CHAPTER 17

Coyotes

Coyotes in Yellowstone National Park: the influence of dominance on foraging, territoriality, and fitness

Eric M. Gese

A coyote *Canis latrans* pauses during its travels in Yellowstone National Park © E. M. Gese.

Studies on the behavioural ecology of coyotes (*Canis latrans*) are inherently difficult due to their nocturnal and secretive habits. In Yellowstone National Park (YNP), Wyoming, the coyote population has not been subject to human persecution for several decades, allowing for direct observation of their behaviour, interactions among pack members, and how they deal with changes in their environment. From January 1991 to June 1993, over 2500 h of direct observation were collected on members of five resident packs, five transient individuals, and eight dispersing animals, in the Lamar River Valley

of YNP. The presence of a dominance hierarchy within the resident packs greatly influenced access to food resources, individual fitness (i.e. mating opportunities, survival, and dispersal), and regulation of pack size. Alpha animals had the greatest access to ungulate carcasses in winter, diligently defended their territory against intruders, and consequently achieved a high degree of fitness in terms of acquiring all mating opportunities and reproductive success. Subordinate individuals (betas and pups) in the pack had less access to resources (mates and food), lower survival, higher dispersal rates, and thus reduced fitness as compared to alpha animals. Non-territorial coyotes (transients and dispersers) had even lower survival (mainly dispersing animals), no mating opportunities, and little access to ungulate carcasses during winter when resources were scarce. Being dominant and territorial was advantageous in coyote society by insuring access to mates, food, and space.

Introduction

The coyote, is an opportunistic, generalist predator that has expanded its distribution to most of North America and is probably one of the most widely researched canids. Yet, its typically nocturnal, secretive behaviour mean there have been only two studies—both in Grand Teton National Park, Wyoming—based on direct observation of wild coyotes (Camenzind 1978b; Bekoff and Wells 1986).

The coyote population in YNP has not been persecuted for several decades, and thus is tolerant of humans to an extent that has facilitated our studies of how coyotes deal with fluctuations in temperature, snow depth, snow-pack hardness, and food availability (e.g. Gese *et al.* 1996a–c). This chapter synthesizes the findings of over 2500 h of observation on coyotes in the Lamar River Valley, YNP, Wyoming (Gese *et al.* 1996a–c; Gese and Ruff 1997, 1998; Gese 2001b).

Study area

The study was conducted in a 70-km^2 area in the Lamar River Valley, YNP, Wyoming (Fig. 17.1; 44°52′N, 110°11′E), about 2000 m above sea level. Long, cold winters and short, cool summers characterize the climate in the valley (Dirks and Martner 1982; Houston 1982). Mean annual temperature and precipitation is 1.8°C and 31.7 cm, respectively, with most of the annual precipitation falling as snow (Dirks and Martner 1982; Houston 1982). Habitats included forest, mesic meadow, mesic shrub-meadow, riparian, grassland, sage-grassland, and road (see Gese *et al.* 1996a for habitat descriptions).

Figure 17.1 Yellowstone National Park, Wyoming where the study was conducted.

Predominant ungulate species included elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), bison, (*Bison bison*), and bighorn sheep (*Ovis canadensis*). A few moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*) inhabited the valley, and pronghorn antelope (*Antilocapra americana*) were present during summer. A major food source for coyotes during winter was elk carrion (Murie 1940; Houston 1978; Gese *et al.* 1996a). Small mammal species included microtines (*Microtus* spp.), mice (*Peromyscus* spp.), pocket gophers (*Thomomys talpoides*), and Uinta ground squirrels (*Spermophilus armatus*).

General methodology

The sampling design and methodologies for recording behavioural observations of coyotes were described in Gese *et al.* (1996a–c), Gese and Ruff (1997, 1998), and Gese (2001). In general, coyotes >5 months

of age were captured with padded leg-hold traps with attached tranquilizer tabs, weighed, sexed, ear-tagged and radio-collared, and the vestigial first premolar of the lower jaw was extracted for ageing (Linhart and Knowlton 1967). Pups (8–12 weeks old) were captured at the den, ear-tagged, and surgically implanted with an intraperitoneal transmitter. We classified coyotes by age as pups (<12 months old), yearlings (12–24 months old), or adults (>24 months of age). Coyotes were also classified as residents or transients based upon their social interactions and affinity for one area (Bowen 1981; Gese *et al.* 1988). Members of a resident pack were further classified into different social classes, including alphas (dominant breeding adults), betas (adults and yearlings subordinate to the alphas but dominant over pups), or pups (young of the year subordinate to both alphas and betas), based upon the separate male and female dominance hierarchies observed in the pack (see Gese *et al.* 1996a–c for details on methodology).

Coyotes were observed with a 10–45× spotting scope from vantage points located throughout the valley during October–July; high grass (>1 m) precluded observation in August and September. We collected nocturnal observations using an 11× night-vision scope. Behavioural observations followed Gese *et al.* (1996a,b) in which we randomly sampled packs, and stratified individuals within each pack to allow for similar sampling of each sex and social class. We used focal-animal sampling (Lehner 1979; Martin and Bateson 1993), recording all behaviours for a single individual using a program on a notebook computer, or on a tape recorder and transcribed later. Whenever possible, we recorded the location at which behaviours (e.g. bed sites, dens, howling, scent-marking, predation, carcasses) occurred to the nearest 10-m grid intersection using the Universal Transverse Mercator (UTM) grid system on a 1 : 24,000 US Geological Survey topographic map. Snow depth, hardness, and layering were recorded every 1–2 days by excavation of a snow pit. Additional climate information was recorded at a permanent weather station within the study area. Available ungulate carcass biomass in the valley was estimated weekly (see Gese *et al.* 1996a). The sampling unit for all statistical tests was the individual coyote (Machlis *et al.* 1985). Statistical analyses of behaviours are described in Gese *et al.* (1996a–c) and used the software program SYSTAT (Wilkinson *et al.* 1992) following the recommendations in Steel and Torrie (1980), Sokal and Rohlf (1981), and Zar (1996).

Environmental conditions

The first winter (1990–91) of behavioural observations in YNP was mild, with little carcass biomass available to the coyotes in the valley (Fig. 17.2(a)). Maximum snow depth was 30 cm and the amount of known carcass biomass was <170 kg/wk. Coyotes were dependent upon small mammals, mostly voles, as their major food item during that winter. The second winter (1991–92) was characterized by deeper snow cover and higher carcass biomass (Fig. 17.2(b)). That winter had an early snowfall followed by a thaw, which re-froze into an ice layer on the ground and subsequently led to an early initiation of winter die-off of ungulates. Maximum snow depth was 46 cm, and known carcass biomass exceeded 200 kg/wk for 10 weeks. The third winter (1992–93) was similar to the second winter, with deep snow cover and high carcass biomass (Fig. 17.2(C)). Maximum snow depth was 63 cm, and for 6 weeks known carcass biomass was >200 kg/wk.

Social organization and dominance

From January 1991 to June 1993, we observed 49 resident coyotes from 5 packs for 2456 h and 5 transients for 51 h; 8 animals identified as dispersers were observed for 53 h. Of the 54 coyotes observed, 29 were males, 23 were females, and 2 unmarked coyotes were of unknown sex. We collared or implanted 31 coyotes with radio-transmitters, and 23 were unmarked but recognizable from physical characteristics. The coyotes in the Lamar River Valley were organized into relatively large packs (up to 10 individuals) with distinct territories (Fig. 17.3). These resident packs remained spatially stable, except in the last winter (1992–93) when the Soda Butte pack usurped a part of the Norris pack territory (Fig. 17.3(c); see Gese 1998 for details). Transient home ranges overlapped the resident territories. Territorial boundaries of resident packs were scent-marked and actively defended;

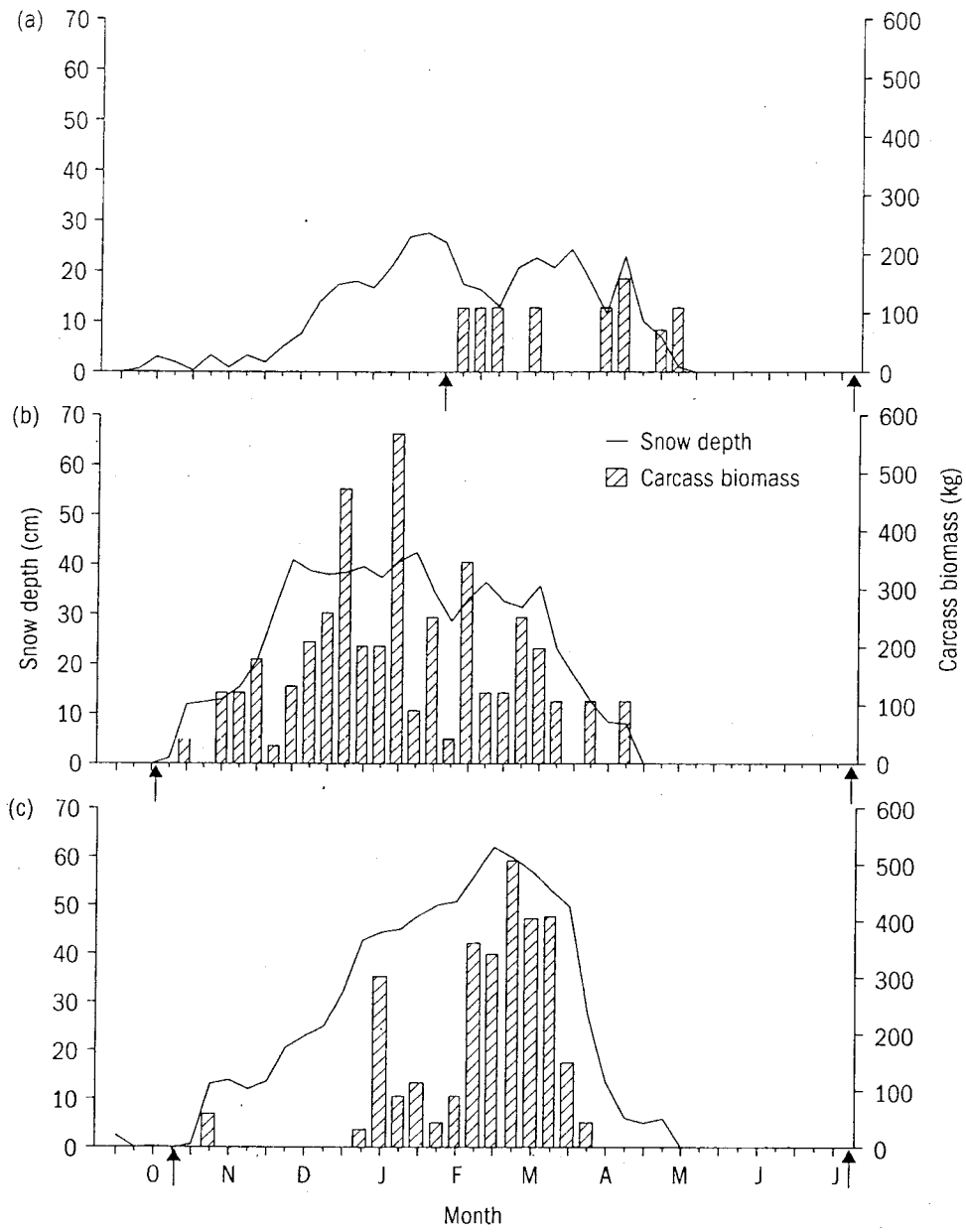

Figure 17.2 Mean snow depth and carcass biomass for each week during the winters of (a) 1990–91, (b) 1991–92, and (c) 1992–93 in the Lamar Valley, YNP, Wyoming. Arrows indicate the time span of data collection for each winter.

transient home ranges were not scent-marked or defended (Gese and Ruff 1997; Gese 2001). Each resident pack was comprised of an alpha pair and associated pack members, usually related offspring (Hatier 1995; Gese *et al.* 1996c). Associate animals that remained in the pack over winter usually helped feed and care for the offspring whelped by the alpha pair the subsequent spring (Hatier 1995). Dominance matrices for each pack demonstrated the presence of a social order or dominance hierarchy among both females and males (Gese *et al.* 1996c), similar to that described in a wolf pack (*Canis lupus*; Mech 1970). The presence of a dominance hierarchy in these packs played a major role on pack dynamics, foraging ecology, territorial maintenance, and ultimately individual fitness. The large packs we observed were probably a consequence of the combination of abundant prey biomass (Bekoff and Wells 1981; Geffen *et al.* 1996) and the lack of exploitation in the study area (Knowlton *et al.* 1999; Frank and Woodroffe 2001). For details on individuals observed and pack histories, see Gese *et al.* (1996a–c) (Fig. 17.4).

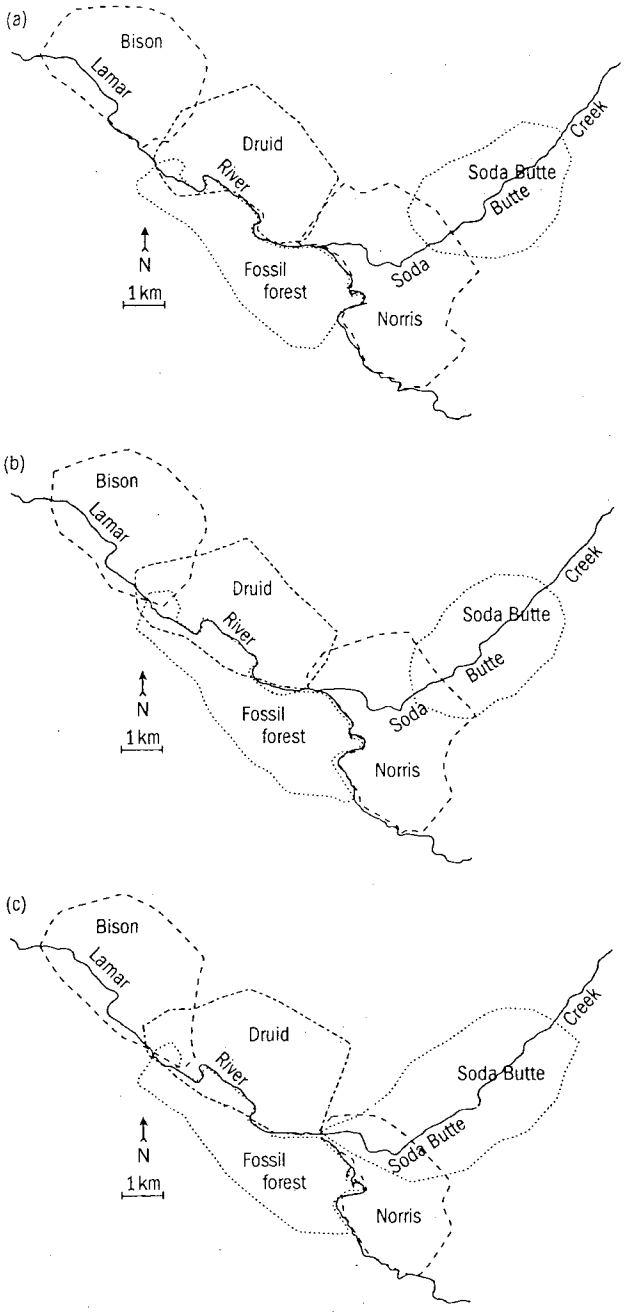

Figure 17.3 Spatial distribution and territorial boundaries of the five resident coyote packs occupying the Lamar River Valley in the winters of (a) 1990–91, (b) 1991–92, and (c) 1992–93, YNP, Wyoming.

Figure 17.4 The alpha male of the Soda Butte pack dominates the beta male (his 2-yr old son) at an elk calf (*Cervus elaphus*) the alpha pair just killed © E. M. Gese.

Behavioural activity budgets

The behavioural activity budgets of the coyotes in the Lamar River Valley changed throughout the year (Fig. 17.5). In the fall, coyotes spent much of their time travelling (60%) and hunting small mammals (13%). During winter, as snow depth increased and ungulate carcasses became available, coyotes travelled less (24%), hunted small mammals less (2%), and fed more on ungulate carcasses (2%) and rested (66%). During spring, the coyotes returned to travelling and hunting small mammals, with a corresponding decrease in the amount of time spent resting and feeding on ungulate carcasses. The ungulate carcasses that coyotes fed on during summer were mostly elk calves they killed, plus scavenging the remains of old carcasses from the previous winter. Transient coyotes showed similar proportions of activity as resident animals except for the amount of time spent feeding on carcasses. Members of resident coyote packs spent an average of 2% of their time feeding on carcasses, while transients spent only 0.3% feeding on carcasses ($t = 1.927$, $P = 0.056$). Transients, which were solitary animals, were at a disadvantage when attempting to obtain, feed on, or defend a carcass (Gese *et al.* 1996a). Bekoff and Wells (1981, 1982, 1986) reported similar changes in behavioural activity budgets of coyotes in Grand Teton National Park, Wyoming, in relation to social organization, and changes in snow depth and carcass availability.

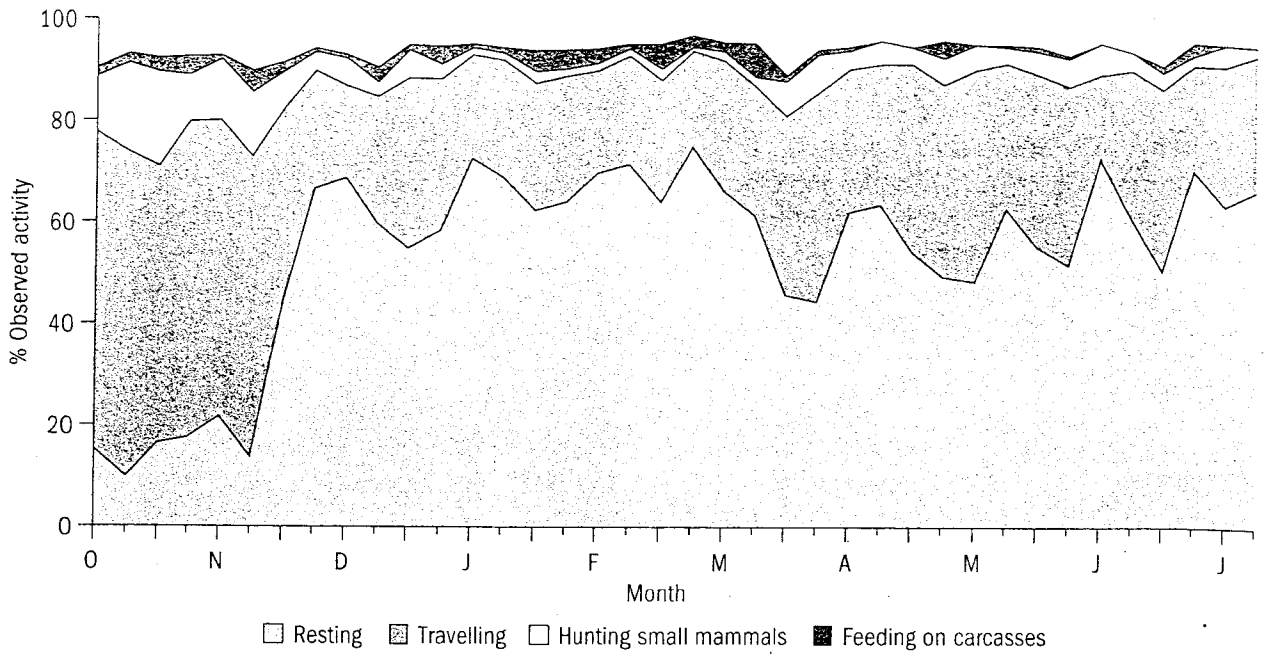

Figure 17.5 Amount of time coyotes were observed to spend resting, travelling, hunting small mammals, and feeding on carcasses each week during the three winters (1991-93) combined, YNP, Wyoming.

Foraging ecology

Coyotes hunted elk calves in early summer, while the calves were vulnerable during the first few weeks of life. Coyotes also hunted ground squirrels during summer when the squirrels emerged from hibernation. Voles were the principal small mammal food and constituted most of prey biomass ingested by coyotes year round. Even though large coyote packs existed, small mammals were always hunted by coyotes alone (Gese *et al.* 1996b). During the 2507 h of observation, we recorded 6433 prey detections of small mammals, 4439 attempts to capture prey, and 1545 captures of small mammals by coyotes. Many extrinsic and intrinsic factors influenced predation rates and capture success of small mammals by coyotes (Gese *et al.* 1996b). Habitat was a major factor influencing predation rates by coyotes on small mammals. Detection rates, attempt rates, and capture rates of small mammals by coyotes significantly varied among the various habitats (detection rate: $F = 39.82$, df = 6, 1668, $P < 0.001$; attempt rate: $F = 31.305$, df = 6, 1668, $P < 0.001$; capture rate: $F = 14.84$, df = 6, 1668, $P < 0.001$) with detection, attempt, and capture rates of small mammals being highest among mesic habitats (Table 17.1). Most *Microtus* species are associated with mesic habitats (Getz 1985). Dense vegetation also provides mechanical support for snow cover influencing the amount of subnivean space available at the ground surface for microtine passages (Spencer 1984). Coyotes readily exploited these habitats containing the highest prey densities and spent most of their time hunting small mammals in these habitats (Gese *et al.* 1996b).

Table 17.1 Influence of habitat type on detection, attempt, and capture rates (# prey/hour spent active) of small mammals by coyotes in the Lamar River Valley, YNP, Wyoming, 1991-93

Habitat type	Detection	Attempt	Capture
Shrub-meadow	8.0	5.4	1.8
Mesic meadow	7.3	5.2	1.6
Sage-grassland	4.6	3.1	1.0
Grassland	4.4	3.1	1.1
Riparian	2.2	1.3	0.5
Forest	1.4	1.0	0.4
Road	0.7	0.5	0.0

Table 17.2 Influence of snow depth on detection, attempt, and capture rates (# prey/hour spent active) of small mammals by coyotes in the Lamar River Valley, YNP, Wyoming, 1991-93

Snow depth	Detection	Attempt	Capture
None	5.8	3.5	1.7
Low (5-15 cm)	8.4	5.9	1.9
Moderate (16-25 cm)	5.0	3.2	1.0
Deep (26-40 cm)	3.7	2.6	0.9
Very deep (>40 cm)	3.4	2.4	0.5

Another important factor influencing predation on small mammals by coyotes was snow depth (Fig. 17.6). Snow depth was classed into none, low (5–15 cm), moderate (16–25 cm), deep (26–40 cm), and very deep (>40 cm). Detection rates, attempt rates, and capture rates of small mammals by coyotes varied among the different snow depth classes (detection rate: $F = 28.38$, df = 4, 1670, $P < 0.001$; attempt rate: $F = 24.35$, df = 4, 1670, $P < 0.001$; capture rate: $F = 15.26$, df = 4, 1670, $P < 0.001$) (Table 17.2; Fig. 17.6). Low snow cover actually increased prey detection rates, predation attempt rates, and capture rates of rodents by coyotes compared with bare ground. As snow depth increased, detection rates, attempt rates, and capture rates of small mammals by coyotes declined (Fig. 17.6).

Age and experience of the coyote was also a major factor influencing predation on small mammals. We found that even under the same environmental conditions (snow depth, habitat, snow-pack hardness, and wind speed), pups detected or showed that they detected more prey per hour than did older coyotes (Fig. 17.6). We believe that this higher detection rate by pups may have been due to increased responsiveness to an auditory cue (whether prey or not). It appeared that older coyotes may filter out irrelevant sounds from the environment and were more selective towards cues associated with prey (Gese *et al.* 1996b). Older coyotes also reduced the proportion of prey they attacked during adverse conditions, while pups continued to attack a high proportion of prey that they detected (possibly due to lack of experience). Alternatively, and more plausible, is that

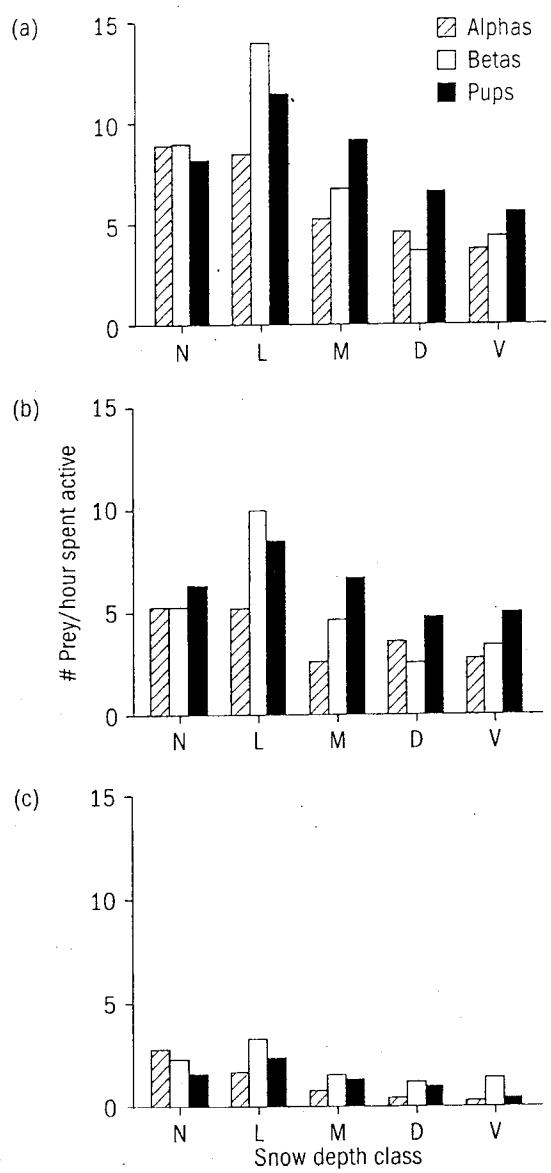

Figure 17.6 Rates (# prey/hour spent active) of small mammal (a) detection, (b) attempt, and (c) capture, for alpha, beta, and pup coyotes across varying snow depth classes in mesic-meadow habitat, YNP, Wyoming, 1991-93. Snow depth classes were: N (no snow), L (low, 5-15 cm), M (moderate, 16-25 cm), D (deep, 26-40 cm), and V (very deep, >40 cm).

reduced access to ungulate carcasses (Gese *et al.* 1996a) may have forced pups to hunt small mammals under adverse conditions in order to survive and remain in the pack (Gese *et al.* 1996c).

During winter, the presence of a dominance hierarchy in the coyote packs dictated the level of resources acquired by individual members of the

pack (Gese *et al.* 1996a). During winter as snow depth increased, access to small mammals (encounter, attempt, and capture rates) declined (Fig. 17.6; Gese *et al.* 1996b). However, as this snow cover limited access to the small mammal prey base by coyotes, it made foraging for plant material more difficult for ungulates (mainly elk). As winter progressed and the elk became nutritionally stressed, animals died due to malnutrition (Craighead *et al.* 1973; Houston 1978), or were weakened and killed by coyotes (Gese and Grothe 1995). Surprisingly, only 2–3 coyotes were needed to kill even an adult elk, but these elk were in extremely poor nutritional condition. Gese and Grothe (1995) reported several instances of coyote predation on elk and found that predation attempts on ungulates almost always involved the alpha pair (the alpha male was the main attacker) and the remainder of the pack did not participate in the attack, but were often observed to be watching the attack.

Once a kill had been made or an ungulate succumbed to winter stress, the resident pack would begin feeding on this resource. However, not all pack members fed equally (Gese *et al.* 1996a). Apparently, pups were restricted from feeding on the carcass by the older members of the pack (Fig. 17.7). The carcass was monopolized by the alpha pair first, then the higher ranking beta animals, then the lower ranking individuals, and lastly the pups (Fig. 17.7; Gese *et al.* 1996a). Even though these pups were the offspring of the alpha pair and usually related to the older betas in the pack, this restriction of access to the carcass indicated that the pups had to fend for themselves. Parent–offspring conflict (Trivers 1972, 1974), was apparent within these coyote packs as food resources became restricted during winter. In response to this resource partitioning, pups adopted a different foraging strategy and spent more time hunting small mammals even when conditions were poor (Fig. 17.7; Gese *et al.* 1996a,b; Fig. 17.8).

Evidence of resource partitioning in relation to social dominance has been found in other social carnivores. In the Namib Desert, spotted hyaenas (*Crocuta crocuta*) showed a linear dominance hierarchy when feeding on a carcass, in which subordinate animals eventually gained access to large carcasses, but not small carcasses (Tilson and Hamilton 1984).

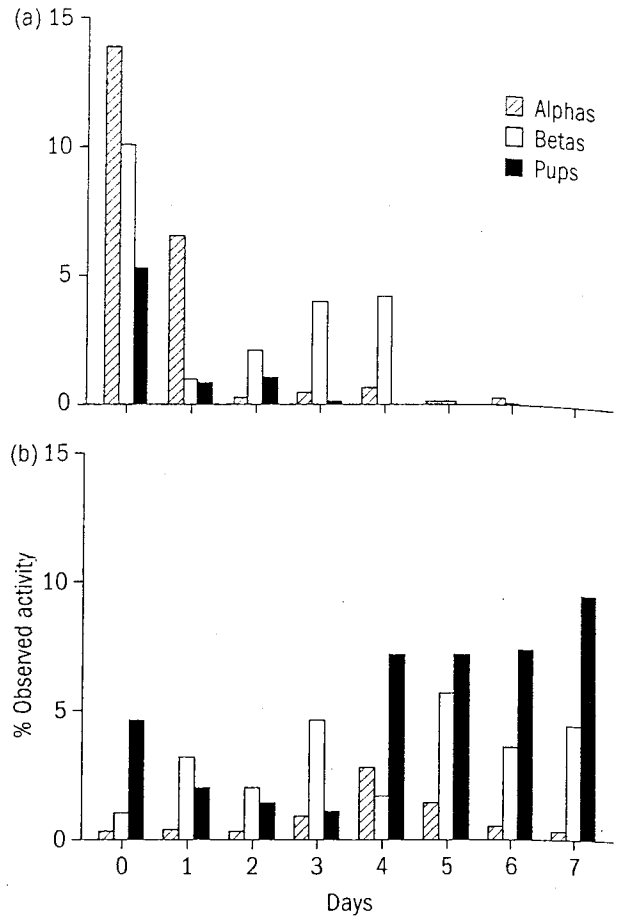

Figure 17.7 Amount of time alpha, beta, and pup coyotes were observed to spend (a) feeding on a carcass and (b) hunting small mammals, on the day (day 0) and the proceeding 7 days after an elk died or was killed by coyotes, YNP, Wyoming, 1991–93.

A correlation between social rank and feeding typified female spotted hyenas in the Masai Mara National Reserve in Kenya (Frank 1986), brown hyenas (*Hyaena brunnea*) (Owens and Owens 1978), and wolves (Zimen 1976), amongst others.

Influence of food availability on regulation of pack size

During our study, winter severity (mainly snow depth) determined ungulate carcass biomass, which in turn influenced coyote pack size as mediated by social dominance within the resident pack. Access to

Figure 17.8 Coyote *Canis latrans* pouncing through the snow to capture a vole underneath © E. M. Gese.

food resources during the winter bottleneck not only influenced coyote pack size, but also appeared to influence reproduction the subsequent spring. During the first winter, carcass biomass was low due to low snowfall. With limited food resources, competition for ungulate carcasses was high with access to those few carcasses determined by social rank within the pack (i.e. resource partitioning; Gese *et al.* 1996a). Subordinate individuals (i.e. low-ranking betas and pups) with limited access to ungulate carcasses attempted to compensate for this shortfall by hunting small mammals (Gese *et al.* 1996b). Those that could capture and subsist on small mammals often remained in the pack, but others that were less successful hunters of small prey dispersed (Gese *et al.* 1996c). With low prey biomass in the valley, coyote packs through the winter of 1990–91 remained small ($\bar{x}$ = 4.6 coyotes/pack in January) as pups from the previous year dispersed early (Gese *et al.* 1996a,c). Litter size (at den emergence) that spring (1991) averaged 5.0 pups/pack (Gese *et al.* 1996a). During the second winter (1991–92), increased snowfall resulted in an increase in available ungulate biomass in the form of winter kill. With more ungulate carcass biomass available, more of the pack had access to these resources and subsequently fewer individuals were forced to disperse (Gese *et al.* 1996c) and seek resources elsewhere, dispersal occurred later in winter, and pack size increased correspondingly ($\bar{x}$ = 5.8 coyotes/pack in January). Litter size increased to 7.8 pups/pack with one pack producing 2 litters (only the litter whelped by the alpha female survived beyond 4 months of age). During the final winter (1992–93), with similar high ungulate biomass in the valley, some coyotes did not disperse until late winter and pack size increased to 6.6 coyotes/pack (in January); litter size was not accurately determined that spring (Gese *et al.* 1996c).

The relationship between food abundance and regulation of canid populations has been documented (e.g. Zimen 1976; Keith 1983; Knowlton and Stoddart 1983; Fuller 1989; Fuller and Sievert 2001). Food abundance regulates coyote numbers by influencing reproduction, survival, dispersal, space-use patterns, and territory density (Todd *et al.* 1981; Todd and Keith 1983; Mills and Knowlton 1991; Knowlton *et al.* 1999). Coyote populations will increase and decrease with changes in food availability, particularly in areas with cyclic lagomorph populations. In areas where hares comprise a significant portion of the coyote diet, coyote numbers will rise and fall as snowshoe hare (*Lepus americanus*) or black-tailed jackrabbit (*Lepus californicus*) numbers change (Clark 1972; Todd *et al.* 1981; Knowlton and Stoddart 1992; O'Donoghue *et al.* 1997). The mechanisms for these responses are changes in ovulation rates and litter sizes, and changes in the percentage of adult and yearling coyotes that bred (Todd *et al.* 1981; Todd and Keith 1983). Food abundance also influences coyote numbers through its affect on dispersal of pups in winter (Gese *et al.* 1996c). In addition,

food shortages can increase mortality rates, especially among juvenile coyotes as they disperse into unfamiliar areas (Knowlton *et al.* 1999).

Territorial maintenance and defence

The territory of an animal has been defined as the area that an animal will defend against individuals of the same species (Burt 1943; Mech 1970). Territoriality allows animals to exclude potential competitors from access to mates, food, space, and cover. Failure to defend the territory may have far-reaching consequences for the resident pack (e.g. Gese 1998). Canids use both direct and indirect mechanisms to maintain territorial boundaries, including scent-marking (Peters and Mech 1975; Camenzind 1978; Rothman and Mech 1979; Barrette and Messier 1980; Bowen and Cowan 1980; Wells and Bekoff 1981), howling (Harrington and Mech 1978a,b, 1979), and direct confrontation of intruders (Camenzind 1978; Bekoff and Wells 1986; Mech 1993, 1994). During this study, the importance of the presence of the dominance hierarchy in the resident packs was exemplified in the role pack members played in territory maintenance. Observations of the coyotes revealed that they defended their territorial borders both directly through confrontation of intruding animals, and indirectly via scent-marking and howling (Gese and Ruff 1997, 1998; Gese 2001). We found that the alpha pair of the pack was principally responsible for maintaining and defending the territory, with peak defence occurring during the breeding season.

Scent-marking

During observations of scent-marking behaviour, we recorded 3042 urinations, 451 defecations, 446 ground scratches, and 743 double-marks (Gese and Ruff 1997). Rates of urination, double-marking, and ground-scratching varied seasonally and among social classes (Fig. 17.9). Overall, alpha, beta, and pup

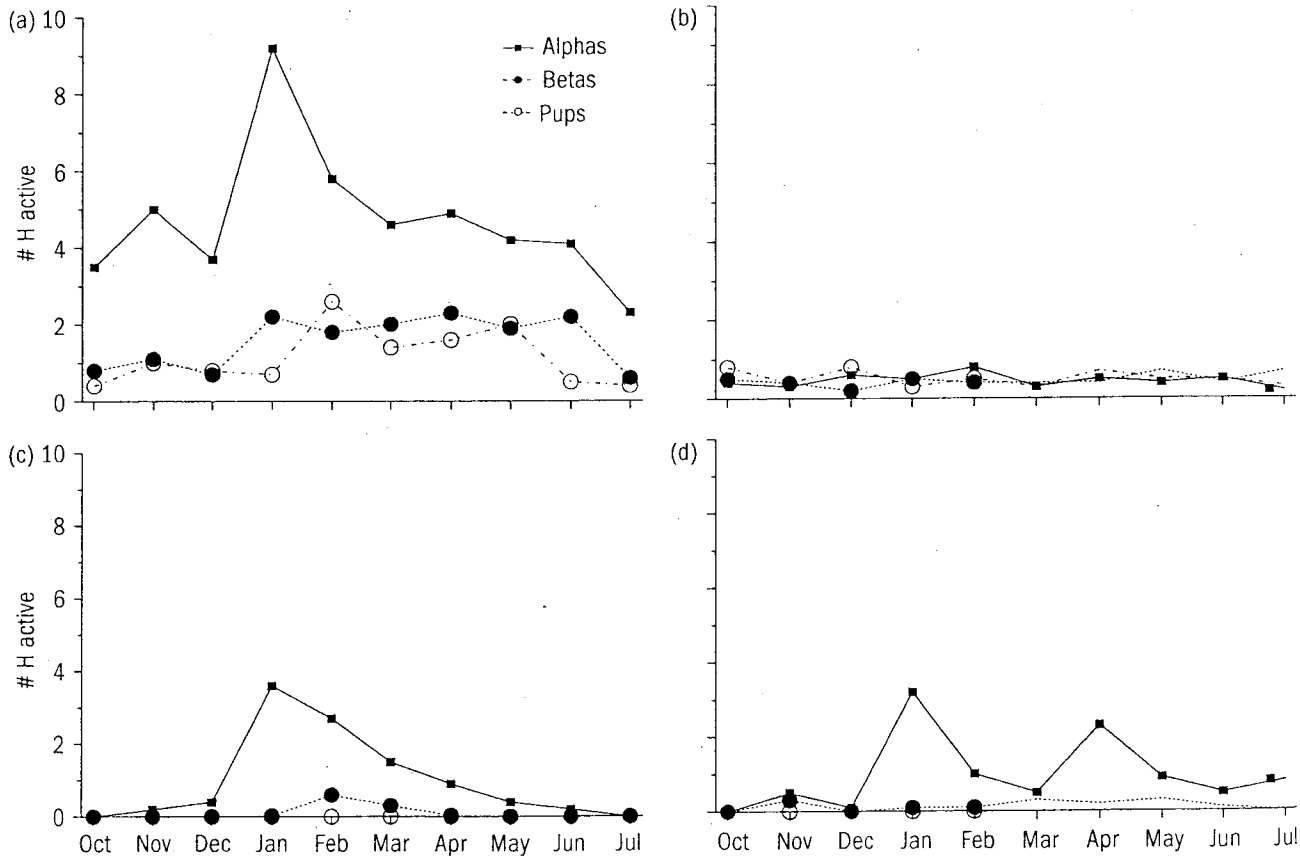

Figure 17.9 The rate of (a) urinations, (b) defecations, (c) double-marks and (d) ground scratches for alpha, beta and pup coyotes from October to July, YNP, Wyoming, 1991-93.

coyotes scent-marked at a rate of 5.1, 1.7, and 1.4 marks/h active, respectively. Double-marks were performed an average of 1.3, 0.1, and 0 marks/h active for alpha, beta, and pup coyotes, respectively. Scent-marking peaked during the breeding season (Fig. 17.9). We found that the alpha pair scent-marked the boundaries, using urinations, double-marking, and ground scratching, at a higher rate (6.0 marks/h) and frequency than in the core (2.7 marks/h) of their territory ($t = -3.039$, df = 82, $P = 0.003$). Beta coyotes participated to some degree in scent-marking, but not at the level of the alpha pair (Fig. 17.9; Gese and Ruff 1997). Pups seemed not to participate in scent-marking duties. Defecation rate was relatively constant all year (Fig. 17.9) and among social classes (0.5, 0.5, and 0.8 defecations/h for alphas, betas, and pups, respectively), and appeared to be relatively unimportant as a scent-marking signal (Gese and Ruff 1997). Asa *et al.* (1985) speculated that urine may be a better compound for scent-marking because faeces may not be as readily available for deposition as urine. Studies on the scent-marking of wolves (Peters and Mech 1975) and coyotes (Wells and Bekoff 1981) have reported similar results with territorial canids scent-marking more along the boundaries of their territory and dominant members scent-marking at higher rates than subordinates (see also Sillero-Zubiri and Macdonald 1998). Scent-marking increased during the breeding season when pair bonds are strengthened and breeding synchrony was initiated (Bekoff and Diamond 1976; Kennelly 1978). Scent-marking in dominant wolves changed seasonally and was correlated with changes in testosterone (Asa *et al.* 1990). Scent-marking by canids appears to influence demarcation of territorial boundaries and also provides internal information to members of the resident pack (Macdonald 1979a, 1985; Wells and Bekoff 1981). Scent-marks do not prevent animals from crossing territorial boundaries, but may serve as subtle repellents eliciting avoidance by potential intruders.

Howling

Another indirect means of territory maintenance that followed the same pattern as scent-marking was howling or long-range vocalizations. We recorded 517 howling events during the 2507 h of behavioural observations. Rates of howling varied seasonally and among the social classes (Fig. 17.10). The alpha pair spent more time howling (0.59%) and howled at a higher rate (0.33 howls/h) than both beta (0.15% and 0.10 howls/h) and pup (0.14% and 0.11 howls/h) coyotes (Gese and Ruff 1998). These alpha animals also howled at a greater frequency when near territorial boundaries (56% of howls) and howling rates peaked before and during the breeding season, then declined in the pup-rearing season (Fig. 17.10). In contrast, transient animals did not howl and appeared to maintain a 'low profile' and did not advertise their presence either through howling or scent-marking. Howling appeared to serve as a territorial spacing function that was mainly performed by the alpha pair. Research on howling among wolves and coyotes have found similar results with howling rates peaking during the breeding season, alpha members howling more frequently than subordinate individuals, and howling playing an important role in territory maintenance (Harrington and Mech 1978a,b, 1979, 1983; Walsh and Inglis 1989). Seasonal changes in howling rates among alpha animals may be related to increased pair-bond behaviour, hormonal changes, and territorial maintenance during the breeding season, with the decline possibly related to a reduced need to advertise their presence outside of the breeding season (Zimen 1976; Harrington and Mech 1978*a*; Gese and Ruff 1998).

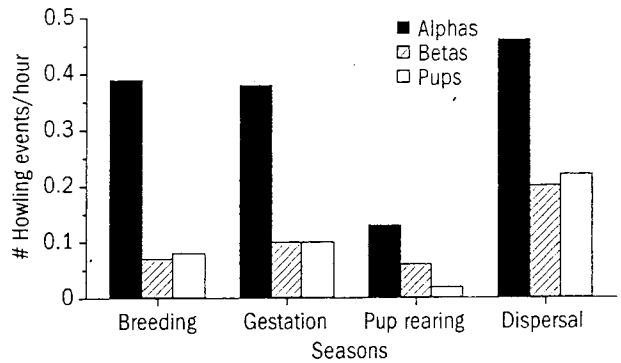

Figure 17.10 Howling rate for alpha, beta, and pup coyotes during the biological seasons, YNP, Wyoming 1991–93.

Direct defence

When intruding animals ignore indirect mechanisms of territory defence, canids must employ direct

confrontation of intruders to reinforce territory boundaries (Camenzind 1978; Bekoff and Wells 1986; Mech 1993, 1994). Defence of a territory is usually a task undertaken by the dominant alpha pair (Mech 1970, 1993). We observed 112 instances of territorial defence by resident coyotes evicting trespassing animals (Gese 2001). These chases averaged 2.87 min in duration (range 0.3–26.8 min). Similar to the findings on howling and scent-marking rates, the alpha pair (mainly the alpha male) was most likely to be involved in territorial defence (87% of evictions). Beta coyotes were less likely to be involved (48% of the chases), while pups participated little in territorial defence (7% of the evictions). Pursuits of intruding coyotes terminated at the territory boundary and were followed by a robust session of howling and scent-marking at the border by the resident animal(s). Physical contact between the resident animals and intruders was observed, but consisted of ritualized displays of dominance and submission, with few serious injuries occurring. In contrast to the high mortality among wolves associated with a territorial trespass (e.g. Van Ballenberghe and Erickson 1973; Mech 1994), no intruding coyotes were killed during encounters with a resident pack. Intruders generally retreated from the resident territory quickly and often without any physical contact occurring between the residents and intruder(s). The group of coyotes pursuing an intruder or group of intruders usually had a numerical advantage over the group being chased (Gese 2001). Howling seems to serve as a long-distance warning to intruders, scent-marking as the visual and olfactory signal used at shorter distances, and direct confrontation if intruders ignored all the other territorial signals (Gese and Ruff 1997, 1998; Gese 2001).

Individual fitness

When we examined the benefits of a dominance hierarchy within the resident packs in terms of reproductive success and survival (i.e. fitness; Davies 1978), several key findings became evident. While the alpha coyotes have the risk of injury when confronting intruders or attacking large prey, they benefit greatly in terms of survival and reproduction (Gese 2001). We found that the alpha coyotes are the ones providing all of the reproductive output into the population with 93.7% of the alphas observed breeding and 66.1% of their pups being recruited into the population (Table 17.3). Even though one beta female produced a litter of pups, those pups did not survive to be recruited into the population (i.e. they all perished in <3 months). In addition, pup coyotes and dispersing coyotes had the lowest survival rates (0.64 and 0.13 annual survival rates for pups and dispersers, respectively). Most dispersing coyotes moved outside the park into areas where human persecution was more prevalent. Beta (0.96 annual survival) and alpha coyotes (0.91) had equal survival, but betas did not contribute to the reproductive effort (but may benefit

Table 17.3 Comparison of various reproductive, demographic, and foraging parameters between territorial and non-territorial coyotes, YNP, Wyoming, 1991–93

	% animals breeding	% pups surviving to 5 months	Annual survival rate	Annual dispersal rate	% time feeding on carcass	Small mammal capture rate (#/h)	Capture success (%)
Territorial							
Alphas (16)	93.7	66.1	0.91	0.03	2.7	2.3	38.2
Betas (31)	6.2	0	0.96	0.14	3.2	2.5	37.2
Pups (43)	0	-	0.64	0.30	0.6	2.2	27.6
Non-territorial							
Transients (5)	0	-	1.00	0.17	0.3	2.0	32.3
Dispersers (8)	0	-	0.13	B	0.4	0.6	22.0

Note: Numbers in parentheses are sample size for that cohort.

through inclusive fitness by helping related offspring; Hamilton 1964). Transient coyotes also had high survival, but again, produced no offspring (Table 17.3). In terms of dispersal rates, alpha coyotes rarely dispersed, while dispersal was much more common among betas, pups, and transients (Table 17.3). Alphas and betas had the greatest access to ungulate carcasses during winter, while pups, transients, and dispersers had little access to carcasses (Table 17.3). All cohorts of coyotes (alphas, betas, pups, and transients) were equally adept at capturing small mammals, while dispersing coyotes had the lowest success hunting small mammals (Table 17.3; Gese *et al.* 1996c). By defending a territory, the alpha pair benefited the most in terms of food resources, mating, space, and survival, when compared to other resident pack members (betas and pups) and non-territorial coyotes (transients and dispersers; Gese 2001). Essentially, within the coyote social system, the fitness of the alpha animals far exceeded all the other cohorts even when the risk of injury from territorial defence is considered (although the risk to the alphas seems almost non-existent).

In summary, in YNP, coyotes adapted to changes in prey abundance, availability, and vulnerability throughout the year, as well as changes in snow depth and temperature by modifying their behaviour, foraging strategies, and activity budgets. Differences in prey density within certain habitats were exploited by all coyotes as they spent more time hunting small mammals in habitats containing the highest reward. The presence of a dominance hierarchy in the resident pack, in conjunction with territoriality, allowed resident animals (particularly the alpha pair) more access to food, mates, and space and appeared to be evolutionary advantageous in coyote society.

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Edited by DAVID W. MACDONALD
and CLAUDIO SILLERO-ZUBIRI

Wildlife Conservation Research Unit, University of Oxford

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