

Interspecific Killing among Mammalian Carnivores

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ABSTRACT: Interspecific killing among mammalian carnivores is common in nature and accounts for up to 68% of known mortalities in some species. Interactions may be symmetrical (both species kill each other) or asymmetrical (one species kills the other), and in some interactions adults of one species kill young but not adults of the other. There is a positive significant relationship between the body masses of solitary killer species and body masses of their victim species, and grouping species kill larger victims than solitary species. Interactions and consumption of the victim appear more common when food is scarce or disputed. In response to killers, victim species may alter their use of space, activity patterns, and form groups. Consequences of interspecific killing include population reduction or even extinction, and reduction and enhancement of prey populations, and may therefore have important implications for conservation and management of carnivores and their prey.

Keywords: carnivores, interspecific killing, intraguild predation, mesopredator release, population and community effects.

Direct (e.g., interference competition, predation) and indirect (e.g., exploitative competition, trophic cascades) interactions among species regulate natural populations and shape community structure (Case and Gilpin 1974; Estes and Palmisano 1974; Menge and Sutherland 1987; Paine et al. 1990; Bengtsson et al. 1994; Wootton 1994; Menge 1995). Despite great interest in such interactions, the actual influence of direct and indirect effects on food-web structure is still far from clear (Pianka 1988; Pimm 1991; Strauss 1991). This is especially true for food webs that include terrestrial mammalian carnivores, some of which are

thought to act as keystone species in the top-down control of terrestrial ecosystems (Terborgh and Winter 1980; Terborgh 1992; McLaren and Peterson 1994). One factor affecting carnivore populations is interspecific killing by other carnivores (sometimes called intraguild predation; Polis et al. 1989), which has been hypothesized as having direct and indirect effects on population and community structure that may be more complex than the effects of either competition or predation alone (see, e.g., Latham 1952; Rosenzweig 1966; Mech 1970; Polis and Holt 1992; Holt and Polis 1997). Currently, there is renewed interest in intraguild predation from a conservation standpoint since top predator removal is thought to release other predator populations with consequences for lower trophic levels (termed "mesopredator release"; Soulé et al. 1988; Meffe et al. 1994).

In theory, interspecific killing might remove a source of mortality for the killer or its offspring (Eaton 1979) or free up food resources that would be consumed by the victim (Polis et al. 1989), or killers might accrue energetic benefits from consuming their victims, although victims generally feature little in the diet of their killers (discussed later). Unfortunately, however, we have no comprehensive knowledge of interspecific killing in carnivores, which impedes our understanding of its evolution, ecological importance, and conservation significance. Through a survey of published literature (see the appendix), we sought to document the distribution of interspecific killing among mammalian carnivores, to examine patterns of interactions, to determine whether consumption of victims occurs, to ascertain both direct and indirect effects on populations of victim species, and to identify implications for conservation and management.

Distribution of Interspecific Killing

Interspecific killing is common among mammalian carnivores. We uncovered 97 different pairwise interactions, involving 54 different victim and 27 killer species (table 1). The number of species killed was greater than the number of killer species for all families except felids. Figures in table 1 are conservative because we only considered cases in which there was unequivocal evidence that inter-

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Table 1: Interspecific killing among mammalian carnivores summarized by family

| Family | Number of interactions where one species was killed | Number of species killed | Number of interactions where a species was the killer | Number of killer species |
|------------|---|--------------------------|---|--------------------------|
| Herpestids | 4 | 4 (10.8) | ... | ... |
| Viverrids | 2 | 2 (5.9) | ... | ... |
| Felids | 17 | 9 (24.3) | 47 | 12 (32.4) |
| Hyaenids | 5 | 3 (75.0) | 7 | 2 (50.0) |
| Ursids | 5 | 4 (44.4) | 4 | 2 (22.2) |
| Canids | 37 | 14 (40.0) | 34 | 8 (22.9) |
| Procyonids | 2 | 1 (5.6) | 0 | ... |
| Mustelids | 25 | 17 (27.0) | 5 | 3 (4.8) |
| Total | 97 | 54 (22.8) | 97 | 27 (11.4) |

Note: Parentheses refer to the percentage of species in the family, following Wozencraft (1989).

actions led to the death of an individual (i.e., direct observations of encounters or dead animals with clear evidence of having been killed by another mammalian carnivore species). Although data on carnivore diets also point to numerous instances of carnivores being prey (e.g., see Rosenzweig 1966 and Erlinge 1981 for some mustelid species; Mills 1990 for brown hyena *Hyaena brunnea*; and Bailey 1993 for leopard *Panthera pardus*), these could represent carrion feeding. Therefore, information from dietary studies was not considered here. We also excluded instances in which a domestic species was the killer because domestic species may have been trained to kill other species (e.g., *Canis familiaris*).

Canids, mustelids, and felids (as victim) and felids and canids (as killer) were the families most involved in the interactions (table 1). The species that were most often victims were the red fox in seven pairwise interactions; domestic dog in five; bat-eared fox *Otocyon megalotis* in four; and African wild dog *Lycaon pictus*, cheetah *Acinonyx jubatus*, the arctic fox *Alopex lagopus*, American marten *Martes americana*, and lion each in three pairwise interactions. Regarding killer species, those of the genera *Panthera* and *Lynx* were in 79% of the pairwise interactions involving felid species ($n = 47$), with the leopard, the lion *Panthera leo*, the Eurasian lynx *Lynx lynx*, and the Spanish lynx *Lynx pardinus*, being the most important killers accounting for 13, nine, six, and six pairwise interactions, respectively. Species of genus *Canis* and *Vulpes* accounted for 85% of interactions that involved any canid species being the killer ($n = 34$). The gray wolf *Canis lupus*, with 12, the red fox *Vulpes vulpes*, with nine, and the coyote *Canis latrans*, with eight, are the species most often cited as killers.

The families least recorded as either killing other carnivores or being killed (herpestids, viverrids, and procyonids; table 1) are those that have received little study. In addition, these families include small and medium-sized

species, which reduces the likelihood of finding their remains or even the remains of species killed by them as their victims are small (discussed later). In fact, of the 27 killer species, 37.0% are heavier than 50 kg, 44.4% lie between 10 and 50 kg, and only 18.5% are smaller than 10 kg. For victims, the figures are 16.7%, 25.9%, and 57.4%, respectively.

Patterns of Interaction

Age, size, and patterns of grouping play a significant role in the outcome of interactions between mammalian carnivores. Smaller species may kill cubs, young, or subadult individuals of the larger species (fig. 1A; four of seven instances; see the appendix), but in general, larger species usually kill both adult and juvenile individuals of the smaller species (fig. 1B; 24 of 26 instances; see the appendix). One of the two exceptions to the latter finding was two records of wolves killing adult black bears *Ursus americanus* (Rogers and Mech 1981; Paquet and Carbyn 1986). In both instances, the wolves were in packs (see later discussion). Mutual killings have also been recorded (see the appendix). Some interacting species are able to kill only nonadults of the other (fig. 1C; e.g., red foxes and European badgers *Meles meles*), one species kills both adults and nonadults of the second, whereas the second kills only nonadults of the first species (fig. 1D; e.g., lions and spotted hyenas *Crocuta crocuta* and lions and leopards), or both species kill both adults and nonadults of the other (fig. 1E; e.g., lions and African wild dogs or Asian wild dogs *Cuon alpinus* and tigers *Panthera tigris*). In the last two cases, grouping has an important role in the final result of the interaction (see Eaton 1979).

Relative body mass of interactants (i.e., mass of victim/mass of killer) is significantly higher for species killed by carnivores that group than for solitary species ($N = 6$, mean = 3.84 ± 1.85 SE vs. $N = 9$, mean = 0.47 ± 0.10 ,

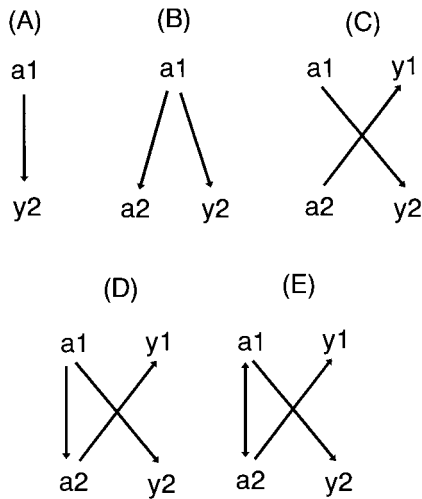


Figure 1: Patterns of interspecific killing in mammalian carnivores. Numbers denote species; letters denote adult (*a*) and nonadult (*y*) individuals. Arrows indicate direction from killer to victim. Asymmetrical age-structured patterns arise when species 1 may kill either (A) only nonadults or (B) both age classes of species 2. Mutual killings exist in which (C) both species kill nonadults of the other, (D) species 1 kills both adults and nonadults of species 2, but species 2 can only kill nonadults of species 1, and (E) both species kill each age class of the other.

respectively; $t = 2.27$, $df = 13$, $P = .041$; fig. 2). Indeed, carnivores that group can kill species that weigh up to 12 times their own body mass (fig. 2), similar to that found for prey (Earle 1987). Only in the case of brown bears *Ursus arctos* killing black bears has a solitary carnivore been recorded as killing a potentially heavier carnivore. The records, however, were of an adult brown bear killing cubs of black bears (Ross et al. 1988) or an adult male brown bear (ca. 190–200 kg) killing adult female black bears (ca. 98–99 kg; Mattson et al. 1992; Smith and Follmann 1993). Therefore, heavier individuals also killed smaller individuals in these cases. Moreover, mass of bears varies considerably between populations (e.g., see Nowak 1991).

Figure 2 shows that the weight of victim increases with weight of solitary killers ($\log \text{weight of victim} = -0.065 + 0.731 \times \log \text{weight of killer}$, $\text{adj. } R^2 = 0.66$, $F = 16.78$, $P = .0046$, using the heaviest species killed by each of the eight solitary killers known to kill adults of other species and the actual weights of the interacting bears of the killings reported by Mattson et al. [1992] and Smith and Follmann [1993]). For solitary species, there seems to be a threshold above which the victim cannot be killed. For example, in southwestern Spain the Spanish lynx kills 2–7-kg species, such as the European genet *Genetta genetta*, Egyptian mongoose *Herpestes ichneumon*, red fox, and domestic cat, but not

badgers that weigh between 7 and 9 kg (Palomares et al. 1996).

Consumption of Victims

Some carnivores consume their victims. Of 21 killer species where information was available, killers always totally or partially ate their victims in 10 cases, either did or did not eat them in eight cases, or never ate them in three (see the appendix). There are no clear taxonomic or behavioral patterns to these data except that all consumers have been reported as feeding on carrion. Characteristics of the victims did not seem to affect consumption, as the same species was sometimes eaten but at other times was not, either by the same or different killer species (e.g., killed cheetahs, coyotes, red foxes, domestic dogs, kit foxes *Vulpes macrotis*, bat-eared foxes, stoats *Mustela erminea*, and European pine martens *Martes martes*).

Availability of alternative prey may be a determinant of both interspecific killing and consumption (Macdonald 1977; Polis 1981; Ackerman et al. 1984; Stephenson et al. 1991) as the diets of sympatric carnivores often show great overlap (e.g., see Kruuk 1972; Delibes 1980; Major and Sherburne 1987; Lindström 1989; Smits et al. 1989; Theberge and Wedeles 1989; Paquet 1992; Mills and Biggs 1993; Palomares 1993; Karanth and Sunquist 1995; Okarma 1995, Okarma et al. 1997). For example, Ballard (1982) found that the number of kills contested by wolves and bears was higher in areas of low prey density. In 36 cases, authors of carnivore studies in northern latitudes

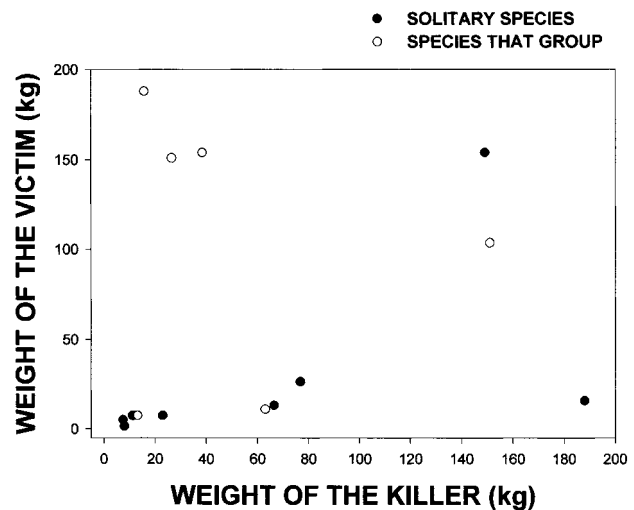


Figure 2: Body mass of victims plotted against body mass of killers. For killers, solitary species are filled circles, and group living species are open circles. When more than one data set was available for a given killer species, only data of the heaviest victim are shown.

Table 2: Extent of mortality resulting from interspecific killing in mammalian carnivores

| Species killed | Percentage of mortalities | Killer species | Region | Sources |
|----------------------|---------------------------|-------------------------------|----------------------------------|---|
| African wild dog | 13–50 | Lion, spotted hyena | Botswana, South Africa, Tanzania | Mills and Biggs 1993; Creel and Creel 1996, 1998 |
| American marten | 4 | Red fox | Ontario | Thompson 1994 |
| Black-footed ferret | 33 ^a | Coyote | Wyoming | Forrest et al. 1988 |
| Bobcat | 12 ^a –62 | Coyote, cougar | Idaho | Knick 1990; Koehler and Hornocker 1991 |
| Cheetah | 68 ^b | Lion, spotted hyena, leopard | Tanzania | Laurenson 1994, 1995 |
| Coyote | 43–67 ^a | Cougar, wolf | Alaska, Idaho | Koehler and Hornocker 1991; Thurber et al. 1992 |
| Egyptian mongoose | 0–67 ^a | Spanish lynx | Spain | Palomares and Delibes 1992; F. Palomares, unpublished data |
| European badger | 9 ^a | Red fox | Spain | E. Revilla, unpublished data |
| European genet | 33 ^a | Spanish lynx | Spain | Palomares and Delibes 1994 |
| Kit fox | 50–76 ^a | Coyote, red fox | California | O'Farrell 1984; Ralls and White 1995; Cypher and Spencer 1998 |
| Lion | 8 ^b | Leopard, hyena | Serengeti | Schaller 1972 |
| European pine marten | 50 ^a | Red fox | Scandinavia | Lindström et al. 1995 |
| Raccoon | 11 ^a | Coyote | Iowa | Judson et al. 1994 |
| Red fox | 13 ^a | Spanish lynx | Spain | F. Palomares et al., unpublished data |
| Spotted hyena | 55 | Lion | Serengeti | Kruuk 1972 |
| Striped skunk | 22 and 17 ^{a,c} | American badger | North Dakota | Sargeant et al. 1982 |
| Swift fox | 45 ^a | Coyote, North American badger | Alberta | Carbyn et al. 1994 |

^a Refers to known deaths from a radio-tracked sample of the population.

^b The figure indicates only cub and/or young mortality.

^c Figures are for litter and adult mortality, respectively.

reported the date of carnivore interactions. Twenty-four (67%) took place during the cold season (November–March) when prey is less available, which suggests that competition over food may have been important, although tracking carnivores in snow may have inflated this figure. Regarding consumption, Boyd and O'Gara (1985) report a coyote killed but not consumed by a cougar *Felis concolor*, near a prey carcass but four other coyotes killed by cougars away from carcasses that were eaten. Also, while defending or usurping food caches, cougars killed coyotes and bobcats *Felis rufus* but did not eat them, perhaps because alternative food was on hand (Koehler and Hornocker 1991).

Direct Effects of Interspecific Killing on Victim Populations

Mortality resulting from interspecific killing can be high, ranging from 43% to 68% of mortalities, as, for example, in cheetah, bobcat, spotted hyena, African wild dog, coyote, European pine marten, kit fox, or Egyptian mongoose (table 2); arctic fox populations on islands or at the limits of their distribution may even be extirpated by red foxes (Bailey 1992; Hersteinsson and Macdonald 1992). Two of five radio-tracked common palm civets *Paradoxurus hermaphroditus* were also killed by undetermined carnivores in Nepal (Joshi et al. 1995). Negative relationships exist

between densities of cheetahs and both lions and spotted hyenas, densities of African wild dogs and both lions and spotted hyenas, and Egyptian mongooses and Spanish lynx (Laurenson 1995; Creel and Creel 1996; Palomares et al. 1998). In each case, interspecific killing between pairs of these species has been witnessed repeatedly. Furthermore, Laurenson (1995), Lindström et al. (1995), Olsson et al. (1997), and White and Garrott (1997) suggest, respectively, that interspecific killing may be limiting the population density of cheetahs by lions in the Serengeti; European pine marten and European badgers by red foxes and wolves, respectively, in Scandinavia; and kit foxes by coyotes in North America.

More circumstantial evidence suggests that populations of weasels, stoats, North American badgers *Taxidea taxus*, leopards, coyotes, red foxes, wolverine *Gulo gulo*, raccoons *Procyon lotor*, and brown bears may all be reduced through interspecific killing (Latham 1952; Robinson 1953; Pullainen 1965; Schaller 1967; Mech 1970; Linhart and Robinson 1972; Carbyn 1982; Erlinge et al. 1982; Dekker 1989; Johnson et al. 1989; Stephenson et al. 1991; Thurber et al. 1992). Nevertheless, there are many studies in which interspecific killing occurs only infrequently. Here, species may be avoiding each other (see later discussion), such as black bears avoiding brown bears (Miller et al. 1997) or cheetahs avoiding lions (Durant 1998), or, alternatively, rates of killing may actually be low, as in the case of red foxes that share dens with European badgers in which only a few instances have been noted despite intensive study (Neal and Cheeseman 1996).

Indirect Effects of Interspecific Killing on Victim Populations

Shifts in Space Use

Victim species may occupy areas that do not overlap with the killer species' home ranges, or they may use different habitats. Red foxes have been reported as using the periphery of coyote home ranges or different habitats from coyotes where they occur sympatrically, and coyotes have been noted as using areas between wolf home ranges (Fuller and Keith 1981; Voigt and Earle 1983; Major and Sherburne 1987; Sargeant et al. 1987; Dekker 1989; Harrison et al. 1989; Theberge and Wedeles 1989; Thurber et al. 1992). European genets and Egyptian mongooses avoid suitable habitats where densities of Spanish lynx are high (Palomares et al. 1996), as do wild dogs and cheetahs where lions are common (Mills and Gorman 1997; Durant 1998). Predator avoidance apparently increases fitness at least in one species. Female cheetah lifetime reproductive success was significantly negatively correlated with the proportion of cheetah family sightings in which lions were close by

(Kelly et al. 1998), and individual females that respond quicker to playbacks of lions and spotted hyenas had higher reproductive success (S. M. Durant, unpublished data). Other mechanisms to avoid being killed include the use of a large number of dens as may occur in California kit foxes (White et al. 1994).

Temporal Segregation

Victims may adjust their activity patterns to reduce encounters with killer species (Litvaitis 1992; Johnson et al. 1996) although evidence for this is circumstantial. In Kruger National Park, lions hunt mainly at night, wild dogs in early morning, and cheetahs around the middle of the day (Mills and Biggs 1993). Although cheetahs hunt during the hottest period, it may help them reduce kleptoparasitism and interference from lions and spotted hyenas (Schaller 1972). Rudzinski et al. (1982) attempted to evaluate interactions between red and arctic foxes by conducting trials in enclosures. Rarely were both species active simultaneously, and activity of arctic foxes decreased when red foxes were present. Nevertheless, clear temporal segregation has been found rarely in studies of resource partitioning between sympatric potentially interacting carnivores (e.g., Major and Sherburne 1987; Litvaitis and Harrison 1989).

Group Formation

Grouping allows medium and small-sized carnivores to obtain antipredator advantages or compete more successfully for food (Kruuk 1975; Eaton 1979; Lamprecht 1981; Gittleman 1989). It has been shown (Caro 1994) that adolescent cheetahs in groups were more effective at deterring spotted hyenas than singleton adolescents. After hypothesized benefits of group hunting were excluded, it was concluded that antipredator benefits were the principal factor favoring litter mates' temporary associations following independence. Dwarf mongooses *Helogale parvula*, experienced lower predation rates with increased group size (Rasa 1986). G. Koehler (unpublished data) observed a group of three coyotes mobbing and successfully chasing a cougar.

Most African carnivores that form groups successfully defend prey more often than solitary individuals (Kruuk 1972; Schaller 1972; Fanshawe and FitzGibbon 1993; Mills 1993). For instance, Carbone et al. (1997) demonstrated that wild dogs hunting in small groups (one to two individuals) would be particularly vulnerable to kleptoparasitism by spotted hyenas, whereas intermediate-sized groups may be most effective at meeting nutritional demands. Also, in North America, large packs of coyotes

successfully defend carcasses against cougars and bears in Yellowstone National Park (D. Boyd, unpublished data).

Changes in Prey Populations

For some time, it has been surmised that when the killer species disappears from an area, smaller predators may be released, which places additional pressure on prey populations. As illustrations, the extinction or decline of many bird species on Barro Colorado Island (Terborgh and Winter 1980), in eastern North America (Sargeant et al. 1984; Wilcove 1985), and in southeastern Spain (Suárez et al. 1993) was inferred as being due to mesopredator release owing to the absence of top carnivores. A few studies have quantified the effect of large carnivore presence on populations of prey. For example, Soulé et al. (1988) showed that presence or absence of coyotes affected the abundance of smaller carnivores such as gray foxes *Urocyon cinereoargenteus* and feral cats *Felis domesticus* in canyons around San Diego. These in turn affected the abundance of birds so that in the absence of coyotes, the number of bird species was depressed. Sovada et al. (1995) studied duck nesting success in upland areas of North America where coyotes or red foxes occurred and found that nesting success was higher in areas dominated by coyotes. In southwestern Spain, high densities of the Spanish lynx may benefit European rabbits *Oryctolagus cuniculus* by controlling Egyptian mongooses that also feed on rabbits (Palomares et al. 1995). Although these three studies reached their conclusions based on known interactions among predator species, other explanations such as alteration of natural habitats or human presence need to be excluded (Wright et al. 1994; Litvaitis and Villafuerte 1996).

Implications for Conservation

Some endangered species such as cheetah and wild dog suffer consequences of interactions with larger carnivores that in certain areas have increased owing to protection policies (Caro and Laurenson 1994; Creel and Creel 1996; Gorman et al. 1998; Kelly et al. 1998). Also, reintroductions of the endangered swift fox *Vulpes velox* and black-footed ferret *Mustela nigripes* in North America have been jeopardized by coyote predation (Carbyn et al. 1994; S. Forrest, unpublished data). Solutions to these conservation problems are difficult because reduction of larger predators is distasteful. In situations in which they have been proposed (Forrest et al. 1985), managers must be given detailed knowledge of killer species' diets before implementing any program of biological control (Schmidt 1985; Waage and Mills 1992).

Protection of larger carnivores may play an important role in the control of less desirable species. By conserving

the Spanish lynx, the negative impact of red foxes and Egyptian mongooses on small game populations can be ameliorated (Palomares et al. 1995). Similarly, protecting coyotes may reduce the effect of red foxes on ducks in North America (Sargeant et al. 1984; Sovada et al. 1995) because foxes can be killed by coyotes. Managing certain carnivores may therefore be a low-cost and effective method for increasing abundance of some prey species. Furthermore, knowledge of the importance of dominant predators and their positive indirect effects on prey of concern may provide a basis for the conservation of some threatened species (as in Spanish lynx; Nowell and Jackson 1996), which otherwise might be viewed as being in conflict with game management objectives.

Conclusions

Interspecific killing appears common in communities of mammalian carnivores of North America, Africa, and Europe, although ecological and behavioral factors affecting it are poorly understood. Further study of interspecific killing between more pairs of species and in different environments should provide insights as to whether life-history characteristics and productivity of an area affect intensity of the interactions and consumption of victims.

To understand the consequences of interspecific killing in mammalian carnivores, we need quantitative data on carnivore and prey populations. For example, theoretical models of intraguild predation suggest that predator coexistence arises when the victim species is superior at exploitative competition for a shared resource, but the killer species gains significantly from the consumption of the victim. At present, however, interspecific interactions have been revealed through qualitative rather than quantitative measures, and future efforts should be directed in determining to what extent various densities of a given species alter abundance or behavior of the other. Realistically, the feasibility of gaining such knowledge in mammalian carnivores is low because they are scarce, difficult to see and to catch, move over large areas, and may be threatened. Natural experiments, large-scale environmental management decisions, together with the long-term monitoring of communities or the selection of suitable ecologically similar areas for comparison, are perhaps the only ways of inferring the ecological consequences of killing among mammalian carnivores (Diamond 1986; Sarrazin and Barbault 1996; also see Bender et al. 1984). Such information is nevertheless essential to construct explanatory, semi-quantitative theories of ecological communities.

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S. Forrest, K. Frafjord, J. O. Helldin, S. Knick, G. M. Koehler, H. Kruuk, T. Kvam, J. A. Litvaitis, D. S. Maehr, S. Minta, D. Monson, H. Okarma, K. Ralls, E. Revilla, A. Rodríguez, I. Thompson, and three anonymous referees for making helpful comments and for providing additional references and unpublished information.

APPENDIX

Table A1: Instances of interspecific killing among mammalian carnivores

| Killed species | Killer species | Age class of victim | Consumption of victim | Sources |
|---|--|---------------------|-----------------------|---|
| <i>Acinonyx jubatus</i> (cheetah) | <i>Crocuta crocuta</i> (spotted hyena) | a | C | Laurenson 1995 |
| <i>A. jubatus</i> | <i>Panthera leo</i> (lion) | b | NC | Schaller 1972; Laurenson 1994, 1995 |
| <i>A. jubatus</i> | <i>Panthera pardus</i> (leopard) | a | SC | Kruuk and Turner 1967; Schaller 1972; Mills 1990; Laurenson 1995 |
| <i>Ailurus fulgens</i> (red panda) | <i>P. pardus</i> | b | ... | Yonzon and Hunter 1991 |
| <i>Alopex lagopus</i> (Arctic fox) | <i>Ursus maritimus</i> (polar bear) | ... | ... | Chesemore 1975 |
| <i>A. lagopus</i> | <i>Vulpes vulpes</i> (red fox) | b | ... | Frafjord et al. 1989; Tannerfeldt 1997; A. Angerbjörn, unpublished data; J. Linnell, unpublished data |
| <i>A. lagopus</i> | <i>Gulo gulo</i> (wolverine) | ... | ... | Tannerfeldt 1997 |
| <i>Canis aureus</i> (golden jackal) | <i>C. crocuta</i> | b | NC | Kruuk 1972 |
| <i>Canis familiaris</i> (domestic dog) | <i>Canis latrans</i> (coyote) | ... | C | Bider and Weil 1984 |
| <i>C. familiaris</i> | <i>Canis lupus</i> (gray wolf) | b | (C) | Fritts and Paul 1989; J. Linnell, unpublished data |
| <i>C. familiaris</i> | <i>Lynx pardinus</i> (Spanish lynx) | ... | ... | Valverde 1967 |
| <i>C. familiaris</i> | <i>Lynx lynx</i> (Eurasian lynx) | ... | C | Okarma et al. 1997 |
| <i>C. familiaris</i> | <i>P. pardus</i> | ... | C | Seidensticker et al. 1990; Johnsingh 1992 |
| <i>C. latrans</i> | <i>C. lupus</i> | b | (C) | Berg and Chesness 1978; Carbyn 1982; Paquet 1991; Thurber et al. 1992; Boyd et al. 1994 |
| <i>C. latrans</i> | <i>Felis concolor</i> (mountain lion) | b | (C) | Ackerman et al. 1984; Boyd and O'Gara 1985; Koehler and Hornocker 1991 |
| <i>C. lupus</i> | <i>Ursus arctos</i> (brown bear) | b | (C) | Ballard 1980; Hayes and Baer 1992; S. Minta, unpublished data |
| <i>Canis mesomelas</i> (black-backed jackal) | <i>P. pardus</i> | ... | C | Kruuk and Turner 1967; Mills 1990 |
| <i>C. mesomelas</i> | <i>P. leo</i> | ... | NC | Stander 1992 |
| <i>Civettictis civetta</i> (African civet) | <i>P. pardus</i> | ... | C | Bailey 1993 |
| <i>C. crocuta</i> | <i>P. leo</i> | b | NC | Kruuk 1972; Eloff 1984; Mills 1990 |
| <i>C. crocuta</i> | <i>P. pardus</i> | a | C | Bailey 1993 |
| <i>Cuon alpinus</i> (dhole) | <i>Panthera tigris</i> (tiger) | b | ... | Schaller 1967 |

Table A1 (Continued)

| Killed species | Killer species | Age class of victim | Consumption of victim | Sources |
|---|---------------------------------|---------------------|-----------------------|--|
| <i>C. alpinus</i> | <i>P. pardus</i> | ... | C | Johnsingh 1992 |
| <i>Cynictis penicillata</i> (yellow mongoose) | <i>Felis caracal</i> (caracal) | ... | ... | Cavallini 1993 |
| <i>Enhydra lutris</i> (sea otter) | <i>U. arctos</i> | ... | C | Monson and DeGange 1995 |
| <i>Felis catus</i> (domestic cat) | <i>L. pardinus</i> | b | NC | Palomares et al. 1996 |
| <i>F. catus</i> | <i>L. lynx</i> | ... | ... | Liberg 1997 |
| <i>F. concolor</i> | <i>C. lupus</i> | a | (C) | White and Boyd 1989; Boyd and Neale 1992; Boyd et al. 1994 |
| <i>Felis libyca</i> (African wild cat) | <i>F. caracal</i> | ... | ... | Mills 1990 |
| <i>F. libyca</i> | <i>P. pardus</i> | ... | C | Mills 1990 |
| <i>Felis pardalis</i> (ocelot) | <i>Panthera onca</i> (jaguar) | ... | ... | Mondolfi and Hoogesteijn 1986 |
| <i>Felis rufus</i> (bobcat) | <i>F. concolor</i> | ... | NC | Koehler and Hornocker 1991 |
| <i>F. rufus</i> | <i>C. latrans</i> | b | ... | Knick 1990 |
| <i>Genetta genetta</i> (European genet) | <i>L. pardinus</i> | b | NC | Palomares et al. 1996; F. Palomares, unpublished data |
| <i>G. gulo</i> | <i>C. lupus</i> | b | NC | Burkholder 1962; Boles 1977 |
| <i>Helogale parvula</i> (dwarf mongoose) | <i>C. mesomelas</i> | ... | C | Lamprecht 1978 |
| <i>Herpestes ichneumon</i> (Egyptian mongoose) | <i>L. pardinus</i> | b | NC | Palomares et al. 1996; F. Palomares, unpublished data |
| <i>Hyaena brunnea</i> (brown hyena) | <i>C. crocuta</i> | ... | ... | Mills 1990 |
| <i>H. brunnea</i> | <i>P. leo</i> | ... | NC | Eloff 1984; Mills 1990 |
| <i>Ictonyx striatus</i> (striped polecat) | <i>H. brunnea</i> | ... | C | Mills 1990 |
| <i>Lutra canadensis</i> (river otter) | <i>C. lupus</i> | ... | C | Route and Peterson 1991 |
| <i>Lutra lutra</i> (European otter) | <i>L. pardinus</i> | ... | ... | Valverde 1967 |
| <i>L. lutra</i> | <i>L. lynx</i> | ... | ... | Liberg 1997 |
| <i>Lycaon pictus</i> (African hunting dog) | <i>C. crocuta</i> | a | C | Creel et al. 1995; Ginsberg et al. 1995 |
| <i>L. pictus</i> | <i>P. leo</i> | b | NC | Mills and Biggs 1993; Creel and Creel 1996 |
| <i>L. pictus</i> | <i>P. pardus</i> | b | ... | S. Creel, unpublished data |
| <i>Martes americana</i> (American or pine marten) | <i>V. vulpes</i> | b | ... | Thompson 1994 |
| <i>M. americana</i> | <i>C. lupus</i> | b | ... | Paragi et al. 1996 |
| <i>M. americana</i> | <i>Martes pennanti</i> (Fisher) | ... | ... | Raine 1983 |

Table A1 (Continued)

| Killed species | Killer species | Age class of victim | Consumption of victim | Sources |
|---|--|---------------------|-----------------------|---|
| <i>Martes martes</i> (European pine marten) | <i>V. vulpes</i> | b | NC | Lindström et al. 1995 |
| <i>M. martes</i> | <i>L. lynx</i> | b | C | Okarma et al. 1997; H. Okarma, unpublished data; J. Linnell, unpublished data |
| <i>Meles meles</i> (Eurasian badger) | <i>V. vulpes</i> | a | NC | Neal and Cheeseman 1996; E. Revilla, unpublished data |
| <i>Mellivora capensis</i> (ratel) | <i>P. leo</i> | ... | NC | Eloff 1984 |
| <i>Mephitis mephitis</i> (striped skunk) | <i>C. lupus</i> | ... | C | Boyd et al. 1994; D. Boyd, unpublished data |
| <i>M. mephitis</i> | <i>Taxidea taxus</i> (North American badger) | b | NC | Sargeant et al. 1982; Rossatte 1987 |
| <i>Mustela erminea</i> (stoat) | <i>A. lagopus</i> | ... | C | K. Frafjord, unpublished data |
| <i>M. erminea</i> | <i>V. vulpes</i> | ... | NC | Mulder 1990 |
| <i>Mustela frenata</i> (long-tailed weasel) | <i>Urocyon cinereoargenteus</i> (gray fox) | ... | ... | Latham 1952 |
| <i>M. frenata</i> | <i>V. vulpes</i> | ... | NC | Latham 1952 |
| <i>Mustela nigripes</i> (black-footed ferret) | <i>C. latrans</i> | b | (C) | S. Forrest, unpublished data |
| <i>Mustela nivalis</i> (least weasel) | <i>V. vulpes</i> | ... | NC | Latham 1952; Macdonald 1977 |
| <i>M. nivalis</i> | <i>U. cinereoargenteus</i> | ... | ... | Latham 1952 |
| <i>Mustela putorius</i> (polecat) | <i>V. vulpes</i> | ... | NC | Mulder 1990 |
| <i>Mustela vison</i> (American mink) | <i>A. lagopus</i> | ... | C | K. Frafjord, unpublished data |
| <i>Nyctereutes procyonoides</i> (raccoon dog) | <i>C. lupus</i> | ... | ... | H. Okarma, unpublished data |
| <i>N. procyonoides</i> | <i>L. lynx</i> | ... | ... | H. Okarma, unpublished data |
| <i>Otocyon megalotis</i> (bat-eared fox) | <i>P. leo</i> | ... | (C) | Eloff 1984 |
| <i>O. megalotis</i> | <i>P. pardus</i> | ... | C | Mills 1990 |
| <i>O. megalotis</i> | <i>A. jubatus</i> | ... | C | Mills 1990 |
| <i>O. megalotis</i> | <i>H. brunnea</i> | ... | C | Mills 1990 |
| <i>P. leo</i> | <i>C. crocuta</i> | a | ... | Schaller 1972 |
| <i>P. leo</i> | <i>L. pictus</i> | b | C | Pienaar 1969 |
| <i>P. leo</i> | <i>P. pardus</i> | a | ... | Schaller 1972 |
| <i>P. pardus</i> | <i>P. leo</i> | b | C | Kruuk and Turner 1967; Schaller 1972 |
| <i>P. pardus</i> | <i>P. tigris</i> | ... | C | Seidensticker 1976; Johnsingh 1992 |

Table A1 (Continued)

| Killed species | Killer species | Age class of victim | Consumption of victim | Sources |
|---|--|---------------------|-----------------------|---|
| <i>P. tigris</i> | <i>C. alpinus</i> | b | C | Schaller 1967 |
| <i>Procyon lotor</i> (raccoon) | <i>F. concolor</i> | ... | C | Maehr et al. 1990 |
| <i>P. lotor</i> | <i>C. latrans</i> | ... | C | Clark et al. 1989; Hasbrouck et al. 1992; Judson et al. 1994; W. R. Clark, unpublished data |
| <i>Proteles cristatus</i> (aardwolf) | <i>P. pardus</i> | ... | C | Mills 1990 |
| <i>Suricata suricatta</i> (suricate) | <i>P. leo</i> | ... | NC | Eloff 1984 |
| <i>T. taxus</i> | <i>C. latrans</i> | a | C | Rathbun et al. 1980 |
| <i>Ursus americanus</i> (American black bear) | <i>C. lupus</i> | b | C | Rogers and Mech 1981; Horejsi et al. 1984; Paquet and Carbyn 1986 |
| <i>U. americanus</i> | <i>U. arctos</i> | b | C | Ross et al. 1988; Mattson et al. 1992; Smith and Follmann 1993 |
| <i>U. arctos</i> | <i>C. lupus</i> | a | C | Ballard 1982 |
| <i>U. maritimus</i> | <i>C. lupus</i> | ... | C | Ramsay and Stirling 1984 |
| <i>Vulpes chama</i> (cape fox) | <i>P. pardus</i> | ... | C | Mills 1990 |
| <i>Vulpes macrotis</i> (kit fox) | <i>C. latrans</i> | b | (C) | O'Farrell 1984; Ralls and White 1995; Cypher and Spencer 1998 |
| <i>V. macrotis</i> | <i>V. vulpes</i> | b | C | Ralls and White 1995; K. Ralls, unpublished data |
| <i>Vulpes velox</i> (swift fox) | <i>C. latrans</i> | ... | ... | Carbyn et al. 1994 |
| <i>V. velox</i> | <i>T. taxus</i> | ... | ... | Carbyn et al. 1994 |
| <i>V. vulpes</i> | <i>C. latrans</i> | b | (C) | Sargeant and Allen 1989 |
| <i>V. vulpes</i> | <i>C. lupus</i> | ... | (C) | Mech 1970; A. Delibes, unpublished data; H. Okarma, unpublished data |
| <i>V. vulpes</i> | <i>F. rufus</i> | ... | C | Petraborg and Gunvalson 1962 |
| <i>V. vulpes</i> | <i>L. pardinus</i> | b | NC | Palomares et al. 1996; F. Palomares, unpublished data |
| <i>V. vulpes</i> | <i>Lynx canadensis</i> (North American lynx) | b | C | Stephenson et al. 1991 |
| <i>V. vulpes</i> | <i>L. lynx</i> | b | C | Haglund 1966; Capt et al. 1993; Sunde 1996; Liberg 1997; Sunde and Kvam 1997; H. Okarma, unpublished data; J. Linnell, unpublished data |
| <i>V. vulpes</i> | <i>M. meles</i> | a | NC | Neal and Cheeseman 1996 |

Note: Information on the age class of the victim (a = the killer species only dispatches nonadult individuals of the victim species; b = the killer dispatches both young and adult individuals or only adults of the victim species) and whether they were consumed by the killer (C = consumed, (C) = sometimes consumed, NC = not consumed) are presented when known. Ellipses indicate that information is unknown. Species follow Wozencraft (1989).

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