Adaptations to Intraguild Competition in Mesocarnivores

By

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B.S. (University of Washington, Seattle) 2002

DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Ecology

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

Approved:

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Committee in Charge

2008

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ABSTRACT

Carnivores are unique among mammals because their primary competitors are often also their primary predators. Intraguild interactions play a prominent role in shaping ecological communities, so over evolutionary time one might expect species that co-occur with a large number of larger, behaviorally dominant species to evolve adaptations to ameliorate the risks of intraguild competition. Here I use several different mesocarnivore species and carnivore communities, including cheetahs (*Acinonyx jubatus*) and scavengers in Serengeti National Park, American carnivores and striped skunks (*Mephitis mephitis)* to investigate behavioral, ecological and physiological adaptations to intraguild interactions.

Cheetahs are frequently victims of kleptoparasitism and are sometimes killed (both adults and cubs) by larger predators that come to scavenge from their kills. I examined the propensity of cheetahs of different sexes and reproductive condition to hide carcasses after making a kill, to be vigilant at kills and to depart promptly from a kill after feeding with respect to several ecological factors and scavenger presence. I found that females accompanied by cubs behaved in ways to reduce the risk of cubs being killed while male cheetahs tried to reduce their risk of being killed by dangerous scavengers. I also investigated the factors that influence scavenger arrival at kills and found that scavengers were more likely to arrive at larger kills while terrestrial scavengers were less likely to locate kills situated in tall grass. Spotted hyenas (*Crocuta crocuta*) and jackals (*Canis* spp.) were each likely to be present simultaneous with vultures, although there was little concordance of order of arrival.

Another method of reducing competitive pressure is niche partitioning. There are 77 carnivore species in the Americas that belong to six taxonomic families. Each species shares its geographic range with numerous other species. Carnivore families mediate competition and predation risk through the use of alternative habitat types, strata (terrestrial, arboreal, fossorial or aquatic), activity pattern and diet. I found that dietary generalists, like the families Canidae and Ursidae, co-occur with more potential competitors than families with more specialized diets and the Mustelidae family may reduce competition by being arboreal or aquatic. I also found that members of the Procyonidae and Mephitidae are under great predation pressure than other families. Members of Procyonidae reduce this threat by being arboreal whereas the Mephitidae likely reduce predation through the use and advertisement of noxious secretions.

As with all member of Mephitidae, striped skunks possess a potent defense against predators. They are also aposematically colored, which warns potential predators that they are noxious. I conducted several field experiments in California to explore the reaction of mammalian carnivores to skunks and the specific cues used by predators to identify dangerous prey. Carnivores were found to avoid taxidermy mounts of striped skunks and to generalize skunks' noxious qualities to both other black and white colored animals and cryptically colored skunk-shaped animals. There was also an effect of local skunk abundance on carnivore behavior, suggesting that instead of innately avoiding contrastingly colored prey, it is necessary for carnivores to learn about skunk defenses through experience.

Mammalian carnivores use several strategies to adapt to the competitive and predation risks posed by other members of the carnivore guild. The data presented here suggest that several facets of carnivore behavior, niche occupation and physiology are greatly influenced by intraguild competition. It is through the use of these strategies that mammalian carnivores are able to coexist within a suite of potentially dangerous competitors.

ACKNOWLEDGEMENTS

The member of my dissertation committee, Tim Caro, Dirk Van Vuren and Andy Sih reviewed several drafts of this volume and provided much needed and appreciated advice. Special thanks to Tim Caro for his patience and guidance over the years and for his attempts to motivate me via 2 am (PST) text messages from Tanzania.

Chapters 1 and 2 were a collaborative effort between Tim Caro, Sarah Durant of the Zoological Society of London and me. Several people and organizations were instrumental in collecting the data we used. We would like to thank the Tanzania Commission for Science and Technology, Tanzania Wildlife Research Institute and Tanzania National Parks for permission and Ndutu lodge for logistical support during field work. We thank the staff and volunteers from the Serengeti Cheetah project for their help with data collection. Funding was provided to me by the University of California, the National Science Foundation and the Valentine Eastern Sierra Reserve Research Grant. Sarah Durant was funded by Wildlife Conservation Society, Frankfurt Zoological Society, National Geographic Society, Peoples Trust for Endangered Species, the Howard Buffett Foundation and the Times Christmas Appeal 1998 and Tim Caro was funded by the Royal Society and the National Geographic Society. Thanks also to Sarah for playing host to my adventures in London and to Tim for financing them.

Chapters 4 and 5 are the results of a project that was conducted at 10 research sites throughout California; accordingly I have scores of people to whom I owe a debt of gratitude. I would like to thank Vance Russell and Rodd Kelsey of Audubon California for the use of Bobcat Ranch. Thanks to Sus Danner and Heather Brady at the Big Sur Land Trust for their help in facilitating my research at Mitteldorf Preserve. Jeff Brown and Faerthen Felix were extremely helpful during my time at Sagehen Natural Reserve. Thanks also to Dan Dawson, Cabot Thomas and Kim Rose at the Valentine Eastern Sierra Reserve for their patience after I abandoned Valentine Camp out of fear of bears destroying my project and facilitating Plan B at the Sierra Nevada Aquatic Research Lab. Thanks also to J.D. Delbar for working tirelessly fix my furnace.

I would like to thank all of the staff and volunteers at Fort Ord Public lands, including Bruce Delgado and Eric Morgan. A huge thanks to Jessie Quinn, who was kind enough to let me stay at her rented trailer in Seaside and a massive thanks to Geriann Albers, Mark Elbroch and Daniel Jackson who actually had to live with me.

Thanks to Shorty Boucher and Shane Waddell for all of their help at Quail Ridge. I would like to give a special thanks to Shane for handling an unfortunate well pump situation and for risking life and limb to help me locate a fox mount pilfered by an enormous male mountain lion. It should be noted that Shane did bring a large shovel on this expedition and it is not entirely clear, should we be attacked, whether this shovel would be used beat off the mountain lion or to cripple me, and thus facilitate his own escape. Fellow researcher Karen Mabry also braved the chaparral in search of my fox's carcass and it should be noted that Karen did not bring a shovel, nor a weapon of any kind.

Thanks to the Sacramento Valley Conservancy and particularly Tammy Mebane for her advice on how best to deal with the nefarious, and often criminal, activities of the local folk. Thanks also to the Sacramento County Sheriff's department for their prompt response to my reports of gunfire in my general direction.

Thanks also to Kurt Merg and Feynner Arias at Big Creek. Feynner deserves a special thank you for rescuing me after an unfortunate Mule break-down and for showing me the alarming speed that can be attained if one turns a Mule off when going downhill. This is a trick which I now happily employ with every Mule, Gator or Rhino I can get my hands on. Finally thanks to Feynner and Terry to sharing their home, food and wine with me.

I would also like to thank the staff and volunteers at Cosumnes River Preserve for their patience with the series of unfortunate events that happened to coincide with, or result from, my research at CRP. First and foremost, thanks to Harry McQuillen for being point-man for all the fall-out and for reassuring me that it was okay that I was terrifying volunteers, orchestrating bee-attacks, inviting auto accidents with my mounts sets and spooking thousands of migratory birds.

Thanks also to Jennifer Buck, Mark Ackerman for liaising with the rice farmers and Holden Brink for his good humor and who, for the record, does not possess a pony-tail.

I would like to thank Rhett Woerly for entertaining my hare-brained ideas and allowing me to accompany him on various mis-adventures around McLaughlin Natural Reserve. Special thanks also to Paul Aigner and Cathy Koehler for tracking down and recovering my beloved fox from hunting-shack purgatory and for tolerating the aforementioned adventures. During various failed and successful visits to McLaughlin entertainment was provided by Adam Smith, Rick Lankau, Angela and Burl, Anne-Marie Panetta and Kris Hulvey.

On a personal note I would like to thank Danielle Brown and Chantal Stoner for keeping me in good spirits and Mark Elbroch for his mount-stealing-mountain-lion advice and his determined mount-stealing-coyote tracking. I would also like to thank my family: Susan and Bruce Hunter, Chris and Annie Ussin-Hunter and my husband, Mike Cobb for his love, support and patience listening to me blather endlessly about my project. Mike also proved to be courageous under fire as he drove me around Deer Creek Hills every evening as bullets rained down on us. Bernice Hunter-Cobb kept me company and kept me warm at Fort Ord and Mitteldorf Preserve. Finally, thanks to Oscar Hunter-Cobb for showing me that the most important things in life start, and end with a good meal.

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INTRODUCTION

The ecological role of mammalian carnivores has traditionally been thought to be limited to controlling prey populations but in recent years it has become clear that stable, intact carnivore guilds play an important role in structuring entire biological communities (*e.g.* Crooks and Soule 1999, Berger *et al.* 2001, Terborgh *et al.* 2001, Ripple and Beschta, 2004, Wilmers *et al.* 2003, Steneck 2005, Sergio *et al.* 2008). This is because ecologically dominant carnivores influence recruitment and the population dynamics of subordinate species (hereafter, termed mesocarnivores) through both direct predation and competition for shared resources (Laurenson 1995, Switalski 2003, Creel *et al.* 2001). When top carnivore populations are reduced either through natural population fluctuations or human exploitation, mesocarnivores can become functionally released from competition which can have ramifications for lower trophic levels (*e.g.* Rogers and Caro 1998, Crooks and Soule 1999, Berger *et al.* 2001, Schmidt 2003, Wolff and Van Horn 2003, Finke and Denno 2004, Ripple and Beschta, 2004, Berger *et al.* 2008). These relationships, broadly termed intraguild competition, can take the form of exploitative competition or interference competition. In exploitative competition animals compete indirectly for a finite resource - a food item consumed by one individual cannot be consumed by another and a den site that can only be occupied by one animal at a time. In contrast, interference competition takes place when two animals compete directly for a resource, especially food, and can result in the death of one of the competitors (Linnell and Strand 2000).

New recognition of the ecological implications of intraguild competition has focused recent research on carnivore interactions (*e.g.* Palomares and Caro 1999, Linnell & Strand 2000, Creel *et al.* 2001, Donadio and Buskirk 2006; St. Pierre *et al.* 2006, Roth *et al.* 2008) and we now believe that intraguild competition is ubiquitous among mammalian carnivores. There have been several attempts to use theoretical models to illustrate the interspecific relationships that are most likely to facilitate species coexistence (*e.g.* Polis *et al.* 1989, Holt and Polis 1997, Křivan 2000, Revilla 2002, Roth *et al.* 2008). The result of most of these efforts is a number of simple three-species models (intraguild predator, intraguild prey and a shared prey species) that follow three key assumptions: 1. the subordinate guild member must be superior competitor for a common resource, 2.the dominant guild member must gain some energetic advantage from preying upon and consuming the subordinate guild member and 3.intraguild predation is asymmetric, wherein the cost of interacting is always greater to one species (intraguild prey) then the other (intraguild predator). However, carnivore communities are often extensive. Caro and Stoner (2003) found African carnivores, on average, share geographic range and habitat preferences with 26 other species, of which 22 species share the same diet and 15 species are potential predators. Thus simplistic interaction models likely under represent the diversity of competitive relationships between multiple guild members utilizing multiple prey sources.

It is difficult to disentangle the influence of exploitative competition and interference competition on species' ecology and behavior, particularly for predatory animals, when the act of feeding itself represents a convergence of these risks with predators attracted both to the food being consumed and the individual consuming it (Carbone *et al.* 1997, Creel *et al.* 2001, Horner *et al.* 2002, Donadio and Buskirk 2006). In order to mitigate these pressures, mesocarnivores should adopt strategies to minimize the risks posed by agonistic interactions with heterospecifics (Linnell and Strand 2000, Caro and Stoner 2003). Spatial and temporal avoidance by two or three guild members has been well documented (*e.g.* Durant 1998, Fedriani *et al.* 2000, Neale and Sacks 2001, St. Pierre *et al.* 2006, Selas and Vik 2007) and has been the primary focus of much of the research on carnivore coexistence. Less attention has been paid to behaviors used to minimize competitive interactions (but see Durant 2000, Kimbrell *et al.* 2007) and the physiological means of deterring attack (*e.g.* Ruxton *et al.* 2004, Caro 2005) in mammalian carnivores. The aim of this dissertation is to explore adaptations to intraguild competition by mesocarnivores through behavioral mediation (Chapters 1 and 2), community-wide niche partitioning (Chapter 3) and physiological defenses (Chapters 4 and 5).

Chapter 1 adds to the growing body of literature examining how animal behavior can mitigate the influence of dangerous competitors on vulnerable mesocarnivore populations. I analyzed sex-specific differences in anti-predator behaviors exercised by cheetahs (*Acinonyx jubatus*) at kill sites. While known primarily for their speed and proficiency as hunters, cheetahs are susceptible to exploitation by larger carnivores, particular at their kills (Caro 1987). Lions and spotted hyenas frequently scavenge from cheetah kills, are the primary cause of cheetah cub mortality (Laurenson 1995) and have been reported to kill adult cheetahs on occasion (du Pienaar 1969). Thus, it is vitally important for cheetahs to balance time spent feeding with anti-predator behaviors, like moving a kill to dense vegetation, being vigilant and departing from kills promptly after feeding.

Kills procured by cheetahs and other East African carnivores are scavenged by a number of mammalian and avian species and it is believed that there is a mutualistic relationship between vultures and carnivores with vultures relying on carnivores to create scavenging opportunities and carnivores in turn using vultures to locate carcasses to scavenge (Creel *et al.* 2001). In order make predictions about how mesopredators, like cheetahs, can avoid attracting scavengers, it is important to understand the ecological conditions that facilitate the detection of carcasses by both terrestrial and avian scavengers. In Chapter 2 I investigate how environmental factors and the presence of conspecifics or heterospecifics affects whether, and in what order scavengers arrive at carcasses.

The outcome of these two studies (Chapter 1 and Chapter 2) further underscores the importance of evaluating interspecific interactions in the context of entire animal communities. Several studies have found disparate diets, activity patterns, and habitat use between competing carnivores (*e.g.* Houston 1978, Ray and Sunquist 2001, Frajford 2003, St. Pierre *et al.* 2006). While niche specialization is critical to the evolution of large, diverse animal communities

(Hutchinson 1959, Kronfeld-Schor and Dayan 1999, Bastolla *et al.* 2005), community-wide resource partitioning has been largely ignored in studies of intraguild competition (but see Caro and Stoner 2003). In Chapter 3 I examine the potential of 77 species of American carnivore to ameliorate the risk of intraguild competition from other carnivores using an existing database of geographic ranges and a literature review of preferred habitat types, habitat strata (i.e. terrestrial, arboreal, fossorial and aquatic), activity patterns and diet to assess the relative risk of competition and predation faced by each carnivore family, and how species can reduce the risk of both interference and exploitative competition. In the process of completing the analyses for Chapter 3 it became clear that one family in particular, Mephitidae (skunks) were at particularly high risk of predation by virtue of being of small body size and being active in the same habitats, during the same hours as the most of their potential predators.

Aposematic signals indicate that the bearer is noxious or unpalatable and are exhibited by all members of the family Mephitidae. These warning signals are most effective if their meaning is reinforced regularly, therefore the efficacy of aposematic signaling may be improved if predators are encountered frequently (Guilford and Dawkins 1991, Ruxton *et al.* 2004, Mappes *et al.* 2005). In Chapters 4 and 5 I investigate the effectiveness of aposematic coloration in striped skunks (*Mephitis mephitis*) by examining the behavior of wild mammalian carnivores in northern California. In Chapter 4, I examine the behavior of carnivores near taxidermy mounts of striped skunks and see whether there were predator species-specific differences in how skunk mounts were treated. Aposematic signals, like those found in skunks are probably perceived differently by different predators (Endler and Mappes 2004, Mappes *et al.* 2005) across the range of micro-habitats and light environments found in nature.

The specific visual cues used by other mammalian carnivores to distinguish skunks from other, non-noxious species are poorly understood. Several potential signaling modalities have been studied in aposematic taxa (Gamberale-Stille and Tullberg 1999, Jetz et al. 2001, Hristov and Conner 2005, Papaj and Newsome 2005, Haugland et al. 2006), although there has been little attempt to tease apart the specific deterrent value of signal attributes. For most predator-prey systems we know little about the relative importance of specific indicators of prey defense. In Chapter 5 I used reciprocally colored skunk and grey fox (*Urocyon cinereoargenteus*) taxidermy mounts to ascertain the importance of skunk coloration and skunk shape in eliciting avoidance behaviors. I used video cameras to record the behavior of any visiting species and correlated these behaviors with mount characteristics and the relative abundance of skunks at each research site.

My work shows that the mechanisms by which carnivores coexist extends far beyond the traditional spatial- versus temporal-avoidance paradigm. For endangered cheetahs the ability of individuals to survive in the presence of lions and hyenas can have an immediate impact on population viability (Kelly and Durant 2000) whereas an entire scavenger community depends upon large carnivores to provide a steady supply of large animal carcasses, to persist (Richardson *et al*. 1986, DeVault *et al*. 2003). American carnivores offer an illustration of how fine-scale niche differentiation can facilitate the coexistence of multiple species that depend on a common resource base, while aposematic skunks demonstrate the elegance of physiological adaptations, no matter how distasteful, in mediating intraguild conflict. The potential energetic and survivorship costs suffered by co-occuring guild members is substantial for many species (Creel and Creel 1996, Carbone *et al*. 1997, Durant 1998, Fedriani *et al*. 2000, Selas and Vik 2007) and my work highlights a number of evolutionary pathways to mitigate interspecific competition including individual animal behavior, species' ecology and physiological adaptations.

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CHAPTER 1

To flee or not to flee: Predator avoidance by cheetahs at kills

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ABSTRACT

Mammalian carnivores are unusual because their primary competitors for food are often their primary predators. This relationship is most evident at persistent kills where dominant competitors are attracted to both the carcass (as a free meal) and to the killers (as potential prey). Cheetahs (*Acinonyx jubatus*) are frequent victims of kleptoparasitism and cubs, and sometimes adults, are killed by lions (*Panthera leo*) or spotted hyenas (*Crocuta crocuta*). Between 1980 and 2002 we observed 639 kills made by cheetahs in Serengeti National Park, Tanzania. These kills were often visited by scavengers, including relatively innocuous species such as vultures and jackals and potentially dangerous species, like spotted hyenas and lions. We used cheetah behavior at kills to test a number of predictions about how cheetahs should minimize risk at kill sites given they face an increased risk of predation of themselves or their cubs. In particular, we examined the propensity of cheetahs of different age/sex classes to hide carcasses after making a kill, vigilance at kills and the delay in leaving after finishing feeding with respect to ecological factors and scavenger presence. The behavior of single females at kills did not suggest that they were trying to avoid being killed, but the behavior of males, often found in groups, was in line with this hypothesis. In contrast, the behavior of mother cheetahs at kills appeared to be influenced greatly by the risk of cubs being killed. Our results suggest that cheetahs use several behavioral counterstrategies to avoid interspecific predation of self or cubs.

INTRODUCTION

Behavioral ecologists have established a strong theoretical basis for predicting how animals should behave under risk of predation (*e.g.* Sih 1987, Lima and Dill 1990, Lima 1998a). Central to these predictions is balancing access to food while minimizing vulnerability to predators. Questions of anti-predator behaviors have traditionally focused on species for whom the process of feeding is risky because it either distracts from anti-predator vigilance or involves being away from refuges and therefore greater exposure to predators. In the case of intraguild killing however, the act of feeding represents a convergence of competition and predation pressure because potential predators are attracted both to the resource being consumed and the individual consuming it (Palomares and Caro 1999, Donadio and Buskirk 2006). Interspecific interactions between mammalian carnivores can greatly influence population dynamics (Laurenson 1995, Carbone *et al*. 1997, Switalski 2003) and the risks of direct killing and the killing of offspring by dominant guild-members can play a prominent role in shaping the behavior of subordinate species (*e.g.* Cooper 1991, Fanshawe and Fitzgibbon 1993, Carbone *et al*. 1997, Stander *et al*. 1997).

Cheetahs (Acinonyx jubatus) in Serengeti National Park (SNP), Tanzania have been studied for 30 years where they suffer kleptoparasitism and are killed by lions (*Panthera leo*), spotted hyenas (*Crocuta crocuta*) and occasionally by leopards (*Panthera pardus*) (Caro 1987, Durant 1998, 2000a, 2000b). In SNP cheetahs lose 10-12% of their kills (Schaller 1972, Caro 1994) to behaviorally dominant scavengers and while healthy adult cheetahs are rarely killed by other carnivores (Burney and Burney 1979), lions and hyenas kill 73% of dependent cubs (Laurenson 1994). The frequency and nature of these agonistic interactions between cheetahs and larger carnivores can seriously impact the long term viability of the SNP cheetah population (Kelly *et al*. 1998, Kelly and Durant 2000).

Here we use an extensive data set to address three behaviors that cheetahs may use to minimize encounters with larger carnivores: (i) moving the carcass to a safer microhabitat before feeding, (ii) being vigilant (proportion of feeding time spent visually scanning the surrounding habitat) and (iii) leaving a kill promptly after feeding. Since cheetahs are at risk of being killed and kleptoparasitized by the same species it is difficult to differentiate those behaviors aimed at minimizing each type of risk. While the risk of kleptoparasitism can have a tremendous influence on cheetah behavior before a kill is consumed, it likely has minimal impact on cheetah behavior during and after feeding. Once a cheetah has chosen a location and begun to feed there is little it can do to avoid scavengers. Cheetahs in SNP seldom move their kills after beginning to feed, never defend their kills from lions, seldom defend their kills from hyenas and never cache or return to their kills after feeding. Therefore behaviors observed in theses circumstances (i.e. vigilance while feeding and delay to leave a kill once finished feeding) can be ascribed almost entirely to the risk of being killed or injured by dangerous scavengers drawn to the kill.

Cheetahs are most often observed in one of three age/sex categories: adult males (alone or in coalitions), single females and females with cubs (Caro 1994). The risk of being killed varies for cheetahs of differing sexes and reproductive condition. For example, through forming coalitions male cheetahs both increase competitive access to females and may reduce risk of being killed by larger carnivores, through both dilution and intimidation of scavengers (Caro 1994). Females are more vulnerable to predators, as a consequence of being solitary and smaller than males. Mother cheetahs face the additional risk of cubs being killed by scavengers but must balance the risks to self and offspring with anti-predator behaviors, feeding themselves and allowing cubs adequate access to a kill (Caro 1987, Caro 1994, Laurenson 1994). Thus, we expected cheetahs of different sexes and reproductive condition to behave in a way that reflects actual risk of being killed by dangerous scavengers. For example we expected a decrease in anti-predator behaviors with increasing coalition size in male cheetahs (Elgar 1989, Bednekoff and Lima 1998a, Caro 2005) and we expected mother cheetahs to engage in frequent anti-predator behaviors when accompanied by young cubs (less than 4 months old), because young cubs are killed at much higher rates than older cubs (Laurenson 1995) and are physically unable to outrun predators (Caro 1987). We also expected mother cheetahs with many cubs to be willing to incur greater costs of defence than mothers with few cubs as the energetic investment necessary to replace a large litter is greater than that for a small litter (Clutton-Brock 1991, Winkler 1987).

In general, we expected the vigorousness of cheetah predation avoidance behavior to reflect the risk posed to feeding cheetahs, with cheetahs being more apt to move, more vigilant and leaving sooner from those carcasses consumed in a comparatively dangerous environment or when more vulnerable cheetahs are present (Table 1.1). For example, large kills are more costly to obtain, take a longer time to consume (Caro 1994) and are more easily detected by scavengers, when compared to small kills (Blumenschine 1986, Sunquist and Sunquist 1989, Stander *et al*. 1997, Domiguez-Rodrigo 2001) and carcasses situated in open habitats are more easily detected than those concealed by vegetation or shade (Sunquist and Sunquist 1989, Stander *et al*. 1997). In addition, these behaviors may be state-dependent, with energetically stressed cheetahs willing to tolerate a greater risk of being killed if it allows them more time to feed (Sweitzer and Berger 1992, Lima 1998a,b).

METHODS

Study area and observations

Observations took place at 639 cheetah kills made by 186 different individuals, including 59 adult males and 127 adult females with an average of 3.0 kills per individual. Ten individuals could not be identified. Kills included 282 kills from 1980-1984 (TMC) and 357 kills from 1991-2004 (SMD) in SNP. Cheetahs preyed upon at least 11 species (Table 1.2). Given documented differences in carcass detectability and persistence time according to size (Blumenschine 1986), we used two weights to discern differences in cheetah behavior and scavenger arrival: carcasses weighing 0-10kg (N=417) and those weighing more than 10 kg (N=213) in edible mass (Blumeschine and Caro 1986). Cheetahs were observed during daylight hours from a distance of 0 to 150m with binoculars. Individuals were identified by spot patterns (Kelly 2000). Cub age was estimated by comparing body size to that of known aged individuals (Caro 1994). TMC made continuous observations of family groups, typically relocating and following animals for between 1 and 7 consecutive days with observations of males collected *ad hoc*. SMD recorded cheetah behavior and scavenger arrival on kills discovered *ad hoc* as well as during continuous observations.

Cheetah kills

Prior to each hunt the belly size of the cheetahs was rated on a scale from 1, when the animal was emaciated, to 14 when the abdomen was visibly distended. This measure was used to estimate an individual's level of hunger. The abdomen of pregnant females does not become prominent until into the last month of pregnancy (TMC, pers obs) so it was assumed that belly sizes of single females were due to stomach content, not reproductive condition. Similar belly size estimates have been used reliably in cheetah and lion studies (Frame and Frame 1981, Packer 1986).

Time of day, habitat type (plains or plains-woodland border), prey species and age, belly size before and after feeding, grass height where the kill was consumed, as well as the presence or absence of shade was recorded for each kill. Once the prey had been captured and killed, the observation vehicle was driven to the carcass, stopping at a minimum of 15 to 20 m away. Mammalian or avian scavengers were not drawn to the vehicle in other circumstances; observer presence at kills is therefore unlikely to have attracted potential scavengers, however, it may have deterred shy scavengers. To mitigate this effect, observers were careful to not move vehicles after taking up position. A kill was considered to have been moved if cheetahs dragged the carcass away from the kill site before beginning to feed. The distance a kill was moved was either estimated (TMC) or measured with GPS (SMD). Any difference in vegetation height between the kill site and the feeding site was also recorded. In adult groups, a randomly selected focal animal was timed with a stopwatch to determine the total time cheetahs spent feeding at a kill. In the case of females with cubs the mother was always the focal animal.

Vigilance was measured as the sum of time the focal cheetah spent on a kill visually scanning its surroundings, divided by total time elapsed from the start of feeding to the cessation of feeding. Scan lengths were measured with either one (TMC) or multiple stopwatches (SMD) and were recorded from the beginning to the end of feeding, regardless of whether cheetahs remained near the kill after feeding. In addition to moving and vigilance behavior, SMD noted the delay for cheetahs to leave a kill after having finished feeding. Delay in leaving was only measured at kills where cheetahs fed unmolested and appeared to depart from the carcass voluntarily.

Scavengers

In our analyses we considered four scavenger groups: vultures (*Torgos tracheliotus, Trigonoceps occipitalis, Gyps africanus, G. rueppellii, Neophron percnopterus, Necrosyrtes monachus*), jackals (*Canis mesomelas, C. aureus*), spotted hyenas and lions. Leopards were never seen at a kill. Despite differences in behavior and feeding ecology of the vulture species, we considered them together as a single scavenger group (Kruuk 1967, Houston 1975). Other scavengers at cheetah kills included marabou storks (*Leptoptilos crumeniferus*) and tawny eagles (*Aquila rapax*) but they were present at very few kills (<10) and were therefore excluded from our analyses.

Data analysis

For each kill cheetah hunger (based on belly size), grass height where the kill was consumed (estimated to 20 cm), whether or not the kill was eaten in shade, time of day and prey size, together with their two-way interactions were examined for their influence on whether a kill was moved, vigilance at a kill and the delay in leaving a kill. Kills where feeding cheetahs appeared to have been disturbed by tourist presence (visually survey tourist vehicles or abandoning a kill) were excluded from all analyses.

A priori we suspected that cheetah behavior at kills may have been affected by ambient temperature. No direct measure of temperature was made so kills were grouped according to time of day and included in each analysis of cheetah behavior as a potential confounding variable. Kills made between 1000 and 1600 hours, when temperatures are typically highest, were grouped into one category and those kills made during the cooler hours before 1000 and after 1600 hours were grouped into a second category.

A kill was considered to have been moved if the cheetah dragged or carried the kill away from the kill site before beginning to feed. Mother cheetahs were not seen to bring kills to their cubs, instead cubs approached prey once their mother had subdued it. Therefore we assumed that mother cheetahs moved carcasses to seek a preferential location. Cheetah belly size before feeding was used in moving and vigilance analyses whereas belly size at the end of feeding was used for all delay in leaving analyses as these were the most relevant measures in each situation.

Presence or absence of vultures, jackals, hyenas and lions as well as all two-way interactions were analyzed for moving and vigilance. Jackals were rarely present during SMD's observations and as a result were excluded from analyses of delay in leaving.

For female cheetahs with young, we analyzed moving kills, vigilance and delay in leaving with respect to cub age and cub number. Cub age was scored as either young (<4 mos) or old (>4 mos) and was determined by size, with young cheetahs approximately one-third of the mother's height or smaller and older cubs one-half the mother's height or taller (Caro 1994). For analyses of adult male behavior the number of cheetahs present was included in all analyses.

A combination of t-tests and general linear models were used for analyses. Analyses of moving a kill were fitted to a binomial distribution, cheetah vigilance was arcsine transformed and fitted to a normal distribution and delay in leaving (+1) was fitted to an exponential distribution. In all analyses non-significant variables ($p>0.05$) were removed step-wise according to least significance. All analyses were conducted using GenStat version 5.1 (Payne *et al*. 1987).

Cheetah identity was included as a factor in all analyses and did not exert any significant effect on any of our measures of behavior so we analyzed our data treating multiple observations of the same cheetah as independent.

RESULTS

Cheetahs

The data set used in this study included observations from adult males (both singly and in coalitions), single females, females with cubs, lactating females and adolescents. All of the observed cheetah kills (639 kills) were included in our analyses of scavenger presence; however we used only the appropriate subset of data when analyzing the behavior of males, single females and females with cubs. Males were observed at 115 kills, single females were observed at 102 kills and mother cheetahs with cubs were observed at 348 kills. There were an additional 74 observations of adolescent, lactating females or unidentifiable cheetahs. Males were seen either singly (n=15 kills) or in coalitions of 2 (n=15) or 3 (n=25) animals.

Moving a kill

Approximately 65% of the 491 cheetah kills observed from the end of a successful hunt were moved from the kill site to another location before the cheetahs began to feed. Lack of appropriate cover may have affected whether cheetahs moved carcasses, although cheetahs did move kills great distances suggesting they put substantial effort into seeking desirable conditions. The mean distance a kill was moved was 64.5m (s.e. 5.8m); one individual moved a kill over 712 m. Males were significantly more likely to move large kills than small kills, to move kills to areas of taller vegetation, and to move kills into shade, although males were less likely to move kills during the hottest hours of the day (Table 1.3). There was a significant interaction between hunger and prey size with males with smaller belly sizes more likely to move large kills (χ^2= 11.76, df=2, p=0.006). Hungrier males were also more likely to move kills during the hottest hours of the day (χ^2=5.78, df=2, p=0.016). For single females, only prey size and belly size had an impact on their propensity to move kills, with females moving large kills more than small kills and moving kills more often with smaller belly size when compared to larger belly sizes (Table 1.3). Females with cubs were less likely to move large kills than small kills, however there was a significant interaction between prey size and time of day with mothers more likely to move large kills during the hottest hours of the day, than small kills (χ^2=7.9, df=2, p=0.005). Mother cheetahs were also more likely to move kills into areas with taller grass than to areas with shorter grass height and more likely to move kills into areas shadier than the kill site. Cub age was also an important factor, with females with young cubs more likely to move kills than females with older cubs (Table 1.3).

Vigilance

Vigilance of all age/sex classes was significantly affected by prey size, with males, single females and females with cubs all more vigilant at larger kills, when compared with small kills (Table 1.4). Mother cheetahs were more vigilant at kills in taller grass, when compared with kills eaten in shorter grass. Mother cheetahs with young cubs were significantly more vigilant when compared with mothers with older cubs and mothers with many cubs were more vigilant than those with few cubs.

Delay in leaving

Male cheetahs tended to depart sooner from large kills than small kills and left kills eaten in shade sooner than kills consumed in the open (Table 1.5). The number of males in a coalition also affected the timing of departure, with groups of many males leaving a kill sooner than single males. Single females tended to depart sooner from small kills than large kills and left kills consumed in taller grass sooner than kills consumed in short grass (Table 1.5). Females also departed from a kill more quickly if they were satiated and remained near a kill for a greater length of time during the hottest part of the day than in cooler times of the day. There was a significant interaction between belly size and grass height with females departing sooner from kills in shorter grass if they were satiated, when compared to kills in taller grass (χ^2=11.53, df=2, p=0.007). Mothers with cubs remained near large kills longer than small kills, departed sooner from kills consumed in tall grass when compared to kills consumed in short grass, and departed from kills more promptly when they had larger belly sizes (Table 1.5). The number of dependent cubs also significantly influenced the delay in leaving, with mothers with many cubs tending to leave a kill before mothers with few cubs.

Scavengers

Of the 460 kills observed from the time cheetahs began feeding until they finished, vultures were present at 32.0%, spotted hyenas at 12.4% and lions at 2.4%. Jackals were rare during SMD's observations but were present at 14.2% of TMC's observations (they were excluded from analyses of delay in leaving, as TMC did not record this). Sixty-nine of the 605 kills, where the conclusion of cheetah feeding was witnessed, were abandoned to approaching scavengers (11.4%). Hyenas were responsible for the majority of stolen kills (78% of 69 kills), followed by lions and other cheetahs (15% and 3 %, respectively). The remaining kills (4%) were abandoned after feeding cheetahs were disturbed by noisy tourists or other, non-scavenging wildlife. While females with cubs were somewhat more likely to abandon kills to other carnivores (12.4% of kills) than either adult males (7.8%) or adult females (7.8%), there was no statistically significant difference between these groups (χ^2=2.63, df=2, p=0.27).

We found that jackals and hyenas were both significantly less likely to arrive at kills that were moved (Table 1.6). The eventual presence of vultures, jackals, hyenas or lions at kills made by males or by single females did not significantly impact the rate of vigilance of the feeding cheetahs, whereas mothers with cubs were significantly more vigilant at kills that attracted vultures than those kills that did not (Table 1.7). There was a significant interaction between hyenas and the number of cubs present; mother cheetah vigilance increased with increasing litter size at kills where hyenas were present (t_{166}=-4.36, p=0.049).

Males and single females both departed from sooner from kills with the presence of vultures. For mothers with cubs, however vulture and jackal presence did not impact the delay in leaving a kill, though lions and hyenas both significantly expedited the departure of mothers and their cubs from kills (Table 1.8).

DISCUSSION

Cheetahs in this study interacted with several predator species at their own kills including spotted hyenas and lions, the former known to kill cheetah cubs, and the latter known to kill both adults and cubs (Burney and Burney 1979, de Pienaar 1969, Eaton 1974, Frame and Frame 1981, Laurenson 1994). We presented a number of predictions that might support the hypothesis that cheetahs employ counterstrategies to avoid being predated at kills but these were not always clear cut. For example the propensity of cheetahs to move small kills more than large kills may have more to do with the physical ability of gracile cheetahs to move large prey than evidence of a lack of concern about attracting dangerous scavengers. Also, increased wariness in taller grass (increased vigilance: mother cheetahs; prompt departure: single females and mother cheetahs) may the result of an inability for cheetahs to detect approaching danger. Finally, we cannot always distinguish between cheetahs attempting to avoid predation and avoiding kleptoparasitism in our interpretation of results. That said, a number of themes emerge from this study (Table 1.9).

For male cheetahs, five results supported the hypothesis that cheetahs were trying to avoid predation and two were against. Nonetheless, three out of the five could also be interpreted as behaviors to avoid kleptoparasites. Thus, there is only equivocal evidence that male behavior at kills is principally geared toward avoiding threat of predation. This might have been expected since male cheetahs are quite bold in the presence of scavengers, particularly when compared to female cheetahs. Group living affords male cheetahs a number of fitness benefits, including improved territory acquisition and defense and perhaps increased foraging efficiency (Caro 1994) but group living also has potential risks. For example, male coalitions tend to hunt large prey (Caro 1994) but large prey tend to attract more scavengers (Blumenschine 1986, Domingues-Rodrigo 2000). Several males might be more visible to potential predators (Cullen 1960, Vine 1973), although past studies of social carnivores suggests that animals in groups are less vulnerable to predation at kills than single animals (Cooper 1991, Carbone *et al*. 1997). That males left kills more quickly when in large groups suggests that risk of attracting dangerous scavengers may be high when coalition size is large.

Our results were ambiguous for single females with two findings in support of the predator avoidance hypotheses and three against. Although alone, and perhaps difficult to detect, single females were in no way immune from the attentions of predators. Our results suggest, however, that the energetic and opportunity costs of vigorous predator-avoidance behaviors may be too great for single females; rather they try to eat and depart from their kills as rapidly as possible. Trade-offs between predation or kleptoparasitism risks and speed of eating have not been addressed directly in the literature and requires more attention. Giving-up-densities (Brown *et al*. 1999) have been used to assess perception of risk in rodents, however this measure is not appropriate for large non-divisible food items, like those eaten by cheetahs

Adult cheetahs are rarely killed by dangerous scavengers, although predation is the chief source of mortality for cheetah cubs (Laurenson 1994). While some of our findings supported attempts to reduce predation on mothers themselves, others refuted it. Nonetheless a great majority supported mothers trying to reduce cub predation. Young cubs are likely to require more time to escape from approaching predators and therefore we expected mothers with young cubs to be more wary of potential predators than mothers with old cubs and while this was the case with moving a kill and vigilance, we did not find a significant impact of cub age on the delay for mothers to depart from a kill. This outcome was unexpected and can have major fitness consequences; SMD observed a mother cheetah and cubs remain near a kill after finishing feeding, despite a growing number of vultures and one of the cubs was subsequently killed by a scavenging lion.

Larger litters have larger energetic demands than small litters and as a result mother cheetahs spend more time searching for food as litter size increases (Caro 1989). While provisioning offspring is energetically costly forcing mother cheetahs to hunt frequently, Caro (1987) found that cheetah mother vigilance at kills was significantly associated with anti-predator measures, as opposed to searching for additional prey. Mother cheetahs should invest more in larger litters as larger litters carry a greater replacement cost (Winkler 1987, Montgomerie and Weatherhead 1988, Clutton-Brock 1991). Our findings that mothers are more vigilant with larger litters are contrary to those found by Caro (1987), who found that litter size had no impact on mothers' vigilance. There is also some evidence to suggest that risk of predation increases with litter size (see Caro 1987) and this difference in risk may further explain increased vigilance with large litters. An alternative explanation may be that vigilance was recorded as the percentage of time a mother spent at a kill but not feeding and, while we interpolated vigilance from this percentage, mothers may have been raising their heads and pausing to allow their cubs to feed, rather than scanning for approaching scavengers. This may explain the greater recorded "vigilance" of mothers with more cubs. Juvenile feeding priority has been recorded in feral domestic cats (*Felis catus*) (Yamane *et al*. 1997) and given that cub survival must depend to some extent on their speed of development and the resulting ability to outrun predators, mother cheetahs may be willing to forego self-feeding opportunities to maximize feeding opportunities for their offspring.

Conclusions

Classic examples of the tradeoff between foraging and predation suggest that prey animals can either inhabit safe environments where there is no food or forage in places that make them vulnerable to predation (*e.g.* Werner 1983, Sih 1986, Lima 1988b, Lima and Dill 1990, Hilton *et al*. 1999, Martin *et al*. 2003). For meso-carnivores this tradeoff is more complicated, as the nature of their food resources makes them vulnerable to predation and to having their kills stolen. This simultaneous risk makes it is difficult to tease apart behavioral decisions made with regard to the relative risks of predation and kleptoparasitism and although the measures used in this study could not easily distinguish between avoidance of predators or kleptoparasites, our results do indicate that single females did not appear to using behavioral measures to avoid dangerous scavengers at kills. In contrast, males may use strategies to avoid being killed, despite the low risk and high cost of these behaviors, and mother cheetahs behaved to reduce the risk of cub predation.

ACKNOWLEDGEMENTS

We thank the Tanzania Commission for Science and Technology, Tanzania Wildlife Research Institute and Tanzania National Parks for permission. We thank Lindsay Turnbull, Isla Graham, Jos Milner, Jane Wisbey, Ian and Ghislaine Sayers, John Shemkunde, and Sultana Bashir for help with data collection. Funding was provided to JSH by the National Science Foundation and the University of California, to SMD by Wildlife Conservation Society, Frankfurt Zoological Society, National Geographic Society, Peoples Trust for Endangered Species, the Howard Buffett Foundation and the Times Christmas Appeal 1998 and to TMC by the Royal Society and the National Geographic Society. SMD is grateful to everyone at SWRC, SENAPA, the late Hugo van Lawick and his team, Frankfurt Zoological Society, Greg and Maria Russell, and Ndutu lodge for logistical support during field work. This study was conducted in full compliance with the laws and regulations governing scientific study in Tanzania.

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Table 1.1 Predictions for cheetah behavior in support of hypotheses for avoiding interspecific killing of adults and cubs. Potential outcomes marked “N/A” are not appropriate or relevant and for those marked “No prediction,” we made no explicit prediction about the direction of any significant effects. Cub age was scored as young (1) or not-young (0) therefore a positive expected result means that we expected behavior to be exhibited significantly more often then the mother was accompanied by young cubs as compared to older cubs.

	Avoid being killed	Avoid cubs being killed
Moving a kill		
Prey size	+[*]	+
Grass height	+[*]	+
Shade	+[*]	+
Belly size (start)	+[*]	No prediction
Number of adults	-[*]	N/A
Cub age	N/A	+
Number of cubs	N/A	+
Vigilance		
Prey size	+	+
Grass height	-	-
Shade	+	+
Belly size (start)	+	No prediction
Number of adults	-	N/A
Cub age	N/A	+
Number of cubs	N/A	+
Delay in leaving		
Prey size	-	-
Grass height	+	+
Shade	+	+
Belly size (end)	No prediction	No prediction
Number of adults	+	N/A
Cub age	N/A	-
Number of cubs	N/A	-

[*] potential outcomes that might also support avoiding kleptoparasitism

Table 1.2   Prey species from 639 cheetah kills. The juvenile category includes all classes of subadult animals (i.e. newborn, fawn, yearling, subadult). Starred categories (*) are those prey which were estimated to weigh less than 10 kg. For most species, juvenile or adult animals could be placed discretely in one of the two weight classes; twenty-five juvenile Thomson's gazelle kills were estimated to be greater than 10 kg and were included as such in all analyses.

Species	Juvenile	Adult
Thomson's gazelle (*Gazella thomsoni)*	322^{*}	108
Hares *(Lepus spp.*)	59^{*}	28^{*}
Wildebeest *(Connochaetes taurinus)*	45	2
Grant's gazelle *(Gazella granti)*	27^{*}	15
Reedbuck *(Redunca redunca)*	2^{*}	8
Burchell's zebra *(Equus burchelli*)	3	0
Impala *(Aepyceros melampus)*	2	0
Warthog (*Phacochoerus aethiopicus*)	2	0
Eland *(Taurotragus oryx)*	2^{*}	0
Hartebeest *(Alcelaphus buselaphus)*	2	0
Dik-dik *(Madoqua kirki)*	0	1^{*}
Bat-eared fox *(Otocyon megalotis)*	0	1^{*}

Table 1.3. Ecological and demographic factors influencing the propensity of cheetahs to move kills. These analyses include data from at total of 376 kills made by males, single females and females with cubs that were observed from when a kill was made until the cheetah started eating. Significant main effects ($p \leq 0.05$) are in bold type and significant 2-way interactions are noted in the text. Cheetah identity did not have a significant influence on the propensity for cheetahs to move kills and was not included in the final model.

	Coefficient	Dispersion	Statistic	p-value
Males				
Prey size	7.94	1	$\chi^2_1 = 9.64$	**0.002**
Grass height	0.0717	1	$\chi^2_1 = 14.26$	**< 0.001**
Shade	2.58	1	$\chi^2_1 = 4.76$	**0.029**
Belly size (start)	-0.126	1	$\chi^2_1 = 0.27$	0.60
Time of day	-0.355	1	$\chi^2_1 = 6.03$	**0.014**
Number of males	-0.806	1	$\chi^2_1 = 3.24$	0.07
Individual identity	-	-	$\chi^2_{58} = 1.41$	1.00
Single females				
Prey size	7.5	1	$\chi^2_1 = 5.22$	**0.022**
Grass height	-0.0394	1	$\chi^2_1 = 2.47$	0.17
Shade	7.8	1	$\chi^2_1 = 0.097$	0.76
Time of day	1.789	1	$\chi^2_1 = 3.64$	0.06
Belly size (start)	-0.478	1	$\chi^2_1 = 4.31$	**0.038**
Individual identity	-	-	$\chi^2_{49} = 1.03$	1.00
Females with cubs				
Prey size	-1.845	1	$\chi^2_1 = 13.6$	**< 0.001**
Grass height	0.0489	1	$\chi^2_1 = 30.1$	**< 0.001**
Shade	4.05	1	$\chi^2_1 = 38.5$	**< 0.001**
Belly size (start)	-0.0197	1	$\chi^2_1 = 0.04$	0.84
Time of day	-0.050	1	$\chi^2_1 = 0.01$	0.92
Cub age	1.701	1	$\chi^2_1 = 26.8$	**< 0.001**
Number of cubs	0.291	1	$\chi^2_1 = 2.67$	0.10
Individual identity	-	-	$\chi^2_{234} = 1.81$	1.00

Table 1.4 Ecological and demographic factors influencing vigilance at cheetahs kills. These analyses include 236 kills made by each of the three primary age/sex groups and observed for the duration of cheetah feeding where the percentage of time at kill spent being vigilant was recorded. Significant main effects ($p \leq 0.05$) are in bold type and all significant 2-way interactions are noted in the text. Cheetah identity did not have a significant influence on the vigilance of cheetahs at kills and was not included in the final model.

	Coefficient	Dispersion	Statistic	p-value
Males				
Prey size	0.1191	1	$t_{38} = 2.02$	**0.05**
Grass height	0.00206	1	$t_{38} = 1.30$	0.20
Shade	0.076	1	$t_{38} = 0.57$	0.57
Belly size (start)	0.0151	1	$t_{38} = 0.94$	0.35
Time of day	0.0865	1	$t_{38} = 1.49$	0.14
Number of males	-0.0020	1	$t_{38} = 0.06$	0.95
Individual identity	-	-	$F_{9,38} = 0.05$	0.99
Single females				
Prey size	1.666	1	$t_{26} = 2.55$	**0.017**
Grass height	-0.00677	1	$t_{26} = 1.71$	0.10
Shade	0.183	1	$t_{26} = 1.63$	0.12
Time of day	-0.1020	1	$t_{26} = 1.54$	0.14
Belly size (start)	0.0094	1	$t_{26} = 0.50$	0.62
Individual identity	-	-	$F_{14,26} = 0.03$	1.00
Females with cubs				
Prey size	0.1211	1	$t_{169} = 3.49$	**< 0.001**
Grass height	0.0028	1	$t_{169} = 3.20$	**0.002**
Shade	0.0332	1	$t_{169} = 0.72$	0.47
Belly size (start)	-0.0155	1	$t_{169} = 1.65$	0.10
Time of day	0.0513	1	$t_{169} = 1.74$	0.84
Cub age	0.1309	1	$t_{169} = 4.28$	**< 0.001**
Number of cubs	0.0400	1	$t_{169} = 2.15$	**0.033**
Individual identity	-	-	$F_{41,169} = 0.06$	1.00

Table 1.5 Ecological and demographic factors influencing cheetah delay in leaving a kill. These analyses include 147 kills made by males, single females or mothers with cubs, for which the delay in leaving a carcass was recorded. Significant main effects ($p \leq 0.05$) are in bold type. Significant 2-way interactions are noted in the text. Cheetah identity did not have a significant influence the delay for cheetahs to leave a kill and was not included in the final model.

	Coefficient	Dispersion	Statistic	p-value
Males				
Prey size	-0.238	0.819	$\chi^2_1 = 5.30$	**0.021**
Grass height	0.0055	0.832	$\chi^2_1 = 3.05$	0.08
Shade	-0.819	0.819	$\chi^2_1 = 8.09$	**0.003**
Belly size (end)	0.0107	0.796	$\chi^2_1 = 0.031$	0.58
Time of day	-0.193	0.774	$\chi^2_1 = 2.04$	0.15
Number of males	-0.3731	0.819	$\chi^2_1 = 50.54$	**< 0.001**
Individual identity	-	-	$\chi^2_{31} = 1.35$	1.00
Single females				
Prey size	1.011	0.49	$\chi^2_1 = 83.4$	**< 0.001**
Grass height	-0.0072	0.49	$\chi^2_1 = 13.34$	**< 0.001**
Shade	-0.133	0.49	$\chi^2_1 = 0.06$	0.81
Belly size (end)	0.0215	0.49	$\chi^2_1 = 9.90$	**< 0.001**
Time of day	0.2636	0.49	$\chi^2_1 = 39.8$	**< 0.001**
Individual identity	-	-	$\chi^2_{33} = 0.04$	1.00
Females with cubs				
Prey size	0.0658	1.70	$\chi^2_1 = 4.29$	**0.038**
Grass height	-0.0008	1.70	$\chi^2_1 = 4.21$	**0.040**
Shade	-0.0628	1.68	$\chi^2_1 = 2.57$	0.11
Belly size (end)	-0.0164	1.70	$\chi^2_1 = 6.57$	**0.010**
Time of day	0.0137	1.70	$\chi^2_1 = 0.15$	0.70
Cub age	-0.0288	1.70	$\chi^2_1 = 0.44$	0.50
Number of cubs	-0.0396	2.19	$\chi^2_1 = 7.29$	**0.007**
Individual identity	-	-	$\chi^2_{83} = 4.43$	1.00

Table 1.6 The effects of moving a kill on the eventual arrival of scavengers using 460 kills that were observed from the time a kill was made to the time a cheetah finished feeding. Therefore, it is known whether or not kills were moved and whether or not particular scavengers arrived. Significant main effects ($p \leq 0.05$) are in bold type and significant 2-way interactions are noted in the text. Variables with inadequate sample sizes are signified with N/A.

	Coefficient	Dispersion	Statistic	p-value
All cheetahs				
Vulture	-0.144	1	$\chi^2_1 = 0.03$	0.86
Jackal	-0.731	1	$\chi^2_1 = 4.4$	**0.036**
Hyena	-0.863	1	$\chi^2_1 = 5.6$	**0.018**
Lion	1.01	1	$\chi^2_1 = 1.0$	0.31
Males				
Vulture	-1.296	1	$\chi^2_1 = 2.23$	0.13
Jackal	1.91	1	$\chi^2_1 = 2.36$	0.12
Hyena	2.21	1	$\chi^2_1 = 3.23$	0.07
Lion	N/A	N/A	N/A	N/A
Number of cheetahs	-0.689	1	$\chi^2_1 = 1.67$	0.19
Single females				
Vulture	6.4	1	$\chi^2_1 = 0.21$	0.65
Jackal	-2.03	1	$\chi^2_1 = 2.52$	0.11
Hyena	N/A	N/A	N/A	N/A
Lion	8.5	1	$\chi^2_1 = 0.0$	1.00
Females with cubs				
Vulture	0.066	1	$\chi^2_1 = 0.13$	0.72
Jackal	0.048	1	$\chi^2_1 = -0.156$	0.69
Hyena	-0.156	1	$\chi^2_1 = 0.063$	0.80
Lion	-8.0	1	$\chi^2_1 = 0.0$	1.00
Cub age	1.386	1	$\chi^2_1 = 14.3$	**< 0.001**
Number of cubs	-0.133	1	$\chi^2_1 = 0.207$	0.65

Table 1.7 Cheetah vigilance at kills with scavenger species present, including 460 kills that were observed from the end of a successful hunt until the cheetah(s) finished feeding. By limiting analyses to these data it is possible to assess vigilance as percent of time at kill but not feeding and the presence or absence of particular scavenger species. Significant results ($p \leq 0.05$) are in bold type. Variables with inadequate sample sizes are signified with N/A. There were no significant 2-way interactions.

	Coefficient	Dispersion	Statistic	p-value
All cheetahs				
Vulture	0.1203	1	$t_{279} = 4.36$	**< 0.001**
Jackal	-0.0498	1	$t_{279} = 1.28$	0.20
Hyena	-0.2121	1	$t_{279} = 5.18$	**< 0.001**
Lion	0.1490	1	$t_{279} = 1.78$	0.08
Males				
Vulture	0.0	1	$t_{24} = 0.0$	1.00
Jackal	-0.001	1	$t_{24} = 0.0$	1.00
Hyena	-0.255	1	$t_{24} = 1.87$	0.07
Lion	N/A	N/A	N/A	N/A
Number of cheetahs	-0.0111	1	$t_{24} = 0.18$	0.86
Single females				
Vulture	N/A	N/A	N/A	N/A.
Jackal	-0.0301	1	$t_{23} = 0.34$	0.74
Hyena	N/A	N/A	N/A	N/A
Lion	0.233	1	$t_{23} = 1.14$	0.27
Females with cubs				
Vulture	0.1254	1	$t_{166} = 3.40$	**< 0.001**
Jackal	0.0012	1	$t_{166}= 0.03$	0.97
Hyena	0.087	1	$t_{166} = 0.51$	0.61
Lion	0.210	1	$t_{166} = 1.52$	0.13
Cub age	0.315	1	$t_{166} = 2.98$	**0.003**
Number of cubs	0.0892	1	$t_{166} = 2.62$	**0.01**

Table 1.8 The effects of scavenger presence on cheetah delay in leaving a carcass using 460 kills that were observed from the end of a successful hunt until the cheetah(s) finished feeding. Significant results ($p \leq 0.05$) are in bold type. Variables with inadequate sample sizes are signified with N/A. There were no significant 2-way interactions.

	Coefficient	Dispersion	Statistic	p-value
All cheetahs				
Vulture	0.0682	2.16	$\chi^2_1 = 5.88$	**0.024**
Jackal	N/A	N/A	N/A	N/A
Hyena	0.930	2.14	$\chi^2_1 = 2.73$	0.10
Lion	0.868	2.16	$\chi^2_1 = 5.46$	**0.019**
Males				
Vulture	0.601	1.37	$\chi^2_1 = 15.95$	**< 0.001**
Jackal	N/A	N/A	N/A	N/A
Hyena	0.404	1.41	$\chi^2_1 = 1.09$	0.30
Lion	N/A	N/A	N/A	N/A
Number of cheetahs	-0.1718	0.780	$\chi^2_1 = 27.81$	**< 0.001**
Single females				
Vulture	0.195	2.58	$\chi^2_1 = 3.69$	**0.05**
Jackal	N/A	N/A	N/A	N/A
Hyena	0.857	2.47	$\chi^2_1 = 2.75$	0.10
Lion	N/A	N/A	N/A	N/A
Females with cubs				
Vulture	0.0223	2.11	$\chi^2_1 = 2.51$	n.s.
Jackal	N/A	N/A	N/A	N/A
Hyena	0.252	2.02	$\chi^2_1 = 5.49$	**0.019**
Lion	0.859	1.94	$\chi^2_1 = 4.20$	**0.040**
Cub age	-0.0340	1.92	$\chi^2_1 = 1.94$	0.16
Number of cubs	-0.0254	1.82	$\chi^2_1 = 5.13$	**0.024**

Table 1.9. Significant main effects with respect to our hypotheses of adult killing, cub killing for males, single females and females with cubs. Starred (*) outcomes concurrently support avoidance of kleptoparasitism. Some of the significant results that did not support our hypotheses were ambiguous (†) and neither supported nor were contradictory to our predictions. As such these should be interpreted as weak evidence, when compared to other outcomes.

Age/Sex	Hypothesis	Significant results in support of hypothesis	Significant results that do not support hypothesis
Males	Adult killing	1. Move more with large prey* 2. Move to taller grass * 3. Move to shade* 4. More vigilant at larger kills 5. Leave sooner from large kills	1. Leave sooner from shade 2. Leave sooner with increasing group size
Females	Adult killing	1. Move more with large prey* 2. More vigilant at large kills	1. Move more when hungry 2. Leave sooner from small kills 3. Leave sooner in taller grass†
Females With cubs	Adult killing	1. Move to taller grass * 2. Move to shade* 3. More vigilant at large kills 4. Leave sooner when well-fed	1. Move more with small prey† 2. More vigilant in taller grass † 3. Leave sooner from small kills 4. Leave sooner in taller grass †
	Cub killing	1. Move to taller grass* 2. Move to shade* 3. Move more with young cubs 4. More vigilant at large kills 5. Move vigilant with young cubs 6. More vigilant with more cubs 7. Leave sooner when well-fed 8. Leave sooner with more cubs	1. Move more with small prey† 2. More vigilant in taller grass† 3. Leave sooner with small prey 4. Leave sooner in taller grass†

CHAPTER 2

Patterns of scavenger arrival at cheetah kills in Serengeti National Park, Tanzania

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ABSTRACT

Scavenging by large bodied vertebrates is observed in many ecosystems but has rarely been quantified. Here we document the timing and order of scavenger arrival at 639 cheetah kills in Serengeti National Park, Tanzania, focusing on ecological and heterospecific factors that may impact detectability of carcasses to small, medium and large sized vultures, jackals, spotted hyenas and lions; all of these scavengers were more likely to be present at the carcasses of large-bodied prey. Lions and spotted hyenas were less likely to locate kills in tall grass; medium sized vultures were likely to arrive before both large and small vultures; whereas spotted hyenas and vultures were likely to be present at kills simultaneously. Despite numerous anecdotal accounts, we did not find that hyenas use alighting vultures as a means of locating food. Our findings, therefore show that other scavengers and environmental variables affecting carcass detectability both influence the costs of scavenging in the terrestrial ecosystem.

INTRODUCTION

For terrestrial and avian scavengers, scavenging is an important way to gain access to food because carrion is a valuable source of protein but the mechanisms used by scavengers to locate carrion are largely unknown (DeVault *et al.* 2003). In Serengeti National Park, Tanzania, there are several opportunistic and obligate vertebrate scavengers and consequently this ecosystem has been the site of many of the most influential studies of scavenging behaviour (Kruuk 1967, Pennycuick 1972, Houston 1974, 1975, 1979, Blumenschine 1986). As many as eleven species of birds occasionally feed on animal carcasses in Serengeti and eight species obtain a substantial portion of their diet from scavenging, including seven species of vulture (white-backed griffon, *Gyps africanus;* Ruppell's griffon, *G. rueppellii*; Egyptian, *Neophron percnopterus*; hooded, *Necrosyrtes monachus*; Lammergeyer, *Gypaetus barbatus*; white-headed, *Trigonoceps occipitalis* and lappet-faced, *Torgos tracheliotus*) and marabou storks (*Leptoptilos crumeniferus*). Scavenging behaviour by terrestrial carnivores in Serengeti has been recorded in lions (*Panthera leo*) (Kruuk 1972, Schaller 1972), spotted hyenas (*Crocuta crocuta*) (Kruuk 1972, Schaller 1972), black-backed and golden jackals (*Canis mesomelas* and *C. aureus*) (Kruuk 1972) but rarely in leopards (*Panthera pardus*) (Houston 1979) or cheetahs (*Acinonyx jubatus*) (Caro 1994).

A number of ecological and heterospecific factors are thought to affect the detectability of carcasses and therefore opportunities for scavenging. The activity cycle of carnivores should dictate when scavenging can occur. For example, many carcasses result from kills by crepuscular and nocturnal predators, like lions and hyenas, but vultures are thought to scavenge only during the day. Large carcasses persist for significantly longer than small carcasses and thereby tend to attract more scavengers (Blumenschine 1986). Habitat may also be important because, in Serengeti, both ungulate and carnivore biomass is greater on the plains than in the woodlands (Sinclair 1979, Blumenschine 1986, Domínguez-Rodrigo 2000). Competition among scavengers is thought to be higher in open areas than in woodlands because carcasses and feeding animals can be seen more easily in the open than in areas with tree cover (Blumenschine 1986, Domínguez-Rodrigo 2000). Finally, anecdotal accounts suggest scavengers use heterospecifics to locate carrion (*e.g.* Kruuk 1972, Schaller 1972, Creel *et al.* 2001); indeed there may be a strict arrival order of vultures at carcasses (Kruuk 1967, Houston 1975). To date, the relationships between scavenging and these factors are largely speculative, with few empirical studies addressing the importance of ecological and heterospecific interactions affecting carcass availability.

Large carnivores actively defend their kills from approaching scavengers and can remain near their kills, continuing to feed off them for some time, and in addition there can be competition between scavengers for access to high-quality meat. At cheetah kills, however, the potential risk of death or injury associated with scavenging large carnivore kills are virtually nonexistent because cheetahs are notorious for leaving their kills quickly and seldom consume an entire carcass (Houston 1979). They rarely, if ever, defend their kills and never return to a carcass, after having abandoned it. Therefore, in this study, we use cheetah kills as a tool to examine the factors that influence scavenger arrival at carcasses in East Africa.

METHODS

All observations took place at 639 cheetah kills from 1980-1984 (TMC) and 1991-2004 (SMD) in Serengeti National Park, Tanzania. Kills were divided into two categories of prey size, given differences in carcass detectability and persistence times (Blumenschine 1986), 0-10 kg (n=416 kills) and >10kg (n=213 kills). Kills were found either on the plains or plains-woodland border with habitat designation being based on the height and density of vegetation (see Sinclair 1979 for a complete description). The height of any grass in which a carcass lay in was estimated by eye in 20cm increments (0-20cm; 20-40cm; 40-60cm, 60-80cm, 80-100cm). Whether or not a kill was shaded by tree cover was noted too.

We focused on the 10 most common scavengers in the Serengeti: six vulture species (white-backed, lappet-faced, white-backed griffon, Ruppell's griffon, hooded and Egyptian vultures), two jackal species (black backed and golden jackals), spotted hyenas and lions. Marabou storks and tawny eagles (*Aquila rapax*) were present at very few kills (<10) and were not considered in these analyses.

TMC noted scavenger arrival time and numbers arriving by recording data at 2-minute intervals from the time cheetahs began to feed at a carcass (typically 0-5 minutes after a kill was made) until feeding ended. Scavengers were considered present at a kill if they were within 500 m of the feeding cheetahs. SMD recorded the time that the first vulture species arrived at each kill and total vulture number every five minutes from when the prey was first brought down. Vulture numbers and composition were again recorded when cheetahs finished feeding and when cheetahs left a kill. All of these observations took place during daily observations of cheetah family groups and *ad hoc* encounters with cheetah at kills.

To analyze presence or absence of a particular scavenger species at each kill, we used a subset of 458 kills, excluding those kills where observations started after the cheetahs began feeding. For the remainder of the analyses the entire data set was used (639 kills). Our analyses were conducted using a combination of SPSS (vers. 9.0) and GenStat (7th ed.). Vultures were tested both as a single scavenger classification and were also separated into three groups (small, medium and large vultures) based on body size and feeding ecology (Kruuk 1967, Hertel 1994). Presence or absence of each scavenger grouping (small: hooded and Egyptian vultures, medium: white backed and Ruppell's griffon and large vultures: white-headed and lappet-faced vultures), jackals, spotted hyenas and lions) was fitted to a binomial distribution and tested, with a general linear model, against time of day, prey size, habitat type, grass height and shade together with all 2-way interactions. Lions and hyenas were also grouped where noted. Non-significant variables were eliminated step-wise with the least significant variables removed first. To assess any heterospecific attraction between scavenger species we compared the ranked arrival order of all scavengers, using a Wilcoxon's sign rank test to detect the magnitude of difference in arrival order between species pairs.

RESULTS

Of the 458 kills observed in their entirety, vultures appeared at 32% (147 kills), spotted hyenas at 71 (15.5%) and lions at only 15 kills (3.3%). Of TMC's observations, jackals were present at 40 of 282 kills (14.2%) (Figure 2.1). In general, terrestrial scavengers tended to arrive sooner after a kill was made than did vultures (Figure 2.2). In 69 of the 431 kills for which a definitive outcome is known, cheetahs were eventually forced off their kills by scavengers (12.9%). The majority of these carcasses were surrendered to spotted hyenas (54 of 69 lost kills; 78%). Lions and other cheetahs accounted for 15% and 3% of kills lost, respectively, and in 4% of kills that were abandoned, cheetahs were forced off by various other non-scavengers (i.e. tourist interference, warthogs *Phacochoerus africanus*, baboons *Papio anubis*).

Ecological factors

There was no significant difference in the time of day that jackals, hyenas, lions or vultures arrived at cheetah kills (Table 2.1). We found that larger carcasses drew significantly more vultures, jackals, hyenas and lions than small kills. Carcasses on the plains-woodland border or concealed by shade were no less likely to be discovered by large or small vultures, jackals, lions and hyenas then those in open grassland. However, medium sized vultures were significantly more likely to arrive at kills on the plains than on the plains-woodland border (χ^2=4.0, df=1, n=273, p=0.046) although they were unaffected by shade. Furthermore, hyenas and lions were each more likely to arrive at kills in shorter grass (χ^2=4.4, n=429, df=1, p=0.036 and χ^2=6.1, df=1, n=429, p=0.014, respectively).

Heterospecific attraction

Overall, there were strong correlations between vulture presence and the presence of hyenas (χ^2=11.7, df=1, n=456, p<0.001) and jackals (χ^2=12.9, df=1, n=280, p<0.001). There was a strong association between the presence of all three vulture classifications at cheetah kills (Table 2.2). Small vulture presence was associated with large vulture presence (χ^2=15.6, df=1, n=282, p<0.001). Medium vulture presence was significantly related to both large (χ^2=25.1, df=1, n=282, p<0.001) and small vulture presence (χ^2=34.1, df=1, n=282, p<0.001) at carcasses. Medium vulture presence was also correlated with jackal (χ^2=8.0, df=1, n=282, p=0.004) and hyena presence (χ^2=6.5, df=1, n=282, p=0.01). Finally, small vultures were also related to hyena presence (χ^2=4.6, df=1, n=282, p=0.03).

There was little concordance between arrival order, with most scavenger groups equally likely to be the first species at a kill (Figure 2.3). Medium-sized vultures were significantly more likely to arrive at kills before large vultures (Wilcoxon's sign rank test, n=20, p=0.014), however, and small vultures were somewhat more likely to arrive after medium-sized vultures (Wilcoxon's sign rank test, n=16, p=0.08). We found hyenas and vultures to be equally likely to proceed each other at kills. When kills were divided by those stolen early (<5 min after a kill was made) and those stolen late (>5 min) we found that vultures arrived before hyenas and lions significantly more frequently at kills that were stolen late (Wilcoxon's sign rank test, n=11, p=0.029) and conversely, vultures arrived significantly later than hyenas and lions at kills stolen early (Wilcoxon's sign rank test, n=9, p=0.020).

DISCUSSION

Avian scavengers

Large-sized vultures.

Kruuk (1967) found that in Serengeti the largest vultures (white-headed and lappet-faced) tended to arrive earliest at a kill and feed off strips of flesh torn from the carcasses. They are suspected to kill their own prey periodically (Petrides, 1959, Kruuk, 1967). We found that these species tended to co-occur with other vultures and were frequently the second vulture group to arrive at a kill. Pennycuick (1972) and Houston (1975) both suggested that these species were dependent on temperature-driven thermal-updrafts and were therefore less active during the early hours of the day. However, our quantitative analyses found no effect of time of day on the probability of large-sized vultures arriving at cheetah kills.

Medium-sized vultures.

Of vultures living in Serengeti, only medium-sized (Ruppell's griffon and white-backed) vultures are considered obligate scavengers (Houston 1979). Bone fragments, disarticulated by hyenas and other bone-crushing carnivores are an important part of griffon vulture diet (Richardson *et al.* 1986). Kruuk (1967) noted that these vultures tend to arrive at carcasses after the lappet-faced and white-headed vultures. We found the opposite result, with medium-sized vultures more likely to precede the larger sized vultures at kills. Houston (1974) found griffon vultures located carrion by sight alone, rarely discovering carcasses concealed in trees or otherwise covered. In this study, we found a similar result, with Ruppell's and white-backed vultures less likely to arrive at kill made on the plains-woodland border than kills on the plains.

Small-sized vultures.

Hooded and Egyptian vultures are the smallest vultures in Serengeti and were infrequently seen at cheetah kills. Kruuk (1967) found these species tended to arrive last at carcasses. We found weak support for this, with small-sized vultures tending to arrive after medium-sized vultures. These species are unable to access much material on a dead animal, instead feeding primarily on scraps on the ground around carcasses (Petrides 1959, Kruuk 1967). Their feeding method makes the presence of other vulture species very important. These two species rarely arrived first at a kill and co-occurred with other vultures at the vast majority of kills at which they were present. Small-sized vultures may be attracted to other vultures landing both as a cue to food and because they depend on other vultures to facilitate their feeding. Hooded and

Egyptian vultures both supplement carrion with insects, dung and small vertebrates (Houston, 1979) and may therefore be less dependent on carrion than the other vultures.

Terrestrial scavengers

Jackals.

While black-backed and golden jackals persist largely by hunting small vertebrates and foraging on vegetative matter (Lamprecht 1978), Kruuk (1967) suggested the jackals compete heavily with vultures and are even occasionally killed by lions and hyenas at carcasses. Based on fecal analyses, however, carrion accounts for only 3% of jackal diets (Houston 1979). Similarly, Blumenschine (1986) found no measurable impact of jackal scavenging on carcass persistence. Jackals were present only at 14% of TMC's cheetah kills and were only rarely observed by SMD. They seem to be associated with vultures, in general, but not to follow vultures to kills, as has been suggested for lions and hyenas. Jackals rely little on carrion and are potentially at risk from both cheetahs and other scavengers at carcasses.

Spotted hyenas.

Of the three hyenids in Serengeti, only the spotted hyena is thought to feed significantly from carrion (Pienaar 1969, Waser 1980). Despite a reputation as predominant scavenger, spotted hyenas hunt the majority of prey they consume (Kruuk 1972, Tilson and Henschel 1986, Cooper 1990, Gasaway *et al.* 1991) although they tend to scavenge the majority of the food eaten during the day (Kruuk 1972). We found that presence of hyenas were strongly related to presence of vultures. Kruuk (1972) characterized the relationship between hyenas and vultures as 'a complicated relationship of mutual benefit and competition' (p. 146), where hyenas provide scavenging opportunities to vultures and hyenas use landing vultures as a cue to a food source. Terrestrial scavengers sometimes locate cheetah kills by witnessing the hunt itself, cuing in on heterospecifics (i.e. alighting vultures) or stumbling across a feeding cheetah by chance. Our data show that hyenas were more likely to arrive at kills before vultures if kills were lost early, suggesting that for early losses they had most likely witnessed the hunt itself and were alerted to the carcass by fleeing prey. However, hyenas were more likely to arrive at kills after vultures if kills were lost late, suggesting that if hyenas did not witness a hunt itself, they were likely to be responding to cues such as alighting vultures to scavenge.

Lions.

Lions are thought to scavenge purely opportunistically, killing the majority of their prey and utilizing fresh carrion when encountered (Schaller 1972), nonetheless they are considered one of the most important mammalian scavengers in Serengeti (Houston 1974). As the most behaviorally dominant carnivore in the Serengeti ecosystem, lions frequently displace other carnivores from their kills to scavenge carcasses. While they were not significantly associated with any other scavenger group and were present at very few kills, lions forced cheetahs off their kills in all cases. Lions and hyenas compete intensely for food resources (Kruuk 1972, Schaller 1972, Cooper 1991), however, these species never co-occurred at kills in the study.

Long-term studies have yielded some information about the habits and behaviour of scavenging animals but this study addresses differences in the heterospecific and ecological parameters that influence carcass detectability across scavenging taxa. Our key finding is that while a number of ecological factors affect what species arrive at kills, these effects are experienced differently by different species, depending on how they locate food, their physical ability to handle it and whether or not they supplement carrion with other food. Terrestrial carnivores, especially lions and hyenas, were somewhat more affected by ecological factors than avian scavengers. Terrestrial carnivores may depend on smell to locate some carcasses whereas vultures use primarily sight and even sound (Kruuk 1967, Moshe and Yom Tove 1978). These different ways of locating carcasses, together with the tight association between some scavenger species, may differentially help scavenging animals locate carrion and thereby influence the costs and benefits of pursuing a scavenging strategy for locating food.

ACKNOWLEDGEMENTS

We thank the Tanzania Commission for Science and Technology, Tanzanian Wildlife Research Institute and Tanzania National Parks for permission. We also thank Lindsay Turnbull, Isla Graham, Jos Milner, Jane Wisbey, Ian and Ghislaine Sayers, John Shemkunde, and Sultana Bashir for help with data collection. Funding was provided to JSH by the National Science Foundation, SMD by Wildlife Conservation Society, Frankfurt Zoological Society, National Geographic Society, Peoples Trust for Endangered Species, the Howard Buffett Foundation and the Times Christmas Appeal 1998 and to TMC by the Royal Society and the National Geographic Society. SMD is grateful to everyone at SWRC, SENAPA, Hugo van Lawick's team, Frankfurt Zoological Society, Greg and Maria Russell, and Ndutu lodge for logistical support during field work.

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Table 2.1 Main effects of ecological factors affecting scavenger presence at kills.

Species Independent Variable	Coefficient	Deviance	df	Significance (p-value)
Large vulture				
time of day	-1.11	0.5	1	*n.s.*
prey size	1.066	6.7	1	0.01
grass height	-0.0146	1.7	1	*n.s.*
shade	0.198	0.1	1	*n.s.*
habitat type	0.563	2.1	1	*n.s.*
Medium vulture				
time of day	-0.66	0.3	1	*n.s.*
prey size	2.959	74.2	1	<0.001
grass height	-0.01023	1.1	1	*n.s.*
shade	-0.256	0.2	1	*n.s.*
habitat type	0.692	4.0	1	0.046
Small vulture				
time of day	-2.18	1.7	1	*n.s.*
prey size	1.402	9.7	1	0.002
grass height	-0.0231	2.9	1	*n.s.*
shade	0.865	1.7	1	*n.s.*
habitat type	0.377	0.6	1	*n.s.*
Jackal				
time of day	0.924	1.4	1	*n.s.*
prey size	0.887	5.5	1	0.019
grass height	-0.0095	0.9	1	*n.s.*
shade	-0.660	0.8	1	*n.s.*
habitat type	-0.079	0.0	1	*n.s.*
Spotted hyena				
time of day	-0.26	0.1	1	*n.s.*
prey size	1.495	3.8	1	0.05
grass height	-0.01770	22.4	1	<0.001
shade	-0.151	0.1	1	*n.s.*
habitat type	0.470	1.7	1	*n.s.*
Lion				
time of day	-5.25	0.00	1	*n.s.*
prey size	1.315	3.93	1	0.046
grass height	0.0382	7.14	1	0.007
shade	1.411	2.04	1	*n.s.*
habitat type	1.387	1.47	1	*n.s.*

Table 2.2 Associations between scavenger species at kills.

	Small vulture	Medium vulture	Large vulture	Jackal	Spotted hyena	Lion
Small vulture						
Medium vulture	<0.001					
Large vulture	<0.001	<0.001				
Jackal	*n.s.*	0.004	*n.s.*			
Spotted hyena	0.03	0.01	*n.s.*	*n.s.*		
Lion	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	

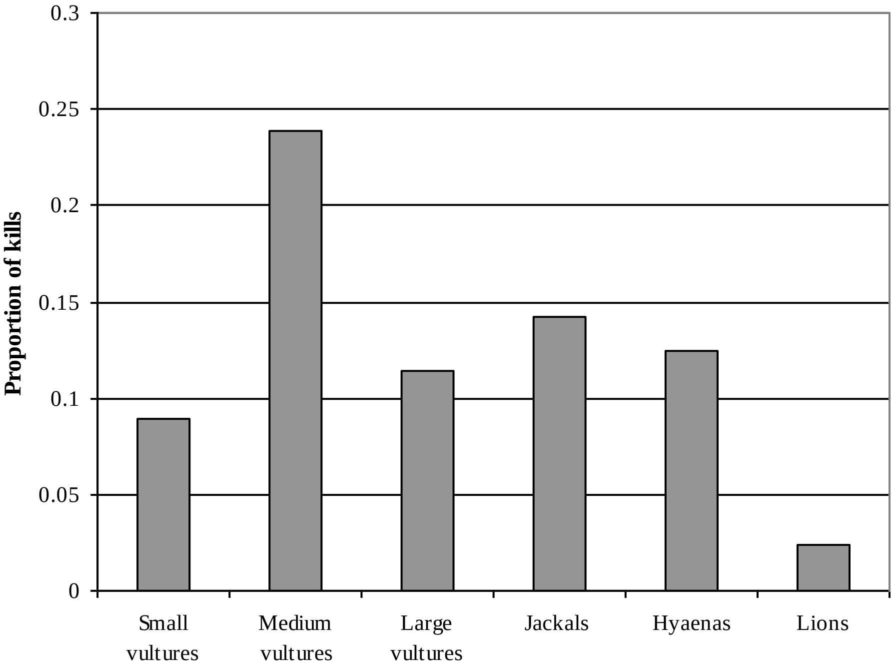

Figure 2.1. The proportion of kills with scavenger species present.

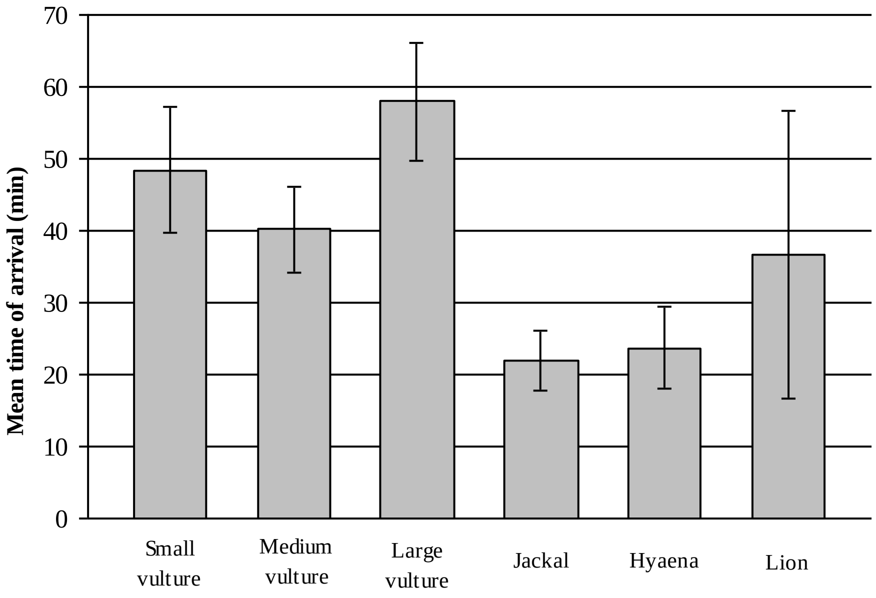

Figure 2.2. Mean (+/- S.E.) arrival time of scavengers after cheetahs began feeding.

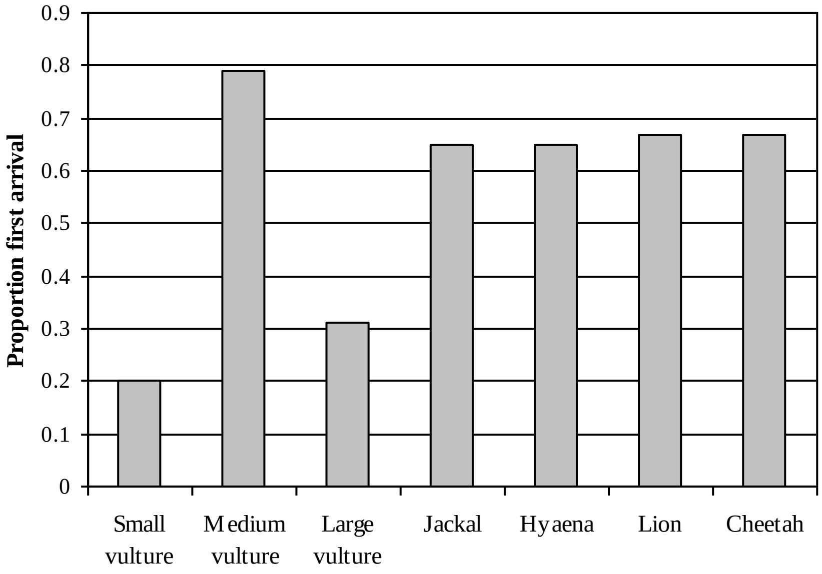

Figure 2.3. The proportion of arrivals at kills where species was the first scavenger to arrive.

CHAPTER 3

Interspecific competition and predation in American carnivore families

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ABSTRACT

Intraguild interactions play a prominent role in shaping ecological communities, so over evolutionary time one might expect that species that co-occur with a large number of competitors would evolve morphological and behavioral adaptations to ameliorate risks of intraguild competition and predation. In four different sets of analyses that took account of habitat stratum, habitat type and activity pattern on competition and predation pressure, significant differences were found in the extent to which American carnivore families potentially encounter other carnivores. Members of largely omnivorous families, Canidae and Ursidae, co-occur with a greater proportion of potential competitors than members of families with more specialized diets. We found that members of the Mustelidae family may reduce competition by being arboreal or aquatic, and that members of the Procyonidae and Mephitidae are potentially under great predation pressure but the former reduce this threat by being arboreal whereas Mephitidae likely reduce predation through advertising noxious secretions. In one analysis, conspicuous species with both contrasting facial and body coloration co-occurred with more potential predators than other less striking species of carnivore suggesting that intraguild predation is an evolutionary driver of contrasting coat coloration in carnivores. These quantitative analyses suggest that several facets of carnivore niche occupation and morphology have evolved in response to intraguild pressures.

INTRODUCTION

Small and middle-sized mammalian carnivores are often adversely affected by larger sympatric members of their guild (Palomares *et al*. 1996, Crooks and Soule 1999, Palomares and Caro 1999, Fedriani *et al*. 2000, Donadio and Buskirk 2006). Such interspecific competition takes the form of exploitation, namely competing indirectly for a shared resource (hereafter, competition) or interference, a direct encounter between species that can result in intraguild predation (hereafter, predation). Prey species, including carnivores themselves, use a number of anti-predator defenses to evade predators including morphological (*e.g.*, Merilaita and Lind 2005), behavioral (Lima and Dill 1990) and physiological (*e.g.*, Creel *et al*. 2007) adaptations and the mechanisms by which different carnivores avoid competitive interactions have been the focus of several studies over the last decade (Durant 1998, Ray and Sunquist 2001, Tannerfeldt *et al*. 2002, Frafjord 2003, Sheinin 2006). Currently, however, it is difficult to disentangle the extent to which biological attributes such as activity pattern or habitat preferences of a species have evolved to avoid predators as opposed to being adaptations to enhance foraging (but see Creel *et al*. 2005). Furthermore, ecological circumstances surrounding the evolution of some putative predator avoidance mechanisms are unknown. For example, the evolution of aposematic coloration of Mephitidae and some Mustelidae is well recognized (Ortolani and Caro 1996, Ortolani 1999, Newman *et al*. 2005) but, extraordinarily, the factors responsible for its evolution have never been addressed.

Here, we first examine the extent to which American carnivores face potential competition and also predation risk from other carnivores using three sorts of measures. In so doing, we are able to assess whether different carnivore families ameliorate risk using different habitat strata, habitat type and activity pattern. Second, we explore the extent to which these same biological traits differentially reduce competition or predation risk in the six North American carnivore families (see Donadio and Buskirk 2006 for a similar approach). We use geographic range overlap as a proxy for competitive interactions (see Stoner and Caro 2003, Donadio and

Buskirk 2006, Davies *et al*. 2007) allowing us to examine a large sample of mammalian carnivore potential interactions and thereby circumvent the problem of carnivores being rare and living at low population densities which makes it so difficult to assess competitive relationships. Our study is a large scale analysis that focuses on the ways in which carnivores avoid potential intraguild predators and competitors.

METHODS

Carnivore species

Seventy-seven species of terrestrial American carnivores, belonging to six families (Canidae, Felidae, Mephitidae, Mustelidae, Procyonidae and Ursidae) were included in our analyses. Marine otters were excluded because the majority of their intraguild interactions are with marine taxa not included in this study. Similarly, polar bears (*Ursus maritimus*) both compete with and prey upon members of the principally marine suborder Pinnipedia and are not represented here. Two Procyonid species (*Nasua nelsoni; Procyon pygmaea*) as well as the populations of *Urocyon cinereoargenteus* and *Potos flavus* on the island of Cozumel were excluded from all analyses due to uncertainties in taxonomic status (Decker and Wozencraft 1991, Cuaron *et al*. 2004). Additionally, *Procyon maynardi*, from the Bahamas, and *Procyon gloveralleni* and *Procyon minor* from the Lesser Antilles were excluded as these insular species probably originated from introduced *Procyon lotor* (Helgen and Wilson 2003). *Procyon insularis* was excluded due to a lack of genetic, ecological and behavioral knowledge. Finally, red wolves (*Canis rufus*) were excluded due to genetic ambiguity resulting from interbreeding with domestic dogs (*Canis familiaris*) and coyotes (*Canis latrans*) (Wayne and Jenks 1991, Nowak 2002).

Phylogenetic relationships between species included in this study follow the carnivore supertree of Bininda-Emonds *et al*. (1999) with six exceptions. 1. Following Dragoo and Honeycutt (1997), skunks were considered a monophyletic family (Mephitidae). 2. We included three species of spotted skunk (*Spilogale putorius; S. gracilis* and *S. pygmaea)* (Jones *et al*. 1992, Ferguson and Laviere 2002). 3. *Vulpes velox* and *V. macrotis* were designated separate species (Dragoo *et al*. 1990, Mercure *et al*. 1993, Wozencraft 2005). 4. Following Garcia-Perea (1994) and Wozencraft (2005) we considered 3 species of pampas cats (*Lynchailurus braccatus*, *L. colocolo* and *L. pajeros*)**.** 5. *Conepatus mesoleucus* and *C. leuconotus* were considered a single species (*C. leuconotus)* (Dragoo *et al*. 2003). 6. *Pseudalopex fulvipes* was considered a sister species to *P. gresieus* (Sillero-Zubiri *et al*. 2004) (Figure 3.1).

Data compilation

Contemporary digital range maps for American carnivores were obtained from NatureServe (Patterson *et al*. 2003) because historical range maps were available for only very few species. No digital maps were available for polar bears (here included as a competitor) so competition with other terrestrial carnivores was estimated using a combination of published polar bear range maps (Demaster and Stirling 1981) and digital range maps of potentially sympatric species. Two species were considered to overlap geographically if there was any area of overlap in their ranges whatsoever regardless of the size or percentage of entire range (but see Davies *et al*. 2007). Species were systematically compared on their ecological and behavioral attributes to infer risks of competition and predation from other carnivores.

Ecological data

Many behavioral, morphological and even physiological aspects of species' biology may function to mitigate impacts of pressure (Ruxton *et al*., 2004, Caro, 2005). We chose three behavioral and one morphological trait that were easy to documented categorically in Mammalian Species accounts, Emmons (1997), Reid (1998), Nowak (1999) and Sunquist and Sunquist (2002).

Habitat strata

Carnivore species were classified as arboreal if they lived >50% of the time in trees, or as terrestrial, fossorial or aquatic according to the habitat stratum that was used predominantly. In cases where two or more strata were used with approximately equal frequency, species were assigned to all relevant categories.

Habitat type

Eleven different habitat type designations were used to capture the diversity of biomes throughout the Americas: agricultural lands, arid, coastal areas, forest, high elevation forest, riparian areas, high elevation grasslands, scrubland, open areas, tundra and wetlands. Carnivore species that occurred in transitional areas (swampy-grassland, gallery forest, etc.) were included in each appropriate habitat classification.

Diet

Although quantitative data exist for diet of a small minority of species, data for most species are crude and we were forced to use coarse dietary categories. Species were classified as carnivorous, insectivorous, frugivorous or omnivorous. Carnivorous species were defined as those that feed principally on vertebrates but may supplement meat with vegetative matter, invertebrates or carrion. Insectivorous and frugivorous carnivores were those for whom insects or fruits constitute the majority of their diet, respectively, although we recognized that species in both categories eat small vertebrates, invertebrates and carrion occasionally. Species for which vertebrates do not make up the majority of their diet and feed opportunistically on a wide variety of edible material were considered omnivorous. Following Donadio and Buskirk (2006), carnivorous, insectivorous and frugivorous carnivores were assumed to compete only with co-occurring species of the same dietary category, whereas omnivores were considered to compete with all co-occurring species, regardless of dietary category (Morris 2005).

Social structure

Carnivores were placed into one of five social categories: solitary, pair-living, family groups, bands and packs. Classifications were based on the most common social associations of adult animals, excluding seasonal consorts and mothers with dependent offspring. Family groups were defined as an adult pair cohabitating with their sub-adult offspring, beyond the period of juvenile dependency. Bands were defined as social groups composed primarily of adult females and their young but males that are usually solitary. Finally, pack species live in groups of multiple adult males and females. Species with variability (n=10 species) in social grouping across their geographic range were placed in the largest recorded grouping category.

Activity pattern

Activity cycles were categorized as diurnal, nocturnal, crepuscular or cathemeral. While diurnal and nocturnal animals were considered to have separate activity patterns, cathemeral and crepuscular animals were considered to overlap with both nocturnal and diurnal species. Carnivores with variable activity cycles were conservatively scored as overlapping with species of all activity categories. Species with unknown activity cycles were excluded from analyses of activity patterns.

Coloration

Two categories of contrasting coloration were used to assess the potential role of aposematism in mitigating competition or predation pressure. These were facial contrast and body contrast. We considered contrasting coloration to be an abrupt demarcation between white and dark (either dark brown or black) markings. Facial contrast was defined as contrasting coloration occurring on the head, or between the ears, or between face and muzzle. Body contrast was defined as areas of contrasting coloration over the entire body, excluding head, throat and tail. All species were evaluated from color photographs, if available. For equivocal species we used a minimum of three photos to evaluate contrasts, obtained from a number of sources including IUCN taxon advisory groups, Macdonald (1984), Nowak (1999), Wilson and Ruff (1999) and Sunquist and Sunquist (2002). Species with frequent melanistic variation (i.e. *Gulo gulo*, *Eira barbara*) were excluded from analyses.

Body size

Species' body weights were taken from an average of male and female mean body weights (see Caro and Stoner 2003); in cases where no explicit mean was available, minimum and maximum recorded weights were averaged. Although body weight is a coarse measure particularly for those species with marked sexual dimorphism (Dayan *et al*. 1989) or those with great latitudinal variation in body mass, differences in body mass provide a crude indication of predatory abilities and vulnerabilities.

Data organization and analyses

The level of competition or predation experienced by each species was assessed in three ways: (i) worst-case, (ii) single-trait, and (iii) multi-trait indices. (i) In the worst-case analyses all geographically co-occurring species that were either omnivorous or shared the same diet with the focal species were viewed as *potential competitors*. Those species that routinely eat flesh (omnivorous or carnivorous) and are of appropriate size were viewed as *potential predators* of the focal species. Following Palomares and Caro (1999), we considered each focal species at risk of being killed by a solitary species that was equal in size or of greater body mass, or by social species equal to or greater than one-quarter of the focal species' body mass. (This differs from Donadio and Buskirk (2006) who found that predation was less likely between carnivores differing greatly in size but it is unlikely to matter given the paucity of large carnivore species in the Americas, especially when ursids are excluded, see below). We disregarded possible lethal interactions between insectivorous and frugivorous carnivores as we assumed these to be relatively insignificant. Evaluating the proportion of co-occurring species (i.e., number of species overlapping in geographic range divided by all species of carnivores in the Americas) that are potential competitors or predators of the focal species allows us to assess whether species belonging to some families co-occur with competitive or dangerous species more than do species in other families. Competition and predation indices were analyzed at the level of taxonomic family to reflect the shared evolutionary history of the species in each family (Gittleman 1985, Donadio and Buskirk 2006).

(ii) Our worst-case indices focus on geographic range overlap and are agnostic to antipredator defenses making them rather crude. A more sensitive indicator of competition or predation pressure should incorporate the ecology and behavior of prey species. We therefore separately examined all co-occurring species for similarities and differences in the use of three traits: habitat stratum, habitat type and activity pattern. These indices were organized in two ways, as single-trait analyses, and additively, as multi-trait analyses (see next paragraph). For the single-trait models, each of three key traits (habitat stratum, habitat type and activity pattern) was examined for each of the 77 focal species separately. All geographically co-occurring species that shared the same trait of interest with the focal species were then totaled. In our competition (but not predation) analyses it was not considered necessary for other species to show the same activity pattern with the focal species, so species with different activity patterns were still included as potential competitors.

(iii) Multi-trait predation and competition indices were calculated by totaling the number of co-occurring species that shared the same habitat stratum and the same habitat type and the same activity pattern with the focal species. This was done for both potential competitors, and potential predators (i.e., carnivores larger than the focal species in a social species). Note, as with the single-trait models, activity pattern was considered unimportant in predicting competitive pressure and was omitted from this analysis.

The absolute numbers of single and multi-trait competitors or predators of each focal species was divided by the total number of geographically overlapping species to derive a series of single- and multi-trait competition and predation indices, which accounted for interspecific differences in the number of co-occurring species. In summary, the single-trait models assess the potential for competitive or predatory interactions amongst species that have one behavioral or ecological characteristic in common (i.e., habitat stratum, habitat type or activity pattern) with the focal species, whereas the multi-trait model refers to the potential for competitive or predatory interactions amongst species that have all three of these variables in common with the focal species.

(iv) In a final set of analyses we switched from describing different types of competition or predation based on the three indices (i-iii) and the effects of biological traits on reducing risk, and instead examined the role that biological traits might play in each carnivore family in reducing intraguild competition or predation. Here between-trait differences were used to examine changes in competition or predation indices as one moves from the coarsest analysis (worst-case) to more fine-scale analyses. Thus, the worst case competition or predation index was subtracted from each of the three single-trait indices so as to evaluate the importance of various traits in reducing competition or predation for each carnivore family. This was also carried out for the with respect to the multi-trait index.

Note that all analyses of competition and predation indices were based on an assumption that each focal species encounters other carnivore species with near equal regularity, regardless of geographic location. There are however, distinct and well-documented macroecological patterns in ecosystem productivity and mammalian physiology and behavior that are correlated with latitude (i.e. Badgley and Fox 2000, Silva *et al*. 2001, Diniz-Filho and Torres 2002) Despite these patterns, an *a priori* analysis of covariance for species found only at low (between 23’30° N and 23’30° S latitude) and high (north of 23’30° N and south of 23’30° S) latitudes revealed no significant differences between the number of overlapping species and geographic range size (ANCOVA, F=0.866, p=0.429) according to latitudinal position. Therefore it was assumed that latitudinal position of each species had no impact on the frequency with which it encountered heterospecifics.

We used carnivore family as the unit of analysis because we were interested in large scale evolutionary processes and knew *a priori* that many aspects of species biology such as feeding behaviour and activity pattern are highly constrained by family affiliation (Donandio and Buskirk

2006). (In contrast, coloration is far more labile across carnivore species and we used a species analysis there, controlling for phylogeny). All competition and predation indices were analyzed using Kruskal-Wallis non-parametric tests, ordered by family. Significant outcomes were tested further with *post-hoc* multiple contrasts (Tukey's Rank Sums Test (RST)) to investigate where significant differences lay.

The relationships between indices of competition and predation pressure and coloration were evaluated in two ways. First, we examined whether or not black (or dark) and white-colored species co-occurred geographically with a higher proportion of competitive or dangerous species than non-contrasting species (worst-case indices). Second, coloration was tested against the multi-trait competition and predation indices to examine if additive effects of habitat stratum and habitat type and, in the case of predation, activity pattern differed between contrasting and non-contrasting species. Analyses were conducted using both F-statistics using individual species and CAIC independent contrasts (CAIC v.2.6.9, Purvis and Rainbaut 1995) to control for phylogeny (Harvey and Pagel 1991).

RESULTS

General patterns

Of the 77 species included in these analyses, 18 belonged to the Family Canidae, 14 to Felidae, 9 to Mephitidae, 19 to Mustelidae, 13 to Procyonidae and 4 to Ursidae. Species were scored as either arboreal: 19 species, aquatic: 8 species, fossorial: 4 species, and/or terrestrial: 65 species (Appendix 3.1). There were seven diurnal species, 38 nocturnal species and 32 species with activity patterns that varied, either seasonally or throughout their geographic range. In total, 46.8% of all species were carnivorous, 39.0% were omnivorous, 6.5% were insectivorous and 7.8% were frugivorous. Most American carnivores (53 species) were largely, if not entirely solitary, although some species were commonly seen in pairs (17 species) or family groups (4 species). Only two species were known to form packs and three species lived in bands. The social grouping of six species was unknown. There was much variation in habitat type, with the preferences of many species changing with habitat availability throughout their range (Appendix 3.1).

Body size has traditionally been considered the single most influential factor determining the direction and strength of intraguild dynamics (Polis *et al*. 1989, Donadio and Buskirk 2006). The distribution of body mass in American carnivores spans four orders of magnitude and while most families contained both large and small members species' body sizes differed significantly according to family (Kruskal-Wallis test, χ^2=27.87, df=5, p<0.001). Mephitidae were significantly smaller than both Ursidae (Tukey's RST, Q=4.08, p<0.001) and Felidae (Tukey's RST, Q=3.05, p<0.05) while Mustelidae and Procyonidae were significantly smaller than Ursidae (Tukey's RST, Q=3.67, p<0.005 and Q=3.52, p<0.01, respectively). For all species, the mean geographic range overlap was with 31.5 species (SD±13.1) and, of those co-occurring species, an average of 24.4 (±13.1) species shared the same habitat stratum; an average of 24.4 (±13.6) species shared the same habitat type; and an average of 29.0 (±13.2) species shared the same activity pattern.

Between carnivore families in the Americas, there were no significant differences between them in the absolute number of geographically overlapping species (χ^2=4.527, df=5, p=0.476), nor were there differences in the absolute number of species sharing the same geographic area and stratum (χ^2=3.255, df=5, p=0.661), geographic area and habitat type (χ^2=3.862, df=5, p=0.569) or geographic area and activity pattern (χ^2=6.641, df=5, 0.249).

Competition

The risk of competition under the worst-case model differed across families (Table 3.1). The Canidae were under significantly greater worst-case competition pressure than either Felidae or Mustelidae. Members of the Ursidae shared significantly more competitors with the same habitat strata than members of either Procyonidae or Mephitidae. There were no significant differences between families in the proportion of competitors that utilized the same habitat types used by the focal species. The multi-trait analysis yielded only one weakly significant difference: Canidae were under significantly greater competitive pressure than Procyonidae (Table 3.1; Figure 3.2*a*).

Between-trait competition indices that identify which biological traits help one reduce competition risk uncovered only one significant finding: that procyonids reduce the number of potential competitors through selection of habitat strata more than do felids (Table 3.1).

Predation

The majority of significant differences in the analyses of predation risk were between those families whose members are small (Mephitidae, Mustelidae and Procyonidae) and the family whose members are large (Ursidae). In the analyses of the (coarse) worst-case predation index, Mephitidae, Mustelidae and Procyonidae were each at a significantly greater risk of predation than the Ursidae (Table 3.2). In the single-trait analyses, Mephitidae also shared each habitat strata, habitat type and activity pattern with a greater proportion of potential predators than Ursidae. Compared to ursids, mustelids co-occurred with a significantly greater proportion of species using the same habitat strata, and procyonids co-occurred with a significantly greater proportion of species using the same habitat type. In the multi-trait analyses Mephitidae shared habitat strata, type and activity pattern with a significantly greater proportion of potential predators than either Procyonidae or Ursidae. Mustelids shared habitat strata, type and activity pattern with a significantly greater proportion of potential predators than Ursidae (Table 3.2; Figure 3.2*b*).

By comparing the worst-case predation index and each single-trait and the multi-trait model it was possible to assess the relative importance of each antipredator avoidance candidate mechanism across families (Table 3.2). Procyonidae eliminated a greater proportion of dangerous co-occurring species once their use of habitat stratum was considered than did either

Canidae or Ursidae. The additive effects of strata, habitat type and activity pattern also benefited Procyonidae significantly more than did the Canidae, Felidae or Ursidae (Table 3.2).

A posteriori it was clear that the extremely large body size of bears and hence their low predation risk was likely skewing our predation index results; by comparison all of the other families appeared statistically indistinguishable. Therefore, we repeated all of the analyses dropping Ursidae (Table 3.2). With the exclusion of bears there were no significant differences between the five smaller families for the worst-case predation index. There were a number of significant differences between families when individual behavioral traits were taken into account, however. Members of the Mephitidae shared geographic range and habitat strata with a greater proportion of potential predators than did the Procyonidae. Mephitidae also shared the same geographic range and habitat type with a greater proportion of predators than either Canidae or Felidae, and the same activity pattern with more predators than members of the family Canidae. However, when all of these traits were considered together (multi-trait analysis) the only significant contrast was between Mephitidae and Procyonidae, with members of the Mephitidae co-occurring with more potential predators using the same habitat type, strata and activity pattern than members of the Procyonidae (Table 3.2).

Finally, considering between-traits analyses that assess antipredator benefits of biological traits, members of the Family Procyonidae avoided significantly more potential predators through selection of habitat strata, type and activity pattern than either Canidae or Felidae (Table 3.2).

Contrasting coloration

Eighteen of 77 species of American carnivores have black and white faces or bodies. Contrasting coloration among American carnivores occurs in species belonging to the families Mephitidae, Mustelidae, Procyonidae and Ursidae (Figure 3.1). There were no significant relationships between various indices of competition pressure and contrasting coloration. Nor did black and white-colored carnivore species tend to co-occur with a higher proportion of potential predator species than non-black and white species (Figure 3.3). There was however, a significant relationship between each contrasting facial (F=4.95, df=1, p=0.029) and contrasting body (F=8.17, df=1, p=0.006) coloration and the multi-trait predation index: black and white species co-occurred with more potential predators than non-black and white species even after accounting for the three behavioral/ecological avoidance mechanisms (Figure 3.4). There were however no significant relationship between predation or competition risk and body and facial coloration when employing phylogenetic controls.

DISCUSSION

This study made a number of assumptions concerning our different indices of competition and predation. First, no attempt was made to measure sympatric carnivore density and this is likely to be an important factor affecting contemporary intraguild competition and predation. Second, any geographic range overlap was sufficient for us to categorize two species as being potential competitors even though such overlap might vary between 5% and 100%. We used this generous criterion because we were concerned about making arbitrary cut-off points and suspected range maps for lesser known species were somewhat inaccurate. Third, body size was explicitly used to define potential competitors and predators but a carnivore might be driven off prey or killed by an individual smaller than itself (see Hunter *et al*. 2007). Until we have more studies of intraguild interactions in carnivores, however, we need to make these or similar assumptions to come to general conclusions about carnivore ecology, behavior and evolution.

Caro and Stoner (2003) characterized the potential for interspecific competition and predation on a species-by-species basis for African carnivores and found that African carnivores geographically overlapped with a mean of 41.0 other species. Here we found that American carnivores overlapped with an average of 31.5 other species. American and African carnivores share geographic range and habitat type with a similar number of other species with means of 24.4 and 25.9, respectively. African and American carnivores seem to be under similar competition risk, sharing habitat type and diet with a mean of 22.4 and 20.6 potential competitor species respectively. American carnivores shared the same geographic range and habitat type with a mean of 13.1 potential predator species but African carnivores were at risk from a mean of only 8.6 other carnivore species that might eat them.

Patterns of competition

Carnivores must compete with one another for a limited resource, animal biomass, that is both difficult to obtain and to defend against conspecifics and heterospecifics (Creel *et al*. 2001, Hunter *et al*. 2007) and meta-analyses have shown that competitive interactions between carnivores are frequent when dietary overlap is high (Donadio and Buskirk 2006). Omnivores were considered to compete with other species here and, predictably, in the worst-case and single-trait analyses omnivorous families appeared to be under greater competitive pressure than more specialized families. Nonetheless, the dietary flexibility that defines omnivory likely facilitates species coexistence beyond the coarse categorization used in this study. Multi-trait analyses showed no significant differences among the six families, however. This suggests that although primarily omnivorous families (Ursidae and Canidae) were at a greater risk of competition than other families, they may functionally reduce their competition pressure through the utilization of alternative of habitat strata and habitat types.

It is worth noting that the competition pressure faced by insectivorous species is likely somewhat overestimated in our analyses, as previous studies have suggested that insectivorous carnivores take prey of proportionally smaller size and utilize a wider range of prey sizes than other carnivores (Vézina 1985) and probably have no measurable impact on the foraging success their competitors (Moehlman 1986).

Patterns of predation

In a review of published literature Palomares and Caro (1999) found interspecific killing among carnivores to be common, with intraguild predation accounting for as much as 68% of known mortality. Given that Ursidae are the largest terrestrial carnivores on earth, however, it was not surprising that we found that they are under particularly low predation pressure; by contrast, the predation pressure experienced by all the other families appeared to be similar. When bears were excluded from the analyses, however, it was clear that the members of Mephitidae, that have the smallest mean body size of the six families, are under particularly high potential predation pressure. The Procyonidae had the second smallest mean body size but, surprisingly, were under the least potential predation pressure, at least according to multi-trait analyses, illustrating how small species may reduce intraguild predation pressure through altering their spatial and temporal resource use.

Adaptations to avoid competition and predation

Larger, *behavioral*ly dominant carnivores can greatly influence population dynamics and recruitment of subordinate carnivores through both predation and competition for resources. According to theory, coexistence between dominant and subordinate species is only possible when the subordinate species is a superior competitor for a shared resource (Holt and Polis 1997, Revilla 2002). The size and complexity of the carnivore guild challenges this assertion, however. Instead, partitioning resources through spatial and temporal variation in habitat use has likely contributed to the maintenance of diverse carnivore communities (Rosenzweig 1966, Van Valkenburgh 1985, Jacomo *et al*. 2004). While it is difficult to separate cause and effect, this study suggests that evolutionary adaptation to specific habitat strata, habitat types and activity patterns may have been shaped, at least partially by intraguild interactions.

Spatial avoidance

Spatial avoidance can be accomplished in at least two ways: through habitat selection and living in different habitat strata. All six American carnivore families used similar habitat types but they used different habitat strata to reduce competition in the case of Mustelidae, and to reduce predation, in the case of Procyonidae. Mustelid species are under greatest competitive pressure and their ability to be arboreal or aquatic may help to facilitate their coexistence with more competitively dominant carnivores. The Procyonidae was the only predominantly arboreal family and as a consequence was under extremely low predation pressure.

Temporal avoidance

Temporal avoidance of predation is well documented in mammals (*e.g.*, Penn and MacDonald 1995, Kronfeld-Schor and Dayan 2003) and is likely to be especially prevalent in small carnivores subject to predation. The Procyonidae eliminated a substantial proportion of potential predators through the selection of their activity pattern. Members of Procyonidae fit into two general categories: predominantly arboreal and nocturnal or terrestrial and diurnal. In contrast, potential predators of procyonids tended to be both terrestrial *and* nocturnal. The nocturnal habits of the frugivorous members of this family may also help to minimize direct competition with primates for access to fruiting trees. The Mephitidae are all nocturnal, as are most of their potential predators, but they may avoid predation through the use of noxious anal secretions (Ortolani and Caro 1996, Ortolani 1999). Moreover, the highly contrasting warning coloration present in all members of Mephitidae stands out when viewed in low light conditions (Ortolani and Caro 1996) so perhaps nocturnality, while inherently dangerous for this family, serves to maximize the effectiveness of this warning signal.

Contrasting coloration

Contrasting coloration is present in four of the six families of American carnivore. Ursidae, Procyonidae, Mustelidae and Mephitidae all have partially or entirely plantigrade foot posture so when faced with a potential predator these species are at a distinct disadvantage as they unlikely to be able to outrun their predators (Van Valkenburgh 1993). It is therefore important for plantigrade species, especially those of small body size, to be able to avoid predators. As previously discussed, most Procyonidae are semi- to entirely arboreal (Eisenberg 1981) and thereby avoid a substantial proportion of potential predators whereas the Ursidae are at low risk of predation due primarily to their extremely large body size. The remaining two families, Mephitidae and Mustelidae are under particularly high predation pressure. The black and white coloration of the Mephitidae warns of a potent anti-predator defense (noxious anal secretions; Ortolani and Caro 1996). Several members of the family Mustelidae and a few members of Procyonidae also possess contrasting facial and body markings and some mustelids use anal secretions to deter predators (Ortolani and Caro 1996). They are also known for being particularly pugnacious; such aggression may be another form of anti-predator defense but has not been studied explicitly (King 1989, Newman *et al*. 2005, Caro in press).

In conclusion, this large scale study of carnivores on the North and South American continents suggests that intraguild competition and predation have potentially affected aspects of carnivore species' habitat choices, activity patterns and even morphology. Procyonids reduced competition by being arboreal and Mephitids reduced threat of predation by advertising their noxious secretions. While such analyses need to be repeated on other continents, they suggest that the time has come to stop taking basic aspects of species biology such as warning coloration as a given, but instead to try to interpret them as responses to ecological pressures moulded by predation pressure and other factors. That predation pressure apparently shapes species' biology in carnivore families suggests that it must be a driving force in altering fundamental aspects of herbivore biology too.

ACKNOWLEDGEMENTS

Data were obtained in part from NatureServe in collaboration with Bruce Patterson, Wes Sechrest, Marcelo Tognelli, Gerardo Ceballos, The Nature Conservancy—Migratory Bird Program, Conservation International—CABS, World Wildlife Fund—US, and Environment Canada—WILDSPACE. Funding was provided by the National Science Foundation and the University of California. We thank Tom Schoener, Andy Sih and an anonymous reviewer for helpful suggestions and Mike Cobb for developing software to assist in statistical analyses.

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Table 3.1. Differences between carnivore families in indices of competition. Outcomes of Kruskal-Wallis non-parametric tests and *post hoc* multiple contrasts (Tukey's Rank Sums Test, $Q_{0.05,6}$=2.936) for any differences in competition risk between American carnivore families at various levels of data organization. Significant contrasts where the family in front of > sign denotes that its species are under significantly greater potential competition risk from other carnivores than members of the family following the sign.

Model	n	p-value	Significant contrasts	Q-value	p-value
Worst-case	6	0.001	Canidae > Felidae Canidae > Mustelidae	3.93 3.09	$p<0.002$ $p<0.05$
Single-trait					
Strata	6	0.006	Ursidae > Procyonidae Ursidae > Mephitidae	3.19 3.21	$p<0.05$ $p<0.02$
Habitat type	6	0.502	none	N/A	N/A
Multi-trait	6	0.058	Canidae > Procyonidae	3.04	$p<0.05$
Between-trait differences					
Worst-case and Strata	6	0.015	Procyonidae > Felidae	3.48	$p<0.01$
Worst-case and Habitat	6	0.078	none	N/A	N/A
Worst-case and Multi-trait	6	0.208	none	N/A	N/A

Table 3.2. Differences between carnivore families in indices of predation. Outcomes of Kruskal-Wallis non-parametric tests and *post hoc* multiple contrasts for differences in predation risk between American carnivore families at various levels of data organization. Families in front of > signs are under significantly greater potential predation risk from other carnivores than members of the family following the sign.

			All families					Ursidae excluded		
Model	n	p- value	Significant contrasts	Q-value	p-value	n	p-value	Significant contrasts	Q-value	p-value
Worst-case	6	0.001	Mephitidae > Ursidae	3.67	p<0.005	5	0.028	none	N/A	N/A
			Mustelidae > Ursidae	3.27	p<0.02					
			Procyonidae > Ursidae	3.51	p<0.01					
Single-trait										
Strata	6	0.004	Mephitidae > Ursidae	3.72	p<0.005	5	0.043	Mephitidae > Procyonidae	3.37	p<0.01
			Mustelidae > Ursidae	3.10	p<0.05					
Habitat type	6	<0.001	Mephitidae > Ursidae	4.01	p<0.001	5	0.005	Mephitidae > Canidae	3.03	p<0.05
			Procyonidae > Ursidae	3.55	p<0.01			Mephitidae > Felidae	3.06	p<0.05
Activity	6	0.003	Mephitdae > Ursidae	3.95	p<0.002	5	0.042	Mephitidae > Canidae	2.95	p<0.05
Multi-trait	6	<0.001	Mephitidae > Procyonidae	3.64	p<0.005	5	0.001	Mephitidae > Procyonidae	3.80	p<0.002
			Mephitidae > Ursidae	3.70	p<0.005					
			Mustelidae > Ursidae	3.23	p<0.02					
Between-trait differences										
Worst-case & Strata	6	0.001	Procyonidae >Canidae	3.54	p<0.01	5	0.004	Procyonidae > Canidae	3.66	p<0.005
			Procyonidae > Ursidae	3.80	p<0.005					
Worst-case & Habitat	6	0.124	none	N/A	N/A	5	0.778	none	N/A	N/A
Worst-case & Activity	6	0.013	none	N/A	N/A	5	0.031	Procyonidae > Felidae	2.91	p<0.05
Worst-case & Multi-trait	6	<0.001	Procyonidae > Canidae	4.25	p<0.001	5	<0.001	Procyonidae >Canidae	4.42	p<0.001
			Procyonidae > Felidae	3.13	p<0.05			Procyonidae > Felidae	3.28	p<0.02
			Procyonidae > Ursidae	4.66	p<0.001					

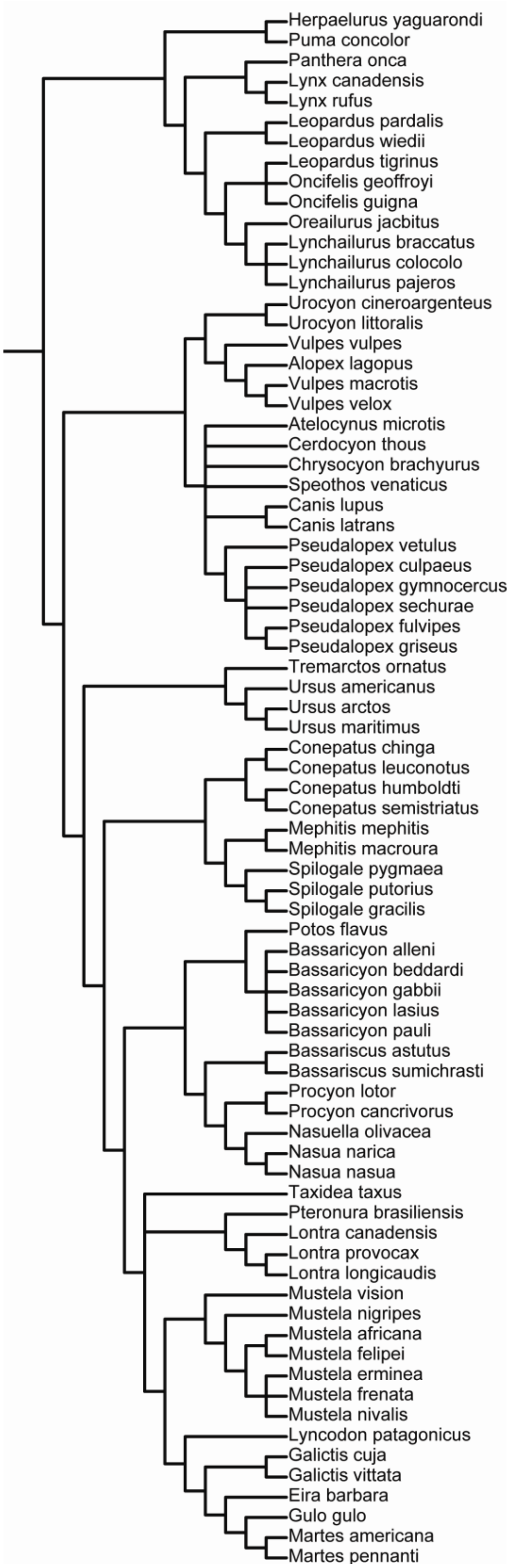

Figure 3.1. Phylogenetic tree of American carnivores.

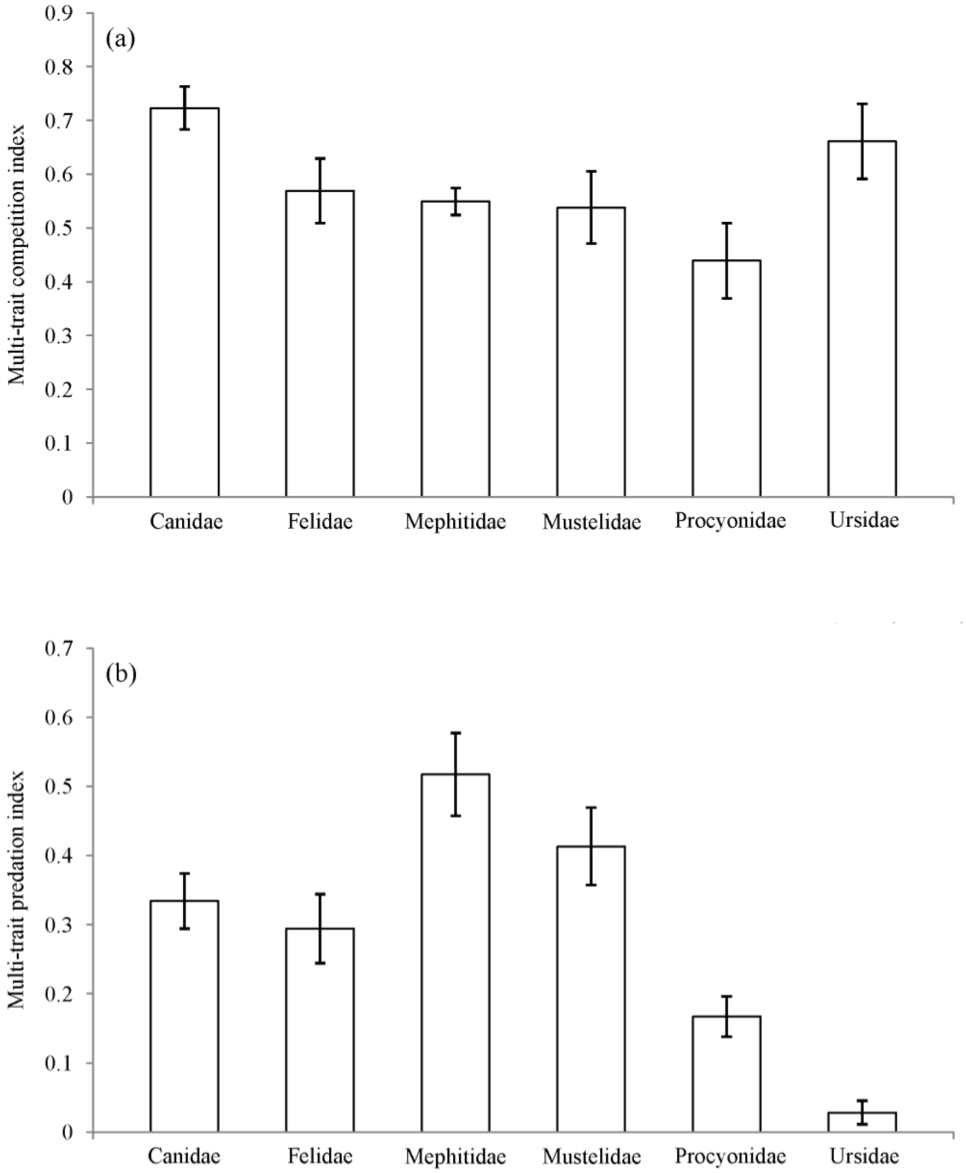

Figure 3.2. Mean and standard error of multi-trait competition index (*a*) and predation index (*b)* for each of the 6 families of American carnivore. Kruskal-Wallis tests and subsequent Tukey's Ranks Sums multiple contrast tests did not yield any significant contrasts for competition indices between families. For the predation indices there were significant differences between Mephitidae and Ursidae, Mephitidae and Procyonidae and Mustelidae and Ursidae (Table 3.2).

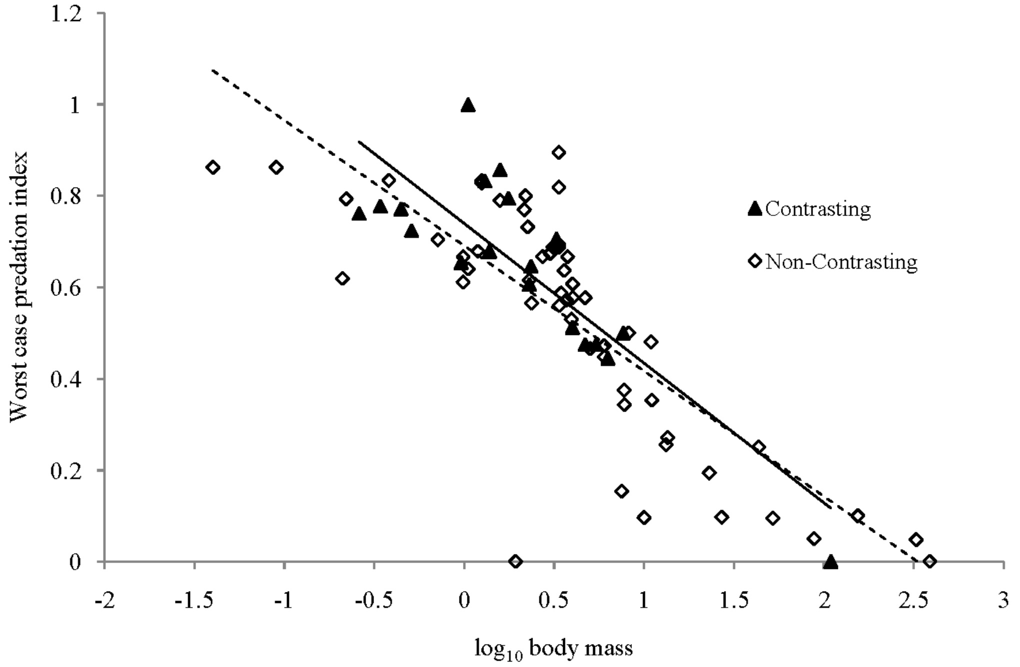

Figure 3.3. Species with contrasting facial and/or body colouration compared to those species without contrasting colouration for the worst-case predation index. There were no significant differences between the two categories of colouration. The solid line is the best fit line for contrasting coloured species while the broken line is the best fit line for non-contrasting species.

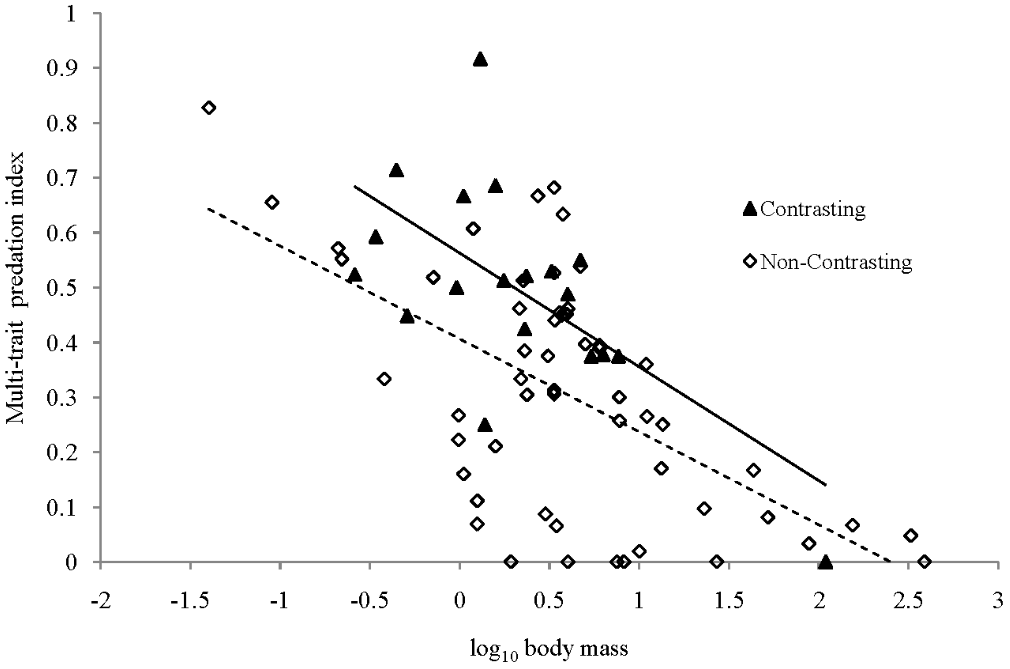

Figure 3.4. Species with contrasting facial and/or body colouration compared to those species without contrasting colouration. Contrasting species had a significantly greater multi-trait predation index than more cryptically coloured species (facial contrast: p=0.029, body contrast: p=0.006). The solid line is the best fit line for contrasting coloured species, the broken line is the best fit line for non-contrasting species.

APPENDIX 3.1. Ecological and behavioral data for American carnivores.

Species	Body mass (kg)	Diurnal	Nocturnal	Crepuscular	Cathemeral	Varies	Unknown	Solitary	Pair	Family	Pack	Band	Unknown
Alopex lagopus	3.10		x			x			x				
Atelocynus microtis	7.75		x					x					
Canis latrans	13.25		x	x				x	x	x			
Canis lupus	43.25					x					x		
Cerdocyon thous	6.00		x						x				
Chrysocyon brachyurus	23.00		x	x				x					
Pseudalopex culpaeus	2.72		x					x					
Pseudalopex fulvipes	4.00					x		x					
Pseudalopex griseus	4.69		x						x				
Pseudalopex gymnocercus	2.19		x					x					
Pseudalopex sechurae	3.35		x					x					
Pseudalopex vetulus	7.73	x							x				
Speothos venaticus	6.00	x								x	x		
Urocyon cineroargenteus	3.69		x						x				
Urocyon littoralis	1.93	x							x				
Vulpes macrotis	2.30		x						x				
Vulpes velox	2.37		x						x	x			
Vulpes vulpes	3.75		x	x					x				
Lynx rufus	5.00		x					x					
Herpaelurus yaguarondi	13.50	x		x				x					
Leopardus pardalis	2.25		x			x		x					
Leopardus wiedii	3.45		x					x					
Leopardus tigrinus	3.35		x					x					
Lynchailurus braccatus	3.35						x	x					
Lynchailurus colocolo	3.35		x					x					
Lynchailurus pajeros	10.90						x	x					
Lynx canadensis	11.03		x			x		x					
Oncifelis geoffroyi	3.59		x	x				x					
Oncifelis guigna	2.15					x		x					
Oreailurus jacobitus	4.00		x					x					
Panthera onca	88.13		x					x					
Puma concolor	52.00					x		x					
Conepatus chinga	1.76		x					x					
Conepatus humboldti	1.30		x					x					
Conepatus leuconotus	2.30		x			x		x					
Conepatus semistriatus	3.99		x					x					
Mephitis macroura	0.96		x					x					
Mephitis mephitis	3.25		x					x					
Spilogale gracilis	0.44		x					x					
Spilogale putorius	0.34		x					x					
Spilogale pygmaea	0.26		x					x					

Appendix 3.1 (*cont.*)

Species	Body mass (kg)	Diurnal	Nocturnal	Crepuscular	Cathemeral	Varies	Unknown	Solitary	Pair	Family	Pack	Band	Unknown
Eira barbara	3.94	x						x					
Galictis cuja	1.58					x		x		x			
Galictis vittata	2.35		x	x				x	x	x			
Gulo gulo	12.23		x					x					
Lontra canadensis	8.20		x	x						x			
Lontra longicaudis	10.00			x									x
Lontra provocax	7.50		x					x					
Lyncodon patagonicus	1.05						x						x
Martes americana	0.71		x					x					
Martes pennanti	3.38					x		x					
Mustela africana	0.22						x						x
Mustela erminea	0.09				x			x					
Mustela felipei	0.38						x						x
Mustela frenata	0.21					x		x					
Mustela nigripes	0.51		x										x
Mustela nivalis	0.04					x		x					
Mustela vison	1.19		x					x					
Pteronura brasiliensis	27.00	x							x				
Taxidea taxus	7.65					x		x					
Bassaricyon alleni	1.25		x					x	x				
Bassaricyon beddardi	1.25		x					x	x				
Bassaricyon gabbii	0.99		x					x	x				
Bassaricyon lasius	1.58		x					x	x				
Bassaricyon pauli	1.58		x					x	x				
Bassariscus astutus	0.99		x					x	x				
Bassariscus sumichrasti	1.05		x					x					
Nasua narica	4.70	x										x	
Nasua nasua	3.93	x										x	
Nasuella olivacea	1.38						x					x	
Potos flavus	3.00		x					x					
Procyon cancrivorus	5.40		x										x
Procyon lotor	6.29		x					x	x				
Tremarctos ornatus	109.3		x	x									x
Ursus americanus	154.3					x		x					
Ursus arctos	325.7					x		x					
Ursus maritimus	387.5					x		x					

Appendix 3.1 (*cont.*)

Species	Carnivorous	Omnivorous	Frugivorous	Insectivorous	Terrestrial	Arboreal	Aquatic	Fossorial	Agricultural	Arid	Coastal	High elevation forest	Riparian
Alopex lagopus		x			x						x		
Atelocynus microtis		x			x		x		x	x			
Canis latrans		x			x				x	x			
Canis lupus	x				x						x		x
Cerdocyon thous		x			x								
Chrysocyon brachyurus		x			x								
Pseudalopex culpaeus		x			x					x		x	
Pseudalopex fulvipes		x			x								
Pseudalopex griseus		x			x								
Pseudalopex gymnocercus		x			x					x			
Pseudalopex sechurae		x			x					x			
Pseudalopex vetulus		x			x								
Speothos venaticus	x				x		x						
Urocyon cineroargenteus		x			x				x	x			
Urocyon littoralis		x			x								x
Vulpes macrotis		x			x								
Vulpes velox		x			x								
Vulpes vulpes		x			x				x	x			
Lynx rufus	x				x					x			x
Herpaelurus yaguarondi	x				x					x		x	
Leopardus pardalis	x				x							x	
Leopardus wiedii	x					x						x	x
Leopardus tigrinus	x				x				x			x	
Lynchailurus braccatus	x				x								
Lynchailurus colocolo	x				x					x		x	
Lynchailurus pajeros	x				x					x		x	
Lynx canadensis	x				x				x				
Oncifelis geoffroyi	x				x								x
Oncifelis guigna	x				x	x							x
Oreailurus jacobitus	x				x								
Panthera onca	x				x					x			x
Puma concolor	x				x					x			
Conepatus chinga		x			x					x			
Conepatus humboldti		x			x				x				
Conepatus leuconotus				x	x								
Conepatus semistriatus				x	x				x			x	
Mephitis macroura				x	x				x				
Mephitis mephitis				x	x				x				
Spilogale gracilis				x	x						x		x
Spilogale putorius		x			x	x							
Spilogale pygmaea		x			x						x		

Appendix 3.1 (*cont.*)

Species	Carnivorous	Omnivorous	Frugivorous	Insectivorous	Terrestrial	Arboreal	Aquatic	Fossorial	Agricultural	Arid	Coastal	High elevation forest	Riparian
Eira barbara		x			x	x			x			x	
Galictis cuja					x				x	x	x	x	
Galictis vittata	x				x				x				
Gulo gulo	x				x							x	x
Lontra canadensis	x						x						x
Lontra longicaudis	x						x						x
Lontra provocax	x						x						x
Lyncodon patagonicus	x				x								
Martes americana	x				x	x							x
Martes pennanti	x				x								
Mustela africana	x				x								x
Mustela erminea	x				x	x	x	x					x
Mustela felipei	x				x		x						x
Mustela frenata	x				x	x			x	x		x	
Mustela nigripes	x				x			x		x			
Mustela nivalis	x				x	x		x	x	x	x		x
Mustela vison	x				x		x						x
Pteronura brasiliensis	x						x						x
Taxidea taxus	x				x			x	x	x			
Bassaricyon alleni			x			x							
Bassaricyon beddardi			x			x							
Bassaricyon gabbii			x			x							
Bassaricyon lasius			x			x							
Bassaricyon pauli			x			x							
Bassariscus astutus		x			x	x							x
Bassariscus sumichrasti		x				x						x	
Nasua narica		x			x	x				x			x
Nasua nasua		x			x							x	x
Nasuella olivacea		x			x							x	
Potos flavus			x			x							x
Procyon cancrivorus		x			x						x		x
Procyon lotor		x			x	x			x	x	x		x
Tremarctos ornatus		x			x							x	
Ursus americanus		x			x								
Ursus arctos	x				x						x		x
Ursus maritimus	x				x						x		

Appendix 3.1 (*cont.*)

Species	Paramo	Scrub	Forest	Open	Tundra	Wetlands	Facial ContraSt	Body Contrast
Alopex lagopus					x			
Atelocynus microtis			x			x		
Canis latrans			x	x				
Canis lupus		x	x	x	x	x		
Cerdocyon thous			x	x				
Chrysocyon brachyurus				x		x		
Pseudalopex culpaeus		x	x	x				
Pseudalopex fulvipes			x					
Pseudalopex griseus			x	x				
Pseudalopex gymnocercus			x	x				
Pseudalopex sechurae								
Pseudalopex vetulus				x				
Speothos venaticus			x	x				
Urocyon cineroargenteus			x					
Urocyon littoralis		x	x	x				
Vulpes macrotis				x				
Vulpes velox				x				
Vulpes vulpes			x	x	x			
Lynx rufus			x	x		x		
Herpaelurus yaguarondi			x	x		x		
Leopardus pardalis		x	x			x		
Leopardus wiedii			x	x		x		
Leopardus tigrinus	x		x	x		x		
Lynchailurus braccatus			x	x		x	?	
Lynchailurus colocolo		x						
Lynchailurus pajeros		x					?	
Lynx canadensis			x			x		
Oncifelis geoffroyi			x					
Oncifelis guigna			x					
Oreailurus jacobitus	x							
Panthera onca			x	x		x		
Puma concolor		x	x	x				
Conepatus chinga				x				x
Conepatus humboldti			x	x			x	x
Conepatus leuconotus		x	x					x
Conepatus semistriatus		x	x	x			x	x
Mephitis macroura		x	x	x			x	x
Mephitis mephitis		x	x	x			x	x
Spilogale gracilis			x	x			x	x
Spilogale putorius			x				x	x
Spilogale pygmaea			x				x	x
Eira barbara		x	x	x				
Galictis cuja		x	x	x		x	x	x
Galictis vittata			x	x			x	x

Appendix 3.1 (*cont.*)

Species	Paramo	Scrub	Forest	Open	Tundra	Wetlands	Facial ContraSt	Body Contrast
Gulo gulo			x		x		?	?
Lontra canadensis								
Lontra longicaudis								
Lontra provocax								
Lyncodon patagonicus				x			x	
Martes americana			x					
Martes pennanti			x					
Mustela africana			x			x		
Mustela erminea		x	x					
Mustela felipei							?	
Mustela frenata				x				
Mustela nigripes				x			x	
Mustela nivalis		x	x	x				
Mustela vison			x	x		x		
Pteronura brasiliensis								
Taxidea taxus				x			x	
Bassaricyon alleni			x					
Bassaricyon beddardi			x				?	
Bassaricyon gabbii			x					
Bassaricyon lasius			x				?	
Bassaricyon pauli			x					
Bassariscus astutus								
Bassariscus sumichrasti			x					
Nasua narica			x				x	
Nasua nasua		x	x				?	
Nasuella olivacea	x						x	
Potos flavus			x					
Procyon cancrivorus			x			x	x	
Procyon lotor		x	x	x	x	x	x	
Tremarctos ornatus				x			x	
Ursus americanus			x					
Ursus arctos			x	x	x			
Ursus maritimus					x			

Appendix 3.1 (*cont.*)

Species	Sources
Alopex lagopus	Nowak 1999, Audet *et al.* 2002, Tannerfeldt *et al.* 2002, Frafjord 2003, Sillero-Zubiri *et al.* 2004
Atelocynus microtis	Berta 1986, Nowak 1999, de la Rosa and Nocke 2000, Munoz-Duran 2002, Sillero-Zubiri *et al.* 2004
Canis latrans	Reid 1998, Nowak 1999, de la Rosa and Nocke 2000, Neale and Sacks 2001, Guerroro *et al.* 2002, Sillero-Zubiri *et al.* 2004
Canis lupus	Mech 1974, Nowak 1999, Sillero-Zubiri *et al.* 2004
Cerdocyon thous	Berta 1982, Nowak 1999, Juarez and Marinho-Filho 2002, Jacomo *et al.* 2004, Sillero-Zubiri *et al.* 2004
Chrysocyon brachyurus	Dietz 1985, Nowak 1999, Juarez and Marinho-Filho 2002, Jacomo *et al.* 2004, Sillero-Zubiri *et al.* 2004
Pseudalopex culpaeus	Novaro 1997, Nowak 1999, Sillero-Zubiri *et al.* 2004
Pseudalopex fulvipes	Sillero-Zubiri *et al.* 2004, Vila *et al.* 2004
Pseudalopex griseus	Nowak 1999, Munoz-Duran 2002, Sillero-Zubiri *et al.* 2004
Pseudalopex gymnocercus	Nowak 1999, Munoz-Duran 2002,Sillero-Zubiri *et al.* 2004
Pseudalopex sechurae	Nowak 1999, Munoz-Duran 2002,Sillero-Zubiri *et al.* 2004
Pseudalopex vetulus	Nowak 1999, Juarez and Marinho-Filho 2002, Jacomo *et al.* 2004, Sillero-Zubiri *et al.* 2004
Speothos venaticus	Reid 1998, Nowak 1999, Richard-Hansen *et al.* 1999, de la Rosa and Nocke 2000, Sillero-Zubiri *et al.* 2004
Urocyon cineroargenteus	Neale and Sacks 2001, Rau *et al.* 1995, de la Rosa and Nocke 2000, Guerroro *et al.* 2002, Sillero-Zubiri *et al.* 2004
Urocyon littoralis	Moore and Collins 1995, Sillero-Zubiri *et al.* 2004
Vulpes macrotis	McGrew 1979, Nowak 1999, Sillero-Zubiri *et al.* 2004
Vulpes velox	Egoscue 1979, Nowak 1999, Sillero-Zubiri *et al.* 2004
Vulpes vulpes	Lariviere and Pasitschniak-Arts 1996, Nowak 1999, Tannerfeldt *et al.* 2002
Lynx rufus	Lariviere and Walton 1997, Neale and Sacks 2001, Sunquist and Sunquist 2002
Herpaelurus yaguarondi	de Oliveira 1998a, Richard-Hansen *et al.* 1999, de la Rosa and Nocke 2000, Guerroro *et al.* 2002, Sunquist and Sunquist 2002
Leopardus pardalis	Murray and Gardner 1997, Richard-Hansen *et al.* 1999, de la Rosa and Nocke 2000, Sunquist and Sunquist 2002, Haines *et al.* 2005
Leopardus wiedii	de Oliveira 1998b, Richard-Hansen *et al.* 1999, de la Rosa and Nocke 2000, Sunquist and Sunquist 2002
Leopardus tigrinus	de la Rosa and Nocke 2000, Sunquist and Sunquist 2002
Lynchailurus braccatus	Garcia-Perea 1994
Lynchailurus colocolo	Garcia-Perea 1994, Sunquist and Sunquist 2002
Lynchailurus pajeros	Garcia-Perea 1994
Lynx canadensis	Tumlison 1987, Sunquist and Sunquist 2002
Oncifelis geoffroyi	Ximenez 1975, Munoz-Duran 2002, Sunquist and Sunquist 2002
Oncifelis guigna	Dunstone *et al.* 2002, Munoz-Duran 2002, Sunquist and Sunquist 2002
Oreailurus jacobitus	Yensen and Seymour 2000, Garcia-Perea 2002, Sunquist and Sunquist 2002, Perovic *et al.* 2003
Panthera onca	Seymour 1989, Richard-Hansen *et al.* 1999, de la Rosa and Nocke 2000, Sunquist and Sunquist 2002, Scognamillo *et al.* 2003

Appendix 3.1 (*cont.*)

Species	Sources
Puma concolor	de la Rosa and Nocke 2000, Sunquist and Sunquist 2002, Scognamillo *et al.* 2003
Conepatus chinga	Travaini *et al.* 1998, Donadio *et al.* 2001
Conepatus humboldti	Fuller *et al.* 1987, Zapata *et al.* 2001
Conepatus leuconotus	Reid 1998, de la Rosa and Nocke 2000, Cervantes *et al.* 2002, Dragoo *et al.* 2003
Conepatus semistriatus	Emmons, 1997, de la Rosa and Nocke 2000, Cervantes *et al.* 2002
Mephitis macroura	de la Rosa and Nocke 2000
Mephitis mephitis	Wade-Smith and Verts 1982, Nowak 1999
Spilogale gracilis	Nowak 1999, Verts *et al.* 2001
Spilogale putorius	Kinlaw 1995, Nowak 1999, de la Rosa and Nocke 2000
Spilogale pygmaea	Medellin *et al.* 1998, Nowak 1999
Eira barbara	Presely 2000, Richard-Hansen *et al.* 1999, de la Rosa and Nocke 2000
Galictis cuja	Nowak 1999, Yensen 2003
Galictis vittata	Nowak 1999, de la Rosa and Nocke 2000, Yensen and Tarifa 2003
Gulo gulo	Pasitschniak-Arts and Lariviere 1995, Nowak 1999
Lontra canadensis	Lariviere and Walton 1998
Lontra longicaudis	Emmons 1997, Lariviere 1999b, de la Rosa and Nocke 2000
Lontra provocax	Lariviere 1999c
Lyncodon patagonicus	Nowak 1999
Martes americana	Clark *et al.* 1987, Nowak 1999, Zielinski and Duncan 2004
Martes pennanti	Powell 1981, Nowak 1999, Zielinski and Duncan 2004, Zielinski *et al.* 2004
Mustela africana	Izor and Peterson 1985, Ferrari and Lopes 1992, Emmons 1997, Nowak 1999
Mustela erminea	King 1983, Nowak 1999
Mustela felipei	Izor and Peterson 1985, Nowak 1999,
Mustela frenata	Sheffield and Thomas 1997, Nowak 1999, de la Rosa and Nocke 2000
Mustela nigripes	Hillman and Clark 1980, Nowak 1999
Mustela nivalis	Nowak 1999
Mustela vison	Lariviere 1999a, Nowak 1999
Pteronura brasiliensis	Nowak 1999
Taxidea taxus	Long 1973, Nowak 1999
Bassaricyon alleni	Glaston 1994, Nowak 1999
Bassaricyon beddardi	Glaston 1994, Nowak 1999
Bassaricyon gabbii	Glaston 1994, Nowak 1999, de la Rosa and Nocke 2000
Bassaricyon lasius	Glaston 1994, Nowak 1999
Bassaricyon pauli	Gaston 1994, Nowak 1999
Bassariscus astutus	Poglayen-Neuwall and Toweill 1988, Glaston 1994, Nowak 1999, de la Rosa and Nocke 2000
Bassariscus sumichrasti	Glaston 1994, Reid 1998, Nowak 1999, de la Rosa and Nocke 2000
Nasua narica	Glaston 1994, Gompper 1995, Nowak 1999, de la Rosa and Nocke 2000
Nasua nasua	Glaston 1994, Gompper and Decker 1998, Nowak 1999, Richard-Hansen *et al.* 1999
Nasuella olivacea	Hillman and Clark 1980, Nowak 1999, Rodriquez-Bolanos *et al.* 2003

Appendix 3.1 (*cont.*)

Species	Sources
Potos flavus	Ford and Hoffmann 1988, Glaston 1994, Martinez-Meyer *et al.* 1998, Nowak 1999, Richard-Hansen *et al.* 1999, de la Rosa and Nocke 2000
Procyon cancrivorus	Glaston 1994, Emmons 1997, Reid 1998, Richard-Hansen *et al.* 1999, de la Rosa and Nocke 2000
Procyon lotor	Lotze and Anderson 1979, Gehrt and Fritzell 1999, Nowak 1999, de la Rosa and Nocke 2000, Guerroro *et al.* 2002
Tremarctos ornatus	Nowak 1999, Munoz-Duran 2002, Cuesta *et al.* 2003, Katten *et al.* 2003
Ursus americanus	Nowak 1999, Lariviere 2001
Ursus arctos	Pasitschniak-Arts 1993, Nowak 1999
Ursus maritimus	DeMaster and Stirling 1981, Nowak 1999

CHAPTER 4

Differential responses of sympatric carnivores to taxidermic mounts of aposematic striped skunks *Mephitis mephitis*

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ABSTRACT

The bright black and white coloration of striped skunks (*Mephitis mephitis*) is one of the most familiar forms of aposematism but little is known about how mammalian carnivores interact with skunks. Here I explore whether skunk coloration serves as a deterrent to potential predators and examine the light environments and micro-habitat characteristics where this signal is most effective. By videotaping the behavior of all carnivores near taxidermic mounts of striped skunks and control sites, I show that mammalian carnivores avoid skunks and approach them hesitantly, particularly on darker nights. I also conducted individual species analyses and found that three sympatric carnivore species, coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and raccoons *(Procyon lotor)* actively avoid striped skunks indicating aposematism may be effective at a distance. Grey foxes (*Urocyon cinereoargenteus*), however, do not avoid approaching skunk mounts although they rarely make contact with them suggesting that they are deterred by skunks when close. These results show that sympatric carnivores are differentially affected by warning coloration in this quintessential aposematic mammal.

INTRODUCTION

Noxious or dangerous prey have an interest in communicating their unpalatability or defenses to potential predators. This interspecific communication often takes the form of conspicuous, contrastingly colored, aposematic warnings signals that make the bearer easier to detect, recognize and readily differentiated from both its background and cryptic prey (Guilford 1985, Guilford and Dawkins 1991, Sherratt and Beatty 2003, Ruxton *et al*. 2004). The goal of these signals is to modify predator behavior and to discourage attacks from predators who, in the absence of the signal, may attempt to capture and kill the signaler (Mappes *et al*. 2005).

Perceptual and cognitive differences between the various receivers of these warning signals likely contribute greatly to the evolution of aposematic signals (Endler and Mappes 2004) and lighting conditions and the structure of the environment may be important in determining the efficacy of aposematic signaling (Endler 1992). For example, black and white coloration is thought to be most effective in low-light conditions (Hailman 1977, Ortolani 1999) and, accordingly, the fraction of moon illuminated may be influential in how potential predators perceive aposematic prey. Black and white coloration is also thought to be most beneficial when it contrasts with the local environment, allowing predators to easily detect and avoid aposematic animals (Ruxton *et al*. 2004).

Striped skunks (*Mephitis mephitis*) are one of most common North American carnivores and are often identified by their warning coloration. Comparative data show that the black and white pelage of skunks warns predators of their ability to spray attackers with noxious secretions (Ortolani and Caro 1996). Little is known, however, about the actual anti-predator benefits conferred by aposematic signaling in striped skunks and the circumstances under which and to whom it is most effective. In the western United States skunks are potentially killed by several mammalian carnivores including: grey foxes (*Urocyon cinereoargenteus*), red foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*), bobcats (*Lynx rufus*), mountain lions (*Puma concolor*), black bears (*Ursus americanus*), coyotes (*Canis latrans*) and badgers (*Taxidea taxus*) (Wade-Smith and

Verts 1982, Hansen *et al*. 2004, Hunter and Caro *in press*). Beyond a few anecdotal accounts (*e.g.* Walton and Lariviere 1996; Prange and Gehrt 2007), however, there has been no experimental examination of the predator behavior when confronted by a striped skunk.

Here I investigate the reaction of potential predators to striped skunks at eight sites across a range of environmental conditions in northern California. I used baited taxidermic mounts of striped skunks with motion-triggered infra-red video cameras to observe different mammalian predator species in proximity to skunk mounts. Exceedingly little is known about the sources and rates of predator mortality in striped skunks so it is difficult to make predictions as to the relative importance of aposematic signaling to different predator species (Hansen *et al*. 2004, Gehrt 2005, Prange and Gehrt 2007). The high luminance contrast of skunk pelage likely makes skunks conspicuous to multiple predator species. (Hailman 1977, Prudic *et al*. 2006), although unknown differences in predatory behavior, wariness and dietary conservatism may make skunk aposematism more effective against some species and less effective against others (Endler and Mappes 2004).

One function of warning coloration is alerting potential predators to the presence of a noxious animal from sufficient distance to minimize recognition errors and thereby avoid ill-advised attacks (Ruxton *et al*. 2004, Caro 2005). Using habitat thickness as a proxy for visibility I examined differences in the detectability of skunk mounts across predator species. I expected to find that skunk mounts were visited less often in more open environments where there is minimal signal attenuation (Endler 1992). Lastly, juxtaposition of absorptive black and reflective white coloration appears more contrasting in dimmer light (Hailman 1977, Birren 1988). Therefore, I expect skunk mounts to elicit a stronger avoidance response on darker, low moon light nights (Hailman 1979, Ortolani 1999).

METHODS

Data collection

Data were collected at 8 sites in northern California, USA. These were: Big Creek Natural Reserve (University of California Natural Reserve System (UCNRS)), Bobcat Ranch (Audubon California), Cosumnes River Preserve (Bureau of Land Management (BLM), The Nature Conservancy), Deer Creek Hills (Sacramento Valley Conservancy), Fort Ord Public Lands (BLM), McLaughlin Natural Reserve (UCNRS), Mitteldorf Preserve (Big Sur Land Trust) and Quail Ridge Natural Reserve (UCNRS) from June 2006-November 2007 (Figure 4.1)

Camera stations

Camera stations were established along trails or roads and were randomly spaced at 250m, 500m, 750m or 1km intervals. Each camera station set consisted of two treatment types: a station with a taxidermic mount of a striped skunk and a control station that had a camera, but no mount. All stations were baited with a mixture of salmon meat, sun-rendered trout oil, and beaver castorium (Buckeye Trap Supply; Ashland, OH). Infra-red cameras (Leaf River; Taylorsville, MS) were placed on wooden stakes at a height of 25-30cm at a distance of approximately 4 m from the bait. The habitat characteristics in the immediate area of the camera stations were assigned to one of two coarse categories: open or closed. Open areas were areas of grassland or oak woodlands with no woody vegetation less than 4 m in height within 3 m of the station. Closed habitat included areas of chaparral or other dense undergrowth within 3 m of the station. Mounts were anchored with stakes driven into the ground until they were flush with the substrate, then secured to the stakes using zip ties. Mounts were washed initially to remove any dye odors, were sprayed daily in the field with a carbon-based deodorizing spray (Carbon Blast, Robinson Labs Inc; Cannon Falls, MN), and were handled with latex gloves to minimize the transmission of human odors.

When approached by a potential predator live skunks engage in a series of escalating displays culminated with an expulsion of noxious anal secretions. Skunk mounts were positioned facing across the road or trail with their tail arched behind them but not mimicking the raised tail alarm position often seen as the first warning signal (Lariviere and Messier 1996). Cameras were set to trigger at 1 min intervals and to record 1 min of digital video footage. The result was a near continuous record of the behavior of visiting species. Videos were downloaded every morning and stations were baited every evening. During the day, mounts were covered to minimize color fading from sun exposure and cameras were switched off. Mount sets were run for five consecutive nights and relocated four times per site (a minimum of 1 km from the location of any previous mount set) for a total of 20 sampling nights per site of each, control and skunk stations.

Carnivore behavior

Videos obtained from camera-stations were scored using several criteria. Visits by the same species at the same mount station within any 10 minute period were considered to be repeat visits by the same individual and were only counted as one visit. Once an animal appeared on camera the species identity, number of animals and approximate age (adult or juvenile) were noted. Because young carnivores are often more curious than adults (*e.g.* Caro 1994) and likely have limited prior experience with skunks, visits by juveniles were excluded from all analyses, unless accompanied by an adult animal. In cases where more than one adult animal was present the first individual to appear on camera was used as the focal animal for all behavioral observations. If a visiting animal moved toward the bait/mount the number and length of all pauses in their approach were recorded. A pause was defined as an animal freezing, for any length of time, in its approach towards the mount or bait station. Once an animal got near the bait it could either turn and move away, off camera, or continue forward and make contact (sniff, lick, bite or rub) with the bait or mount. On occasions when this occurred, the total time elapsed from when the animal began to move toward the bait until when it made contact (including any pauses) was recorded (time to contact). The length of time the animal remained in contact with the bait or mount was also noted (time in contact).

Data analyses

Five behavioral variables were analyzed for carnivores collectively (all species, excluding skunks) and three behavioral variables were analyzed for individual species who visited in sufficient numbers to warrant statistical analysis (coyote, grey fox, bobcat and raccoon). For grouped analyses whether camera stations were visited, whether animals paused in their approach and whether they made contact with the bait or mount were compared across skunk and control stations as was the total amount of time that an animal paused was recorded, as was the time taken to make contact with the bait or mount. Species-level analyses were limited to likelihood of visiting, pausing and making contact with mounts or bait and compared across stations type. Animal behavior was also compared between species. The focus of this study was the behavior of predators so visits by skunks were excluded from grouped analyses but were included for comparisons between species to provide a contrast, as skunks were not expected to avoid skunk mounts for fear of being sprayed (Wade-Smith and Verts 1982). Animal behavior was also analyzed with respect to the fraction of moon illuminated (per United States Naval Observatory) and habitat type; cloud cover was negligible throughout the study period. Data were analyzed using SPSS (vers. 16). Data from all carnivore species lumped together were analyzed using analyses of variance (ANOVA) for normally distributed dependent variables (using F distributions) or generalized linear models for binomially distributed dependent variables (using χ^2 distributions). Camera station type (skunk or control) was used as a factor and habitat type and moonlight were used as covariates. Data were analyzed for main effects and 2-way interactions and non-significant ($p<0.1$) were dropped stepwise from each model. Due to small sample size and non-normal data distributions individual species were analyzed using nonparametric rank ANOVAs, Mann-Whitney U-tests and Fisher's exact tests. Statistical power was calculated for non-significant results of interest using G*Power 3 (Faul *et al*. 2007).

RESULTS

Striped skunk mount stations were visited 55 times by 6 species (coyote, grey fox, bobcat, raccoon, striped skunk, mountain lion) and control stations received 89 visits from 7 species (coyote, grey fox, bobcat, raccoon, striped skunk, mountain lion and Virginia opossum) at 8 research sites for a total of 160 station nights at each, skunk mount and control stations (Table 4.1).

When all species were analyzed together (excluding skunks) mammalian carnivores were significantly less likely to visit skunk stations than control stations (χ_1^2=14.519, n=324, p<0.001). Animals were also more likely to pause when approaching skunk stations than control stations (χ_1^2=7.006, n=80, p=0.008). Overall, animals were more apt to make contact with camera stations with increasing moonlight (χ_1^2=4.678, n=69, p=0.031) but this effect was especially pronounced for control stations, while there was little effect of moonlight on contacts at skunk stations (moonlight x camera station type: χ_1^2=4.433, n=69, p=0.035). Carnivores took longer to make contact with camera stations both in open environments rather than closed environments ($F_{1,45}$=11.294, p=0.002), and with decreasing moonlight ($F_{1, 45}$=4.067, p=0.050). There was also a significant interaction between moonlight and station type for time taken to make contact, with animals taking less time to make contact with skunk mounts on brighter nights ($F_{1,45}$=5.241, p=0.027).

In individual species analysis, coyotes, bobcats and raccoons were each less likely to visit skunk stations than control stations (Fisher’s Exact Tests: coyote: p=0.009, bobcats: p=0.055, raccoons: p=0.020; Table 4.2, Figure 4.3). Grey foxes were equally likely to visit skunk and control stations (χ_1^2=1.883, n=282, p=0.170, *w*=0.95), although foxes were more likely to pause when approaching skunk stations than control stations (χ_1^2=3.494, n=45, p=0.062) and were significantly less likely to make contact with skunk stations than control stations (Fisher’s Exact Test, n=45, p=0.017; Figure 4.3). There were non-significant difference in the likelihood of coyotes, bobcats and raccoons each to make contact between mount types (Table 4.2), although for all of these species statistical power was extremely low (<0.1), so sample sizes were likely too small to detect a difference.

There was no effect of moonlight or habitat type on individuals species behavior at skunk mounts, although bobcats were more likely to visit control stations on darker nights (Mann-Whitney U, Z=-2.58, n=15, p=0.010) while raccoons and foxes were more likely to visit control stations on brighter nights (raccoons; Mann-Whitney U, Z=-1.76, n=12, p=0.078; foxes: Mann-Whitney U, Z=-2.241, n=33, p=0.025). Raccoons were more apt to visit control stations in open habitats than closed habitats (Fisher's Exact Test, n=12, p<0.001). Bobcats were somewhat more likely to pause when approaching the control station in closed habitat (Fisher's Exact Test, n=15 p=0.091).

Interspecific comparisons

The rates of visitation, likelihood of pausing and likelihood of making contact at skunk stations and control stations were compared across all species (including skunks). Skunks were significantly more likely to visit skunk stations than coyotes (Fisher's Exact Test, n=37, p=0.015) and raccoons (Fisher's Exact Test, n=44, p=0.037) and somewhat more likely to visit than bobcats (Fisher's Exact Test, n=49, p=0.084). However, skunks approached other skunk mounts carefully and were more likely to pause in their approach than coyotes (Fisher's Exact Test, n=16, p=0.005) or perhaps bobcats (Fisher's Exact Test, n=14, p=0.10).

Foxes were the most frequent visitor at skunk stations and were significantly more likely to visit these stations than coyotes (Fisher's Exact Test, n=67, p=0.05) and were more likely to pause at control stations than skunks (Fisher's Exact Test, n=24, p=0.009). Coyotes were exceedingly wary of skunk stations and never made contact with the mount which differed from skunks (Fisher's Exact Test, n=17, p=0.029), and perhaps raccoons (Fisher's Exact Test, n=14, p=0.097) and foxes (Fisher's Exact Test, n=44, p=0.087).

There was a significant difference across species in visitation to control stations according to moon light (Rank ANOVA; $\chi_4^2=21.384$, n=82, p<0.001) with raccoons and foxes visiting on brighter nights than bobcats (Tukey's HSD—raccoons: Q=3.68, p<0.005; foxes: Q=4.18, p<0.001) and foxes more visiting on brighter nights than skunks (Tukey's HSD, Q=2.60, p<0.1). There was no effect of habitat type on the likelihood of visiting, pausing at or making contact with skunk stations, however there were a number of significant differences among species at control stations. Foxes were more likely than skunks (Fisher's Exact Test, n=28, p=0.004) and raccoons (Fisher's Exact Test, n=20, p=0.036) and somewhat more likely than coyotes (Fisher's Exact Test, n=22, p=0.06) to visit control stations in closed habitat. Foxes were significantly more likely to make contact with the bait in closed habitat than skunks (Fisher's Exact Test, n=13, p=0.05), coyotes (Fisher's Exact Test, n=13, p=0.05) and possibly raccoons (Fisher's Exact Test, n=13, p=0.10).

DISCUSSION

Evolution should favor aposematic signals that are effective against all predators (Endler and Mappes 2004; Prudic *et al*. 2006). The objective of this study was to evaluate the behavior of potential skunk predators towards skunk mounts and to explore how two environmental characteristics (moonlight and habitat type) might influence predator perception of striped skunks. All of the species included here are documented or highly probable skunk predators (see Wade-Smith and Verts 1982, Hunter and Caro *in press*). Furthermore, the attraction of carnivores to heterospecifics has been well documented, with animals attracted to the presence of other species as a means of locating food resources (Palomares & Caro 1999, Creel *et al*. 2001, Hunter *et al*. 2007). The focus of this study was mammalian predators, although there has been some suggestion that great horned owls (*Bubo virginiana*) are important skunk predators (Wade-Smith and Verts 1982), but there is little empirical evidence supporting this claim in either owl diet studies (*e.g.* Cromrich *et al*. 2002, Schowalter *et al*. 2002) or skunk ecology studies (*e.g.* Sargeant 1982, Hanson *et al*. 2004).

Mammalian carnivores were reluctant to visit striped skunk mounts and approached skunk mounts more hesitantly than control stations, suggesting that mammalian predators actively avoid skunks. For raccoons and bobcats, it seems that if their interest was sufficient to approach the skunk mount, they were willing to make contact with it. On occasions when these species visited they were equally likely to make contact at skunk and control stations, although due to low statistical power these results should be interpreted with caution. Grey foxes, however, were equally likely to visit the two station types but were far less likely to make contact with skunk stations. Coyotes were nervous around the skunk stations: they rarely visited and never made physical contact, although they visited so rarely that it is difficult to draw conclusions about coyote behavior with confidence. Perhaps not surprisingly striped skunks were far more likely to visit the skunk stations than most other carnivores and approached the skunk mounts with greater trepidation than other species.

There was an effect of moonlight on visitation to all camera stations with animals less likely to visit on darker night. I also found that mammalian carnivores took more time to make contact with skunk mounts on darker nights. Hailman (1977) posited that black and white coloration is more effective deterrent in low light conditions; the degree of luminance (brightness) contrast between black and white coloration may make the white dorsal stripe appear brighter on darker nights (see also Prudic *et al* 2006). Habitat type had no effect on carnivore visitation to skunk mounts, although bobcats were more likely to pause and raccoons were less likely to visit control stations in closed habitat.

Little is known about species-specific differences in scotopic vision which is important for understanding how mammalian carnivores perceive their environment at night (Hailman 1977, Hubel 1988). Accordingly, it is difficult to make predictions about how a particular species might perceive a particular interspecific signal. The high luminance contrast of skunk coloration however is likely maximally conspicuous to a broad range of visual systems under a broad range of environmental conditions (Hailman 1977, Prudic *et al*. 2006).

It is possible that some aposematic signals are cryptic from a distance and conspicuous when viewed from close-up (Marshall 2000, Ruxton *et al*. 2004, Tullberg *et al*. 2005, Bohlin et al 2008) although, near and far are relative measures. It is possible that coyotes, bobcats and raccoons recognized and avoided skunk stations from a sufficient distance to avoid triggering the camera; for these species striped skunk coloration may function as a warning signal from a significant distance. In contrast, grey foxes were no less likely to visit skunk stations than control stations but they were less likely to make contact with skunk mounts, if they visited. For foxes, it seems that skunk aposematic signals are most effect deterrents when viewed from a relatively near distance.

Several anecdotal accounts suggest that when predators do approach closely, skunk displays are quite effective in driving their would-be predators off. Walton and Lariviere (1994) observed a striped skunk rebuffing two coyotes by merely displaying and Prange and Gehrt (2007) observed a coyote fleeing after being sprayed and a red fox fleeing from a displaying skunk. Furthermore, it appears that skunks often do not attempt to avoid their predators (Crooks and Soule 1999, Sovada *et al* 2000). While studying coyote avoidance by skunks Prange and Gehrt (2007) played coyote howls and observed skunks foraging within 20-50m of the playback speaker, apparently unaffected by the proximity of a “coyote.”

In conclusion, this study demonstrates an aversion of mammalian carnivores to striped skunks and finds that black and white coloration causes greater hesitancy to approach on darker nights, although for specific carnivores this avoidance was manifested in different ways; coyotes, bobcats and raccoons avoided skunk mounts outright while grey foxes investigated the mounts but rarely made contact with them, suggesting that skunk aposematic signally deters foxes from nearby but coyotes, bobcats and raccoons from a distance. In order to deter predatory attacks aposematic animals, like striped skunks, should use warning signals that exploit the disparate perceptual abilities of an entire suite of potential predators. While it is difficult to ascertain the cognitive or psychological factors that influence how predators see aposematic prey, species-specific differences in approach frequency and behavior are important to consider when evaluating the efficacy of aposematic signaling as an anti-predator strategy.

ACKNOWLEDGEMENTS

Many thanks to Tim Caro, Andy Sih and Dirk Van Vuren for commenting on earlier versions of this manuscript. Funding was provided by the National Science Foundation, the University of California and a Valentine Eastern Sierra Reserve Research Grant.

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Table 4.1. Total number of visits at control and skunk stations at eight research sites in California, USA. Several *C. latrans* visits (Control: 5, Skunk: 3) were made by subadult animals and were excluded from all analyses

Species	Control	Skunk
C. latrans	14	4
D. virginiana	1	0
L. rufus	15	7
M. mephitis	12	15
P. concolor	2	1
P. lotor	12	4
U. cinereoargenteus	33	24

Table 4.2. Statistics for mammalian predator behavior at control and skunk stations. Bold p-values indicate statistical significance at α=0.05. Data were tested using chi-squared analyses, Mann-Whitney U tests and Fisher's Exact Test as dictated by sample size and data distributions

Species	Statistic	p-value
C. latrans		
Visit	-	0.009
Pause	-	n.s.
Total pause	Z=-1.414	n.s.
Contact	-	n.s.
Time-to-contact	N/A	N/A
L.rufus		
Visit	-	0.055
Pause	-	n,s
Total pause	Z=-1.155	n,s
Contact	-	n,s
Time-to-contact	N/A	N/A
P. lotor		
Visit	-	0.020
Pause	-	n,s
Total pause	N/A	N/A
Contact?	-	n,s
Time-to-contact	N/A	N/A
U. cinereoargenteus		
Visit	χ^2=1.883	n,s
Pause	-	0.106
Total pause	Z=-0.937	n,s
Contact	-	0.017
Time-to-contact	Z=-0.613	n.s.

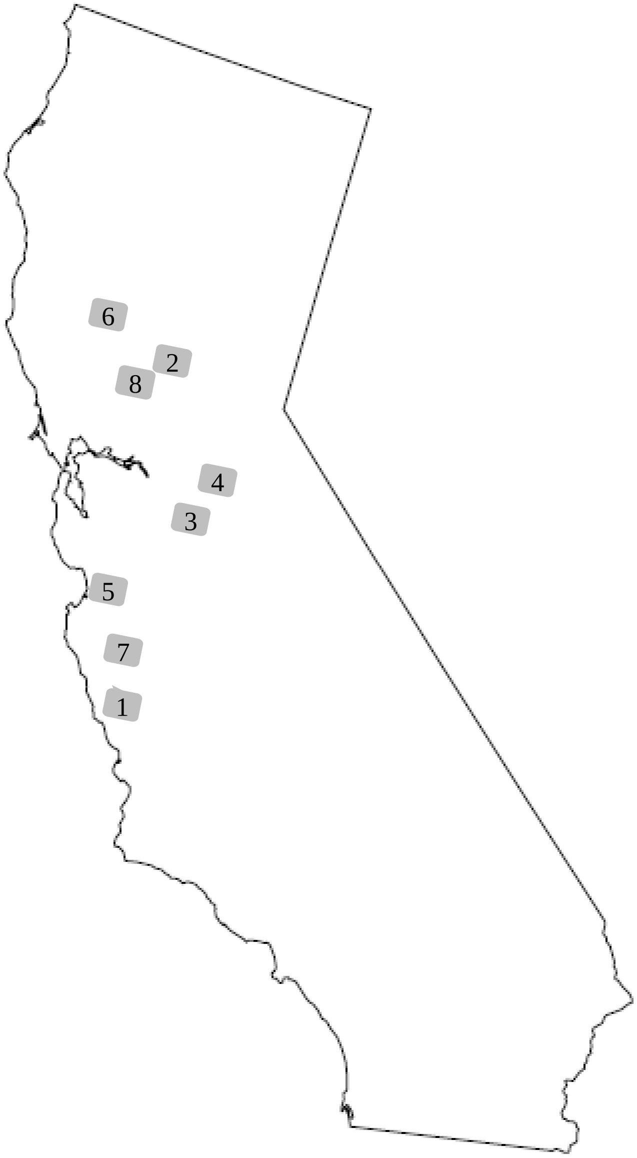

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Figure 4.1. Numbered markers indicate the following research sites in northern California, USA: 1. Big Creek Natural Reserve, 2. Bobcat Ranch, 3. Cosumnes River Preserve, 4. Deer Creek Hills, 5. Fort Ord Public Lands, 6. McLaughlin Natural Reserve, 7. Mitteldorf Preserve, and 8. Quail Ridge Natural Reserve.

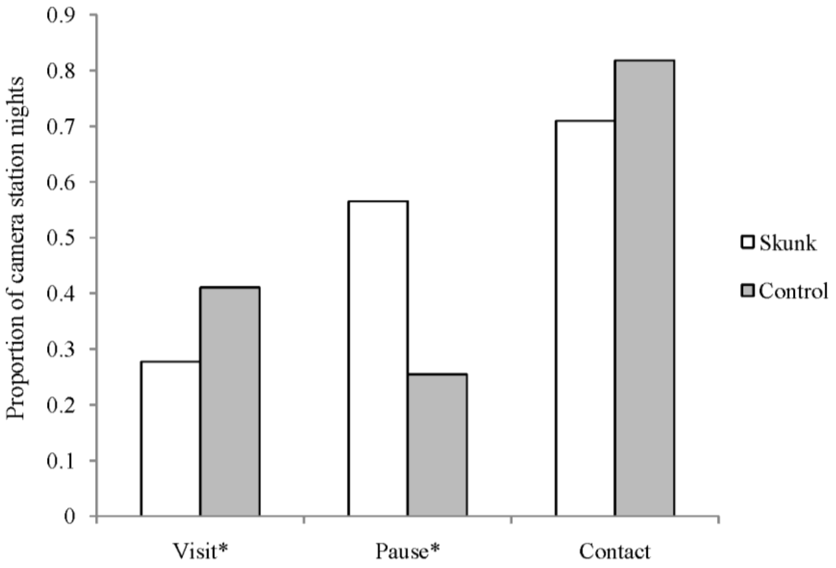

Figure 4.2. The proportion of sampling nights when carnivores visited, paused and made contact with skunk (open bars) and control (grey bars) stations. Pause and contact measures are conditional on visitation. Starred (*) bars indicate a statistically significant difference according to camera station type ($p<0.05$).

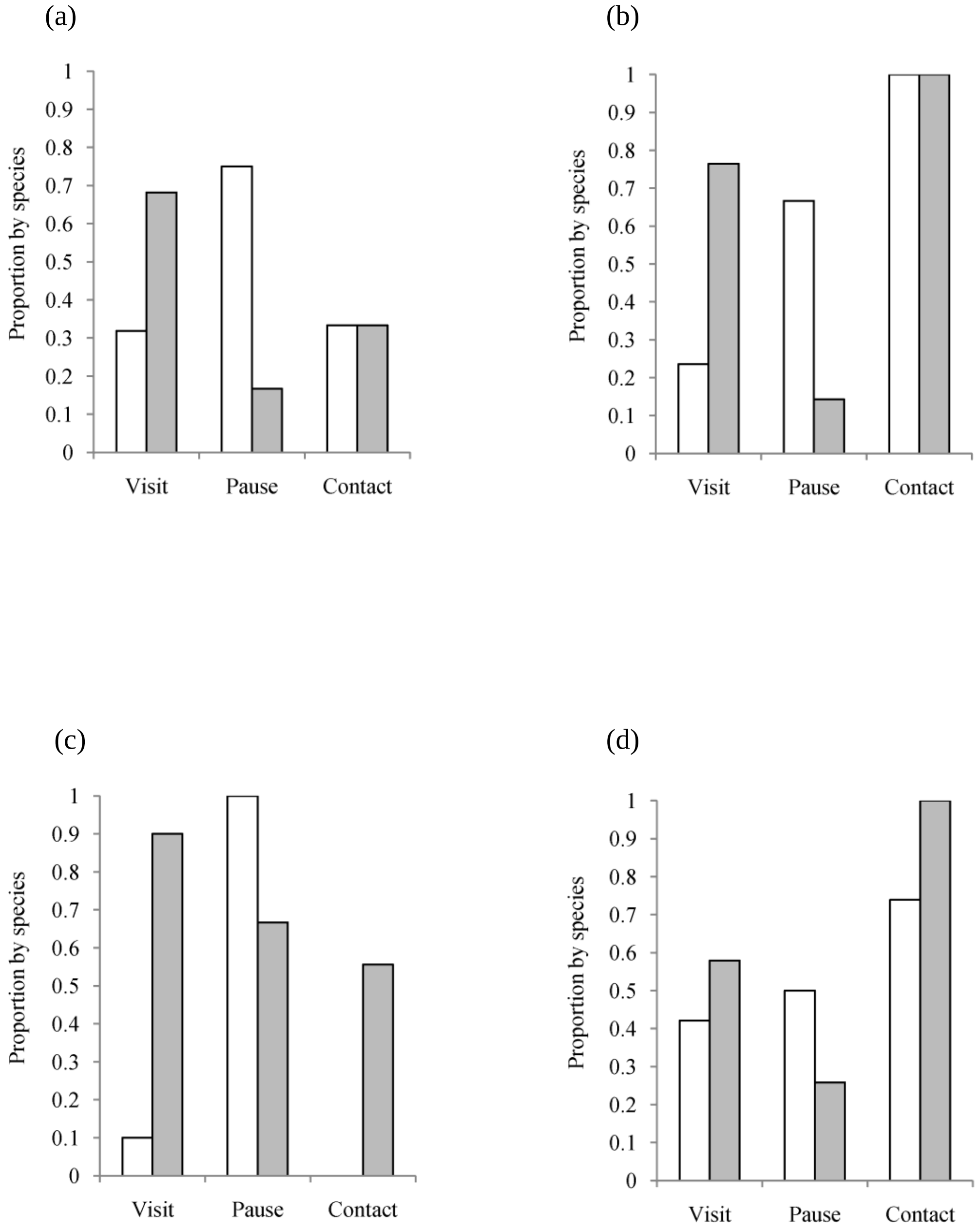

Figure 4.3. The proportion of each species' visitation and the likelihood of pausing and making contact at skunk stations (open bars) and control stations (closed bars). Species are (a) bobcat, (b) raccoon, (c) coyote and (d) grey fox.

CHAPTER 5

Familiarity breeds contempt: effects of striped skunk color, shape and local abundance on wild carnivore behavior

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ABSTRACT

Contrasting coloration in animals is widely seen as a warning signal but the extent to which it actually affects predator behavior in the wild and the way predators recognize such coloration is poorly understood. Here I use naturally and reciprocally colored taxidermy mounts of striped skunks (*Mephitis mephitis*) and grey foxes (*Urocyon cinereoargenteus)* to explore the impact of aposematic coloration and shape on the behavior of wild mammalian carnivores. Mounts were baited and all visiting species were recorded with remote video cameras at 10 wilderness sites in California, USA. I found mammalian carnivores approached black and white mounts more hesitantly than grey colored mounts but also reacted negatively to skunk shaped mounts. Carnivores were less likely to visit black and white mounts and approached skunk shaped mounts more reluctantly at sites with greater skunk abundance, suggesting that rather than simply possessing an unlearnt wariness toward contrastingly colored prey, it is necessary for carnivores to learn about skunks' noxious qualities through experience. There were also some differences in behavior among sympatric carnivores, with raccoons spending more time and being more vigilant near fox mounts than skunk mounts, and grey foxes spending more time in proximity to skunk mounts than fox mounts. These findings suggest that color and shape are both important components of aposematic signals in wild animals and that experience facilitates predator recognition of distasteful prey.

INTRODUCTION

Aposematic signaling communicates to potential predators that some prey species would be unwise to attack because they are toxic or dangerous (Ruxton et al. 2004; Caro 2005, Mappes et al. 2005). The efficacy of aposematism depends on predators' ability to learn to avoid dangerous prey, the ability to remember previous encounters, and the ability to discriminate between dangerous and palatable prey (Guilford & Dawkins 1991, Ruxton et al. 2004). Many studies have used coloration as the primary variable to investigate aposematism (e.g. Lindstrom et al. 2001, Sherratt and Beatty 2003, Exnerova et al. 2007, Ham et al. 2007). Background contrast (Roper 1994**,** Ruxton et al. 2004**,** Prudic et al. 2007), body shape (Gamberale-Stille and Tullberg 1999, Papaj and Newsome 2005), and olfactory (Roper and Marples 1997, Rowe and Guildford 1999a, Jetz et al. 2001) and auditory warning signals (Hristov and Conner 2005, Haugland et al. 2006) have been investigated to a lesser extent, although usually in concert with contrasting coloration. Most of these signals have been shown to augment the deterrent properties of warning coloration (e.g. Rowe and Guilford 1999b, Roper and Marples 1997, Ruxton et al. 2004), but there has been little attempt to tease apart the individual value of these signal modalities. The cues used by predators to differentiate aposematic prey from undefended prey presumably vary considerably across taxa (Endler and Mappes 2004, Mappes et al. 2005), and for most predator-prey systems we know little about the relative importance of specific indicators of prey defense.

For aposematism to be effective predators must learn quickly to avoid unpalatable, warningly colored prey and preferentially pursue and consume cryptic prey (i.e. Alatalo & Mappes 1996, Lindstrom et al. 1999a, Sherratt and Beatty 2003, Exnerova et al. 2007). While there is some evidence of an innate aversion of predators to specific colors and patterns similar to those found in aposematic prey (Smith 1977, Schuler and Roper 1992, Lindstrom et al. 1999b), these aversions are heightened with prior experience with noxious prey (Gittleman and Harvey 1980, Alatalo and Mappes 1996, Gamberale-Stille and Tullberg 1999, Gamberale-Stille 2001, Sherratt and Beatty2003). If learning plays a significant role in shaping aversions to aposematic animals one could expect the deterrent value of these signals to scale with local abundance or density of aposematic prey. Several studies have shown that gregariousness provides a selective advantage for aposematic prey (e.g. Guilford 1990, Gagliardo and Guildford 1993, Sherratt and Beatty 2003, Ruxton et al. 2004, Mappes et al. 2005), but it remains to be seen how variability in encounter frequency affects the behaviors of wide ranging predators towards aposematic prey, particularly when these interactions are separated in space and time.

Striped skunks (*Mephitis mephitis*) are perhaps the most familiar example of aposematism in vertebrates and are characterized by black pelage with bright white markings on their head and dorsum. They have wide bodies, short legs and a large, black and white, plume-like, tail. When threatened, skunks can spray a noxious compound from their anal glands a distance of up to 6 m (Wade-Smith and Verts 1982). Skunks are potentially preyed upon by a suite of mammalian and avian predator (Wade-Smith and Verts 1982, Hunter and Caro *in press*), although, surprisingly, several studies have found that predator mortality has little influence on skunk populations (Hanson et al. 2004, Gehrt 2005, Prange and Gehrt 2007). Skunks are largely avoided by their predators (Hunter, *submitted*), and on those occasions when predators approach skunks their anti-predator displays are extremely effective at deterring any predatory attack (Walton and Lariviere 1994, Prange and Gehrt 2007). In addition to warning coloration, experienced predators might use the characteristic body shape of striped skunks to recognize their noxious quality. Despite the frequency with which skunks are cited as an example of aposematism, very little is known about the specific visual cues predators use to differentiate skunks from undefended prey.

Studies of predator response to aposematic prey have typically been conducted in a highly controlled laboratory setting using naïve hand-reared or wild caught birds and novel prey (Ruxton et al. 2004; but see Brodie and Janzen 1995, Buasso et al. 2006). To date, there has been little attempt to quantify the role of experience on predator responses to aposematic prey in a field setting. Forced interactions between captive predators and prey may obfuscate the degree to which predators avoid aposematic prey in a landscape, particularly for species, like striped skunks, for which direct contact is not required for their defense to be deployed. This study focuses on mammalian carnivores and explores the deterrent effects of aposematic coloration on intraguild predators. I used taxidermy mounts of striped skunks and grey foxes (*Urocyon cinereoargenteus*) *in situ* to assess the relationship between natural predator-prey dyads. First I ask which striped skunks attribute, body shape, coloration, or the interaction between the two is most likely to elicit an avoidance response in skunk predators? Secondly, does the local abundance of striped skunks influence the behaviors of predators around skunks and skunk colored mounts?

METHODS

Camera stations

Data were collected at 10 sites throughout northern California from June 2006 through November 2007 (Figure 5.1). Each camera station set consisted of five treatment types: black-and-white skunk, grey skunk, black-and-white fox, grey fox and a control (baited, with no mount). Black and white skunks and grey fox mounts were made from tanned skunk and fox skins. Black and white fox mounts were made using fox skins dyed with commercial hair dye and bleach. Dyed and bleached skunk skins were used for the grey skunk mounts but, due to the difficulty of replicating the grey fox pelage using dye alone, the dorsum and crown of the head was cut out of dyed skunk skins and grey fox fur was sewn in its place. All mounts were washed initially to remove any dye odors, were sprayed daily in the field with a carbon-based deodorizing spray (Carbon Blast, Robinson Labs Inc; Cannon Falls, MN), and were handled with latex gloves to minimize the transmission of human odors.

Striped skunks and grey foxes co-occur throughout much of their geographic ranges (Wade-Smith and Verts 1981, Fritzell and Haroldson 1982). While they belong to different taxonomic families (skunks: Mustelidae, foxes: Canidae) they are both omnivorous and habitat generalists and are of similar size (skunks: 3.3kg, foxes: 3.7kg, Hunter and Caro *in press*). Furthermore, grey foxes are cryptically colored and are comparably long-legged (Fritzell and Haroldson 1982), thus fox mounts differed from striped skunks mounts both in coloration and body shape. It should be noted however that fox mounts were 20-25cm taller than skunk mounts and could appear more intimidating to other carnivores.

Camera stations were established along trails or roads in random order at 250 m intervals and were baited with a mixture of salmon meat, sun-rendered trout oil, and beaver castorium (Buckeye Trap Supply; Ashland, OH). Infra-red cameras (Leaf River; Taylorsville, MS) were placed on wooden stakes at a height of 25-30 cm, at a distance of approximately 4 m from the bait. Mounts were anchored to the ground with stakes that were driven into the ground until they were flush with the substrate, then secured to the stakes using zip ties. When approached by a potential predator skunks engage in a series of escalating displays culminated with the expulsion of noxious secretions. Skunk mounts were positioned facing across the road or trail with their tail arched behind them, so as not to mimic the raised tail alarm position often seen as the first warning signal (Lariviere & Messier 1996). Cameras were set to trigger at 1 min intervals and to record 1 min of digital video footage. The result was a near continuous record of the behavior of visiting species. Videos were downloaded every morning and stations were baited every evening. During the day, mounts were covered to minimize fading caused by prolonged exposure to the sun, and cameras were switched off. Camera station sets were run for 5 consecutive non-rainy nights and relocated four times per site (a minimum of 1 km from the location of any previous mount set) for a total of 20 camera nights per site of each, control and mount stations.

An attempt was made to sample each site equally (four camera station sets at each site), but this was not possible at two sites. At one site a grey skunk mount was stolen by a coyote, resulting in 3 fewer station nights than any of the other treatment types, and at a second site excessive human activity resulted in premature closure of two camera station sets.

Carnivore behavior

The videos obtained from camera-stations were scored using several criteria. Visits by the same species at the same mount station within any 10 minute period were considered to be repeat visits by the same individual and these occasions were counted as one visit. Once an animal appeared on camera, the species identity, number of animals, and age (adult or juvenile) were noted. Because young carnivores are often more curious than adults (e.g. Caro 1994) and likely have limited prior experience with skunks, visits by juveniles were excluded from all analyses, unless accompanied by an adult animal. In cases where more than one adult animal was present the first animal on camera was used as the focal animal for all behavioral observations. If a visiting animal moved toward the bait or mount, the number and length of all pauses in their approach were scored. A pause was defined as an animal freezing for any length of time in its approach to the mount or bait station. Once an animal got near the bait, it could either turn and move off camera or continue forward and make contact (sniff, lick, bite, or rub) with either the bait or mount. On occasions when animals made contact, the total time elapsed from when an animal came into view until it made contact with the mount or bait (including any pauses) was recorded (time-to-contact). The length of time the animal remained in contact with the bait or mount was also noted (time-in-contact). Finally, mean scan length was calculated from scan number and duration during each carnivore visit. Vigilance was defined as an animal turning away from the mount and fixing its gaze beyond camera view.

Track stations

In the western United States skunks are potentially killed by several mammalian carnivores, including grey foxes, red foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*), bobcats (*Lynx rufus*), mountain lions (*Puma concolor*), black bears (*Ursus americanus*), coyotes (*Canis latrans*), and badgers (*Taxidea taxus*) (Wade-Smith & Verts 1982; Hansen et al. 2004). In order to evaluate the relative abundance of skunks and skunk predators at each of the study sites, track stations were placed at 250m intervals along roads or trails. Track stations were lined with a 1-m diameter circle of fine-weave landscaping cloth, staked to the ground with 15 cm nails and covered with approximately 1 cm of sifted mixture of white sand moistened with mineral oil. Bait (trout oil, salmon meat and beaver castorium) was placed directly on the sand in the center of the station. Track stations were checked every morning and were re-baited, nightly for five consecutive nights. The number of stations deployed at each site varied (26 to 40) depending on road and trail accessibility. The relative abundance of carnivores across sites was calculated using the following methodology set forth by Crooks (2002):

$$\text{Relative Abundance} = \ln\left[\left(\frac{v_j}{(s_j n_j)}\right) + 1\right]$$

where v_j is the number of track station visits by the focal species at site j, s_j is the number of stations at site j, and n_j is the number of nights that track stations were run at site j. Track stations, particularly those with natural substrate, are likely to detect the presence of most carnivores (Gompper et al. 2006) and are a more economical means of sampling large areas than are camera traps. For brevity, relative abundance will hereafter be referred to as abundance.

Data analyses

My study focused on the behavior of predators towards skunks, so visits by skunks were excluded from statistical analyses except where noted. Eight behavioral variables were analyzed based on video observations: (i) visits, (ii) pauses, (iii) contacts, (iv) total pause length, (v) mean pause length, (vi) time to contact, (vii) time spent in contact, and (viii) mean vigilance scan length. *A priori* it was clear that several environmental factors may affect how easily mounts were seen by visiting species and were therefore included as covariates. Habitat type was organized into two coarse categories: open and closed. Open habitat was grassland or oak woodland with no woody vegetation less than 4 m in height within 3 m of the station. Closed habitat included was chaparral or other dense undergrowth within 3 m of the station. Several sites, particularly those near the coast, had a near-nightly influx of marine fog which may have made the mounts difficult for visiting species to see from a distance. To evaluate the influence of foggy conditions on animal behavior an EasyUSB data logger (Lascar Electronics; Erie, PA) was attached to the camera stake at the control station and was used to record relative humidity hourly. When more than one camera station set was run concurrently the data logger was randomly assigned to one of the control stations. Animal behavior was also analyzed with respect to the fraction of moon illuminated (per United States Naval Observatory) on each sampling night to examine the influence of lunar illumination..

Continuous data were tested using analyses of covariance (ANCOVAs), and binomial data were tested using generalized linear models, using SPSS (vers 16). Mean pause length, time to contact, time in contact, and mean scan length were natural-log transformed (+1) to achieve normality. For ANCOVAs, mount shape (skunk or fox) and mount color (black and white or grey) were included as fixed-factors and species identity was included as a random-factors. Habitat type, relative humidity, moon fraction, relative abundance of striped skunks, and relative abundance of foxes were treated as covariates and analyzed for main effects and 2-way interactions. Generalized linear models were fit to a binomial distribution. Mount color and shape were analyzed for main effects and 2-way interactions with species identity, habitat type, relative humidity, moon fraction, and the relative abundance of striped skunks and grey foxes. All terms and 2-way interactions were included in the initial model and non-significant terms (p-value greater than 0.10) were deleted stepwise. I conducted several statistical tests on the same data set so I used sequential Bonferroni corrections (Rice 1989) to minimize the likelihood of making type I errors, although these corrections do increase the risk of committing type II errors (Moran 2003, Nakagawa 2004). The corrected significance of results are noted in the text, with (*) denoting $p < 0.\ 5$ and (**) denoting $p<0.01$.

RESULTS:

Camera stations were visited by 8 species including coyotes, grey foxes, raccoons, bobcats, striped skunks, Virginia opossums, mountain lions and black bears for a grand total of 307 visits at all station types (947 station nights) across 10 sites (Table 5.1).

Species abundance

In 1505 track station nights across the 10 sites there were 445 carnivore visits from several species including grey fox (n=190, 42.7%), striped skunk (n=91, 20.4%), raccoon (n=53, 11.9%), coyote (n=39, 8.8%), Virginia opossum (*Didelphis virginiana*, n=33, 7.4%), bobcat (n=15, 3.4%), long tailed weasel (*Mustela frenata*, n=8, 1.8%), spotted skunk (*Spilogale gracilis*, n=4, 0.9%), mountain lion (n=3, 0.7%), American mink (*Mustela vison*, n=3, 0.7%), river otter (*Lontra canadensis*, n=1, 0.2%), American badger (n=1, 0.2%), and four unidentifiable tracks (0.9%). The relative abundance of carnivores varied greatly across sites (Table 5.2).

Effects of color

There was no effect of mount color on visitation but animals were significantly more likely to pause in their approach to black and white colored mounts (χ_1^2=5.961, p=0.015, Figure 5.2). There was no effect of color on the length of time animals paused (mean or total) in their approach, but there was a significant interaction between mount color and moon fraction with visiting species more likely to pause in their approach to black and white mounts on darker, low moon fraction nights (χ_2^2=5.404, p=0.067). Carnivores approached black and white mounts very cautiously, taking significantly longer to make contact with black and white mounts when compared to grey mounts ($F_{1,51}$=4.563, p=0.037). There was a significant interaction effect of moon fraction and color, with animals avoiding contact with grey mounts on brighter nights (χ_2^2=5.042, p=0.025).

Effects of shape

Carnivores were significantly less likely to visit skunk shaped mounts than fox shaped mounts (χ_1^2=22.396, p<0.001**, Figure 5.2), and were particularly averse to visiting skunk mounts in closed habitat (χ_2^2=26.949, p<0.001**). There was no effect of mount shape on likelihood of pausing in approach or total or mean pause length, although animals were less likely to make contact with fox mounts than skunk mounts (χ_1^2=4.708, p=0.030, Figure 5.2) and were reluctant to make contact with foxes on foggier nights (higher relative humidity) (χ_2^2=7.812, p=0.020). Carnivores did take a significantly longer time to get near enough to make contact with skunk mounts when compared to fox mounts ($F_{1,51}$=21.513, p<0.001**). Once they made contact though, animals spent significantly more time in contact with skunk-shaped mounts than fox-shaped mounts ($F_{1,43}$=4.180, p=0.049), somewhat more so on clearer (low rel. humidity) nights ($F_{1,43}$= 2.845, p=0.099). Finally, visiting carnivores were more vigilant at skunk mounts with decreasing moonlight ($F_{1,46}$=3.927, p=0.054).

There was also a significant interaction between species identity and mount shape for time spent in contact with mounts ($F_{1,43}$=3.037, p=0.020); foxes spent more time in contact with skunk mounts (t_{43}=2.454, p=0.018) than fox mounts, and raccoons spent more time in contact with fox mounts (t_{43}=2.430, p=0.019) than skunk mounts. There was also a significant interaction between shape and species identity for mean scan length with raccoons more vigilant at fox mounts than at skunk mounts (t_{46}=2.617, p=0.012).

Effects of environmental variables

Several environmental factors influenced animal behavior. Visiting species were more likely to visit all mount types in closed habitat rather than open habitat (χ_1^2=42.303, p<0.001**). Total pause length was related to moon fraction with animals pausing for longer with increasing moon fraction ($F_{1,50}$=3.348, p=0.073). Animals took longer to make contact in open environments ($F_{1,55}$=14.846, p<0.001**) and spent more time in contact with mounts on clearer (low relative humidity) nights ($F_{1,43}$=4.234, p=0.046) and darker (low moon fraction) nights ($F_{1,43}$=5.765, p=0.021). Carnivores were also more vigilant on clearer nights ($F_{1,46}$=10.383, p=0.002*).

Effects of skunk abundance on predator behavior

Visitation at all mount stations was influenced by skunk abundance, with fewer visits, to all mount stations, with increasing local skunk abundance (χ_1^2=13.70, p<0.001**). This effect was not driven by overall carnivore abundance. An *a posteriori* test yielded a significant effect of carnivore abundance (excluding skunks) on species abundance but the trend was opposite the effect of skunk abundance; visitation was more likely at sites with more carnivores (t_{1072}=5.328, p<0.001**). There was a parallel significant interaction between fox abundance and mount shape, with fox mounts less likely to be visited in places with higher fox abundance (χ_1^2=28.586, p<0.001**). There was also a significant interaction of color and skunk abundance, with visitation at black and white colored mounts decreasing with increasing skunk abundance (χ_1^2=4.299, p=0.038).

Skunk abundance was also related to likelihood of pausing, with animals more likely to pause in their approach with increasing skunk abundance (χ_1^2=4.493, p=0.034). Skunk abundance was also related to mean scan length, with animals tending to be more vigilant in areas with higher skunk abundance ($F_{1,46}$=4.763, p=0.034). *A posteriori* tests revealed non-significant effects of overall carnivore abundance on the likelihood of pausing and scan length. There was a significant interaction between shape and skunk abundance with animals more likely to pause at skunk-shaped mounts with increasing skunk abundance (χ_1^2=4.178, p=0.041). There was no effect of skunk abundance on mean pause length, total pause length, or time to contact the mounts. The likelihood of approaching near enough to make contact was unrelated to skunk abundance, although more time was spent in contact with mounts in areas of higher fox abundance ($F_{1,43}$=6.036, p=0.018).

DISCUSSION

The taxidermy mounts used in this study affected the behavior of wild carnivores, although different mounts produced different responses. For example, in some cases “predatory” attacks were made, including a mountain lion attacking and mauling a black and white fox mount, and a coyote extricating a grey skunk mount from its anchor and running off with it.

Black and white coloration elicited stronger reactions from mammalian carnivores than did grey coloration when paired with both skunk and fox shapes. In order for aposematism to provide a selective advantage it is not necessary for aposematic prey to avoid their predators completely (Cott 1940, Ruxton et al. 2004), as long as possessing these signals discourages predator attacks (Guilford and Dawkins 1991, Ruxton et al. 2004, Mappes et al. 2005). Black and white mounts in this study were not avoided altogether by mammalian predators, although visiting carnivores approached them extremely cautiously, particularly on darker nights, when black and white colored animals appear maximally contrasting (Hailman 1977, 1979, Ortolani 1999). Conspicuous coloration is thought to allow predators to readily distinguish noxious from palatable prey, facilitates associative learning and enhances memorability of aposematic signals (Gittleman and Harvey 1980, Lindstrom et al. 2001, Guilford 1990, Guilford and Dawkins 1991, Ruxton et al. 2004) and the results of this study suggest that skunk coloration achieves this regardless of body form.

In addition, the distinctive skunk shape also gave pause to visiting carnivores. Skunk shaped mounts, both black and white and grey, were visited less often and approached more hesitantly than fox shaped mounts. The influence of body shape has rarely been addressed explicitly in past studies of aposematism, although cryptic forms of aposematic prey are frequently offered to captive predators with differing results. For example, Gamberale-Stille and Tullberg (1999) found that experienced domestic chicks did not generalize the negative experience with aposematic prey to less colorful morphs of the same shape. In contrast Exnerova (2007) found interspecific differences in reaction to aposematic prey, with some species of wild caught tits more apt to handle non-aposematic than aposematically colored prey, whereas other species were equally reluctant to handle non-aposematic as aposematic forms. My study found experienced mammalian carnivores to behave cautiously near skunk mounts, regardless of whether the mounts possessed the distinctive black and white skunk coloration. If predators generalize aposematic traits to prey with the same physical form as familiar aposematic prey, studies that compare aposematic and non-aposematic morphs of the same prey species may conflate the separate effects of coloration and body shape as predator deterrents. Therefore, it may be difficult to ascertain the efficacy of an aposematic signal or infer predator psychology from comparative analyses of feeding behavior on different color morphs of single prey species.

Aggregations of aposematic prey have been shown to elicit stronger avoidance behaviors than solitary aposematic prey, and accordingly gregariousness is considered a likely mechanism for facilitating the initial evolution of aposematic phenotypes (Endler 1988, Gagliardo and Guilford 1993, Riipi et al. 2001, Speed 2000, 2001, Ruxton et al. 2004, Caro 2005). While the genesis of the argument for the importance of gregariousness is kin-selection theory (for a review see Ruxton et al. 2004), spatial aggregation may be equally important for maintaining the effectiveness of aposematic signals, regardless of the relationship between individuals (Endler 1988). The present study suggests that the survivorship benefits conferred by proximity to other aposematic individuals might be reasonably extended to densities at a landscape scale (Ruxton et al. 2004) where the frequency with which aposematic prey are encountered in the environment is potentially instrumental in reinforcing warning signals and increasing the memorability of these signals to predators (Endler 1988, Guilford and Dawkins 1991, Ruxton et al. 2004, Mappes et al. 2005). My study showed that in places where skunk abundance was low mammalian carnivores readily visited black and white mounts but at sites where skunks were relatively common carnivores avoided black and white mounts, regardless as to whether they were skunk or fox shaped. Similarly, carnivores were more apt to pause at skunk shaped mounts at sites where skunks were more common. Striped skunks are ubiquitous throughout the state of California

(Jameson and Peeters 2004) so while the research sites used in this study varied in skunk abundance anecdotal sightings data indicate, at a minimum, all sites had a skunk presence in the recent past. Therefore, I am reasonably confident that adult carnivores at these sites have had some prior experience with skunks. While unlearnt wariness may play some role in the avoidance of aposematic prey (Smith 1977, Schuler and Hesse 1985, Schuler and Roper 1992, Exnerova et al. 2007), any innate aversions are likely modified by the frequency of interactions with noxious prey.

The local abundance of skunks also had an unexpected impact on behavior near all mount types, with mammalian carnivores approaching all mounts more cautiously with increasing skunk abundance. It is possible that predators are more reluctant to approach other carnivores in areas where aposematic animals are frequently encountered. In mammalian carnivores, interspecific interactions commonly take place near food resources (Palomares and Caro 1999, Creel et al. 2001, Hunter et al. 2007), and perhaps it is in these circumstances where other carnivores frequently come in contact with skunks, which may necessitate approaching the baited mount stations cautiously. There were also some effects of fox abundance on carnivore behavior, with fox mounts more likely to be visited at sites with lower fox abundance. This result was likely been driven by conspecific visits by grey foxes. Fox abundance also influenced the time spent in contact with mounts. While other species typically spent less than 30 seconds in contact with the mounts or bait it was not uncommon for grey foxes to lick at the bait for a full minute uninterrupted, thus it is not surprising that at sites with large fox populations there would be a significant increase in the amount of time spent in contact with the mounts.

Different predators vary in their perceptual and cognitive abilities but evolution should favor aposematic signals that are effective against all predator species (Endler and Mappes 2004, Ruxton et al. 2004, Mappes et al. 2005, Prudic 2007). The analyses in my study were limited to two potential visual cues that potential predators may use to identify skunks (coloration and body shape), but there are specific behaviors that skunks engage in when confronted by a predator

(Lariviere and Messier 1996). These displays have been shown to be quite effective in rebuffing potential predators (Walton and Lariviere 1994, Prange and Gehrt 2007) and would likely amplify any aversion noted in this study. Past studies on birds have found that behavior around aposematic prey varies significantly with predator species (Evans and Waldbauer 1982, Exnerova et al. 2003, 2007), however in this study the response to alternative mount shapes and colors did not vary substantially according to carnivore species identity, with all species reacting similarly to black and white mounts and skunk shaped in most cases. Grey foxes did spent more time in contact with skunk mounts than fox mounts but this observation may reflect some intra-specific interaction between grey foxes and fox mounts, rather than a true affinity for skunk mounts. Raccoons moved away from skunk mounts more quickly than fox mounts but were more vigilant at fox mounts than skunk mounts, although this may simply be an artifact of increased time near fox mounts. Raccoons and skunks share substantial dietary overlap (Azevedo et al. 2006), so raccoons may frequently interact with skunks near food resources and therefore be particularly averse to skunk shaped mounts.

In conclusion, the data presented here underscore the importance of warning coloration in eliciting avoidance behavior by wild predators and additionally show that body shape is important. There were a few significant effects of species identity but, by and large, mammalian carnivores reacted equally strongly to the mounts. Finally, the importance of skunk abundance suggests that experience promotes learning of aposematism in mammalian carnivores and that this effect is enhanced when skunks occur in greater numbers.

ACKNOWLEDGEMENTS

I would like to thank Tim Caro, Andy Sih and Dirk Van Vuren for commenting on previous versions of this manuscript. Thanks so much to the following reserve, preserve and public lands staff for all their support: M. Ackerman, P. Aigner, F. Arias, V. Boucher, H. Brady, J. Brown, J. Buck, S. Danner, D. Dawson, B. Delgado, F. Felix, R. Kelsey, C. Koehler, H. McQuillen, T. Mebane, E. Morgan, K. Merg, V. Russell, R. Worley and S. Waddell. Special thanks to S. Waddell and M. Elbroch for their mount recovery efforts. Funding was provided by the National Science Foundation, the University of California, Davis and a grant from the University of California Valentine Eastern Sierra Reserve.

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Table 5.1. Number of visits by mammalian carnivore at control, black and white (B&W) skunk, black and white fox, grey skunk and grey fox stations at 10 research sites.

Species	Control	B&W skunk	B&W fox	Grey skunk	Grey fox
C. latrans	14	4	0	2	0
D. viginianus	1	0	1	0	3
L. rufus	15	7	7	15	6
M. mephitis	11	15	6	6	7
P. lotor	13	4	14	9	15
P. concolor	2	0	4	0	1
U. cinereoargenteous	33	24	25	24	17
U. americanus	0	0	0	1	1

Table 5.2. Relative abundance of mammalian carnivores at 10 research sites in California (for calculation method seen text). Site identity is as follows: BC=Big Creek Natural Reserve, BR=Bobcat Ranch, CRP=Cosumnes River Preserve, DCH=Deer Creek Hills, FO=Fort Ord Public Lands, MC=McLaughlin Natural Reserve, MP=Mitteldorf Preserve, QR=Quail Ridge Natural Reserve, SH=Sagehen Natural Reserve, SN=Sierra Nevada Aquatic Research Laboratory.

Species (N^o station nights)	BC (170)	BR (135)	CRP (145)	DCH (145)	FO (200)	MC (145)	MP (135)	QR (150)	SH (150)	SN (130)
C. familiaris	-	-	-	-	0.010	-	-	-	-	-
C. latrans	0.017	0.036	0.007	0.007	0.039	-	0.007	-	0.089	0.045
D. viginiana	0.040	-	0.053	-	-	0.007	-	0.007	-	-
F. catus	-	-	-	-	0.005	-	-	-	-	-
L. canadensis	-	-	0.007	-	-	-	-	-	-	-
L. rufus	0.018	-	-	0.007	0.015	0.007	0.015	0.013	0.020	-
M. mephitis	-	0.044	0.117	0.007	0.131	0.069	0.007	0.148	-	0.023
M. frenata	0.029	-	-	-	0.005	-	-	-	0.007	0.008
M. vision	-	-	0.021	-	-	-	-	-	-	-
P. lotor	-	0.051	0.177	0.007	0.068	-	-	-	0.007	0.015
P. concolor	-	-	-	-	0.005	-	0.015	-	-	-
S. gracilis	0.023	-	-	-	-	-	-	-	-	-
T. taxus	-	-	-	-	0.005	-	-	-	-	-
U. cinereoargenteous	0.444	0.092	-	-	0.230	0.020	0.099	0.119	0.007	-
Unknown	0.012	-	-	-	-	-	-	-	-	-

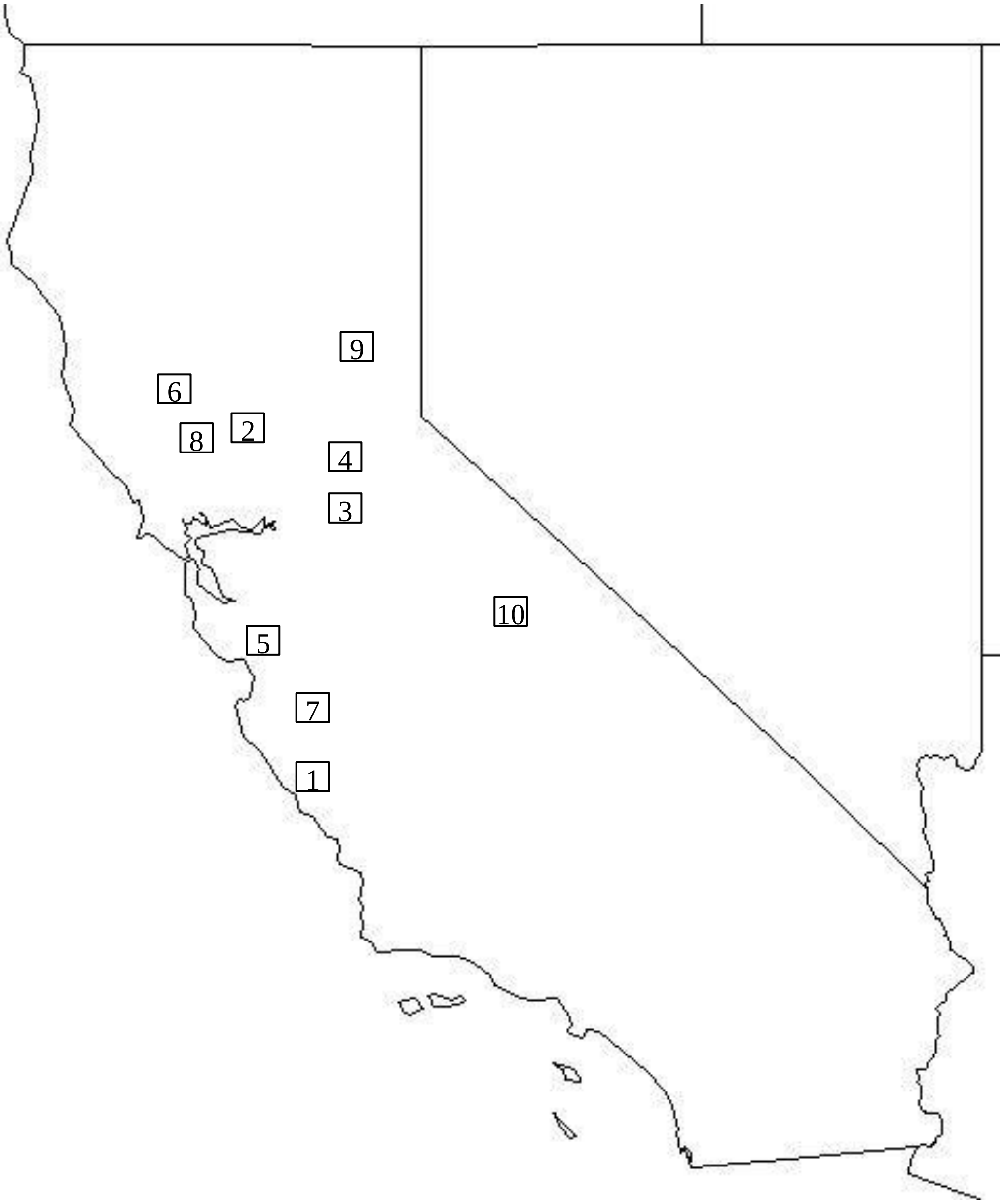

Figure 5.1. Numbered markers indicate the following research sites: 1. Big Creek Natural Reserve (University of California Natural Reserve System (UCNRS)); 2. Bobcat Ranch (Audubon California); 3. Cosumnes River Preserve (Bureau of Land Management (BLM), The Nature Conservancy); 4. Deer Creek Hills (Sacramento Valley Conservancy); 5. Fort Ord (BLM); 6. McLaughlin Natural Reserve (UCNRS); 7. Mitteldorf Preserve (Big Sur Land Trust); 8. Quail Ridge Natural Reserve (UCNRS); 9. Sagehen Natural Reserve/Tahoe National Forest (UCNRS); 10. Sierra Nevada Aquatic Research Laboratory/Inyo National Forest. (UCRNS/USFS).

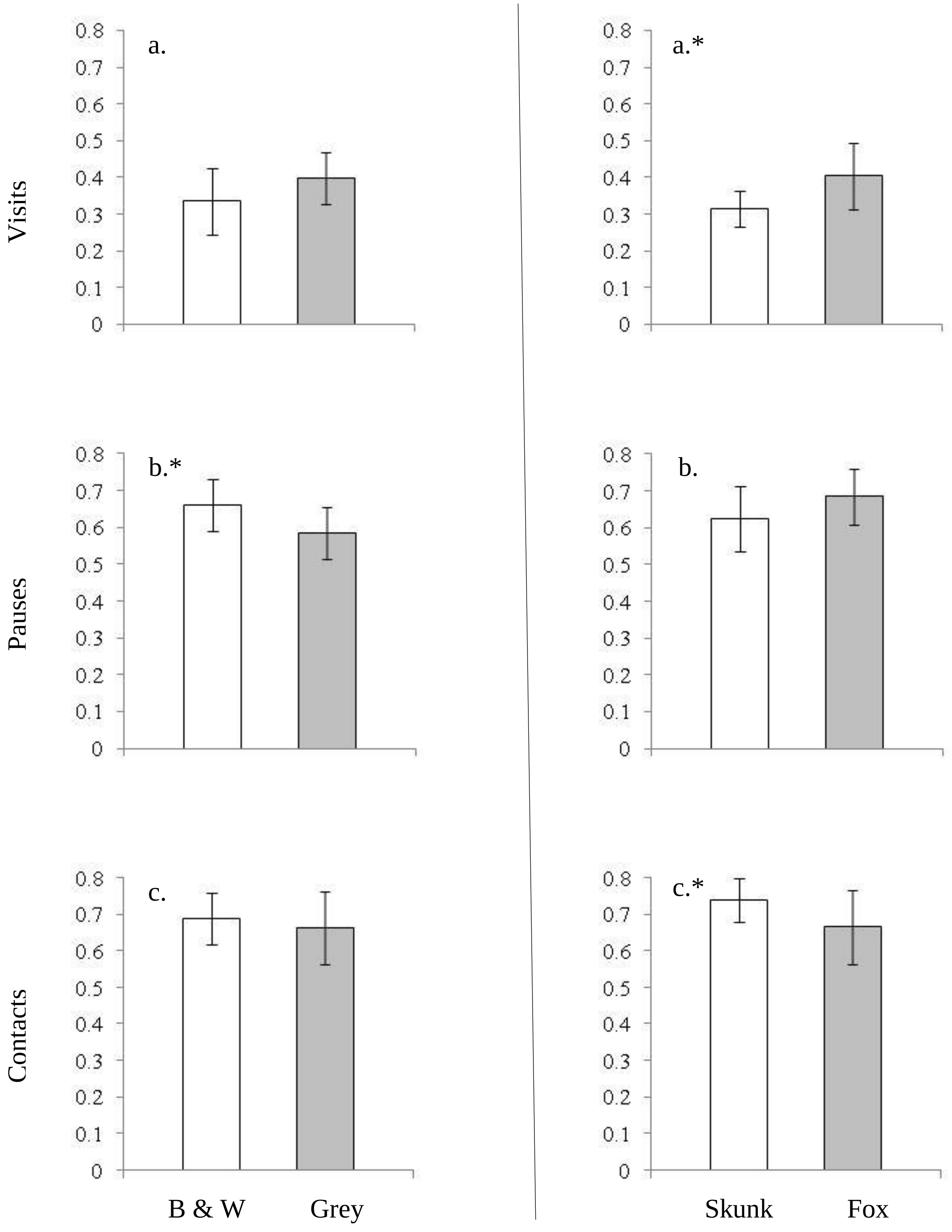

Figure 5.2. Mean (±S.E.) proportion of total visits (a), proportion of pauses (b), and proportion of contacts (c) according to mount color and mount shape. Mount colors (left column) were black and white (B&W, open bars) or grey (grey bars) and mount shapes (right column) were skunk-shaped (open bars) or fox-shaped (grey bars). Starred (*) graphs denote a significant differences in generalized linear models.