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The Social Ecology of Coyotes

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Motion-picture films about the American West almost always depict coyotes in the same way, as solitary animals howling mournfully on the top of a distant hill. In reality coyotes are protean creatures that display a wide range of behavior. They are characterized by highly variable modes of social organization, ranging from solitary (except for the breeding season) and transient individuals to gregarious and stable groups that may live in the same area over a long period of time. Between the two extremes are single individuals and mated pairs that tend to remain in one area. Indeed, a single coyote may in its lifetime experience all the different grades of sociality. This remarkable flexibility in the ways coyotes interact with one another can best be understood by examining their ecology, or the ways they interact with their environment.

It is generally accepted that most animal characteristics are the product of an interaction between inherited predispositions and the environment. In other words, although the cumulative passing of genes by successfully reproducing individuals establishes certain tendencies in each animal, many observable traits are subject to modification by proximate, or immediate, factors in the animal's environment. Thus many of an animal's traits, in particular behavioral ones, can be viewed as adaptations to the environments in which the animal has lived or is living. For example, the Dutch ethologist Hans Kruuk, who has done intensive studies of hyenas, has concluded that for many large carnivores, which typically have few predators (other than man), the nature of food resources is an important proximate factor that influences social behavior. More precisely, it appears that variations in the sociality of carnivores of the same species can often be traced to differences in their food supply.

For the past three years we have been observing the behavior of coyotes in the wild, mostly in Grand Teton National Park near the town of Jackson in northwestern Wyoming. Our studies indicate 130 that the social organization of coyotes is indeed a reflection of their food resources and that three variables have a direct and significant impact in this regard: the size of the available prey, the prey's spatial distribution and its temporal, or seasonal, distribution. We shall report on our findings about both the specific behavioral adaptations coyotes seem to make to different types of food supply and the advantages these adaptations seem to confer. Before we undertake to sort out this aspect of the complex relation between coyotes and their environment we shall briefly describe the animals and the setting in which we are studying them.

Coyotes *(Canis latrans)* belong to the same mammalian family as jackals, foxes, wolves and domestic dogs. There are 19 recognized subspecies of coyotes, but because the animals are currently more mobile than they used to be and crossbreed to a greater extent there seems little reason to retain the more refined classification. Coyotes mate once a year and are generally monogamous, so that the same pair may mate in the same area over long periods, often returning to the same den site year after year. (Coyotes bear their young in holes in the ground, which they may or may not dig for themselves; the coyotes we observed generally made use of holes that had already been excavated by badgers.)

In a study of coyotes in the Canadian province of Alberta, Donald Bowen of the University of British Columbia noted that coyotes living in packs not only eat, sleep and travel in close association with one another but also tend to exhibit dominance relations. Franz J. Camenzind, who has studied coyotes on the National Elk Refuge adjoining the town of Jackson, has made similar observations. In general pack

members are more sociable with one another than they are with outsiders, such as single coyotes living in the same area or passing through. It appears that most members of a coyote pack are genetically related. Indeed, the basis of coyote social structure is probably the mated pair supplemented by those offspring that do not leave the pack when they are old enough to care for themselves.

Typically only one male and one female breed in each pack. Some of the nonbreeding individuals may help to raise other members of the pack, most probably their younger siblings, and to defend food supplies, mainly against other coyotes. Packs may also include nonbreeding hangers-on, probably also offspring of the mated pair in the pack,' that continue to live in the vicinity of the pack but interact very little with it. (It is possible that these individuals benefit from such a minimal association by "inheriting" a breeding area after a parent leaves it or dies.)

Coyotes are found in diverse habitats in Canada, Central America and most of the states of the continental U.S., but even within a single geographical setting their social behavior can vary dramatically. Our primary site for the long-term observation of wild coyotes is the area around Blacktail Butte in the southeastern corner of Grand Teton National Park. This is a particularly good place for a study of behavior and ecology because the animals that live in the park are relatively unaffected by man. Moreover, from Blacktail Butte, which rises some 300 meters from the surrounding valley floor, it is easy to observe coyotes going about their normal activities. Our findings for the Blacktail Butte area have been supplemented by observations of coyotes one of us (Bekoff) made with the aid of several students in Rocky Mountain National Park in Colorado. In the Moraine Park section of that park, where the study was carried out, the environmental conditions were quite different from those found at Blacktail Butte, and so in many cases comparing data from the two locations has helped us to identify variables influencing social behavior. We have also done experiments with animals in captivity, so that relevant competing variables could be more closely controlled.

For studies such as ours it is important to be able to identify various members of a wild population, but in the case of coyotes distinguishing characteristics such as size (ranging from eight to 20 kilograms for males) and coat color (a highly variable blend of white, gray, brown and rust) may change with time. As a result it has been necessary to capture and mark individual coyotes, and for this purpose we generally rely on foot traps, the jaws of which are wrapped with thick cotton padding to reduce the likelihood of injury to the trapped animal. To keep the coyote from thrashing around in the trap we frequently attach a tranquilizer pellet, which the animal usually swallows. The tranquilizer sedates the trapped coyote but does not render it unconscious. The trap lines are covered on foot, on skis or by automobile every six to eight hours so that the coyotes are restrained no longer than is necessary.

Once a coyote has been captured it becomes extremely docile, and so when we find a coyote in one of our traps, we immediately release it and then proceed to weigh it, note its sex, make an assessment of its physical condition and estimate its age. Next we attach a colored identification tag to each ear and fit it with a collar bearing a small radio transmitter. In this way after the coyote is released we can identify it even when it is out of sight, and we can always tell which coyotes are associating with one another. Because the area around Blacktail Butte is quite open, however, we are usually able to see the coyotes (with binoculars or a spotting telescope if not with the eye), and the radio transmitters serve primarily for the gathering of data on wide-ranging movements of individuals and groups.

There are many ways in which the nature of food resources might influence the social behavior of coyotes. For example, when large prey animals such as ungulates (hoofed mammals) are available, several carnivores (including lions, wolves, jackals and African wild dogs) have been seen to band together in packs for cooperative hunting. Pack living may also be an adaptation for the defense of major food supplies such as caches of carrion. The observations of David Macdonald of the Animal Behavior

Research Group at the University of Oxford indicate that this is the case for golden jackals *(Canis aureus)* found in Israel. We have observed that for coyotes, at least in the conditions under which we are observing them, group hunting is a rare and generally unsuccessful undertaking. In fact, from our vantage on Blacktail Butte we have never seen either a group of coyotes or a single coyote attacking a large live ungulate. On the other hand, our findings and Bowen's indicate that coyotes do group together to defend certain food resources.

In the area around Blacktail Butte there is a significant seasonal fluctuation in "the food items that sustain coyotes. In "summer" (the period from May through October) the coyotes feed mainly on rodents such as pocket gophers, field mice and Uinta ground squirrels. In "winter" (the period from November through April) the major food supply is the carrion of ungulates such as deer, moose and in particular elk that have died from causes other than coyote predation. To put it another way, in summer the coyotes hunt and kill small prey that are generally distributed widely over the area in which the coyotes live and in winter they feed on large dead prey (mainly elk) that because of the formation of herds and legal hunting by human beings during a limited season generally tend to be distributed as isolated clumps of carrion. The increased availability of carrion in winter is a widespread phenomenon, largely as a result of the higher ungulate mortality in that season.

Members of a coyote pack gather around the carcass of an elk in the snow on the National Elk Refuge adjoining the town of Jackson, Wyo. Coyotes display remarkably flexible patterns of social organization, ranging from transient individuals and mated pairs to large, stable groups that tend to remain in one area. Studies of these animals in the wild indicate that pack living represents an adaptation to large, clumped food resources such as the carrion of ungulates (hoofed mammals), whereas solitary living is associated with the availability of small live prey such as rodents. Coyotes have rarely been observed to prey on the large ungulates (elk, moose and so on) whose carrion generally sustains them in winter; the elk shown in this photograph died of other causes.

Our basic hypotheses about the role that the size of food items and their spatial and seasonal distribution play in molding coyotes' social behavior suggest that it should be possible to see variations in the sociality not only of populations of coyotes with access to different food resources but also within a single population from season to season. To determine the effects of the seasonal fluctuation of prey at Blacktail Butte we compared the sizes of the coyote groups we found there in summer and in winter. Between September, 1977, and August, 1979, we made more than 1,000 sightings of 35 marked coyotes and about 15 unmarked ones and found that in the summer months, when rodents were the major food resource, the average group size was 1.3 individuals and that in winter the average rose to 1.8. Hence the availability of large, clumped prey items did seem to be correlated with heightened sociability in these coyotes.

Pack member defends carrion (not visible) by "threat gaping" at an intruding coyote to chase it away. The two coyotes at the lower right belong to the same pack as the coyote at the center does and so remain unthreatened near the carrion. Ability to successfully defend such a food supply appears to be one of principal advantages of pack living. Photograph was taken by Franz J. Camenzind.

Moreover, we made another interesting discovery when we compared our findings with Camenzind's for coyotes on the National Elk Refuge. Camenzind's observation site is only about seven kilometers from our own, but since many more elk winter there, the supply of ungulate carrion is larger and denser. Camenzind found that on the elk refuge the coyote groups were also larger, with an average group size of 1.6 individuals in summer and three in winter. This finding suggests that the increased availability of ungulate carrion in winter not only serves to increase sociability in that season but also may have a cumulative effect, resulting in increased gregariousness the following summer. It is also interesting to note that in the Moraine Park area of Rocky Mountain National Park, where for three successive winters there was virtually no ungulate carrion, the situation was quite different. The coyotes were forced to depend on small rodents throughout the year, and the average group size in both summer and winter was 1.1.

We also compared the frequency with which three coyote social groupings—single individuals, mated pairs and packs of three or more individuals—were sighted at the various observation areas over an entire year. For example, at Blacktail Butte 35 percent of our sightings were of packs and about 50

percent were of single individuals, either transients passing through an area occupied by a pack (or by a mated pair) or solitary coyotes living on the edges of the area. On the carrion-rich elk refuge, however, only about 15 percent of Camenzind's observations were of single coyotes and about 60 percent were of packs. It would appear that in the vicinity of Black tail Butte, where ungulate carrion is scarcer and is clumped in only a few small areas, fewer individuals can live in packs that defend these resources. The remaining coyotes, which are generally excluded from the clumped carrion, must forage widely for food, either alone or as a mated pair. This conclusion is supported by the fact that at the Rocky Mountain National Park site, where there was almost no carrion, 97 percent of the sightings were of single individuals.

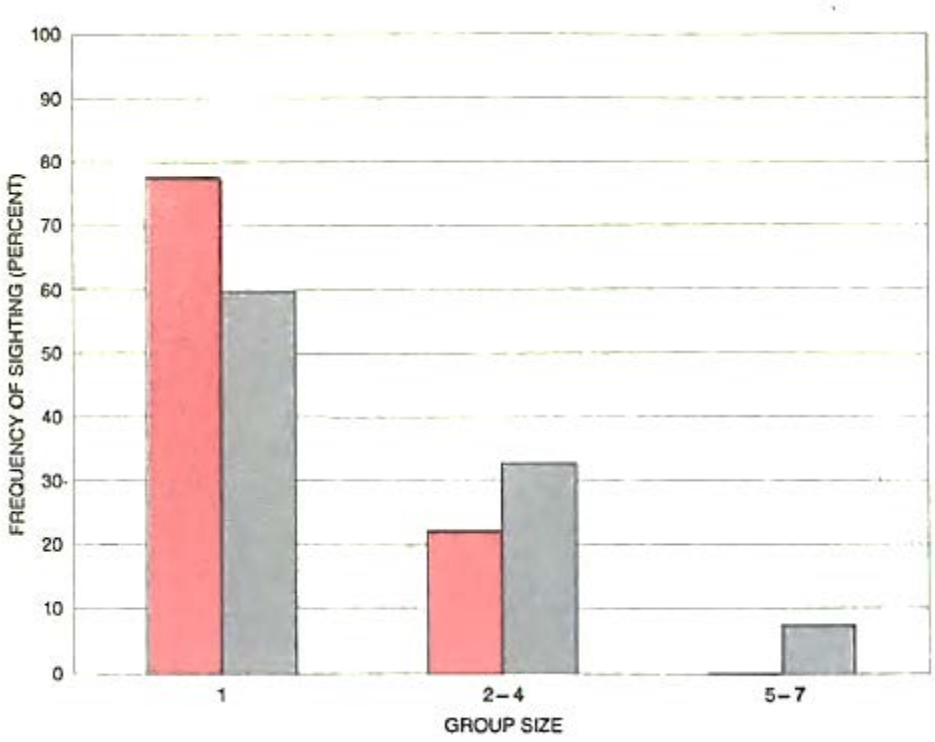
Three-week-old coyote pups require feeding and protection and remain dose to the hole in the ground that serves as their den. (Although coyotes may excavate their own den, these pups are in an abandoned badger hole their parents enlarged.) Coyote pops begin to make forays away from the den when they are two to three months old, and they may strike out on their own when they are six to nine months old. It seems that most members of a coyote pack are genetically related and that the basis of coyote social structure is probably the mated pair supplemented by a number of nondispersIng offspring. In most instances only one male-female pair in a pack breeds.

In order to gain a better understanding of the nature of coyote groupings and the advantages of the adaptation to defendable resources we did not have to cover a large area. Indeed, the observation over the past three years of two groups of coyotes with contiguous home ranges in the vicinity of Blacktail Butte has provided us with ample evidence of the ways in which food supply can influence social behavior. (An animal's home range is defined as the area it covers routinely in the course of its daily activities.)

For example, in the winter of 1978-79 there was a significant difference in the quantity of elk carrion found on the two home ranges. Completely by chance (no attempt was made to control the distribution of carrion in the Blacktail Butte area) Group *A* had about 17 percent of the available carrion and Group *B* about 83 percent. As might be expected, Group *A* was the smaller one, consisting from November, 1978, through April, 1979, of only a single mated pair. All the young of the pair from previous years had

dispersed. In the same period Group *B* had four members: a mated pair, an adult male born to them in 1977 and a male yearling born to them in 1978. (The older nonbreeding male helped to raise its siblings born in 1978.) The group also included two female hangers-on, one that was born to the mated pair in 1978 and another that we believe was born to them in 1977; these individuals rarely interacted with the members of the pack but were allowed to remain in their vicinity. From November, 1978, through the following May (and beyond) the four main members of Group *B* were highly cohesive: eating, sleeping, traveling and defending carrion in close association with one another. In this period only 6 percent of the sightings of pack members were of single individuals and more than 50 percent were of all four pack members together. From November through April the male and female of Group *A* were observed together 71 percent of the time, and on the remaining occasions each animal was seen in the vicinity of other coyotes, although not in close association with them.

Seasonal variation in the sociability of coyotes may reflect a seasonal fluctuation in the availability of different prey items. This chart compares the frequency with which groups of different sizes were sighted from Blacktail Butte in Grand Teton National Park In Wyoming during the "summer" season (May through October) and the "winter" season (November through April). In summer *(color),* when coyotes sustained themselves by catching rodents, they were significantly Jess social than in winter *(light gray),* when ungulate carrion was available.



It has been observed that when coyotes other than a mated pair spend a winter together, there is an increased probability they will also spend the summer together. Our observations of the two groups in the area of Blacktail Butte indicate that when winter food is in good supply, older pups may continue to share at least a part of their parents' home range, and that if the pups remain in association with their parents throughout their first winter, there is a good chance that as yearlings they will remain through the following summer and perhaps beyond. It is interesting to note that two of the young that left the home range of Group *A* (the mated pair) in the fall of 1978 returned to it (from the National Elk Refuge, where they had

spent the winter) the following spring, their return coinciding with the seasonal increase in rodents on the parental home range. These yearlings have remained solitary, not helping to raise their younger siblings, and in general they appear to be less closely bonded to their parents than the yearlings in Group, which never left the pack.

During the past winter (1979-80) there has been another interesting development in the relation between food availability and social organization in the coyote groups living in the vicinity of Blacktail Butte. In the previous two winters heavy snows fell in our study area in December, but this year snow did not blanket the home ranges of Group *A* (the mated pair) and Group *B* (the pack) until late January. As a result rodents were available in greater number and for a longer period than they had been in the preceding winters, supplementing the usual winter supply of elk carrion. In the previous two winters all the young from Group *A* had dispersed by November, but this year a juvenile born in April, 1979, was still with its parents in February. (In Group *B* three juveniles born in April, 1979, still remained with the pack in February.) Thus it appears that a naturally occurring change in the coyotes' food resources resulted in a change in their social organization, at least over a short period of time. The consequences of this change will be investigated in the future.

Social bonding is not the only aspect of coyotes' social behavior that is affected by variations in the food supply. Such variations also have a strong influence on how the animals make use of space. For the purposes of this discussion it is important to understand the distinction between a home range, the area an animal or a group of animals covers routinely in the course of its daily activities, and a territory. A home range has a flexible, undefended boundary, so that the home ranges of different individuals or groups may overlap considerably. A territory, on the other hand, is defined as the area that an individual or group occupies to the almost complete exclusion of other animals of the same species and that it will actively defend against them. In some geographical areas coyotes clearly defend their territory against other animals, but in other areas there is no evidence that they are territorial. Our own findings indicate it is only coyotes in packs that are territorial; individuals with a fixed home range but living alone or in mated pairs are not. Consider the two coyote groups we observed in the area of Blacktail Butte.

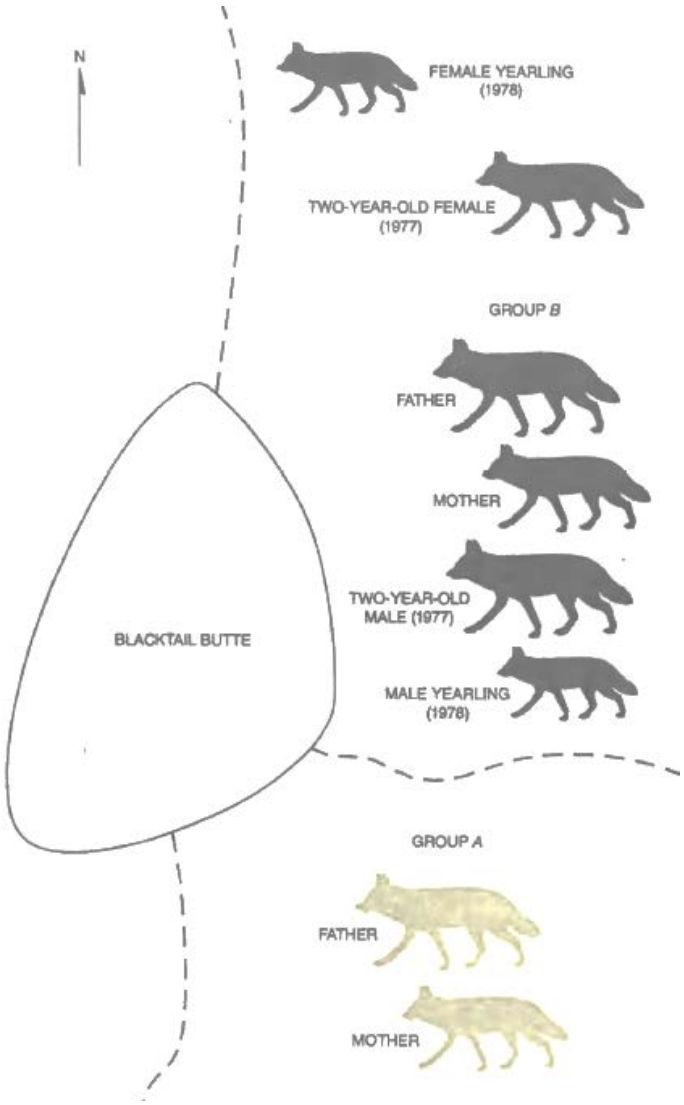
The four members of Group *B* maintained as a group a territory with rigorous boundaries between themselves and Group *A,* the mated pair. They also repelled many other coyotes from their territory, sometimes chasing an intruder for as much as two or three kilometers. (In April, 1979, we saw the breeding female of the pack chase an intruding coyote for a kilometer only a few days after she had given birth to a litter, and when she returned to the den, her mate chased the intruder for three more kilometers.) On the other hand, the two members of Group *A* were never seen defending a part of their home range against any other coyote. These findings, which are confirmed by those of other workers, indicate that the intensity with which an area is defended by individuals or groups is related to the presence of a large, clumped food resource.

We also found that a shortage of food clearly brings about increased trespassing into neighboring home ranges and territories, particularly those in which desired food items can be found. For example, although Group *A,* the mated pair, made frequent forays into the territory defended by Group *B,* no member of Group *B* was ever observed intruding onto the home range of Group *A* In fact, the members of the pack rarely left their own territory, which is not surprising considering the wealth of ungulate carrion in it.

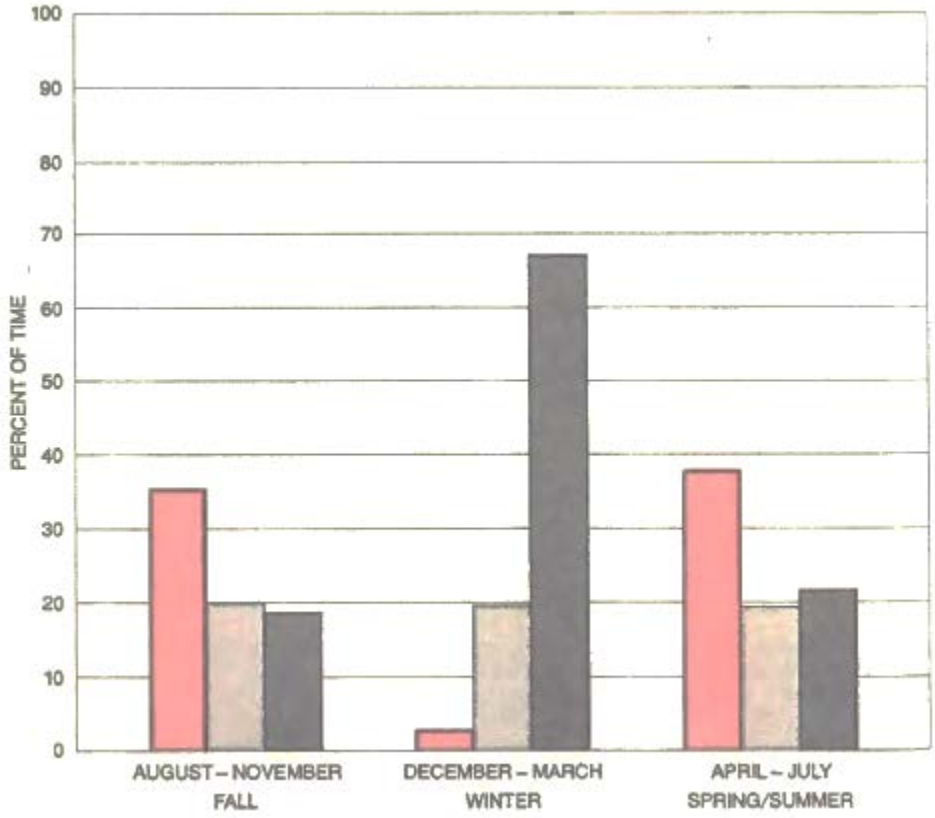
The sizes of coyotes' home ranges and territories vary markedly, although not consistently, with the locale, the season and the year and also with the age and the sex of the individuals. When we measured the home ranges of 10 adults in the Blacktail Butte area, we found that the average size was 21.1 square kilometers, with no discernible differences according to sex. When we classified the home-range sizes according to the coyotes' social groupings, however, we found that solitary individuals and mated pairs,

which are excluded from carrion in winter, have a larger home range, with an average size of 30.1 square kilometers. Pack members, which defend a food resource in winter and tend to remain in their own territory, have an average home range of only 14.3 square kilometers. The sizes of pack members' home ranges also show considerably less variation, probably because of the clumped distribution of ungulate carrion.

Two coyote groups inhabiting contiguous home ranges in the area around Blacktail Bntte had access to significantly different amounts of elk carrion in the winter of 1978-79. (A home range Is defined as the area an Individual or a pack travels routinely In the course of its daily activities.) The home range of Group *A* held 17 percent of the available carrion, whereas the home range of Group *B* held 83 percent. As is shown here, the sizes of the groups differed accordingly: Group *A (color)* consisted of only a mated pair, all the young from previous years having dispersed; Group *B (gray)* consisted of a mated pair, a two-year-old male born to them In 1977 and a male yearling born to them In 1978. (One of the advantages of pack living may be that a breeding female receives help in caring for her young; the two-year-old in Group *B* helped to raise its siblings born in 1978.) Pack also included two hangers-on: a female born to the mated pair in 1978 and a female believed to have been horn to them in 1977. These coyotes rarely interacted with their parents or siblings but were allowed to remain near them.



Relative amounts of time that coyotes in the area of Blacktail Butte devoted to the activities of hunting *(color),* traveling *(light* gray) and resting *(dark* gray) in different seasons are shown. In winter, when the coyotes depended mainly on elk carrion, the animals hunted less and rested more than they did at other times of the year. Coyotes generally mate in the winter months, and their relative inactivity in this season may be beneficial for the breeding females. A comparison of the winter activities of traveling and resting for mated pairs living in packs and those living alone reveals additional energy savings for the former. Percentages are based on 668 coyote-hours of observation (one coyote-hour is defined as observation of one coyote for one hour) from September, 1977, through August, 1979.



Pack living confers advantages not only in the defense of food resources against competitors but also in reproductive activities. Coyotes generally mate in the period from January to April, the date varying from one locale to another. The female coyote's pregnancy rate, her productivity and her pups' rate of survival are clearly related to the general state of her health, which in turn is closely linked to the quantity and quality of the food available to her before and during pregnancy, that is, to the winter food supply. Therefore the increased ease with which pack members are often able to locate food items may represent an important reproductive advantage. Moreover, when we examined the amounts of time coyotes invest in other types of activity in winter and summer, we made an interesting discovery.

Coyotes typically are active in the early morning and early evening, but when we compared the time 50 coyotes (35 of them marked) devoted to hunting and resting, we found that in winter, when carrion is available but the food supply is usually low, much less time is spent hunting and considerably more is spent resting than is the case in summer, when small rodents are readily available but must be found, caught and killed. The higher ratio of resting time to hunting time may be generally beneficial for pregnant females, which must conserve energy for the nutritional demands placed on them during the nine-week gestation period and afterward. (There are six pups in an average coyote litter, and they are altricial, or

dependent, at birth, requiring feeding and protection for the first few months of their life.) If females living in packs are able to spend more time resting than females living alone with their mate, then the pack-living females might reproduce more successfully. Moreover, as we have mentioned, females living in packs are more likely to receive help in raising their offspring.

Our findings about the pack-living adaptation of coyotes are supported by data gathered for golden jackals and hyenas, and we have been able to draw some general conclusions that should be tested with other species of carnivores. We have found that in situations where there are "haves" and "have-nots" with respect to the winter food supply (that is, individuals living in an area where a food resource is large and clumped as opposed to individuals living in one where the resource is scarce) the haves (1) are more social and cohesive than the have-nots, (2) are territorial and will defend the food resources, (3) have a more compressed home range, (4) are subject to higher rates of intrusion by members of the same species on the areas where the food is clumped and (5) in winter are able to travel less and so rest more. And the advantages of pack living can include any of the following: (1) food can be more successfully defended, particularly in winter; (2) food items can be more readily located; (3) individuals, particularly sexually mature females, can conserve energy needed for reproduction and care of the young, and (4) help, in the form of feeding and protection, can be provided for the young by individuals other than parents (most likely older siblings). Whether or not pack living confers an advantage in the acquisition of large prey remains an open question.

So far we have mainly discussed the pack-living adaptation to defendable food resources, but solitary living is also an adaptation to a particular food resource. For the coyotes we observed from Blacktail Butte the resource is rodents: prey items that coyotes cannot defend against other coyotes and that are difficult to share except with pups. Our studies have shown that even coyotes living in cohesive groups become temporarily solitary when they are hunting rodents. Hence just as it is important to study the various patterns of behavior associated with the group defense of territory and food, so it is important to study the various patterns of behavior associated with solitary predation. Not much is known about how wild coyotes locate and capture prey, but we have done several experiments to throw some light on this type of behavior.

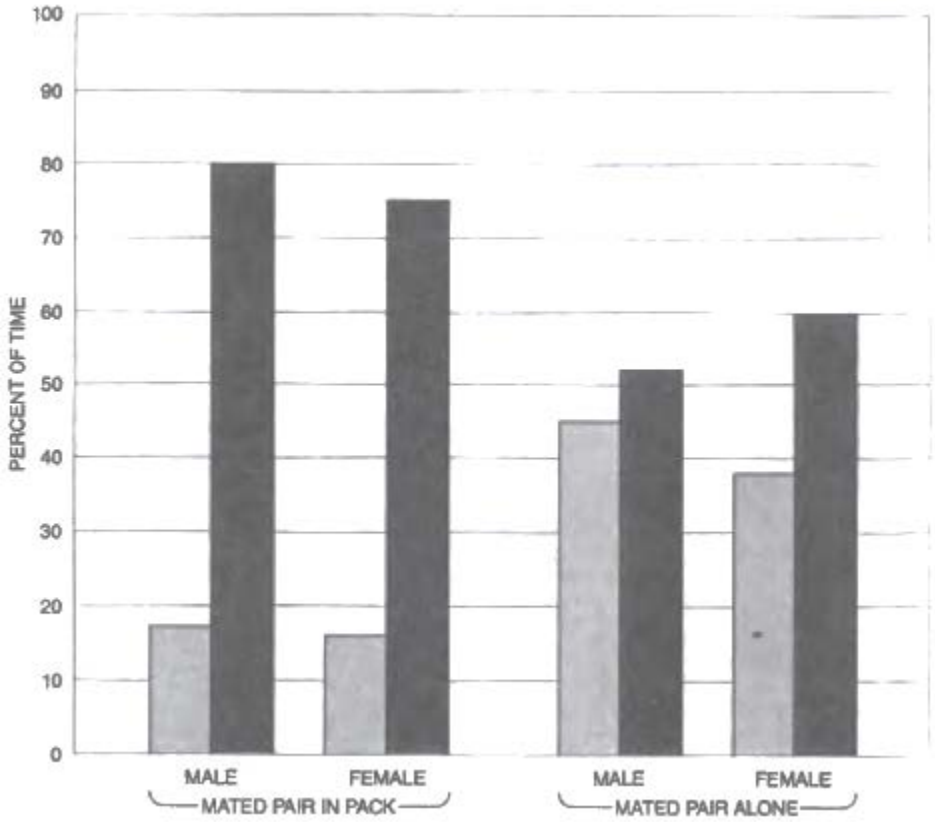
To begin with, the process by which any predator locates prey is complex, and different species of carnivores go about the task quite differently. Visual, auditory and olfactory stimuli are all clearly important and in nature probably interact to elicit the predator's response to the prey. It is interesting, however, to try to determine the relative importance of these three types of stimuli for coyotes and to try to relate such findings to the natural history of the species. The experiments required for the purpose are best done with captive coyotes, under conditions in which external stimuli can be rigorously controlled.

In the first set of experiments, conducted at Colorado State University in collaboration with Philip N. Lehner, coyotes were placed in a small room 30 meters square with a hidden rabbit. The time individual coyotes needed to find the rabbit with all possible combinations of the three types of stimuli was measured. Visual stimuli were suppressed by eliminating all light from the room (in which case the coyotes were tracked by means of infrared motion-picture photography), auditory stimuli by using a dead rabbit as prey and olfactory stimuli by either blowing a masking odor into the room (the odors from a rabbit colony) or by irrigating the coyote's nasal mucous membranes with a zinc sulfate solution.

The results of the experiments showed that when visual cues were present, the absence of auditory or olfactory ones led to only minor changes in the duration of the coyote's search for its prey. For example, with all three stimuli available the average search time was 4.4 seconds; with nothing but visual cues available the figure rose only to 5.6 seconds. With visual cues removed and only olfactory and auditory ones present, the average search time rose to about 36.1 seconds, or eight times the duration with all

three types of stimuli. When auditory cues alone were present, the search time decreased slightly, to an average of 28.8 seconds; when olfactory cues alone were present, it went up to 81.1 seconds. With all three types of stimuli suppressed, it took the coyotes an average of 154.8 seconds, or more than 2.5 minutes, to find the prey by means of touch.

Mated female in a pack spends significantly mon time resting *(dark gray)* and significantly less time traveling *(light gray)* in winter than a female living alone with her mate, as is shown by this chart comparing these two activities for the breeding male and female in Group *A* (the mated pair) and Group *B* (the pack) in the vicinity of Blacktail Butte. Females living in packs have not been observed to reproduce more successfully than other females, but it appears that if food became a limiting factor, then the pack-living females' substantial net energy savings might give them a reproductive advantage.

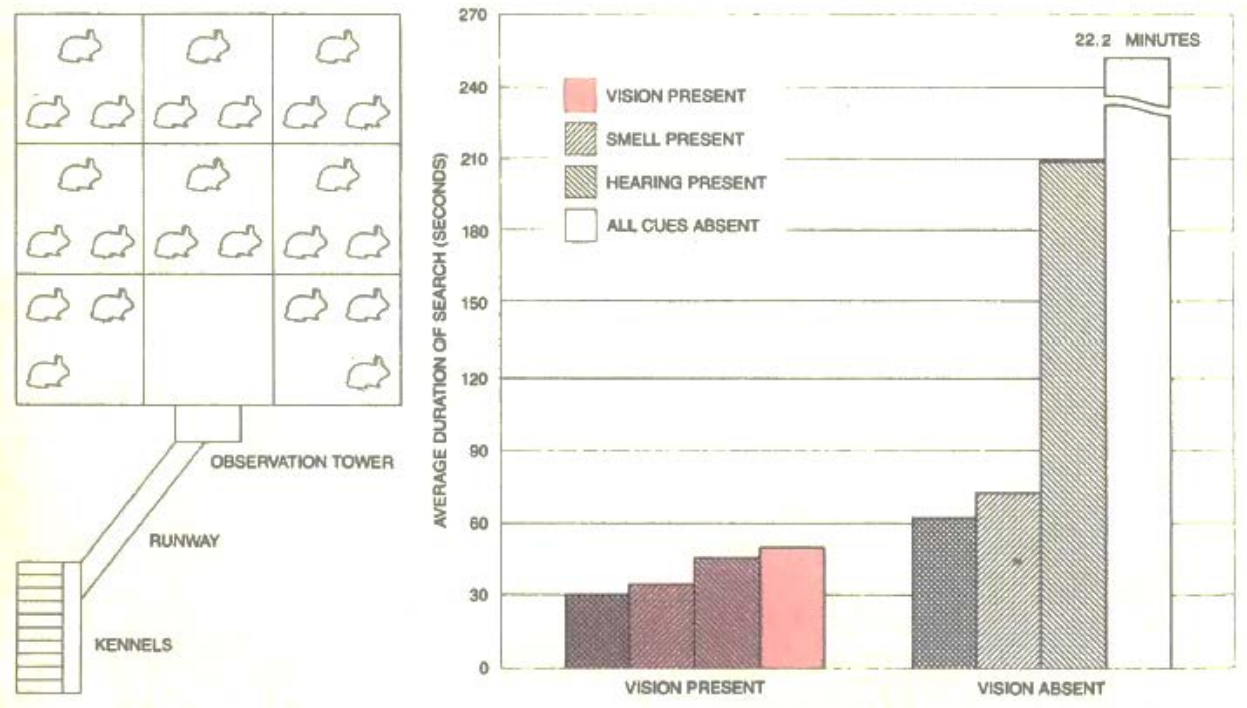


Thus under these experimental conditions the senses that facilitate the location of prey for the coyote are, in decreasing order of their importance, sight, hearing and smell. The fact that vision is of primary importance is confirmed by the results of another series of experiments in which coyotes were presented simultaneously with a hidden rabbit making sounds (breathing, rustling and so on) and a visible rabbit making no sound. The visible rabbits were without exception captured first. The coyote probably evolved on open plains covered with low-growing grasses, where prey would be highly visible, and its heavy reliance on vision is presumably the result of adaptation to this habitat.

In order to replicate the coyote's natural hunting environment more closely a similar set of experiments was run outdoors in a large fenced-in area (6,400 square meters) at the Maxwell Ranch, owned by Colorado State University. With the larger search area and the larger number of distracting factors outdoors the average search times were all higher, but once again vision proved to be the most important sense in locating prey. Here, however, smell proved to be more important than hearing: the coyotes could

find the rabbits faster with visual and olfactory cues present (when they needed an average of 34.5 seconds) than with visual and auditory cues present (when they needed an average of 43.7 seconds). Similarly, with only olfactory stimuli present the coyotes took an average of 72.7 seconds to locate the prey, and with only auditory stimuli the average search time rose to 208.8 seconds. When all three types of stimuli were present, the average search time was 30.1 seconds; when all three were suppressed, the average rose to about 22.2 minutes.

Experimental setup for determining the relative importance of the senses of vision, smell and bearing for coyotes in locating prey is shown at the left. In each trial a rabbit is placed at random at any one of 24 possible locations In a large outdoor enclosure (6,400 square meters); a coyote is admitted to the enclosure, and the time required for it to find the rabbit is recorded. The procedure was repeated for five coyotes with all possible combinations of the three types of sensory stimuli present. Visual cues were eliminated by testing coyotes on a dark night (and observing them with a "starlight scope," which intensifies available light); auditory cues were eliminated by using a dead rabbit as prey, and olfactory cues were eliminated by irrigating coyotes' nasal mucous membranes with zinc sulfate solution. Average time required to locate prey under each condition is shown at right. Results of trials with visual cues present *(color) h*ave been separated from those with visual cues suppressed, showing that In locating prey coyotes' most Important sense is vision. Hearing is least important.



The differences between the results of the indoor experiments and those of the outdoor ones can be explained by taking into account the effects of the wind. Airborne olfactory stimuli are clearly important directional cues to a hunting coyote, as is indicated by the fact that outdoors, where smell was more important than hearing, 83.9 percent (47 out of 56) of the approaches to the rabbit were made from the downwind side. Similarly, at our study site in Grand Teton National Park we found that 74.9 percent of all the approaches we observed to mice by wild coyotes were from the downwind side. In addition, in the outdoor experiments where only olfactory cues were available to the coyotes, a significant correlation was observed between wind velocity and approach distance, or the distance at which a hunting coyote

becomes aware of the location of its prey. More precisely, as the wind velocity increased the approach distance increased as well, so that when the wind was 10 kilometers per hour, the approach distance was about two meters, whereas when the wind rose to 40 kilometers per hour, the approach distance increased to about five meters.

Hence although the coyote seems to depend most heavily on vision when it is hunting, it appears to have effective backup systems that can be relied on when certain types of sensory cues are absent or inadequate. When prey are visible, pursuit based on visual cues is most likely to start before olfactory or auditory cues can come into play, but when the prey is well hidden, the coyote probably relies on some combination of olfactory and auditory cues. (The exact combination probably depends on the wind conditions and the amount of noise made by the prey.) Coyotes are highly efficient predators and can clearly switch back and forth between these various hunting modes in order to take maximum advantage of whatever the environmental conditions are at the time.

How does the coyote actually kill the prey it locates? Information on the subject may be useful not only to biologists interested in the comparative and evolutionary aspects of predatory behavior but also to those concerned with the control and management of predators. Here it will be most convenient to distinguish between prey animals that are smaller than the coyote and those that are larger. (Coyotes do occasionally prey on large live animals, although as our observations of the coyotes in the area of Blacktail Butte indicate, this form of predation is rare.)

To begin with, we have observed seven distinct activities that can be included in the predatory behavior of a coyote when its prey is a small animal such as a rodent. In sequence they are long-distance searching (in which the coyote traverses large areas and scans the ground cover for a sign of prey), close searching (in which the coyote pokes around in the ground cover), orientation (in which the coyote assumes an alert posture, perhaps sniffing or pricking its ears to determine the exact location of detected prey), stalking (in which the coyote slowly and stealthily approaches its prey), pouncing (in which the coyote first rears up on its hind legs and then falls forward on its front legs to pin the prey to the ground), rushing (in which the coyote makes a rapid dash toward the prey) and finally killing. A coyote generally kills a rodent by biting it in the area of the head, and in many cases the coyote will also shake the prey vigorously from side to side.

It is important to understand that not all these activities are always included in a single predatory sequence. For example, we found that if the prey is a smaller rodent such as a field mouse, a coyote does not usually rush the rodent but simply stalks it and then pounces on it, pinning it to the ground so that a killing bite can be delivered. When the prey is a larger rodent such as a Uinta ground squirrel or a Richardson's ground squirrel, however, the coyotes we observed rushed it in more than 90 percent of the cases and pounced only rarely.

The success of the coyote's predatory sequences in catching and killing rodents varies considerably. Our data indicate that coyotes are successful between 10 and 50 percent of the time. We have not yet identified all the variables that influence the rate of success, but ground squirrels seem to be easier to catch than mice. The hunger level of a coyote may also be important. Observations in captivity reveal that satiated coyotes often play with a rodent before killing and eating it, and frequently the rodent escapes. Similar observations have been made in the field.

We also wondered whether the predatory skills of coyotes improve with age, and so we compared the time that nine young coyotes from three to six months old and 15 adults spent in the activities of searching, orienting and stalking when they were hunting mice or ground squirrels. The adults, it turned out, spent less time searching and orienting, and in addition the times adults devoted to these activities

were much less variable than those of the pups. There was no difference in the time spent stalking, however, an activity to which coyotes in both age groups devoted an average of about 5.5 seconds. Therefore it would appear that the pups are less effective than the adults in locating their prey, but once the prey has been located coyotes in either age group will stalk briefly and then go in for the kill. Studies of coyotes in captivity also reveal that pups only 30 days old are capable of carrying out a successful predatory sequence on a mouse. In other words, although coyotes of that age rarely have an opportunity to kill a small rodent in the wild, they clearly have the ability.

Turning to the subject of how coyotes kill large wild prey, such as sheep, deer, elk and moose, there are for a number of reasons few observations from which useful generalizations can be drawn. To begin with, coyote kills are often indistinguishable from those of other wild predators or even domestic dogs. Moreover, it has been noted that most healthy ungulates living in the same locale as coyotes are able to defend themselves against a single coyote, so that instances of such predation are rare and hence difficult to observe. The few data that do exist indicate that two or more coyotes are usually required to take down, say, a healthy adult deer. In most cases coyotes appear to kill either young ungulates or weak ones, typically by attacking the head, neck, belly and rump. It is generally believed coyotes do not have any significant detrimental effect on wild ungulate populations.

The effects of coyote predation on domestic sheep are less clear-cut, which brings us to a more controversial aspect of coyote biology, namely the management and control of coyotes. Coyotes are said to have a significant detrimental effect on the sheep industry, and as a result for a century coyotes have been a particular target of predator-control programs. At present large amounts of time, energy and money (in many cases from public funds) are being devoted to such efforts. The returns on the investment are small, in terms both of reducing coyote populations and of preventing livestock losses and damage. The failure of the control and management programs is due essentially to the lack of sufficient background information on the behavioral and population dynamics of coyotes.

Indeed, very little is known about the predatory habits of wild coyotes with regard to domestic sheep. Guy Connolly and his colleagues at the United States Fish and Wildlife Service have found that even when coyotes are confined with sheep, their predatory behavior is surprisingly inefficient. In these experiments coyotes killed sheep in only 20 out of 38 encounters. Moreover, both the average time that elapsed before the coyotes attacked the sheep (47 minutes) and the average time that elapsed before the sheep were killed (13 minutes) were quite long, totaling an hour. The defensive behavior of the sheep deterred the coyotes in only 31.6 percent of the cases, and so it is understandable that the coyotes would take their time before killing the sheep. Of course, there are no instances of such inefficient predation in natural predator-prey interactions, where the prey either flees or actively fights off the predator as long as it can. It is clear, however, that sheep, which have been subjected to artificial selection by the great domesticator *Homo sapiens,* have been left virtually defenseless against predation.

Coyotes do kill sheep, then, as well as other livestock and poultry. Many studies have shown, however, that factors other than coyote predation can cause considerably heavier losses. For example, it was reported in a recent study that in the early 1970's the value of the losses of ewes and lambs in the state of Idaho amounted to $2,343,438. Of this total 36 percent could be attributed to disease, 30 percent to unspecified causes and 34 percent to predation; only 14.3 percent of the losses could be attributed to predation by coyotes. Moreover, there are data to indicate that not all coyotes are sheep killers and that the indiscriminate killing of coyotes in areas where sheep are being killed is an ineffective method of control. A recent study of livestock predation in 15 Western states issued by the Animal Damage Control Program of the Department of the Interior concluded that the relation between such predation and the population dynamics of coyotes is obscure.

In a sense the coyote is victimized by success: it is threatened because it takes advantage of livestock that have been robbed of most of their defenses by shortsighted practices of domestication. It is to be hoped that in the future defensive behavior will be bred back into livestock. For the present one can only assume that the failure of predation control is due to a lack of basic knowledge about predatory species, a problem that can be remedied by further studies of behavior and ecology of the kind we have described here.

We have found the coyote to be a particularly good subject for such investigations. Further field study will be needed to determine to what extent our findings can be applied to other coyote populations, to closely related species and to carnivores in general. In the meantime coyotes should be appreciated as animals that have adapted remarkably well to the pressures exerted by their environment, including harassment by man and the severe restriction of their natural habitats.