Food Habits of Feral Carnivores: A Review of Stomach Content Analysis

Susan M. Landry, BS
H. J. Van Kruiningen, DVM, PhD

Introduction

A good deal of disagreement exists within the veterinary profession about the proper diet for dogs, some nutritionists advocating meat and fat rations and questioning the need for carbohydrates, and others describing a necessity for carbohydrates and suggesting deleterious effects from high meat protein diets.[25,38,50] The proliferation of commercial dog food products and the hyperbolic television advertising associated with them have compounded the dilemma for the veterinarian and the dog-owning public.[62]

The authors became concerned about canine rations because recent studies suggest that canine acute gastric dilatation may be related to diet.[57] The disease occurs with greatest frequency in the best-cared-for animals, in dogs fed exclusively soybean-cereal grain-expanded dog food products.[57] Acute gastric dilatation occurs shortly after a meal and has been shown to be fermentative in origin.[44,57]

We conducted a review of the available wildlife literature, with the intent that the information gathered concerning food selection among feral carnivores might influence future considerations regarding the feeding of domestic carnivores.

Review of the Literature

Food habits of feral carnivores have long been of interest to wildlife specialists, who have attempted to elucidate predator-prey relationships and their fluctuations. Three methods have been used to determine the foods of feral carnivores: (1) examination of stomach contents; (2) scat analysis; and (3) direct observation.

In the examination of stomach contents, samples are floated in water and then dried in ovens. This is a common method. A partial identification is accomplished by inspection of undigested fur, bones, feathers, plant material, teeth, scales, and other such tissue. Identification is completed by microscopic study, comparing these materials with reference collections.[1,29,30,54] Stomach contents are relatively easy to identify, and this method allows for distinction between carrion and freshly killed material.

From the Department of Pathobiology, University of Connecticut, Storrs, Connecticut 06268.

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Address reprint requests to Dr. Van Kruiningen.

Table 1

Food Habits of Coyotes, as Determined by Examination of Stomach Contents

Location	Number of Specimens	Empty (%)	Contents[a]	Reference
Arkansas	227	26	Poultry, persimmons, insects, rodents	15
California	3,982	44	Rodents, rabbits, deer	7
Central Alberta	344	ND	Carrion, mice, microtines, snowshoe hare	37
Kansas	1,451	ND	Rabbits, rodents, carrion	14
Maine	66	23	Plants, small mammals, snowshoe hare	42
Missouri	895	14	Rabbits, mice and rats, poultry	23
Northern Louisiana	43	ND	Rodents, rabbits, persimmons	63
Texas	137	31	Carrion, rodents, insects, rabbits	34
Utah-Idaho	186	25	Jackrabbits, all rodents, deer	3
17 States	14,829[b]	13.6	Rabbits, carrion, rodents	53

[a] Arranged in order of occurrence.
[b] In addition, 29.4% were filled with debris and were not analyzed.
ND = not determined.

In the scat analysis, fresh feces are collected, floated in water, and dried in ovens. Identification is based on comparisons with reference collections. This method provides a larger sample size than stomach contents, but identification is more difficult.

Direct observation of animals' feeding is the third method used. Ear tagging devices and radio telemetry[2,47] permit precise tracking of an animal's movements, thus allowing first hand observation. This method of monitoring is especially valuable for studying endangered species or animals on game preserves.

We chose to review stomach content analyses because they offer more information than scat analysis and greater numbers than have been studied by direct observation.

Coyote

Economic losses to farmers resulted in extensive studies of the coyote's predatory behavior. Sportsmen and trappers have made a large number of specimens available for research. Thus, the food habits of this canid are well delineated [Table 1]. Sperry,[53] in a 5-year study encompassing 17 states and all seasons, ranked rabbits as the primary food of coyotes. Carrion and rodents were next in importance. Similar findings have been reported for various regions.[8,35,56,59]

Geographic influences on selection by the coyote are exemplified in a study of 2222 stomachs from California.[7] Regional differences among four areas of the state are documented [Table 2]. The intake of rabbits in the eastern region is twice that of other regions, while the deer intake is almost one-half, suggesting a proportional relationship. This type of relationship is also seen in the coastal region where coyotes appear to prey predominantly on the rodent population, resulting in a decreased intake of rabbits, sheep, and birds.[7] Other examples of regional influence can be seen. Stomachs of coyotes from Texas contain fruits of native plants;[34] poultry remnants are a common finding in stomachs of coyotes from such states as Arkansas, Nebraska, and Missouri, where broiler production is a prominent industry.[16] These findings suggest that the coyote is an opportunistic scavenger.

Table 2

Comparison of Food Habits of Coyotes from Four Regional Areas[a] in California

Food	Coastal	Northeast	Inland	Eastern	Total
Rodent	63.1	49.8	46.8	41.5	49.1
Rabbit	16.5	32.1	29.0	48.9	29.3
Deer	21.1	27.7	14.1	9.6	18.5
Sheep	4.9	8.8	11.1	10.6	8.7
Other stock	17.2	13.7	15.4	17.2	14.6
Miscellaneous	37.3	25.5	33.8	40.4	30.7
Birds	15.7	18.3	16.9	25.5	18.1
Plant	8.6	5.4	18.7	5.3	12.5

[a] Percent frequency of occurrence (Ferrel et al[7]).

Table 3

Seasonal Variations in Food Habits of Coyotes[a]

	Season			
	Spring	Summer	Fall	Winter
	Stomachs Examined			
Food	102	51	181	436
Rabbits	48.6[b]	35.2	47.7	58.1
Poultry	17.0	27.4	12.8	8.5
Livestock	16.5	17.5	7.2	7.6
Mice and rats	5.4	5.6	9.0	9.5
Other mammals	6.6	6.7	8.3	7.5
Carrion	5.0	4.3	4.3	6.6

[a] From Korschgen.[23]
[b] Volume basis.

In an analysis of 770 stomachs of coyotes in northwestern Missouri, rabbits were the staple food. The percent occurrence, however, varied seasonally and annually, the changes reflecting the population densities of rabbits. The greatest consumption of rabbits occurred in the winter—58.1% by volume compared to 35.2% in summer [Table 3]. Mice and rats were found more frequently and in greater quantity in fall and winter months.[23] This report is at variance with other studies,[37,53] which report highest consumption of rodents during the summer and fall. It may be more difficult for coyotes to find and capture smaller animals in the snow. A slight increase in the amount of carrion consumed in the winter months has been reported.[37,52,53]

Unusual foods and/or quantities of food merit mention. Items such as leather,[42,53] paper, and tinfoil[42] have been found in coyote stomachs. Dirt, sticks, pebbles, and bark are often found in coyotes that have been trapped. Stomachs filled with insects have been reported.[15] Farmers cultivating watermelons have experienced heavy losses from coyotes.[15] Persimmons are frequently found in stomachs and, in areas where they are plentiful, comprise a significant part of the coyote's diet.[15,23,63]

Fox

The fox, like the coyote, has been the subject of much research. Foxes have also been considered extensive predators of domestic livestock. Analysis of food habits of the fox indicate that this canid is an opportunistic carnivore, consuming items that are easily obtained.[31]

The major foods of foxes are small mammals such as rabbits and rodents.[4-6,17,19-21,26,27,48,49,64] Although these foods are similar to coyote foods, there are differences. Some reports indicate that rodents are more important to foxes as a staple food,[17,19] though this is not borne out by available data [Table 4]. In addition, the red fox eats less rabbit and more of other game than the coyote.

The importance of game birds in the fox diet is debatable.[4] Instances can be found where game birds are a major food item.[10] This choice of prey probably occurs when there are large populations of birds or when populations of rabbits and rodents are low. Inspection of fox stomachs often reveals that this animal is not strictly carnivorous. Apples, grasses, persimmons, plums, and miscellaneous vegetation are often found.[17,19,27] A comparison of red and gray fox stomach contents shows different preferences. Plants appear more frequently and in greater volume in gray foxes. This difference is especially noticeable in winter months.[6,19,48]

Table 4

Food Habits of Foxes, as Determined by Examination of Stomach Contents

Location	Number of Specimens	Empty (%)	Contents[a]	Reference
Central Massachusetts	57	ND	Apples, shrews, mice	27
North Florida, South Georgia, South Carolina	171	ND	Rabbits, rodents, birds, insects	64
New York	134	ND	Rabbits, mice	49
New York, New England	229	10	Mice, rabbits, grasses	17
Minnesota[b]	34	14.7	Mice, rabbits, poultry	19
Minnesota[c]	58	8.6	Mice, rabbits, vegetation, fruits	19
Iowa[b]	79	44	Rodents, rabbits, birds	48
Iowa[c]	33	42	Rodents, rabbits, plants	48
Iowa[b]	50	ND	Rabbits, mice, birds (chickens, pheasants)	6
Missouri	1,170	14	Hares and rabbits, mice and rats, poultry	24
Wisconsin	29	ND	Rabbits, small mammals, carrion	20
Wisconsin	59	ND	Rabbits, rodents, birds	6
Wisconsin	59	ND	Rodents, rabbits	41
Pennsylvania	147	ND	Chickens, rabbits, pheasants	26
Pennsylvania	147	ND	Rabbits, woodchuck, deer	5
Indiana	211	ND	Rabbits, mice	21
Ohio	89	ND	Opossum, rabbits, squirrels	13
North Dakota	200	ND	Mice, game birds, rabbits	32
Victoria	1,229	21.3	Rabbits, sheep, carrion, mice	4

[a] Contents arranged in order of importance.
[b] Red foxes.
[c] Gray foxes.
ND = not determined.

Wolf

The food habits of wolves are modulated by their social behavior. Food is often obtained by a cooperative effort of the pack. As a result of the animal's size and pack society, the wolf can successfully prey on a variety of animals [Table 5].[33]

Historically, the food of wolves appeared to have been buffalo, antelope, elk, deer, caribou, and moose.[66] Today, when populations are adequate, these animals still comprise the major part of the diet of wolves. Caribou and moose remnants predominate in wolf stomachs in northern regions. In areas where man has settled and substituted domestic livestock for food, the wolf has done likewise. Tissues from livestock occurred 456 times in an analysis of 3346 wolf stomachs. Stomachs were obtained from states west of the 100th meridian and reflect the agriculture of that region.[66] Wolves select animals requiring the least amount of energy to hunt and kill. Domestic livestock are unable to defend themselves effectively and are easily captured.

Table 5

Food Habits of Wolves, as Determined by Examination of Stomach Contents

Location	Number of Specimens	Empty (%)	Contents	Reference
Texas and Oklahoma[a]	72	ND	Rabbits, domestic stock, rodents, carrion	66*
Texas, Oklahoma, Louisiana, Arkansas	31	ND	Cottontails, jackrabbits, carrion, deer	66*
Michigan, Minnesota[b]	8	ND	Carrion, deer, rabbit, mouse	66*
Minnesota	10	ND	Deer, carrion	66*
New Mexico, Arizona	10	ND	Domestic livestock, carrion, deer, rabbit	66*
West of 100th Meridian[c]	3,346	ND	Domestic livestock, deer, carrion, rabbit	66*
Michigan	8	ND	Deer, snowshoe hare	55
Minnesota	51	ND	Deer remains in 80% of stomachs	55
Northern Alberta	95	ND	Remnants of bison in 41%	11
Manitoba	75	ND	Caribou 60%; moose 21%	22
Alaska	131	ND	Caribou, moose, deer, beaver	22

[a] Red wolves.
[b] Gray wolves.
[c] This location also includes some from eastern Texas, Oklahoma, Arkansas, and Michigan (17 states).
ND = not determined.
* Order of importance could not be determined from data given.

Flesh, hair, and bones of deer are found in stomachs of wolves from all regions. Deer also are eaten in greater numbers than is represented by their populations. This suggests that deer are preferred food.[33]

Beaver tissue and carrion are common findings in wolf stomachs. Carrion is utilized as food, particularly by animals that have been handicapped by injuries from traps or by worn teeth and in areas of low prey populations. Minor food items eaten by wolves are rabbits, hares, birds, and fish.[66] Insects, invertebrates, and fruits, such as plums, watermelons, and berries also are seen in wolf stomachs. Infrequently, snowshoe hares are reported as a major food source. The size and social behavior of wolves would suggest that the hare probably does not contribute significantly to the wolf diet.

Bobcat

Bobcats eat mice, hares, rabbits, squirrels, and porcupines [Table 6]. Deer are also considered an important food item, but there is some controversy as to how this animal is obtained. Bobcats have been observed consuming carcasses of deer with gunshot wounds.[40,45] Eyewitness accounts have also documented instances of bobcats preying on live deer.[16,39,65] The actual preference of the bobcat, whether for freshly killed meat or for carrion, cannot be determined from the information available.

The frequency of porcupines in the bobcat diet is significant. Bobcats do not seem to be adversely affected by quills.[18,40,45,61] Porcupines are frequently found in bobcat stomachs even in areas where porcupine population densities are low and where other bobcat food is plentiful.[12,28,40] This suggests that porcupines are preferred food.[28,40]

Minor food items are birds, skunks, and fish.[12,18,45] Leaves, twigs, soil, and other such debris also are commonly found.[12] Since bobcats are ground feeders, the presence of these items is probably the result of accidental ingestion. Green grass is also found frequently enough to be considered a food item. The nutritional value of grass in the bobcat's diet, however, has not been determined.

Table 6

Food Habits of Felidae, as Determined by Examination of Stomach Contents

Location	Number of Specimens	Empty (%)	Contents[a]	Reference
BOBCAT:				
New England	224	27	Varying hares, deer, rabbit, porcupine	40
Vermont	143	2	Mice, deer, hares and rabbits	18
Utah, Nevada	86	38	Hares and rabbits, mule deer, deer mouse	12
Maine	101	12.8	Deer, hare, squirrel	61
Minnesota	50	ND	Hare, deer, porcupine	45
COUGAR:				
Utah, Nevada	401[b]	31	Domestic sheep, mule deer, porcupine	43
South Central British Columbia	132	9	Deer, snowshoe hare, porcupine	51
LYNX:				
Alberta and MacKenzie District	75	ND[c]	Snowshoe hare, microtines, birds	58
Central Alberta	13	ND	Snowshoe hare, carrion, ruffed grouse, red squirrel	36
Newfoundland	40	ND	Snowshoe hare, microtines, caribou, birds	46

[a] Contents arranged in order of importance.
[b] Represents total number of specimens: 30, summer, 245, winter.
[c] Number of empty stomachs could not be determined from data available.
ND = not determined.

Cougar

Little is known of the food habits of cougars. Deer supply the major portion of the diet—outnumbering the total of all other prey [Table 6].[43] Other important foods are porcupines and lagomorphs.[43,51] Tissues from horses, cows, coyotes, bobcats, skunks, and beavers also have been recovered from cougar stomachs. This data indicate that this felid prefers to eat large animals. The intake of lagomorphs may be an indication of availability rather than of preference. Low population densities of larger animals may force utilization of rabbits and hares for food. The cougar will also consume grasses in both winter and summer.[43] Brown, coarse, giant ryegrass has been found in the stomachs of cougars. This type of grass is avoided by livestock even in winter. Nutritional benefits of this grass for the cougar are unknown.

Lynx

Knowledge of food habits of the lynx is also sparse. The major food supply of this felid is the snowshoe hare [Table 6]. Microtines and birds are next in importance.[36,46,58] Lynx will also utilize red squirrels,[36] fish,[46] grass,[46,58] and birds, particularly ducks.[46,58]

The importance of the snowshoe hare is emphasized by the frequency of occurrence and/or percentage biomass. In Central Alberta,[36] snowshoe hares represented 75.7% biomass, carrion second at 9.8%, and ruffed grouse at 9.2%. In Alberta and MacKenzie districts,[58] snowshoe hares occurred with a 52% frequency, while the second ranked food item, microtus, occurred with a 22% frequency. The absolute dependence of the lynx on the snowshoe hare has been attributed to what is termed "feline specialization."[58] Felines choose their foods with respect to their own size. The lynx is a medium-sized feline, and thus is limited to capturing small animals.

Discussion

From these many studies into the food habits of feral carnivores, it may be concluded that the staple diet of carnivores living in a natural setting includes other animals, carrion, and occasionally fruits and grasses. The larger the predator, the larger the prey. Wolves and cougars possess the capability to bring down large species of prey and thus eat less frequently than other carnivores and tend to engorge when they do. While the domestic dog is regarded as a descendent of the wolf, outcrossings with other canid species appears to have been responsible for many of our domestic breeds.[9] Most of our domestic breeds possess the conformation, size, ferocity, and hunting capability similar to that of the coyote and the fox, carnivores that hunt individually, catch and kill small animals, eat carrion, and occasionally eat fruits or grasses. The data suggested that medium- and small-sized carnivores are sometime hunters, sometime scavengers, eating what they can get their claws on. Anatomically, our domestic breeds of dogs possess gastrointestinal systems similar to those of the feral carnivores studied. They share in common strong carnassial teeth, simple stomachs of great digestive capability, thickly muscled esophagus, stomach and intestine, residual cecae, and simple non-sacculated colons.

Recognizing the limitations inherent in stomach analyses as traditionally performed, it nevertheless appears reasonable to surmise from these reports that carnivores in their natural environments consume diets high in animal protein, bulk, and roughage (not plant fiber, but indigestible or poorly digestible parts of animal carcasses, such as bone, cartilage, scales, fin, fur, feather, tendon, and teeth), and low in carbohydrates and caloric density (the fat content of the flesh of wild rabbits equals 5%).[60]

The medium and small feral carnivores undoubtedly eat several times daily (nightly really), catching as catch can, with periods of rest or fruitless scavenging or hunting in between. From stomach analyses it can also be recognized that canivores masticate their prey minimally and prefer to swallow large bollets, *ie*— portions of carcasses with indigestible elements included.

An understanding of the food habits of feral carnivores should influence the diets and feeding practices we impose upon domestic carnivores.

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