

Intrinsic and extrinsic factors influencing coyote predation of small mammals in Yellowstone National Park

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

Abstract: We examined the intrinsic (age, sex, and social status) and extrinsic factors (snow depth and hardness, temperature, cloud cover, wind speed, and habitat) influencing coyote (*Canis latrans*) predation of small mammals 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. We observed 6433 prey detections by coyotes during which coyotes made 4439 attempts to capture prey, resulting in 1545 successful prey captures. The age of the coyote influenced prey-detection rates, predation attempts, and capture rates, plus the proportions of prey attacked after being detected and capture success. Pups had higher prey-detection rates and higher attempt rates than alphas and betas, but capture rates were similar. Snow depth and hardness and habitat type were factors influencing detection rates, predation attempt rates and capture rates. Coyotes hunted mainly in mesic meadows and shrub-meadows, where prey-detection rates, predation attempt rates, and capture rates were highest. Snow depth influenced coyote predation on small mammals, prey-detection rates, predation attempt rates, and capture rates being highest in low snow cover and lower in deeper snow. Our findings indicated that young, inexperienced coyotes detected and attacked small mammals at a higher rate than older coyotes. Yearlings and adults were more selective, and thus detected and attempted to capture prey at a lower rate than pups. Overall, however, pups and older coyotes captured similar numbers of prey per hour.

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 résidents de 5 meutes, plus 5 individus de passage) pendant 2507 h, entre janvier 1991 et juin 1993. Nous avons observé 6433 cas de détection de proies par les coyotes, suivies de 4439 tentatives de capture et 1545 captures réussies. L'âge des coyotes influence les taux de détection, de tentative de capture et de capture des proies, de même que la proportion des proies attaquées après détection et la proportion des captures réussies. Les chiots font plus de détections et de tentatives de capture que les coyotes alpha ou bêta, mais les taux de capture sont les mêmes chez tous les groupes d'âge. La profondeur de la couche de neige, sa dureté et le type d'habitat influencent les taux de détection, de tentative de capture et de capture. Les coyotes chassent surtout dans les prairies mésiques et les prairies buissonneuses où les taux de détection, de tentative de capture et de capture sont le plus élevés. L'épaisseur de la couverture de neige influence la prédation exercée par les coyotes sur les petits mammifères; les taux de détection, de tentative de capture et de capture sont plus élevés lorsque la couche de neige est moins profonde et moins élevés lorsque la couche de neige est plus profonde. Nos résultats indiquent que les jeunes coyotes inexpérimentés détectent et attaquent les petits mammifères à des taux plus élevés que les coyotes plus âgés. Les jeunes de 1 an et les adultes sont plus sélectifs et leurs taux de détection et de tentative de capture sont donc moins élevés que ceux des chiots. Dans l'ensemble cependant, les chiots et les coyotes plus âgés capturent des nombres semblables de proies par heure.
[Traduit par la Rédaction]

Introduction

Predation has been defined as the killing and eating of living individuals of one species by another species (Taylor 1984). Observing the predatory behavior of coyotes (*Canis latrans*)

is difficult, owing to their secretive and nocturnal nature. Studies on the predatory behavior of coyotes have usually involved observing captive animals (Bekoff 1978; Vincent and Bekoff 1978; Wells 1978; Wells and Lehner 1978), predation on wild ungulates (Truett 1979; Wenger 1981; Gese and Grothe 1995), or coyotes preying on livestock (Jansen 1974; Connolly et al. 1976). Little is known about the behavior of coyotes preying on small mammals in the wild. In only one previous study of wild coyotes have direct observations of their predatory behavior been recorded (Wells and Bekoff 1982). These authors found that adults and pups were equally successful in capturing prey, but the pups captured only grasshoppers. Capture success was not affected by wind speed, was greater in shallow snow than in deep snow, and was influenced by grass height (Wells and Bekoff 1982).

Received June 6, 1995. Accepted October 24, 1995.

E.M. Gese¹ and R.L. Ruff. Department of Wildlife Ecology, University of Wisconsin, Madison, WI 53706, U.S.A.

R.L. Crabtree. Biology Department, Montana State University, Bozeman, MT 59717, U.S.A.

¹ Present address: U.S. Department of Fisheries and Wildlife, Denver Wildlife Research Center, Utah State University, Logan, UT 84322-5295, U.S.A.

However, many questions about the influence of intrinsic and extrinsic factors on coyote predation remained unanswered.

The observable and diurnally active nature of coyotes in Yellowstone National Park allowed for the examination of the influence of intrinsic and extrinsic factors on coyote predation of small mammals. Gese (1995) examined the influence of intrinsic and extrinsic factors on coyote activity budgets, with particular emphasis on the amount of time coyotes spent hunting. Hunting by coyotes was influenced by social status, snow depth, available carcass biomass, and habitat type, and further, coyotes spent more time hunting in habitats with the highest prey-detection and prey-capture rates. Overall, pups spent more time hunting small mammals than did alpha and beta coyotes, especially during times of deep snow and high carcass biomass, when pups fed less on carcasses (Gese 1995). Once a coyote was hunting small mammals, we utilized direct observations to examine the following questions in regard to the act of predation: (i) do intrinsic factors, including sex, age, and social status of the coyote, influence prey-detection rates, predation attempts, and capture rates of small mammals? (ii) do extrinsic factors, including snow depth, snowpack hardness, temperature, cloud cover, wind speed, and habitat type, influence prey-detection rates, predation attempts, and capture rates of small mammals by coyotes? (iii) do intrinsic and extrinsic factors influence the length of time coyotes spend approaching, pursuing, and handling a prey item?

Study area

The 70-km² study area is located at about 2000 m above sea level in the Lamar River Valley, Yellowstone National Park, Wyoming (44°52'N, 110°11'E). Winters are long and cold, with most of the annual precipitation falling as snow (Houston 1982). Mean annual precipitation and temperature is 31.7 cm and 1.8°C, respectively (Houston 1982). Habitats identified in the study area included forest, riparian, grassland, sage-grassland, mesic meadow, mesic shrub-meadow, and road (Gese 1995).

Ungulate prey species within the park included elk (*Cervus elaphus*), bison (*Bison bison*), mule deer (*Odocoileus hemionus*), pronghorn antelope (*Antilocapra americana*), moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), and white-tailed deer (*Odocoileus virginianus*). During winter, elk carrion was a major food source for coyotes and was a result of winterkill (Murie 1940) or coyote predation (Gese and Grothe 1995). Small mammals available year-round as prey items to coyotes included microtines (*Microtus* spp.), mice (*Peromyscus* spp.), and pocket gophers (*Thomomys talpoides*). Uinta ground squirrels (*Spermophilus armatus*) were available as prey for coyotes only during spring and summer.

Methods

We captured coyotes with padded leg-hold traps with attached tranquilizer tabs (Balsler 1965). Coyotes were immobilized (Cornely 1979) for removal from the trap and processing. We weighed, sexed, ear-tagged, and radio-collared the coyotes and extracted the first vestigial premolar from the lower jaw for aging by analysis of cementum annuli (Linhart and Knowlton 1967). We captured pups at the den when they were 10–12 weeks old, ear-tagged them, and surgically implanted an intraperitoneal transmitter. We assigned coyotes to one of three age-classes: pup (<12 months old), yearling (12–24 months old), or adult (>24 months old).

We classified each coyote as either a member of a resident pack or a transient (Bowen 1981; Gese et al. 1988). We further classi-

fied coyotes within the resident pack into different social classes based upon the separate male and female dominance hierarchies observed within each resident pack. Social classes included alphas (dominant, breeding adult male and female), betas (adults and yearlings subordinate to alphas but dominant over pups), and pups (young of the year subordinate to both alphas and betas) (Schenkel 1947, 1967; Rabb et al. 1967; Mech 1970). Coyotes classified as pups remained in that class until the next litter became mobile and independent of parental feeding in September. An individual was moved into the next age and social class as it grew older and elevated its rank within the pack hierarchy.

We made direct open-field observations of transmitter-equipped and unmarked (identifiable by physical characteristics) coyotes in the Lamar River Valley during daylight hours, usually between 07:00 and 20:00 h. We collected nocturnal observations using an 11× night-vision scope (Litton Electron Devices, Tempe, Arizona). We conducted observations on coyotes from October to July; the >1 m high grass in August and September precluded observation in those 2 months. To avoid repeated sampling of the same group or individuals (Morrison et al. 1992), we randomly chose coyote packs to be observed before going into the field. We then stratified individuals within the pack (based upon previous sampling effort) to allow for systematic selection of the animal to be observed in the pack.

An observer sat at a site overlooking the pack territory, and using radiotelemetry and a 10–45× spotting scope, located the individual scheduled for observation. If that individual was not located, the observer attempted to locate the next animal on the priority list. If no animal could be located, the observer moved to the next randomly chosen pack. The animal chosen was then observed using focal-animal sampling (Lehner 1979; Morrison et al. 1992) and all activities performed by that individual were continuously recorded. Predatory behavior was recorded to within 1 s using a program on an Atari Portfolio notebook computer or on a tape recorder and transcribed later. The behavior program recorded the type of behavior the animal performed, the time it was performed, and the habitat where it occurred. To minimize observer error (Lehner 1979; Martin and Bateson 1993), each observer was trained by the senior author for a minimum of 5–7 days to maintain reliable and consistent interpretation of behaviors. Predatory behaviors recorded were stalk, rush, rush-pounce, pounce, head thrust, search, orient, dig, and eat, following descriptions by Murie (1940), Bekoff (1978), and Wells and Bekoff (1982).

The act of predation can be regarded as a sequence of events or decisions made by the predator (Wells and Bekoff 1982; Sih 1993). First, the animal must decide to hunt. Once hunting is initiated, the animal must encounter or detect prey. If it detects or encounters prey, the animal must decide if it will attempt to attack or capture the prey. Once it attempts to capture the prey, the attempt may end in success or failure. Lastly, if the predator successfully captures the prey, it may or may not consume it. Thus, we examined the influence of intrinsic and extrinsic factors at each stage of the predation sequence. Prey detection occurred when a coyote oriented or stalked, and included all attempts to capture prey. An attempt occurred when a coyote actively pursued a prey item and was a subset of all detections (i.e., coyotes did not try to capture all prey detected). A capture occurred when a coyote successfully acquired the prey item and was a subset of all attempts (i.e., not all attempts were successful). The success or failure of the attempt was recorded and the prey item consumed was identified when possible, or classified as a small rodent, large rodent, bird, or unknown.

Using a computer program, we summed the numbers of prey detections, predation attempts, and successful captures by prey item for each habitat. We calculated a standardized rate (number per hour) for all detections, predation attempts, and captures when the coyote was active (i.e., we excluded the time the coyote was bedded) for each day a coyote was observed. We calculated the

Table 1. Influence of sex, social status, habitat type, snowpack hardness, cloud cover, snow depth, temperature, and wind speed on prey-detection rates, predation attempt rates, and capture rates by coyotes in Yellowstone National Park, Wyoming, 1991–1993.

Source	df	Detection rate		Attempt rate		Capture rate	
		F	P	F	P	F	P
Sex	1	0.89	0.346	3.56	0.060	2.04	0.154
Status	2	14.96	<0.001	22.92	<0.001	3.37	0.034
Habitat	6	41.05	<0.001	31.93	<0.001	14.39	<0.001
Snowpack hardness	3	7.84	<0.001	10.34	<0.001	3.21	0.022
Cloud cover	3	0.06	0.981	0.14	0.936	0.33	0.802
Snow depth	1	51.95	<0.001	31.82	<0.001	14.44	<0.001
Temperature	1	0.76	0.384	1.70	0.192	0.18	0.666
Wind speed	3	0.87	0.454	0.70	0.549	0.91	0.432
Error	1652						

proportion of prey detected that coyotes attempted to capture (percent attempted) and the proportion of attempts resulting in capture (percent captured). We also measured the time (in seconds) that a coyote spent approaching (time from detection to attack), attacking (time from attack to capture or failure), and handling (time spent eating) each prey item.

Weather conditions were recorded at the end of the observational period. Cloud cover was classed as clear, low (5–25% overcast), moderate (26–50% overcast), or heavy (>50% overcast). Wind speed was classed as calm, light (2–8 km/h), moderate (9–24 km/h), or high (≥ 25 km/h). Temperature was recorded to the nearest 3°C. Snow depth and hardness were recorded every 1–2 days by excavation of a snow pit. Hardness of the snowpack was measured as soft (powder snow or no crust, snow did not support a coyote's weight), moderate (a crust was present and occasionally supported the weight of a walking coyote), or hard (a thick crust was present and consistently supported a walking coyote's weight).

All statistical tests were performed using SYSTAT (Wilkinson et al. 1992). Multiway analyses of variance (ANOVA) followed a factorial design (Steel and Torrie 1980; Sokal and Rohlf 1981) and included only the main effects. ANOVA with repeated measures was not performed because some animals died, dispersed, or were not observed in every environmental condition. Tukey's test of all possible comparisons was performed when one-way ANOVA indicated a significant difference among groups. For all statistical tests involving rates and proportions, the sampling unit was the individual coyote observed each day. We used days on which the coyote was observed to be active for ≥ 0.5 h and detected ≥ 1 prey item (i.e., we could only assume that coyotes were hunting rodents if they were active and showed an interest in small mammals). We did not use days on which coyotes were not observed hunting. For examining the length of time spent approaching, attacking, and handling prey, the sampling unit was each predatory sequence (i.e., approach, attack, and consume if successful).

Results

From January 1991 to June 1993, we observed 54 coyotes (49 residents from 5 packs, plus 5 transients) for 2507 h during which we observed 6433 prey detections, 4439 attempts to capture prey, and 1545 captures: an overall success rate of 35%. Of the 54 coyotes observed, 29 were males, 23 were females, and 2 nonmarked coyotes were of unknown sex. Thirty-one coyotes were radio-collared or implanted, and 23 were recognizable from physical characteristics. Pack

size, age, and social structure of the coyotes belonging to the 5 resident packs over the three winters in the Lamar River Valley were summarized in Gese (1995).

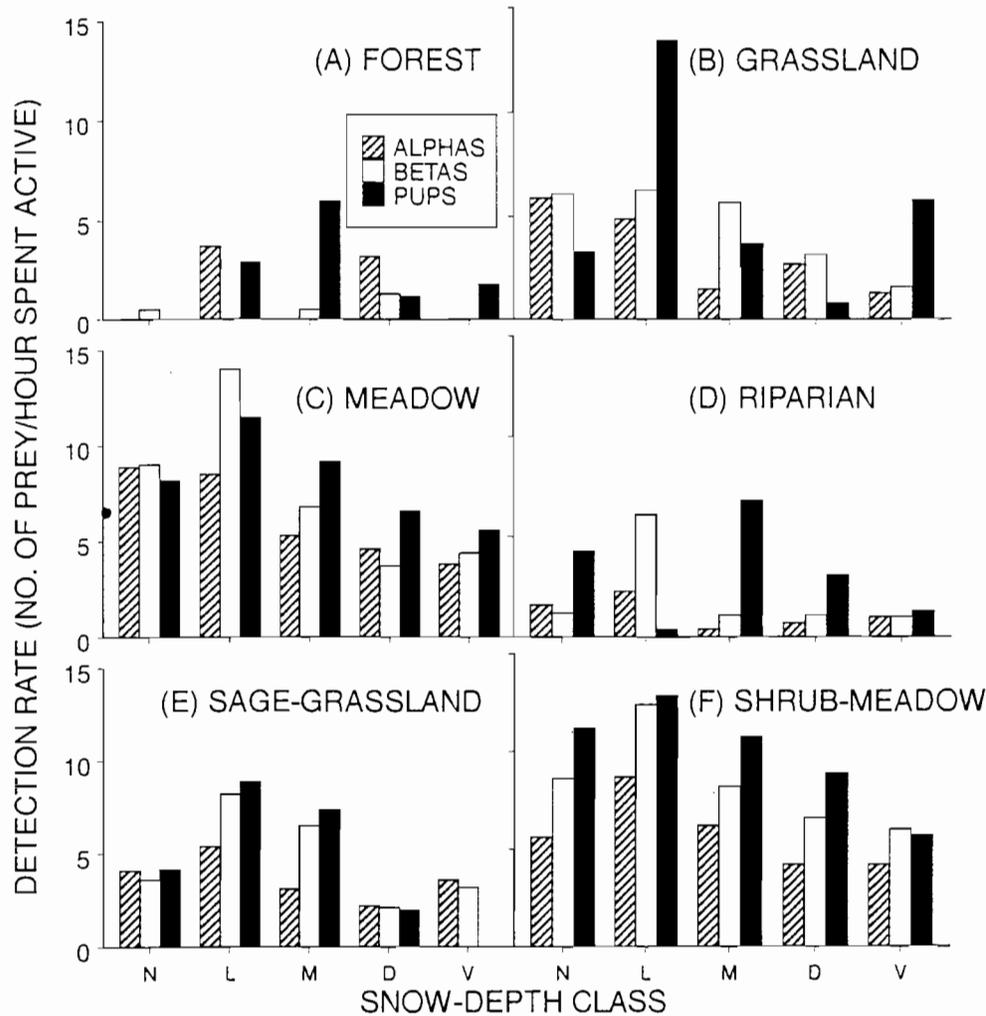
Prey-detection rates

We found that the social status of the coyote, habitat type, snow depth, and snowpack hardness all significantly influenced the rates of detection of small mammals by coyotes (Table 1). Prey-detection rates by coyotes averaged 8.0, 7.3, 4.6, 4.4, 2.2, 1.4, and 0.7 prey/h for shrub–meadow, mesic meadow, sage–grassland, grassland, riparian, forest, and road habitat, respectively ($F_{[6,1668]} = 39.82$, $P < 0.001$) (Fig. 1). Coyotes had the highest prey-detection rates in mesic meadows and shrub–meadows ($P < 0.001$), followed by grasslands and sage–grasslands ($P = 0.99$). Prey-detection rates in forests, riparian areas, and along roads were similar ($P > 0.95$), and all significantly lower than in all the other habitat types ($P < 0.001$).

The previous analysis examined the influence of snow along a continuous gradient. For purposes of comparison, we classed snow into five depth categories: no, low (5–15 cm), moderate (16–25 cm), deep (26–40 cm), and very deep (>40 cm). Prey-detection rates by coyotes averaged 5.8, 8.4, 5.0, 3.7, and 3.4 prey/h for days with no, low, moderate, deep, and very deep snow, respectively ($F_{[4,1670]} = 28.38$, $P < 0.001$) (Fig. 1). Prey-detection rates were highest during days of low snow ($P < 0.001$) and declined as snow depth increased, reaching their lowest during days of deep or very deep snow ($P < 0.04$).

Prey-detection rates were different among the three coyote social classes ($F_{[2,1672]} = 17.66$, $P < 0.001$) (Fig. 1). Overall, pups had higher prey-detection rates than alphas ($P < 0.001$) and betas ($P = 0.003$), while those of betas were higher than those of alphas ($P = 0.002$). This difference occurred only in mesic meadow, sage–grassland, and shrub–meadow habitats (F tests, $P < 0.05$). For forest, grassland, riparian, and road habitats, the social classes had similar detection rates (F tests, $P > 0.08$). Among the different snow-depth classes, pups had higher prey-detection rates than alphas and betas during days with low, moderate, or deep snow (F tests, $P < 0.05$). All social classes had similar detection rates during days of no or very deep snow (F tests,

Fig. 1. Prey-detection rates for alpha, beta, and pup coyotes across varying snow-depth classes in six different types of habitat in Yellowstone National Park, Wyoming, 1991–1993. N, none; L, low; M, moderate; D, deep; V, very deep (for a description of snow-depth classes see the text).



$P > 0.15$). The influence of social status was further illustrated when we plotted the prey-detection rates of different-aged coyotes through the winter (Fig. 2A). Pups had higher prey-detection rates during winter, yet by their second winter these coyotes as yearlings exhibited detection rates similar to those of adults.

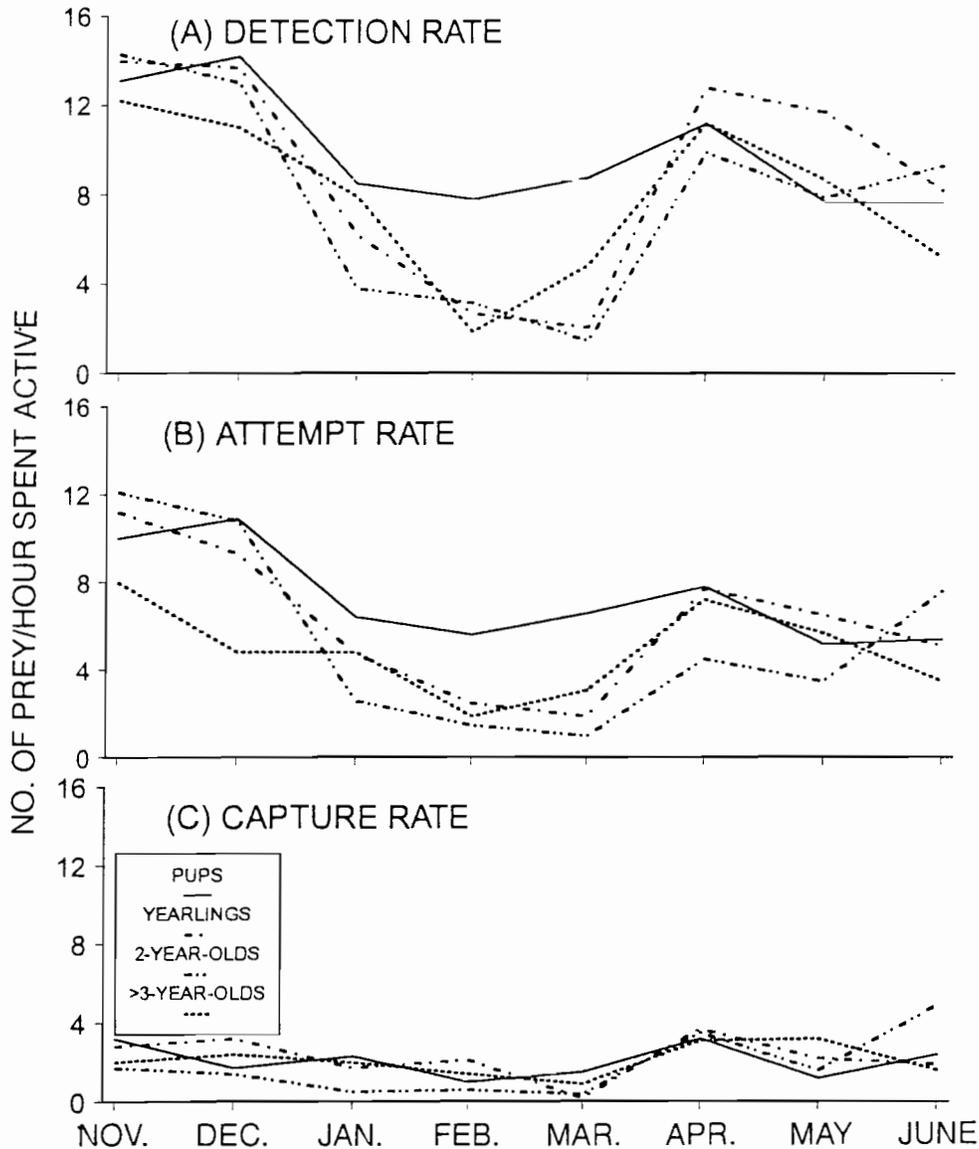
Coyotes had different prey-detection rates under varying snowpack hardness ($F_{[2,1671]} = 13.47$, $P < 0.001$) (Fig. 3A). Coyotes had higher prey-detection rates during days with soft snow than during days with moderate and hard snowpack ($P < 0.01$). Alphas had lower prey-detection rates than betas ($P = 0.008$) and pups ($P = 0.016$) during days with soft snowpack (Fig. 3A); pups and betas had similar rates ($P = 0.97$). During days with moderate snowpack, all social classes had similar prey-detection rates ($F_{[2,256]} = 1.73$, $P = 0.18$). When hard snowpack was present, pups had higher prey-detection rates than alphas ($P = 0.001$) and betas ($P = 0.001$), while betas had higher detection rates than alphas ($P = 0.004$).

For all coyotes combined, prey-detection rates averaged 5.7, 5.7, 5.9, and 6.1 prey/h for days with calm, light, moderate, and high winds, respectively ($F_{[3,1671]} = 0.23$,

$P = 0.87$). During calm days (Fig. 4A), alphas had lower prey-detection rates than pups ($P = 0.001$) and betas ($P = 0.008$); pups and betas had similar prey-detection rates ($P = 0.36$). During days with light winds (Fig. 4A), alphas had lower prey-detection rates than pups ($P = 0.001$) and betas ($P = 0.016$), while pups and betas did not differ ($P = 0.18$). Prey-detection rates did not differ among the social classes during days with moderate and high winds (F tests, $P > 0.09$).

Annual fluctuations and cycles of microtine populations are well documented (Taitt and Krebs 1985). Thus, we examined if rates of detection of small mammals by coyotes changed during the 3 years of study. We assumed that changes in vole numbers would be reflected in rates of detection by coyotes. Because snow depth influenced detection rates and snow depth varied daily and annually, we assessed changes in detection rates for days with no snow during each year (i.e., we removed the influence of snow). Using the same ANOVA with the variables previously described (sex, social status, habitat, cloud cover, temperature, wind speed), with the addition of years, we found that the detection rates of prey by coyotes were not influenced by year, sex, cloud cover, temperature, or wind speed (F tests, $P > 0.10$). If vole

Fig. 2. Influence of coyote age on detection rates (A), predation attempt rates (B), and capture rates (C) in November–June, Yellowstone National Park, Wyoming, 1991–1993.



numbers changed during the 3 years, it was not reflected in yearly changes in detection rates. However, detection rates could reach a threshold (i.e., a coyote may not be able to detect prey at densities beyond a maximal rate because of physical, spatial, and (or) temporal constraints).

Predation attempt rates

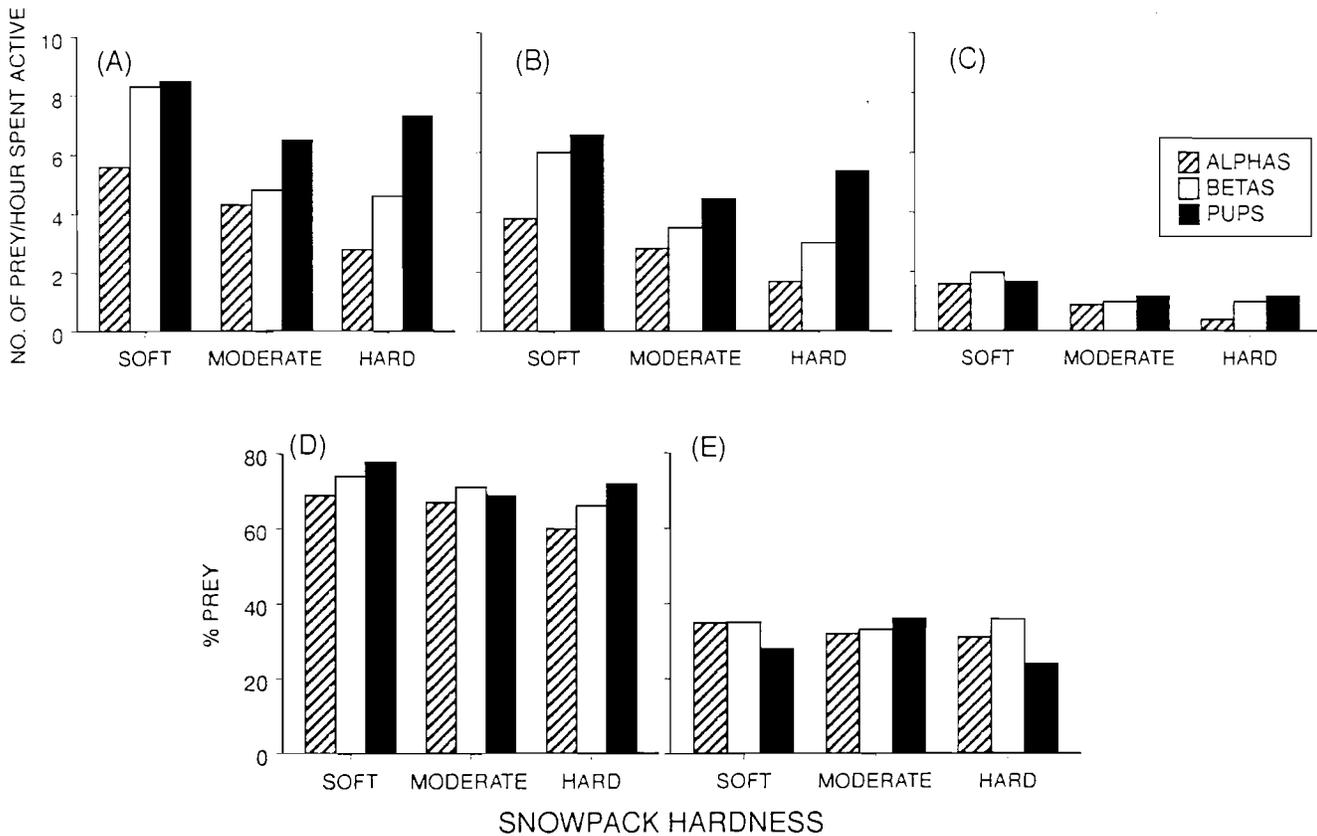
We found that social status, habitat type, snow depth, and snowpack hardness significantly influenced predation attempt rates on small mammals by coyotes (Table 1). The rate averaged 5.4, 5.2, 3.1, 3.1, 1.3, 1.0, and 0.5 prey/h for shrub–meadow, mesic meadow, grassland, sage–grassland, riparian, forest, and road habitat, respectively ($F_{[6,1668]}$, $P < 0.001$). Coyotes had the highest attempt rates in both ($P = 0.98$) mesic meadow and shrub–meadow compared with all other habitats ($P < 0.003$), moderate attempt rates in both ($P = 0.98$) grassland and sage–grassland, and

similar ($P > 0.90$) low attempt rates in forests, riparian areas, and along roads (Fig. 5).

Predation attempt rates by coyotes varied with snow depth ($F_{[4,1670]} = 24.35$, $P < 0.001$) (Fig. 5), the mean being 3.5, 5.9, 3.2, 2.6, and 2.4 attempts/h during days with no, low, moderate, deep, and very deep snow, respectively. Coyotes had the highest attempt rates during days with low snow ($P < 0.001$), similar lower rates during days with no, moderate, or deep snow ($P > 0.11$), and the lowest rates on days with very deep snow ($P < 0.05$) (Fig. 5).

Attempt rates by coyotes varied among the social classes ($F_{[2,1672]} = 24.57$, $P < 0.001$) (Fig. 5). Pups had higher attempt rates than both alphas ($P = 0.001$) and betas ($P = 0.001$), and betas had higher rates than alphas ($P = 0.001$). Not only were attempt rates higher, but pups and betas also attempted to capture a higher proportion of prey detected than did alphas ($P < 0.025$); pups and betas attempted to

Fig. 3. Influence of snowpack hardness on detection rates (A), predation attempt rates (B), capture rates (C), percentage of prey attempted (D), and percentage of prey captured (E) by coyotes in Yellowstone National Park, Wyoming, 1991–1993. Snowpack classes are described in the text.



capture similar proportions of prey detected ($P = 0.96$). This difference in attempt rates among social classes occurred only in grassland, meadow, sage-grassland, and shrub-meadow (F tests, $P < 0.04$), not in forests, riparian areas, or along roads (F tests, $P > 0.12$). In these four major habitats used for hunting (Gese 1995), pups always had the highest attempt rates, followed by betas, then alphas (Fig. 5). Like detection rates, attempt rates were higher for pups than for alphas and betas during days with low, moderate, deep, or very deep snow (F tests, $P < 0.03$), but not during days with no snow ($F_{[2,448]} = 0.41$, $P = 0.66$). Pups had high attempt rates throughout their first winter, but rates were similar to those of adults when they were yearlings (Fig. 2B).

The attempt rate averaged 5.5, 3.6, and 3.4 attempts/h during days with soft, moderate, and hard snowpack, respectively ($F_{[2,1671]} = 15.37$, $P < 0.001$) (Fig. 3B). For all social classes combined, coyotes had the highest attempt rates on days with soft snowpack ($P < 0.001$) and similar ($P = 0.62$) low attempt rates during days with moderate or hard snowpack. Pups and betas had similar ($P = 0.78$) higher attempt rates than alphas ($P < 0.006$) during days with soft snowpack. All three social classes had similar attempt rates during days with moderate snowpack ($F_{[2,256]} = 1.95$, $P = 0.14$). During days with hard snowpack, pups had higher attempt rates than alphas ($P = 0.001$) and betas ($P = 0.001$), and betas had higher attempt rates than alphas ($P = 0.003$). While attempt rates differed among the social classes during

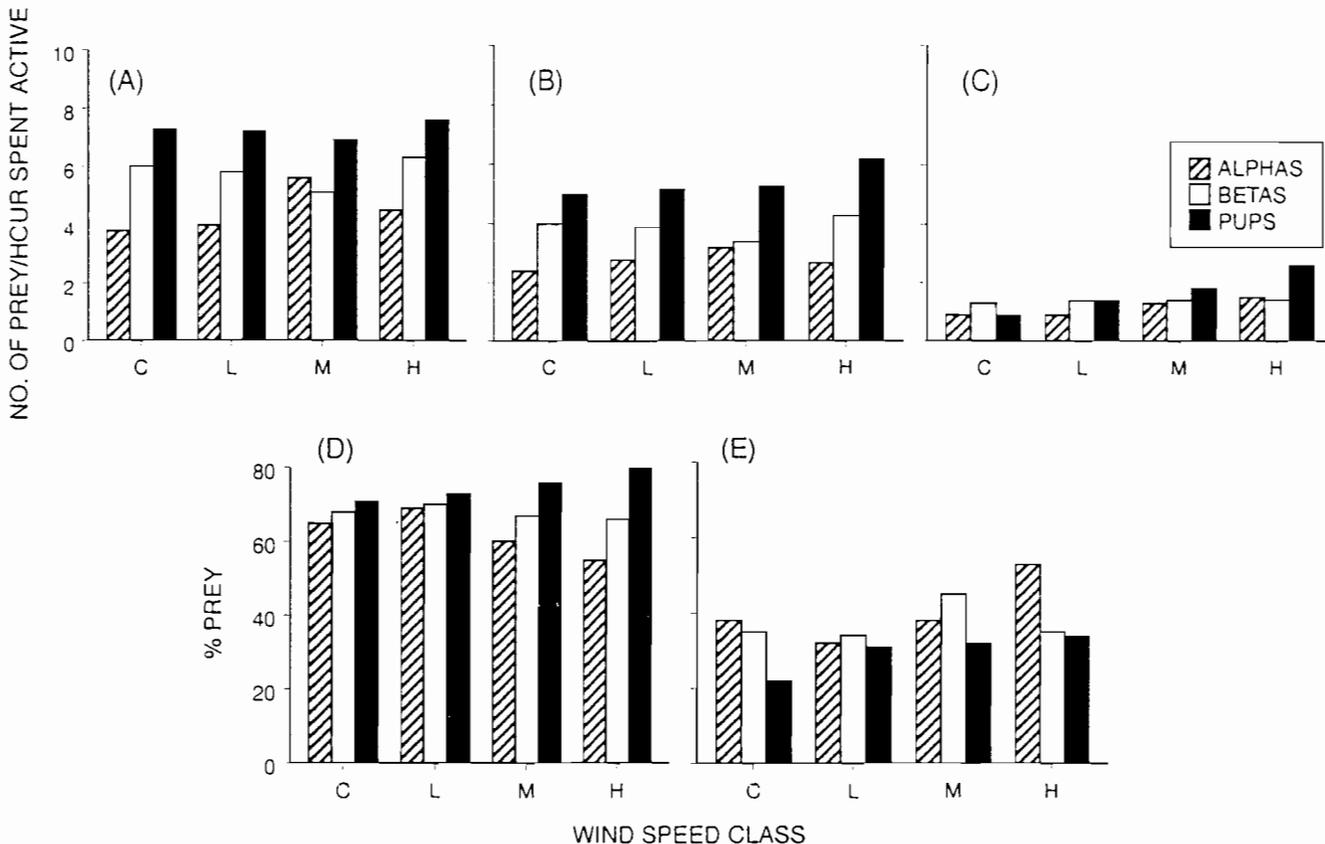
days with different snowpack hardness, the proportions of prey detected that coyotes of different social status attempted to capture did not differ (Fig. 3D). During days of soft ($F_{[2,229]} = 1.78$, $P = 0.17$), moderate ($F_{[2,149]} = 1.83$, $P = 0.16$), or hard snowpack ($F_{[2,331]} = 2.40$, $P = 0.09$), pups, betas, and alphas attempted to capture similar proportions of prey detected.

For all coyote social classes combined, attempt rates did not differ among wind-speed classes ($F_{[3,1671]} = 0.17$, $P = 0.92$). However, attempt rates among social classes did differ at each level of wind speed (Fig. 4B). During days with calm or light winds, betas and pups had similar attempt rates ($P > 0.10$), which were significantly higher than those of alphas ($P < 0.05$). During days of moderate or high winds, pups again had higher attempt rates ($P < 0.009$), while alphas and betas had similar ($P > 0.15$) lower attempt rates. While attempt rates differed among social classes, the proportions of prey detected that coyotes attempted to capture (Fig. 4D) did not differ among the social classes during days with calm ($F_{[2,250]} = 0.41$, $P = 0.66$) or light winds ($F_{[2,319]} = 0.57$, $P = 0.57$). During days with moderate or high winds, pups attempted to capture a greater proportion of prey detected than alphas ($P < 0.05$) and betas ($P < 0.07$).

Prey-capture rates

Social status, habitat type, snow depth, and snowpack hardness all influenced capture rates of small mammals by coyotes

Fig. 4. Influence of wind speed on detection rates (A), predation attempt rates (B), capture rates (C), percentage of prey attempted (D), and percentage of prey captured (E) by coyotes in Yellowstone National Park, Wyoming, 1991–1993. C, calm; L, light wind; M, moderate wind; H, high wind (wind speed classes are described in the text).



(Table 1). Prey-capture rates by coyotes averaged 1.8, 1.6, 1.1, 1.0, 0.5, 0.4, and 0 prey/h in shrub-meadow, mesic meadow, grassland, sage-grassland, riparian, forest, and road habitat, respectively ($F_{[6,1668]} = 14.84$, $P < 0.001$). Coyotes had higher prey-capture rates in both ($P = 0.99$) mesic meadow and shrub-meadow habitat than in all other habitats ($P < 0.05$) (Fig. 6). Coyotes had intermediate capture rates in both ($P = 0.99$) grassland and sage-grassland ($P < 0.05$), while capture rates were lowest in riparian areas, forests, and along roads ($P < 0.05$). For all habitats combined, prey-capture rates by coyotes averaged 1.7, 1.9, 1.0, 0.9, and 0.5 prey/h during days with no, low, moderate, deep, and very deep snow, respectively ($F_{[4,1670]} = 15.26$, $P < 0.001$). Coyotes had similar ($P = 0.82$) high capture rates during days with low or no snow ($P < 0.003$) and lower rates during days with moderate, deep, or very deep snow (Fig. 6).

While ANOVA indicated that prey-capture rates were influenced by the social status of coyotes, multiple comparisons showed that for all habitats combined, capture rates did not differ among pups, betas, and alphas ($P > 0.06$). Disparity in prey-capture rates among coyote social classes occurred only in riparian habitat ($F_{[2,214]} = 2.88$, $P = 0.05$) (Fig. 6D), where pups had higher capture rates than alphas and betas ($P < 0.06$). While pups had higher prey-detection (Fig. 2A) and attempt rates (Fig. 2B) than yearlings and adults throughout the winter, the rates at which prey were

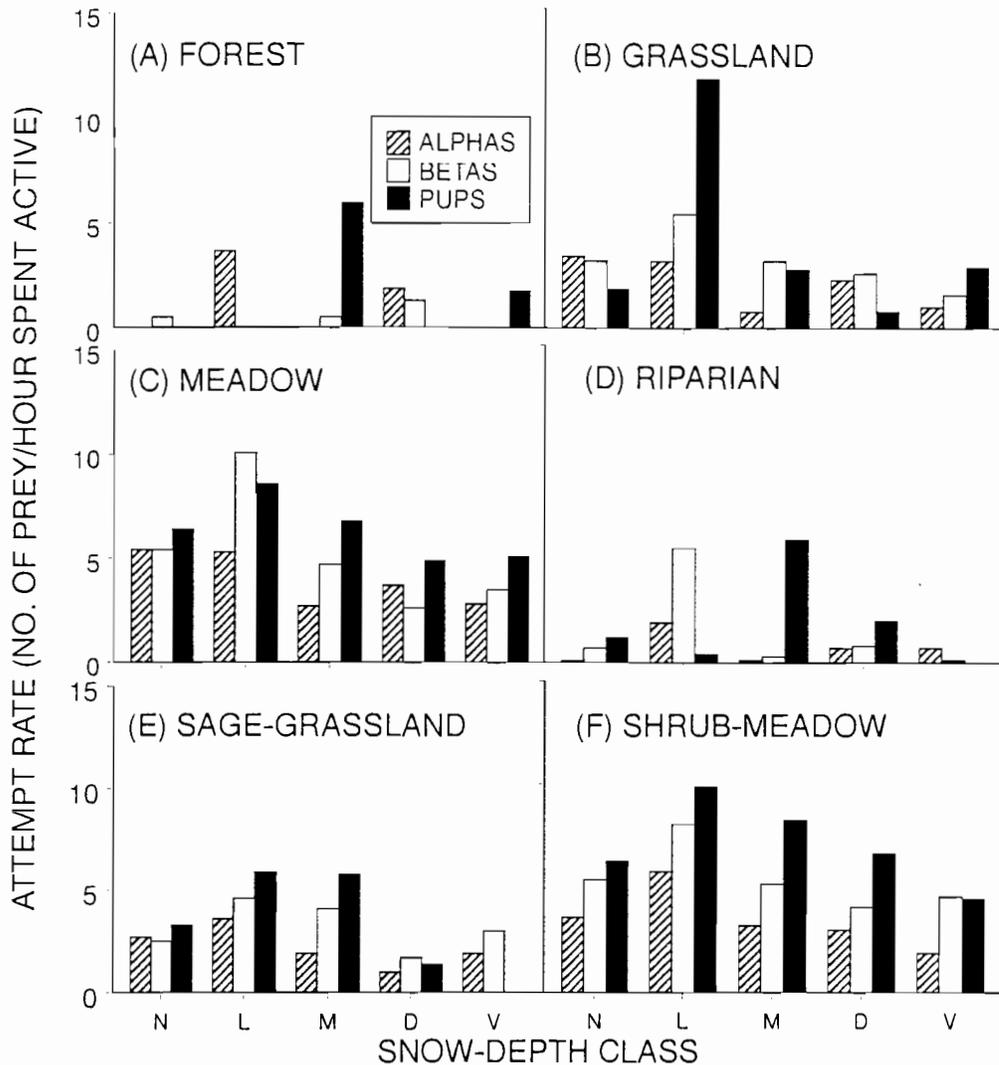
captured were similar among pups, yearlings, and adults (Fig. 2C). During days of no, low, moderate, or very deep snow, prey-capture rates did not differ among the social classes (F tests, $P > 0.06$) (Fig. 6). During days of deep snow, pups had higher prey-capture rates than alphas ($P = 0.04$) but not betas ($P = 0.23$); capture rates for alphas and betas did not differ ($P = 0.49$).

Capture rates of small mammals by coyotes differed among snowpack hardness classes ($F_{[3,1671]} = 14.37$, $P < 0.001$) (Fig. 3C). Coyotes had the highest capture rates ($\bar{x} = 1.8$ prey/h) during days of soft snowpack ($P < 0.001$) and lower capture rates during days with moderate ($\bar{x} = 1.0$ prey/h) or hard snowpack ($\bar{x} = 0.9$ prey/h). Capture rates did not differ among the social classes during days of soft ($F_{[2,340]} = 0.86$, $P = 0.42$) or moderate snowpack ($F_{[2,256]} = 0.38$, $P = 0.68$). During days with hard snowpack, pups and betas had similar ($P = 0.65$) higher capture rates than alphas ($P < 0.001$) (Fig. 3C). Prey-capture rates for coyotes were not influenced by wind speed (Table 1, Fig. 4C).

Proportions of prey attacked and captured

The previous analyses showed that detection rates, predation attempt rates, and capture rates of small mammals by coyotes were influenced by social status, habitat type, snow depth, and snowpack hardness. Next, we examined if intrinsic and extrinsic factors similarly influenced the proportion of detected prey that the coyotes attempted to capture, and capture suc-

Fig. 5. Prey attempt rates for alpha, beta, and pup coyotes across varying snow-depth classes in six different habitats in Yellowstone National Park, Wyoming, 1991–1993. For a description of snow-depth classes see Fig. 1 and the text.



cess. The proportion of detected prey that coyotes attempted to capture was influenced by social status ($F_{[2,941]} = 6.11$, $P = 0.002$), snow depth ($F_{[1,941]} = 4.08$, $P = 0.04$), and snowpack hardness ($F_{[2,941]} = 2.21$, $P = 0.086$). Overall, alphas attacked a lower proportion of prey detected than betas ($P = 0.013$) and pups ($P = 0.024$); pups and betas attacked similar proportions of prey detected ($P = 0.95$). Coyotes attacked a lower percentage of prey during days with no snow than on days with deep snow ($P = 0.009$), but there were no differences among days with no, low, moderate, and very deep snow ($P > 0.10$).

The proportion of attempts leading to a successful capture was influenced by habitat type ($F_{[6,824]} = 2.42$, $P = 0.025$), snowpack hardness ($F_{[2,824]} = 3.69$, $P = 0.012$), and social status of the coyote ($F_{[2,824]} = 2.64$, $P = 0.07$). For all habitats combined, pups captured a lower proportion of prey whose capture they attempted than alphas and betas ($P < 0.05$) did, while alphas and betas experienced similar capture success ($P = 0.89$). Apparently, the decision to attack and the ability to capture prey were very important stages in the

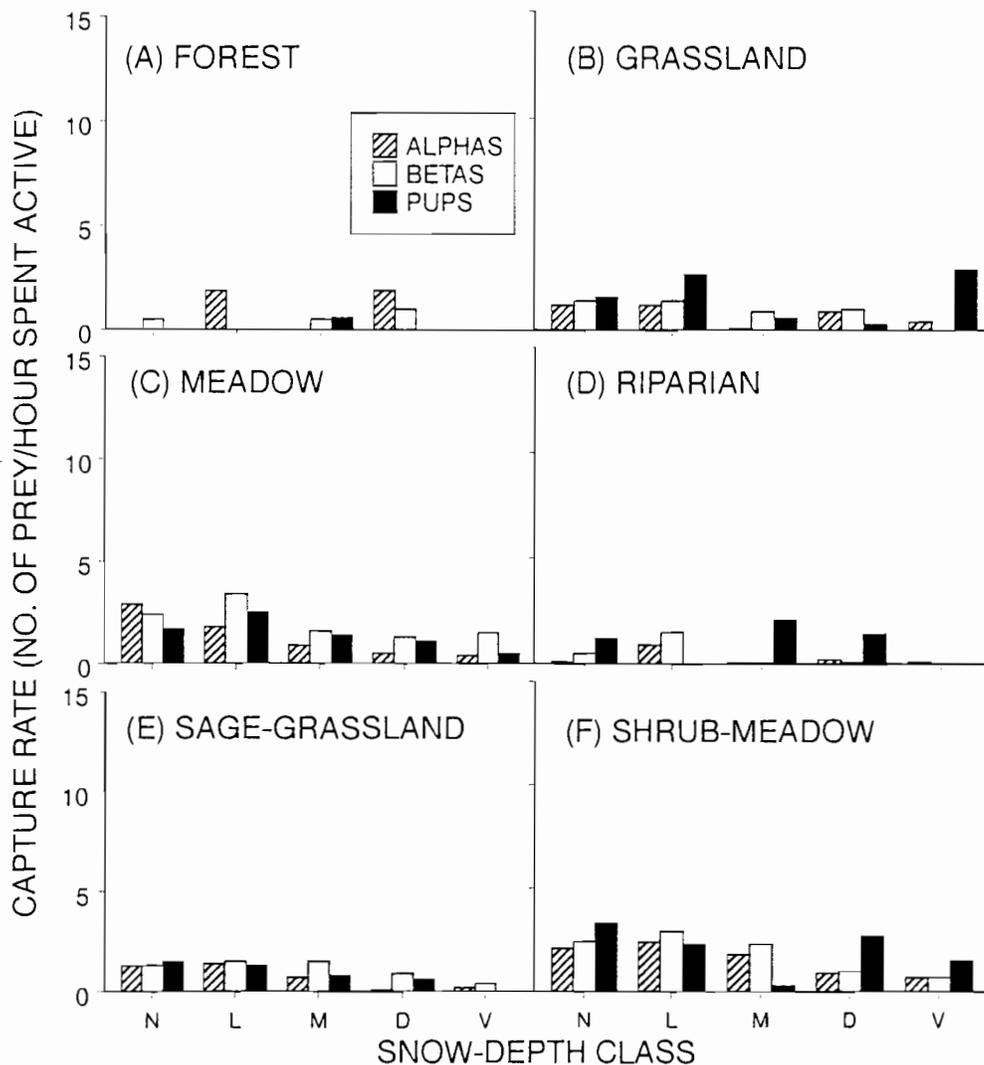
predation sequence among alphas, betas, and pups. Pups detected prey at a high rate and attempted to capture prey more frequently than older coyotes, yet captured prey at a rate similar to alphas and betas (Figs. 2C and 6) because pups captured a lower proportion of prey attacked than alphas and betas did (Fig. 7).

We found that habitat type influenced prey-detection rates, predation attempt rates, and capture rates by coyotes. While the proportion of prey detected that were attacked was not influenced by habitat type ($F_{[6,941]} = 1.24$, $P = 0.28$), we did find that habitat type influenced capture success. When hunting in the forest and riparian areas, coyotes had higher capture success than when hunting in grasslands, mesic meadows, shrub-meadows, and sage-grasslands (Fig. 7), but the capture rates in these two habitats were very low.

Length of time approaching and attacking prey

We recorded 1130, 2059, and 1096 approach and attack times for pups, betas, and alphas, respectively. All the coyotes hunted small mammals alone and spent a mean of 29 s

Fig. 6. Prey capture rates for alpha, beta, and pup coyotes across varying snow-depth classes in six different habitats in Yellowstone National Park, Wyoming, 1991–1993. For a description of snow-depth classes see Fig. 1 and the text.

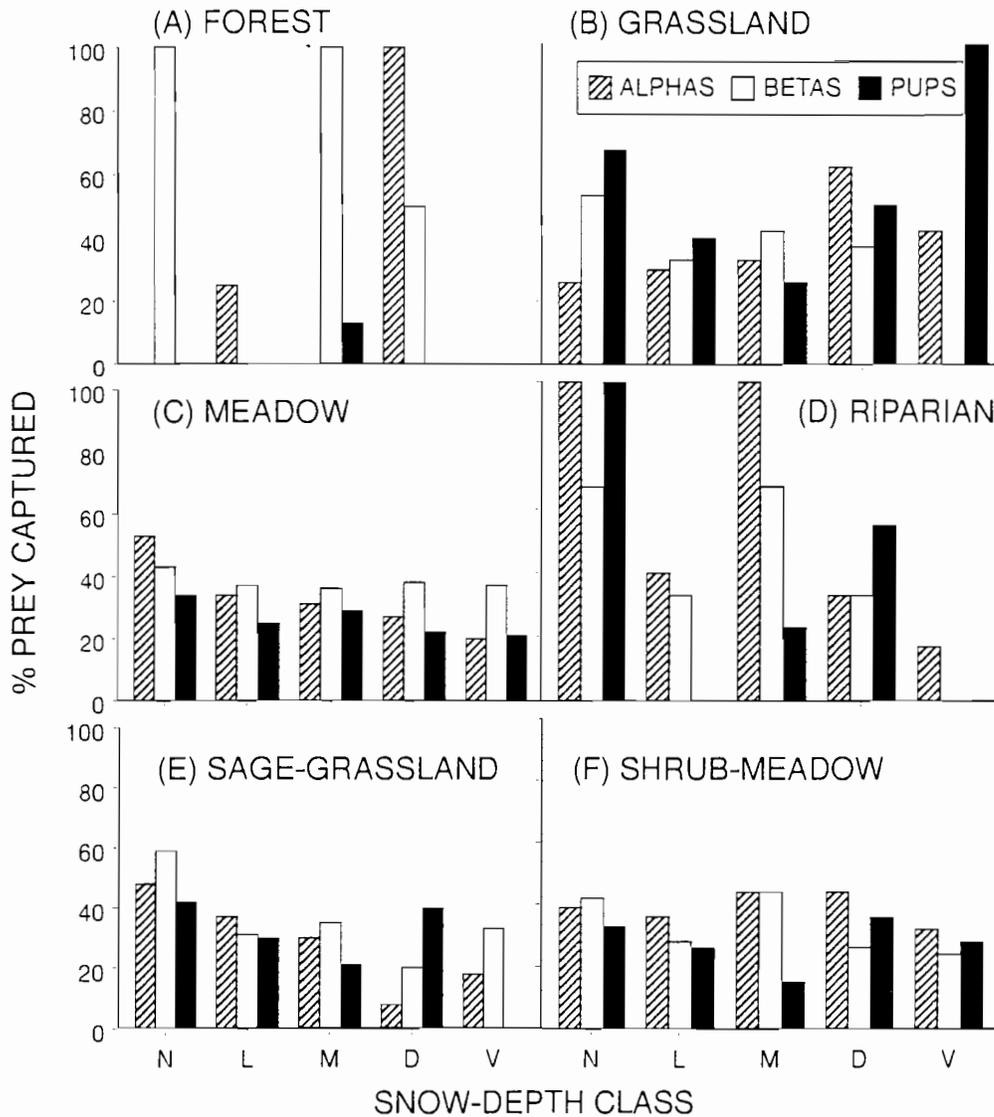


approaching the prey they had detected. The social status of the coyote ($F_{[2,4264]} = 8.06$, $P < 0.001$), snowpack hardness ($F_{[3,4264]} = 4.56$, $P = 0.003$), and snow depth ($F_{[1,4264]} = 4.15$, $P = 0.042$) all influenced the length of time coyotes spent approaching a prey item they detected. Approach times were longest during days with very deep snow ($P < 0.010$), but did not differ during days with no, low, moderate, or deep snow ($P > 0.45$) (Table 2). Pups, betas, and alphas spent a mean of 22, 31, and 34 s, respectively, approaching a prey item ($F_{[2,4283]} = 7.06$, $P < 0.001$). For all snow-depth classes combined, the mean approach time for pups was shorter than for alphas ($P < 0.001$) and betas ($P = 0.001$), which had similar approach times ($P = 0.55$). During days with no, deep, and very deep snow, approach times among the social classes did not differ (F tests, $P > 0.10$). During days with low snow (Table 2), the mean approach time for betas and pups was shorter than for alphas ($P = 0.001$); pups and betas had similar approach times ($P = 0.99$). During days with moderate snow depth, pups had a

shorter mean approach time than alphas ($P < 0.001$) and betas ($P = 0.006$), and betas had a shorter approach time than alphas ($P = 0.019$). Snowpack hardness had an influence during days with low snow, approach times being longer when snowpack was hard than when it was soft ($P = 0.001$) or moderate ($P < 0.001$); approach times during days with soft and moderate snowpack were similar ($P = 0.45$). During days with deep snow, approach times were longer when snowpack was hard than when it was moderate ($P = 0.035$) (Table 2).

Coyotes spent a mean of 47 s attacking a prey item. The length of time spent attacking a prey item was influenced by social status of the coyote ($F_{[2,4257]} = 2.92$, $P = 0.033$), snowpack hardness ($F_{[3,4257]} = 4.48$, $P = 0.004$), snow depth ($F_{[1,4257]} = 21.93$, $P < 0.001$), and the technique used in the attack ($F_{[5,4257]} = 94.35$, $P < 0.001$). Attack times were shortest during days with either no ($\bar{x} = 29$ s) or low snow ($\bar{x} = 38$ s), and longest during days with moderate ($\bar{x} = 63$ s), deep ($\bar{x} = 68$ s), or very deep ($\bar{x} = 72$ s) snow

Fig. 7. Percentages of prey captured by alpha, beta, and pup coyotes across varying snow-depth classes in six different habitats in Yellowstone National Park, Wyoming, 1991–1993. For a description of snow-depth classes see Fig. 1 and the text.



($P < 0.001$) (Table 3). Alphas, betas, and pups spent a mean of 40, 49, and 48 s, respectively, attacking a prey item ($F_{[2,4282]} = 2.27, P = 0.07$).

Six techniques were employed by coyotes when attacking prey. Most attacks involved a pounce (pounce and rush-pounce, 74.8%) or digging (12.4%). Rushing the prey item was observed in 5.6% of the attacks, usually when ground squirrels were hunted. A head thrust (without a prior pounce) or searching constituted 2.2 and 4.9% of the attacks, respectively. The technique used (i.e., rush, rush-pounce, dig, pounce, search, or head thrust) influenced the length of the attack ($F_{[5,4281]} = 152.03, P < 0.001$) (Table 3). When coyotes employed digging to capture the prey, the attack ($\bar{x} = 141$ s) lasted longer than a pounce ($\bar{x} = 35$ s), rush-pounce ($\bar{x} = 38$ s), rush ($\bar{x} = 21$ s), head thrust ($\bar{x} = 18$ s), or search ($\bar{x} = 14$ s) ($P < 0.001$); the attacks were similar in length for the other five techniques ($P > 0.07$).

Attack times were longest during days with hard snowpack ($P < 0.05$) but similar during days with soft and moderate snowpack ($P = 0.22$). We also found that attacks resulting in a successful capture averaged 43 s, while unsuccessful attacks averaged 49 s ($t = -2.006, 4285$ df, $P = 0.045$).

Prey captured and handling times

We observed 1545 captures of prey by coyotes. The coyote capturing the prey consumed 98.6% of the items, cached 0.5% of them, gave 0.4% and 0.3% to the pups and alpha female, respectively, and 0.1% escaped. These proportions include only whole prey and not regurgitations of prey to the pups or alpha female at the den. Only alpha males were observed provisioning the alpha female with whole prey during the period of gestation and pup rearing. Alphas, betas, and pups from the previous year brought food to the current litter of pups at the den.

Table 2. Time (s) spent approaching prey by alpha, beta, and pup coyotes across five snow-depth classes and three snowpack-hardness classes, Yellowstone National Park, Wyoming, 1991–1993.

Snow depth	Snow hardness	Alphas			Betas			Pups		
		\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>
None	None	26	2.2	423	30	2.2	654	21	2.7	156
Low	Soft	35	5.2	216	26	2.3	422	17	1.7	334
	Moderate	22	5.8	64	16	1.9	179	38	9.6	37
	Hard	77	25.6	30	17	5.1	21	37	7.9	82
Moderate	Soft	29	10.8	34	31	4.6	200	15	3.4	75
	Moderate	46	8.6	63	20	6.4	36	32	8.3	77
	Hard	68	15.1	49	35	4.3	173	13	1.8	118
Deep	Soft	30	5.9	50	35	7.6	43	30	8.4	37
	Moderate	16	6.0	20	21	11.1	10	10	2.2	38
	Hard	39	17.5	43	35	4.4	144	24	3.8	98
Very deep	Soft	27	5.1	27	98	38.1	29	33	10.1	15
	Moderate	17	4.2	25	28	6.0	53	13	61.4	21
	Hard	50	23.6	52	54	14.5	94	26	7.7	44

Table 3. Time (s) spent by coyotes when attacking a prey item by digging, head thrusting, pouncing, rush–pouncing, rushing, and searching in snow of five different depth classes, Yellowstone National Park, Wyoming, 1991–1993.

Snow depth	Dig			Head thrust			Pounce			Rush–pounce			Rush			Search		
	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>
None	147	22	74	17	6	30	25	2	632	21	2	231	19	2	172	15	5	107
Low	121	11	119	21	8	34	31	2	809	35	3	344	27	6	44	7	2	49
Moderate	158	17	118	15	6	13	44	3	486	61	7	188	20	4	12	15	6	16
Deep	124	9	144	22	8	10	46	6	297	61	12	42	23	9	9	11	3	30
Very deep	158	18	97	10	5	12	47	8	262	40	9	39	23	14	5	39	17	15

Small rodents (*Microtus* spp. and *Peromyscus* spp.), large rodents (pocket gophers and ground squirrels), birds, and unknown prey items composed 78.0, 9.3, 0.5, and 12.1%, respectively, of the items captured and consumed by coyotes. We were unable to differentiate between the numbers of voles and mice in the small-rodent component captured by coyotes. We found that ground squirrels and pocket gophers composed 40 and 60%, respectively, of the large rodents captured. Of the bird component captured by coyotes ($n = 8$), 6 appeared to be acquired by nest predation in the summer (unidentified species) and 2 were grouse (Galliformes).

Coyotes spent a mean of 21 s consuming a prey item. The length of time spent handling or consuming the prey item was influenced by its size ($F_{[3,1493]} = 124.77$, $P < 0.001$). Small rodents ($\bar{x} = 9$ s) were consumed in a shorter time ($P < 0.003$) than were all other food items. Consumption times for large rodents ($\bar{x} = 60$ s), birds ($\bar{x} = 55$ s), and unknown prey items ($\bar{x} = 47$ s) did not differ ($P > 0.05$). The sex and social status of the coyote did not influence the consumption time of prey items.

Hunting by transient coyotes

Transient coyotes had limited access to carcasses (Gese

1995) and had to hunt for small mammals in areas frequently utilized by the resident pack. Because transients may need to be more wary to avoid being chased by members of the resident pack, we examined if approach times and attack times were shorter for transient coyotes than for resident alphas, betas, and pups. We found that transient coyotes spent a mean of 36 s ($n = 155$) approaching a prey item, which was similar to the time for alphas ($P = 0.97$) and betas ($P = 0.72$) but longer than that for pups ($P = 0.05$). Pups had the shortest approach time of all coyotes. Transient coyotes spent a mean of 51 s ($n = 155$) attacking prey, similar to all the other social classes in a resident pack ($P > 0.50$). Handling times of prey were similar between transients, alphas, betas, and pups ($P > 0.30$). Detection rates ($P > 0.25$), predation attempt rates ($P > 0.14$), and capture rates ($P > 0.80$) for transients were similar to those for alphas, betas, and pups. Our sample sizes of transient coyotes ($n = 5$) and hours observed ($n = 51$ h) limited our analysis of transient hunting behavior. However, our results indicated that transient coyotes appeared to be equally successful hunters of small mammals as residents, and their main disadvantage with regard to foraging appears to be limited access to ungulate carcasses in the winter (Gese 1995).

Discussion

Murie (1940) first described the behavior employed by coyotes when hunting small mammals in Yellowstone National Park. The hunting behavior and predatory sequence of coyotes have since been described and documented in captivity (Fox 1969; Bekoff 1978; Vincent and Bekoff 1978; Wells 1978; Wells and Lehner 1978). However, only one study has quantified the predatory behavior of free-ranging coyotes (Wells and Bekoff 1982). These authors found that snow depth and grass height were extrinsic factors influencing capture success, while wind speed did not affect it. Among intrinsic factors, they found that the age of the coyote did not influence capture success, but pups were capturing only grasshoppers.

We found that many extrinsic factors influenced predation rates and capture success of coyotes on small mammals. Habitat type influenced the detection rates, predation attempt rates, and capture rates of small mammals by coyotes, as well as capture success. The highest detection rates, predation attempt rates, and capture rates were in mesic meadows and shrub-meadows, followed by grasslands and sage-grasslands, and the rates were lowest in forests and riparian areas and along roads. Most *Microtus* species are associated with mesic habitats (Getz 1985). Mesic meadows and shrub-meadows provide food and cover for microtines (Birney et al. 1976; Spencer 1984; Getz 1985). Dense vegetation also provides mechanical support for snow cover, thereby influencing the amount of subnivean space available at the ground surface for microtine passages (Spencer 1984). Coyotes readily exploited these mesic habitats, spending much of their time hunting small mammals in them, where prey-detection rates, predation attempt rates, and capture rates were highest. As snow depth increased, coyotes increased their use of these mesic areas, particularly pups, which spent less time feeding on carcasses and more time hunting small mammals than did alphas and betas (Gese 1995).

We found that coyotes hunting in forests and riparian areas experienced higher capture success than when hunting in other habitats. However, we emphasize that although capture success was higher, the rates of capture were lower in these two habitats than in other habitats. The understory of the forests was rather open, and may have had less snow cover, owing to interception of snow on tree crowns (Ozoga 1968; Carpenter and Wallmo 1981). We defined riparian areas as rocky and sandy shores, riverbanks, and gravel bars (Gese 1995). These areas were typically windblown, resulting in low snow cover, and provided little escape cover for small mammals. In contrast, the other four habitats contained either tall sedges (*Carex* spp.) or dense grasses, which would have provided cover during snow-free periods and mechanical support for microtine passages under the snowpack. They were also interspersed with clumps of woody vegetation, mainly sage (*Artemisia tridentata*), willow (*Salix* spp.), and shrubby cinquefoil (*Potentilla fruticosa*), all of which provided escape cover for small mammals and resulted in lower capture success.

Similar to Wells and Bekoff (1982), we found that snow depth greatly influenced coyote predation on small mammals. Low snow cover increased prey-detection rates, predation attempt rates, and capture rates of rodents by coyotes.

This low snow cover may have provided the coyotes with a quieter substrate for walking, or given a false sense of security to the small mammals. Microtines do increase their activity during the first snowfall, possibly to lay out a system of passages while the snowpack is soft (Spencer 1984) or the risk from aerial predators is reduced. However, as snow depth increased, detection rates declined. This may have been a consequence of reduced auditory cues penetrating the snowpack to the coyote, reduced microtine activity under deep, hard-packed snow (Pruitt 1984), or a reduced interest in hunting small mammals when feeding on ungulate carcasses increased (Gese 1995). Whether coyotes detect and locate small mammals by the vocalizations produced by microtines (Wolff 1985) or the sounds produced by rodents moving through their passageways remains unknown. In general, snow cover appeared to be more important in reducing access to small mammals, as indicated by reduced detection rates, predation attempt rates, and capture rates, and less of an influence on the percentage of prey attacked and captured.

While we found that snow depth influenced detection rates, predation attempt rates, and capture rates of small mammals by coyotes, as well as the proportion of prey detected that they attempted to capture, snow depth did not influence capture success. We believe this indicates that snow depth may be an important factor in a coyote's decision whether to attack a prey item once it is detected, and less important in their ability to capture the prey item. Perhaps past experience during the same day or preceding days allows the coyotes to assess the probability of accurately locating and successfully capturing prey at a particular snow depth, and based on that knowledge they may choose not to attack the prey item detected. Experience was an important factor in the difference in predatory skills between pups and older coyotes, thus assessment of current environmental conditions by a hunting coyote could also occur on a daily, if not hourly, basis.

Snow depth also influenced the length of time coyotes spent approaching and attacking small mammals. Wells and Bekoff (1982) similarly found that the duration of a predatory sequence increased during periods of deep snow. Increased snow depth and hardness probably lengthened approach times by dampening the noise generated by prey movements and vocalizations, thereby reducing a coyote's ability to locate the prey item quickly. Attack times also increased with deeper snow and harder snowpack, likely as a consequence of reduced penetration into the snowpack when a coyote pounced. Increased snow depth would also increase the distance between predator and prey during the attack phase of the predatory sequence. Increased snow depth and snowpack hardness also influenced capture success because longer attack times would provide greater opportunities for prey to escape into passages beneath the snowpack.

We found that even under the same environmental conditions (snow depth, habitat, snowpack hardness, and wind speed), pups detected or showed that they detected more prey per hour than older coyotes. We believe that this higher detection rate by pups may be due to increased responsiveness to an auditory cue (whether prey or not). Older coyotes appeared to filter out irrelevant sounds from the environment

and were more selective of cues associated with prey. Older coyotes also reduced the proportion of prey they attacked during adverse conditions (i.e., days with hard snowpack or deep snow), while pups continued to attack a relatively high proportion of prey that they detected. Alternatively, reduced access to carcasses (Gese 1995) may have forced pups to hunt small mammals during days with adverse conditions. During fall and spring, pups detected and attempted to capture prey at a similar rate to older coyotes. During winter, pups detected and attacked prey at a higher rate than older coyotes, possibly in response to resource partitioning among the social classes and the need to compensate for this food deficiency.

Captive studies by Fox (1969), Bekoff (1978), and Vincent and Bekoff (1978) documented that the predatory behavior and prey-killing patterns of coyotes develop early in life. Vincent and Bekoff (1978) found that the social rank of pups within a litter was not related to prey-killing ability; however, all the study animals were pups. Wells and Bekoff (1982) found that adults and juveniles did not differ in their capture success when hunting rodents. In contrast, we found that the age and social status of the coyote did influence predation on small mammals. Pups had higher detection rates and higher predation attempt rates on small mammals than did older coyotes, yet captured prey at a similar rate to older coyotes, owing to the lower capture success of pups. Pups also had shorter approach times than older coyotes, but attack times were similar among the social classes. Age also played a role in the duration of a predatory sequence and the final outcome of a predatory attempt. Pups attacked quickly (short approach time), while older coyotes took more time approaching prey. An older coyote has possibly learned that a longer approach time allows it to improve the locational accuracy of its predatory attack and simultaneously reduce the distance between predator and prey before it attacks. Experience played a role when coyotes cooperatively hunted large prey (Gese and Grothe 1995), and our results indicated that experience, as indicated by the age of the coyote, was also important when hunting small mammals. We concluded that while pups used the same predatory behavior as older coyotes, they apparently underwent a period of learning during their first winter and were more experienced hunters of small mammals by their second winter.

Acknowledgements

We thank P.A. Terletzky, E.R. Schauster, A.M. Whittaker, A.W. Calio, M.L. Pangraze, L. Sox, L.P. Yengoyan, D.E. Rozen, M.J. Johnson, S. Grothe, K. Hatier, W.J. Roach, and V. Vergara for assistance in data collection; J.D. Varley, B. Chan, C. Daigle-Berg, and B. O'Dea of the National Park Service for logistical support; J.R. Cary and J. Coleman for computer programming; and P. Arcese, J.R. Baylis, R.A. Garrott, and W.P. Porter for manuscript review. Funding and support were provided by the Department of Wildlife Ecology and the College of Agricultural and Life Sciences at the University of Wisconsin—Madison, the Max McGraw Wildlife Foundation, the U.S. Fish and Wildlife Service, the U.S. National Park Service (Cooperative Agreement 1268-1-9001 to R.L. Crabtree), the National Geographic Society, the Biology Department at Montana State Uni-

versity, Earthwatch, and the Hornocker Wildlife Research Institute.

References

- Balser, D.S. 1965. Tranquilizer tabs for capturing wild carnivores. *J. Wildl. Manage.* **29**: 438–442.
- Bekoff, M. 1978. Behavioral development in coyotes and eastern coyotes. *In* *Coyotes: biology, behavior, and management*. Edited by M. Bekoff. Academic Press, New York. pp. 97–126.
- Birney, E.C., Grant, W.E., and Baird, D.D. 1976. Importance of vegetative cover to cycles of *Microtus* populations. *Ecology*, **57**: 1043–1051.
- Bowen, W.D. 1981. Variation in coyote social organization: the influence of prey size. *Can. J. Zool.* **59**: 639–652.
- Carpenter, L.H., and Wallmo, O.C. 1981. Rocky Mountain and intermountain habitats, part 2: habitat evaluation and management. *In* *Mule and black-tailed deer of North America*. Edited by O.C. Wallmo. University of Nebraska, Lincoln. pp. 399–421.
- Connolly, G.E., Timm, R.M., Howard, W.E., and Longhurst, W.M. 1976. Sheep killing behavior of captive coyotes. *J. Wildl. Manage.* **40**: 400–407.
- Cornely, J.E. 1979. Anesthesia of coyotes with ketamine hydrochloride and xylazine. *J. Wildl. Manage.* **43**: 577–579.
- Fox, M.W. 1969. Ontogeny of prey-killing behavior in Canidae. *Behaviour*, **35**: 259–272.
- Gese, E.M. 1995. Foraging ecology of coyotes in Yellowstone National Park. Ph.D. thesis, University of Wisconsin, Madison.
- Gese, E.M., and Grothe, S. 1995. Analysis of coyote predation on deer and elk during winter in Yellowstone National Park, Wyoming. *Am. Midl. Nat.* **133**: 36–43.
- Gese, E.M., Rongstad, O.J., and Mytton, W.R. 1988. Home range and habitat use of coyotes in southeastern Colorado. *J. Wildl. Manage.* **52**: 640–646.
- Getz, L.L. 1985. Habitats. *Spec. Publ. Am. Soc. Mammal.* No. 8. pp. 286–309.
- Houston, D.B. 1982. *The northern Yellowstone elk: ecology and management*. Macmillan Publishing Co. Inc., New York.
- Jansen, C.D. 1974. Behavior patterns observed in coyote–sheep interactions. M.Sc. thesis, Colorado State University, Fort Collins.
- Lehner, P.N. 1979. *Handbook of ethological methods*. Garland STPM Press, New York.
- Linhart, S.B., and Knowlton, F.F. 1967. Determining age of coyotes by tooth cementum layers. *J. Wildl. Manage.* **31**: 362–365.
- Martin, P., and Bateson, P. 1993. *Measuring behaviour: an introductory guide*. 2nd ed. Cambridge University Press, London.
- Mech, L.D. 1970. *The wolf: the ecology and behavior of an endangered species*. Natural History Press, Garden City, N.Y.
- Morrison, M.L., Marcot, B.G., and Mannan, R.W. 1992. *Wildlife–habitat relationships*. University of Wisconsin Press, Madison.
- Murie, A. 1940. Ecology of the coyote in the Yellowstone. U.S. Natl. Park Serv. Fauna Ser. No. 4.
- Ozoga, J.J. 1968. Variation in microclimate in a conifer swamp deeryard in northern Michigan. *J. Wildl. Manage.* **32**: 574–585.
- Pruitt, W.O., Jr. 1984. Snow and small mammals. *Carnegie Mus. Nat. Hist. Spec. Publ.* No. 10. pp. 1–8.
- Rabb, G.B., Woolpy, J.H., and Ginsberg, B.E. 1967. Social relationships in a group of captive wolves. *Am. Zool.* **7**: 305–311.
- Schenkel, R. 1947. Expression studies of wolves. *Behaviour*, **1**: 81–129.
- Schenkel, R. 1967. Submission: its features and function in the wolf and dog. *Am. Zool.* **7**: 319–329.
- Sih, A. 1993. Effects of ecological interactions on forager diets: competition, predation risk, parasitism, and prey behavior.

- In Diet selection: an interdisciplinary approach to foraging behavior. Edited by R.H. Hughes. Blackwell Scientific Publications, Cambridge, Mass. pp. 182–211.
- Sokal, R.R., and Rohlf, F.J. 1981. Biometry. W.H. Freeman and Co., New York.
- Spencer, A.W. 1984. Food habits, grazing activities, and reproductive development of long-tailed voles, *Microtus longicaudus* (Merriam), in relation to snow cover in the mountains of Colorado. Carnegie Mus. Nat. Hist. Spec. Publ. No. 10. pp. 67–90.
- Steel, R.G.D., and Torrie, J.H. 1980. Principles and procedures of statistics: a biometrical approach. McGraw-Hill Book Co., New York.
- Taitt, M.J., and Krebs, C.J. 1985. Population dynamics and cycles. Spec. Publ. Am. Soc. Mammal. No. 8. pp. 567–620.
- Taylor, R.J. 1984. Predation. Chapman and Hall, New York.
- Truett, J.C. 1979. Observations of coyote predation on mule deer fawns in Arizona. J. Wildl. Manage. 43: 956–958.
- Vincent, L.E., and Bekoff, M. 1978. Quantitative analyses of the ontogeny of predatory behaviour in coyotes, *Canis latrans*. Anim. Behav. 26: 225–231.
- Wells, M.C. 1978. Coyote senses in predation: environmental influences on their relative use. Behav. Processes, 3: 149–158.
- Wells, M.C., and Bekoff, M. 1982. Predation by wild coyotes: behavioral and ecological analyses. J. Mammal. 63: 118–127.
- Wells, M.C. and Lehner, P.N. 1978. The relative importance of the distance senses in coyote predatory behaviour. Anim. Behav. 26: 251–258.
- Wenger, C.R. 1981. Coyote – mule deer: interaction observations in central Wyoming. J. Wildl. Manage. 45: 770–772.
- Wilkinson, L., Hill, M., Welna, J.P., and Birkenbeuel, G.K. 1992. SYSTAT for Windows: statistics, version 5 ed. SYSTAT, Inc., Evanston, Ill.
- Wolff, J.O. 1985. Behavior. Spec. Publ. Am. Soc. Mammal. No. 8. pp. 340–372.