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FINAL REPORT

THE MAMMALIAN PREDATOR COMMUNITY

OF WIND CAVE NATIONAL PARK

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ABSTRACT

The purpose of this study was to describe the mammalian carnivore community of Wind Cave National Park and to discover the factors which determine its structure. The initial phase of the project was devoted to surveys of Park records, State records, and local trappers for accounts of carnivores in the southern Black Hills and to a thorough description of the Park's current predator community. Historical records suggest that coyotes, badgers, and bobcats are the carnivore species most consistently present, coyotes comprising the bulk of individuals. Foxes, raccoons, skunks, and other members of the weasel family have been rare or absent. The second year of this project dealt with radiotracking some of the Park's coyotes and with an experimental introduction of skunks. The report concludes that the carnivore fauna of Wind Cave National Park is less diverse than that of the surrounding southern Black Hills and discusses the causative factors that may underlie this phenomenon.

INTRODUCTION

This study was motivated by the concerns of personnel at Wind Cave National Park (WCNP) that the species diversity of the Park's mammalian carnivore community is unreasonably low, that certain species common in the southern Black Hills, such as raccoons (Procyon lotor) and striped skunks (Mephitis mephitis), are rare or absent, and that the causes underlying these patterns are not obvious.

The factors which structure carnivore communities are not well understood. Since the traditional focus of wildlife ecology has rested heavily upon individual species rather than upon the communities they comprise, little of the published literature on carnivores addresses the issues of species interaction and community structure. Some speculation has been published on the topic (e.g. Rosenzweig 1966, Schmidt 1986), but the amount of reliable data is not great.

The tendency of wildlife biologists to explain the ecology of species in terms of habitat parameters is only partially justified with carnivores. To be sure, some carnivores have specific habitat requirements. Mink (Mustela vison) and otter (Lutra canadensis), for example, tend to be associated with aquatic and riparian habitats. Small carnivores may be subject to predation themselves and

so restricted to secure habitats. And a great deal of evidence suggests that habitat use and home-range sizes of predators are related to the distribution and abundance of prey (e.g. Litvaitis et al. 1986) and thereby to the habitat affinities of those prey. Beyond this, the community ecology of carnivores gets complicated.

To deal with the Park's concerns, the following specific research objectives were identified:

1. determine, as best as possible, the history of the mammalian carnivore community in WCNP,
2. assess the structure of the existing predator community within and adjacent to the Park,
3. develop population indices for the predatory species inside the Park,
4. assess the impact of management practices within WCNP on the predator community, and finally
5. generate a set of hypotheses to explain the absence of certain species of carnivores and a concomitant set of management recommendations for how these species might be allowed to reestablish populations within the boundaries of WCNP.

The first year's work was meant to focus on objectives 1-3; the second year's work would treat objectives 4 and 5.

METHODS

Wind Cave National Park is situated at the southern tip of the Black Hills of South Dakota. The vegetation and topography of the area have been described by Turner (1974). The Park itself is a mosaic of pine forests and short-grass prairie. From the perspective of a carnivore, WCNP consists primarily of a set of discrete prairie dog towns with seasonally available deer and antelope fawns and elk and bison carrion.

Objective 1, the discovery of the history of WCNP's carnivore fauna, was achieved by examination of Park records. These consisted of reports of past superintendents and wildlife observations collected by Park biologists. These records were organized systematically and placed on computer databases.

Objective 2, the assessment of the existing carnivore community, both within and adjacent to the Park, required several methods. The first was a thorough examination of the Park in both summer and winter for predators and predator signs (tracks, scats, etc.). This effort also included monitoring 5 ungulate carcasses and 71 trap-nights of live trapping with wire cage traps.

The second was the placement of scent stations throughout the Park in 1988. The scent stations consisted of circular areas, 1 square m in area, from which vegetation

was cleared and over which a thin layer of fine soil was sifted. A small plaster disc was placed in the center of each scent station. The discs were impregnated with a predator attractant, synthetic fatty-acid scent, produced by the USDA. These stations were examined 24 hrs after placement for tracks of carnivores.

The Park was divided into two strata of roughly equal size for scent-station sampling. Since historical records indicated that the diversity of carnivores was greater in the western half of the Park, approximately twice the density of scent stations was located in that stratum. Within a stratum the location of each station was chosen at random. A total of 200 scent stations was placed inside the Park.

The third and fourth methods addressed the issue of what species of carnivores live in the southern Black Hills in the vicinity of the Park. The third method was a poll of 11 fur trappers living in the vicinity of WCNP. In addition, records of the local Animal Damage Control officer and the South Dakota Department of Game, Fish, and Parks were examined for evidence of local carnivores.

The fourth method was a direct assessment by means of scent stations of carnivore communities in areas adjacent to the Park. Seventy-five stations were located in Custer State Park in 1989 in areas comparable in vegetation to Wind Cave. An additional 50 stations were placed in the

Angostura Reservoir Area south of Hot Springs. These stations were set out and counted at the same time of year and using the same procedures as the scent station survey in the Park in 1988.

Objective 3, the development of population indices, proved to be impractical, except for coyotes. Other species were too rare to provide a reliable index for a reasonable amount of work. Scat transects tend to provide the most cost-effective index to coyote numbers. Eighteen one-mile-long transects were established on the Park in the summer of 1989. To get more detailed information on coyotes than these transects could provide, efforts were made to capture coyotes in the winter and early summer of 1989 and equip them with radio transmitters. A total of 4 coyotes, 2 adult males and 2 adult females, were captured with snares, sedated with ketamine hydrochloride, and equipped with radiocollars manufactured by Advanced Telemetry Systems, Bethel, Minnesota.

Objective 4 was approached by selecting a target species, striped skunks, and mounting an experimental reintroduction. Five skunks were equipped with radiocollars and released in the Park in the summer of 1989. One was released outside the Park. My expectation was that the fates of these animals would provide information that could reflect upon why the Park seems to be unsuitable for skunks.

RESULTS AND DISCUSSION

The historical records of predators are summarized in Fig. 1. These data are presented only as presence or absence records, since systematic sampling methods for predators have never been employed by Park personnel. The records fall into three groups, as far as quality is concerned. The first spans the period from the establishment of WCNP to 1925. In this interval carnivores were seen as barriers to the successful establishment of a herd of pronghorn antelope (Antilocapra americana) and were actively removed. Although one can question the motives of the managers at that time, they were at least systematic in recording the numbers of coyotes and bobcats killed. The second interval extended from 1925 to the mid 1970's. During this period systematic records were kept for no more than a few years at a stretch. The final period extends from 1978 to the present. Records in this interval are largely anecdotal but were made in such detail that they can be considered reliable. One can safely infer from these data the following:

1. Coyotes, bobcats, and badgers are consistently seen on the Park. Coyotes have always been common; badgers less so. Bobcats have been rare, perhaps rarer now than in the 1920's.

2. Cougars (Felis concolor) are occasionally seen on the Park, but not every year and never for long.
3. Striped skunks and raccoons have always been rare on the Park, particularly in recent years.
4. Other mustelids, weasels and ferrets, are extremely rare. Black-footed ferrets (Mustela nigripes) were introduced into the Park in the mid-1950's but have not been seen since.
5. Red foxes and swift foxes (Vulpes velox) have never been recorded on the Park.

Given the spotty nature of Park records, my primary goal in 1988-1989 was to provide an accurate account of the existing carnivore community. Evidence was obtained in that year of coyotes, bobcats, badgers, one fox, and one raccoon. Bobcat tracks were seen during the winter in Wind Cave Canyon. Fresh badger diggings were seen on several of the prairie dog towns and along Beaver Creek during the summer. Fox tracks were seen in lower Reeves Gulch during the summer, and a fox was sighted at a distance. This animal could not be positively identified to species, although the small size suggests that it was a swift fox. One raccoon was glimpsed briefly in the vicinity of the Park's headquarters. Live traps set at Cold Spring Creek, Beaver Creek, Reeves Gulch, the Headquarters area, and the bison trap caught no carnivores. The five elk and bison carcasses were used extensively by coyotes, but no other species was

seen near them.

By their rarity, these observations suggest that no species except the coyote is common on the Park. Figure 2 displays all evidence of coyotes gathered in 1988-1989. Of the 200 scent stations set out, 189 yielded data; the remainder were destroyed by bison. The 26 scent stations visited by coyotes are indicated with open circles. The x's indicate either direct sightings or signs of coyotes in the summer of 1988. The c's represent captures, sightings, or signs of coyotes in the winter of 1989.

Figure 3 displays the results of the telemetry effort with coyotes begun in the winter and extending through the summer of 1989. Four animals were captured, 2 females and 2 males. These animals were labeled with numbers that reflected the frequencies of their transmitters, so that, for example, the transmitter of female 025 broadcast at 151.025 MHz. Ground telemetry proved to be quite difficult in the western portions of the Park. My graduate student made a single attempt to locate every animal from the air on August 23, 1989.

Female 025 was captured February 26, 100 m west of NPS 6 in Red Valley. She was relocated 13 times, usually in the southern portion of Red Valley, although once, on March 1, she left the Park to the east. She was last located September 2. This animal was an adult and quite large, possibly a young territory-holding animal, although gross

examination showed no evidence of recent breeding activity; the mammae and vulva were not enlarged.

Female 037, a yearling, was captured in Reeves Gulch, about 3/4 mi north of Beaver Creek Canyon on January 27. At that time she showed bare spots on her rump, indicating that she may have been breeding. She was located twice more in March and not at all thereafter, which indicates either that the transmitter failed or that she dispersed from the Park prior to August 23.

Male 064 was captured on January 22 in the Bison Flats prairie dog town. This animal was a mature male. Its testes were completely descended, and its teeth showed wear. It was located twice more, the last location being March 1. Attempts to locate it after that, both on the ground and from the air, were unsuccessful.

The last animal captured, male 084, was snared on August 4. This male showed signs of age; one canine was broken and then worn smooth and it had several old scars on its muzzle and legs. Attempts to relocate this animal were unsuccessful.

I interpret these data to indicate the following:

1. Female 025 may have been a new territory holder, since females normally leave their natal territories fairly young.
2. Female 037 was a yearling female caught just before dispersal.

3. Male 064 was a territory-holding male that was displaced during the spring.

4. Male 084 was an old male that had been ejected from a territory and was just passing through the Park.

These inferences require that I assume that the transmitters did not fail. It is extremely unlikely that 3 of 4 commercially built transmitters would have failed within a few months of being placed in service. It is equally unlikely that their signals could not have been detected from the air. The logical conclusion is that the coyote population of WCNP exhibits a good deal of interchange with that of the surrounding area.

In Fig. 4 I summarize all the locational data and draw preliminary boundaries of coyote territories on the Park. Beaver Creek Canyon is a conspicuous territory boundary. Many scats were discovered along the creek, and I once observed a howling contest over a bison carcass between adjacent coyotes at the confluence of Beaver Creek and Reeves Gulch. The pair occupying the northwest territory appeared to have reproduced successfully in 1988; one young coyote was seen in September, and small tracks associated with large tracks were seen in late August of that year. The three locations of male 064 suggest that the southwestern corner of the Park comprises another territory. The locations of female 025 clearly demark a third territory in the southeastern portion of the Park. And the large

number of signs and scent station visitations in the mid and northeastern portions of the Park suggest an additional territory. None of the territories is without at least one substantial prairie dog town. I must emphasize that these are preliminary boundaries. An intensive telemetry study would almost certainly result in alteration of these lines and might even suggest an additional discrete territory in the northeast corner.

The 18 scat transects (Fig. 5) were all located along roads and trails. The numbers by each represent scats deposited in a 5-day period during the summer of 1989. The fact that no more than 1 scat was found on any transect may make this method imprecise for any but qualitative uses.

The primary source of information for the composition of the carnivore community in areas adjacent to the Park was a survey of 11 local fur trappers. All 11 returned the form. Their answers, summarized in Table 1, indicate that the southern Black Hills contain substantial populations of coyotes, red foxes, skunks, and raccoons. Occasionally trappers caught swift foxes, bobcats, mink, and badgers. The most noteworthy result of this survey is that red foxes, raccoons, and skunks, three species absent or uncommon on WCNP, seem to be reasonably abundant within five mi of the Park's boundary. Table 2 lists data for 1987-1988. These are dominated by the activity of a single trapper who spent little time working near WCNP. Interpretation of Tables 1

Table 1. Fur trapper survey of the southern Black Hills, 1988-1989. The data are the total numbers of animals captured.

<u>SPECIES</u>	<u>PROXIMITY TO WIND CAVE NATIONAL PARK</u>				
	<u>< 1 MI</u>	<u>1-3 MI</u>	<u>3-5 MI</u>	<u>> 5 MI</u>	<u>TOTAL</u>
Coyote	10	6	24	98	138
Red fox	0	1	8	69	78
Swift fox	0	0	0	4	4
Bobcat	0	1	4	13	18
Mink	0	0	0	23	23
Badger	0	3	1	21	25
Striped skunk	0	15	22	121+	158+
Raccoon	5	4	6	82	97

Table 2. Fur trapper survey of the southern Black Hills, 1987-1988.

<u>SPECIES</u>	<u>PROXIMITY TO WIND CAVE NAT. PARK</u>				
	<u>< 1 MI</u>	<u>1-3 MI</u>	<u>3-5 MI</u>	<u>> 5 MI</u>	<u>TOTAL</u>
Coyote	2	0	1	4	7
Red fox	0	0	4	31	35
Striped skunk	0	0	7	23	30
Badger	0	0	0	6	6
Raccoon	5	4	2	9	20

and 2 much beyond this is unwarranted, since no information is available on how much effort was directed toward trapping in each of the 4 zones.

A less accurate measure of what lives near the Park is provided by complaints to State Animal Damage Control personnel. Table 3 lists those for the period July 1, 1987 to June 30, 1988. Perhaps not surprisingly, coyotes were the source of the most complaints.

For a period of 10 yrs ending in 1980, USDA/ADC personnel ran a series of scent-station transects all over the West. Two of those lines were in the vicinity of the southern Black Hills. Line 13 was near Jewel Cave, and line 14 lay somewhat west of the Black Hills. Table 4 lists the species whose tracks were detected at these scent stations in the years 1977, 1978, and 1980 (Bean 1981) and the actual number of visitations. The identification of gray wolf tracks is unlikely to be accurate; the tracks of this species are often indistinguishable from those of large dogs.

Until 1980-1981, the South Dakota Department of Game, Fish, and Parks kept county-by-county records of fur harvests in the State. Table 5 lists these data for Custer County. Skunks, raccoons, and coyotes were the most common animals taken. Substantial numbers of red foxes were taken, relatively few badgers, minks, and bobcats.

Table 3. Animal complaints received by state ADC personnel in the southern Black Hills, July 1, 1987 - June 30, 1988.

Coyote	67
Fox	3
Raccoon	5
Skunk	3
Mink	1

Table 4. USDA/ADC scent station survey 1977, 1978, and 1980, South Dakota lines 13 and 14. Data are the number of visitations.

SPECIES	LINE 13	LINE 14
	1977	
Coyote	8	31
Kit (Swift) fox	1	0
Bobcat	1	0
Skunk	1	0
Gray wolf	1	0
	1978	
Coyote	22	90
	1980	
Coyote	9	0

A more precise comparison between the Park and adjacent areas is given by scent-station data. Table 6 compares WCNP to an adjacent area of Custer State Park and to a comparable area south of Hot Springs near the Angostura Reservoir by means of an index of scent-station visitation. The absence of raccoons and skunks in the Park and the presence of a single fox track have already been noted. Two additional features of this table merit attention. The first is that raccoons seem to be reasonably common both on Custer State Park and in the Angostura area. Those areas both differ from Wind Cave primarily in having more riparian habitat. To assess the effect of this difference, Table 7 partitions the data in Table 6 into upland and riparian areas for the two comparison samples. Raccoon visitation seems to be concentrated in riparian areas.

The second feature of Table 6 worthy of note is its information about skunks. This species seems to be absent both from Custer S. P. and from WCNP. Its presence in the Angostura area in 1989 is doubly impressive because of anecdotal evidence of a general collapse in the Black Hills skunk population in 1989. The primary difference between Wind Cave and Custer on the one hand and Angostura on the other is the density of coyotes. They are abundant in the parks and are severely depressed in the Angostura area.

I note anecdotally that two skulls collected south of Hot Springs by the Park's former research biologist were

Table 5. Fur harvest in Custer Co., South Dakota, 1980-1981.

<u>SPECIES</u>	<u>NO. HARVESTED</u>
Coyote	225
Red fox	87
Bobcat	19
Raccoon	258
Skunk	192
Badger	39
Mink	35

Table 6. Scent-station visitation in WCNP, Custer S. P. and the Angostura Reservoir area. The data are visits per 50 scent-station nights. Numbers in parentheses are the total scent-station nights in each area.

<u>SPECIES</u>	<u>WCNP (189)</u>	<u>CUSTER S. P. (73)</u>	<u>ANGOSTURA (44)</u>
Coyote	6.9	11.6	1.1
Fox	.3	0	1.1
Bobcat	0	.7	0
Raccoon	0	4.1	2.3
Skunk	0	0	3.4

Table 7. Scent-station visitation index by habitat type.

	<u>CUSTER S. P.</u>		<u>ANGOSTURA</u>	
	<u>Upland (49)</u>	<u>Riparian (24)</u>	<u>Upland (34)</u>	<u>Riparian (10)</u>
Coyote	14	6.3	1.5	0
Fox	0	0	0	5
Bobcat	1	0	0	0
Raccoon	1	10.4	0	10
Skunk	0	0	2.9	5

identified as gray foxes. While none of this species has been caught by trappers recently, the skulls suggest that it may on occasion be resident in the area.

To further probe the absence of common species from the Park, my graduate student mounted a release of radiocollared skunks in the summer of 1989. The 5 animals he released in the Park were trapped in the vicinity of the southern Black Hills and then held in captivity for 12-23 days. The results were less than satisfactory, due both to the unanticipated propensity of skunks to move large distances after release and to the difficulty of ground telemetry in the western half of the Park. Nonetheless, a short narrative is instructive.

Skunk E1 was a large (4.75 kg) adult male captured near Oral, SD on July 5, 1989 and released at the confluence of Cold Spring and Beaver Creeks on July 19. It was lost immediately. Its transmitter was discovered in December 1989 or January 1990 on the Streeter Ranch approximately 9 km SE of the release point.

Skunk E2, a juvenile female (1.5 kg) was captured near the Cheyenne River on July 2. She was released near the junction of Reeve's Gulch and Beaver Creek Canyon on July 19 and was never relocated.

Skunk E3, an adult female (2.45 kg) was captured near Oral, SD on July 21. She was released in Beaver Creek Canyon, 1 km below the SD 87 bridge. Upon release she

remained near Beaver Creek for about 16 hrs until it grew dark. Then she left the canyon and was lost.

Skunk E4 was a juvenile female (1.15 kg) caught in the Bismarck Lake campground in the Black Hills National Forest on July 27. She was released on August 15 at the horse corral above Park headquarters. She immediately struck out west for the Park's boundary and was lost after one hour.

Skunk E5, an adult male (3.55 kg), was captured near Oral, SD on August 10. It was held in a cage in Beaver Creek Canyon for one week prior to its release on August 22. The next day it was located from the air at a site 8 km down the canyon from where it was released. A subsequent effort to locate this animal from the ground was unsuccessful.

Transmitter failure is not a likely explanation of the disappearance of these animals. Two of the 5 clearly moved off the Park, and it is likely that the remaining 3 did also. Whether their somewhat surprising tendency to move following either a hard or soft release was motivated by features of the Park or simply by the novelty of the release site is unclear.

HYPOTHESES

The following conclusions appear to be justified. The dominant species in the mammalian carnivore community of the southern Black Hills is the coyote. This appears to be true both in WCNP and in surrounding areas. The Park and

adjacent areas exhibit some conspicuous differences. The Park's carnivore community is less diverse in general. Foxes are relatively common off the Park. My observation in 1988 is the first documented record of a fox in the Park's history. Raccoons and skunks are common in the vicinity of the Park, occasionally to the point of being pests. They are rare on the Park. Single observations of skunks and raccoons in the last couple of years are the first since the mid-1960's.

On the basis of this study I cannot definitively answer the question of why this difference exists. I can, however, construct a series of hypotheses to identify the range of alternative answers. This consists of the following:

Hypothesis 1: WCNP is too small to provide a minimum of one home range for a missing species.

Hypothesis 2: WCNP does not contain potentially suitable habitat for a missing species.

Hypothesis 3: WCNP contains potentially suitable habitat, but because of management policies, that habitat has been rendered unacceptable.

Hypothesis 4: Adequate habitat is available, but interactions with other carnivore species act to exclude a missing species.

These four hypotheses should not be considered equally plausible nor equally applicable to all species. I shall discuss each in turn.

Hypothesis 1: The physical size of WCNP is well in excess of that required for all carnivores whose historic range includes the Black Hills, with the exceptions of wolves (Canis lupus) and cougars. Wolves are endangered in the West and do not exist in the vicinity of the Park. The home range size of cougars is at least 25 square mi for males and from 5-20 square mi for females in areas undisturbed by humans (Hornocker 1969). These estimates would probably need to be increased by a factor of at least 2 for the Black Hills. This means that a male could be expected to spend only a fraction of its time in the Park. And if any portion of WCNP is deemed unattractive by a female, then its home range could not be contained within the Park's boundaries. This hypothesis, therefore, seems to be the simplest explanation of the episodic occurrence of cougars.

Hypothesis 2: Off the Park, raccoons seem to be associated most closely with riparian habitats. The extent of riparian habitat on the Park is quite limited. This hypothesis may, therefore, be a plausible candidate for why raccoons appear to avoid the Park. The absence of foxes, skunks, and other small mustelids is less easily explained since, with the exception of mink, these are less tied to riparian habitats. Nonetheless, this hypothesis cannot be ruled out.

Hypothesis 3: The impacts of management policies upon habitat characteristics relevant to predators can be divided into three categories, ungulate impact, prairie dog impact,

and human impact. The primary result of maintaining large ungulate herds on the Park is to provide a substantial amount of food for the larger carnivores. This food is in the form of deer and antelope fawns and perhaps the occasional elk calf in the spring and early summer followed by carrion in the late summer and autumn. The carrion is provided primarily by bull elk and bison that die as a result of the stress of the rut.

Coyotes profit most from this food supply. They attend carcasses and clean them up fairly quickly. The availability of ungulate young and carrion is thought to change the social structure of coyote populations, making the young less prone to disperse and coyotes more of a pack species. Although this study was not designed to address this issue, on the basis of our observations I am inclined to believe that the Wind Cave coyotes are not more social than is typical in the West. My student and I rarely found coyotes together. When we did it was usually at carrion sites and then only parents with young of the year.

It is difficult to envision how carrion and other manifestations of ungulates might directly impair the success of smaller carnivore species. Nonetheless large herds of ungulates have many direct and indirect impacts upon ecosystems, so this hypothesis must remain a possibility.

The decision of the Park to allow prairie dogs to

persist has resulted in about 280 ha of active colonies distributed throughout the Park. Most signs of bobcats, badgers, and coyotes occur in the vicinity of these colonies, and they must be considered the Park's primary prey resource. Other carnivores, with the exceptions of skunks and raccoons, also consume prairie dogs; therefore, it is unlikely that current prairie dog management interferes directly with the missing species.

Human impact is difficult to judge. On the one hand carnivores tend to be shy of humans, and the western portion of the Park is heavily used by visitors. On the other hand, the middle and eastern portions of the Park are very lightly used and should be suitable for shy species. Two of the missing species, raccoons and skunks, seem to habituate quite well to humans. I conclude that this does not seem to be a plausible hypothesis, short perhaps for cougars.

Hypothesis 4: If anything can be said of the last 20 years of ecological research on community structure, it is that the importance of competitive and predator-prey interactions to structuring communities cannot be overemphasized. The best of this research has been experimental and has, as a consequence, emphasized communities of animals tractable to experimental manipulation (Paine 1980).

Mammalian carnivore communities are not amenable to experimentation; therefore, we are only beginning to understand the importance of biological interactions among

their constituent species (Eaton 1979, Schmidt 1986). Several kinds of descriptive data suggest that competition may occur. Linhart and Robinson (1972) discovered that a decline in coyotes (Canis latrans) in Wyoming was apparently accompanied by increases in other mammalian carnivores, particularly red fox (Vulpes vulpes). Wagner (1988) discovered a comparable rise in population indices of bobcat (Felis rufus), badger (Taxidea taxus), and red fox in response to suppression of coyotes by poisoning in Utah and Wyoming. And Rowell (1991) found widespread negative associations in visits to scent stations throughout the West between coyotes and red foxes, gray foxes, raccoons, and skunks. But competition in the Carnivora is confused by the fact that individuals not only share resources, they also kill and eat one another. Such intraguild predation is currently being recognized as posing special problems in community ecology (Polis et al. 1989).

In a few cases the mechanism of competition is reasonably well understood. For example, foxes tend to be excluded from coyote home ranges in a variety of locations (Small 1971, Voigt and Earle 1983, Sargeant et al. 1987, Major and Sherbourne 1987, Theberge and Wedeles 1989, Harrison et al. 1989). Weak evidence suggests that wolves exclude coyotes (Mech 1966, Carbyn 1982). But the extent to which this kind of behavioral interaction is a factor in other species' interactions is not clear.

I am forced to conclude that this hypothesis must be taken seriously, especially as it relates to the relationships of coyotes with smaller carnivores.

In summary, each of these four hypotheses is likely to be applicable to some components of the problem of the missing carnivore species. I doubt that any can be definitively ruled out without resorting to experimental management. When dealing with ambiguity of this sort, scientists often resort to the logical tool called Occam's Razor or the Law of Parsimony. In operational terms, this states that hypotheses should be ranked, for purposes of further research, in order of their ease of falsifiability. Ease of falsifiability means the difficulty of proving a hypothesis wrong in terms of time, manpower, and expense.

By this criterion, these four hypotheses are relatively easy to rank. Hypothesis 1 is clearly the most difficult to falsify. It requires increasing the size of the Park, something which might be desirable for a variety of reasons but which is clearly not fast, easy, nor cheap.

Hypothesis 2 is next most difficult. The quality of the Park's riparian habitats might be improved by selective exclusion of ungulates, but this would be both expensive and potentially disruptive to the Park's bison and elk herds. The primary problem is that, because of the Park's geology, water tends not to remain on the surface. Any attempt to increase the linear extent of stream flow is almost certain

to be difficult, expensive, and perhaps ecologically harmful.

The difficulty of testing hypothesis 3 varies, depending upon precisely what form of the hypothesis one considers. Ungulate impacts could be assessed by excluding them from a portion of the Park for a period of at least 5 yrs. Considering the fact that carnivores are quite mobile and have large home ranges, the area to be fenced off would need to be large, at least 2000 ha. This would mean that the total ungulate population on the Park would need to be reduced proportionally and is obviously not inexpensive.

Prairie dog impacts could be assessed rather more easily, by eliminating one of the more isolated dog towns and accompanying this with both before-and-after and simultaneous-control studies.

An experimental assessment of human impacts would require more hypothesis development to design. The problem at present is that human use is highly concentrated in the western portion of the Park and is, therefore, difficult to separate from habitat differences. To vary patterns of human use would almost certainly require alteration of road use and might be quite expensive.

With the exception of the effects of prairie dogs, variants of hypothesis 3 tend to be difficult and expensive to test. And the possibility that prairie dogs have a direct negative effect on small carnivores is the least

likely aspect of that hypothesis.

Hypothesis 4 ranks as the easiest to test. It would require that a portion of the Park be kept free of coyotes for a period of 5 yrs and compared to an untouched part. This would be most easily done with the eastern half of the Park and could probably be accomplished at little cost.

In terms of simplicity, therefore, I would rank the competitive effects model simplest, followed by the human management model then the habitat model and finally the

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