



Some observations on the predator-prey complex in the Gallatin valley
by Cecil P Haight

A THESIS Submitted to the Graduate Committee in partial fulfillment of the requirements for the
degree of Master of Science In Zoology
Montana State University
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Abstract:

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IN THE GALLATIN VALLEY

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ABSTRACT

Some observations of predator-prey relations were made on a section of land in the midst of first grade irrigated farming land lying just west of the Montana State College campus. The study was carried out between October 1, 1939 and April 1, 1941.

Scat and pellet analyses and field observations were made to try to establish some of the relations between the raptors and predators and the prey species on the area.

Despite ample opportunity to prey on domestic animals all predation was on wild populations, mainly on meadow mice. Insects were taken in significant quantities when they were available. All the predators ate a considerable amount of carrion in the winter. Predators on this area had no detrimental effect on normal prey populations.

INTRODUCTION

The study of predation is a relatively new aspect of animal ecology. Few workers have investigated this field in detail, hence any concrete evidence offered in interpretation of predator-prey relations is valuable in helping to complete the picture.

A survey of literature reveals the need of accurate data on local predation patterns and the attendant collection of habit variation in different areas. This project was undertaken in order to gather data which would fill in part of another gap in this field.

A DEVELOPMENT OF IDEAS

Early in the Middle Ages written records were made of the destructiveness of "vermin" to small game and domestic animals. These predators were hunted unceasingly and no sportsman's code was invoked against the manner of their capture. The ancient thought that predators are "vermin" to be exterminated bore the implication that any carnivore (predator) taking an animal which man wanted for himself was a thief and should be punished accordingly. The idea persists in the minds of many even today.

However, people in general, and naturalists in particular, are beginning to realize the incalculable value of predatory species. The relationships of predator and prey species, the interrelations of predators--the contemporary concept of predation--is yet immature; the earliest intensive study of these interrelations was begun little more than a decade ago. Several pioneers in the study of predation were McAtee, Stoddard, Leopold, and Errington. These, and others, have set forth concisely various phases of the predation theory which earlier were not understood or

were unknown.

Many people do not realize what far reaching effects may result from some seemingly minor disturbance in the biota of an area. Breckenridge (1938) suggests that most hunters advocating predator control "do not seem to appreciate what tremendously complex and powerful natural forces they are opposing in trying to bring about an unnatural, Utopian situation where game is continuously abundant. . . They do not stop to figure out that if they kill off all the hawks and owls that prey to some extent on game species, they are at the same time removing effective and natural checks on ground squirrels, mice, rabbits and like forms that in turn destroy cover (and food) for game birds."

Leopold (1933) quotes McLean as saying, "There is a growing tendency on the part of scientists to defend the predator as indispensable to the welfare of the animal preyed upon." Cahalane (1939), reporting on research done in Yellowstone National Park, Modoc Lava Beds, and Mt. McKinley National Monuments, says, "Results of studies brought to conclusion indicate that control (of coyotes) at present is not desirable. Rather, on the contrary, coyotes under present circumstances are exercising a beneficial influence by removing diseased and crippled waterfowl and surplus prey mammals." These crippled and surplus animals would have to disappear anyway, by migration, starvation, disease, or death.

The ecological concept of predation is so infinitely variable that laws governing predator-prey relations are difficult to formulate. Even though definite rules for interpretation may not yet be made, certain generalizations convenient for interpretation of data are in order.

Leopold (1933) distinguished five different types of predation:

- 1) Accident--chance predation.
- 2) Habit--acquired taste starting with accidental predation.
- 3) Education or "sucker list"--taking prey till it becomes too wary for capture.
- 4) Starvation--preying on victims of unfavorable environment.
- 5) Sanitary--culling weak, diseased, or dumb individuals.

A sixth type of predation has been suggested, one which is perhaps very important in dealing with the effects of predation on prey species, this is psychological predation. When a hawk so harries a covey of quail that they refuse to venture far enough from their shelter to obtain adequate food, and when they do venture even a short distance away a magpie or a small song bird swooping close will send them back to cover, then the psychological phase of predation occurs. The damage is not directly physical but is indirectly so by wearing the prey down through the medium of fear. At times this factor may be most important in predation.

Predation includes not only culling out unfit individuals, but also a regulatory action on the movements and distribution of the prey, thus preventing static and over-crowded populations. Henderson and Craig (1932) intimate this in saying, "On our western plains and mountains, coyotes, wolves and other predatory mammals had long lived in proximity to deer, rabbits and other mammals, in such equilibrium as neither to exterminate them nor to permit them to become overabundant."

Leopold (1933) presents the relatively new concept that alternative foods for predators may act as "buffers" between game populations and their predators. This buffer action results because of sheer numbers or because of greater availability. Buffers are alternative foods of staple rank.

Errington and Stoddard agree with Leopold in recognizing the value of buffer species and the tremendously complex and variable relations of predators to buffers to game. Not only may buffers be beneficial to game, they may also bring about conditions detrimental to them. Cyclic behavior of buffer species may, during progressive phases, afford protection to game species and during the regressive phases may throw an unusually heavy load on the game, thus causing them much distress.

Five deleterious effects which buffers may have on game species are listed by Leopold (1933):

- 1) When present in concentration they may act as bait for predators not normally in the area.
- 2) They are intermediate hosts of disease and parasites of many of the game species.
- 3) They throw a load on the game species during the winter because of hibernation or unavailability through deep snow.
- 4) Diurnal buffers are not available to nocturnal predators and vice versa, thus the "balance" of populations is changed from night to day.
- 5) Buffers may act in direct competition with the game for food or may become predatory on the game itself.

Buffers are closely tied up with the food habits of predators.

Concerning apparent predilections of predators McAtee (1932) asserts that "Within size limits, animals of practically every kind accessible to birds are preyed upon, and so as we consider the records for group after group a tendency for the number of captures to be in proportion to the abundance of the animal concerned is unmistakable. Availability is undoubtedly the chief factor involved in the choice of food, and predation therefore tends to be in proportion to population." Hence, as buffer species are usually present in large numbers, they constitute a rather large part of the diet

of predators. Errington (1935) presents a modification of McAtee's principle, "Material or heavy predation upon vigorous adult winter bobwhites appeared largely confined to that proportion of the population which was in excess of the environment properly to accommodate." A combination of these two propositions suggests that predation tends to be in proportion to the population in excess of the normal carrying capacity of the range.

Mills (1937) brings out the fact that "information now being obtained by game management specialists tends to show that predators have but little effect on normal populations of game species, and that the check which predatory species apply to the increase of these valuable forms is negligible." Errington (1936) states, "The trimming down by predation of excess population that must disappear anyway, is incidental."

Food habits, then, are determined by local conditions, and vary as much as those conditions. Composite studies of predator food habits are only a general guide to local problems according to Leopold (1933). Results of local studies cannot be transferred from one locality to another with any expectation of success, but they are invaluable in completing the composite of a regional food habits survey.

The exceedingly complex pattern of predation must be interpreted with care. Laboratory examination of pellets and scats alone will not yield a true picture of the food habits of a predator, nor will field observation by itself give a true picture. Both sources of data must be carefully considered in relation to the multitudinous environmental factors, each of which contributes its share in making the predator-prey pattern of that particular locality just what it is.

DESCRIPTION OF THE AREA

This particular area was chosen because of accessibility from the college. During the course of the study, October 1, 1939 to March 1, 1941, many short trips were made to it as well as all day observations.

The area under consideration is one section (640 acres) lying a half mile west of the Montana State College campus (Sec. 14, T 2 S, R 5 E, Montana Principal Meridian). The section is located in the midst of the irrigated farming section of the upper Gallatin Valley. From this point the land slopes upward to the mountains about six miles distant to the south and east. The area is moderately level with a gentle declivity to the north. This section is classified as first grade irrigated farming land with interspersed tongues of fourth grade land running up the seepage sloughs and along some of the ditches.¹ In this kind of farming district all possible land is under cultivation and comparatively little headland is left around the fields; for the most part clean farming is practiced.

Four operators control a quarter of a section each, thus dividing it into: 1) State College experimental plots and pasture, 2) pasture for dairy stock and sheep with small fields, and 3) and 4) two diversified farming units. Particularly in the latter the pastures and the crop areas are well dispersed among one another so that a maximum of edge effect results. There are three main pasture areas on the section resulting from land too wet to cultivate easily--fourth grade land--or from the need of pasture for dairy stock.

¹Land classification maps, unpublished, Mont. Agric. Exp't. Station in cooperation with the Bureau of Chem. and Soils, Bozeman, Montana.

Along the fence rows, large irrigation ditches, and along many of the sloughs there are several large trees and a considerable amount of brush. (See appended map, Plate I, for details of cover.) The brushy cover consists mainly of various age classes of willow (Salix spp.), alder (Alnus sp.), wild rose (Rosa sp.), and snowberry (Symphoricarpos sp.). Around the farm yards and scattered along the fences and ditches there are cottonwoods (Populus angustifolia) and large willow trees (Salix sp.). The grass in the pastures is mainly blue grass (Poa sp.), with some slough grass (Juncus sp.), brome (Bromus sp.), and sedges (Carex sp.).

"The climate of the Gallatin Valley in general is similar to that of other intermountain valleys of the northwest. It is continental in character and is subject to wide extremes of seasonal and daily temperatures, a difference of 30° F sometimes occurring within 24 hours. Winds are variable in both movement and direction, in the daytime the winds may be prevailing from the west or southwest, and at night they very often shift to the southeast. Locally some of the coldest winds in winter are from the east. During the winter warm "chinook" winds are also of variable occurrence. . . The mean annual temperature at the agriculture college at Bozeman is 41.4° F. . .". (DeYoung and Smith, 1931).

The fall and early winter of 1939 were extended and mild almost to an extreme.¹ There was no snow and relatively little moisture until the last week in December, during which time the temperature was moderate with only occasional freezes. Until the first of January, 1940, the weather

¹See Table V. Summary of weather conditions in the Gallatin Valley during the period of investigation.

was open so that upland game birds, mice and rabbits could obtain food directly from the ground and from very low vegetation.

The first two months of 1940 showed an unusually heavy snowfall. When leaving the road during January and February it was necessary to travel on skis, and on several occasions the depth of snow at random points on the area was determined to vary between 14 inches and two feet, with drifts near brush rows five feet or more in height. During the time this heavy blanket of snow was on the ground none of the short vegetation or plants with pliable stalks was available to animals living above the snow.

Because the first snows were heavy and fell on a relatively frost-free ground, the warmth of the ground below drew the few inches of frost from the surface leaving soft ground under the snow throughout the winter. There was no snow on the ground after March 20 and practically no freezing weather from that date on into the summer. The spring and summer were average for the valley with average monthly temperatures from 36°F. in March to 67°F. in August and average rainfall for that period 1.67 inches per month. The vegetation on the section was heavy thus affording abundant food and cover for game through the spring and summer.

September and October, 1940, were warm and damp. The cover and food plants remained in good condition and green until the middle of the following month. Little movement of game and predators occurred till the first of November, 1940, since the weather and food conditions were ideal for fall. The first snow fell during the first week of November and winter weather set in immediately although for no length of time was the

snow excessively deep as during the previous winter. With exception of one week in December the winter months of 1940-41 might be considered mild. The spring was normal, the snow having all melted by mid-March and the vegetation showing signs of spring growth almost immediately in the warm days that followed. Field observations and collection of other data were terminated March 31, 1941.

TECHNIQUES EMPLOYED IN THE STUDY

Two main attacks were made on the problem--1) actual observation in the field and 2) interpretation of scat and pellet analysis. Approximately ten hours a week were spent in observation on the section with the exception of the summer of 1940 when 6-8 hours were spent in the field by an inexperienced field worker. Systematic observation on the section with the aid of field glasses, interpretation of sign, and collection of specimens, scats and pellets yielded a considerable amount of valuable supplementary data. Some facts were obtained from the farmers on the section.

Laboratory examination of scats and pellets followed techniques used by the Fish and Wildlife Service. The items were recorded by number occurring in each scat or pellet. A quantitative measurement of the amounts of each food item eaten was not kept. These data were separated according to season as it was not feasible to keep an accurate monthly check on the dates of dropping.

THE FAUNA

The following table (Table I) shows the number of significant predator and prey species observed on the section at the end of each

season as indicated. (The seasons are three month periods--December, January and February being winter, etc.) For convenience in study the animals have been placed into more or less natural groups--raptors, carnivores, other birds, and other mammals. Arabic numerals indicate the number of individuals observed on the area in that season; Roman numerals indicate the month of that particular season in which the migrant or hibernating animals were first or last seen according to the time of year.

An accurate count was obtained of all the predators except weasels. A careful estimate after checking tracks and sign would place the actual number seen at about half the number present.

A satisfactory check was made on the number of birds present except during the spring when it is estimated that only three-fourths of the partridges were flushed. This number is based on the number of partridges seen during the previous month and the number of adult birds flushed in the fall.

It was extremely difficult to get population numbers of the small mammals so index figures are used to show their abundance. These indices are used to show the fluctuation within a species only, and not the relative size of populations of different species on the area (although this is indicated in a slight degree). In the fall of 1939 the Microtus population had reached the upper limit of its cycle and during the spring of 1940 had been reduced to a fraction of its former size. Estimates of numbers of active runways and numbers seen in a given length of time suggest that the number had dropped to less than a tenth of the previous

Table I. Numbers of principal species observed on the area by season.

	Fall 63	Winter 04-64	Spring 07	Summer * 07	Fall 07	Winter 11-07	Spring 11
RAPTORES							
<i>Circus hudsonius</i>	3	1-i	3-iii	1	3-iii	--	--
<i>Buteo borealis calurus</i>	4-iii	--	1-iii	3	2-iii		
<i>Buteo lagopus s.johannis</i>	2-iii	1	1-i		1-iii		
<i>Bubo virginianus occidentalis</i>	1	1	1	1	1	1-ii	
<i>Asio wilsonianus</i>	2	2-ii					
CARNIVORES							
<i>Canis latrans</i>	1	1	1	1	1	1	
<i>Mephitis hudsonica</i>	2				1		
<i>Mustela longicauda</i>	5		1		3	6	
<i>Felis domesticus</i>	6	2			4	5	2
OTHER BIRDS							
<i>Perdix p. perdix</i>	22	9	10	2	36	25	12
<i>Phasianus colchicus torquatus</i>					5	4	3
<i>Pica pica hudsonia</i>	100±	100±	100±	100±	100±	100±	100±
<i>Passer domesticus</i>	(large numbers around all buildings and brush)						
<i>Falco sparverius</i>	3-iii			2	2-i		
OTHER MAMMALS							
<i>Microtus pennsylvanicus modestus</i>	10	10	5	1	1	2	3
<i>Microtus nanus</i>							
<i>Lepus townsendi</i>	4	7	2	1	2	4	1
<i>Citellus richardsonii</i>			x-ii	x-i	x-i		x-i
<i>Ondatra zibethica</i>	2	1	1	1	1	1	

*Summer figures inaccurate, data collected by inexperienced field man

population. The reason for this sudden decrease is unknown. Numbers of jack rabbits on the section were obtained quite accurately after the first snowfall. The number of ground squirrels was not obtained but a seemingly constant, moderate population remained on the area, increasing in the spring and decreasing slowly in the summer and fall to a number about constant for any spring census. This tendency of populations to remain near the maximum carrying capacity of the range has been noted by many. King is quoted by Errington (1938) as observing an increased vulnerability of a top-heavy ruffed grouse population in Minnesota during the winter. By spring the unusually large number of grouse starting was reduced to a number about average for the two previous springs.

THE BIOLOGICAL COMPLEX

Weather and Animal Movements

Predator and prey populations changed considerably during the time of the study. This is only natural because any small change in environment may itself change a pattern or may set off a series of subsequent changes which will have a much greater effect on the population. Adams (1925) recognized the dynamic quality of ecological processes. "There is no fixed relative balance of nature, it is always undergoing change; the major relative balance was changed by the Indians, and much more by the European. . . These changes impose new relative balances upon all wildlife, including predators, and thus this unending process of adjustment to change continues."

Most of the changes on the study area can be traced directly to weather conditions and population shifts (Plate II).

Two American rough-legged hawks arrived on the area November 22, 1939, and remained there throughout the winter. The red-tails left the first of December and the last marsh hawk was seen the middle of the same month. The prey animals remained in good condition during the fall, which was a time of overlapping periods of stay of the migrant raptors, so that the prey species went into the winter in unusually good condition.

The winter residents of the section included two rough-legs, one great horned owl, two long eared owls, a coyote, at least one skunk, and about twelve weasels; 25 European partridges, 7 jack rabbits, and a large population of meadow mice.

Heavy, deep snow in the first three months of 1940 worked a hardship on most of the predator and prey animals, but raptors, and mice which lived under the snow almost entirely, were not effected as greatly as the others. Coyotes continually blundered in the deep snow and had difficulty getting footing for a sudden spring. Rabbits fared little better; true, they stayed on top of the light crust most of the time, but when startled they would kick through the crust and be hard put to regain their footing so they could escape. The partridges got along moderately well but were vulnerable to attack when they were down in the snow or away from the brush. Their initial spring in the air was considerably hampered by the depth of the snow and the first few wing beats lost impetus by striking the snow.

All the snow had melted by the last of March and about that time the first marsh hawk returned for the summer. Nearly two weeks later the red-tails arrived. During that time the rough-legs were returning to

their summer haunts in the north. In the spring and early summer there was a sudden and radical decrease in the mouse population so that it became only a fraction of that of the previous summer. The summer was average for the valley.

A summer census showed present on the area three red-tails, four marsh hawks, one great horned owl, one coyote, a skunk, and 12 weasels; 35 European partridges, four jack rabbits, a small population of mice, and a moderate population of ground squirrels.

The arrival of grasshoppers and other insects in the spring took a considerable load from the vertebrate prey for nearly all of the predators on the area ate considerable quantities of insects during the summer as scat and pellet analyses showed. In the early fall several ring-necked pheasants (Phasianus colchicus torquatus) migrated to the area thus introducing a new element into the population configuration.

The disappearance of insects with the advent of cold weather shifted the diet of these predators almost completely to mice again. The food and cover plants on the area were frozen in mid-fall and the prey species were more exposed and in poorer condition for winter weather which set in the latter part of October.

The winter of 1940-41 was somewhat colder and more extended than the previous winter. This winter population was composed of one great horned owl, one coyote, at least one skunk, a dozen weasels; 20 partridges, three ring-necked pheasants, five jack rabbits and a moderate population of mice. No other raptors wintered on the area and the owl that had been resident there for some time shifted his hunting to more favorable parts

about the first of February. On termination of the study March 31, 1941, no hawks had returned from the south and the partridge population was reduced to about 18-20, otherwise no population changes were evident for the spring of 1941.

During the winter the apparently less available food and the decrease in the amount of satisfactory cover tended to keep the predators more widely distributed than in the summer. It was found that the animals daily hunted almost all of the area within their normal daily cruising radius. There seemed to be less overlapping of hunting territory among similar predators than in the summer. It was found that scavenging was more prevalent in the winter months, presumably because of lack of sufficient amounts of other foods. Definite evidence of both carnivore and raptore scavenging was found in the snow in the remains of chickens, magpies and a newborn calf picked clean.

Increased predator pressure, caused in part by the influx of migratory species, somewhat decreased the relative availability of the prey species (aside from the super-abundant mice in 1939-40) for a short time in the fall and for a slightly longer time in the spring (see plate II).

There was very little direct antagonism between owls and hawks but there was a great deal of direct competition in the way of pressure on the same prey species, the hawks exerting pressure in the daytime and the owls at night. In the early morning and late evening hawks and owls were seen hunting over the same area simultaneously, but this was not common. These two raptores effected a never-ending pressure on rodent populations and the threat of accidental predation on game species was always present,

day and night.

A coyote, two skunks and about 12 weasels roamed the area constantly, the weasels seldom covering an area more than a hundred yards in radius during one day. Except a few hours at noon these mammals hunted the area almost unceasingly, some of them hunting throughout the night. Nearly the entire section was systematically hunted the year round by at least six house cats. Thus another factor was added to the already complex "balance" existing on the section.

Flora-fauna Relationships

There are certain ecological associations which generally need no explanation, but when interpreting predator-prey phenomena it is well to have the details of the situation well in mind.

Wild populations tend to exist in proportion to the amount of edge-effect. It is expected that animals will be found most frequently next to those edges; the data gathered on this study are in no way contradictory.

Along sloughs and ditches in pastures there was a rather constant population of meadow mice. Here they were in their preferred habitat--wet ground with a heavy overgrowth of grass which permitted them to build their tunnels on top of the soil yet remain hidden. Hummocks of ground on which willows stood in the sloughs gave the mice a good place in which to build their nests and push their tunnels. The rank, green vegetation which grows in the sloughs afforded the mice a never ending supply of green food material, even in winter. The marsh hawk, which shows a

predilection for meadow mice, was seen coursing over the sloughs and wet pasture lands. Red-tailed hawks and occasionally rough-legs were seen quartering the sloughs in search of prey. In the evening owls hunted the same area. The crepuscular coyote hunted the sloughs taking heavy toll of the mice it found there. Although weasels and skunks were less specific in the choice of land which they hunted, they were often seen snooping here and there up and down the sloughs in search of prey.

Wet ditches, and the wet ground near them, present a different type of flora--one transitional between hydrophytic and mesophytic. The grass found there was still mainly blue grass with a heavier mixture of the more wiry Carex and Elymus. There were numerous forbs along the ditches and a rather dense stand of rose bush, snowberry, willows, and alders alternated with stretches on which the only cover was tall grass (Elymus and Bromus) and various forbs. There were some mice here but considerably fewer than along the sloughs. The tall grass and brush afforded excellent cover for rabbits and partridges the year round. Invading the ditches and small streams in the more open areas were a few muskrats which easily fell prey to the larger predators because of lack of cover. Red-tailed and American rough-legged hawks and a great horned owl hunted along these ditches and moist areas. Coyotes, skunks, and house cats found ample stalking cover. During the day hawks were seen loafing and owls sleeping in the willows, alders, and occasional tall cottonwoods along the ditches. The hawks and magpies used the brush as resting cover at night as did the owls, skunks, and coyote in the daytime. Animals flushed from cover and signs left behind proved this point. Numerous small birds, including a large number of

English sparrows, inhabited this brushy area all year and domestic chickens frequently hunted along it.

There were three farms on the area and seven adjoining it; all of these units had some chickens which, particularly in summer, foraged as far as half a mile from the buildings. These chickens fed along fences and brush where the hawks, owl, and coyote were to be found hunting or resting, yet the only predator action against them (as far as could be ascertained) was scavenging on dead chickens dumped out by the farmers.

The pasture areas on the section were either dry or had sub-irrigated borders along ditches and sloughs. The dominant cover in the pastures was blue grass with scattering brome and timothy in parts. Along the fence rows there was some rose brush and alder as well as a few lone cottonwoods. The more damp parts of the pastures were well populated by meadow mice and were freely run over by jack rabbits. In the spring, summer and fall numerous ground squirrels (Citellus richardsonii) were found in the pastures, particularly along fences and high ditch banks. The pastures were hunted by all the raptors on the area, and their borders were thoroughly patrolled by coyotes, skunks, and weasels. The damp pasture land seemed to be the hunting ground most in common to the predators of this area.

The fields on the section were of three types during the winter: fall plowing, alfalfa, or wheat stubble. The plowing supported practically no game or buffer populations except for the few individuals along the borders of the fields where they apparently had migrated from the populous neighboring areas.

The alfalfa supported heavy populations of meadow mice and along the edges furnished food for the rabbits and partridges in the summer. Early in the winter the wheat stubble offered cover and food to a large population of meadow mice and numerous partridges. Many coyote scats and skunk sign were seen along the edges of the stubble fields. The partridges spent a large part of their time in the edge of the stubble, around straw piles and along brushy fence rows during the entire time of study. In the summer when growing crops were found on most of the field areas, the rodent and game populations moved in quite rapidly to take advantage of the abundant food and cover which crop land offers.

The change of cropping practices and consequent shift of plowed areas on the section during the summer and fall of 1940 had a very marked effect on the position and movement of animal populations. With the late summer plowing of large portions on the east side of the section all populations shifted west to pastures and unplowed crop lands. By noting the types of farming practices on the various parts of the section (see plate I) it is possible to place approximately the positions of concentrations of smaller prey and hence also the areas where one would find the predators.

Predation Patterns

Mice: In winter the meadow mice on the area were found to build nests above the ground and under the snow. A little dome iced over by the heat of their bodies resulted and almost invariably a small vent was formed directly above the nest. Bailey (1913) notes this behavior in the Microtus of Glacier Park. "When the first snow falls they (Microtus) plow little

tunnels over the surface of the ground, and these become hardened and throughout the winter are avenues of travel. . . Many winter nests are built on the surface of the ground and occupied until the snow disappears." From these nests on top of the ground tunnels ramified through the snow, as extensive in a horizontal plane as are their subterranean tunnels in summer.

Weasels and skunks made a habit of visiting these nests which they located by the small vent. Weasels frequently explored the inside of the little iced domes, sometimes even working out into the tunnels, only to come back out through the place they entered and go on to another nest. Skunks hunted about these "houses" in a manner similar to the weasels but less frequently actually entered the nest. Piper (1909) says, "They (skunks and weasels) are most persistent enemies of mice." Magpies opened the mouse nests as soon as they could reach them through the opening in the snow.

The deep snow and the frost free ground were a boon to the mice. They built their homes and tunnels securely under a foot or more of snow, gathered green food all winter long and lived comparatively free from attack. Hawks and owls were seen to dive into the snow after mice, frequently completely burying themselves and emerging now and then with a mouse, but more often without it. The predatory mammals lived little better, usually returning from a plunge into the snow with empty claws. In spite of these depredations the mice lived comparatively free from disturbance while the snow was deep on the ground. And in spite of their relative security they furnished the staple winter food of all the predators on the area as can be

seen in tables II, III, and IV.

Ground squirrels: Ground squirrels, which are preyed upon considerably by the larger raptores and predatory mammals, ceased their activity for the most part by the last week in September and hence their buffer action disappeared. No October pellets or scats contained ground squirrel remains. Their hibernation occurred at a time when predator pressure was increased by the influx of migratory raptores. By the middle of March the ground squirrels came out of hibernation, just after the winter resident raptores had gone north. Their appearance from hibernation at this time relieved some of the stress on other populations at a time when breeding, choice of nesting sites, etc., made the latter intolerant of their winter concentrations and less cautious in their habits.

Several early April scats and pellets showed predation had already begun on the ground squirrels. Fur and bone fragments in scats and pellets, and skulls lying in the field showed that ground squirrels were preyed on quite consistently as long as they were available. The last three of Leopold's five deleterious effects of buffers (p.9) applied aptly to the ground squirrels. At the same time they were of great value in reducing pressure on other species throughout the summer.

Coyote: The coyote, a native of the plains country, has stayed there while the farmers have moved in around it. By changing its ways so as to live with the farmer it has been able to stay in its old territory in spite of efforts to exterminate it.

At times it hunted practically in the farm yards as tracks proved. Frequently during the winter coyote tracks were followed along the willow

patches, brushy fence rows, and out across open fields. The tracks showed that the coyote had been hunting these areas quite carefully, not overlooking any possibilities--mice, rabbits, partridges, or whatever else might occur in its path. In late November, 1939, the remains of a large muskrat killed and eaten by a coyote were found under a willow about fifty yards from a small stream. This was without doubt a case of accidental predation. The place where the muskrat was caught was close to a fence and dry ditch which the coyote habitually used while hunting that side of the pasture. In another part of the section a marsh hawk was killed by a coyote. Fresh tracks and a newly dropped scat were found a short distance from the kill. Apparently the coyote had discovered the hawk early in the morning as it was sleeping on the ground near some scrub willows in a slough and had killed it.

Table II summarizes the food habits of the coyote as determined by scat analysis only. Other sign found in the field show that the coyote had also eaten a muskrat, carrion chicken, a magpie, a marsh hawk, a jack-rabbit, and a ground squirrel. The birds were taken in the winter, the mammals in the spring and fall.

Mice formed the main food of the coyote throughout the year but other mammals also were taken during the summer; the larger size of the latter prey would make them an important factor in the coyote's diet. Insects were taken in large enough numbers to make them important during the warmer months. Column B shows that they were found in quite large numbers in $1/6$ to $1/3$ of the summer scats. Birds were preyed on only during the winter and then were an infrequent item. The sparrow-size

Table II. Seasonal summary of coyote scat analysis. Column "A"--average number of food items per scat, column "B"--number of scats in which that food item appeared. (See plate III.)

Total number of scats	1939				1940				1941					
	Fall		Winter		Spring		Summer		Fall		Winter		Spring	
	29		24		12		6		23		12		6	
	A	B	A	B	A	B	A	B	A	B	A	B	A	B
MAMMALS	4.28	29	3.75	24	4.83	12	3.67	6	4.17	23	4.33	12	1.83	6
Microtus	4.21	29	3.75	24	4.67	12	3.67	6	4.17	23	4.33	12	1.83	6
Citellus	.03	1												
Others	.04	1			.16	2								
INSECTS	.52	5			.83	4	.50	1	4.65	6				
Acrididae	.17	3			.33	3	.33	1	.17	3				
Coleoptera	.17	2							3.00	3				
Noctuidae larvae									1.43	2				
Others	.18	3			.50	1	.17	1	.05	1				
BIRDS			.13	3	.25	3			.09	2	.08	1		
Sparrows (?)			.09	2	.25	3			.09	2				
Partridges											.08	1		
Others			.04	1										
PLANTS	.21	4	.09	2	.25	2			.13	2	.08	1		
Grass, straw	.17	4	.05	1	.25	2			.13	2	.08	1		
Others	.04	1	.04	1										
MISCELLANEOUS	.07	2	.13	3	.08	1			.17	3				

See appendix, table VII, for individual scat analysis.

birds usually taken could be hardly more indicative of food habits than a single mouse. It is quite possible that many of these avian prey were taken by sanitary predation. Some extraneous plant material was found in nearly every scat analyzed, only exceptional items or amounts were noted in the table. Miscellaneous items included a considerable amount of sand (grit from the gizzard of a partridge), 4 Nematode parasites, proglottids from a Cestode, one small Gastropod, and some wood, stones and dirt.

Skunk: From the few skunk scats available (see table X) it appears that skunks fed almost entirely on mice in the winter and on insects and mice in the summer. A summer scat (not included in the table) found at the beginning of the study consisted entirely of grasshopper remains. Those taken during the study usually had at least one mouse represented.

European partridge: During the winter months the partridges became extremely wary and it was difficult to approach within 50 yards before they flushed. In winter the partridges could be seen along the ditch banks where there was little snow picking up seeds, green grass, and gravel, and taking dust baths. At other times they frequented straw piles and the stubble next to brush rows. They would scratch through 6-8 inches of snow to get food and grit underneath. By mid-March the partridges were already paired and claiming nesting grounds.

In spring, summer and fall they were more secretive in their habits and lay well, flushing suddenly at short distances. Throughout the summer they spent most of the time out in the fields and in pastures within a hundred yards of cover. In the fall they congregated in coveys of from 6-20 members. Shortly after heavy winter set in the coveys broke into smaller groups and several left the area, so that by spring there were

from 8-10 pairs left on the section. Apparently 9-10 pairs is the approximate carrying capacity of this section for nesting partridges. In this region the partridge population is limited mainly by the amount of available food in winter, and secondarily in most instances by the amount of cover.

Hawks: All observations on hawks were made according to species but it was not feasible to separate pellets, so pellet analyses were grouped as food habits of "hawks on the area".

Marsh hawks may be seen any time in the daylight hours coursing back and forth across sloughs or fields hunting mice. They fly tirelessly only 4-6 feet above the ground, making sudden plunges earthward as they see some quarry. Occasionally they rest a few minutes sitting on the ground, or when worried by a group of magpies they may take shelter in some brush for a short time. On no occasion were these hawks seen to eat anything but mice, although it is quite probable that they hunt small ground squirrels in the summer. The marsh hawk eats many insects during the warmer months.

The red-tails are the hawks one commonly sees circling high in the air. When hunting they may quarter the fields and pastures like the marsh hawk or spend much time sitting on a post or in a tree watching for some larger prey. During the summer the red-tails apparently prey to a considerable extent on ground squirrels, but in the spring and fall they have to rely almost entirely on mice for sustenance.

The American rough-legs come down from their far north nesting region to winter in the northern states. From their arrival in November

till their departure in February or March their staple food is mice. At times they may chance on a partridge, jackrabbit, or in hard weather may even "stoop" to eating carrion, as do most other predators in the winter. The rough-legs were watched carefully and were observed to prey only on mice during their stay here in the winter.

A summary of hawk pellet analyses is given in table III. No pellets were found in the winter and spring of 1941 because the summer hawks had all migrated south before winter set in, no northern hawks wintered here, and the summer residents had not returned when the study was terminated.

Though there were fewer hawks in the entire valley in the winter of 1940-41 the absence of hawks from this particular section may have been closely associated with the local scarcity of mice. Dymond (1939) believes "It is the prey which determine the number of their predators. Predators do effect to some extent the numbers of their prey but the initiative lies with the prey."

The staple food of hawks on the section at any time was mice. Ground squirrels were preyed upon in the warmer months. A rabbit, a pocket gopher (Thomomys talpoides) and an unidentified small carnivore were also taken in the summer. The pocket gopher must have been picked up in the foothills 5-6 miles away as none have been found in the intervening area. These mammals formed a material portion of the diet of the hawks resident on the area in the summer. When available, insects were taken in quantities sufficient to make them a rather important source of food. Some birds were taken but they probably played an insignificant

TABLE III. Seasonal summary of hawk pellet analysis. Column "A"--average number of food items per pellet, column "B"--number of pellets in which that food item appeared. (See plate IV.)

Total number of pellets	1939				1940				1941					
	Fall		Winter		Spring		Summer		Fall		Winter		Spring	
	50		23		31		63		54		0		0	
	A	B	A	B	A	B	A	B	A	B	A	B	A	B
MAMMALS	1.96	50	2.28	23	2.41	31	1.75	63	1.70	54				
Microtus	1.94	50	2.28	23	2.39	31	1.70	63	1.68	54				
Citellus							.03	2	.02	1				
Others	.02	1			.02	1	.02	1						
INSECTS	.34	9			.35	7	.68	20	.52	19				
Acrididae	.20	7			.03	1	.29	11	.23	10				
Coleoptera	.08	1			.10	3	.36	9	.21	8				
Coleoptera larvae	.02	1					.03	2	.04	2				
Noctuidae larvae	.				.16	1			.02	2				
Others	.04				.06	2			.02	1				
BIRDS	.02	1	.05	1	.03	1	.03	2	.06	3				
Sparrows (?)	.02	1	.05	1	.03	1	.03	2	.06	3				
PLANTS	.08	2	.04	1	.13	3			.06	3				
Grass, straw	.02	1	.04	1	.10	1			.					
Forbs	.02	1							.04	2				
Grain	.04	2			.03	1			.02	1				
MISCELLANEOUS					.06	2								

role in the food habits of these hawks.

Owl: The great horned owl hunts nocturnally, picking up whatever prey its powerful talons can grasp. Table IV shows the food habits of the great horned owl as learned from pellet analysis.

The owl left the area early in February, 1941, so few pellets were found in the winter and none in the spring.

The principal food of this raptor was mice. Ground squirrels played a small part in the food of the owl because they are strictly diurnal and the owl is crepuscular and nocturnal. Insects, mainly the larger beetles and grasshoppers, were taken quite often. Birds are a significant, though hardly important, item in the owl's diet. They were taken, perhaps, mainly through accidental predation.

Magpies: Magpies were sometimes seen worrying marsh hawks or red-tails after they had caught a mouse or some other bit of prey. The magpies even tried to rob the big rough-legs that wintered on the area. They are a most omnivorous bird—robbing granaries, killing mice, stealing from other birds of prey, hunting out carrion and otherwise eating almost anything they can find. Frequent evidence of predation on mice was seen throughout the winter, sweeping tail marks, a bit of viscera and fur in the snow testified to this habit of magpies. Almost invariably one or two magpies were frightened from any carrion that happened to be lying exposed.

General: Despite some radical changes in the predator and prey populations during the time of study the predation pattern remained essentially unchanged throughout that time. The following plate and tables clearly indicate the nature of predation that occurred on the area

