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Coyotes and recolonizing wolves: social rank mediates risk-conditional behaviour at ungulate carcasses

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Wolf, *Canis lupus*, recolonization of the Greater Yellowstone Ecosystem provides a rare opportunity to identify behaviours facilitating coexistence between sympatric canids. We investigated interactions between coyotes, *Canis latrans*, and recolonizing wolves at ungulate carcasses in Montana's Madison Range. We used a field-experimental study design consisting of a two-level carcass treatment (wolf presence, wolf absence) to assess factors influencing coyote risk assessment, carrion consumption and aggressive encounters with wolves. Socially dominant coyotes (alphas and betas) responded to wolf presence by increasing the proportion of time spent vigilant while scavenging. Vigilance behaviour was more pronounced when scavenging closer to structurally complex vegetation where lateral occlusion inhibited the ability of coyotes to scan for, and possibly escape from, returning wolves. Despite greater time spent vigilant, alpha coyotes consumed the greatest amount of carrion biomass by feeding on carcasses in earlier stages of consumption when organs and large muscle tissues were still present. This finding suggests that alpha coyotes might trade off greater risk for higher-quality food items. Coyotes would aggressively confront wolves: numerical advantage by coyotes and the stage of carcass consumption were influential in determining whether coyotes were able to displace wolves from carcasses. Coyotes relied on a gradient of risk-sensitive behaviours, ranging from elevated vigilance to aggressive confrontation, to manage risk associated with wolf presence. Identification of these behaviours, and their sensitivity to numeric and social factors, is an important step in elucidating mechanisms of resource partitioning in social canids.

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In carnivores, asymmetric competition can affect the subordinate competitor by limiting spatial distributions (Fuller & Keith 1981), constraining habitat selection (Mills & Gorman 1997), reducing prey encounter rates (Palomares et al. 1996), reducing food intake or requiring increased hunting effort (Gorman et al. 1998), and increasing mortality rates (Palomares & Caro 1999). While the above effects are mostly well understood, there is a paucity of data describing the mechanistic details. Indeed, it remains difficult to identify behaviours that mediate asymmetry in interactions because when competitors have been sympatric over long periods of time, mechanisms may be subtle

(Abramsky et al. 1986) and facilitating behaviours may be undetectable. For example, risk of being killed by a recolonizing dominant competitor (e.g. interspecific killing: Palomares & Caro 1999) should be greatest, and most detectable, during initial interactions. However, over subsequent interactions, a subordinate competitor should accrue knowledge of the threat posed by a dominant competitor and optimize behaviour to mitigate risk (e.g. spatial avoidance: Creel et al. 2001). Ideally then, investigations into mechanisms of resource partitioning are particularly suited to systems where competitive interactions can be observed along a naïve–savvy continuum (Berger et al. 2001) in the subordinate competitor. Fortunately, wolf, *Canis lupus*, recolonization of the Greater Yellowstone Ecosystem (GYE), U.S.A., has provided a rare opportunity to identify mechanisms of resource partitioning with presumably naïve coyotes, *Canis latrans*.

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In most cases, coyotes and wolves do not engage in contest competition for live prey (Paquet 1992; Arjo & Pletscher 1999), but rather compete for access to carcasses (Fuller & Keith 1981; Paquet 1992; Wilmers et al. 2003). Accordingly, prey kill sites should be focal areas of intense competition, and the energetic costs and benefits of maintaining or gaining access should impel behaviours that mediate the outcome of competitive interactions. For example, large carnivores can expend considerable energy while hunting (e.g. ≥25 times the basal metabolic rate, BMR; Gorman et al. 1998), and should be highly motivated to maintain primacy in carcass access until the energetic deficit incurred from catching and killing prey has been overcome (Caro 1994; Gorman et al. 1998). Accordingly, we would expect wolves to vigorously defend against kleptoparasitism until the marginal benefit of remaining at a prey carcass decreases with respect to future energetic gains. Several factors can affect the perceived marginal value of a carcass, including the presence of other prey items (Ballard 1982), loss of biomass to scavengers (Vucetich et al. 2004), or risk of attack from competitors (Creel et al. 2001). Logically, then, carcasses should have a temporally declining value to wolves; as value declines, wolves should be less likely to mount a vigorous defence against kleptoparasitism. For coyotes, scavenging wolf-killed prey carries substantial risk of injury or death (Paquet 1992), and the net benefit realized largely depends on energy expended in managing risk. Thus, coyotes should, over time, perceive gradations of less vigorous carcass defence by wolves and become more aggressive in attempts at usurpation when defence begins to wane. Clearly, if coyotes are able to perceive and take advantage of temporal declines in risk, it would represent a behaviour crucial in facilitating coexistence with wolves, and illustrate the importance of risk assessment in mediating asymmetric interactions between canids.

Evidence suggests that general threat-alleviating behaviours, including increased vigilance (Lima 1987a), reduced foraging time (Hughes & Ward 1993; Abramsky et al. 2002), changes in group size or configuration (Creel & Winnie 2005), preemptive aggression (Bertram 1978; Gese 1999) and retreat to refuge habitats (Formanowicz & Bobka 1988; Blumstein & Daniel 2002), either independently or interactively, may prove crucial in mediating interspecific interactions in social carnivores. For example, in asymmetrically subordinate canids, numeric superiority apparently facilitates detection of encroaching competitors (Eaton 1979), mediates the duration over which a kill is retained under threat of kleptoparasitism (Fanshawe & FitzGibbon 1993; Creel & Creel 1996) and influences the willingness to aggregate and mob intruding allospecifics (Cooper 1991; Creel et al. 2001). Furthermore, because the social status of competitors can significantly influence the outcome of intraspecific interactions (Gese 2001), social status may interact with other behaviours to influence the outcome of interspecific interactions. Mechanisms of risk-conditional behaviour between asymmetric competitors remain a relatively unexplored facet of sympatry.

We investigated behavioural interactions between coyotes and wolves to determine the mechanisms and costs of risk assessment and mitigation by coyotes while scavenging wolf-killed prey. Three a priori predictions were made concerning the effect of ecological and social variables on vigilance behaviour and energy intake rate. First, we predicted that coyote social status and wolf presence would interact to elevate vigilance rates; socially dominant coyotes should be more vigilant when scavenging wolf-killed carcasses. In many social species, dominance hierarchies will affect foraging behaviour of individuals. For example, subordinate individuals may be forced to trade off foraging with vigilance behaviour and suffer reduced energy intake (Rands et al. 2006). However, dominant coyotes typically are the social class that aggressively responds to intruding conspecifics (Gese 2001), and we predicted that they would display the same behaviour in response to allospecifics. Second, we sought to determine whether there was an energetic cost to risk-sensitive coyotes. We predicted that, when scavenging wolf-killed prey, increased vigilance would result in diminished carrion consumption by coyotes regardless of social class. Finally, we predicted that numerical advantage would be a critical factor in determining whether coyotes were able to gain access to carcasses by displacing wolves. We believe that directly observing interacting coyotes and wolves provides a rare opportunity to elucidate mechanisms of risk assessment, which may prove important in understanding how sympatric canids partition resources.

METHODS

Study Site and Animals

The study took place in the Northern Madison Study Area (NMSA; 680 km^2), located in southwest Montana's Madison Range of the Rocky Mountains, U.S.A., from December through May of 2003–2005. The NMSA is approximately 50 km northwest of Yellowstone National Park, and is bordered on the east by the Gallatin River, on the west by the Madison River, and on the south by the Spanish Peaks of the Gallatin National Forest. Shrub/steppe habitat (535 km^2) dominates valleys and benches on the NMSA; coniferous forest (145 km^2) makes up approximately 23% of the remaining area. Elevations range from 2500 m in the Spanish Peaks to 1300 m on the Madison River floodplain, and mediate an ecological gradient varying from dry grassland/juniper, *Juniperus scopulorum*, savannah at lower elevations to closed canopy Douglas fir, *Pseudotsuga menziesii*, or lodgepole pine, *Pinus contorta*, forests on moist sites at higher elevations. High elevation dry sites occur on southern exposures and ridgelines, and are predominantly mountain big sage, *Artemisia tridentada vaseyana*/grassland mosaics. Temperatures range from highs of 21–32°C in summer to lows of −34°C in winter.

A single wolf pack (Bear Trap pack) composed of two adults and two yearlings recolonized the NMSA in the winter of 2003. The Bear Trap pack represented the recolonizing front in the Madison Range and, based on yearly ground and aerial surveys beginning in 2000, were the first wolves known to occur on the NMSA (V. Asher, Turner Endangered Species Fund, personal observation). Annual wolf pack size ranged from two to eight individuals (0.003–0.011 wolves/km^2), one of which (yearling

female) was radiocollared and subsequently dispersed. Over the duration of the study, the Bear Trap pack averaged five individuals, and the same alpha male and female were present throughout the study. We captured and radiocollared coyotes using foothold traps and aerial netgunning. Coyotes were distributed over the entire NMSA (0.19–0.25 coyotes/km^2) and resided in multigenerational packs. Prewhelping pack size was four adults, and average litter size was six pups. Coyotes were subjected to hunting, and we estimated that approximately 20% of the coyote population was killed annually. Ungulate numbers varied slightly during the study. After the arrival of wolves, abundance of elk, *Cervus elaphus* ($\overline{X}_{2003-2005} \pm SE = 2416 \pm 423$) increased 5% in 2003, declined 24% in 2004, and increased 33% in 2005. Declining elk abundance in 2004 was attributed to a large herd (ca. 550–650 animals) temporarily leaving the study area (Atwood et al. 2007). Abundance of mule deer, *Odocoileus hemionus* ($\overline{X}_{2003-2005} \pm SE = 425 \pm 133$) increased by an average of 16% over the duration of our research.

Procedures

We used a field-experimental design consisting of two treatment levels: (1) wolf presence, wolves fed on wolf-killed or manually placed carcasses and (2) wolf absence (control), no evidence was detected that wolves visited manually placed carcasses. Manually placed carcasses were road-killed ungulates that were collected opportunistically and stored in a freezer truck, then thawed to ambient temperature before placement on the study site. We relied on guidance from a logistic regression model of NMSA wolf-kill site characteristics (Atwood et al. 2007) to ensure that road-killed ungulate carcasses were placed in habitat and physiographical associations representative of where wolf-killed ungulates were found. Although we were not able to randomize the 'wolf presence' treatment, we were able to randomize the control treatment; all coyote packs observed were exposed to both treatment levels at least once (mean interval between successive treatment/ control periods for an individual and a pack was 67 days). The NMSA was privately owned, and wolves were not harassed by humans. As a result, wolves were readily observable during diurnal feeding bouts. We did not monitor carcasses during potential nocturnal feeding bouts, but visited manually placed carcasses daily to detect evidence (e.g. scat, tracks and broken long bones) of wolf visits. When a wolf visit was detected, we reclassified manually placed carcasses as 'wolf presence' treatments beginning when the wolf visit was first detected and lasting the duration of carcass exploitation. We used all-occurrence sampling (sensu Lehner 1996) to gather behavioural data on coyotes and wolves at carcasses using 15–45× spotting scopes. Each observation session included associated measures of the proportion of time that coyotes spent vigilant while scavenging, feeding bout duration, stage of carcass consumption, scavenger social status, coyote and wolf group sizes, and distance to protective cover (measured via a range finder).

Observation sessions were continuous and occurred during daylight hours usually between 0700 and 2000 hours. For manually placed carcasses, observation sessions began the morning following carcass placement. For wolf-killed carcasses, observation sessions began immediately following carcass detection (see Atwood et al. 2007 for methods used to detect carcasses). Coyote social status was determined by generating dominance matrices (Gese et al. 1996) based on intraspecific interactions; only data from coyotes of known social status were used in subsequent analyses. Following Gese et al. (1996), social classes were defined as alphas (dominant, breeding adult males and females), betas (adults subordinate to alphas but dominant over yearlings and pups) and subordinates (yearlings and pups subordinate to both alphas and betas). Protective cover was defined as vegetation tall and dense enough to conceal an animal from view (Molvar & Bowyer 1994). Scavenging was defined as biting, tearing or chewing food with a lowered head. A coyote was considered vigilant when its head was raised and it was in an alert position (i.e. gaze steady and directed forward with erect ears and a semierect tail), or it was actively scanning (including neck movement) the environment. We omitted periods in which the scavenging behaviour of focal coyotes was interrupted by social interactions with packmates, elimination behaviour, or resting. The proportion of time spent vigilant by individual coyotes was summed over the period that a carcass was observed to determine a mean. To counteract the tendency of the variance to increase with shorter observation times, we excluded data from individuals observed fewer than 15 min. Observations were made of both marked (≥1 radiocollared individual per pack observed) and unmarked but identifiable (pelage coloration, pelage pattern and physical characteristics; Gese et al. 1996) coyotes. All observations were made by the same person (T.C.A.).

To determine whether there was a cost associated with elevated vigilance, we first needed to estimate the absolute amount of carrion biomass coyotes consumed while scavenging. Wilmers & Stahler (2002) estimated active consumption rates (ACR; ACR = g/min ingested × feeding bout duration) for captive coyotes feeding on ungulate carcasses, and found that rates differed based on the stage of consumption. On average, coyotes ingested carrion at a rate of 230 g/min when feeding on organs, entrails and major muscles; consumption rates dropped to 60 g/min when feeding on minor muscles, hide and stripping bones (Wilmers & Stahler 2002; Wilmers et al. 2003). At the beginning and end of each daily observation period, we approached carcasses close enough to estimate the stage of consumption. We then used stage-based ACR estimates of consumption provided in Wilmers & Stahler (2002) to determine the daily amount (g) of carrion biomass ingested by coyotes. Individual consumption amounts were summed over the period that a carcass was observed to determine a mean for each coyote. Mean absolute biomass (g) consumption was then used as a metric to estimate the energetic cost of vigilance behaviour.

Statistical Methods

We used generalized linear mixed models (GLMM) to characterize risk assessment and the energetic costs of

vigilance by scavenging coyotes. This method enables the fitting of random terms and therefore accounts for repeated sampling across error terms. In our study, we sampled some of the same individuals repeatedly and included individual identity and coyote pack as random factors in the models with first-order autocorrelation as a covariance structure. We used restricted maximum likelihood (REML) methods for model estimation and Satterthwaite's F tests to gauge effects (McCullagh & Nelder 1991). We first conducted analyses to determine whether coyote foraging time and biomass consumption differed when wolves fed upon wolf-killed or manually placed carcasses. For these analyses, we compared effects of carcass type fed upon by wolves (manually placed or wolf-killed), year, coyote social rank and carcass species. Subsequent analyses included effects of treatment type, coyote social rank, coyote group size, sex, foraging duration and distance from protective cover. In these latter analyses, treatment type consisted of two levels: control (i.e. wolves never visited a manually placed carcass) and wolf presence (i.e. wolves visited and fed at a manually placed or wolf-killed carcass). We tested all two-way interactions of fixed factors and made a posteriori pairwise comparisons using least squares means tests (Zar 1999).

We used Akaike's information criterion (AIC), adjusted for small sample sizes (AIC$_c$; Burnham & Anderson 2002), to choose the best models, starting with all fixed effects, covariates, random factors and interactions. Although all final models reported here refer to REML models, AIC$_c$ values were calculated from maximum likelihood models to make comparisons meaningful (Burnham & Anderson 2002). To induce homoscedasticity, vigilance data (proportion of time spent vigilant while foraging) were arcsine square-root transformed and biomass consumption data were natural logarithm transformed (Neter et al. 1996). To further guard against pseudoreplication, we examined vigilance data for serial correlation by plotting residuals against their lags (lag-1 autocorrelation: plotting e_i against $e_i - 1$), and calculating the correlation coefficient (r) (Zar 1999). Lag-1 autocorrelation approximates the true serial correlation of multiple observations taken from the same individual (Pyper & Peterman 1998).

To determine whether numeric superiority and/or stage of carcass consumption mediated the duration over which a kill was retained, we first needed to quantify the outcome of agonistic interactions. We defined a discrete agonistic interaction as the duration over which aggressive behaviours (e.g. bluff attack, biting, chasing, vocal harassment; Schenkel 1967) were used by coyotes and wolves with the intent of maintaining or usurping carcass access. Eviction of the competing species was equated with success. Success in agonistic interactions (S) of coyotes with group size j was then calculated using a modification of the equation proposed by Henderson & Hart (1995), where $S = (N$ interactions won by $j_{coyotes}/N$ interactions lost by $j_{coyotes}) \times (N$ wolves supplanted/$j_{coyotes}$). This equation takes both the proportion of interactions won and the proportion of individuals supplanted by a coyote group into account. Based on the group size success score (S_j), a rank number, from least to most successful, was assigned to each coyote group size (j). We

analysed whether consumption stage (stages I and II, organs, entrails and major muscles, or stages III and IV, minor muscles, hide, bone stripping; Wilmers et al. 2003) influenced the vigour of carcass defence by wolves using a Wilcoxon two-sample test (Zar 1999). We used chi-square analysis to determine whether success in carcass defence by wolves was independent of carcass source (i.e. wolf-killed or manually placed, road-killed carcass). Significance for all tests was set at an alpha of 0.05.

RESULTS

We observed 54 individual coyotes (12 packs; 23 collared, 31 uncollared) and six individual adult wolves (Bear Trap pack) of known social status for 1429 h at 93 ungulate carcasses. Sixty-one carcasses were observed throughout the duration of their availability, beginning either before (in the case of manually placed carcasses) or shortly after wolves or coyotes began feeding. Fifty-five per cent of the carcasses were white-tailed deer, *Odocoileus virginianus*, 35% were elk, 7% were bison, *Bison bison*, and 3% were mule deer. Forty-seven per cent of the carcasses were wolf kills; wolves fed upon an additional 15 manually placed carcasses. Carcasses fed upon by both wolves and coyotes lasted a mean $\pm$ SE of 78 ± 11.4 h, whereas those fed upon solely by coyotes lasted 91 ± 22.6 h. Carcasses also were fed upon by black bears, *Ursus americanus*, grizzly bears, *Ursus arctos*, golden eagles, *Aquila chrysaetos*, bald eagles, *Haliaeetus leucocephalus*, ravens, *Corvus corax*, and magpies, *Pica pica*. One collared adult coyote (beta female; winter 2004) and two uncollared pups (6−11 months old; winters of 2003 and 2005) were found killed by wolves; by comparison, three collared adults were killed by cougars, *Puma concolor*. All coyote mortalities attributed to interspecific killing occurred near ($\leq$200 m from carcass) sites of wolf- or cougar-killed prey. Portions of eight coyote pack territories (95% fixed kernel) and five pack core areas (60% fixed kernel) fell within areas characterized by intense wolf activity, and coyotes were not displaced from these areas throughout the duration of our research (Atwood 2006).

Vigilance

The proportion of time that coyotes spent vigilant (GLMM: $F_{1,107} = 0.81$, $P = 0.36$) and the amount of carrion biomass consumed ($F_{1,107} = 1.74$, $P = 0.10$) did not differ between years, carcass species, or whether carcasses that were fed upon by wolves were wolf kills or manually placed roadkill, so data were pooled for subsequent analyses. The most parsimonious GLMM model explaining coyote vigilance contained treatment (wolf presence or wolf absence; $F_{1,82.3} = 16.66$, $P = 0.0001$) at carcasses, the interaction between social rank and distance from cover ($F_{2,63.6} = 11.02$, $P = 0.001$), and the interaction between social rank and total foraging time ($F_{2,92} = 5.89$, $P = 0.02$; Table 1). Least square means tests indicated that the proportion of time spent vigilant by coyotes was greatest for alphas, but betas also responded to wolf presence by increasing vigilance. Compared to control

Table 1. Response variables, explanatory variables, model rank, AIC_c value and significant effects (restricted maximum likelihood models), with individual identity and coyote pack as random effects, for the top three generalized linear mixed models

Response	Fixed factors, covariates, interactions	Rank	AIC_c	Significant variables
Vigilance	Treatment, rank×cover, rank×forage time	1	98.6	All
	Treatment×rank, rank×cover, group size	2	104.7	Treatment×rank, rank×cover
	Treatment, rank, forage time, group size	3	114.3	Treatment, rank
Biomass consumption	Rank×forage time	1	218.9	Rank×forage time
	Treatment, rank×forage time	2	226.3	Rank×forage time
	Rank, treatment, cover, forage time	3	236.1	Rank, forage

treatments, alphas increased vigilance by 32% when scavenging carcasses that were visited by wolves ($\overline{X} \pm SE$ proportion of time spent vigilant: wolves present: 0.49 ± 0.03, $N = 18$ individuals; wolves absent: 0.37 ± 0.02, $N = 21$ individuals). For betas, vigilance increased by 48% when carcasses were visited by wolves (wolves present: 0.40 ± 0.03, $N = 8$ individuals; wolves absent: 0.27 ± 0.04, $N = 11$ individuals). When feeding at control carcasses, the proportion of time that dominant (alpha and beta) coyotes spent vigilant increased with increasing distance from protective cover (Fig. 1a, b), and dominants fed at carcasses for longer periods ($\overline{X} \pm SE = 10.38 \pm 1.02$ min, $N = 21$ individuals). At carcasses visited by wolves, the proportion of time that dominant coyotes spent vigilant increased with decreasing distance from cover (Fig. 2a, b), and dominants minimized feeding time ($\overline{X} \pm SE = 6.94 \pm 0.56$ min, $N = 18$ individuals). Subordinate coyotes showed no measurable response to wolf presence ($\overline{X} \pm SE$ proportion of time spent vigilant: wolves present: 0.25 ± 0.03, $N = 14$ individuals; wolves absent: 0.25 ± 0.01,

$N = 17$ individuals). Lag-1 autocorrelation of vigilance was low for all coyote social ranks (alpha: $r = 0.06$, $N = 26$ individuals; beta: $r = 0.01$, $N = 11$ individuals; subordinate: $r = 0.006$, $N = 17$ individuals).

Feeding Bouts and Biomass Consumed

Although socially dominant coyotes spent more time vigilant, they did not incur a cost in terms of diminished carrion consumption. A GLMM model containing only the interaction of social rank with total foraging time (rank × forage time: $F_{2,28.7} = 7.66$, $P = 0.0009$; Table 1) provided the most parsimonious explanation of biomass consumption. Unlike the top model of coyote vigilance, mean biomass consumption did not differ based on treatment type ($F_{1,84.2} = 0.37$, $P = 0.69$; Fig. 3) or distance from protective cover ($F_{1,67.2} = 0.01$, $P = 0.94$). At control carcasses, foraging bout durations of alphas were similar to those of betas and subordinates (Table 2), yet alphas
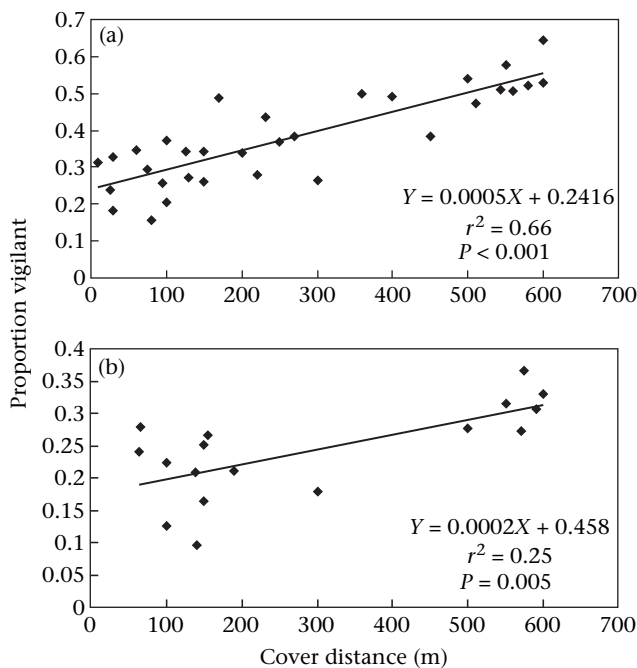

Figure 1. Proportion of time spent vigilant relative to distance from protective cover for (a) socially dominant (alphas and betas) coyotes scavenging control (wolves absent) carcasses and (b) socially subordinate coyotes scavenging control carcasses.
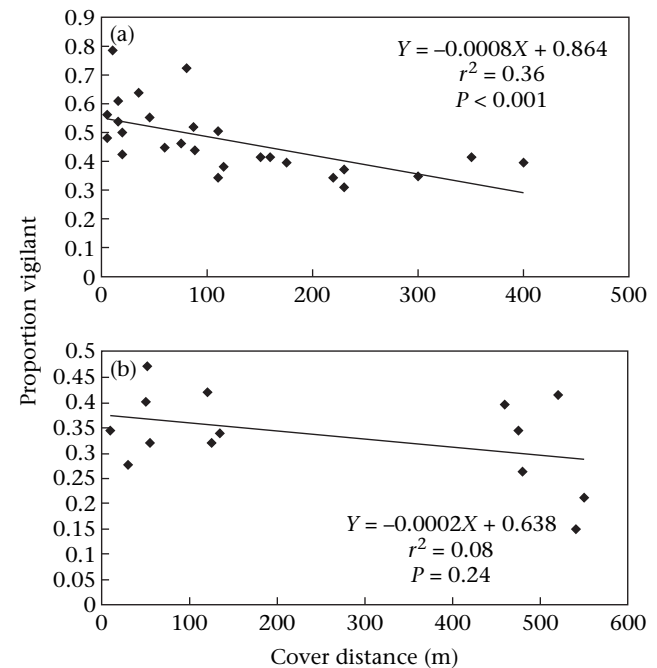

Figure 2. Proportion of time spent vigilant relative to distance from protective cover for (a) socially dominant (alphas and betas) coyotes scavenging wolf treatment carcasses and (b) socially subordinate coyotes scavenging wolf treatment carcasses.
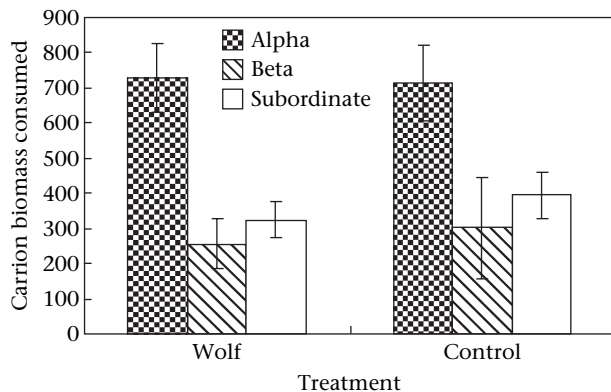
Figure 3. Mean ± SE absolute estimate (g) of carrion biomass consumed by alpha, beta and subordinate coyotes relative to carcass treatment level.

ingested substantially more carrion biomass (Fig. 3). In the presence of wolves, mean foraging time for alphas decreased by 16%, but absolute estimates of carrion consumption remained qualitatively similar ($\overline{X} \pm$ SE carrion consumed: wolf present: 729 ± 96 g, $N = 18$ individuals; wolf absent: 714 ± 108 g, $N = 21$ individuals; Fig. 3). In contrast, mean foraging time for betas dropped substantially in the presence of wolves, as did biomass consumption (Fig. 3). Interestingly, mean foraging time for subordinates increased at wolf-killed carcasses, whereas carrion consumption decreased by 18% (Fig. 3). Consumption was greater for alphas because they fed more frequently on carcasses during the initial stages of consumption (stages I and II, organs, entrails and major muscles: ACR = 230 g/min; Wilmers et al. 2003). For alphas, 64% of observations involved ingestion of organs, entrails and major muscles, compared to 27% for both betas and subordinates.

Agonistic Interactions

We observed 36 bouts of agonistic interactions involving six different coyote packs and the Bear Trap wolf pack (Table 3). At least one alpha coyote was present during 27 (75%) of the 36 bouts. Seventeen bouts (47%) ended with

Table 2. Feeding time, number of individuals observed and 95% confidence interval (CI) of scavenging alpha, beta and subordinate coyotes relative to ungulate carcass treatment level

Treatment	Social status	N	$\overline{X}$(SE)	95% CI
			Feeding time (min)	
Wolf presence	Alpha	18	4.12 (0.70)	2.75−5.49
	Beta	8	2.50 (1.10)	0.34−4.66
	Subordinate	14	5.02 (1.71)	1.67−8.37
Wolf absence (control)	Alpha	21	4.16 (0.50)	3.18−5.14
	Beta	11	5.01 (2.39)	0.33−9.69
	Subordinate	17	4.73 (0.95)	2.87−6.59

coyotes supplanting wolves from carcasses, all of which occurred during the last stages of carcass consumption (Wilcoxon two-sample test: $Z = 3.57$, $N = 36$, $P = 0.0002$; stages III and IV, ingestion of minor muscles, hide and bone stripping; Wilmers et al. 2003). Both alpha coyotes were present in 16 (44%) of the 17 bouts where wolves were supplanted, and coyote group size (range 2−6 adults) was numerically superior to wolf group size (range 1−3 adults) in those 16 bouts. Thirteen bouts involved groups of two to six coyotes supplanting the alpha male wolf, and three bouts involved groups of two to four coyotes supplanting one to two yearling wolves. However, whether the contested carcass was a wolf-kill was critical to the likelihood of coyotes supplanting wolves: based on chi-square analysis and the corresponding odds ratio, coyotes were 5.3 times less likely to supplant wolves from wolf-killed carcasses ($\chi_1^2 = 5.39$, $P = 0.02$).

DISCUSSION

Our study revealed four novel observations of how coyotes on our site responded to wolf recolonization. We first showed that coyotes assessed risk when scavenging carcasses. Coyotes displayed risk-sensitive foraging behaviour by increasing the proportion of time spent vigilant when wolf presence was detected. Second, responsibility for risk assessment and carcass defence fell most heavily on socially dominant coyotes. Alpha coyotes were always more vigilant than betas and subordinates, and alphas and betas substantially elevated vigilance when wolf presence was detectable. Third, heightened vigilance in alpha coyotes did not adversely affect the amount of carrion biomass consumed. Alpha coyotes consumed more carrion biomass than betas and subordinates regardless of treatment level. Finally, coyotes would aggressively confront wolves to gain or maintain carcass access.

Vigilance of scavenging coyotes was sensitive to effects of social status, treatment level and distance from vegetative cover. Socially dominant coyotes (alphas and betas) responded to wolf presence by increasing the proportion of time spent vigilant; alphas were substantially more vigilant (22% higher, on average) than betas. There are two plausible scenarios for this hierarchical-dependent vigilance: (1) within a pack, vigilance may mediate social competition (Rands et al. 2006), and/or (2) vigilance may ameliorate negative interactions within and between adjacent packs. In the latter, heightened vigilance in dominants may reflect intimidation behaviour associated with intrapack dynamics. That is, alphas, and to a lesser degree betas, may spend a greater proportion of time vigilant to monitor the behaviours and to constrain feeding attempts of subordinate pack members. Indeed, Gese et al. (1996) found that alpha and beta coyotes in Yellowstone National Park (pre-wolf reintroduction) had the greatest access to carcasses and, similar to our study, fed first while subordinates waited. Once dominant individuals were sated, the subordinates fed. Under this intrapack hierarchy construct, subordinates should not elevate vigilance unless they are trying to cheat, by feeding at carcasses when dominant individuals are absent. Thus, it seems

Table 3. Summary of interacting coyote and wolf group sizes, number of aggressive confrontations, carcass condition, and their relevance to postconfrontation carcass primacy

Preconfrontation carcass primacy*	Postconfrontation carcass primacy	Group size difference (coyotes−wolves)	Number of confrontations†	Stage of carcass consumption‡
Coyote	Coyote	1	4	III−IV
		4	1	III−IV
Coyote	Wolf	−1	3	III−IV
Wolf	Wolf	0	1	III−IV
		1	2	I−II
		2	2	I−II
		−1	7	I−II
		−2	4	I−II
Wolf	Coyote	1	4	III−IV
		3	1	III−IV
		4	5	III−IV
		5	2	III−IV

*Carcass primacy refers to the species that had singular access to the carcass.
†Confrontations were defined as discrete aggressive interactions between coyotes and wolves ending when access to a carcass was either retained by a defender or ceded to a challenger.
‡Stages I and II include consumption of organs, entrails and major muscles; stages III and IV include consumption of minor muscles and hide.

logical that hierarchical-dependent vigilance may also be a potent behaviour for mitigating conflict with other competitors, given its effectiveness in ameliorating intrapack competition. In this case, vigilance would not be used to intimidate, but to gather nuanced information essential to assessing risk, such as postures, speed of approach and competitor group size.

Coyote social status interacted with distance from complex vegetative cover to influence the proportion of time spent vigilant. Several studies have documented changes in the allocation of time to vigilance under varying amounts of cover. Evidence generally supports the notion that animals spend more time alert when foraging away from shrub or tree cover (Barnard 1980; Leger et al. 1983; Cassini 1991; Otter 1994; Tchabovsky et al. 2001). However, the nexus between vegetative cover and vigilance is probably far from simple; cover that provides concealment can also obstruct vision and hinder escape (Lima 1987b; Lima & Dill 1990; Schooley et al. 1996; Sharpe & Van Horne 1998; Blumstein et al. 2004). In addition, differences in forager behaviour may further complicate the relationship between cover and vigilance. For example, the dispersion of data points in Figs 1a, b and 2a, b reflected differences in feeding behaviours between dominant and subordinate coyotes. Dominant coyotes fed more frequently on carcasses during the initial stages of consumption and often tore off large food items, then moved short distances away before consuming them. Subordinates, on the other hand, fed more frequently on carcasses during the final stages of consumption and were often relegated to stripping flesh from bone. As a result, subordinates usually consumed these small food items without leaving the carcass. We found evidence that dominant coyotes spent more time vigilant when scavenging near shrub cover than when foraging away from cover. Presumably, this occurs because lateral occlusion by shrub cover interferes with the ability of coyotes to scan the environment, which is necessary when scavenging prey recently killed by wolves.

The level of risk perceived has been found to influence the decision of whether animals should flee (Ydenberg & Dill 1986; Lima & Dill 1990) or retaliate (Geist et al. 2005). If our ability to extend inference to observations was restricted to vigilance behaviour, then we might have arrived at the specious conclusion that elevated vigilance was a generalized strategy used by NMSA coyotes regardless of threat level perceived. In fact, when vigilance behaviour is viewed in concert with observations of agonistic interactions with wolves, it becomes apparent that heightened vigilance is simply a first-order response to the likelihood of a threat. In other words, increased vigilance represents an attempt to preempt a threat; as coyotes perceive escalations in wolf threat-level (e.g. detection of past or immediate physical presence), they use commensurate mitigating behaviours. In this sense, vigilance is properly placed at one end of a continuum of behaviours that coyotes rely on when managing a gradient of risk associated with wolves. At the opposite end of this continuum is aggressive confrontation (Geist et al. 2005). These divergent risk-sensitive behaviours might reflect discrepant levels of fearfulness (Stankowich & Blumstein 2005) influenced by experience with an aggressor (i.e. knowledge of the attack behaviour), and/or by characteristics of interacting agents (e.g. differences in group size or social status).

Perhaps the most unexpected finding of our study was that coyotes would, on occasion, aggressively confront wolves in attempts to gain or maintain access to carcasses. Coyotes confronting wolves as a response to escalating risk would seem paradoxical. Rather than fleeing, preemptively engaging a putative aggressor would seem to further escalate the likelihood of injury. However after analysing interactions with wolves, it becomes apparent that coyotes' decisions to confront competitors are partially informed by knowledge that differences in social status and/or group size can exacerbate or ameliorate risk. In the confrontation bouts where coyotes successfully displaced wolves from carcasses, both alpha coyotes were

present, coyotes were numerically superior to wolves, and no injuries were sustained. Numeric superiority has been found to be a primary determinant in the outcome of interspecific interactions for African social carnivores (Cooper 1991; Fanshawe & FitzGibbon 1993; Creel et al. 2001), and Gese (2001) found that competitor social status significantly affected the outcome of intraspecific interactions in coyotes. Thus, it is not surprising to find coyotes relying on both factors to assess risk and guide decision-making when interacting with wolves. The extent to which numeric superiority and the presence of dominant individuals is influential in coyotes displacing wolves from carcasses is likely to depend on how invested wolves are in maintaining primacy.

The stage of carcass consumption probably mediates the vigour with which wolves defend against kleptoparasitism (Wilmers et al. 2003; Vucetich et al. 2004) and may also influence the level of risk that coyotes will tolerate. Our prediction that elevated vigilance in dominant coyotes would depress carrion consumption rates was incorrect. In fact, alpha coyotes consumed substantially more carrion biomass than other social classes, despite similar feeding bout durations. This occurred because alpha coyotes engaged in riskier behaviour by more frequently scavenging carcasses in the early stages of consumption (stages I and II), whereas betas and subordinates primarily fed on carcasses in the latter stages of consumption (stages III and IV). Carcasses in the early stages of consumption should be vigorously defended by wolves; as the carrion resource depreciates, wolves invest less energy in defence, and risk to scavenging coyotes should decline concomitantly. By exploiting carcasses in the early stages of wolf consumption, alpha coyotes appeared to trade greater risk for greater biomass consumption. However, by consuming greater biomass than betas and subordinates over feeding bouts of similar duration, and minimizing total time spent at carcasses visited by wolves (i.e. time spent foraging), alpha coyotes probably reduced their exposure to risk (Charnov 1976; Pyke et al. 1977). Whether betas and subordinates were minimizing time or maximizing energy was ambiguous and confounded by differences in vigilance behaviour; betas and subordinates spent more time feeding on carcasses in the later stages of consumption, but betas were substantially more vigilant than subordinates.

Vigour in defence of carcasses by wolves should also depend on density of local food resources. Several previous studies showed that interspecific killing among carnivores can be dependent on prey density (e.g. Palomares & Caro 1999). For example, Ballard (1982) showed that number of kills contested by wolves and brown bears was higher in areas of low prey density. Over the duration of our research, there was a net increase in prey (elk and mule deer) relative abundance (Atwood et al. 2007), which may have attenuated the vigour displayed by wolves in defending carcasses. While it is likely that NMSA wolves would defend carcasses more vigorously against coyotes during times of low prey density, our data do not allow us to explore that possibility.

It can be argued that wolf recolonization of the GYE has most affected how coyotes behave when exploiting carrion resources. Before to wolf recolonization of the NMSA, ungulate carrion availability was limited to cougar-killed prey, which can be hard to detect owing to caching, and to winter-kill or animals that succumbed to wounds sustained during the hunt season. In the case of the latter two, both were temporally discrete occurrences. The NMSA was privately owned and public access to hunters was tightly restricted to a 3-week cow elk hunt in December. Winter-kill generally occurred at the end of severe winters (late March/early April), and the extent of carrion available primarily depended on stochastic, climatic factors. It is worth noting that the few instances we detected of coyotes preying on adult ungulates occurred at the end of severe winters. Thus, where wolves have recolonized, the formerly ephemeral carrion resources have since become spatiotemporally constant (Wilmers et al. 2003) foci of substantial risk. In response to this change, coyotes appear to have developed trenchant behaviours of risk assessment when exploiting wolf-killed carrion. The mechanisms of risk assessment, such as stimuli indicating wolf presence (e.g. urine, scat, and actual presence), coyote social status and numerical advantage, mediate the behaviours that coyotes use in their attempts to maintain or usurp carcass access. Our study is the first to consider and confirm the interactive effect of group size and social status as influential in the outcome of competitive interactions in social canids. However, we caution that our findings reflect the responses of coyotes to activity associated with a single wolf pack and should not be generalized to coyote−wolf interactions at a broader scale without further study.

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