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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.

Keywords: agonism; *Canis latrans*; *Canis lupus*; resource partitioning; scavenging; social dominance

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. $\geq$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