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Draft

DEMOGRAPHICS AND DISPERSAL OF COYOTE (*Canis latrans*) PUPS

Jeffrey W. Blatt

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OF COYOTE (*Canis latrans*) PUPS

In Partial Fulfillment

of the Requirements for the degree

Masters of Science

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by

Jeffrey William Blatt

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Approved for the Graduate Faculty

Dr. Sheldon Johnson, Committee Chair

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Abstract

Acknowledgements

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Introduction

The populations of many large predatory mammals such as the wolf, cougar, and grizzly bear have been much reduced in the contiguous United States largely because of loss of wildlife habitat and conflict with man's pastoral activities. However, one medium sized carnivore, the coyote (*Canis latrans*), has adapted remarkably well to man's encroachment on its habitat (Stoel 1976). This is due primarily to coyote's adaptability and resilience. An increase in coyote research in recent years (Harrison 1992, Harrison et al. 1991, Fulmer 1990, Crabtree 1989, Harrison and Gilbert 1985, Bekoff and Wells 1986) has gained a better understanding of the sociodemographics of the adult coyote. One major area that has received little attention is the population dynamics of sub-adult coyotes. With the relatively short life span of the coyote, the influx of these animals has a significant influence on the condition of the adult population. This study investigates some aspects of coyote pups contribute to the demographics and behavior of the adult population.

Home range

Althoff (1978), Andelt (1985) and Harrison et al. (1991) presented data on home ranges of coyote pups before independence from adults; however, other investigators reported movements of coyotes trapped and radio collared after attaining some degree of independence (Andelt and Gipson 1979, Berg and Chesness 1978, Bowen 1982, Hibler 1977, Messier and Barrette 1982, Woodruff 1977). Comparisons of absolute measurements among these studies are confounded by different methods of measuring home ranges, different ages for defining pups, and combine data from yearlings and pups of the year. Relative measures of home range size show gradually increases from early summer to autumn, with a pronounced increase corresponding to dispersal.

Sex ratio

Data on sex ratios of coyotes through out their first 12 months of life are scare. Most data on sex ratios are collects ancillary to adult population studies, or are only collected at one time period in the first year (Knowlton 1972, Bowen 1978, Holzman et al. 1992). Of the studies that obtained sex ratios before dispersal (Andrews and Boggess 1978, Bekoff and Wells 1986, Gese et al. 1989, Nellis and Keith 1976, and Hallett 1977) a strong 1:1 sex ratio is apparent, although Moore and Millar (1984) found a sex ratio favoring males in colonizing populations.

Associates

There have been many studies (e.g. Andelt 1982, Bekoff and Wells 1986, Berg and Chesness 1978, Camenzind 1978a, Gese et al. 1989) showing that the most common social unit of coyotes as a mated pair with possibly one or more non-breeding adults. It is suspected that these non-breeding adults, or associates, are young from previous litters of the mated pair, although the precise relationship of these animals is still uncertain.

Dispersal

Differences in reported social behaviors primarily have been attributed to variations in dispersal patterns in pups (Andelt 1985, Bekoff and Wells 1986, Bowen 1982, Messier and Barrette 1982). Most studies of social organization, however, concentrated on the spatial relationships of yearling (1 year old) and adult (≥ 2 years old) coyotes (Andelt 1985, Bekoff and Wells 1986, Berg and Chesness 1978, Bowen 1981, Camenzind 1978b, Messier and Barrette 1982). Of the studies that have focused on pup movement the most extensive are Harrison (1992) and Harrison et al. (1991).

Dispersal rates of pups before their first year of life have been show to be high compared to that of adults (Althoff et al. 1981, Althoff and Gipson 1981, Bekoff and Wells 1986, Berg and Chesness 1978, Bowen 1978, Gese et al. 1989, Harrison 1992). Dispersal timing of studies in North America and Canada has been consistently observed from October to January of their first year (Althoff et al. 1981, Andrews and Boggess 1978, Berg and Chesness 1978, Chesness and Bremicker 1974, Gese et al. 1989, Harrison 1992, Nellis and Keith 1976, Pyrah 1984, Windberg et al. 1985); however, delayed dispersal at >1 year of age also has been reported (Andelt 1985, Harrison 1986, Nellis and Keith 1976). The distribution of dispersal dates within these ranges varies.

Several studies have reported on dispersal direction (Andrews and Boggess 1978, Berg and Chesness 1978, Davison 1980, Gese et al. 1989, Howard 1960, Knowlton and Stoddart 1983, Nellis and Keith 1976, Pyrah 1984), but many of these did not distinguish between pup and adult dispersal. Several papers on small mammals (e.g. Krebs et al. 1973) have addressed dispersal as a population regulation mechanism, but little has been done for canids (Lidicker 1962, Knowlton and Stoddart 1983).

Early researchers concluded that female coyote pups dispersed farther than males (Robinson and Cummings 1951, Knowlton 1972) and in greater proportions (Hibler 1977, Knowlton 1972). These conclusions were based on tag returns (Robinson and Grand 1958) or on sex ratios of harvested animals (Knowlton 1972), but both methods have inherent biases (Harrison 1992). Other studies of sex-specific dispersal of coyotes have yielded conflicting results. Nellis and Keith (1976) and Windberg et al. (1985) noted a greater mean recovery distance for females, and Hibler (1977) and Windberg et al. (1985) reported a greater proportion of females dispersing. Similarly, several studies have reported the longest dispersal treks by females(e.g., Hibler 1977, Gese et al. 1989). In contrast Hawthorne (1971), Davison (1980) and Harrison et al. (1991) observed no differences in dispersal movements between sexes, and Berg and Chesness (1978) reported greater dispersal distances by males.

Mortality

Few studies have reported on mortality of pups. Like pup sex ratios, pup mortality is usually reported secondarily in studies of adult demographics. The degree to which this data is confounded by pup dispersal is seldom investigated.

Most pup mortality studies only look at mortality for the first year as a whole. These studies have found pup mortality to be high (Andelt 1982, Davison 1980, Gese et al. 1989, Hallett 1977, Knudsen 1976, Nellis and Keith 1976, Robinson and Cummings 1951, Windberg et al. 1985). Pup mortality relative to adult mortality is also consistently high (Andelt 1982, Camenzind 1978a, Gese et al. 1989, Nellis and Keith 1976, Pyrah 1984, Windberg et al. 1985). The majority of these studies have found human caused mortality to be the predominant form (Andelt 1982, Andrews and Boggess 1978, Bowen 1978, Davison 1980, Hallett 1977, Knudsen 1976, Nellis and Keith 1976, Pyrah 1984, Tzilkowski 1980, Windberg et al. 1985). Mortality of dispersers is particularly high (Bekoff and Wells 1986, Gese et al. 1989, Tzilkowski 1980, Windberg et al. 1985, Harrison 1992) as is mortality outside the home range (Harris 1983, Rucker 1975, Woodruff 1977, Althoff 1978, and Litvaitis 1978)

Objectives

The overall objective of this study is to investigate demographics and dispersal of coyotes in their first year of life. Four specific objectives are ...

- Investigate home range size during the first year of life.
- Document sex ratios through the first year of life.
- Characterize natal dispersal direction and distance.
- Estimate the causes, and magnitude, of coyote mortality in the first year of life.

Methods

Study area

The study was conducted on the Arid Lands Ecology (ALE) Reserve a 330 km^2 of protected land on the United States Department of Energy's Hanford Site in Benton County, Washington (Rickard and Poole 1989, Thorp and Hinds 1977) (Figure 1). The study area is topographically dominated by the Rattlesnake Hills and Yakima Ridge. Elevations range between 200 and 1000 meters. Most of the yearly precipitation falls in late autumn and winter, averaging 17 cm on the Columbia River plain to 23 cm in the Rattlesnake Hills (Thorp and Hinds 1977).

The vegetation of the ALE Reserve is characteristic of the shrub-steppe ecoregion of semi-arid south-central Washington (Daubenmire 1970). Stands are dominated by the *Artemisia tridentata/Agropyron spicatum* association (big sagebrush/bluebunch wheatgrass). Other major understory species are *Poa sandbergii* (sandberg's bluegrass), and *Bromus tectorum* (cheatgrass brome). Periodic wildfires, most recently in August 1984, have removed the sagebrush from approximately 70% of the study area, leaving the overstory with a patchy distribution of sage brush (Rickard and Poole 1989). A variety of woody riparian species is associated with a few small, natural springs (e.g., Rattlesnake Springs). The land use surrounding the reserve is of two distinct varieties. To the south and west cultivation agriculture is the predominant land use. The majority of the Hanford Site, to the north and east, has been left unchanged since its inception in 1943 (Rickard, 1972).

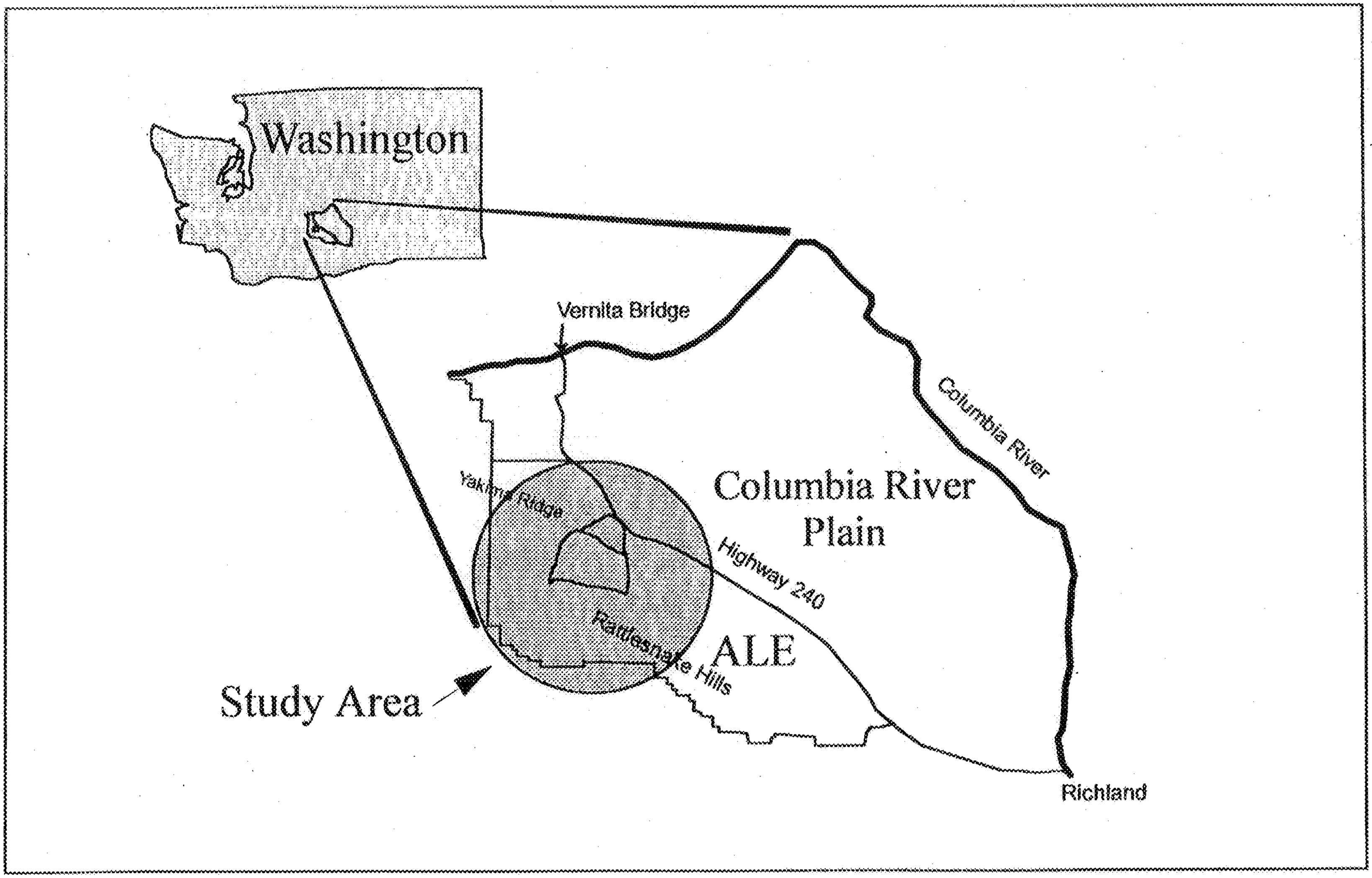


Figure 1: Location of Arid Land Ecology (ALE) Reserve on the U.S. DOE Hanford site and the study area, shaded circle. The road system inside ALE is for reference.

The fauna is characteristic of a relatively undisturbed shrub-steppe ecosystem. The dominant mammals are resident mule deer (*Odocoileus hemionus*), elk (*Cervus canadensis*), black-tailed hare (*Lepus californicus*), badger (*Taxidea taxus*), porcupine (*Erethizon dorsatum*), deer mouse (*Peromyscus maniculatus*), great basin pocket mouse (*Perognathus parvus*) and bobcat (*Lynx rufus*). The dominant raptors are the burrowing owl (*Speotyto cunnicularia*), marsh hawk (*Circus cyaneus*), red-tailed hawk (*Buteo jamaicensis*) (Rickard and Poole 1989). Potential food competitors of the coyote are badger, marsh hawk, red-tailed hawk, and bobcat.

Coyote Population

From Fall 1984 to Spring 1989, Crabtree (1989) conducted an extensive study on the demographics of the coyotes and estimated a population density of approximately one coyote per square mile, with a relatively top heavy age structure. Eleven adjacent territories had been marked with at least one radio-collared animal per territory. Most of these territorial boundaries have been well defined.

The levels of exploitation of coyotes are not consistent around the boundaries of ALE. Predator control is practiced regularly along the southern and eastern boundaries. The major forms of predator control are leg-hold trapping, shooting and litter exterminating. The land to the north and east, consisting primarily of the Hanford Site, have had no human exploitation. Onsite disturbance has been minimal. Since 1967, the coyote population has not been hunted or trapped for furs or for population control (Rickard 1972).

Overview

Pups were initially marked using one of two techniques. Primarily the pups were equipped with a subcutaneous radio-transmitter and then later fitted with an expandable radio collar. Secondarily, if the first technique failed for any reason, the pups were traps at an older age and fitted with a standard (non-expanding) radio collar.

The first technique was used to mark pups at a very early age. Leg-hold traps were used to capture potentially breeding adult animals. These animals were equipped with standard radio-collars, and released. Collared adults, closely monitored just prior to whelping, were used to find the locations of active dens. Two representative pups were subsequently fitted with subcutaneous radio-transmitting implants. The implants allowed for the monitoring of the litter as a whole. Data early mortality and sex ratios prior to 90 days of age were collected from these animals. The implants were also used to aid in the relocation of these animals at a later time so that each pup of the litter could be fitted with more powerful expandable radio collars. These collars accounted for the increasing neck diameter of the growing pups.

The second technique involved Leg-hold trapping pups directly and was postponed until the pups were older (greater than 5 months). The trapping of older pups was implemented identically to that of adults in the first technique. Because of the size of the pups at this age, standard radio collars were used. Coyotes, at this age, still had strong affinity with their natal territory so that their parents and siblings could still be determined. Sixteen pups were captured in this manner.

Data collected from radio collared pups (either standard or expandable) was used to calculate mortality, sex ratio, home range size, and dispersal for animals older than 90 days. Data was collected on 57 individuals from 13 territories and 14 groups whose social structure was not determined. Coyotes were monitored from spring 1984 to fall 1987, but most of the animals were captured and released in the spring of 1986 and 1987.

Animal Procurement

Number Three, offset jaw, steel leg-hold traps were used to capture adults and older pups. To reduce injury to the animal the traps were equipped with rubber pads and tranquilizer tabs fastened to the side (Balser 1965). The tabs contained 300 mg to 500 mg of propriopromazine HCL, inside a gauze pouch that was coated with bees wax. The captured animal, in an effort to escape, would chew at the tab and ingest the tranquilizer. This would help to quiet the animal until it was removed from the trap. The radio transmittered adult females were then closely monitored from aircraft and from the ground during the beginning of the denning season.

A total of nine dens ~~was~~ were located. Pups from these dens were marked when they were, on the average, twenty-seven days old (7 to 47 days). They were captured by excavating their dens with shovels. Before excavating, pup age and relative size were determined through direct observation, as well as investigating the size and number of pup tracks around the den opening.

On initial inspection of the den, estimates were made of the direction and depth of the litter chamber. A vertical shaft was then carefully excavated to intercept the tunnel just before the litter chamber. This often took several attempts. All existing entrances were either blocked or covered with a net to prevent the pups from escaping.

Implant Procedures

Each captured pup was measured (body length and hind foot length), weighed, and sexed. Age was determined by tooth eruption patterns and body measurements (Geir 1968, Bekoff and Jamieson 1975). Individuals were marked with a one inch square piece of colored flagging attached with epoxy to the hair on top of their head.

The radio implants where only used during 1987. During that year, one or two pups were selected from each den to be implanted with a light weight, subcutaneous, short range radio-transmitter (Figure 2a and 2b). The heaviest male and female of each litter were selected for radio implanting.

The implanted transmitters were of two types. One was designed with two disk-shaped batteries and a coiled antenna (Figure 2a); the other contained a flat-box battery and a straight antenna (Figure 2b). Both where coated with Elvax, an inert surgical wax to help prevent infection. The implants had a battery life of sixty days and weighed 10.6 grams, an average of less than 1.5% of the pup's body weight.

Transmitters were surgically implanted at the den sites to reduce the amount of handling time, and stress on study animals. The animals were anesthetized with a 0.5 cc to 1.5 cc subcutaneous dose of 85 percent Ketaset® (Ketamine hydrochloride) (Beck 1976) and 15 percent Rompun® (Xylazine hydrochloride). The transmitters were placed subcutaneously on the pups dorsal surface just posterior to the scapulas. This position was used to prevent the animal from irritating the incision site. A loop of suture was used to anchor the implant to the muscle until the incision healed. The skin was then closed with gut suture and Vetbond™ (n-butyl cyanoacrylate) adhesive. The average duration of the field surgery was approximately one hour.

All of the field surgery procedures had been discussed with and reviewed by Kathy Babson, DVM, of the Moscow Animal Care Clinic, Idaho; and Richard Weller, DVM, of ~~Battelle~~ PNL, Richland, Washington. Mock implantation's were also performed with Dr. Babson.

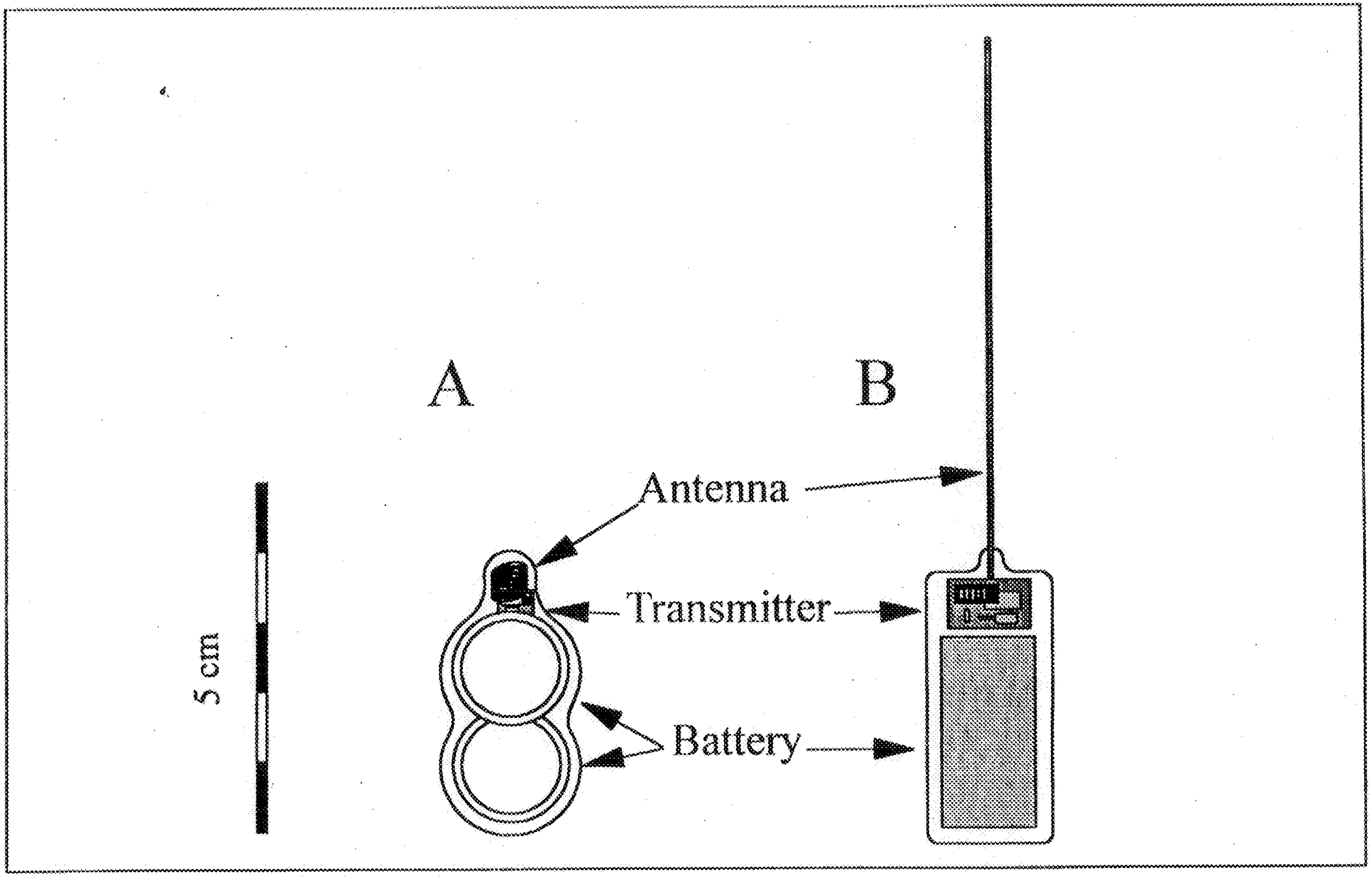


Figure 2: Diagram of the two types of subcutaneous radio implants used to mark coyote pups.

A total of forty-nine coyote pups from eleven home ranges was collected. From those collected, fifteen pups from eight litters were implanted. Although the implants served the purpose they were intended for, this procedure can not be recommended. Later field inspection of pups revealed that all pups showed signs of infection, with the majority being extensive. Eighty percent of the implants were removed by the pups or conspecifics prior to collaring.

Each pup was placed back in the den near its main entrance. The selected one or two pups that had been implanted were allowed to recover from the anesthesia in the security of an empty field pack. They were then returned to the den. Residual human disturbance was minimized by filling in all excavated holes, brushing over foot prints, and removing all foreign debris from the area. All handling of the pups was done with surgical gloves to reduce the amount of human scent left on the pups.

Animal Collaring

In order to follow movement and investigate mortality over time pups from the marked litters were equipped with expandable radio-collars. An attempt was make to collar all of the pups in each den not just pups that had been previously implanted. When the pups reached approximately seventy-seven days of age, eighteen pups from eight home ranges were recaptured by either hand netting or excavation of the dens. The expandable collars had a longer battery life, greater transmitting range, and were more reliable than the implants.

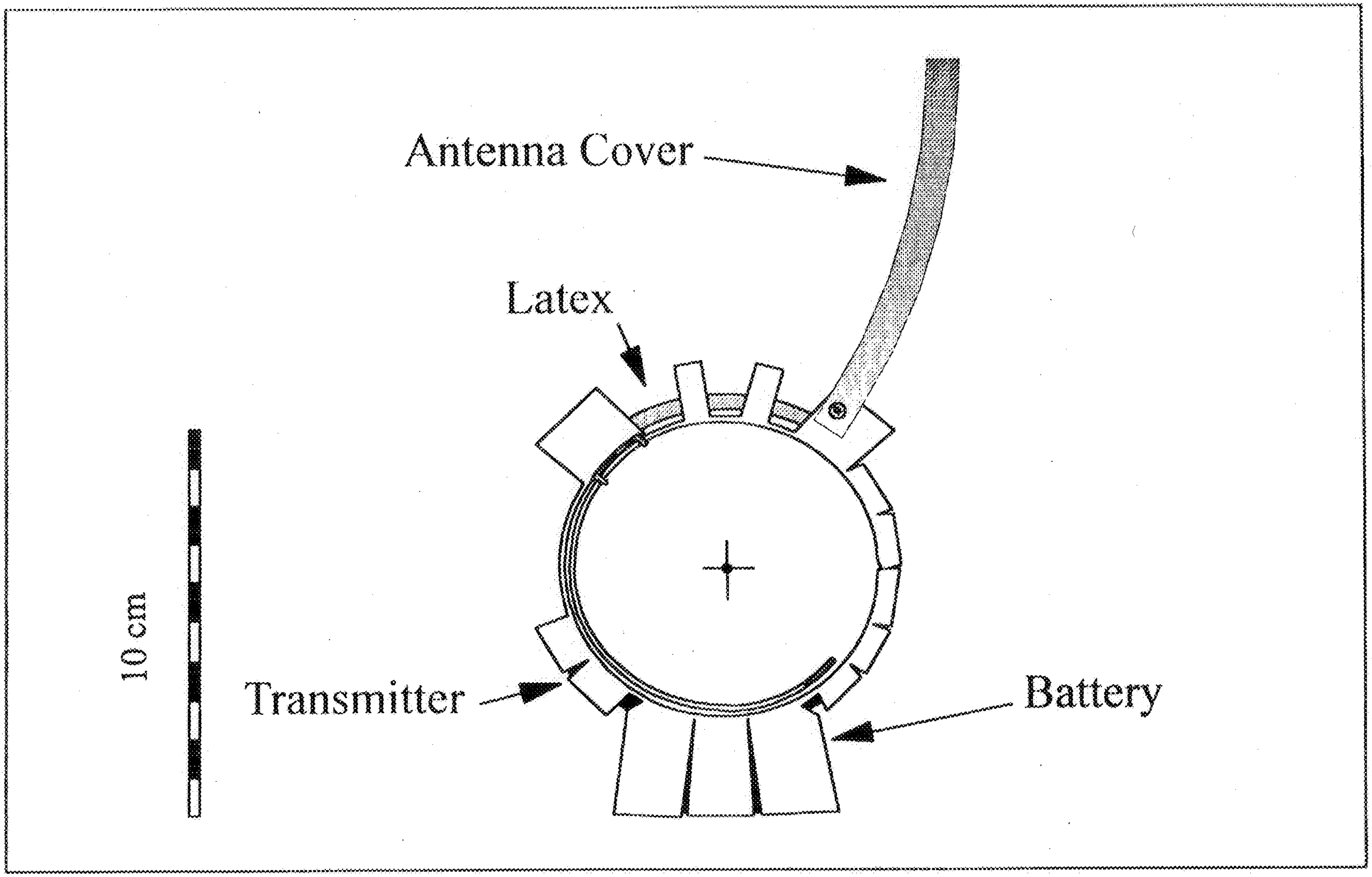


Figure 3: Diagram of the expandable collar used to monitor movement of coyote pups.

The expanding feature of the collar enabled the collar's diameter to increase as the pups grew (Figure 3). Three straps of latex tubing, 4 mm in diameter stretched to differing tensions, held the collar closed. As the latex straps were exposed to the ultraviolet rays of the sun, they gradually disintegrated. Because of the increasing tensions of the latex, the straps broke sequentially, allowing for gradual expansion. Over time the collars would then expand to the full adult neck size. The collars initial and final diameter could be adjusted at the time of fitting. This adjustment gave a range of ±2.0 cm to both maximum and minimum circumferences. The collar had an expected battery life of two years, weighed 140 grams, and averaged 4.0% of a pup's body weight (decreasing to an average 1.4% at adulthood).

Before production of the expandable collar, an initial material-evaluation study was performed to find a suitable latex for the expanding feature. Sixteen different materials were tested for ultraviolet deterioration (Perham, unpublished data). This was done by exposing them to ambient sunlight and temperature, and monitoring the materials' condition. Five penned coyote pups were fitted with the prototype collar, to test collar efficiency. The animals were housed in an outdoor pen so that the collars would be exposed to an environment similar to that experienced by wild pups.

The prototype design was used during the 1986 field season. Six coyotes were fitted and released. After observing the 1986 design in the field, the collar was redesigned. The main body of the collar, which was made of a PVC-like plastic, was too rigid. The new design used a rubber-like material, polyurothane. In 1986 the latex was covered by a light hardware cloth mesh to protect it from being chewed by other pups. There was no visual evidence of pups chewing on the collars so the mesh was eliminated, as well as several fastening rivets and wires. Twelve pups were fitted with this new design in 1987.

Animal Measurements

The captured pups were marked with numbered ear tags, each with a distinctly colored ear flag. The following data were collected from each animal, body length, head length, tail length, foot length, head girth, neck girth, body girth, body weight, gender, and general observed health. A blood sample was taken to assess specific health parameters. Each coyote was then fitted with a radio-collar. The collar allowed monitoring of the animals for the rest of the year without rehandling them.

Tracking

Radio-tracking methods included fixed station tracking, ground tracking with hand-held antennas, and aerial tracking (early morning surveys). Location data were collected by radio-tracking each radio-collared pup and its parents.

A system of eight null-peak fixed tracking stations was set up on the study site (Figure 4). A null-peak tracking station consisted of two antennae mounted side by side, in parallel, at the top of a mast. The mast was mounted in a stationary stand so that the entire antenna array could be rotated 360 degrees.

In 1986 single hand-held locations of the adults and pups were taken three times a week. In 1987 multiple locations were taken once a week, mainly using the null peak tracking system. These locations consisted of one location every half hour during a four hour period after dusk and again for three hours before dawn.

After the onset of dispersal, aerial locations were obtained biweekly. Periodic visual observations were used to monitor the health of each coyote. Dispersal was defined as the movement of an animal from its place of origin to an area where it reproduced or would have reproduced had it survived (Howard 1960).

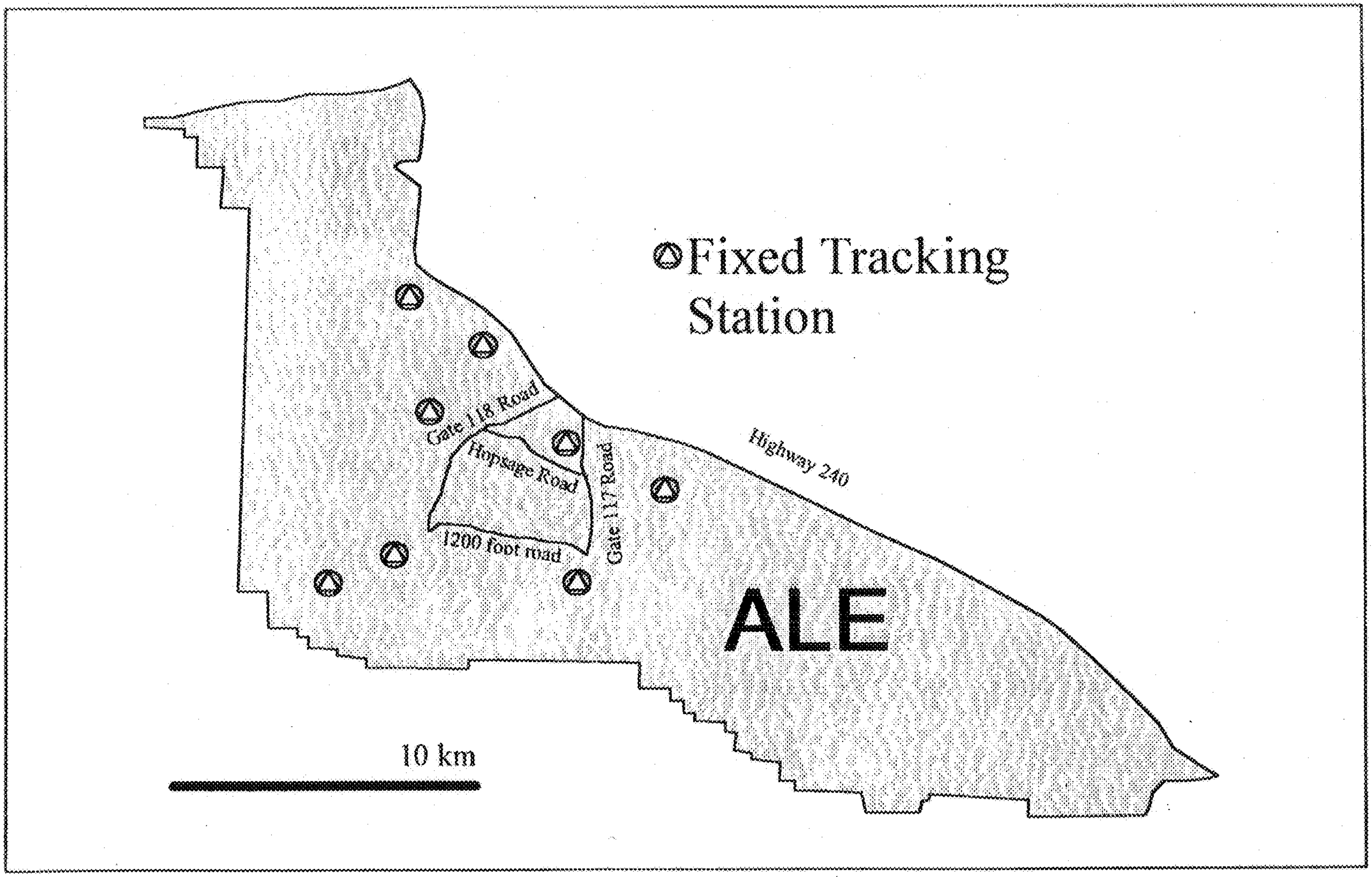


Figure 4: Map of the Arid Lands Ecology (ALE) ~~Resevation~~ Reserve with the locations of the fixed tracking stations. The interior road system is for reference.

Life History Time Periods

I divided the year into six periods that correspond to behavioral stages in the first year of a coyote's life:

Implanting:	April 15	to May 24
Early rearing:	May 25	to July 14
Late rearing:	July 15	to dispersal (about Oct. 14)
Dispersal:	dispersal	to December 31
Breeding:	January 1	to February 14
Denning:	February 15	to April 14

Data Analysis

Five of the eight territories monitored (Hopsage, Yakima Ridge, Benson Ranch, Cold Creek, and Packrat) provided enough data to estimate the pups home range. The home range size was calculated on a monthly basis. Pup and adult home ranges were calculate separately. The monthly locations of all the pups in a home range were combined to calculate the pup home range for that month. The same was done for the adults.

A software package called Program Home Range (Ackerman et al. 1990) was used to calculate the home range boundary. The program calculates home range boundaries with the harmonic mean method (Dixon and Chapman 1980, Spencer and Barrett 1984, Worton 1987, Worton 1989). The harmonic mean estimate is based on a utilization distribution, calculated on a rectangular grid of square cells. This grid is used to calculate the nonparametric harmonic mean distribution from the animal's location data. I choose to use the 75% utilization contour as the boundary. This choice was in part subjective, but since it was used to calculate the boundary for all home ranges, and all comparisons were relative, this was justifiable. The program calculated the coordinates of the boundary line, the area within that boundary and the arithmetic center of the area within the boundary.

Dispersal information was collected from 18 coyotes. Coyote locations were plotted on a map. A line was draw from the center of the animals natal territory to the center of activity of the animal after dispersal, or the last known location of that animal. The length and angle of this straight line were used as the dispersal distance and direction respectively. If a coyote died during the dispersal period and had initiated dispersal it was recorded as an unsuccessful dispersal.

All sex ratios are represented as the ratio of females to all animals at given points in time. Sex ratios were calculated for the start of each life history period.

Cause of mortality was determined by physical inspection and placed in one of five categories (Disease, Predation, Traffic collision, Trapped, or Shot). If the pup was found dead with no sign of wounds and was in an emaciated condition the cause recorded as disease.

Because of the small sample size of mortality data, analysis was performed in two ways. First, a mortality ratio was calculated. This ratio consisted of the number of animals that died in a time period to the number of total animals monitored through that time period. Secondly, the data was analyzed with the use of a software package called MicroMort (Heisey and Fuller 1985). This program takes into account the amount of time in each of the time periods the animals were monitored. It first calculates a daily survival rate and then calculates the survival rate for the entire time period from the daily rate. One of the assumptions of this method is that mortality rates must be constant throughout the time period.

Results

Thirty five animals where monitored during the first year of life. The amount of monitoring time varied with each animal. Figures 5 and 6 show the amount of time during the first year of life each animal was monitored. Figure 5 shows the time for the animals equipped with expandable radio-collars and Figure 6 shows the time for the animals captured as older pups and collared with standard radio-collars. The results of this study are grouped into four major categories; home range, dispersal, sex ratio, and mortality. Study animals spent most of their time below 680 meters.

Home range size

Table I and table II contains the data from Program Home Range. Table I contains pup home range sizes and table II contains adult home range sizes. The data are broken down for each of the five home ranges. Three pup home ranges in this study (Benson Ranch, Hopsage, Yakima Ridge) contained enough data to calculate monthly home range sizes consecutively from June to October. The "Number of Animals" column represents the number of individual animals that contributed to the estimates. The "Number of Locations" column represents the sum of the locations from all animals contributing to the estimates.

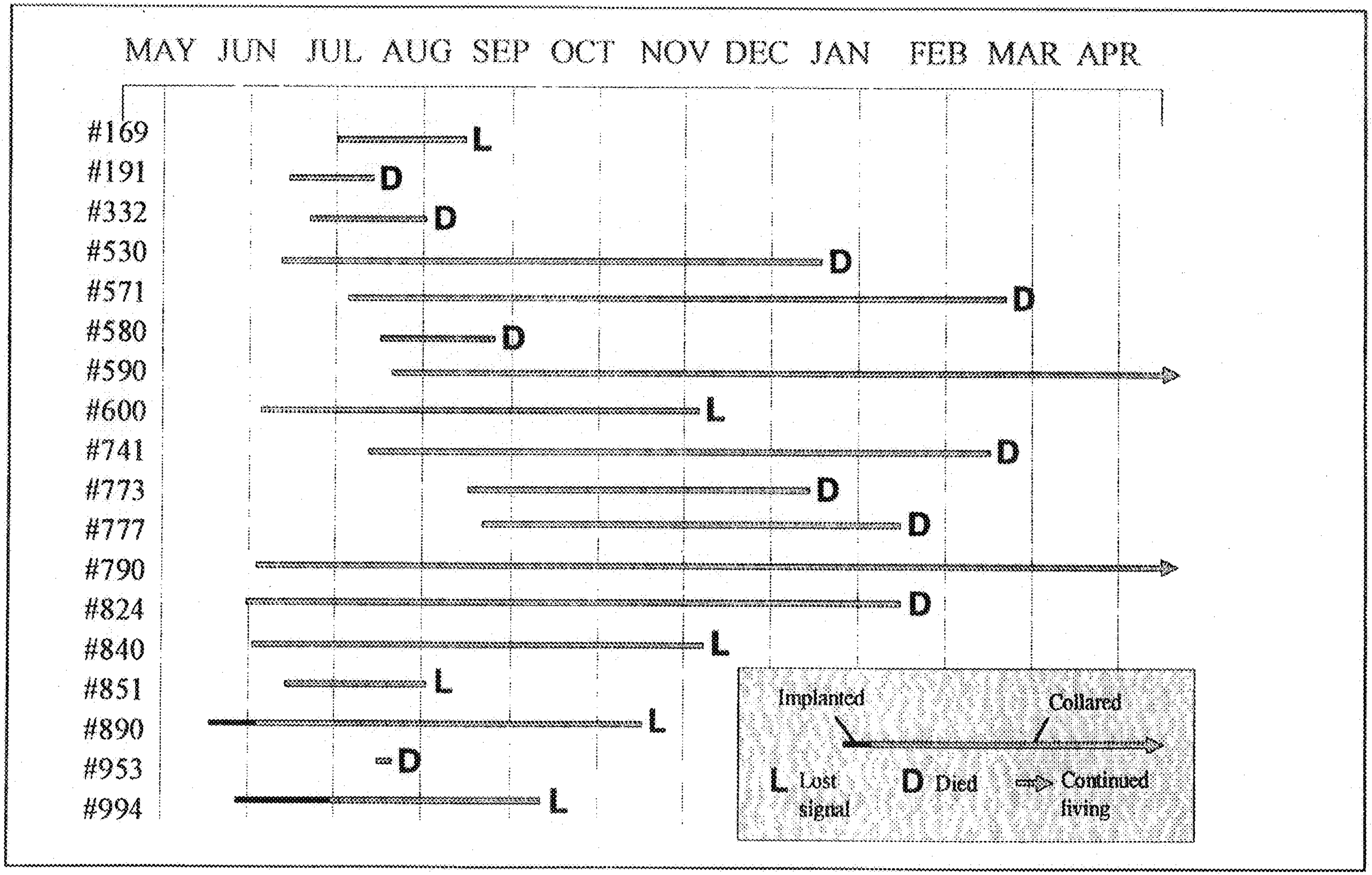


Figure 5: Time table showing the monitoring time line for each coyotes fitted with an expandable collar.

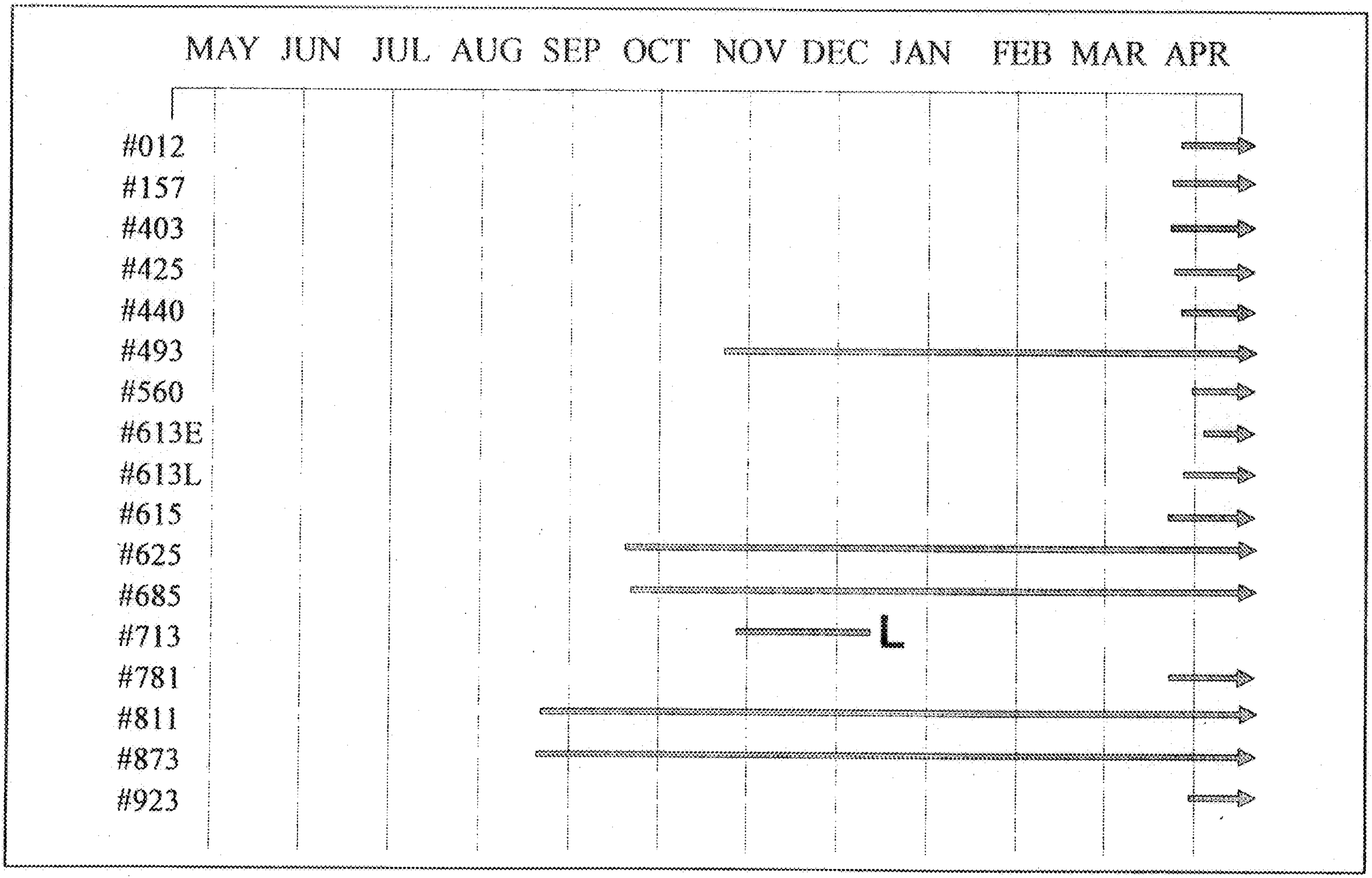


Figure 6: Time table showing the monitoring time line for each coyotes fitted with a standard (nonexpanding) collar. See legend for Figure 5.

Table I: Pup home range size data from Program Home Range. The data is broken down by parrental terretory.

Pup home range size summary				
Territory	Month	Area in km2	Number of	
			Animals	Locatio ns
Benson Ranch	6/86	3.35	2	18
	7/86	6.45	2	81
	8/86	3.62	2	32
	9/86	7.50	2	35
	10/86	5.51	2	35
Cold Creek	6/87	3.14	3	31
	7/87	1.40	1	7
Hopsage	7/86	1.29	1	22
	8/86	5.98	3	31
	9/86	11.62	3	55
	10/86	7.23	2	33
	11/86	21.98	3	23
Packrat	7/87	2.80	2	21
	8/87	1.31	2	11
Yakima Ridge	6/86	7.88	1	42
	7/86	2.27	1	47
	8/86	2.15	1	18
	9/86	4.69	1	14
	10/86	2.20	1	18

Table II: Adult home range size data from Program Home Range.

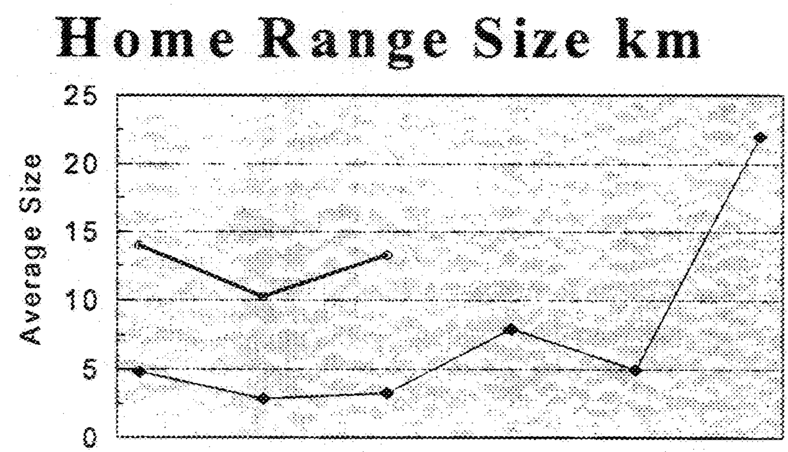
Adult home range size summary				
Territory	Month	Area in km2	Number of	
			Animals	Locations
Benson Ranch Adults	6/86	15.32	1	50
	7/86	8.17	1	45
Cold Creek Adults	6/87	9.30	1	54
	7/87	9.02	1	41
Hopsage Adults	6/86	16.82	1	47
	7/86	12.26	1	51
Packrat Adults	7/87	13.46	1	39
	8/87	13.24	1	29
Yakima Ridge Adults	6/86	14.33	2	105
	7/86	8.25	2	99

Table III and figure 7 show's average home range sizes for pups and adults by month. There was no significant trend up or down in the size of the pup home ranges through time (β_1=2.77, α=0.05, r^2=0.5114)

Figures 8 through 16 are example plots, of the 75 percent utilization contour, that Program Home Range calculates. Figures 8 through 12 show the "Yakima Ridge" home range from June through October of 1986. The first two plots (Figures 8 and 9) show a comparison between the adults and the pups 75 percent contour. Figures 13 through 16 show the "Hopsage" pups from August through November of 1986.

Table III: Summary home range utilization data, by month.

Month	Pup home range			Adult home range		
	Avgerage km^2	n	Varience	Avgerage km^2	n	Varience
6	4.79	3	2.68	13.94	4	3.26
7	2.84	5	2.11	10.23	5	2.46
8	3.27	4	2.05	13.24	1	n/a
9	7.94	3	3.49	-	-	-
10	4.98	3	2.56	-	-	-
11	21.98	1	n/a	-	-	-
Overall	5.39	19	22.57	-	-	-
Pre-November	4.47	18	7.68	-	-	-



Months	June	July	August	Sept.	Oct.	Nov.
Adults —	13.94	10.23	13.24	*No Data*	*No Data*	*No Data*
Pups —◆—	4.79	2.84	3.27	7.94	4.98	21.98

Figure 7: Average home range sizes of both adult and pup coyotes.

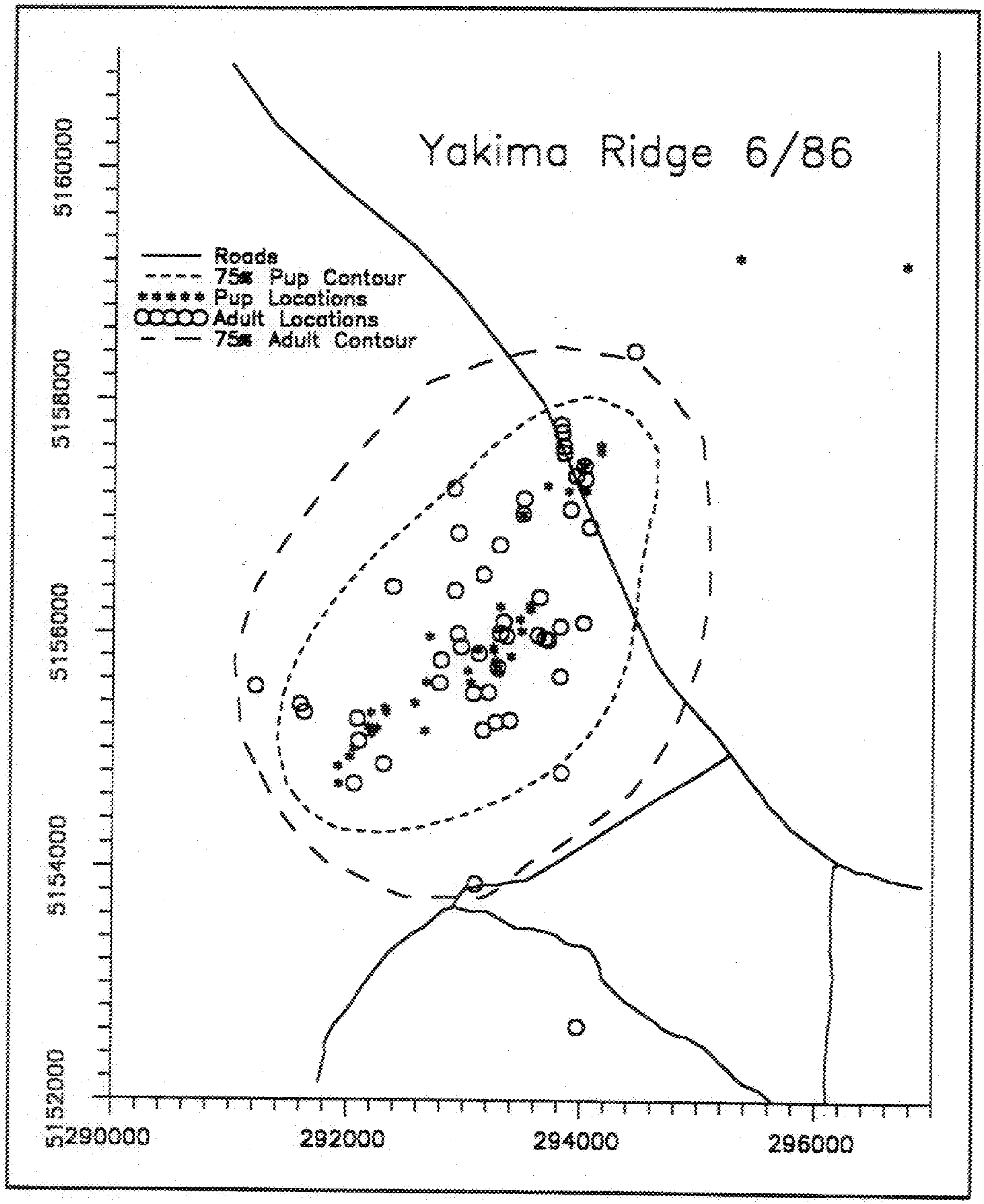


Figure 8: Yakima Ridge 6/86 75% Adult and 75% pup utilization distribution contour.

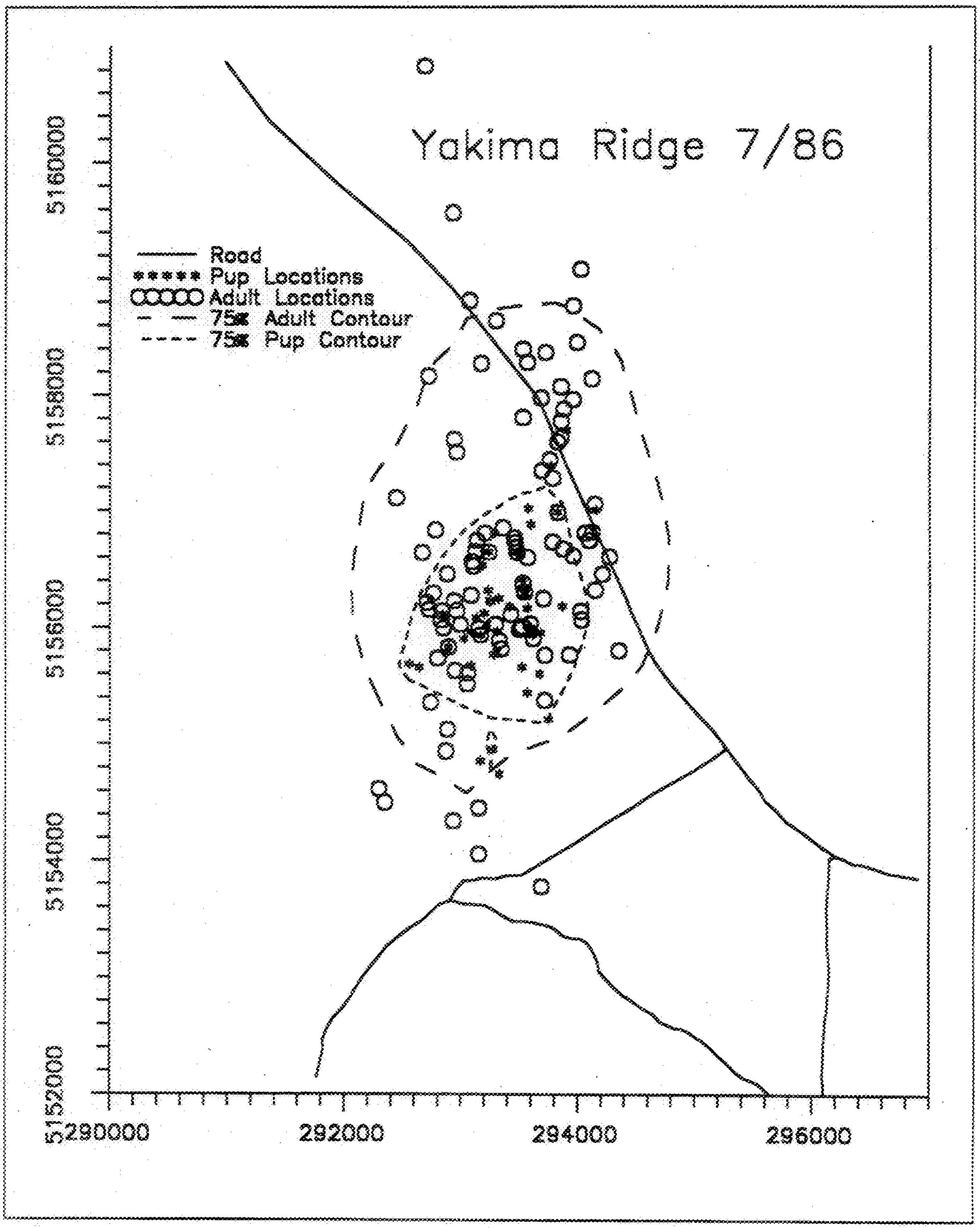


Figure 9: Yakima Ridge 6/86 75% Adult and 75% pup utilization distribution contour.

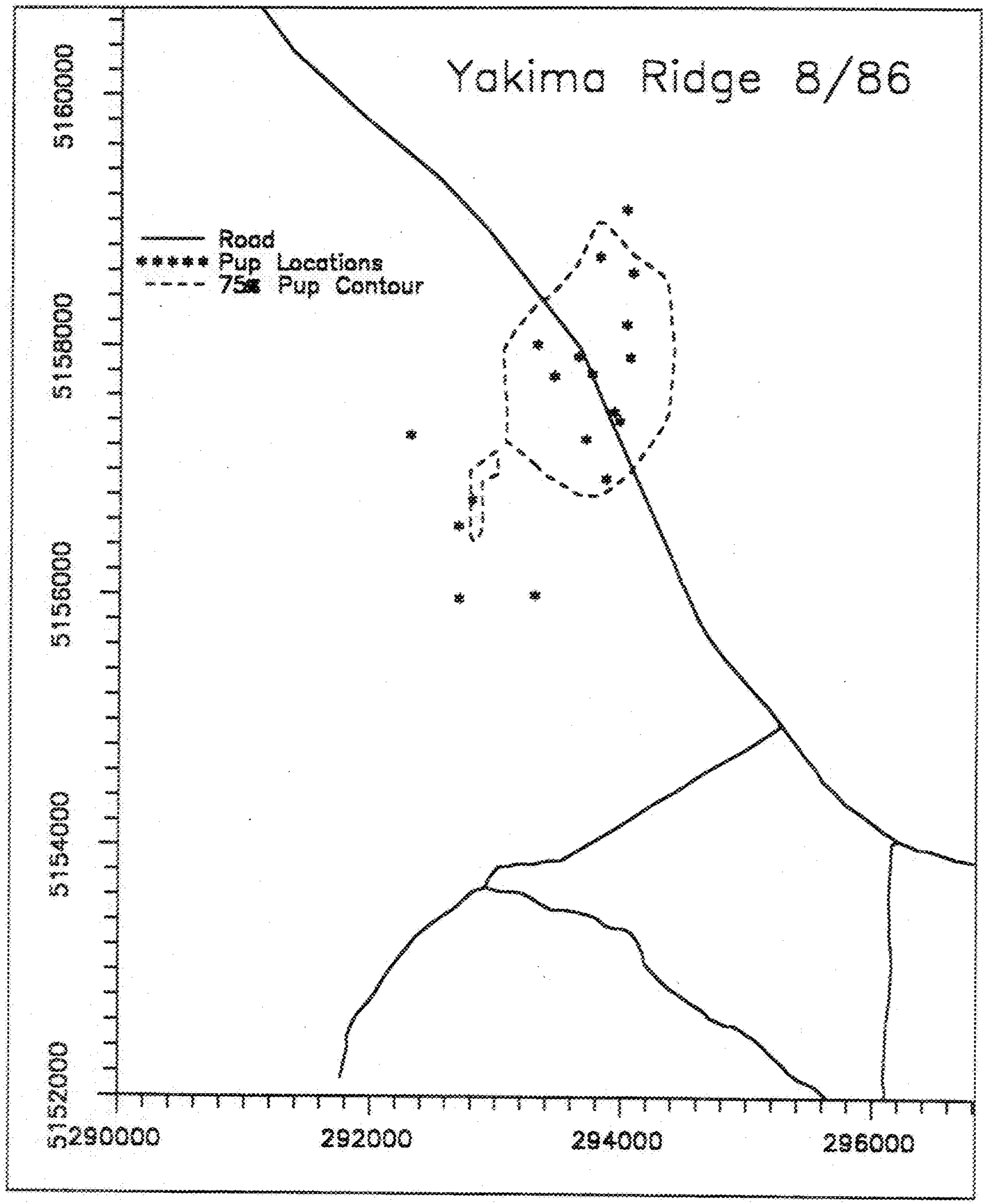


Figure 10: Yakima Ridge 8/86 75% pup utilization distribution contour.

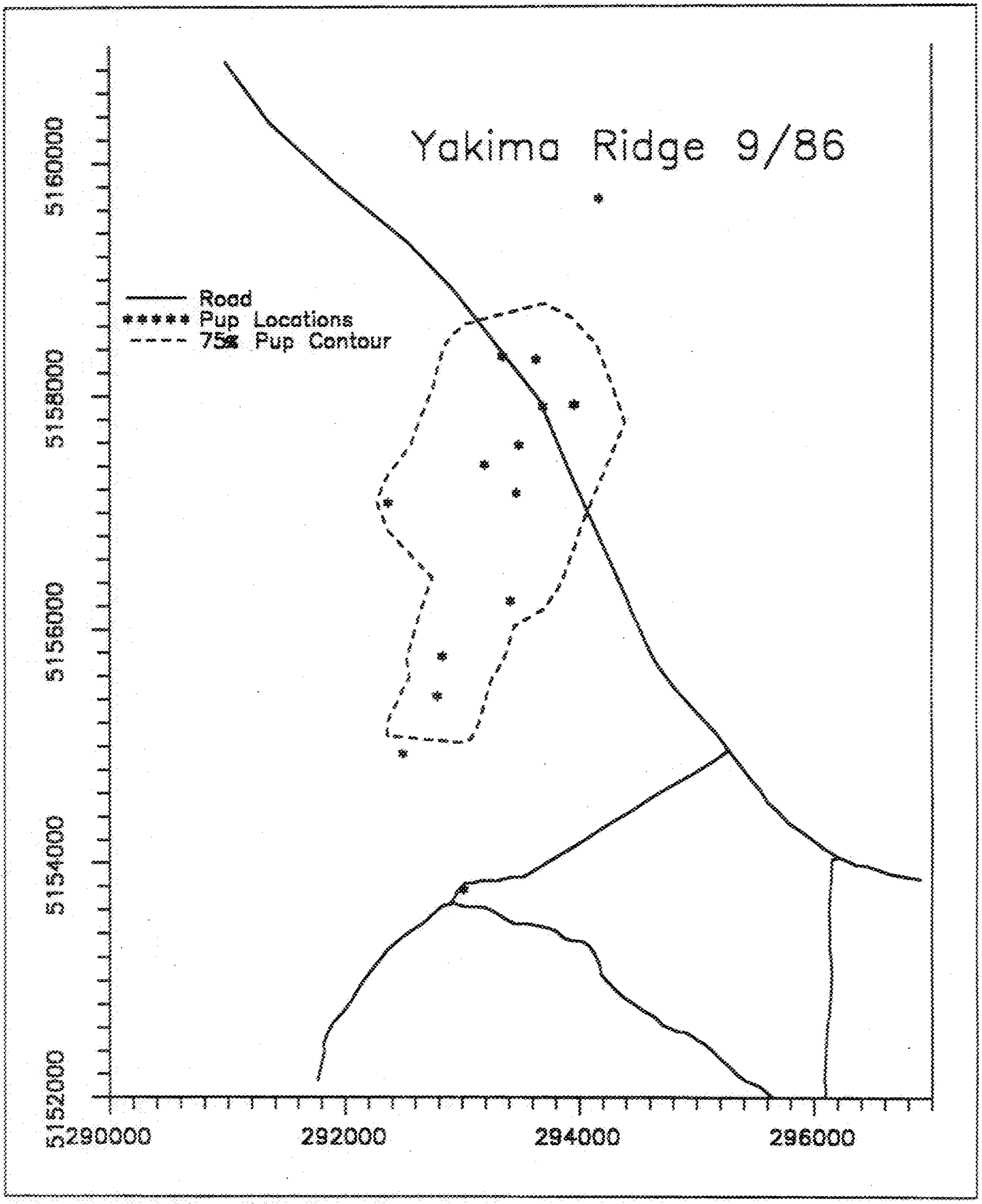


Figure 11: Yakima Ridge 9/86 75% pup utilization distribution contour.

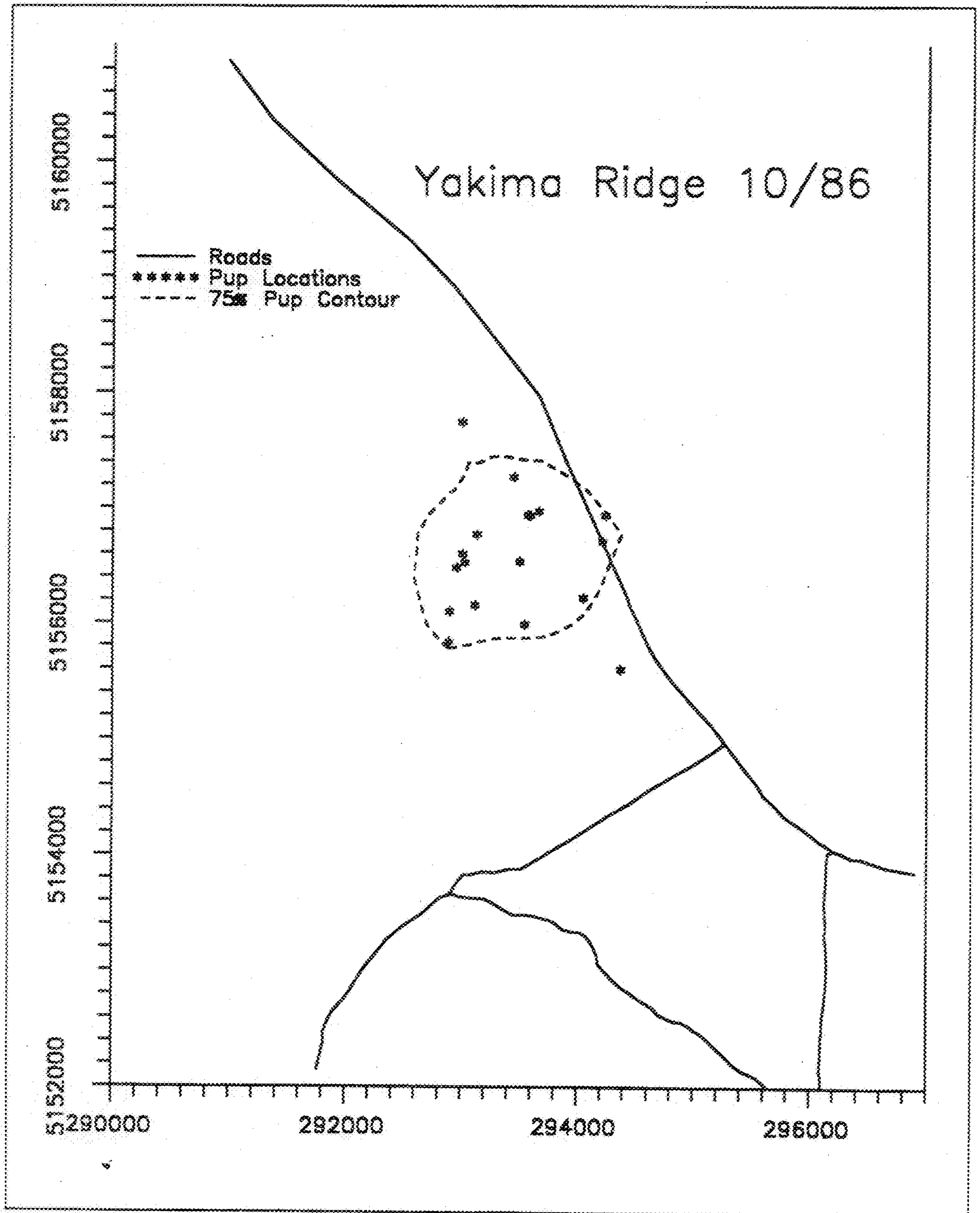


Figure 12: Yakima Ridge 10/86 75% pup utilization distribution contour.

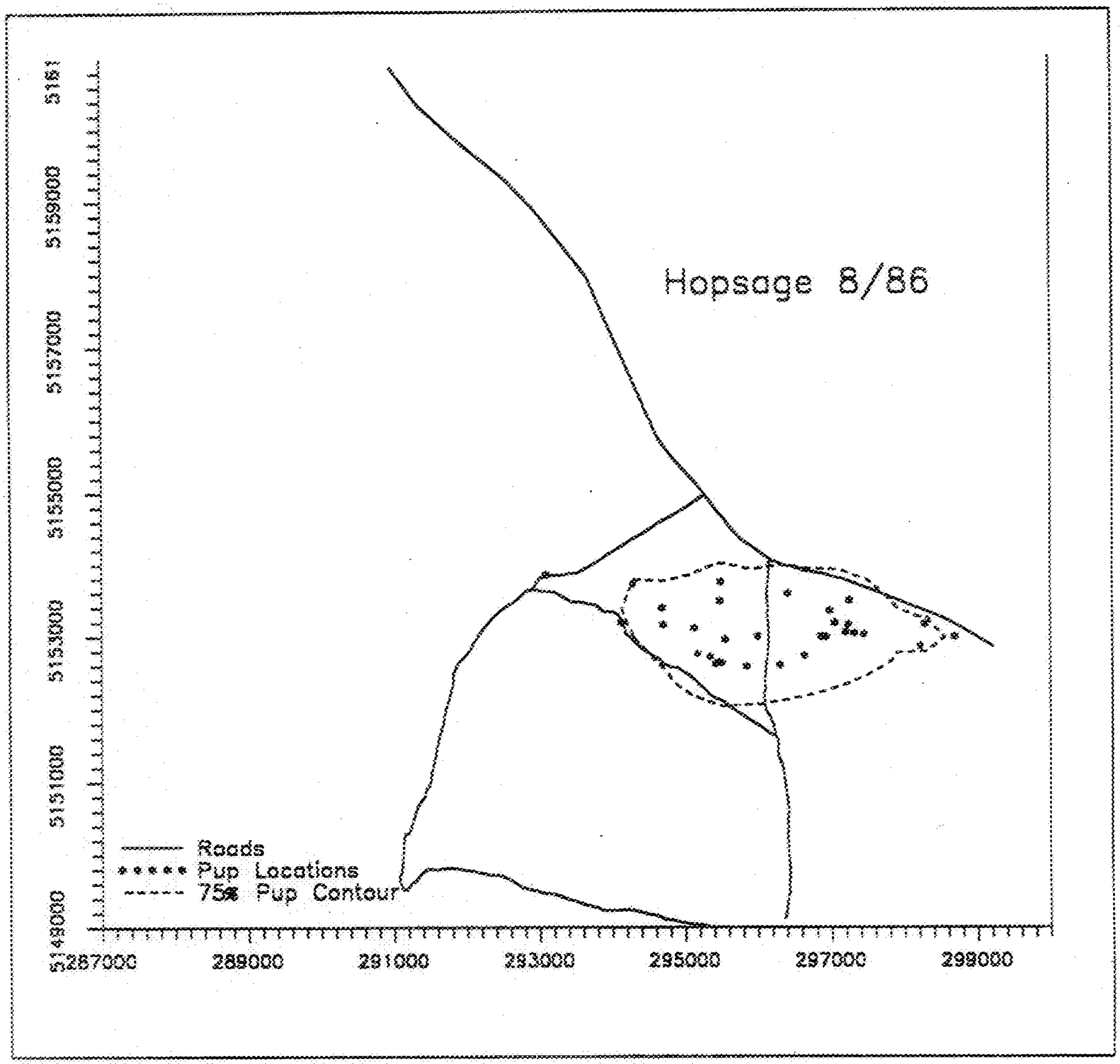


Figure 13: Hopsage 8/86 75% pup utilization distribution contour.

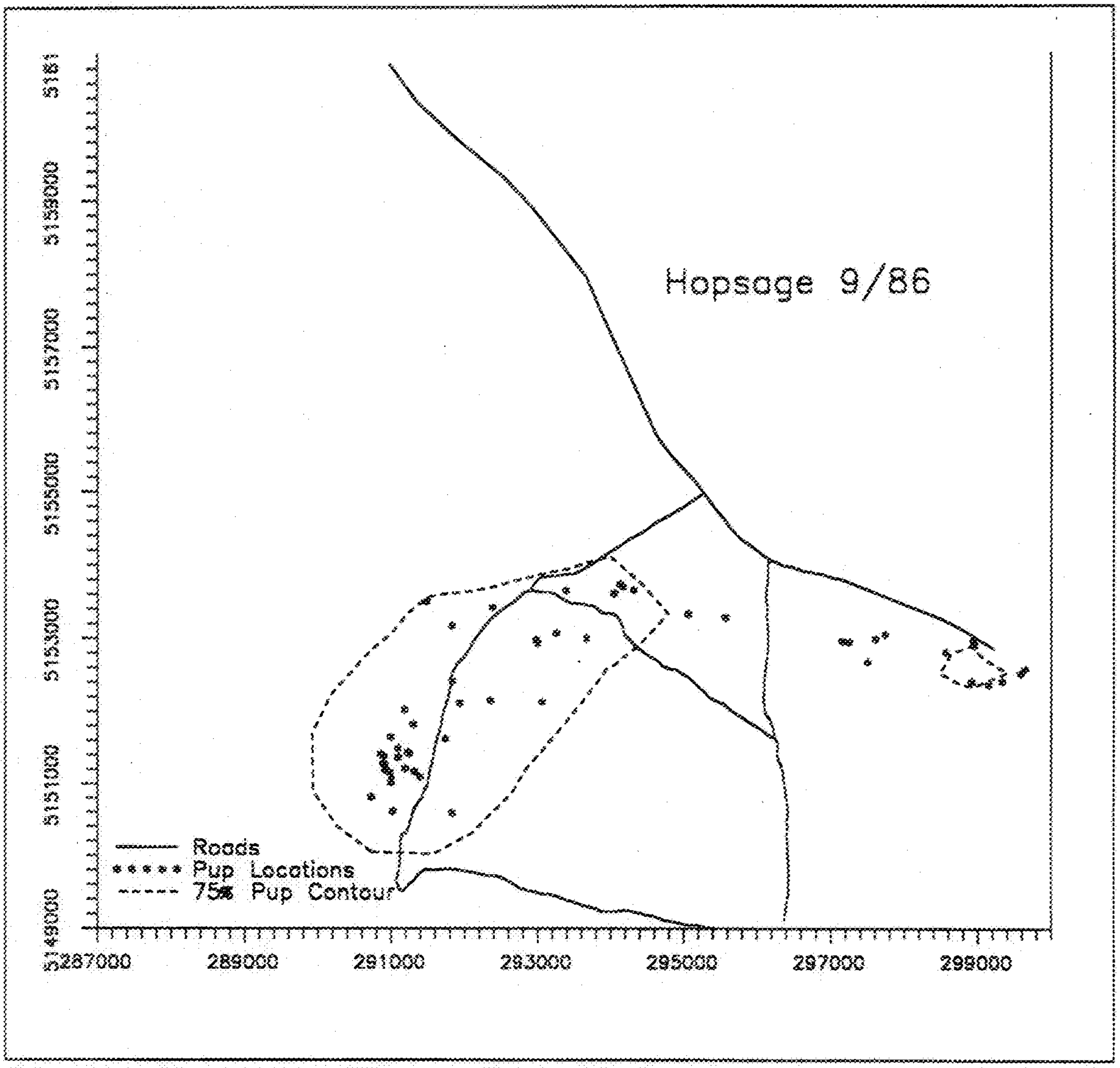


Figure 14: Hopsage 9/86 75% pup utilization distribution contour.

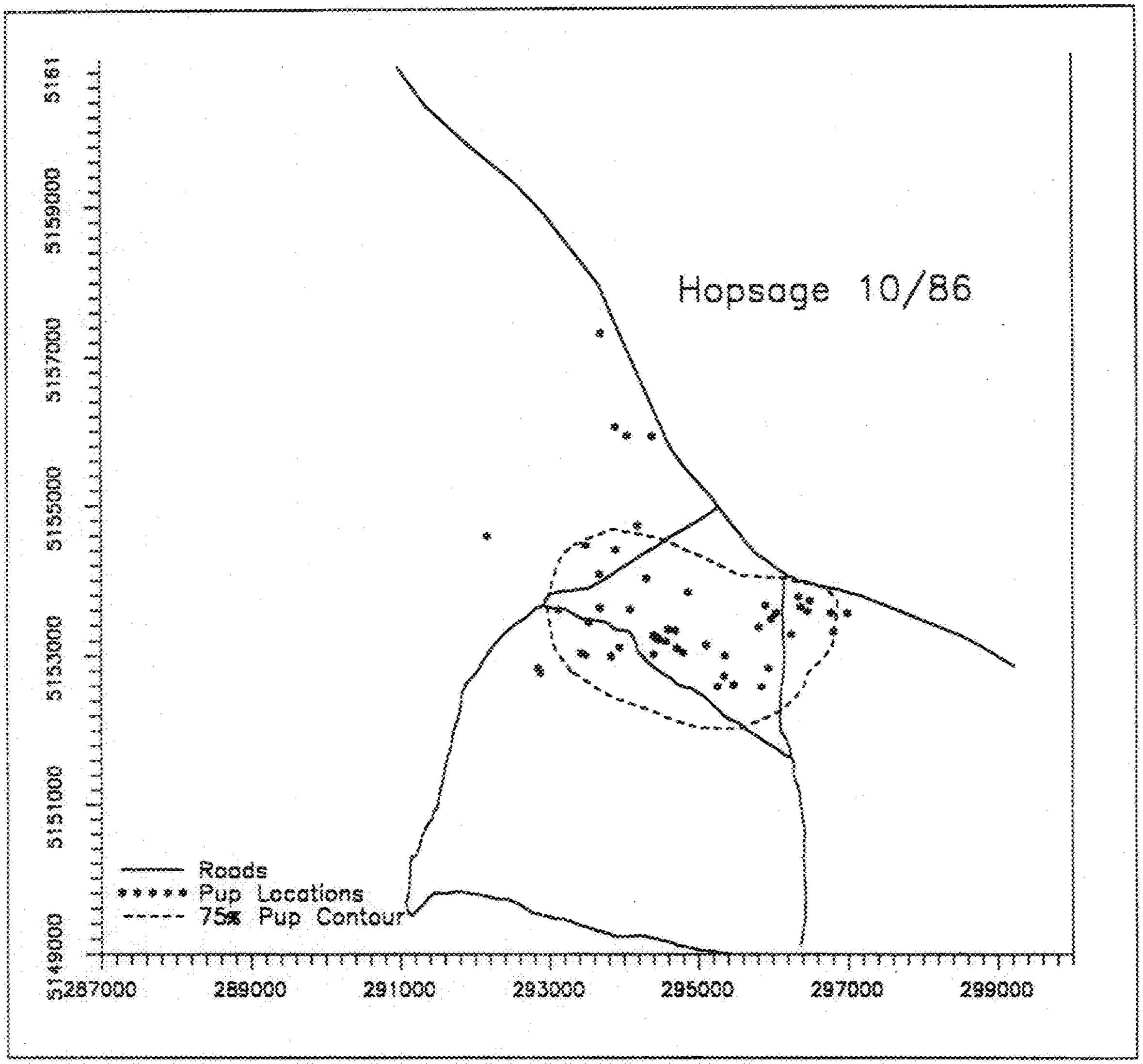


Figure 15: Hopsage 10/86 75% pup utilization distribution contour.

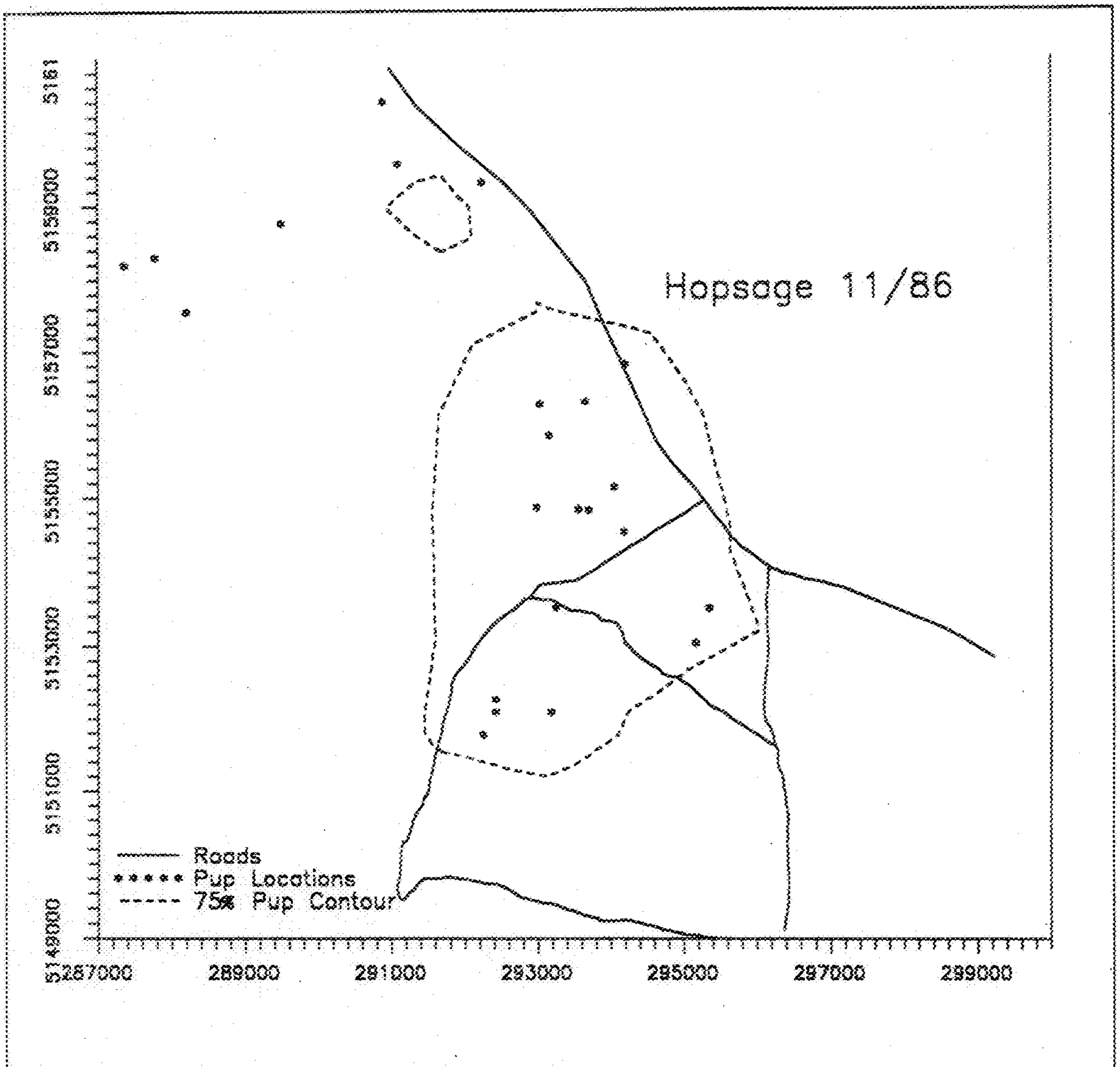


Figure 16: Hopsage 11/86 75% pup utilization distribution contour.

Sex ratios

Sex ratios were estimated at the beginning of 7 time periods (Table IV and Figure 17). The ratio never varied significantly from 50/50 (α=0.05, β_1=-0.0000577, r^2=0.246).

Table IV: Sex ratio data.

At the beginning of	Females	Males	Female Sex Ratio
Implant	25	18	0.58
Early Rearing	6	8	0.43
Late Rearing	9	11	0.45
Dispersal	8	9	0.47
Breeding	5	6	0.45
Denning	9	10	0.47
At One Year	9	9	0.50
Successful Dispersers	4	4	0.50
Unsuccessful Dispersers	1	1	0.50

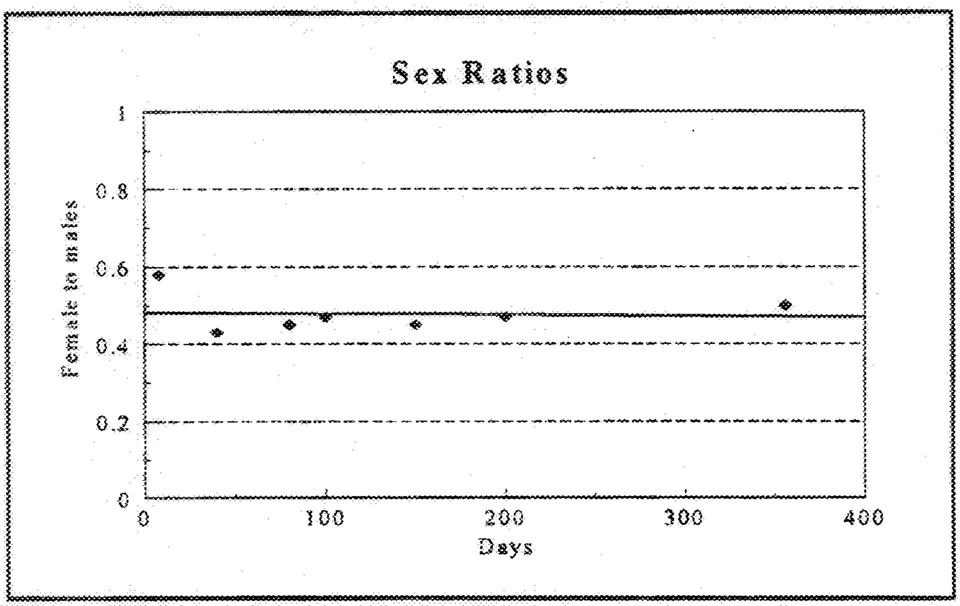


Figure 17: Sex ratios through the first year.

Dispersal

Dispersal data ws collected from 17 pups. The different classes used for dispersal are as follows. A successful disperser is an animal that lived through the dispersal period. Unsuccessful dispersers died during the dispersal period. If an animals signal was lost, or insufficient locations were obtained during the dispersal period the animal was classified as Dispersal Undetermined. An Associate is an animal that lived through the dispersal period and returned to its natal home range during the next year. All dispersing animals traveled far enough to emigrate from the study population. For three animals (#169, #713, and #840) (Figures 5 and 6) radio contact was lost just after the age of dispersal, but the animals had begun to disperse.

Table V outlines the dispersal results. Of the 17 animals that survived to the age of dispersal, 16 attempted dispersal, resulting in a pup dispersal rate of 94.11%. Two animals died during dispersal (#530, #773), resulting in a successful dispersal rate of 80.00%

Table V: Dispersal distances and direction by sex and class.

Class	Animal	Sex	Distance km	Direction
Successful Disperser	493	F	10.7	172°
	625	M	25.0	285°
	685	F	24.7	278°
	741	M	7.7	280°
	777	M	14.3	209°
	571	M	5.4	210°
	790	F	4.8	188°
	873	F	53.1	140°
Unsuccessful Dispersers	530	M	18.5	185°
	773	F	22.0	225°
Dispersal Undetermined	811	F	-	-
	169	F	-	-
	994	F	-	-
	600	M	-	-
	840	M	-	-
	713	M	-	-
Associate	590	M	-	-

Table VI shows the average dispersal distances by sex and success class. Figures 18 and 19 show this same information graphically. Due to the disproportionately long distance that #873 traveled this data was analyzed twice, once including #873 and once excluding #873. With #873 included, the average dispersal distance of females was significantly longer than males (Avg_{FEMALE}=23.06 Avg_{MALE}=14.18 α=0.05). There was no significant difference between successful and unsuccessful dispersers(Avg_{SUCC}=18.21 Avg_{UNSUCC}=20.25 α=0.05). Excluding 873, there was no significant difference between females and males (Avg_{FEMALE}=15.55 Avg_{MALE}=14.18 α=0.05), but unsuccessful dispersers moved significantly farther than successful dispersers (Avg_{SUCC}=13.23 Avg_{UNSUCC}=20.25 α =0.05). Because several of the dispersing animals died during, or just after dispersal the dispersal distances are conservative.

Table VI: Summary dispersal data.

Class	Average Distance in km	Sample Size	Varience
Females	23.06	5	18.67
Males	14.18	5	7.98
Successful dispersal	18.21	8	16.18
Unsuccessful dispersal	20.25	2	2.48
All animals	18.62	10	14.32

The dispersal directions for successful dispersers and unsuccessful dispersers was exclusively south, southwest and west (Figures 17 and 18). The average dispersal direction was 217° ± 35.6° (α=0.05).

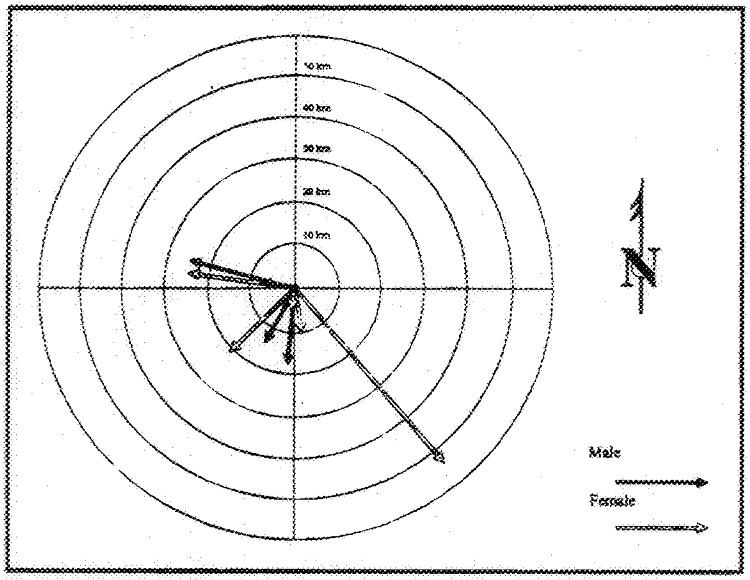


Figure 18: Dispersal distance and direction by sex.

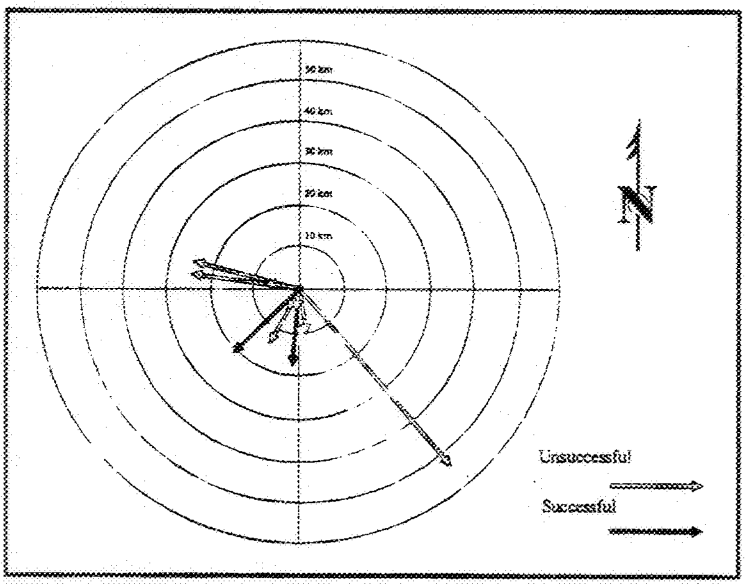


Figure 19: Dispersal distance and direction by success class.

Mortality

Estimates of early mortality (between birth and the time the pups were collared) were complicated by sporadic observations and low sample sizes. The only reliable data that could be quantified were maximum and minimum mortality rates for the first ninety days of life (Figure 21). This was calculated by conducting a census of animals known to be alive, known to be dead, and those that where unknown for each day during the first 90 days (Figure 20). The minimum mortality rate assumes all unknown animals where alive. Maximum mortality assumes that all unknown animals were dead.

Table VII through X show mortality rates of animals after the age of collaring. Table VI shows the ratio of the number of animals that died in a time period to the number of animals monitored through that time period. Table VII through X show the results obtained by MicroMort. The results from MicroMort better represent the amount of time each animal was monitored and takes into account the length of each time period. The straight ratios are shown because the estimates of the MicroMort program maybe biased do to the small sample sizes and the assumption of the technique used by MicroMort (mortality must be constant within a time period). MicroMort requires time periods to start on rigid dates. This also may distorts the MicroMort estimates, because the start of the dispersal period varied with each animal. The results of each of these methods are shown in figure 22.

Table VII and figure 23 show the mortality rates by season. Table VIII and figures 24 and 25 have mortality rates broken down by sex and by season. Finally table IX and figures 26 and 27 break up morality by mortality type and season.

Table VII: Mortality estimates by ratio.

Time Period	Number of Pups Monitored	Number of Mortalities	Mortality Rate
Early Rearing	14	1	0.0714
Late Rearing	19	3	0.1579
Dispersal	12	2	0.1667
Breeding	11	3	0.2727
Denning	18	0	0.0000

Table VIII: Mortality estimates by MicroMort.

Coyote Mortality by Season				
Category	Estimate	Variance	95% Confidence Intinterval	
			Low	High
Early Rearing	0.1114	0.0110	0.000*	0.3170
Late Rearing	0.1747	0.0083	0.000*	0.3537
Dispersal	0.1250	0.0068	0.000*	0.2867
Breeding	0.1655	0.0114	0.000*	0.3747
Denning	0.0790	0.0058	0.000*	0.2277
Overall	0.4212	0.0128	0.1992	0.6432

* = lower limit truncated to 0.0

Table IX. Mortality estimates by sex and season

Coyote Mortality by Sex and Season					
Category		Estimate	Variance	95% Confidence Interval	
				Low	High
Female	Early Rearing	0.0000	0.0000	0.0000	0.0000
	Late Rearing	0.0000	0.0000	0.0000	0.0000
	Dispersal	0.1395	0.0167	0.000*	0.3922
	Breeding	0.0000	0.0000	0.0000	0.0000
	Denning	0.0000	0.0000	0.0000	0.0000
Overall Female		0.0730	0.00513	0.000*	0.2135
Male	Early Rearing	0.2267	0.0395	0.000*	0.6163
	Late Rearing	0.3419	0.0253	0.0303	0.6535
	Dispersal	0.1131	0.0113	0.000*	0.3214
	Breeding	0.3179	0.0341	0.000*	0.6796
	Denning	0.1867	0.0282	0.000*	0.5161
Overall Male		0.6984	0.0176	0.4380	0.9587

* = Lower limit truncated to 0.0

Table X. Mortality estimates by type and season.

Coyote Mortality by Mortality Type and Season					
Mortality type		Estimate	Varience	95% Confidence interval	
				Low	High
Shot or Trapped	Early Rearing	0.0000	0.0000	0.0000	0.0000
	Late Rearing	0.0000	0.0000	0.0000	0.0000
	Dispersal	0.1250	0.0068	0.000*	0.2867
	Breeding	0.0828	0.0063	0.000*	0.2380
	Denning	0.0000	0.0000	0.0000	0.0000
Overall Shot or Trapped		0.0985	0.0031	0.000*	0.2082
Disease	Early Rearing	0.0000	0.0000	0.0000	0.0000
	Late Rearing	0.1747	0.0083	0.000*	0.3537
	Dispersal	0.0000	0.0000	0.0000	0.0000
	Breeding	0.0828	0.0063	0.000*	0.2380
	Denning	0.0790	0.0058	0.000*	0.2277
Overall Disease		0.2114	0.0078	0.0385	0.3842
Traffic Collision	Early Rearing	0.1114	0.0110	0.000*	0.3170
	Late Rearing	0.0000	0.0000	0.0000	0.0000
	Dispersal	0.0000	0.0000	0.0000	0.0000
	Breeding	0.0000	0.0000	0.0000	0.0000
	Denning	0.0000	0.0000	0.0000	0.0000
Overall Traffic Collision		0.1114	0.0110	0.000*	0.3170

* = Lower limit truncated to 0.0

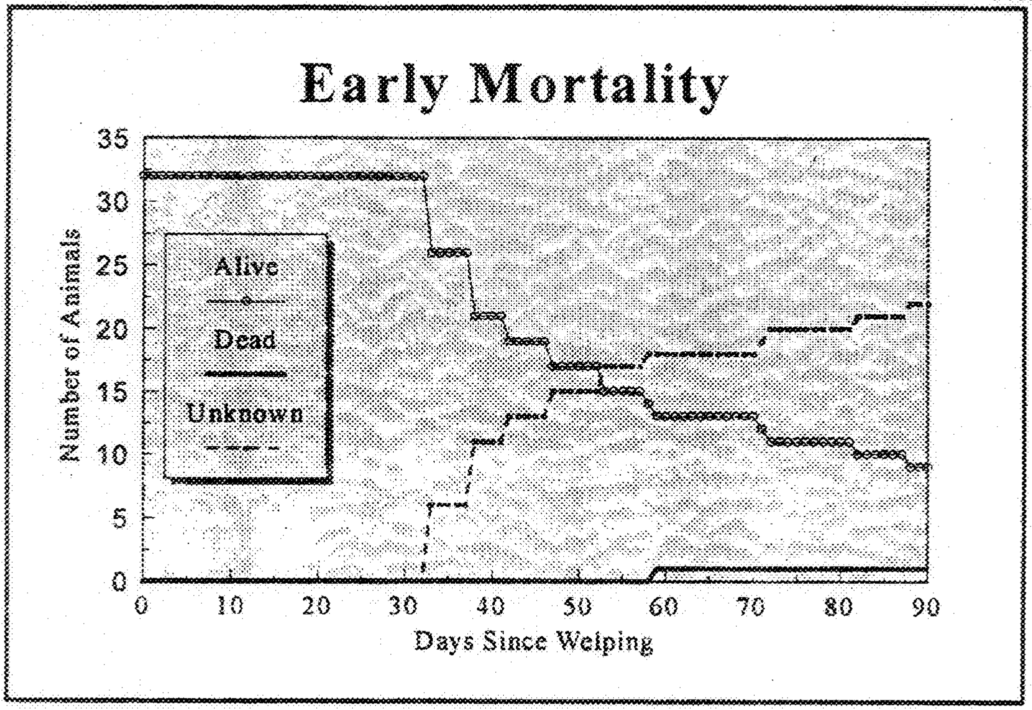


Figure 20: Component of early mortality calculation.

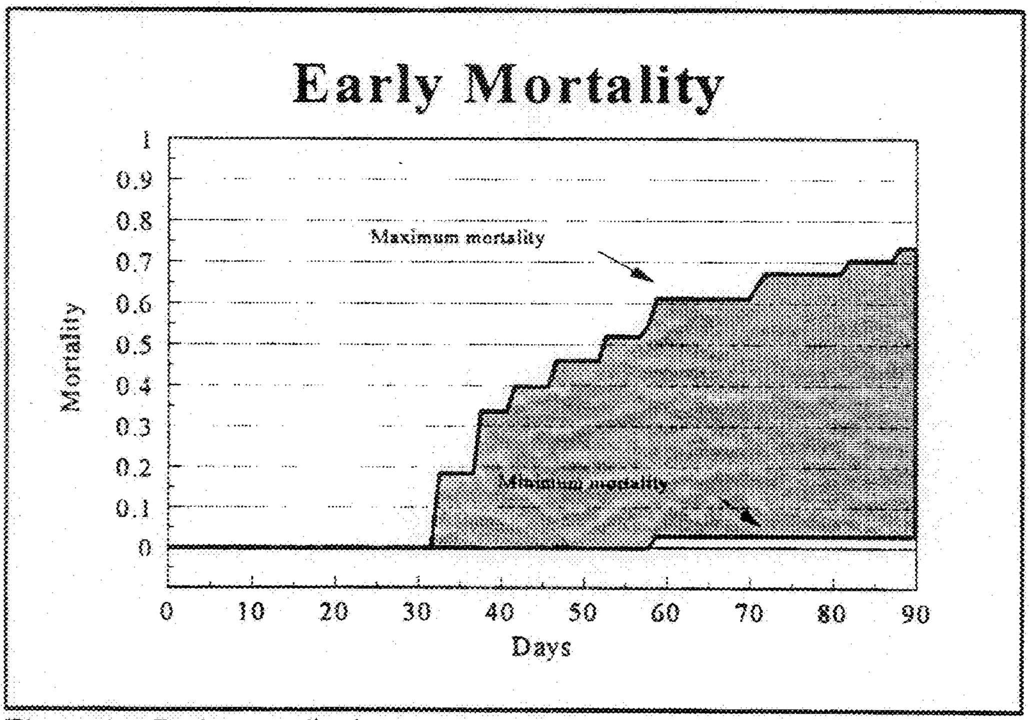


Figure 21: Early mortality in coyote pups.

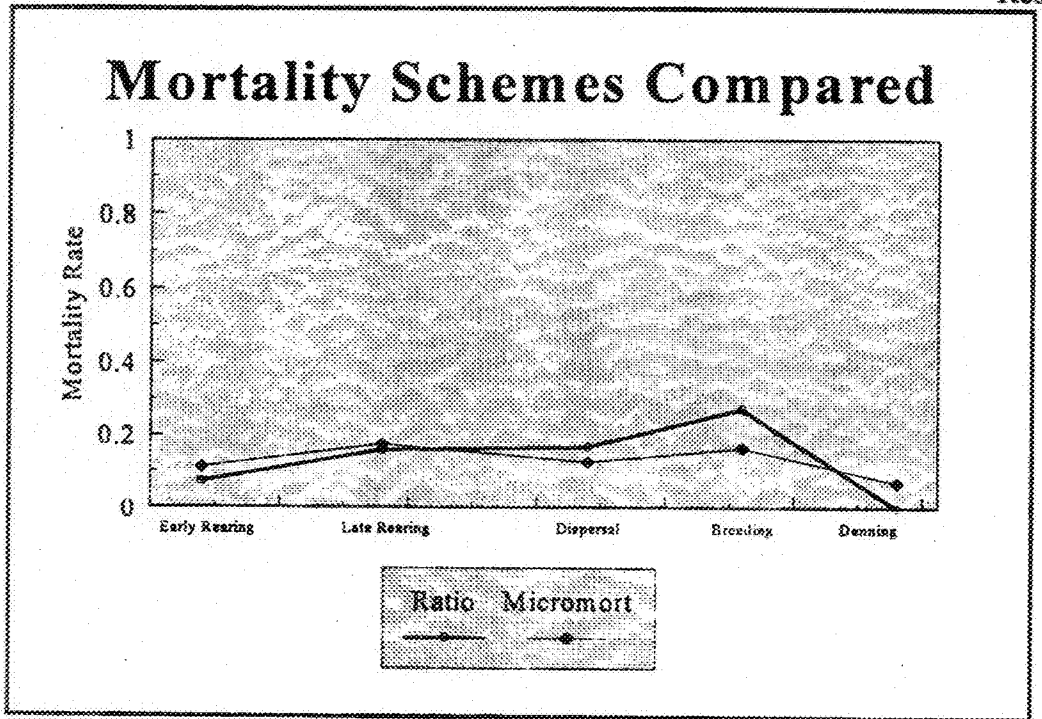


Figure 22: MicroMort and Ratio mortality methods compared.

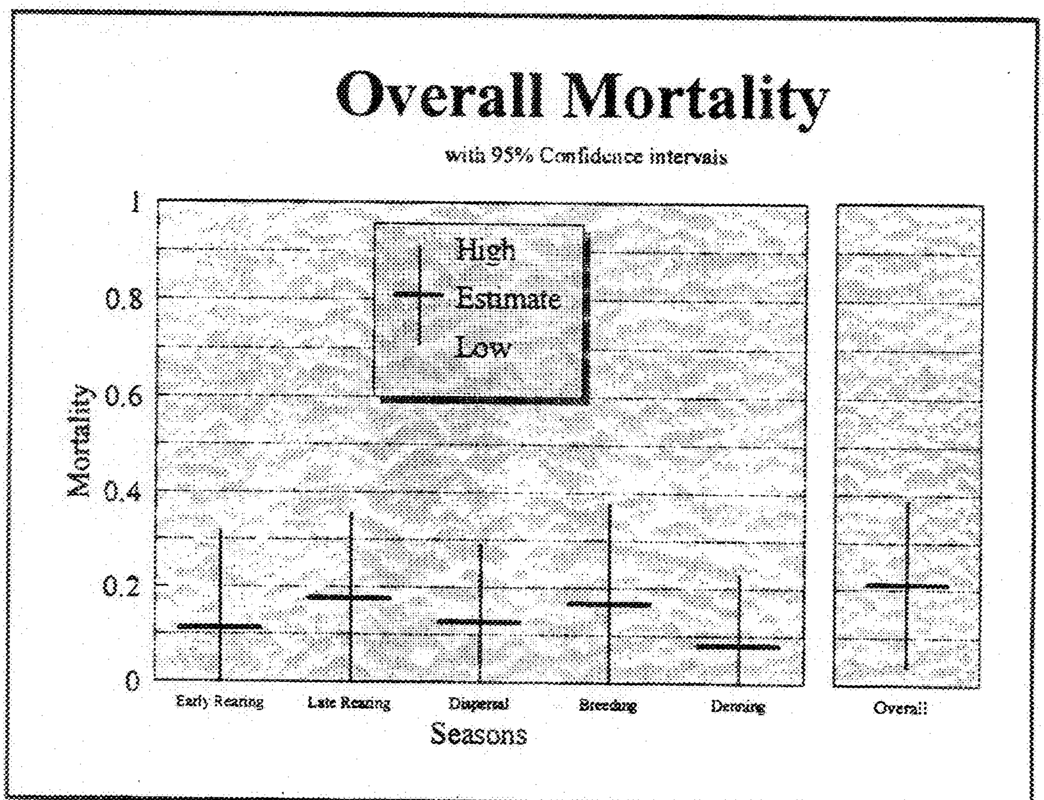


Figure 23: Overall mortality of pups by season.

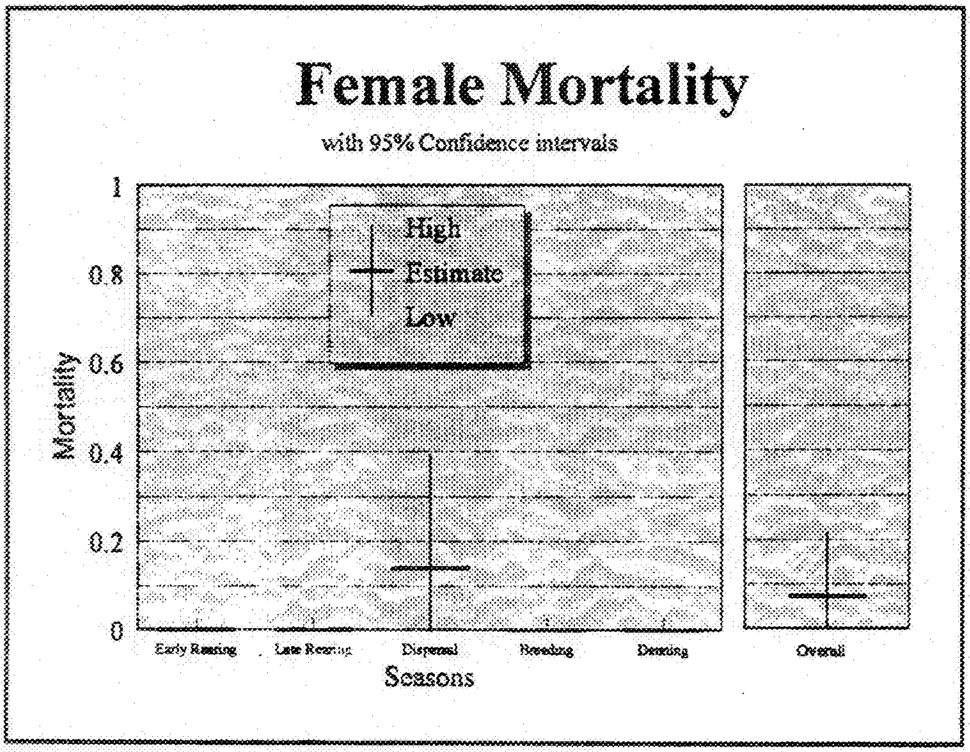


Figure 24: Mortality of female pups by season..

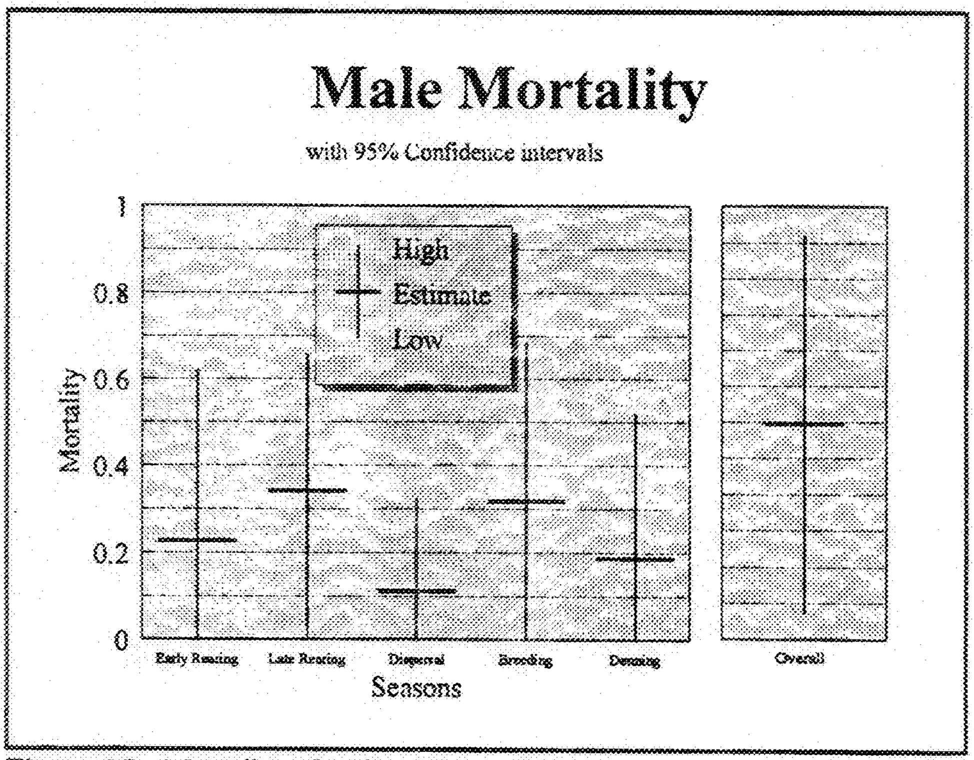


Figure 25: Mortality of male pups by season..

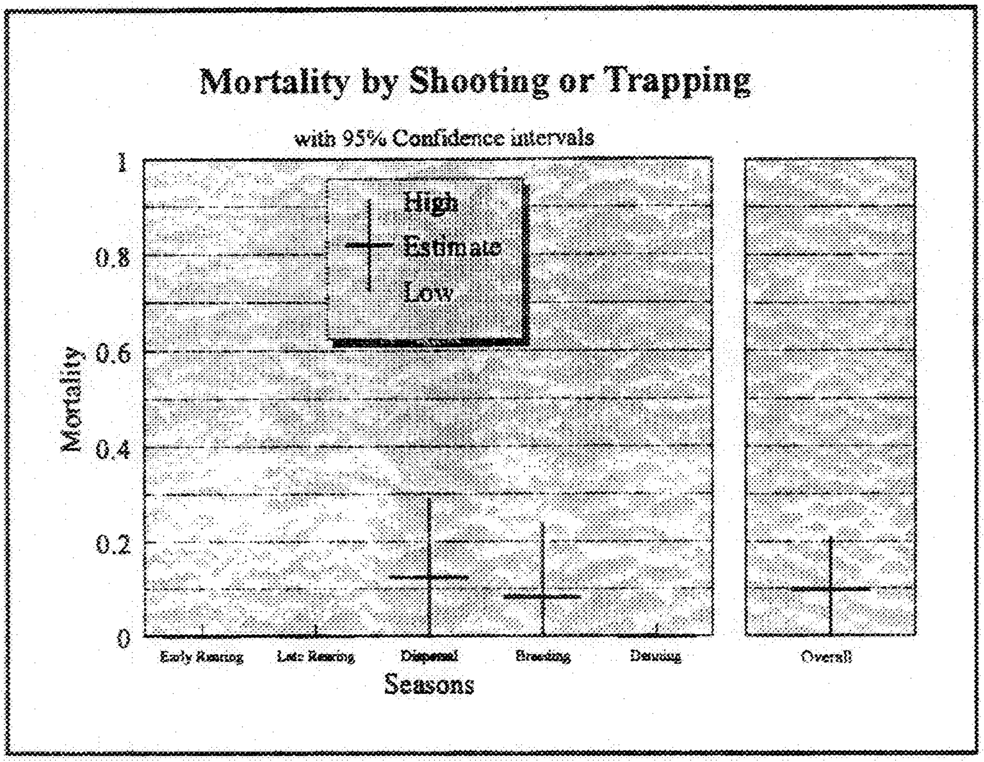


Figure 26: Human caused mortality of pups by season.

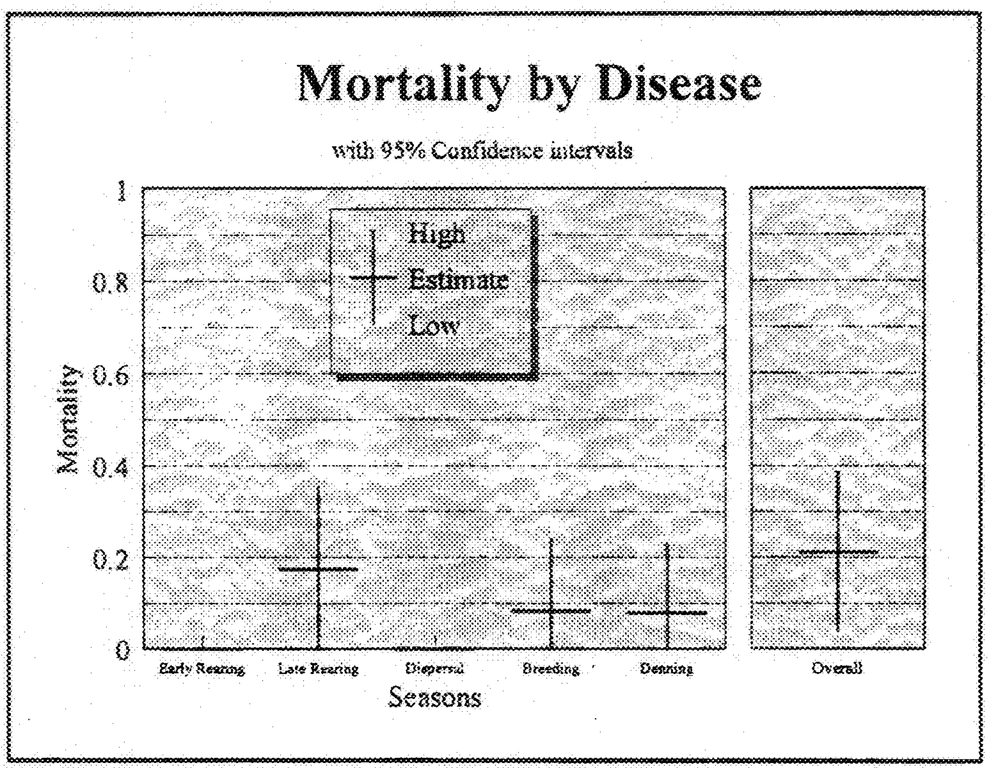


Figure 27: Disease caused mortality of pups by season.

Discussion

Home range

Home range size

Home range size of pups in past studies is varied (Table XI). One reason for the wide range of estimates (2.4 - 56.0 km^2) is because of method of calculation. More importantly, the time of year the movement data was collected can greatly influence the estimate. A pup's home range grows dramatically within the first year (Berg and Chesness 1978, Harrison et al. 1991, Messier and Barrette 1982). Estimates taken later in the year will incorporate dispersal and exploratory Behaviour that will inflate the estimate It is the inclusion of dispersal movement that produced many of the larger home range sizes in table XI. It is also important to note that home range estimates of pups early in the year may be influenced to a great extent by the home range size of the adults. Predispersal pup home ranges in this study (3.32 km^2) were always smaller than corresponding adult home ranges (11.48 km^2) as was also noted by Andelt (1985), Harrison et al. (1991) and Springer (1982).

Table XI: Summary of pup home range size from the literature.

Study	km^2	Monitoring period	n
Althoff 1978 [a] [d]	2.8	<12 months	4
Andelt 1985 [a]	2.6	<9 months	4
	2.4	9-20 months	6
Andelt and Gipson 1979 [a]	53.0	9-16 months	1
Berg and Chesness 1978 [b]	5-8	<12 months	50
Danner 1976	2.6	<12 months	6
Danner and Smith 1980	6.7	<12 months	6
Harrison et al. 1991 [c]	6.65	<7 months	6
Hibler 1977	56.2	<12 months	19
Litvaitis and Shaw 1980 [a]	0.98	2-4 months	4
Messier and Barrette 1982 [c]	2.2	0-8 months	12
	30.3	8-12 months	3
Springer 1982 [a]	54.3	<12 months	6
Rucker 1975	7.6	<12 months	2
Woodruff 1977	22.8	<12 months	2
This study	4.61	<12 months	5

[a] Minimum area (Mohr 1947)
[b] Minimum area (Dalke and Sime 1938)
[c] Minimal convex polygon (Mohr 1947)
[d] Type I home ranges only

Only a few studies estimated home range size for several time periods within the first year. These studies show a gradual increase in pup home range size from late spring to autumn, with a pronounced increase during dispersal (Althoff 1978, Andelt 1985, Harrison et. al. 1991, Messier and Barrette 1982). Although the data in this study showed no significant increasing trend, the November home range size of the "Hopsage" group suggests that the expansion of home ranges may have been present. An extended tracking period may have revealed similar increases in the other home ranges. The adult home ranges in this study showed a constant size. The November "Hopsage" home range grew 422% over the previous five months. Harrison et al (1991) found an increase of 194% during October. Absolute home range sizes in Harrison et al. (1991) were most comparable to this study while Andelt (1985) were smaller (Figure 28).

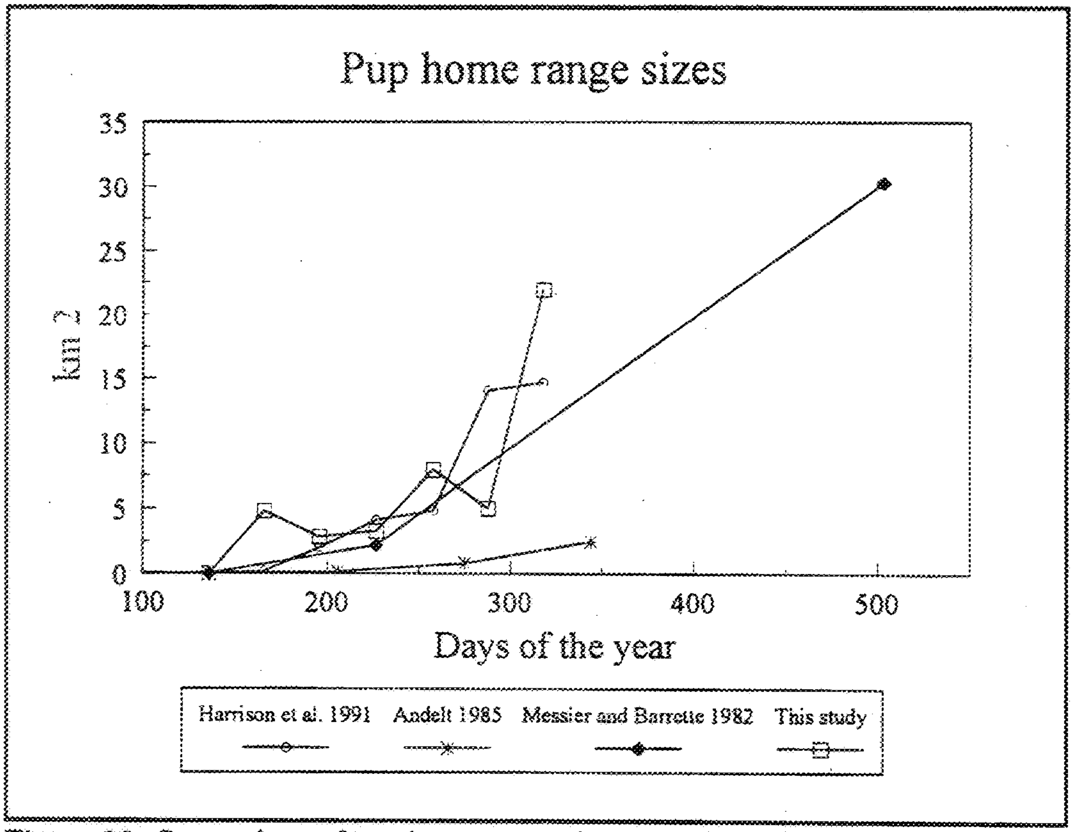


Figure 28: Comparison of pup home range size through the first year of life.

Exploratory movement

A possible explanation for the non distinct increase in home ranges in this study maybe a result of little exploratory behavior preceding dispersal. Well-established populations having little human exploitation and fixed territory boundaries would have few neutral areas between territories. This would add to the difficulty of extra-territorial movements. Harrison et al. (1991) noted that none of the first autumn dispersers made exploratory movements outside of the family home range before dispersal.

Of the exploratory movements recorded in this study one by the "Hopsage" group was most notable (Figures 13 to 16). Prior to September adult and pups had home ranges similar to figure 13. In September the pup movements showed a distinct displacement to the west (Figure 14). An elk carcass was later located roughly in the middle of this new home range. Unfortunately the adults could not be monitored during this period. This suggests that home range boundaries of the juveniles may break down when large amounts of food are readily available. During the month of October the pups return to their original home range location (Figure 15). The next month (Figure 16) shows an expansion of their home range characteristic of the onset of dispersal. Other reports of exploratory behavior are numerous in the literature (Althoff 1978, Andelt 1982, Andelt and Gipson 1979, Bowen 1982).

Sex Ratio

This study is the only study in the literature that has documented sex ratios of a cohort of wild coyotes for multiple periods in the first year of life. The results of this study as well as several others (Gese et al. 1989, Nellis and Keith 1976, Hawthorne 1971) found a 1:1 sex ratio for all ages of pups up to 1 year of age. On the basis of the monogamous breeding system of the coyotes (Harrison 1992, Harrison and Gilbert 1985, Kleiman and Brady 1978), a relatively even sex ratio would be expected.

Associate

Many studies have show that coyote pups don't always disperse in their first year (Andelt 1982, Bowen 1978, Camenzind 1978b, Harrison 1986, Hawthorne 1971, Knudsen

1976, Nellis and Keith 1976). Only one pup in this study stayed with its natal home range (5.9%). Gese et al. (1989) noted 18% (4 of 22) of the pups stayed. After spending some time outside it's natal home range, pup #590 returned before the following spring. In a colonizing population, where a lot of open uncontested areas are present, it would be beneficial for as many pups as possible to disperse and start new territories. This would increase the reproductive output of the population as a whole. Thus, fewer animals should be associates. In well-established populations it might be more beneficial for some animals to remain with its parental territory. The security of the territory could reduce its risk of mortality, and the opportunity to experience the raising of a litter could increase its success as a future parent. Benefits to the breeding pair could be the raising of a healthier litter with the aid of more adult animals in the group. This would reduce the number of dispersing animals but the reproductive potential of each animal would be increased.

Dispersal

Despite the existence of many theories concerning various aspects of mammalian dispersal, very little is known about long-distance movements of wide-ranging carnivores such as coyotes (Bekoff and Wells 1986). Little is known about the interactions among coyotes and spacing mechanisms involved in their distribution over time and space (Althoff 1978)

Overall dispersal rate

Dispersal is the most difficult of all population processes to investigate (Caughley 1977). The parameters that affect dispersal are unique to each population, making it difficult to compare rates among populations. First year dispersal rate in most coyote populations exceeds 60% (Table XII). The dispersal rate in this study was one of the highest reported (94.1%).

Table XII: Summary of natal dispersal rates from the literature.

Study	Pup Dispersal Rate
Althoff et al. 1981	100%
Andelt 1982	22%
Bekoff and Wells 1986	57%
Berg and Chesness 1978	70%
Bowen 1978	62.5%
Gese et al. 1989	81.8%
Harrison 1992	87.5%
This study	94.1%

Dispersal timing

All of the pups in this study dispersed between October 15 and December 31. This is consistent with the dates reported in the literature (Althoff et al. 1981, Andrews and Boggess 1978, Berg and Chesness 1978, Chesness and Bremicker 1974, Gese et al. 1989, Harrison 1992, Nellis and Keith 1976, Pyrah 1984, Windberg et al. 1985). Harrison (1992) noticed two peak dispersal periods (Oct.-Nov. and Feb.-Mar.). The dispersal dates in this study had an even distribution.

Dispersal distance

The minimum dispersal distance observed in this study was 4.8 km. This was enough to traverse at least two home ranges from the natal home range. Pusey (1980) stated maximizing distance from the natal area would reduce the probability of inbreeding depression. The average dispersal distance observed in this study of 18.62 km compares with most other studies (Table XIII).

Dispersal direction

Many researchers have speculated about dispersal direction being guided by population density (Knowlton and Stoddart 1983, Howard 1960). Gese et al. (1989) noted that dispersal may be an important population regulating mechanism with coyotes moving from high-density to low-density areas. The distinctive southwest dispersal direction in this study is most likely attributed to the surrounding population structure. All of the land to the north and west of the study area consists of the Hanford Reservation. There has been no hunting or trapping on this land for 20 years. Area for new home ranges is not frequently available. The populations in this area are relatively stable (Springer 1982) compared to the land to the south and west. This land is predominated by cultivated agriculture. Predator control in these areas disrupts pack formation leaving more land uncontested and available for colonization by dispersers. Other studies have also documented dispersal towards low density areas (Andrews and Boggess 1978, Berg and Chesness 1978, Davison 1980, Gese et al. 1989, Pyrah 1984); however Nellis and Keith (1976) reported that pups in Alberta dispersed in random directions. Andelt (1985) stated that dispersal was not a population regulating mechanism in his study.

An area that has remained unexplored is how pups determine which direction to disperse. A random search path could be used but this would reveal more extensive exploratory movements than is reported in the literature. A possible tool that coyotes would have at their disposal to monitor local densities is territorial vocalizations. Fulmer (1990) and others have added to the understanding of the functions of vocalizations, but much more data would be needed to test the above hypothesis

Sex interactions with rate and distance

Dobson (1982) states, male dispersal predominates in mammals with polygynous systems, whereas both sexes usually disperse in monogamous mammals. These patterns appear associated with sex-specific competition for mates (Harrison 1992). Harrison

(1992) and Windberg et al. (1985) found greater female than male dispersers. In contrast Moore and Miller (1984) and Robinson and Grand (1958) reported more male dispersers. Other studies found no significant sex difference in dispersers (Andrews and Boggess 1978, Davison 1980 in Idaho, Hawthorne 1971, Nellis and Keith 1976). This study also found no sex differences. Coyotes do not appear to be limited to a specific sex ratio for animals that colonize new areas. If any consistent trend is to be found, more data needed.

Dispersal distances among sexes also show little consistency in the literature. Andrews and Boggess (1978), Davison in Idaho (1980), Harrison (1992), and Hawthorne (1971), found no difference in dispersal distance. Davison in Utah (1980), Nellis and Keith (1976), Windberg et al. (1985) found that female dispersed farther while Berg and Chesness (1978) and Robinson and Grand (1958) reported that male dispersed farther. My data shows a tendency for females to disperse over longer distances, but this result is dependent on the inclusion of a possible outlier (#873).

It seems probable that, because of the variation in all of the dispersal characteristics reviewed, coyotes are utilizing different dispersal strategies dependent on local conditions. Studying these characteristics is very important in determining the range of behaviors but may be of little use in describing a single coyote dispersal theory. Bekoff (1977) states with the appearance of recent data on a variety of mammalian species, it is becoming clear that "universal" hypotheses about dispersal; based one single underlying mechanisms may have limited applicability.

Table XIII: Average dispersal distances of coyote pups by sex.

	Females		Males		Total	
	km	n	km	n	km	n
Andelt 1982	-	-	-	-	7.1	
Andrews and Boggess 1978 [a]	68.6	12	61.6	14	64.8	26
Berg and Chesness 1978	-	-	-	-	48	35
Bowen 1978	51.4	3	17.2	2	37.7	5
Garlough 1940 [b]	34.4	38	45.9	51	40.9	89
Gese et al. 1989	-	-	-	-	59	11
Harrison 1992	94	11	113	9	102.5	20
Hawthorne 1971	6.4	8	5.2	8	5.8	16
Nellis and Keith 1976	26.4	22	14.1	28	21.1	50
Pyrah 1984	-	-	-	-	52.2	11
Robinson and Grand 1958 [c]	-	-	-	-	16.9	146
Windberg et al. 1985	15.3	16	3.7	6	12.4	22

[a] For animals that moved >16 km (10 miles), pup and adults combined. The age structure was very young (57% pups).
[b] Adults and pups (97.8% pups).
[c] Using Robinson and Cummings (1951) data.

Mortality

Early mortality

Low observation rate during the first 90 days of life inhibited my ability to collect adequate mortality data. The data that was collected suggests that there was no extreme mortality rate, either high or low (Figure 20). Gier (1968) reported 50% mortality in the first 3 months, Nellis and Keith (1976) found 8.6% mortality from birth to 40 days and Anderson (unpubl.) found 9% mortality from denning to 40 days. Andelt (1982) indicated that mortality in the first 1 to 2 months my be high in Texas. Considerably more data will be needed to reach any definite conclusions. Knowledge of early mortality, as a tool for management, is vital. Management practices focus on young animals at den sites or adult animals, while having little understanding of the link between these two age classes or its effect on subsequent generations.

Comparison of mortality calculation methods

The two procedures for calculating mortality after the date of collaring showed similar results (Figure 22). Thus, the premise will be made that the data meets the assumptions of the Micromort program. The detailed analysis that Micromort produced does have some interesting trends.

Annual pup mortality

The overall annual pup mortality rate of 0.42 in this study is comparable to other studies (Table XIV). Pup mortality in general is high with respect to adults (Andelt 1982, Camenzind 1978b, Gese et al. 1989, Nellis and Keith 1976, Pyrah 1984, Windberg et al. 1985).

Table XIV: Summary of pup mortality from the literature.

Study	Location	Years	Period	Mortality
Anderson unpubl.	Alberta	1964-68	Denning - 40 days	9%
Andelt 1982	Texas	1978-79	June-November	36-64%
Davison 1980	Utah	-	First year	77%
	Idaho	-	First year	55%
Gese et al. 1989	Colorado	1983-86	First year	49%
Gier 1968	Kansas	1948-51	Denning - July	50%
Hallett 1977	Missouri	1976	May - Fall	56%
Knudsen 1976	Utah	1973	Denning - December	72%
		1974	Denning - December	41%
Nellis and Keith 1976	Alberta	1964-68	Denning - 40 days	8.6%
			40 days - 1 year	68%
Robinson and Cummings 1951	Wyoming	1945-50	First year	~68%
Windberg 1985	Texas	1974-82	First year	58%

Causes of mortality

Studies in the past have reported mortalities in the form of shooting (Windberg et al. 1985), trapping (Windberg et al. 1985, Andelt 1982), traffic collisions (Windberg et al. 1985), disease, and to a lesser predation (Andelt 1982). In this study mortality manifested itself in two forms; disease and human caused (shooting, trapping, and traffic collisions). Every study reviewed that investigated pup mortality reported some degree of human caused mortalities. The degree of human caused mortality was usually high (Table XV). Considering the extent of human influences on coyote populations it will be a challenge to determine pup mortality in the absence of human exploitation.

There has been no study that has reported an undisturbed coyote population in excess of its carrying capacity and yet coyotes can maintain viable population in the presence of considerable human exploitation. This exemplifies the incredible ability of the coyote to regulate its own densities. The understanding of the variety of regulating mechanisms of the coyote is far from being complete.

Specific pathogens that contributed to mortalities of pups in this study could not be determined. One animal #570, was diagnosed as having had been exposed to parvo-virus at some point in its life. Pathogenic mortality was highest during late rearing, although it had a significant influence later in the year.

Table XV: Human caused pup mortality

Study	Human mortality
Andelt 1982	38%
Davison 1980	89% Utah 78% Idaho
Hallett 1977	54%
Knudsen 1976 [a]	92%
Nellis and Keith 1976	29%
Pyrah 1984	79%
Tzilkowski 1980 [a]	93%
Windberg et al. 1985	51%

[a] Pups and adults combined.

Sex specific mortality

Since only one female was known to die, this mortality data may be heavily influenced by males. The single female was killed by a trapper during the dispersal period. Most males died during late rearing and breeding. The higher overall male mortality is puzzling because of the strong 1:1 sex ratio during all seasons. Either an increase in the proportion of males or a greater female mortality rate would have been expected. Windberg et al. (1985) reported even sex specific mortality of pups.

Dispersal and mortality

Dispersal may be one of the most risky ventures undertaken by a coyote pup (Bekoff and Wells 1986). Mortality during dispersal is usually high (Bekoff and Wells 1986, Gese et al. 1989, Harrison 1992, Tzilkowski 1980, Windberg et al. 1985). Bekoff and Wells (1986) report that 56% (9 of 16) dispersers died compared to 20% (1 of 5) nondispersers. Harrison (1992) found a 53% mortality for dispersers and a 28% mortality for nondispersers. Gese et al. (1989) noted a 77% (10 of 13) dispersal mortality rate. Windberg et al. (1985) also reports greater pup mortality from November to February.

Harrison (1992) states dispersal entails inherent risks expressed as reduced survival rates of dispersing individuals relative to non-dispersing individuals. Dispersal increases chance encounters with hunters, vehicles and traps. Coyotes appear to be more vulnerable to trapping and man-induced mortality in areas less familiar to them (Althoff 1978, Harris 1983, Litvaitis 1978, Rucker 1975, and Woodruff 1977). Pyrah (1984) also notes that most mortality occurred outside the home range. All human caused deaths in the current study were during the dispersal and breeding periods (except for one auto caused death during early rearing). Human caused mortality was not only highest during dispersal, it was the only known cause of mortality.

Despite reduced survival of dispersers, the observed pattern of complete dispersal by both sexes of juvenile coyotes suggests that either reproductive benefits may compensate for higher overall mortality rates of dispersers, or that most individuals have no choice; thus, they may be forced to disperse by siblings or parents (Harrison 1992). Despite lower overall survival rates of dispersers, individuals forced to disperse may reduce their immediate risks of being injured or killed by conspecifics. Dispersal also probably enhances reproductive potential by reducing probability of inbreeding, or by increasing chances of encountering a potential territory that is unoccupied by a dominant coyote of the same sex.

There is no reference in the literature to dispersal distance as it related to the success of the disperser. Unfortunately this study does not have the sample size to shed much light on the subject. A greater dispersal distance of an individual would increase its chance of encountering optimal habitat to establish a territory. On the other hand the greater time spent dispersing would increase the chance of encountering humans or aggressive conspecific. The results of this study suggest that it is better to establish a home range as soon as possible, even at the cost of habitat quality.

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