



SPECIAL ISSUE: PREDATION

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Indirect Effects of Carnivores on Livestock Foraging Behavior and Production

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Introduction

Direct effects of predation (i.e., killing of animals) can result in significant economic losses to livestock producers. A recent publication by the USDA, Wildlife Services (2002) identified the following losses: (1) livestock losses attributed to predators, predominantly coyotes (*Canis latrans*), reach about \$71 million annually; (2) cattle and calf losses to predators in the United States totaled 147,000 head during 2000. A National Agricultural Statistics Service (NASS) study valued these losses at \$51.6 million; (3) sheep and lamb losses to predators in the United States totaled 273,000 in 1999. A NASS study valued these losses at \$16.5 million; (4) In Arizona, New Mexico, and Texas, the three major goat-producing states, 61,000 goats and kids were lost to predators in 1999. A NASS study valued these losses at \$3.4 million. Although direct losses of livestock due to depredation are often conspicuous and economically significant, they likely underestimate the total loss to producers because they do not consider indirect effects of carnivores as a result of livestock being exposed to the threat of predation without being killed.

Laundré et al. (2001) suggested that behavioral responses by prey species to impending predation might have more far-reaching consequences for ungulate behavioral ecology than the actual killing of individuals by predators. Potential negative, *indirect* impacts associated with the mere presence of predators include, but are not limited to, increased vigilance and reduced foraging efficiency by prey species, and being

forced by predators to forage in suboptimal habitats that contain lower quality or quantity of nutrients, and higher levels of toxins. Moreover, overuse of and lowered carrying capacity in suboptimal habitats could contribute to resource degradation (e.g., overgrazing in marginal habitats, increased erosion and sedimentation) and lower producer profits due to declines in livestock production (e.g., weight gain, body condition, lamb or calf crop). Thus, indirect impacts of predation may have negative impacts on the ecological integrity of the land, as well as negative impacts on personal, local, and regional economies that depend on livestock production. However, there is little or no published information that addresses indirect effects of carnivores on domestic ungulates.

The purpose of this paper is to discuss how the mere threat of predation might influence foraging efficiency and vigilance, diet and habitat selection, skin-gut responses, and social behavior in wild and domestic ungulate prey species. Because there is little or no published information on domestic ungulates concerning these subjects, we rely heavily on wild ungulate studies that have attempted to quantify or qualify the indirect effects of predation. Our aim is to use the wildlife literature as a springboard to stimulate discussion among producers, wildlife damage management professionals, and researchers regarding ways to quantify and address the indirect effects of carnivores on domestic ungulates. We first discuss the evidence from the wildlife literature that supports indirect effects of carnivores on wild ungulates, and then relate that evidence to its potential implications for domestic livestock foraging behavior and production.

Evidence From The Wildlife Literature

Foraging Efficiency and Vigilance

Foraging efficiency is generally higher in the absence of predators because ungulates are not hindered from selecting diets from habitats that contain high nutrient densities and low toxin levels (Laundré et al., 2001). Foraging in high-quality, predator-free habitats affords prey species the opportunity to exhibit maximum selectivity among nutritious plants and plant parts. Conversely, when herbivores sense or encounter predators, foraging efficiency may decrease due to increased vigilance and corresponding lower intake in high-quality habitats, increased energy expenditures caused by avoidance or escape maneuvers, or by being forced into lower-quality habitats where nutrients are less available and less digestible (Lima and Dill, 1990). Decreased animal production could result due to any of these scenarios.

Vigilance has been defined in previous studies as when an animal stands with its head raised while looking around, and is not lying, feeding, moving to another feeding spot, or engaged in a maintenance behavior like grooming or nursing (Hunter and Skinner, 1998; Laundré et al., 2001). Wild ungulates and other prey species increase vigilance while foraging in or near risky habitat (e.g., dense vegetation or water holes), while occupying more hazardous areas within a social group (e.g., group periphery), or while foraging during more hazardous times of the day (Underwood, 1982; Lagory, 1986; Scheel, 1993; Bednekoff and Ritter, 1994; Molvar and Bowyer, 1994). Predation risk and corresponding vigilance levels vary across space and time, with species of predator,

and with predator:prey ratios (Brown and Alkon, 1990; Brown, 1992, 1999; Brown et al., 1999; Gese and Knowlton, 2001; Kotler et al., 1994). Increased vigilance by prey species generally comes at the expense of lower foraging efficiency. For example, female elk (*Cervus elaphus*) with calves increased their vigilance rates from 20 to 48% in the presence of wolves, which meant they sacrificed nearly half their foraging effort (Laundré et al., 2001).

Diet and Habitat Selection

When predation risk is high, prey species may move to lower-quality foraging areas that have higher-security value (Brown, 1999), or may choose to occupy the periphery of a predator's territory that may be safer. This, in turn, may negatively influence a prey species' ability to preferentially select high-quality habitats and diets that meet their physiological and nutritional needs. Caribou (*Rangifer tarandus*) resided on Pic Island in Lake Superior to escape wolf (*Canis lupus*) predation on the mainland even though the mainland provided a higher quantity and quality of forage (Ferguson et al., 1988). Mech (1977) found higher densities and survival rates for white-tailed deer (*Odocoileus virginianus*) with home ranges located along the edge of wolf pack territories, suggesting that wolf predation was greater for deer whose home ranges significantly overlapped wolf territories. Mule deer (*Odocoileus hemionus*) subject to predation by mountain lions (*Puma concolor*) reduced use of patches where predation risk was high and increased use of similar quality food patches located in safer areas (Altendorf et al., 2001).

Predators directly affect prey numbers by killing offspring, but also indirectly influence production of female ungulates by altering their preferred diet and habitat selection patterns (Edwards, 1983). This is significant because adequate nutrition is widely recognized as a key component necessary for recruitment, especially for females that must consume adequate diets to conceive, carry a fetus to term, nurse and protect their offspring from predators until weaning. Female ungulates carrying fetuses or traveling with offspring at heel frequently sacrifice their own foraging efficiency to protect their progeny from predators. For example, female caribou dispersed into moun-

tainous areas giving up better quality forage in the lowlands, apparently to avoid wolves during the calving season (Bergerud et al., 1984). Similarly, pregnant bighorn ewes (*Ovis canadensis*) migrated from low-elevation winter range to high-elevation lambing areas before plant growth had commenced, ostensibly to avoid predation during lambing (Festa-Bianchet, 1988). Elk and bison (*Bison bison*) cows were more vigilant in areas with wolves than in wolf-free areas in Yellowstone National Park (Laundré et al., 2001). Lactating moose with active juveniles were more vigilant (i.e., spent less time foraging) than those with inactive young, and spent more time near protective cover than nonlactating cows when subjected to grizzly bear (*Ursus arctos*) and wolf predation (White and Berger, 2001).

Skin-Gut Defense System

In natural systems where predation plays a significant role, safe and unsafe areas of the landscape can rapidly change across space and time because predators move across the landscape in response to their prey (Lima, 2002). Nutrient and toxin contents of plants also change seasonally and across landscapes but at a much slower rate when compared to predation and other potential external threats. To cope with these challenges, animals have evolved the skin-gut defense system to protect themselves from risks in their foraging environment (Garcia and Holder, 1985; Garcia et al., 1985). The skin and gut defense systems are neurologically and physiologically interlinked but produce fundamentally different responses in animals (e.g., place aversions via skin defense versus flavor aversions via gut defense), and operate across dissimilar time scales ranging from seconds (skin defense) to hours (gut defense). The skin-defense system protects animals from danger in their external environment (e.g., predators, electric shock), while the gut-defense system mediates hazards associated with an animal's internal environment (e.g., over-ingestion of plant toxins or nutrients).

Social Group Responses

Some wild ungulate prey species form social groups in response to impending predation. The formation of social groups is believed to increase protection from predators by enhancing sensory capabilities, confusing the search

image of predators, increasing predator:prey ratios, and allowing herd members located within the group's core to dedicate more time to foraging and ruminating (Lagory, 1986; Benekoff and Ritter, 1994; Hunter and Skinner, 1998).

An oft-cited example of how ungulates cooperate socially to mitigate imminent predation is how musk ox (*Ovibos moschatus*) change herd conformation, density, and shape (i.e., perimeter size) in response to an imminent wolf attack (Miller and Gunn, 1984). Similarly, male bighorn sheep form a "musk ring" to protect the herd from carnivores (Shank, 1977). Mule deer form large cohesive groups and make a stand to fight off coyote attacks, as opposed to white-tailed deer that use their speed to outrun coyotes (Lingle, 2001). Risenhoover and Bailey (1985) reported that foraging efficiency of mountain sheep was positively related to group size, and that foraging groups of more than ten animals appeared to be a behavioral adaptation enabling sheep to use less secure habitats. Frid (1997) reported that Dall sheep (*Ovis dalli*) became less vigilant as group size increased, while California bighorn sheep groups consisting of five or less individuals had lower foraging efficiency than larger groups because of more interruptions to scan the environment, i.e., increased vigilance (Berger, 1978).

Some ungulates have been observed to form "nurseries" to cooperatively guard offspring while mother forages. For example, lactating Nubian ibexes (*Capra ibex*) selected richer feeding areas, spent more time feeding per day, and foraged further from escape cover when their young were cached in a "nursery" compared to lactating females with young at heel (Kohlmann et al., 1996). The establishment of nurseries apparently allowed lactating ibex to select and consume more nutritious diets while other herd members protected their young from predators.

Potential Implications for Domestic Livestock

Foraging Efficiency and Vigilance

Productivity of wild and domestic ungulates is largely a function of forage intake ($I = g/\text{minute}$ or kg/day), which has been characterized as the product of

bite rate (BR = bites/minute), bite size (BS = g/bite), and foraging time (FT = time foraging/day), i.e., $BR * BS * FT = I$ (Stuth, 1991). Ungulates increase, decrease, or maintain forage intake by adjusting any of these three variables in response to changing foraging conditions. Animals that consume more food in relation to energy expended traveling and searching for food are said to forage more efficiently, and typically gain more weight and produce more young than animals with lower intake levels and higher energy outputs (Osugi, 1974; Sevi et al., 1999).

The term "feeding station" describes when an ungulate stops walking, plants its two front feet, lowers its head, and bites a plant (Stuth, 1991). When forage quality is high (e.g., high levels of cell contents, low levels of cell wall and plant toxins), animals learn to select plants and plant parts that offer higher BS than what is available on average within the feeding station. Under these conditions, BR and FT may decrease because of the compensatory response of animals to select plants and plant parts that offer higher BS. On the other hand, when forage quality is low, animals may spend more time harvesting the forage within a feeding station, but less time searching for high-quality forage when walking between feeding stations. Under this scenario, BR may increase as animals try to compensate for lower BS and reduced FT because they require longer rumination times to digest low-quality diets.

As discussed earlier, wild ungulates increase vigilance when in the presence of predators at the expense of forage intake due to a reduction in BR, BS, FT, or all three of these factors. Predators may also force prey species to abandon high-quality habitat for lower-quality habitat, which can reduce ingestion of nutrients for the reasons described above (i.e., increased BR of lower quality forage to compensate for lower BS and FT). Moreover, when prey are forced by predators to utilize unfamiliar habitats in which they have little or no experience they may eat less, suffer more from malnutrition, and spend more time walking than animals foraging in familiar environments. All of these factors may weaken animals and further increase their risk to predation (Provenza and Balph, 1990). Domestic ungulates that

are restricted to smaller foraging areas due to the presence of predators could also overgraze and decrease forage and animal productivity. Any of these scenarios would have a negative impact on individual animal productivity in the short-term and overall profitability of livestock operations in the long-term.

Diet and Habitat Selection

Domestic ungulates learn to avoid or select foods on the basis of post-ingestive feedback (Howery et al., 1998a). Animals learn to ingest nutritious foods by associating a food's flavor (taste and smell) with its post-ingestive consequences (reviewed by Provenza et al., 1992; Provenza, 1995). If ingestion of a food is followed by satiety or nutritional benefit (or, internal malaise or illness), preference for the food increases (decreases) and the animal will seek (avoid) the food when it is encountered in the future. If toxicity of a food decreases (or, if its nutrient content increases), the food is no longer paired with negative feedback and intake may increase. Conversely, intake of a food may decrease when its toxicity increases or nutrient content decreases. Animals learn which foods to eat or avoid through constant sampling and updating flavor:post-ingestive associations of foods that change in toxin or nutrient content across space and time. Any change in liking of a food (typically quantified as a change in intake) is known as a "hedonic shift."

As with dietary preferences, animals develop habitat preferences as a result of prior experience. Bailey et al. (1996) proposed the concept of a "site value rating" where lower ratings or expectations are assigned to foraging habitats or sites that contain high levels of plant toxins. According to this model, domestic ungulates learn to rarely revisit sites that contain plants with high levels of toxins, or habitats associated with abiotic constraints that limit access to forage by domestic herbivores (e.g., distance from water, percent slope). Hence, Bailey et al.'s site value ratings in habitat selection are analogous to hedonic values assigned to foods in the parlance of conditioned flavor preferences or aversions (Provenza, 1995).

Although no field studies have been conducted to determine if site value ratings (or hedonic values) can be esti-

mated for habitats or sites based on the probability of predation attacks, it is widely recognized that domestic ungulates learn to avoid handling facilities if the movement through these facilities is associated with pain and fear (Grandin and Deesing, 1998). Alternatively, animals form place preferences and easily move through handling facilities that are associated with a food reward (Hutson, 1980). It therefore seems reasonable to hypothesize that domestic animals learn to form aversions and avoid locations or habitats associated with predators (e.g., dense vegetation or other forms of stalking cover), although this needs to be tested in the field (Launchbaugh and Howery, 2004).

Skin-Gut Defense System

In controlled experiments where electric shock is used to mimic non-lethal insults to the skin-defense system (Garcia and Holder, 1985), livestock were trained to completely avoid a high-quality habitat associated with visual cues and electric shock (Cibils et al., submitted). Cattle instead foraged near lower-quality habitat that was "safe". The tendency for cattle to shun high-quality habitat following an insult to the skin-defense system is analogous to wild ungulates avoiding high-quality food patches associated with predators (Brown, 1999; Altendorf et al., 2001; Laundré et al., 2001; Lingle, 2001; White et al., 2001; Miller, 2002). Avoidance of high-quality habitats occupied by predators could negatively impact livestock weight gain, animal condition, and overall performance for reasons described earlier.

Social Responses

The phrase "strength in numbers" characterizes how wild and domestic ungulates frequently use group behavior to respond to impending predation. The following anecdotal examples need experimental confirmation, but indicate how domestic herbivores respond to and are impacted by impending predation.

Cattle production suffered in Wyoming when cows and calves were stalked and killed by grizzly bears (Terry Schramm, Grazing Behavior Symposium presentation, Univ. of Idaho, Moscow, 1999). Cattle formed groups to ward off grizzly bear attacks and restricted themselves to areas where predation risk was

reduced which resulted in overuse of the range.

In eastern Arizona, where calf losses to wolves on one ranch were estimated to be 50% in 2002, cattle were observed to huddle and move together in smaller groups (Darcy Ely, personal communication). Cattle "were always on the move and never in the same area during a 24-hour period" while grazing an 8,000-acre pasture in wolf country (Darcy Ely, personal communication). Other behaviors observed included increased vigilance, cows running through fence lines, cows fighting wolves to protect their calves, diarrhea, increased stillborns and abortions, and cows and calves running from domestic cow dogs after being exposed to wolves. By fall roundup, cow dogs could no longer control cattle movements. Cows that lost their calves to wolf predation had spoiled teats due to lack of suckling, and new calves had to be bottle-fed the following year. Cows with spoiled teats eventually had to be culled. Incessant wolf predation resulted in the decision to truck cows to a wolf-free allotment that did not have adequate forage quantity and quality. Cows were not observed to rebreed while on this allotment (Darcy Ely, personal communication).

When sheep are herded they are apparently afforded more protection from predators than cattle because herders can move sheep out of areas with predator problems. However, predator attacks still occur at night when sheep are bedded (Mark Pedersen, personal communication). Sheep pursued by predators at night likely suffer from exhaustion and weight loss, which can negatively influence forage intake and reproductive performance of both males and females. Rams need food and rest to service 50 to 60 ewes, and ewes that lose weight may not cycle or carry lambs to term compared to rested animals (Mark Pedersen, personal communication). When a band of 2,000 sheep are chased by predators they move "shoulder to shoulder like an amoeba" which can damage soils and vegetation, especially when wet (Mark Pedersen, personal communication). In addition to increased energy expenditure as a result of being harassed by predators at night, animals also have less time to ruminate, which can reduce digestibility of plant material harvested earlier in

the day. Thus, harassment by predators may directly cause weight loss due to increased energy expenditure associated with running and loss of sleep, but may also indirectly reduce the ability of ruminants to convert plant nutrients into weight gain due to decreased rumination time.

Conclusions

More research is needed to better understand the potential impacts of indirect, nonlethal predation on domestic livestock behavior and production. Increased understanding could allow managers to manipulate animals, forage, and habitats in ways that lower both the direct and indirect effects of predation, increase livestock production, and that prevent herbivore distribution problems that may cause resource degradation (Howery et al., 1996, 1998b). Additionally, increased understanding will provide for the development of long-term, sustainable, profitable, and environmentally sound, pest-management systems for agriculture, promotion of reduced risk pest-management practices, and protection and conservation of ecosystem quality and diversity.

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