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Large carnivores that kill livestock: do "problem individuals" really exist?

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During recent decades there has been an almost worldwide reversal in the management of large carnivores. Rather than being categorized as "vermin" and subject to government-financed extermination campaigns, most large carnivores are presently highly regarded by the public and management is directed at species recovery and conservation (Mech 1995, 1996; Bangs and Fritts 1996). However, where these measures have been successful and carnivore populations have increased, many former conflicts have reappeared or increased in magnitude. The most significant of these is the conflict with herders caused by carnivore depredation on livestock. The problem is world-wide but appears to be especially acute in areas where carnivores have returned after having been temporarily absent (Blanco et al. 1992, Quigley and Crawshaw 1992, Oli et al. 1994, Cozza et al. 1996, Kaczensky 1996). Reducing these carnivore-livestock conflicts is a prerequisite to successfully conserving large carnivore species (Linnell et al. 1996, Sagør et al. 1997)

The paradigm of livestock-killing "problem individuals"

Regardless of whether a carnivore conservation strategy is based on separating carnivores and livestock (zoning) or conserving both in a multi-use landscape (Linnell et al. 1996), experience has shown that there will likely need to be some form of removal (either lethal or non-lethal control) of individual carnivores in response to depredation events on livestock (Dorrance 1983; Fritts et al. 1985, 1992; Mech 1995). Because of the lack of social acceptance for widespread control and costs of such operations when using poison is forbidden (Saunders et al. 1995), the paradigm of selective removal of so-called "problem individuals" has arisen.

Conceptually, there are 2 possible categories of problem individuals, depending on the scale of the livestock-carnivore distribution matrix. In a coarse-grained matrix, where most individual carnivores do not have livestock within their home ranges, a problem animal may be any individual in the wrong place (type 1). However, in a fine-scale matrix, where all individuals have livestock within their home ranges, a problem individual is one that kills more livestock/encounter than other individuals (type 2). The underlying assumption of the problem-individual paradigm is that only a small proportion of the individuals in a carnivore population are responsible for most livestock depredation. This assumption has rarely, if ever, been tested. This review examines the evidence for and against the existence of individuals or a demographic group, within a carnivore population, that might kill a disproportionate share of livestock. The review is intended to discuss management issues concerning large carnivore species and livestock, but where data are lacking on larger species, we rely on papers on smaller carnivore species or predation on wild prey to illustrate a biological point.

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Inexperienced juveniles or infirm adults?

Domestic livestock lack virtually all of their ancestors' anti-predator behaviors, and represent a relatively easily killed prey when compared to wild prey species of similar size. It is often expected that either inexperienced juvenile or old and infirm adult predators take advantage of this resource and prey on livestock to a greater extent than prime-age adults. There have been surprisingly few studies of the ontogeny of hunting skills among free-ranging carnivores, although 5 detailed studies have been conducted on sea otter (*Enhydra lutris*, Payne and Jameson 1984), Eurasian otter (*Lutra lutra*, Watt 1993), cheetah (*Acinonyx jubatus*, Caro 1994), spotted hyena (*Crocuta crocuta*, Holekamp et al. 1997), and polar bear (*Ursus maritimus*, Stirling and Latour 1978). These studies have shown that young animals are poorer hunters than older animals, take longer to catch each prey item, and feed on prey that are easier to kill. No systematic data are available for recently independent individuals, although sub-adult tigers (*Panthera tigris*) appear to use less efficient killing techniques than adult tigers (Seidensticker and McDougal 1993). Juvenile and yearling bobcats (*Lynx rufus*) are sometimes in poorer condition and kill smaller prey than adults in some (Litvaitis et al. 1986, Matlack and Evans 1992), but not all, study populations (Fritts and Selander 1978). Despite this indication of poorer hunting success among juveniles, starvation has rarely been documented as a major cause of mortality among recently independent large carnivores (Logan et al. 1986, Mech 1987, Lindzey et al. 1988, Harrison 1992, Schwartz and Franzmann 1992). These studies do not support the existence of either type of problem individual.

Among those individuals controlled following depredation events, there is rarely any indication that young carnivores are involved to a greater extent than expected by chance (Horstman and Gunson 1982, Esterhuizen and Norton 1985, Aune 1991, Armistead et al. 1994, Riley et al. 1994, Cunningham et al. 1995). The few exceptions are where conflicts occur near a protected area. In such situations, it is often young animals, especially males, that are more likely to disperse and therefore to come into areas of conflict (Anderson 1980, Saberwal et al. 1994). This supports the existence of the "individual in the wrong place" (type 1) category of problem individual. Despite the logic of the argument, there is little evidence for the hypothesis that juveniles kill a disproportionate number of livestock/encounter than adults (type 2).

It has long been a common adage that old or sick individuals could turn to livestock when unable to hunt wild prey, although the evidence for this is minimal. Apart from a few observations of old or injured snow leopards (*Unicia unica*) being involved in depredation (Fox and Chundawat 1988), the only consistent evidence comes from jaguars (*Panthera onca*) in Central and South America. In one study, 10 of 19 and, in another, 10 of 13 jaguars shot for livestock depredation showed signs of injury, mainly old wounds from shotgun pellets, which may have affected their ability to hunt wild prey (Rabinowitz 1986, Hoogesteijn et al. 1993). Most other studies have found that livestock killers are in good health (Aune 1991, Riley et al. 1994). This does not provide firm evidence for either type of problem individual.

Table 1. Sex ratio (males: female) of carnivores shot or trapped in response to depredation on livestock. The sex ratio of animals controlled for other complaints (aggression, feeding on garbage, etc.), marked for research, or known to exist in the population is presented as an index of sex ratio "availability."

Species	Depredation control		Other harvest / availability		Reference[a]
	M: F	n	M: F	n	
Cougar	4:1	10	1:1	20 (oth. complaints)	1
	6:1	26[b]	1:1	97 (total marked)	2
	0:3	3[b]	1:1	57 (total marked)	3
	3:1	22	1:1	22 (total marked)	4
Jaguar	3:1	4			5
Leopard	2:1	>100			6
	2:1	145			7
Lion	7:3	10[b]	1:1	185 (pop. survey)	8
	3:1	79			9
Grizzly bear	2:1	23	1:1	48 (oth. complaints)	10
Black bear	18:0	18			11
	6:1	76			12
	3:1	30			13
Wolf	1:1	107			14

[a] 1=Aune 1991, 2=Ashman et al. 1983, 3=Anderson et al. 1992, 4=Cunningham et al. 1995, 5=Hoogestejn et al. 1993, 6=Hamilton, in Bailey 1993, 7=Esterhuizen and Norton 1985, 8=Stander 1990, 9=Anderson 1980, 10=Riley et al. 1994, 11=Horstman and Gunson 1982, 12=Armistead et al. 1994, 13=Johnson and Griffel 1982, 14=Fritts et al. 1985.

[b] Indicates samples based on radiocollared or marked animals. All other samples are unmarked.

Which sex is usually involved in livestock predation?

Both sexes are usually implicated in livestock depredation, but there is an almost universal trend for males to be represented more than females among individuals shot or trapped following depredation events (Table 1). This pattern holds for numerous solitary species, including cougar (*Puma concolor*), jaguar, leopard (*Panthera pardus*), lion (*Panthera leo*), grizzly bear (*Ursus arctos*), and black bear (*Ursus americanus*), but not for social species like wolves (*Canis lupus*). Although the sex ratio of the overall population is often unknown, there are few, if any, cases of natural carnivore populations having a male-biased sex ratio. It seems unlikely that this sex bias is due only to a greater vulnerability of males to depredation control techniques. The existence of the same pattern among samples of radiocollared animals (Cunningham et al. 1995), and the finding of a difference in sex ratio between individuals controlled following depredation versus those controlled for other offenses (Aune 1991, Riley et al. 1994), indicate that the pattern is real.

Additional evidence supporting a male bias comes from the few studies of depredation rates of individual carnivores. In a study of radiocollared leopards on a Kenyan ranch, only a single male leopard was implicated in killing livestock in overnight corrals (Mizutani 1993). In a cougar study in Arizona, all 6 radiocollared males were eventually shot in connection with depredation on cattle, whereas only 2 of 8 females had the same fate (Cunningham et al. 1995). Jorgensen (1983), studying black bear behavior in an area with sheep, reported that only 3 male bears were ever close to sheep flocks and, of these, only 1 could be directly implicated in a depredation event. Studies of coyote (*Canis latrans*) depredation behavior in captivity indicated that adult, paired individuals, especially males, were much more likely to kill sheep than young, unpaired, or female individuals (Connolly et al. 1976). Studies of free-ranging coyotes also support this conclusion (Sacks et al. 1999). In contrast, Knight and Judd (1983) reported that all radiocollared grizzly bears, regardless of gender, killed sheep if their ranges overlapped with grazing flocks.

Why do males kill more livestock than females? Most carnivore species display some degree of sexual dimorphism (Gittleman and Van Valkenburgh 1997). Linked to this has been the finding of gender differences in diet for many species (Fritts and Selander 1978, Litvaitis et al. 1984, Birks and Dunstone 1985, Matlack and Evans 1992, Pulliainen et al. 1995, Sunde and Kvam 1997). Whereas body size may explain a greater role for males in killing larger livestock like cattle, it is unlikely that females of most large carnivore species are too small to kill sheep and goats. Alternative explanations lie in gender-specific predation behavior (Vaudry et al. 1990). Either the larger home ranges and wider-ranging movements of male carnivores may simply result in greater encounter rates with livestock, or there may be something intrinsic in male behavior that promotes greater risk taking (Sukumar 1991, Wilson et al. 1994). Until a study controls for livestock distribution and gender-specific movement patterns, we will not be able to distinguish between the 2 possible types of problem individual which males may represent.

Surplus killing—problem individuals or natural behavior?

Finding multiple uneaten or only partially eaten carcasses of livestock species (surplus killing) is a common component of carnivore depredation on livestock (Andelt et. al. 1980, Mysterud 1980, Horstman and Gunson 1982, Fox and Chundawat 1988, Stuart 1988, Anderson et al. 1992, Fritts et al. 1992) and is widely claimed by livestock herders to indicate the presence of a "problem individual" in the area. However, there is much evidence that surplus killing is merely an extension of natural "multiple killing" behavior, where multiple prey items that require more than one meal to consume are killed in a single event but are then fully consumed over a prolonged period. Many small carnivores catch more prey than they can eat at once and cache them for later use (Oksanen et al. 1985, Jedrzejewska and Jedrzejewski 1989, Vander Wall 1990, Madsen et al. 1992, Macdonald et al. 1994). Among larger carnivores, multiple killing is less common but still widespread. Examples include wolves, Eurasian lynx (*Lynx lynx*), lions, cougars, and grizzly bears preying on a diverse range of lagomorphs and wild ungulates (Haglund 1966, Schaller 1972, Mech 1988, French and French 1990, Stander 1992, Carbyn et al. 1993, Dale et al. 1995, Mech et al. 1995). The implications are that killing multiple prey items is adaptive when the opportunity exists. It has been proposed that, whereas searching behavior may be inhibited by killing and satiation, further killing behavior is not (Kruuk 1972). However, the well-developed anti-predator behavior of most wild prey species (Caro and Fitzgibbon 1992) means there are rarely opportunities to make multiple kills. This explains why, in virtually all cases of surplus killing (i.e., excessive multiple killing) of wild prey, there is some factor or unusual conditions that increase prey vulnerability. Examples include thunderstorms (Kruuk 1972), deep snow (Eide and Ballard 1982, Patterson 1994), and concentrations of vulnerable neonates (Miller et al. 1985).

Unusual conditions prevail in almost all circumstances where livestock are concerned. Unnaturally high densities of easily caught prey that lack most of their natural anti-predatory instincts and that are often placed in accessible (from the carnivore's view) but confined (from the livestock's view) areas present special situations for carnivores. Natural selection should not be expected to have favored behavior to kill only as much as can be eaten in a single meal under such artificial circumstances. Therefore, it is unlikely that surplus killing of livestock reflects the existence of a problem individual of either type, although there may still be differences in the way individuals react to a given situation where the potential for surplus killing exists (type 2).

Animal personality—do individuals exist?

A prerequisite for the occurrence of type-2 problem individuals among carnivores that kill livestock is the existence of individuality among wild carnivores. Most researchers who have studied individuals of any mammalian species are likely to have subjectively recognized that different individuals appear to behave slightly differently (Bekoff 1977). Primatologists have long recognized individuality as a serious area of research, and have even started to use the expression "personality" to describe individuals with consistent but different behavioral patterns (Stevenson-Hinde 1983). The same methods have been successfully applied to domestic cats and to a single wild carnivore species, the brown bear (Fagen and Fagen 1996, Feaver et al. 1986).

Although formal analyses of patterns of personality have not been applied to individual carnivores of other species, the literature contains anecdotes supporting existence of individual behavioral traits. Among a sample of 5 radiocollared female cougars, only 1 consistently hunted and killed mountain sheep (*Ovis canadensis*), which were available to all (Ross et al. 1997). Only 1 of 8 radiocollared leopards killed livestock (Mizutani 1993). Different clans of spotted hyenas displayed slightly different hunting behavior (Mills 1990). Stander (1990) was able to identify individual lions that repeatedly killed available livestock, whereas other individuals did not. Claar et al. (1986) reported that only 2 of 20 radiocollared grizzly bears killed livestock that were available to most of the bears. Hard data are rare because of 2 problems. First, large carnivores are intrinsically difficult to study; second, investigator observation of predation is rare. It is therefore difficult to gather enough data on each individual to quantify a consistent individual predation parameter; however, such work is vital. We need to stop regarding variation as an inconvenience and examine the individuals as individuals. The leopard and lion examples are the firmest evidence available for the existence of type 2 problem individuals. We desperately need data on the ontogeny of search image, prey-recognition behavior, and the switching behavior of carnivores when both wild and domestic prey are available. However, it should be clear that carnivores are such complex and long-lived organisms that the potential for individuality, and therefore the formation of problem individuals, exists. The framework for the analysis of shyness-boldness behavior proposed by Wilson et al. (1994) offers a good starting point for such work.

Livestock husbandry: does it influence the development of problem individuals?

We hypothesize that the livestock herding technique is a main factor leading to the possible formation of problem individuals. In systems where sheep, goats, or cattle are constantly herded, kept on open fields, or confined at night inside a fence, corral, or boma (Kruuk 1980, Mizutani 1993, Linnell et al. 1996), predation on livestock requires the development of specialized behavior by the predator. To successfully kill livestock, the predator has to either bypass the shepherd and his dogs, enter open habitat, or cross physical barriers. Individuals must learn how to access this food source. These behaviors all require learning and are unlikely to develop in young animals or naturally more cautious females (Sukumar 1991). However, in grazing systems such as those used in Norway (Sagør et al.

1997), where sheep are free-ranging and unattended in natural carnivore habitat such as forests and mountains, there is unlikely to be any perceptual difference between a sheep and natural ungulate prey, apart from the sheep being easier to kill. The scattered distribution of sheep throughout a carnivore's normal hunting habitat also will increase encounter rates between carnivores and sheep, without any search behavior required by the carnivore. We hypothesize that under these conditions, problem individuals (type 1 or 2) are less likely to appear because most individuals have opportunity to kill livestock without developing specialized behaviors. This could explain why losses of domestic sheep in Norway are so much higher than for any other country (Warren and Mysterud 1995, Aanes et al. 1996, Kaczensky 1996, Sagør et al. 1997), despite an abundance of wild prey species.

Identifying and managing "problem individuals"

Even if problem individuals exist, management is still difficult. For example, Gipson (1975) documented that the probability of killing an offending coyote with traps was relatively low for livestock offenses. Management based on the selective removal of problem individuals is dependent on selective control methods and the ability to define and identify problem individuals. Livestock protection (toxic) collars are the only guaranteed method of controlling the individual involved in depredation (Connolly and Burns 1990, Burns et al. 1996). However, the method is clearly not suitable for areas where husbandry is so lax that most individual carnivores within an area may kill livestock occasionally. Trapping on the carcass may be effective for felid species that habitually return to a kill, but also may trap other individuals or other species like wolverine (*Gulo gulo*), bear, or wolves that are scavenging a kill made by another individual. Following scent from a fresh kill with trained dogs also may be a valid approach to control the correct individual. Despite such problems, any form of selective control is ecologically preferable to widespread population reduction. Although translocation is often used as a non-lethal alternative to remove an individual, there are many problems with the routine use of this approach (reviewed in Linnell et al. 1997). In effect, the most effective solutions in the case of rare or endangered species are to modify husbandry techniques or zone landuse to reduce or prevent depredation, rather than relying on reaction after the event (Linnell et al. 1996).

Conclusions

There is reason to believe that individuals or demographic groups within a carnivore population can show different behavioral traits. This could, in theory, produce "problem individuals" that are often assumed to be responsible for most cases of livestock depredation. Adult males are involved in more depredation events than any other age or gender class, and there is little evidence that juvenile or old individuals prey disproportionately on livestock. Surplus killing should be regarded as an extension of natural multiple killing behavior rather than as evidence of a problem individual. Field data do not yet allow us to determine whether there are in fact any individual differences when livestock availability and differential encounter rates are considered. The only way to obtain the field data is to intensively monitor the movements and predation behavior of different individuals in relation to the distribution of livestock. Such work is difficult and expensive, but vital to determine whether there is any scientific basis to the established management paradigm of problem-individual removal. We hypothesize that most individuals of large carnivore species will at least occasionally kill accessible livestock that they encounter. If true, this implies that problem individual control will need to remove most individuals that have the possibility to encounter livestock. This may be acceptable if carnivore conservation is based on livestock-free wilderness areas or landuse zones, but it will not function in multi-use landscapes where livestock are dispersed throughout the area where carnivores are to be conserved.

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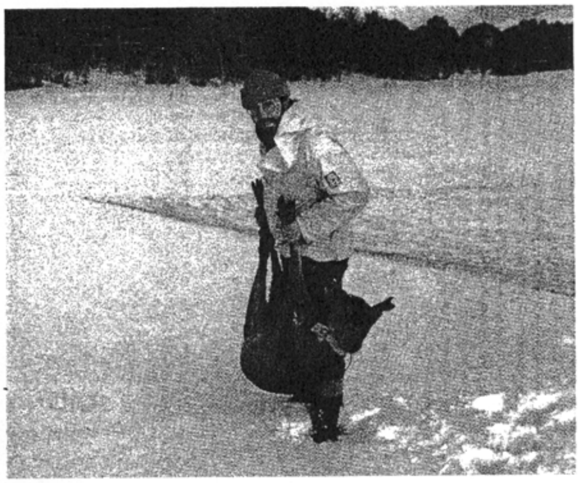

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