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BEHAVIORAL INTERACTIONS BETWEEN COYOTES, *CANIS LATRANS*, AND WOLVES, *CANIS LUPUS*, AT UNGULATE CARCASSES IN SOUTHWESTERN MONTANA

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Key words: behavioral interaction, Canis latrans, Canis lupus, *carcass, confrontation, coyote, scavenge, wolf.*

Wolf (*Canis lupus*) recolonization of the Greater Yellowstone Ecosystem (GYE) provides an excellent opportunity to document competitive interactions between sympatric canids. To date, information regarding interactions between wolves and coyotes (*Canis latrans*) has been primarily descriptions of partitioned space use (Paquet 1991), extent of dietary overlap (Paquet 1992, Arjo 1998, Arjo and Pletscher 1999), adverse effects on coyote survival and demography (Crabtree 1998), and influences on coyote foraging patterns (Switalski 2003). The results of competitive interactions between coyotes and wolves may be ambiguous, particularly in areas where coyotes have become habituated to the presence of wolves. Although wolves may kill coyotes, they also provide significant scavenging opportunities by killing large prey not directly vulnerable to coyotes (Fuller and Keith 1981, Paquet 1991, Wilmers et al. 2003). These kill sites are likely focal areas for competitive interactions and provide an opportunity to elucidate factors that mediate the outcome of resource partitioning between coyotes and wolves. However, to date, no observations of prolonged interactions between these canids have been published.

From March 2004 through February 2005, I observed behavioral interactions between wolves (Bear Trap pack) and coyotes (n = 5 packs) at elk (*Cervus elaphus*), bison (*Bison bison*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*Odocoileus virginianus*) carcasses in the upper Madison Range, southwestern Montana (45°47′N, 111°9′W). Using a 15–45X spotting scope, I conducted all-occurrence sampling (Lehner 1996) to collect 62 hours (in 8 separate periods) of data on interactions between coyotes and wolves. An observation period was the time during which I observed an individual ungulate carcass (n = 8) being exploited by coyotes and wolves. Thus, an observation period began when I located a carcass and terminated when the carcass was abandoned by wolves and coyotes. A confrontation (≥1 individual displaying aggressive behavior) was defined as a discrete aggressive behavioral interaction. Successive confrontations were not always independent; that is, serial discrete confrontation behaviors often were nested within a prolonged interaction dynamic during an observation period. Coyote group sizes ranged from 1 to 6 adults and wolf group size ranged from 1 to 6 adults and pups. Social status and sex of coyotes and wolves had been determined prior to the observations. All wolf pups observed were >6 months old.

Coyotes exploited carcasses in numerically superior numbers (n = 4 packs; group size range 2–6 adults) relative to wolves during 6 out of 8 (75%) observation periods (Table 1). During the 6 observation periods, alpha coyotes were always present and alphas and subordinates (betas and pack associates; present during 5 of the 6 periods) were able to feed at carcasses between wolf feeding bouts (Table 1). Numerically superior coyotes were able to maintain exclusive access to a carcass during 1 (12.5%) observation period (21 December 2004) when adult wolves were present and during 2 periods (25%; 17 January 2005 and 19 February 2005) when a wolf pup was present (Table 1). During the 1st period, 3 wolves (alpha pair and pup) observed the coyotes feeding at the carcass but did not attempt to feed (Table 1).

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TABLE 1. Observation period, group composition and sizes, carcass type, canid with primary carcass access, and hours spent observing coyote-wolf interactions at ungulate carcasses in southwestern Montana, March 2004–February 2005.

Date	Coyote pack	Coyote group		Wolf group		Carcass type	Carcass access[a]	Observed feeding	Hours observed
		Size	Composition	Size	Composition				
16 Mar 04	Little Lamar	5	alpha pair 3 subordinates	6	alpha pair 2 subordinates 2 pups	white-tailed deer	wolf	all wolves	7
23 Jun 04	Carpenter Creek	6	alpha pair 4 subordinates	1	alpha male	elk	wolf and coyotes[b]	all coyotes alpha wolf	8
25 Jun 04	Little Lamar	5	alpha pair 3 subordinates	1	alpha male	elk	wolf and coyotes[b]	all coyotes alpha wolf	9
28 Jun 04	Cow Camp	2	alpha pair	1	alpha male	elk	wolf and coyotes[b]	coyote pair alpha wolf	8
21 Aug 04	East Fork	1	alpha male	3	alpha pair 1 pup	bison	wolf	all wolves	4
21 Dec 04	Carpenter Creek	6	alpha pair 4 subordinates	3	alpha pair 1 pup	white-tailed deer	coyote	all coyotes	6
17 Jan 05	Little Lamar	4	alpha pair 2 subordinates	1	pup	bison	coyote	all coyotes	9
19 Feb 05	East Fork	3	alpha pair 1 subordinate	1	pup	mule deer	coyote	all coyotes wolf pup[c]	5

[a]Carcass access refers to the species able to maintain primary access to the carcass (i.e., the ability to feed at will).
[b]Coyotes attempted to evict the alpha male wolf from the carcasses but were unsuccessful (i.e., the wolf fed at will).
[c]The wolf pup fed after the coyotes abandoned the carcass.

In the latter 2 periods, a wolf pup remained bedded in dense aspen (*Populus tremuloides*) and mountain big sage (*Artemisia tridentata vaseyana*), respectively, while coyotes fed (Table 1). During 3 (37.5%) observation periods (23 June 2004, 25 June 2004, and 28 June 2004), numerically superior coyote packs were able to exploit elk carcasses in the presence of an alpha male wolf (Table 1) by partitioning access temporally. During these 3 periods, coyotes fed only after the wolf had finished and moved 20–50 m away to bed. Thus, coyotes always fed within view of the wolf, but did not attempt to feed while the wolf was feeding.

In the presence of coyotes, wolves (group size range 1–6 individuals) fed at will at carcasses during 5 of 8 (62%) observation periods (Table 1). During 1 observation period (21 August 2004), 3 wolves fed at a bison carcass while an alpha male coyote approached to within 200 m of the carcass and bedded (Table 1). The single coyote did not feed until the wolves had abandoned the carcass and moved 800 m into dense timber. During another observation period (16 March 2004), 6 wolves (2 pups and 4 adults, including the alpha pair) monopolized a white-tailed deer carcass, and a pack of 5 adult coyotes did not attempt to feed until the wolves had abandoned the carcass (Table 1).

During 3 observation periods (23 June 2004, 25 June 2004, and 28 June 2004), I observed 39 confrontations (involving 8 different coyotes and 4 different wolves) between groups of 1–6 coyotes and single adult wolves (Table 2). Thirty-three (85%) of the confrontations were initiated by coyotes: 11 led by alpha females (Carpenter Creek and Little Lamar packs), 6 led by alpha males (Carpenter Creek and Cow Camp packs), 10 led by a beta female (Little Lamar pack), and 6 led by other subordinates (Carpenter Creek, Little Lamar, and Cow Camp packs; Table 2). Sixty-seven percent of the coyote-initiated confrontations involved groups of ≥3 coyotes, and 22% involved groups of 2; a single coyote was involved in 11% of the confrontations (Table 2). In all confrontations, aggressive coyotes were unsuccessful in displacing wolves from carcasses. In 6 (15% of total) confrontations, the alpha male wolf initiated aggressive behavior directed at an alpha female coyote (25 June 2004, Little Lamar pack) resulting in modest retreats of 5–15 m by the coyote. The aggression appeared to result from

TABLE 2. Characteristics, behaviors, and outcomes of behavioral interaction between coyotes and wolves at ungulate carcasses in southwest Montana, March 2004–February 2005.

Date	Coyote pack	Coyote group		Wolf group		No. of confrontations	Mean duration (min)	Coyote behavior	Wolf behavior
		Size	Aggressor status	Size	Social status				
23 Jun 04	Carpenter Creek	2	alpha female	1	alpha male	2	6.0	barking	no response
		2	alpha male	1	subordinate male	2	3.0	barking	no response
		5	subordinate female	1	alpha male	2	1.1	barking	no response
25 Jun 04	Little Lamar	5	alpha female	1	alpha male	4	8.5	barking	no response
						3	0.2	nipping	chased coyote
		1	alpha female	1	subordinate male	2	3.0	barking	no response
		5	beta female	1	alpha male	7	3.3	barking	no response
						3	0.1	nipping	chased coyote
		6	subordinate	1	alpha male	3	3.1	barking	no response
28 Jun 04	Cow Camp	5	alpha male	1	alpha female	4	4.0	barking	no response
		4	subordinate	1	alpha male	1	40.8[a]	barking	no response

[a]Note that this datum is from a single observation and is not a mean value.

the alpha female approaching too close to the wolf while it was bedded with food.

Switalski (2003) observed wolves chasing coyotes away from carcasses in Yellowstone National Park but did not comment on group size or social status of individual competitors, both of which may be important factors mediating the outcome of interspecific interactions. In 6 of the observation periods, numerically superior packs of coyotes attempted, and were successful in maintaining, access to carcasses in the presence of numerically inferior groups of wolves. When wolf group size was equal to or greater than coyote group size, wolves were able to monopolize carcasses and coyotes did not attempt to feed until wolves had abandoned or moved substantial distances (>800 m) from the carcass. Although coyotes were unsuccessful in maintaining exclusive access to carcasses (i.e., wolves fed at will) during all but 3 observation periods (21 December 2004, 17 January 2005, and 19 February 2005), the coyotes were not summarily evicted by wolves from the immediate vicinity. In the 2 observation periods during which wolves completely monopolized carcasses (16 March 2004 and 21 August 2004), they were the first to feed and thus had access to muscle and organ tissues. As suggested by Wilmers et al. (2003), wolves may place a temporally declining value on a carcass because it is highly valued initially for the large muscle and organ tissues. Accordingly, wolves may be more aggressive in defending and maintaining exclusive access to more valued resources. Carcass value may degrade once these resources are depleted, and wolves must then weigh the cost of staying to defend a carcass of marginal value against the benefit of abandoning it to acquire a new prey item. Greater carcass value, combined with wolf numerical superiority, may result in a more vigorous defense of such carcasses, thereby inhibiting coyote exploitation of the resource until abandonment by wolves.

For coyotes to benefit from scavenging subsidies from larger predators, they must maximize the benefits of exploiting the prey item while minimizing the costs of gaining access. Predation on ungulates by coyotes involves considerable risk of injury, and success rates are usually low (Paquet 1992). Therefore, it is advantageous for coyotes to scavenge wolf-killed prey, provided they can manage the risk posed by wolves. In my estimation, the coyote packs were not naive to the potential danger posed by wolves. A pup from one of the interacting packs (East Fork pack; pack size = 4 adults) was killed by wolves in fall 2003, as was a beta female coyote (observed on 25 June 2004 harassing the alpha male wolf; Table 2) from an adjacent pack (Little Lamar pack; pack size = 5 adults). These 2 coyote packs occupied territories having high wolf activity and were observed avoiding wolf-killed carcasses when the complete wolf pack (6 adults) was present. Coyotes, like wolves, may be more vigorous in attempts at usurping carcasses when valued muscle and organ tissues are present. Coyotes having prior experience with wolves may exploit carcasses in larger groups to maintain access and manage risk while scavenging.

The confrontation behavior exhibited by coyotes was primarily initiated by dominant animals and may have been in response to a perceived threat to themselves or packmates, either via interspecific killing (Palomares and Caro 1999) or loss of the carcass as a food source. Gese et al. (1996) noted that alpha coyotes were able to maintain higher carcass access rates than subordinates and, as a result, may be more experienced in predator detection or deterring kleptoparasitism at carcasses. The aggressive behavior coyotes directed towards single wolves may have been attempts to usurp carcasses. Attempts at usurpation failed when the single wolf was an alpha, but were successful when the wolf was a pup. The observation that coyotes attempted to usurp carcasses from alphas and pups may suggest that social status of the wolves was not of primary importance in risk assessment by coyotes. Rather, I believe that numeric superiority may mediate coyote risk-taking behavior at carcasses. However, the behaviors I report represent too small a data set to extend observation to inference, and I view these data as helpful in identifying variables to consider in attempts to understand a complex dynamic process. Further attempts to elucidate these interactions likely will be important in understanding how competition influences canid community structure.

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