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COYOTE-FOOD BASE RELATIONSHIPS
IN JACKSON HOLE, WYOMING

by

John L. Weaver

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

of

MASTER OF SCIENCE

in

Wildlife Science

Approved:

Utah State University
Logan, Utah

1977

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Numerous individuals contributed in making my study of coyotes in Jackson Hole a rich and memorable experience.

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John L. Weaver

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ABSTRACT

Coyote-Food Base Relationships in Jackson Hole, Wyoming

by

John L. Weaver, Master of Science

Utah State University, 1977

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

I measured three variables of coyote-food base relationships in Jackson Hole, Wyoming, during the period July, 1973, to July, 1975. Field work provided estimates of relative coyote and prey abundance as well as observations on coyote feeding behavior during winter. Laboratory analysis of 1,500 coyote scats revealed feeding patterns while feeding trials with captive coyotes allowed refinement in interpretation of scat analysis.

Deer mice and chipmunks comprised most of the rodent biomass captured in traps in the fall, while ground squirrels accounted for much of the rodent biomass in the spring. Field voles declined from 1973 to 1974 throughout much of the study area.

Northern pocket gophers, field voles, and Uinta ground squirrels were the principal foods in the May-October diet of coyotes. They fed primarily upon ungulate carrion during winter.

Because substantial differences in weight between adult and juvenile ground squirrels and pocket gophers make age classification important in calculating biomass, I developed a technique for identifying age classes based upon measurements of tooth remains in coyote scats. Feeding trials with captive coyotes indicated that heavier prey are detected in scats more often than lighter ones. Differences in weight multiplied by differences in detectability for the three principal rodents varied by factors of 1.1 to 2.6.

Carrion from hunter-killed and winter-killed elk supplied food for coyotes from October to May. The abundance and temporal availability of carrion varied substantially between areas.

Up to six-fold differences in coyote population indices occurred between areas. These differences were attributed primarily to differences in the amount of ungulate carrion available during winter. The possible influence of nutrition upon coyote natality, mortality, and movements are contemplated.

(98 pages)

INTRODUCTION

The coyote (Canis latrans), a widespread predator in the western United States, is a major figure in the current controversy concerning predation on domestic sheep (Cain *et al*. 1972, Wagner 1972, 1974). It is the primary target of a private-state-federal cooperative program to alleviate depredations, primarily through reduction of offending populations. An environmental awareness, however, is prompting the American public to question single-value, utilitarian approaches to predator management. The concept of land as a whole organism (Leopold 1953) with predators an integral part, seems to be gaining acceptance.

The many diverse values attached to predators might best be served by more intensive management. The finesse of such efforts will depend, in part, upon greater knowledge of the species' ecology (Knowlton 1972). Understanding the relative importance of intrinsic and extrinsic factors influencing species demography seems requisite to sound predator management.

A direct relationship between food supply and predator population density has been hypothesized for various raptors (Southern and Lowe 1968, Rusch *et al*. 1972, McInvaille and Keith 1974), felids (Nellis *et al*. 1972, Schaller 1972), canids (Ables 1969, Englung 1970, Macpherson 1969, Jordan *et al*. 1967, Van Ballenberghe *et al*. 1975, Clark 1972, Todd and Keith 1976), and hyaenids (Kruuk 1972).

Testing the hypothesis that food resources determine predator population levels requires quantitative measurement of two basic variables (Solomon 1949, Holling 1959): (1) relative abundance of food, and (2) relative numbers of the predator. These should encompass a wide range of values to delineate functional relationships. A third variable--predator food habits--identifies what constitutes "food."

Although numerous studies have documented food habits of coyotes in various areas of the country (Knowlton 1964), only three, to my knowledge, secured measurements on all three variables. Gier (1968) suggested that coyote populations in Kansas fluctuated with changes in densities of small rodents. Knowlton (1972) compared two areas in Texas and reported a similar relationship between rodent abundance and coyote numbers. In South Texas, a 40 percent decline in the average coyote density index was noted following a radical decline in packrat (Neotoma micropus) and cotton rat (Sigmodon hispidus) populations (Knowlton et al. 1971). Clark (1972) reported that coyote populations in Curlew Valley along the Utah-Idaho border fluctuated with the density of blacktailed jackrabbits (Lepus californicus). In each case, however, interpretation of the effects of food base upon coyote density was confounded by human exploitation of the coyotes.

The goal of this study was to measure these three variables of a coyote-food base relationship in an area where the influence of human exploitation of coyotes was minimal. The National Elk Refuge and portions of Grand Teton National Park and Teton National Forest in Jackson Hole, Wyoming, were chosen as a seemingly appropriate area in which to conduct such a study.

The specific objectives were to:

(1) determine coyote feeding patterns

(2) estimate abundance of coyote foods

(3) estimate relative abundance of coyotes, and

(4) examine functional response (change in numbers of prey consumed by individual predators) and numerical response (change in predator density) of coyotes to changes in food base.

My approach in analyzing coyote-food base relationships has been to compare data (1) between three areas with different environmental conditions, and (2) in each area during the course of natural fluctuations in the food base (q.v. Wagner 1969).

DESCRIPTION OF STUDY AREA

A 550-km^2 area (henceforth called the "study area") in Jackson Hole, an intermountain basin in Teton County, Wyoming (Fig. 1), was selected to investigate coyote-food base relationships. The study area, oriented along a northeast-southwest axis, was 38 km long and 8 km to 24 km wide.

Physiography

The physiography and geologic history of Jackson Hole has been discussed in detail by Fryxell (1930) and Love and Reed (1968). The precipitous fault-block Teton Mountains rise to 4185 m along the west side of the study area. The Washakie Mountains frome the valley on the north, the Mount Leidy Highlands and Gros Ventre Mountains on the east, and the Snake River Mountains on the south.

A comparatively flat glacial outwash plain forms the floor of the valley. Elevation of the floor ranges from 1890 m at the southern end of the study area to 2072 m at the northern end. Glacial moraines, "potholes" formed by melting ice blocks, and terraced benches along the entrenched Snake River provide minor physical relief. Isolated buttes rise as much as 400 m above the valley floor.

Jackson, Jenny, and Leigh Lakes border the study area on the northwest. The Snake, Gros Ventre, and Buffalo Rivers and their tributaries traverse Jackson Hole.

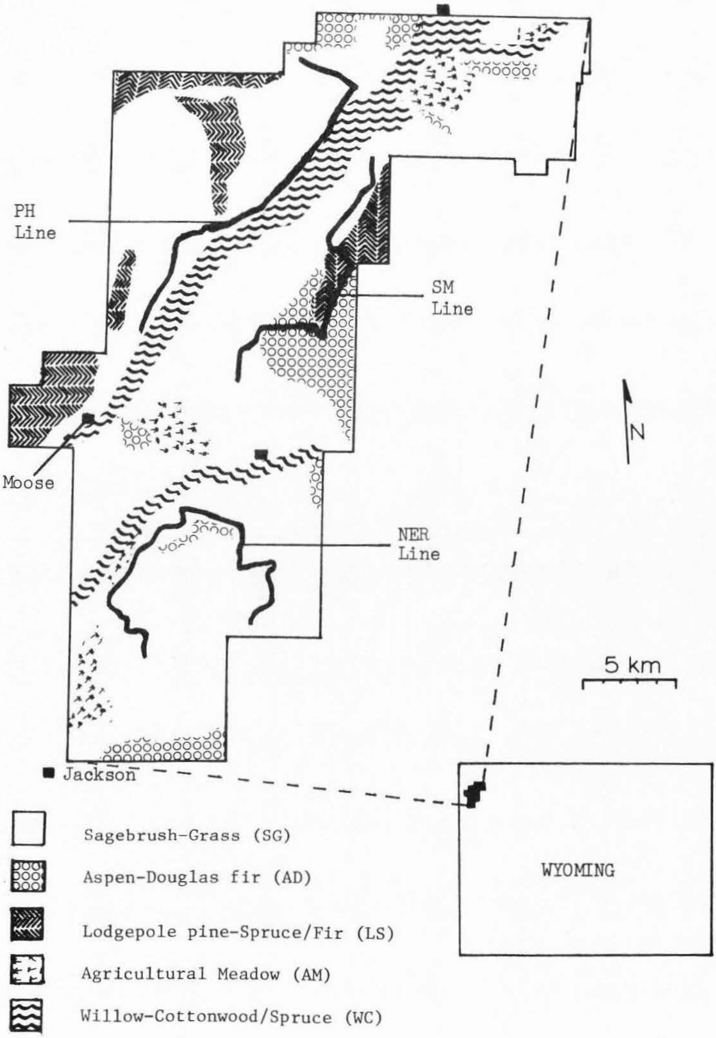

Figure 1. Location, boundaries, vegetation, and the coyote-prey index lines of the Jackson Hole study area.

Climate

Alyea (1966) classified the climate in Jackson Hole as "cold-snowy-forest-climate with humid winters." United States Department of Commerce Weather Bureau records for a 25-year period (1950-1975, excluding 1959) at the village of Moose, near the center of the study area, show a mean annual temperature of 2.41 C (Table 1), ranging from a monthly mean of 15.73 C in July to -9.92 C in January. Mean temperatures decrease by about 1.65 C from the southern end of the study area to the northern end (Dirks 1974).

Cold air masses move into Jackson Hole in winter, and cold air drainage from the surrounding mountains can maintain very low temperatures for several days. Minimum temperatures of -38 C (January 3, 1974) and -35.2 C (January 12, 1975) were recorded at Moose during this study.

Approximately 70 percent of the mean annual precipitation of 61.47 cm falls as snow. A decreasing gradient in snowfall occurs from north to south and from west to east across the study area. Average snow depths at Moose during the winters of 1973-74 and 1974-75 are shown (Fig. 2).

Vegetation

Classification and distribution of vegetation types were patterned after Oswald (1966), Houston (1968), Cole (1969), and Sabinske (1972). Plant nomenclature followed Shaw (1975).

Table 1. Mean monthly temperature and precipitation at Moose, Wyoming, 1950 through 1975.

Month	Temperature (C)	Precipitation (cm)
January	-9.92	8.89
February	-7.85	6.40
March	-4.73	6.35
April	1.38	4.32
May	6.46	4.22
June	10.45	5.28
July	15.73	2.24
August	14.91	2.97
September	10.21	3.56
October	4.68	3.53
November	-3.14	6.10
December	-9.32	8.03
Mean or Total	2.41	61.47

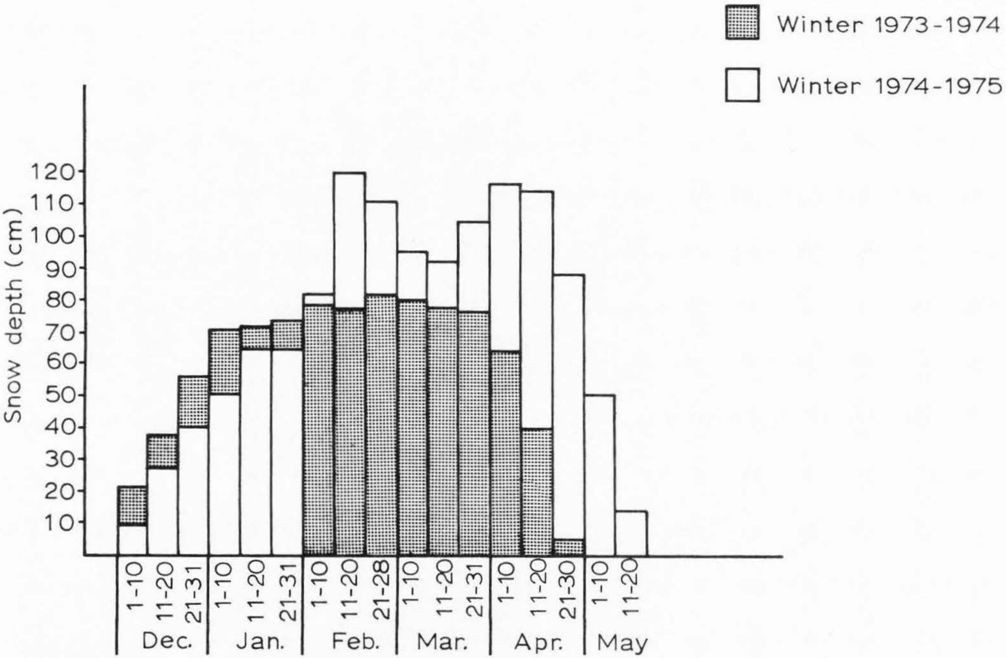

Figure 2. Average snow depth at Moose, Wyoming, by 10-day intervals, during winters of 1973-74 and 1974-75.

Vegetation "type" is a collective term denoting major units of vegetation. "Characteristic" plants were conspicuous components of the vegetation with a high frequency of occurrence in closely related successional stages. "Associated" plants comprised up to one-quarter of the field layers of forest and shrub types, often had a high frequency of occurrence in either field or overstory layers, or had a plant cover equal to, or greater than, characteristic plants in certain local stands. This terminology follows Houston (1968).

From extensive field observations, I classified and mapped the study area into five vegetation types (Fig. 1).

Sagebrush-Grass (SG) covered 58 percent of the study area. It occurred on glacial outwash plains and river terraces throughout the valley and on west and south slopes of moraines. Big sagebrush (*Artemesia tridentata* Nutt.), low sagebrush (*A. arbuscula arbuscula* Nutt.), bitterbrush (*Purshia tridentata* (Pursh) DC.), and junegrass (*Koeleria macrantha* (Ledeb.) Shultes) were characteristic species. Species composition and abundance, however, was not constant (Sabinske 1972). Low sagebrush occurred only west of the Snake River while big sagebrush was more abundant east of the river. Bitterbrush appeared with big sagebrush only south and east of Moose. Reasons for these patterns are not fully understood (Sabinske 1972). Lupine (*Lupinus* spp.), balsamroot (*Balsamorrhiza sagitata* (Pursh) Nutt.), buckwheat (*Eriogonum* spp.), Idaho fescue (*Festuca idahoensis* Elmer), and bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & Sm.) occurred in association.

Lodgepole pine-Spruce/Fir (LS) comprised 5 percent of the study area. It occurred on valley moraines and on the north and east slopes of buttes and foothills. Lodgepole pine (Pinus contorta var. latifolia Engelm.) was the characteristic species and occurred frequently in pure stands. Subalpine fir (Abies lasiocarpa (Hook.) Nutt.) and Englemann spruce (Picea englemannii Parry ex Engelm.) succeeded lodgepole pine in certain areas. Huckleberry (Vaccinium scoparium) Leib and V. membranaceum Dougl.), arnica (Arnica cordifolia Hook.), pinegrass (Calamagrostis rubescens Buckl.), and Geyer's sedge (Carex geyerii) accompanied these trees.

Aspen-Douglas fir (AD) covered 9 percent and occurred on wetter areas of the glacial outwash plain and on all aspects of buttes and foothills. Aspen (Populus tremuloides Michx.) was the characteristic and dominant species, but Douglas fir (Pseudotsuga menziesii (Mirb.) Franco) appeared on the drier aspects of some hillsides. Geranium (Geranium spp.), fireweed (Epilobium angustifolium L.), and western chokecherry (Prunus virginiana L. var. melanocarpa (A. Nels.) Sarg.) were associated species.

Willow-Cottonwood-Spruce (WC) covered 13 percent. It occurred on alluvial soils along the floodplain of rivers and streams. Characteristic species were various willows (Salix spp.) and narrowleaf cottonwood (Populus angustifolia James) representing a seral stage succeeded by blue spruce (Picea pungens Engelm.). Russet buffaloberry (Shepherdia canadensis (L.) Nutt.), thinleaf alder (Alnus incana (L.) Moench.), red osier dogwood (Cornus stolonifera Michx.), balsam poplar (*Populus balsamifera* L.), and sedges (*Carex* spp.) were associated species.

Fauna

Negus and Findley (1959), Halloran (1962), and Long (1965) presented species accounts of mammals occurring in Jackson Hole. The Uinta ground squirrel (*Spermophilus armatus*), least chipmunk (*Eutamias minimus*) and yellowpine chipmunk (*E. amoenus*), red squirrel (*Tamiasciurus hudsonicus*), northern flying squirrel (*Glaucomys sabrinus*), northern pocket gopher (*Thomomys talpoides*), beaver (*Castor canadensis*), deer mouse (*Peromyscus maniculatus*), red-backed vole (*Clethrionomys gapperi*), three species of field vole (*Microtus montanus*, *M. pennsylvanicus*, and *M. longicaudus*), muskrat (*Ondatra zibethica*), western jumping mouse (*Zapus princeps*), porcupine (*Erethizon dorsatum*), yellow-bellied marmot (*Marmota flaviventris*), snowshoe hare (*Lepus americanus*), and white-tailed jackrabbit (*L. townsendii*) inhabit the study area in varying densities and provide food for coyotes.

Elk (*Cervus elaphus*), moose (*Alces alces shirasi*), mule deer (*Odocoileus hemionus*), pronghorn antelope (*Antilocapra americana*), and bison (*Bison bison*) are larger mammals that contribute to the coyote's food base, usually in the form of carrion. No domestic sheep lived on the study area.

Craighead and Craighead (1956:378-379) listed birds commonly found in Jackson Hole.

Coyotes are not the only consumers of these animals. The pine marten (Martes americana), ermine (Mustela erminea), long-tailed weasel (M. frenata), and badger (Taxidea taxus) are common mammals who also use these prey species. The red-tailed hawk (Buteo jamaicensis), Swainson's hawk (B. swainsoni), rough-legged hawk (B. lagopus), marsh hawk (Circus cyaneus), great horned owl (Bubo virginianus), and raven (Corvus corax) are present on the area at least part of the year. Craighead and Craighead (1956) detailed some of the mechanics of raptor predation.

Land Use

According to the Teton County Assessor's Office, approximately 97 percent of the county is publicly owned. Other than small scattered private inholdings, land within the study area is administered by the National Park Service, U. S. Forest Service, and U. S. Fish & Wildlife Service. In 1968 the county population was estimated at 6800. The local economy is based on tourism.

METHODS

Data were collected during 16 months of field work between July, 1973, and July, 1975. Prey indices, coyote scats, and coyote indices were obtained along 24.5-km lines in three areas (Fig. 1): Pothole (PH), National Elk Refuge (NER), and Shadow Mountain (SM).

Relative Abundance of Food

Relative abundance of various components of the food base (excluding ungulate carrion) was sampled systematically with a common design (Fig. 3). Systematic samples are often more easily drawn and executed in the field than random ones, provide similar precision if the populations are distributed randomly, and allows subsampling of the units for analysis (Cochran 1963:230).

A 24.5-km-long section of unimproved dirt road in each of three areas was designated as a line. Twenty-five transects, alternating to the left and right of the line, were distributed at 1-km intervals along each line. Each transect extended 90 m perpendicular to the axis of the line and consisted of ten stations distributed at 10-m intervals. The first station was located immediately adjacent to the road edge. These stations served as the sampling units.

Percent distribution of transects by vegetation is shown in Table 2.

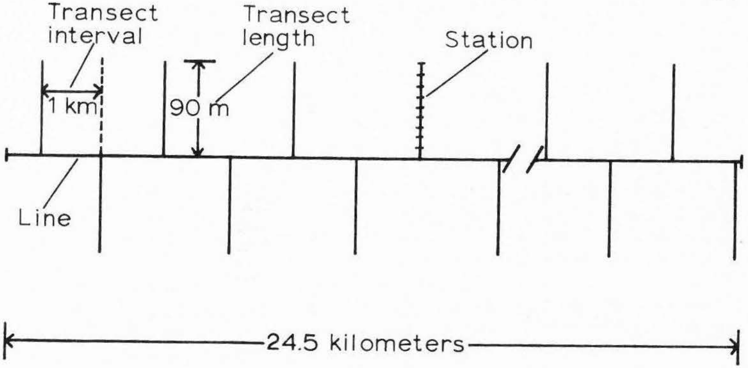

Figure 3. The common design used to sample some components of the food base.

Table 2. Distribution of prey abundance transects by vegetation in the Jackson Hole study area. Number of transects per line in parentheses.

Vegetation type	Percent of area	Percent of transects	Percent of transects by line PH (25)	NER (25)	SM (25)
SG	58	76	100	88	40
LS	5	12			36
AD	9	9		4	24
AM	15	3		8	
WC	13				

Rodent snap-traps

Relative rodent densities were estimated with snap-traps using the design outlined above. One M-4 rat snap-trap with expanded treadle (Carley and Knowlton 1971) was placed at each station and baited with a mixture of rolled oats and peanut butter. Traps were checked at approximately the same hour for each of four consecutive days. Species, sex, age (adult or juvenile), and body weight of trapped animals were recorded. Sprung and inoperable (treadle not sensitive enough to release killing bar) traps were noted and reset.

Pocket gopher mound counts

Studies by Richens (1965) and Reid *et al*. (1966) suggested that mound counts could serve as useful indices of abundance for northern pocket gophers. Richen's definition of this sign was accepted: a "mound" is the pile of soil pushed above ground level from one gopher hole. Earth plugs, or holes that have been filled with soil (Reid *et al*. 1966), were not counted since their detectability varied between vegetation types.

Relative abundance of pocket gophers was sampled with a modification of the common design. Two circular plots, each 7.2 m in diameter (0.00405 ha) were distributed randomly along each transect. The number of mounds within each plot was counted. Because a preliminary inspection of the data indicated large variation between circular plots on the same transect, I sampled again using a strip 0.45 m wide and the length of the transect (0.00405 ha). Mound counts along all transects were made in mid-August, 1974.

To relate mound counts to numbers of pocket gophers, mounds were counted on plots approximately 60 m square and gophers were trapped. Each plot was grided such that 36 circular subplots, 7.2 m in diameter, were established for replicates (Fig. 4). Mounds were counted both on the subplots and on the total plot. Macabee gopher traps were then placed in all active burrow systems within the plot and checked for three days. Eight plots--four in the sagebrush-grass vegetation type, and one each in the other four types--were sampled between mid-August and mid-September, 1974.

Grasshopper flushing counts

Relative abundance of grasshoppers was estimated with the common design by a flushing technique similar to the one used by the United States Department of Agriculture (USDA 1969). As the transects were walked, I visualized a plot 0.3 m square on the ground at each station ahead and counted grasshoppers flushing off each plot. Three counts were taken at two-week intervals during August, 1973.

Ungulate carrion estimates

Although coyotes did kill elk and mule deer on the study area, they normally fed on ungulates in the form of carrion. The number of elk shot during the hunting season within the study area was obtained from records compiled by Grand Teton National Park, National Elk Refuge, and Wyoming Game and Fish Department. The number of elk dying during the winter, and the extent to which they were scavenged by coyotes, was estimated by personal observations and by reports from Park and Refuge personnel.

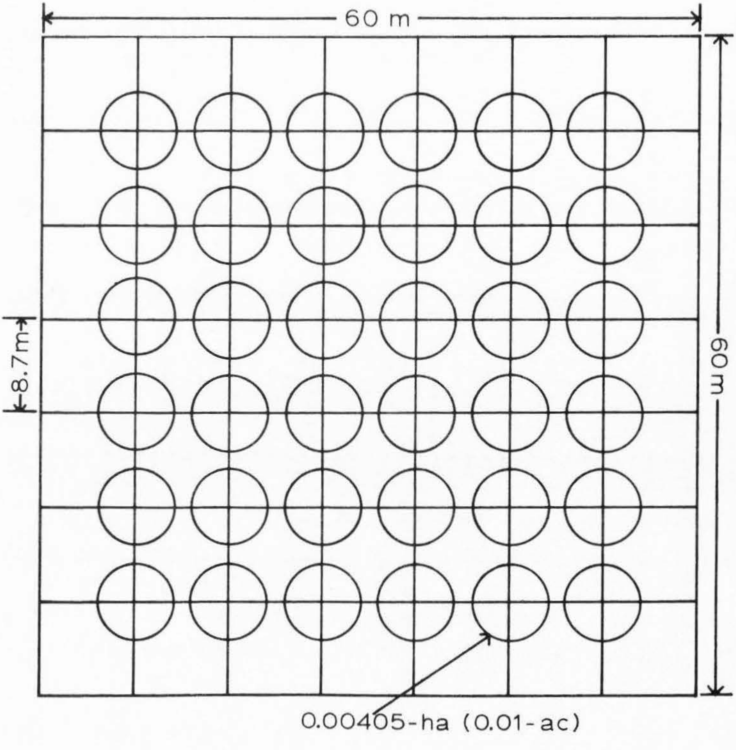

Figure 4. Design of grid used to calibrate mounds of northern pocket gophers.

Coyote Food Habits

Coyote food habits were assessed by collecting scats monthly from May to November ("summer") along 129 km of standard routes (including the three lines) and while snowtracking coyotes from January to March ("winter"). Additional scats were collected elsewhere in the field whenever encountered. The date, location, and vegetation type were recorded for each scat.

Scat analysis

Scats were examined in the laboratory by breaking apart the dried material by hand and identifying the constituents under a binocular dissecting microscope. A reference collection of study skins, skeletal material, and slides of guard hairs of animals occurring on the study area aided in identification. The number of vertebrate individuals detected was determined by using the diagnostic part (mandibles, teeth, bones, tails, and feet) that gave the highest count (Murie 1935). In scats containing only hair of a particular species, only one individual of that species was tallied. Fruit, vegetation, and insects were segregated and weighed to the nearest 0.1-g.

Snowtracking

Additional observations on coyote food habits and feeding behavior during the winter were obtained by tracking them over snow. This technique has been used in previous predator studies (Murie 1936, Stebler 1939, Ozoga 1963, Nellis and Keith 1968, and others).

Murie (1936) considered it "practically equivalent to observing an animal for a long period of time under natural conditions."

During the first winter (1974), coyote trails throughout the study area were selected randomly and followed. On any particular day the first coyote tracks encountered were backtracked until a bed was located or the tracks were lost. I would then return to the original interception point and follow the trail until the animal(s) was jumped, tracks were lost, or darkness prevented further tracking. During the second winter, the same group (henceforth called the "Glacier View" group) of coyotes was followed as often as possible over a 55-day period.

When two or more coyotes were traveling together and close enough that all trails could be observed, I multiplied that portion of the distance trailed by the number of coyotes. Thus, the logged distance was expressed in "coyote-km." During the two winters, approximately 400 coyote-km were logged.

Relative Abundance of Coyotes

Secretive, highly mobile predators occurring in low densities are difficult to census and coyotes are no exception. In this study two independent indices were obtained for comparison of trends.

Scent-station surveys

Standard carnivore scent-station surveys (Linhart and Knowlton 1975), used by the Fish & Wildlife Service throughout 17 western states, were established along the three lines. Each survey line consisted of 50 scent stations alternating left and right at 0.5-km intervals along the road. A station was a circle of sifted earth 1 m in diameter located immediately adjacent to the road edge. In the center a small, perforated plastic capsule containing about 1 g of granular fermented-egg attractant was supported 2.5 cm above the ground with a wooden applicator stick. Each line was checked daily for at least three, and preferably five, consecutive days. Only the presence of coyote tracks was recorded with no attempt to determine how many animals were involved. Scent-station surveys were run in the spring (late May-early June) and fall (early September) of each year.

Scat collection rates

The number of scats collected along the lines provided another index of coyote numbers (Clark 1972). Scats were collected at monthly intervals, but the index was based on pooled values due to small sample sizes.

RESULTS

Relative Abundance of Foods

Murie (1935) reported that coyotes in Jackson Hole fed primarily upon field voles, pocket gophers, grasshoppers, and elk (chiefly as carrion). During this study, indices of these foods were obtained.

Rodents

Squirrels and cricetid mice. Trapping indices are commonly expressed as the number of animals captured per unit of effort, where effort is often defined as "trap-night." As traps become filled, sprung, or otherwise nonfunctional, however, they no longer contribute to the effort. Hence, some correction seems necessary. Nelson and Clark (1973) suggested subtracting half a trapping unit from the initial number of traps for each trap sprung. Effort, though, does not decline at a constant decrement; rather, it decreases proportional to the number of traps still operable ("surviving") at any time during the trap night. I calculated effort using the following equation provided by Dr. L. C. Stoddart (1975):

$$E = \frac{N_t/N_o - 1}{\log_e N_t/N_o}$$

where E = effort

N_o = initial number of traps

N_t = N_o minus number of traps sprung (with or without rodents or otherwise nonfunctional).

Efforts calculated with the Nelson and Clark equation and with the Stoddart equation are similar until a high (70%) proportion of traps are snapped (Fig. 5). With the Nelson and Clark equation, even when all traps are snapped, the effort is still 0.5. With this situation, however, effort remains undefined since one does not know at what point during the trapping period the last trap was snapped.

Several aspects of rodent abundance are presented (Table 3). For comparisons of rodent numbers within and between lines to be valid, one must assume that all individuals regardless of species, have an equal and independent chance of capture. Hence, the indices must relate in some relatively constant, if unknown, manner to actual densities. Biomass indices then follow by multiplying the number captured by an average weight for the species (based on trapped individuals). Catch and biomass indices allow comparisons between lines, seasons, and years. Percent of total catch and percent of total biomass permit comparisons between species for a particular line, season, or year. It should be kept in mind, however, that these indices are not calibrated.

Since biomass estimates are derived, in part, from the numbers of various rodent species trapped, rodent composition along each line was examined. On the Pothole line, deer mice (82-88%) and chipmunks (11-14%) comprised most of the catch (Table 3). On the National Elk Refuge, these two species accounted for 70-87% and 16-11%, respectively, of the fall captures. Ground squirrels made up 29% of the spring 1974 catch on this line. Along the Shadow Mountain line during the

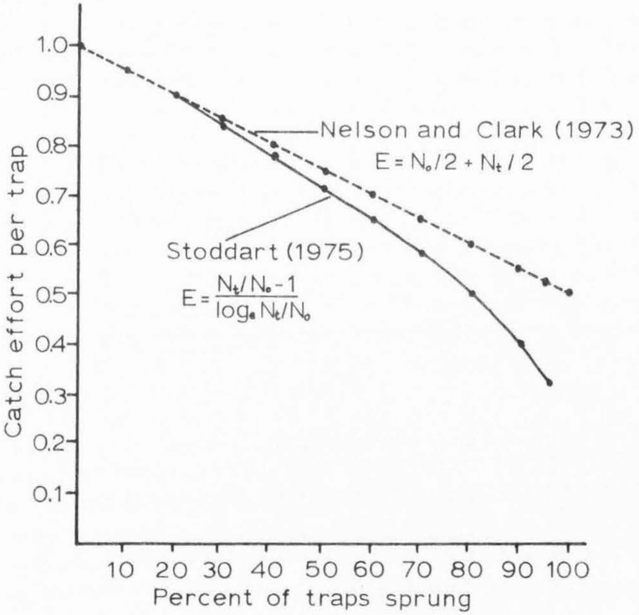

Figure 5. Comparison of catch effort using Nelson and Clark (1973) and Stoddart (1975) correction equations.

Table 3. Catch per trap night (corrected for trap effort), percent of total catch, total biomass, and percent of total biomass, by rodent species for the three lines, Jackson Hole, Wyoming, 1973-74.

	POTHOLE			NATIONAL ELK REFUGE			SHADOW MOUNTAIN		
Species	Fall '73	Spg '74	Fall '74	Fall '73	Spg '74	Fall '74	Fall '73	Spg '74	Fall '74
Trap Effort[a]	750	661	709	596	698	578	753	666	720
Total Biomass	8140	4075	4280	4420	8385	2750	9180	18055	5925
Deer Mouse									
Catch (no./eff)	0.322	0.130	0.159	0.128	0.040	0.107	0.187	0.045	0.129
% of Total Catch	87.6	81.9	85.0	69.7	36.8	87.3	54.7	26.5	56.7
Biomass(g)	6440	2600	3180	2560	800	2140	3740	900	2580
% of Total Biomass	76.8	69.8	75.2	53.9	9.5	74.4	36.8	5.0	42.1
Field Vole									
Catch	0.004	0.003	--	0.024	0.001	0.002	0.016	0.005	0.021
% of Total Catch	1.1	1.9	--	12.8	1.3	1.4	4.7	2.7	9.1
Biomass (g)	100	75	--	600	25	50	400	125	525
% of Total Biomass	1.5	1.6	--	16.7	0.3	5.0	4.5	0.7	9.9
Chipmunk									
Catch	0.040	0.020	0.027	0.029	0.034	0.014	0.103	0.025	0.063
% of Total Catch	10.9	12.4	14.3	15.6	31.6	11.3	29.8	14.2	28.1
Biomass (g)	1600	800	1080	1160	1360	560	4120	1000	2520
% of Total Biomass	20.3	17.4	24.2	25.5	13.2	20.6	41.7	4.5	39.3
Ground Squirrel									
Catch	--	0.002	--	--	0.031	--	0.001	0.078	--
% of Total Catch	--	1.0	--	--	28.9	--	0.4	46.0	--
Biomass (g)	--	400	--	--	6200	--	200	15600	--
% of Total Biomass	--	8.4	--	--	77.0	--	4.6	82.0	--
Other[b]	--								
Catch	--	0.005	0.001	0.003	0.001	--	0.032	0.019	0.013
% of Total Catch	--	2.9	0.8	1.8	1.3	--	9.4	10.7	6.1
Biomass (g)	--	200	20	100	--	--	720	430	300
% of Total Biomass	--	2.7	0.5	3.9	--	--	7.6	7.8	8.6

[a] Adjusted from a potential 1000 trap-nights.

[b] Jumping mouse, red-backed vole, red tree squirrel, northern flying squirrel, short-tailed weasel

fall, deer mice (55-57%) and chipmunks (28-30%) were predominant, with jumping mice (Zapodidae) and red-backed voles ("Other") common in the coniferous forests. Ground squirrels made up 46% of the catch in spring 1974.

Considerable spatial and seasonal variation in rodent biomass occurred along the three lines (Table 3, Fig. 6). Shadow Mountain provided the greatest catch in rodent biomass, followed by the Potholes and the National Elk Refuge. A two-fold increase in biomass in spring along the SM and NER lines was directly attributable to ground squirrels, since the biomass of other rodents was lower at this season (Table 3). Ground squirrels became inactive before I trapped in the fall. Rodent biomass was lower in fall 1974 than in fall 1973 along each line (Fig. 6). Field voles decreased markedly on the National Elk Refuge by June 1974, especially in meadows and willow marshes where high densities had prevailed in 1973. Miscellaneous trapping throughout the study area in June 1974 confirmed the widespread decline in vole abundance in these habitats.

Northern pocket gophers. Counts of accumulated gopher mounds revealed they were most numerous along the Shadow Mountain line, less common on the Pothole line and least abundant on the National Elk Refuge (Table 4). Since the tallies between the circular subplots varied substantially along many of the transects, I counted mounds within a strip 0.45-m-wide the length of the transect in an attempt to reduce the variance. Although this method did not appreciably diminish variation, it yielded significantly ($p < 0.01$) higher average

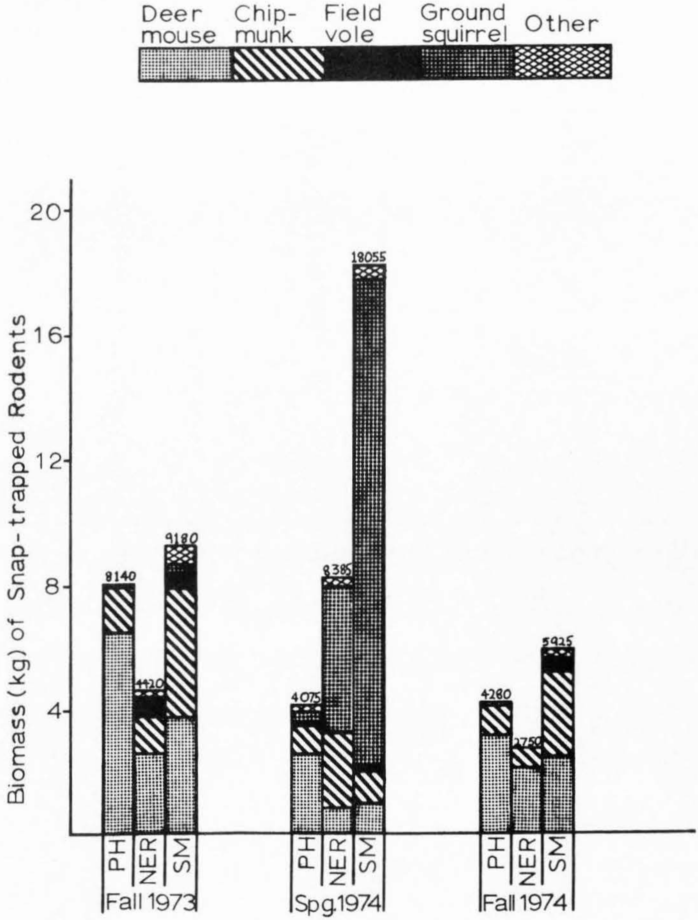

Figure 6. Biomass of rodents snap-trapped along the Pothole (PH), National Elk Refuge (NER), and Shadow Mountain (SM) lines in Jackson Hole, Wyoming.

Table 4. Counts of northern pocket gopher mounds along three lines, Jackson Hole, Wyoming, August 1974

Line	Circle Plot		Strip Plot	
	Mean	95% Conf. Int.	Mean	95% Conf. Int.
PH	2.1	± 0.7	5.6	± 1.8
NER	0.9	± 0.4	2.0	± 1.2
SM	2.1	± 0.9	3.2	± 1.8

numbers of mounds (Table 4). Part of this difference may relate to plot shape. Long, narrow plots provide more edge than circular ones so the observer more frequently has to decide whether a mound lies within or outside the plot. A bias toward including them may exist.

Since the number of mounds may not directly reflect the number of pocket gophers in different habitats, calibration of mound counts seemed essential. This was achieved by counting mounds on 40,000-sq.ft. plots, then trapping gophers for three days. The number of pocket gophers trapped per hectare ranged from 0 on a plot within Lodgepole pine-Spruce/Fir to 46 on one plot within Sagebrush-Grass dominated by low sage (Table 5). These catches are low compared with other studies (Richens 1965, Reid et al. 1966, Turner et al. 1973) which trapped at the same time of year.

Curiously, there was a high correlation (r = 0.98) between the ratio of mounds counted in subplot counts to the total number of mounds and the number of gophers trapped (Fig. 7). As gopher density

Table 5. Number of gopher mounds per hectare based on 0.00405-ha (0.01-acre) subplots (36 per grid), number of gopher mounds per hectare based on total count, number of northern pocket gophers trapped per hectare, and number of mounds per gopher, Jackson Hole, Wyoming, August-September, 1974. Parenthetical values are 95 % confidence intervals. Grids are presented in chronological order.

Vegetation type	Date	(A) No. mounds/ha subplots	(B) No. mounds/ha total count	(C) No. gophers/ trapped/ha	(D) No. mounds/gopher
SG	13 Aug.	604 (±183)	753	16	47.1
SG	17 Aug.	261 (±120)	632	8	79.0
SG	21 Aug.	2387 (±368)	1658	46	36.0
LS	28 Aug.	0 (-)	0	0	-
WC	29 Aug.	103 (±126)	234	5	46.8
AD	4 Sept.	460 (±213)	479	24	20.0
AM	12 Sept.	473 (±189)	524	19	27.6
SG	21 Sept.	994 (±473)	1498	13	115.2

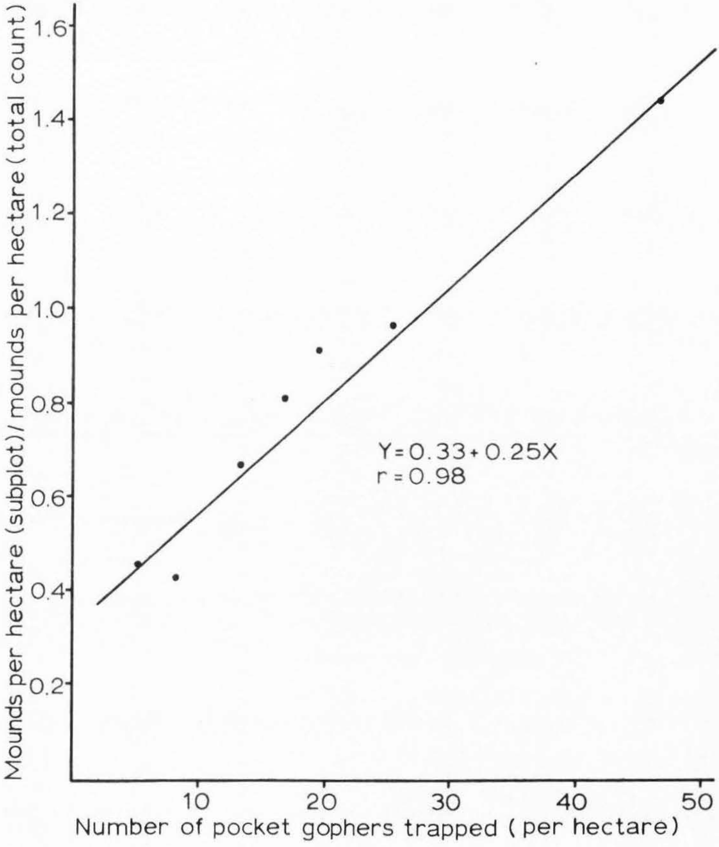

Figure 7. Regression of ratio of number of gopher mounds per ha within subplots to total number of mounds upon number of northern pocket gophers trapped per ha. The correlation is significant at the 0.01 probability level.

increased so did the percentage of mounds inside the subplots relative to those outside. Although the subsamples were not normally distributed, the correlation seems stronger than chance alone and suggests some consistent bias was operating.

Reid et al. (1966) calibrated pocket gopher signs in Colorado in a manner that differed from mine in two respects. First, they counted fresh mounds (made during a two-day interval) whereas my counts were of mounds built since snowmelt (3-4 months). Secondly, their subplots covered 16 percent of the grid while mine comprised about 40 percent. A comparable regression using their data (Reid et al. 1966:330) suggested no comparable bias ($r = 0.17$).

Transect mound counts were calibrated using the number of mounds (based upon total count) per gopher for each vegetation type (Col. D, Table 5). No mounds were found on the Lodgepole pine-Spruce/Fir plot, so an average value of 50 mounds per gopher was used for transects in that type. The average number of mounds per gopher of the four Sagebrush-Grass plots was used for that calibration.

Other published calibration values are from aspen-open parkland vegetation types (Richens 1965, Reid et al. 1966, Turner et al. 1973). The value of 20 mounds per gopher from my one plot in Aspen-Douglas fir accords well with those studies. The values for Sagebrush-Grass are higher and variable which may reflect differences in soil, characteristic and associated plants, or density and age structure of the gopher population (Turner et al. 1973).

Results from both circular and strip plots generally indicate similar trends in pocket gopher abundance between lines. Gophers were most numerous on Shadow Mountain, less common on the Potholes, and least abundant on the National Elk Refuge (Table 6). Since the 90% confidence intervals overlap, the differences between lines cannot be considered statistically significant.

Grasshoppers

The grasshopper flushing index was highest on the National Elk Refuge, lower on the Potholes, and lowest on Shadow Mountain, with all differences being statistically significant (Table 7).

Ungulate carrion

Each fall the viscera, heads, and lower legs of hunter-killed elk become available to coyotes. No hunting was allowed in the Pothole section of the study area, but east of the Snake River within Grand Teton National Park and on the National Elk Refuge, hunting was allowed on a permit basis. Hunter-killed elk were more common in the Shadow Mountain area than on the National Elk Refuge (Table 8), with virtually none in the Pothole area.

The geographical distribution of ungulate carrion shifts during the winter. About 7,500 elk winter on the National Elk Refuge each year with an average of 75 (1 percent) dying between November and May; 75 died in winter 1972-73, 125 (1.5 percent) in 73-74, and 50 (0.7 percent) in 74-75. Cows and calves comprised 48 percent and 36 percent, respectively, of these losses. No quantitative estimates of ungulate numbers (elk, moose, and mule deer) or mortality rates

Table 6. Number of northern pocket gophers per hectare based upon mound counts on 25 transects along each line, Jackson Hole, Wyoming, August, 1974. See text for calibration procedure.

Line	Circle Plot			Strip Plot		
	Mean	90% Conf. Int.	s/x	Mean	90% Conf. Int.	s/x
PH	7.4	± 2.6	1.0	19.8	± 5.4	± 0.8
NER	4.2	± 2.2	1.5	11.3	± 6.8	± 1.8
SM	13.8	± 8.4	1.8	19.8	+ 11.6	± 1.7

Table 7. Number of grasshoppers flushed per m^2, Jackson Hole, Wyoming, August, 1973.[a]

Line	No./m^2	90% Conf. Int.
PH	1.4	± 0.2
NER	8.0	± 0.8
SM	0.6	± 0.2

[a] Based upon three counts (August 1, 15 and 31) comprised of 250 plots along each line.

Table 8. Number of elk killed during hunting seasons 1972-74, Jackson Hole, Wyoming. Data from records compiled by Grand Teton National Park, National Elk Refuge, and Wyoming Game and Fish Department.

Line	1972	1973	1974
PH		no hunting allowed	
NER	59	77	48
SM[a]	520	500	315

[a] Includes half the kill in Unit 74 (within and adjacent to the study area) and the total kill in Units 75 and 76 (3 km southwest of Shadow Mountain).

were obtained for the Pothole or Shadow Mountain areas. Relative inaccessibility of these sections and the low densities of ungulates rendered most sampling attempts ineffective and/or inefficient. My subjective impression is that 100-300 ungulates spend part of the winter along the Snake River and the eastern foothills of the study area, but some of them "push" down to the Refuge later in the winter. Thus, ungulates are essentially absent from much of the Pothole area during the winter except for a few animals along the immediate floodplain of the Snake River. If mortality rates of these herds approximate that of the National Elk Refuge herds, then 10-30 animals die each winter.

The temporal distribution of dying ungulates also merits consideration. Monthly elk mortality figures for the National Elk Refuge from the three winters were pooled since there was no significant

(Friedman nonparametric test) difference in monthly deaths between years. About 48 percent of the winter elk mortality occurred in January and February with 37 percent in March and April (Table 9). The temporal pattern of elk winter mortality elsewhere is unknown, but I believe a smaller fraction of them die during early winter (November-January) than on the National Elk Refuge.

Coyote Feeding Patterns

No single method of predator scat analysis is ideal; each provides unique information and allows interpretations not possible with others (Latham 1951). Food habits data are presented here in three ways: (1) percent occurrence in the scats (sampling units), (2) percent of items identified, and (3) relative biomass of the principal rodents consumed.

Assuming random sampling, percent occurrence in scats indicates how pervasive the food item is in the diet of the population and is not unduly biased by food preferences of individual predators. Limitations include one individual item scoring as much as ten, and small items equating with larger ones. Percent of identified items partially corrects for this but assumes that all individuals are equally detectable. Again, small items such as field voles count as much as ground squirrels. Percent biomass adjusts for weight differences among prey species.

Spatial and temporal variations in coyote food habits, based upon analysis of 1506 scats and 400 coyote-km of snowtracking, were

Table 9. Monthly elk mortality on the National Elk Refuge, Jackson Hole, Wyoming. Data were pooled for winters 1972-73 through 1974-75. (Data courtesy of R. Robbins.)

Month	Number	Percent
November	3	1.49
December	13	6.47
January	51	25.37
February	46	22.89
March	36	17.91
April	39	19.40
May	13	6.47
Total	200	100.00

examined to reveal feeding patterns. Percent of identified items and relative percent biomass were used in interpreting the data.

Spatial aspects

Mammals comprised 94 percent or more of all vertebrate items identified in scats collected between May and October on all lines (Tables 10-12). Pocket gophers, field voles, and ground squirrels dominated the diet (76-82%) although their relative importance varied between lines. Coyote feeding patterns were similar along the Pothole and Shadow Mountain lines where pocket gophers and field voles together accounted for 73 and 66 percent of the items identified and ground squirrels 9 and 10 percent, respectively (Tables 10 and 12).

Table 10. Summer food habits of coyotes along Pothole Line, Jackson Hole, Wyoming, 1973-74. Sample sizes in parentheses.

	Percent Occurrence in Scats					Percent of Items				
	Overall	1973		1974		Overall	1973		1974	
		PRE[a]	POST[a]	PRE	POST		PRE	POST	PRE	POST
Group and Species	(185)	(20)	(19)	(104)	(42)	(461)	(61)	(44)	(291)	(65)
MAMMAL	95	100	100	96	86	94	92	98	92	97
Rodent	85	100	84	88	71	87	92	82	84	89
Pocket Gopher	55	60	58	52	55	40	38	43	37	49
Ground Squirrel	15	20	--	24	--	9	8	--	13	--
Field Vole	54	80	42	59	33	33	43	39	30	31
Other[b]	13	10	--	15	14	5	3	--	4	9
Ungulate	16	--	37	19	10	6	--	16	7	6
Elk	13	--	37	14	5	5	--	16	5	3
Mule Deer	--	--	--	--	--	--	--	--	--	--
Other[c]	3	--	--	5	5	1	--	--	2	3
Lagomorph and other Mammals	3	--	--	4	2	1	--	--	1	2
BIRD	15	25	5	18	5	6	8	2	7	3
INSECT[d]	12	15	11	13	10					
VEGETATION[d]	22	20	16	28	12					
FRUIT	9	--	--	6	26					

[a] Pre- and post-ground squirrel aestivation.

[b] Deer mouse, western jumping mouse, chipmunk, porcupine, muskrat, beaver.

[c] Moose, domestic cow.

[d] Distinction of individuals was not attempted.

Table 11. Summer food habits of coyotes along National Elk Refuge Line, Jackson Hole, Wyoming, 1973-74. Sample sizes in parentheses.

Group and Species	Percent Occurrence in Scats					Percent of Items				
	Overall	1973		1974		Overall	1973		1974	
		PRE[a]	POST[a]	PRE	POST		PRE	POST	PRE	POST
	(621)	(259)	(90)	(192)	(80)	(1231)	(659)	(186)	(282)	(94)
MAMMAL	87	95	89	81	74	94	94	97	93	95
Rodent	78	95	80	68	41	82	88	88	76	57
Pocket Gopher	28	30	33	23	28	20	18	24	22	30
Ground Squirrel	29	42	3	33	--	22	26	1	31	--
Field Vole	49	73	70	23	18	37	42	59	18	18
Other[b]	7	5	9	7	10	3	2	4	5	9
Ungulate	20	12	19	24	41	11	5	9	16	36
Elk	17	10	13	21	33	8	4	6	14	28
Mule Deer	1	--	1	2	3	1	--	1	1	2
Other[c]	3	3	4	2	8	2	1	2	1	6
Lagomorph and other Mammals	2	2	--	1	3	1	1	--	1	2
BIRD	5	14	7	19	6	6	6	3	7	5
INSECT[d]	25	22	33	25	21					
VEGETATION[d]	32	35	38	28	21					
FRUIT[a]	17	2	13	28	44					

[a] Pre- and post-ground squirrel aestivation

[b] Deer mouse, western jumping mouse, chipmunk, porcupine, muskrat

[c] Moose, domestic cow, horse

[d] Distinction of individuals was not attempted

Table 12. Summer food habits of coyotes along Shadow Mountain Line, Jackson Hole, Wyoming, 1973-74. Sample sizes in parentheses.

	Percent Occurrence in Scats					Percent of Items				
	Overall	1973		1974		Overall	1973		1974	
		PRE[a]	POST[a]	PRE	POST		PRE	POST	PRE	POST
Group and species	(135)	(61)	(23)	(35)	(16)	(309)	(176)	(45)	(71)	(17)
MAMMAL	95	95	96	91	100	95	96	95	95	100
Rodent	79	89	83	74	44	84	90	82	78	70
Pocket Gopher	53	62	65	43	31	43	44	49	42	29
Ground Squirrel	17	23	--	23	--	10	11	--	17	--
Field Vole	39	51	43	26	19	23	26	33	13	23
Other[b]	16	25	--	9	19	8	9	--	6	18
Ungulate	20	15	26	24	25	9	5	13	13	24
Elk	13	8	22	14	19	6	3	11	7	18
Mule Deer	7	7	4	11	6	3	2	2	6	6
Lagomorph and other Mammals	4	2	--	3	6	2	1	--	4	6
BIRD	9	10	9	11	--	4	3	5	5	--
INSECT[c]	13	16	13	11	6					
VEGETATION[c]	35	39	30	37	19					
FRUIT[c]	10	8	4	23	--					

[a] Pre- and post-ground squirrel aestivation.

[b] Western jumping mouse, red-back vole, porcupine, muskrat.

[c] Distinction of individuals was not attempted.

On the National Elk Refuge, however, gophers and voles constituted 57 percent of the items and ground squirrels 22 percent (Table 11).

Ungulates, primarily elk, made up 6 percent of identified items in scats from the Pothole line, 11 percent on the National Elk Refuge, and 9 percent on Shadow Mountain, Lagomorphs (1-2%) were rare items in the diet of Jackson Hole coyotes.

Birds comprised 4-6 percent of vertebrate items. Identification to species was not attempted, but the presence of egg shell fragments in the majority of instances suggested that ground-nesting passerines were preyed upon. Most bird remains were observed in June and July scats.

Insects, vegetation, and fruit were tabulated on a percent occurrence in scats-basis only. Insects (primarily grasshoppers) occurred in about 25 percent of NER scats and in about 12 percent of PH and SM scats. Vegetation in amounts greater than one gram occurred in 22-35 percent of scats. In some cases an entire scat was composed of vegetation. Fruit occurred in 17 percent of NER scats, 10 percent of SM scats, and 9 percent of PH scats.

Temporal aspects

The aestivation and hibernation of rodents marks a significant phenological change in the coyotes' food supply. To examine their response, I compared food habits data for three periods: (1) pre-Uinta ground squirrel aestivation (May-August), (2) post-Uinta ground squirrel aestivation (September-October), and (3) winter (January-March).

Following ground squirrel aestivation, pocket gophers increased by 5-10 percent of the items identified (except for the small sample from Shadow Mountain in 1974) while field voles remained relatively constant or increased by 5-15 percent (Tables 10-12). Consumption of ungulates and fruit also increased while insects decreased, each change due primarily to changes in availability.

During the winter, ungulates--mostly elk--comprised 81 percent of items identified and occurred in 87 percent of scats (Table 13). Field voles made up 12 percent of items, but this figure is biased by collections from coyotes hunting in meadows where Microtus were common. Murie (1940) reported that elk and deer (mainly as carrion) made up "practically the entire food supply" during the winter for Yellowstone coyotes. Coyotes in Michigan (Ozoga 1963) and in Alberta (Nellis and Keith 1976) also relied upon ungulate carrion for winter food.

Snowtracking of coyotes throughout the study area (1974) and of the Glacier View group (1975) confirmed this reliance upon ungulate carrion (Table 14). The importance of field voles was perhaps exaggerated again by following coyotes in localized vole habitats. Although I did not trail coyotes over the National Elk Refuge due to elk management considerations, I suspect similar feeding patterns prevailed there during the winter.

The Glacier View group was trailed 19 of 55 days between January 15 and March 11, 1975. The group consisted of two adults who were joined by a smaller coyote about February 5. From January 15 to

Table 13. Winter food habits of coyotes in Jackson Hole, Wyoming, based upon analysis of scats collected from January through March, 1974 and 1975. Sample sizes in parentheses.

Group and Species	Percent Occurrence in Scats (315)	Percent of Items (370)
MAMMAL	95	98
Rodent	12	15
Pocket gopher	1	1
Field vole	11	13
Other	1	1
Ungulate	87	81
Elk	82	74
Mule deer	1	1
Other	7	6
Other mammal[a]	3	2
BIRD	2	2
VEGETATION	4	--

[a] Including unidentified bone and meat residue.

Table 14. Classification of food items found along 400 km of coyote trails from January through March, 1974 and 1975, Jackson Hole, Wyoming.

Group and Species	Kills	Carrion	Caches
MAMMAL	41	84	20
Rodent	39	--	--
Pocket Gopher	1	--	--
Field Vole	37	--	--
Red Squirrel	1	--	--
Ungulate	2	83	20
Elk	2	69	20
Mule Deer	--	--	--
Domestic Cow	--	8	--
Moose	--	6	--
Other Mammal[a]	--	1	--
BIRD	2	--	--
Ruffed Grouse	1	--	--
Mallard Duck	1	--	--
UNIDENTIFIED	--	--	8

[a] Coyote pup.

February 17--33 days--these coyotes killed one mallard duck and gnawed upon old ungulate bones. Although they spent some time apparently hunting snowshoe hares in the floodplain forest along the Snake River, I never found indications of success. The coyotes would return again and again to old ungulate carcasses to chew whatever bones were left, often digging through 4-5 feet of snow to reach them. While the Glacier View group was not tracked continuously, their scats approximate their food habits on the off days since digestion of an item usually occurs within 18-30 hours after ingestion (Weaver and Hoffman unpubl. data). The available evidence suggests that coyotes may go weeks with very little fresh food.

If the weather is not extremely cold, several coyotes can "clean up" elk or moose carcass in 1-3 days. It seems likely that much of these carcasses must be cached since it is doubtful that even many coyotes could consume 300-1000 pounds so quickly. Usually I did not discover winter-killed ungulates soon enough to find fresh caches. On the morning of February 18, 1975, however, I observed the Glacier View group (3 coyotes) feed on two cow elk that had died the previous night. If a cache is defined as any part of a carcass which is buried further than 25 m from the original carcass site, these coyotes made 16 known caches during the next two days. Ten of the caches were more than 400 m from the carcasses. No apparent pattern in cache location relative to landmarks was discerned. One cache contained a 78-g chunk of fresh meat. One elk and half of the other had been stripped bare by the third day.

Two probable elk kills by coyotes were recorded during this study. In one instance a calf elk was apparently held at bay in a cold stream for several hours and killed at the edge of the bank. In another case, a cow elk was chased off a steep rim and killed after wedging her leg between two trees lying on the ground.

Conversion to biomass for principal rodents

Pocket gophers, ground squirrels, and field voles dominated the diet of Jackson Hole coyotes from May to October. Their relative importance between areas has been shown using percent of items identified. The analysis thus far obscures importance relative to each other, either on or between areas, since there may be a 12-fold difference in weight between species (e.g., 300 g adult ground squirrels and 25 g adult field voles). Hence, a conversion to biomass is desirable.

Other investigators (Rusch _et_ _al_. 1972, Nellis _et_ _al_. 1972, and McInvaille and Keith 1974) converted to biomass by multiplying average adult weight for a species by its percentage of items identified. Two assumptions are implicit in that calculation: (1) all individuals detected are adults, and (2) all ingested individuals are detected.

I checked these assumptions before making biomass conversions because (1) there is a 175 g (240 percent) difference between average weights of juvenile and adult Uinta ground squirrels (June) and a 27 g (140 percent) difference between average weights of juvenile and adult northern pocket gophers (August-September), and (2) Murie (1946) reported only about half the field voles consumed by a captive coyote was detected in its scats.

Age classification. I developed a technique for separating age classes of pocket gophers and ground squirrels based upon measurements of tooth remains in coyote scats. Four dental measurements were made on individuals (trapped on study area) of known age-class of these two species: (1) length of upper molariform row, (2) length of lower molariform row, (3) length of beveled surface of upper incisor, and (4) length of beveled surface of lower incisor (Fig. 8). Age determination of pocket gophers was based upon size of reproductive organs (Hansen 1960) and body weight while age of ground

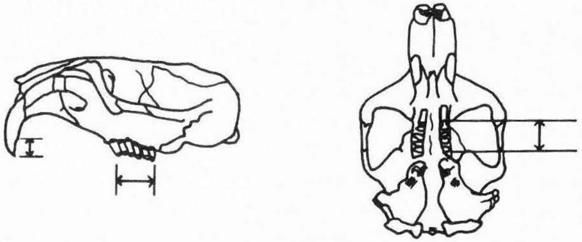

Figure 8. Measurements of molariform row and beveled surface of incisor used in age determination of northern pocket gophers and Uinta ground squirrels in coyote scats.

squirrels was based upon body size. The means between age classes for both northern pocket gophers and Uinta ground squirrels were significantly ($p < 0.05$) different for all four measurements (Table 15).

On the basis of these measurements, individuals of known age-class were classified into age categories by discriminant analysis. This is a technique (Cooley and Lohnes 1971, Tatsuoko 1970) appropriate for distinguishing groups of individuals using linear combinations of measurements. The BMD 07M computer program (Dixon 1970) performed the analysis stepwise with variables entered one at a time in the order of their ability to distinguish groups. The program classified individuals into either adult or juvenile and printed their associated posterior probabilities. The classification criterion was the minimum Mahalanobis distance between groups. In calculating the posterior probability, the BMD program did not assume equal covariance matrices.

Table 15. Comparison of dental measurements between adults and juveniles of northern pocket gophers and Uinta ground squirrels. Parenthetical values are one standard error.

Species	Variable	Length (mm) Adults	Length (mm) Juveniles	F-value
Pocket gopher:	sample size	18	27	
	lower molariform row	6.33 (0.39)	5.54 (0.08)	38.25**
	upper molariform row	6.09 (0.05)	5.46 (0.08)	34.09**
	lower incisor bevel	4.16 (0.13)	3.64 (0.11)	9.87**
	upper incisor bevel	3.37 (0.18)	2.92 (0.08)	6.77 *
Ground squirrel:	sample size	73	50	
	upper incisor bevel	4.03 (0.07)	1.91 (0.09)	363.78**
	upper molariform row	9.19 (0.09)	6.70 (0.11)	324.11**
	lower incisor bevel	4.99 (0.08)	3.19 (0.09)	228.76**
	lower molariform row	8.73 (0.10)	7.04 (0.13)	108.05**

*Significant at the 0.05 level.

**Significant at the 0.01 level.

Variables and combinations of variables used in age classification of unknown-age teeth remains from coyote scats are ranked in Table 16 by their relative discrimination ability. For pocket gophers, molariform row lengths were better classifying measurements than lengths of the incisor bevels. One explanation might be that in these fossorial animals the adults wear back the anterior ends of the incisors, thereby shortening the bevel length. With ground squirrels, the upper tooth measurements (both molariform row and incisor bevel) were better criteria than lower teeth. Part of this was due to tooth eruption phenology of the juveniles. Fourteen of 50 juveniles trapped on July 1 had recently erupted the last lower molar and thus biased results toward adults. Although including these individuals in the analysis reduced the discriminating ability of this measurement, it seemed appropriate since the scat collections encompassed the period ground squirrels were active (until about August 20).

Of the 665 pocket gophers detected in coyote scats, 407 (57 percent) were used to determine age ratios. The others either had no measurable tooth remains or were rejected due to a posterior probability less than 0.80. About 80 percent of the pocket gophers detected and classified were juveniles. Of the 506 ground squirrels found in scats, 371 (72 percent) had satisfactory measurements for age determination. About 60 percent of these were juveniles.

As the first step toward conversion to relative biomass, pocket gophers and ground squirrels detected in coyote scats from the three lines were classified adult or juvenile, based on dental measurements.

Table 16. Individual northern pocket gophers and Uinta ground squirrels correctly assigned to age class by discriminant analysis of dental measurements. Classification criterion was the minimum Mahalanobis distance. All categorizations significant at the 0.01 probability level.

		Individuals Correctly Assigned to Age Class				
		Adult		Juvenile		
Species	Variables	No.	%	No.	%	Approximate F-value
Pocket gopher	(sample size)	(18)		(27)		
	lower molariform row	16	89	20	74	71.82
	upper molariform row	18	100	20	74	59.17
	lower molariform row and lower incisor bevel	16	89	24	89	38.81
	upper molariform row and lower incisor bevel	18	100	24	89	36.82
	upper molariform row and upper incisor bevel	16	89	20	74	31.00
	lower incisor bevel	14	78	18	67	18.98
	upper incisor bevel	12	67	21	78	14.70
Ground squirrel	(sample size)	(73)		(50)		
	upper molariform row	72	99	40	80	722.96

Table 16. Cont.

Species	Variables	Individuals Correctly Assigned to Age Class				Approximate F-value
		Adult		Juvenile		
		No.	%	No.	%	
	upper incisor bevel	68	93	50	100	641.77
	upper molariform row and upper incisor bevel	72	99	45	90	603.47
	lower incisor bevel	71	97	42	84	486.04
	lower molariform row and lower incisor bevel	72	99	42	84	290.47
	Lower molariform row	73	100	32	64	252.48

These age ratios were assumed applicable to all individuals detected (Table 17).

Adjustments for detectability in coyote scats. The number of individual prey detected in coyote scats, however, may not equal what was consumed. A feeding experiment with captive coyotes was conducted from December 18, 1975, to January 3, 1976, to determine what percent of ingested individuals of various rodent species could be detected in scat analysis. Six adult coyotes, three of each sex, were fed 10 different diets with known numbers of rodents. Five diets contained a single rodent species while 5 combined 2-3 species. Daily intake was a constant 600 g. Scats were collected every 6 hours throughout the experiment, weighed wet, dried in a 60 C oven for 72 hours and

Table 17. Adjusted age composition of northern pocket gophers and Uinta ground squirrels detected in summer coyote scats, Jackson Hole, Wyoming, 1973-74. See text for method of age determination.

		Pocket Gopher			Ground Squirrel		
Year	Line	Total	Adult	Juvenile	Total	Adult	Juvenile
1973	PH	42	5	37	5	2	3
	NER	161	37	124	175	71	104
	SM	99	24	75	19	9	10
1974	PH	140	24	116	37	17	20
	NER	90	25	65	93	33	60
	SM	35	6	29	12	5	7

reweighed. All scats were analyzed in the same manner as field-collected scats. Each coyote was weighed following 48 hours of deprivation at the beginning and end of the experiment. Results are shown in Table 18.

The percent of ingested individuals detected in scat analysis was regressed upon prey body weight (Fig. 9). The equation $Y = 105.72 \log X - 113.17$, was fitted ($r = 0.87$) to the data points. The relationship suggests that heavier prey species are detected more often than smaller ones. Parts of a single individual can be excreted in several scats. Since each scat is a sampling unit, frequency of detection can be greater than 100 percent. Hence, adjustments for detectability are necessary for different-sized prey.

These adjustments were made for field voles and adult and juvenile pocket gophers and ground squirrels using average body weights from animals trapped on the study area. The following calibrations were computed from the regression equation:

(1) field vole (25 g) - 2.89 consumed : 1 detected,

(2) juvenile pocket gopher (63 g) - 1.29 : 1,

(3) adult pocket gopher (90 g) - 1.07 : 1,

(4) juvenile ground squirrel (125 g) - 0.92 : 1, and

(5) adult ground squirrel (300 g) - 0.67 : 1.

These values were used to adjust numbers of field voles, pocket gophers, and ground squirrels detected (Table 17) to number consumed (Table 19).

From the adjusted number of rodents consumed, I computed biomass for four rodent species.

Coyote	Deer Mouse			Pocket Mouse			Kangaroo Rat			Juvenile Ground Squirrel			Adult Ground Squirrel		
	C	D	%	C	D	%	C	D	%	C	D	%	C	D	%
Dizzy (♀)	79	8	10	45	7	16	23	15	65	4	3	75	4	3	75
Mitzy (♀)	77	18	23	44	11	25	21	12	57	5	7	140	4	7	175
Shabi (♀)	77	25	32	43	9	21	22	14	64	4	6	150	4	6	150
Blue (♂)	74	14	19	42	8	19	22	12	55	4	2	50	4	9	225
Brujo (♂)	61	12	20	44	14	32	23	18	78	4	5	125	4	5	125
Untag (♂)	33	18	55	32	8	25	12	6	50	0	0	--	1	0	0
Mean			27			23			62			108			125
95% Conf. Int.			±16			±6			±10			±50			±83

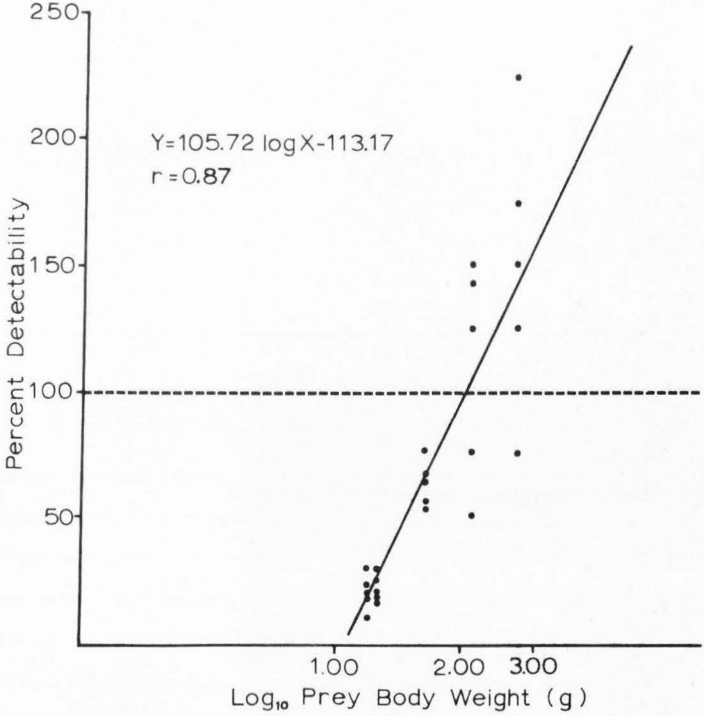

Figure 9. Percent of ingested individuals detected in scat analysis regressed upon prey body weight (Log_{10} X). Dashed line represents unity of consumption and detection. The correlation is significant at the 0.01 probability level.

Table 19. Number and age composition of three species of rodents represented in coyote scats. Estimates from Table 17 for pocket gophers and ground squirrels and from Tables 10-12 for field voles adjusted using calibration values in parentheses.

		Field Vole	Northern Pocket Gopher			Uinta Ground Squirrel		
Year	Line	Total (2.89)	Total	Adult (1.07)	Juvenile (1.29)	Total	Adult (0.67)	Juvenile (0.92)
1973	PH	124	54	6	48	4	1	3
	NER	1101	200	40	160	144	48	96
	SM	176	123	26	97	15	6	9
1974	PH	309	182	32	150	29	11	18
	NER	202	111	27	84	77	22	55
	SM	32	43	6	37	9	3	6

consumed for each of the three principal rodents during summer by multiplying number consumed (Table 19) and the average body weight for the respective age classes. Biomass of a species divided by the total biomass of all three species gave a <u>relative</u> biomass percentage for that species (Fig. 10). These percentages, while not directly comparable to the percentages for identified items in Tables 10-12, show somewhat similar trends. In the Pothole and Shadow Mountain areas, pocket gophers and field voles were the dominant rodents consumed on a biomass basis. Ground squirrels assumed greater prominence in the coyote diet on the National Elk Refuge. Following the decline of field voles during the winter and spring of 1974, their relative biomass in the coyotes' diet decreased by nearly one-half along all

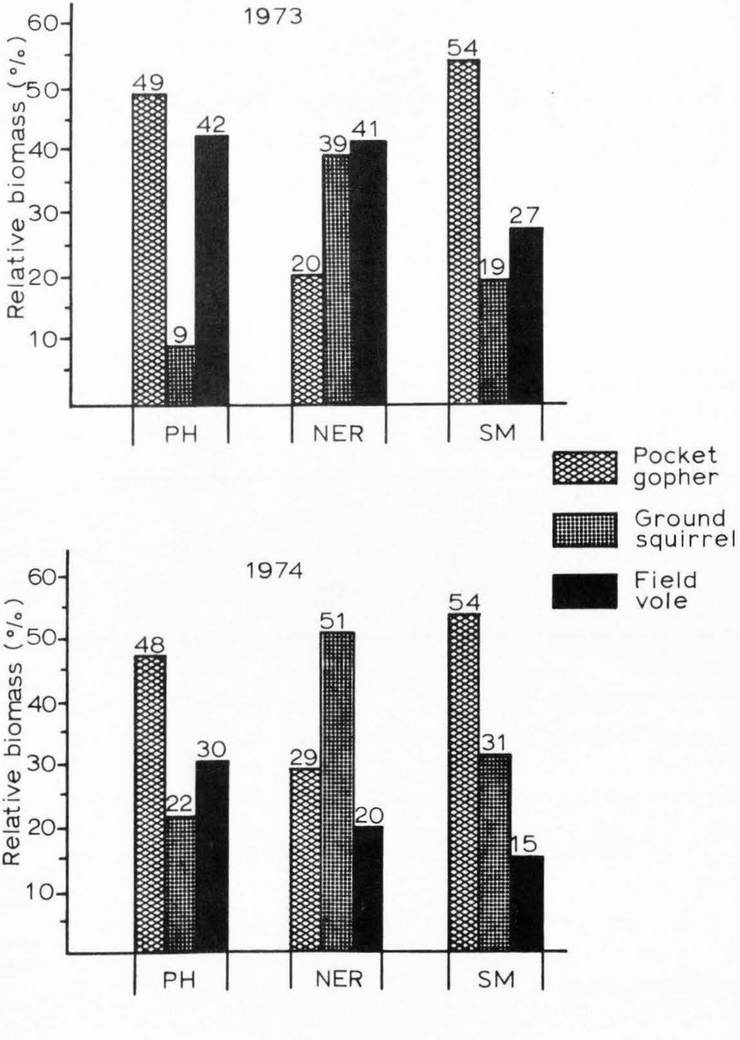

Figure 10. Relative biomass of three principal rodents in summer diet of coyotes, Jackson Hole, Wyoming, 1973 and 1974.

lines. Coyotes near the Potholes and Shadow Mountain shifted more to ground squirrels than to pocket gophers whereas those on the National Elk Refuge increased their consumption of each on a biomass basis about equally.

Biomass conversions become important when the weight and detectability relationships between species diverge. For example, there is a 12-fold difference in weight between adult ground squirrels and field voles but only a 4.6-fold difference in detectability. Between field voles and juvenile pocket gophers, there are 2.5-fold differences in weight and 2.1-fold differences in detectability; hence, little is gained from making biomass conversions for comparing these two species. The net effects of these relationships are depicted in Table 20.

Table 20. Net effect of differences in weight (W_2/W_1) multiplied by differences in detectability (D_2/D_1) for three rodent species. Value of one indicates offsetting weight and detectability.

	Field Vole	Pocket Gopher Juvenile	Pocket Gopher Adult	Ground Squirrel Juvenile
Pocket Gopher Juvenile	1.13			
Pocket Gopher Adult	1.33	1.18		
Ground Squirrel Juvenile	1.59	1.41	1.20	
Ground Squirrel Adult	2.79	2.47	2.08	1.75

Relative Abundance of Coyotes

The scent-station and scat collection indices of coyote abundance were scaled to a common base by setting the mean values observed for each equal to 100. Individual observations were then adjusted by the equation:

$$x_i = \frac{X_i}{\overline{X}} \times 100$$

where x_i = adjusted index

X_i = observed value

$\overline{X}$ = average of all observed values for the index method

The composite index was my best estimate of the relative population density for any particular line because it was based upon an average of the two independent indices. Therefore, it should be less subject to sampling error than either index method alone.

The composite index and its constituent indices suggested that coyotes were most abundant on the National Elk Refuge, less abundant on Shadow Mountain, and least common near the Potholes (Table 21). Differences between areas were greatest in 1973.

Both the scent-station and the scat collection indices indicated that coyote numbers increased on the Pothole and decreased on the National Elk Refuge from fall 1973 to fall 1974 (Table 21, Fig. 11). Changes in the two indices for Shadow Mountain between years did not agree. The scent-station index suggested a slight increase whereas the scat collection index pointed to a substantial decline. The

Table 21. Relative and composite coyote population indices, Jackson Hole, Wyoming, 1973-75.

Line	Index	Fall 1973	Spring 1974	Fall 1974	Spring 1975
PH	Scent Station	26[a](41[b])	83 (134)	57 (92)	54 (87)
	Scat Collection[c]	34[a](9)		92 (24)	
	Composite[a]	30		75	
NER	Scent Station	176 (283)	167 (268)	117 (188)	207 (332)
	Scat Collection	218 (57)		92 (24)	
	Composite	197		105	
SM	Scent Station	82 (132)	72 (116)	101 (163)	58 (93)
	Scat Collection	126 (33)		38 (10)	
	Composite	104		70	

[a] See text for adjustment procedure.

[b] Unadjusted values in parentheses.

[c] Number per day per km x 1000.

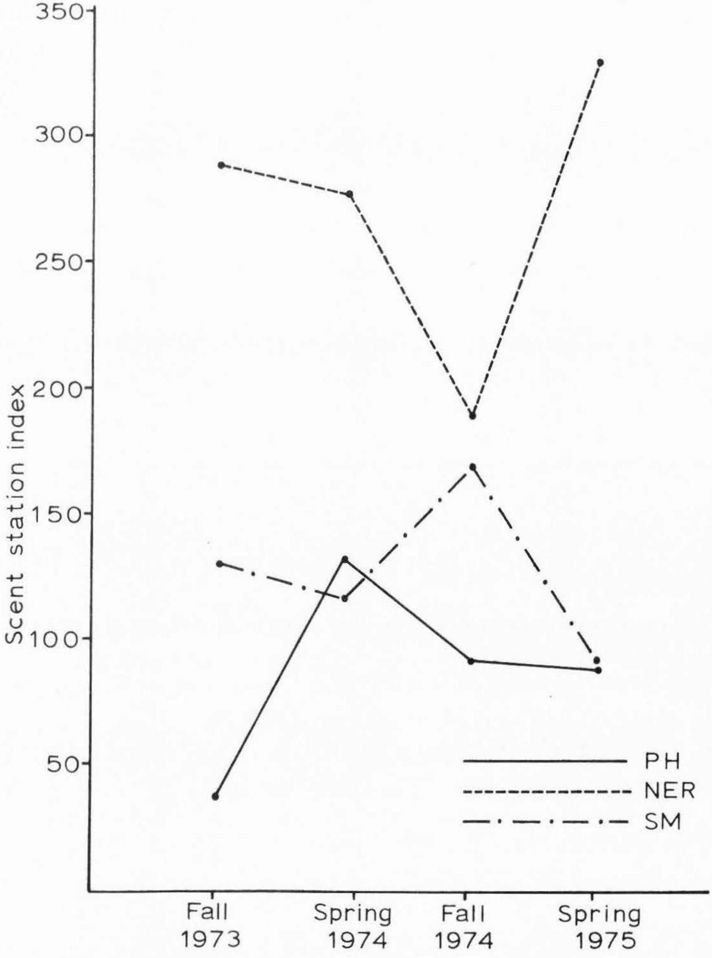

Figure 11. Semi-annual coyote scent-station indices (unadjusted values) for the three lines, Jackson Hole, Wyoming, 1973-75.

number of scats collected each month during the summer and fall was similar for the two years except for unusually large numbers found in September and October, 1973. Changes in defecation behavior or movements may have caused some of this variation.

DISCUSSION

If we are to develop models which simulate responses of coyote populations to their food supply, it is necessary to measure and characterize the functional and numerical relationships involved. If a link between food base and coyote numbers is established, do we have to inventory all food resources at all times to predict coyote densities and changes thereof? Or can we identify key prey species and/or seasons? Do coyotes "switch" (i.e., increase predation pressure [Murdoch 1969:337]upon other prey) should one species decline in numbers?

This discussion examines functional and numerical responses of Jackson Hole coyotes to changes in their food base. Since density is determined by an interaction of natality, mortality, and movements, the possible influence of nutrition upon these demographic parameters will be explored.

Functional Response

Field voles were the only rodent for which I had two years of data both on availability and utilization by coyotes. The relative abundance of voles appeared to decrease between fall, 1973, and fall, 1974, on the Pothole and National Elk Refuge lines but increase on the Shadow Mountain line (Table 3). The number of voles per coyote scat declined substantially between summers in each area (Tables 10-12).

Thus, there was a strong positive functional response in two of three areas.

Another set of data involved the coyotes' functional response to aestivation of Uinta ground squirrels, one of three principal rodents in their summer diet. The number of food items identified per coyote scat was determined for six foods: Uinta ground squirrel, northern pocket gopher, field vole, ungulate, insect, and fruit. Individual rodents were tallied whereas occurrences of the other three represented one "individual." Scats collected between May and August were termed "pre-aestivation;" those in September and October, "post-aestivation."

The total number of these foods per coyote scat ranged from 1.84 to 2.87 prior to ground squirrel aestivation and from 0.87 to 2.38 afterwards (Fig. 12). It decreased from pre- to post-aestivation both years on the Pothole and Shadow Mountain areas but increased on the National Elk Refuge. The occurrence of ground squirrels in coyotes' diet declined to zero post-aestivation as coyotes showed a positive functional response. The number of pocket gophers and field voles per scat decreased post-aestivation on the Pothole and Shadow Mountain areas but not on the National Elk Refuge. Use of insects generally decreased, while consumption of fruit increased (except on Shadow Mountain). The major shift, though, was to ungulates. Changes in consumption by coyotes of insects, fruit, and ungulate may have reflected a change in their availability.

The feeding pattern of coyotes changed markedly after ground

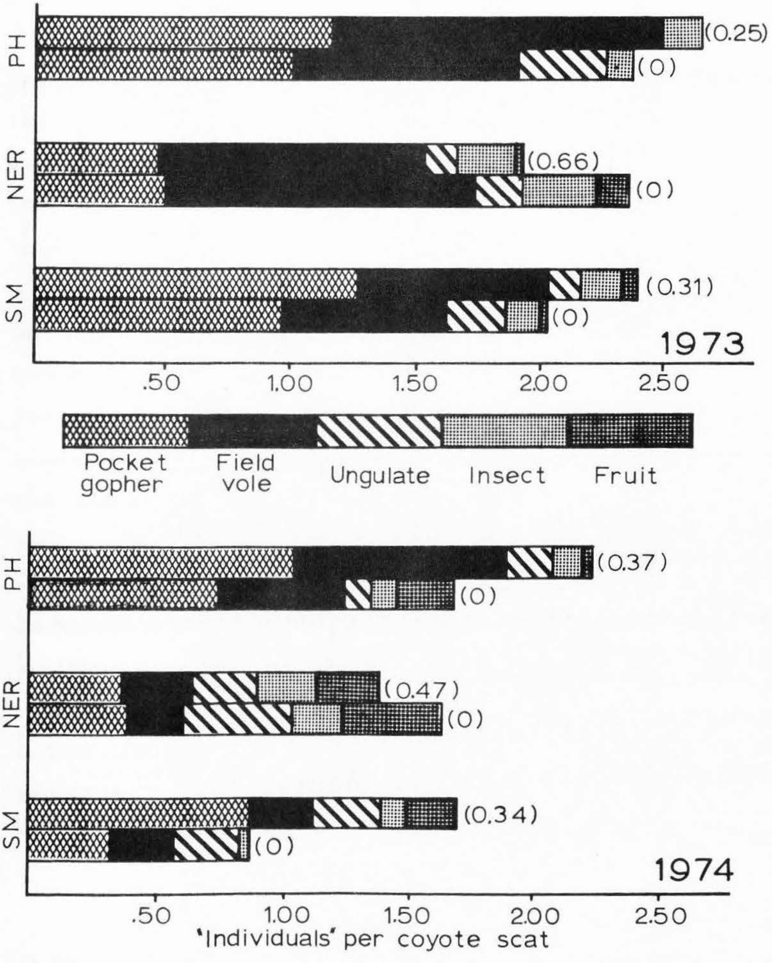

Figure 12. Functional response and dietary shifts of Jackson Hole coyotes to aestivation of Uinta ground squirrels. Bar segments are the number of "individuals" per coyote scat for five foods. Upper bar refers to pre-aestivation, lower bar to post-aestivation. Parenthetical values are number of ground squirrels per coyote scat.
]

squirrel aestivation. Based on number of foods per scat, coyotes apparently did not compensate for the disappearance of a principal food. Furthermore, since the weight-to-detection ratio of ground squirrels to field voles is 1.6-2.8:1 and to pocket gophers is 1.2-2.5:1 (Table 20), any shift to those two rodents would have to be substantial to account for differences in biomass.

It is possible that coyotes could have achieved this by consuming more ungulate. The tally of ungulates in scats is based upon their hair and it is difficult to calibrate the amount of ungulate consumed. When coyotes chew through the hide and feed on flesh, little hair shows up in the scats, which are mostly meat residue. On the other hand, coyotes may gnaw on the hide when little but skin and skeleton remains. These scats are composed entirely of hair. Whatever the case, I do not believe one can assume that each visit to carrion constitutes a "meal" as some suggest (Nellis _et al_. 1972, Brand _et al_. 1976).

Finally, knowledge of the energy provided by various foods such as fruit, insects, and mammals would place their importance in better perspective.

Numerical Response

Assessing the numerical response of coyote populations to changes in their food base was confounded in this study (as in others) by human exploitation of coyotes (Tzilkowski and Knowlton 1976). Much of this exploitation occurred during fall and winter on or near Shadow

Mountain and the National Elk Refuge where coyotes usually were more abundant. Hence, the influence of food supply upon coyote abundance might have been more evident in the absence of human exploitation.

Coyote numbers were greatest on the National Elk Refuge, lower on Shadow Mountain, and lowest on the Potholes in 1973 (Table 21). Numerical differences were not as marked the following year, but the Refuge still harbored more coyotes than the other areas.

To evaluate the impact of summer food supply upon coyote numbers, I compared the relative abundance of field voles, Uinta ground squirrels, and northern pocket gophers in 1974 between areas (Fig. 13). These rodents accounted for the majority of vertebrate items identified in the May-October coyote scats along each line (Tables 10-12). Since abundance was expressed as indices with different units for each species, they could not be combined and regressed against coyote abundance.

Although there were substantial differences in relative abundance of these principal rodents between areas, relative coyote densities did not correspond. All three were most common on Shadow Mountain, yet coyote indices were lower there. Comparing overall rodent abundance for the other two areas was difficult because the ground squirrel index was greater on the National Elk Refuge than on the Pothole while the pocket gopher index was smaller. Nonetheless, the area (Shadow Mountain) with the greatest abundance of principal summer foods did not have the most coyotes, while the area (National Elk Refuge) with the highest coyote index did not have the largest

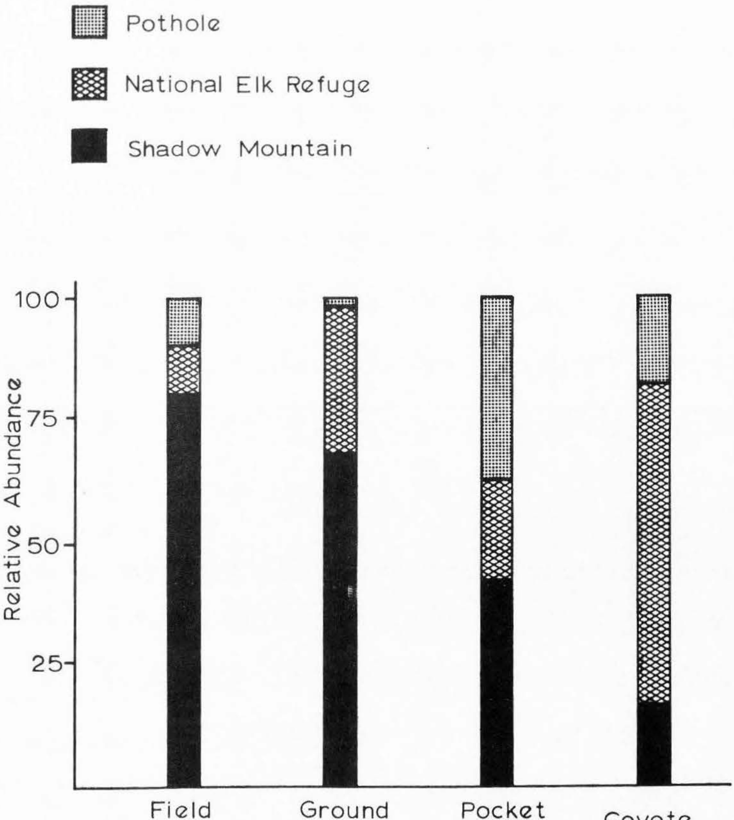

Figure 13. Comparison among the three index lines in Jackson Hole, Wyoming, of the proportional distribution of field voles, Uinta ground squirrels, northern pocket gophers in summer, 1974, and of coyotes in spring, 1975.

supply of important rodents. Thus, the summer food base clearly was not the major determinant of coyote population levels in Jackson Hole.

During late fall and winter, coyotes fed primarily upon ungulate (chiefly elk) carrion (Tables 14 and 15). The viscera, and often the feet and head, of hunter-killed elk were present during October and November. The carcasses of "winter-killed" elk were the primary source of food from December through April. Carrion from both sources was available in late fall.

The amount of carrion present was computed in the following manner. The numbers, sex, and age of hunter-killed elk in the three areas was obtained from records compiled by Park, Refuge, and Game and Fish biologists and segregated into calf, adult cow, and adult bull classes. The average live weight of animals in these classes--109, 232, and 286 kg respectively (Greer and Howe 1964)--was multiplied by the percent which the viscera comprised of hunter-dressed elk--34, 33, and 32 percent respectively (Quimby and Johnson 1951).

The known number in each sex-age class of elk which died between November and May on the National Elk Refuge (Table 9) was multiplied by the appropriate live weight. In locales visited by coyotes from the Pothole and Shadow Mountain areas, I subjectively estimated 200 and 100 wintering elk, respectively. Since winter environmental conditions there seem more rigorous than on the Elk Refuge, I arbitrarily set the average winter mortality rate of elk in those areas at 5 percent (compared to a known 1 percent on the Refuge). The sex and age composition of winter-killed elk on the Refuge, as well as relative mortality rates between winters, was applied to calculations for the Pothole and Shadow Mountain areas.

These estimates represent the biomass of elk carrion present from October to May. Differences in this food supply between areas was substantial (Fig. 14). Since no hunting was allowed within the Pothole area and relatively few elk wintered there or nearby, very little ungulate carrion was available to these coyotes during winter. Elk carrion on the Shadow Mountain area (40,277 and 28,195 kg during 1973-74 and 1974-75, respectively) was 12 to 20-fold more abundant than on the Potholes and 1.3 to 2-fold more than on the National Elk Refuge. The amount of carrion decreased by 30 percent on Shadow Mountain, and by more than 50 percent on the Potholes and National Elk Refuge from 1973-74 to 1974-75 (Fig. 14). Some of the carrion biomass, including rumen, skull and leg bones, may not be edible, which could substantially reduce the amount from hunter-killed elk actually available to coyotes.

A linear regression of the spring (late May-early June) coyote scent-station index upon the log of the amount of elk carrion present from both sources October-May yielded a poor correlation ($r = 0.36$). A plot of the log of only carrion from winter-killed elk upon coyote abundance in the spring produced a much better correlation ($r = 0.84$, Fig. 15). This numerical response suggests that carrion from elk dying throughout the winter played a more prominent role in determining coyote numbers in spring than did visceral remains of elk killed by hunters during fall (more of which may be non-edible). It may be

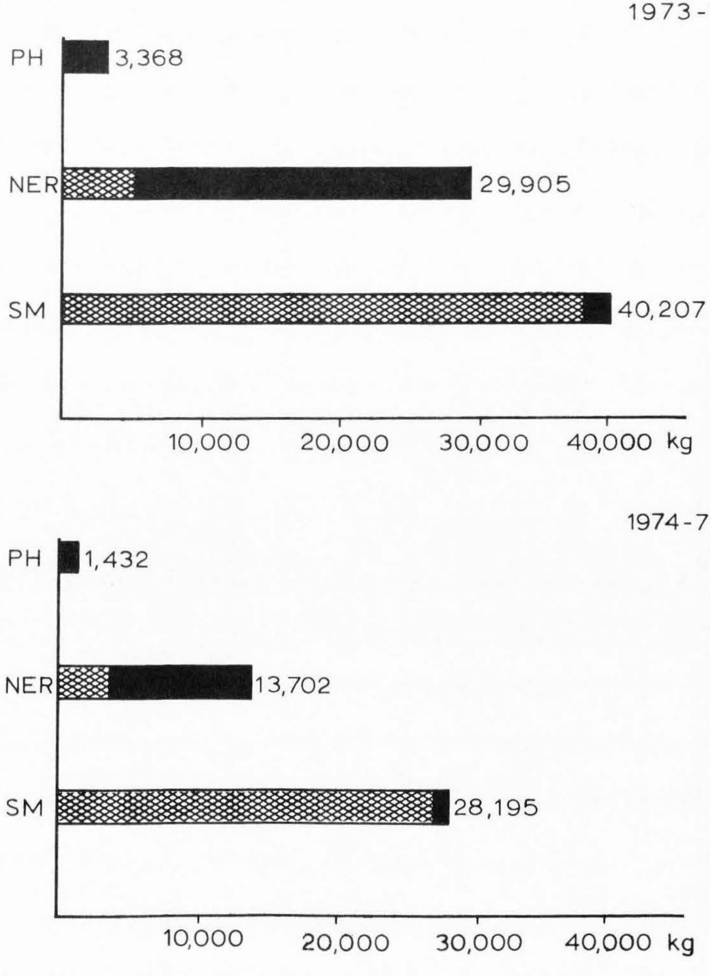

Figure 14. Estimated biomass of carrion from hunter-killed (light bar) and winter-killed (dark bar) elk, October-May, 1973-74 and 1974-75 in three areas of Jackson Hole, Wyoming.

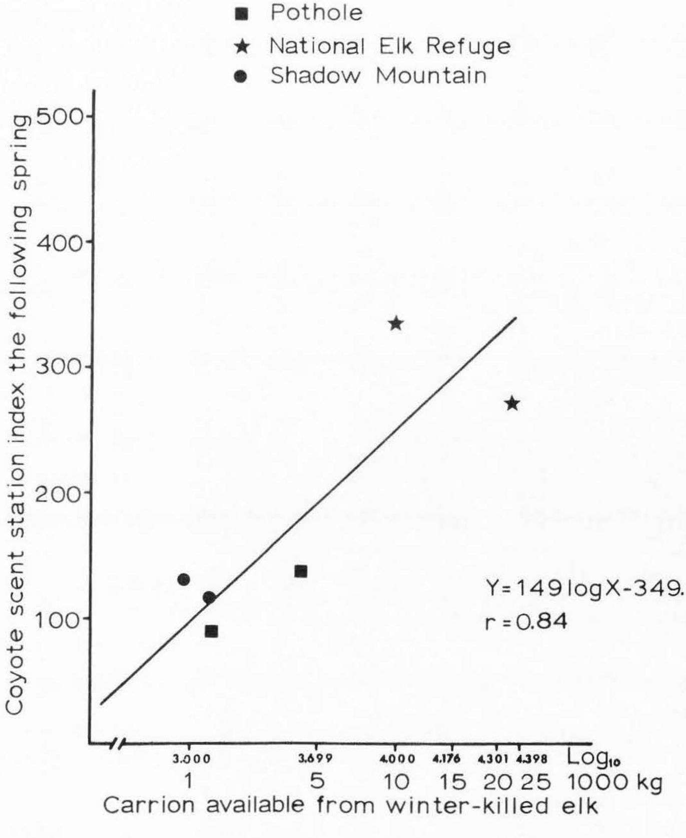

Figure 15. Spring coyote scent-station index regressed upon $\log_{10}$ of the carrion available from winter-killed elk, Jackson Hole, Wyoming. The correlation is significant at the 0.05 probability level.

significant that elk mortality on the Elk Refuge was well distributed from January through April (Table 9), rather than concentrated during a short time period.

The relationship between winter food supply--elk carrion--and coyote populations seems clear. Where little carrion was available, coyotes were scarce (Potholes); where carrion was ample, coyotes were abundant (National Elk Refuge). Although human exploitation of coyotes could confound interpretations, much of it occurred near the Elk Refuge. Hence, the influence of winter food base may have been more striking had exploitation been less.

To summarize, differences in coyote population levels between three areas in Jackson Hole were attributed primarily to differences in ungulate carrion available during winter. Although difficulties in comparing rodent indices precluded a full analysis, food resources during summer appeared less influential.

Influence of Nutrition Upon Demographic Mechanisms

Natality, mortality, and movements are demographic mechanisms which determine population density. Nutrition--the quantity and quality of food--is one of several factors which may influence any or all of these mechanisms.

Natality

Variations in performance at any point in the reproductive process can affect the reproductive efficiency of a female population. Productivity varies with the (1) age of first estrus (puberty),

(2) percentage of females which breed, (3) number of ovulations, (4) number of eggs fertilized and implanted, and (5) number of implanted blastocysts which survive gestation. Knowlton (1972) suggested that all of these parameters may be important in coyote populations.

Much work has been done with domestic farm animals to determine the effects of nutrition upon reproduction, and it may be instructive to survey those findings. Experiments with dairy and beef cattle and sheep suggest that lower levels of nutrition during periods of growth preceding puberty significantly lengthen the time before the test animals experienced their first estrus. Low levels of nutrition delayed puberty an average of over 7 months in four breeds of dairy and beef cattle (Jaubert 1954). In another study, 26.4 percent of the ewe lambs fed supplemental amounts of food while on winter range entered estrus, but only 13.6 percent of the control group (Burfening _et_ _al_. 1971). Of 13 white-tailed deer yearlings fed at low levels of nutrition for a 6-week period prior to estrus, only 6 bred whereas all 8 of the yearlings on a maintenance nutrition level bred (Verme 1969). Gier (1968) reported that none of the yearling female coyotes examined in Kansas had bred in years when rodent remains constituted less than 3 percent of stomach contents during winter. In winters when the rodent percentage rose to 5 or more, at least 50 percent of the yearling females examined bred.

That higher nutrition increased the percentage of adult females breeding has also been demonstrated with a variety of animals (Blakely _et_ _al_. 1963, Dunn _et_ _al_. 1969, Short _et_ _al_. 1968, Verme 1969). Gier

(1968) found that in a "good mouse year" 83 percent of the adult female coyotes bred, whereas in a "bad mouse year," only 60 percent bred.

Although ovulation rates are subject to genetic selection, nutrition can be an influence. Ovulation seems affected both by absolute bodyweight at breeding time (Foote _et_ _al_. 1959, Fletcher 1971, and Ruttle and Montgomery 1972) and the plane of nutrition immediately prior to breeding ("flushing") (Allen and Lamming 1961, McGillivray _et_ _al_. 1962, Ray and McCarthy 1965, Verme 1969). Absolute bodyweight may have the greater effect. Flushing seems particularly valuable if the animal was in poor condition prior to estrus (Clark 1934, Pike and Boaz 1972).

According to Nalbandov (1958), if the timing is proper and adequate quantities of viable sperm are present, fertilization rates of many multiparous animals approach 100 percent. Higher nutrition seems to have a slight but positive effect upon fertilization and implantation rates (El-Shiekh _et_ _al_. 1955, Edey 1970, Hill _et_ _al_. 1970).

Although evidence from numerous studies with various animals is conflicting, it appears possible that a higher plane of nutrition may actually decrease embryo survival.

To summarize: while nutrition affects all aspects of the reproductive process, its most significant impact is upon the number of females, particularly yearlings, breeding and upon the number of ova shed.

Knowlton (1972) suggested that, although productivity of coyote populations could be increased by increasing litter sizes, pregnancy rates of females, especially 10-month old pups, might be the reproductive variable having the greatest impact. Hence, the role of nutrition in determining the potential productivity of yearling females could be important.

Mortality

Our knowledge of causes and magnitude of natural mortality in carnivore populations is limited. Several studies suggest that survival of young may be linked directly to available food supply. Nellis et al. (1972) reported that lynx kitten survival from birth until winter ceased during three years of low hare densities. Schaller (1972:190) claimed that 28 percent of African lion cubs 6-12 months old in one area of Serengeti died of starvation. Wolf (Kuyt 1972) and arctic fox (Macpherson 1969) pup survival in northern Canada were directly correlated with local densities of prey. Van Ballenberghe et al. (1975) reported a pup mortality rate of 56 percent in the first seven months of life for an unexploited wolf population in northeastern Minnesota. They suggested that food availability may be an important factor influencing post-natal pup mortality. Kruuk (1972:61) found two 1-month-old and one 2-month-old spotted hyaena cubs which died of starvation.

Knudsen (1976) reported that differences in jackrabbit availability during 1972-74 did not account for observed differences in coyote pup mortality rates. He pointed out, however, that this finding (in contrast to the studies cited above) may result from having only two years of data. Murie (1940) observed numerous coyotes in Yellowstone during the winter which appeared emaciated and tentatively classified cause of death of several coyotes found in January and February as starvation.

Knowlton (1972) suggested that in Texas some post-whelping pup mortality occurs but that mortality of very young pups is low. His speculation involved a hypothetical unexploited population that had stabilized with the environment. This aspect of coyote ecology remains obscure, however, and research on truly unexploited populations is needed.

Movements

Egress from an area by a substantial segment of a population, if not compensated by ingress, can reduce local densities. This may be a response to environmental stresses such as deep snow, reduced food availability, or other factors.

Tagging studies (McLean 1932, Hawthorne 1971) suggest that in areas of heavy winter snowfall, residence by coyotes is seasonal, with altitudinal spring and fall migrations. Robinson and Cummings (1951) concluded that about half the tagged coyotes resident in summer in Yellowstone National Park moved to lower areas during fall, before heavy snows and prior to ungulate migrations. But half of these returned in late winter and early spring.

In central Alberta, where coyotes were dependent upon livestock carrion during the winter, Todd and Keith (1976) tested the hypothesis that elimination of this food source would reduce winter coyote density through egress. Since the coyote density-winter food base relationship there resembles that in Jackson Hole, a review of their findings might be instructive.

Coyotes on the Alberta experimental areas responded to carrion removed in 1972-73 by increased use of meadow voles and snowshoe hares. Egress resulted in a major decline of the initially high coyote population on one township by mid-winter. High coyote numbers on the two control (no carrion removal) townships dropped sharply after mid-winter, again presumably through egress.

In 1973-74, due to deeper snow and scarcity of native prey, coyotes were more reliant upon livestock carrion. Major coyote responses to carrion removal evidently occurred before early winter. The control areas held greater coyote densities over winter, 19.0 vs. 12.4 coyotes per township. Coyotes remaining on the carrion-free areas were consistently more widely dispersed. Todd and Keith believed that transient members of the winter coyote population were most affected by carrion removal.

Synthesis

One goal in population ecology is to discern and characterize environmental factors that maintain equilibrium and/or determine mean density, two distinct but related demographic features (c.f. Wagner

1969). My investigation focused primarily on the influence of food upon the relative level of coyote populations in three areas.

Animals require energy in the form of food for body maintenance and growth as well as reproduction. Hence, the functional response of coyotes to changes in their food base may be considered a prelude to the numerical response. Efficiency in predicting numerical responses of coyote populations may depend, in part, upon the variability of their functional response.

Studies of coyote food habits in Jackson Hole (O. Murie 1935) and in Yellowstone National Park (A. Murie 1940) disclosed feeding patterns similar to those of the present study (Table 22).

Summer scats were more prevalent than winter ones in Olaus Murie's work, while Adolph Murie's collection covered the April to November period. Their data has been re-calculated to facilitate direct comparisons.

The major differences between their findings and mine were the higher percent of ground squirrels and lower percent of ungulates and lagomorphs in the present study. The Murie brothers attributed the low consumption of ground squirrels to their scarcity on their study areas. The higher percent of ungulates in the diet of Yellowstone coyote may be due to a great abundance of elk. Long-time Jackson Hole residents state that lagomorphs, especially jackrabbits, have not been common since the 1940's.

In some northern states across the country, coyotes are dependent upon carrion for energy during winter because few other foods are

Table 22. Coyote food habits in Jackson Hole (this study and Murie 1935) and Yellowstone National Park (Murie 1940), Wyoming. Sample sizes in parentheses.

Group and Species	Percent of Vertebrate Items		
	Jackson Hole		Yellowstone Nat. Park
	This Study (2557)	Murie 1935 (1772)	Murie 1940 (7672)
MAMMAL	95	96	97
Rodent	84	72	71
Pocket gopher	26	21	25
Ground squirrel	20	1	1
Field vole	34	29	40
Other[a]	4	21	5
Ungulate	10	13	21
Elk	7	9	19
Mule deer	1	1	1
Other[b]	2	3	1
Lagomorph and other mammals	1	11	5
BIRD	5	4	3

[a] Snowshoe hare, marmot, muskrat, porcupine, beaver, deer mouse, jumping mouse, weasel.

[b] Antelope, moose, bison, domestic cow.

available (Murie 1940, Ozoga 1963, this study). Differences in coyote numbers between areas of Jackson Hole have been attributed primarily to differences in abundance of ungulate carrion during winter.

Food abundance may have influenced coyote natality, mortality, and/or movements. Coyotes in Jackson Hole breed during February and March (Camenzind unpubl. data, Tzilkowski unpubl. data). Availability of ungulate carrion at that time may vary with severity of the winter. In areas or years of low carrion supply, coyotes may leave before breeding season. Of those remaining, fewer females--especially yearlings--may breed successfully. Some coyotes may perish from starvation or other causes whose effect has been potentiated by undernutrition (Sinclair 1977).

Without compensation between these agents of population change, we may find large differences in coyote abundance between areas or years of low and high carrion supply.

In areas where the biota is more diverse and available year-round, however, responses by coyotes may be quite different. The ability of coyotes to switch to alternate foods may assume greater importance.

My data on this aspect of coyote behavior are not unequivocal (Fig. 12). Following the aestivation of Uinta ground squirrels, coyote predation upon field voles and northern pocket gophers did not intensify. Consumption of fruit and ungulate, though, did increase as they became more available. Perhaps the cost-benefit ratio in energy for securing them is less than for rodents.

Hence, both the abundance and temporal availability--whether a single key species or the total array--of food may influence coyote numbers. The full range of coyote population responses to food resources awaits further investigation.

Summary

Coyote-food base relationships were investigated on a 550-km^2 area in Jackson Hole, Wyoming, from July, 1973, to July 1975. Prey indices, coyote scats, and coyote indices were obtained along three

24.5-km lines. Relative abundance of summer food was estimated from snap-trapping of various rodents, mound counts and subsequent trapping of pocket gophers, and flushing counts of grasshoppers. Ungulate carrion available during fall and winter was estimated from records compiled by agency biologists and personal observations in the field. Coyote feeding patterns were assessed by collecting scats monthly from May to November, and January to March, and analyzing them in the laboratory, and by snowtracking coyotes January to March. Feeding experiments with captive coyotes aided interpretation of food habits. Standard carnivore scent-station surveys and scat collection rates provided indices of coyote abundance.

Considerable areal and seasonal variation in biomass of rodents trapped occurred along the three lines. Shadow Mountain provided the greatest amount, followed by the Potholes and the National Elk Refuge. Deer mice and chipmunks accounted for 75 percent or more of the fall biomass along all lines. A two-fold increase in biomass occurred in spring 1974 along Shadow Mountain and the National Elk Refuge due to ground squirrel abundance above ground. Rodent biomass decreased along each line from fall 1973, to fall 1974. Field voles had declined throughout much of the study area by June, 1974. Calibrated counts of pocket gopher mounds revealed that gophers were most numerous along the Shadow Mountain line, less on the Potholes, and least on the National Elk Refuge. Grasshoppers occurred in greatest densities on the Refuge. Carrion from hunter-killed elk in the fall was most abundant on Shadow Mountain, but much of it (rumen contents, skull, leg bones) may not have been edible. Most of the elk carrion available during winter was concentrated on the National Elk Refuge.

Pocket gophers, field voles, and ground squirrels dominated the coyote summer diet, though their relative occurrence varied between lines. Grasshoppers and fruit were frequent in scats during August and September. Coyotes depended upon ungulate carrion during winter, but they can survive for weeks on little fresh food. When weight and detectability relationships between prey species are different, food habits data should be converted to a biomass basis.

Coyotes may not have fully compensated, energy-wise, for the aestivation of Uinta ground squirrels, a principal component of their summer diet. The number of field voles per coyote scat decreased following a major decline in vole abundance.

Both a composite index and its two constituent indices suggested that coyotes were most abundant on the National Elk Refuge, less numerous on Shadow Mountain, and least common on the Potholes. Short-term variations in coyote abundance occurred.

Differences in relative coyote densities between areas were attributed primarily to differences in ungulate carrion available during winter. Summer food resources seemed less influential.

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