (9.70 km^2) for family groups. Storm et al. (1976) reported families staying within an area of $4 \times 2.4 \text{ km}$. The range of all these studies was 0.6 to 9.7 km^2 which is considerably smaller than the 83 km^2 reported in this study.

Shaw (1975), studying the red wolf in Texas, reported a mean home range size of 44.2 km^2 . This value is slightly more than half the value reported for coyotes in this study, but exceeds the value of 26 km^2 for adult male coyotes in Texas (Table 5). It also exceeds the range of values presented for red fox.

Stebler (1944), working with timber wolves in upper Michigan, found that adults may have a home range of 130 mi^2 (336 km^2). Thompson (1952) reported home ranges of 40 to 50 mi^2 (103 to 129 km^2) for timber wolves in Wisconsin. Mech (1966) found that a pack of approximately 16 animals covered an area of 105 mi^2 (271 km^2). Kolenosky and Johnston (1967) reported a mean value of 40 km^2 for wolves in Ontario. Mech and Frenzel (1971) reported that a pack of five animals in northeastern Minnesota used a range of approximately 43 mi^2 (111 km^2), whereas lone wolves covered areas many times this size. Van Ballenberghe et al. (1975) also working in Minnesota reported a range of values from 49 to 192 km^2 for seven animals.

Caution should be used in interpreting the home range values of individual timber wolves when only the size for the pack is known. Some authors (Stebler 1944, Thompson 1952) divide the total range for the pack by the number of animals comprising the pack and use this value as a home range figure for individual animals. However individual members of a pack travel together (especially during winter) and therefore traverse approximately the same area as the pack. Van Ballenberghe found that home ranges of radio-tagged individuals approximated the territories of their respective packs.

The general trend appears to be larger home range requirements as the size of canid species increases. Greater food requirements of the larger canids may force them to use larger tracts of land for their sustenance provided selected prey biomass is the same. Schoener (1971) found that mammals, birds and reptiles maintain increased home range or territory size with increase in body weight.

Observations Related to Home Range Boundaries

Relationship of capture sites to home range boundaries

Among all age and sex categories, coyotes were more frequently trapped along the margins or outside their assessed home ranges than inside. Coyotes appear to be more vulnerable to trapping in areas which are less familiar to them. Welker (1961) found that animals generally become more cautious when confronted with less familiar environments. Metzgar (1967) found that transient white-footed mice engage in more exploratory behavior than do residents. Animals in more novel environments apparently are not only more attentive to

stimuli, but also tend to investigate the area more thoroughly.

This does not imply that animals do not thoroughly explore the confines of their home ranges, but they may have done so at some previous time. After animals have become familiar with a particular environment, they may engage less in exploration and replace this activity with more routine use of the home range (habituation). Welker stated that repeated presentation of mild stimuli eventually fail to elicit the responses which they once did. During habitual travel the animal may repeatedly and inadvertently bypass trap sets without detecting, or responding to, the scent stimulus.

An alternative explanation is that coyotes detect the trap scent, but avoid, rather than approach, novel stimuli while in familiar areas. Barnett (1963) found that wild rats (Rattus norvegicus) show strong aversion to novelty when in familiar surroundings (neophobia), but replace avoidance behavior with investigative responses in a totally new environment. Perhaps the only place coyotes tend to approach the novelty associated with a trap site is near the periphery or outside the familiar surroundings of its "home."

Another possibility might involve a change in location, or size, of the home range as a result of the trapping experience. Prior to that, home range boundaries may have included the trap site. While this remains a viable alternative pending evidence to the contrary, I currently do not suspect appreciable changes in use of areas as a result of being trapped.

Relationship of mortality sites to home range boundaries

No coyote was killed within its respective home range, and more

coyotes were killed outside the home range than along the periphery. Storm et al. (1976) reported that the proportion of red foxes killed by shooting increased with recovery distance. Coyotes outside of their respective home ranges apparently lack advantages which the home range provides (familiarity with environment). The same factor which influenced vulnerability to traps outside the home range may also be operating where man-induced mortality is involved.

Males were more frequently killed outside their respective home ranges than females (Table 6). Males also spent more total time in sally activity than females (Table 7). This suggests that the proportion of coyotes killed outside the home range may be correlated with exposure to less familiar territory. This trend was consistent among other age and sex classifications, except juvenile males suffered the greatest mortality outside the home range while adult males spent the greatest total amount of time in sally activity. To some degree, increased exposure may be compensated by greater experience.

Fate of individuals

The percent of adult female coyotes killed as the result of man-related activities was significantly less than for other age and sex classifications (Table 9). Speculation on this difference again focuses on the relative amounts of exploratory or transient behavior. Adult females spent less total time in sally activity than did adult males and juvenile males (Table 7). Although adult females spent more time in sally activity than juvenile females, the "wisdom" associated with experience may have compensated. The fact that no adult female was known to disperse may be partially due to the small number of

instrumented females. However synthesis of the percent dispersing, relative total time spent in sally activity (third lowest of age and sex groups) and percent of adult females designated as wanderers (also third lowest), suggests adult females may be less inclined to use unfamiliar areas than other groups.

Although differences were not found to be statistically significant, mortality was highest for wanderers (Table 9). This may be pertinent in view of what has been said concerning the advantages of confining movements to familiar areas. The implication is that wanderers may be removed from the population at a faster rate, proportionately, than coyotes with more compact, and presumably familiar, ranges.

Differential patterns of areal use

Speculating on the causes of disjunct and wandering patterns of areal use, I suggest that some habitats may not be as ecologically important to the animal as those utilized more intensely. Another explanation for less contiguous patterns is that social stress from con-specifics may force coyotes to take up less contiguous home ranges.

The concept that familiarity with the environment may be advantageous to coyotes was discussed in the preceding sections. When conditions permit, coyotes may "prefer" contiguous home ranges to separating home areas or wandering. In so doing they reduce exposure to strange environments. Christian (1970) reported that many, if not most, mammals operate to reduce exposure to new or changing habitats. However, food scarcity or intraspecific strife may alter conditions, forcing subordinates to establish less centralized home ranges.

not show any statistical difference, there are indications that wanderers may suffer higher mortality rates than other groups. On the other hand, Storm et al. (1976) did not find marked differential mortality between resident and transient red foxes.

Specific factors influencing vulnerability are unknown, but the following are commonly suggested as possibilities: (1) escape from predators is hindered by lack of familiarity with terrain; (2) physical condition may deteriorate due to disease, poor cover, lack of food, and/or aggression from residents; and (3) transients may spend more time moving about the environment, covering greater distances than residents, to compensate for the lack of familiarity. Peters and Mech (1975) reported that lone wolves may be nomadic in areas up to 20 times the size of a territory. As a result, they may be more exposed to predators (hunters).

Linear Movements Outside the Home Range

Sallies

Although brief forays away from the home range are discussed in a theoretical sense by Burt (1943), Brown (1966), and Jewell (1966), few studies on canids have reported quantitative results on sally activity. Niewold (n.d.) described various irregular excursions away from the activity area (home range) of red fox. He describes four categories of irregular movements based on distance from the home range, number made per month and degree of irregularity. In the Curlew Valley study, no attempt was made to differentiate types of sallies. However Niewold's category of "direct trips between activity areas" was excluded from sally activity here because of the lack of exploratory implications.

The most obvious differences noted in sally activity (Table 7) was adult males spending considerably more time per sally and more total time per month than any other age group. Males spent approximately twice as much total time in forays as did females of their age group.

Niewold reported that male red foxes engaged more frequently (number per unit time) in excursions than did females, as did juveniles in this study; the trend however was reversed among adults in Curlew Valley. Reasons for these differences are not explained.

The importance of sally activity to the animal has been discussed by several authors. Burt (1943) suggests that sallies are exploratory in nature. Welker (1961) stated that exploration, along with play, are crucial to animals learning about, and remaining "in touch" with, the surrounding environment and associated changes that takes place. Metzgar (1967) stated that white-footed mice are more susceptible to predation when they are unfamiliar with the surrounding area, implying that knowledge of the environment gained through previous exploration aids residents in escaping from predators. Brown (1966) and Jewell (1966), working with small mammals, and Peters and Mech (1975), working with wolves, suggest that peripheral extensions to home ranges are made as the result of discovering unoccupied areas through exploratory efforts. Sallies may serve the purpose of familiarizing animals with the environment in and around the home area as well as increasing the awareness of changes therein.

Niewold reported three factors which may serve as motivation for such excursions by red fox: (1) seasonal fluctuations in food items causing animals to seek out other food sources; (2) increases in sexual

activity motivating males to search for females; and (3) high population densities forcing some foxes to search for other areas of habitation.

Dispersal

None of the adult females were known to disperse (Table 8). This is emphasized by the fact that no adult female was among the group of animals that "disappeared" after release. Dispersal may have been a factor accounting for some "missing" animals.

As a group, in Curlew Valley juveniles more commonly dispersed than adults (46 to 19 percent respectively). The frequency of juvenile males known to disperse was less than juvenile females (33 to 53 percent respectively). On the basis of tag returns, primarily from juveniles, Robinson and Cummings (1951), also, found that females not only had a greater tendency to disperse than males (44 to 32 percent respectively) but they dispersed further (37 to 34 km respectively). Knowlton (1972) also suggested that females were more prone to seek out new areas than males. Storm et al. (1976) found that juvenile red foxes were also more prone to disperse than adults (62 to 24 percent respectively). However he found that among juveniles, males were more prone to disperse than females (80 to 37 percent respectively). The 46 percent of juvenile coyotes dispersing in this study was somewhat less than the 62 percent for red fox reported in Storm.

The percentage of juvenile coyotes known to disperse was unexpectedly low. One reason may be that exploitation rates appreciably reduced the coyote population density. Consequently some of the motivational stimuli (social stress, food and cover shortage) commonly

associated with dispersal may have been removed. Another factor potentially influencing the low percentage reported here is that 14 of 48 juveniles released with transmitters were "lost" to the monitoring system shortly after release. Animals which "disappeared" suddenly after release may include a greater proportion of dispersing animals than those which stayed within the monitoring system. Evidence in support of the latter hypothesis was obtained by comparing the percentage of "lost" animals involved in dispersal to the percentage not lost. Of 11 "lost" animals that were recovered, 6 (54 percent) had dispersed; of 36 non-lost animals, only 7 (19 percent) had dispersed.

Another segment of the population which may be included in "lost" animals are those juveniles which dispersed early (late September through early October). Substantial juvenile mortality occurred shortly after release (late fall through early winter). By January 28 (last date a juvenile was known to be engaged in dispersal activity), 12 juveniles (25 percent of those instrumented) had been killed. Early dispersing, younger animals may be more vulnerable to man-induced mortality than animals that disperse later after acquiring more "experience." Preliminary logistical problems in assessing movements may have prevented detecting these animals in their dispersal efforts.

Although a smaller percentage of adults were known to disperse, on the average they dispersed further than juveniles (56 and 42 km respectively). Robinson and Cummings (1951) found that adults moved shorter distances than juveniles (\bar{x} = 31 and 42 km respectively). Their results for juveniles are similar with observations in this study, but comparisons indicate considerably longer dispersal distances for adults in this study. Chesness (1974) stated that the mean dispersal

distances of juvenile males and females was 24.3 mi (39.1 km) and 17.0 mi (27.3 km) respectively. His value for juvenile males is considerably larger than the 9 km reported by this study. However, this study reports substantially larger distances (54 km) for juvenile females. Omitting animal 5003, which was killed 281 km distant, the value reported by Chesness is again larger.

In addition to coyote No. 5003, another (tag return) was shot 224 km from its release point. The rapidly declining food base may have encouraged some animals to engage in longer movements. On the other hand, Storm et al. (1976) suggested long dispersal distances by red foxes (beyond 75 miles) may involve individuals genetically inclined to do so.

Juvenile coyotes generally began dispersal activity between late September and late November, such activity ceasing between late November and late January. Knowlton (1972) indicated that dispersal in Texas became important in November, reached a peak in January, and decreased in intensity through March. Chesness (1974) reported that juvenile coyotes dispersed during October and November. Since only one adult animal was detected during onset of dispersal (January 13), little can be said about dispersal periods for adults.

Some authors (Arnold and Schofield 1956, Storm 1972, and Storm et al. 1976) indicate a greater proportion of red foxes in north-central United States were recovered north of release points than to the south. However the trend could have been a result of unequal hunting and trapping pressure (Storm 1972). Coyotes in Curlew Valley tended to disperse in more northerly and westerly directions. Results were not dependent upon tag returns, but determined primarily from telemetry

results.

A Prediction Equation for Home Range Size

Since home ranges of only five of the animals monitored appeared to stabilize during the study period (Figures 5-8), an equation capable of predicting the ultimate home range size seemed desirable. Metzgar and Sheldon (1974) developed an index to estimate home range size based on the trend (slope) of existing data. A similar procedure was used in this study, based on characteristics of the five animals with asymptotic home ranges. Since the mean slope (b) of the regression equations for animals with adequately described home ranges was not significantly different ($p > .05$) from the entire group of adult coyotes, the sub-sample used to develop the index was representative of the entire sample.

Rationale for development of a predictive equation

A general positive correlation between the rate of expansion of assessed home range (slope of curve) and the corresponding asymptotic value (Figure 6) was noted. Apparently the rate at which the home range appeared to expand was a function of the size of the home range. The rate referred to here is not hourly, but daily, weekly or monthly. Sargeant et al. (n.d.) found little variation in rates (mph) of travel of different foxes, but considerable variation in the total distance traveled due to greater amounts of time spent traveling. This equates to some longer time interval-based rate, such as a day or week. Hence animals with larger home ranges may travel greater distances per temporal unit to cover their larger "holdings."

The development of the home range equation involved describing the slope-asymptote relationship, which was accomplished in two phases. First a linear regression was fitted to plots for the five adult animals individually during the period of "home range expansion" (Figure 16). A linear relationship was selected since the plots appeared more linear than curvilinear. Then the corresponding asymptotes were plotted as functions of the slope coefficients (b value from phase I) for each animal (Figure 17).

Four regression equations were fitted through the slope-asymptote calculations: (1) $Y = a + bX$, (2) $Y = a + b/X$, (3) $Y = a + b X$, and (4) $Y = a + \log_e X$. Three criteria, namely (1) the coefficient of determination (r^2), (2) proximity of the extrapolated curve to the origin, and (3) how well the curve visually fit the data trend, were used in selecting the relationship which best described the plots of the second phase. The curvilinear relationship, $Y = a + b \log_e X$, where X is equivalent to the slope (from phase I) and Y the home range value, was selected as the most accurate predictor.

Home range size based on the predictive equation

Results in Table 11 suggest adult females have slightly larger home ranges than adult males, with mean values of 20.2 and 17.8 km² respectively; the difference was not significant ($p > .05$). These index-estimated values were similar to mean values for coyotes whose home ranges had been adequately described.

Use of the index for estimating juvenile home ranges did not seem warranted since none of the home ranges of juveniles was adequately described, even though three had been monitored between 5-8 months

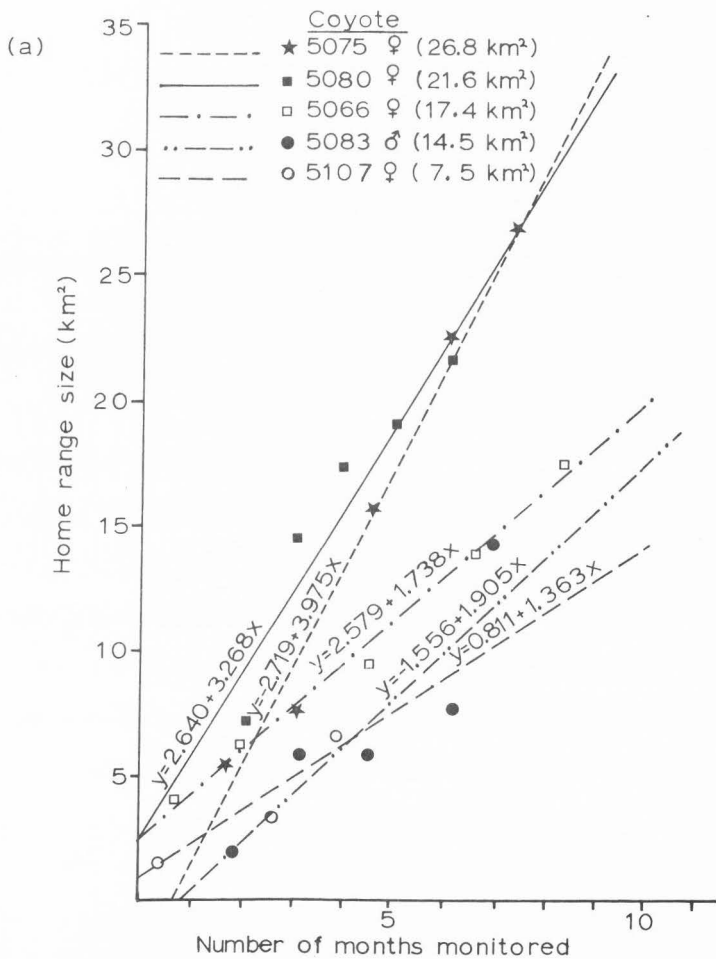


Figure 16. Linear relationship between assessed home range size and number of months five coyotes were monitored.

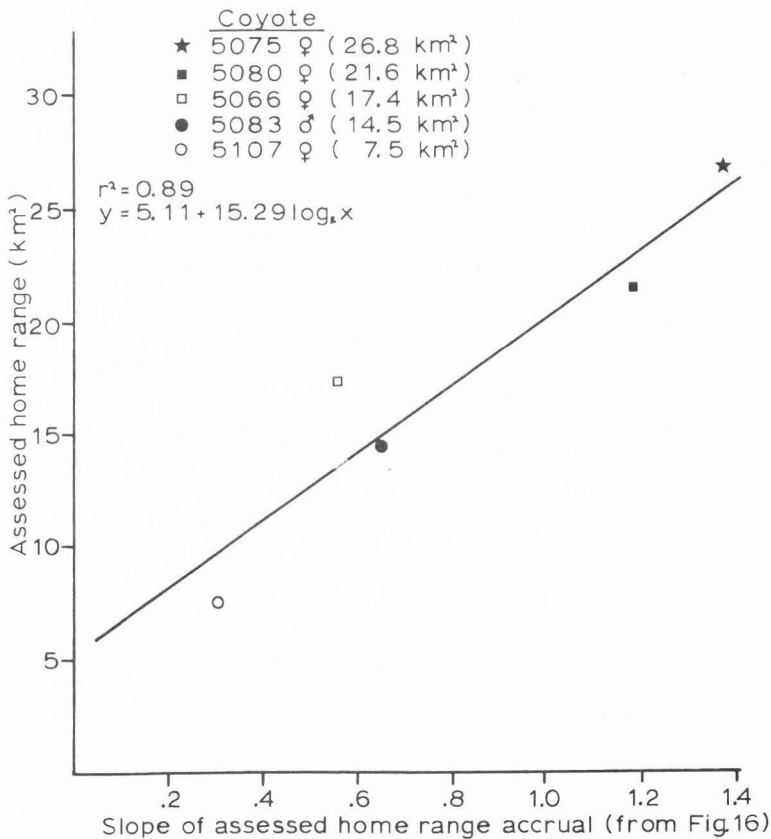


Figure 17. Relationship between rate of accrual in assessed home range ($\text{Log}_e X$) and ultimate size of the home range of 5 adult coyotes in Curlew Valley.

Table 11. Home range sizes for adult coyotes in Curlew Valley based on the predictive equation

Sex	Animal number	Number locations	Number months monitored	Home range size (km ²)		
				Asymptotic	Non-asymptotic	Equation
Male						
	5110	96	6		11.8	20.2
	5050	50	5		3.8	15.6
	5082	43	2		5.8	26.2
	5083	323	10	14.5		[16.1] ^a
	5089	77	5		4.7	1.1 ^b
	5053	65	5		10.8	27.6
	5113	110	5		5.6	16.2
Means excluding asymptotic values					7.1 (3.36) ^c	17.8 (9.58)
Means including asymptotic values					8.1 (4.15)	17.3 (8.83)
Female						
	5080	314	10	21.6		[24.4]
	5081	92	6		14.4	20.9
	5075	312	11	26.8		[24.0]
	5066	264	13	17.4		[15.6]
	5107	150	7	7.5		[7.7]
	5106	170	7		15.4	19.5
Means excluding asymptotic values					14.9 (0.71)	20.2 (0.99)
Means including asymptotic values					17.2 (6.58)	19.0 (6.42)

^aValues in brackets are estimates of asymptotic home ranges predicted from the index.

^bExtrapolated from below the predictive range of the index.

^cParenthetical values are standard deviations.

(Figure 8).

Validation of the equation

An attempt was made to determine the accuracy of the predictive qualities of the equation by applying it to a comparable data set. Data from a study in South Texas by Carley and Knowlton (unpublished data) seemed appropriate, although the assessed home ranges had not distinctly stabilized. Animals had been monitored for a minimum of 8 months and 303 locations, and five animals appeared to be approaching the asymptotic levels (Figure 18). Predicted home range values were compared to the near-asymptotic values (Table 12). Values derived from the prediction equation were essentially twice the near-asymptotic values observed in the field. These discrepancies suggest the relationship between the expansion rate in assessed home ranges of coyotes and the asymptote (maximum home range size) may not apply across habitats and that the predictive equation derived does not apply to other populations. Several qualifications should be mentioned before abandoning the possibility of a general equation: (1) the sample from which the equation was derived was small, comprised of only five animals; (2) the home range values for the Texas coyotes were from an extrapolated portion of the predictive relationship, since the largest home range value for Texas was smaller than the smallest value for Curlew Valley; (3) the Y-intercept of 5.11 in Figure 17 argues against a linear relationship as portrayed since presumably such an equation should pass through the origin; (4) home ranges of the Texas animals had not completely stabilized; and (5) the monitoring schedules used in the two studies were not identical.

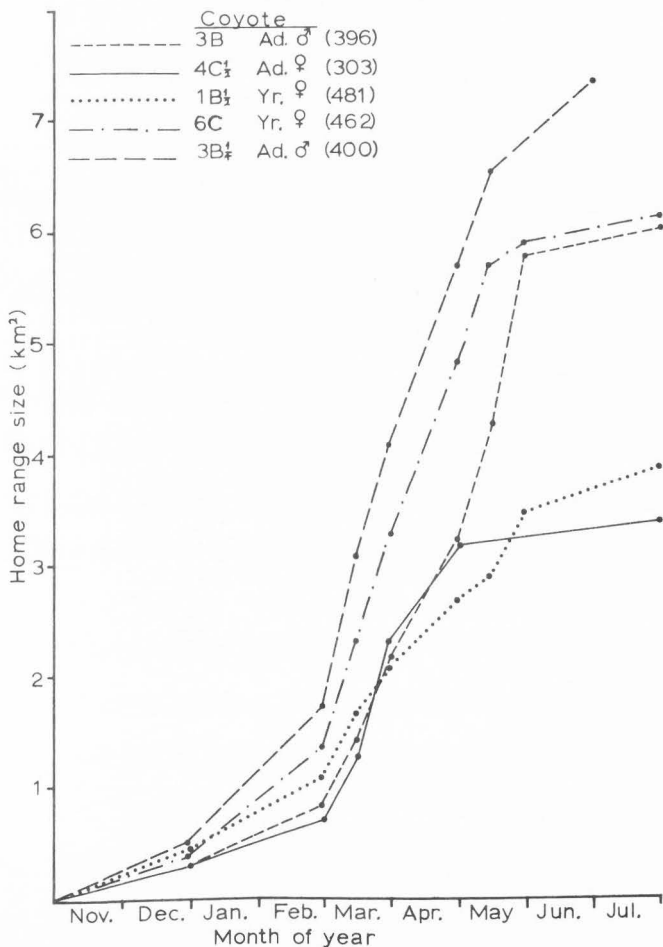


Figure 18. Expansion of assessed home ranges of five coyotes in South Texas. Numbers in parens represent total number of relocations.

Table 12. Home ranges (in km²) of South Texas coyotes predicted from the predictive equation for Curlew Valley

Animal No.	Sex	Age	Observed home range (near-asymptotic level)	Predicted home range (from Curlew equation)
4C $\frac{1}{2}$	Female	Adult	3.39	8.75
1B $\frac{1}{2}$	Female	Yearling	3.85	0.24
6C	Female	Yearling	6.11	11.84
3B	Male	Adult	6.00	11.70
3B $\frac{1}{2}$	Male	Adult	7.30	14.51

Seemingly, development of a general equation between home range size and the rate of expansion of the assessed home range warrants further exploration. Obviously, parameters of the assessment (relocation) schedule would influence the nature of the equation. The nature of the predictive equation in the lower range of values deserves better definition.

SUMMARY

Between fall 1972 and summer 1974, 87 coyotes were equipped with radio-collars in Curlew Valley. A total of 5059 relocations were obtained, with 79 percent of them from 36 animals. Among the latter, movement patterns were identified, including total area utilized, home range, sallies, and dispersal.

Total area utilized was determined by connecting outlying points to form irregular polygons. While this is an easy representation of animals gross utilization of space, it over-estimates real use of space and fails to discriminate between different activities. Mean values obtained for total area utilized were: 90 km^2 for adult males; 138 km^2 for adult females; 68 km^2 for juvenile males and 46 km^2 for juvenile females.

Home range boundaries were established according to contours based on (1) frequency of visitations to specific locations, and (2) density (or absence) of relocations. Home ranges described were irregular (ameboid) in shape and did not conform to any specific geometric form. In assessing home range size as a function of the time the animals were monitored, or number of relocations, only five home ranges (one adult male and four adult females) appeared to stabilize

and were thought to be adequately described. From characteristics of the rate of home range expansion and the asymptote in home range size of these 5 animals, an equation was developed to estimate the ultimate size of home ranges of other adults. These averaged 20.2 km^2 for females and 17.8 km^2 for males. Since no juvenile animals were among those with stable home range sizes, it did not seem reasonable to use the equation to estimate home ranges for this group. Size of areas are listed, however, along with the number of relocations and time period over which the data were gathered.

Three patterns were recognized with regard to coyote home ranges: (1) contiguous ones; (2) others with two or more disjunct areas that were commonly used, frequently several kilometers apart; and (3) wandering animals with relatively small areas that could be construed to be a home range. In addition, there was some evidence to suggest mutual avoidance between members of the same sex but not between members of the opposite sex.

Analyses of capture and mortality sites as well as fates of individual coyotes suggest that coyotes may be more vulnerable to human-related activities when outside their respective home ranges than within them. This increased vulnerability may be related to the animal's unfamiliarity with surroundings at that time. Appreciably fewer adult females were shot by hunters compared to other sex and age groups. Adult females also were less prone to pursue activities outside the home area.

Sallies (excursions) away from the home area averaged 4.9, 4.6, 3.9 and 3.3 kilometers respectively for adult females, adult males, juvenile males, and juvenile females. Adult females also engaged in

more sallies per unit of time ($\bar{x} = 7.9$ per month) than other groups. On the other hand, adult males spent the greatest amount of time per sally ($\bar{x} = 16.2$ hours) and the most time per month in sally activity (72.9 hours).

Mean dispersal distances noted were 56 km for adult males, 9 km for juvenile males, and 54 km for juvenile females. No adult female was known to disperse. Although juveniles were more apt to disperse than adults (46 and 19 percent respectively), adults tended to disperse further (56 vs. 42 km respectively). The greatest dispersal noted was 281 km.

The need for standardization of terminology with regard to home range is discussed. Without commonality in definitions and in the methods of assessing home ranges, there is little value in comparing results obtained by studies in different habitats, or under varying conditions. Since home ranges are dynamic, measurements should be related to specific time intervals.

LITERATURE CITED

- Ables, E. D. 1969. Home range studies of red foxes (Vulpes vulpes). J. Mammal. 50(1):108-120.
- Altmann, A. and J. Altmann. 1970. Baboon Ecology. Univ. of Chicago Press, Chicago and London. 220 pp.
- Arnold, D. A. and R. D. Schofield. 1956. Home range and dispersal of Michigan red foxes. Papers of the Michigan Acad. of Sci., Arts and Letters Vol. 41 (1955 meeting).
- Balser, D. S. 1965. Tranquilizer tabs for capturing wild carnivores. J. Wildl. Mgmt. 29(3):438-442.
- Barnett, S. A. 1963. A study in Behavior. Methuen and Co. LTD, London. 288 pp.
- Blair, W. F. 1953. Population dynamics of rodents and other small mammals. Advances in Genetics. 5(1):1-41.
- Brandt, D. H. 1962. Measures of the movements and population densities of small rodents. Univ. of Calif. Publ. in Zool. 62(2):105-183.
- Brown, L. E. 1962. Home range in small mammal communities. In Survey of Biol. Prog., Bentley Glass, ed. 4:131-179.
- _____. 1966. Home range and movements of small mammals. Symp. Zool. Soc. London No. 18:111-142.
- Burg, J. R. and C. D. Jorgensen. 1973. Home range of small mammals: a reliable estimate. J. Mammal. 54(2):483-487.
- Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. J. Mammal. 24(3):346-352.
- Calhoun, J. P. and J. U. Casby. 1958. The calculation of home range and density of small mammals. U.S. Dept. of H.E.W., Publ. Health Mono., No. 55. 24 pp.
- Camenzind, F. J. 1974. Territorial and social behavior of free-ranging coyotes. Proc. Coyote Research Workshop, Denver, Colo.
- Chesness, R. A. 1974. Home range, territoriality and sociability of coyotes in north-central Minnesota. Proc. Coyote Research Workshop, Denver, Colo.

- Christian, J. J. 1970. Social subordination, population density and mammalian evolution. *Science* 168(3927):84-90.
- Clark, F. W. 1972. Influence of jackrabbit density on coyote population change. *J. Wildl. Mgt.* 36(2):343-356.
- Danner, D. A. 1976. Coyote home range, social organization, and scent post visitation. M.S. thesis, Univ. of Arizona, Tuscon. 86 pp.
- Dice, L. R. and P. J. Clark. 1953. The statistical concept of home range as applied to the recapture radius of the deer mouse (Peromyscus). *Contrib. No. 62, Lab. Vert. Biol., Univ. Mich., Ann Arbor.* 15 pp.
- Errington, P. L. 1963. Muskrat populations. Iowa St. Univ. Press, Ames, Ia. 665 pp.
- Gipson, P. S. 1972. Home range and activity of the coyote (C. latrans frustror) in Arkansas. *Proc. Annual Conf. of the Southeastern Assoc. of Game and Fish Commissioners.* 26:82-95.
- Harrison, J. L. 1958. Range of movements of some Malayan rats. *J. Mammal.* 39(2):190-206.
- Hawthorn, J. M. 1971. Coyote movements in the Sagehen Creek Basin, N. E. California. *Calif. Fish and Game.* 57(3):154-161.
- Hayne, D. W. 1949. Calculation of size of home range. *J. Mammal.* 30(1):1-18.
- Heezen, K. L. and J. R. Tester. 1967. Evaluation of radio-tracking by triangulation with special reference to deer movements. *J. Wildl. Mgt.* 31(1):124-141.
- Howard, W. E. 1960. Innate and environmental dispersal of individual vertebrates. *Amer. Midl. Nat.* 63(1):152-161.
- Jewell, P. A. 1966. The concept of home range in mammals. *Symp. Zool. Soc. London*, No. 18. p 85-109.
- Knowlton, F. F. 1972. Preliminary interpretation of coyote population mechanics with some management implications. *J. Wildl. Mgt.* 36(2):369-382.
- _____, C. J. Carley, R. T. McBride, and Div. Wildl. Serv. 1972. *Mammal Damage Control Research--Predators and Predator-Prey.* Ann. Prog. Rept., Denver Wildl. Res. Ctr., Denver, Colo. 30 pp.
- Knudsen, J. J. 1976. Demographic analysis of a Utah-Idaho coyote population. M.S. thesis, Utah State Univ., Logan. 195 pp.

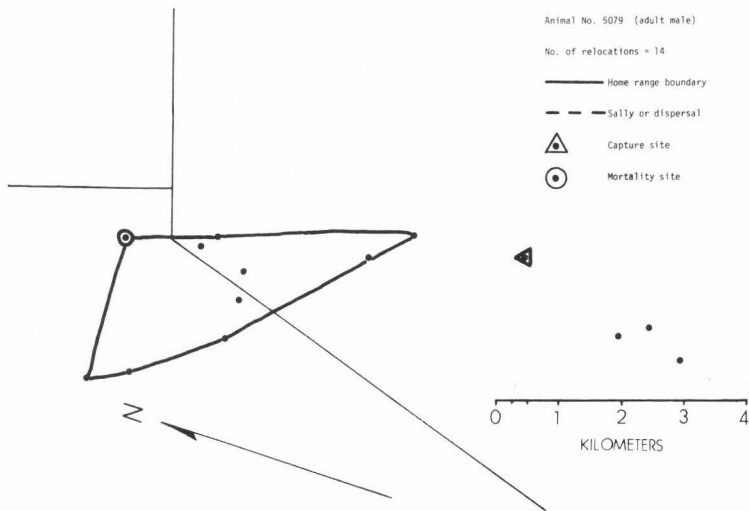
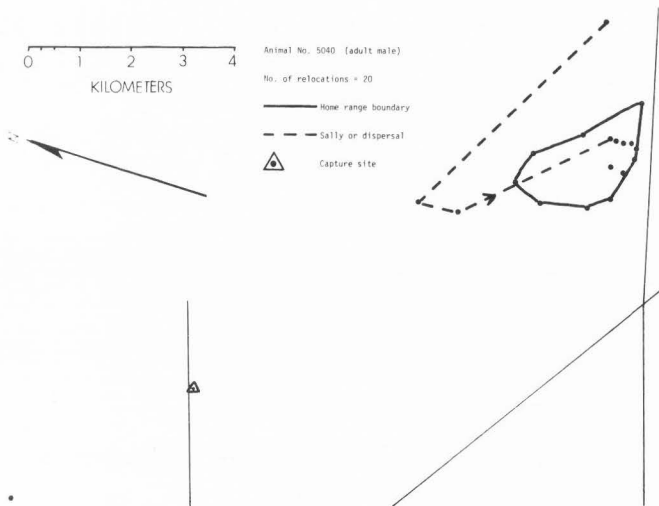
- Kolz, A. L., G. W. Corner and R. E. Johnson. 1973. A multiple-use wildlife transmitter. Spec. Sci. Dept., Wildl. No. 163. Denver Wildl. Res. Ctr. 11 pp.
- Kolenosky, G. B. and D. H. Johnston. 1967. Radio-tracking timber wolves in Ontario. Amer. Zool. 7(2):289-303.
- Manville, R. H. 1949. A study of small mammals in Northern Michigan. Misc. Publ. Mus. Zool., Univ. Mich. 73(1):1-83.
- Mech, L. D. 1966. The wolves of Isle Royale. Fauna of the National Parks of the U.S., Fauna Series 7, U.S. Dept. of the Interior. 210 pp.
- _____. and L. D. Frenzel, Jr. 1971. Ecological studies of the timber wolf in northeastern Minnesota. North Central Forest Expt. Sta., For. Serv., U.S. Dept. of Agric. Res. Paper N C 52. 62 pp.
- Metzgar, L. H. 1967. An experimental comparison of screech owl predation on resident and transient white-footed mice (Peromyscus leucopus). J. Mammal. 48(3):387-391.
- _____. 1972. The measurement of home range shape. J. Wildl. Mgt. 36(2):643-645.
- Metzgar, L. H. and A. L. Sheldon. 1974. An index of home range size. J. Wildl. Mgt. 38(3):546-551.
- Mohr, C. O. and W. A. Stumpf. 1966. Comparison of methods for calculating areas of animal activity. J. Wildl. Mgt. 30(2):293-304.
- Nelson, L. Jr. 1968. Distortion of observed home range patterns in radio-telemetry tracking studies. Dept. Wildl. Res., Utah State Univ., Logan. 11 pp.
- Niewold, F. J. J. n.d. Irregular movements of the red fox (Vulpes vulpes) determined by radio tracking. Pop. Ecol. of Game Spp.: 331-337.
- Odum, E. P. and E. J. Kuenzler. 1955. Measurement of territory and home range size in birds. Auk 72(2):128-137.
- Ozoga, J. J. and E. M. Harger. 1966. Winter activities and feeding habitat of northern Michigan coyotes. J. Wildl. Mgt. 30(4):809-818.
- Peters, R. P. and L. Mech. 1975. Scent-marking in wolves. Amer. Scient. 63(6):628-637.
- Robinette, W. Leslie. 1966. Mule deer home ranges and dispersal in Utah. J. Wildl. Mgt. 30(2):335-349.

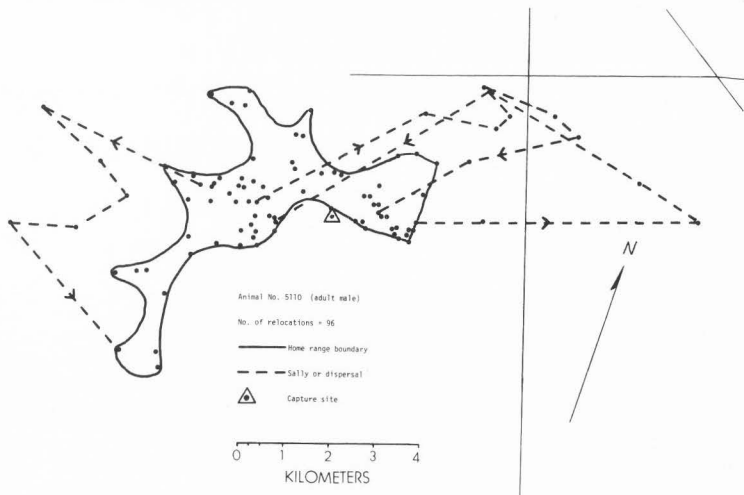
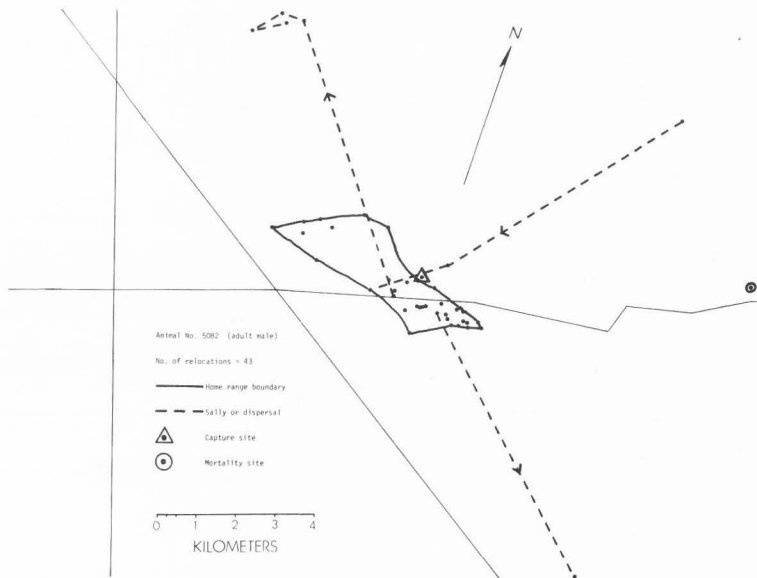
- Robinson, W. B. and M. W. Cummings. 1951. Movements of coyotes from and to Yellowstone National Park. U.S. Fish and Wildlife Service, Spec. Sci. Rept., Wildl. No. 11. 17 pp.
- _____, and E. F. Grand. 1958. Comparative movements of bobcats and coyotes as disclosed by tagging. J. Wildl. Mgt. 22(2):117-122.
- Sanderson, G. C. 1966. The study of mammal movements--a review. J. Wildl. Mgt. 30(1):215-235.
- Sargeant, A. B., D. W. Warner, and D. B. Siniff. n.d. Activity patterns in a wild red fox population. (unpubl. manuscript).
- Saunders, J. K. Jr. 1963. Movements and activity of the lynx in Newfoundland. J. Wildl. Mgt. 27(3):390-400.
- Schoener, T. W. 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics. 2:369-404.
- Shaw, J. H. 1975. Ecology, behavior, and systematics of the red wolf (Canis rufus). Ph.D. Dissert. Yale Univ., New Haven. 110 pp.
- Shillito, J. F. 1963. Observations on the range and movements of a woodland population of the common shrew, Sorex araneus L. Proc. Zool. Soc., London. 140(3):533-546.
- Snyder, R. L. 1961. Evolution and integration of mechanisms that regulate population growth. Proc. Natl. Acad. Sci. 47(4):449-455.
- Stebler, A. M. 1944. The status of the wolf in Michigan. J. Mammal. 25(1):37-43.
- Stoddart, L. C. 1975. Population dynamics, movement and home range of black-tailed jackrabbits (Lepus californicus) in Curlew Valley. Prog. Rept., Utah State Univ., Logan. 30 pp. (mimeo).
- Storm, G. L. 1972. Population dynamics of red foxes in north-central U.S. Ph.D. Dissert., Univ. Minn., St. Paul. 227 pp.
- _____, R. D. Andrews, R. L. Phillips, R. A. Bishop, D. B. Siniff and J. R. Tester. 1976. Morphology, reproduction, dispersal, and mortality of midwestern red fox populations. Wildl. Monog., No. 49. 82 pp.
- Tester, J. R. and D. B. Siniff. 1965. Aspects of animal movements and home range data obtained by telemetry. Trans. N. Amer. Wildl. and Nat. Resour. Conf. 30:379-392.
- Tanaka, R. O. 1963. Truthfulness of the delimited area concept of home range in small mammals. Kochi Women's Univ. Bull. (Nat. Sci. Ser.) 11(7):6-11.

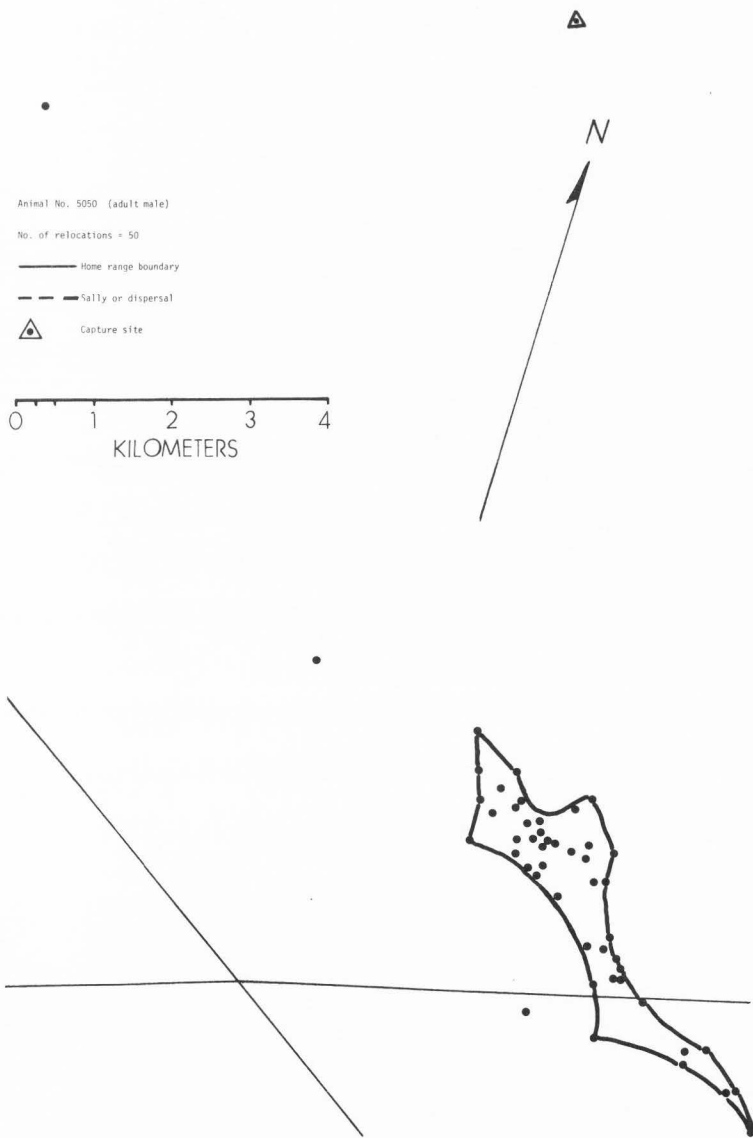
- Thompson, D. Q. 1952. Travel, range, and food habits of timber wolves in Wisconsin. *J. Mammal.* 33(4):429-442.
- Welker, W. I. 1961. An analysis of exploratory and play behavior in animals. In *Functions of Varied Experience* by D. W. Fiske and S. R. Maddi. Dorsey Press, Inc., Homewood, Ill. 175-226 pp.
- Van Ballenberghe, V. A., W. Erickson and D. Byman. 1975. Ecology of the timber wolf in northeastern Minnesota. *Wildl. Monog.* No. 43. 43 pp.

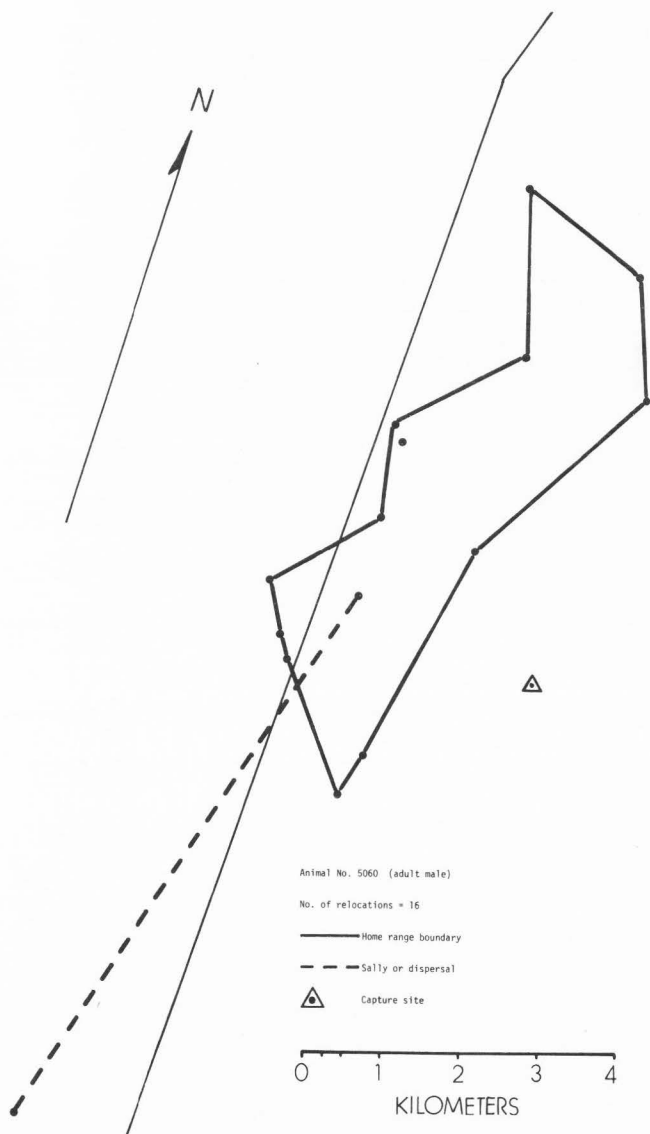
APPENDIX

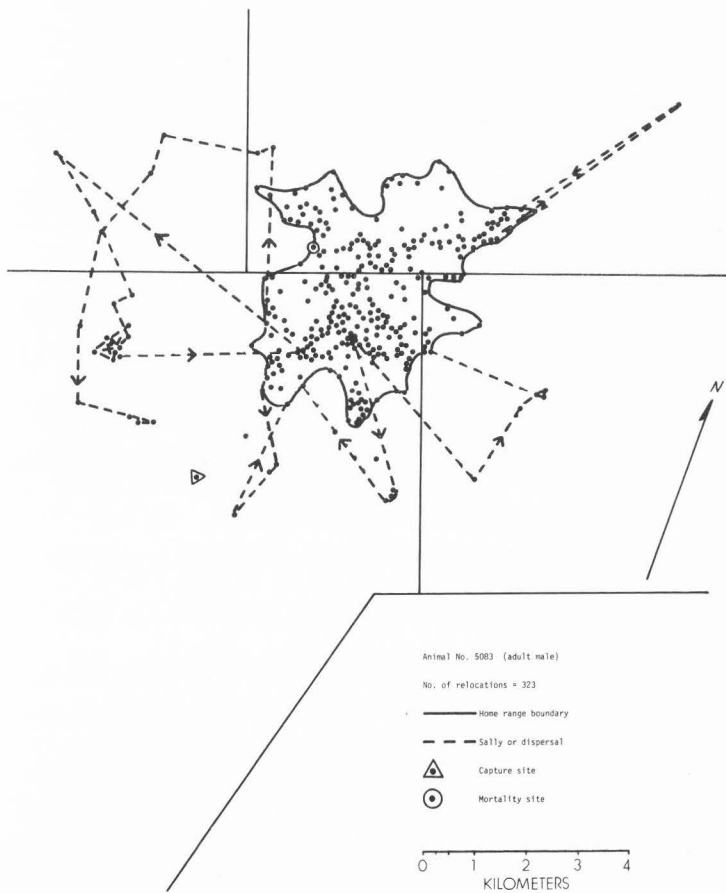
Home Ranges of Coyotes in Curlew Valley

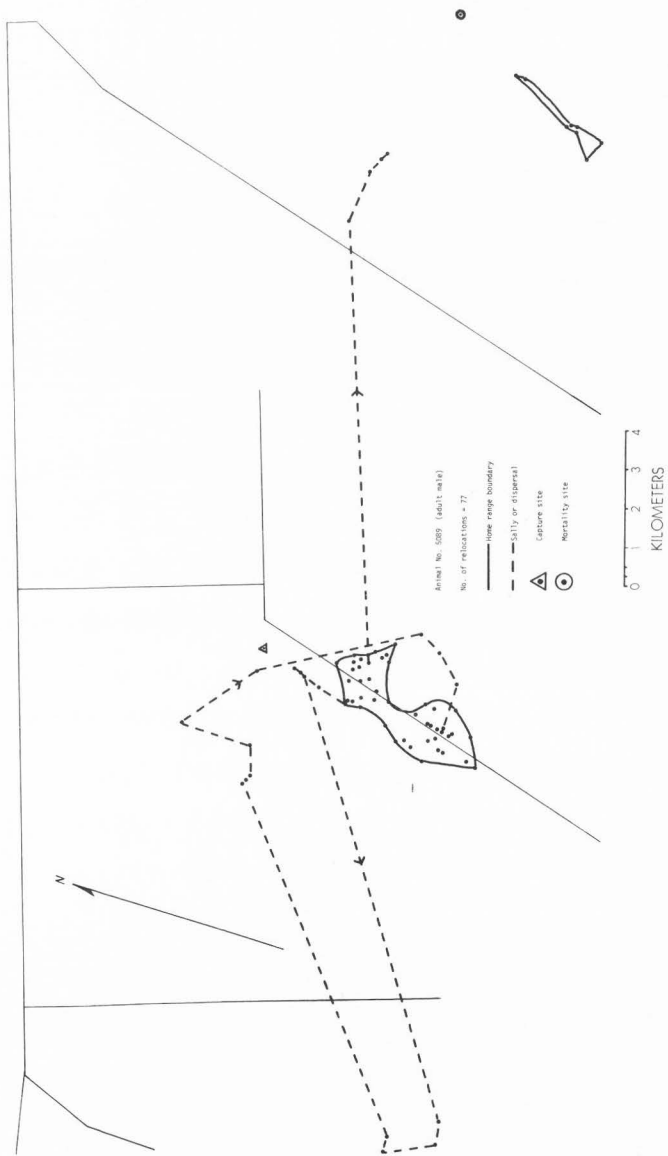


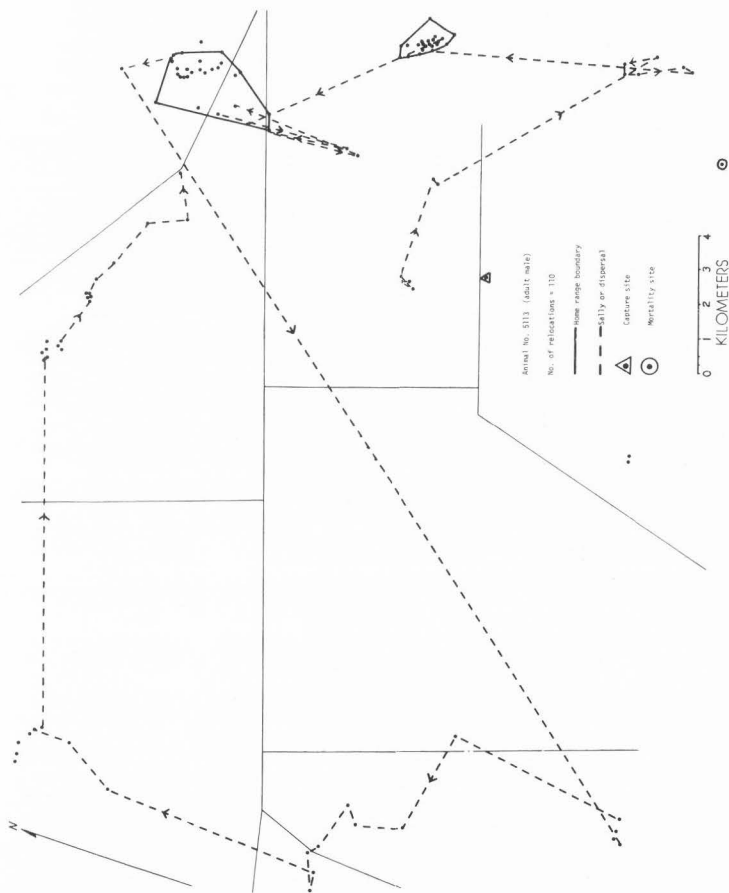


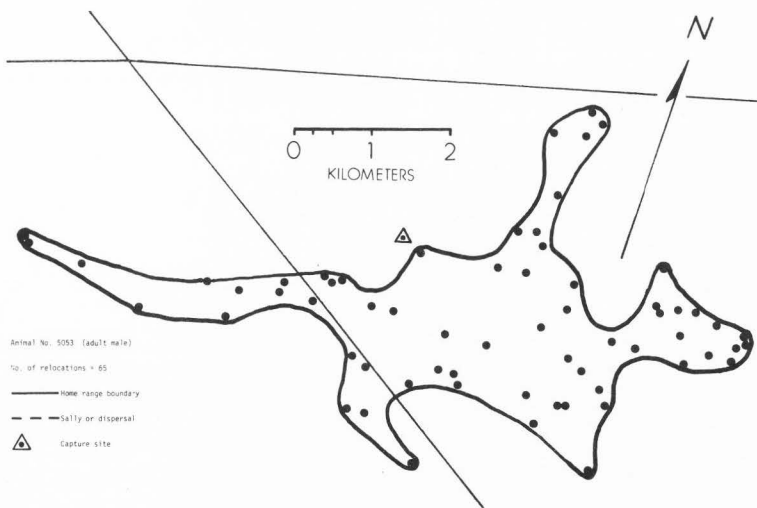
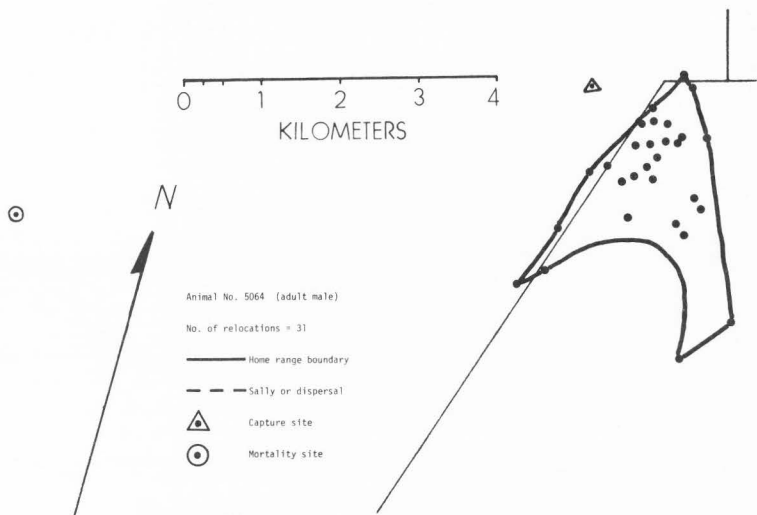




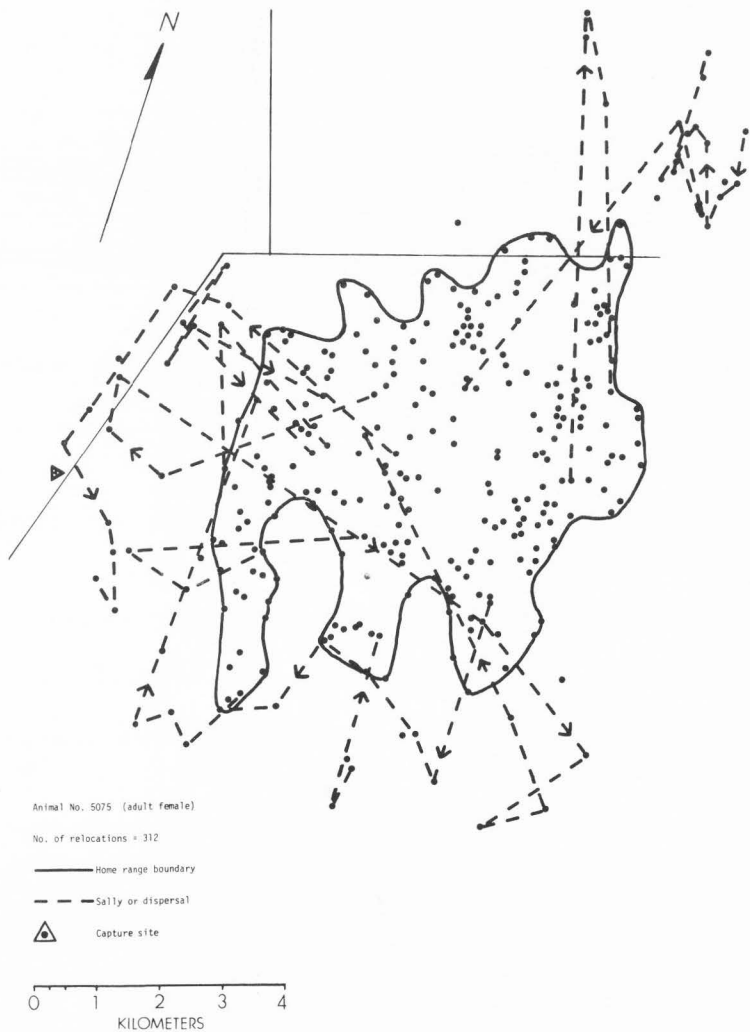


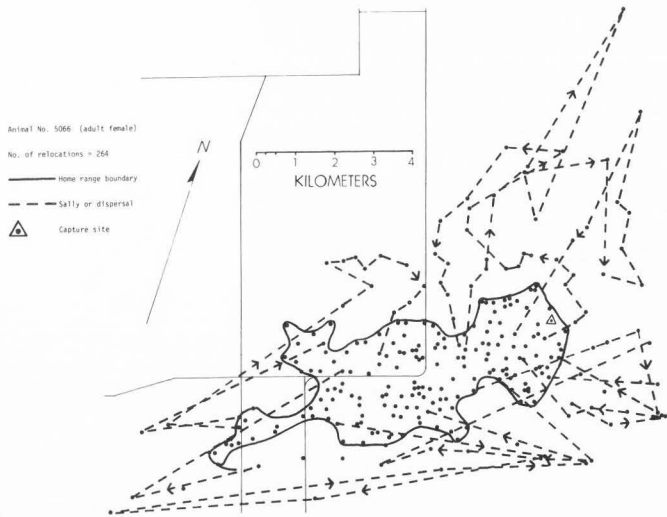
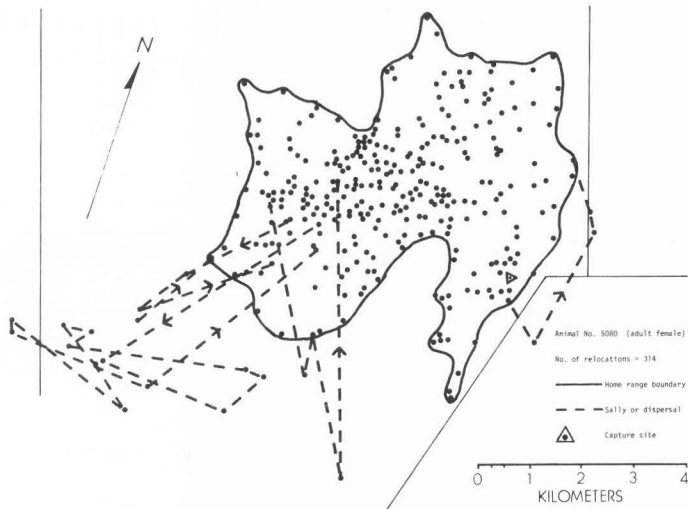




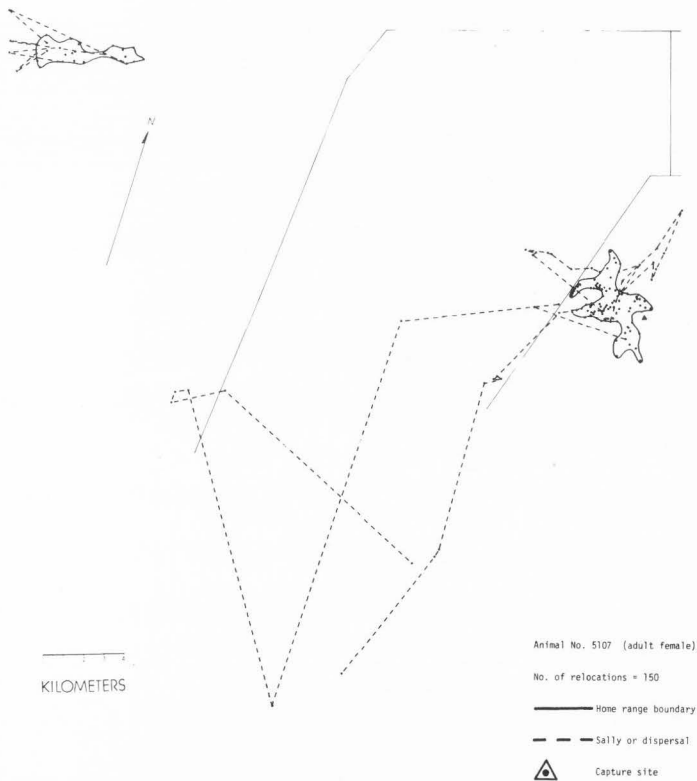


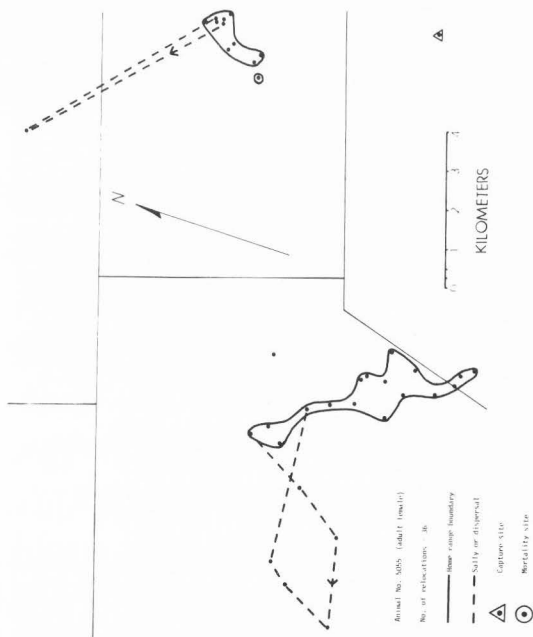


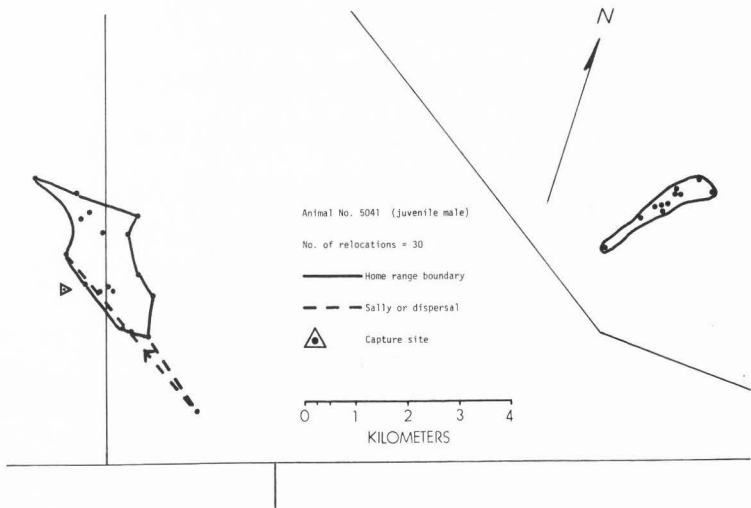
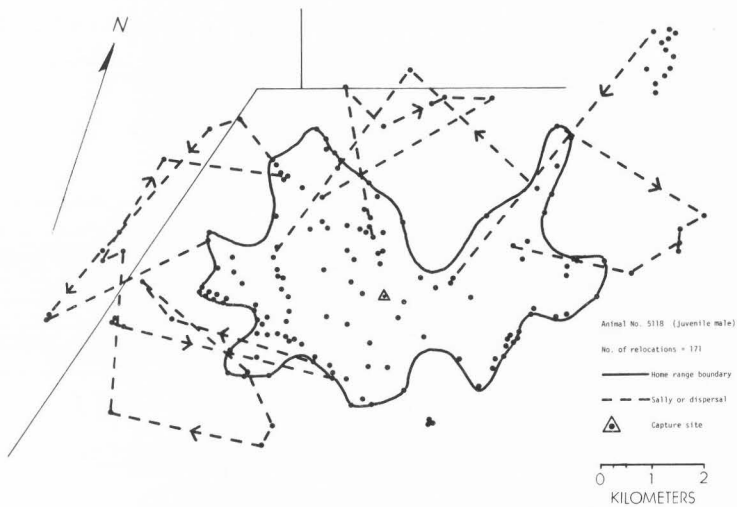


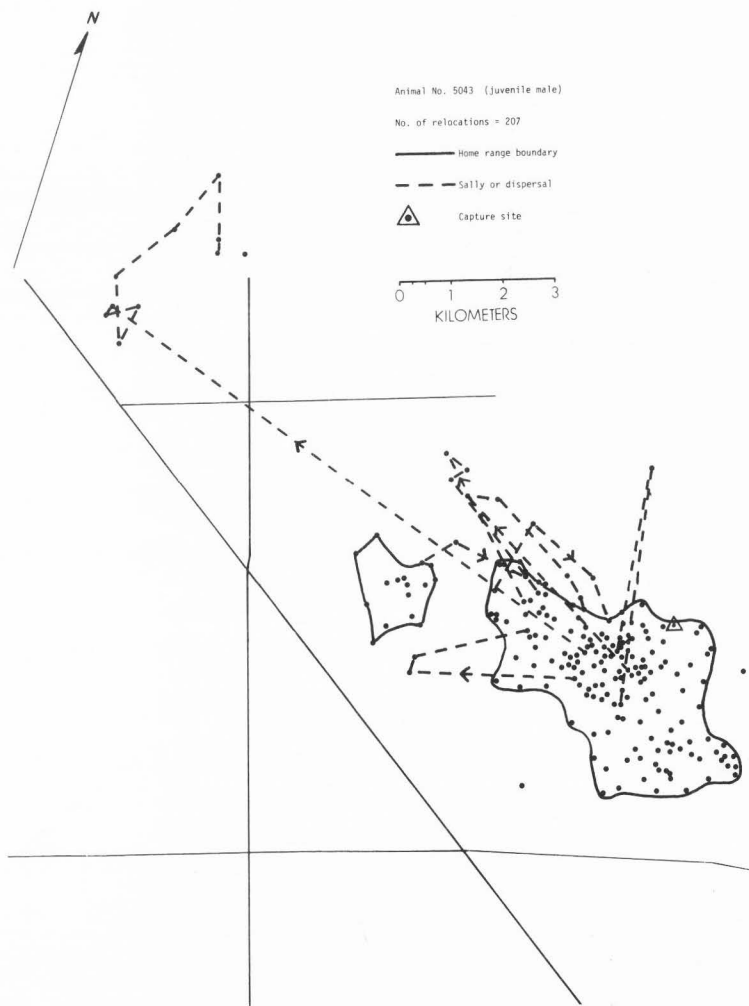


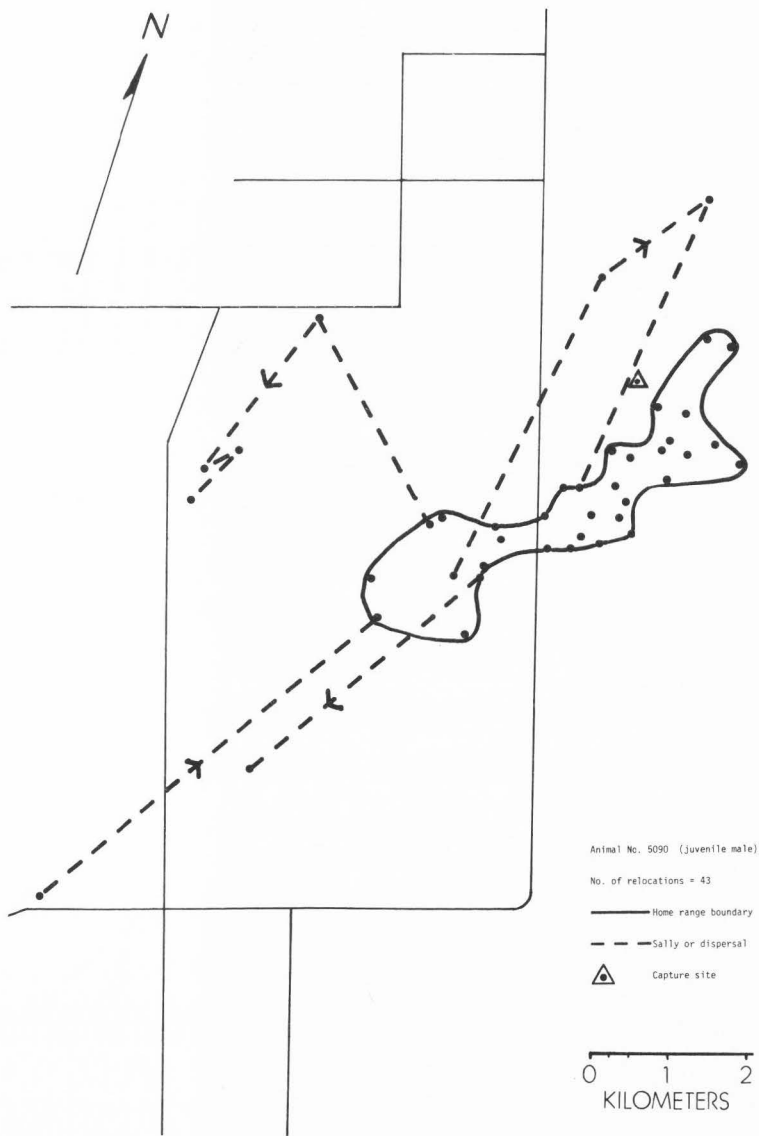


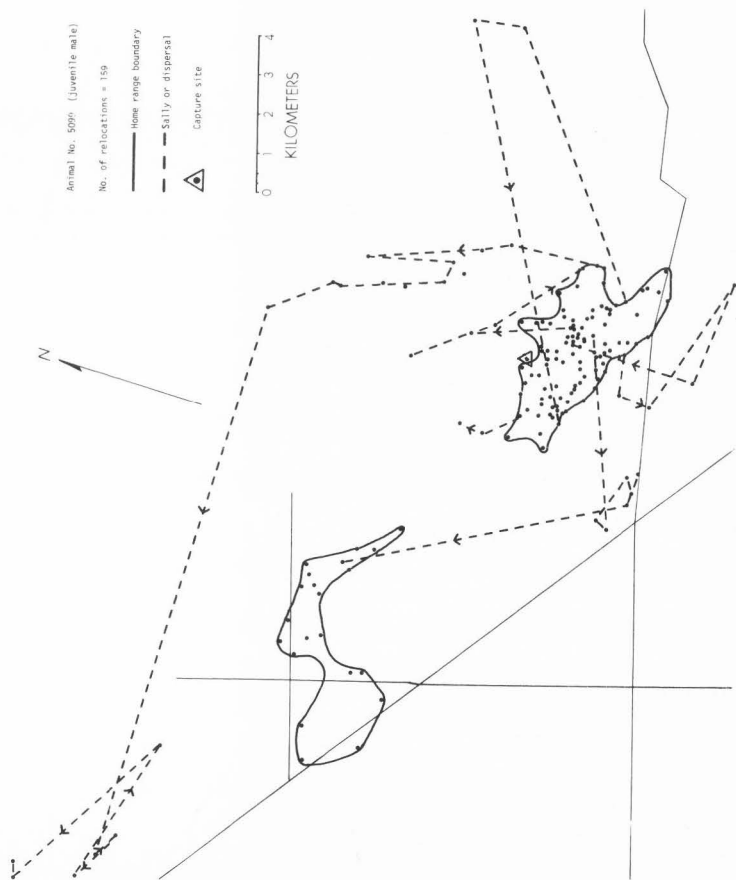












Animal No. 5105 (juvenile male)

No. of relocations = 45

— Home range boundary

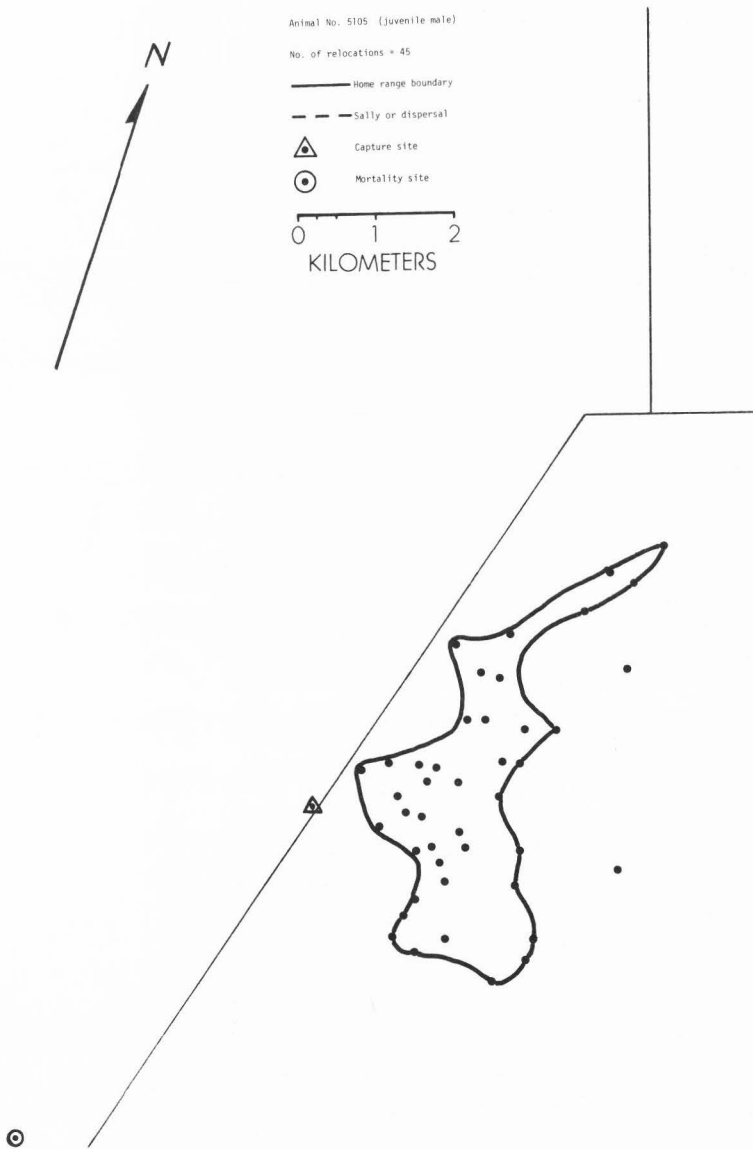
- - - Sally or dispersal

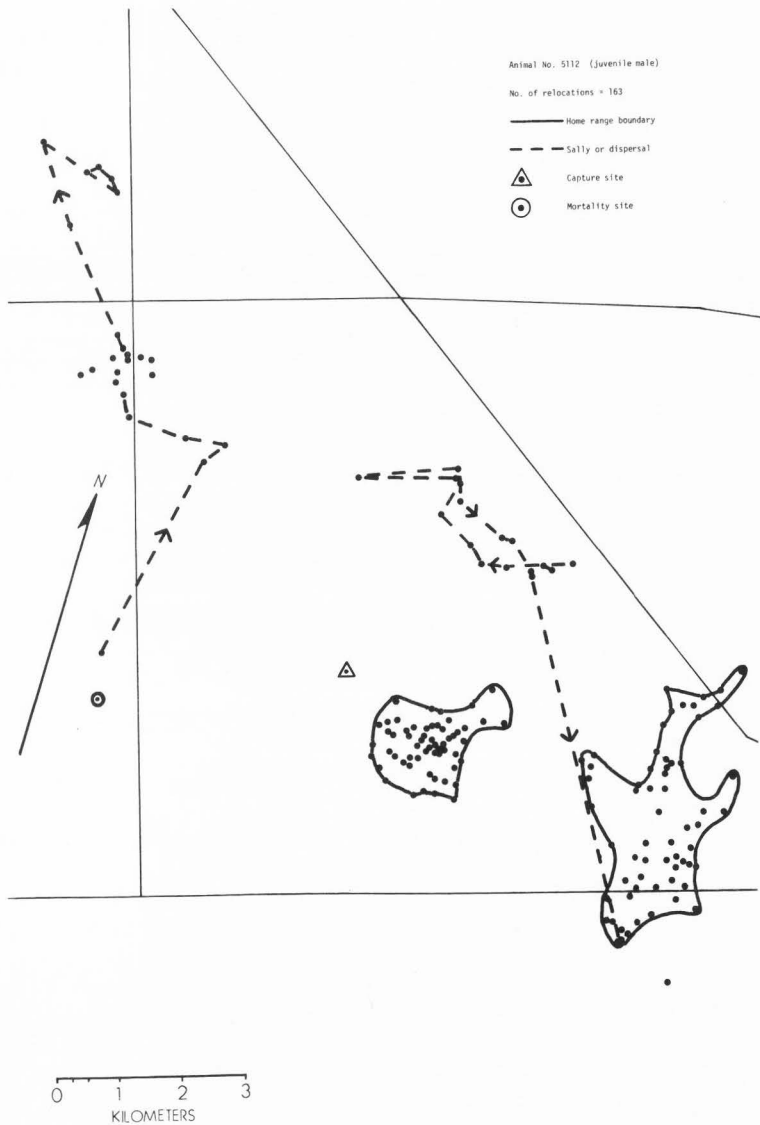
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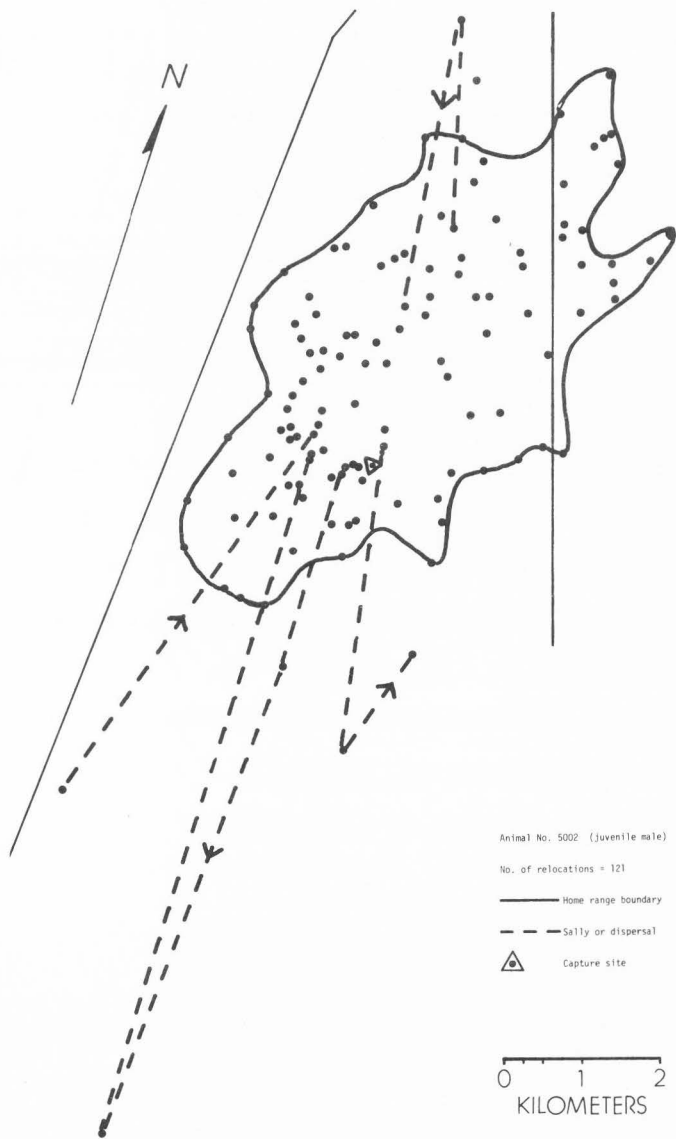
⊙ Mortality site

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KILOMETERS









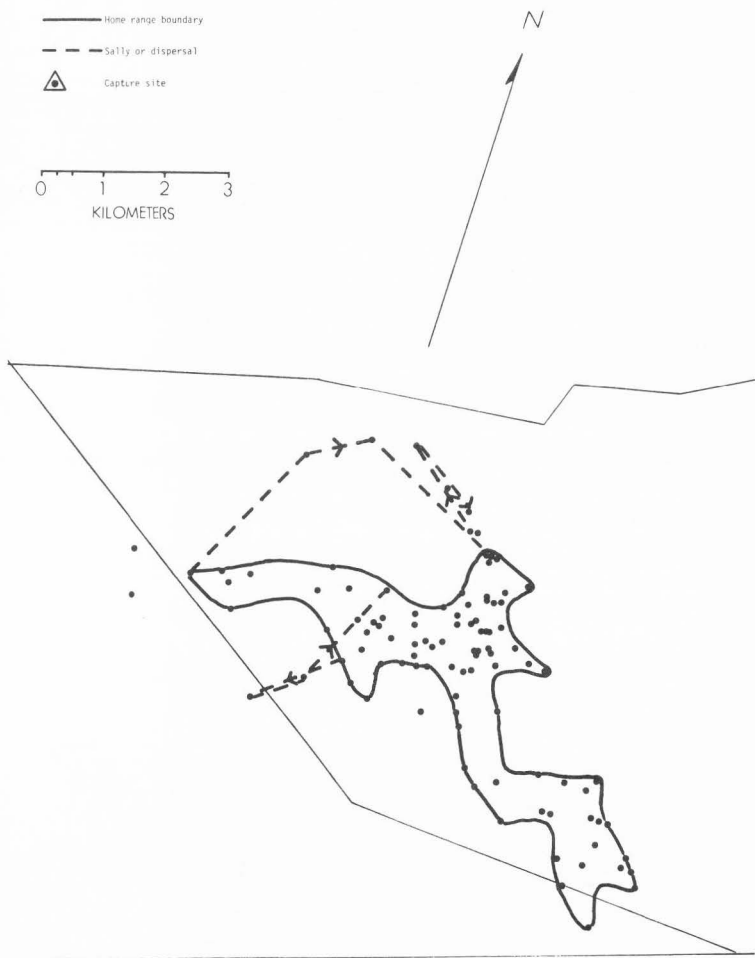
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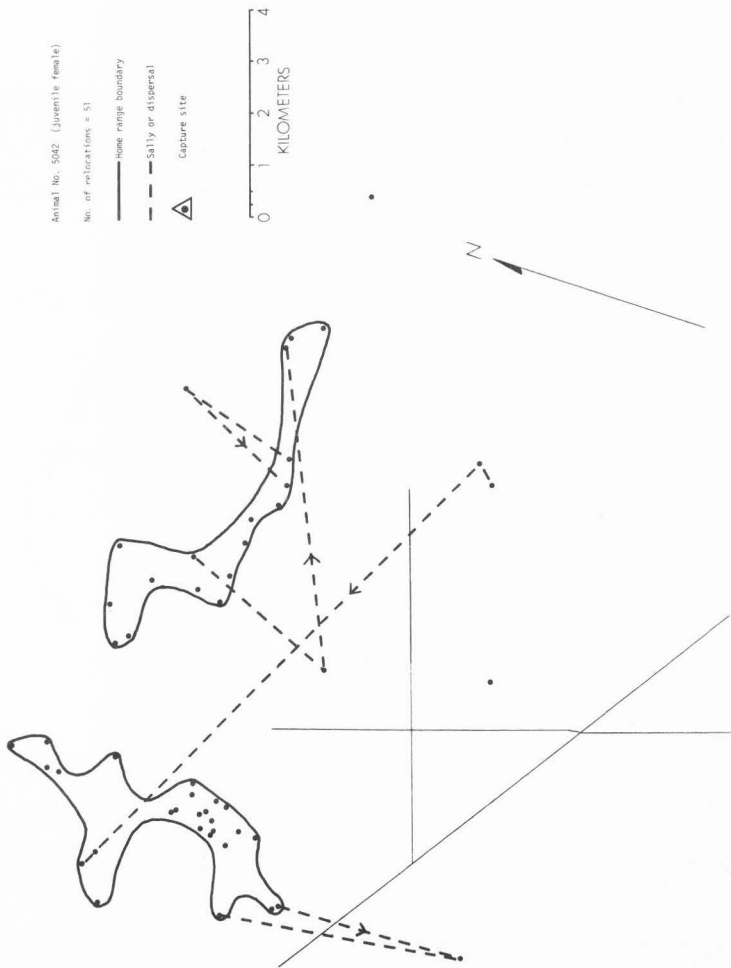
No. of relocations = 103

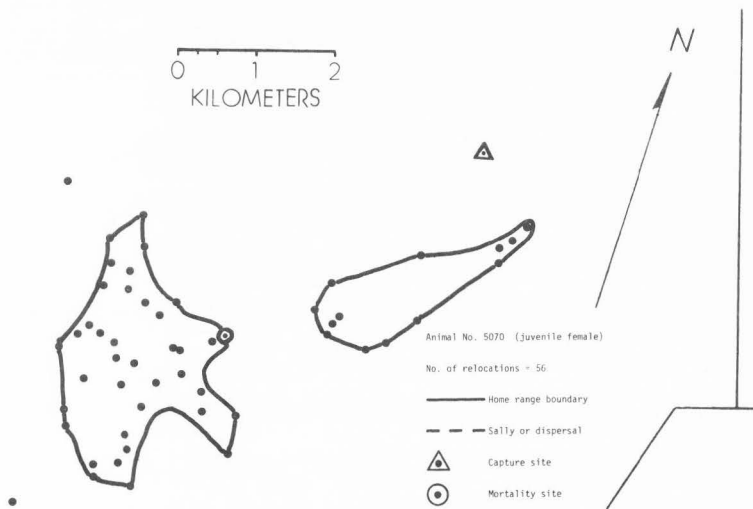
— Home range boundary

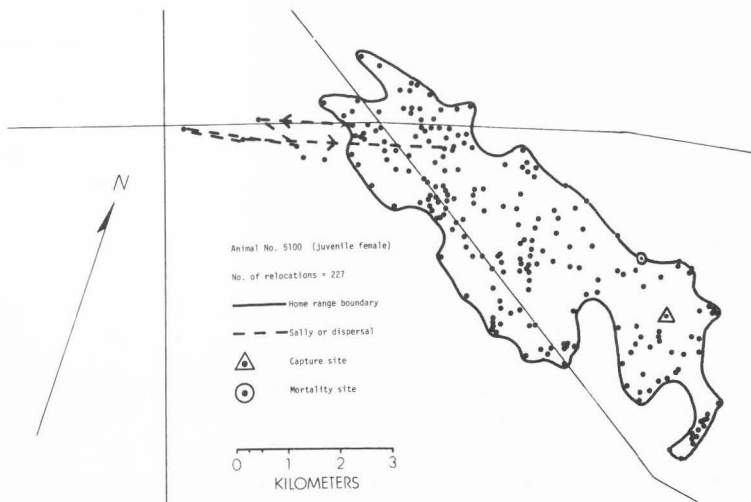
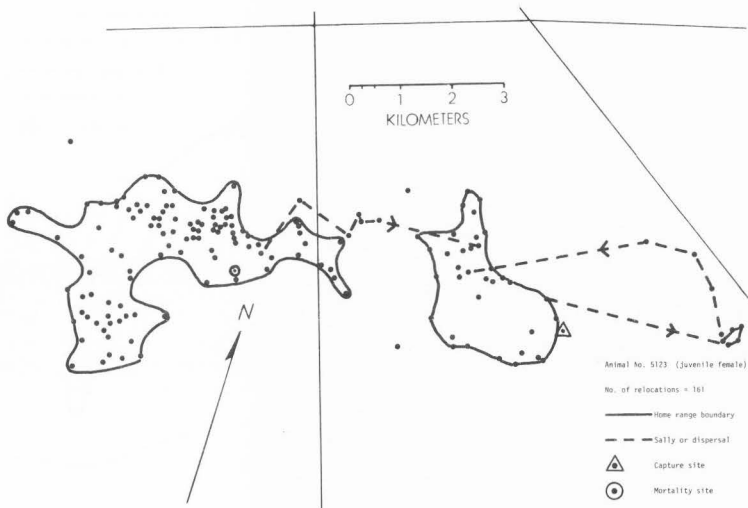
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▲ Capture site









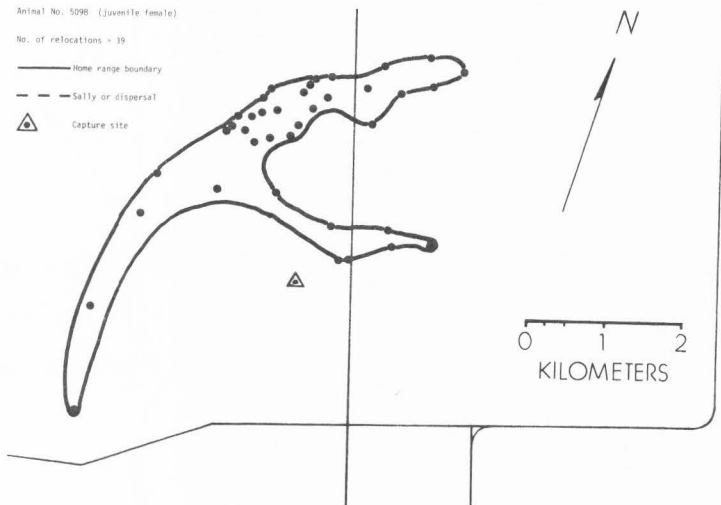
Animal No. 5098 (juvenile female)

No. of relocations = 39

— Home range boundary

- - - Sally or dispersal

△ Capture site



Animal No. 5088 (juvenile female)

No. of relocations = 24

— Home range boundary

- - - Sally or dispersal

△ Capture site

