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DREWEK, JOHN, JR.

BEHAVIOR, POPULATION STRUCTURE, PARASITISM, AND OTHER ASPECTS OF COYOTE ECOLOGY IN SOUTHERN ARIZONA

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BEHAVIOR, POPULATION STRUCTURE, PARASITISM, AND OTHER ASPECTS OF COYOTE ECOLOGY IN SOUTHERN ARIZONA

by

John Drewek Jr.

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WITH A MAJOR IN WILDLIFE BIOLOGY

In the Graduate College

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As members of the Final Examination Committee, we certify that we have read

the dissertation prepared by John Drewek Jr.

entitled BEHAVIOR, POPULATION STRUCTURE, PARASITISM, AND OTHER ASPECTS OF COYOTE ECOLOGY IN SOUTHERN ARIZONA

and recommend that it be accepted as fulfilling the dissertation requirement

for the Degree of Doctor of Philosophy.

Lyle K. Sowls	4-24-80 Date
Raymond E. Reed	4-24-80 Date
E. Lendell Cockrum	4-24-80 Date
Ted H. Noon	4/24/80 Date
Roger Hungerford	24 April 1980 Date

Final approval and acceptance of this dissertation is contingent upon the candidate's submission of the final copy of the dissertation to the Graduate College.

I hereby certify that I have read this dissertation prepared under my direction and recommend that it be accepted as fulfilling the dissertation requirement.

Lyle K. Sowls	4-24-80
Dissertation Director	Date

STATEMENT BY AUTHOR

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SIGNED: John Hnewck Jr.

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ABSTRACT

A study of the coyote in southern Arizona was initiated to gain insight into basic ecological relationships and to provide a basis for more detailed future studies.

The behavioral portion of the study was conducted on the Santa Rita Experimental Range (SRER), where apparent minimum home ranges for 6 radio-tracked coyotes ranged in size from 0.5 to 7.9 square miles, and averaged 4.2 square miles. The relatively small home ranges may have reflected high coyote density and abundance of food during the period of study. Females tended to occupy larger areas than did males. Home ranges appeared to be a composite of foraging ranges, each of which had its own center of activity. Generally home ranges exhibited the property of linearity. Coyotes typically became active before dusk and remained so until midmorning of the following day, with cooler weather extending activity periods.

Based upon annuli counts from canine teeth of 378 coyotes, the age distribution within the general population was as follows: 0-1 year old, 32.8%; 1-2, 14.3%; 2-3, 15.3%; 3-4, 12.2%; 4-5, 11.4%; 5-6, 5.0%; and over 6 years, 9.0% of the sample. The average age was 3.2 years (s.d. 2.4), with one animal reaching just under 14 years of age. Subsamples representing different years, causes of death, and counties had significantly different age class distributions. Also, coyote age class structures from various regions of North America exhibited highly significant variations.

Of 273 known-sex coyotes, the ratio was 154 males: 119 females. Males tended to outlive females; for coyotes over 5 years of age males significantly outnumbered females. The control practices of trapping and poisoning killed a highly significant majority of male coyotes. Hypothetically, disproportionate sex ratios were part of a mechanism whereby coyote populations maintained a balance with their environment.

Reproductive tracts from 22 males and 20 females were examined. Males produced spermatozoa from January to June. There was no evidence of breeding among juvenile females.

Over 100 coyote specimens were examined for parasites. Information on the occurrence of ectoparasites tended to be of qualitative value. The species identified were Pulex simulans, Echidnophaga gallinacea, Thrassis arizonensis, Heterodoxus spiniger, and Otobius megnini. The 15 species of helminths recovered consisted of 5 cestodes, including Taenia pisiformis (56% infection rate), T. multiceps (22%), T. macrocystis (6%), T. hydatigena (1%), and Mesocestoides sp. (6%); 8 nematodes, including Ancylostoma caninum (38%), Filaroides osleri (3%), Toxascaris leonina (43%), Physaloptera rara (51%), P. sp. (1%), Rictularia cahirensis (3%), Mastophorus numidica (1%), and Dirofilaria immitis (2%); and 2 acanthocephalans, including Oncicola canis (46%) and Pachysentis canicola (1%). Pups and females were subject to greater collective endoparasite burdens. Variations in incidence and intensity of infection were also noted with year, season, and county.

A general picture of food habits was obtained by examining 101 coyote stomachs. By percentage of overall volume, stomach contents were: larger mammal, 25.4%; smaller mammal, 35.0%; bird, 16.4%;

reptile, 0.1%; invertebrate, 6.4%; and vegetable matter, 16.2%. Much of the larger mammal material was carrion. Statistical analyses revealed that there were significant differences in the diets of pups and females versus adults and males, respectively, while variations in diet between years, seasons, and counties did not appear significant.

By percentage of organic weight, contents of 619 coyote scats from the SRER were: larger mammal, 15.8%; smaller mammal, 49.9%; bird, 0.8%; reptile, 0.2%; insect, 5.4%; and vegetable matter, 27.9%. Variations in recovered weights of the major food categories between seasons were highly significant. The proportion of native fruits and insects in the scats increased greatly in summer and fall, and appeared responsible for moderating predation upon smaller mammals for several months.

INTRODUCTION

The coyote (Canis latrans) has become one of the more familiar and truly controversial wild mammals of the American West. Characterized by rather large, pointed ears, tapered face, and bushy tail, this medium-sized wild dog averages less than 30 pounds (13.6 kg.) in weight. Though 19 subspecies of the coyote have been described (Young and Jackson 1951), but one, C. l. mearnsi Merriam 1897, occurs naturally throughout Arizona (Cockrum 1960). It is a small form, colorful both literally and figuratively, and is adaptable within limits to people and their structures. Adaptability enables the animal to survive in a variety of habitats, including mountain and desert, agricultural and pristine, rural and urban. However, it is most typically found in the lower Sonoran life zone, below 5,000 feet (1.5 km.) in elevation, preferring grassland and scrub habitats. The animal's success is also attributable to its non-specialization, for a wide variety of foods are acceptable fare; the coyote may be scavenger, predator, or vegetarian as opportunity affords.

During this century the coyote has expanded its range across North America (Ames 1975; Bekoff 1978) and purportedly increased in numbers. However, historical references indicate that the animal was plentiful in primitive America (Smith 1866; Dobie 1961). In southern Arizona, within the bounds of normal population fluctuations, the coyote has probably always been numerous. It was well known to early

Indians of the region as evidenced by the appearance of its likenesses on Hohokam pottery and occasionally on petroglyphs, and by records of its exploits in tribal folk tales (Olin 1954). As early as 1763 a Spanish padre noted that coyotes preyed upon untended sheep and poultry of that day (Rudo Ensayo 1951). Davis (1973) provided several references to the abundance of coyotes in southern Arizona during the early nineteenth century. Similarly, Young and Jackson (1951:80, 154, 168) indicated that coyotes occurred in numbers in this region in the early twentieth century. The coyote remains numerous in Arizona today (Linhart and Knowlton 1975), though the animal's numbers are often underestimated because of its adeptness at avoiding human encounters.

The intrusion of European man upon the primeval American ecosystem resulted in an alteration of "the balance of nature." In the West most noticeably native herbivores were gradually reduced in numbers or eliminated and replaced with domestic animals. Predators continued to prey upon herbivores, but now this niche had been filled by livestock. Depredations led to a predator control effort that eventually involved the U.S. Government and exterminated or greatly reduced the numbers of many larger predators. The coyote survived. In fact, so successful was the coyote that it was labeled an "archpredator, the scourge of the western country" (Goldman 1930), and soon became the major target of the predator control program.

In recent decades predators have become increasingly appreciated as "resources of inherent interest and value" (Leopold 1964), and the coyote has fared well in this respect. The animal's ecological values were early recognized. Since its chief foods, rabbits and rodents, are potential pests in their own right, the check the coyote provides on their populations has benefited man. Another less apparent merit of predators such as the coyote is their subtle culling effect upon game populations, thereby strengthening the stock. Scavenging by the coyote cleans the environment. The animal has recreational and commercial value as well, for it provides excellent sport hunting, and, subject to the whims of fashion, its pelt has considerable worth. Furthermore, the coyote has a less tangible aesthetic value; its howl is a symbol of the western wilderness. Also the wily coyote has scientific value. Why has this predator thrived when so many other wildlife species have declined? Could the answer be useful in the management of these other species?

Certainly it would be naive to think that depredation is not a problem, but in light of the new status of the coyote in the public eye, the wholesale killing of coyotes in an effort to reduce livestock losses has become unacceptable. The growing complaint against indiscriminate predator control programs and general dissatisfaction with handling of the depredation problem led to the formation of a special investigatory committee whose evaluation of the situation culminated in the Cain report (Cain et al. 1972). This report had immediate and far reaching effects upon the policy and practice of the predator control program. Among the more worthwhile results was a stimulation of coyote research. While previous coyote studies dealt predominantly with food habits, by 1974 over 120 investigations dealing with all aspects of coyote ecology were underway (Knowlton 1973, 1974). Perhaps the most comprehensive study of the coyote predated the Cain report, however. The 15-year-long effort of H. T. Gier (1968), who studied multiple aspects of the animal's ecology in Kansas, had a strong influence on the designing of this project.

This study was conceived to provide basic information about the coyote in southern Arizona. To accomplish this, a set of somewhat specific objectives was formulated. The first involved delimiting the animal's home range. Because radio telemetry was the technique of choice, it was a simple matter to monitor daily behavior patterns as well. Secondly, the sex and age distribution within the overall population was investigated, for this information is basic to an understanding of population dynamics. As the project developed, it was decided to also record such reproductive information as became available. Thirdly, the incidence of parasites afflicting the coyote was cataloged. While a thorough investigation of coyote diseases was prohibitive, an effort was made to detect ill coyotes while pursuing other objectives in field and laboratory. A series of coyote heads were tested in an attempt to detect rabies. And finally, a general picture of coyote food habits was obtained by identifying contents of a series of stomachs representing coyotes from a wide area of southern Arizona, and by analysis of scats representing a localized group of coyotes.

Southern Arizona provided its own set of challenges, and these had to be considered in undertaking the study. It is an area of diverse environment and varied topography, a mixture of mountain ranges and broad valleys. The Arizona climatic pattern is characterized by winter and summer rains separated by drought-like periods. Except for the higher mountains, summers are hot while winters are mild. The large number of assorted habitats are occupied by a great variety of vertebrates, including over 400 species of birds and over 100 species of mammals (Lowe 1964).

The diverse environment combined with the adaptability of the coyote presented some difficulty in planning and, later, in interpreting results. Traveling across southern Arizona one encounters, in effect, a succession of coyote subpopulations, each conforming to the dictates of its own time and place. Cottonfields have been converted to pecan orchards, rangelands have been converted to housing developments, cattle feedlot operations have been disbanded, and so on. Individual coyotes as well as entire subpopulations adapted to prevailing circumstances. Limitations imposed on a broad ecological study of the coyote by this situation should be kept in mind by the reader as he proceeds through this report. For the purposes of this study it was supposed that the various groups of coyotes had enough in common that some generalizations would be valid. While the broad approach was pursued as much as possible, some phases of the study had to be qualified. Perhaps the best example was the behavioral phase of the research; information obtained from radio tracking was limited to a specific group of animals and results should be applied cautiously to coyotes generally. Whenever sufficient data existed, analyses were attempted to evaluate the effects of time and place, as well as sex, age, and cause of death. Also comparisons were made with results obtained by other coyote researchers from across North America. Hopefully, these comparative analyses have pointed to areas where more detailed study would be worthwhile.

The project was initiated in July, 1970, with major support provided by the Arizona Cooperative Wildlife Research Unit until August, 1973. That period was utilized primarily to accumulate data. Subsequent analysis and organization of information proceeded, except for a few lengthy interruptions, until the present time. This report, the culmination of that effort, attempts to comprehensively present procedures and results in a meaningful way.

At the outset this project was broad, heuristic, and ambitious, and eventually several facets of the work were of necessity curtailed. How well the original goals have been fulfilled the reader will decide. Certainly this report leaves ample room for further study; hopefully it will stimulate some. Hopefully too it has made a contribution toward answering an appeal made by the Cain committee for a factual basis upon which to base better management of the coyote.

MATERIALS AND METHODS

Coyote Behavior

The Study Area

Virtually all of the behavioral phase of this study, including all radio telemetry work, was conducted on the Santa Rita Experimental Range (SRER) and in its immediate vicinity. The area, located about 30 miles (48 km.) south of Tucson (see Fig. 5, p. 22), is maintained as a research facility by the U.S. Forest Service, and general accounts of the tract were provided by U.S. Department of Agriculture (1952) and Martin and Reynolds (1973).

The study area slopes from the foothills of the Santa Rita Mountains on the east down to the vicinity of the Santa Cruz River on the west, with the elevation dropping from over 4,600 feet (1400 m.) to less than 2,900 feet (885 m.) over a distance of 9 miles (14.5 km.). Roughly 80 square miles (20,720 ha.) comprise the SRER.

Climate is dry and mild. Precipitation varies slightly with elevation, but the overall average is about 14 inches (35.6 cm.) per year.

The SRER can be classified as mesquite-grassland. The dominant shrub is mesquite (*Prosopis juliflora*), but several chollas (*Opuntia spp.*), prickly pear (*O. engelmanni*), catclaw (*Acacia greggi*), and ocotillo (*Fouquieria splendens*) are common. Saguaro (*Carnegiea gigantea*) is less common. Along the western edge of the area some nearly pure stands of creosote bush (Larrea divaricata) exist. Occurrence of grasses varies with elevation, grass cover being more prevalent at the higher levels. Common species include cottontop (Trichachne californica), bush muhly (Muhlenbergia porteri), and a number of three awns (Aristida spp.), gramas (Bouteloua spp.), and lovegrasses (Eragrostis spp.). A variety of forbs, notably Astragalus spp., Lupinus spp., and numerous mustards, among others, tend to be more seasonal in occurrence.

Changes in vegetative cover, particularly that of grasses and forbs, can be striking from the dry season (April-June) to the wet season (July-September), and occasionally from one year to the next.

The SRER was divided into over 20 fenced pastures upon which two private cattle operations ran stock in regulated grazing regimes. Both were cow-calf operations. Because of these, water was available from stock tanks which were regularly spaced across the range.

Other occurrences and operations of interest on the SRER during this study included aerial spraying and other methods of mesquite control, which were being tested on a portion of the range. Road improvement, involving extensive bulldozing and grading, was accomplished during the spring of 1973. A number of small fires, probably resulting from vandalism, broke out in the summer of 1973. A succession of other range, entomology, and small animal studies were constantly in progress. Legal hunting seasons for deer (Odocoileus hemionus) and javelina (Tayassu tajacu) were held in September and February, respectively, each year. Though the range was otherwise posted against public access, varmint hunting occurred seasonally and other forms of recreation occurred throughout the year.

Live Trapping and Handling of Coyotes

Steel traps were used to capture coyotes alive. An assortment of number 3 and 4 double long-spring traps were available for this purpose. To minimize injury to animals caught, each jaw was wrapped with a 4 x 8 inch (10 x 20 cm.) piece of burlap which was then secured to the jaw at 4 points with thin wire. The burlap had to be replaced often, as captured coyotes chewed and tore it off. However, burlap appeared to be the best material for this purpose. A light weight canvas was also tried, but provided a smooth surface which allowed captured coyotes to pull free. An appropriate length of heavy duty common door spring was attached across a loop of the trap chain in such a manner that the fully expanded spring was parallel to the chain; this prevented tugging directly against the chain. Traps were old and generally had relatively weak springs. In those cases where trap springs were strong, the jaws were offset to prevent their complete closure when the trap was snapped. Finally a tranquilizer tab was employed as described by Balser (1965) to sedate captured animals. Diazepam was the drug used in the tabs. Figure 1 illustrates a steel trap modified for capturing coyotes alive.

Traps were placed using techniques described by Young (1936), Henderson (1972), and Wade (1973). All sets were made in sandy washes employing both bait and scent techniques. When set, traps were checked each morning. Captured coyotes were held with a manually operated noose at the end of a 6 foot (1.8 m.) length of 1/2 inch (1.3 cm.)

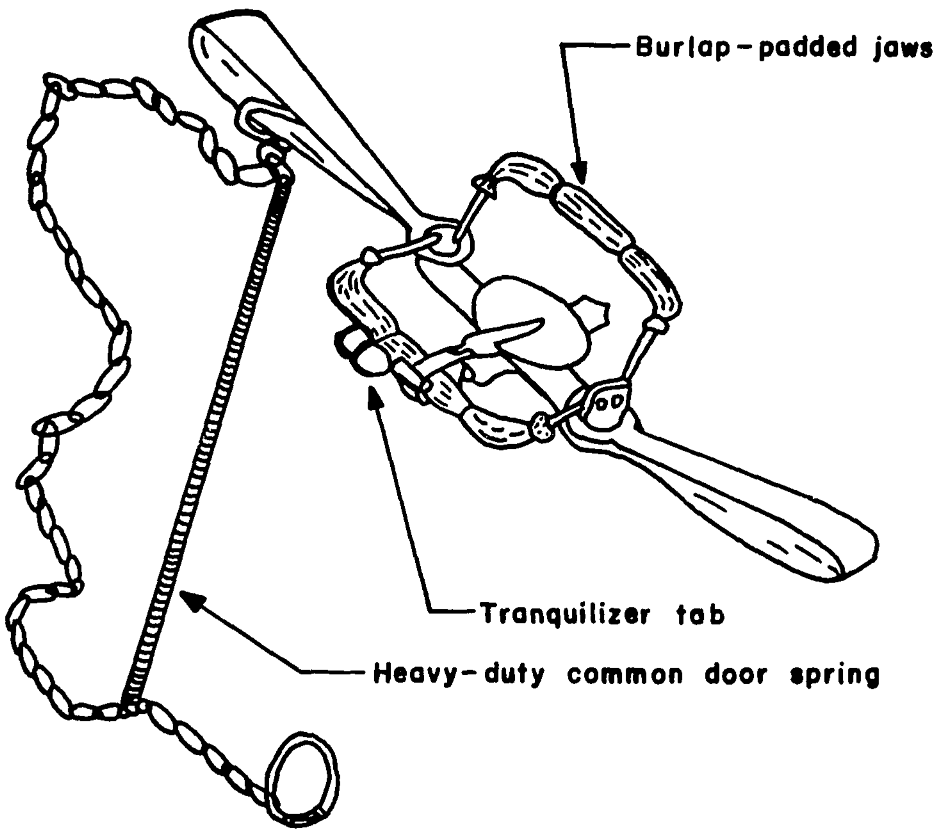


Figure 1. Steel trap modified for capturing coyotes alive.

diameter pipe, muzzled, hobbled, removed from the trap, and carried to a holding cage. Trap wounds were washed and topical medication applied in the field. The majority of animals were examined by a veterinarian and treated as necessary before release.

All released coyotes were tagged with a numbered aluminum small animal ear tag (Best Yet Aluminum Ear Tags, Aluminum Marker Works, Beaver Falls, Pa.) placed along the lower leading edge of the auricle. Some of these animals were also marked with different combinations of colored patches made by using Analin dye (American Cyanamid Co., Princeton, N.J.) as suggested by Day (1973) to produce red hair, and dilute picric acid to produce yellow hair. Dyes were applied with a comb.

Ages of live coyotes were estimated by means of incisor wear, utilizing a technique presented by Gier (1968).

Telemetry Equipment

Transmitting Gear. A dozen transmitters were constructed using the basic circuit design of Beaty (1971). The circuit incorporated a crystal-controlled oscillator, an amplifier stage, and a frequency doubler to produce radio signals in the 148 Mhz. range (see Fig. 2). Once operating satisfactorily transmitters were cast in a resin potting compound and secured to a collar of one inch (2.5 cm.) wide nylon webbing. Two types of transmitting antennas were employed. A 9 inch (23 cm.) whip antenna was utilized on half the units, while a log-spiral antenna in use by the Arizona Game and Fish Department was employed on the remainder. Once transmitter, antenna, and battery were

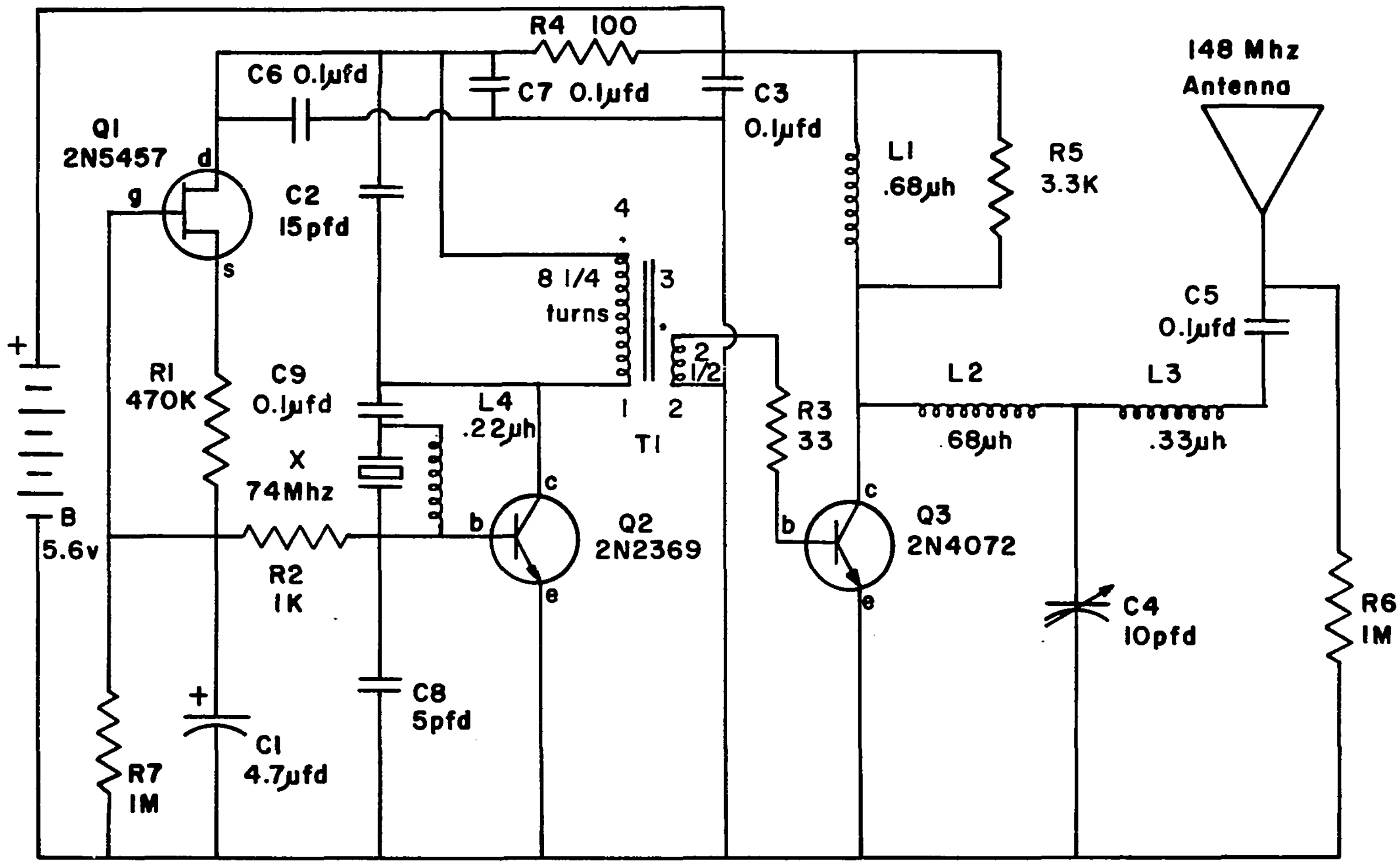


Figure 2. Schematic diagram of 148 Mhz transmitter utilized for coyote study. -- Adapted from Beaty, personal communication 1971.

in place, these components were sealed to the collar with a protective fiberglass covering. Two leads were left exposed, and these were connected to complete the circuitry just before the units were placed on coyotes. A plastic tag requesting return and bearing appropriate information was also attached to the collar. Completed radio collars weighed approximately a half pound (180 to 230 g.). The 2 types are illustrated in Figure 3.

All transmitter assemblies were field tested before use. A minimum acceptable range at which a signal could be detected was set at one mile (1.6 km.); maximum ranges of over 2 miles (3.2 km.) were obtained with some units. However, such ranges were seldom attained once units were placed on coyotes, for then transmitters were closer to the ground and the radio signal more attenuated by vegetation and terrain.

Components and materials were selected to minimize weight of the transmitter collars, yet insure satisfactory operation. Brander and Cochran (1969) suggested that the entire transmitter package should be less than 6% of the animal's body weight, so as to least interfere with normal behavior. To provide a wide margin of safety in this respect, juvenile and yearling coyotes were not radio collared. Burt (1943) pointed out that adolescent animals have not yet established home ranges at any rate, so their exclusion was desirable.

All coyotes fitted with a radio collar were also given a commercial flea collar and dusted for ectoparasites. I felt that these measures would reduce mechanical abuse of the collars resulting from

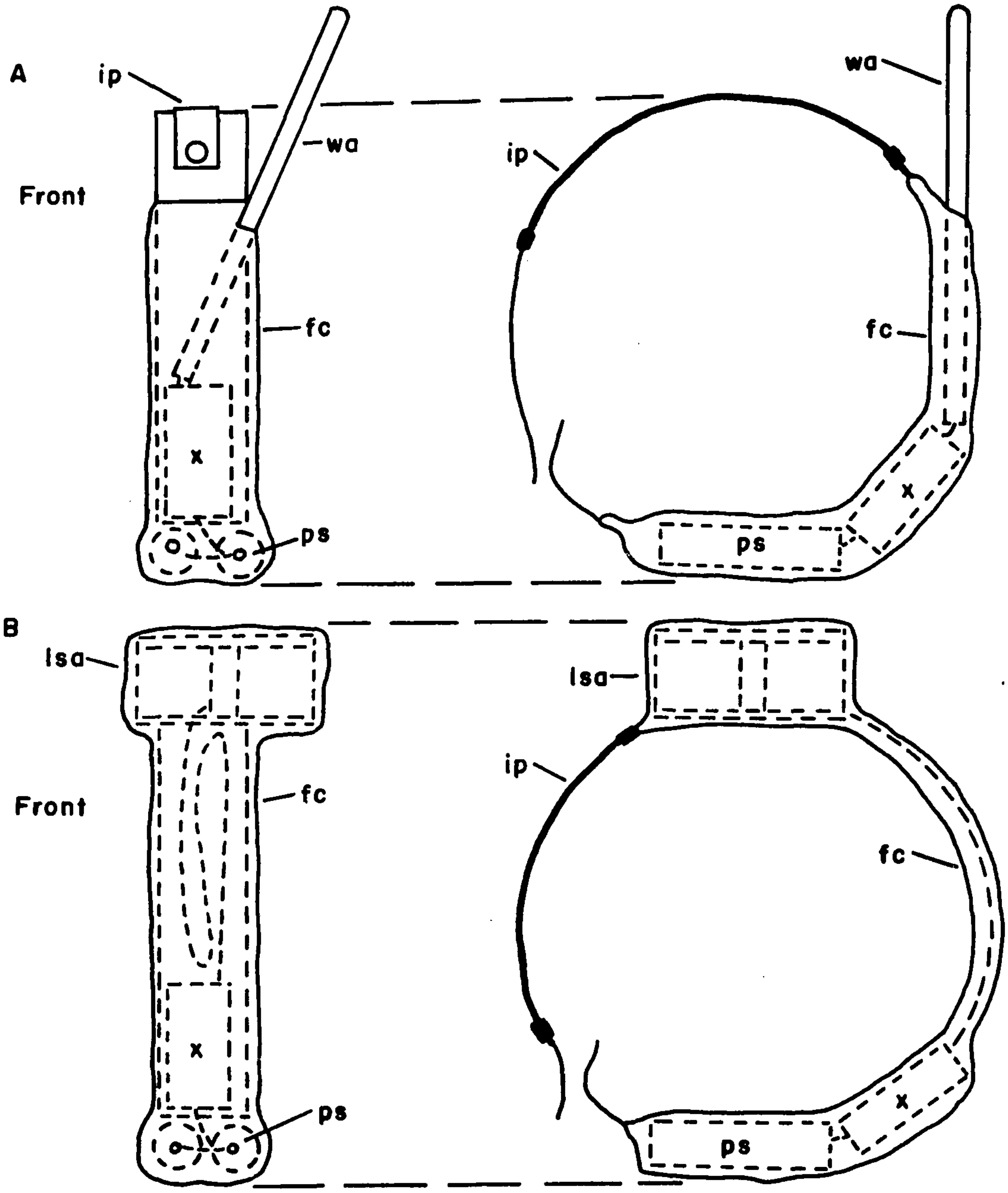


Figure 3. Radio-collar construction. -- A, with whip antenna; and B, with log-spiral antenna. Major components: ps=power supply; x=transmitter; wa=whip antenna; lsa=log-spiral antenna; ip=information plate; fc=fiberglass casing.

scratching to alleviate irritation beneath the collar where ectoparasites were likely to accumulate.

Receiving Gear. A Sharp CBT-55 receiver modified by Beaty was used to track instrumented coyotes. This unit had 5 channels tuned to frequencies of 148.5, 148.6, 148.7, 148.8, and 148.9 Mhz.

A 3-element,2-meter yagi (Hy-Gain Model 23, Hy-Gain Electronics Corp., Lincoln, NB.) trimmed for reception at 148 Mhz. was the basic receiving antenna. Initially this antenna was hand held while radio checks were made at intervals along roads or as less accessible areas were traversed on foot. As the study progressed, however, this procedure proved inefficient and a better system was devised. Brackets made of one inch (2.5 cm.) wide angle iron, a 30 inch (0.76 m.) x 1¼ inch (3.2 cm.) base and an 8 foot (2.4 m.) x 3/4 inch (1.9 cm.) mast made of galvanized pipe, and a modified car-top carrier were assembled into a workable mobile antenna support. The brackets and base were bolted to the side of the vehicle assigned to the project and the supporting frame clamped onto the vehicle roof so that the antenna mast could be set up and disassembled with relative ease during field operations. The entire antenna assembly is illustrated in Figure 4. The mast was used to support either a single yagi or, for improved directivity, horizontally stacked yagis 10 feet (3 m.) above ground level. When stacked, yagis were separated by one wavelength (80 inches or 2 m.) on a beam of ½ inch (1.3 cm.) pipe. The antenna array was set perpendicular to the long axis of the vehicle as it was moved slowly along, thus providing a continuous scan along one side of the road. Because

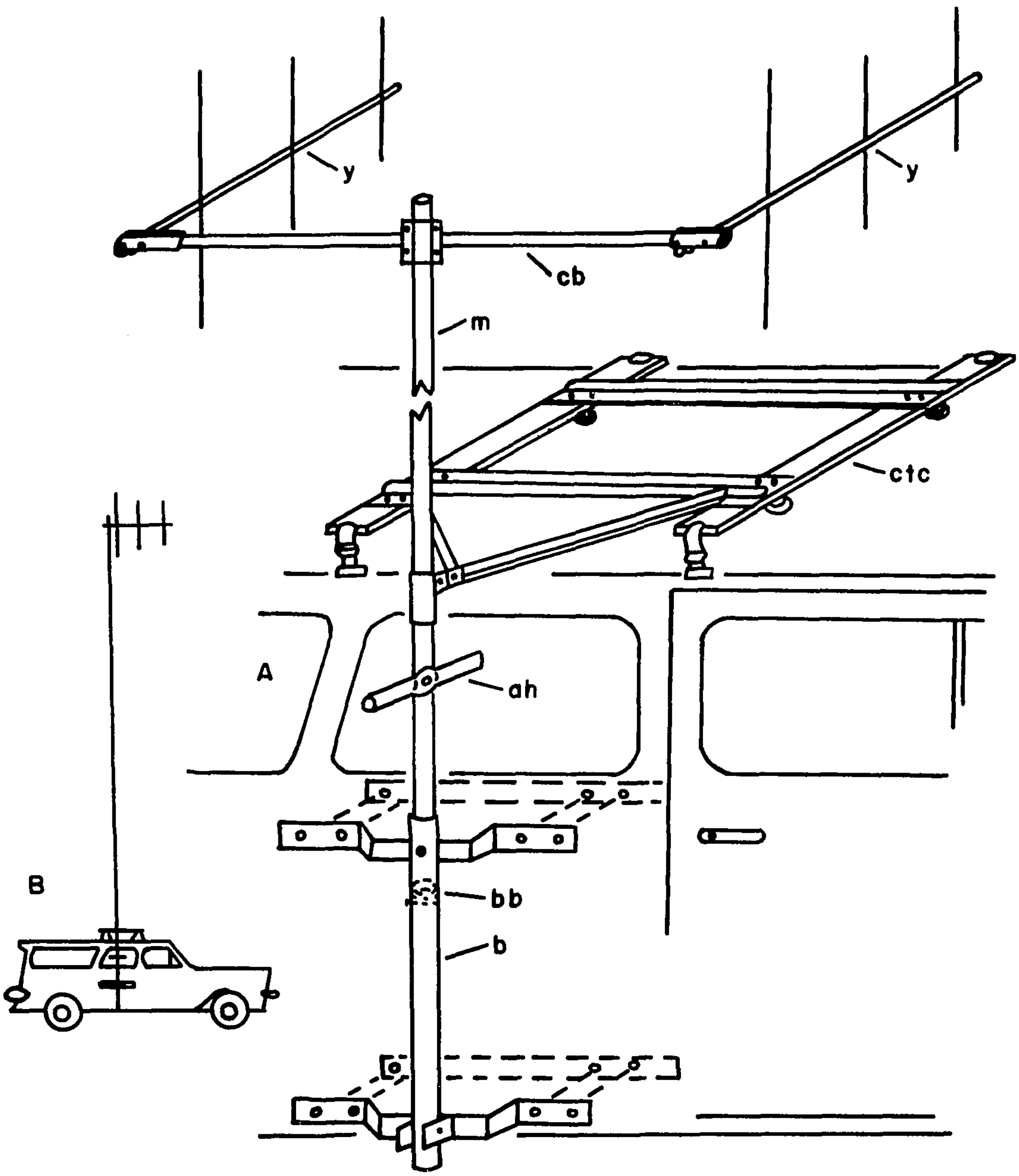


Figure 4. Receiving antenna system. -- A, mast with stacked yagis; and B, tower with single yagi. Major components: bb=ball bearings; ah=alignment handle; y=yagi; b=base; m=mast; cb=cross beam; ctc=car top carrier (modified).

of the natural east-to-west slope of the study area the vehicle could be driven to the higher eastern edge and allowed to coast downhill, thereby eliminating static produced in the receiver by the running vehicle engine. When a signal was encountered the vehicle was stopped, the antenna rotated to give maximum signal strength, and a bearing taken with a hand held compass (Silva 15T, Silva Inc., LaPorte, IN.). Fixes were obtained by triangulation.

While the accuracy of the system was not precisely measured, it was apparent from field testing for signal range that bearings taken to the transmitters were accurate. During subsequent field work collared coyotes were regularly located by following a bearing to the transmitter.

When the vehicle was stationary, a set of 3 telescoping lengths of aluminum tubing could be inserted into the mast to form a tower 28 feet (8.5 m.) tall. This extended mast supported a single yagi. Results suggested that use of the tower increased the detectable range of transmitters by several hundred yards (m.). It could be used only while the level vehicle remained stationary, and its use under breezy conditions would have required addition of guy lines. The tower is illustrated in Figure 4B.

Radio Tracking Procedure

The procedure used for locating and monitoring radio tagged coyotes evolved during the field study, and resulted from consideration of research objectives, effective range of the transmitted signal, and reaction of tagged coyotes to the observer. Since the primary concern of the field study was to estimate home range size,it was desirable to obtain as many locations as possible for each instrumented coyote. Field time was spent primarily in searching for these animals. Only one frequency could be monitored at a time; however, the vehicle was often stopped at advantageous points and a check made for other frequencies as applicable. When an animal was located its position was determined by taking bearings to the transmitter from different locations.

Coyote activity was monitored by parking the vehicle and noting changes in signal characteristics and direction. Numerous fixes were not taken while observing activity since this would have involved moving the vehicle back and forth, a procedure which apparently affected the behavior of some coyotes. Good fixes were obtained at least at the beginning and end of prolonged monitoring periods.

Particularly during the later months of field work when several coyotes were instrumented at the same time, monitoring of activity was minimized and most of the time was spent searching. When a signal was detected, the location of the instrumented coyote was established and then the search phase resumed for other instrumented coyotes.

An effort was made to take all bearings from locations readily identifiable on a map, such as surveyed corners, road junctions, intersections with fences, and so on. When this was not possible, distances to such locations were measured using the vehicle's odometer. Magnetic bearings had to be adjusted for 13 degrees of declination present at the study area.

Mapping Home Ranges

Home range, for purposes of this report, was defined as the apparent area occupied by a radio-tagged coyote during the period that it was periodically located. All reliable location information was used to delineate home ranges, including capture sites, radio fixes, and sightings. Radio fixes were defined by the intersection of two or more bearings to the transmitter obtained from different locations. These were plotted as points on a map.

Area of home range was estimated using two different methods. The minimum home range method illustrated by Mohr (1947) involved connecting outermost location points to form a polygon. Area was measured with a planimeter (KE No. 62 0000, Keuffel and Esser Co., Morristown, N.J.). The second method, described by Gipson and Sealander (1972), involved drawing an ellipse of dimensions and oriented as determined by the spread of location points, and centered at the geometric center of the points. In this case the area was readily calculated using the dimensions of the ellipse. The first method tends to underestimate home range, as noted by Hayne (1949) and Stickel (1954), while the second probably overestimates it; the area of the true home range may be intermediate. Both methods are illustrated in the home range figures for the various coyotes. Since, according to Tester and Siniff (1965), the geometric center of points has no particular significance from the standpoint of the animal's behavior, in the home range diagrams that follow the ellipse has been shifted so as to encompass the maximum number of points. It was felt that this procedure more accurately reflected the position of home ranges on the map.

Eliciting Vocalizations

A mechanical siren powered by an electric motor and operated from the study vehicle's electrical system was used at irregular intervals in an attempt to stimulate coyote howling. A survey route was established through the study area with 10 stops at one mile (1.6 km.) interspaces. The siren was sounded at each stop three times with a short waiting period between each blast. This technique was used along the survey route 17 times during the study. While results were probably inconclusive from the standpoint of censusing, some useful information on coyote behavior was gained.

Varmint Calling

When time permitted during field operations a predator call (Circe Calls, Goodyear, AZ.) was used to attract coyotes. The technique used has been described by Popowski (1971), Henderson (1973), and others. It was hoped some sightings of marked coyotes would result. Efforts frequently resulted in response by coyotes. Though no sightings of marked coyotes resulted, some meaningful behavioral information accrued.

Coyote Population Structure

Obtaining Specimens

The age and sex structure of the coyote population of southern Arizona was estimated from a large sample of carcasses, skulls, and lower jaws representing the entire area.

To obtain coyote specimens the assistance of the Division of Wildlife Services (DWS) of the Bureau of Sport Fisheries and Wildlife (presently the Animal Damage Control Division of the Fish and Wildlife Service), U.S. Department of Interior, was solicited. DWS field personnel were responsible for controlling coyote numbers in response to various complaints. As a matter of convenience to them, field agents were asked to collect only that portion of the lower jaw containing the canine teeth from coyotes killed during control activities. A small number of entire carcasses were also donated to the project as circumstances allowed. Tags were supplied to field personnel upon which they were asked to record date of kill, sex, general locality, and county of origin for each coyote.

Specimens were also obtained from several other sources. The Tucson Varmint Callers, a local hunting club, was asked to participate, and responded by bringing in entire carcasses and a smaller number of heads and jaws. Arizona Game and Fish Department personnel, the game management unit for the U.S. Army at Fort Huachuca, ranchers, trappers, and students also provided some specimens. Road-killed coyotes were retrieved when reported or when encountered during field activities.

Overall 384 specimens were collected from October, 1970, through June, 1973, including 67 in 1970, 218 in 1971, 81 in 1972, and 18 in 1973. The geographical source of specimens is shown in Figure 5.

Aging Specimens

The number of cementum layers appearing in canine teeth was the basis for determining the age of specimens. This procedure had advantages over techniques employed by Gier (1968) and Rogers (1965), chief of which was the ability to detect the older age classes. The

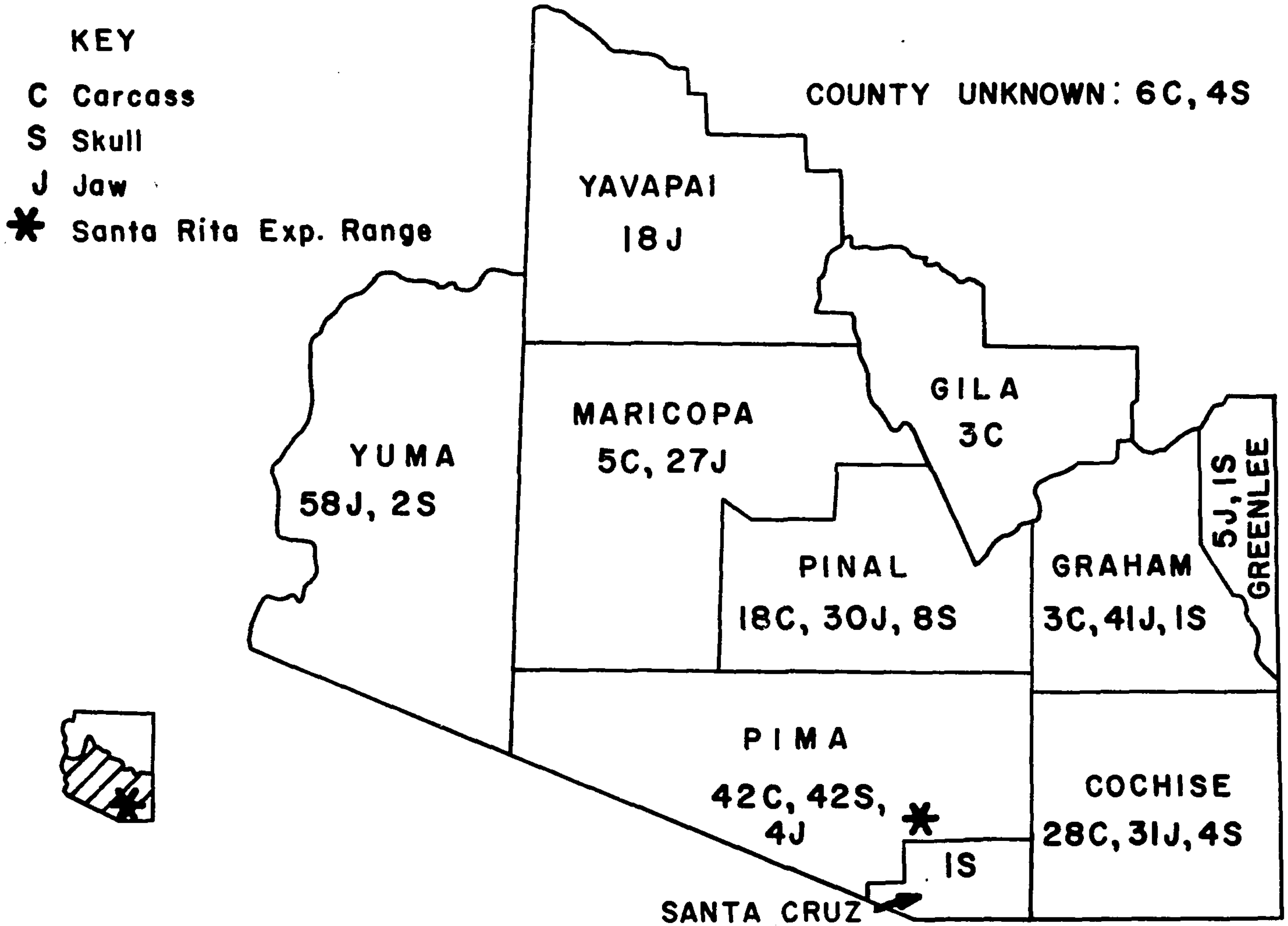


Figure 5. Origin of coyote specimens by county.

general use of annuli in teeth for aging purposes was discussed by Klevezal and Kleinenberg (1967). With modifications, the technique described by Linhart and Knowlton (1967) was employed. A control sample of known-age specimens, as cautioned by Allen and Kohn (1976), was unavailable from southern Arizona to verify criteria for assignment of age classes.

One canine tooth was extracted from the lower jaw of each specimen. When the tooth could not be readily pulled,the mandible was boiled in water until the tooth loosened. After extraction the tooth was cleaned and stored in a small vial of 10 percent formalin solution. When a number of teeth were accumulated they were arranged in a flexible plastic ice cube tray and embedded in catalyzed resin as suggested by Erickson and Seliger (1969). After the resin had set for several days about 8 cross sections of roughly 35 to 50 microns in thickness were cut from the root of each tooth using a high speed bone sectioning saw (Gillings-Hamco Thin Sectioning Machine, Brownwill Scientific Co., Rochester, N.Y.). Sections were washed with a commercial detergent, rinsed with water, and decalcified by soaking in a solution of one part formalin, 5 parts formic acid, and 20 parts water. After rinsing thoroughly in water the sections were stained by immersion in hematoxylin stain (Humason 1967:137) for 20 minutes. This was followed by another thorough rinse. Subsequently the sections were dehydrated and prepared for mounting by a series of 70, 85, 95, and 100 percent ethyl alcohol baths, respectively, and then by soaking in xylene. The sections were finally mounted in Permount® (Fisher Scientific Co., Fair Lawn, N.J.) on glass slides.

Cementum annuli were counted with the aid of a compound microscope at a magnification of 100 power. A series of specimens were read at each sitting and the results recorded. After an interval ranging from a few weeks to several months the same slides were again studied. In this way each specimen was reviewed at least three times, and if there was a discrepancy in readings for any specimen it was resolved if possible by a fourth count. Because of variance in annuli counts 40 teeth were sectioned, stained, and mounted a second time in an effort to obtain better defined cementum layers in the sections. Four specimens were eventually discarded because annuli were not clearly discernible.

Sexing Specimens

When entire carcasses were available I classified the specimen as to sex. In those cases where I was unable to see the carcass, I depended upon the sex information provided by the contributor.

Statistical Procedures

Age class distribution was first tabulated for the entire sample, and then subdivided regardless of other criteria according to year of death, month of death, sex of specimen, cause of death, and county of origin. In each tabulation the maximum number of specimens for which relevant information was known was used. The composite age class distribution was compared to similar data presented by other researchers for other locations.

Life tables were constructed from composite age distribution data for the entire sample and for each sex using procedures and formuli presented by Quick (1963). Technically life tables should be derived from figures which accurately reflect age distribution within a stable population. Pooled data suggested a rather stable general coyote population across southern Arizona, but further analysis indicated that age distributions varied between years, locations, and so on. Nonetheless, interpretation of life tables yielded some useful general concepts.

Numerous statistical tests were employed to aid in interpretation of data. Age distributions representing various subsamples were compared by means of chi-square contingency tables of appropriate size, as described by Steel and Torrie (1960:366). Care was taken to maintain fewer than 20 percent of the chi-square cells with an expected value of less than 5 and no cells with an expected value of less than one (Siegel 1956:178).

Sex ratio was tabulated for the entire sample and for subsamples defined,regardless of other criteria,by year of death, month of death, age class, cause of death, and county of origin. The composite sex ratio was compared with similar data presented by other researchers for other locations.

Two distinct statistical procedures were applied to each category of sex specific data. Chi-square contingency tables were again employed to compare sex ratios between the various categories. A simpler 1 x 2 chi-square test was applied to determine the significance of variation from an expected even sex ratio within each category; a value of 5 per cell was considered minimal for a legitimate test (Siegel 1956:46). Because corrections for continuity lowered chi-square values,they were applied only when results at least approached significance.

As was standard procedure throughout this report, results of statistical testing were considered non-significant (n.s.) when the probability of chance occurrence exceeded 10 percent, approaching significance (a.s.) when the probability level ranged from 5 to 10 percent, significant (*) when the probability level ranged from one to 5 percent, and highly significant (**) when the probability of chance occurrence was below one percent.

Coyote Reproductive Analysis

Reproductive information was obtained by removing and examining sex organs from 42 coyote carcasses. These materials were stored in 10 percent formalin solution until processed.

Reproductive organs from 22 males were checked for the presence of spermatozoa. Hamlett (1938) noted, "As it is only while spermatozoa are present in the epididymis that the male is fertile, the limits of the breeding season can be determined by ascertaining at what time of year the epididymis contains sperm." A slit was made through the epididymis and teste with a razor blade, after which the tissue was spread and pressed against a glass microscope slide to make a smear. While large masses of spermatozoa could be detected at a magnification of 100 power, positive identification was made at 450 power.

Ovaries and uteri were collected from 20 females. Uteri were cut open over their entire lengths and examined for evidence of pregnancy. Ovaries were sliced at intervals lengthwise with a razor blade and examined macroscopically for corpora lutea.

Sections taken from some testes and some ovaries were stained and mounted permanently on glass slides. Since most carcasses were contributed by hunters or retrieved from roadways, the animals had been dead and unrefrigerated for hours before they were processed. Autolysis, particularly within ovaries, presented a problem in interpreting sections microscopically.

Coyote Parasites and Diseases

Collecting and Identifying Parasites

Entire coyote carcasses obtained from a variety of sources in conjunction with other aspects of this study were utilized in obtaining parasitological information for coyotes in southern Arizona.

Each carcass from which the hide had not been removed was examined for ectoparasites. These were collected as encountered and preserved in a 70 percent alcohol solution. When time permitted, a representative sample was cleared by soaking in a 2 percent potassium hydroxide solution, treated, and permanently mounted on microscope slides to facilitate identification. Remaining untreated specimens were identified as wet mounts.

Because carcasses obtained for study had generally been dead for some time, it was doubtful that they yielded a true index of ectoparasite incidence. As a check, coyotes live trapped for the behavioral portion of this study were examined for ectoparasites. When encountered, these were collected and treated as above.

Identification of fleas was made by reference to the key provided by Hubbard (1947). Other useful texts included those of

Cox (1950), I. Fox (1940), and Holland (1949). Lice were identified with the aid of descriptions provided by Harrison and Johnston (1916) and Werneck and Thompson (1940). Ticks were identified by reference to the Agricultural Research Service's Manual on Livestock Ticks (1965).

After examining a number of carcasses for endoparasites a standardized procedure evolved. The viscera of each animal was extracted, including the esophagus and trachea and all organs through the rectum. All organs were examined critically for helminths. The trachea was opened lengthwise, as were the bronchi and bronchioles down into the lungs. The lungs were palpated, sliced at intervals, and inspected macroscopically for abnormalities. The liver and spleen were also palpated, cut into pieces, and examined with the naked eye. The kidneys were cut open to expose the lumen; the urinary bladder was opened and examined. The heart was cut open to expose all chambers. The stomach was opened and the stomach wall and contents were inspected; stomach contents received special handling as outlined in the Coyote Food Habits section of this report. The intestine from the pyloric sphincter through the rectum was stripped from the mesentery and the resulting free tube was flushed with tap water. Contents were caught in gallon jars. After these contents were allowed to settle for some time, excess liquid and debris were poured off, and the contents washed and rewashed by adding tap water, agitating, allowing to settle, and decanting. Eventually the remaining material consisted of undigested food fragments and helminths. The contrast provided by pouring this material into a black tray allowed collection of parasites with relative ease. With the exception of the first several specimens, the intestine was then opened for its entire length and inspected for parasites embedded in the mucosa, and for other abnormalities. The caecum was also opened and critically examined.

Cestodes were placed in physiological saline (Humason 1972:533) and refrigerated for several hours to allow them to die, then preserved in a solution of acetic acid, formalin, ethyl alcohol, glycerin, and water. A representative sample from each positive coyote was appropriately treated, stained, and permanently mounted on microscope slides according to the instructions of Dewhirst (personal communication 1971). Scolices were sliced and mounted in such a manner that the rostellum and crown of hooks could be viewed from above; this facilitated counting and measuring of hooks. Mature and gravid proglottids were stained and mounted to allow examination of uteri and other internal structures useful in taxonomy. Having established which species were likely to be encountered, all remaining tapeworms from all coyotes were identified by counting and measuring hooks on unstained scolices viewed as wet mounts.

Nematodes were collected and preserved in a 10 percent formalin solution. A representative sample of each species was soaked in lactophenol (Humason 1972:144) to clear the worms and allow examination of internal structures. All were prepared and examined as temporary wet mounts. Acanthocephalans were generally handled in the same way.

To detect possible trichinosis, a portion of the diaphragm of a number of coyotes was collected. These tissue samples from 6 coyotes were digested in a pepsin-hydrochloric acid solution to determine if <u>Trichinella</u> larvae were present. The remaining tissue samples were pressed between two heavy glass plates and viewed microscopically to detect any encysted larvae.

Endoparasites were identified by reference to general texts, and then a more detailed search of the literature was made as needed. For this study The Zoology of Tapeworms (Wardle and McLeod 1952) served as the basic reference for cestodes, Nematode Parasites of Domestic Animals and of Man (Levine 1968) served the same purpose with regard to nematodes, and Acanthocephala of North American Mammals (Van Cleave 1953) served as the authority for identifying acanthocephalans. Other useful texts included those of Abuladze (1964), Lapage (1962), Petrochenko (1958), Soulsby (1968), and Yamaguti (1961). Keys such as those presented by Erickson (1944) tended to impart a false sense of confidence to parasite identification, when in fact possibilities other than those presented in the key existed and had to be investigated.

Statistical Procedures

A statistical analysis was conducted using data from the six most common species of parasites. Two parasite-host relationships were tested, intensity and incidence of infection. Numbers of parasites per host measured intensity, while proportion of infected animals measured incidence of parasitism. Intensity of infection was tested for each of the six species as well as for all intestinal helminths collectively. Incidence was tested for each of the six species only. No significant differences would have been detected by testing the proportion of animals infected with the collective intestinal helminths, since few animals were found to be free of these parasites.

Testing of these two parasite-host relationships was done for five different categories. These were age class, sex, year of death, season of death, and county of origin of the host coyote. Only two age classes were utilized: animals less than one year old, and animals over one year of age. Animals killed from May, 1970, through April, 1971, versus those killed from May, 1971, through April, 1972, supplied the two sets of data used for testing differences by year. Season and quarter of the year were equated for purposes of this analysis. Data from three counties, Cochise, Pima, and Pinal, were used to test for geographical variation in these parasite-host relationships.

The Mann and Whitney 2-sample ranked test (Steel and Torrie 1960:405) was used to test for differences in numbers of parasites per coyote by age class, by sex, and by year of death, while the Kruskal and Wallis ranked test (Steel and Torrie 1960:406) was used to test differences in intensity of infection by season and by county. A 2 x 2 chi-square test (Steel and Torrie 1960:371) was used to test differences in incidence of infection for all five categories.

Detecting Diseases

While examining carcasses for parasites a special effort was made to note any gross pathology which might indicate disease. During field operations behavior of free ranging coyotes was observed in an effort to detect any abnormal behavior which might be indicative of morbidity. The Department of Veterinary Science, University of Arizona, provided valuable assistance by studying suspicious tissue samples, running serology tests, examining water samples, and, in one instance, autopsying a coyote which had been shot after exhibiting symptoms suggestive of severe illness. A series of coyote heads were submitted to the Arizona State Department of Health, Laboratory Division, in Phoenix, where fluorescent antibody tests for rabies were performed on them.

Coyote Food Habits

Analyzing Stomach Contents

Stomachs from coyote carcasses obtained from various sources, primarily for other phases of this project,were utilized to gain a broad picture of the food habits of coyotes in southern Arizona. Occasional carcasses were stored temporarily in a walk-in freezer until they could be processed. Stomachs were generally examined the same day that they were removed from carcasses. Each was cut open lengthwise and the contents dumped into a large, fine-mesh seive. Materials adhering to the stomach wall were washed into the seive and then the entire contents gently rinsed with tap water.

Following the recommendations of Martin and Korschgen (1963) that at least two expressions of quantitative data be presented when reporting food habits information, items composing the contents of stomachs were recorded by frequency of occurrence and relative volume. The appearance of any item in a stomach, regardless of the number of individuals present, was considered a single occurrence. Relative volume was estimated in a simple 2-step process. First, the volume of the entire contents was scored from 1/10 to 10/10 of a specified maximum volume of roughly 2 quarts (2,000 ml.). A stomach containing a pint of material (about 500 ml.) would be scored 3/10, for example.

Second, the percentage of the total volume of the contents composed of each item was estimated. To aid in these estimations a 12 x 18 inch (30 x 45 cm.) plexiglass panel upon which a grid of one inch (2.5 cm.) squares had been etched in checkerboard fashion was employed as suggested by Dixon (1925). Estimates were made no closer than 5 percent. Materials composing less than 5 percent of the bulk of any stomach scored over 1/10, and all contents of stomachs scored less than 1/10 were recorded as present in trace amounts. The algebraic product of the figures obtained by the two steps was the relative volume for a particular food item. Relative volumes were then totaled by item for all stomachs and the sums used to compute the relative volume of each item for the composite sample. Decimal values resulting from this procedure should not be interpreted as an indicator of accuracy. I felt that this technique resulted in no gross errors, and that results correctly reflected volumetric relationships, while time consuming and tedious attempts to measure volume were bypassed.

Intestinal contents were not utilized, for digestion altered volumetric relationships and would have unduly complicated the analysis.

<u>Analyzing Scat Composition</u>

To obtain a better year-round picture of coyote food habits, scats or droppings were collected routinely during field operations on the SRER and in its immediate vicinity. These represented each month of the year beginning with September, 1971, through June, 1973.

Scats were gathered along roadways, dry washes, and cattle trails, and around earthen stock tanks. Only droppings judged to be fresh, that is, less than a few days old, were collected. Older droppings were cleared away from sites visited regularly. Weathering and the activity of dung beetles, particularly during the warmer months, tended to prevent erroneous collection of dated scats. Confusion of coyote scats with the droppings of bobcats (Lynx rufus), badgers (Taxidea taxus), javelina, and foxes (Urocyon and Vulpes) was a possibility. Coyotes were more common on the study area than any of these other species; foxes in particular were quite uncommon. Field signs were used as much as possible to identify scats. Tracks of coyotes along sandy washes and dusty roads were useful, as were scrape marks sometimes left on the ground by coyotes after scent marking. Stations where coyotes regularly defecated were located and these depositories were raided at intervals. The possibility that some droppings of other species were inadvertently collected was probably slight.

Each scat was placed in a plastic sandwich bag along with a bit of paper upon which was written an identifying number. Individual scats were then stored in large paper bags by month of collection. Climatic conditions generally insured that scats were dry when collected, but several which had not thoroughly dried developed saprophytic growths in storage and were subsequently discarded. All scats were analyzed during the period July through November, 1974.

Tabulations were made by frequency of occurrence and estimated weight of food items. Lockie (1959) found percentage weight of undigested matter was the most worthwhile means of presenting data obtained from fecal analyses. Each entire scat was weighed air dry. Then the scat was soaked in water to soften the contents and allow separation without damage to brittle components, such as dry hairs, insect wings and cuticle, leaves, and so on. The fecal mass was separated by type of item. At the outset all fractions were weighed to aid in estimations, but eventually this practice was followed only occasionally or when a scat with unusual composition was encountered. No greater than 5 percent accuracy was attempted. Items recorded in trace amounts composed less than 5 percent by weight of the organic content of a scat. Estimated weights were then tabulated by item for all scats, and the percentage composition for each item calculated from these totals. Again, resultant decimal values should not be considered as indicators of accuracy.

Identifying Remains

Identification of remains of food items was much easier from stomachs than from scats. I found that coyotes were not delicate feeders; rather they gulped food in large chunks,and smaller items such as mice and fruits were sometimes swallowed whole. Thus stomach contents were often identifiable as to species. While occasionally this was possible in scats, it seemed an unwarranted effort to attain this level of accuracy, since the main purpose of the scat analysis was to obtain a general picture of seasonal trends in coyote feeding habits.

Where only hair was found in a stomach, identification was limited to the categories of rodent or lagomorph, and deer, cow, coyote, or javelina. Hair keys provided by Adorjan and Kolenosky (1969), Mayer (1952), Spence (1963), and Stains (1958) were useful in identifying hairs in a general way, but the final criterion generally had to be comparison with hairs from known specimens. Porcupine quills were readily identifiable. A skull key presented by Glass (1964) was an asset in identifying teeth and skull fragments. A Field Guide to the Mammals (Burt and Grossenheider 1964) also proved useful in identifying mammalian remains. A collection of assorted hairs, teeth, bones, feet, and tails was gradually accumulated for comparative purposes. Other appropriate field guides were regularly consulted: that of Peterson (1961) served as an aid in identifying bird remains, that of Cochran and Goin (1970) served this purpose for reptilian remains, while that of Borror and White (1970) was useful for insect identification. Seeds and fruits were identified from the seed guide of Martin and Barkley (1961) and by comparison with a local seed collection. Often tentative identifications were confirmed by consulting with mammalogists, herpetologists, and entomologists at The University of Arizona.

Statistical Procedures

Coyote food habits based upon stomach analysis were compared for categories of coyotes differentiated by age class, sex, year and season (quarter) of death, and county of origin, regardless of other criteria, respectively. Major food groups considered for comparisons were larger mammal, smaller mammal, bird, invertebrate, and vegetable foods. Comparison of frequency of occurrence of major food categories was accomplished using a 2 x 2 chi-square test described by Steel and Torrie (1960:371). Due to the nature of the volumetric food habits data, nonparametric tests seemed appropriate for determining whether observed differences were significant. Statistical comparisons of relative volumes of major food categories representative of coyotes of different age class, sex, and year of collection were made by applying a Mann and Whitney ranked test (Steel and Torrie 1960:405). The large number of tie values resulting from stomachs containing none of a specific item necessitated applying a correction factor as presented by Siegel (1956:124). Comparisons of relative volumes for coyotes collected during different quarters of the year and in different counties were made by applying a Kruskal and Wallis ranked test (Steel and Torrie 1960:406) with appropriate correction for tied values.

Similarly tests of seasonal variation in frequency of occurrence of various items in scats employed a 2 x 2 chi-square test, and seasonal variations in relative weights of food items in scats were compared using the Kruskal and Wallis ranked test with correction for tied values.

RESULTS AND DISCUSSION

Coyote Behavior

Trapping Success

Coyotes were captured with relative ease on the study area. This was due to the high density of coyotes combined with good trapping conditions, including generally dry weather and an abundance of sandy washes,which were often used as travel ways by coyotes and which provided numerous trap sites. Only when I attempted to capture an animal in a specific location did I sometimes encounter difficulty, possibly because that area was not being intensively used by coyotes at the time.

The total trapping effort consisted of 210 set-nights. In trapper parlance, double-trap sets were used, and therefore two traps placed for a 24 hour period comprised one set-night. During this effort there were 81 detectable visits, often resulting in snapped traps. A total of 21 coyotes were captured, 3 additional coyotes were caught but escaped, and 6 non-target animals were captured. The average figure of 10 set-nights per coyote captured is quite low, but cannot be used as an index of coyote density, since sets were only made at selected locations and traps were removed when the desired number of suitable animals were captured. An effort was made to capture the minimum number of coyotes necessary to carry the available radio collars.

Pertinent information on the 21 captured coyotes is provided in Table 1.

Trauma sustained by coyotes in the trapping process ranged from no detectable injury to death. The degree of injury appeared to be directly related to the length of time the animals spent in a trap. Trapped coyotes chewed and tore away the burlap trap-jaw padding and, once this was removed, were subject to cuts where the jaws held them. Females, because they appeared to be more excitable, were more subject to injury and prone to self-mutilation. Of the 21 captured coyotes, 16 sustained relatively minor injuries, mostly cuts and swelling, while 5 suffered more serious injuries, including deep cuts with heavy bleeding, sprains and luxations with severe swelling, broken toes, and chewing of the trapped foot below the trap jaws. Three coyotes died as a result of the trapping process. These types of injuries are common to animals captured with steel traps, even when protective measures are taken, as reported by Payne, Jenkins and Provost (1966) and by Gipson and Sealander (1972). A better means of capturing coyotes alive would be highly desirable.

Radio Telemetry Success

Twelve coyotes were fitted with radio collars and released on the SRER during 1972 and 1973. Performance of the telemetry system was often less than optimal, but half of the instrumented animals were located regularly enough and over a long enough span of time to provide information on home ranges, while most of the animals provided at least some behavioral information. Duration of the tracking period,

Table 1. Data on coyotes trapped, marked, and released on the Santa Rita Experimental Range during 1972 and 1973.

No.	Sex	Est. Age (Yrs)	Date Captured (D-M-Yr)	Type of Set	Capture-Release Location	Date Released (D-M-Yr)	Last Contact (D-M-Yr)	Radio Freq. (Mhz)	Ear Tag No.	Dye Color
1	F	2	21- 6-72	Bait	NE¼,S36 T18SR14E	21- 6-72	21- 6-72	148.9	900	Yellow Red
2	M	1	22- 6-72	Bait	NE¼,S22 T18SR14E	23- 6-72	23- 6-72	None	899	Yellow
3	M	2	22- 6-72	Bait	NW¼,S21 T18SR14E	22- 6-72	22- 6-72	None	898	Yellow
4	M	4	22- 6-72	Scent	NE¼,S15 T18SR14E	Found Dead in Trap		None	None	None
5	M	4	10- 7-72	Bait	SW¼,S15 T18SR14E	11- 7-72	16- 7-72	148.8	897	Yellow
6	F	4	14- 7-72	Scent	SW¼,S21 T18SR14E	15- 7-72	15- 7-72	None	896	Yellow Red
7	M	2	11-11-72	Scent	SE¼,S23 T18SR14E	12-11-72	27-12-72	148.7	895	None
8	F	3	11-11-72	Bait	SW¼,S23 T18SR14E	12-11-72	17-12-72	148.9	894	None
9	M	2	13- 1-73	Bait	SE¼,S34 T18SR14E	14- 1-73	19- 2-73	148.8	893	Red
10	F	6	14- 1-73	Bait	NE¼,S6 T19SR15E	15- 1-73	7- 4-73	148.5	892	Yellow Red
11	F	6	28- 2-73	Scent	NE¼,S14 T18SR14E	1- 3-73	1- 3-73	None	891	Red

Table 1--Continued.

No.	Sex	Est. Age (Yrs)	Date Captured (D-M-Yr)	Type of Set	Capture-Release Location	Date Released (D-M-Yr)	Last Contact (D-M-Yr)	Radio Freq. (Mhz)	Ear Tag No.	Dye Color
12	M	4	4- 5-73	Bait	NE¼,S14 T18SR14E	6- 5-73	11- 5-73	148.5	889	None
13	F	1	6- 5-73	Scent	NW¼,S6 T19SR15E	Euthanized		None	887	None
14	M	3	6- 5-73	Scent	SE¼,S1 T19SR14E	9- 5-73	14- 6-73	148.6	888	None
15	F	1	12- 5-73	Bait	SE¼,S5 T19SR15E	14- 5-73	14- 5-73	None	886	Red
16	F	3	14- 5-73	Scent	SE¼,S23 T18SR14E	16- 5-73	26- 6-73	148.6	885	Yellow Red
17	F	2	21- 5-73	Scent	SE¼,S23 T18SR14E	22- 5-73	22- 5-73	148.7	884	Red
18	F	1	25- 5-73	Scent	NW¼,S8 T19SR15E	Died of Trap Injuries		None	None	None
19	M	2	29- 5-73	Bait	SE¼,S30 T18SR15E	30- 5-73	16- 6-73	148.7	883	Red
20	M	4	7- 6-73	Bait	NW¼,S23 T18SR14E	8- 6-73	9- 8-73	148.9	881	Red
21	M	1	7- 6-73	Bait	NE¼,S6 T19SR15E	8- 6-73	8- 6-73	None	882	Red

that time during which radio signals were detected and the instrumented animal located, ranged from a few hours to 82 days. Tracking periods for the 12 animals are shown in Figure 6.

Coyotes 1 and 17 were not relocated after the day of their release. Poor results were also obtained with coyotes 5, 12, and 19. Premature failure of the transmitters seemed the most probable cause of these results. Coyote 17 exhibited a high blood titer for leptospirosis, though the possibility of her death from the disease seemed slight (see Coyote Parasites and Diseases: Leptospirosis); also, the condition of this animal's mammae indicated that she had recently nursed pups. Coyote 12 was located on only 2 different days after his release. Together with the fact that these fixes were approximately 2-3/4 miles (4.4 km.) from his release site, a substantial distance when compared to typical movements of other instrumented coyotes on the study area, this suggested that he may have been a transient. Coyote 19 was relocated regularly for a period of about two weeks during which time the performance of his transmitter was poor.

Coyotes 5 and 8 provided another problem. The effective range of their transmitters diminished after their release, and often after radio contact was established they moved out of radio range into large tracts that were inaccessible by vehicle. Although some behavioral information was obtained, the extent of their wanderings could not be determined.

Coyotes 7 and 14 were both large adult males whose home ranges butted against the mountains to the east. Coyote 14 actually foraged

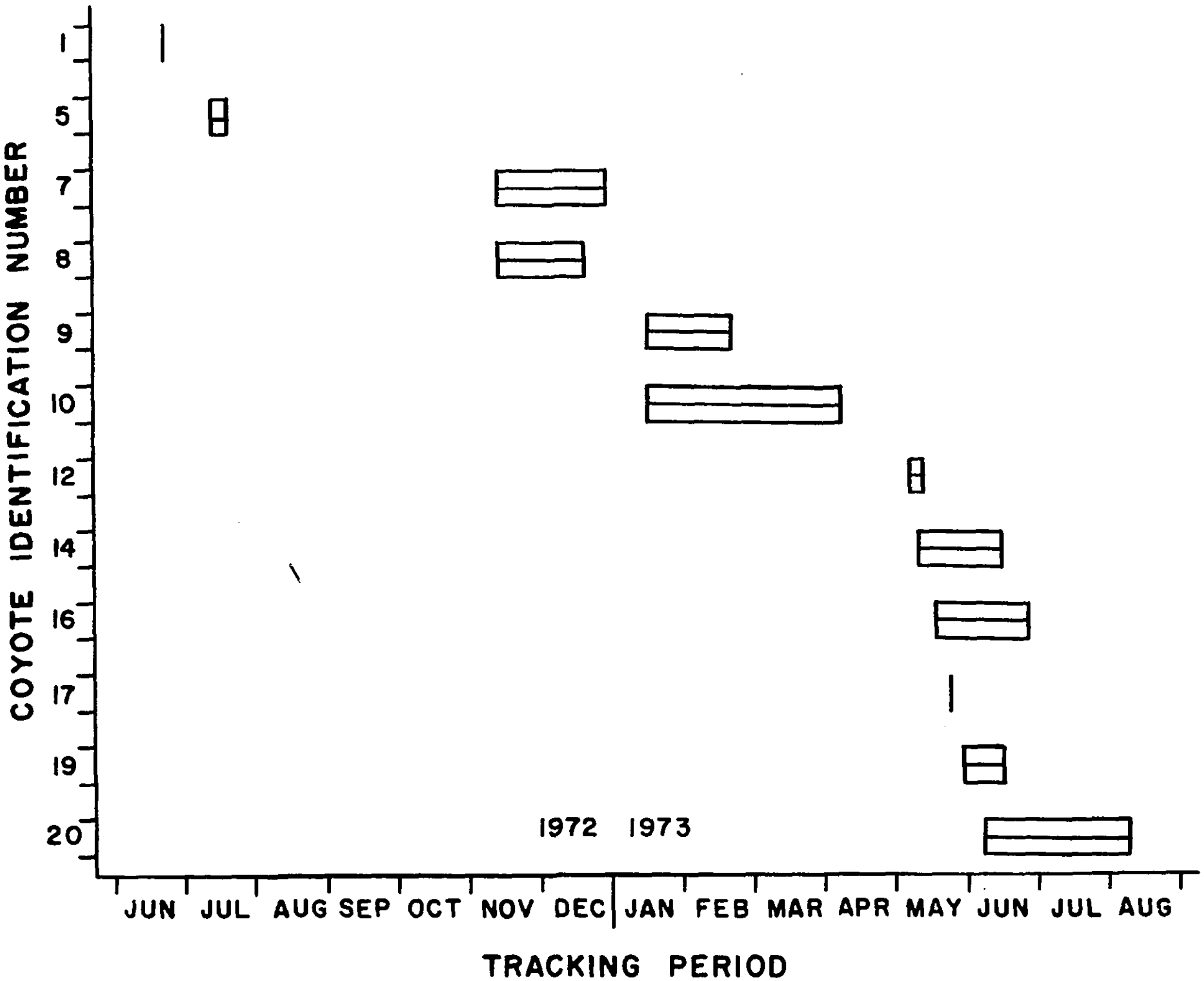


Figure 6. Periods during which the behavior of 12 individual coyotes was monitored by radio telemetry.

among the foothills, but was never located at elevations above roughly 4200 feet (1280 m.).

Apparent loners, coyotes 9 and 20 utilized smaller areas nearer the center of the SRER. Both animals had been injured in trapping.

Coyote 10 provided the best data of any of the instrumented animals. Her transmitter operated for nearly three months and she was located on virtually every visit to the SRER during that period. Often a member of a very vocal social group, her movements tended to be gradual and unhurried, except when attempting to avoid the observer.

In contrast to 10, coyote 16 may have been a loner, and traveled extensively within her home range. One movement of a minimum straight line distance of 4.0 miles (6.4 km.) between two fixes over 8½ hours was the maximum recorded for any coyote monitored.

Coyote 10 appeared to be in proestrous when released. However in the following weeks she did not exhibit any denning behavior, nor was the presence of pups at any particular location suggested by her actions. Similarly there was no indication that coyote 16 had produced a litter during the period that she was radio tracked.

Analysis of Coyote Home Range

Estimated Size of Home Range. Home range was defined as the apparent area occupied by an instrumented coyote during the period that telemetric data were obtained from it. Data from six of the radio-tagged animals was considered complete enough to provide an estimate of the size of their home range. Two means of obtaining estimates, the minimum and elliptical home range methods, are illustrated for each of the six coyotes in Figures 7 through 12. As can be seen from these diagrams, minimum home range tended to be conservative while elliptical home range probably overestimated the area used by an animal. As suggested by Burt (1943), the true home range was probably ameboid in shape.

The estimated areas obtained by the two methods are presented in Table 2. Using the minimum home range method, the average area occupied was 4.2 square miles (1090 ha.), with extremes ranging from 0.5 square miles (130 ha.) to 7.9 square miles (2055 ha.). Using the elliptical home range method all areas were somewhat larger, averaging 5.9 square miles (1538 ha.) with extremes ranging from 0.7 square miles (168 ha.) to 10.5 square miles (2714 ha.).

A number of other researchers and writers have estimated the size of coyote home ranges and, for purposes of comparison, some of these are presented in Table 3. There appeared to be much variation with geographical area. Indeed there was considerable variation among the estimates from coyote to coyote on the SRER. These variations are considered more fully in the following discussion.

Sources of Variation in Size of Home Range.

Sex of Coyote: It was apparent that females had larger home ranges than did males. The average minimum home range for female coyotes 10 and 16 was 7.2 square miles (1865 ha.), while average minimum home range for male coyotes 7, 9, 14, and 20 was 2.7 square miles (699 ha.). Statistically this difference was significant ($t=3.085$, $df.=4$, $0.05>P$). Even if the unusually small home range of coyote 20 was excluded from

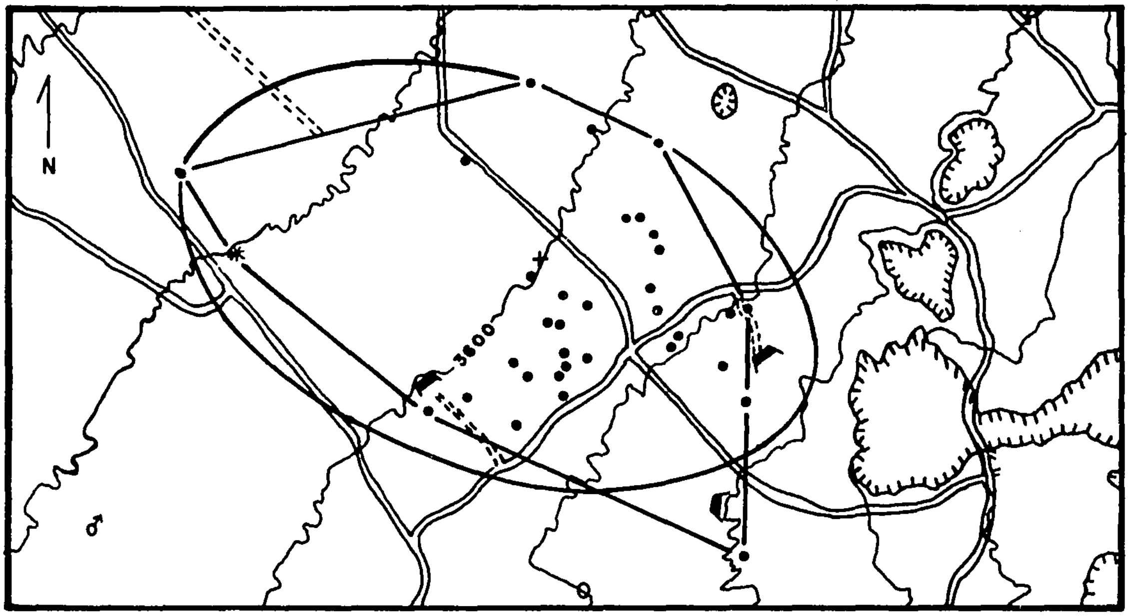
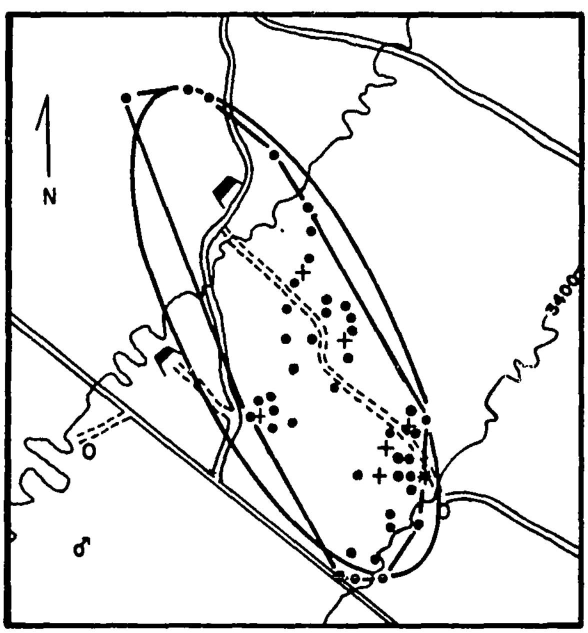


Figure 7. Minimum and elliptical home ranges of coyote 7. -- See Figure 8B for legend.



Legend

•	Radio fix
+	Sighting
✱	Capture site
—	Home range boundary
═	Primary road
⋮⋮	Jeep trail
〰	Contour line (contour interval, 200 feet)
	Hill
	Earthen stock tank
o	Metal stock tank
B	Scale: 1 inch = 1 mile

Figure 8. Minimum and elliptical home ranges of coyote 9. -- B, legend for Figures 7 through 12.

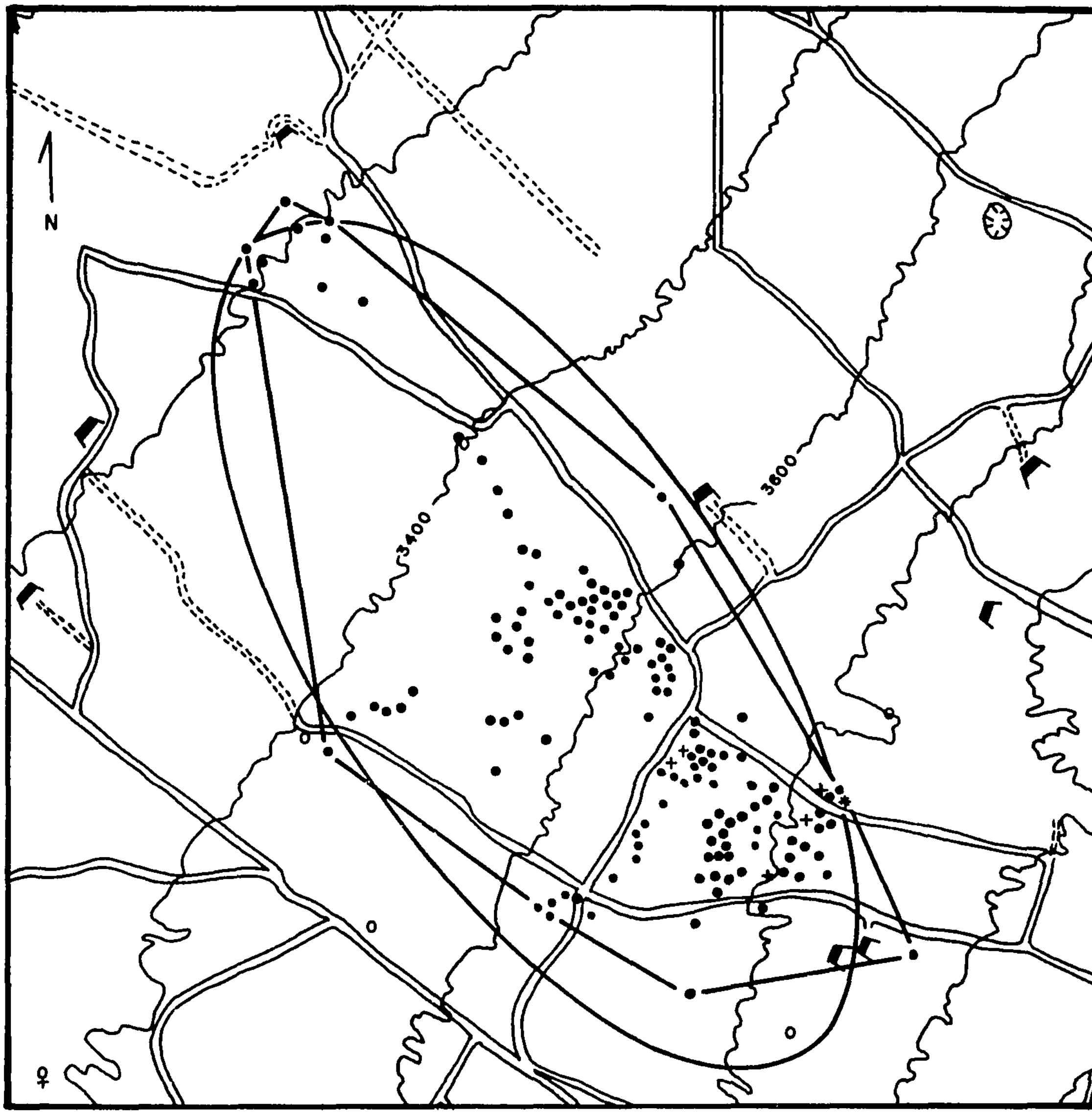


Figure 9. Minimum and elliptical home ranges of coyote 10. -- See Figure 8B for legend.

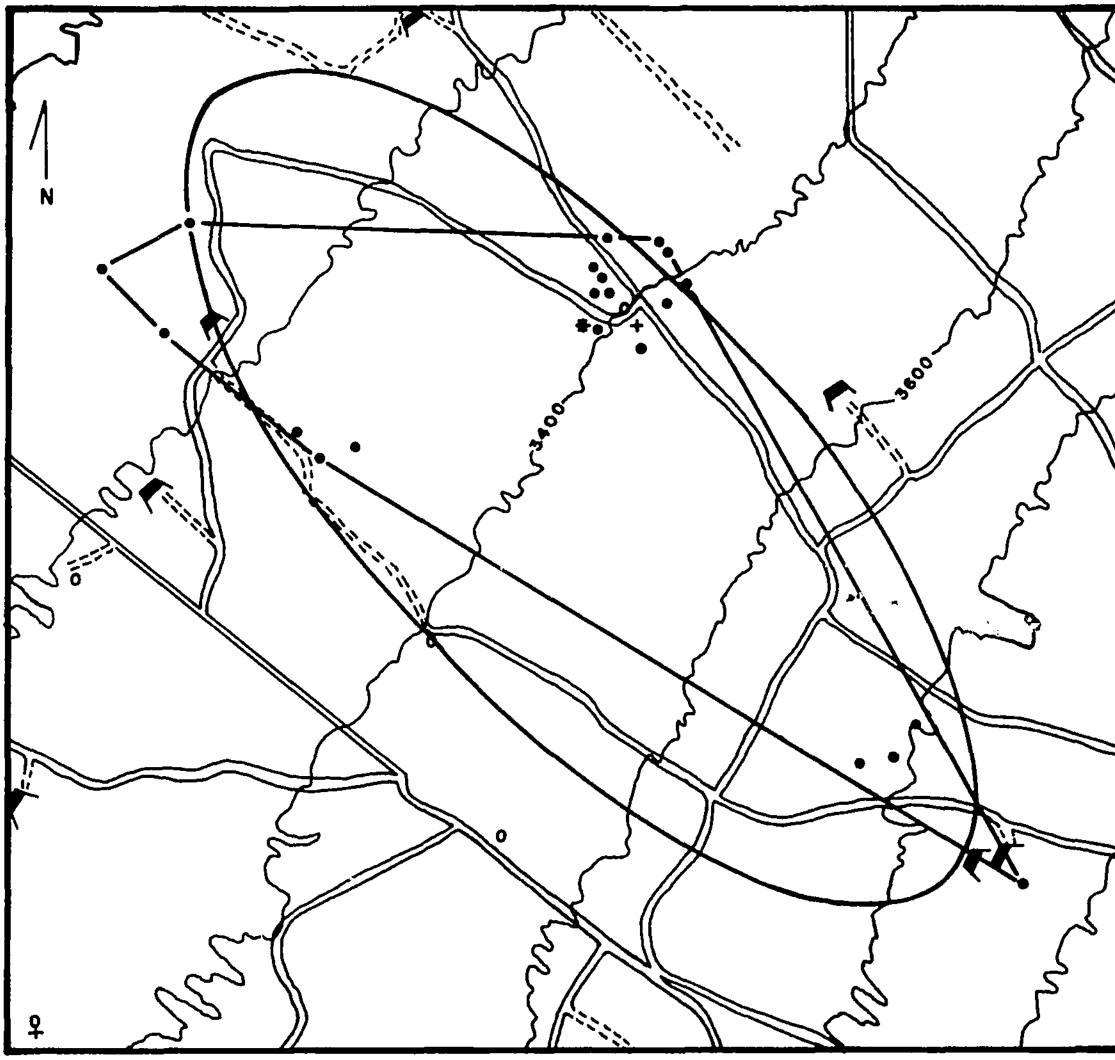


Figure 10. Minimum and elliptical home ranges of coyote 16. -- See Figure 8B for legend.

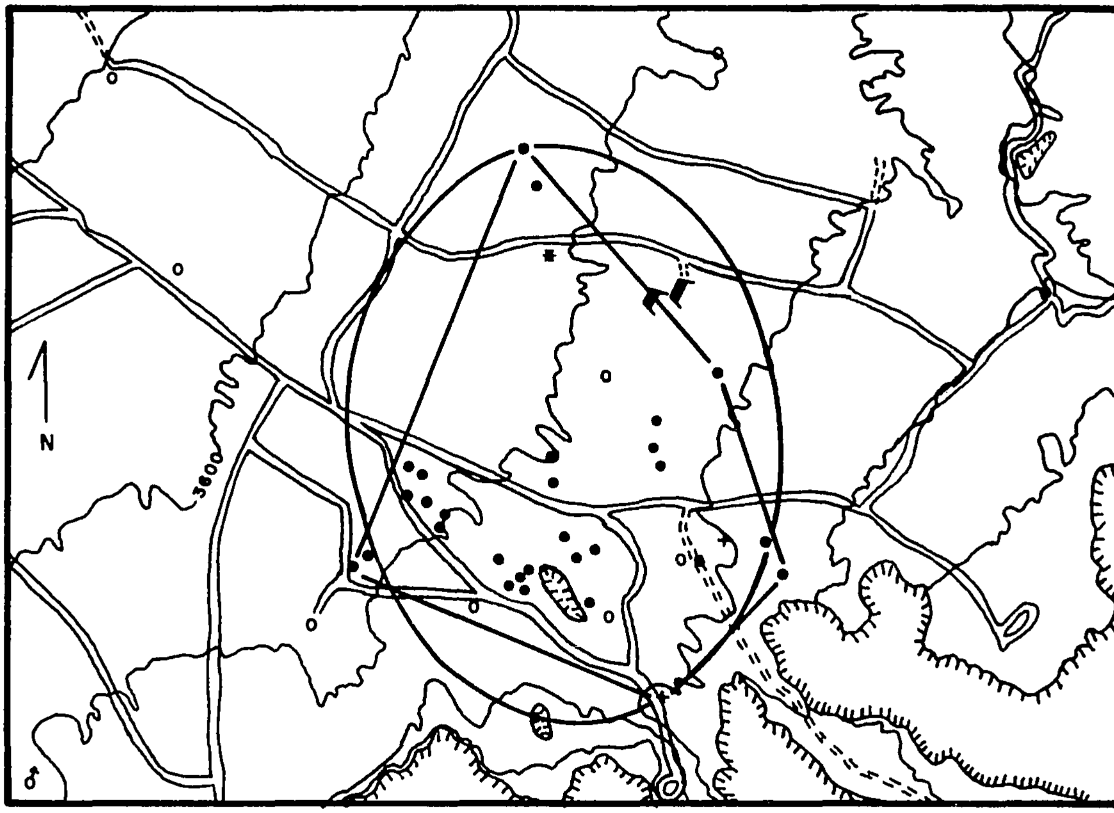


Figure 11. Minimum and elliptical home ranges of coyote 14. -- See Figure 8B for legend.

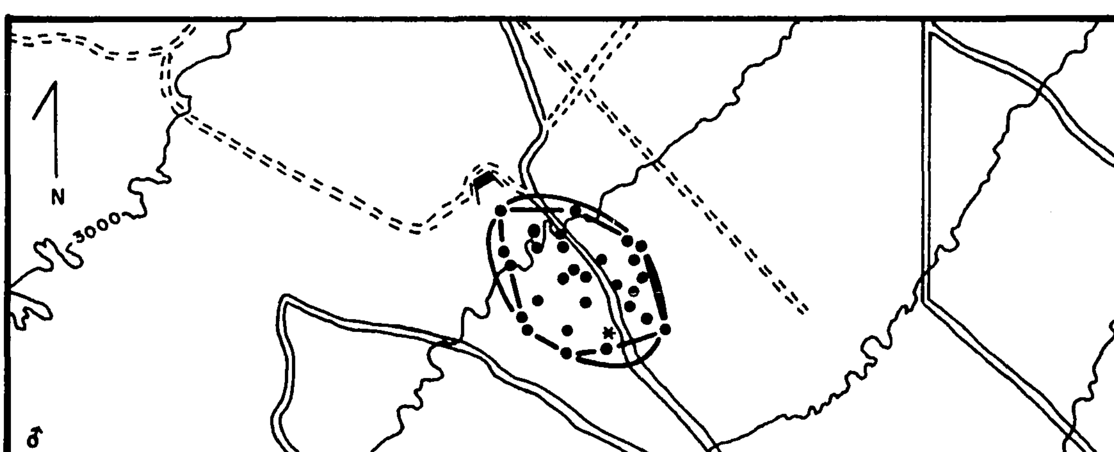


Figure 12. Minimum and elliptical home ranges of coyote 20. -- See Figure 8B for legend.

Table 2. Estimated size of coyote home ranges on the Santa Rita Experimental Range in 1972 and 1973.

Coyote	Minimum Home Range			Elliptical Home Range		
	Sq. Mi.	Acres	Hectares	Sq. Mi.	Acres	Hectares
7	4.58	2931.20	1186.22	5.79	3705.60	1499.61
9	1.98	1266.56	512.56	3.36	2150.40	870.24
10	7.93	5077.76	2054.91	9.75	6240.00	2525.25
14	3.83	2450.56	991.71	5.60	3583.94	1450.40
16	6.46	4131.84	1672.10	10.48	6707.02	2714.32
20	0.50	320.00	129.50	0.65	416.00	168.35
Average	4.21	2696.32	1091.17	5.94	3800.49	1538.03

Table 3. Size of coyote home ranges as estimated by different investigators.

Investigator	Location	Home Range Size	How Determined
Andelt and Gipson 1979b	Nebraska	21.4 sq. mi. (average)	Radio telemetry
Chesness and Bremicker 1974	Minnesota	13.7 sq. mi. (average)	Radio telemetry
Danner 1976	Arizona (SRER)	21.0 sq. mi. (adult average)	Radio telemetry
Fitch 1948	California	7 sq. mi.	Based on assumed cruising radius
Fitch 1958	Kansas	7.85 sq. mi.	Calculated from movement data
Gipson and Sealander 1972	Arkansas	8.8 sq. mi.	Radio telemetry
Henderson 1972	Kansas	3-4 mi. dia. when pups young; 25-30 mi. dia. for adults otherwise	Unknown
McLean 1934	California	5 sq. mi. per day	Unknown
Ozaga 1963	Michigan	20-25 sq. mi.	Snow tracking
Ozaga and Harger 1966	Michigan	36-50 sq. mi.	Snow tracking
Ryden 1974	Wyoming	Approx. 5 sq. mi.	Direct observation
Seton 1929	No. Amer.	20-30 sq. mi.	Personal observation

the calculations, male minimum home ranges averaged 3.5 square miles (906 ha.), roughly half that of females, and the difference remained significant ($t=3.286$, d.f.=3, $0.05>P$).

According to Cockrum (1962:112), among mammals males usually have larger home ranges than females. However, exceptions are not uncommon and examples have been reported by Manville (1949:53, 58), Marchinton and Jeter (1966), and Blair (1940), among others.

Live-trapping, marking, and re-trapping has long been employed as a technique for determining the size of the home range of smaller mammals (Cockrum 1962:106). Before the advent of radio telemetry some information on coyote movements was disclosed by utilizing this method. Reporting the results of such a study in Yellowstone Park, Robinson and Grand (1958) noted that females traveled greater distances between capture sites than did males. Movements of 102 females averaged 11.1 miles, while the average movement of 110 males was 7.9 miles, movement having been measured as airline distance from tagging to recapture sites. Nearly a third of these coyotes were mature when tagged. However, in Wyoming these same researchers found the converse true; movements of 51 males averaged 28.5 miles and of 38 females averaged 21.4 miles. In the Wyoming portion of the study nearly all animals were tagged as pups, hence movements were probably more a measure of dispersal than of travel within an established home range. Hawthorne (1971) in a similar tag and recapture study in northeastern California discovered that female coyotes moved greater distances than males, averages for adults being 4-3/4 versus 4 miles, and for juveniles 4 versus 3-1/4 miles. Differences in movements by the sexes were slight and not statistically significant. Assuming that movements between capture sites were directly related to size of home ranges, results of both studies were compatible with findings on the SRER in the sense that females had larger ranges than males.

In contrast, Gipson and Sealander (1972) after a radio tracking study of Arkansas coyotes reported that the size of adult male home ranges averaged 12.8 square miles, while that of females averaged 5.1 square miles. Similarly Chesness and Bremicker (1974) found that among Minnesota coyotes male home ranges averaged 26.2 square miles while female home ranges averaged 6.3 square miles. Results of these studies agreed with the general rule that males tend to have larger home ranges and conflicted with findings on the SRER during this study.

A complete explanation of variation in size of coyote home range between the sexes awaits further research. It was evident that this relationship reversed itself from one area to another. Possibly, as suggested by Robinson and Grand (1958), there was a link to the ecology of the area. In a coyote population that has reached the upper density level for its habitat, such as occurred in Yellowstone Park in the absence of predator control, female ranges exceeded those of males, while in areas not filled to capacity, male ranges exceeded those of females. This reasoning was consistent with observations on the SRER where a large coyote population existed during the period of study.

The mechanism behind this phenomenon may have been related to the dominance status of the sexes. Unfortunately references to sex-related dominance in coyotes are scant in the literature. Snow (1967) did not comment on this point in her observations on coyote behavior, while Brown (1973) found that a single male pup became dominant over three female pups in a coyote litter he studied. Bekoff and Jamieson (1975) observed a male pup that eventually assumed dominance over a litter consisting of three males and three females. Ryden (1974) reported behavior of wild coyotes which supported the contention that males tend to dominate females. In wolves (Canis lupus) males were generally dominant over females, and this relationship appeared to be related to size (Fox 1972). Females tend to be smaller in physical stature among coyotes (see Appendix A) as well as among wolves. During this project females were noticeably more nervous and threatening when handled and more difficult to radio track because of their tendency to avoid human contact, behavior which was interpreted as submissive in nature. This seemed a reasonable inference, since Brown (1973:71) noted threatening behavior and flight were characteristic of submissive coyotes. Theoretically, when a large population of coyotes occupy an area, submissive animals would be more harried and would have to cover more area to satisfy their needs. This speculation is consistent with limited field observations, but does require much more verification under controlled conditions.

Another factor which might cause females to occupy larger home ranges may have been a tendency of progeny to associate with their mothers for prolonged periods. Females tended to be group members as a result. A discussion of the relationship between group size and home range follows.

Group size: Some coyotes were members of social groups, presumably family groups. Classification of a radio-tagged coyote as a group member or as a loner was based upon sightings and/or proximity to other coyotes as determined by listening to vocalizations over an extended period while the radio-tagged animal was being monitored. Home ranges of group members would be expected to be larger than ranges of single animals, for a larger food supply would be necessary to support the company. The largest recorded minimum home range was that of coyote 10, an animal that was definitely a group member, while the smallest was for coyote 20, which from all indications was a loner.

Season of Year: Coyote home ranges may have been smaller in summer than in winter. Unfortunately the same animals were not tracked in both seasons. Coyotes 7, 9, and 10 were tracked during the period November through April, and their average minimum home range was 4.8 square miles (1243 ha.). Coyotes 14, 16, and 20 were tracked during the period May through August, and their average minimum home range was 3.6 square miles (932 ha.). This difference was not statistically significant ($t=1.518$, d.f.=4, $0.3>P>0.2$).

Seasonal variation in home range size would be largely a function of available food supply. That home range and food supply are tied together followed logically from the writing of McNab (1963), who related size of home range to metabolic rate, and has been suggested by the work of Ables (1969), Yerger (1953), Marshall and Jenkins (1966), and others. While data from this study were inadequate to clearly demonstrate this point, it was notable that the very small apparent home range of coyote 20 occurred during a season of plenty. Heavy spring rains had produced lush vegetation throughout the SRER, with a resultant increase in the numbers of small mammals and lagomorphs. A heavy crop of prickly pear fruit was also available within this animal's home range during the tracking period. Coyote 20 would have had difficulty securing a living in so small an area during the winter season when small mammals were less available and fruits were absent.

Seasonal migration of coyotes between the SRER and the adjoining Santa Rita Mountains could not be substantiated during this study, though mule deer did move down onto the SRER during the winter months.

Density of Population: Coyotes were numerous on the study area during the years 1972 and 1973. An average density figure of 0.77 coyotes per square mile was derived using data obtained from howling responses elicited by a siren. However, this figure was probably an underestimate, since procedures followed in censusing violated numerous guidelines developed later by Wolfe (1974). On two occasions radio-tagged coyotes within a quarter mile (0.4 km.) of the siren failed to vocalize, while at other times spontaneous vocalizations suggested the presence of 12 or 15 coyotes per square mile.

A crude empirical estimate of two coyotes per square mile for the SRER seemed reasonable. This figure proved to be consistent with economic density figures computed for carnivores by Mohr (1947) and was certainly not inconceivable, since Knowlton (1972) reported densities as high as five to six coyotes per square mile.

Results of this study indicated that estimated coyote home ranges on the SRER were smaller than reported for coyotes elsewhere. This was shown in Table 3. The dense coyote population on the study area may have been an important factor in determining home range size. Other researchers, including Brown (1966), Ellis (1964), and Yerger (1953), have noted contracted home ranges within dense populations.

Injury: Two male coyotes which had sustained debilitating injuries when captured were released with radio collars attached. Coyote 9 sustained a severe sprain and swelling of the left front foot and lower leg, while coyote 20 suffered a broken toe and other damage to the right front foot. Their injuries may have contributed to the restricted movements of these animals. However, statistically the sizes of their home ranges did not differ significantly ($t=3.59$, d.f.$=2$, $0.1>P>0.05$) from those of other male coyotes. Gipson and Sealander (1972) reported movements of coyotes with broken feet were unaffected by their injuries, and even a coyote with a broken leg moved about freely. Coyote 9 was sighted 36 days after his release and appeared to have recovered full use of his injured limb.

Coyote 9 spent much time in the neighborhood of a stock tank-corral complex where small mammals were common, while coyote 20 was radio tracked during summer when small mammals and prickly pear fruits were plentiful in his environs. It was probably the ready availability of food that allowed these coyotes to survive in relatively restricted areas.

Other Properties of Home Range.

Biological Center of Activity: Use of the home range was not uniform; some portions of the occupied area were frequented more often than others. Heavily used areas included favored resting areas and hunting grounds. Such areas have been termed "biological centers of activity" by Ables (1969) as opposed to the geometric "center of activity" described by Hayne (1949).

Biological centers of activity were best illustrated by coyote 10, but other coyotes which were radio tracked for more than a few days also showed a tendency to favor certain portions of their home ranges. Such high use areas appeared as clumps of points when radio fixes were plotted on home range maps. Because of the small size of the total area occupied, this phenomenon was least apparent for coyote 20.

Foci of activity shifted about with time, a coyote centering its activity in one area for as long as several days before use of a different area was accentuated.

Establishment of homesites defined by Manville (1949) as retreats occupied more or less regularly could not be documented. On those occasions when a coyote returned to the same general area to rest, it appeared that specific bedding sites were used but once. Even coyote 20 shifted his rest sites about within his restricted home range. It has been well established that coyotes utilize dens during the whelping season, but such behavior was not observed for any instrumented animal during this study.

Foraging Ranges: The total home range was composed of a series of smaller ranges within which the animal lived for a time before moving on to a new area. The idea of subranges was embraced within the concept of periodic ranges put forth by Mohr (1947), who noted that the area of home range changed weekly, seasonally, and so on. However, Francis and Stephenson (1972) applied the term "foraging range" to such areas, and this term more appropriately described the observed phenomenon.

Use of different foraging ranges appeared to be typical for coyotes for which radio contact was maintained for at least several weeks, except again for coyote 20. This feature was best illustrated by coyote 10, because radio contact was maintained on a more regular basis over a longer period than for the other coyotes. Her foraging ranges are illustrated in Figure 13. Divisions between different sub-ranges were made when the behavior of the animal indicated a shift in the area occupied. In the case of coyote 10 foraging ranges showed consistency in size, averaging 2.8 square miles (725 ha.). There was also a definite downslope, east-to-west shift in her ranges during the tracking period. Shifts in foraging ranges in different directions were noted at various times for other coyotes.

Biological centers of activity existed within each foraging range. Occasional rather lengthy forays were made from these foci in different directions, and these account largely for extensive overlap between the sub-ranges. During these forays the coyote probably encountered circumstances which eventually determined which direction the next shift would take. Such changes in foraging ranges appeared to occur periodically, and it seemed reasonable to describe the lifetime home range of a coyote as a composite of foraging ranges.

Essential Habitat Features: Foraging ranges provided an opportunity to evaluate the importance of different habitat features. On

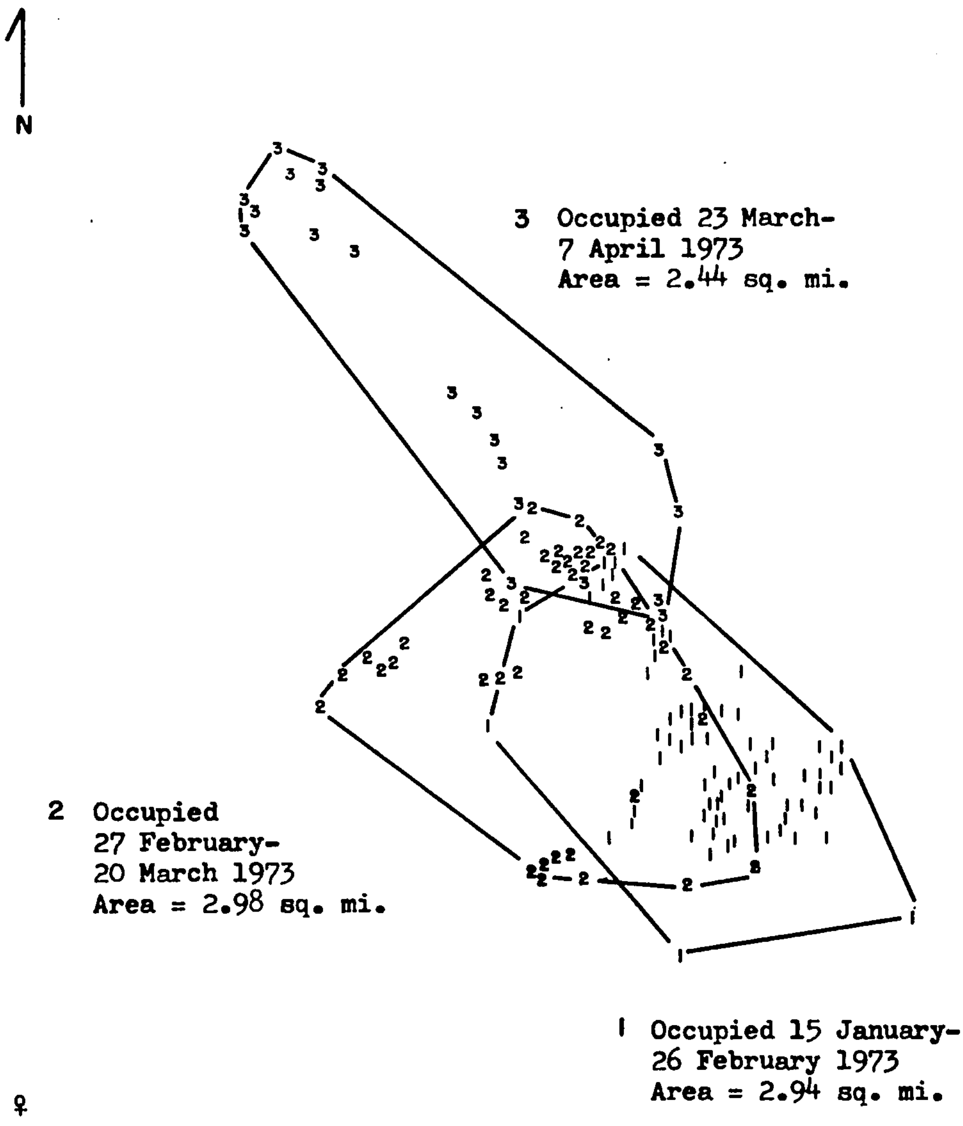


Figure 13. Minimum foraging ranges of coyote 10. -- Scale: 1 inch = 1 mile.

the study area cover was provided chiefly by mesquite and other shrubby vegetation. Food sources included small mammals, lagomorphs, carrion, and various fruits in season. Cover and food sources were generally well distributed and, based upon subjective field observations, amply represented within each foraging range.

Water was readily available from stock tanks of two types. Earthen tanks were designed to catch runoff resulting from precipitation, and were often dry seasonally. Metal tanks had water piped to them and generally held it throughout the year. While home ranges generally included one or more stock tanks within their boundaries, foraging ranges did not necessarily include water sources. Coyotes were occasionally seen visiting stock tanks for water, but observations indicated that they did not do so on any regular basis. Water apparently was not an essential feature of coyote habitat.

Linearity: According to Stumpf and Mohr (1962) linearity is a common property of home ranges of diverse animals. By linearity is meant that the range is longer than wide, or oblong rather than circular in outline. As can be seen from Figures 7 through 12, coyote home ranges as delineated by this study tended to be linear.

Using the major and minor diameters of the elliptical home ranges as measures of length and width, and using the ratio of width to length as a measure of linearity,as did Stumpf and Mohr (1962), the ratio varied from 1:1.35 for the nearly round home range of coyote 14 to 1:2.52 for the very elongated home range of coyote 16. Averaging lengths and widths for the six coyotes for which home ranges were computed, the average ratio was 1:1.96, while a composite range produced by superimposing the home ranges one upon another resulted in a ratio of 1:2.52. These figures indicated that coyote home ranges were indeed linear.

The shape of coyote home ranges on the SRER appeared to be affected by ease of travel. Coyotes frequently traveled along the dry, sandy washes that dissected the area. Often radio-tagged coyotes appeared to use washes while being monitored, particularly when making a lengthy movement. These washes provided excellent travel ways which avoided rough terrain and harsh vegetation. Coyotes also made use of roadways and cattle trails for travel. Maintained roads appeared to be used less than older, unmaintained backroads where encounters with man were less likely. Coyote tracks were sometimes seen following a track of a backroad for a half mile or more. Many of these roads and trails ran parallel to major washes, often along ridges, thereby evading rougher topography.

Washes had a more subtle influence on coyote movements as well. Brushy vegetation frequently bordered washes, providing cover for cottontails (Sylvilagus auduboni) and other small mammals, and thereby influenced the hunting patterns of coyotes.

Because of the effect of washes and ridges on the travel habits of coyotes, drainage pattern appeared to influence the shape of coyote home ranges. To test this relationship, the average slope was calculated for the major and minor diameters of the elliptical home ranges, and these slopes were compared. The average slope of the major axes was 134.4 feet per mile (25.5 m./km.), while that of the minor axes was 56.9 feet per mile (10.8 m./km.), a difference which was highly significant ($t=3.59$, d.f.=10, $0.01>P>0.001$). The result of this simple test supported the contention that coyote home ranges were elongated with slope. The explanation for this appeared to be that coyotes tended to travel in and along dry washes, which of course ran down slope.

The exception to the general rule was coyote 14. The slope of the minor axis of his elliptical home range exceeded that of the major axis, indicating that the range was not oriented with slope. Much of this animal's range was among foothills and broken terrain where the washes tended to be steep-sided and strewn with boulders and therefore not good travel ways.

Coyote Activity Pattern

Daily Routine. Coyotes generally became active before dusk, continued to hunt through the night, and often remained active for a few hours after daybreak. They generally rested through the midday period. Their activity period allowed them to take advantage of crepuscular and nocturnal prey species.

A composite picture of coyote activity by hour of the day is presented as Figure 14. Data upon which this figure was based were obtained by lumping radio fixes for all coyotes. Fixes were judged active, inactive, or activity status undetermined. Those fixes for which activity status could not be determined were not considered, nor were fixes where observer interference was a possibility.

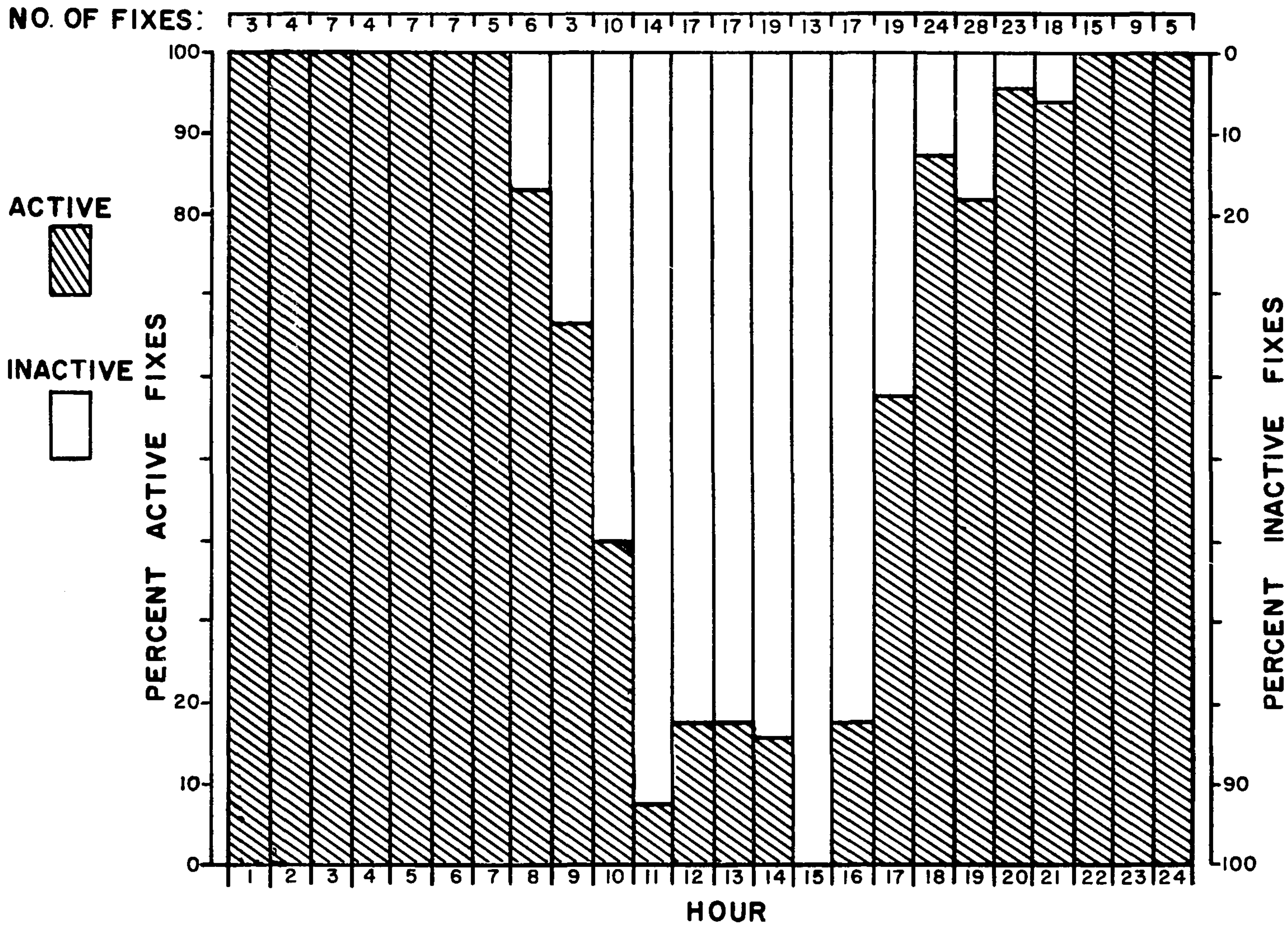


Figure 14. Coyote activity by hour of the day.

Effect of Season. The typical activity pattern found coyotes inactive during the hot midday periods of summer, while during the cooler winter months they became active earlier and remained active later in the day. To illustrate this seasonal change coyotes 7, 8, 9, and 10 were considered "winter" coyotes and coyotes 5, 12, 14, 16, 19, and 20 "summer" coyotes. The activity status of each fix was evaluated as already described. "Summer" coyotes became inactive as early as the 0800 hour and remained inactive as late as the 2000 hour, with no activity recorded for any of these animals from 1100 through 1700. In the winter, in contrast, some active fixes were recorded for every hour except 1500, while inactive fixes were recorded from 1000 to 1900 hours, with one additional inactive fix recorded during the 2100 hour.

Effect of Weather. Coyotes tended to be active during foul weather, that is, under rainy, snowy, misty, or blustery conditions. This was particularly noticeable during daylight hours when coyotes normally were inactive. Comparing the number of active to inactive fixes during daylight hours for foul versus fair weather, coyotes proved to be more active in foul weather at a highly significant level ($X^2 = 11.2$, $0.005>P$). In foul weather 70.6 percent of 17 daytime fixes were judged active. A similar comparison of activity for nighttime fixes showed no significant difference between fair and foul weather ($X^2 = 0.1$, $0.75>P>0.50$), but coyotes were normally active during these hours.

Daytime activity in inclement weather sometimes caused a shift in the normal diel activity pattern. For example, on 13 February, 1973, foul weather prevailed on the SRER and coyote 10 remained active through the early afternoon, finally becoming inactive by 1500 hours. She then remained at rest until 2140 when contact was broken off. Under normal conditions she would have been active before this hour. A similar situation developed on 12 March, 1973.

These activity patterns suggested that the relationship between physical exertion and body temperature affected coyote activity. In hot weather coyotes remained relatively cool by remaining inactive, while during cold or inclement weather they remained warm by moving about.

Other Aspects of Coyote Behavior

Resting Sites. Use of dens was apparently minimal among SRER coyotes. No use of dens by instrumented coyotes was detected, though evidence of den use by other coyotes was found during the whelping season. Instrumented coyotes were encountered at a variety of different resting sites during the course of field work. Examples follow.

On 12 July, 1972, coyote 5 rested in the bottom of a dry wash against the base of a vertical 8 foot (2.4 m.) bank, a well shaded, very cool spot. Four days later the same animal was roused from a bed under a bushy mesquite tree in an otherwise relatively pure stand of creosote bush. The site offered shade and was slightly elevated on a small ridge between washes. The ground was bare except for scattered detritus.

Coyote 10 and at least four other coyotes in her company were bedded together in the shade of a grove of broad-topped mesquite trees bordering a dry wash on 29 January,1973. Here the ground was grassy. Two beds were located by observing the actions of my dog, and their position confirmed by the presence of crushed vegetation where the animals had been lying. The resting coyotes had been separated by several yards, each against the trunk of a tree. On the very windy afternoon of 4 April, 1973, coyote 10 was bedded on the lee side of a ridge formed at the junction of two washes, roughly 5 feet (1.5 m.) above the level of the bottom of the wash. While the animal slipped away without being sighted, my dog again located her bed. In this case the coyote had been lying beneath a shrubby catclaw which did not shade out the warming sun. The coyote had been resting in a form made in a dense growth of tall grass, predominantly bush muhly, which grew beneath and around the brush. Three such forms were apparent, but one was not well defined and appeared to have been used only briefly or at some earlier time. The two well defined forms were separated by only a few feet.

On 19 February, 1973, coyote 9 was found bedded against the base of a shady mesquite tree located on a flat, grassy area about 200 yards (180 m.) from a backroad. The site resembled dozens of similar ones available in the vicinity. The ground had a sparse grass cover.

Observations suggested that no particular rule could be formulated for the location of coyote resting sites. Coyotes appeared to rest in a variety of locations dictated by physical comfort as much as any other factor. All locations would have been comfortable from a human standpoint.

Hunting Behavior. Hunting activity was monitored for coyotes 5, 7, 9, 10, 14, 16, and 20. While hunting, coyote movements were not great, and often movement defined by a change in direction of a bearing of a radio signal did not occur for periods of 10 or 20 minutes. Yet changes in intensity and other characteristics of the radio signal indicated activity. Apparently coyotes hunted in a very deliberate fashion, moving along slowly and, one can speculate, looking, listening, and sniffing out various small prey, carrion, fruits, or other possible food items. Such activity sometimes moved the coyote along on a more or less directed course, while at other times the animal doubled back and criss-crossed an area so that the point at which the activity eventually stopped was not far removed from where it had begun. This type of behavior was typical of coyotes during their waking hours.

No evidence of capturing of prey by running it down was noted. Brown (1973) stated that coyotes are coursers, but this means of capturing prey was not typical of hunting by coyotes on the SRER.

Purposeful, relatively rapid movements from one location to another were recorded on a few occasions. During these movements coyotes traveled at a steady pace for distances upward of a half-mile (0.8 km.). Such movements possibly carried coyotes from one hunting area to another or returned them to a favored resting area.

Escape Behavior. Rapid movements in one direction commonly resulted from efforts by a coyote to escape from the immediate vicinity of the observer. A number of times when instrumented coyotes encountered the observer or the study vehicle they immediately moved away. Distances involved regularly exceeded a half-mile (0.8 km.), and rate of movement indicated that the animals actually ran at times. Such activity was regarded as non-typical behavior, and probably stemmed from the trauma of being captured and handled.

Escape behavior presented some problems in interpretation of data. It was apparent that coyotes were quite capable of detecting the presence of the observer at considerable distances. This ability became less impressive as more time was spent in the field, for moving vehicles could be heard for miles across the range, particularly during the hours of darkness when conditions were otherwise quite still. Also, wind often carried scent to coyotes,enabling them to detect the observer at considerable distance.

A striking example of this type of behavior occurred on 26 February, 1973, while monitoring coyote 10. This animal was located at about 17 00 hours as she moved southward. Her movement was gradual and it became apparent that,if the animal held her course,she would cross the road upon which the study vehicle was parked,to the west of it. After about an hour signal direction indicated that coyote 10 was very close to the road. At 17 55 a single unmarked coyote came out onto the road from the vicinity of 10 and at a distance of roughly 200 yards (180 m.). This animal remained in view nosing along the roadside for a time, eventually moved out of view to the north from where it had come, then returned to the road and continued to move about in view, stopping to look northward several times. A second larger unmarked coyote then stepped into view from the north side of the road, hesitated a moment to look directly at the vehicle and observer, and then moved quickly out of view to the south. The first coyote trotted down the road to investigate something, stopped to look into the brush to the south where the second coyote had disappeared, and then moved off to the south and out of view. The instrumented animal, however, never did show herself. The bearings of her radio signal indicated that she apparently backtracked over the course she had taken to the road, and by 18 35 was moving away to the west in a direction roughly parallel to the road. During this observation the vehicle had remained stationary, though the observer did move around to take bearings. A light breeze was in the coyotes' favor.

Male Versus Female. In the process of capturing and handling live coyotes a definite difference was noted in the temperament of the sexes. Females were always more excitable, were more likely to injure themselves in the traps, exhibited accelerated respiration and heart rate when handled, and tended to be hyperactive, to threaten, or to cower in the presence of humans while in captivity. Adult males, while not docile, seemed more adaptable to captivity and remained relatively calm. Adult males accepted food in the form of dead rabbits, and ate in the presence of humans, while females would back to the far end of the holding cage when food was presented, and ate only after being left alone.

After release the difference in behavior persisted. Females avoided the observer and study vehicle whenever they detected either, moving rapidly away from the vicinity. This was particularly apparent with coyote 8 which was often already moving away when her signal was detected. Since her transmitter performance was poor, this compounded the problem of tracking her. Similar behavior may have contributed to the lack of success in tracking coyotes 1 and 17. Males appeared less concerned when encountering the observer in the field. Generally they simply resumed their normal activity after a few minutes, though they did avoid contact. Coyote 7 did move rapidly away from the study vehicle on one occasion, but coyote 9, even when followed closely on foot, simply moved away, then stood watching the observer approach, then moved away again, appearing ready to resume his normal activity as soon as he was left to do so.

Vocalizations. Coyote howling was commonly heard on the study area during those hours when the animals were normally active, and apparently served a number of communicative functions. Vocalizations appeared to allow members of the same social groups to maintain contact and move about as a unit, while at the same time providing a means whereby members of different social groups could avoid each other. A more obvious purpose was that of warning others of possible danger. On a number of occasions when I blundered into a band of coyotes, or vice versa, warning howls were given and the animals moved away. Spontaneous howling appeared to reach a peak during late winter, and this was probably related to breeding activity. During the balmy night of 6 February, 1973, and the following morning, for example, coyotes howled continuously at intervals of 20 to 30 minutes on the SRER. Howling maximized the chances of sexually mature animals locating each other.

Several types of vocalizations were noted; onomatopoeic terms for these were generally inadequate. Characteristic howling sessions, usually involving several coyotes, were most commonly heard. These involved much variation and defied accurate description. Warning calls given by disturbed coyotes exhibited more excitement and were more hurried than typical howls, and often involved only a single animal. Yipping was commonly used by coyotes in a teasing sense, particularly when they confronted my dog in the field. Occasionally when I was detected by a coyote responding to a varmint call, the animal would retreat and yip at me from out of sight. Barking much like that of a domestic dog was elicited on several occasions with a siren. Apparently barking indicated a state of high excitement or agitation. Rarely growls and whines were heard, but these and other more restrained articulations could generally be detected only by maintaining more intimate contact than was possible with wild, free ranging coyotes. Various coyote vocalizations have been described by Brown (1973) and McCarley (1975).

It often appeared that a specific coyote was responsible for initiating a howling chorus. On several occasions a blast from the siren would be followed by complete stillness for a time before a single coyote would howl, and suddenly several others would join in. This could be a stirring experience when the animals were at close range in the darkness. That this behavior originated with family discipline was suggested by an event which took place in the early morning of 1 July, 1973. After a wail from the siren at about 0340 hours,a group of young coyote pups began yapping in response at a distance of about 100 yards (92 m.). Their response was abruptly ended, however, when an adult coyote gave a sharp bark. After a short hesitation a single pup resumed its yapping, but again the adult quieted it with a curt bark. No further vocalizations could be induced.

Coyotes appeared to have a limited capacity for howling. Once an animal howled it was a minimum of 20 or 30 minutes before it would do so again. This became evident when coyotes could be heard in the distance along the route to be taken during a siren survey, but subsequently could not be induced to vocalize again when the siren was in close proximity to their location. Wolfe (1974) noted similar occurrences while censusing coyotes with a siren. This phenomenon was also apparent when observing captive coyotes displayed at the Arizona-Sonora Desert Museum near Tucson. Children often elicited vocalizations from these captive coyotes by squealing at them. However, after a robust howling session the animals did not respond further by howling for some time, though they often continued to whine and yodel in response to the bombardment of stimuli. Pimlott (1960) reported a similar limited capacity for howling among wolves. It appeared that vocalizing required what Lorenz (1970:308) called "response-specific energy," and howling could be triggered only when sufficient "arousal pressure" had accumulated.

While most coyote howls seemed at first indistinguishable to the untrained human ear, a few animals did have distinctive voices. Some individuals also appeared to have a characteristic rhythm to their calls. Thus in a gross way certain animals were recognizable. In view of the analysis of wolf howls by Theberge and Falls (1967), identification of different coyotes by their vocalizations seemed possible.

Vocalizations appeared to be a promising source of much behavioral information about coyotes. The potential use of howling for censusing has been explored by Wolfe (1974). Young and Dobyns (1945) mentioned the use of howling to locate dens. If individuals could be identified from their howls, knowledge of such things as home ranges, activity patterns, group associations, and a variety of other ecological relationships might be learned.

Intraspecific Interaction

Loose Associations. Coyotes frequently associated in groups of two or more. Some observations of coyotes in groups have already been cited in foregoing discussion. These and other similar observations indicated that captured-and-released coyotes were readily accepted by their associates, despite various markings and the presence of radio collars. Some instrumented coyotes of both sexes were confirmed group members. This was most often determined by noting the correlation between movements of a radio-tagged coyote and other vocalizing coyotes. Applying this criteria, coyotes 5, 8, 10, and 14 were at times judged group members, while the status of 7, 12, 16, and 19 were less apparent. These latter animals tended to be non-vocal and their associates, if they had any, may have had this same trait. From all appearances coyotes 9 and 20 were loners. Both frequented areas through which groups of vocal coyotes passed, yet their movements bore no relationship to those of the vocalizing groups. Interestingly,home ranges of both coyotes 9 and 20 were relatively small in comparison to those of other radio tracked coyotes.

Association of coyotes in groups could also be deduced from simply listening for uninstrumented coyote vocalizations over a prolonged period. At times a group of coyotes would be heard howling at one location, and some time later would be heard howling again from a different location, indicating that they were moving as a unit.

While often vocalizing coyotes were too close to each other to determine their spatial relationship, when they were separated they tended to maintain a linear configuration. On 12 July, 1972, coyote 5 was monitored while hunting. He was in company of at least two other coyotes, as indicated by occasional howling over a two hour period. The animals were spread over a distance of a few hundred yards and moved roughly abreast of each other. In this way the hunters covered ground more efficiently than they could have individually.

On several occasions lines of uninstrumented vocalizing coyotes were detected. Such lines sometimes contained four or five coyotes and were spread over distances of a quarter mile (0.4 km.) or more at times. During two of these observations the linear configuration was sustained for at least 30 to 40 minutes, the period over which contact was maintained.

On three occasions more than one coyote responded to a varmint call. When this happened the animals invariably appeared one after the other from the same direction, as though they had been traveling in file. The success of varmint calling itself probably depends to a large degree upon this pattern of association. I surmise that when a group member hears the sound of a distressed rabbit he investigates, feeling another member of the group has made a kill.

Besides contributing to hunting efficiency, association in groups improved coyote security. For example, on 17 March, 1973, an attempt to catch sight of coyote 10 by following her radio beam into the wind was foiled when a second coyote,whose position could not have been known,was inadvertently disturbed and gave warning calls.

Due to the dense vegetation on the SRER direct observation of coyotes was difficult. Often coyotes were seen crossing roads, but generally only a single animal was observed. On 24 August, 1972, a coyote came out on the road to yip and scold for a time as my dog and I had breakfast. By carefully scanning the area behind the animal with binoculars a second coyote was detected moving through the sheltering brush about 200 yards (180 m.) further away. Since aggregations were at times spread out over considerable distances, the tendency of coyotes to associate with one another could be underestimated if based upon visual contacts alone.

Coyote associations were "loose" in the sense that they were readily dissolved. Group members sometimes moved off in different directions for unknown reasons. Documentation of such an occurrence was given in the preceding discussion of escape behavior. Presumably separated group members met again and reunited periodically.

Whether social groups consisted of animals related by blood was problematical. Fox (1971:26) speculated that coyotes may hunt as a family unit until the mother returns to estrus, at which time the youngsters are driven away. He also suggested that association in groups may be a function of food availability, with an abundance of food in one locality leading to temporary aggregations. Both situations were possibilities on the SRER.

These temporary associations could not be considered "packs" in the sense of the highly structured groups formed by wolves and described by Mech (1966:57-65, 1970:38) and Fox (1971:23).

Territoriality. The status of coyotes on the SRER with regard to territoriality was somewhat ambiguous. No defense of territory was observed during this study. At different times coyotes freely passed through the established home ranges of instrumented coyotes, and groups of vocalizing coyotes sometimes occurred in close proximity to one another. Radio tracked coyotes tended to shift their foraging ranges about and appeared to have little permanent attachment to any tract of land. These observations intimated that territorial behavior was unimportant.

However, coyotes often appeared to distribute themselves evenly over the SRER. Groups of vocalizing coyotes as a rule avoided moving into areas already occupied by other vocalizing or instrumented coyotes. Of the coyotes that were radio tracked few had home ranges which overlapped extensively, and those that did were not tracked simultaneously, so that the overlap may have been more apparent than real. This spacing was probably not due to territorial behavior in the sense of active defense of a tract of land, but to a tendency to avoid competition while hunting for food.

Territorial behavior in coyotes has been described by Camenzind (1978) and Ryden (1974) in Wyoming, Andelt and Gipson (1979b) in

Nebraska, and Chesness and Bremicker (1974) in Minnesota. Gipson and Sealander (1972) were unable to determine if coyotes were territorial in their Arkansas study.

Social Organization. From field observations it was obvious that coyote social organization on the study area was somewhat complicated. The basic component of the population appeared to be a group of relatively old, established residents. These animals occupied definite home ranges and presumably bred and raised young periodically.

A second major component of the population probably consisted of the offspring of residents. During their first year of life young coyotes were probably closely associated with their parents, but gradually became more independent. The dense coyote population in the region over the span of this study would have made it difficult for youngsters to become established on their own. Therefore they probably associated with their parents longer and, even after beginning to wander, probably rejoined their parents regularly.

A third category of coyotes were transients. Young coyotes originating elsewhere no doubt explored the study area occasionally in their search for vacant habitat. However, the transient component probably also included adults displaced from their home ranges by human activity. Loss of wildlife habitat in the Santa Cruz Valley between Tucson and Mexico has been striking in recent years. The greater Tucson area has been growing by over 2,000 residents per month ("City population up 27,000 in '71," The Arizona Daily Star, May 12, 1972, p. 2A). The community of Green Valley directly west of the SRER has also enjoyed accelerated growth. Similarly, southward the communities of Amado, Tubac, and Rio Rico have been expanding. Loss of habitat to agriculture, mining, and highway and road construction has also been considerable. While such development occurred virtually up to its boundaries, the SRER remained a piece of prime coyote habitat.

Camenzind (1978) observed similar elements of social organization among coyotes on the National Elk Refuge in Wyoming. He described the degrees of social structure as nomads, aggregations, packs, and resident pairs.

Coyote Population Structure

Analysis of Age Structure

The Composite Sample. Ages were obtained for 378 coyotes representing southern Arizona. The number (d'_x) and proportion (d_x) of animals falling within each age class is shown in Table 4, and the composite population structure is illustrated in Figure 23 (see p. 102). Based upon ages in years for the entire sample, the average age of a southern Arizona coyote was 3.23 years (standard deviation [s.d.] = 2.42 yr).

While most coyotes did not survive beyond the early years of life, some did live to an old age. Two specimens were aged at nearly 13 years and another at just under 14 years of age. Study of tooth sections from one considerably older animal resulted in cementum layer counts ranging from 12 to 26; my judgment was that there were 17 annuli present. Taking into account the month of death (April), this coyote

Table 4. General life table based upon a composite sample of 378 coyotes collected from October, 1970, through May, 1973.

x	d'_x	d_x	l_x	q_x	L_x	e_x
0 - 1	124	328	1000	328	836.0	2.73
1 - 2	54	143	672	213	600.5	2.82
2 - 3	58	153	529	289	452.5	2.45
3 - 4	46	122	376	324	315.0	2.24
4 - 5	43	114	254	449	197.0	2.08
5 - 6	19	50	140	357	115.0	2.36
6 - 7	9	24	90	267	78.0	2.39
7 - 8	8	21	66	318	55.5	2.08
8 - 9	9	24	45	533	33.0	1.81
9 - 10	2	5	21	238	18.5	2.31
10 - 11	2	5	16	313	13.5	1.88
11 - 12	1	3	11	273	9.5	1.50
12 - 13	2	5	8	625	5.5	0.88
13 - 14	1	3	3	1000	1.5	0.50
Totals	378	1000				

Explanation of symbols:

x = age class
d'_x = number of animals in sample from each age class
d_x = proportion of the population composed of each age class
l_x = number of survivors per 1000
q_x = number of mortalities per 1000
L_x = mean number of animals living between age classes
e_x = mean years of further life expectancy

was almost 19 years of age. Because of the ambiguity in the count, however, this specimen was not considered in the analyses which follow.

Knowlton (1972) reported coyotes reaching 13.5 and 14.5 years of age, Manville (1953) reported a captive coyote living to an age of 15 years, and Linhart and Knowlton (1967) recorded 21 years as the age of one very old captive coyote.

A life table constructed from the composite sample data is presented in Table 4. Based upon a cohort of 1000, it is a convenient means of presenting statistics basic to an understanding of population dynamics. These statistics include the proportion of the population composed of each age class (d_x), number of survivors per thousand (l_x), mortality rate (q_x), mean number of animals living between age classes (L_x), and mean years of further life expectancy (e_x).

The survival and mortality curves of Figure 15 were based upon the l_x and q_x statistics, respectively. For southern Arizona, coyote survivorship showed a rapid drop in the early years of life through about age 5 years, after which the curve tailed off gradually for older aged coyotes. Mortality was greatest in the first year of life (32.8 percent), then moderated somewhat until age 5, thereafter dropping off very gradually until age 14 when the oldest animal died. Relatively few animals reached old age, and there was no resultant steep drop-off due to deaths associated with senescence.

Expectation of further life was greatest for yearlings, that is, animals in the 1-2 year old age class, at 2.82 years, and dropped more or less gradually with advancing age subsequently. The e_x value of 2.73 for coyotes in the 0-1 year old age class was no doubt inflated

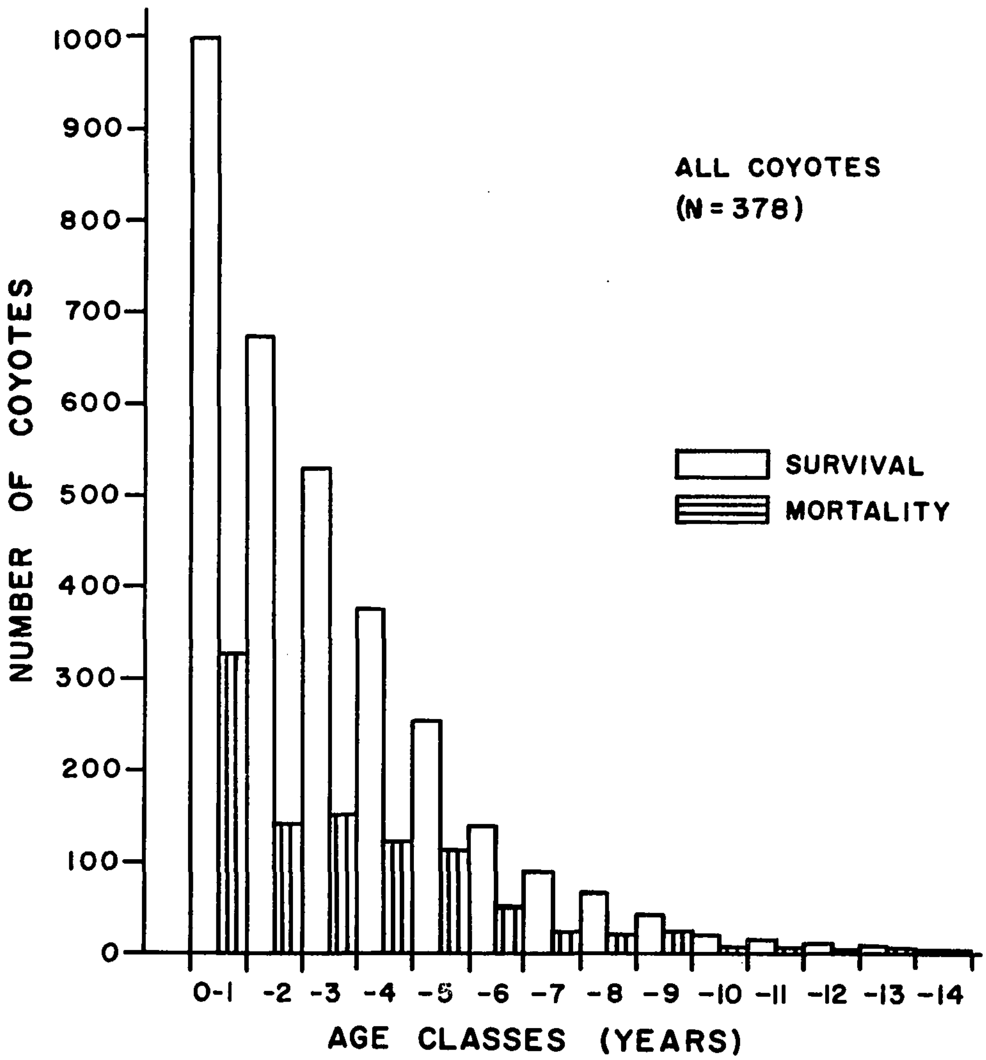


Figure 15. Survivorship and mortality by age classes based upon a composite sample of 378 coyotes from southern Arizona.

because pups were usually over 6 months old when sampled; the probable large undetected mortality of younger pups did not contribute to the life table statistics.

It should be remembered that the 378 specimens upon which the life table was based were gathered over a period of 32 months and represented a variety of habitats over a vast area. Interpretations should be of a general nature only.

By Year of Death. Available information suggested that May 1 approximated the period of peak parturition among coyotes in southern Arizona (Hamlett 1938; also see Coyote Reproductive Analysis). It seemed appropriate that a coyote year be defined from May 1 through the following April 30. Dividing the composite coyote sample accordingly insured that effects of various phenomena would be more accurately reflected within the different age classes.

Based upon sampling completed in year 1, May, 1970 through April, 1971, and year 2, May, 1971, through April, 1972, histograms representing the respective population structures are presented in Figure 16.

Comparison of the histograms for the two years brought out certain differences and clarified somewhat inconsistencies in the composite data. For example, the depressed size of the 1-2 year old age class in the pooled data resulted from depressed numbers in that age class in both years 1 and 2. The fact that the relatively small 1-2 year old component for the year May, 1970-April, 1971, was carried over and appeared as a relatively small 2-3 year old age class in the

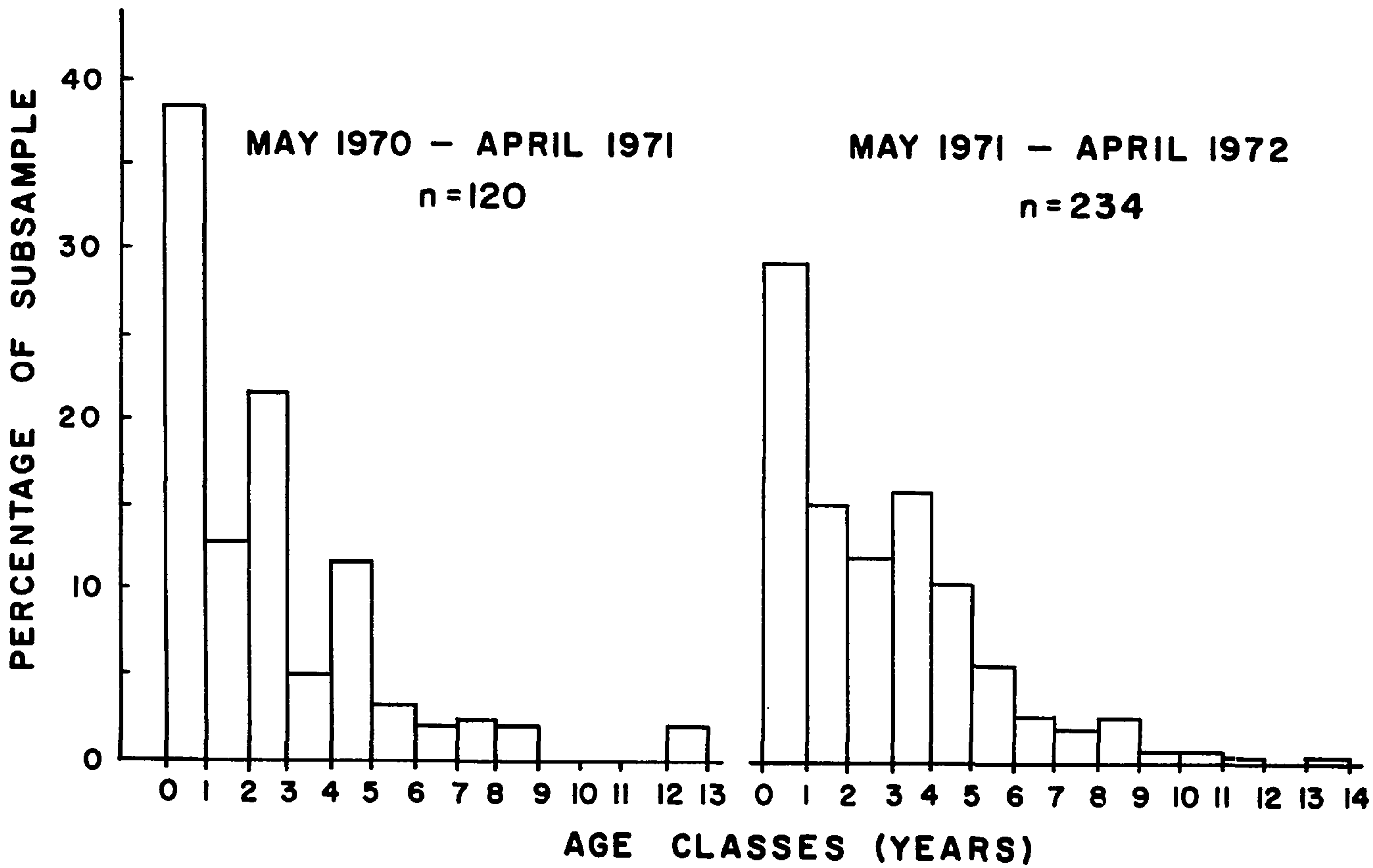


Figure 16. Comparison of coyote subsample age class structures for 2 successive years.

following year seemed good evidence that the phenomenon was real. Likewise the relatively large 2-3 year old category in the first year appeared as a relatively large 3-4 year old age class in the second year. Inconsistencies in similar relationships for older age classes were difficult to explain, but probably resulted from sampling error, particularly since smaller numbers of specimens typically represented older age classes.

The depressed size of the 1-2 year old age class in both years suggested a low reproductive rate and/or poor survival of pups. The proportion of the sample composed of pups, animals in the 0-1 year old age class, was somewhat smaller than in several other areas (see Figure 23, p.102), where populations were sampled by comparable means, intimating relatively poor reproductive success among southern Arizona coyotes.

Statistical comparison of the southern Arizona age structures between the two years by means of a chi-square 2 x 8 contingency table indicated a significant difference ($X^2 = 16.7$, d.f.=7, $0.025>P>0.010$). The 0-1, 2-3, and 3-4 year old age classes contributed most to the chi-square value. The greatest contribution was due to variation in the numbers of coyotes falling within the 3-4 year old category, and unfortunately appeared to have no logical basis; this flaw in the data may have resulted from sampling error. Logically one would have expected the greatest difference to have occurred in the 0-1 year old category. The number of pups within the population each year was dependent upon various factors, including the vagaries of the previous breeding season, range conditions during gestation, and the various maladies affecting survival of young pups, whereas the numbers of coyotes falling into older age categories were subjected to mortality factors which were much less age specific. In this study sampling of younger pups may have been inadequate to detect such a difference if it occurred.

By Month of Death. The numbers of coyote specimens representing each month ranged from a low of two for July and for August to a high of 55 for January. The age structure of the monthly samples is shown by Figure 17.

Pups first appeared in the sample at five months of age. These inexperienced coyotes were vulnerable and composed a large portion of the sample for the next several months. Attrition of their numbers was apparently rapid through their first year of life. No clear monthly trends were apparent for older aged coyotes.

By Sex of Coyote. Known-sex specimens were tabulated by age class and year of collection. To aid comparisons, age pyramids (Fig. 18) were constructed from these data. A small number of specimens collected after the second year of the study were included in the composite data.

Based upon the composite sample, average age for 152 males was 3.28 years (s.d.=2.42), while average age for 117 females was slightly lower, 2.86 years (s.d.=2.56).

The pooled data were expanded into sex-specific life tables (Tables 5 and 6), and into mortality and survival curves for each of the sexes (Figs. 19 and 20). Comparison of the curves indicated that

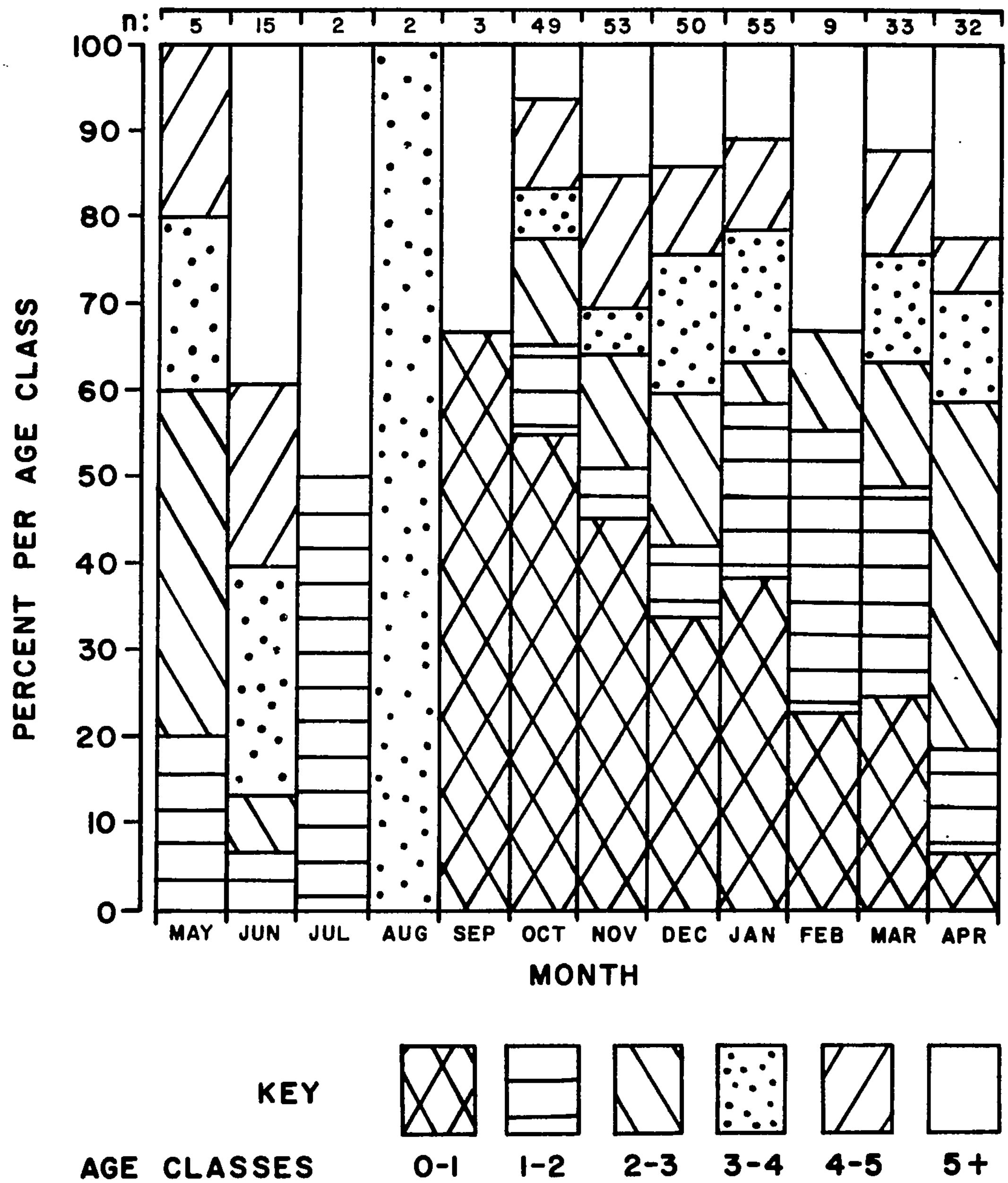


Figure 17. Monthly variation in age class distribution within composite coyote sample.

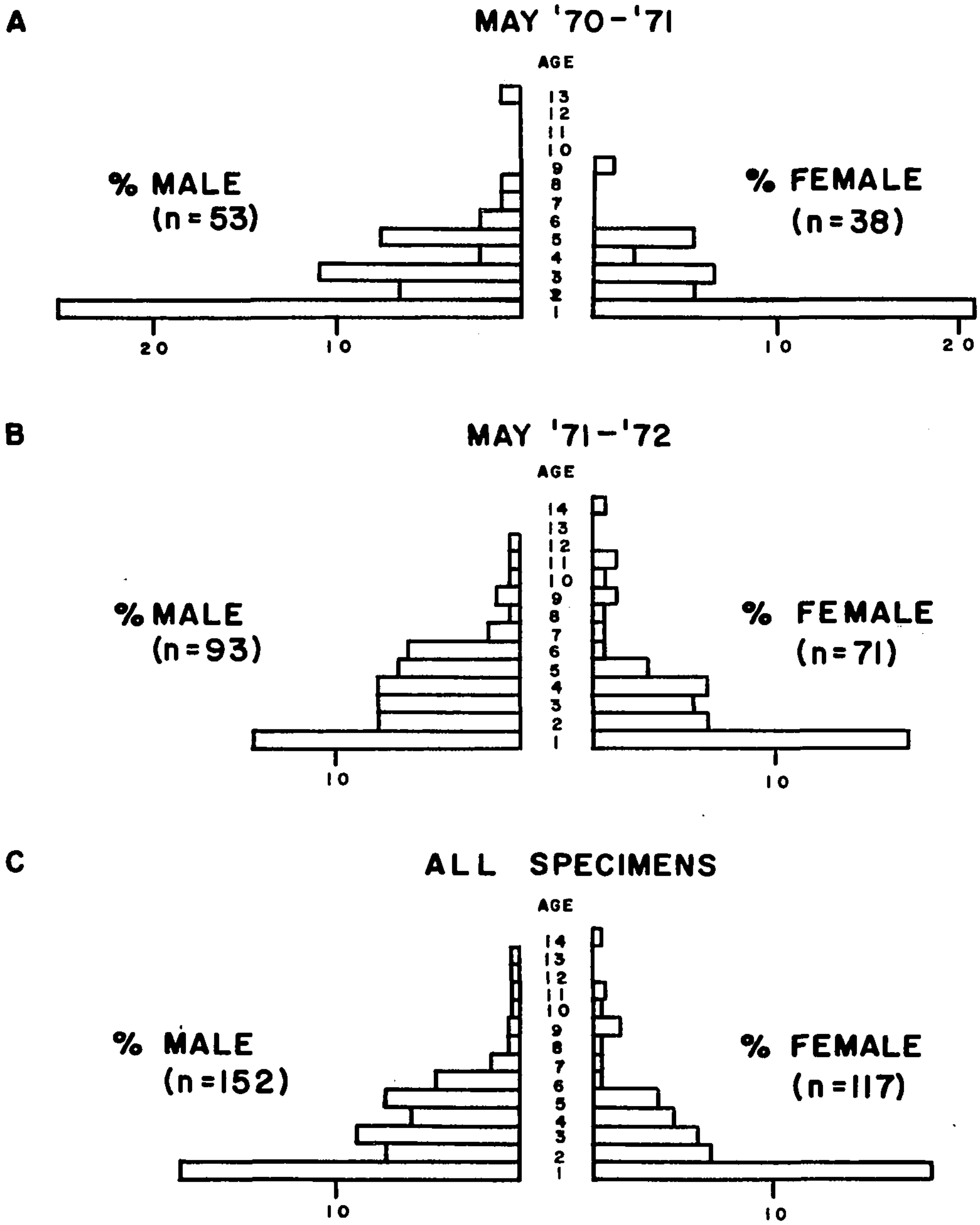


Figure 18. Sex-specific coyote age class distributions. -- A, specimens collected from May, 1970, through April, 1971. B, specimens collected from May, 1971, through April, 1972. C, all known-sex specimens.

Table 5. Sex-specific life table based upon a sample of 152 male coyotes collected from October, 1970, through April, 1973.

x	d'_x	d_x	l_x	q_x	L_x	e_x
0 - 1	50	329	1000	329	835.5	2.78
1 - 2	19	125	671	186	608.5	2.90
2 - 3	24	158	546	289	467.0	2.45
3 - 4	16	105	388	271	335.5	2.25
4 - 5	19	125	283	442	220.5	1.90
5 - 6	12	79	158	500	118.5	2.01
6 - 7	4	26	79	329	66.0	2.51
7 - 8	2	13	53	245	46.5	2.50
8 - 9	2	13	40	325	33.5	2.15
9 - 10	1	7	27	259	23.5	1.94
10 - 11	1	7	20	350	16.5	1.45
11 - 12	1	7	13	538	9.5	0.96
12 - 13	1	7	6	1000	3.0	0.50
Totals	152	1001				

Note: Explanation of symbols given in Table 4.

Table 6. Sex-specific life table based upon a sample of 117 female coyotes collected from October, 1970, through May, 1973.

x	d'_x	d_x	l_x	q_x	L_x	e_x
0 - 1	50	427	1000	427	786.5	2.35
1 - 2	18	154	573	269	496.0	2.73
2 - 3	16	137	419	327	350.5	2.55
3 - 4	12	103	282	365	230.5	2.55
4 - 5	10	85	179	475	136.5	2.73
5 - 6	1	9	94	96	89.5	3.76
6 - 7	1	9	85	106	80.5	3.10
7 - 8	1	9	76	118	71.5	2.41
8 - 9	4	34	67	507	50.0	1.66
9 - 10	1	9	33	273	28.5	1.86
10 - 11	2	17	24	708	15.5	1.38
11 - 12	0	0	7	0	7.0	2.50
12 - 13	0	0	7	0	7.0	1.50
13 - 14	1	9	7	1000	3.5	0.50
Totals	117	1002				

Note: Explanation of symbols given in Table 4.

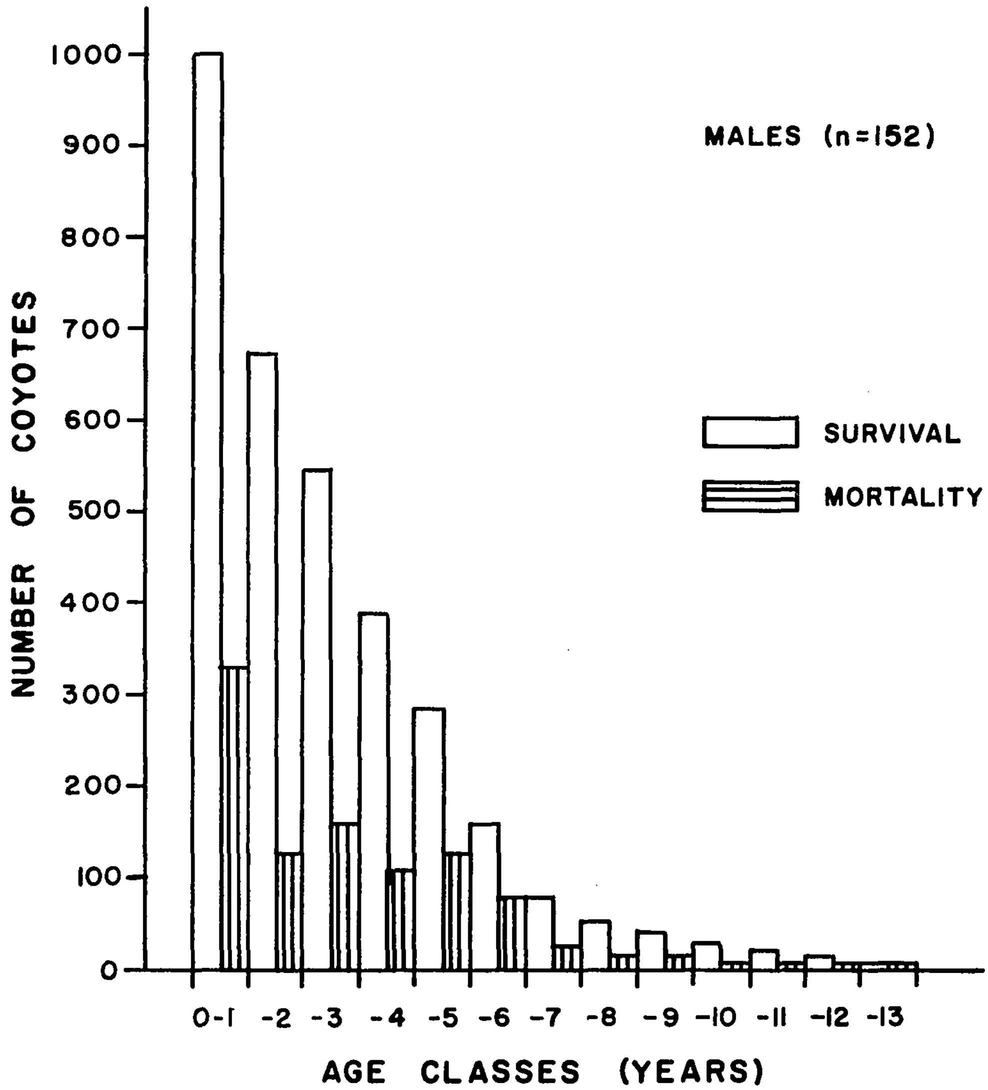


Figure 19. Survivorship and mortality by age classes based upon a subsample of 152 male coyotes from southern Arizona.

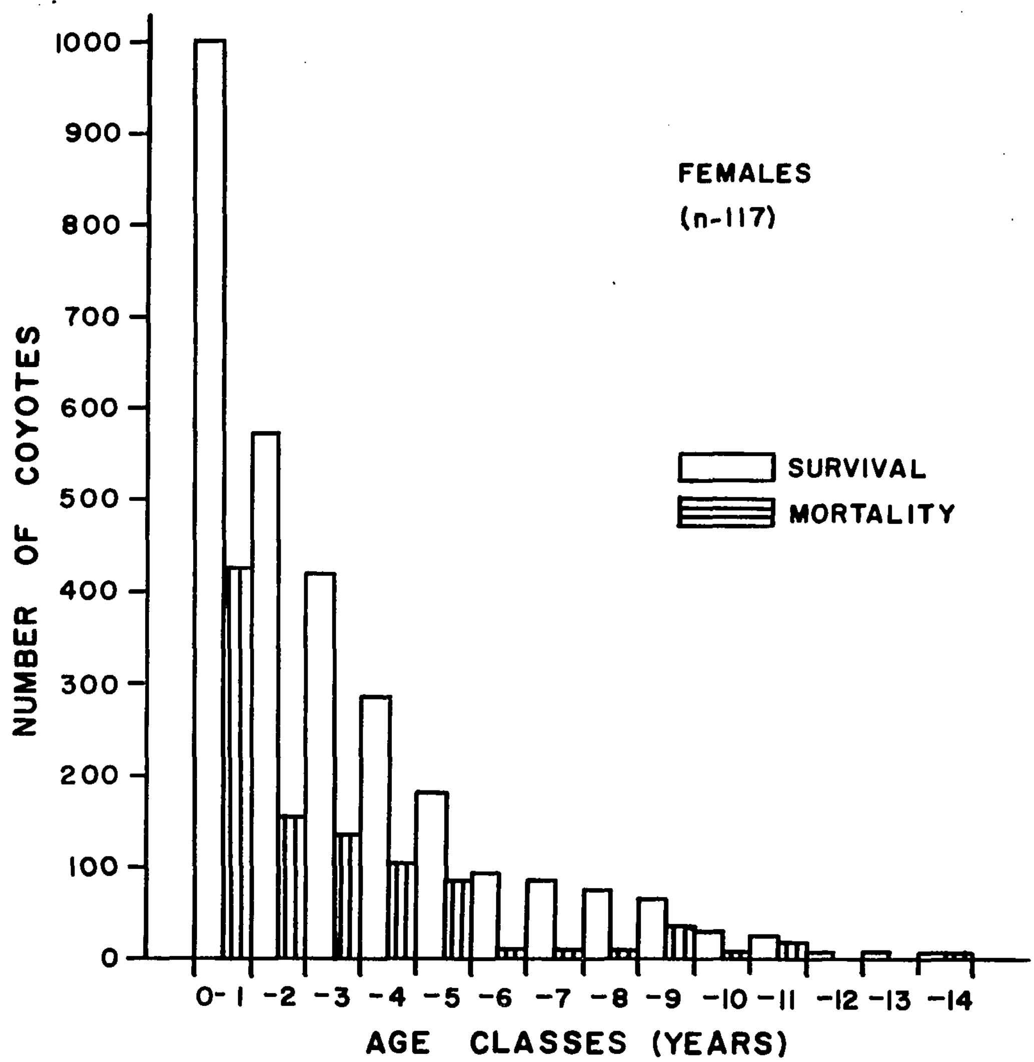


Figure 20. Survivorship and mortality by age classes based upon a subsample of 117 female coyotes from southern Arizona.

for coyotes less than one year of age, mortality of females was considerably greater than that of males. For coyotes of either sex over one year old, both mortality and survivorship were roughly comparable, tailing off more or less gradually with advancing age. A peculiar feature developed in the life table statistics for females because of the small number of animals representing age classes over 5 years of age. As a result, mortality rate and survivorship appeared to change little for female coyotes between ages 5 and 8 years. This was reflected by a striking difference in the mean further life expectancies of the sexes. For males, yearlings exhibited the greatest e_x at 2.90 years, while for females the greatest e_x of 3.76 years occurred for 5 year olds. Once females reached 5 years of age they appeared relatively invulnerable for the following 2 or 3 years. A similar increase in mean further life expectancy for males in late middle age was less exaggerated. Relatively few animals lived beyond age 8 years. Except for one female of age 13 years, males tended to outlive females.

A series of statistical comparisons of the age structures of the sexes was conducted utilizing chi-square contingency tables of appropriate sizes. Results are summarized in Table 7, and indicate no statistically significant differences between age distribution of males versus females within the composite data, nor within either year, nor between the first two years of this study.

By Cause of Death. The age structure of samples of coyotes killed by three different means is shown graphically in Figure 21. Road-killed coyotes were found along roads and highways, and presumably

Table 7. Results of chi-square comparisons for various combinations of age distribution data tabulated by sex and year.

Comparison	X^2	Degrees of Freedom	Probability
Composite sample:			
Male versus Female	12.0	7	0.25>P>0.10
May 1970 - April 1971:			
Male versus Female	2.0	5	0.90>P>0.75
May 1971 - April 1972:			
Male versus Female	10.0	7	0.25>P>0.10
Male:			
Year 1 versus Year 2	10.1	6	0.25>P>0.10
Female:			
Year 1 versus Year 2	6.3	5	0.50>P>0.25

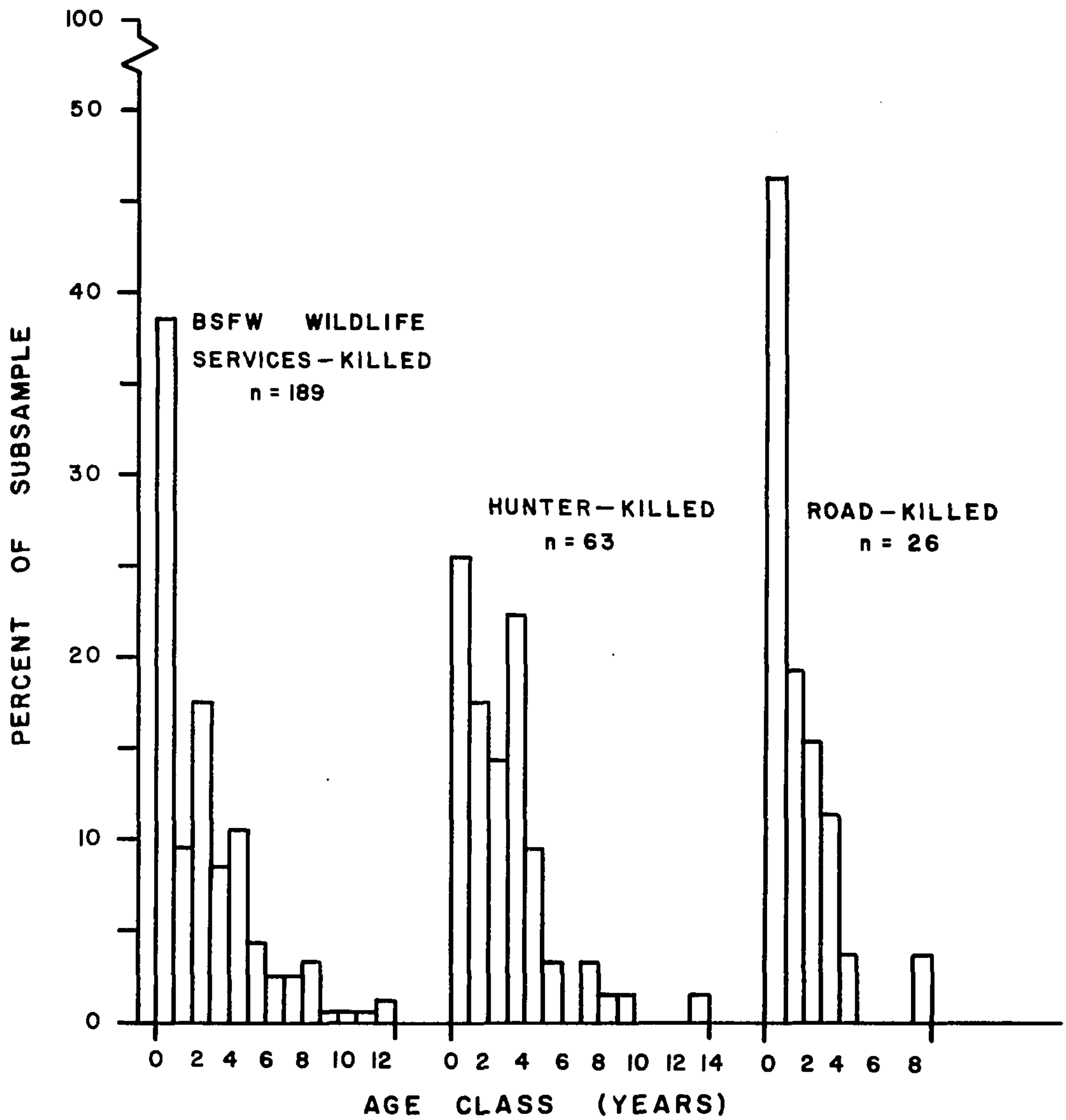


Figure 21. Coyote age class distributions for subsamples representing cause of death.

all died as a result of being struck by vehicles. Hunter-killed coyotes were shot, the great majority after responding to varmint calls; varmint calling was a popular sport among southern Arizona hunters. Animals killed by DWS were taken by means of traps or poisoned baits.

Comparison of the three sets of data by means of a chi-square 3 x 5 contingency table indicated that the age distributions differed significantly ($X^2 = 17.9$, d.f.=8, $0.025 > P > 0.010$). This result suggested that the age classes were not equally susceptible to the different sources of mortality.

It appeared that pups were particularly vulnerable to accidental death on roadways, while coyotes in the older age classes apparently had learned to avoid vehicles.

Coyotes ranging from 1 to 5 years of age were well represented among hunter-killed animals. Speculatively, these animals were more likely to be group members; sexually active coyotes probably bred successfully and younger coyotes probably associated with their parents for some time. Members of family groups were probably more susceptible to varmint calling, as already suggested in the behavioral discussion of this report (see Coyote Behavior: Loose Associations). A bias might have been introduced if hunters were reluctant to contribute small pups that they had shot. However, in soliciting coyotes from hunters I stressed the importance of obtaining as many of their kills as possible, including young animals. Also, most coyote hunting activity occurred in winter and spring after hunting seasons for more popular game species had ended, by which time pups had very nearly reached the physical stature of adults.

The sample of coyotes taken by DWS control activities may have been skewed somewhat toward pups, suggesting that learning was a factor in avoiding control devices. Otherwise the age classes of coyotes taken by trapping or poisoning appeared to be representative; these control techniques probably took members of older age classes in proportion to their numbers.

By County of Origin. Certainly county boundaries have no significance to free ranging coyotes; however, in Arizona counties tended to be large entities that served as convenient means for geographical division (see Fig. 5).

The age structure for coyote specimens grouped by county of origin is presented graphically in Figure 22 for six southern Arizona counties from which relatively large numbers of specimens were obtained. A chi-square 6 x 5 contingency table indicated that observed differences in age distribution were significant ($X^2 = 33.0$, d.f.=20, $0.050 > P > 0.025$).

Cochise, Pima, and Pinal counties provided enough specimens during each of the first two years of study to allow further statistical analysis. Relevant age structure information is presented in Table 8. The outcome of various statistical comparisons utilizing chi-square contingency tables of appropriate size are summarized in Table 9. Results suggested that age structure variations from year 1 to year 2 for the three counties were not significant. When the composite coyote sample was considered earlier the variation in age structure between these 2 years was significant, probably due to the cumulative effect of lumping together subsamples from several different counties.

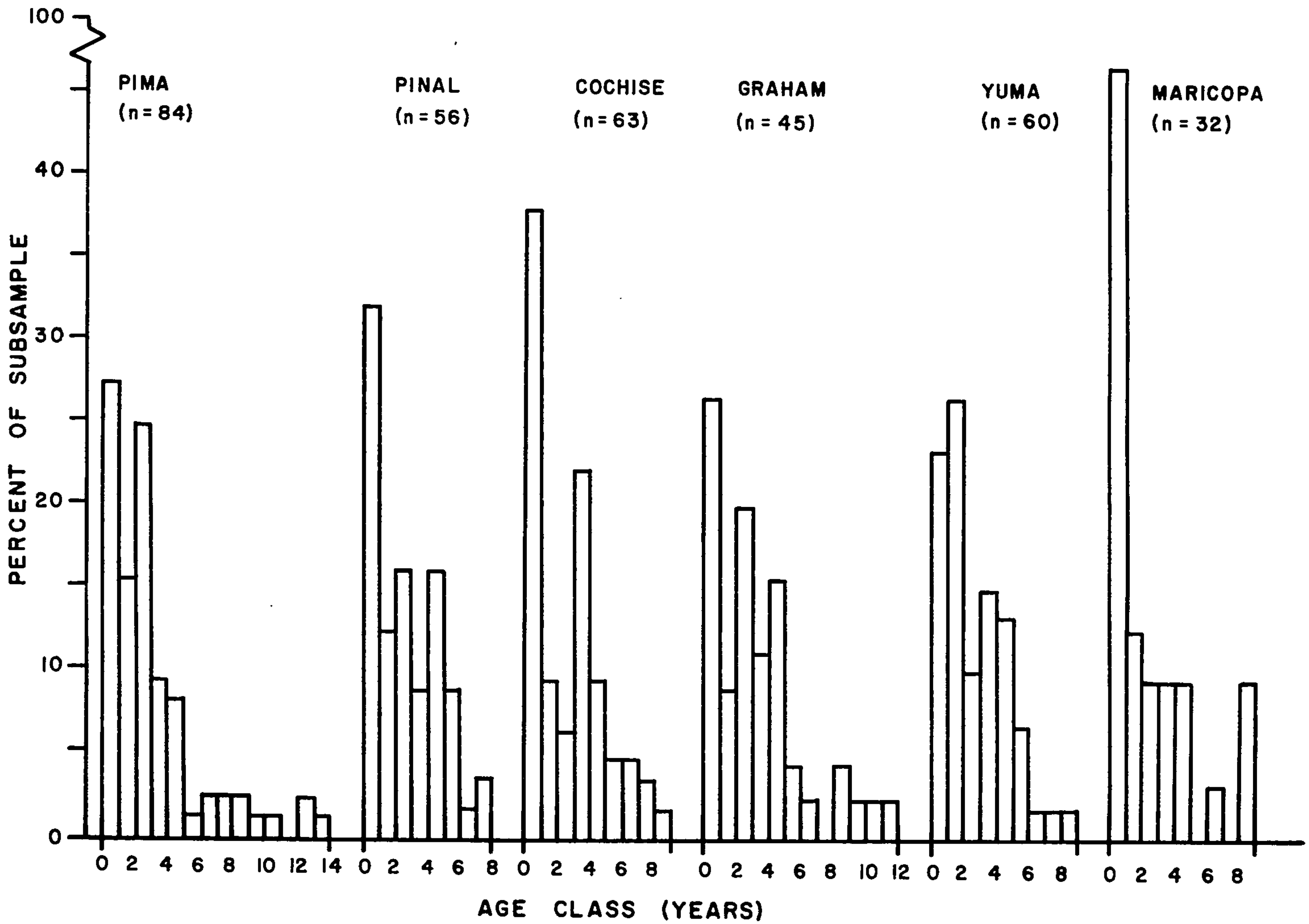


Figure 22. Coyote age class distributions for subsamples representing 6 southern Arizona counties.

Table 8. Age class distribution within coyote subsamples from Cochise, Pima, and Pinal counties during successive years.

	May 1970 - April 1971						May 1971 - April 1972					
	Cochise		Pima		Pinal		Cochise		Pima		Pinal	
Age Class	N	%	N	%	N	%	N	%	N	%	N	%
0 - 1	10	58.8	5	13.5	12	41.4	14	30.4	7	28.0	6	22.2
1 - 2	1	5.9	7	18.9	5	17.2	5	10.9	3	12.0	2	7.4
2 - 3	1	5.9	13	35.1	5	17.2	3	6.5	6	24.0	4	14.8
3 - 4	2	11.8	4	10.8	0	0.0	12	26.1	3	12.0	5	18.5
4 - 5	1	5.9	2	5.4	5	17.2	5	10.9	2	8.0	4	14.8
5 - 6	0	0.0	0	0.0	1	3.4	3	6.5	1	4.0	4	14.8
6 - 7	1	5.9	1	2.7	0	0.0	2	4.3	0	0.0	1	3.7
7 - 8	0	0.0	2	5.4	1	3.4	2	4.3	0	0.0	1	3.7
8 - 9	1	5.9	1	2.7	0	0.0	0	0.0	0	0.0	0	0.0
9 - 10	0	0.0	0	0.0	0	0.0	0	0.0	1	4.0	0	0.0
10 - 11	0	0.0	0	0.0	0	0.0	0	0.0	1	4.0	0	0.0
11 - 12	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
12 - 13	0	0.0	2	5.4	0	0.0	0	0.0	0	0.0	0	0.0
13 - 14	0	0.0	0	0.0	0	0.0	0	0.0	1	4.0	0	0.0
Totals	17	100.1	37	99.9	29	99.8	46	99.9	25	100.0	27	99.9

Table 9. Results of chi-square comparisons for various combinations of age distribution data tabulated by county and year.

Comparison	X^2	Degrees of Freedom	Probability
Cochise county:			
Year 1 versus Year 2	4.2	2	0.25>P>0.10
Pima county:			
Year 1 versus Year 2	2.8	3	0.50>P>0.25
Pinal county:			
Year 1 versus Year 2	6.3	3	0.25>P>0.10
May 1970 - April 1971:			
Cochise vs. Pima vs. Pinal	15.2	6	* 0.025>P>0.010
May 1971 - April 1972:			
Cochise vs. Pima vs. Pinal	1.1	4	0.90>P>0.75

*Significant

Age distribution during the year May, 1970, through April, 1971, proved to be significantly different between Cochise, Pima, and Pinal counties ($X^2 = 15.2$, d.f.=6, $0.025 > P > 0.010$). However, in the following year no significant variation was detected between the three counties.

This analysis suggested that fluctuations in the age class distribution of coyotes occurred rather gradually within counties from year to year, but that such variation between counties could be significant. Apparently fluctuations in age structure from one locale to another were not always synchronous, and probably were a reflection of local conditions acting upon coyote numbers. Since southern Arizona was an area of roughly 57,000 square miles (147,600 sq. km.) and included a wide variety of habitats, this situation was not unexpected.

Comparison with Other Studies. A number of studies have been made of age structure within coyote populations from other regions of western North America. Several of these can be compared with the coyote age distribution found in southern Arizona by viewing the histograms of Figure 23.

The Kansas data was derived from Gier (1968) by averaging values for the different age classes for the years 1954, 1955, 1956, and 1957. Aging of Kansas coyotes was based upon incisor wear. New Mexico coyote age structure was taken directly from Rogers (1965). Aging in the New Mexico study was accomplished by noting closure of certain skull sutures and wear on the first upper molar. In the latter two studies accurate aging beyond about 5 years was not possible.

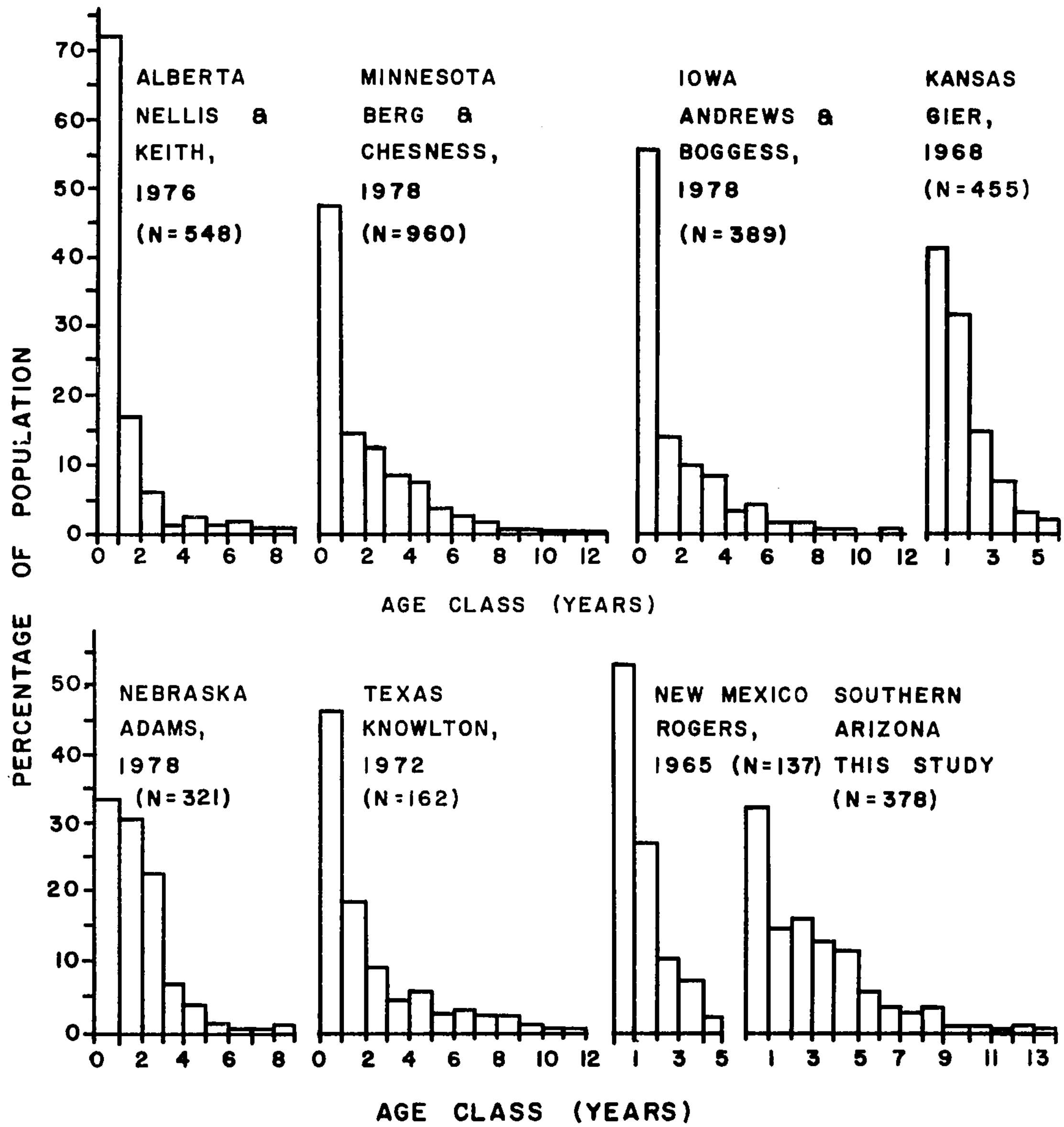


Figure 23. Coyote age class distributions representing 8 different regions of western North America.

Nellis and Keith (1976) were the source of age structure information for Alberta coyotes. Ages were estimated by an unspecified "composite" method.

In the remaining studies aging of coyotes was based upon counts of tooth annuli. The Texas data resulted from pooling figures presented by Knowlton (1972). The age class distribution for Iowa coyotes was derived from a histogram presented by Andrews and Boggess (1978), and that for Minnesota coyotes originated with Berg and Chesness (1978). The data from Nebraska was taken as presented by Adams (1978), though a discrepancy in figures was apparent in his report.

Comparison of the composite age distributions from the eight different regions by means of a chi-square 5 x 8 contingency table revealed a highly significant difference between them ($X^2 = 425.0$, d.f.=28, $0.005>P$).

An interesting feature of the age distributions of Figure 23 is that the southernmost regions appeared to harbor a greater proportion of longer-lived coyotes. Indeed, the major source of variation between the age class arrays was the number of animals in the 4+ year old group. In the Arizona sample over 25 percent, and in the Texas sample over 20 percent of the specimens were over 4 years of age. Some older aged individuals may have appeared in the New Mexico data had the tooth annuli method of aging been employed. Gier (1968:55) felt that few Kansas coyotes lived beyond 6 years of age. The oldest coyotes reported from adjacent southeastern Nebraska were 9 years of age (Adams 1978). Similarly Crowe and Strickland (1975) examined 225 coyotes from southeastern Wyoming and found only six in the 5-10 year old category. Ogle (1969) aged 30 Washington state coyotes and found none older than 7 years. Using figures derived from Andrews and Boggess (1978), 11.3 percent of Iowa coyotes fell into the 4+ year old category. In an earlier, parallel study of age structure in Iowa, Mathwig (1973) examined canine teeth from 139 coyotes and found none over 6 years of age. The highest proportion of coyotes over 4 years of age for a northern state was reported by Berg and Chesness (1978) in Minnesota, where 17.3 percent occurred in that age grouping, with 6 coyotes between 9 and 12 years old accounting for less than one percent of the total sample. Though Nellis and Keith (1976) reported a few old coyotes from Alberta, including a 13.5 year old individual, only 5 percent of the animals exceeded 4 years of age. The longer lives enjoyed by some coyotes in southern regions may be related to the lack of harsh winter weather and the greater availability of food year round.

The second major source of variation between age distributions from the diverse regions was the size of the 0-1 year old age class. Among wildlife populations generally this is expected to be the largest age group, but, largely because of the limited mobility of the young, it is difficult to sample accurately. A preponderance of animals less than a year old implies an expanding population (Odum 1959:171), or one subjected to heavy mortality. The Alberta and Iowa data particularly suggested poor survivorship among coyotes. By comparison the Arizona data intimated a relatively unexploited population.

Analysis of Sex Ratio

The Composite Sample. Of 273 total specimens for which sex was known, 154 were male and 119 were female. These figures reflect a significant departure from an even sex ratio ($X^2 = 4.2$, d.f.=1, $0.050>P>0.025$).

By Year of Death. Known-sex coyotes collected during the first year of the study consisted of 54 males and 39 females. There was no significant variation from an even sex ratio ($X^2 = 2.4$, d.f.=1, $0.25>P>0.10$). During the following year 94 males and 71 females were tallied. The observed difference between these figures and an expected 1:1 ratio approached significance ($X^2 = 2.9$, d.f.=1, $0.10>P>0.05$). The relatively few known-sex specimens collected subsequently consisted of 7 males and 8 females.

Sex ratios by year and for the pooled data are illustrated in Figure 24. Comparison of observed sex ratios between years, using the three sets of data for years 1, 2, and subsequently, revealed no significant difference ($X^2 = 0.7$, d.f.=2, $0.75>P>0.50$).

Assuming a reasonably accurate sampling, the pooled and yearly sex ratios suggested that within the general population males tended to predominate slightly. Comparison of figures between years indicated that this relationship did not vary significantly from one year to the next over the period for which data were available.

By Month of Death. When the composite known-sex sample was divided according to month of death, the data presented in Table 10

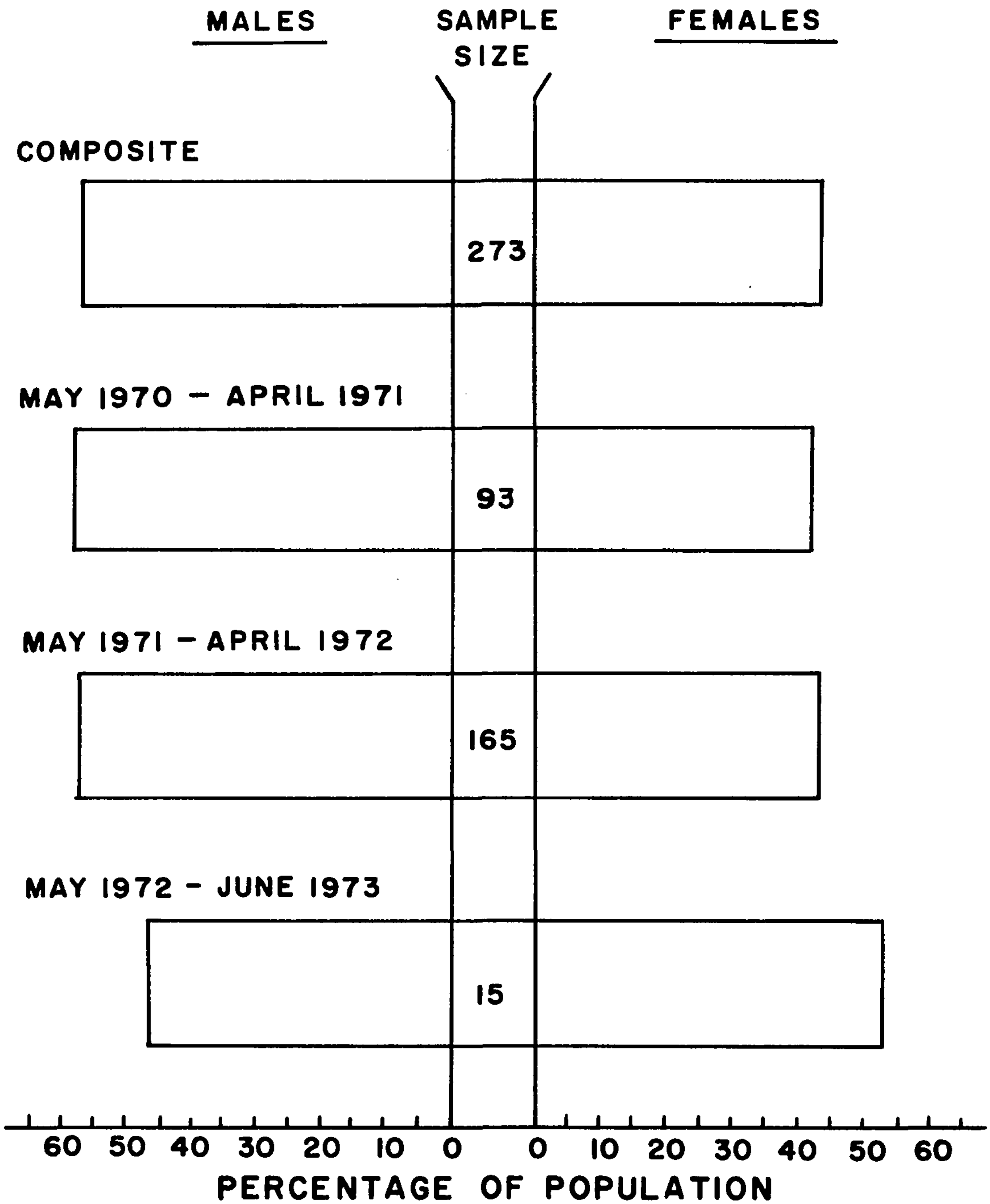


Figure 24. Ratio of the sexes within the composite sample and yearly subsamples of coyotes.

Table 10. Sex ratios within composite known-sex sample tabulated by month, quarter, and half-year, and results of chi-square testing of variation from an even (1:1) ratio.

Period	N	Male	Female	X^2	Probability
January	55	31	24	0.89	0.50>P>0.25
February	9	5	4		-No test-
March	31	16	15	0.03	0.90>P>0.75
Quarter 1	95	52	43	0.85	0.50>P>0.25
April	9	7	2		-No test-
May	3	0	3		-No test-
June	8	6	2		-No test-
Quarter 2	20	13	7	1.80	0.25>P>0.10
First ½ yr.	115	65	50	1.96	0.25>P>0.10
July	2	0	2		-No test-
August	2	0	2		-No test-
September	3	1	2		-No test-
Quarter 3	7	1	6		-No test-
October	50	26	24	0.08	0.90>P>0.75
November	50	27	23	0.32	0.75>P>0.50
December	51	35	16	6.35	0.025>P>0.010*
Quarter 4	151	88	63	3.82	0.10>P>0.05 a.s.
Second ½ yr.	158	89	69	2.53	0.25>P>0.10
Overall	273	154	119	4.23	0.050>P>0.025*

*Significant

a.s. = approaching significance

resulted. Variation from an even sex ratio was tested for significance within each month, and the resulting chi-square values also appear in Table 10. Note that in seven of the months too few known-sex specimens were available to allow a legitimate test. (A value of five per cell was considered minimal for legitimacy.) For this reason values representing quarter-year and half-year periods were tested as well. Variations in sex ratios between quarters (X^2 = 5.8, d.f.=3, 0.25>P>0.10) and between half-years (X^2 = 0.008, d.f.=1, 0.95>P>0.90) were not significant. Sex ratios of coyotes representing the four quarters of the year are illustrated in Figure 25.

Knowlton (1972:375) suggested that limited activity by gravid females resulted in a preponderance of males in spring population samples. If true, this explanation would have accounted for the prevalence of males in quarter 2. The disproportionate number of females appearing in the summer sample (quarter 3) was probably more the effect of chance and small sample size than an indication of increased foraging by bitches attempting to support litters of pups.

By Age Class of Coyote. The ratios of males to females occurring within each age class for all specimens for which sex was known are presented in Table 11, along with results of tests of significance for variation from an even sex ratio within each age class. Sex ratios tended to be even during the early years of life, but eventually males began to predominate until the variation became significant in the older age classes (see Fig. 26). The same trend appeared when the data for individual years were examined, except that the predominance of

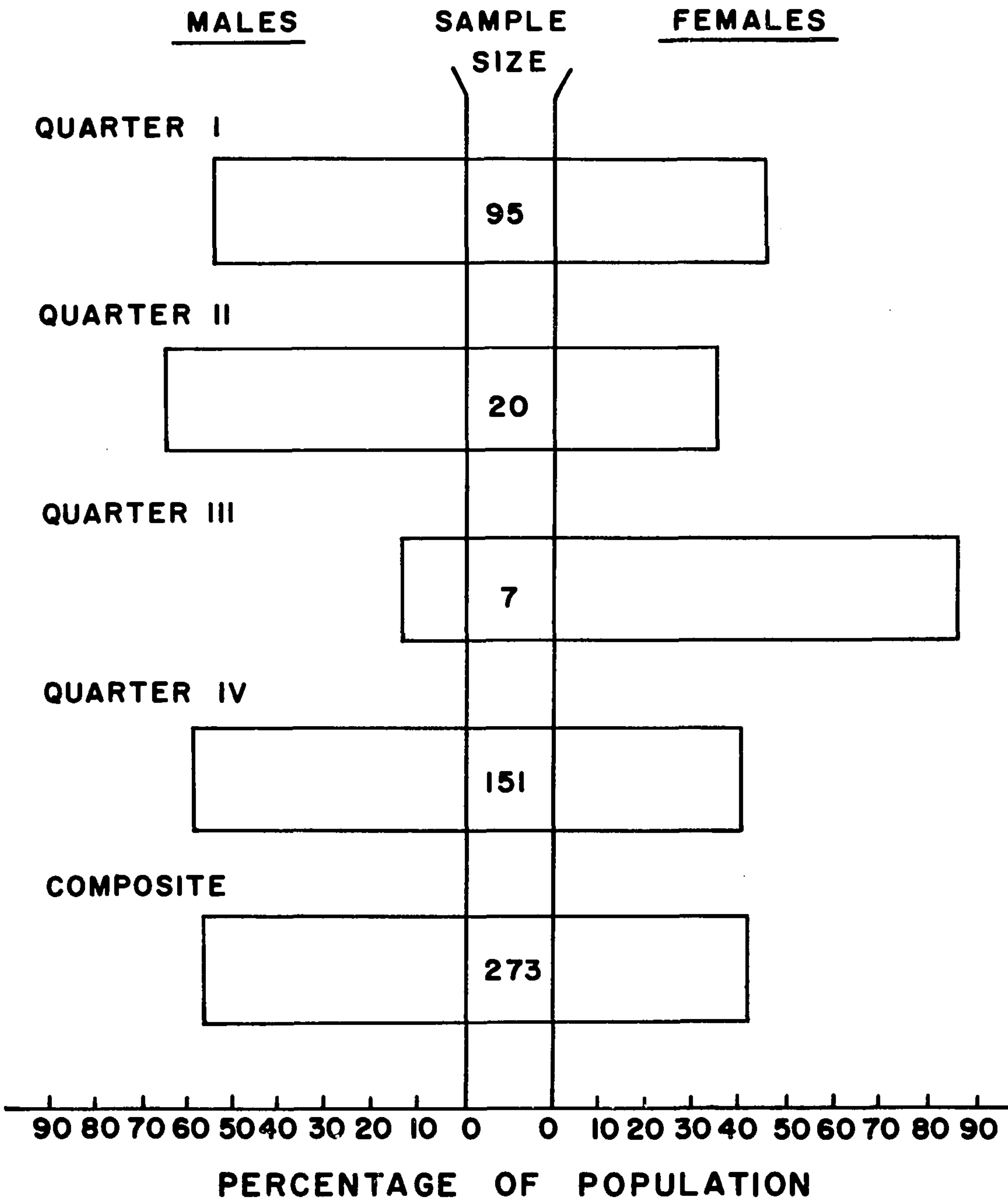


Figure 25. Ratio of the sexes within quarterly coyote subsamples.

Table 11. Sex ratios within composite known-sex sample tabulated by age class, and results of chi-square testing of variation from an even (1:1) ratio.

Age Class (yrs.)	N	Male	Female	X^2	Probability
0 - 1	100	50	50	0.00	P>99.5
1 - 2	37	19	18	0.03	0.90>P>0.75
2 - 3	40	24	16	1.60	0.25>P>0.10
3 - 4	28	16	12	0.57	0.50>P>0.25
4 - 5	29	19	10	2.21	0.25>P>0.10
5+	35	24	11	4.11	0.05>P>0.025*
Overall	269	152	117	4.30	0.05>P>0.025*

*Significant

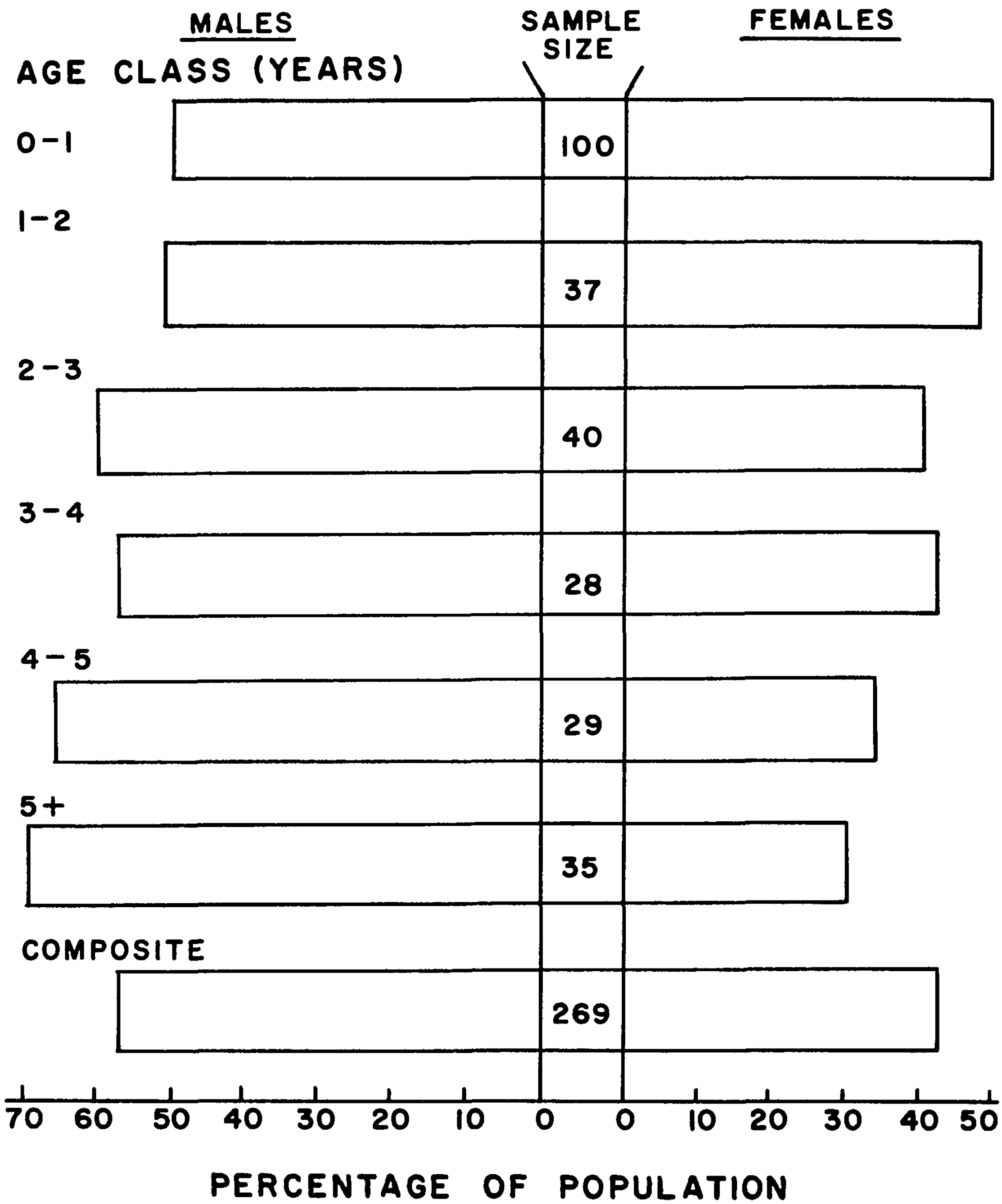


Figure 26. Ratio of the sexes within coyote age classes.

males never reached a significant level. Treatment of the data by individual years resulted in limiting the number of age classes that could be tested, for the subdivided data left fewer chi-square cells with sufficient values (≥ 5) to provide legitimate tests.

Variation in sex ratios between age classes were tested for three arrays of data representing the composite sample and years 1 and 2 of the study. No significant differences were detected between age classes in any case. Results of statistical testing have already been presented in connection with the discussion of sex specific age distributions, and appear in Table 7. These results implied that sex ratios did not vary significantly from one age class to another.

By Cause of Death. When coyote specimens were tabulated by cause of death and sex, the figures presented in Table 12 resulted. A simple chi-square test was applied to determine the significance of departure from an even sex ratio within each category, and results also appear in Table 12. Visual comparison of sex ratios by cause of death can be made by viewing the histograms of Figure 27.

Among road-killed coyotes, females predominated. Sample size was relatively small and this relationship was not statistically significant ($X^2 = 1.0$, d.f.=1, $0.50>P>0.25$).

Hunter-killed coyotes exhibited a sex ratio which more closely approximated 1:1; variation from an even sex ratio was insignificant ($X^2 = 0.27$, d.f.=1, $0.75>P>0.50$). This could be interpreted as support for the hypothesis that members of family groups were more likely to respond to varmint calling (see Coyote Behavior: Loose Associations), for both sexes appeared about equally vulnerable.

Table 12. Sex ratios within composite known-sex sample tabulated by cause of death, and results of chi-square testing of variation from an even (1:1) sex ratio.

Cause of Death	N	Male	Female	X^2	Probability
Road-killed	25	10	15	1.00	$0.50 > P > 0.25$
Hunter-killed	60	32	28	0.27	$0.75 > P > 0.50$
DWS-killed	157	98	59	9.20	$0.005 > P$ **
Overall	242	140	102	5.66	$0.025 > P > 0.010$*

*Significant

**Highly significant

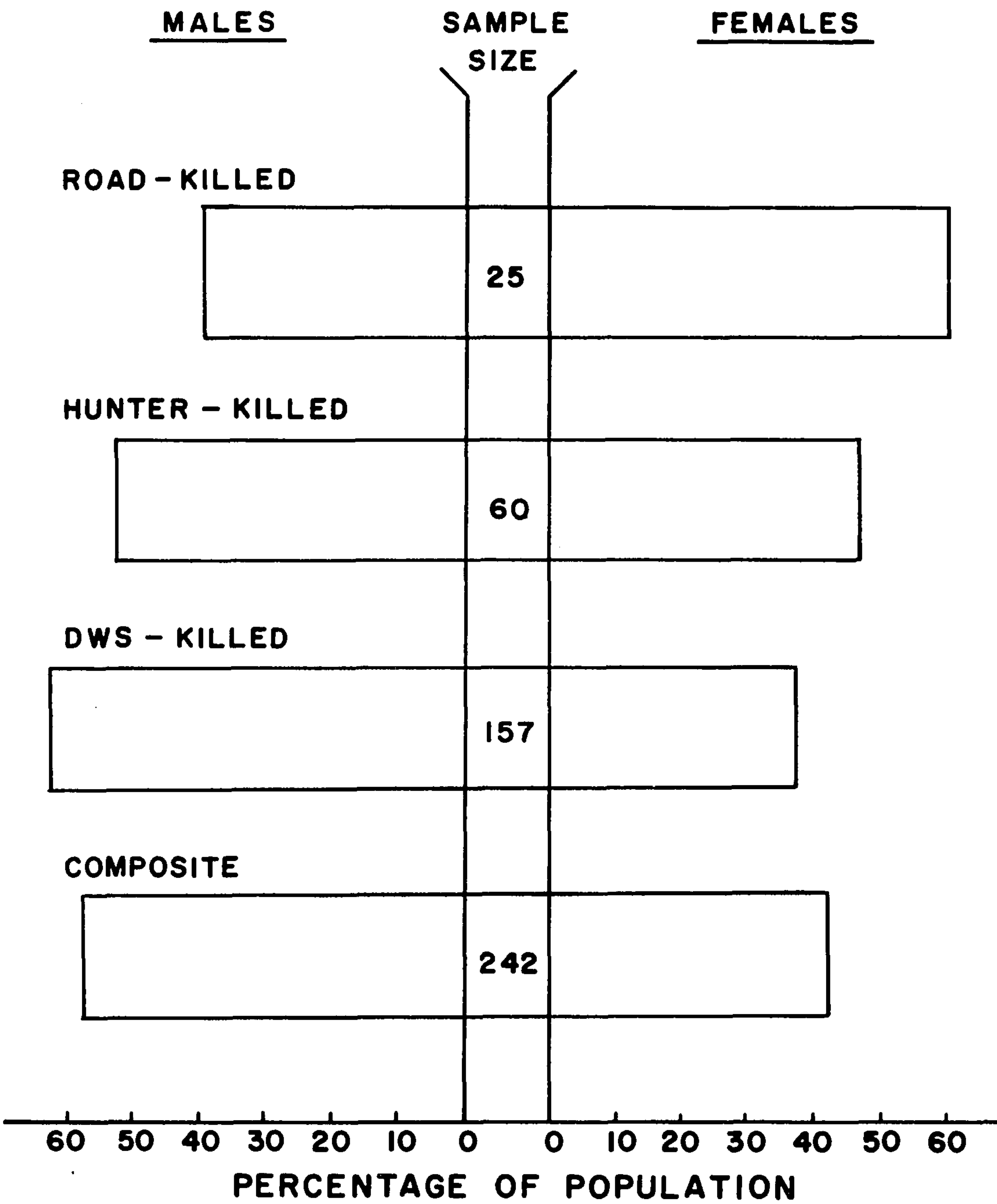


Figure 27. Ratio of the sexes within coyote subsamples representing 3 different causes of death.

Most interesting were the results obtained from comparison of the sexes of coyotes taken by trapping and poisoning. Both means of killing coyotes appeared to be much more effective against males, for statistical testing indicated a highly significant departure from an expected 1:1 sex ratio. Scent, primarily urine, was used to attract coyotes to traps; this may have been more effective in attracting males. Scent also played a part in attracting coyotes to poisoned bait, but in this case it was food related and probably not sex specific.

A hypothetical reason for the observed preponderance of males among DWS-killed coyotes may have been their general mien. If males tended to be bolder and less suspicious of threatening situations, as contended in discussions of coyote behavior and food habits elsewhere in this report (see Coyote Behavior: Male versus Female, and Coyote Food Habits: Analysis by Sex of Coyote), their likelihood of being killed by these control methods would be greater than would be the case for shyer, less aggressive females. Dobie (1961) noted that females were generally more distrustful and difficult to trap.

Comparing sex ratios between the three categories of causes of death resulted in a chi-square value which only approached significance ($X^2 = 5.2$, d.f.=2, $0.10>P>0.05$).

<u>By County of Origin</u>. Sex ratios obtained from coyote subsamples representing southern Arizona counties are presented in Table 13. Ratios within counties were compared with an expected even sex ratio by means of a chi-square test, and results appear in Table 13 as well. Sex ratios by county are presented graphically in Figure 28.

Table 13. Sex ratios within composite known-sex sample tabulated by county of origin, and results of chi-square testing of variation from an even (1:1) sex ratio.

County	N	Male	Female	X^2	Probability
Cochise	53	31	22	1.53	0.25>P>0.10
Gila	3	2	1		-No test-
Graham	45	32	13	7.20	0.01>P>0.005**
Greenlee	6	5	1		-No test-
Maricopa	30	11	19	2.13	0.25>P>0.10
Pima	53	23	30	0.92	0.50>P>0.25
Pinal	53	32	21	2.28	0.25>P>0.10
Santa Cruz	1	1	0		-No test-
Yavapai	18	11	7	0.89	0.50>P>0.25
Yuma	7	4	3		-No test-
Overall	269	152	117	4.30	0.05>P>0.025*

*Significant

**Highly significant

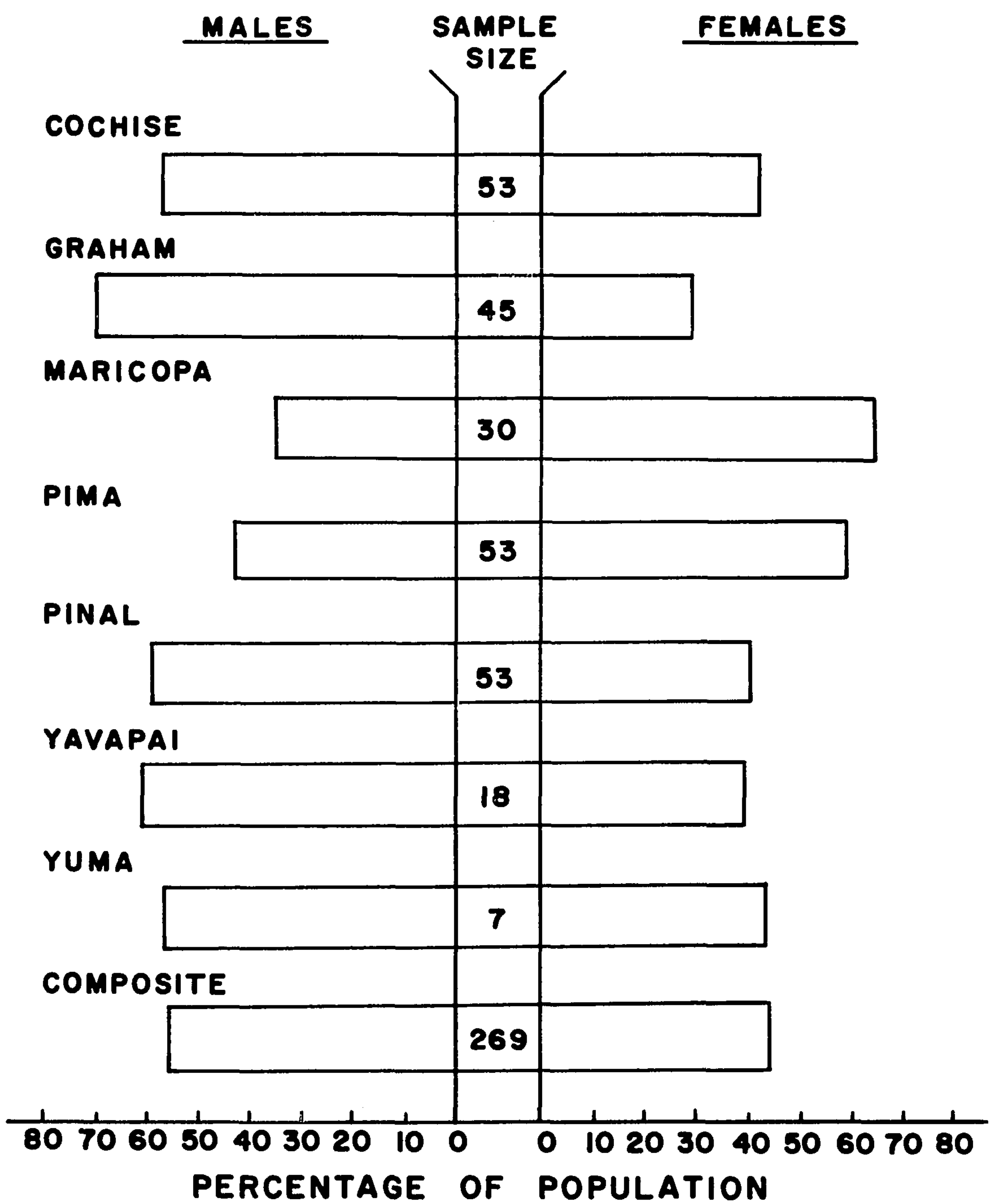


Figure 28. Ratio of the sexes within coyote subsamples representing southern Arizona counties.

Comparing the sex ratios visually (Fig. 28) it is obvious that there was regional variation. Too few specimens were available from several of the counties to allow meaningful statistical comparisons. For the five counties represented by relatively large numbers of known-sex coyotes, sex ratios within counties tended to diverge less dramatically from an expected even ratio. The exception was the Graham County sample in which males outnumbered females by more than two to one, and the variation was highly significant.

The sex-specific data for Cochise, Graham, Maricopa, Pima, Pinal, and Yuma counties were compared to determine if the observed disparity in ratios between counties was statistically significant. These counties were selected because they were represented by larger numbers of coyotes, and their use was consistent with the earlier comparison of age distributions between counties. The observed differences between counties proved to be significant ($X^2 = 12.7$, d.f.=5, $0.05>P>0.025$), indicating that sex ratios did not vary uniformly between these subsamples. How well actual subpopulations of coyotes were represented by the sampling was problematical.

<u>Comparison with Other Studies</u>. Several researchers have reported sex distributions within coyote populations from different regions across western North America. Data from different reports have been assembled in Table 14; results of testing for significant departure from an even sex ratio within the population samples are also presented. Sex ratios among coyotes from the different regions are compared graphically in Figure 29. Many investigators felt that

Table 14. Sex distribution within samples of coyote populations from different regions of North America, and results of chi-square testing of variation from an even (1:1) sex ratio.

Reference	Region	N	Male	Female	X^2	Probability
Adams 1978	Nebraska	321	158	163	0.08	0.90>P>0.75
Andrews and Boggess 1978	Iowa	805	428	377	3.23	0.10>P>0.05 a.s.
Berg and Chesness 1978	Minnesota	1558	813	745	2.97	0.10>P>0.05 a.s.
Crowe and Strickland 1975	Wyoming	225	98	127	3.74	0.10>P>0.05 a.s.
Gier 1968	Kansas	2059	1064	995	2.31	0.25>P>0.10
Knowlton 1972	New Mexico	85	47	38	0.95	0.50>P>0.25
Knowlton 1972	Arivaca, Arizona	79	50	29	5.06	0.025>P>0.010*
Knowlton 1972	Kaibab, Arizona	44	25	19	0.82	0.50>P>0.25
Knowlton 1972	Texas (1964)	18	14	4	-No test-	
Knowlton 1972	Texas (1965)	46	27	19	1.39	0.25>P>0.10
Knowlton 1972	Texas (1966)	49	23	26	0.09	0.75>P>0.50
Knowlton 1972	Texas (1967)	49	13	36	9.88	0.005>P**
Mathwig 1973	Iowa	149	86	63	3.55	0.10>P>0.05 a.s.
Nellis and Keith 1976	Alberta	548	269	279	0.18	0.75>P>0.50
Rogers 1965	New Mexico	146	66	80	1.34	0.25>P>0.10
Present Study	Southern Arizona	273	154	119	4.23	0.05>P>0.025*

a.s. = approaching significance
*Significant
**Highly significant

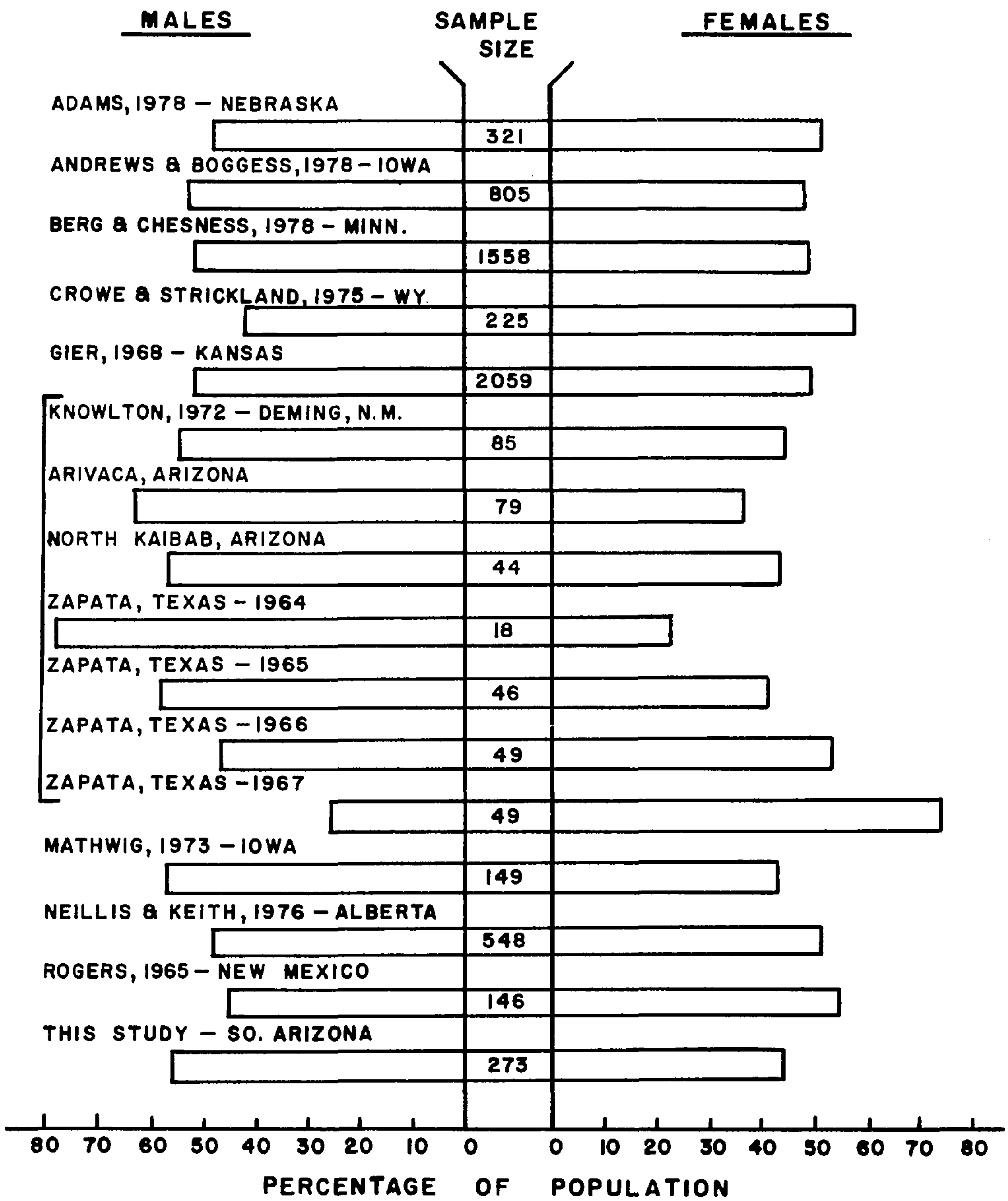


Figure 29. Ratio of the sexes within coyote samples representing different regions of western North America.

males and females were about equally represented, but occasionally a significant shift in favor of one sex or the other took place. The disparity between composite sex ratios representing 13 different regions proved to be statistically significant (X^2 = 22.5, d.f.=12, 0.05>P>0.025).

Integrated Analysis: Variation in Age Structure and Sex Ratio with Year and County of Origin

It was clear that coyote age distributions and sex ratios, as represented by population sampling, varied with year and location. These fluctuations probably reflected adjustments within the population toward the carrying capacity for coyotes. A lesser amount of variation possibly resulted from sampling error, for there were some differences in sources of specimens from one year and county to the next.

Cochise, Pima, and Pinal counties supplied sufficient numbers of specimens for the first two years of the study to attempt further analysis. The respective samples tabulated by sex and year are presented in Table 15. Also appearing in Table 15 are results of chi-square comparisons of observed sex ratios with expected even sex ratios. In the second year, observed variations from an even sex ratio in Pima county proved to be significant, and in Pinal county highly significant.

Results of statistically testing the data within counties between years, and between counties within years are summarized in Table 16. The sex ratios for Cochise county coyote samples remained stable during the two years. However, in Pima county an apparent reversal in sex ratio occurred from year 1 to year 2, for males outnumbered females

Table 15. Coyote population samples from three southern Arizona counties tabulated by sex and year, and results of chi-square comparisons of observed sex ratios with an expected even sex ratio.

County	Year	N	Male	Female	X^2	Probability
Cochise	Year 1	17	10	7	0.53	0.50>P>0.25
	Year 2	36	21	15	1.00	0.50>P>0.25
Pima	Year 1	16	11	5	2.25	0.25>P>0.10
	Year 2	23	6	17	4.35	0.05>P>0.025*
Pinal	Year 1	28	12	16	0.57	0.50>P>0.25
	Year 2	25	20	5	9.00	0.005>P**

*Significant
**Highly significant

Table 16. Results of chi-square comparisons for various combinations of sex distribution data tabulated by year and county. -- See Table 15.

Comparison	X^2	Degrees of Freedom	Probability
Cochise County:			
Year 1 versus Year 2	0.07	1	0.90>P>0.75
Pima County:			
Year 1 versus Year 2	5.36	1	0.025>P>0.010*
Pinal County:			
Year 1 versus Year 2	6.14	1	0.025>P>0.010*
Year 1:			
Ccchise vs. Pima vs. Pinal	2.87	2	0.25>P>0.10
Year 2:			
Cochise vs. Pima vs. Pinal	14.34	2	0.005>P**

*Significant
**Highly significant

by more than two to one in year 1, while in year 2 females outnumbered males by almost three to one. A similar but diametrically opposite situation appeared in Pinal county between the two years, with females slightly more common than males in year 1, and a reversal again taking place in year 2, with males becoming four times more common than females. In both Pima and Pinal counties the variation between years was statistically significant (Table 16). Comparison of the sex ratios between counties within years indicated that most of the variation occurred in year 2.

It seemed reasonable that observed differences in sex ratios were attributable to dissimilarities in recruitment or survivorship of the sexes rather than due exclusively to small differences in sources of specimens. A major source of recruitment was natality. Information on the sex ratios of pups taken in these counties and the proportion of the total sample represented by pups for each of the two years is summarized in Table 17. It was apparent from these data that imbalanced sex ratios among coyotes in the 0-1 year old age class were a major source of inequality in the sex ratios of the overall samples. Presumably this disparity among pups arose from an unequal sex ratio at birth, sex-specific prenatal or postnatal mortality, dispersal favoring one sex, or a combination of these factors.

Odum (1959:171) indicated that the proportion of young animals in a population could be a key to whether that population is expanding or declining. Trend in the size of the 0-1 year old category appeared to be a better criterion. With this in mind, a second relationship was inherent in the data of Table 17. The percentage of the sample

Table 17. Number, percentage of subsample, and sex ratio of coyotes in the 0-1 year old age class from Cochise, Pima, and Pinal counties tabulated by year.

County	Subsample Size	Number of Pups	Percent Pups	Known-sex Specimens Number of Pups	Male Pups	Female Pups
			May 1970-April 1971			
Cochise	17	10	58.8	10	5	5
Pima	37	5	13.5	4	4	0
Pinal	29	12	41.4	12	4	8
			May 1971-April 1972			
Cochise	46	14	30.4	14	7	7
Pima	25	7	28.0	6	1	5
Pinal	27	6	22.2	6	6	0

represented by pups increased in Pima County from year 1 to year 2, and as the 0-1 year old age class expanded, the sex ratio among pups shifted in favor of females. Since females were the productive element, their presence increased population growth potential. Alternately, the percentage of pups in the Pinal County sample decreased from year 1 to year 2, and as the 0-1 year old age class was reduced male pups predominated. Circumstances in Cochise County were less clear, but probably represented a more stable situation, with pups composing a substantial portion of the population in both years and sex ratios remaining balanced.

Very similar data were obtained by Knowlton (1972:374), who presented age and sex frequencies for coyotes taken in Zapata County, Texas, from 1964 through 1967. Over this four year period a gradual shift in sex ratio took place from a predominantly male sample in 1964 to one composed primarily of females in 1967 (see Fig. 29). The variation in sex ratio between years was highly significant ($X^2 = 17.5$, d.f.=3, 0.005 P). When the 0-1 year old component comprised a greater proportion of the overall sample the percentage of females increased. Pups accounted for 55.1 percent of the Zapata County specimens in 1967, with females outnumbering males 23 to 4 within that age class. Knowlton (1972:375) presented additional sex and age information based upon field examination of coyote carcasses which showed the same relationships between sex ratios and percentages of juveniles in the samples.

Similarly, Mech (1975) pointed out disproportionate sex ratios among wolf pups. In areas supporting dense wolf populations males predominated, and conversely in areas of low wolf density females predominated among pups.

In addition to an unequal sex ratio in the 0-1 year old category, changes in sex ratio of the general population may have resulted from differential movements of the sexes among older coyotes. As already discussed (see Coyote Behavior: Size of Home Range: Sex of Coyote), female coyotes residing on the densely populated SRER were prone to travel greater distances than males. Robinson and Grand (1958) and Knowlton (1972) also reported greater movements of females from dense coyote populations. Nellis and Keith (1976) and Chesness and Bremicker (1974) observed greater dispersal distances for females generally. It follows that female coyotes would be the more likely to move into less populated areas which provided the necessities of life.

While male coyotes were also capable of traveling great distances, variations in their numbers may have been more closely tied to sex-specific mortality. Notwithstanding the fact that males tended to outlive females, under some circumstances they appeared to sustain greater losses. Already noted was the preponderance of males taken by DWS control measures. Among various big game species a greater natural death rate among males has been documented (Taber and Dasmann 1954; Cowan 1950). However, based upon the bulk of coyote data that he examined Knowlton (1972) felt that males did not sustain substantially higher mortality than females.

Additionally, Nellis and Keith (1976) found that in two instances where the sex ratio significantly favored females, coyote populations were depressed. Knowlton (1972:377) indicated that females were more prevalent in areas of intensive control. Presumably in both cases coyote populations were attempting to expand toward carrying capacity.

Observed variations in sex ratios among southern Arizona coyotes and consistent observations among coyotes and wolves reported elsewhere suggested that disproportionate sex ratios were part of a stabilizing mechanism which acted to keep coyote populations in balance with their environment. In simplified terms, when coyote numbers were reduced below carrying capacity it appeared that the population responded with increased reproduction and quite possibly ingress. Females were favored during this recruitment phase, thereby enhancing reproductive potential. Gier (1968) and Knowlton (1972) have noted that litter size and the percentage of female pups which successfully bred increased where coyote numbers were depressed. The combination of the three phenomena, that is, a sex ratio skewed in favor of females, larger litters, and a greater incidence of breeding among female pups, provided a means whereby coyote populations could rebound quickly after they had been substantially reduced, by intensive control activities for example. The connection between a population's sex ratio and its status with regard to carrying capacity requires verification via more substantial, carefully controlled population sampling and analysis.

Coyote Reproductive Analysis

Males

Of 22 sets of male sex organs examined, only three pairs did not contain spermatozoa. Of these negative specimens, one set was from an animal killed in June and the others were from coyotes killed in November. A second June coyote had a few spermatozoa remaining in one epididymis, while the other contained no sperm. Of the male sex organs processed none represented December. However, an animal killed in January was producing very large numbers of spermatozoa. It appeared then that in southern Arizona male coyotes generally become sterile by June and remained so for approximately six months, regaining their fertility by January. These results were in agreement with the findings of Hamlett (1938), but suggested a breeding season slightly longer than reported by Gier (1968) for coyotes in Kansas.

Males less than one year of age were fertile. Four males less than a year old had produced spermatozoa during the breeding season, while one killed in November was sterile. Gier (1968) found male pups were fertile in Kansas as well. Because of the low social status of pups and because of the predominance of males in the overall population (see Coyote Population Structure: Analysis of Sex Ratio of the Composite Sample), juvenile males were presumably of no importance in the total coyote reproductive picture.

Females

Of 20 uteri examined, six showed signs of pregnancy ranging from the presence of fetuses to the post-partum bands described by Gier (1968). Only females killed from March through July exhibited such evidence. Possibly prolonged storage of the tissues in a formalin solution caused fading of placental scars, for none were well defined in animals taken during the remainder of the year. In fact, pigmentation bands were often lacking even where swellings of the uterus indicated implantation sites. Specimens showing positive indications of conception are listed in Table 18 along with related information.

The average number of implantation sites per gravid female was 4.5. Only 8 ovaries were available for analysis from these animals, and coincidentally the average number of corpora lutea present was also 4.5.

Based upon this small sample, the youngest females to conceive were 3 year olds, and these had relatively small litters. Of the females examined, all those 3 years of age and older that were killed during the period from March through July were or had been pregnant; two 2 year olds and two one year olds killed during this period showed no evidence of pregnancy.

Two specimens, numbers 24 and 26, contained fetuses of measurable size. Employing measurements presented by Gier (1968) and assuming a 60 day gestation period to age these embryos, dates of conception were calculated as February 27 and March 15, respectively, and dates of parturition would have been April 27 and May 13, respectively.

Gier (1968) reported that under favorable conditions up to 70 percent of females one year of age bred, but under unfavorable circumstances less than 10 percent did so. Knowlton (1972) found that this age class usually did not make an appreciable contribution to general productivity in Texas. This was probably the case in southern Arizona as well. The younger age classes remained a potentially important factor in coyote productivity, however. As discussed by Knowlton (1972),

Table 18. Relevant information on all coyote bitches that showed positive indications of pregnancy within their uteri.

Specimen Number	Month Killed	Age (mos.)	Total Implantations
24	April	36	3
26	April	36	2
30	June	38	3
33	June	62	6
34	July	111	5
79	March	47	8

productivity appeared to be inversely related to density. Had the general coyote population been depressed, presumably younger animals would have made a greater contribution. Unfortunately reproductive information gathered during this study was too scanty to permit a detailed analysis by year or location which might have shed more light upon the importance of younger females in the total reproductive picture.

Coyote Parasites and Diseases

Ectoparasites

Of 101 coyote carcasses which I examined for ectoparasites, only 17 (16.8 percent) were positive for them. Carcasses were seldom those of recently killed animals, and therefore a true index of ectoparasitism was not obtained from this survey. Gier and Ameel (1959) noted that, except in cold weather, fleas left the carcass of a dead host within a few hours after death. Other ectoparasites probably behaved similarly. This reasoning seemed to be substantiated by the fact that of 21 live-trapped coyotes examined, 13 (61.9 percent) carried ectoparasites. The accuracy of these figures is also suspect, however, because on four occasions two coyotes were captured within a short time and were held in close contact in the same cage temporarily, during which time transfer of external parasites may have occurred.

Ectoparasite data obtained from coyote carcasses and from live coyotes are summarized in Tables 19 and 20, respectively.

Because of the error inherent in collecting ectoparasites from old carcasses, and because collections from live animals were

Table 19. Occurrence of ectoparasites on 101 coyote carcasses from southern Arizona.

Ectoparasite	Number Positive Coyotes	Percent Positive Coyotes
Siphonaptera	10	9.9
Pulex simulans	10	9.9
Echidnophaga gallinacea	1	1.0
Thrassis arizonensis	1	1.0
Mallophaga	3	3.0
Heterodoxus spiniger	3	3.0
Acarina	5	5.0
Otobius megnini	5	5.0

Table 20. Occurrence of ectoparasites on 21 live coyotes from southern Arizona.

Ectoparasite	Number Positive Coyotes	Percent Positive Coyotes
Siphonaptera	11	52.4
Pulex simulans	11	52.4
Echidnophaga gallinacea	2	9.5
Mallophaga	4	19.0
Heterodoxus spiniger	4	19.0

sometimes made under less-than-ideal conditions in the field, numbers of recovered ectoparasites probably do not reflect true infestation levels. All live-trapped animals were taken from a relatively small area (SRER) of good coyote habitat.

Fleas.

Pulex simulans: This flea was the most common ectoparasite observed during this study. It was recovered in numbers ranging from 1 to 22 ($\bar{x} = 6.9$) from 9.9 percent of the carcasses, and in numbers from 1 to 14 ($\bar{x} = 4.5$) from 52.4 percent of the live animals.

Gier and Ameel (1959) found P. simulans to be the most common flea of Kansas coyotes also. Eads (1948) found the closely related P. irritans to be very common on Texas coyotes, occurring on 98.9 percent of 90 coyotes in numbers averaging 22.5 per host. P. irritans was also listed as a common parasite of coyotes by Young and Jackson (1951) and Parker and Howell (1959). Smit (1958) described the differences between these two pulicids. Critical examination of specimens taken from southern Arizona coyotes during this study revealed that most had features characteristic of P. simulans, including longer maxillary palps, a greater number of bristles on sternum VII, and a broad aedeagal sclerite. The differences between these two species in southern Arizona were apparently not so striking as reported by Gier and Ameel (1959), for some specimens had intermediate characteristics.

Echidnophaga gallinacea: In this study 14 specimens of the sticktight flea were recovered from one coyote carcass, and two live-trapped coyotes yielded one and three specimens. In every case this flea occurred together with *P. simulans* on the host. Eads (1948) found 22 specimens of this species on a single coyote from Texas.

Thrassis arizonensis: A single specimen of this flea was recovered with *P. simulans* from a coyote. *T. arizonensis* normally parasitizes rodents, and it is reasonable to assume that it occurred accidentally on the coyote after transfer from prey to predator.

Lice.

Heterodoxus spiniger: This louse, originally identified as a parasite of marsupials, is commonly found on canids in warm climates. In the present study it was recovered from 3 percent of the carcasses in numbers ranging from one to 26 ($\bar{x} = 12$), and from 19 percent of the live coyotes in numbers ranging from one to 14 ($\bar{x} = 6.8$). However, numbers are not representative of infestations on live coyotes. Of the four live coyotes carrying *H. spiniger* two yielded only one specimen each, but the other two coyotes supported much heavier infestations of which only a portion of the lice were collected. In the most severe case approximately 50 lice parasitized the host coyote, which had multiple abrasions from scratching and chewing to alleviate the attendant irritation. Similar abrasions were noted on one carcass from which nine lice were recovered.

H. spiniger and *P. simulans* sometimes occurred together on the same host.

Eads (1948), Hopkins (1949), and Emerson (1962) previously reported this louse from coyotes.

Ticks.

Otobius megnini: I recovered nymphs of the spinose ear tick from 5 percent of the coyote carcasses in numbers ranging from one to two. Two coyotes yielded two of the nymphs, one from each ear. This parasite lodged deeply in the ear and was detected only by cutting open the auditory canal. It was not recovered from any live coyotes.

The coyote was listed by Bishopp and Trembley (1945) as a host for *Ornithodoros megnini* (synonymous with *Otobius megnini*) as well as for several other ticks. A series of Texas coyotes examined by Eads (1948) yielded six species of ticks, including *O. megnini*; he regarded general tick infestation of coyotes as light. Stiles and Baker (1935) also list a number of ticks as parasites of coyotes. No other ticks were recovered from coyotes during the course of this investigation. This was surprising since engorged ticks were frequently observed on jackrabbits and my dog occasionally acquired common dog ticks, *Rhipicephalus sanguineus*, while in the field.

Endoparasites

I recovered endoparasites from 97 of 103 carcasses examined, and even this high rate of infection, because of the condition of some of the carcasses, was conservative. Occasionally pieces of viscera were lacking from road-killed coyotes and hunter-killed coyotes that had been shot with high-powered rifles. Ninety-nine carcasses were critically examined for intestinal parasites, and of these only two animals were found to be completely free of them. Occurrence of endoparasites in southern Arizona coyotes is summarized in Table 21.

Table 21. Occurrence of endoparasites in 103 coyotes from southern Arizona.†

Endoparasite	Number Positive Coyotes	Percent Positive Coyotes
Cestoda	62	62.6
Taenia pisiformis	55	55.6
Taenia hydatigena	1	1.0
Taenia macrocystis	6	6.1
Taenia multiceps	22	22.2
Mesocestoides sp.	6	6.1
Nematoda	79	79.8
Ancylostoma caninum	38	38.4
Filaroides osleri	3	2.9
Toxascaris leonina	43	43.4
Physaloptera rara	50	50.5
Physaloptera sp.	1	1.0
Rictularia cahirensis	3	3.0
Mastophorus numidica	1	1.0
Dirofilaria immitis	2	1.9
Acanthocephala	46	46.5
Oncicola canis	45	45.5
Pachysentis canicola	1	1.0

†Only 99 carcasses examined for intestinal helminths.

Cestodes. Of 99 coyote carcasses examined for them, 62 (62.6 percent) were infected with tapeworms of at least five different species.

Taenia pisiformis: This species was the most common cestode found, occurring in 55.6 percent of the coyotes examined in numbers ranging from one to 93 ($\bar{x}$ = 11.4). However, mature specimens were recovered from only 28 coyotes in numbers ranging from one to 21 ($\bar{x}$ = 5.4). Information on the occurrence of the various growth stages of T. pisiformis recovered is presented in Table 22.

T. pisiformis is a common coyote parasite, having been reported from all of 69 Oklahoma coyotes by Self and McKnight (1950), from 1758 of 1850 (95 percent) Kansas coyotes by Gier and Ameel (1959), from 48 of 67 (72 percent) Michigan coyotes by Dunatchik (1967), from 29 or 43 (67 percent) Manitoba coyotes by Samuel, Ramalingam and Carbyn (1978), from 41 of 75 (55 percent) Utah coyotes by Butler and Grundmann (1954), from 24 of 61 (39 percent) Minnesota coyotes by Erickson (1944), from 23 of 75 (31 percent) Alberta coyotes by Holmes and Podesta (1968), and from 66 of 339 (19 percent) Ontario coyotes by Freeman, Adorjan, and Pimlott (1961). This no doubt reflects the universal importance of lagomorphs, which serve as intermediate hosts for this taeniid, in the diet of coyotes.

Gier and Ameel (1959) reported as many as 150 mature, 250 immature, and 600 scoleces from an individual coyote, with an overall average of 43 specimens per coyote. Both the incidence and number of cestodes per coyote were considerably lower in southern Arizona. This probably reflected more diverse food habits (see Coyote Food Habits) as compared to Kansas, where leporids composed over 50 percent of the

Table 22. Occurrence of developmental stages of cestodes recovered from southern Arizona coyotes.

Cestode and Growth Stage	Number Positive Coyotes	Total Cestodes	Min.	Max.	Average
<u>Taenia pisiformis</u>	55	627	1	93	11.4
Scoleces	22	193	1	58	8.8
Immature	31	283	1	65	9.1
Mature	28	151	1	21	5.4
<u>Taenia hydatigena</u>	1	4	4	4	4.0
Scoleces	1	4	4	4	4.0
Immature	0	0	0	0	0.0
Mature	0	0	0	0	0.0
<u>Taenia macrocystis</u>	6	23	1	9	3.8
Scoleces	2	2	1	1	1.0
Immature	5	21	1	8	4.2
Mature	0	0	0	0	0.0
<u>Taenia multiceps</u>	22	674	1	109	30.6
Scoleces	18	393	1	77	21.8
Immature	6	155	1	64	25.8
Mature	7	126	1	60	18.0
<u>Mesocestoides sp.</u>	6	160	1	151	26.7
Scoleces	3	153	1	150	51.0
Immature	3	3	1	1	1.0
Mature	3	4	1	2	1.3

coyote diet (Tiemeier 1955; Gier 1968). It was most interesting to note that mature worms occur in relatively small numbers in both locations. Ameel (1955) reported 25 mature tapeworms as about maximum, with an average infection consisting of less than 10. These figures were comparable to those found in this study and may reflect the maximum burden of this species that can be supported by a mature coyote.

Gier and Ameel (1959) conjectured that tapeworm infections at the levels generally found in coyotes were no more than mildly detrimental to the hosts. According to Abuladze (1964) the usual manifestation of infection, if severe enough, was digestive tract disturbance, including irregular appetite, alternating diarrhea and constipation, and a chronic catarrhal condition. In heavier infections obstruction, invagination, and even perforation of the intestine were possible. In observations of infections in domestic dogs (*Canis familiaris*), symptoms developed most intensively in puppies, leading to depression and progressive emaciation, with death an eventual possibility (Abuladze 1964). It seems reasonable to infer similar reactions in coyotes. Gier and Ameel (1959) have shown that coyote pups can become infected very early in life. Since the various taeniids attack their hosts in the same manner, the resulting pathology is probably similar regardless of the species of cestode involved.

A means whereby coyotes may accidentally clear themselves of tapeworms was stumbled upon in the course of this study. In cases where fecal matter plugged the rectum, this material was forced out prior to flushing the intestine as previously described. In one such instance this material consisted largely of the shredded pods of mesquite beans, entangled among which were portions of several mature tapeworms. No scoleces were observed, but otherwise the tapes appeared to be relatively complete. Subsequently, about 10 mature tapeworms were recovered from the intestine of this coyote. Coarse vegetation occasionally ingested by coyotes may serve to scour cestodes from their intestines. Supportive of this hypothesis, minimum incidence and intensity of cestode parasitism occurred during quarter III (see Tables 23 and 24, pp. 155, 156) concurrently with peak consumption of mesquite beans by coyotes (see Coyote Food Habits).

Taenia hydatigena: In this study one coyote yielded four scoleces which I identified as *T. hydatigena*. No mature specimens were found. This species is apparently seldom common in coyotes, as suggested by reported incidences of 3 of 43 (7 percent) in Manitoba by Samuel, Ramalingam and Carbyn (1978), 3 of 67 (4 percent) in Michigan by Dunatchik (1967), 2 of 75 (3 percent) in Utah by Butler and Grundmann (1954), 1 of 75 (1 percent) in Alberta by Holmes and Podesta (1968), and 3 of 339 (1 percent) in Ontario by Freeman et al. (1961). An exception was the occurrence of *T. hydatigena* in 19 of 61 (31 percent) coyotes in Minnesota as reported by Erickson (1944).

Intermediate hosts include deer, sheep, and other ruminants, all of which may be of lesser importance in the coyote diet generally. Grundmann (1958) recovered the infective larvae of this taeniid from a rabbit and a rodent in Utah, and Abuladze (1964) reported that the cysticerci occur in rodents in Russia. That such instances are uncommon in these small mammals, which comprise a large percentage of coyote prey, was suggested by the infrequent occurrence of *T. hydatigena* in coyotes.

Taenia macrocystis: Wardle and McLeod (1952) placed this species in the genus *Hydatigera*, whereas Abuladze (1964) referred it to *Taenia*. In view of the findings of Esch and Self (1965), *Taenia* appeared to be the correct genus.

In the present study six coyotes (6.1 percent) harbored this tapeworm in small numbers in its developmental stages. Apparently it has not been previously reported from the coyote, and the fact that no mature specimens were recovered may indicate that the coyote is an unsuitable host. Intermediate stages occur in lagomorphs and wild Felidae reportedly serve as the common definitive hosts.

Taenia multiceps: The taxonomy of this species has undergone considerable revision. Using criteria presented by Wardle and McLeod (1952), the two species *Multiceps multiceps* and *M. serialis* were indistinguishable, except that *M. serialis* produced daughter cysts in the intermediate host. Examination of a number of larval stages, which were quite common in jackrabbits from this region, revealed that adventitious cysts were the rule, hence *M. serialis* seemed to be the proper classification. Further research, however, revealed that Clapham (1942) had shown *M. multiceps* and *M. serialis* to be one species, the presence of adventitious cysts resulting from an intermediate host reaction. Clapham's conclusions were accepted for this study, though other authorities felt *M. serialis* was a valid species (Abuladze 1964). Cameron (1926) indicated that even the genus *Multiceps* might be invalid. Subsequently Esch and Self (1965) have shown that this indeed was true, and members of the genus *Multiceps* should be relegated to the genus *Taenia*.

T. multiceps was relatively common in southern Arizona coyotes, occurring in 22.2 percent of those autopsied in numbers ranging from one to 109 ($\overline{x}$ = 30.6). Mature specimens, however, only occurred in 7.1 percent of the coyote sample in numbers ranging from one to 60 ($\overline{x}$ = 18.0).

This species was also recovered from 3 of 75 (4 percent) Alberta coyotes by Holmes and Podesta (1968). Dunatchik (1967) reported *Multiceps serialis* from 4 of 67 (6 percent) coyotes that he examined in Michigan. *Multiceps packii* was found in 4 of 75 (5 percent) Utah coyotes by Butler and Grundmann (1954) and in 8 of 17 (47 percent) Utah coyotes by Conder and Loveless (1978), while Erickson (1944) reported the same species in 1 of 61 (2 percent) of the Minnesota coyotes that he examined. Erickson (1944) also reported *Multiceps sp.* from 7 of 61 (11 percent) coyotes in his sample.

Mesocestoides sp.: I recovered mesocestoids from six coyotes (6.1 percent), generally in very small numbers. Four mature specimens were recovered from three coyotes, but another coyote yielded 150 mesocestoid scoleces.

Because of the extensive overlap in characters between species, the great variability of these characters, and the poor condition of some specimens, it was difficult to identify these tapeworms as to species. Using criteria presented by Voge (1955), two specimens were tentatively identified as *M. corti*. No specific identification was attempted from the scoleces alone.

Gier and Ameel (1959) recovered specimens of *M. corti* from 3 of 1850 (0.2 percent) coyotes in Kansas. *M. kirbyi* was first described from several California coyotes, and since has been reported from 3 of 17 (18 percent) and 8 of 75 (11 percent) coyotes from Utah by Conder and Loveless (1978) and Butler and Grundmann (1954), respectively, and from 1 of 75 (1 percent) coyotes from Alberta by Holmes and Podesta (1968). An unidentified mesocestoid was recovered from one coyote in Ontario by Freeman et al. (1961).

As is apparent from findings of this study, coyotes may be subjected to heavy infections with tetrathyridia, the mesocestoid larvae infective for the definitive host. However, it appears that few of these develop into mature forms. Apparently members of this genus are not serious parasites of coyotes.

Other Cestodes: Two cestodes, *Dipylidium caninum* and *Echinococcus granulosus*, were conspicuous by their absence in southern Arizona coyotes. Both have been recovered elsewhere from a relatively small portion of the coyote population in small numbers. *D. caninum* is a common tapeworm of canids, and has been reported from coyotes in Utah by Butler and Grundmann (1954) and in Kansas by Gier and Ameel (1959). *E. granulosus* in coyotes has been reported from Michigan by Dunatchik (1967), from Ontario by Freeman et al. (1961), from Alberta by Holmes and Podesta (1968), and from California by Liu et al. (1970). *E. granulosus* is responsible for development of hydatid cysts, and so has great public health significance. Both of these species are quite small, but since numerous minute scoleces of other cestodes were recovered it was unlikely that these forms would have been overlooked had they been present.

Nematodes. Nematodes were the most common group of parasites encountered. Information on their occurrence in coyotes from southern Arizona is summarized in Table 21.

Ancylostoma caninum: In this study the dog hookworm occurred in 38.4 percent of 99 coyotes autopsied for intestinal helminths in numbers ranging from one to 82 ($\bar{x}$ = 8.8).

This parasite is commonly recovered from the coyote. Thornton, Bell and Reardon (1974) reported finding it in each of 13 coyotes examined from Texas, Franson et al. (1978) encountered it in 72 of 144 (50 percent) Iowa coyotes, Dunatchik (1967) reported an infection rate of 22 in 67 (33 percent) among Michigan coyotes, Gier and Ameel (1959) found an incidence of 463 of 1850 (25 percent) in Kansas coyotes, Conder and Loveless (1978) identified *A. caninum* from 2 of 17 (12 percent) Utah coyotes, Erickson (1944) found 2 of 61 (3 percent) Minnesota coyotes infected, and Holmes and Podesta (1968) found it in 1 of 75 (1 percent) Alberta coyotes. From fecal samples gathered in southern Texas, Mitchell and Beasom (1974) estimated a minimum infection rate of 90.4 percent there.

Reportedly *A. caninum* was rare in southern Arizona less than 20 years ago (Dewhirst, personal communication 1980), but widespread irrigation practices combined with influx of people and their pets have resulted in its becoming common.

Hookworms are voracious blood consumers. The adults live in the small intestine, where they attach themselves to the intestinal wall, lacerate the tissue, and secrete an anticoagulant to insure the free flow of blood. Much blood is lost because the parasites often move to new attachment sites, leaving open wounds behind. Clark et al. (1961)

found infected domestic dog pups lost an average of 0.07 cc. of blood per hookworm per day. T. A. Miller (1965) reported that immunity to infection developed with age, with pups being highly susceptible. Compounding the threat to young animals, infection may be acquired prenatally, with even lighly infected females producing heavily infected pups (Foster 1935). Heavy infection results in progressive anemia and other debilitating effects which could lead to death. Gier and Ameel (1959) and Mitchell and Beasom (1974) note the importance of this parasite as a factor in coyote mortality.

Filaroides osleri: This parasite was found in nodules at the junction of trachea and bronchi in 3 of 103 (2.9 percent) of the coyotes that I examined for it. Individual worms were not counted. Later, nodules containing nematodes, probably *F. osleri*, were detected in the trachea of a road-killed coyote autopsied as a classroom demonstration.

Price (1928) first reported *Oslerus osleri*, synonymous with *F. osleri*, as a coyote parasite from a single case in Texas, Since, Samuel, Ramalingam and Carbyn (1978) reported this parasite from 20 of 43 (47 percent) Manitoba coyotes, Thornton et al. (1974) reported it from 4 of 13 (31 percent) coyotes taken in southern Texas, Dunatchik (1967) found *F. osleri* in 17 of the 67 (25 percent) Michigan coyotes that he examined, Conder and Loveless (1978) reported it in 3 of 17 (18 percent)Utah coyotes, Morrison and Gier (1978) found it in 68 of 395 (17 percent) coyotes representing the Great Plains, Holmes and Podesta (1968) recorded an incidence of 11 in 75 (15 percent) in Alberta coyotes, and Erickson (1944) detected it in 3 of 61 (6 percent) Minnesota coyotes.

The life cycle is incompletely known, though slugs and snails are suspected intermediate hosts,since they serve this purpose for other closely related metastrongyles. Olsen and Bracken (1959) felt that mice might serve as transport hosts. Dorrington (1965) reported direct transmission in dogs under experimental conditions.

Morgan and Hawkins (1949) noted that nodules may range up to 10 mm. in size, and if very numerous could cause death from suffocation. Such an infection in a domestic dog was reported by Mills and Nielsen (1966), but presumably a severe infection in a wild coyote would simply result in its undetected death. No such gross pathology was observed in southern Arizona coyotes. In the most severe case, nodules up to 8 mm. in diameter were scattered up the trachea to about 3 inches (7.6 cm.) above its bifurcation, but no more than a quarter inch (0.6 cm.) below it. No significant blockage of air resulted.

Levine (1968) stated that young animals were probably more susceptible than older ones. Thornton et al. (1974) reported that of four infected coyotes, two were juveniles. In the present study only one of three infected coyotes was less than a year old, though the other two animals were less than 2 years of age. Due to its low incidence _F. osleri_ is probably not an important factor in coyote population dynamics in southern Arizona at this time.

Toxascaris leonina: One of the more common parasites identified during this investigation, this ascarid occurred in 43.4 percent of the coyotes examined for intestinal helminths in numbers ranging from 1 to 73 ($\bar{x}$ = 13.8). This species is relatively easy to confuse with the related _Toxocara canis_. The condition of unwinged spicules in males and smooth-shelled ova in females of T. leonina proved useful criteria for differentiating between the two.

T. leonina is a common and widespread parasite of carnivores (Levine 1968). In other studies, Samuel, Ramalingam and Carbyn (1978) reported 28 of 43 (65 percent) Manitoba coyotes infected, Holmes and Podesta (1968) observed this ascarid in 39 of 75 (52 percent) Alberta coyotes, Franson et al. (1978) found it in 56 of 144 (39 percent) Iowa coyotes, Butler and Grundmann (1954) found an infection rate of 28 of 75 (37 percent) in Utah, Gier and Ameel (1959) reported an incidence of 610 of 1850 (33 percent) in Kansas, and Conder and Loveless (1978) found it in 5 of 17 (29 percent) Utah coyotes. Dunatchik (1967) found only 1 of 67 (1 percent) Michigan coyotes carrying this nematode, and postulated that the cool summer climate of the Lake States accounted for the generally low rates of infection there. However, the finding of T. leonina in 72 percent of 200 Alaskan wolves by Rausch and Williamson (1959) appeared to refute this hypothesis.

Butler and Grundmann (1954), Gier and Ameel (1959), and Levine (1968) all indicate that younger animals are more susceptible to infection. This worm lives on intestinal contents, and therefore is a competitor with its host for nourishment. Infected puppies show signs of unthriftiness, enlarged abdomens, and digestive disturbances, and in severe cases intestinal blockage and rupture may occur (Levine 1968). Heavy infection of coyote pups could result in their deaths. Infections may be perpetuated about dens where the soil is contaminated by infected adults (Butler and Grundmann 1954). Gier and Ameel (1959) presented evidence that coyote pups became infected very early in life, probably by way of infected nipples. Larvae of *T. leonina* do not normally migrate through the host (Wright 1934), which suggests that prenatal infection is of no consequence. Sprent (1959) reported that mice might harbor infective larvae, and the importance of small mammals in the coyote diet suggests that infection via such transport hosts may be significant.

Physaloptera rara: This spirurorid proved to be the most common nematode of southern Arizona coyotes, occurring in 50.5 percent in numbers ranging from one to 97 ($\bar{x} = 9.8$). Stomach worms were generally free in the stomach, though on occasion I found one attached to the stomach wall. They apparently moved about freely after the host was killed, and were often found in the esophagus, occasionally were flushed from the intestine, and if the stomach was pierced by a shot were found within the abdominal capity.

Also the most frequently encountered nematode parasitizing Michigan coyotes, *P. rara* was reported from 41 of 67 (61 percent) by Dunatchik (1967). Stomach worms, the great majority of which were *P. rara* were found in 925 of 1850 (50 percent) Kansas coyotes by Gier and Ameel (1959). Erickson (1944) reported a relatively low incidence, 3 of 65 (5 percent) from Minnesota coyotes.

Physaloptera sp.: One coyote harbored a single physalopterid which I was not able to identify as to species. This specimen was a slightly damaged male, apparently immature, with a definite prepuce-like sheath partially enclosing the posterior end. *P. praeputialis* or *P. pseudopraeputialis* appeared to be the most likely possibilities.

Unidentified physalopterids have been reported from 96 of 144 (67 percent) Iowa coyotes by Franson et al. (1978), from 3 of 13 (23 percent) Texas coyotes by Thornton et al. (1974), from 8 of 65 (12 percent) Minnesota coyotes by Erickson (1944), from 3 of 43 (7 percent) Manitoba coyotes by Samuel, Ramalingam and Carbyn (1978), and from 1 of 17 (6 percent) Utah coyotes by Conder and Loveless (1978). Occasionally food habits investigators report finding stomach worms: Mathwig (1973) reported 54.3 percent of 151 coyote stomachs from Iowa, Fichter, Schildman and Sather (1955) found 44.7 percent of 747 coyote stomachs from Nebraska, and Sperry (1941) noted 1.6 percent of 14,829 stomachs representing 15 western states contained unidentified physalopterids.

Members of the genus _Physaloptera_ subsist by attaching themselves to the stomach wall and sucking blood from their host. Movement of the worms to different attachment sites results in numerous bleeding lesions. The level of infection generally found in adult coyotes is not particularly injurious, whereas survival of coyote pups with infections exceeding 50 worms is doubtful (Gier and Ameel 1959).

Rictularia cahirensis: In the present investigation three coyotes yielded four female specimens of this small but somewhat spectacular spirurorid. Taxonomy of the genus is confused, many species having been described from insufficient material. Using criteria presented by Skrjabin, Sobolev and Ivashkin (1967), specimens recovered in southern Arizona seemed to fit most closely the description of _R. splendida_. Gibbs (1957) placed _R. splendida_ and another species in synonomy with _R. cahirensis_, and his conclusions were accepted for this report. Although _R. splendida_ was listed as a parasite of coyotes by Young and Jackson (1951), no other recent studies have identified this parasite from coyotes. In view of the small numbers of worms present, the infrequency of infection, and the lack of knowledge about the pathogenicity of this nematode, even for dogs, it appears to be of little importance to the coyote.

Mastophorus numidica: One coyote harbored three specimens, a male and two females, of this species. Again taxonomy is confused and specific identification somewhat difficult. Descriptions and illustrations presented by Chitwood and Chitwood (1950), Read and Milleman (1953), and Yamaguti (1961) proved useful.

Butler and Grundmann (1954) reported Protospirura numidica (synonymous with M. numidica) from 1 of 75 (1 percent) coyotes in Utah. Sperry (1941) recovered P. numidica and the related M. muris from coyote stomachs examined while gathering food habits data. Members of the genus Mastophorus commonly parasitize rodents, an important component of the coyote diet, and in view of Sperry's findings it seems probable that some coyote parasitism may result from ingesting infected rodents. The presence of few worms coupled with low incidence of infection again seems to indicate that this nematode is generally unimportant to the coyote.

Dirofilaria immitis: I recovered the dog heartworm from 2 of 103 coyotes examined for it. A few mature worms were recovered from the right ventricle of an extremely old coyote, while in the second animal, a 9 month old female, a mass of worms filled the right ventricle and a number extended out into the pulmonary artery.

Dr. Stephen Bowen, Command Veterinarian, Yuma Proving Ground, Arizona, during a Venezualian equine encephalitis surveillance program near Yuma,noted the frequent occurrence of microfilariae in coyote blood samples. Subsequently Bowen (personal communication 1973) found 19 of 25 coyotes (76 percent) collected from May, 1972, through January, 1973, positive for heartworm. All coyotes were taken within 20 miles of the Colorado River,where they presumably had ample exposure to mosquito vectors capable of transmitting the parasite.

Elsewhere, Thornton et al. (1974) found the dog heartworm in 3 of 13 (23 percent) coyotes from Texas, Graham (1975) identified *D. immitis* from 11 of 133 (8 percent) coyotes from Kansas and Colorado; Franson, Jorgenson and Boggess (1976) found it in 8 of 220 (4 percent) Iowa coyotes, Ellis (1958) found 1 of 25 (4 percent) coyotes infected in Oklahoma, and Gier and Ameel (1959) reported finding 9 infected hearts in 900 (1 percent) Kansas coyotes examined.

Heartworm infection can certainly be a debilitating condition in dogs. According to Levine (1968) symptoms may not appear until 8 or 9 months after infection. Infected animals tire easily, develop poor physical condition, extreme weakness, progressive anemia, and other symptoms. Congestive heart failure is the usual cause of death (Hartley 1938). One would reasonably expect effects of infection to be more serious in coyotes, since they lead a more rigorous life.

Evaluating *D. immitis* from the standpoint of its effect on coyote populations is an interesting problem. Generally the incidence of infection is low and the overall effect on the population negligible. Under such conditions the conclusion of Schlotthauer (1964) that wild mammal populations do not serve as highly significant reservoirs of heartworm infection would generate little controversy. However, under favorable conditions such as appear to exist along the Colorado River in southwestern Arizona, a majority of hosts may become infected and provide a very large reservoir for infection. Because coyotes in that area remain abundant,the effect of such a situation on their populations remains to be clarified by further research.

Other Nematodes: Trichinella spiralis occurs in a wide variety of animals, though the natural hosts are carnivores. It is well known in the pig and rat (Levine 1968), and has been reported parasitizing diverse forms from the horned owl (Zimmerman et al. 1962) to whales (Rausch 1951). It is of special interest because it is readily transmissible to man.

Rausch et al. (1956) found encysted larvae in 1 of 8 (12.5 percent) coyote diaphragms from Alaska, Zimmerman et al. (1962) found 5 of 44 coyotes (11.4 percent) in Iowa infected with T. spiralis, while Olsen (1960) found the larvae encysted in 1 of 193 coyote tongues (0.5 percent) from Colorado. In the present study 45 coyote diaphragm tissue samples were examined for larvae and none were found. No mature worms were recovered from intestinal flushings.

Several other more common canine helminths are notable for their apparent absence in southern Arizona coyotes. Toxocara canis was not identified from Arizona coyotes, though it does occur among domestic dogs in southern Arizona (Dewhirst, personal communication 1972). T. canis was not recovered from a large series of Kansas coyotes examined by Gier and Ameel (1959); it was recovered from single coyotes in Utah by Butler and Grundmann (1954) and by Conder and Loveless (1978), and in Alberta by Holmes and Podesta (1968). Whipworms, *Trichuris vulpis*, were not found during this study though all caeca were examined for them. Also absent from southern Arizona coyotes was the giant kidney worm, *Dioctophyme renale*, although it has been reported from coyotes elsewhere (Brunetti 1959; Holmes and Podesta 1968). *Spirocerca lupi* has been previously recorded from coyotes (Thornton et al. 1974; Dunatchik 1967), as has the lungworm, *Capillaria aerophila* (Morrison and Gier 1978; Holmes and Podesta 1968), although neither could be detected during the present study.

Acanthocephalans. I identified spiny-headed worms of two species from 46 of 99 coyotes examined for intestinal helminths. These forms are not commonly reported from coyotes, but appear to parasitize them regularly in southern Arizona. This finding is in harmony with the theory presented by Van Cleave (1953) that mammalian acanthocephalans are concentrated in southern states where they have geographical continuity with the same or related species in mammals of Central and South America.

Oncicola canis: This rather small acanthocephalan occurred in 45 of 99 coyotes (45.5 percent) in numbers ranging from 1 to 123 ($\bar{x}$ = 15.6). Price (1928) recovered *O. canis* from a coyote in Texas, but few accounts of this parasite in coyotes have appeared since. Price (1926) felt *O. canis* occurred only rarely in dogs, and infection was generally asymptomatic. Reportedly symptoms similar to those of rabies are characteristic of severe infection (Petrochenko 1958). One would expect heavy infections to cause enteritis and other symptoms similar to those reported for taeniid tapeworm infections, since both forms imbed their probosci in the intestinal wall. It is interesting that hydrophobic symptoms have been reported for severe tapeworm infections as well (Abuladze 1964). Relatively little research has been conducted on *O. canis*, and even its life cycle remains unknown.

Pachysentis canicola: I recovered five specimens identified as *P. canicola* from a single coyote. This appears to be the first record of this parasite from the coyote. It has been previously reported from foxes and skunks (Van Cleave 1953) and so is not an unexpected parasite of the coyote. *P. canicola* is even less known than *O. canis*, but very probably results of infection are similar.

Statistical Analysis of Endoparasitism

Six species of parasites were recovered consistently enough to allow a meaningful analysis of intensity and incidence of infection based upon age class, sex, year of death, season of death, and county of origin of the host coyotes. These species were *Taenia pisiformis*, *Taenia multiceps*, *Oncicola canis*, *Ancylostoma caninum*, *Toxascaris leonina*, and *Physaloptera rara*. Average intensity and incidence of infection data appear in Tables 23 and 24, respectively.

By Age Class of Hosts. All but one species of intestinal helminth showed a greater average number of parasites per coyote host less than a year of age than for older animals. If these parasites were lumped together, pups averaged 61.2 intestinal helminths each, while adult hosts averaged 29.3 each, a difference which was highly

Table 23. Intensity of endoparasite infection expressed as average number of helminths per infected coyote.

		Intestinal helminths collectively	*Taenia pisiformis*	*Taenia multiceps*	*Oncicola canis*	*Ancylostoma caninum*	*Toxascaris leonina*	*Physaloptera rara*
Age	Less than 1 year	61.2	15.0	39.8	21.9	6.2	21.6	11.8
	Over 1 year	29.3	9.8	21.5	12.6	9.7	11.7	9.0
Sex	Male host	24.5	9.2	36.5	8.1	6.6	11.8	7.8
	Female host	49.1	13.8	24.8	20.7	10.8	15.7	11.4
Year	May 1970-April 1971	21.7	10.1	43.3	5.6	2.5	8.3	4.5
	May 1971-April 1972	40.6	11.9	28.5	18.0	7.9	13.3	12.7
Season	Quarter I	32.2	9.1	26.8	11.2	5.5	10.9	8.0
	Quarter II	25.1	23.3	1.3	5.1	10.9	13.0	2.0
	Quarter III	39.8	2.0	1.0	21.5	25.8	28.0	10.0
	Quarter IV	44.1	9.7	45.5	25.6	4.9	15.7	13.1
County	Cochise	30.5	13.9	11.0	11.4	10.2	13.7	6.9
	Pima	41.0	11.3	26.2	20.0	9.1	17.7	11.3
	Pinal	48.6	8.0	61.8	4.1	4.4	7.9	11.6

Table 24. Incidence of endoparasite infection expressed as number of infected coyotes over total number of coyotes examined.

		Intestinal helminths collectively	*Taenia pisiformis*	*Taenia multiceps*	*Oncicola canis*	*Ancylostoma caninum*	*Toxascaris leonina*	*Physaloptera rara*
Age	Less than 1 year	24/24	17/24	11/24	14/24	10/24	10/24	15/24
	Over 1 year	71/74	37/73	11/73	32/73	28/73	32/73	34/74
Sex	Male host	52/55	29/54	11/54	23/54	18/54	21/54	23/55
	Female host	44/45	26/45	11/45	23/45	20/45	22/45	27/45
Year	May 1970-April 1971	22/23	10/22	4/22	10/22	3/22	12/22	11/23
	May 1971-April 1972	61/62	39/62	14/62	30/62	26/62	23/62	32/62
Season	Quarter I	37/39	21/39	8/39	22/39	8/39	21/39	22/39
	Quarter II	16/16	9/15	3/15	7/15	10/15	2/15	4/16
	Quarter III	5/6	2/6	1/6	2/6	4/6	2/6	3/6
	Quarter IV	39/39	23/39	10/39	15/39	16/39	18/39	21/39
County	Cochise	27/27	20/27	6/27	9/27	14/27	7/27	16/27
	Pima	38/42	18/41	9/41	22/41	17/41	23/41	21/42
	Pinal	17/17	10/17	6/17	8/17	5/17	9/17	8/17

significant ($z = 3.269$, $P = 0.0005$). However, when these helminths were considered by species, differences in numbers were less striking. Numbers of _T. pisiformis_ per pup averaged 15.0 while for adults the average was 9.8, and this difference was significant ($z = 1.825$, $P = 0.03$). In no other species was the difference in numbers of parasites per coyote by age class found to be significant. In the five remaining species, probabilities of the recorded differences being due to chance ranged from 10.0 to 37.5 percent. Only in the case of _A. caninum_ did the average intensity of infection in adults exceed that in pups, 9.7 versus 6.2 worms per coyote, respectively.

The proportion of coyotes less than a year old infected with _T. multiceps_ and the proportion of older coyotes infected with this cestode differed at a highly significant level ($X^2 = 8.1$, $0.005>P$); 45.8 percent of the younger coyotes were infected while only 15.1 percent of the adults were. The other five species of helminths showed no significant differences in the incidence of infection by age class ($0.975>P>0.10$). Generally at least a slightly greater proportion of pups was infected.

These findings were consistent with what was suspected about the development of immunity with age in coyotes. Unfortunately a serious bias existed within the juvenile sample. The majority of contributors to the study began killing coyotes in the fall with the onset of hunting season and continued through spring when depredation control efforts increased. As a result pups were represented predominantly by coyotes 6 to 12 months of age. By this age they were approaching adulthood. Animals less than 6 months of age were of special interest, but were represented in the sample by only two road-killed specimens. Had a larger number of younger pups been sampled, differences by age class may have been accentuated.

Franson et al. (1978) reported a significant decline in numbers of *A. caninum*, *T. leonina*, and *Physaloptera sp.* with increasing age of coyote hosts in Iowa. Frequency of infection with these helminths also declined with advancing age, although this trend proved significant only in the case of *A. caninum*.

By Sex of Hosts. After comparing numbers of parasites per coyote by sex of host, it was apparent that females harbored greater parasite burdens than did males. If numbers of parasites were pooled, males averaged 24.5 and females 49.1 intestinal helminths per coyote, a difference which was statistically significant ($z = 1.957$, $P = 0.025$). Considering the parasite species individually only *O. canis* yielded a significant difference in numbers of worms by sex of host, averaging 8.1 per male and 20.7 per female coyote ($z = 1.988$, $P = 0.023$). *A. caninum* and *T. leonina* closely approached significance in this regard ($z = 1.593$, $P = 0.056$; and $z = 1.555$, $P = 0.061$, respectively), while the differences for the other helminths were insignificant ($0.32<P<0.44$).

Differences in the proportion of infected coyotes by sex were not statistically significant for any of the six species of helminths tested, though in all cases a greater proportion of females were infected. The greatest divergence appeared in the case of *P. rara* where the difference was 41.8 percent of males versus 60.0 percent of females infected ($X^2 = 2.6$, $0.25>P>0.10$). In the cases of other species of parasites the probability of differences being chance ranged from 25 to 90 percent.

Generalizing from these findings, it appeared that females were susceptible to greater collective endoparasite burdens, though incidence of infection was not significantly greater than for males. The greater intensity of infection among bitches may have been related to physiological stress associated with pregnancy and lactation, to behavioral differences, to food habits differences, or to other factors. These findings have importance since the female segment of the population was primarily responsible for reproduction. By influencing the condition of females, parasitism might act to control population growth.

Franson et al. (1978) found no significant differences in numbers of parasites or frequency of infection with respect to sex of host coyotes from Iowa.

By Year of Death of Hosts. Numbers of endoparasites recovered from coyotes killed from May 1, 1970, through April 30, 1971 (year 1) were generally lower than numbers of endoparasites recovered from those killed from May 1, 1971, through April 30, 1972 (year 2). When intestinal helminths were considered collectively, worm burdens averaged 21.7 and 40.6 worms per coyote in year 1 versus year 2, respectively, a difference which was statistically significant ($z = 1.969$, $P = 0.024$). In the case of *T. leonina* the difference of 8.3 versus 13.3 worms per coyote for years 1 and 2, respectively, was highly significant ($z = 2.659$, $P = 0.004$). Differences in intensity of infection data for the other species of helminths tested were not significant, though significance was approached in the case of *P. rara* ($z = 1.503$, $P = 0.067$).

A statistical comparison of incidence of infection for the two years revealed a significant difference for only one species. In year 1, 13.6 percent of the coyotes were infected with *A. caninum* while in the following year the infection rate for this parasite jumped to 41.9 percent, a difference which was statistically significant ($X^2 = 4.6$, $0.05 > P > 0.025$). For the other five species of helminths tested differences in the proportion of infected coyotes for the two years were not significant ($0.995 > P > 0.10$).

Apparently conditions more favorable for transmission and maintenance of infections by the majority of these helminths were encountered by coyotes in year 2 than in year 1. Because of the complexity of the ecology of the various parasites it is difficult to say why this was so, but subtle differences in weather, in prey populations, in coyote populations, and in less obvious factors could have been responsible. What was important from the standpoint of the present study was that both intensity and incidence of infection, and hence the impact of parasitism upon the coyote population, varied between years.

By Season of Death of Hosts. Because only 16 coyotes represented quarter II and only six coyotes were taken in quarter III, this discussion of endoparasitism by season should be accepted qualifiedly. Generally numbers of endoparasites per infected coyote were at their lowest level in spring (quarter II), and subsequently rose to their seasonal high in fall and winter (quarters IV and I). This trend was best reflected by numbers of intestinal helminths collectively, which averaged 25.1 worms per infected coyote in quarter II, 39.8 in quarter III, 44.1 in quarter IV, and then dropped to 32.2 in quarter I. Average numbers for individual species tended to be slightly more erratic by season, reflecting individual differences in life cycle and probably the greater influence of chance on the smaller sample sizes for coyotes infected with each species compared to those infected with any helminth. In no case were the numbers of worms significantly different by season, though in the cases of the two cestodes, *T. pisiformis* and *T. multiceps*, these figures approached significance ($H = 6.754$, $P = 0.084$; and $H = 6.592$, $P = 0.089$; respectively). For the other four species and for intestinal helminths collectively probabilities for observed differences occurring by chance ranged from 20.4 to 92.7 percent.

Differences in the proportions of infected coyotes by season showed no consistent pattern for the six species of parasites tested, as can be seen in Table 24.

The proportion of coyotes infected with cestodes was at its lowest level in summer, but rose during the cooler seasons, probably reflecting the increased importance of lagomorphs, the chief intermediate hosts for these parasites, in the coyote diet (see Coyote Food Habits). Seasonal differences in the incidence of cestodes in coyotes were not statistically significant ($0.95>P>0.50$).

Also insignificant statistically were seasonal variations in the proportion of coyotes harboring acanthocephalans ($0.95>P>0.10$).

In the case of A. caninum the difference in proportions of infected coyotes between quarters I and II was highly significant ($X^2 = 8.4$, $0.005>P$), and approached significance between quarters I and III ($X^2 = 3.6$, $0.10>P>0.05$) and I and IV ($X^2 = 2.9$, $0.10>P>0.05$). The pattern of high incidence in the warmer months and low incidence in the cooler months occurred only for the dog hookworm. Conditions required for development of infective larvae, that is temperatures of 25-30°C and a moist environment (Levine 1968) occurred most consistently during quarters II and III, and apparently most infected coyotes acquired hookworm during this period. Because neither intermediate nor transport hosts were of importance in the hookworm life cycle, incidence of infection appeared to increase rapidly when conditions for transmission were met. Levine (1968) noted that the life span of A. caninum ranged from a few months to 2 years. In adult coyotes having a good immune mechanism the shorter life span may have been more characteristic. Infected coyotes probably shed hookworms continually, and once cooler fall weather arrived conditions favorable for reinfection did not occur until the following spring. Such reasoning was supported by data on intensity of infection. Beginning with quarter I, average numbers of hookworms per infected coyote were 5.5, 10.9, 25.8, and 4.9, respectively. Also contributing to the decrease in incidence, of course, was attrition of the coyote population itself, with infected coyotes presumably at a disadvantage..

The proportion of coyotes infected with T. leonina differed at a significant level between quarters I and II ($X^2 = 5.7$, $0.025>P>0.01$) and approached significance between quarters II and IV ($X^2 = 3.7$,

$0.10>P>0.05$). The seasonal pattern of incidence for this nematode reflected a low rate of infection in quarter II, and a gradual increase as more coyotes were exposed to infection as the year progressed. The use of transport hosts by this parasite, as suggested by Sprent (1959), would explain why incidence of infection continued to increase for a time after environmental conditions were no longer favorable for development of infective ova. The sharp decline in rate of infection between quarters I and II may have resulted from death of a number of infected hosts, from natural death of worms, or from shedding of them during a period when reinfection was unlikely.

In the case of _P. rara_ the proportion of infected coyotes did not differ significantly by season. However, differences in incidence of infection approached significance between quarters I and II ($X^2 = 3.3$, $0.10>P>0.05$) and quarters II and IV ($X^2 = 2.7$, $0.10>P>0.05$). This situation was similar to that for _T. leonina_ and lent itself to the same explanation.

By County of Origin of Hosts. Coyote-parasite relationships were compared for three counties in southern Arizona from which adequate coyote samples were obtained: 27 coyotes from Cochise, 42 from Pima, and 17 from Pinal counties yielded the parasite data used in these tests.

Comparing numbers of endoparasites per infected coyote by county revealed a statistically significant difference for only one species, _T. multiceps_ ($H = 6.477$, $P = 0.041$). This cestode ranged in average numbers per coyote from 11.0 in Cochise county to 61.8 in

Pinal county. Differences in intensity of infection for the other five species of helminths tested and for all intestinal helminths collectively were not significant ($0.87>P>0.32$).

Analysis of the incidence of infection in the three counties revealed a significant difference for two species of parasites, and in both cases this difference occurred between coyotes from Cochise versus Pima counties. T. pisiformis occurred in 74.1 and 43.9 percent of the coyotes examined from Cochise and Pima counties, respectively, and this difference was significant ($X^2 = 4.85$, $0.05>P>0.025$). Also significant was the difference in incidence of infection with T. leonina, which occurred in 25.9 and 56.1 percent of the coyotes examined from Cochise and Pima counties, respectively ($X^2 = 4.85$, $0.05>P>0.025$). All other observed differences in incidence of infection from these three counties were insignificant ($0.95>P>0.10$).

Of the two host-parasite relationships investigated, intensity of infection was the less variable. This could be interpreted as an indication that coyotes were able to sustain about the same degree of parasitism regardless of where they lived. Variability in incidence of infection was much more important. One explanation would be differences in opportunity for infection between the counties. Generally the greatest differences in host-parasite relationships were recorded between Cochise and Pima counties, and the least differences between Pima and Pinal counties. Of the three counties Cochise was unique in that it fell within a faunal area characterized largely by grassland rather than by the desert shrub more typical of the other two counties

(Swarth 1929). This implied differences in availability of prey and in climate, both of which were primary considerations in the transmission of parasites. For example, a simplified explanation of the greater incidence of *T. pisiformis* in Cochise county might be that a lusher flora supported a larger cottontail population, which provided greater opportunity for infection. Obviously many other factors influence parasitism, and a detailed explanation of all observed differences is beyond the scope of this report.

Diseases

Rabies. First in importance among the zoonoses because its existence endangers domestic livestock and even human life, rabies is perennially detected in a number of wildlife species in southern Arizona. While the majority of cases involve skunks and bats, a small number of rabid coyotes have been reported each year ("Animal Rabies Summary," *Arizona Veterinarian*, December 1968; January 1970; August 1971 and 1972; and January 1973). Perhaps the largest outbreak in recent years occurred in the spring of 1977 when several rabid coyotes were detected near Tucson in Pima county.

In an attempt to detect the disease, I submitted 27 coyote heads taken from animals killed by various means in four southern Arizona counties to the Laboratory Division of the Arizona State Department of Health in Phoenix. Four heads were submitted for testing in 1971, 19 in 1972, and four in 1973. A fluorescent antibody test was performed upon material from each specimen. All results were negative.

While the coyote has not figured to any appreciable extent in the general rabies picture, epizootics in coyotes have occurred from time to time. Gier (1948) reported serious outbreaks of the disease among coyotes in 1915-1916 on the West Coast and in 1943 in New Mexico, while Schoening (1956) reported another outbreak among coyotes in Oregon, California, Nevada, and Idaho in 1950. Such serious situations have not developed in southern Arizona in recent years in spite of potentially dangerous outbreaks of the disease among skunks in Santa Cruz county in 1968-69 ("Rabies in Arizona," Arizona Public Health Epidemiology, February and August 1969), among dogs in the Yuma area and among domestic cats (*Felis domesticus*) in Tucson in 1964 ("Rabies in Arizona," Arizona Public Health Epidemiology, March 1965). An outbreak of rabies among coyotes and dogs in the vicinity of Tucson in the spring of 1977 was apparently controlled by the standard procedures of population reduction and immunization of pets.

Southern Arizona supports a large, almost contiguous population of coyotes. The fact that a few rabid coyotes are encountered in this region yearly, and yet have not triggered an epizootic, suggests that many of the concepts about rabies in wildlife as outlined by Sikes (1970) and other may be inaccurate. So little is known about the effect of this disease among coyotes that this discussion must draw upon information gained from studying rabies in other species. The notion that rabid animals spread the disease by wandering widely was refuted by Gier (1948), who felt that infected animals probably did not travel far after becoming sick. Substantiation came from Storm and Verts (1966), who discovered that movements of a radio-tagged rabid skunk were not significantly different from those of healthy skunks. Though the disease commonly originates with the bite of an infective animal, other possible means of transmission include consumption of infected prey (Ramsden and Johnston 1975), contact with urine from infected animals (Debbie and Trimarchi 1970), and the aerosol route (Sikes 1970). Not all animals exposed to the virus develop fatal rabies (Carey and McLean 1978). Younger animals are more susceptible (Tierkal 1959). Verts (1967) has shown that the stress of pregnancy and lactation increased the infection rate among female skunks. Other stress factors would probably increase susceptibility as well. The population control potential of rabies has been documented among foxes by Parker et al. (1957); these researchers noted that even after a significant decrease in fox numbers, the disease remained enzootic in the remaining sparse population. Apparently not unlike the southern Arizona coyote situation, Parker et al. (1957) found high fox populations adjacent to enzootic regions and postulated some unknown ecological barrier to account for this. It is clear that our understanding of the course of rabies among coyotes, and among other wildlife species as well, is inadequate, and further research is needed.

Oral Papillomatosis. Based upon the gross appearance of wartlike lesions about the lips and mouth, oral papillomatosis was diagnosed in two of the coyotes examined during the course of this study. In the first case pulpy masses of wartlike growths covered the lips and extended onto the cheeks and gums, particularly on the left side of the head, while the tongue was unaffected. In the second case much smaller but very similar growths appeared on the lower lips, more noticeably on the right side. In neither case was the condition especially debilitating. In both cases the afflicted animals were females and appeared otherwise normal, except that both harbored relatively heavy endoparasite burdens. Both animals were killed by varmint hunters, the first on 14 August, 1971, and the second on 29 January, 1972, but of particular interest is the fact that both came from the same locale, north of Bowie in Cochise county.

Young and Jackson (1951:109) reported "buccal papillomata" from Mohave county, Arizona, in 1945, when 10 to 15 percent of local coyotes had severe infections. Subsequently this disease was identified in coyotes from Texas by Trainer, Knowlton and Karstad (1968), from Saskatchewan and Alberta by Broughton et al. (1970), from Alberta by Samuel, Chalmers and Gunson (1978) and by Nellis (1973), and from Manitoba by Greig and Charlton (1973). These authors generally agree that unless spectacular the disease is often overlooked.

Leptospirosis. On 28 March, 1973, I encountered an extremely weak and obviously very ill coyote during field operations on the SRER. The animal was shot, but later autopsy revealed no gross abnormalities. The test for rabies proved negative. Histologic examination of kidney tissue samples from the animal revealed an accumulation of lymphocytes and macrophages in the interstitial stroma, presence of tubular casts, thickening of Bowman's capsule, and chronic glomerulitis. These findings suggested the possibility of a leptospiral infection (Bicknell 1973; Smith, Jones and Hunt 1972:562-565).

Subsequently blood samples were drawn from nine coyotes of both sexes and different ages which were live-trapped on the SRER for the behavioral phase of the present study. Serology tests for *Leptospira canicola* were positive in four cases, and one of these was also positive for *L. icterohaemorrhagiae*. Another serotype, *L. pomona*, was also tested, but results were negative in every case. These three serotypes are the most common in North America, with *L. canicola* commonly causing leptospirosis in dogs (Roth 1970).

Andrews and Ferris (1966) found that the distribution of leptospirosis among wildlife was facilitated because the animals shared a common piece of habitat. According to Roth (1970) leptospirae are passed in the urine of infected animals and may survive for several weeks in moist soil or stagnant ponds. It seemed probable that the extremely wet spring of 1973, with rainfall accumulations of over 4 inches above normal on the SRER in March alone (ESSA 1973), provided conditions favorable for the spread of the disease. Stock ponds seemed likely sources of infection, although no leptospirae were found in water samples taken from eight different stock watering areas on the study area in early June. The coyote's use of urine for scent marking (Kleiman 1966) provided an obvious means of transmitting the disease organisms. Another likelihood was transmission through direct physical contact between coyotes during social interactions about common feeding sites, or during the mating season which reaches its peak in February in southern Arizona. Acquisition of leptospirosis by coyotes from rodent prey was also a possibility, as rodents have been shown to carry antibodies to *L. canicola* (Cirone et al. 1978).

Because coyote numbers reach their low point in the annual cycle each spring (Gier 1968; Knowlton 1972), it was difficult to evaluate the effect of the disease upon the SRER coyote population. In the absence of any data on their numbers, but based upon my contact with coyotes on the SRER for three years, it appeared that their population was depressed more than normally expected by late spring of 1973. Riders for the Santa Rita Ranch who were very familiar with the area agreed. Possibly leptospirosis was a factor in the deaths of some coyotes during this period.

Though leptospirosis has been reported commonly in wildlife, there has been scant reference to the disease in coyotes. Trainer and Knowlton (1968) reported serologic evidence of *L. canicola* in one of 33 Texas coyotes. More recently Cirone et al. (1978) detected leptospiral antibodies in all of 12 California coyotes that they screened; 9 serotypes were represented, with one coyote apparently carrying antibodies to all 9.

Other Diseases. A number of other diseases are potentially important to coyotes, though relatively little is known of them in wild populations. Probably foremost among these is distemper. Trainer and Knowlton (1968) reported serologic evidence of this disease in a third of 33 Texas coyotes that they screened. Gier and Ameel (1959) found that under laboratory conditions coyote pups were especially susceptible to distemper, and once contracting the disease their prognoses were unfavorable, while adult coyotes appeared to have developed an immunity to infection. Murie (1940) suspected distemper as the disease that reduced coyote numbers in Yellowstone Park in the late 1930's. Gier (1968) felt this disease was indeed one capable of controlling coyote populations.

Infectious canine hepatitis (ICH) also has serious implications for coyotes. Again little is known of the disease in the wild, but coyotes have been experimentally infected. Cabasso (1970) noted that prognosis for young animals was poor, but recovery was followed by a durable immunity. Serologic reactors to the disease were found in 17 of 33 coyotes from Texas by Trainer and Knowlton (1968). That ICH can seriously afflict coyotes was substantiated by Ryden (1974), who reported that the disease killed 90 percent of the pups born in one year on the National Elk Refuge. Camenzind (1978) also reported an outbreak of ICH there.

Coccidioidomycosis is primarily a respiratory disease caused by the fungus *Coccidioides immitis* and enzootic in the American Southwest. Straub, Trautman and Greene (1961) reported the disease in 3 of 5 coyotes from southern Arizona. During the present study no evidence of coccidioidomycosis was observed. Respiratory tracts from two coyotes were examined by Dr. R. E. Reed, Department of Veterinary Sciences, but otherwise it was unlikely that any but the most severe infections would have been detected. Another fungal infection, histoplasmosis, was expected but undetected among Kansas coyotes by Gier and Ameel (1959).

A general synopsis of the diseases of coyotes is provided by Gier, Kruckenberg and Marler (1978).

Coyote Food Habits

Food Habits as Determined from Stomach Contents

Over 80 categories of food items were recovered from 101 coyote stomachs, including remains of mammalian, bird, reptilian, invertebrate, and vegetable foods. The large variety reflected the diverse feeding habits of coyotes in southern Arizona. Relatively few items were present in large quantity regularly enough to be considered staples of the diet, however. Of the 101 stomachs, 9 were empty while 11 contained materials in trace amounts only.

Frequency of occurrence and relative volume of all items identified from coyote stomach contents are presented in Table 25. Relative volumes were estimated no closer than 5 percent, yet when overall percentage figures were derived decimal fractions resulted. Percentage figures are presented to one decimal place for comparative purposes only, and should not be interpreted as being otherwise significant.

Lists of items occurring in coyote stomachs should be accepted cautiously and not without related ecological information. Stomachs utilized in the present study were collected from an extensive geographical area over a span of more than 2 years. Often adequate background information was lacking. Some amplification is given in the following pages. Rather than attempting a point-by-point comparison with similar coyote food habits studies conducted at other times in other localities, the reader is invited to make his own comparisons by referring to Table 33 (see p. 220).

Table 25. Contents of 101 coyote stomachs collected in southern Arizona from October, 1970, through June, 1973, expressed in percentage of occurrence and percentage of total volume.

Item	Percentage Occurrence	Percentage Volume
All Mammal	68.3	60.4
Larger Mammal	28.7	25.4
Cow (*Bos taurus*)	9.9	10.9
Sheep (*Ovis aries*)	2.0	1.0
Pig (*Sus scrofa*)	2.0	5.1
Cat (*Felis domesticus*)	3.0	1.3
Mule deer (*Odocoileus hemionus*)	3.0	4.8
Unidentified deer (*Odocoileus sp.*)	2.0	0.3
Javelina (*Tayassu tajacu*)	2.0	1.3
Coyote (*Canis latrans*)	5.9	0.2
Unidentified	3.0	0.5
Smaller Mammal	54.5	35.0
Lagomorph	26.7	20.9
Antelope jackrabbit (*Lepus alleni*)	2.0	3.0
Blacktailed jackrabbit (*Lepus californicus*)	3.0	2.0
Unidentified jackrabbit (*Lepus sp.*)	4.0	0.5
Desert cottontail (*Sylvilagus auduboni*)	10.9	14.4
Unidentified cottontail (*Sylvilagus sp.*)	5.0	0.8
Unidentified lagomorph	2.0	0.2
Rodent	37.6	14.1
Porcupine (*Erethizon dorsatum*)	1.0	2.3
Kangaroo rat (*Dipodomys sp.*)	5.9	3.2
Pocket mouse (*Perognathus sp.*)	6.9	0.9
Packrat (*Neotoma sp.*)	5.0	3.6
Cotton rat (*Sigmodon hispidus*)	4.0	1.4
Deer mouse (*Peromyscus sp.*)	3.0	0.4
House mouse (*Mus musculus*)	3.0	2.0
Rock squirrel (*Spermophilus variegatus*)	2.0	Trace
Chipmunk (*Eutamias sp.*)	1.0	0.4
Unidentified small rodent	11.9	0.1

Table 25--*continued*. Contents of 101 coyote stomachs.

Item	Percentage Occurrence	Percentage Volume
Bird	26.7	16.4
Chicken (*Gallus gallus*)	4.0	7.1
Pheasant (*Phasianus colchicus*)	5.0	6.4
Gambel's quail (*Lophortyx gambelii*)	1.0	0.3
Unidentified quail	2.0	0.2
Sparrow (*Fringillidae*)	2.0	0.5
Inca dove (*Scardafella inca*)	1.0	Trace
Brewer's blackbird (*Euphagus cyanocephalus*)	1.0	0.1
Unidentified passerine	5.0	0.8
Unidentified raptor	2.0	1.1
Unidentified bird	5.0	Trace
Reptile	5.0	0.1
Lizard (Sauria)	3.0	Trace
Iguanid (Iguanidae)	2.0	Trace
Spiny lizard (*Sceloporus sp.*)	2.0	Trace
Teiid (Teiidae)	2.0	Trace
Snake (Serpentes)	3.0	0.1
Coachwhip (*Masticophis sp.*)	1.0	Trace
Shovel-nosed snake (*Chionactis occipitalis*)	1.0	Trace
Unidentified	1.0	0.1
Invertebrate	41.6	6.4
Centipede (*Scalopendra sp.*)	2.0	0.1
Insect	41.6	6.3
Grasshoppers, crickets, etc. (Orthoptera)	22.8	6.3
Grasshopper	18.8	5.0
Short-horned (Acrididae)	2.0	4.9
Melanoplus sp.	1.0	3.1
Boopodon sp.	1.0	0.2
Unidentified grasshopper	16.8	0.1
Cricket (Gyrillidae)	3.0	1.3
Cockroach (Blattidae)	1.0	Trace

Table 25--*continued*. Contents of 101 coyote stomachs.

Item	Percentage Occurrence	Percentage Volume
Insect (continued)		
Beetles (Coleoptera)	8.9	Trace
Dermestid (Dermestidae)	1.0	Trace
Unidentified beetle	7.9	Trace
Moths (Lepidoptera)	1.0	Trace
Cocoon only	1.0	Trace
Flies (Diptera)	12.9	Trace
Maggots only	12.9	Trace
Ants (Hymenoptera)	2.0	Trace
Myrimicinae	2.0	Trace
Novomessor sp.	1.0	Trace
Unidentified insect	6.9	Trace
Vegetable	80.2	16.2
Fruit	34.7	14.1
Mesquite (*Prosopis juliflora*)	23.8	9.4
Prickly pear (*Opuntia sp.*)	4.0	1.4
Grape (*Vitis sp.*)	1.0	1.8
Watermelon (*Citrullus vulgaris*)	1.0	0.2
Pecan (*Carya illinoensis*)	1.0	0.1
Peanut (*Arachis hypogaea*)	2.0	1.2
Apricot (*Prunus armeniaca*)	1.0	Trace
Orange (*Citrus sinensis*)	1.0	Trace
Apple (*Malus pumila*)	1.0	Trace
Corn (*Zea mays*)	1.0	Trace
Juniper (*Juniperus sp.*)	1.0	0.1
Hackberry (*Celtis sp.*)	1.0	Trace
Assorted seeds	4.0	Trace
Grass	41.6	1.0
Assorted twigs, leaflets, etc.	39.6	1.0

Table 25--continued. Contents of 101 coyote stomachs.

Item	Percentage Occurrence	Percentage Volume
Inorganic	25.7	0.2
Sand	11.9	Trace
Clay	1.0	Trace
Dirt	5.0	Trace
Gravel - Pebbles	18.8	0.1
Miscellaneous	12.9	0.3
Plastic	1.0	Trace
Paper (milk carton, etc.)	3.0	Trace
Leather (boot, glove)	2.0	0.2
Cellophane	3.0	Trace
Monofilament	1.0	Trace
Burlap	2.0	0.2
Heavy cloth webbing	1.0	Trace
Empty	8.9	0.0
Total	-	100.0
Number	101	
Volume		62,200 ml.

Mammalian Foods. Mammals comprised the most important food category of southern Arizona coyotes. Mammalian remains occurred in 68.3 percent of the stomachs and composed 60.4 percent of the total volume of stomach contents. Though this result was in general agreement with findings of other coyote food habits studies, the proportions were somewhat smaller here. For example, in an often quoted study Sperry (1941:9) found more than 90 percent of coyote food consisted of mammals. The lower figures for southern Arizona coyotes reflected a more diverse diet.

Larger Mammalian Foods: The most important item within the larger mammal category was cow, which contributed 10.9 percent to the overall volume of coyote food. No attempt was made to differentiate between fresh meat and carrion. In most cases the condition of materials and the presence of scavenging insects provided strong evidence that the remains originated as carrion.

Dead cattle were often readily available to coyotes. Arizona cattle died from a variety of causes, and newsworthy cases were periodically reported by the media. In some areas drought was blamed for considerable losses nearly every year (Heltsley 1971, 1972; Moore 1973). According to Anderson (1974) regular heavy drought losses on the extensive Papago Indian Reservation resulted from poor management. Periodically screw worm (*Callitroga americana*) outbreaks have resulted in mortality among cattle (Gilman 1972) and probably among deer and other mammals as well. Occasionally, often because of associated climatic conditions, poisonous plants became a problem (Burnham 1972; "Cattle die of poison from weed," *The Arizona Daily Star*, June 20, 1973,

p. 5B). Cattle deaths have also resulted from road accidents ("Steers run loose near Cortaro," The Arizona Daily Star, Dec. 15, 1972, p. 17A), rustling ("Rustlers kill 6 head of cattle," The Arizona Daily Star, Sept. 25, 1973, p. 2A; Beard 1973), domestic dog attacks ("Dogs blamed for death of Catalina steer," The Arizona Daily Star, Oct. 21, 1975, p. 16A; Denley 1978), and unknown causes ("Three more mutilated cattle found," The Arizona Daily Star, Oct. 11, 1975, p. 7B). Major sources of beef carrion were feedlots. Cattle sometimes succumbed to shipping fever after being hauled to feedlots, or died of other natural causes once there. Often carcasses were regularly available at dumps nearby, where varmint hunters took advantage of concentrations of scavenging coyotes. Two coyotes known to have been shot under such circumstances contributed a third of the total beef bulk encountered.

Complicating the picture of coyote consumption of cattle was the fact that once a cow died, coyotes probably continued to visit the carcass to nibble upon the remains for an extended period. Fichter et al. (1955) observed coyotes returning to an old cow carcass for at least 18 months. McLean (1934), Ferrel, Leach and Tillotson (1953), and Gier (1968) also noted that remains of large mammals contributed to coyote stomach contents for long periods.

Researchers agree that coyotes do not generally pose a problem to cattle (Sperry 1941; Fichter et al. 1955; Fitch and Packard 1955; and others). However, the possibility of predation upon young calves does exist. In the present study a July stomach contained remains of a small calf. Whether the coyote had killed the calf or it had died of other causes was problematical.

Coyote-cattle relationships on the SRER are treated later in the discussion of scat composition.

Domestic sheep remains were recovered from only two stomachs in small amounts. Relatively few of the coyote stomachs used in this study represented areas where large numbers of sheep were pastured. In the two cases in question the remains consisted of patches of wool, hide, and gristle. No fresh meat was found.

Pig remains occurred in two stomachs. The coyotes involved were taken in the vicinity of a dump where refuse from nearby hog ranches was discarded. Conversation with the hog ranchers revealed that no predation on pigs had occurred. They reported that pigs occasionally died of a variety of causes; frequently sows lying upon piglets resulted in mortality of the young animals. All pig remains found in coyote stomachs originated as carrion.

Remains of domestic cats were recovered from the stomachs of three coyotes. In one instance the cat remains were associated with wads of burlap, and it seemed probable that the cat had died of some cause other than coyote predation, and had been carried in a burlap sack to a dump.

Deer remains occurred in five stomachs and comprised roughly 5 percent by volume of all coyote foods. Over 90 percent of deer bulk came from two coyotes taken on the Fort Huachuca military reservation in June, 1971. While retrieving some coyote skulls from a dump on the reservation I noted deer remains there, and learned that several deer had recently been struck by vehicles while crossing roads on the base. Possibly their carcasses were the source of the deer residue found in coyote stomachs. Remaining deer bulk consisted of hide, hair, ears, but no flesh. No fawn remains were recovered, though few stomachs represented the summer months when fawns are born in this area. Truett (1979) has reported coyote predation on mule deer fawns in southern Arizona.

Javelina remains were identified in relatively small amounts in two stomachs. One of these coyotes had been killed in December, the second in February. Since legal hunting for javelina occurred concurrently, the remains found in the February stomach may have represented refuse from a field-dressed animal.

Coyote remains were detected in six stomachs. In most cases these consisted of small amounts of hair, possibly ingested in grooming. However, in one instance two ears and patches of hide and hair indicated that coyotes did consume their own kind. This was not an unusual discovery, for similar findings were reported by O. Murie (1935), Sperry (1941), Ferrel et al. (1953), and others.

Smaller Mammalian Foods: In view of the results of other coyote food habits research (see Table 33, p. 220), it was not surprising to find that rabbits collectively were the most important coyote food category. Leporids occurred in over a quarter of the stomachs and composed 20.9 percent of coyote stomach contents by volume. The single most common food item was the cottontail, which accounted for 15.2 percent of the total bulk. The larger jackrabbits were encountered less frequently.

Small rodents were an important component of the coyote diet, and were represented by at least 8 genera. No single species prevailed, as commonly noted in other areas (O. Murie 1935; A. Murie 1940; Ellis 1958; Hawthorne 1972; and others). Rather, a number of different species contributed relatively small proportions, although together they were second only to leporids as a major prey category (see Table 25).

Bird Foods. The most important item volumetrically within the bird category was domestic chicken. In two of the four stomachs containing chicken, remains consisted of heads, feet, feathers, and other refuse probably discarded after the fowl were butchered. The bulk of chicken remains, including flesh, were found in the two remaining stomachs. Poultry were sometimes observed foraging near rural and suburban residences, apparently being raised on a casual basis. As noted by Fichter et al. (1955), coyotes will enter farmyards to steal chickens, so it would not be surprising for them to take freely wandering fowl.

A second major component of the bird category was pheasant. Remains were found in stomachs of five of seven coyotes taken near a commercial preserve where sportsmen paid for the privilege of shooting these birds. In a few cases the remains consisted of what appeared to be refuse from dressed birds, but other stomachs contained considerable amounts of flesh. In one instance the flesh contained shotgun pellets. Birds which had escaped shooters were recaptured and released again before hunters, so that even predation upon cripples was unwelcome. This situation was considered non-typical and biased somewhat the food habits data in favor of the bird category.

The remaining classes of birds contributed relatively little volumetrically. Quail remains appeared to be largely residue from field-dressed birds taken during hunting seasons; this finding was consistent with the conclusions of Truett and Day (1966). Remains of a dove were found in the stomach of a road-killed suburban coyote at a time when doves were dying as a result of disease, probably trichomoniasis. A variety of other birds were represented in small amounts. Bebb (1934) suggested that the source of many of these birds might be highway mortalities. Another possibility was dead birds resulting from shooting; many people entertain themselves by plinking birds. Raptors perched conspicuously on poles and wires make particularly inviting targets.

Reptilian Foods. Lizard and snake remains were occasionally recovered, but contributed little to the overall coyote diet. An interesting discovery was the occurrence of an entire specimen of a shovel-nosed snake in one stomach. This species is a mimic of the coral snake and its bright coloration purportedly afford it protection from predation.

Invertebrate Foods. Insects were frequently ingested by coyotes, though only grasshoppers and crickets were found in large numbers. Particularly in late summer and fall these orthopterans were important food items. The stomach of a single coyote killed in November, 1971, held an estimated 820 grasshoppers of the genera *Melanoplus* and *Boopodon*, common range pests. One might be skeptical about a coyote's ability to capture so many of the elusive insects. Dr. Floyd

Werner, an entomologist at The University of Arizona, suggested that coyotes could catch large numbers of grasshoppers in the early morning hours when they were sluggish because of low temperatures. The coyote mentioned above was killed in the morning, lending support to this theory.

O. Murie (1935), Sperry (1941), Ferrel et al. (1953), Fichter et al. (1955), and others have reported large numbers of insects or spiders consumed by individual coyotes.

Maggots, dermestid beetles, and ants were probably consumed along with carrion. Their presence substantiated the importance of scavenging to coyotes.

Vegetable Foods. Fruits of various sorts were a significant component of the coyote diet, occurring in almost 35 percent of all stomachs and comprising over 14 percent of the total bulk. By far the most important of these was the mesquite bean. The beans became available in late summer and persisted through fall, providing a food source for an extended period. Coyotes sometimes fed exclusively upon them. One November stomach contained over a quart (950 ml.). Laboratory results reported by Meinzer, Ueckert and Flinders (1975) indicated viability of mesquite seeds was drastically reduced after passing through coyotes, intimating that these animals are unimportant in the spread of this tree, contrary to the contention of Jaeger (1950).

At least 11 other fruit items were identified from coyote stomachs. Of the commercially important items, most were present in small amounts and in association with other debris, suggesting that they originated from scavenging of garbage. Remains of grapes and peanuts may have resulted from depredation of vineyard and field.

The importance of fruit was not properly reflected by this stomach analysis, since relatively few coyotes were collected during the late summer and early fall when many fruits were most available. This situation appeared to have developed in numerous other coyote food habits studies as well (Rogers 1965; Gier 1968; Ozaga and Harger 1966; Mathwig 1973; and others); even where animals were collected year round a disproportionate number represented the winter period when coyotes were normally pursued.

Studies by A. Murie (1951), Wilson (1967), Small (1971), and Niebauer and Rongstad (1977) indicated that fruits of native vegetation were important components of the coyote diet. On Texas rangeland native fruits composed 46 percent by volume of the annual diet of coyotes studied by Meinzer et al. (1975). Even in Michigan, Ozaga and Harger (1966) found that coyotes searched abandoned orchards for frozen apples, which were a substantial part of their winter diet. In light of these studies and the present one, the statement by Sperry (1941) that over 98 percent of the coyote's diet consists of food of animal origin seems to underrate considerably the importance of fruits, particularly in the Southwest.

Grass was consumed in quantity by several coyotes. O. Murie (1935) intimated grass might be a regular part of the coyote's diet, as such leafy vegetables as spinach and lettuce are in man's diet. In opposition, Fichter et al. (1955) stated that grass was not a true food.

Gier (1968) suggested that grass might serve as a tonic, source of vitamins, or vermicide.

The high incidence of leaves, twigs, and assorted vegetative fragments, including many instances of small amounts of grass, probably resulted from accidental ingestion during attempts to capture small prey or while consuming food items from the ground.

Miscellaneous Stomach Contents. A variety of what were generally considered non-food items were found in coyote stomachs. Small amounts of sand and dirt were no doubt ingested incidentally with food. However, pebbles and small stones were found in 19 stomachs, and it appeared that they were purposely consumed for some unknown reason. A mass of clayey soil was found in one stomach along with numerous chips of bone from an unidentified larger mammal; possibly the clay had been consumed because it had absorbed fluids from carrion. Pieces of a milk carton and cellophane food wrappers were associated with other debris, indicating that they were eaten while the coyote in question scavenged garbage. Leather fragments and chips of plastic may have been consumed because they had appealing flavors.

Analysis of Food Habits as Determined From Stomach Contents

By Age Class of Coyote. Frequency of occurrence and relative volume of the various categories of food items found in stomachs of adult coyotes versus pups are presented in Table 26. Adults were defined as animals 2 years of age and older; pups were less than one year old. All pups were over 5 months of age and most were capable of

Table 26. Frequency of occurrence and relative volume of major food categories found in coyote stomachs by age class of coyote.

Item	Adult Percentage Occurrence	Adult Percentage Volume	Pup Percentage Occurrence	Pup Percentage Volume
All Mammal	66.7	67.6	70.8	47.0
Larger Mammal	35.2	36.8	25.0	7.5
Cow	14.8	16.3	4.2	0.9
Smaller Mammal	48.1	30.8	62.5	39.5
Rabbit	27.8	18.7	29.2	23.4
Rodent	27.8	12.1	50.0	16.1
Bird	27.8	11.6	29.2	15.6
Reptile	3.7	0.2	4.2	Trace
Invertebrate	37.0	5.7	58.3	12.1
Vegetable	77.8	14.6	87.5	24.0
Inorganic	33.3	0.1	12.5	0.5
Miscellaneous	11.1	0.3	8.3	0.8
Empty	13.0	0.0	4.2	0.0
Total	-	100.1	-	100.0
Number	54		24	
Volume		38,000 ml.		12,800 ml.

foraging for themselves when killed. Disparity in the diets of these two age groups may have reflected differences in learning, status, ability, and behavior generally.

The volumetric proportion of larger mammal remains consumed by adult coyotes approached 5 times the proportion found in pups ($z=1.76$, n.s., $P=0.08$). Ability to kill larger mammals was probably an unimportant factor, since most of these remains originated as carrion. The discrepancy in frequency of occurrence of larger mammal foods between the age classes was less striking than was the difference in bulk ($0.75>P>0.50$); apparently youngsters had opportunity to consume larger mammals nearly as often as adults, but did not consume as much.

Possibly these observations reflected the dominance of older coyotes over pups. Probably adults satisfied their hunger before allowing younger animals to approach a large carcass. Such a situation was illustrated by an observation made by Cahalane (1947) of coyotes killing and feeding upon deer. Though the ages of the coyotes observed by him were unknown, the dominant coyote ate its fill before allowing the others to eat. Similarly Wells and Bekoff (1978) reported one adult kept other subdominant coyotes away from a cow carcass while it fed.

A greater proportion of the diet of pups consisted of smaller mammals, birds, invertebrates, and fruits. These foods were small enough that once captured or located they could be consumed by the individual without social status becoming a factor. Statistical testing indicated that coyotes less than a year old consumed a significantly greater volume of smaller mammals ($z=2.05$, $P=0.04$) and vegetable matter ($z=2.17$, $P=0.03$) than did adults, while volumetric differences observed in the bird and invertebrate categories were not significant ($0.50>P>0.09$). Variations in frequency of occurrence of smaller mammal, bird, invertebrate, and vegetable foods were not statistically significant ($0.90>P>0.10$).

The yearling age group, animals between 1 and 2 years of age, exhibited food habits generally intermediate between adults and juveniles. The small number of yearling stomachs containing measurable volumes of food materials precluded a more elaborate comparison.

Hawthorne (1972) was able to collect 23 fecal samples from live-trapped juvenile coyotes, and analyzed these along with 384 scats, which presumably represented all age classes, collected on his study area in northern California. Relationships between the food categories by age class of coyote were very similar to those observed in the present study. For example, larger mammals were utilized less frequently and accounted for smaller volume in the scats of juveniles as compared to scats from the general population. Small mammals, birds, invertebrates, and other foods occurred more frequently in juvenile scats. Hawthorne concluded that juvenile coyotes utilized virtually the same foods as adults, but in somewhat different proportions. This generalization applied to coyote feeding trends observed in southern Arizona as well.

By Sex of Coyote. Presumably the same foods were available to both sexes. Behavioral differences probably accounted for variations in diet by sex of coyote. Comparison of stomach contents of male versus female coyotes can be made by referring to Table 27.

Table 27. Frequency of occurrence and relative volume of major food categories found in coyote stomachs by sex of coyote.

	Male Percentage		Female Percentage	
Item	Occurrence	Volume	Occurrence	Volume
All Mammal	67.3	56.5	69.6	64.9
Larger Mammal	34.5	26.8	21.7	23.6
Cow	14.5	13.4	4.3	8.0
Smaller Mammal	47.3	29.7	63.0	41.3
Rabbit	23.6	18.4	30.4	23.8
Rodent	34.5	11.3	41.3	17.5
Bird	32.7	24.6	19.6	6.9
Reptile	3.6	0.2	6.5	Trace
Invertebrate	38.2	6.1	45.7	6.6
Vegetable	76.4	11.8	84.8	21.4
Inorganic	23.6	0.2	28.3	0.1
Miscellaneous	10.9	0.6	15.2	Trace
Empty	9.1	0.0	8.7	0.0
Total	-	100.0	-	99.9
Number	55		46	
Volume		33,600 ml.		28,600 ml.

The data indicated that female coyotes relied more upon smaller mammals, insects, and fruits, while larger mammals and birds were of greater importance to males. Some specific differences were obscured by combining data into general categories. A more detailed comparison of the larger mammal category by sex of coyote, for example, revealed that male stomachs contained 13.4 percent by volume of cow remains, while for female stomachs cow comprised 8.0 percent of the bulk. Where large carcasses were involved, dominance status may have again affected feeding habits. Also, observed differences may have resulted from a greater boldness of males and a more cautious disposition of females (see Coyote Behavior: Male versus Female). The greater mass of the bird category consisted of chicken and pheasant, items which probably required a certain amount of risk to obtain; males were apparently more prone to take this risk for a meal, whereas females appeared content to forage for more natural foods. However, Andelt and Gipson (1979a) reported that both male and female coyotes were responsible for turkey depredations on a Nebraska ranch; possibly other foods were less available there.

The relative volume of smaller mammals in female stomachs was significantly greater than that in male stomachs ($z=2.35$, $P=0.019$), while the greater volume of vegetable matter consumed by females approached significance ($z=1.84$, $P=0.066$). Also approaching significance was the greater volume of bird found in male stomachs ($z=1.80$, $P=0.072$). Larger mammals, cow, and invertebrates exhibited no significant variation in relative volumes ($0.17>P>0.10$). Observed dissimilarities in frequency of occurrence of the major food categories was not statistically significant ($0.75>P>0.10$).

Documentation of differences in food habits of the sexes is rare in the coyote literature. McLean (1934) tabulated the occurrences of deer remains in stomachs by sex of coyote; of 537 coyotes examined 53 male and 47 female coyotes had consumed deer. Data necessary to test the significance of these figures statistically was not presented.

After studying food habits of bobcats in Arkansas, Fritts and Sealander (1978) reported that females consumed significantly more rats and mice than did males, and postulated that smaller physical size and home ranges of females may have been responsible. These factors appeared of lesser importance among coyotes in southern Arizona.

By Year. Data derived from stomach contents representing year 1 (May 1, 1970, through April 30, 1971) versus year 2 (May 1, 1971, through April 30, 1972) are presented in Table 28 in the form of percentage of occurrence and relative volume of the various food categories. Though fewer stomachs were collected in year 1, roughly the same proportion of stomachs represented each quarter of the year in both years. While no stomachs were collected in the third quarter of year 1, only 3 represented that period in year 2.

Coyote feeding habits appeared to be surprisingly stable between the two years. The disparity in the volume of bird consumed approached significance ($z=1.65$, $P=0.099$), but could be traced to the atypical presence of pheasant in several stomachs in year 1. Otherwise variations in relative volumes from year 1 to year 2 were

Table 28. Frequency of occurrence and relative volume of major food categories found in coyote stomachs by year.

Item	Year 1 Percentage Occurrence	Year 1 Percentage Volume	Year 2 Percentage Occurrence	Year 2 Percentage Volume
All Mammal	64.0	58.6	64.5	60.3
Larger Mammal	36.0	29.4	29.0	23.9
Cow	20.0	12.3	8.1	10.5
Smaller Mammal	44.0	29.2	50.0	36.4
Rabbit	20.0	18.1	27.4	22.2
Rodent	32.0	11.1	32.3	14.2
Bird	36.0	25.8	19.4	9.8
Reptile	8.0	0.2	3.2	0.1
Invertebrate	44.0	1.6	40.3	9.3
Vegetable	76.0	13.4	77.4	20.0
Inorganic	36.0	Trace	25.8	0.3
Miscellaneous	8.0	0.4	12.9	0.3
Empty	12.0	0.0	9.7	0.0
Total	-	100.0	-	100.1
Number	25		62	
Volume		24,000 ml		36,500 ml.

statistically insignificant ($0.73 > P > 0.36$). Similarly, frequency of occurrence of the major food categories did not vary significantly between years ($0.95 > P > 0.10$).

Tiemeier (1955), Korschgen (1957), and Gier (1968) presented more elaborate data on variation in coyote food habits from year to year. These authors concurred that availability determined to a large extent what foods coyotes consumed. Fitch and Packard (1955) have shown that dramatic differences can occur in the coyote diet in different years.

By Season. To fairly depict seasonal variations in the coyote diet a large number of coyote stomachs should have been collected during each quarter. Because the majority of carcasses were donated to the study by varmint hunters, relatively few stomachs were available for the months April through September when hunting activity was minimal. A more accurate picture of seasonal feeding trends was obtained from the scat analysis appearing later in this report.

In terms of relative volume, larger mammals appeared to be of greatest importance in the coyote diet during quarters II and III. This observation contrasted sharply with results obtained from scat analysis and the findings of other researchers, and probably resulted from inadequate sampling (Table 29). Other studies have shown that larger mammals, usually originating as carrion, were a major food during the winter and early spring (Sperry 1934; Aiton 1938; Ellis 1958; Hawthorne 1972; and others).

Table 29. Frequency of occurrence and relative volume of major food categories found in coyote stomachs by quarter (season) of the year.

Item	Quarter I Percentage Occ.	Quarter I Percentage Vol.	Quarter II Percentage Occ.	Quarter II Percentage Vol.	Quarter III Percentage Occ.	Quarter III Percentage Vol.	Quarter IV Percentage Occ.	Quarter IV Percentage Vol.
All Mammal	69.2	55.0	80.0	94.8	83.3	64.6	61.0	49.7
Larger Mammal	25.6	11.3	46.7	60.6	33.3	41.7	24.4	19.6
Cow	10.3	6.2	0.0	0.0	16.7	37.5	12.2	14.5
Smaller Mammal	51.3	43.8	73.3	34.2	83.3	22.9	46.3	30.1
Rabbit	35.9	33.4	20.0	21.2	33.3	11.0	19.5	11.7
Rodent	25.6	10.4	60.0	13.0	83.3	11.9	34.1	18.4
Bird	15.4	29.2	33.3	2.4	16.7	4.4	36.6	13.6
Reptile	10.3	0.3	6.7	Trace	0.0	0.0	0.0	0.0
Invertebrate	43.6	4.4	33.3	Trace	83.3	3.8	36.6	11.2
Vegetable	74.4	10.5	93.3	2.7	100.0	27.3	78.0	24.7
Inorganic	20.5	0.1	40.0	Trace	50.0	Trace	22.0	0.3
Miscellaneous	10.3	0.5	26.7	0.1	0.0	0.0	12.2	0.4
Empty	7.7	0.0	6.7	0.0	0.0	0.0	12.2	0.0
Total	-	100.0	-	100.0	-	100.1	-	99.9
Number	39		15		6		41	
Volume		21,800 ml.		10,600 ml.		4,800 ml.		25,000 ml.

Smaller mammals assumed their greatest importance during the winter-spring period, though they were well represented during each season and therefore were considered staples in the coyote diet. The bulge in the relative volume of the bird category during quarters I and IV was attributed largely to the presence of pheasant remains in the stomachs of several coyotes collected where shooting of pen-raised birds occurred. Insect bulk reached its highest point in the fourth quarter, and appeared to reflect directly the availability of grasshoppers. Likewise the volume of fruit in the stomachs reflected availability; however, the importance of fruits was underrated since relatively few summer stomachs were available.

No statistically significant differences were detected for the five food categories tested with respect to relative volume between quarters of the year ($0.99>P>0.10$). Except for differences in the bird category between quarters I and IV ($X^2 = 3.61$, $0.10>P>0.05$) and the invertebrate category between quarters III and IV ($X^2 = 2.96$, $0.10>P>0.05$) which approached significance, testing of the data indicated that seasonal variations in frequency of occurrence of these food categories was insignificant ($0.95>P>0.10$).

Information on seasonal variations in coyote food habits has been provided by numerous investigators, including Bond (1939), Sperry (1941), Ferrel et al. (1953), Korschgen (1957), Ellis (1958), Ozaga (1963), Gier (1968), Meinzer et al. (1975), and others.

By County of Origin of Coyote. Enough stomachs were available from Cochise, Pima, and Pinal counties to allow comparison of the coyote diet between counties. Frequency of occurrence and relative volume for the different food categories are listed by county in Table 30.

While Pima and Pinal counties were characterized by desert-scrub vegetation, Cochise county was more typically grassland. Coyotes from Pinal county largely represented agricultural areas. Variation in diet between counties theoretically reflected differences is availability of food items. However, because of the small sample size, in a few instances a large bulk of a specific item in a small number of stomachs biased relative volume figures. Within the larger mammal category, materials from Pima county stomachs consisted mostly of cow and hog residue. While Cochise county coyotes had consumed almost as much cow, their apparent diet was weighted by deer remains from Fort Huachuca. Pinal county stomachs contained the same variety of larger mammals in more moderate amounts. Pima county coyotes had consumed rodents more frequently and in slightly greater volume than had coyotes from the other two counties. Rabbits contributed almost a third of the bulk of the apparent diet of coyotes from Cochise county, although rabbits occurred almost as frequently in stomachs of coyotes from Pima and Pinal counties. The inflated volume of the bird category in Pinal county was because of pheasant eaten by several coyotes, and in Pima county was because of consumption of chicken by two coyotes. Other birds contributed little volumetrically. A single coyote which had filled its stomach with grasshoppers was responsible for the increased volume of invertebrates consumed by Cochise county coyotes. More often remains of invertebrates were found in trace amounts and contributed

Table 30. Frequency of occurrence and relative volume of major food categories found in coyote stomachs by county of origin.

Item	Cochise Percentage Occ.	Cochise Percentage Vol.	Pima Percentage Occ.	Pima Percentage Vol.	Pinal Percentage Occ.	Pinal Percentage Vol.
All Mammal	63.0	76.9	73.2	52.8	66.7	36.6
Larger Mammal	33.3	31.6	24.4	24.9	33.3	14.4
Cow	11.1	9.3	9.8	9.7	5.6	4.7
Smaller Mammal	48.1	45.3	65.9	27.9	44.4	22.2
Rabbit	29.6	31.6	24.4	10.9	22.2	9.1
Rodent	25.9	13.8	56.1	16.9	27.8	13.1
Bird	11.1	3.5	34.1	20.9	38.9	46.7
Reptile	0.0	0.0	7.3	0.2	5.6	Trace
Invertebrate	40.7	11.4	51.2	1.3	16.7	Trace
Vegetable	77.8	8.1	85.4	24.8	66.7	15.7
Inorganic	37.0	0.1	22.0	Trace	16.7	0.9
Miscellaneous	0.0	0.0	19.5	Trace	11.1	Trace
Empty	11.1	0.0	4.9	0.0	16.7	0.0
Total	-	100.0	-	100.0	-	99.9
Number	27		41		18	
Volume	17,600 ml.		25,200 ml.		8,600 ml.	

little to bulk. Insects appeared to be a comparatively infrequent food item for Pinal county coyotes. Fruits consumed by coyotes from Cochise and Pima counties were predominantly mesquite beans, while in Pinal county grapes from a single stomach made a large contribution to the total volume of vegetative food.

Statistical testing of the observed variations in relative volumes of the five major food categories between the three counties revealed no statistically significant differences ($0.995>P>0.25$). The more frequent occurrence of bird in Pima versus Cochise and in Pinal versus Cochise county stomachs approached significance ($0.10>P>0.05$). The difference in frequency of occurrence of invertebrates in stomachs of coyotes from Pima versus Pinal county proved significant ($X^2 = 4.84$, $0.05>P>0.025$). No other significant differences in frequency of occurrence were detected ($0.95>P>0.10$).

Strong regional dissimilarities in diet as reported for Arkansas bobcats by Fritts and Sealander (1978) were not apparent for coyotes inhabiting southern Arizona. Such differences as did occur were probably because of the unusual contents of a few stomachs. While available habitat differed somewhat, apparently the same foods were available to coyotes from all three counties. Ferrel et al. (1953), Fichter et al. (1955), Ellis (1958), and Gipson (1974), among others, have noted sectional variations in coyote food habits within a state.

Food Habits as Determined from Scat Composition

The composition of 619 coyote scats collected on the SRER from September, 1971, through June, 1973, is summarized in Table 31.

Table 31. Composition of 619 coyote scats collected on the Santa Rita Experimental Range from September, 1971, through June, 1973, expressed in percentage occurrence and percentage of total organic weight.

Item	Percentage Occurrence	Percentage Weight
All Mammal	82.9	65.6
Larger Mammal	39.9	15.8
Cow (*Bos taurus*)	33.0	12.4
Dog (*Canis familiaris*)	0.2	Trace
Deer (*Odocoileus*)	2.8	1.7
Javelina (*Tayassu tajacu*)	2.3	1.7
Coyote	1.9	Trace
Unidentified	0.3	Trace
Smaller Mammal	61.6	49.9
Lagomorph	23.6	21.8
Jackrabbit (*Lepus*)	5.8	7.8
Cottontail (*Sylvilagus*)	0.7	0.7
Unidentified	17.1	13.4
Rodent	46.0	28.1
Bird	5.0	0.8
Bird	4.0	0.8
Eggshell	1.1	Trace
Reptile	1.9	0.2
Insect	17.3	5.4
Vegetable	66.6	27.9
Mesquite bean (*Prosopis juliflora*)	15.7	9.5
Prickly pear tuna (*Opuntia*)	13.3	9.9
Graythorn berry (*Condalia*)	4.7	3.5
Assorted Other	44.4	5.1
Total Organic Content	-	100.0
Organic matter	100.0	74.8
Inorganic matter	52.0	25.2
Total Number/Weight	619 /	14,150 g.

Twenty-five categories of items are listed by percentage of occurrence and percentage of total organic weight. Less detail is provided than was the case for stomach contents, for identification of items was more difficult. A major purpose of the scat analysis was to clarify the year round coyote food habits picture, for which a more general categorization was adequate.

A major advantage of investigating food habits through scat analysis was that the subject population was not disturbed, as it would have been had animals been killed to enable stomach analysis. The major criticism of the technique was that only undigestible residue could be used as a basis for monitoring food habits. Often quantitative relationships were distorted. For example, mesquite beans contained much fibrous material and often appeared little altered by the coyote digestive system, whereas prickly pear tunas contained much juicy pulp which was digested away, leaving only rind and seeds. Numerical relationships were also distorted. O. Murie (1946) noted that, because residue from a large food item was likely to appear in several droppings, scat analyses tend to overestimate the importance of larger mammals and underestimate the importance of smaller food items. These considerations complicate interpretation of the data presented in Table 31.

Proper evaluation of the data also hinges upon a knowledge of ecological background information, some of which is presented in the following discussion.

Mammalian Foods.

Larger Mammalian Foods: Cow: Of the larger mammalian foods, only domestic cattle remains were a major component of scats, occurring in 33 percent and representing 12.4 percent of their organic weight. While occassionally an entire scat consisted of cow hair, more often much smaller amounts of hair were found mixed with remains of other food items or inorganic material.

During field operations on the SRER particular attention was paid to the relationship between coyotes and cattle. Santa Rita Ranch (SRR) personnel felt coyotes seldom if ever attacked older cattle, but because of circumstantial evidence suspected coyotes of killing young calves occasionally. Mr. Bill MacWilliams, Jr., manager of the SRR and a leaseholder on a major portion of the SRER, felt that he lost a few calves to coyotes there every year.

Coyotes often associated closely with cattle. On several occasions radio-tagged coyotes were monitored as they moved about among congregations of cows and calves. When such areas were surveyed on foot later no evidence of coyote predation could be found. I was accompanied in the field by a dog adept at locating carrion, so it seemed unlikely any such predation in the vicinity was overlooked. During the calving season coyotes probably foraged among cattle searching for afterbirth, and it appeared that they occasionally fed upon fresh manure. Cattle sometimes trampled and crushed the dens and burrow systems of rodents, most notably those of kangaroo rats, thereby exposing their inhabitants and creating an inviting situation for coyotes. Cattle appeared to be quite capable of protecting their calves. They invariably chased my dog when they encountered it, and on one occasion were observed chasing a coyote, which escaped by running under a fence into a different pasture.

During the period that coyote droppings were being collected, several cattle died on the SRER. The most common cause of death appeared to be calving complications. Young cows which had conceived for the first time were most frequently involved, according to SRR personnel. Sometimes both cow and calf died, but more often the cow survived. Riders from the SRR covered the range almost daily during the extended calving season, and gravid cattle that they felt would have difficulty were corraled until after calving. Some of these animals died despite special care, and the carcasses were disposed of at a dump near SRR headquarters where coyotes gathered to feed upon the carrion.

On 28 March, 1973, Mr. Gilbert Garcia, SRR foreman, informed me that he had just observed a coyote feeding upon a newborn calf. The rather large calf was quickly located, the remains salvaged, and an autopsy performed by Dr. Ted Noon, D.V.M., Department of Veterinary Science, University of Arizona. Indications were that the calf died as a result of dystocia, possibly related to its large size. Abdominal viscera were unavailable, having been removed by the coyote(s). Examination of the lungs revealed fluid in the trachea and bronchi, possibly resulting from aspiration during a fetal dystocia (Noon, personal communication 1980). Though I did not observe the cow in question, Mr. Garcia described her as "weak and wobbly," which suggested that she had indeed suffered trauma during calving.

Range cattle occasionally died from other causes as well. Heavy precipitation sometimes generated mortality from a phenomenon known as nitrate poisoning. Numerous cases were reported in Pima County after heavy spring rains in 1973, and this malady may have been responsible for the deaths of two cows found on the SRER at that time. Under dry conditions poisonous plants may have become a threat. Of several poisonous forms, Astragulus, Haplopappus, and Lupinus were particularly prominent on the SRER, though they were seldom consumed in quantity so long as other forage was available.

Observations of coyotes feeding upon the fresh carcasses of a dead cow and calf found at an earthen stock tank (Middle Tank) in January, 1973, were typical. Presumably calving difficulties had caused the mortality. The calf carcass disappeared quickly; after a few days no trace of it remained. The cow carcass was fed upon by coyotes, ravens, and vultures until after several days all that remained was a hollow shell. Tracks indicated that coyotes continued to visit the remains months after little in the way of food value was left. It was not determined that they continued to consume the residue, but they may have. It appeared that eventually the carcass served as a scent post.

Cattlemen frequently mentioned "tail-pulling" as evidence of attempted coyote predation upon cattle. A single bob-tailed cow was observed on the SRER. Attacking coyotes allegedly caught cows or calves by the tail and bit or pulled it off as their intended prey escaped. While such behavior by coyotes was never witnessed, Cape hunting dogs (Lycaon pictus) while hunting in packs often hold large

African ungulates by their tails when attacking (van Lawick-Goodall 1970). One SRR rider suggested that bob-tailing resulted when cows inadvertently stepped upon the tails of other,reclining cattle; when a pained animal jumped to its feet it could lose its tail.

A major source of cattle carrion was a dump within two miles (3.2 km.) of the west boundary of the SRER. A cattle feedlot operated by Farmers' Investment Corporation (FICo) sustained regular losses from various causes. Carcasses were dragged to the dump where coyotes and other scavengers gathered to feed. While attempting to radio track coyotes, some of the instrumented animals moved off the SRER in the direction of this carcass disposal area. Consequently a considerable amount of time was spent afoot traversing the intervening tract searching for radio signals. Numerous scats were collected during these forays. Also, many scats were picked up about three earthen stock tanks near the west boundary of the SRER. It was probable that coyotes which fed at the FICo dump visited these stock tanks occasionally. Hence it was not unreasonable to assume that the origin of much of the cow material recovered during scat analysis was the FICo dump.

Larger Mammalian Foods: Other Larger Mammal: Other larger mammals contributed relatively little to the overall coyote diet on the SRER. Deer remains, mostly hair, comprised 1.7 percent by weight of the organic material found in all scats. Of the 2.7 percent of the scats which contained deer residue, measurable amounts were recovered from August through January, with only traces of hair found in three June and September droppings.

During the time of this study mule deer were common on the SRER. Their numbers swelled somewhat during the winter and early spring, suggesting a seasonal migration from the adjacent Santa Rita Mountains. White-tailed deer (O. virginianus) were never observed on the SRER, though they occurred in the mountains immediately eastward. Based upon personal observation, productivity of the SRER deer appeared to be good. Numerous fawns were observed during the summers, and twins were not unusual. No remains of spotted fawns were recovered from coyote scats.

Remains of javelina occurred in 2.3 percent and comprised 1.7 percent of the organic weight of all scats examined. These figures were comparable to those obtained for deer. Javelina were frequently sighted on the SRER in numbers ranging from 1 to 17. One November scat contained hair and hoof fragments of a juvenile.

Remains of other large mammals did not occur in significant amounts. Domestic dog remains were almost certainly carrion; two dogs were found shot to death along roads on the SRER in 1973. Occasionally a scat contained a small amount of coyote hair, probably ingested during grooming.

Smaller Mammalian Foods: On the SRER rabbits and rodents were the most popular coyote food items. Taken together these staples occurred in 61.6 percent of the scats and comprised 49.9 percent of the weight of organic remains.

Leporids comprised 21.8 percent by weight of the organic component of the scats, and occurred at a frequency of 23.6 percent. Reportedly rabbit populations were depressed during the time of this study. Jackrabbits of two species, Lepus californicus and L. alleni, were commonly seen, but cottontails were only noted occasionally near pockets of favorable habitat. Road counts made at irregular intervals and at different times of day provided at least some index of jackrabbit abundance. A low figure of 0.28 jackrabbits per mile (1.6 km.) resulted from averaging counts of all hares seen while driving through the SRER on 12 occasions from February through June, 1972. After heavy spring rains, a high figure of 1.37 jackrabbits per mile (1.6 km.) was recorded in June, 1973.

Unfortunately a complication was introduced into the food habits investigation by the behavioral phase of this study. Carcasses of rabbits and hares resulting from independent research elsewhere (Madsen 1974) were utilized as bait during the live-trapping process. These carcasses were eventually consumed by coyotes. Also, a bait station was maintained for several months during the study at a specific location (SE¼, S23, T18S, R14E) using roughly two rabbit carcasses per week. This situation developed from an attempt to learn something of coyote movements by feeding them bait containing glass beads, as suggested by the work of Sowls and Minnamon (1963) and, later, to learn if such a food source would have any effect upon behavior of radio-tagged animals. Colored beads were mixed in 5 pound (2.3 kg.) portions of ground horsemeat, and one portion per week along with the rabbits was left at the site. After a 10 week period only rabbit carcasses were left as bait. Subsequent recovery of beads was minimal; a total of 6 bead-containing scats were collected and these were all found within 0.8 miles (1.29 km.) of the bait station. Scats containing beads were not utilized for food habits data. The small number recovered suggested that the bait station had little effect on the food habits investigation. To minimize possible influence, scats encountered within a few miles of the baited site were not collected.

Rodents collectively constituted the single most important food category, composing over 28 percent of the composite organic weight. Their remains occurred in slightly over 46 percent of the scats examined. Numerous small rodent species were available on the SRER. While no special effort was made to distinguish between them, packrat, kangaroo rat, pocket mouse, and porcupine remains were at times conspicuous in the scat content.

Estimated densities of Heteromyids and Cricetids over the period of scat collection were obtained from Courtney and Vaughan (personal communication 1976). Based upon trapping data from a small portion of the SRER, their figures ranged from a low of 8.7 animals per acre (21.4/ha.) in the fourth quarter of 1971 to a high of 11.6 animals per acre (28.6/ha.) in the third quarter of 1972. Generally densities were lowest during the winter when many species hibernated or aestivated, and were highest at the end of summer when young of the year swelled populations.

Bird and Reptilian Foods. Though plentiful on the SRER, birds and reptiles were very minor items in the coyote diet. Gambel's quail were abundant, particularly in the neighborhood of stock tanks. Scaled quail (*Callipepla squamata*) became increasingly common during the time of the study. Especially during the winter, very numerous flocks of

Fringillids foraged through the low brush and on the ground across the area. Yet birds occurred in only 4 percent of the scats and contributed less than one percent to the organic weight. Occurrence of white eggshell fragments in 7 scats collected in April, June, and August suggested that coyotes may have occasionally raided nests of birds.

Reptiles occurred in less than 2 percent of all scats despite the abundance of a variety of lizards and snakes. A large part of the reptilian component probably originated as carrion, for snakes were occasionally found dead on roadways after having been run over by vehicles.

Insect Foods. Insect remains had a high frequency of occurrence in scats. Their importance was underrated when evaluated on a weight basis, for usually only bits of hard anatomy survived the digestive process. Grasshopper remains became increasingly prevalent in droppings through late summer, and by fall and early winter composed a considerable portion of the coyote diet. Numerous scats were recovered which consisted almost entirely of such residue. The overall data were somewhat weighted by scats collected in late 1971 when great numbers of grasshoppers were available. Nonetheless these insects had to be considered an important seasonal food of SRER coyotes. The species involved were chiefly members of the genus *Melanoplus*. A large and conspicuous grasshopper, *Taeniopoda sp.*, was very common in late 1971, but traces of it were seldom found in scats; apparently it was unpalatable or possessed some other protective mechanism.

Vegetable Foods. When available seasonally, fruits of mesquite, prickly pear, and graythorn were of major importance to SRER coyotes. Additionally, an occasional scat consisted almost exclusively of grass or forb leaves, particularly in spring. The frequent occurrence of assorted bits of vegetation in scats probably represented incidental ingestion along with other food items. While the contribution of vegetative foods to the composite scat sample was a considerable 28 percent of organic weight, in late summer over 80 percent by weight of monthly organic scat content was composed of vegetative materials, mostly remains of mesquite beans and prickly pear tunas. That the importance of fruits to coyotes was not a local phenomenon was indicated by an even greater dependence upon them reported by Meinzer et al. (1975) for Texas coyotes (see Table 33, p. 220).

Annual variation in production of fruits was best illustrated by graythorn, which because of heavy spring rains in 1973 produced a bumper crop that year, whereas in 1972 graythorn berries were much less in evidence. The increased production of other fruits in 1973 was less striking.

Inorganic Materials in Scats. An extraordinary amount of inorganic material, mostly sand, occurred in the SRER coyote scats. Fifty-two percent of all droppings contained such material, and it contributed 25.2 percent to the total scat weight. This situation appeared to be unique for the SRER, for measurable amounts of inorganic matter did not regularly occur in stomachs examined during the present study, nor have other researchers reported such findings.

That coyotes consumed soil to alleviate some mineral deficiency seemed a remote possibility, for coyotes from the area appeared to be in good physical condition.

Sand in quantity might have been ingested by coyotes in a number of ways. Young and Jackson (1951:91) noted that in the Southwest coyotes in search of water often dug holes 2 or 3 feet deep in dry washes. Such a watering site was discovered on the study area (SE¼, S32, T18S, R14E). Dug by coyotes, sign indicated that the hole was also used by deer and various birds. In a similar manner in an apparent effort to find water, coyotes often dug into the bottoms of large earthen stock tanks after they dried up seasonally. Animals attempting to lap water from such holes undoubtedly ingested considerable amounts of soil, for the liquid in them was usually no less than thin mud.

As pointed out by A. Murie (1940), Young and Jackson (1951:91), and others, coyotes cache food, that is, bury it temporarily to return, uncover, and consume it later. Such behavior would contribute inorganic matter to the scat content, since some soil would adhere to buried foods, particularly to flesh.

The major source of sand in the scats, however, appeared to be related to the disposition of dead cattle at the FICo dump mentioned earlier. Cattle dying at the FICo feedlot were dragged to the dump site where they were periodically bulldozed into shallow pits and covered with a thin layer of soil. Such measures would not deter scavenging coyotes. In the process of feeding on carrion handled in this way, coyotes no doubt ingested considerable amounts of inorganic matter. Possibly they purposely consumed soil that had absorbed fluids from decomposing carasses. As noted by Tiemeier(1955) amount of decay has little effect upon carrion consumption by coyotes. Of 195 scats containing inorganic materials in greater than trace amounts, 65 percent also contained evidence of cow, and when relatively large amounts of soil occurred at least a few cow hairs were almost invariably present. Both occurrence and weight of cow and inorganic matter appeared to vary together seasonally, suggesting a positive relationship between the two items. These findings suggested that the FICo dump was a major food source for coyotes in the general vicinity. As already noted, the collection of numerous scats near the western boundary tended to bias the scat collection in favor of coyotes feeding at the carcass disposal area.

Analysis of Seasonal Variation in Scat Composition

A general picture of seasonal variation in coyote food habits on the SRER as determined from scat analysis can be obtained by referring to Table 32, which lists freoquency of occurrence and relative weight of the different food categories by quarter of the year. Generally relative weight was the more accurate indicator of a food item's importance. Monthly variation in relative weights of six food categories is illustrated in Figure 30.

The larger mammal category exhibited less seasonal variation than did other major components of the diet. Heaviest use occurred from December through March when 24.8 percent of the weight of organic residue was attributable to larger mammals. Lowest use came in August and September when the corresponding figure was only 2.6 percent.

Table 32. Frequency of occurrence and relative weight of major food categories found in coyote scats by quarter (season) of the year.

Item	Quarter I Percentage Occ.	Quarter I Percentage Wht.	Quarter II Percentage Occ.	Quarter II Percentage Wht.	Quarter III Percentage Occ.	Quarter III Percentage Wht.	Quarter IV Percentage Occ.	Quarter IV Percentage Wht.
All Mammal	98.9	91.0	97.6	80.2	46.8	27.4	76.7	50.8
Larger Mammal	46.5	24.6	42.1	11.0	18.5	5.7	47.3	18.4
Cow	40.0	21.7	37.8	9.3	11.3	5.6	37.0	9.9
Smaller Mammal	69.2	66.5	83.5	69.3	39.5	21.7	45.9	32.4
Lagomorph	34.1	32.5	31.1	32.7	10.5	8.0	13.0	8.6
Rodent	44.9	34.0	66.5	36.5	33.1	13.6	35.6	23.8
Bird	0.5	Trace	9.1	1.9	4.8	Trace	6.2	1.3
Reptile	1.6	0.1	4.9	0.8	0.0	0.0	0.7	Trace
Insect	3.8	2.3	12.2	0.5	21.0	0.9	37.0	17.7
Vegetable	51.4	6.6	51.2	16.5	95.2	71.7	78.8	30.2
Total Organic Content	-	100.0	-	99.9	-	100.0	-	100.0
Organic Matter	100.0	65.9	100.0	73.7	100.0	95.2	100.0	75.2
Inorganic Matter	63.8	34.1	58.5	26.3	25.8	4.8	52.1	24.8
Total Number	185		164		124		146	
Total Weight		4,700 g.		3,750 g.		2,200 g.		3,500 g.

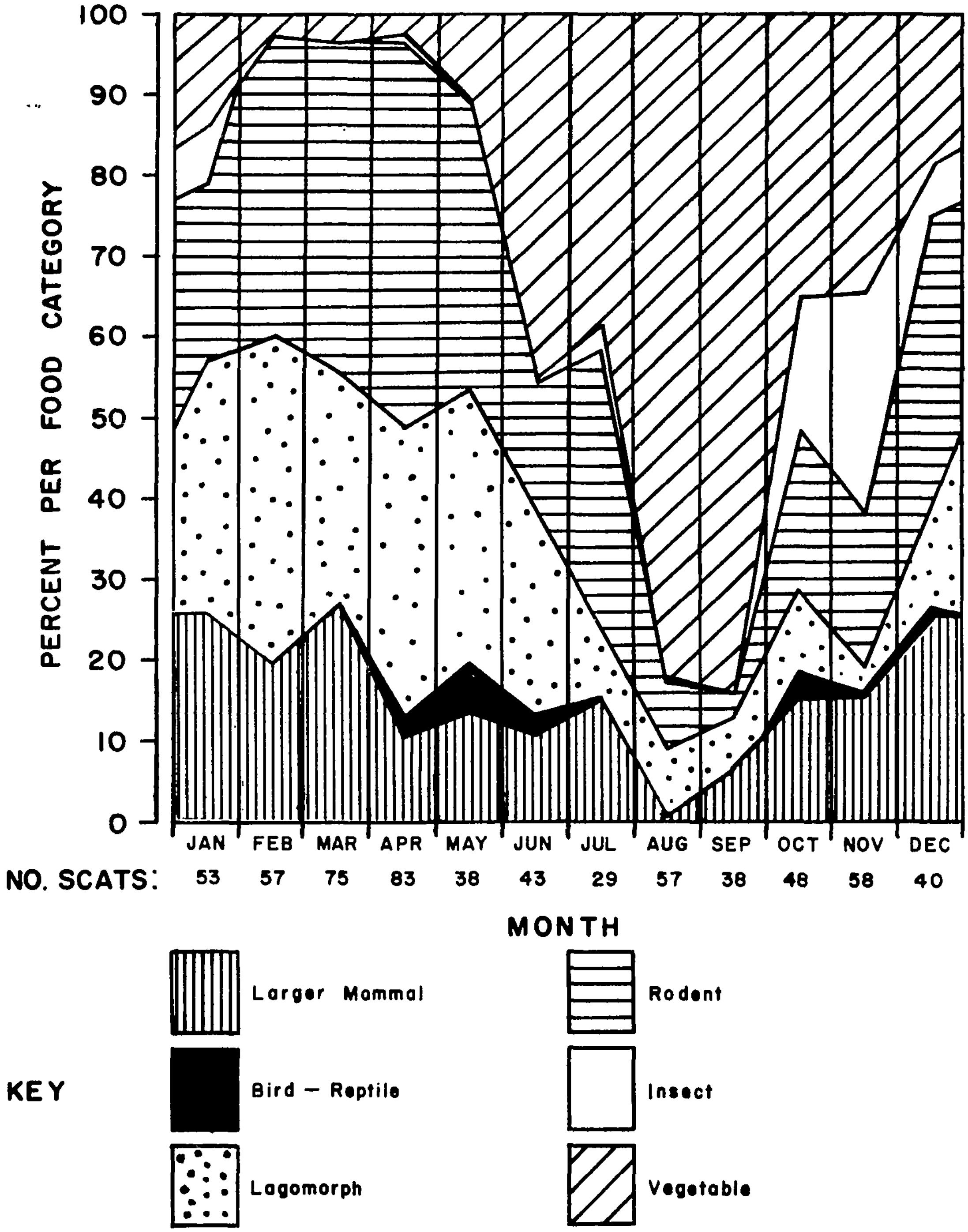


Figure 30. Monthly variation in composition of coyote scats from the SRER.

During the remainder of the year usage remained relatively constant at between roughly 10 and 15 percent of the diet by weight. Statistically the variation in relative weight of larger mammal remains between quarters was highly significant (H=21.2, 0.005>P). Variations in frequency of occurrence of larger mammals between quarters I, II, and IV were not significant (0.95>P>0.25), though their frequency in third quarter scats was lower than in any other quarter at a highly significant level (0.005>P).

Larger mammal material consisted predominantly of cow remains. Considering this item alone, seasonal variation was moderated somewhat. Perhaps this was due to the constant availability of cow carrion from the FICo carcass disposal area. Mortality of range cattle on the SRER per se tended to occur during the extended calving period beginning in January. Therefore it was not surprising that peak usage of cow, marked by a contribution of 21.7 percent to organic weight, was in the first quarter. Through the remaining months of the year, with the exception of the low incidence in August-September, the cow component remained relatively stable at between 7 and 15 percent of the organic weight of scat content.

Contributing to the importance of the larger mammal category in fall and winter was the increased incidence of big game material in scats at that time. Deer remains made their most significant contribution from October through January, during which period 4.9 percent of the organic weight of all scats was attributable to deer, with only trace amounts of deer hair occasionally appearing in scats during the remainder of the year. The seasonal appearance of deer remains suggested that hunter-related mortality was an important factor in making this food available to coyotes. McLean (1934) pointed out the relationship between sport hunting and increased incidence of deer in the coyote diet in California, and others have made similar observations elsewhere since (Ferrel et al. 1953; Knowlton 1964; Ozaga and Harger 1966; and others). An observation of a coyote feeding upon man-killed deer remains was made on the SRER when the site of unusual behavior on the part of a radio-monitored coyote was investigated. In the early morning hours of 22 December, 1972, this coyote located the remains of a deer which had been illegally shot and field dressed, fed upon the offal, and left only scraps of hair, hide, and viscera before moving on.

Similarly javelina were seasonally represented in scats. Measurable javelina residue was found from November through April, and a trace of javelina hair was recovered in a single May scat. Javelina accounted for 2.9 percent of the organic weight of all scats collected during the November-April period. Again hunter-related mortality may have been a factor. Legal hunting for javelina occurred in February each year; to explain the appearance of javelina in scats as early as November one has to assume that some of the animals were killed or crippled during the September deer season, or by other shooting while hunters were in the field.

The small mammal complement of the scats exhibited greater variation over the year, with the percentage of total organic weight due to this component ranging from under 10 percent in September to 85 percent in April, and varying at a highly significant level between quarters (H=72.7, 0.005>P). Variation in frequency of occurrence of smaller mammals between all quarters would have been highly significant (0.005>P), except that between quarters III and IV it was insignificant (0.50>P>0.25).

Within the smaller mammal category the importance of rabbits and rodents varied more or less together. Leporids were of greatest importance in February and April when they composed 40.4 and 36.4 percent, respectively,of the organic weight of all scats collected, and they were of least importance in November and September when the corresponding values were 3.2 and 6.9 percent, respectively. For rodents, maximum usage occurred in April and March when they contributed 48.6 and 40.3 percent, respectively,of total organic weight, while minimum values of 2.6 and 8.4 percent occurred in September and August, respectively. For the smaller mammal category collectively, changes from the late winter-early spring high to the late summer-early fall low usage periods were steady over a period of several months.

Bird remains were never an important component of the scat contents. The highest monthly records were 26 grams, 5 percent of the organic weight, recovered from 2 of 38 May droppings, and 28.5 grams, 3.1 percent by weight of the organic content of 48 October scats. Otherwise bird materials were found in very small amounts or not at all. The periods of peak incidence coincided with increased nesting activity in late spring and with fall sport hunting activity. The small number of scats containing measurable amounts of bird remains precluded a meaningful statistical test of seasonal variation based upon weights. The low frequency of occurrence during quarter I differed from that in quarter III at a significant level (0.05>P>0.025) and from that in quarters II and IV at a highly significant level (0.005>P). Frequency of occurrence of bird remains in scats did not differ significantly between all other quarters (0.95>P>0.25).

Insect remains appeared in substantial amounts from late summer into the winter months. This was particularly true in 1971 when large numbers of grasshoppers occurred on the study area. In October and November, 1971, the months of peak insect consumption, grasshopper remains comprised a remarkable 38.8 and 39.5 percent of the weight of organic remains of 22 and 38 scats, respectively. In contrast, in 1972 the month of heaviest use was July when 14.3 percent of the organic weight of 29 scats was attributable to grasshoppers. The variation in weight of insect remains between quarters proved highly significant (H=88.0, 0.005>P). Changes in frequency of occurrence would have been highly significant (0.01>P) between all quarters, except that between quarters II and III the difference only approached significance (0.10>P>0.05).

The great seasonal importance of the vegetative complement was due to the high incidence of remains of the fruits of graythorn, prickly pear, and mesquite in scats. Graythorn fruit was the first to ripen, and composed by weight 53.3 percent of the organic material found in 34 scats from June, 1973. Evidence of prickly pear tunas began to appear in July each year and traces could still be found in November scats. Their peak usage was recorded in August, 1972, when 64.6 percent by weight of the organic remains consisted of tuna rinds, seeds, and associated debris. Mesquite beans were consumed from July through February, showing much less of a peak in occurrence than did the other two major fruits. In November, 1972, 53.4 percent by weight of the organic material found in 38 droppings consisted of mesquite bean fragments.

An overwhelming preponderance of the August and September scat content consisted of remains of these fruits; in September 84.0 percent by weight of the organic scat material originated from them, while the corresponding value of 82.1 percent for August was only slightly less. Throughout the summer and fall, fruits were of major importance as coyote food. The quarterly variation in weights of vegetative remains proved highly significant statistically ($H=198.8$, $0.005>P$). Except that no significant change took place between quarters I and II ($0.95>P>0.90$), changes in frequency of occurrence in vegetative foods between all quarters was highly significant ($0.005>P$).

Effect of Availability versus Abundance on Seasonal Diet. While availability seemed the controlling factor in determining the importance of insects and fruits as coyote foods, it was apparently much less of a factor in governing usage of certain other items. The larger mammal food category showed less extreme seasonal fluctuations because its major component, cow carrion, was readily available year round. Particularly striking, however, was the fact that the importance of smaller mammals in the coyote diet, as determined by analysis of scat composition and supported by data obtained from examination of stomach contents presented earlier, did not relate directly to abundance. Over the period in which scats were being collected, summer rains began regularly in July of each year, resulting in a dramatic greening of the desert. Madsen (1974) found that desert lagomorphs responded quickly to improved forage developing in the wake of favorable precipitation patterns by reproducing. Probably many rodents responded similarly. Logically then, smaller mammals were most numerous in late summer. This contention was borne out by trapping data obtained by Courtney and Vaughan (personal communication 1976) showing that the greatest density of small rodents occurred in the third quarter of the year. Yet it was precisely at this time that they contributed least to the coyote scat content. Whether measured by frequency of occurrence or weight, evidence of smaller mammals did not peak in coyote scats until months later at a time when they were considerably less numerous. This was almost certainly due to the ready availability of fruits and grasshoppers in late summer and early fall, which removed the burden of predation temporarily from the smaller mammals. Possibly fruits and insects were preferred foods, but more probably it was simply a matter of less effort being required to obtain them. A somewhat similar situation was elaborated upon by Weckwerth and Hawley (1962) in relation to the food habits of the martin (*Martes americana*) in Montana

Comparison with Other Studies

Perhaps the most studied aspect of coyote ecology has been food habits. A digest of many coyote food habits reports is provided in Table 33. Data from cited references has been recombined into the five major food categories used for analysis in the present study, the results of which for comparative purposes appear as the last entry in

Table 33. Digest of coyote food habits studies.

Reference	Location	Sampling Period	No. Stomachs	No. scats	Percentage Based Upon Total	Larger Mammal	Smaller Mammal	Bird	Invertebrate	Vegetable	All Other
Alcorn 1946	Nevada	Nov.-Dec.	9	0	Stomachs	22.2	66.7	0.0	0.0	22.2	22.2
Andrews and Boggess 1978	Iowa	Winter	222	0	Volume	28.1	68.8	2.7	0.0	0.3	0.2
		Summer	0	246	Volume	12.4	55.7	4.4	1.4	25.2	0.8
Berg and Chesness 1978	Minnesota	Winter	1204	0	Weight	65.1	25.7	2.5	0.0	0.0	2.0
Bond 1939	California	Yr. round	9	273	Number	15.2	51.0	6.6	19.6	6.5	1.1
Ellis 1958	Oklahoma (Prairie)	Yr. round	0	358	Volume	3.1	82.4	7.0	1.4	3.3	2.8
	Oklahoma (Ecotone)	Yr. round	0	404	Volume	1.9	89.7	4.7	1.4	1.0	1.3
Ellis and Schemnitz 1958	Oklahoma	Nov.-Dec.-Jan.	16	0	Weight	8.0	91.5	0.0	0.2	0.3	Trace
Ferrel et al. 1953	California	Yr. round	2222	0	Volume	32.1	48.8	4.6	0.0	4.0	10.5
Fichter et al. 1955	Nebraska	Yr. round	747	0	Volume	12.6	64.2	17.7	0.9	1.6	3.1
Fitch 1948	California	Yr. round	0	1173	Weight	0.0	89.1	1.1	0.0	0.0	9.8
Fitch and Packard 1955	Kansas	Oct.-Jan.	0	118	Volume	20.9	75.9	1.2	0.0	0.0	1.8
Gier 1968	Kansas	Winter	1948	0	Weight	26.0	62.0	9.1	0.0	2.1	0.0

Table 33--continued. Digest of coyote food habits studies.

Reference	Location	Sampling Period	No. Stomachs	No. Scats	Percentage Based Upon Total	Larger Mammal	Smaller Mammal	Bird	Invertebrate	Vegetable	All Other
Grater 1943	Nevada-Arizona	Yr. round	0	176	Number	1.0	71.2	5.6	3.6	16.9	1.7
Hawthorne 1972	California	Jan.-Sept.	0	384	Volume	35	50	Trace	Trace	Trace	Trace
Johnson and Hansen 1979	Idaho	Yr. round	0	832	Weight	3.5	86.9	1.5	1.8	1.6	4.7
Knowlton 1964	Texas	Yr. round	265	0	Volume	16.7	36.4	7.4	12.4	19.5	7.7
Korschgen 1957	Missouri	Yr. round	770	0	Volume	10.9	67.8	11.8	0.8	2.0	6.4
			0	326	Volume	1.2	82.5	1.9	0.8	13.1	0.5
Leach and Frazier 1953	California	Apr.-Sept.	19	0	Volume	4.4	85.7	5.3	Trace	4.6	0.0
Mathwig 1973	Iowa	Jan.-Mar.	151	0	Volume	14.0	81.1	4.2	Trace	0.3	Trace
		Apr.-Oct.	0	147	Volume	10.0	56.1	1.3	1.0	29.2	1.8
Meinzer et al. 1975	Texas	Yr. round	94	0	Volume	21.4	31.4	4.5	11.7	23.0	8.0
			0	514	Volume	6.0	35.2	1.1	4.3	50.0	3.6
Murie, A. 1940	Yellowstone	Apr.-Nov.	0	5086	Number	19.2	63.9	3.2	9.6	2.4	1.6
Murie, A. 1951	Arizona	Feb.-July	0	3981	Number	13.6	10.0	1.3	9.5	65.3	0.3
Murie, O. 1935	Jackson Hole	Yr. round	64	714	Number	10.1	60.4	3.6	24.0	1.3	0.7

Table 33--continued. Digest of coyote food habits studies.

Reference	Location	Sampling Period	No. Stomachs	No. Scats	Percentage Based Upon Total	Larger Mammal	Smaller Mammal	Bird	Invertebrate	Vegetable	All Other
Murie, O. 1945	British Columbia	June	0	311	Number	12.8	75.5	7.4	1.0	1.8	1.5
	Western Montana	July	0	286	Number	20.4	71.3	3.5	1.6	1.9	1.3
	Eastern Montana	August	0	67	Number	6.4	53.8	12.9	18.3	3.2	5.4
Nellis and Keith 1976	Alberta	Yr. round	344	0	Volume	44	35	11	0	7	3
Niebauer and Rongstad 1977	Wisconsin	Yr. round	208	3353	Volume	25.6	36.0	4.8	1.3	26.9	5.5
Ogle 1969	Washington	May, July-August	12	0	Stomachs	41.6	66.7	25.0	33.3	8.3	0.0
			0	102	Scats	43.1	44.1	8.8	3.9	0.0	0.0
Ozaga 1963	Michigan	Yr. round	0	247	Volume	22.4	40.3	3.0	4.2	29.5	0.6
Rogers 1965	New Mexico	Winter-Spring	52	0	Volume	11.9	73.8	5.6	1.0	4.9	2.7
Sperry 1941	Western U.S.	Yr. round	8263	0	Volume	42.9	51.3	2.9	1.1	1.7	0.1
Tiemeier 1955	Kansas	Winter	871	0	Weight	25.4[a]	65.3	9.1	0.0	0.0	0.2
Truett and Day 1966	Arizona	Winter	142	0	Weight	23.8	53.4	0.6	0.0	7.0	15.2

Table 33--continued. Digest of coyote food habits studies.

Reference	Location	Sampling Period	No. Stomachs	No. Scats	Percentage Based Upon Total	Larger Mammal	Smaller Mammal	Bird	Invertebrate	Vegetable	All Other
Present Study	Arizona	Yr. round	92	0	Volume	25.4	35.0	16.4	6.4	16.2	0.4
			0	619	Weight	15.8	49.9	0.8	5.4	27.9	0.2

[a]Includes some chicken (Tiemeier 1955).

the table. Because of more limited information presented, findings of several additional studies could not be accurately abbreviated to fit the table. Enough representative studies have been included that a general notion of coyote feeding patterns across the country can be ascertained. Hopefully no damage to any researcher's original intent has been done by recategorizing data; however before drawing anything but general conclusions about coyote food habits in a particular region the original work should be consulted.

Background information about predator and prey species, general food availability, and similar ecological intelligence must be known to properly interpret results of any food habits investigation. The occurrence of items valued by man in stomachs or scats should not by itself be condemning. For example, the frequent appearance of deer remains reported in Michigan coyote scats (90 percent) by Ozaga and Harger (1966) must be evaluated in light of winter die-offs among yarded deer near scat collection sites. Likewise, the statement by Knowlton (1964) that deer composed up to 40 percent of the coyote diet on Welder Wildlife Refuge can be explained knowing that a density of 107 deer per square mile (0.4 deer/ha.) existed there at the time of his research. Nationwide, deer usually did not compose a substantial portion of the coyote diet.

Within the broad categories of Table 33, feeding trends of southern Arizona coyotes appeared comparable to those of coyotes in most other regions. Mammals generally comprised the great preponderance of coyote food. In virtually every study the majority, if not all, of the larger mammals eaten by coyotes originated as carrion.

In southern Arizona less of a winter-spring peak in consumption of carrion was apparent, possibly reflecting greater year-round availability. Generally coyotes depended upon smaller mammals for the bulk of their food. As was the case in southern Arizona, various species of leporids and rodents usually comprised a predominant portion of the diet. Though a comparative newcomer in the Northeast, the coyote maintains a similar diet even there, depending upon snowshoe hares (*Lepus americanus*) and a variety of mice for subsistence (Hamilton 1974). Birds seldom contributed substantially to the diet except where poultry, often carrion, was readily available (Gipson 1974). A regular but small component of coyote food was insects, which became more important seasonally. Fruits also had seasonal impact and often comprised a significant portion of the diet during the summer months. The longer growing season in the Southwest probably accounted for the increased consumption of insects and fruits by coyotes there.

This synopsis of coyote food habits is obviously oversimplified. Many interacting factors make more specific comparisons difficult and beyond the scope of this report. Because of the complex ecology of predators, Latham (1951)has cautioned that evidence of foods encountered in stomachs and scats indicate feeding trends for only a particular time and locality. While this is true in a specific sense, in the general sense used here it appears that Fichter et al. (1955) correctly concluded that the broad outlines of coyote feeding habits, except for some local variations and seasonal shifts, seem to apply everywhere.

SUMMARY AND CONCLUSIONS

Coyote Behavior

Behavioral information was obtained by live trapping, radio tagging, and releasing coyotes, relocating them periodically, and monitoring their activity at intervals by means of radio telemetry. Other observations, particularly those based upon vocalizations, augmented knowledge of coyote behavior.

In view of the frequent injuries sustained by coyotes captured in steel traps despite such precautions as padded jaws, springs connected parallel to trap chains, and tranquilizer tabs, a less harmful means of live trapping should be devised.

Home range was defined as the apparent area occupied by an instrumented coyote while it supplied telemetric data. Minimum home range estimates ranged from 0.5 square mile (130 ha.) to 7.9 square miles (2055 ha.), and averaged 4.2 square miles (1091 ha.) overall. The relatively small size of these home ranges may have been a reflection of the general abundance of food and the high density of coyotes present on the study area during the time of this study.

Considerable individual variation in home range size was noted, and differences appeared to relate to such factors as sex, season, and group size. Unfortunately substantive data were available for too few animals to allow conclusive statements.

Female home ranges averaged over twice the size of male home ranges (7.2 versus 2.7 square miles, 1865 versus 699 ha.), a difference which was statistically significant. Greater movements by females were noted by some other researchers as well, and theoretically may have been a manifestation of a sex-related dominance hierarchy. Females tended to exhibit behavior interpreted as submissive while in captivity as well as when free ranging. Submissive animals would be more harried and require a larger home range in which to survive.

Certain portions of the home range were used more intensively than others, indicating the location of favored hunting and resting areas. The total occupied area could be divided into a series of foraging ranges, parcels of land upon which the animals lived for a time before shifting to a different tract. While food and cover were essential features of good coyote habitat, it appeared that water was not.

Coyote home ranges were characteristically linear, that is, oblong in shape. On the average, length was twice the width. This appeared to result from the tendency of coyotes to travel routes that were dictated by drainage pattern.

Diel activity accommodated crepuscular and nocturnal prey species, with coyotes tending to remain inactive during the midday hours. During the winter season coyotes remained active later and became active earlier in the day.

Physical comfort influenced coyote behavior. For example, rest sites often were selected for comfort insofar as warm sites were used in cool weather and cool sites were used in hot weather. Activity during foul weather and inactivity during hot weather appeared to be means of maintaining body temperature at a comfortable level.

Hunting for food appeared to be the most common occupation. It was typically a very slow and deliberate process. Lengthy journeys were uncommon, though rapid movements of over a half-mile (0.8 km.) were sometimes noted when instrumented coyotes attempted to avoid contact with the observer in the field.

Vocalizations could be interpreted as having several communicative functions. Basically howling served to advertise the location of the vocalist. More intimate vocalizations and their purposes could not be analyzed. The potential value of this behaviorism to researchers must be emphasized.

Coyotes appeared to commonly associate in groups. Such groups presumably consisted of blood-related animals, though this could not be substantiated. Because of the tendency of these groups to disperse widely and dissolve readily, their occurrence may be generally underestimated.

Though there was some conflicting evidence, territoriality in the sense of active defense of a tract of land was not an obvious feature of coyote behavior on the study area.

Coyote Population Structure

The distribution of age classes and the sexes within the coyote population was estimated from examination of a large number of coyote specimens obtained from a variety of sources. General information about southern Arizona coyotes derived from these data was probably quite valid. However, as the composite sample was broken down into smaller subsamples representing counties and months for example, Type I error became an important consideration. How well subsamples represented actual subpopulations was problematical. Conclusions based upon examination of relatively small samples were tentative. Certainly more rigorously controlled investigation of coyote population dynamics would be fruitful.

Based upon a composite sample of 378 coyotes, the average age attained by southern Arizona coyotes was 3¼ years, though some animals lived to in excess of 13 years. Animals in the 1-2 year old age group enjoyed the greatest expectation of further life at 2.8 years. A modest proportion of the composite sample consisted of coyotes less than one year of age, intimating poor reproductive success and/or survival of young animals. A dramatic decline in the size of the 0-1 year old component was observed from age 5 months, when pups first occurred in the sample, until one year of age; no such trend was apparent for older coyotes. The dynamic nature of coyote populations was apparent from observing significant differences in age structures from year to year and county to county.

Based upon 273 known-sex specimens, males predominated in the general population and tended to outlive females. In the older age classes males significantly outnumbered females.

Coyotes representing different age classes and sexes were not equally susceptible to accidental death on roadways, hunting, or control efforts. Pups and females predominated among road-killed specimens. Coyotes of both sexes up to 5 years of age appeared to be vulnerable to popular hunting techniques; it was hypothesized that group members were more responsive to varmint calling. DWS (ADC) control activities consisting of trapping and poisoning were most successful against pups and males. Since these categories represented the non-productive segment of the population, it was possible that non-intensive control efforts did little more than harvest surplus animals, while more intensive control would stimulate population growth. Theoretically varmint calling, if it could be practically implemented, would be a more effective means of controlling coyote numbers, for it struck more directly at the productive segment of the population.

Southern Arizona coyote age class distributions and sex ratios differed significantly from similar data obtained by other investigators from widely separated regions of western North America. This disparity reflected the dynamic nature of coyote populations generally. Compared with coyotes elsewhere, southern Arizona populations had a greater percentage of animals in the older age categories and a reduced number of animals less than one year old. Taken together these features suggested an unexploited population.

Closer examination of fluctuations in age class and male-female distributions between years and localities led to formulation of a hypothetical explanation of how coyote populations maintained an equilibrium with their environment. Imbalance might have originated with changes in coyote carrying capacity, or from depressive effects of parasites, diseases, or artificial control efforts. Available data suggested that a population below the carrying capacity of its environs was characterized by a shift in sex ratio in favor of females, thereby enhancing reproductive potential. A change in the relative numbers of the sexes was inherent within the control practices of trapping and poisoning, which significantly favored the killing of males. Such a change would be facilitated further by natality and ingress, both of which appeared to favor females under the circumstances. An increasing proportion of females coupled with larger litter sizes and greater incidence of pregnancy among pups, both of which have been documented by other research (Gier 1968; Knowlton 1972), provided an effective means of population recovery by means of increased reproductive success. In contrast, a stable or declining population was characterized by fewer pups and a preponderance of males. Hopefully this hypothesis will be tested by further, better controlled research.

Coyote Reproductive Analysis

Based upon the presence or absence of spermatazoa within the epididymi of 22 male coyotes, it appeared that males were capable breeders from January to June. Males in their first year of life produced sperm, but presumably contributed little to the overall reproductive picture.

Six of 20 uteri examined showed signs of pregnancy. The average number of implantation sites was 4.5. Based upon fetal measurements obtained from two gravid bitches, dates of conception and parturition were approximately March 1 and May 1, respectively. There was no evidence that successful breeding occurred among juvenile female coyotes.

Coyote Parasites and Diseases

Southern Arizona coyotes were subject to attack by a large variety of parasites. This was partly the result of the ubiquitous nature of the coyote: because the animal occurred in a wide range of habitats it was exposed to infection by an assortment of parasites. Diverse food habits also predisposed the coyote to parasitism and enabled endoparasites to make use of intermediate and transport hosts.

Though circumstances were often less than optimal for collection of ectoparasites, five species were identified from 101 carcasses and 21 live coyotes that were examined. The flea *Pulex simulans*, the louse *Heterodoxus spiniger*, and the nymph of the tick *Otobius megnini* were most often encountered.

Two potentially dangerous endoparasites were identified in relatively few coyotes. These were *Filaroides osleri*, which infected the respiratory system, and *Dirofilaria immitis*, which attacked the circulatory system. Their incidence was generally low and their importance limited at the time of this study. However, *D. immitis* has been reported in a large proportion of coyotes along the Colorado River in Yuma county, where it may have had local significance. The intestinal nematodes *Ancylostoma caninum* and *Toxascaris leonina* and the stomach worm *Physaloptera rara* seemed of particular importance. Of these the dog hookworm, *A. caninum*, because of its notorious consumption of blood, was possibly the most debilitating. These nematodes occurred frequently, and when present in large numbers were potentially very injurious. The cestodes *Taenia pisiformis* and *Taenia multiceps* occurred consistently enough to be threatening to coyote well being.

Oncicola canis also occurred repeatedly, but because so little is known of the pathogenicity of this acanthocephalan it remains largely an unknown factor in coyote health. Several other helminths were detected infrequently and appeared to be of little importance.

While parasites were generally recovered from adult coyotes in numbers considered to be only slightly debilitating, occasionally a severely infected individual was encountered. Lethal parasitism would have been difficult to detect among wild coyotes, for moribund animals most probably died unnoticed in the wild. Among pups the effects of parasitism were potentially more severe. Young coyotes had not yet developed a good immune mechanism and were more susceptible to infection. The physiological needs of growing pups accentuated the danger of a large parasite burden.

Statistical analyses of data accumulated during the course of this study indicated that coyotes less than a year of age tended to sustain larger parasite loads than did adults, though incidence of infection for specific helminths in young animals was seldom significantly greater than in adults. Also it appeared that females tended to be somewhat more susceptible to attack by endoparasites collectively than were males. Probably related to the ecology of the parasites themselves were the variations in host-parasite relationships with year, season, and geographic location.

Because of the more sophisticated technology necessary for their detection, diseases were recorded much less frequently than were parasites. Of 27 coyote heads submitted for fluorescent antibody testing, none were positive for rabies. Nonetheless across Arizona rabies has been reported in a small number of coyotes annually. Because of its importance more research on the epizootiology of rabies is needed. Oral papillomatosis was detected in two coyotes, both of which were additionally stressed by heavy endoparasite burdens. Serologic evidence of leptospirosis was detected in four of nine coyotes representing a localized subpopulation. Necropsy of one very weak coyote encountered and shot in the area of the apparent outbreak suggested that leptospirosis might have caused at least some fatalities. While no other diseases were detected among southern Arizona coyotes during this study, others have been recorded in coyotes elsewhere. Distemper, infectious canine hepatitis, and rabies seem particularly dangerous, especially to young coyotes.

In considering parasitism and disease in relation to coyotes it should be remembered that relatively little is known about these factors among wild populations. Frequently studies conducted upon the closely related domestic dog or at best coyotes under laboratory conditions must be extrapolated to natural situations. Theoretically parasitism tends to be a chronic, often insidious malady for coyotes, providing them with a constant stress factor and predisposing them to other dangers. The immune response to parasites, particularly to forms inhabiting the intestinal lumen, is much less than the response to disease organisms (Levine 1968:40). In contrast, disease tends to be more acute by nature, traveling rapidly through a population and, if virulent enough, resulting in the deaths of many individuals within a short period. The findings of this study bolstered these generalizations about parasitism, but were too few to allow many conclusions about the effects of diseases among coyotes.

It is particularly difficult to ascribe cause and effect when considering parasitism and disease in relation to coyote ecology. Factors which must be evaluated include weather, food base, virulence of the infection, condition of the host, and quality of the environment, among others. Gier et al. (1978:38) reported one situation where the combination of mange and severe weather resulted in heavy winter losses of coyotes. The effect of parasitism and disease as a population control device may not always be so obvious, however. During the annual population cycle of the coyote, peak numbers occur in late spring after the birth of pups, and a steady decline ensues until the following whelping season (Gier 1968; Knowlton 1972). The sudden swell in the population and the bulk of the subsequent attrition is due to changes in numbers of juvenile coyotes. Indeed generally a reduction is necessary to keep the population in bounds. In view of what is known about the susceptibility of young coyotes, parasitism and disease may be important factors in their demise, and thereby act to control coyote populations in a very subtle way.

Coyote Food Habits

Two independent food habits studies were conducted to determine the feeding patterns of southern Arizona coyotes. The first was an analysis of stomach contents from 92 coyotes. The relative importance of the major food categories was best expressed as percentage of the composite sample volume. Larger mammals, most of which appeared to originate as carrion, composed 25.4 percent of the total volume. The chief item within this category was cow (10.9 percent). The most important food category, smaller mammals, contributed 35.0 percent of the volume. Within this category, leporids accounted for 20.9 percent, and of these cottontails were most prominent, composing 15.2 percent of total volume. A variety of rats, mice, porcupine, and other rodents together accounted volumetrically for 14.1 percent of the diet. Birds composed 16.4 percent of the volume, with chicken accounting for 7.1 percent and pheasant, considered non-typical, supplying 6.4 percent of overall volume. Other birds contributed relatively little. Reptiles appeared to be of no great significance, contributing but 0.1 percent to overall volume. Invertebrates, largely grasshoppers, composed 6.4 percent of the composite volume, but were of greater importance seasonally. Foods of plant origin also had great seasonal significance, though they did compose a substantial 16.2 percent of the overall volume. Chief late summer and fall plant foods were prickly pear and mesquite fruits. Additionally miscellaneous materials accounted for 0.5 percent of the composite sample volume.

Adult coyotes consumed a greater volume of larger mammalian food than did juveniles. Possibly this reflected the dominance of larger coyotes over pups while the animals were feeding upon large carcasses. Pups consumed a significantly greater volume of smaller mammals and vegetable foods than did adults. More limited food habits data available for yearlings suggested food habits intermediate between those of pups and adults.

Female coyotes consumed a significantly greater volume of smaller mammals and also tended to consume more insects and fruits than did males. Males were prone to feed more upon large birds, and to a slightly greater extent upon larger mammals, particularly cattle. Possibly male feeding patterns reflected a dominant status or greater boldness.

Coyote feeding patterns varied surprisingly little between the two years for which data were available. There were also few differences in the diets of coyotes representing three southern Arizona counties. Such variations as did occur could be largely explained by the unusual contents of a small number of stomachs. Apparently conditions were similar enough between years and counties that the same categories of foods were equally available.

In the second investigation, food habits of coyotes living on the Santa Rita Experimental Range were determined by examining 619 scats collected there. Based upon percentage of weight of the organic component of all scats, the major food categories contributed as follows: larger mammal, 15.8 percent; smaller mammal, 49.9 percent; bird, 0.8 percent; reptile, 0.2 percent; insect, 5.4 percent; and vegetable, 27.9 percent. The principal component of the larger mammal category was cow, which composed 12.4 percent of total organic weight. Since dead cattle were readily available year round and special effort had failed to detect predation upon cattle by coyotes, all cow remains probably originated as carrion. Of the smaller mammals, leporids contributed 21.8 percent and rodents, the single most important category, accounted for 28.1 percent of overall organic weight. Birds and reptiles appeared to be of little significance as coyote food. Of special seasonal importance to SRER coyotes were insects and foods of vegetable origin; grasshoppers and fruits of graythorn, prickly pear, and mesquite became major foods in summer and fall.

More than 25 percent of the weight of the composite scat sample was due to inorganic matter, mostly sand. Coyotes may have ingested large amounts of inorganic material while digging for water or when consuming shallowly buried carrion.

Seasonal differences in weights of residue from scats representing larger mammal, smaller mammal, insect, and vegetable food categories were highly significant statistically. This appeared the result of the great seasonal peak in consumption of fruits in summer and fall, which of course resulted in lower use of other foods at that time. In late summer and fall while fruits were most abundant, coyotes deferred consumption of small mammals, though rabbits and rodents reached their maximum yearly density at this time as well. Smaller mammals were of greatest importance in the coyote diet when they were less numerous, in spring several months later.

Within broad limits, southern Arizona coyotes appeared to utilize the same types of foods as coyotes elsewhere. Small mammals were the most important food, as was the case in the great majority of similar investigations. While other research has shown that carrion generally becomes an important coyote food in late winter and spring, southern Arizona coyotes utilized carrion year round. A pronounced increase in consumption of insects and especially fruits occurred in summer and fall in many areas. Fruits and insects were apparently more important to coyotes in the Southwest than in other parts of their range.

APPENDIX A

MEASUREMENTS OF COYOTE SPECIMENS

Table A-1. Average measurements and ranges of measurements (in parenthesis) of coyote specimens listed by sex and age class of specimen.

Age Class (yrs.)	Sample Size	Total Length in Inches (inc. tail)	Tail (in.)	Height at Shoulder (in.)	Weight (lbs.)
Male Coyotes					
0-1[a]	11	45.89 (40-49.5)	12.70 (10.5-13.75)	18.03 (16.25-20.25)	22.43 (13.5-27.25)
1-2	7	47.13 (43.75-50.375)	13.00 (12.5-14.5)	17.90 (17.25-18.5)	24.79 (21.25-29)
2-3	8	46.72 (43-50.25)	12.20 (11-13.75)	18.45 (17.5-19.25)	26.28 (18.25-34)
3-4	5	48.03 (46.375-51.25)	12.80 (11.75-13.625)	18.37 (17.75-18.75)	25.95 (22-31)
4+	14	46.71 (42.25-49.5)	12.44 (9.5-14.75)	18.23 (17-19.5)	24.43 (21-30)
All Ages	45	46.72 (40-51.25)	12.58 (9.5-14.75)	18.20 (16.25-20.25)	24.49 (13.5-34)
Female Coyotes					
0-1[b]	10	41.40 (39.5-44.75)	11.69 (10-12.5)	16.53 (14-18.5)	16.53 (11.5-21.5)
1-2	7	43.86 (40.5-46.5)	12.10 (11.5-12.5)	16.89 (15.5-18.25)	19.00 (13.5-22.75)
2-3	7	44.68 (40.5-47.75)	12.19 (10.75-12.75)	16.96 (15.5-17.75)	20.75 (18.5-25)

Table A-1--continued.

Age Class (yrs.)	Sample Size	Total Length in Inches (inc. tail)	Tail (in.)	Height at Shoulder (in.)	Weight (lbs.)
3-4	7	44.04 (40-48.5)	11.96 (10.5-12.5)	17.39 (15.75-18.5)	20.46 (16.75-24.5)
4+	2	42.88 (40.75-45)	11.75 (11.5-12)	18.88 (17.75-20)	24.00 (23.5-24.5)
All Ages	33	43.27 (39.5-48.5)	11.95 (10-12.75)	17.02 (14-20)	19.23 (11.5-25)

[a]Average age of male pups was 9.4 months (7-11 mos.).

[b]Average age of female pups was 7.0 months (5-11 mos.).

LITERATURE CITED

Ables, Ernest D. 1969. Home-range studies of red foxes (*Vulpes vulpes*). J. Mammal. 50(1):108-120.

Abuladze, K. I. 1964. Essentials of cestodology. Vol. IV. Taeniata of animals and man and diseases caused by them. Acad. of Sci. of the USSR. Helminth. Lab. Israel Program for Scientific Translations, Jerusalem. 549 pp.

Adams, C. E. 1978. Ages of hunter-killed coyotes in southeastern Nebraska. J. Wildl. Manage. 42(2):425-426.

Adorjan, A. S. and G. B. Kolenosky. 1969. A manual for the identification of hairs of selected Ontario mammals. Ont. Dept. of Lands and For. Res. Rep. No. 90. 64 pp.

Agricultural Research Service. 1965. Manual on livestock ticks. U.S. Dept. Agric., Anim. Dis. Eradication Div. ARS 91-49. 142 pp.

Aiton, John F. 1938. Relationships of predators to whitetail deer in Glacier National Park. Trans. N. Amer. Wildl. Conf. 3:302-304.

Alcorn, J. R. 1946. On the decoying of coyotes. J. Mammal. 27(2): 122-126.

Allen, Stephen H. and Stanley C. Kohn. 1976. Assignment of age-classes in coyotes from canine cementum annuli. J. Wildl. Manage. 40(4):796-797.

Ameel, Donald J. 1955. Parasites of the coyote in Kansas. Trans. Kans. Acad. Sci. 58(2):208-210.

Ames, Norma. 1975. Coyote, man, and the fifth world. New Mex. Wildl. 20(1):22-25.

Andelt, William F. and Philip S. Gipson. 1979a. Domestic turkey losses to radio-tagged coyotes. J. Wildl. Manage. 43(3):673-679.

Andelt, William F. and Philip S. Gipson. 1979b. Home range, activity, and daily movements of coyotes. J. Wildl. Manage. 43(4): 944-951.

Anderson, Raymond E. 1974. Papago drought losses: the numbers game. The Arizona Daily Star 133(223):1H.

Andrews, Richard D. and Deam H. Ferris. 1966. Relationships between movement patterns of wild animals and the distribution of leptospirosis. J. Wildl. Manage. 30(1):131-134.

Andrews, Ronald D. and Edward K. Boggess. 1978. Ecology of coyotes in Iowa. In Coyotes: biology, behavior, and management. Ed. Marc Bekoff. Academic Press, New York, N.Y., pp. 249-265.

Arizona Daily Star. 1972-1975. Tucson.

Arizona Public Health Epidemiology. 1965-1969. Rabies in Arizona. Ariz. State Dept. of Health, Phoenix.

Arizona Veterinarian. 1968-1973. Animal rabies summary. Ariz. State Dept. of Health, Phoenix.

Balser, Donald S. 1965. Tranquilizer tabs for capturing wild carnivores. J. Wildl. Manage. 29(3):438-442.

Beard, Betty. 1973. Increased rustling in state blamed on cattle shortage. The Arizona Daily Star. 132(216):1B.

Beaty, David W. 1971. Personal communication: circuit diagram for wildlife transmitter. Telonics, Inc., Phoenix.

Bebb, William. 1934. Source of small birds eaten by coyote. J. Mammal. 15(4):320-321.

Bekoff, Marc. 1978. Introduction. In Coyotes: biology, behavior, and management. Ed. Marc Bekoff. Academic Press, New York, N.Y. pp. xvii-xx.

Bekoff, Marc and Robert Jamieson. 1975. Physical development in coyotes (Canis latrans), with a comparison to other canids. J. Mammal. 56(3):685-692.

Berg, William E. and Robert A. Chesness. 1978. Ecology of coyotes in northern Minnesota. In Coyotes: biology, behavior, and management. Ed. Marc Bekoff. Academic Press, New York, N.Y. pp. 229-247.

Bicknell, E. J. 1973. Report of laboratory examination. Univ. Ariz. Dept. Vet. Sci. Accession No. 73-529. Debilitated coyote.

Bishopp, F. C. and H. L. Trembley. 1945. Distribution and hosts of certain North American ticks. J. Parasit. 31(1):1-54.

Blair, W. Frank. 1940. Home ranges and populations of the jumping mouse. Amer. Midl. Natur. 23(1):244-250.

Bond, Richard M. 1939. Coyote food habits on the Lava Beds National Monument. J. Wildl. Manage. 3(3):180-198.

Borror, Donald J. and Richard E. White. 1970. A field guide to the insects of America north of Mexico. Houghton Mifflin Co., Boston. 404 pp.

Bowen, Stephen L. 1973. Personal communication. Information of occurrence of heartworms in coyotes near Yuma, Arizona. U.S. Army Med. Dept. Activity, Yuma Proving Ground, Yuma, Arizona.

Brander, Robert B. and William W. Cochran. 1969. Radio-location telemetry. In Wildlife Management Techniques. Ed. Robert H. Giles, Jr. The Wildl. Soc., Washington, D.C. pp. 95-103.

Broughton, E., F. E. Graesser, L. N. Carbyn and L. P. E. Choquette. 1970. Oral papillomatosis in the coyote in western Canada. J. Wildl. Dis. 6(3):180-181.

Brown, John B. 1973. Behavioral correlates of rank in a litter of captive coyotes (Canis latrans). M.S. Thesis, Purdue Univ., Lafayette, Ind. 151 pp.

Brown, L. E. 1966. Home range and movement of small mammals. Symp. Zool. Soc. Lond. 18:111-142.

Brunetti, Oscar A. 1959. Occurrence of the giant kidney worm, Dioctophyma renale, in the coyote of California. Calif. Fish and Game 45(4):351-352.

Burnham, John. 1972. Weed identified as cattle foe. The Arizona Daily Star 131(277):2A.

Burt, William H. 1943. Territoriality and home range concepts as applied to mammals. J. Mammal. 24:346-352.

Burt, William H. and Richard P. Grossenheider. 1964. A field guide to the mammals. Houghton Mifflin Co., Boston. 284 pp.

Butler, Joseph M. and Albert W. Grundmann. 1954. The intestinal helminths of the coyote, Canis latrans Say, in Utah. J. Parasit. 40(4):440-443.

Cabasso, Victor J. 1970. Infectious canine hepatitis. In Infectious diseases of wild mammals. Ed. John W. Davis, Lars H. Karstad and Daniel O. Trainer. Iowa State Univ. Press, Ames, Iowa. pp. 134-139.

Cahalane, Victor H. 1947. A deer-coyote episode. J. Mammal. 28(1): 36-39.

Cain, Stanley A., John A. Kadlec, Durward L. Allen, Richard A. Cooley, Maurice G. Hornocker, A. Starker Leopold, and Frederick H. Wagner. 1972. Predator control - 1971. Report to the Council on Environmental Quality and the Department of the Interior by the Advisory Committee on Predator Control. Univ. of Mich. Press, Ann Arbor. 207 pp.

Camenzind, Franz J. 1978. Behavioral ecology of coyotes on the National Elk Refuge, Jackson, Wyoming. In Coyotes: biology, behavior, and management. Ed. Marc Bekoff. Academic Press, New York, N.Y. pp. 267-294.

Cameron, Thomas W. M. 1926. Observations on the genus Echinococcus Rudolphi, 1801. J. Helminth. 4(1):13-22.

Carey, Andrew B. and Robert G. McLean. 1978. Rabies antibody prevalence and virus tissue tropism in wild carnivores in Virginia. J. Wildl. Dis. 14:487-491.

Chandler, Asa C. 1944. A new species of Mesocestoides, M. kirbyi, from Canis latrans. J. Parasit. 30:273.

Chesness, Robert A. and Timothy P. Bremicker. 1974. Home range, territoriality and sociability of coyotes in north-central Minnesota. Paper presented to Coyote Workshop, Denver, Colo. Nov. 14. 17 pp.

Chitwood, B. G. and M. B. Chitwood. 1950. An introduction to nematology. Monumental Printing Co., Baltimore, Md. 213 pp.

Cirone, S. M., H. P. Riemann, R. Ruppanner, D. E. Behymer and C. E. Franti. 1978. Evaluation of the hemagglutination test for epidemiologic studies of leptospiral antibodies in wild mammals. J. Wildl. Dis. 14:193-202.

Clapham, Phyllis A. 1942. On identifying Multiceps spp. by measurement of the large hook. J. Helminth. 20(1-2):31-40.

Clark, Carl H., J. M. Kling, C. H. Woodley and N. Sharp. 1961. A quantitative measurement of the blood loss caused by Ancylostomiasis in dogs. Amer. J. Vet. Res. 22(88):370-373.

Cochran, Doris M. and Coleman J. Goin. 1970. The new field book of reptiles and amphibians. G. P. Putnam's Sons, New York, N.Y. 359 pp.

Cockrum, E. Lendell. 1960. The recent mammals of Arizona: their taxonomy and distribution. The Univ. of Ariz. Press, Tucson, Arizona. 276 pp.

Cockrum, E. Lendell. 1962. Introduction to mammalogy. The Ronald Press Co., New York, N.Y. 455 pp.

Conder, George A. and Raymond M. Loveless. 1978. Parasites of the coyote (Canis latrans) in central Utah. J. Wildl. Dis. 14: 247-249.

Courtney, Mark and Thomas Vaughan. 1976. Personal communication. Small mammal density on the Santa Rita Experimental Range. Thesis in preparation.

Cowan, I. McT. 1950. Some vital statistics of big game on overstocked mountain range. Trans. N. Amer. Wildl. Conf. 15:581-588.

Cox, George W. 1950. The fleas of Texas. Tex. State Health Dept., Div. of Entomol., Austin, Texas. 85 pp.

Crowe, Douglas M. and Dale Strickland. 1975. Population structures of some mammalian predators in southeastern Wyoming. J. Wildl. Manage. 39(2):449-450.

Danner, Dennis A. 1976. Coyote home range, social organization, and scent post visitation. M.S. Thesis, Univ. of Ariz., Tucson. 86 pp.

Davis, Goode P. 1973. Man and wildlife in Arizona: the presettlement era, 1823-1864. M.S. Thesis, Univ. of Ariz., Tucson. 251 pp.

Day, Gerald I. 1973. Marking devices for big game animals. Wildl. Digest, Ariz. Game and Fish Dept. 7 pp.

Debbie, John G. and Charles V. Trimarchi. 1970. Pantropism of rabies virus in free-ranging rabid red fox Vulpes fulva. J. Wildl. Dis. 6:500-506.

Denley, Patrick. 1978. Dogs: pets by day, killers by night. The Tucson Citizen, Wednesday, May 10:10.

Dewhirst, L. W. 1971. Personal communication. Laboratory techniques on mounting cestodes. Professor, Univ. of Arizona, Tucson.

Dewhirst, L. W. 1972. Personal communication. Occurrence of Toxocara canis in Tucson and vicinity.

Dewhirst, L. W. 1980. Personal communication. Incidence of Ancylostoma caninum infection in Tucson and vicinity.

Dixon, Joseph. 1925. Food predilections of predatory and fur-bearing mammals. J. Mammal. 6(1):34-46.

Dobie, J. Frank. 1961. The voice of the coyote. Univ. of Neb. Press, Lincoln, Neb. 386 pp.

Dorrington, J. E. 1965. Preliminary report on the transmission of Filaroides osleri (Cobbold 1879) in dogs. J. S. Afr. Vet. Med. Assoc. 36(3):389.

Dunatchik, David D. 1967. The helminth parasites of Michigan coyotes. M.S. Thesis, Univ. of Mich., Ann Arbor. 48 pp.

Eads, Richard B. 1948. Ectoparasites from a series of Texas coyotes. J. Mammal. 29(3):268-271.

Ellis, Ralph J. 1958. Food habits and control of coyotes in north-central Oklahoma. M.S. Thesis, Okla. State Univ., Stillwater. 45 pp.

Ellis, Ralph J. 1964. Tracking raccoons by radio. J. Wildl. Manage. 28(2):363-368.

Ellis, Ralph J. and Sanford D. Schemnitz. 1958. Some foods used by coyotes and bobcats in Cimarron County, Oklahoma, 1954 through 1956. Proc. Okla. Acad. Sci. for 1957. pp. 180-185.

Emerson, Kary C. 1962. A tentative list of Mallophaga for North American mammals. U.S. Dept. Com., Inst. for Appl. Tech., Clearinghouse for Fed. Sci. and Tech. Inform. 20 pp.

Environmental Science Services Administration. 1973. Climatological data, Arizona. U.S. Dept. Com., ESSA. Vol. 77 (1-13).

Erickson, Arnold B. 1944. Helminths of Minnesota Canidae in relation to food habits, and a host list and key to the species reported from North America. Amer. Midl. Natur. 32:358-372.

Erickson, James A. and William G. Seliger. 1969. Efficient sectioning of incisors for estimating ages of mule deer. J. Wildl. Manage. 33(2):384-388.

Esch, Gerald W. and J. Teague Self. 1965. A critical study of the taxonomy of Taenia pisiformis Block, 1780; Multiceps multiceps (Leske, 1780); and Hydatigera taeniaeformis Batsch, 1786. J. Parasit. 51(6):932-937.

Ferrel, Carol M., Howard R. Leach and Daniel F. Tillotson. 1953. Food habits of the coyote in California. Calif. Fish and Game 39(3):301-341.

Fichter, Edson, George Schildman and J. Henry Sather. 1955. Some feeding patterns of coyotes in Nebraska. Ecol. Mon. 25(1): 1-37.

Fitch, Henry S. 1948. A study of coyote relationships on a cattle range. J. Wildl. Manage. 12(1):73-78.

Fitch, Henry S. 1958. Home ranges, territories and seasonal movements of vertebrates of the Natural History Reservation. Univ. of Kans. Mus. Natur. Hist. Pub. 11(3):63-326.

Fitch, Henry S. and Robert L. Packard. 1955. The coyote on a natural area in northeastern Kansas. Trans. Kans. Acad. Sci. 58(2): 211-221.

Foster, A. O. 1935. Further observations on prenatal hookworm infection of dogs. J. Parasit. 21(4):302-308.

Fox, Irving. 1940. Fleas of eastern United States. The Iowa State College Press, Ames, Iowa. 191 pp.

Fox, M. W. 1971. Behavior of wolves, dogs and related canids. Jonathon Cape Ltd., London. 214 pp.

Fox, M. W. 1972. Socio-ecological implications of individual differences in wolf litters: a developmental and ecological perspective. Behavior. 41(3&4):298-313.

Francis, G. R. and A. B. Stephenson. 1972. Marten home ranges and food habits in Algonquin Provincial Park, Ontario. Ont. Min. of Natur. Resources Res. Rep. No. 91. 53 pp.

Franson, J. Christian, Richard D. Jorgenson and Edward K. Boggess. 1976. Dirofilariasis in Iowa coyotes. J. Wildl. Dis. 12:165-166.

Franson, J. C., R. D. Jorgenson, E. K. Boggess and J. H. Greve. 1978. Gastrointestinal parasitism of Iowa coyotes in relation to age. J. Parasit. 64(2):303-305.

Freeman, R. S., A. Adorjan and D. H. Pimlott. 1961. Cestodes of wolves, coyotes, and coyote-dog hybrids in Ontario. Can. J. Zool. 39:527-532.

Fritts, Steven H. and John A. Sealander. 1978. Diets of bobcats in Arkansas with special reference to age and sex differences. J. Wildl. Manage. 42(3):533-539.

Gibbs, Harold C. 1957. The taxonomic status of _Rictularia affinis_ Jagerskiold, 1909, _Rictularia cahirensis_ Jagerskiold, 1909, and _Rictularia splendida_ Hall, 1913. Can. J. Zool. 35:405-410.

Gier, H. T. 1948. Rabies in the wild. J. Wildl. Manage. 12(2):142-153.

Gier, H. T. 1968. Coyotes in Kansas. Agric. Exp. Sta., Kans. State Univ., Manhattan, Kans. Bull. No. 393. 118 pp.

Gier, H. T. and D. J. Ameel. 1959. Parasites and diseases of Kansas coyotes. Agric. Exp. Sta., Kans. State Univ., Manhattan, Kans. Tech. Bull. No. 91. 34 pp.

Gier, H. T., S. M. Kruckenberg and R. J. Marler. 1978. Parasites and diseases of coyotes. In Coyotes: biology, behavior and management. Ed. Marc Bekoff. Academic Press, New York, N.Y. pp. 37-71.

Gilman, Richard. 1972. Screwworm peril remains serious. Record number of cases. The Arizona Daily Star 131(237):1A.

Gipson, Philip S. 1974. Food habits of the coyote in Arkansas. J. Wildl. Manage. 38(4):848-853.

Gipson, Philip S. and John A. Sealander. 1972. Home range and activity of the coyote (Canis latrans frustror) in Arkansas. Proc. Conf. SE Assoc. of Game and Fish Comm. 26:82-95.

Glass, Bryan P. 1964. Key to the skulls of North American mammals. Dept. of Zool., Okla. State Univ., Stillwater, Okla. 53 pp.

Goldman, E. A. 1930. The coyote - archpredator. J. Mammal. 11: 325-335.

Graham, J. M. 1975. Filariasis in coyotes from Kansas and Colorado. J. Parasit. 61(3):513-516.

Grater, Russell K. 1943. Coyote foods near Boulder Dam. J. Wildl. Manage. 7(4):422-423.

Greig, A. S. and K. M. Charlton. 1973. Electron microscopy of the virus of oral papillomatosis in the coyote. J. Wildl. Dis. 9(4):359-361.

Grundmann, Albert W. 1958. Cestodes of mammals from the Great Salt Lake desert region of Utah. J. Parasit. 44(4):425-429.

Hamilton, William J. 1974. Food habits of the coyote in the Adirondacks. New York Fish and Game J. 21(2):177-181.

Hamlett, G. W. D. 1938. The reproductive cycle of the coyote. U.S. Dept. of Agric. Tech. Bull. No. 616. 11 pp.

Harrison, Launcelot and T. Harvey Johnston. 1916. Mallophaga from marsupials. I. Parasitology. 8:338-359.

Hartley, Joel. 1938. Pathology of Dirofilaria infestation. Zoologica 23(11):235-246.

Hawthorne, Vernon M. 1971. Coyote movements in Sagehen creek basin, northeastern California. Calif. Fish and Game. 57(3):154-161.

Hawthorne, Vernon M. 1972. Coyote food habits in Sagehen creek basin, northeastern California. Calif. Fish and Game 58(1): 4-12.

Hayne, Don W. 1949. Calculation of size of home range. J. Mammal. 30(1):1-18.

Heltsley, Ernie. 1971. Cattlemen facing fiercest drought in 70 years. Dying animals litter Arizona ranges. The Arizona Daily Star. 130(178):1A.

Heltsley, Ernie. 1972. Papagos gird for dry spell. The Arizona Daily Star. 131(60):4A.

Henderson, F. Robert. 1972. Controlling coyote damage. Coop. Ext. Ser., Kans. State Univ., Manhattan, Kans. 24 pp.

Henderson, F. Robert. 1973. How to call coyotes. Coop. Ext. Ser., Kans. State Univ., Manhattan, Kans. 8 pp.

Holland, George P. 1949. The Siphonaptera of Canada. Sci. Ser., Div. of Entomol., Livestock Insect Lab., Kamloops, B.C. 306 pp.

Holmes, John C. and Ronald Podesta. 1968. The helminths of wolves and coyotes from the forested regions of Alberta. Can. J. Zool. 46:1193-1204.

Hopkins, G. H. E. 1949. The host associations of the lice of mammals. Proc. Zool. Soc. Lond. 119:387-604.

Hubbard, Clarence A. 1947. Fleas of western North America. Iowa State College Press, Ames. 533 pp.

Humason, G. L. 1967. Animal tissue techniques. Freeman and Co., San Francisco, Cal. p. 137.

Humason, G. L. 1972. Animal tissue techniques. W. H. Freeman and Co., San Francisco, Cal. 641 pp.

Jaeger, Edmund C. 1950. The coyote as a seed distributor. J. Mammal. 31(4):452-453.

Johnson, Mark K. and Richard M. Hansen. 1979. Coyote food habits on the Idaho National Engineering Laboratory. J. Wildl. Manage. 43(4):951-956.

Kleiman, Devra. 1966. Scent marking in the Canidae. Symp. Zool. Soc. Lond. 18:167-177.

Klevezal, G. A. and S. E. Kleinenberg. 1967. Age determination of mammals from annual layers in teeth and bones. Acad. of Sci. of the USSR. Severtsov Inst. of Anim. Morphol. Israel Program for Scientific Translations, Jerusalem. 128 pp.

Knowlton, Frederick F. 1964. Aspects of coyote predation in south Texas with special reference to white-tailed deer. Ph.D. dissertation, Purdue Univ., Lafayette, Ind. 189 pp.

Knowlton, Frederick F. 1972. Preliminary interpretations of coyote population mechanics with some management implications. J. Wildl. Manage. 36(2):369-382.

Knowlton, Frederick F. 1973. Coyote research newsletter. Unit of Predator Studies, Dept. Wildl. Sci., Utah State Univ., Logan 1(1):2-20.

Knowlton, Frederick F. 1974. Coyote research newsletter. Unit of Predator Studies, Dept. Wildl. Sci., Utah State Univ., Logan 2(1):3-10.

Korschgen, Leroy J. 1957. Food habits of the coyote in Missouri. J. Wildl. Manage. 21(4):424-435.

Lapage, Geoffrey. 1962. Monnig's veterinary helminthology and entomology. Williams and Wilkins Co., Baltimore, Md. 600 pp.

Latham, Roger M. 1951. The ecology and economics of predator management. Penn. Game Comm., Harrisburg, Pa. 96 pp.

Leach, Howard R. and Walter H. Frazier. 1953. A study on the possible extent of predation on heavy concentrations of valley quail with special reference to the bobcat. Calif. Fish and Game 39(4):527-538.

Leopold, A. Starker. 1964. Predator and rodent control in the United States. Trans. N. Amer. Wildl. Conf. 29:27-47.

Levine, Norman D. 1968. Nematode parasites of domestic animals and of man. Burgess Pub. Co., Minneapolis, Minn. 600 pp.

Linhart, Samuel B. and Frederick F. Knowlton. 1967. Determining age of coyotes by tooth cementum layers. J. Wildl. Manage. 31(2): 362-365.

Linhart, Samuel B. and Frederick F. Knowlton. 1975. Determining the relative abundance of coyotes by scent station lines. Wildl. Soc. Bull. 3(3):119-124.

Liu, Irwin K. M., Calvin W. Schwabe, Peter M. Schantz and Malcolm N. Allison. 1970. The occurrence of Echinococcus granulosus in coyotes (Canis latrans) in the central valley of California. J. Parasit. 56(6):1135-1137.

Lockie, J. D. 1959. The estimation of the food of foxes. J. Wildl. Manage. 23(2):224-227.

Lorenz, Konrad. 1970. Studies in animal and human behaviour. Harvard Univ. Press, Cambridge, Mass. 767 pp.

Lowe, Charles H. (Ed.). 1964. The vertebrates of Arizona. The Univ. of Ariz. Press, Tucson. 270 pp.

Madsen, Rees Low. 1974. The influence of rainfall on the reproduction of Sonoran desert lagomorphs. M.S. Thesis, Univ. of Ariz., Tucson. 60 pp.

Manville, Richard H. 1949. A study of small mammal populations in northern Michigan. Misc. Pub. Mus. of Zool. Univ. Mich. 73:1-83.

Manville, Richard H. 1953. Longevity of the coyote. J. Mammal. 34(3):390.

Marchinton, Robert L. and Lewis K. Jeter. 1966. Telemetric study of deer movement-ecology in the Southeast. Proc. Conf. SE Assoc. of Game and Fish Comm. 20:189-206.

Marshall, A. D. and J. H. Jenkins. 1966. Movements and home ranges of bobcats as determined by radio-tracking in the upper coastal plain of west-central South Carolina. Proc. Conf. SE Assoc. of Game and Fish Comm. 20:206-214.

Martin, Alexander C. and William D. Barkley. 1961. Seed identification manual. Univ. of Calif. Press, Berkeley. 221 pp.

Martin, Alexander C. and Leroy J. Korschgen. 1963. Food-habits procedures. In Wildlife Investigational Techniques. Ed. Henry S. Mosby. The Wildl. Soc., Washington, D.C. pp. 320-329.

Martin, S. Clark and Hudson G. Reynolds. 1973. The Santa Rita Experimental Range: your facility for research on semidesert ecosystems. Ariz. Acad. of Sci. 8(2):56-67.

Mathwig, Herbert J. 1973. Food and population characteristics of Iowa coyotes. Iowa State J. Res. 47(3):167-189.

Mayer, William V. 1952. The hair of California mammals with keys to the dorsal guard hairs of California mammals. Amer. Midl. Natur. 48(2):480-512.

McCarley, Howard. 1975. Long-distance vocalizations of coyotes (Canis latrans). J. Mammal. 56(4):847-856.

McLean, Donald D. 1934. Predatory animal studies. Calif. Fish and Game. 20(1):30-36.

McNab, Brian K. 1963. Bioenergetics and the determination of home range size. Amer. Natur. 97(894):133-140.

Mech, L. David. 1966. The wolves of Isle Royale. Fauna of the Nat. Parks of the U.S., Fauna Series 7. Nat. Park Serv., Washington, D.C. 210 pp.

Mech, L. David. 1970. The wolf: the ecology and behavior of an endangered species. The Amer. Mus. of Natur. Hist., The Natural History Press, Garden City, N.Y. 385 pp.

Mech, L. David. 1975. Disproportionate sex ratios of wolf pups. J. Wildl. Manage. 39(4):737-740.

Meinzer, Wyman P., Darrell N. Ueckart and Jerran T. Flinders. 1975. Foodniche of coyotes in the rolling hills of Texas. J. Range Manage. 28(1):22-27.

Miller, T. A. 1965. Influence of age and sex on susceptibility of dogs to primary infection with Ancylostoma caninum. J. Parasit. 51(5):701-704.

Mills, J. H. L. and S. W. Nielsen. 1966. Canine Filaroides osleri and Filaroides milksi infection. J. Amer. Vet. Med. Assoc. 149(1):56-63.

Mitchell, Robert L. and Samuel L. Beasom. 1974. Hookworms in south Texas coyotes and bobcats. J. Wildl. Manage. 38(3):455-458.

Mohr, Carl O. 1947. Table of equivalent populations of North American small mammals. Amer. Midl. Natur. 37(1):223-249.

Moore, Robert. 1973. Cattle growers fighting off Arizona's autumn drought. The Arizona Daily Star. 132(288):1B.

Morgan, Banner B. and Philip A. Hawkins. 1949. Veterinary helminthology. Burgess Pub. Co., Minneapolis, Minn. p. 233.

Morrison, Edward E. and H. T. Gier. 1978. Lungworms in coyotes on the Great Plains. J. Wildl. Dis. 14:314-316.

Murie, Adolph. 1940. Ecology of the coyote in the Yellowstone. Fauna of the Nat. Parks of the U.S., Bull. No. 4. 206 pp.

Murie, Adolph. 1951. Coyote food habits on a southwestern cattle range. J. Mammal. 32(3):291-295.

Murie, Olaus J. 1935. Food habits of the coyote in Jackson Hole, Wyoming. U.S. Dept. Agric. Circ. No. 362. 24 pp.

Murie, Olaus J. 1945. Notes on coyote food habits in Montana and British Columbia. J. Mammal. 26(1):33-40.

Murie, Olaus J. 1946. Evaluating duplications in analysis of coyote scats. J. Wildl. Manage. 10(3):275-276.

Nellis, Carl H. 1973. Prevalence of oral-papilloma like lesions in coyotes in Alberta. Can. J. Zool. 51(8):900.

Nellis, Carl H. and Lloyd B. Keith. 1976. Population dynamics of coyotes in central Alberta, 1964-1968. J. Wildl. Manage. 40(3):389-399.

Niebauer, Thomas J. and Orrin J. Rongstad. 1977. Coyote food habits in northwestern Wisconsin. In Proc. of the 1975 Predator Symp. Ed. Robert L. Phillips and Charles Jonkel. Mont. For. and Cons. Exp. Sta., Missoula, Montana. pp. 237-251.

Noon, T. H. 1980. Personal communication. Results of autopsy of newborn calf. Professor, Univ. of Ariz., Tucson.

Odum, Eugene P. 1959. Fundamentals of ecology. W. B. Saunders Co., Philadelphia, Pa. 546 pp.

Ogle, Thomas F. 1969. Ecology and breeding biology of the coyote. M.S. Thesis, Wash. State Univ., Pullman. 85 pp.

Olin, George. 1954. Mammals of the southwest deserts. SW Mon. Assoc. The Rydal Press, Inc., Santa Fe, New Mex. 112 pp.

Olsen, O. W. 1960. Sylvatic trichinosis in carnivorous mammals in the Rocky Mountain region of Colorado. J. Parasit. 46(5-2):22.

Olsen, O. Wilford and Frank K. Bracken. 1959. Lungworm, Filaroides osleri, in a dog in Colorado. J. Amer. Vet. Med. Assoc. 134:330-334.

Ozaga, John J. 1963. An ecological study of the coyote on Beaver Island, Lake Michigan. M.S. Thesis, Mich. State Univ., East Lansing, Mich. 122 pp.

Ozaga, John J. and Elsworth M. Harger. 1966. Winter activities and feeding habits of northern Michigan coyotes. J. Wildl. Manage. 30(4):809-818.

Parker, D. D. and J. F. Howell. 1959. Host-flea relationships in the Great Salt Lake desert. J. Parasit. 45(6):597-604.

Parker, Richard L., James W. Kelly, E. L. Cheatum and Donald J. Dean. 1957. Fox population densities in relation to rabies. New York Fish and Game J. 4(2):217-228.

Payne, Richard L., James H. Jenkins and Ernest E. Provost. 1966. Tranquilizer-equipped traps as an aid to furbearer census. Proc. Conf. SE Assoc. of Game and Fish Comm. 20:215-219.

Peterson, Roger T. 1961. A field guide to western birds. Houghton Mifflin Co., Boston. 366 pp.

Petrochenko, V. I. 1958. Acanthocephala of domestic and wild animals. Acad. of Sci. of the USSR. Israel Program for Scientific Translations, Jerusalem. Vol. II. 478 pp.

Pimlott, Douglas H. 1960. The use of tape-recorded wolf howls to locate timber wolves. Paper presented to 22nd Midwest Fish and Wildl. Conf., Toronto, Ont. 7 pp.

Popowski, Bert. 1971. Mind over coyote. The Amer. Rifleman. Feb., pp. 36-39.

Price, Emmett W. 1926. A note on Oncicola canis, an acanthocephalid parasite of the dog. Amer. Vet. Med. Assoc. J. 69 N.S. 22(6):704-710.

Price, E. W. 1928. The coyote (Canis latrans texensis), a new host for Oncicola canis (Kaupp) and Oslerus osleri (Cobbold). J. Parasit. 14(3):197.

Quick, Horace F. 1963. Animal population analysis. In Wildlife Investigational Techniques. Ed. Henry S. Mosby. The Wildl. Soc., Washington, D.C. pp. 190-228.

Ramsden, R. O. and D. H. Johnston. 1975. Studies on the oral infectivity of rabies virus in carnivora. J. Wildl. Dis. 11:318-324.

Rausch, Robert. 1951. Biotic interrelationships of helminth parasitism. Public Health Rep. 66(29):928-934.

Rausch, Robert, B. B. Babero, R. V. Rausch and E. L. Schiller. 1956. Studies on the helminth fauna of Alaska. XXVII. The occurrence of larvae of Trichinella spiralis in Alaskan mammals. J. Parasit. 42(3):259-271.

Rausch, Robert and Francis S. L. Williamson. 1959. Studies on the helminth fauna of Alaska. XXXIV. The parasites of wolves, Canis lupus L. J. Parasit. 45:395-403.

Read, Clark P. and Raymond E. Milleman. 1953. Helminth parasites in kangaroo rats. Univ. of Calif. Pub. Zool. 59(3):61-80.

Robinson, Weldon B. and Eugene T. Grand. 1958. Comparative movements of bobcats and coyotes as disclosed by tagging. J. Wildl. Manage. 22(2):117-122.

Rogers, John G. 1965. Analysis of the coyote population of Dona Ana County, New Mexico. M.S. Thesis, New Mex. State Univ., University Park. 40 pp.

Roth, Earl E. 1970. Leptospirosis. In Infectious diseases of wild mammals. Ed. John W. Davis, Lars H. Karstad and Daniel O. Trainer. Iowa State Univ. Press, Ames. pp. 293-303.

Rudo Ensayo. 1951. Arizona Silhouettes, Tucson, Ariz. 159 pp.

Ryden, Hope. 1974. The "lone" coyote likes family life. Nat. Geogr. 146(2):278-294.

Samuel, W. M., G. A. Chalmers and J. R. Gunson. 1978. Oral papillomatosis in coyotes (Canis latrans) and wolves (Canis lupus) of Alberta. J. Wildl. Dis. 14:165-169.

Samuel, W. M., S. Ramalingam and L. N. Carbyn. 1978. Helminths in coyotes (Canis latrans Say), wolves (Canis lupus L.), and red foxes (Vulpes vulpes L.) of southwestern Manitoba. Can. J. Zool. 56:2614-2617.

Schlotthauer, John C. 1964. Dirofilaria immitis in the red fox (Vulpes fulva) in Minnesota. J. Parasit. 50(6):801-802.

Schoening, H. W. 1956. Rabies. In Animal Diseases. The yearbook of agriculture 1956. U.S. Dept. of Agric. pp. 195-202.

Self, J. Teague and Thomas J. McKnight. 1950. Platyhelminths from fur bearers in the Wichita Mountains Wildlife Refuge, with especial reference to Oochoristica spp. Amer. Midl. Natur. 43:58-61.

Seton, Ernest T. 1929. Lives of game animals. Vol. I. Part II: Cats, wolves, and foxes. Doubleday, Doran and Co., Garden City, N.Y. 640 pp.

Siegel, Sidney. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., New York, N. Y., 312 pp.

Sikes, R. Keith, Sr. 1970. Rabies. In Infectious diseases of wild mammals. Ed. John W. Davis, Lars H. Karstad and Daniel O. Trainer. Iowa State Univ. Press, Ames. pp. 3-19.

Skrjabin, K. I., A. A. Sobolev and V. M. Ivashkin. 1967. Spirurata of animals and man and the diseases caused by them. Part 4. Thelazioidea. Acad. of Sci. of the USSR. Helminth. Lab. Israel Program for Scientific Translations, Jerusalem. 610 pp.

Small, Richard Lee. 1971. Interspecific competition among three species of carnivora on the Spider Ranch, Yavapai County, Arizona. M.S. Thesis, Univ. of Ariz., Tucson. 78 pp.

Smit, F. G. A. M. 1958. A preliminary note on the occurrence of Pulex irritans L. and Pulex simulans in North America. J. Parasit. 44(5):523-526.

Smith, Charles H. 1866. Mammalia. Dogs. Vol. I. In The naturalist's library. Ed. W. Jardine. Henry S. Bohn, Covent Garden, Lond. 267 pp.

Smith, H. A., T. C. Jones and R. D. Hunt. 1972. Veterinary pathology. Lea and Febiger, Philadelphia, Pa. 1521 pp.

Snow, Carol J. 1967. Some observations on the behavioral and morphological development of coyote pups. Amer. Zool. 7:353-355.

Soulsby, E. J. L. 1968. Helminths, arthropods, and protozoa of domesticated animals. Williams and Wilkins Co., Baltimore, Md. 824 pp.

Sowls, Lyle K. and Paul S. Minnamon. 1963. Glass beads for marking home ranges of mammals. J. Wildl. Manage. 27(2):299-302.

Spence, Liter E., Jr. 1963. Study of identifying characteristics of mammal hair. Wildl. Dis. Res. Lab., Wy. Fish and Game Comm., Job Comp. Rep. Project No. FW-3-R-10. 121 pp.

Sperry, Charles C. 1934. Winter food-habits of coyotes. J. Mammal. 15(4):286-290.

Sperry, Charles C. 1941. Food habits of the coyote. U.S. Fish and Wildl. Ser., Wildl. Res. Bull. No. 4. 70 pp.

Sprent, J. F. A. 1959. The life history and development of Toxascaris leonina (von Linstow 1902) in the dog and cat. Parasitology 49(3):330-371.

Stains, Howard J. 1958. Field key to guard hair of middle western furbearers. J. Wildl. Manage. 22(1):95-97.

Steel, Robert G. D. and James H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill Book Co., New York, N.Y. 481 pp.

Stickel, Lucille F. 1954. A comparison of certain methods of measuring ranges of small mammals. J. Mammal. 35(1):1-15.

Stiles, C. W. and Clara E. Baker. 1935. Key catalogue of parasites reported for carnivora with their possible public health importance. Nat. Inst. of Health Bull. No. 163:913-1223.

Storm, G. L. and B. J. Verts. 1966. Movements of a striped skunk infected with rabies. J. Mammal. 47(4):705-708.

Straub, M., R. J. Trautman and J. W. Greene. 1961. Coccidioidomycosis in 3 coyotes. Amer. J. Vet. Res. 22(89):811-813.

Stumpf, William A. and Carl O. Mohr. 1962. Linearity of home ranges of California mice and other animals. J. Wildl. Manage. 26(2):149-154.

Swarth, Harry S. 1929. The faunal areas of southern Arizona: A study in animal distribution. Proc. Calif. Acad. Sci. 18(12): 267-383.

Taber, Richard D. and Raymond F. Dasmann. 1954. A sex difference in mortality in young Columbian black-tailed deer. J. Wildl. Manage. 18(3):309-315.

Tester, John R. and Donald B. Siniff. 1965. Aspects of animal movement and home range data obtained by telemetry. Trans. N. Amer. Wildl. Conf. 30:379-392.

Theberge, John B. and J. Bruce Falls. 1967. Howling as a means of communication in timber wolves. Amer. Zool. 7:331-338.

Thornton, Jack E., R. R. Bell and M. J. Rearden. 1974. Internal parasites of coyotes in southern Texas. J. Wildl. Dis. 10(3):232-236.

Tiemeier, Otto W. 1955. Winter foods of Kansas coyotes. Trans. Kans. Acad. Sci. 58(2):196-207.

Tierkel, Ernest S. 1959. Rabies. In Advances in veterinary science. Ed. C. A. Brandly and E. L. Jungher. Academic Press, Inc., New York, N.Y. 5:183-226.

Trainer, D. O. and F. F. Knowlton. 1968. Serologic evidence of diseases in Texas coyotes. J. Wildl. Manage. 32(4):981-983.

Trainer, D. O., F. F. Knowlton and L. Karstad. 1968. Oral papillomatosis in the coyote. Bull. Wildl. Dis. Assoc. 4:52-54.

Truett, Joe C. 1979. Observations of coyote predation on mule deer fawns in Arizona. J. Wildl. Manage. 43(4):956-958.

Truett, Joe C. and Gerald I. Day. 1966. Winter food habits of coyotes and bobcats. Proc. New Mex.-Ariz. Sect., The Wildl. Soc. 5:83-87.

U.S. Department of Agriculture. 1952. The Santa Rita Experimental Range. SW For. and Range Exp. Sta. Tucson, Ariz. 14 pp.

Van Cleave, Harley. 1953. Acanthocephala of North American mammals. Ill. Biol. Monog. 23(1 & 2):1-179.

van Lawick-Goodall, Hugo and Jane. 1970. Innocent killers. Ballantine Books, New York. 285 pp.

Verts, B. J. 1967. The biology of the striped skunk. Univ. of Ill. Press, Urbana. 218 pp.

Voge, Marietta. 1955. North American cestodes of the genus *Mesocestoides*. Univ. Calif. Pub. Zool. 59(5):125-156.

Wade, Dale A. 1973. Control of damage by coyotes and some other carnivores. Coop. Ext. Ser., Colo. State Univ., Fort Collins, Colo. Pub. No. 11.

Wardle, Robert A. and James A. McLeod. 1952. The zoology of tapeworms. Univ. of Minn. Press, Minneapolis. 780 pp.

Weckwerth, Richard P. and Vernon D. Hawley. 1962. Marten food habits and population fluctuations in Montana. J. Wildl. Manage. 26(1):55-74.

Wells, Michael C. and Marc Bekoff. 1978. Coyote-bald eagle interaction at carrion. J. Mammal. 59(4):886-887.

Werneck, Fabio Leoni and Gordon B. Thompson. 1940. Sur les mallophages des marsupiaux d'Australie. Mem. Inst. Oswaldo Cruz. 35(2):411-455.

Wilson, William C. 1967. Food habits of the coyote, *Canis latrans*, in Louisiana. M.S. Thesis, Louisiana State Univ., Baton Rouge. 49 pp.

Wolfe, Gary J. 1974. Siren-elicited howling response as a coyote census technique. M.S. Thesis, Colo. State Univ., Fort Collins. 206 pp.

Wright, Willard H. 1934. Observations on the life history of *Toxascaris leonina* (Nematoda: Ascaridae). Proc. Helminth. Soc. of Wash. 1(2):56.

Yamaguti, Satyu. 1961. Systema helminthum. III. Nematodes of vertebrates. Interscience Pub., Inc., New York. 1261 pp.

Yerger, Ralph W. 1953. Home range, territoriality, and populations of the chipmunk in central New York. J. Mammal. 34(4):448-458.

Young, Stanley P. 1936. Hints on wolf and coyote trapping. U.S. Dept. Agric. Leafl. No. 59. 8 pp.

Young, Stanley P. and Harold W. Dobyns. 1945. Coyote control by means of den hunting. U.S. Dept. of the Int., Fish and Wildl. Ser. Circ. No. 7. 8 pp.

Young, Stanley P. and Hartley H. T. Jackson. 1951. The clever coyote. The Stackpole Co., Harrisburg, Pa. 411 pp.

Zimmerman, W. J., E. D. Hubbard, L. H. Schwarte and H. E. Biester. 1962. <u>Trichinella spiralis</u> in Iowa wildlife during the years 1953 to 1961. J. Parasit. 48(3):429-432.