Threat of predation: do ungulates behave aggressively towards different members of a coyote pack?

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Abstract: Wild ungulates have evolved a variety of antipredator strategies to deter or escape predation by carnivores. Among wild canids, the dominant pair of a pack often initiates attacks upon prey. Previous observations in Yellowstone National Park, Wyoming, showed that the alpha pair in a coyote (*Canis latrans*) pack most often leads attacks on ungulates during winter. We were interested in determining whether ungulates can distinguish (perhaps by body size or posture) which members of a coyote pack are the alpha individuals, and whether they initiate and direct aggressive behavior towards those members of the pack that pose the greatest threat of predation to themselves and (or) their offspring. During 2507 h of behavioral observations on 54 coyotes between January 1991 and June 1993, we observed 51 interactions between coyotes and adult elk (*Cervus elaphus*), bison (*Bison bison*), and pronghorn antelope (*Antilocapra americana*) in Yellowstone National Park. The interactions analyzed here are those in which the ungulate appeared to initiate aggressive behavior towards the coyote(s) and were not a response to an attack by the predators. We found that aggression by ungulates towards coyotes was highest during the summer months, when calves and fawns were present; female ungulates were more frequently aggressive than males. The frequency of aggression of adult ungulates towards small and large groups of coyotes was equal to the frequency of occurrence of these groups. Ungulates directed aggressive behavior more frequently towards alpha coyotes and were less aggressive towards beta coyotes and pups. Large ungulates, particularly elk and bison, appeared to perceive that alpha coyotes posed a greater threat to themselves and their offspring. The smaller ungulate, the pronghorn antelope, directed aggressive behavior equally towards all coyotes. Adult ungulates were probably responding to the larger body size of the alpha coyotes and the tendency of alpha coyotes to travel at the front of the pack.

Résumé : Les ongulés en nature ont acquis un grand nombre de stratégies anti-prédateurs qui leur servent à éviter ou à empêcher la prédation par les carnivores. Chez les canidés sauvages, le couple dominant d'une meute est généralement l'instigateur des attaques. Des observations préalables dans le parc national de Yellowstone ont révélé que c'est le couple alpha d'une meute de Coyotes (*Canis latrans*) qui mène le plus souvent l'offensive contre les ongulés en hiver. Nous avons cherché à percevoir si les ongulés sont capables de distinguer (peut-être à leur taille ou à leur posture) quels membres de la meute sont les individus alpha et s'ils amorcent des comportements agressifs dirigés contre les membres de la meute qui représentent le plus grand risque de prédation pour eux-mêmes et (ou) pour leur progéniture. Au cours de 2507 heures d'observation de 54 coyotes, nous avons été témoins de 51 interactions entre des coyotes et des adultes du Wapiti (*Cervus elaphus*), du Bison d'Amérique (*Bison bison*) et de l'Antilope d'Amérique (*Antilocapra americana*) dans le parc de Yellowstone, Wyoming, de janvier 1991 à juin 1993. Au cours de ces interactions, ce sont les ongulés qui étaient les initiateurs des comportements agressifs envers les coyotes, et il ne s'agissait pas de réactions à des attaques de coyotes. L'agressivité des ongulés envers les coyotes a été maximale au cours des mois d'été, époque où les jeunes et les faons étaient présents; les femelles étaient plus souvent agressives que les mâles. Les ongulés adultes attaquaient les petits groupes aussi souvent que les grandes meutes de coyotes. L'agressivité des ongulés adultes était dirigée plus souvent vers les coyotes alpha et moins souvent vers les coyotes bêta ou les jeunes. Les gros ongulés, particulièrement les wapitis et les bisons, semblaient percevoir que les coyotes alpha étaient plus menaçants que les autres pour eux-mêmes et pour leur progéniture. Les ongulés plus petits, les Antilopes d'Amérique, avaient des comportements également agressifs à l'égard de tous les coyotes. Les ongulés adultes réagissent probablement à la taille plus grande des coyotes alpha et à leur tendance à se déplacer à la tête de la meute.

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Introduction

Predators and prey evolve together, with adaptations on both sides in what has been termed an evolutionary arms race (Krebs and Davies 1987). Predators often test herds of wild ungulates in order to detect the vulnerable individuals in the herd (Mech 1966; Carbyn et al. 1993). Through this testing process, wild carnivores apparently are able to recognize weaknesses in their prey and can then attack a vulnerable individual (Mech 1970; Peterson 1977). Wolves (*Canis lupus*) tend to prey disproportionately on animals that are young and old, in poor nutritional condition, and have jaw necrosis, arthritis, or heavy parasite loads (Murie 1944; Mech 1966, 1970; Pimlott et al. 1969; Mech et al. 1995). Among coyotes (*Canis latrans*), predation on ungulates is most pronounced during the fawning or calving season (Cook et al. 1971; Barrett 1984), with opportunistic predation on adult ungulates occurring in winter (Robinson 1952; Gese and Grothe 1995). In winter in Yellowstone National Park, coyotes killed elk calves or very old elk (*Cervus elaphus*) that were in poor nutritional condition (Gese and Grothe 1995). Cooperative hunting (dependent on pack size) is also an important influence on predation of ungulates (Mech 1966, 1970; Bowyer 1987; Dale et al. 1995), with most attacks on wild and domestic ungulates being initiated by the dominant, breeding members of a wolf or coyote pack (Peterson 1977; Mech 1988; Gese and Grothe 1995; Sacks 1996).

Countering these tests by predators, ungulates have developed antipredator strategies and behaviors (Mech 1977; Geist 1982; Estes 1991; Nelson and Mech 1991). When encountering a predator, ungulates may flee, approach, attack, stand and face the predator, or remain still and go undetected by the predator (Mech 1966, 1970; Garner and Morrison 1980; Nelson and Mech 1985, 1994; Estes 1991). Garner and Morrison (1980) described several instances in which female white-tailed deer (*Odocoileus virginianus*) chased or attacked coyotes during the fawning season; however, the identity of the coyote in these encounters was unknown. In Yellowstone National Park, coyotes preyed upon adult and calf elk and deer in winter; the majority of the attacks were initiated and led by the alpha pair (Gese and Grothe 1995), which were typically the largest individuals in the pack. Of interest is whether ungulates can determine which member of a coyote pack poses the greatest threat of predation to themselves and their offspring, which would allow them to initiate and direct aggressive behavior towards those individuals (i.e., the alpha animals). While collecting data on foraging behavior by coyotes (Gese et al. 1996*a*, 1996*b*), we observed 51 instances of aggressive behavior (chases) initiated by ungulates and directed towards coyotes; in all cases the identity of the coyote(s) involved was known. The decision by an ungulate to chase or attack a particular coyote may be based upon body size, behavior, or posture of the coyote, or its proximity to the ungulate. In this paper we address the following questions: (*i*) Is there a seasonal pattern of aggression (i.e., chases) by ungulates towards coyotes? (*ii*) Do male and female ungulates initiate aggressive behavior towards coyotes with equal frequency? (*iii*) Is there a relationship between displays of aggression by an ungulate and the size of a coyote group? (*iv*) Can ungulates perceive which individuals in a coyote pack pose the greatest threat of predation (i.e., the coyotes most likely to lead an attack) and direct aggressive behavior towards those coyotes?

Methods

Interactions and the responses of ungulates to the presence of coyotes were recorded during behavioral observations documenting the foraging ecology of coyotes, their predation of small mammals, and the factors influencing their dispersal (Gese et al. 1996*a*, 1996*b*, 1996*c*). Observations were recorded from January 1991 to June 1993 in the Lamar River Valley, Yellowstone National Park, Wyoming (44°52′N, 110°11′E). The elevation of the study area was about 2000 m. The climate was typical of the Rocky Mountain region, with long, cold winters and most of the annual precipitation falling as snow (Dirks and Martner 1982; Houston 1982). Habitats in the valley included forests, grassland, riparian areas, sagebrush–grassland, mesic meadow, and shrub–meadow (for complete habitat descriptions, see Gese et al. 1996*a*).

Coyotes older than 5 months were captured with padded, leghold traps with attached tranquilizer tabs (Balser 1965). Each coyote was immobilized (Cornely 1979) and then weighed, sexed, eartagged, and radio-collared. We extracted the first vestigial premolar to estimate age by analysis of cementum annuli (Linhart and Knowlton 1967). We captured pups (10–12 weeks of age) at the den and surgically implanted an intraperitoneal transmitter in each. The coyotes were classified as pups (<12 months old), yearlings (12–24 months old), or adults (>24 months old). Members of resident packs were classified into three social classes according to their position in the dominance hierarchy: alpha coyotes (the dominant, breeding adult male and female), beta coyotes (adults and yearlings subordinate to the alpha coyotes but dominant over pups), and pups (young of the year, subordinate to both the alpha and the beta coyotes) (Schenkel 1947, 1967; Rabb et al. 1967; Mech 1970). A coyote classified as a pup remained in that category until the next litter became mobile and independent of parental feeding in September. Coyotes were reclassified into the next age and social class as they grew older and their rank in the dominance hierarchy rose (Gese et al. 1996*a*, 1996*b*, 1996*c*).

Behavioral observations followed the procedures described in Gese et al. (1996*a*, 1996*b*, 1996*c*). We observed both "transmittered" and unmarked coyotes (the latter were identified by physical characteristics) during daylight hours (07:00–20:00) with a 15–30× spotting scope from a vehicle or from observation points overlooking the valley. Observations of interactions between ungulates and coyotes were documented while watching individual coyotes (Gese et al. 1996*a*, 1996*b*, 1996*c*). Interactions in which an ungulate initiated aggressive behavior (chase or attack) towards a coyote or group of coyotes were recorded. For each ungulate–coyote interaction, we recorded the age (adult or calf), sex, and species of the ungulate initiating the interaction, the social class of the coyote towards which the ungulate charged, and the group size and composition (age and class of individuals) of the coyotes involved in the interaction. We emphasize that the interactions analyzed here were those in which the ungulate appeared to initiate the interaction by chasing or charging the coyote(s), and were not responses to an attack initiated by the coyote(s) (e.g., Gese and Grothe 1995). However, we acknowledge that perhaps either the posture of the coyote or the distance between the coyote and the ungulate may have led the ungulate to respond aggressively towards the coyote; the ungulate may thus have been responding to a subtle threat from the coyote that we were unable to observe and interpret. For this study we did not use the observations presented by Gese and Grothe (1995), because in those interactions the ungulates were reacting to an initial attack by the alpha coyotes; we were interested only in interactions initiated by ungulates.

Results

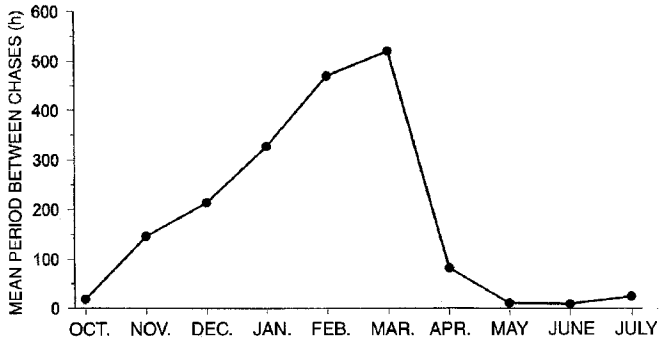
During 2507 h of observation on 54 coyotes from 27 January 1991 to 30 June 1993, we recorded 51 interactions in which an ungulate or group of ungulates aggressively chased or pursued a coyote or group of coyotes. Elk, bison (*Bison bison*), and pronghorn antelope (*Antilocapra americana*) were involved in 36, 10, and 5 of the chases, respectively. All chases were initiated by adult ungulates. Female ungulates were involved in 42 (82%) of the 51 chases; one bull elk chased coyotes, and eight interactions involved bison of unknown sex. Of the 36 chases by elk, 35 involved females. The initiation of aggressive behavior by ungulates towards coyotes had a seasonal pattern (Fig. 1). During the winter, chases of coyotes were infrequent, although coyotes killed ungulates at this time of year (Gese and Grothe 1995). As summer approached, the ungulates, particularly female pronghorn antelope and cow elk, chased coyotes more frequently.

We examined the data to determine if ungulates behaved aggressively towards larger groups of coyotes more frequently than towards smaller groups. Single coyotes and groups of 2, 3, and 4 coyotes were noted at the beginning of 68, 18, 9, and 5% of all observation bouts, respectively. These proportions were used to determine the expected values for aggressive interactions initiated by ungulates towards groups of different sizes (Gese et al. 1996*a*, 1996*b*, 1996*c*). Ungulates chased single coyotes and groups of 2, 3, and 4 coyotes in 31 (61%), 10 (20%), 7 (14%), and 3 (6%) of the observed interactions, respectively, which was not significantly different from the expected distribution (χ^2 = 1.832, df = 3, P = 0.608). Thus, the frequency with which ungulates chased coyote groups of different sizes corresponded to the frequency with which these groups were encountered (i.e., ungulates did not chase large groups of coyotes more frequently than small groups).

We found that ungulates chased coyotes of different social classes differently than expected. The proportions of alpha coyotes (35%), beta coyotes (39%), and pups (26%) in the resident population (Gese et al. 1996*a*, 1996*b*, 1996*c*) were used as the expected values for aggressive behaviors towards coyotes of these classes. Thirty (59%) of the chases by ungulates were directed at an alpha coyote or the alpha pair, whereas only 16 (31%) and 5 (10%) of the chases were directed towards beta coyotes and pups, respectively. The ungulates chased alpha coyotes more frequently than expected, and beta coyotes and pups less frequently than expected (χ^2 = 14.21, df = 2, P = 0.0008). Thus, ungulates initiated and directed aggressive behavior more frequently towards the alpha members of a coyote pack.

We also determined whether the body size of the ungulate influenced the social class of the coyote that was chased. There were 10 interactions involving the largest ungulate (bison); alpha coyotes, beta coyotes, and pups were chased in 70, 20, and 10% of these interactions, respectively, although these social classes constituted 35, 39, and 26% of the spring coyote population, respectively (χ^2 = 5.44, df = 2, P = 0.066). For the 36 chases involving elk, alpha coyotes, beta coyotes, and pups were chased in 61, 33, and 6% of the interactions (χ^2 = 13.08, df = 2, P = 0.0014). For the 5 interactions involving the smallest ungulate (pronghorn antelope), alpha coyotes, beta coyotes, and pups were chased in 20, 40, and 40% of the observations, respectively (χ^2 = 0.72, df = 2, P = 0.69). Thus, it appears that the body size of the ungulate influenced the ungulate–coyote interactions: the smallest species of ungulate (pronghorn antelope) chased all social classes of coyotes equally, and the two larger species of ungulates directed their attacks mostly at the alpha coyotes.

Fig. 1. Mean numbers of hours elapsed between chases of coyotes by ungulates in Yellowstone National Park, Wyoming, from October to July in 1991–1993.



Discussion

Under selective pressure from predators, ungulates have evolved a wide array of antipredator behaviors and strategies (Geist 1982; Estes 1991). Most attacks on wild ungulates by North American canids are initiated and performed by the dominant animals in the pack (Peterson 1977; Mech 1988; Gese and Grothe 1995). Predators have an acute ability to identify vulnerable individuals in a herd of ungulates (Murie 1944; Mech 1966, 1970; Pimlott et al. 1969; Mech et al. 1995) and then direct the attack towards them (Mech 1970). Of interest is whether ungulates are equally capable of detecting the dominant pack members and then initiating and directing aggressive behavior towards them before the predators attack.

Most predator–prey observations are records of ungulates chasing a predator in response to an attack by the predator (Robinson 1952; Hamlin and Schweitzer 1979; Truett 1979; Wenger 1981). Cases in which the ungulate initiated the attack or chase are less well documented (Marion and Sexton 1979; Garner and Morrison 1980). In all of these previous observations the identity of the coyote was unknown. We previously documented that the alpha pair were the principal coyotes involved in attacks on ungulates during winter (Gese and Grothe 1995). Of interest was whether ungulates recognize that the alpha animals pose the greatest threat and therefore whether they initiate aggressive behavior more frequently towards animals in this social class. We observed 51 cases of aggressive behavior in which ungulates chased or attacked coyotes without apparent provocation by the predator. Adult ungulates initiated a chase or attack directed towards alpha coyotes more frequently than expected; beta coyotes and pups were chased less frequently than expected on the basis of their frequency in the population. Based on our observations, we believe that ungulates can distinguish among members of a coyote pack. Ungulates directed aggressive behavior towards the larger individuals (alpha coyotes), which had the greatest tendency to initiate attacks on

adult and young ungulates. However, these attacks were initiated by the ungulates and were not a response to an attack by the predator.

Determining the reason for the ungulates directing aggressive actions towards the alpha coyotes was confounded by several variables. Whether an ungulate's decision to chase the alpha coyotes is based on body size, body posture, behavior, level of activity, or proximity is not known. The mean body mass of male alpha and beta coyotes was 15.2 and 13.4 kg, respectively (t = –2.053, P = 0.027), and that of female alpha and beta coyotes was 12.5 and 10.3 kg, respectively (t = –2.940, P = 0.005). Thus, beta coyotes were typically 12–18% smaller than alpha members of the pack. We could distinguish among the social classes of the coyotes on the basis of body posture and behavior (Gese et al. 1996*a*, 1996*b*, 1996*c*), and ungulates may be equally capable of doing so. In addition, alpha coyotes may display subtle behaviors or postures indicative of hunting that serve as cues for ungulates, yet are undetectable by human observers. We also examined whether ungulates were more likely to attack active coyotes, particularly whether alpha coyotes were chased more frequently because of their activity. Overall, coyotes spend 64% of their time resting and 36% of their time in active behaviors (Gese et al. 1996*a*). In contrast, coyotes were resting or active in 31 and 69% of the ungulate–coyote interactions, respectively. When chases were initiated by ungulates, alpha and beta coyotes and pups were active in 63, 75, and 80% of the interactions, respectively. Thus, alpha coyotes were not chased more frequently because they were more active; in fact, they were active less frequently than beta coyotes and pups. The proximity of the alpha coyotes to the ungulate may also have played a role in eliciting ungulate attacks. Although proximity and travel position of the coyote were not quantified, the alpha individuals were often in front of other pack members while traveling through the territory, hunting and scent-marking (Gese and Ruff 1997). Thus, attacks by ungulates may be directed at whichever coyote is at the front of the group, and this is typically one of the alpha individuals. In all ungulate–coyote interactions involving a group of coyotes, the ungulate appeared to direct its charge towards the alpha animals. These hypotheses are not mutually exclusive, and all may play a role in ungulate–coyote interactions, but the larger body size of the alpha coyotes seems to be a characteristic that would be quickly and readily discerned by an approaching ungulate.

We found that there was a seasonal component to ungulate aggression towards coyotes. The highest rate of aggressive behavior occurred during the fawning and calving season, in response to the threat posed by coyotes to newborn calves and fawns. Aggression by ungulates towards coyotes declined through the fall and winter as the young animals grew older and less vulnerable to predation. Coyotes are proficient predators on young deer, antelope, and elk (Robinson 1952; Cook et al. 1971; Barrett 1984). Thus, it was not surprising that ungulates, particularly females, initiated more attacks and chases during the summer. Attacks by ungulates, in which the front hooves can be used to strike at the predator or the horns used for goring, can deter predators and allow adults and their offspring to escape (Robinson 1952; Truett 1979; Wenger 1981); some attacks are fatal (Mech and Nelson 1990; Estes 1991). Garner and Morrison (1980) documented several cases in which white-tailed deer attacked and chased coyotes. These interactions involved only does; bucks were not aggressive towards coyotes. Maternal defense against predators is the most typical reason in the case of ungulates (Garner and Morrison 1980; Coté et al. 1997), as male ungulates contribute little to parental care. Observations of protective behavior towards offspring by male ungulates are rare; males tend to be more aggressive towards predators when defending themselves, a territory, or a mate (Kruuk 1972; Sinclair 1977; Marion and Sexton 1979). Many studies from Africa have documented both male and female adult ungulates attacking large carnivores when these predators attacked either the adults themselves, other cohorts in the herd, or their offspring (Kruuk 1972; Schaller 1972; Sinclair 1977). The finding that elk and bison directed chases more frequently towards the alpha coyotes, whereas pronghorn antelope directed attacks towards all coyotes equally, indicates that the pronghorn antelope perceived all coyotes as a threat. The larger ungulates apparently perceived the alpha coyotes as the greatest threat.

Cooperative hunting by carnivores is a well-documented strategy for killing large prey (Mech 1970; Kruuk 1972; Schaller 1972). Among coyotes, cooperative hunting has been observed to be employed when they are preying on fawns in summer and adults in winter (Hamlim and Schweitzer 1979; Bowyer 1987; Gese and Grothe 1995), but successful predation does not require the participation of all pack members (Gese and Grothe 1995). Bowyer (1987) indicated that the size of coyote groups was important when they killed mule deer (*Odocoileus hemionus*). However, we documented that coyote group size was not important in determining the success of a predation attempt on an ungulate in winter (Gese and Grothe 1995). The finding that ungulates chased coyote groups of different sizes with a frequency equal to their frequency of occurrence in the population suggests that larger coyote groups do not necessarily pose a greater risk of predation. Our present observations and previous findings (Gese and Grothe 1995) indicate that the success of a predation attempt on an ungulate does not depend on how many coyotes are present but rather on which coyotes are present. The ungulates in Yellowstone National Park appear to be aware of this, and may deter predation by initiating and directing aggressive behavior towards those pack members who are the main instigators of predatory attacks on ungulates.

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