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A winter study of coyote predation on white-tailed deer in the Miller Creek drainage Montana

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A WINTER STUDY OF COYOTE PREDATION ON WHITE-TAILED DEER IN THE MILLER CREEK DRAINAGE, MONTANA

By

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ABSTRACT

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A Winter Study of Coyote Predation on White-tailed Deer in the Miller Creek Drainage, Montana (50 pp.)

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Quantitative data on predation of white-tailed deer (Odocoileus virginianus) by coyotes (Canis latrans) were obtained by investigating deer carcasses from January to March 1975, December 1975 to March 1976, and December 1976 to March 1977. Tracks and necropsies of 23 carcasses revealed that 11 (48%) were definitely killed by coyotes; 8 (35%) were probably killed by coyotes, and 4 (17%) died from unknown causes. One mule deer (Odocoileus hemionus) was killed by a cougar (Felix concolor). Neither parasites, disease, nor malnutrition were important contributing factors. Deer from 3 to 7 years old were most vulnerable; fawns were slightly more vulnerable to coyotes than to hunters, and coyotes killed no yearlings or 2-year-olds. Coyote selection of one sex over the other was not proven. Deer appeared to be most vulnerable to coyote attacks when running downhill. Neither deep nor crusted snow were requirements for successful coyote attacks on deer.

An analysis of 74 coyote scats revealed that deer (55%), meadow voles (Microtus sp.) (32%), and snowshoe hares (Lepus americanus) (19%) were the most frequently occurring food items.

Analysis of meadow vole activity, measured with kerosene-smoked track boards from December 1976 to March 1977, revealed that rodent activity was directly related to minimum temperatures (r^2=.73) and inversely related to percent snow cover (r^2=-.60).

Coyotes killed most deer when rodent activity and minimum temperatures were low and percent snow cover was high, suggesting that coyotes expend more effort to kill deer when rodents are least available.

Browse utilization and pellet group data suggested that the deer population decreased from 1965 to 1977, coincident with the growth of a subdivision at the lower end of the drainage, increased hunting pressure, increased meat prices, and the 1972 presidential order limiting the use of toxicants for predator control.

ACKNOWLEDGMENTS

This section of the thesis was the most difficult to compose, because so many people and organizations contributed to the final product. Some probably feel that their contribution was minimal and therefore inconsequential. However, the help of each, though different, was of great consequence to me, and I am forever grateful.

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John Claxton, Richard Koenig, Richard Mace, James Solomon and John Strank were field assistants par excellence during the 1976-77 winter field season.

Tim Duffner's steady hand drew the maps illustrating the study area, locations of kill sites and areas of intensive search.

My wife, Meg, gave me courage and lent an editorial expertise that made what little I had to write understandable.

And, of course, there were the wild animals that made their living in the Miller Creek drainage. The coyotes and white-tailed deer tried to stay out of my way and, in doing so, gave me a great education and a deeper appreciation of life. My greatest mentors died between January 1975 and April 1977, and I thank them the most.

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CHAPTER I

INTRODUCTION

Few topics generate a more heated debate in the western United States than coyote predation. Coyote predation on white-tailed and mule deer constitutes one facet of the debates. Reports of coyote predation on deer are common in some areas, and uncommon in others.

Conflicting opinions vary from the conviction that coyotes control or even decimate deer populations, to the equally sincere belief that the 30-pound canid is incapable of killing any but the weak, starving, sick, young or aged deer. The conditions claimed necessary for coyotes to kill deer are equally diverse. While some believe that deep crusted snow and iced-over waterways must exist to give coyotes an advantage over the deer, others maintain that snow conditions and topography are irrelevant.

Leopold (1933:231) offered one of the earliest classifications of factors influencing predation on game animals. He suggested the following five groups of factors:

1) density of the prey population;
2) density of the predator population;
3) food preference of the predator;
4) physical condition of the prey and the facilities of escape available; and
5) availability of alternative prey or food items.

In reviewing many studies on predation, Holling (1961) developed a partial theory of predation. Predator and prey densities were universally present components of every predator-prey relationship. Predator characteristics, prey characteristics and environmental factors were "subsidiary variables" which might or might not affect a particular predator-prey relationship.

Biologists studying coyote behavior have concentrated on food preferences as indicated by scat and/or stomach analyses. Coyote diets varied seasonally (Sperry 1933 and 1934, Murie 1935 and 1945, Murie 1940, Tiemeier 1955) and geographically (Murie 1935 and 1945, Bond 1939, Murie 1951, Korschgen 1957). Coyote food habits were also related to habitat (Ozoga and Harger 1966, Reichel 1976), predator density (Clark 1972), prey density (Horn 1941, Clark 1972), and prey behavior (Murie 1940). Several studies specifically reported coyote predation on white-tailed deer (Aiton 1938, Ozoga and Harger 1966, Cook et al. 1971, Ogle 1971, Knowles 1976). Horn (1941), Cook et al. (1971), Trainer (1975) and Knowles (1976) indicated that coyote predation could be limiting the deer populations they studied.

For the past 10 years, ranchers along Miller Creek in western Montana have noted apparently heavy winter predation on white-tailed deer. Concurrently, they believed the deer population was declining and coyote numbers were increasing. Their concern precipitated this study.

During the winter of 1974-75, Metzgar and Prather investigated dead deer reported by Miller Creek-area ranchers. I expanded the investigation during the two succeeding winters and have integrated the data collected by Metzgar and Prather in this report. The specific objectives of this study were to:

1) document the occurrence of coyote predation on white-tailed deer;
2) describe strategies used by coyotes to kill deer;
3) determine factors used by coyotes for selecting individual deer for prey;
4) relate rates of predation on deer to availability of alternate prey items;
5) relate rates of predation to weather and snow conditions;
6) relate rates of predation to changes in deer and coyote densities; and
7) relate predation to topographical and habitat characteristics.

While these data cannot identify the importance of coyote predation on deer, the identification of conditions which permit predation tell us where and when it can occur. It is hoped that the predictive value of this and similar studies will contribute to a flexible and realistic game management policy.

CHAPTER II

DESCRIPTION OF THE STUDY AREA

Location and Topography

Miller Creek drains about 28,000 acres of the northwestern corner of the Sapphire Mountains in western Montana. The creek begins at the Bitterroot Divide, flows northwesterly, and empties into the Bitterroot River south of Missoula (Fig. 1).

Intermittent and permanent secondary streams, fed by springs and runoff, flow into Miller Creek from the east and west. These streams course through deep canyons, with slopes commonly between 40 and 100 percent.

In the area of the most intensive study, elevations range from 1,159 to 2,144 m. Rock outcroppings are numerous, and soil depth is generally shallow.

Vegetation

Coniferous forest covers most of the area. Variations in slope and aspect combine to produce striking contrasts in vegetative cover and composition.

Open stands of ponderosa pine (*Pinus ponderosa*) dominate steep slopes with southern and western aspects. Common understory species are bitterbrush (*Purshia tridentata*), serviceberry (*Amelanchier alnifolia*), ninebark (*Physocarpos malvaceus*), bluebunch wheatgrass (*Agropyron spicatum*), Idaho fescue (*Festuca idahoensis*), and arrowleaf balsamroot (*Balsamorhiza sagittata*).

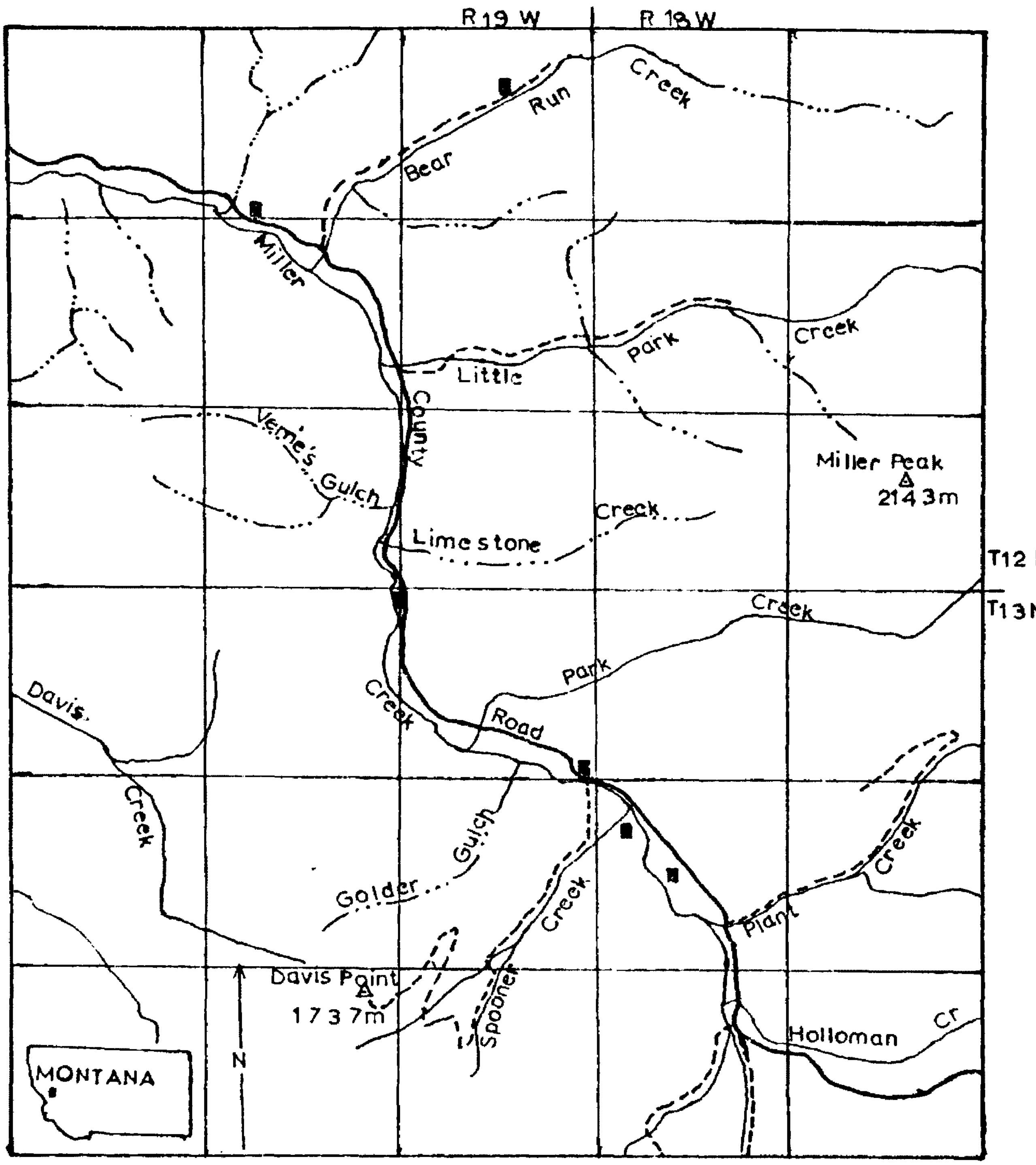


Fig. 1. Map of the study area

Scale
0 .5 1 mi
0 .5 1 1.5 km

■ Home site
—— Improved rd.
------ Unimproved rd.

In contrast, relatively dense stands of Douglas-fir (Pseudotsuga menziesii), western larch (Larix occidentalis), and Engelmann spruce (Picea engelmannii) dominate northern and eastern aspects, as well as the gentle lower slopes with southern and western exposures. Common understory species in these areas are mountain maple (Acer glabrum), snowberry (Symphoricarpos albus), bearberry (Arctostaphylos uva-ursi), creeping Oregon grape (Berberis repens), pinegrass (Calamagrostis rubescens), elk sedge (Carex geyeri), and ninebark.

Because most of the secondary ridges have an east-west orientation with steep northern and southern exposures, these two forest types are distinctly separated along many ridges. Similarly, stream bottoms provide generally narrow ecotones between these two forest types. In stream bottoms, a narrow band of riparian species intermingles with the conifers. Redosier dogwood (Cornus stolenifera), Douglas hawthorne (Crataegus douglasii), thinleaf alder (Alnus tenuifolia), and mountain maple are conspicuous stream-side species.

Superimposed on the area are successional stages induced by fires, logging and grazing. Stands of mature lodgepole pine (Pinus contorta) and western larch saplings mark sites of old fires. Clearcut logging practices have left patches of western larch and Douglas-fir seedlings to grow among piles of slash. Selective logging thinned many ponderosa pine and larch stands. In addition, the extensive logging has ribboned the area with roads and skid trails.

Ranching has left its mark in the area. After homesteading the drainage in the 1880's, ranchers cleared areas with broad fertile stream bottoms and planted exotic graminoids and legumes for hay and winter pastures. Heavy localized grazing by cattle and horses has altered the composition of native species.

Climate

From 1975 to 1977, winter conditions were relatively mild. From December through March, most daytime temperatures were between 0° and -10° C. Winds were infrequent and of low velocity. Snow depths seldom exceeded 30 cm, and steep southern exposures were often free from snow. Ice covered large sections of Miller Creek and its tributaries.

Wildlife

Wintering big game included white-tailed deer at lower elevations, and a few elk (*Cervus elaphus*), moose (*Alces alces*), and mule deer at higher elevations. In addition to the coyote, medium and large-sized predators are sparsely represented by a few bobcats (*Lynx rufus*), cougars, and golden eagles (*Aquila chrysaetos*).

Human Use

The proximity of the Miller Creek drainage to Missoula, a metropolitan area with about 50,000 people, and easy access along a well-maintained county road have made the drainage a popular area of human use. A small subdivision is growing rapidly at the mouth of Miller Creek canyon. During big game hunting seasons, a steady stream of hunters flows through the area. Snowmobiling, target practice, "beer busts," cross-country skiing, trapping, fishing, hiking and camping are other common activities.

Coyotes are shot at regularly throughout the year and trapped during winter, M-44 coyote-getters have been located at one ranch since April 1976.

Most land at lower elevations is privately owned. The remainder is administered by the Lolo National Forest, U.S. Forest Service.

CHAPTER III

MATERIALS AND METHODS

Searching for Dead Deer

Metzgar and Prather began the study in December 1974 by asking Miller Creek ranchers to report dead deer. In January 1975, ranchers in the drainage began notifying them of the discovery of deer carcasses, most of which were near roads. Ranchers reliably reported the locations of carcasses through April 1977.

Concentrating on a small portion of the drainage (Fig. 2), I conducted weekend searches on foot and snowmobile from mid-January through March 1976. Beginning in mid-December 1976, field assistants and I searched portions of the drainage between 5 and 7 days each week and, when snow conditions permitted, trailed coyotes on foot. This search method was continued through March 1977.

Necropsies

Deer carcasses were examined for parasites, size and location of wounds and hemorrhages, condition of articular surfaces of joints, extent of body fat, and abnormalities of skeletal muscles and internal organs.

When possible, femurs were collected and the color and texture of the marrows were recorded (Cheatum 1949). During the second and third winters, I also recorded percent compression of each marrow (Greer 1968). Deer that had white, firm marrows with less than 2 percent compression were assumed to be healthy.

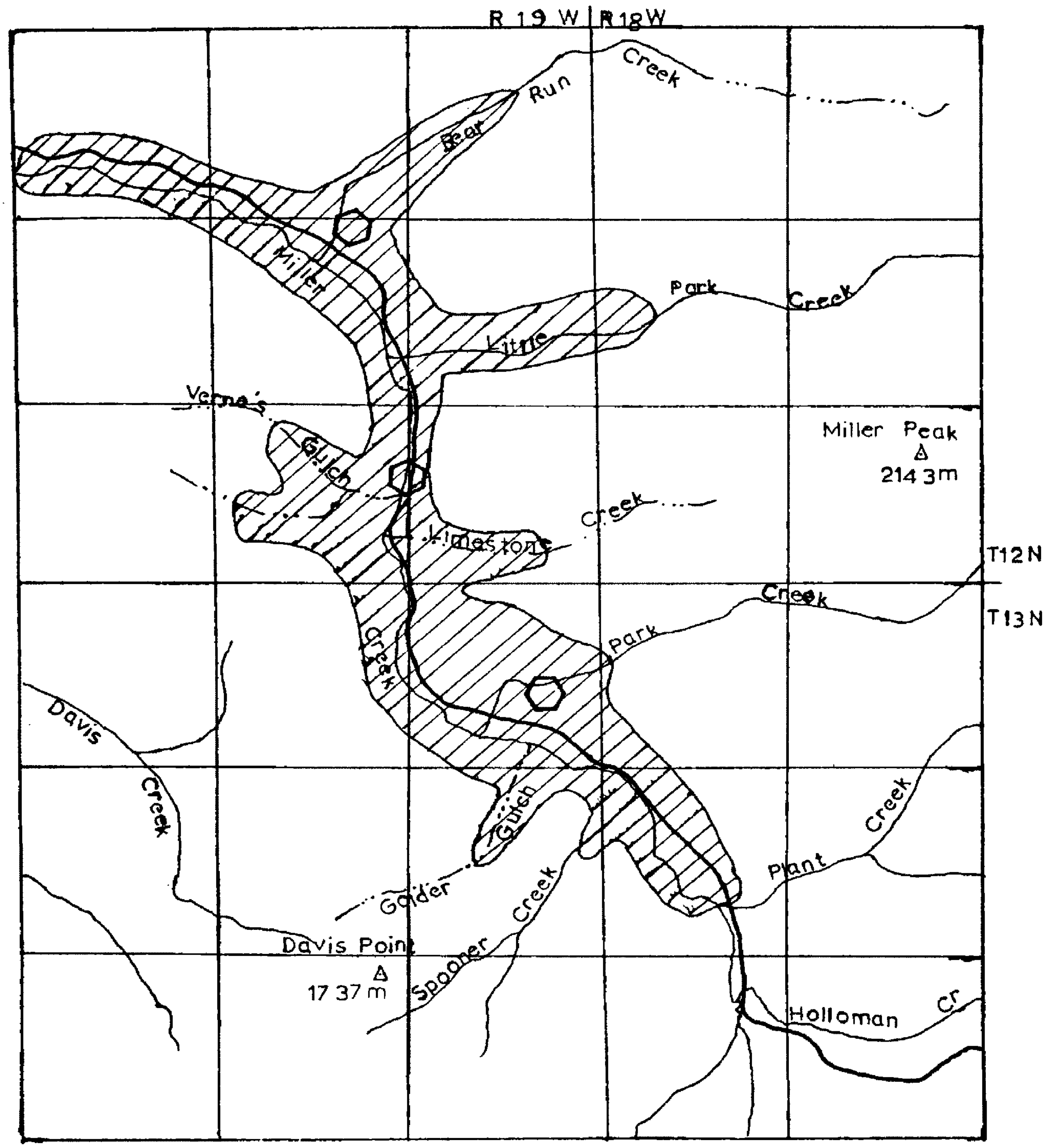


Fig. 2. Locations of intensive search and short snow courses.

Short snow course

Area of intensive search

When possible, lower jaws were collected. The ages of the deer were determined by comparing development and wear of teeth to a collection of known-age jaws and by working with the description of Severinghaus (1949). The presence or absence of antler pedicels and/or suspensory tuberosities on the pelvic girdle (Taber 1956) were criteria for sexual classification of a deer carcass.

Kill Classifications

At the kill site and along chase routes, the locations of deer and coyote tracks, blood spots, deer parts, topographic and cultural features, and major vegetal components were noted and mapped for later reference. Also recorded were snow and weather conditions, and the estimated times of death of the deer.

On the basis of the evidence collected, we classified all dead deer into four categories.

1) Definite coyote-kill: skin punctures and subcutaneous hemorrhaging in the face, throat and hindlegs, associated with coyote tracks along a chase route.
2) Probably coyote-kill: evidence of violent death (e.g., blood-soaked snow, broken brush, far-flung patches of hair and hide, etc.) present with tissue removed from carcass and chase route obscured by feeding activities of coyotes and birds.
3) Possible coyote-kill: coyote tracks associated with the carcass but evidence of violent death and the chase obscured or absent.
4) Mountain lion-kill: punctures and hemorrhaging in dorsal part of neck, crushed cervical vertebra, carcass buried

under twigs and snow, cougar tracks present. One 2½-year-old mule deer buck was in this category.

Temperatures

From mid-January through March 1976 and from early December 1976 through March 1977, I recorded temperatures on 3 consecutive days each week from a maximum-minimum thermometer located in the Miller Creek drainage at about 1,160 m in elevation. Regression analysis of 84 minimum temperatures recorded in Miller Creek and of those recorded in Missoula by the U.S. Weather Service on the same dates revealed a high correlation (r^2=.86) and indicated that Miller Creek (Y) temperatures were consistently lower than Missoula (X) temperatures ($Y=.91X-5.03$). This high correlation permitted an evaluation of the dates of coyote predation on deer in terms of minimum Missoula temperatures for all three winters.

Coyote and Deer Populations

From mid-January through March 1976 and from early December 1976 through March 1977, I attempted to measure changes in coyote and deer densities. In this effort, I counted fresh deer and coyote tracks crossing three short snow courses on 3 consecutive days each week. At those times I also estimated the percent of ground covered by snow. Each snow course was 1.1 km long and hexagonal in shape with 183 m on a side. For the sake of convenience, they were distributed approximately 2 km apart along the county road (Fig. 2). They included stream bottoms, ridges, and portions of north and south-facing slopes.

Attempts to use standard U.S. Fish and Wildlife scent posts to census the coyote population failed. Condensation and freezing at night apparently reduced the effectiveness of the synthetic scent.

A long snow course (8 km) provided supplementary track data on deer and coyotes. This course was covered on foot or snowmobile on 2 consecutive days each week during the last two winters of the study.

Rodent Activity

By using track boards, I measured rodent activity during the last 4 weeks of the second winter and for 15 weeks the third winter. Each board was a kerosene-smoked aluminum plate (15 cm X 7.5 cm) placed in a wooden shelter. I set out 18 boards at a time, one located along each of the six segments of each of the three short snow courses. On 2 consecutive days each week, fresh track boards were distributed and those set out the previous day were collected. When fresh boards were put out, I moved each station about 10 m to minimize rodent habituation and baited the board with rolled oats. The genus of rodent leaving tracks was recorded, and the number of boards each genus tracked was calculated for the 2-day period. A total of 36 track boards was available as a weekly index of rodent activity. Rodent activity, in terms of the number of boards tracked each week, was later compared with minimum Miller Creek temperatures, estimated percent snow cover along short courses, and dates of coyote predation on deer.

I did not use rodent activity data collected from 28 February to 28 March 1976 in this paper because 1) only one deer carcass was found during that time, 2) the data could be related only to snow cover and minimum temperatures during that study period, and 3) the manner of locating and baiting stations was modified during that time.

Coyote Scats

During the last winter of the study, coyote scats were collected along regularly traversed circuits. Later, in the laboratory, the scats were soaked in water, washed over a sieve, and air-dried. I used standard techniques to identify hair (Moore et al. 1974) and teeth and skull fragments (Hoffman and Pattie 1968) and calculated percent frequency of occurrence of identifiable remains.

CHAPTER IV

RESULTS

Predation

Coyotes definitely killed 11 (48%) of the 23 deer carcasses investigated during the three winters, and probably killed another 8 (35%). The remaining four deer (17%) were classified as possible coyote victims.

During the first winter, there were five definite, three probable, and one possible coyote-kills. One definite and two probable coyote-kills were found in the second winter. During the third winter, when search activities were most intensive, I found five definite, three probable, and three possible coyote kills. All carcasses were found in a small portion of the drainage (Fig. 3).

Chase sequences. Backtracking the coyotes' entire approach and chase was possible for only three kills. Coyotes approached the deer from higher elevations, walking slowly at first, stopping occasionally, and then rushing the deer. Coyotes came to within 9, 25, and 91 m of tracks of standing deer, and then ran 101, 185, and 585 m, respectively, before making the kill. For the three sequences, coyotes ran an average of 45 m further than the deer.

Backtracking the deer's entire flight was possible in five sequences. The five fleeing deer ran between 71 and 494 m, averaging 178 m, before succumbing to the coyotes' attack. In six other sequences, where the initial segments of both flight and chase routes were obscured

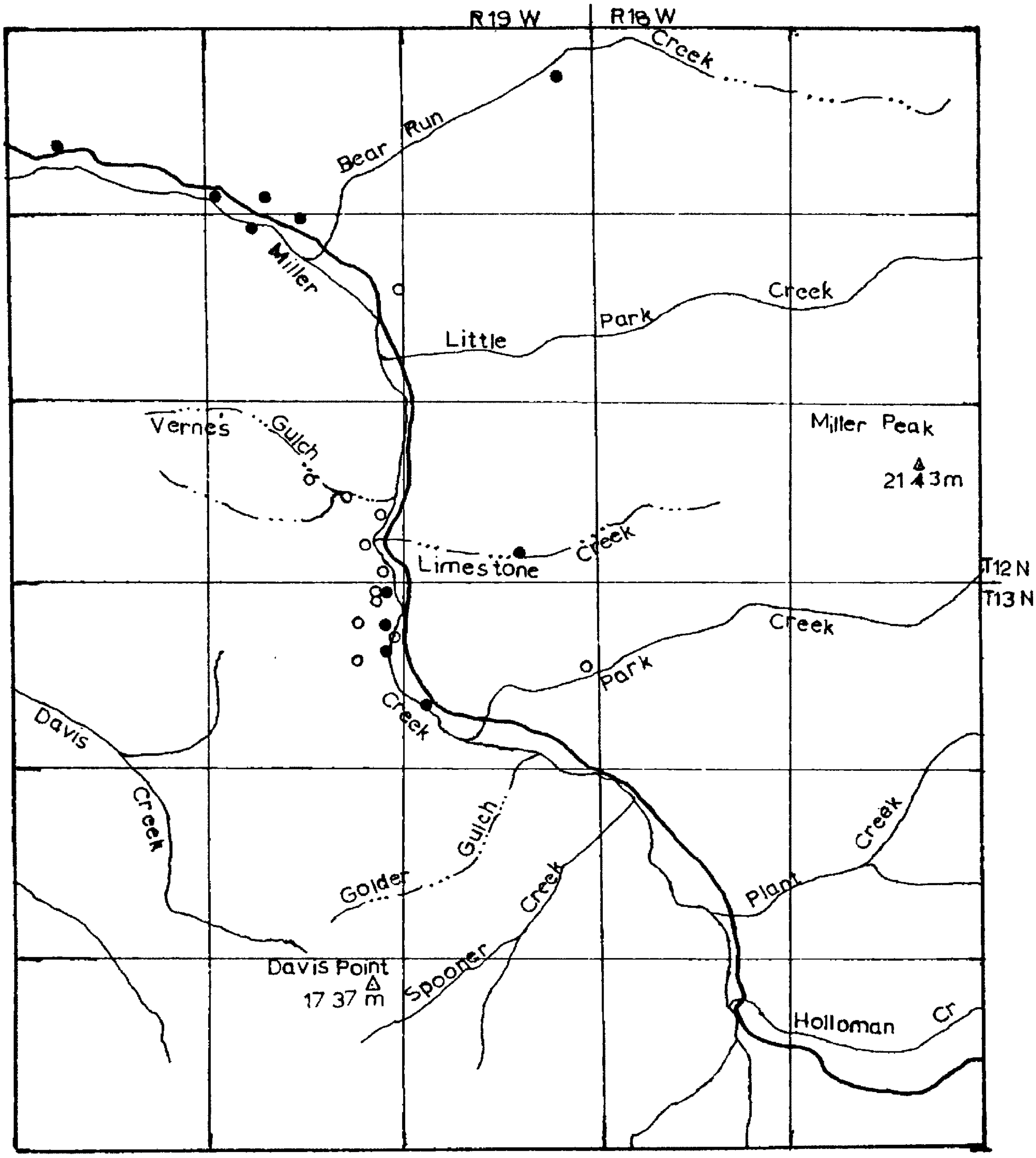


Fig. 3. Location of white-tailed deer carcasses

● Definite coyote-kill site

o Probable or possible coyote-kill site

by subsequent tracking or bare ground, deer and coyotes ran from 46 to 594 m in the snow before the deer was killed.

Comparatively short chases characterized three unsuccessful attacks I recorded while trailing coyotes. In all three instances, coyotes ran upslope toward deer, but stopped running in less than 18 m, as the deer fled uphill.

Tracks along five chase routes clearly revealed that two coyotes made three of the kills; one coyote, one kill, and three coyotes, one kill. In the six other known coyote-kills, two-to-four coyotes made the attacks, but obscured tracks made it impossible to determine their exact number. When more than one coyote attacked and the deer started to turn, one of the coyotes continued a direct pursuit of the deer, while another quartered across the arc to intercept.

In five of the definite coyote-kills, the initial rush of the coyotes was directed toward a lone deer three times, at two deer once, and at seven deer once. In the six other sequences, it appeared that single deer were attacked, but tracks in the area of the initial attack were not clear.

In 10 of the 11 definite coyote-kill-chase sequences, the deer fell at least once, leaving blood and/or hair on the snow or ground, and resumed running before being killed.

Coyotes killed the 11 deer under a variety of snow conditions. One deer was killed with no snow cover; eight when snow was soft and between 0.25 and 18 cm deep, and two, on the same night, in 61 cm of snow, with a crust strong enough to support running coyotes, but not running deer.

Kill sites. Snow at the kill sites was invariably sprayed with bright red blood, and the hot blood draining from the dead or dying deer melted dark red spots into the snow.

Numerous coyote trails radiated from even the very freshly killed deer carcasses, making it difficult to determine the number of feeding coyotes, and sometimes obscuring details along the chase routes. The estimated numbers of feeding coyotes ranged from three to eight at each of the 11 definite-kill sites. Deer hair, hide, blood spots, bones, and packed snow were along the trails where the coyotes had lain feeding. Coyote feces and urine spots were present in quantity around the carcasses and other feeding sites. These signs, associated with rapid and nearly complete consumption of deer definitely killed by coyotes, also appeared at the sites of probable and possible coyote-kills.

The parts of the carcass usually remaining at the kill site included the rumen, small intestine, upper neck and head muscles, vertebral column and attached ribs, portions of the hide, and some long bones with some muscle tissue. Lungs were recovered from only four carcasses. The heart, lungs, kidneys, spleen, and genital tract were present in only one animal investigated. Ham, shoulder and lower neck muscles were often fed upon extensively. It appeared that viscera were eaten first, then the large skeletal muscles.

Vegetation and topographic features. We recorded vegetation and topographic features along the 11 chase routes, even when the detailed chase sequence was obscured. Along nine of the 11 routes, coyotes chased deer downhill (30-to-70% slopes), killing four deer on the steep hillsides and five on flat bottoms at the base of hills. Coyotes chased and subsequently killed the two other deer on relatively flat terrain (1-to-10% slopes); however, in both cases, the chase forced the deer, at some point, to jump down a steep cut to the road about 1.8 m below.

Coyotes chased eight of the 11 deer out of open ponderosa pine stands, killing two in dense riparian shrub growth and six in open hay meadows. After chasing the other three deer through dense Douglas-fir stands, coyotes killed one of them in an open pasture, one in dense conifer cover, and one in a driveway 18 m from a ranch house.

Deer are known to have resisted the coyotes' attack in only two of the 11 definite kills. Both deer, after being wounded along the chase route, made unsuccessful stands against at least two circling coyotes.

Five (45%) of the definite coyote-kills, six (75%) of the probable kills, and two (50%) of the possible kills were within 15 m of a stream. Two of the five deer definitely killed by coyotes lost their footing while trying to cross an iced-over stream and were killed at the stream's edge.

Coyotes killed five deer after chasing them over at least one barbed-wire fence. Two of these carcasses lay next to fences, with deer hair wedged between the wire strands.

<u>Times of kills</u>. The time of day coyotes killed eight deer was estimated on the basis of ranchers' observations, track records, weather conditions, and our own observations in the area. Four kills occurred between 10 p.m. and 5 a.m.; two between 6 and 8 a.m.; one between 8 and 9 a.m., and one between 3 and 6 p.m.

The times of death of three other definite kills were estimated within 24 hours. And, I believe we correctly estimated the time of death within 48 hours for all probable coyote-kills, and within 7 days for possible coyote-kills.

Necropsies

Necropsies of 23 carcasses revealed punctures and hemorrhages in the head, neck, or rump regions of the 11 definitely coyote-killed deer. Although coyotes attacked all three regions of five deer, coyotes wounded only the throat and head regions of four, and just the rump regions of two. Blood in the mouth, nose, trachea, or lungs was common for deer which had been attacked in the neck and head regions. A doe, probably killed by coyotes, found in a creek had water-filled lungs and punctures and hemorrhages in the right flank. In the case of all but one carcass, that of a healthy fawn freshly killed by coyotes, bird and coyote feeding subsequent to the deer's death may have removed some damaged tissue.

The deer examined appeared to have been generally healthy prior to their violent death. The only real exceptions were a 3-year-old doe, definitely killed by coyotes, with a small infected wound in the right ham, and a 6-year-old doe, probably killed by coyotes, with necrotic stomatitis. Although ticks (Dermacentor albipictus) were found on several carcasses, these parasites never appeared in high densities. After the study period, on 30 April 1977, coyotes killed a 5-year-old doe with 27 bot-fly larvae (Cephenemyia phobifera) in her naso-pharyngeal passages. However, no "bots" were found in any of the 23 carcasses examined during the three winters. No evidence of arthropathy was seen in any carcass.

The femurs of 12 deer were collected. Eight were from definite coyote-kills, and four from probable coyote-kills. Eleven bone marrows were white and firm; the marrow from one coyote-killed deer was slightly pink and soft. Of the seven marrows collected during the second and third winters, six compressed less than 2 percent, while the pink-soft marrow, mentioned above, compressed 7 percent.

Sex Ratios

The male:female ratio of 14 known-sex deer carcasses was 1:1. Of the nine known-sex deer definitely killed by coyotes, six (67%) were males and three (33%) were females. All three known-sex deer probably killed by coyotes were females. One deer of each sex was in the possible coyote-kill category.

Comparative data were not available on sex and age structure of the Miller Creek white-tail population. However, of 102 hunter-killed white-tails checked by the Montana Fish and Game Department at nearby Lolo, Montana, during the 1974, 1975 and 1976 fall hunting seasons, 61 percent were males and 39 percent females. The sample size was too small to permit testing the difference between ratios of hunter-killed deer and definitely coyote-killed deer, but the percentages are very similar. A Chi-square test for difference between the ratios of hunter-killed deer and definite and probably coyote-killed deer, combined, revealed no significant difference (X^2=.34, d.f.=1, P=.30).

Age Distributions

The ages of 15 deer were determined by examining the lower jaws. Of the known-age carcasses found, four (27%) were fawns and eleven (73%) were between 3 and 7 years old. There were no yearlings or 2-year-olds. Of the eight known-age deer definitely killed by coyotes, two (25%) were fawns and six (75%) were between 3 and 7 years of age. Coyotes probably killed one fawn and three more deer between the ages of 3 and 7 (Table 1).

The Kolmogorov-Smirnov one-sample test showed considerable difference between the age distributions of hunter-killed deer (Fig. 4a) (Hartkorn and Janson 1975, Firebaugh et al. 1976, and Montana Department Fish Game 1977) and deer definitely killed by coyotes in the study area (Fig. 4b) ($N=8$, $D=.39$, $P<.15$). Furthermore, the age distributions of probable and definite coyote-kills combined (Fig. 4c) and of hunter-killed deer were significantly different ($N=12$, $D=.39$, $P<.05$). The complete absence of 1- and 2-year-old deer killed by coyotes and the presence of 45 percent of the hunter-killed deer in those age categories accounted for the major difference between age distributions. The percent of fawns killed by hunters was slightly less than that killed by coyotes.

Minimum Temperatures

Coyotes killed proportionately more deer on dates with low minimum temperatures. Nearly 73 percent of the estimated dates of death of known coyote-kills occurred when minimum Missoula temperatures were less than -8° C, while only 32 percent of all minimum Missoula temperatures were so low during the three winters (Fig. 5).

The Kolmogorov-Smirnov one-sample test detected a significant difference between the distributions of all minimum Missoula temperatures and minimum temperatures on dates of known coyote-kills ($N=11$, $D=.41$, $P<.05$). The same test applied to the distribution of temperatures on dates of known and probable coyote-kills, combined, and of all minimum Missoula temperatures revealed an even more significant difference ($N=19$, $D=.37$, $P<.01$).

Table 1. Age and sex of definite, probable and possible coyote-killed deer during three-winter study.

Age	Definite			Probable			Possible			Total
	M	F	Unk.	M	F	Unk.	M	F	Unk.	
½	1	1	-	-	-	1	-	-	1	4
1½	-	-	-	-	-	-	-	-	-	0
2½	-	-	-	-	-	-	-	-	-	0
3½	1	1	-	-	-	-	-	-	-	2
4½	1	-	-	-	-	-	-	1	-	2
5½	2	-	-	-	-	-	-	-	-	2
6½	1	-	-	-	2	-	-	-	-	3
7½	-	-	-	-	1	-	1	-	-	2
Unk.	-	1	2	-	-	4	-	-	1	8
Total	6	3	2	0	3	5	1	1	2	23

Fig. 4 Comparison of distributions of age classes of hunter-killed deer from Fish, Petty, and Lolo Creeks (adapted from Hartkorn and Janson 1975, Firebaugh et al. 1976, Montana Dept. Fish Game 1977) (a); definite coyote-killed deer (b); and definite and probable coyote-killed deer (c) for three winter study period.

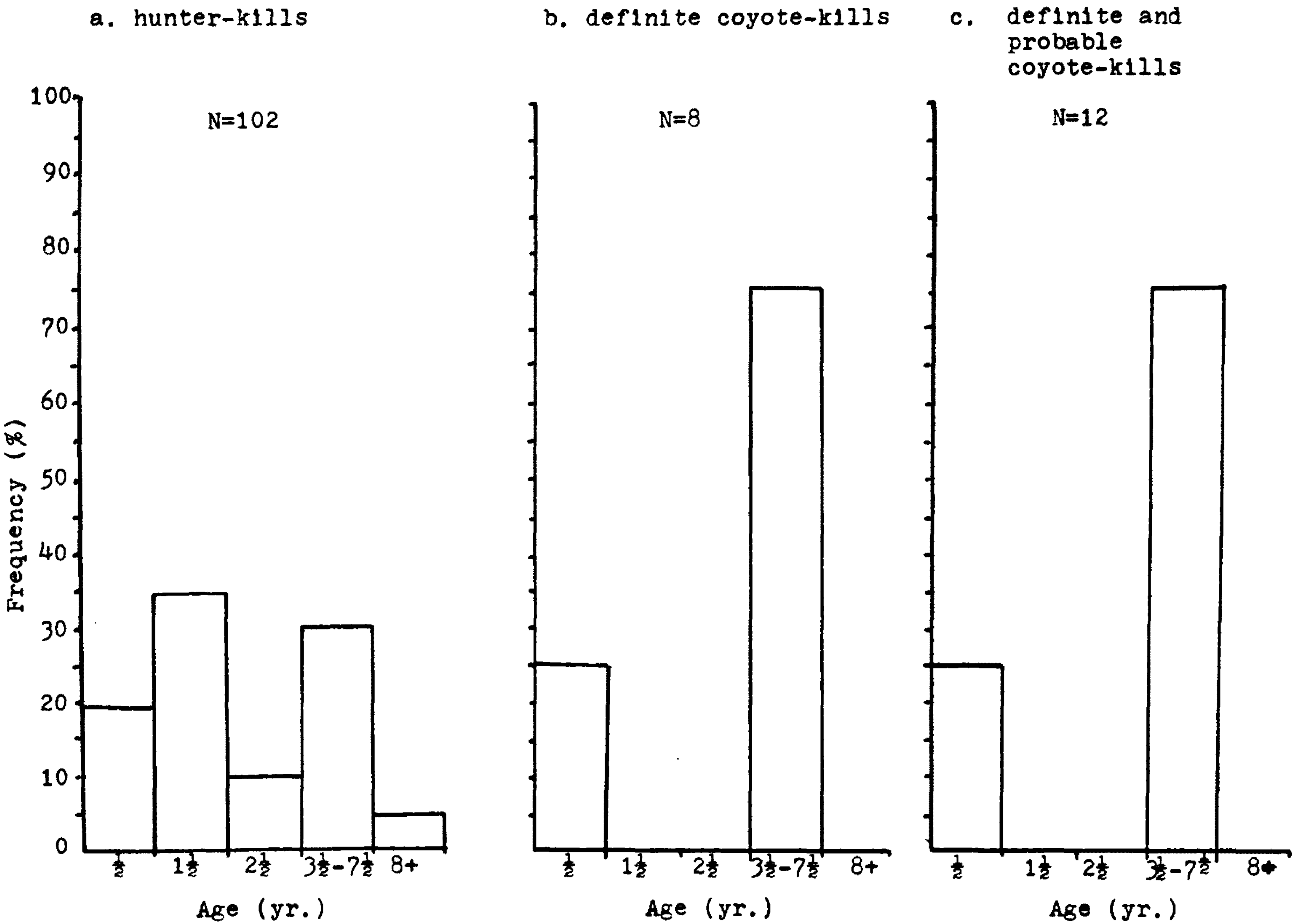
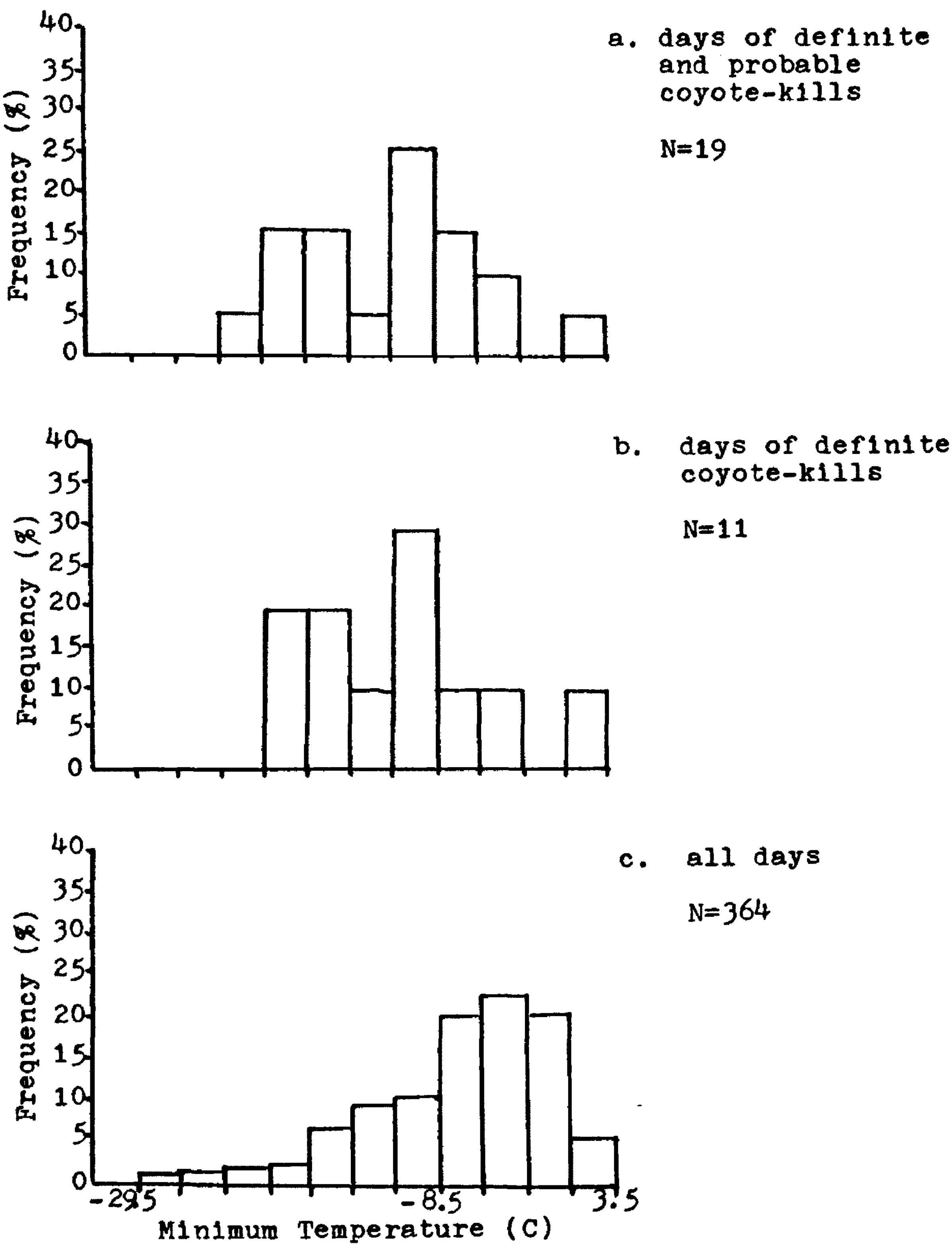


Fig. 5 Comparison of distributions of minimum Missoula temperatures for days of definite and probable coyote-kills (a), days of definite coyote-kills (b), and all days (c) for three winter study periods.



Snow Cover

Snow cover estimates were not made during the first winter of the study, and only one deer was killed while estimates were made during the second. But, during the 1976-77 winter, coyotes killed proportionately more deer on days with high percentages of snow cover. Coyotes killed 50 percent of the deer on days with more than 80 percent snow cover, while snow cover in the study area exceeded 80 percent on only 35 percent of the days sampled (Fig. 6).

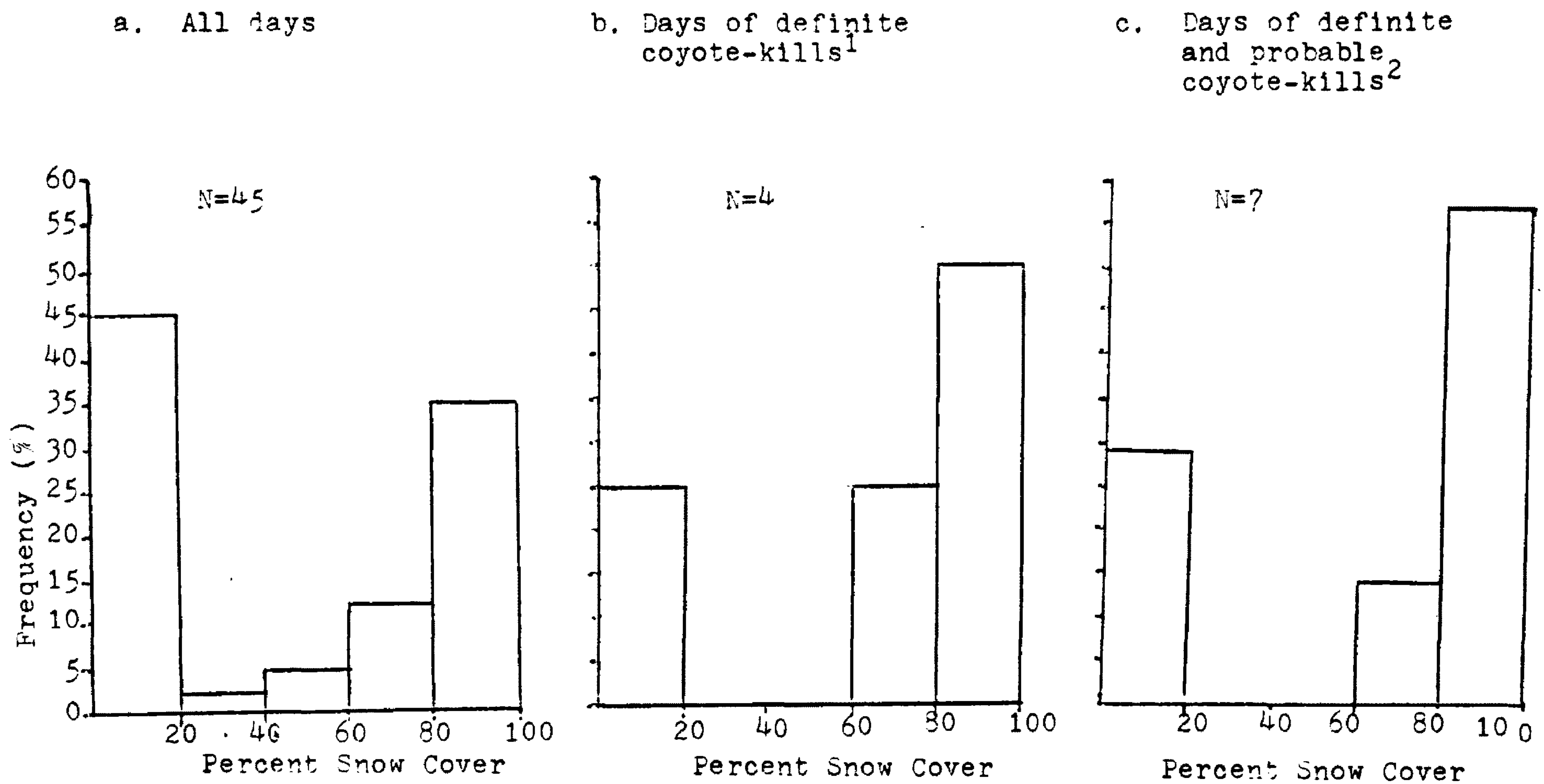
Scat Analysis

During the 1976-77 winter, 74 coyote scats were collected and analyzed. The most frequently occurring items were Odocoileus sp. (55%), Microtus sp. (32%), vegetation (31%), and Lepus americanus (19%) (Table 2). Peromyscus maniculatus (1%), the species most frequently tracking the rodent boards, was not an important food item. Northern pocket gophers (Thomomys talpoides) were present in most of the drainage, but occurred infrequently in coyote scats. Several old cattle carcasses provided some carrion (7%) during the winter of 1976-77.

Rodent Activity

Deer mice and meadow voles tracked the most boards during the 1976-77 winter (Fig. 7). The number of boards tracked by all rodent species for 2-day periods each week was directly related to minimum Miller Creek drainage temperatures (r^2=.73) and inversely related to percent snow cover (r^2=-.47). The number of boards tracked by meadow voles, a major winter food item of coyotes in the Miller Creek drainage, was also strongly related to minimum temperatures (r^2=.73) and percent snow cover (r^2=-.60).

Fig. 6. Comparison of distributions of estimated percent snow cover along snow courses for all days (a), days of definite coyote-kills (b), and days of known and probable coyote-kills, winter of 1976-77.

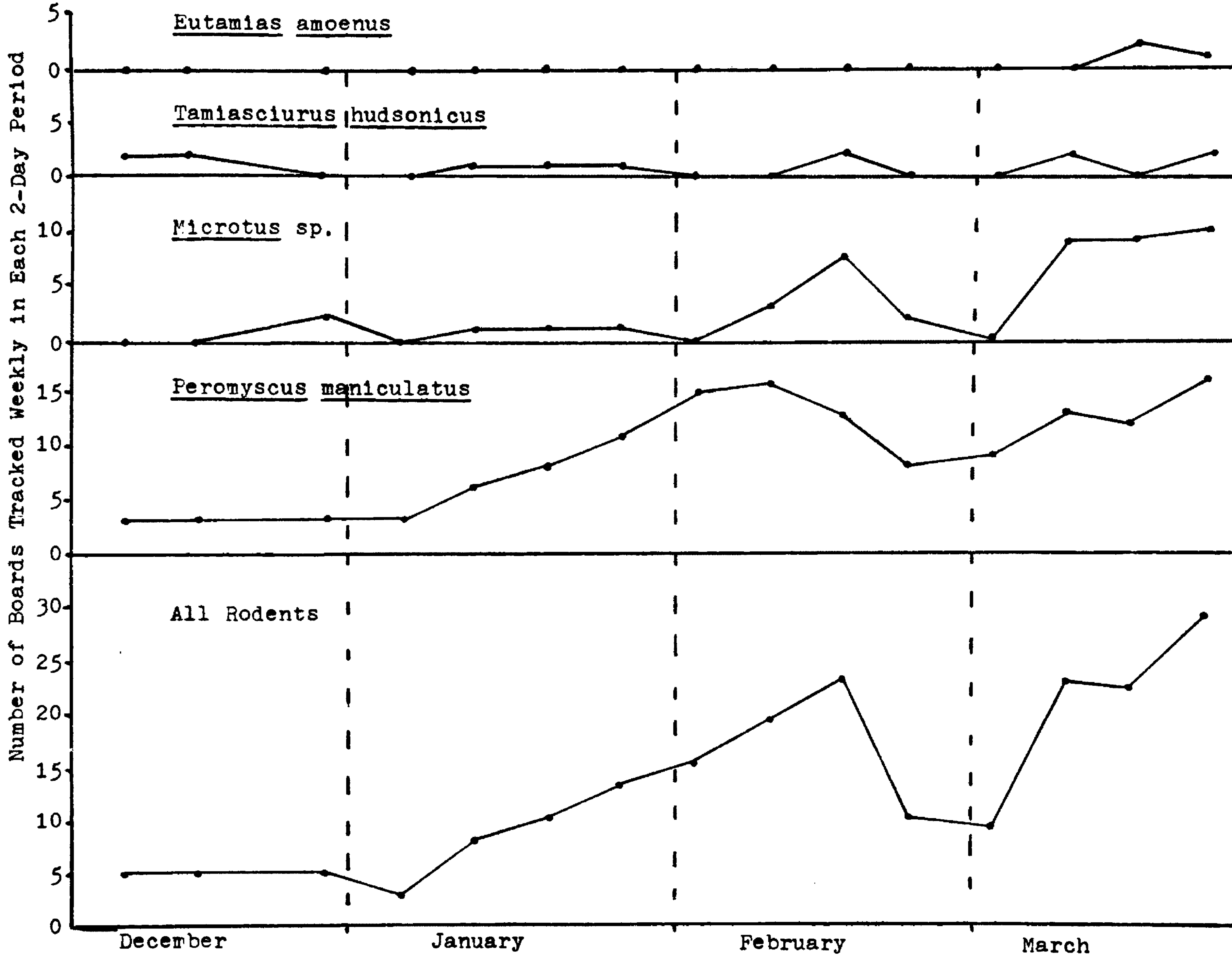


1/ Does not include one kill before snow courses were run.
2/ Does not include four kills before snow courses were run.

Table 2. Frequency occurrence of items in 74 coyote scats collected during 1976-77 winter study period.

Item	(no.)	%
Odocoileus sp.	(41)	55
Microtus sp.	(24)	32
Vegetation	(23)	31
Lepus americanus	(14)	19
Clay and gravel	(13)	18
Unidentified ungulate bone fragments	(7)	9
Bos taurus	(5)	7
Tamiasciurus hudsonicus	(4)	5
Thomomys talpoides	(3)	4
Erethizon dorsatum	(1)	1
Peromyscus maniculatus	(1)	1
Canis latrans	(1)	1
Unidentified bird	(1)	1
Other unidentified	(3)	4

Fig. 7 Number of boards tracked by rodents out of 36 possible during the 1976-77 winter study period.



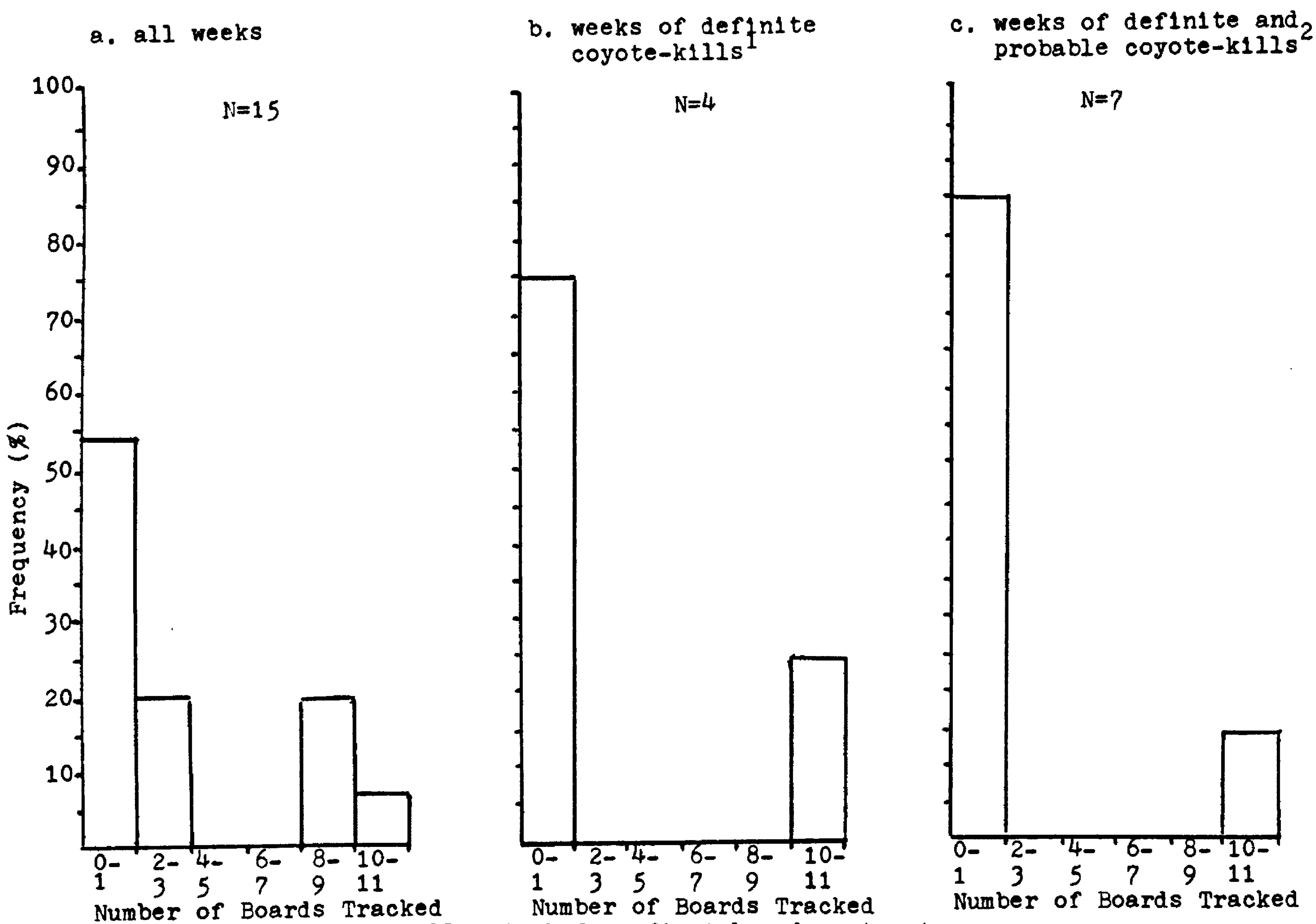
Coyotes killed most of the deer when meadow voles tracked the least number of boards. The Kolmogorov-Smirnov one-sample test detected no significant difference between the distributions of numbers of meadow vole-tracked boards for all weeks and those tracked on dates of known coyote-kills ($N=4$, $D=.22$, $P>.05$). Nevertheless, 75 percent of the known coyote-kills, 86 percent of the known and probable coyote-kills, and 89 percent of all kills occurred when meadow voles tracked only one board or less (Fig. 8).

Predator-Prey Indices

Because 100 percent snow cover was available only 34 percent of the days sampled during the second winter and 19 percent of the third winter (Table 3), I considered the coyote and deer track counts to be unreliable indices of weekly or monthly changes in deer and coyote numbers. For this reason, coyote depredations on deer could not be related to changes in either coyote or deer densities.

Data from the short and long snow courses on days of 100 percent snow cover did reveal coyote:deer track ratios for the last two winters (Table 3). Of particular interest, the number of coyote tracks counted along both long and short courses approached or exceeded the number of deer tracks.

Fig. 8 Frequency distributions of numbers of boards tracked by *Microtus* sp. for all weeks (a), weeks of definite coyote-kills (b), and weeks of definite and probable coyote-kills (c) during 1976-77 winter.



1/Does not include one kill made before first boards set out.
2/Does not include four kills made before first boards set out.

Table 3. Average numbers of coyote and deer tracks crossing snow courses on days with 100 percent snow cover and percent days with 100 percent snow cover for each winter.

Winter	Short Circuits		Long Circuit		Percent days
	Deer	Coyotes	Deer	Coyotes	100% snow cover
74-75[1]	--	--	--	--	--
75-76	12.5	9.1	9.4	10.7	34.4
76-77	1.7	7.0	9.6	8.0	18.7

[1]No measurements or estimates made during first winter.

CHAPTER V

DISCUSSION

The examination of deer carcasses conclusively demonstrated that coyote predation was the major cause of mortality for wintering white-tailed deer in the Miller Creek drainage. Predation, including 11 known and 8 probable coyote-kills, was the direct cause of death in 83 percent of the 23 carcasses examined. Only three of these 19 deer apparently possessed physiological or pathological conditions which could have predisposed them to predation. Coyote tracks and evidence of feeding were present at all 23 carcasses, and, except for the cougar kill, there was never evidence that the cause of any of the deaths was other than coyote predation.

A review of the literature produced no reports of similarly high percentages of deer winter mortality due to predation. Aiton (1938) found that coyotes unmistakably killed 25 percent of the dead white-tailed deer examined in Glacier National Park. Runge and Wobeser (1975) attributed 21.8 percent of the white-tailed deer deaths in Saskatchewan to all forms of predation, but coyotes accounted for only 2.5 percent of the total. Trainer (1975) found that coyotes caused only 24 percent of the total winter mule deer mortality on Steens Mountain in Oregon. These workers reported that malnutrition and overcrowding contributed to predation losses.

In the Miller Creek drainage, neither malnutrition nor overcrowding was apparent. Examination of 12 bone marrows indicated the depredated deer were in generally excellent nutritional condition. Eleven marrows were white and firm, indicating good condition (Cheatum 1949). Based on Greer's (1968) work with elk femurs, the six marrows that compressed zero percent probably had fat contents between 81 and 96 percent. The marrow of a 6½-year-old buck compressed 7 percent, indicating decreased fat content (45-75%).

Although estimates of deer density were outside the scope of this study, numbers appeared to be low, and ranchers in the area believed that the deer population was at an all-time low. Supporting the hypothesis that overcrowding was not a problem, utilization on three permanent Montana Fish and Game Department browse transects located in the drainage ranged from only 0.5 to 32.8 percent for the three winters (Montana Department Fish Game 1965-77).

Rodent Activity

Evidence strongly suggested that coyotes, generally dependent on rodents, switched their hunting strategies from rodents to deer as rodents became less available. Despite their ability to attack and kill deer during relatively warm and snow-free times of the winter, coyotes killed proportionately more deer when minimum daily temperatures and rodent activity were low and percent snow cover was high. Further analysis also revealed that meadow voles, a frequently occurring item in the scats analyzed, were least active when minimum temperatures were low and percent snow cover high. As these small prey items became less active and more difficult to find and capture, coyotes probably increased efforts spent on the riskier and more energy-demanding task of killing deer.

Deer mice were not an important food item, although they tracked more boards than any other rodent. Murie (1940), Ozoga (1963), and Reichel (1976) also noted that deer mice infrequently occurred in coyote scats but, nevertheless, achieved high densities in their study areas. Murie hypothesized that deer mice were adept at eluding coyote attacks. Reichel suggested this anomaly also might be due to a difference in activity patterns or usage of microhabitats by the two species.

Age Distributions

The Miller Creek coyotes killed only fawns and deer from 3 to 7 years of age. No dead deer examined were outside those age classes.

The age distribution of deer killed by coyotes differed greatly from that killed by hunters during the corresponding hunting seasons. The percentage of coyote-killed "prime age" deer far exceeded that harvested by hunters, and may exceed that occurring in the Miller Creek population. Pathological and/or physiological abnormalities, undetected by field necropsies, may accrue in this "prime age" group, reducing its endurance and speed. However, the generally healthy appearance of most carcasses and bone marrows suggested that ailments contributing to susceptibility to predation were not so severe as to have caused the deaths of these animals, regardless of coyote attacks.

Twenty-five percent of the deer definitely killed by coyotes were fawns. Fawns also accounted for 25 percent of the definite and probable coyote-kills, combined. The proportion of fawns in the coyote-killed sample was slightly higher than in the hunter-killed sample. There may have been a bias against fawns in the hunter-killed group if, as is generally believed, hunters selected adult deer over fawns. A bias against fawns may also appear in the coyote-killed sample, because fawns are smaller, more quickly consumed and less likely to be found and identified than older deer (Pimlott 1967, Kolenosky 1972).

In spite of these and other possible biases, the evidence does not indicate that wintering fawns were particularly vulnerable to predation. Wintering fawns in good nutritional state may already be strong enough and fast enough to escape most coyote attacks. Their association with does may lend them added security. If, as was reported by Cook et al. (1971) in Texas and by Trainer (1975) in Oregon, coyotes took large numbers of summer fawns in the Miller Creek drainage, the low occurrence of coyote-killed fawns during the three winters possibly reflected poor summer and fall fawn survival. Ozoga and Harger (1966) in Michigan and Ogle (1971) in Washington believed that fawns were most vulnerable to coyote predation. They reported that, in winters, fawns accounted for 82 and 53 percent, respectively, of the coyote-killed deer.

An interesting note is that yearling and 2-year-old deer, which comprised 45 percent of the hunter-killed sample, did not appear at all in the coyote-killed sample. The top speed of both coyotes (Cottam 1945) and deer (Severinghaus and Cheatum 1956) is about 56 k p h. Yearling and 2-year-old deer may be just enough faster than the younger and older animals to more successfully outdistance pursuing coyotes.

Sex Ratios

In the absence of data on the sex ratio of the Miller Creek white-tailed deer population, it was unclear whether coyotes selected one sex over the other. The sex ratio of deer definitely and probably killed by coyotes, combined, was even. But, of the nine deer of known sex definitely killed by coyotes, the male:female ratio was 170:100.

Neither ratio differed significantly from the sex ratio in the hunter-killed sample, which was probably biased against females because hunters were limited to harvesting only bucks during portions of the regular hunting seasons.

A similar lack of reliable sex ratio data hampered other analyses of the comparative vulnerability of does and bucks to predation. Ogle (1971), reporting that bucks comprised 50 percent of coyote-killed deer, believed that males were no more vulnerable than females. Concluding that bucks were more vulnerable than does to predation by wolves (*Canis lupus*), Pimlott et al. (1969) and Kolenosky (1972) found that bucks accounted for 57 and 71 percent, respectively, of the wolf-kills.

Hunting Strategies

Habitat. Coyotes typically began successful chases uphill from deer, which were forced to flee downhill. In all 11 chases, deer and coyotes either ran downhill or jumped down a steep road cut. Murie (1940), Cahalane (1947), Kramer (1970), and Ogle (1971) also reported coyotes killing deer after downhill chases. Deer often slid considerably further than coyotes when running downhill, and I suspected that, at times, deer slipped and fell rather than being actually knocked down or tripped by coyotes. Falls probably induced some physical damage and undoubtedly caused deer to lose ground to pursuing coyotes.

The location of most chase routes and kill sites in the relatively open ponderosa pine vegetation and hay meadows indicated that deer were more vulnerable, due to their greater visibility, in such habitats. However, the methods used to locate dead animals probably favored finding deer in open areas, such as pine stands and hay meadows, near roads and stream bottoms, and discouraged the discovery of carcasses on upper slopes and in thick timber stands or ravines.

Snow conditions. No evidence supported the hypothesis of Ozoga and Harger (1966) that deep or crusted snow was a requirement for successful coyote attacks. In only two of the 11 successful chases did coyotes run on top of crusted snow while deer, laboring to escape, broke through the crust. Shallow, soft snow cover along the chase routes was the rule rather than the exception and, in one case, no snow was present at any point along the chase route.

Group sizes: Coyotes. A single coyote did kill one fawn during the study, but generally pairs of coyotes chased and killed deer. The advantage in pairs of coyotes attacking was probably two-fold: (1) the distance of the chase was shortened by one coyote quartering across to intercept turning deer, and (2) while one coyote distracted the deer, another could attack an exposed side. The largest recorded number of coyotes attacking and killing a deer was only three, refuting a popular belief that necessarily large "packs" of coyotes make kills.

Group sizes: Deer. Most successful coyote attacks were directed toward single deer. These lone animals probably lacked the security conferred by the greater combined alertness of a group.

Points of attack. Coyotes attacked the face, throat and rump regions of deer. Although the rump was often the point of attack, no instance was found of coyotes actually "hamstringing," or cutting the "Achilles" tendon. White (1973) and Trainer (1975) found hemorrhaged tissue and punctures in the head and throat regions of young coyote-killed deer fawns, but Trainer also noted that coyotes attacked the rump and rear legs more commonly during the winter.

Observing that wolves first attack the rump, then the face, of large prey such as moose, Mech (1970) suggested that attacks to the rump crippled the ungulate and were safest for the wolf. Coyotes may have adopted a similar strategy, but the similarity of deer and coyote speeds may make coyote holds impossible anywhere but the posterior area of a deer.

Over 90 percent of more than 1,200 confirmed coyote attacks on sheep (Ovis aries) on a ranch in western Montana were directed at the head and throat. But at least 20 percent of about 50 white-tailed and mule deer collected on the National Bison Range, Montana, during winter had tears and scars, apparently caused by coyotes, around the anus and hams (B. W. O'Gara, pers. comm.). These observations suggest that coyotes are able to catch slow, short animals by the head and neck, but that coyotes can often catch the faster, taller deer only by the hind-end.

Deer Management Implications

The scarcity of reliable information on predator and prey densities has always hampered analyses of the role of predation on ungulate populations. Securing this type of data in forested and mountainous areas such as western Montana is particularly difficult. Unable to collect population data in the Miller Creek drainage, I directed my efforts toward an analysis of the "subsidiary" variables of coyote predation on white-tailed deer. Based on this analysis, it is inappropriate to conclude that coyotes control the Miller Creek deer population. However, coupled with general observations, my study does suggest some deer management considerations.

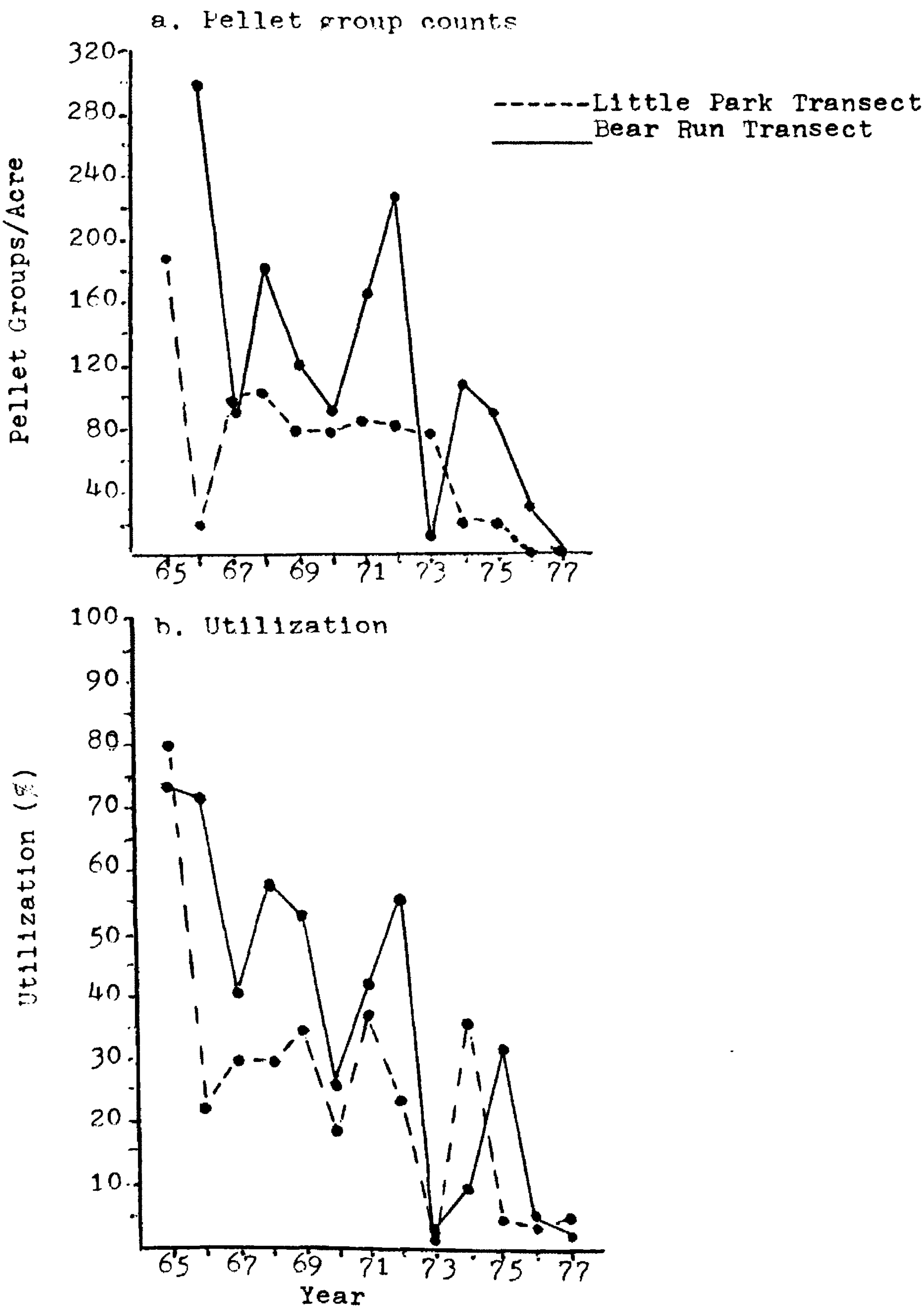
If utilization measurements and pellet group counts accurately reflect deer population trends, deer numbers in the Miller Creek area decreased from 1965 to 1977 (Fig. 9). This apparent decrease in deer numbers coincided with four major, and probably contributing events: (1) an increase in the human population of nearby Missoula and a probable corresponding increase in hunting pressure; (2) a growth in subdivisions and housing at the mouth of the Miller Creek canyon, causing a loss of traditional deer winter range and an expansion of dog (<u>Canis familiaris</u>) numbers; (3) a presidential ban in 1972 on the use of poisons to control predators, likely permitting a greater number of coyotes; and (4) increased market prices of meat, encouraging greater legal and illegal hunting pressure.

Neither disease nor food appeared to be limiting deer numbers, and browse utilization data indicated that the deer population was below carrying capacity.

The role of predation as a regulating force on a prey population will be greatest when prey density is low relative to predator density (Holling 1961, Beason 1974). It appears that from 1965 to 1977 deer numbers decreased, and coyote numbers probably increased with reduced predator control efforts.

Pimlott (1967) believed that, when wolf:deer ratios exceeded 1:100, wolf predation limited deer populations. The literature contains no evaluations of coyote:deer track ratios in terms of actual population densities, but the nearly 1:1 coyote-deer track ratio

Fig. 9. Yearly comparison of pellet group counts (a) and utilization (b) along two transects in Miller Creek drainage, 1965-77 (adapted from Montana Dept. Fish Game 1965-77).



obtained during two winters in the Miller Creek drainage suggests that coyote numbers are relatively high compared with those of deer.

It is clear that even during relatively mild winters, coyotes kill more than an occasionally encountered weak, starving, old or unproductive deer. Most deer killed by coyotes were "prime-age" animals, which, though more susceptible to predation than yearlings and 2-year-olds, nevertheless would have otherwise survived to participate in parturition and rutting activities. The high frequency of deer remains in coyote scats indicated that deer are an important winter food item for the Miller Creek coyotes, and the large percentage of depredated deer suggests that these were live animals, not carrion.

The analysis of relations among rodent activity, temperatures, snow cover, and times of predation indicated that deer are particularly important to coyotes when environmental factors make rodents, especially meadow voles, temporarily unavailable to coyotes. In more difficult winters with lower temperatures and more snowfall, coyotes can be expected to take higher numbers of deer.

While no records are available, human predation in the forms of legitimate hunter harvest and poaching also appeared to be intense in the study area.

Assuming the whitetail population is currently obtaining a lower-than-desired equilibrium, there are four alternative actions that may be taken: (1) reduce hunter harvest, particularly of does and fawns, by implementing a bucks-only season for several years; (2) reduce hunter harvest by shortening the length of the hunting season; (3) conduct intensive predator removal for several years; and/ or (4) increase law enforcement efforts to curtail illegal harvest. If any or all of these actions are undertaken, deer and coyote numbers and hunting pressure must necessarily be monitored to determine the effectiveness of the program. In the event that any or all of these recommendations are realized, further subdivision in the drainage will continue to adversely affect the deer population.

CHAPTER VI

SUMMARY

For three winters from January 1975 through March 1977, certain aspects of coyote predation on white-tailed deer were investigated in the Miller Creek drainage of western Montana. When possible, age, sex and cause of death of the deer were determined. From tracks in the snow, chases were reconstructed.

During the 1975-76 and 1976-77 winters, rodent activity was measured weekly with kerosene-smoked rodent track boards. In addition, I periodically counted tracks of deer and coyotes along snow courses, collected climatological data, and trailed coyotes.

Predation was the major cause of white-tailed deer mortality in the Miller Creek drainage. Of the 23 white-tailed deer carcasses investigated, coyotes definitely killed 11 (48%), probably killed 8 (35%), and possibly killed 4 (17%). None of these deer were yearlings or 2-year-olds. Of the eight known-age deer definitely killed by coyotes, two (25%) were fawns. Predation was concentrated on the "prime-age" class, with six coyote-kills (75%) between 3 and 7 years of age. The greater vulnerability of older animals probably was due to minor ailments accruing with age, resulting in reduced speed and endurance. It was not clear that coyotes selected one sex over the other, although 67 percent of the known-sex coyote-kills were bucks. Evaluation of femur marrows indicated that 11 of the 12 depredated deer from which we collected femurs were in excellent nutritional condition.

Coyotes generally attacked in pairs. They typically chased deer downhill, catching hold of deer in the rump and/or throat regions. Single deer appeared to be most vulnerable. Coyotes did not require deep, crusted snow to gain the advantage over deer. Most deer carcasses were found in open areas close to roads, but methods of searching for carcasses favored such locations.

Analyses of 74 coyote scats revealed that deer (55%), meadow voles (32%) and snowshoe hares (19%) were the most important prey items.

Coyotes killed most deer when minimum Missoula temperatures were less than -8° C, and snow cover was greater than 80 percent. A high correlation (r^2=.86) was obtained for minimum temperatures in the Miller Creek drainage and Missoula. Meadow vole activity was directly related to minimum Miller Creek temperatures (r^2=.73) and inversely related to percent snow cover (r^2=-.60). Most deer were killed when little or no meadow vole activity was recorded. The data imply that coyotes expend more effort hunting deer when snow and low temperatures reduce the availability of meadow voles.

Pellet group and browse utilization data collected in the Miller Creek drainage by the Montana Department of Fish and Game suggested that the deer population decreased from 1965 to 1977. Factors probably influencing this apparent decline were loss of habitat and other disturbances associated with subdivision and home building, increased hunting and poaching pressure accompanying increases in the human population and meat price increases, and higher predation losses to coyotes, resulting from less intensive predator control since 1972.

The conclusion that coyotes control the deer population cannot be made from the kinds of data collected. However, it was clear that coyotes did kill productive animals in a non-compensatory fashion, and coyotes can be expected to kill more deer during more severe winters. The extent to which coyotes kill summer and fall fawns was not known. If these losses were great, as reported for other areas, coyote and human predation may have depressed the population to below carrying capacity.

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