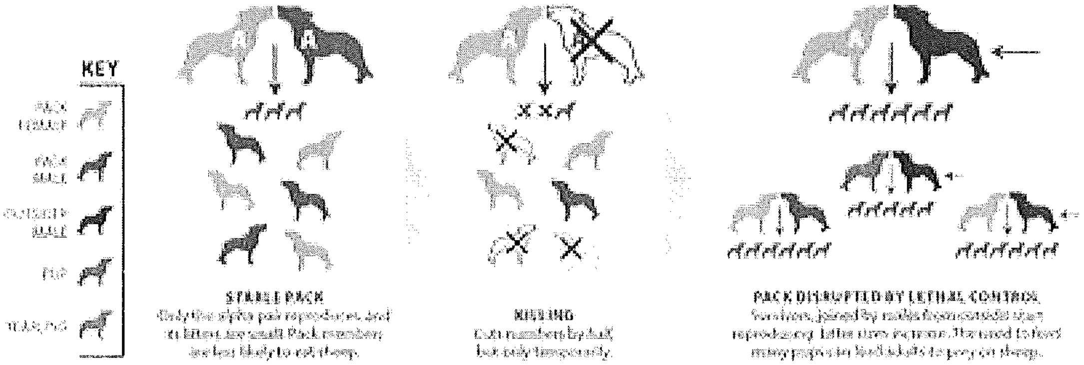
WWW.PROJECTCOYOTELIES.COM

A myth perpetuated by animal rights groups like Project Coyote and the Humane Society of the U.S. is the idea that removing coyotes creates more coyotes. This is simply an unproven theory.

Why **KILLING** Doesn't Work

Shoot or poison coyotes and you will have just as many again within a year or two. Kill one or both members of the alpha pair (A)—the only one that normally reproduces—and other pairs will form and reproduce. At the same time, lone coyotes will move in to mate, young coyotes will start having offspring sooner, and litter sizes will grow.



When Dr. Eric Gese, Professor (USDA National Wildlife Research Center, Predator Behavior and Ecology) was asked for comment on the infographic presented by Project Coyote and The Humane Society of the U.S. his reply was simply put "over simplified and unproven."

Coyote populations are predominantly controlled by available food and suitable habitat. This is Biology 101

A study was conducted by Project Coyote science adviser Robert Crabtree and Dr. Eric Gese. Observed coyotes in Yellowstone National Park. When packs were disrupted, beta animals replaced the lost alphas. The disruption did not result in a coyote mating "free for all" as explained in the HSUS infographic.

Coexistence unnaturally increases coyote carrying capacity by allowing coyotes to come into cities and compete for abundant resources. This inevitably leads to more to habituated coyotes which is a major factor leading to coyote human conflict.

In a book edited by Project Coyote Science advisor Dr. Mark Bekoff "Coyote Biology, Behavior and Management" Guy E. Connoly points out. "Nearly all animal populations fluctuate irregularly within limits that are extremely restricted compared to what is theoretically possible. Population levels of several species of carnivores have been shown to fluctuate in response to variations in the abundance of their principal prey" (Lack, 1954: Keith 1974). "Therefore, it is not surprising that most studies of the factors limiting coyote populations have identified food as the predominant constraint." (McLean 1934: Murie, 1940: Robinson, 1956: Gier, 1968: Clark, 1972: Wagner, 1972: Nellis and Keith, 1976)

REF 1776 - C

Foraging ecology of coyotes (*Canis latrans*): the influence of extrinsic factors and a dominance hierarchy

Eric M. Gese, Robert L. Ruff, and Robert L. Crabtree

Abstract: We examined the influence of intrinsic (age, sex, and social status) and extrinsic (snow depth, snowpack hardness, temperature, available ungulate carcass biomass) factors in relation to time–activity budgets of coyotes (*Canis latrans*) in Yellowstone National Park, Wyoming. We observed 54 coyotes (49 residents from 5 packs, plus 5 transients) for 2507 h from January 1991 to June 1993. Snow depth, ungulate carcass biomass, and habitat type influenced the amount of time coyotes rested, travelled, hunted small mammals, and fed on carcasses. Coyotes decreased travelling and hunting and increased resting and feeding on carcasses as snow depth and available carcass biomass increased. Age and social status of the coyote influenced activity budgets. During times of deep snow and high carcass biomass, pups fed less on carcasses and hunted small mammals more than alpha and beta coyotes. Pups apparently were restricted by older pack members from feeding on a carcass. Thus, pups adopted a different foraging strategy by spending more time hunting small mammals. Coyotes spent most of their time hunting small mammals in mesic meadows and shrub–meadows, where prey densities were highest. Prey-detection rates and prey-capture rates explained 78 and 84%, respectively, of the variation in the amount of time coyotes spent hunting small mammals in each habitat in each winter. Our findings strongly suggested that resource partitioning, as mediated by defense by older coyotes, occurred among coyote pack members in Yellowstone National Park.

Résumé : Nous avons examiné l'influence des facteurs intrinsèques (âge, sexe et statut social) et des facteurs extrinsèques (profondeur de la neige, compacité de la neige, température, biomasse des carcasses d'ongulés disponibles) sur l'activité des Coyotes (*Canis latrans*) dans le parc national de Yellowstone, Wyoming. Nous avons observé 54 coyotes (49 résidants de 5 meutes, plus 5 individus de passage) pendant 2507 h, entre janvier 1991 et juin 1993. La profondeur de la neige, la biomasse des carcasses d'ongulés et le type d'habitat influencent la durée des diverses activités des coyotes, repos, déplacements, chasse aux petits mammifères, consommation des carcasses. Les coyotes se déplacent moins, chassent moins, se reposent plus et se nourrissent plus à même les carcasses lorsque la couverture de neige et la biomasse des carcasses disponibles augmentent. L'âge et le statut social influencent aussi l'activité. Lorsque la couche de neige est épaisse et que la biomasse des carcasses disponibles est importante, les petits se nourrissent moins à même les carcasses et chassent plus les petits mammifères que les coyotes alpha et bêta. Les petits semblent empêchés d'approcher des carcasses par les membres plus âgés de la meute. Ils adoptent donc une stratégie alimentaire différente en passant plus de temps à chasser les petits mammifères. Les coyotes passent la plus grande partie de leur temps à chasser les petits mammifères dans les prairies mésiques et les prairies buissonneuses où la densité des proies est plus élevée. Les taux de détection des proies et de capture des proies expliquent respectivement 78 et 84% de la variation dans la durée de la chasse aux petits mammifères dans chaque habitat, chaque hiver. Nos résultats semblent indiquer qu'il se fait un partitionnement des ressources généré par le comportement de défense des coyotes plus âgés au sein de la meute du parc national de Yellowstone.
[Traduit par la Rédaction]

Introduction

The acquisition of food plays a critical role in the life of any animal, prompting inquiry into where, when, and for how long an animal forages, and how an animal responds and changes its activity budget in relation to the environment (Morrison et al. 1992). Studies of wild carnivores have provided many insights into behavioral budgeting and foraging ecology, but have usually focused on predation on large ungulates (e.g., Mech 1966; Estes and Goddard 1967; Kruuk 1972). Owing to their typically nocturnal activity and secretive nature, plus the difficulty in observing predation on small mammals, studies on the foraging ecology and predatory behavior of coyotes (*Canis latrans*) have usually involved predation on native ungulates (Truett 1979; Wenger 1981; Huegel and Rongstad 1985). Little is known about the behavior and activity budgets of coyotes when they utilize both small mammals and large ungulates as prey. Only one study of wild coyotes has used direct observations to record their time–activity budgets (Bekoff and Wells 1981, 1986). This

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provided a foundation for future behavioral studies of coyotes by examining the influence of food resources, social organization, and snow cover on coyote activity budgets in Grand Teton National Park, Wyoming. However, the influence of sex and social status of an individual coyote, habitat type, prey density, and changing environmental conditions on coyote activity budgets remained unknown.

Coyotes in Yellowstone National Park (YNP) must deal with fluctuations in temperature, snow depth, and food availability. During winter, a coyote must budget its time between hunting, breeding, sleeping, scent marking, defending its territory and mate, socializing with conspecifics, and interacting with other predators. The observable and diurnal nature of coyotes in YNP allowed us to evaluate the intrinsic and extrinsic factors that influence coyote time–activity budgets. Utilizing open field observations in the Lamar River Valley of YNP, we examined the following questions: (*i*) do extrinsic factors (snow depth, snowpack hardness, temperature, carcass biomass) influence coyote activity budgets? (*ii*) do intrinsic factors (age, sex, social status) influence coyote activity budgets? (*iii*) what habitat types do coyotes use and does the use of these habitats change during different environmental conditions? (*iv*) do coyotes of different social status use all habitats similarly? (*v*) do coyotes hunt in habitats containing the highest prey density and does this use change during different environmental conditions? (*vi*) is there a relationship between the amount of time coyotes spend hunting in each habitat and their rate of finding and capturing small mammals? (*vii*) do transient coyotes forage similarly as members of resident packs?

Study area

We conducted this study in a 70-km^2 site located in the Lamar River Valley in YNP, Wyoming (44°52′N, 110°11′E). Elevations in the park range from 1500 to 3400 m, the study area being about 2000 m above sea level. Summers are short and cool, while winters are long and cold, with most of the annual precipitation falling as snow (Houston 1982). Mean annual temperature and precipitation in the Lamar Valley is 1.8°C and 31.7 cm, respectively (Houston 1982). We identified seven habitat types in the study area (modified from descriptions by Despain 1990). (1) Forest: conifer and deciduous forests dominated by Douglas-fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*), and lodgepole pine (*Pinus contorta*). Common snowberry (*Symphoricarpos albus*), creeping Oregon grape (*Mahonia repens*), pinegrass (*Calamagrostis rubescens*), and shiny-leaf spirea (*Spirea betulifolia*) dominate the understory. (2) Mesic meadow: tufted hairgrass (*Deschampsia cespitosa*), various sedges (*Carex* spp.), American bistort (*Polygonum bistortoides*), and graceful cinquefoil (*Potentilla gracilis*) dominate the mesic meadow habitat. (3) Mesic shrub–meadow: willow (*Salix* spp.) and shrubby cinquefoil (*Potentilla fruticosa*) with an understory of sedges and tufted hairgrass occupy wet, poorly drained soils. (4) Riparian: rivers and streams with associated rocky or sandy shores, riverbanks, and gravel bars; includes river ice during winter. (5) Grassland: areas dominated by Idaho fescue (*Festuca idahoensis*), bluebunch wheatgrass (*Agropyron spicatum*), bearded wheatgrass (*Agropyron caninum*), junegrass (*Koelaria cristata*), Sandberg's bluegrass (*Poa sandbergii*), and needlegrass (*Stipa* spp.). (6) Sage–grassland: areas dominated by grasses including Idaho fescue, junegrass, and bluebunch wheatgrass, interspersed with sage (*Artemisia tridentata*) and common rabbitbrush (*Chrysothamnus nauseosus*). (7) Road: paved or gravel roadways.

Seven ungulate species are present in YNP, including elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), pronghorn antelope (*Antilocapra americana*), bison (*Bison bison*), moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), and white-tailed deer (*Odocoileus virginianus*). Elk carrion was a major food item for coyotes during the winter (Murie 1940; this study). Small mammals available as prey to coyotes in the valley consisted of microtines (*Microtus* spp.), mice (*Peromyscus* spp.), pocket gophers (*Thomomys talpoides*), and Uinta ground squirrels (*Spermophilus armatus*).

Methods

Coyotes were captured, sexed, ear-tagged, and radio-collared (Advanced Telemetry Systems, Bethel, Minnesota), and the first vestigial premolar from the lower jaw was extracted for aging by cementum annuli analysis (Linhart and Knowlton 1967). Pups were captured at the den when 10–12 weeks old, ear-tagged, and surgically implanted with an intraperitoneal transmitter (Telonics, Mesa, Arizona). Coyotes were classed as pups (< 12 months old), yearlings (12–24 months old), and adults (> 24 months old). Each coyote was classified as either a member of a resident pack, or as a transient, following Bowen (1981) and Gese et al. (1988). All coyotes within the resident pack were further classified into one of three social classes based upon the separate male and female dominance hierarchies within the pack: alphas (the dominant, breeding, adult male and female), betas (adults and yearlings subordinate to the alphas but dominant over pups), or pups (young of the year that were subordinate to both the alphas and betas), following descriptions by Schenkel (1947, 1967), Rabb et al. (1967), and Mech (1970). A coyote classified as a pup remained in that category until the next litter became mobile and independent of parental feeding in September. Each coyote was classified into the next age and social class as it grew older and elevated its rank within the dominance hierarchy.

The sampling strategy for the collection of behavioral observations was described in Gese et al. (1996). In general, coyote packs were chosen randomly, then we stratified individuals within the pack for systematic selection of the animal to be observed. The animal chosen was observed using focal-animal sampling (Lehner 1979), continually recording all activities performed by the individual coyote. Out-of-sight periods were deleted from the sample, and the sampling period was reduced accordingly (Lehner 1979). We observed both individuals with transmitters and unmarked (identifiable by physical characteristics) during daylight hours (07:00 to 20:00); data on nocturnal activity were collected utilizing a night-vision scope (Litton Electron Devices, Tempe, Arizona). Because of high grass in summer, observation of coyotes was not possible during August and September.

Interpretation of behavioral activities by different observers can cause many problems in a behavioral study (Lehner 1979; Martin and Bateson 1993). To minimize observer error and maintain reliable, consistent data collection, each observer was trained by the senior author for a minimum of 5–7 days by watching an animal simultaneously and establishing criteria for each activity. Behavioral activities were recorded to within 1 s using a program on an Atari Portfolio notebook computer or a tape recorder and transcribed later. The behavior program recorded the type of activity the animal performed, the time the action was performed, and the habitat where the action occurred. Activity categories were (1) resting: the coyote was laying on its side either with its head up and alert or with its head down and assumed to be resting; (2) travelling: the coyote was walking, trotting, or running, occasionally stopping to scan its surroundings; (3) hunting small mammals: the time spent hunting was the total time spent pursuing a prey item, including orienting, stalking, searching, chasing, pouncing, or otherwise pursuing it, but not the time spent travelling between predation attempts because we could not anticipate the coyote's future action (i.e., the coyote could scent mark, interact with another coyote, rest, etc.); (4) feeding on a carcass: the coyote was feeding on an ungulate carcass or scraps from a carcass; (5) socializing: the coyote interacted with a conspecific; this included dominance, submission, or play; (6) howling: the coyote vocalized; (7) marking: the coyote performed a urination or defecation, sometimes followed by scratching the ground; this included searching or smelling the ground prior to urination or defecation; (8) sitting: the coyote sat on its rear haunches; (9) other: searching, digging, and smelling unrelated to prey acquisition, marking, or any of the 8 previously described activities. We summed the times and frequency of each activity, and calculated the percent time spent on each activity by each habitat class. Our major interest was the relationship of activity budgets to foraging ecology. Hence, we analyzed only the 4 major activities (rest, travel, hunt small mammals, feed on a carcass) which constituted or were influenced by foraging. The other activities (socialize, howl, mark, sit, other) combined composed <6% of the total activity budget.

Snow depth and layering were recorded every 1–2 days by excavation of a snow pit. Each layer within the total snow column was measured and the hardness of the layer recorded as soft (powder snow or no crust, snow does not support a coyote's weight), moderate (crust is present and occasionally supports the weight of a walking coyote), and hard snowpack (thick crust is present and consistently supports a walking coyote's weight). Daily total snow depth and maximum and minimum temperatures were recorded at a permanent weather station operated by the National Park Service at the Lamar Valley Ranger Station within the study area.

The number and size of carcasses visited by the coyotes during observational periods were recorded as a measure of alternative food sources other than small mammals. We also scanned the valley each morning for concentrations of coyotes, ravens (*Corvus corax*), magpies (*Pica pica*), or eagles (*Aquila chrysaetos* and *Haliaeetus leucocephalus*), which sometimes indicated the presence of a carcass. For each carcass found, we recorded the species, sex, and age, and the color and consistency of the femur marrow (Bubenik 1982). To estimate the amount of food available to coyotes, we converted each carcass into carcass biomass following Houston (1978) for elk. This conversion took into account the size of the carcass, mass loss during winter, and the amount of food available to the coyotes (i.e., carcass minus rumen and skeleton). We determined the live mass of each bighorn sheep, bison, and mule deer carcass after Geist (1971), Meagher (1973), and Anderson et al. (1974), respectively, and then reduced live mass by 30% to estimate carcass mass at death (Houston 1978). We subtracted another 33% to account for the uneaten mass represented by the stomach and skeleton. This measure of carcass biomass represented a known minimum estimate in the valley only. Coyote packs were randomly watched, thus the biomass estimate should be representative of all packs. However, we do recognize that there were days when a pack was not observed and may have fed on a carcass, or when carcasses may not have been distributed evenly between the pack territories. Also, carcasses in forested habitats or in the hills surrounding the valley may have gone undetected by the observers because of decreased visibility in certain areas.

We also conducted a carcass survey each spring after snowmelt to search for carcasses not detected during the winter observations. Searchers walked 50 m apart and covered all five pack territories in the Lamar River Valley in the spring of 1991 and 1992; the survey in 1993 was incomplete. The location and species of each carcass were recorded, and the sex, age, and condition were determined where possible (i.e., if the carcass had not been completely dismembered and dispersed by scavengers).

For all statistical tests, the sampling unit was the individual coyote (Machlis et al. 1985; Morrison et al. 1992). Percentages of time presented in the results are means unless otherwise indicated. Statistical analyses were performed using SYSTAT (Wilkinson et al. 1992) following a factorial design (Steel and Torrie 1980; Sokal and Rohlf 1981). Multiway analyses of variance (ANOVA) were mixed models with all two-way (first-order) interaction terms included. Pairwise comparisons were performed utilizing Tukey's multiple comparisons test where one-way ANOVAs indicated significant differences among groups. ANOVA with repeated measures was used for many coyotes except those that died, dispersed, or were not observed in all environmental conditions.

Results

We collected 2507 h of observation on 54 coyotes from 27 January 1991 to 30 June 1993. Of the 54 coyotes, 31 were collared or implanted with radio transmitters; 23 animals were not marked but were recognizable from physical charactertistics. We observed 29 males and 23 females; 2 unmarked coyotes were of unknown sex. We observed 11 members of the Bison pack for 498 h, 9 members of the Druid pack for 432 h, 11 members of the Fossil Forest pack for 593 h, 10 members of the Norris pack for 463 h, 8 members of the Soda Butte pack for 470 h, and 5 transient coyotes for 51 h.

Pack histories

Five packs were identified on the study area in YNP. Each pack occupied a distinct territory (Fig. 1) in which boundaries were scent marked and actively defended (E.M. Gese, unpublished data). The social structure of each pack was similar to the dominance hierarchy described in a wolf pack (Mech 1970; Zimen 1981). Each coyote pack was composed of an alpha pair and other pack members, typically offspring from the previous summer and older offspring or older coyotes that were members of the pack at the initiation of the study, i.e., origin or relatedness was unknown (Table 1). The alpha pairs of the Fossil Forest and Soda Butte packs remained intact through all three winters. In the Bison pack, the alpha male was killed by a car in December 1991 and the high-ranking beta male in the pack assumed the alpha position. This male held the alpha position through the winter of 1991–1992, but was replaced by the high-ranking beta male in the pack, which had been subordinate the year before, in the fall of 1992. The former alpha male resumed a beta position. The alpha female was present throughout the three winters. In the Druid pack, the alpha female was present through all three winters but the alpha male was killed by a car in December 1992. The high-ranking beta male filled the alpha role and the alpha female was paired with the new alpha male 4 days after the death of her mate. In the Norris pack, the alpha male was found dead (unknown cause) in January 1993 and the alpha female abandoned the territory for a month and was observed travelling throughout the valley during which time she mated with 3 different males. She returned to the Norris territory at the end of February with the low-ranking beta male from the adjacent territory (Fossil Forest). However, during her absence, the Soda Butte pack usurped half of the Norris territory (Fig. 1C) and continually defended the area against the returning Norris alpha female and her new mate, resulting in no pup production by the Norris pack in 1993 (Table 1).

Environmental conditions

The first winter of study (1990–1991) was considered a mild winter in YNP. Snow depth in the study area reached a maxi-

Fig. 1. Spatial distribution and territorial boundaries of the five coyote packs occupying the Lamar River Valley in the winters of 1990–1991 (A), 1991–1992 (B), and 1992–1993 (C), in Yellowstone National Park, Wyoming.

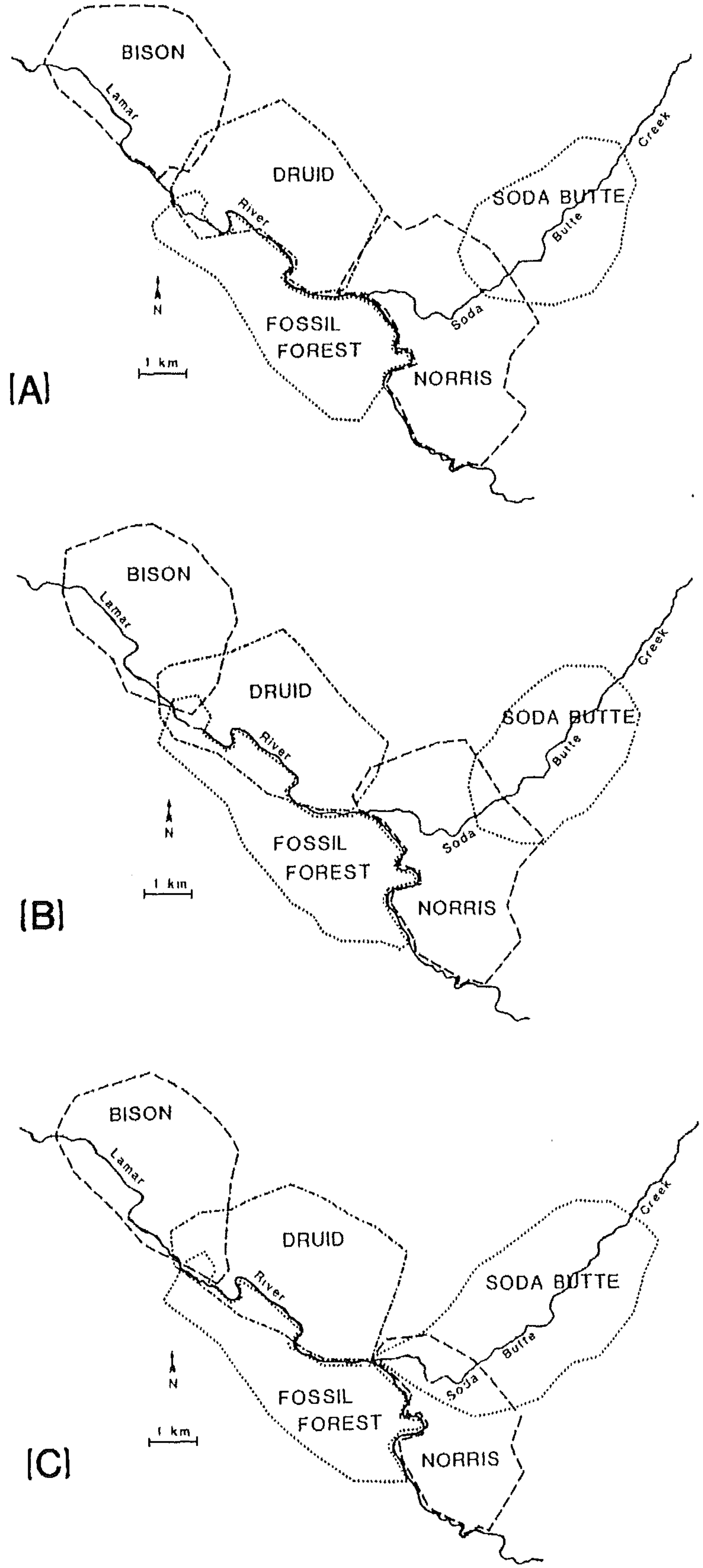


Table 1. Pack size, composition, and litter size of the five coyote packs observed in the Lamar River Valley, Yellowstone National Park, Wyoming, January 1991 to July 1993.

			Composition						
			Alpha		Beta		Pup		
Pack	Winter	Pack size	M	F	M	F	M	F	Litter size
Bison	1990–1991	5	1	1	2	1	0	0	6
	1991–1992	8	1	1	2	2	1	1	12
	1992–1993	10[a]	1	1	3	2	1	1	—[b]
Druid	1990–1991	3	1	1	1	0	0	0	6
	1991–1992	5	1	1	1	0	1	1	5
	1992–1993	7	1	1	2	2	0	1	5
Fossil Forest	1990–1991	5	1	1	1	0	2	0	6
	1991–1992	6	1	1	2	0	1	1	5
	1992–1993	6	1	1	3	1	0	0	—[b]
Norris	1990–1991	4	1	1	1	1	0	0	3
	1991–1992	5	1	1	2	0	0	1	8
	1992–1993	4	1	1	1	1	0	0	—[c]
Soda Butte	1990–1991	6	1	1	0	0	2	2	4
	1991–1992	6	1	1	2	2	0	0	9
	1992–1993	7[d]	1	1	2	2	0	0	—[e]

[a] Includes 1 pup of unknown sex.

[b] A minimum of 2 pups were observed, but the litter was not counted.

[c] One placental scar was counted during necropsy of the alpha female the following winter; the pup was never observed alive.

[d] Includes 1 beta individual of unknown sex.

[e] Litter size was unknown.

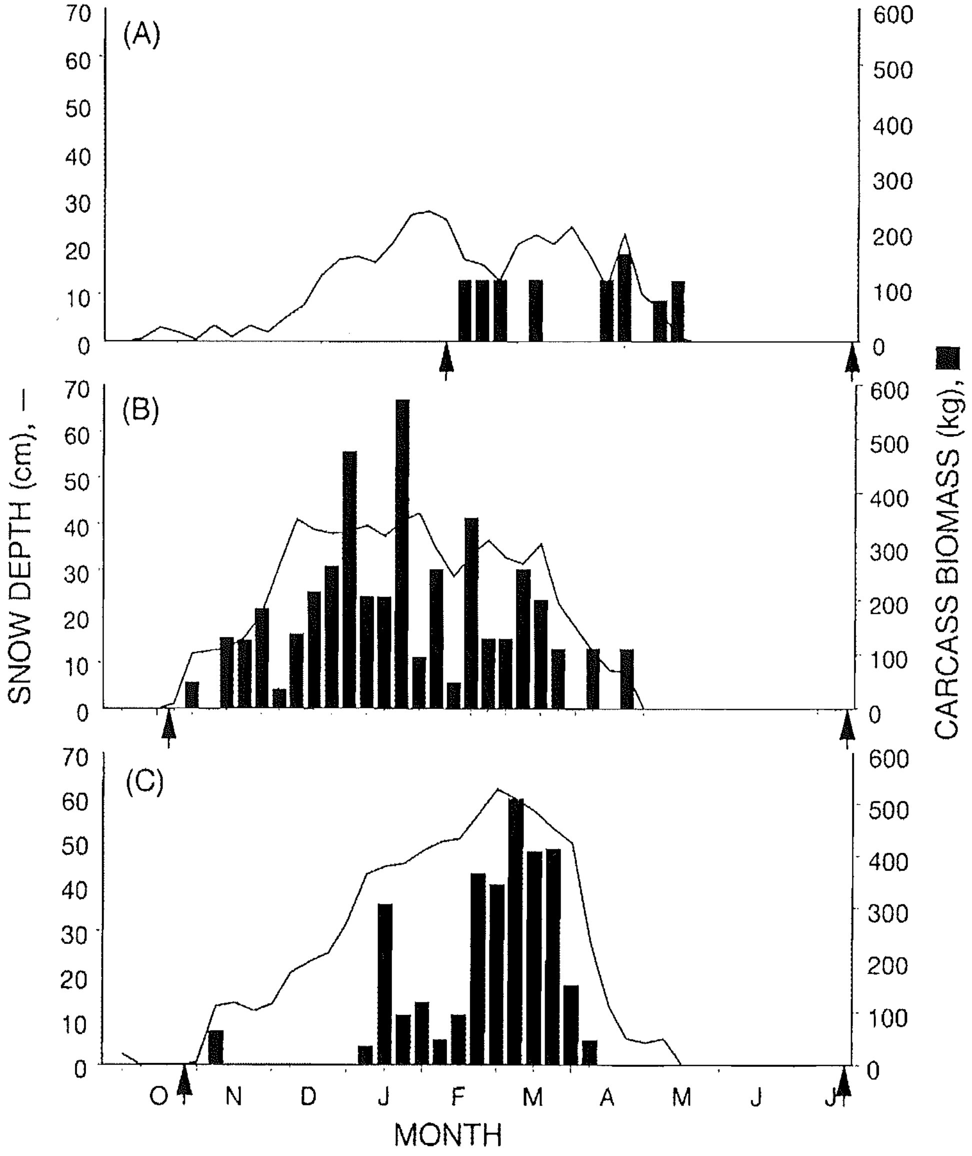
mum of 30 cm and the known carcass biomass was < 170 kg for each week (Fig. 2A). Snow depth was 30 cm for only 7 days of the winter and total known carcass biomass for the remainder of the winter was 900 kg (carcass biomass prior to 27 January was unknown). The second winter of the study (1991–1992) produced deeper snows and higher ungulate carcass biomass (Fig. 2B). The winter was characterized by an early snowfall followed by a thaw, which in turn created an ice layer at ground level that led to an early onset of winterkill of ungulates. Snow depth reached a maximum of 46 cm, with 98 days on which snow depth was >30 cm. Known minimum carcass biomass was >200 kg/week for 10 weeks of the winter; total carcass biomass for the entire winter was 4411 kg. Conditions during the third winter of the study (1992–1993) were characterized by a later onset of snowfall than in the previous winter, maximum snow depth reaching 63 cm in February (Fig. 2C). As in the previous winter, there were 91 days with snow depth >30 cm and 6 weeks with >200 kg of known carcass biomass available to the coyotes. Total known carcass biomass in the valley was a minimum of 3014 kg for the entire winter. In contrast to Bekoff and Wells (1981, 1986), carrion availability increased as the winter progressed (Fig. 2), and the carrion resulted from winterkill or predation, not human hunting.

Winter is the most stressful time for ungulates in YNP, with many elk dying during periods of deep snow (Murie 1940; Craighead et al. 1973; Houston 1978, 1982). Thus, we examined the relationship between environmental conditions and carcass biomass (winterkill or predation) in the Lamar River Valley. Environmental variables included weekly mean snow depth (SNOW), weekly mean minimum temperature (TMIN), weekly mean maximum temperature (TMAX), snowpack hardness (CRUST), and all two-way interactions. Multiway ANOVA showed that 54% of the variation in the amount of carcass biomass (BIOMASS) during a week was explained by SNOW and the interaction between SNOW and TMIN. As snow depth increased and minimum temperature decreased, the amount of carcass biomass increased, i.e., more ungulates died or were killed, thus becoming available as food to coyotes (multiple $r = 0.73$, $P < 0.001$). This relationship between snow depth and carcass biomass was likely due to limited mobility and decreased foraging efficiency of ungulates travelling through deep snow (Beall 1974; Leege and Hickey 1977). Deep snow causes increased energy expenditure (Mattfield 1974; Parker et al. 1984) and reduced physiological condition in ungulates (DelGiudice et al. 1991) and increases their vulnerability to predation and starvation.

Influence of extrinsic factors on activity budgets

The activity budgets of resident coyotes in YNP changed throughout the year (Fig. 3). In the fall, coyotes spent much of their time travelling (60%) and hunting small mammals (13%). During winter, with increased snow depth and carcass availability, coyotes reduced the time spent travelling (24%) and hunting (2%), and spent more time feeding on

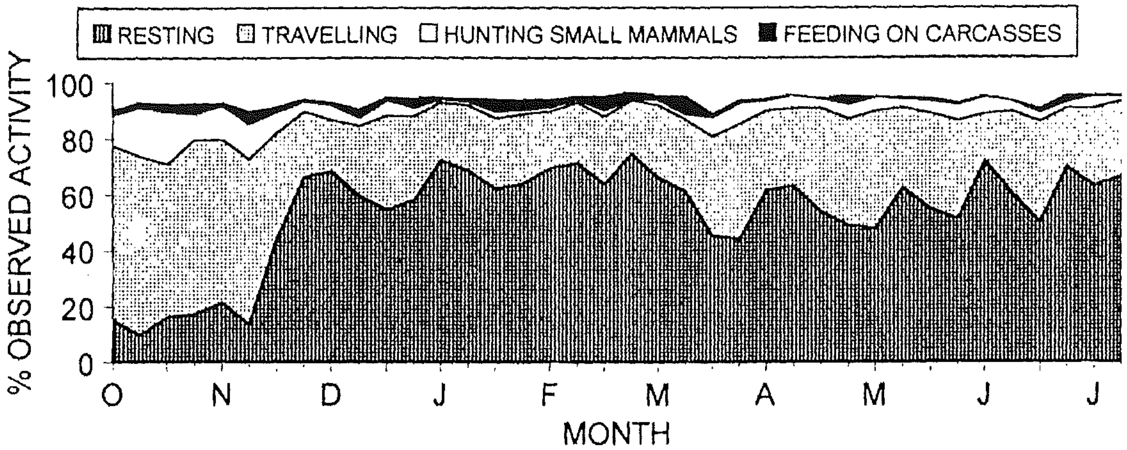
Fig. 2. Mean snow depth and carcass biomass for each week during the winters (October–July) of 1990–1991 (A), 1991–1992 (B), and 1992–1993 (C), in the Lamar River Valley, Yellowstone National Park, Wyoming. Arrows indicate the time span of data collection for each winter.



available carcasses (2%) and resting (66%). In spring, coyotes returned to travelling and hunting small mammals more often as carcass biomass and snow depth declined. Carcasses fed on by coyotes during the summer were the remains of old winter carcasses and depredated elk calves.

Activity budgets of coyotes have been found to be influenced by environmental factors (Bekoff and Wells 1981, 1986). Thus, we first examined the relationship between coyote activity budgets and extrinsic factors quantitatively for all coyotes combined. We examined the influence of the extrinsic factors (SNOW, TMIN, TMAX, CRUST, and BIOMASS) on the amount of time coyotes spent resting, travelling, hunting small mammals, and feeding on a carcass during a 1-week period. Overall, coyotes were observed to spend 59% of their time resting. We found that 46% of the variation in the amount of time coyotes spent resting was explained by four significant environmental variables: SNOW, TMIN, CRUST, and BIOMASS (in decreasing order of importance in explaining variation in the dependent variable; multiple $r = 0.68$, $P < 0.001$). The amount of time spent resting increased with increasing snow depth and carcass biomass, increased hardness of the crust, and decreasing minimum temperature. We observed coyotes travelling 29% of the time. TMIN, the interaction between SNOW and TMIN, BIOMASS, the interaction between SNOW and BIOMASS, and SNOW explained 55% of the variation in the amount of time coyotes spent travelling (multiple $r = 0.74$, $P < 0.001$). Coyotes spent less time travelling as snow depth and carcass biomass increased and minimum temperature decreased. Coyotes spent 4% of their time hunting small mammals. Forty-five percent of the variation in the amount of time coyotes spent hunting was explained by CRUST, TMIN, and SNOW (multiple $r = 0.67$, $P < 0.001$).

Fig. 3. Amount of time coyotes were observed to spend resting, travelling, hunting small mammals, and feeding on carcasses each week during the three winters (1991 – 1993) combined, Yellowstone National Park, Wyoming.



As hardness of the crust and snow depth increased and minimum temperatures decreased, coyotes reduced the amount of time spent hunting. Coyotes spent 2% of their time feeding on carcasses. Only 27% of the variation in the amount of time spent feeding on a carcass was explained by the interaction between SNOW and TMIN (multiple $r = 0.52$, $P < 0.001$). As snow depth increased and minimum temperature decreased, coyotes spent more time feeding on carcasses. Analysis revealed that the amount of carcass biomass was not a significant contributor to the amount of time coyotes were observed to be feeding on carcasses. This was likely because the coyotes fed on carcasses mainly at night. Low temperatures at night appeared to cause many ungulates to finally succumb to malnutrition. We often found coyotes with full stomachs bedded near a carcass in the morning; hence, the amount of time coyotes fed on a carcass was likely underestimated and reduced the amount of variation explained by BIOMASS.

Influence of intrinsic factors on activity budgets

The previous analysis showed that snow depth and carcass biomass were interrelated environmental factors that influenced the activity budgets of coyotes in YNP. Controlling for the influence of these two important variables was necessary when we next examined the influence of intrinsic factors. Thus, we classified the amount of snow cover and carcass biomass into 6 categories based upon the environmental conditions produced over the three winters of the study: (1) no snow cover and no carcass biomass, (2) no snow and low biomass (<200 kg biomass/week), (3) low snow (≤30 cm of snow cover) and no biomass, (4) low snow and low biomass, (5) deep snow (>30 cm of snow) and low biomass, and (6) deep snow and high biomass (≥200 kg biomass/week).

Controlling for snow depth and carcass biomass allowed us to examine the influence of sex, social status, and pack on the amount of time coyotes spent resting, travelling, hunting, and feeding on a carcass. We used multiway ANOVA to examine the influence of the independent variables, which included the sex (SEX) and social status (STATUS) of the coyote, the pack (PACK) in which the coyote was a member, and the snow depth and carcass biomass conditions (CONDITIONS), upon the dependent variable (percent time resting, travelling, hunting, and feeding on a carcass). We found that 74% of the variation in the amount of time coyotes spent resting was mostly explained by CONDITIONS, the interaction between PACK and CONDITIONS, the interaction between STATUS and CONDITIONS, and STATUS (Table 2). Coyotes rested the least during conditions of low snow with both low and no carcass biomass ($P < 0.07$) (Fig. 4A). Social classes differed only during low snow cover and low carcass biomass conditions; pups spent less time resting than alphas ($P = 0.008$) and betas ($P = 0.035$) (Fig. 4A). The amount of time spent resting was not significantly different among alphas, betas, and pups during conditions of no snow and deep snow cover (F tests had $P > 0.10$).

We found that 75% of the variation in the amount of time coyotes spent travelling was principally explained by CONDITIONS, the interaction between PACK and CONDITIONS, the interaction between STATUS and CONDITIONS, and PACK (Table 2). Coyotes travelled the most during conditions of low snow cover ($P < 0.09$) and the least during times of deep snow and high carcass biomasss ($P < 0.07$) (Fig. 4B). The amount of time spent travelling varied among packs, the Fossil Forest pack travelling more than the Bison pack during all conditions ($P < 0.05$). This was likely due to differences in the distribution of food resources. Members of the Fossil Forest pack hunted in numerous meadows spaced throughout their territory (Gese 1995), and carcasses were typically along the periphery of their territory (Fig. 5). In contrast, the Bison pack territory encompassed one large meadow where all pack members hunted rodents (Gese 1995), and carcasses were typically distributed within or near the center of their territory (Fig. 5). The other packs (Druid, Norris, Soda Butte) spent an intermediate amount of time travelling, but were not significantly different from the Fossil Forest and Bison packs ($P > 0.10$).

Seventy-six percent of the variation in the percent time coyotes spent hunting small mammals was mostly explained by CONDITIONS, the interaction between STATUS and CONDITIONS, and STATUS (Table 2). Coyotes spent more time hunting small mammals during conditions of low snow and both no and low carcass biomass than in all other conditions ($P < 0.01$) (Fig. 4C). Among social classes, betas hunted small mammals more than pups during low snow and no

Fig. 4. Amount of time alpha, beta, and pup coyotes were observed to spend resting (A), travelling (B), hunting small mammals (C), and feeding on carcasses (D) under different ecological conditions in Yellowstone National Park, Wyoming, 1991–1993. Snow-cover conditions included no (N), low (L), and deep snow (D). Carcass biomass conditions included no (N), low (L), and high (H).

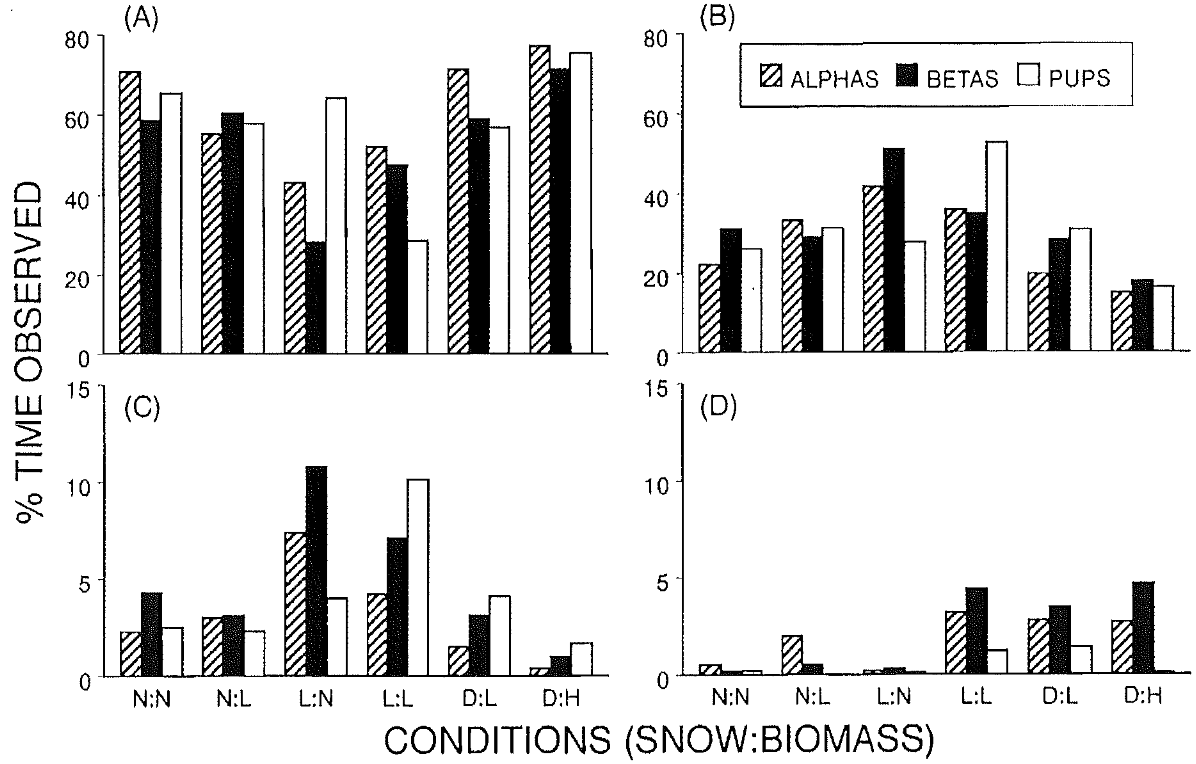


Table 2. ANOVA showing the influence of sex, social status, pack, and environmental conditions on the amount of time coyotes were observed to rest, travel, hunt for small mammals, and feed on carcasses, Yellowstone National Park, Wyoming, 1991–1993.

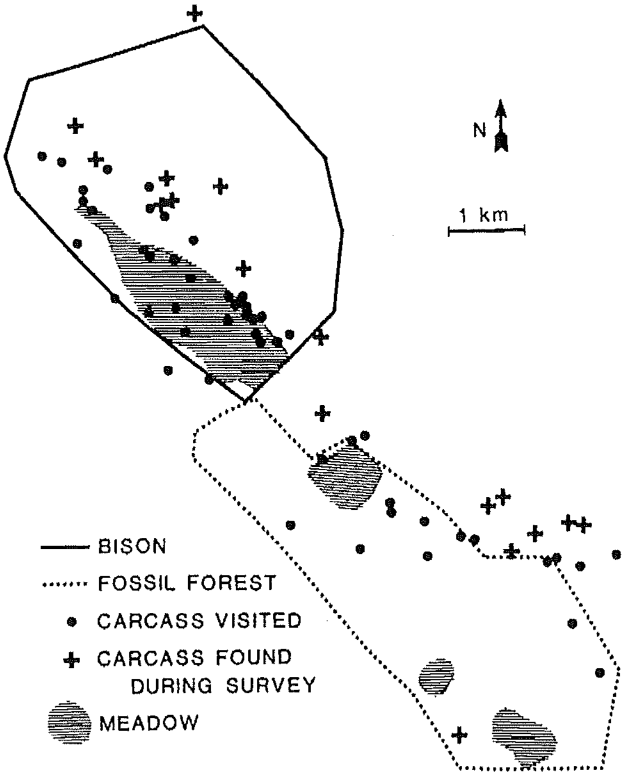
		Rest		Travel		Hunt		Feed on carcass	
Source	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
SEX[a]	1	2.384	0.127	2.918	0.092	0.971	0.328	0.165	0.686
STATUS[b]	2	3.521	0.035	1.903	0.156	4.429	0.015	2.745	0.071
PACK[c]	4	2.339	0.063	3.164	0.019	1.493	0.213	0.027	0.999
CONDITIONS[d]	5	14.500	<0.001	15.170	<0.001	20.311	<0.001	3.414	0.008
SEX × STATUS	2	0.349	0.706	0.719	0.490	0.838	0.437	1.002	0.372
SEX × PACK	4	0.691	0.600	0.758	0.556	1.783	0.141	0.341	0.849
SEX × CONDITIONS	5	0.434	0.824	0.464	0.802	1.796	0.124	1.236	0.301
STATUS × PACK	8	1.037	0.417	1.221	0.299	1.586	0.144	1.154	0.339
STATUS × CONDITIONS	10	3.125	0.002	3.077	0.003	2.827	0.005	0.450	0.916
PACK × CONDITIONS	20	2.000	0.017	1.825	0.033	1.636	0.066	1.115	0.354
Error	74								

[a] Male or female.
[b] Alpha, beta, or pup.
[c] Bison, Druid, Fossil Forest, Norris, or Soda Butte.
[d] Snow depth : carcass biomass = none:none, none:low, low:none, low:low, deep:low, or deep:high.

carcass biomass conditions ($P = 0.06$), while pups hunted significantly more than alphas during conditions of low snow and low carcass biomass ($P = 0.002$), deep snow and low carcass biomass ($P = 0.07$), and deep snow and high carcass biomass ($P = 0.06$) (Fig. 4C).

We found that 51% of the variation in the percent time coyotes spent feeding on carcasses was mostly explained by CONDITIONS and STATUS (Table 2). As expected, coyotes increased the amount of time feeding on carcasses during periods of low and high carcass biomass ($P < 0.07$). However, social classes differed in the amount of time feeding on a carcass. Pups spent less time feeding on a carcass than alphas ($P < 0.09$) and betas ($P < 0.02$) during conditions of both low and high carcass biomass (Fig. 4D).

Fig. 5. Locations of meadows, carcasses visited by coyotes (1991–1993), and carcasses found during spring surveys (1991 and 1992 only) in the Bison and Fossil Forest pack territories, Yellowstone National Park, Wyoming, 1991–1993.



The previous analysis showed that during times when carcasses were present, the older coyotes (alphas and betas) spent more time feeding on carcasses than pups, while pups spent more time hunting small mammals. Thus, we investigated this difference in foraging strategies on a finer time scale. Further evidence of the relationship between social rank within the dominance hierarchy and access to a carcass was illustrated by the amount of time alphas, betas, and pups spent hunting small mammals and feeding on a carcass on the day an ungulate was killed or died, and during the following 7 days. Alphas and betas spent more time feeding on the carcass than pups, while pups spent more time hunting small mammals (Fig. 6). Alphas predominantly fed on the carcass during the first 2 days, while betas fed on it for up to 4 days. In contrast, pups spent little time at the carcass during the first 2 days and no longer came to the carcass after 3 days but hunted small mammals instead. Although we found that the alphas spent <15% of the first day actually feeding on the carcass (Fig. 6B), they spent considerable amounts of time resting near the carcass and deterring other coyotes from feeding or displacing them from the carcass throughout the day. After the alphas relinquished the carcass, the betas spent considerable time at it during the following 2–4 days. When the pups came to the carcass area, they were often deterred from feeding by the dominant, older coyotes at the carcass. The pups would then move away from the area and begin hunting small mammals elsewhere in the territory.

We examined individual variation in behavioral activities (Morrison et al. 1992) within the same social status (sex was not a significant contributor) across changing environmental conditions, using ANOVA with repeated measures. Analyses

Fig. 6. Amount of time alpha, beta, and pup coyotes were observed to spend hunting small mammals (A), and feeding on a carcass (B) on the day an elk died or was killed by coyotes (day 0) and on the following 7 days (days 1–7), Yellowstone National Park, Wyoming, 1991–1993. Data are a composite of 735 h of observation.

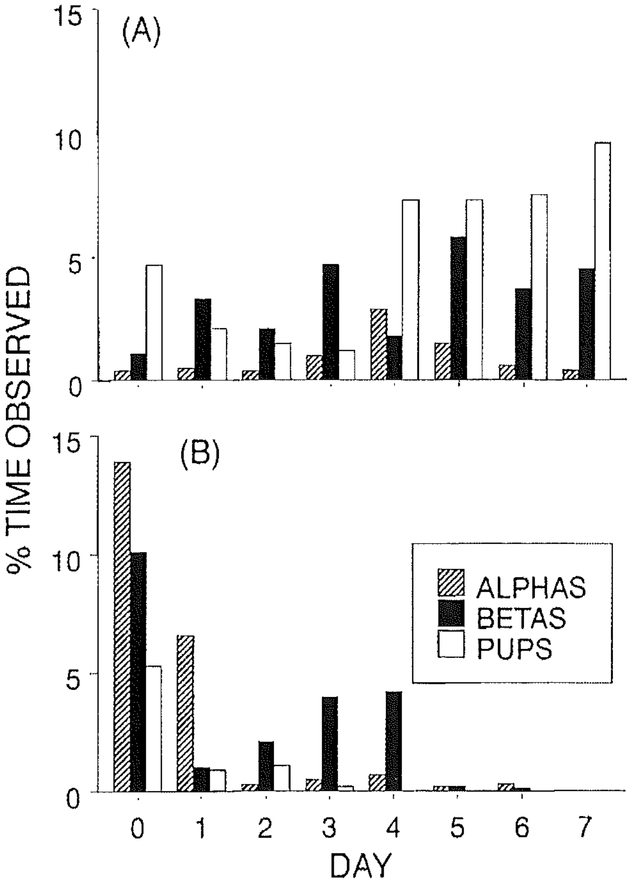


Table 3. The influence of variation between subjects and treatments on the amount of time a behavior was performed by individual coyotes of each social class under changing environmental conditions (ANOVA with repeated measures), Yellowstone National Park, Wyoming, 1991–1993.

		Variation between subjects		Variation between treatments	
Social class	Behavior	*F*	*P*	*F*	*P*
Alpha	Rest	0.32	0.898	5.54	0.001
	Travel	0.49	0.780	6.31	0.001
	Hunt	0.09	0.993	5.20	0.002
	Feed on carcass	1.28	0.297	1.21	0.334
Beta	Rest	0.44	0.775	4.23	0.009
	Travel	0.53	0.712	2.98	0.036
	Hunt	0.36	0.837	6.89	0.001
	Feed on carcass	0.35	0.840	6.46	0.001
Pup	Rest	1.14	0.360	3.52	0.019
	Travel	2.27	0.087	4.83	0.005
	Hunt	0.40	0.809	29.65	0.001
	Feed on carcass	0.31	0.869	2.97	0.039

Table 4. Influence of sex, social status, pack, and environmental conditions on the amount of time coyotes were observed to spend in seven different types of habitat in Yellowstone National Park, Wyoming, 1991–1993.

Source	df	Forest	Mesic meadow	Sage–grassland	Shrub–meadow	Grassland	Riparian	Road
SEX[a]	1	0.53	0.71	1.61	0.01	4.33*	2.13	2.40
STATUS[b]	2	0.91	3.35*	9.85**	0.21	4.50*	0.48	8.04**
PACK[c]	4	10.79**	11.74**	15.31**	4.84**	5.58**	4.47**	1.04
CONDITIONS[d]	5	10.26**	2.99*	2.22	6.36**	0.20	6.52**	8.41**
SEX × STATUS	2	0.48	1.41	0.02	1.01	3.29*	2.48	0.65
SEX × PACK	4	0.23	0.10	0.67	0.29	3.31*	0.32	0.63
SEX × CONDITIONS	5	0.49	0.22	0.38	0.49	1.00	0.92	0.64
STATUS × PACK	8	2.35*	1.62	1.40	1.00	1.38	1.55	4.63**
STATUS × CONDITIONS	10	1.09	1.26	0.76	0.83	0.51	1.10	0.99
PACK × CONDITIONS	20	8.13**	1.55	1.61	1.44	0.67	0.84	0.99
Error	74							

Note: Values in the table are F values followed by the level of significance (*, $P < 0.05$; **, $P < 0.01$).

[a] Male or female.

[b] Alpha, beta, or pup.

[c] Bison, Druid, Fossil Forest, Norris, or Soda Butte.

[d] Snow depth : carcass biomass = none:none, none:low, low:none, low:low, deep:low, or deep:high.

revealed that for all behavioral categories, variation between individuals within each social class did not have a significant influence on the activity budgets of coyotes under changing environmental conditions (Table 3). Variation between treatments was a significant influence, except for the amount of time alpha coyotes spent feeding on a carcass. Our analysis indicated that individuals of the same social status responded similarly in their activity budgets to changes in snow depth and carcass biomass.

Influence of habitat type on activity budgets

Differences in prey density, cover, topography, and other attributes important to coyotes may vary among habitats. Thus, we examined where coyotes performed certain behaviors (i.e., what a particular habitat on the landscape provided to a coyote in relation to foraging and activity budgets). We were not interested in an examination of habitat use versus availability, but changes in habitat use with varying environmental conditions and between coyotes of different social status. Using multiway ANOVA, we found that coyotes changed their use of certain habitats as environmental conditions changed (Table 4, Fig. 7). For all coyotes combined, the amount of time spent in sage–grasslands appeared to decline across environmental conditions ($F = 2.14$, $P = 0.07$) (Fig. 7C). All coyotes increased their use of shrub–meadows as snow and carcass biomass conditions increased (Fig. 7D), the highest use being reached during deep snow cover ($P < 0.05$). Use of riparian areas increased as snow and carcass biomass conditions changed, the highest use being reached during conditions of deep snow and high biomass ($P < 0.05$) (Fig. 7F). Coyotes increased their use of roads during times of low ($P < 0.05$) and deep snow ($P < 0.05$) compared with times of no snow.

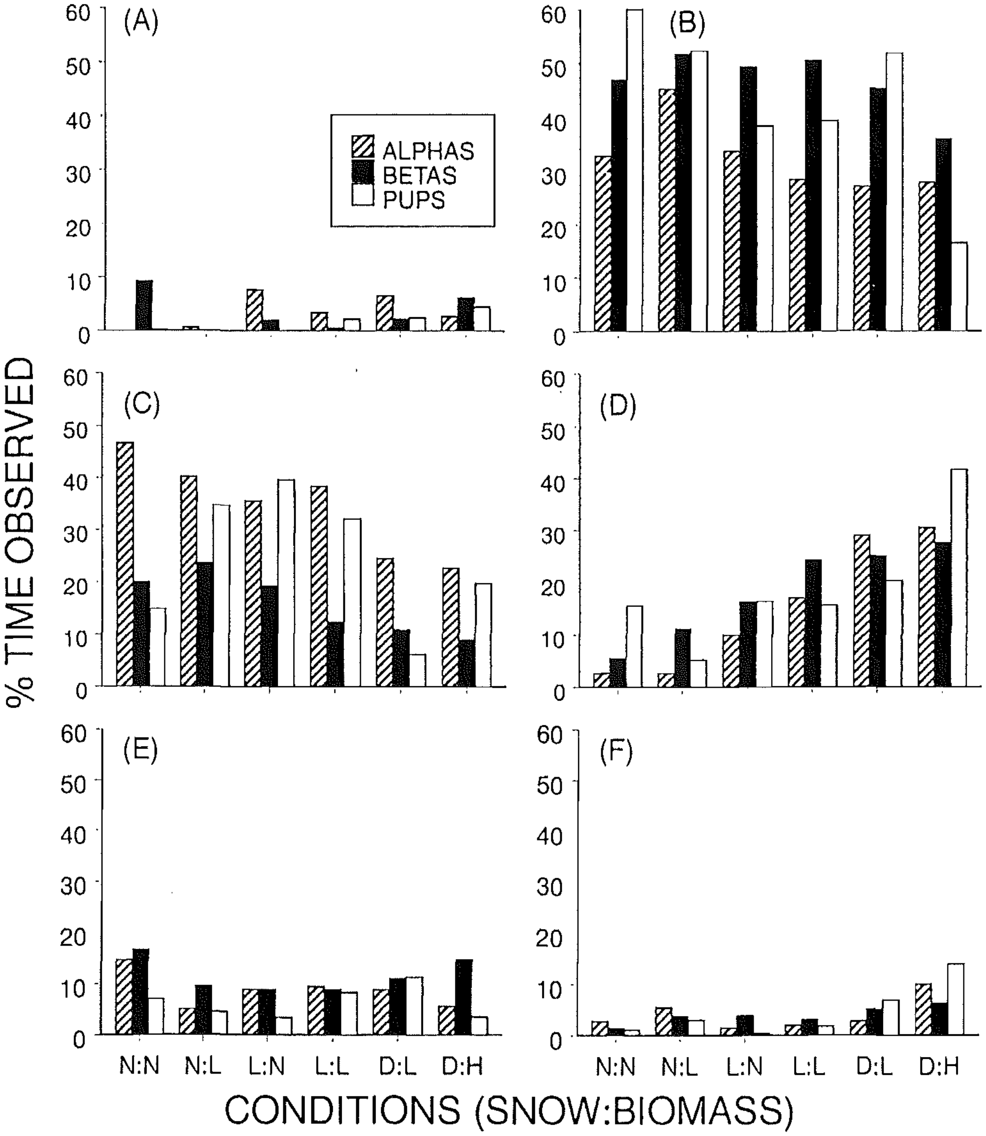
We found that use of some habitats was influenced by social status (Table 4). Among social classes, both pups ($P = 0.07$) and betas ($P = 0.009$) used meadows more than alphas (Fig. 7B) for all conditions combined; pups and betas did not differ in the use of meadows ($P = 0.88$). Alphas used sage–grasslands in higher amounts than betas ($P < 0.001$) across all conditions, but not differently from pups ($P > 0.15$) (Fig. 7C). Pups used mesic shrub–meadows more than alphas and betas during conditions of deep snow and high biomass ($P = 0.05$) (Fig. 7D). Alphas used roads more than betas ($P - 0.003$) but not differently from pups ($P - 0.19$). Use of roads was similar between pups and betas ($P = 0.45$). The pack was also a significant influence on the use of almost all habitats (Table 4), which was expected because of differing habitat components in each pack territory.

Habitat type influenced the amount of time an activity was performed by a coyote. Coyotes spent much of their time resting in sage–grasslands, mesic meadows, and shrub–meadows (Fig. 8A). Coyotes rested little on roads or in riparian areas. Coyotes used roads and riparian areas mostly for travel (Fig. 8B), and increased the use of these two types of habitat as snow depth increased. The frozen rivers and roadways provided a snow-free pathway as snow increased in vegetated habitats. Snow cover was typically lower in these habitats because of plowed roads or wind-blown river ice in the riparian areas. Travelling in mesic meadows and shrub–meadows was mostly in conjunction with hunting. Most of the hunting of small mammals was observed in mesic shrub–meadows, mesic meadows, grasslands, and sage–grasslands (Fig. 8C). Feeding on carcasses was observed mainly in grasslands, sage–grasslands, and forests (Fig. 8D).

Influence of rates of detection and capture of prey on time spent hunting

We found that coyotes spent different amounts of time hunting small mammals in each of the seven identified types of habitat in the study area (Fig. 8C). Prey density within each habitat would most likely influence the proportion of time spent hunting in that habitat, therefore we regressed the proportion of time all coyotes spent hunting small mammals

Fig. 7. Amount of time alpha, beta, and pup coyotes were observed to spend in forest (A), mesic meadow (B), sage–grassland (C), mesic shrub–meadow (D), grassland (E), and riparian (F) habitat under different ecological conditions, Yellowstone National Park, Wyoming, 1991–1993. Snow-cover conditions included no (N), low (L), and deep snow (D). Carcass biomass conditions included no (N), low (L), and high biomass (H).

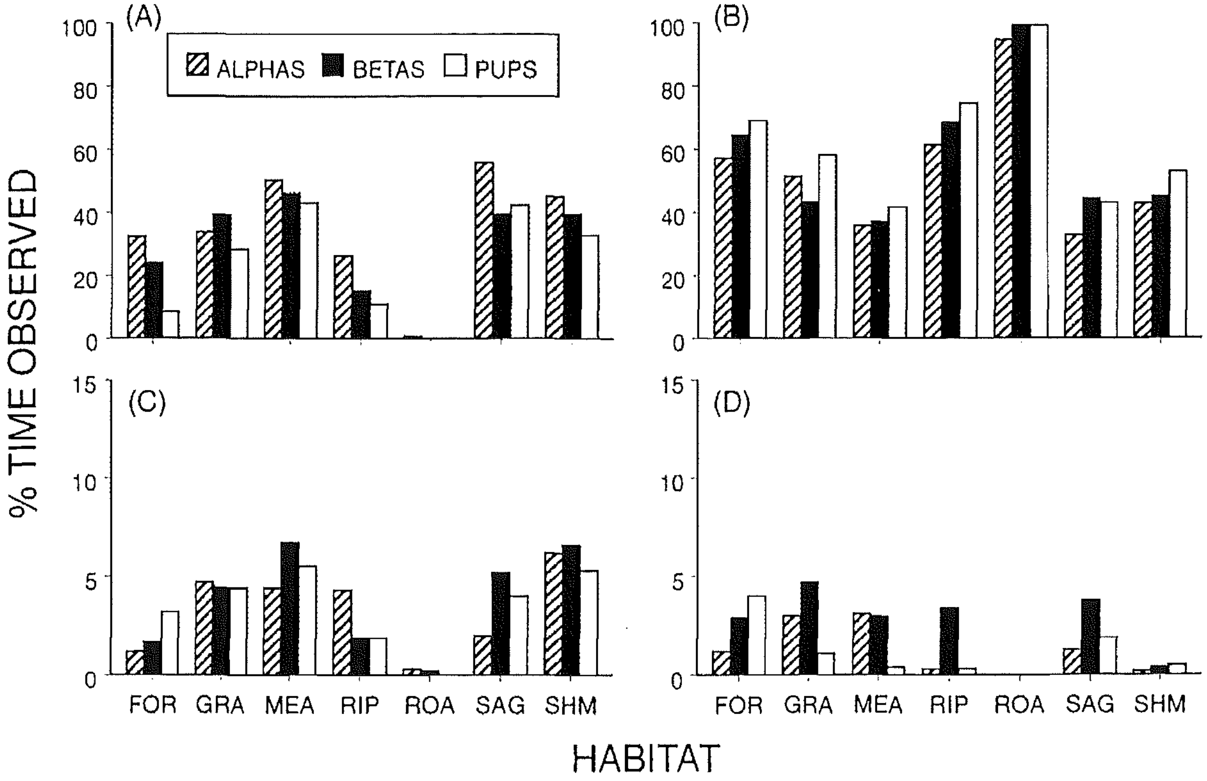


in a habitat on the number of detections and captures of prey per hour spent active in each habitat during each winter. The detection rate was the number of small mammals detected per hour spent active by coyotes, visually determined as a coyote orienting, stalking, pouncing, digging, or rushing a prey item (Gese 1995). The capture rate was the number of prey items that a coyote successfully captured per hour spent active. We found that 78% of the variation in the amount of time coyotes spent hunting small mammals in each habitat was explained by the detection rate of prey in that habitat ($F = 64.97$, $P < 0.001$) (Fig. 9A). Habitats in which coyotes detected small mammals at higher rates were those where coyotes spent more time hunting. Similarly, the rate of prey capture in each habitat explained 84% of the variation in the amount of time coyotes spent hunting in a habitat ($F = 96.87$, $P < 0.001$) (Fig. 9B). As the capture rate of small mammals increased in each habitat, coyotes spent more time hunting in that habitat. The amount of time coyotes spent hunting in a habitat was in proportion to the rates of detection and capture of small mammals in that habitat.

Influence of social organization on activity budgets

Bekoff and Wells (1981, 1986) found a significant influence of coyote social organization on activity budgets. They found that pack members rested more and travelled less than transient coyotes, but there was no difference in the time spent at carrion. We found that the overall proportion of time transient coyotes spent resting, travelling, hunting, and feeding on a carcass did not differ from that spent by members of resident packs ($\chi^2 = 5.51$, 3 df, $P = 0.16$). Paired t tests showed that the mean amount of time residents versus transients rested ($t = 0.356$, $P = 0.72$), travelled ($t = 0.739$,

Fig. 8. Amount of time alpha, beta, and pup coyotes were observed to spend resting (A), travelling (B), hunting small mammals (C), and feeding on carcasses (D) in seven different types of habitat in Yellowstone National Park, Wyoming, 1991–1993. Habitats included forest (FOR), grassland (GRA), mesic meadow (MEA), riparian (RIP), road (ROA), sage–grassland (SAG), and mesic shrub–meadow (SHM).



$P = 0.46$), and hunted ($t = 0.049$, $P = 0.96$) did not differ. However, there appeared to be a difference in the mean amount of time residents (2%) versus transients (0.3%) spent feeding on a carcass ($t = 1.927$, $P = 0.056$). Transients, which were solitary animals in our study area, may be at a disadvantage when attempting to obtain, feed on, or defend a carcass (Bowen 1981; Bekoff and Wells 1981).

Discussion

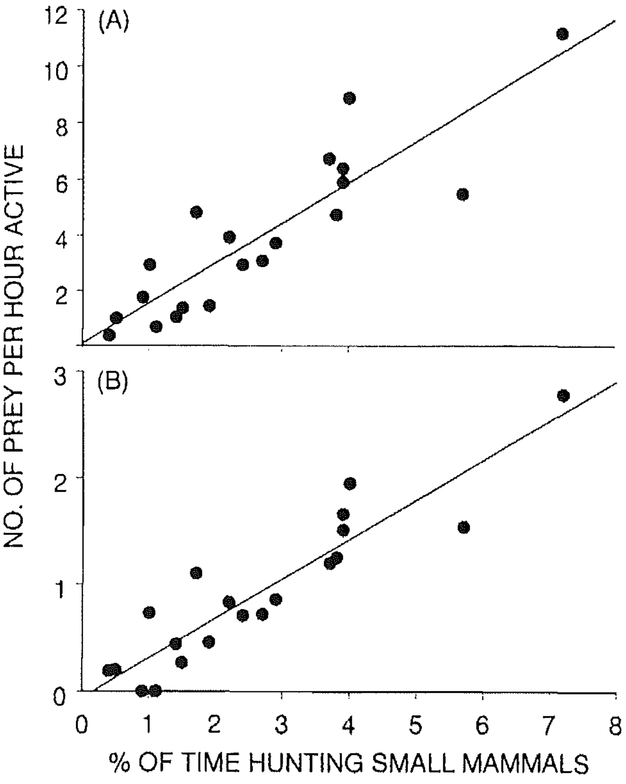
Coyotes have been studied with radiotelemetry throughout the United States and Canada. While telemetry studies have provided information on coyote home-range size, habitat use, movements, and population dynamics, insights into predatory behavior and foraging ecology have been limited to scat analysis and anecdotal observations of coyote predation on large prey. Little is known about the influence of extrinsic factors and social rank on the foraging ecology of coyotes. Bekoff and Wells (1981, 1986) reported only small differences among pack members in the amount of time spent resting, travelling, and feeding on carrion. However, they reported data from only three members of one pack (Bekoff and Wells 1981, p. 798).

Activity budgets of coyotes in YNP changed throughout the year, which is similar to findings reported by Bekoff and Wells (1981, 1986). While coyotes in YNP spent a similar amount of time resting and travelling to coyotes in Grand Teton National Park, we found that they spent less time hunting and feeding on carcasses than coyotes observed by Bekoff and Wells (1981, 1986). However, our estimate of time spent feeding on carcasses was the actual amount of time the coyotes fed, whereas Bekoff and Wells (1981) measured the amount of time coyotes spent at carrion (i.e., within 5–20 m of ungulate carrion).

Extrinsic factors significantly influenced activity budgets of coyotes in YNP. As snow depth and carcass biomass increased, coyotes spent more time resting and feeding on carcasses while reducing the amount of time travelling and hunting small mammals. Increased snow depth and the corresponding increase in carcass biomass allowed coyotes to feed on a large localized food source and reduced the need to hunt small mammals. Increased snow depth and hardness of the crust also reduced capture rates and capture success on small mammals (Wells and Bekoff 1982; Gese 1995). The visual and auditory senses are very important in coyote predatory behavior (Wells and Lehner 1978). A hard crust and deep snow may eliminate visual detection of prey while impairing auditory detection and location of prey. Bekoff and Wells (1981, 1986) found a similar decline in the amount of time coyotes spent hunting during winter versus other seasons, particularly during snowy winters.

We observed that the coyotes spent much of their time resting near carcasses during times of deep snow. The presence of a large food source should lessen the need to travel and hunt for small mammals. Increased costs of locomotion in deep snow may have also influenced the amount of time

Fig. 9. Relationship between the amount of time coyotes spent hunting in each type of habitat during each winter versus prey-detection rate (A), and prey-capture rate (B), Yellowstone National Park, Wyoming, 1991–1993.



coyotes spent travelling. Bekoff and Wells (1981, 1986) similarly found that coyotes rested more, and for longer periods, in winter than in fall and spring–summer, and rested most during snowy winters. Wolves (*Canis lupus*) observed in Minnesota (Mech 1977, 1992) and Alaska (Peterson et al. 1984) spent a large amount of time sleeping and resting and little time feeding on recent kills during winter. Wolves also reduced the time and distance spent travelling during periods of deep snow, possibly in response to increased vulnerability of ungulate prey (Kolenosky 1972; Peterson 1977).

Habitat type influenced the amount of different activities performed by coyotes. Coyotes spent most of their time hunting small mammals in shrub–meadows and mesic meadows (Fig. 8C). In the Lamar River Valley, mesic meadows and shrub–meadows had the highest numbers of microtines, sage–grasslands had lower numbers, and mixed forests had the lowest numbers (M. Harter and R.L. Crabtree, unpublished data). Coyotes appeared to be aware of which habitats contained the highest prey density, and spent more time hunting in those habitats, where they experienced higher rates of detection and capture of small mammals (Fig. 9). Murray et al. (1994) also found, through snowtracking, that coyotes and lynx (*Lynx canadensis*) selected habitats in southwestern Yukon on the basis of snowshoe hare (*Lepus americanus*) abundance, and that coyotes selected habitats where they were most successful in capturing hares.

Coyotes spent the most time feeding on carcasses in forests, grasslands, and sage–grasslands. Coyotes spent little time feeding on carcasses along roads or in mesic shrub–meadows. The increased use of shrub–meadows as snow depth and carcass biomass increased was not in response to high carcass biomass in that habitat, as indicated by the low amount of feeding on carcasses; rather, we believe that it was a consequence of the coyotes' need to hunt small mammals, and because deep snow made hunting rodents difficult (Gese 1995), they hunted primarily in the habitat with the highest prey density and where they were most successful in finding and capturing prey.

Our results indicated that resource partitioning occurred between members of the resident packs in our study area. Pup coyotes fed on carcasses less than alphas and betas during periods of both low and high carcass biomass. Pups appeared to compensate for this deficiency in carcass availability by adopting a different foraging strategy, spending more time hunting small mammals. Apparently, pups were excluded from, or were outcompeted by, older pack members when feeding on carcasses (i.e., resource defense by alphas and betas). While pups were still allowed some access to kills (Gese and Grothe 1995), access was not equal among social classes. We typically observed that when packs were at a fresh kill, the alphas ate their fill, then the betas, and lastly the low-ranking members of the pack, the pups. When other packs became aware of the carcass, particularly if it was on territorial borders, the high-ranking animals would quickly displace the pups or betas at the carcass.

Evidence of resource partitioning in relation to dominance rank has been found in other social carnivores. In the Namib Desert of southwestern Africa, spotted hyenas (*Crocuta crocuta*) showed a similar linear dominance hierarchy when feeding on a carcass. Low-ranking individuals eventually gained access to a large carcass but were excluded from small carcasses (Tilson and Hamilton 1984). The lowest-ranking individuals also fed for a significantly shorter period at large carcasses than higher-ranking hyenas. Frank (1986) found a high correlation between social rank and feeding scores of female spotted hyenas in the Masai Mara National Reserve in Kenya. Not only did high-ranking females have increased access to food, but the feeding scores of cubs were correlated with their mother's dominance rank. Brown hyenas (*Hyaena brunnea*) may also feed in hierarchical order at carcasses (Owens and Owens 1978). Subordinate wolves in captivity were observed to have less access to carcasses than dominant animals, particularly during times of food shortage (Zimen 1976, 1981). There was indirect evidence of resource partitioning among pack members in some red wolf (*Canis rufus*) packs. Through analysis of individually identified scats, juveniles (≤18 months) were found to feed primarily on small mammals, while adults fed mainly on deer (B. Kelly, personal communication). In lions (*Panthera leo*), adult females are subordinate to adult males, but are the primary hunters of ungulates in the pride (Bertram 1976). The females may gain access to the carcass in competition with the males, or may wait and feed after the males have fed.

We found that by fall and early winter, pups were no longer provided with food by their parents or other pack members, and therefore had to find and compete for food themselves. The theory of parent–offspring conflict suggests that at some point in time, parents must stop all help and care of their present litter and invest in their own survival and future offspring (Trivers 1972, 1974). While the pups we observed were directly related to the alpha pair, survival of the breeding pair was apparently more important than survival of the current offspring. In contrast to our findings, the offspring of high-ranking female hyenas were allowed equal access to carcasses (Tilson and Hamilton 1984; Frank 1986). Cubs of high-ranking females could successfully challenge and displace larger hyenas at a carcass. Perhaps the existence of a matriarchal leadership system in hyena clans and a larger body size accounts for this difference in access to food resources and long-term help of young (Frank 1986).

The relationship between dominance and resource partitioning among pack members could be a mechanism regulating coyote pack size, as has been suggested for wolves (Zimen 1976) and spotted hyenas (Tilson and Hamilton 1984). Dispersal plays an integral role in regulating pack size in canid populations (Zimen 1976; Packard and Mech 1980; Knowlton and Stoddart 1983). Pups, being the low-ranking individuals in a coyote pack, are also the age cohort most likely to disperse from the pack (Bekoff and Wells 1986; Gese et al. 1989). These pups may voluntarily leave the pack, as higher ranking siblings (i.e., betas) have better access to carcasses and are typically "biders" waiting to displace the alphas or replace them when they die (see "Pack histories"). Reduced access to carcasses could be a mechanism triggering dispersal of young animals (Zimen 1976), particularly during times of deep snow, when small mammals are difficult to capture (Gese 1995). During times of low food resources, more pups should be compelled to disperse and the size of the pack would remain small. In contrast, during winters of high food resources, more pups should be able to remain and the size of the pack would increase.

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