Living with Large Carnivores: Insights from Diet Choice, Habitat Use, and the Ecology of Fear

BY

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THESIS

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This thesis is dedicated to my loving and patient husband, Paul Orlando, who stood by my side throughout this journey.

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Summary

This thesis focuses on large carnivore behavior in hopes to understand how humans and large carnivores can coexist. Carnivore behavior is examined through diet choice, habitat selection, and the ecology of fear.

The first chapter examines a proposed mechanism of coexistence among carnivores with pumas (*Puma concolor*) and jaguars (*Panthera onca*) as my focal system. I proposed carnivores may coexistence due to a tradeoff in the ability to catch agile prey items and the ability to safely subdue more dangerous prey. I developed a mathematical model, analyzed published diet studies, and examined historic range maps to test the validity of the mechanism of coexistence. I found that all three lines of investigation supported a mechanism of coexistence along a dangerous-agile gradient of the prey for carnivores.

The second chapter examines current and historic puma attacks on humans. I examined published attacks on humans in 12 states from 1890 – 2010. Attack propensity was examined in relation to human density, livestock density, and occurrence of puma hunting. I found puma attacks on humans increase significantly with an increase in human density. Furthermore, with an increase in human density, puma attacks decreased significantly with an increase in livestock density. Sport hunting of pumas had no affect on the propensity of puma attacks on humans.

The final chapter examines temporal and spatial distribution of coyotes (*Canis latrans*) and white-tailed deer (*Odocoileus virginianus*) in the Chicago metropolitan area. Distributions were examined through camera data collected from 2010 and 2011 by the Urban Wildlife Institute. I found that both coyotes and deer were negatively associated

with an increase in housing density and positively associated with an increase in canopy

cover. Deer also exhibited a positive association with water and coyotes.

1. Introduction

1.1 <u>Overview</u>

To me, the importance of possessing a sound ecological knowledge base is to allow for the establishment of successful conservation strategies. This knowledge base needs to be multifaceted and range from understanding behavior and resource needs of an organism without the presence of humans to understanding an organism's response to humans. I believe one of the best examples of taking an all-inclusive approach to conservation efforts is with the tiger (*Panthera tigris*) conservation projects founded by the CEO of Panthera, Dr. Alan Rabinowitz. Tigers are the most critically endangered cat species with only an estimated 3,200 individuals left in the wild. Dr. Rabinowitz developed the largest tiger reserve in the world in Myanamar, the Hukaung Valley Tiger Reserve, in 2004. Realizing space was not the only resource that was critical to tiger conservation, the reserve was also defined based on the healthy varied prey base that was available for tigers. Dr. Rabinowitz realized a lack of a varied wild prey base would increase chances of livestock depredation, consequently greatly hindering the conservation work. Furthermore, he involved the local government and local communities in the establishment of the conservation program.

Dr. Rabinowitz is one of the main reasons I started in the graduated program for Ecology and Evolution and why I am continuing on to receive a degree in Education. His work showed me the importance of understanding the ecological needs of an organism but also the importance of working with and educating the communities that live along side the organism of conservation focus.

My thesis begins with an investigation into coexistence among pumas (*Puma concolor*) and jaguars (*Panthera onca*). The chapter explores a proposed mechanism of coexistence among carnivores along an agile-dangerous gradient of the available prey. The chapter utilizes pumas and jaguars as the inspiration but explores the possibility of a universal carnivore mechanism of coexistence. The second chapter examines historic and current conflict among pumas and humans. This chapter hopes to shed light on possible landscape level drivers of puma attacks in order to reduce the propensity of an attack. Finally, the last chapter explores behavioral changes and habitat selection among coyotes (*Canis latrans*) and white-tailed deer (*Odocoileus virginianus*) in a human-dominated landscape, the Chicago metropolitan area. This chapter explores the acclimation of animals to an urban environment.

The chapters of this thesis are glued together by fundamental ecological knowledge. Each chapter addresses an aspect of what I believe is needed knowledge for successful conservation strategies. This thesis centers on the behavior of large carnivores and is inspired by the quest to learn how humans can coexist with them.

1.2 The journey thus far

My journey into graduate school started on a very different path than the one I am leaving on; however, I have enjoyed the ride. I started the program focused on carnivore conservation with big cats as my model system to explore. I knew I wanted to study behavioral changes in big cats in relation to humans by taking an ecology of fear (Brown *et al*. 1999) approach. However, not knowing what career I wanted after finishing school, I was happy to float along at first, wrapped up in the excitement of studying cats.

I quickly made connections with puma researchers in Western United States. I thank Dr. Ken Logan for inviting me out to his research site on the Uncompahgre Plateau, outside Montrose, Colorado in May 2011. I spent a week out in the field with Dr. Logan, tracking pumas with VHF collars and pug prints, listening to caterwauling by a mating pair of pumas, and helping radio collar two kittens. I will not forget the mixed emotions I had holding the kittens so Dr. Logan could collar them. I was in complete awe and amazement of the kittens but at the same time in fear of the mother returning to the den. I left Colorado with the hopes of developing a research proposal with Dr. Logan and his pumas on the Uncompahgre Plateau.

However, by the time fall semester had started in 2011 I had finally figured out that I wanted to teach science at the middle school level. This meant switching from a Ph.D., which I came into the program as, and finishing as a M.S. This also meant giving up my dream of being a "card carrying cat researcher" (as Dr. Joel Brown put it). It took me two months to call Dr. Logan to tell him of my change of plans and that I had to give up on field research with the cats. However, I leave with three distinct research projects, which I believe, are fundamental to providing insights into large carnivore conservation.

1.3   Coexistence among pumas and jaguars

The first chapter tackles the need to understand behavior and resource needs of carnivores without the presence of humans. Interspecific competition is a major driving force limiting the coexistence of species (Brown 1971, Di Bitetti *et al*. 2010). Interspecific competition can be avoided through morphological, physiological, or behavioral tradeoffs, which in turn will lead to differences in niche use (Tilman 1987). Traditional theories on mechanisms of coexistence among carnivores examine diet

partitioning, such as species of varying size coexist through consuming prey items that correlate to their size (Rosenzweig 1966). The goal of this chapter is to explore a proposed tradeoff between the strength and agility of a carnivore coupled with the dangerousness and elusiveness of a prey as a mechanism of coexistence. We used jaguars and pumas as our model system. Jaguars represent the hulky yet bulky species that is capable of safely subduing dangerous prey but is not as well adapted to catch elusive, agile prey. Pumas represent the agile yet fragile species that is capable of catching elusive, hard to catch prey but is not well adapted to safely subdue dangerous prey. We (my co-authors: Joel Brown, Eric Hancock, and Gordon McNickle) took a three-pronged approach and used published diet data from sympatric pumas and jaguars, historic range overlaps, and a theoretical model to test the mechanism of coexistence. We found that all three lines of evidence supported a mechanism of coexistence along a dangerous-agile gradient of the prey for carnivores.

This chapter allows for an understanding of potential promoters of coexistence among carnivores. It explains the odd occurrence of how similar sized predators can coexist in time and space, and contain similar species in their diets. Understanding the resource needs of carnivores in human absence is a basic requirement that needs to be considered for successful conservation. Current conservation strategies may fall short without understanding how very fine-scale differences in diets can promote coexistence.

1.4   Conflict among pumas and humans

The second chapter explores the most fundamental aspect that limits carnivore-human coexistence: attacks on humans. Puma attacks are relatively rare when compared to other large mammals, such as bears, tigers, lions, or leopards (Loe and Roskaft 2004).

However, a single negative human-wildlife interaction greatly reduces the possibility of coexistence. Puma attacks on humans have been extensively studied on a very fine scale examining case-by-case attacks (Fitzhugh 1988, Beier 1991, 1992, Fitzhugh and Fjelline 1997, Coss *et al*. 2009, Mattson *et al*. 2011). To the best of our knowledge, this is the first attempt to analyze puma attacks on people on a landscape level. A landscape level analysis will allow for a better understanding of potential drivers of puma attacks at a population level. Reducing conflicts between humans and pumas will reduce fear in the public as well as help with the conservation of puma populations (Sweanor and Logan 2010). We examined the affects of human population density, livestock density, and sport hunting patterns on the propensity of a puma attack. We used livestock as a potential sink prey for pumas. A sink prey is a prey item that if solely consumed by the predator would result in negative fitness for that predator. Livestock was used as a representative of sink prey because of the risk associated with them. Very often landowners retaliate against livestock depredation by opportunistically killing the assumed predator (Quigley and Crawshaw Jr 1992, Conforti and de Azevedo 2003).

The potential significance of each of these factors would suggest different management strategies. Without the knowledge of the driver of an attack a successful strategy cannot be implemented. We found that as human population increases the presence of livestock becomes significantly more important in decreasing the propensity of a puma attack on a human. However, livestock depredation is a major human-wildlife conflict in and of itself. This result led us to recommend taking a Win-Win Ecology approach (Rosenzweig 2003) and provide habitat for potential sink prey items such as beavers and porcupines within human habitation to decrease puma attacks on people.

Furthermore, this management suggestion may be valid for other carnivores. The Win-Win Ecology approach would help to reduce wildlife conflict on two fronts: attacks on humans and depredation of livestock.

1.5 **Altered behavior among coyotes and white-tailed deer in relation to humans**

The final chapter deviated from my love of big cats but allowed me to examine direct behavioral changes in mammals in relation to humans. This chapter was developed in collaboration with the Lincoln Park Zoo and their existing camera trap data. Many animals exhibit behavioral plasticity to minimize energy costs and the potential for death (Van Dyke *et al*. 1986, Drew and Bissonette 1997). Animals will shift their activity patterns due to avoidance of predation (Festa-Bianchet 1988), human activity (Van Dyke *et al*. 1986, Arundel *et al*. 2007), prey abundance (Karanth *et al*. 2004), vegetation, and seasons (Beier and McCullough 1990). Temporal and spatial variation in coyote and white-tailed deer activity patterns were analyzed in relation to human factors (distance to urban center, housing density, and road length), habitat factors (percent canopy over and distance to water), and interspecific interactions between white-tailed deer and coyote. We hypothesized (1) coyotes will exhibit a stronger negative association with human factors compared to deer. (2) Deer will exhibit a stronger habitat selection for natural areas compared to coyotes. (3) Deer will exhibit a negative association with coyotes. We found that both coyotes and deer were significantly negatively associated with an increase in housing density and both were significantly positively associated with an increase in canopy cover. However, deer also showed an affiliation with water and coyotes. The affiliation between deer and coyotes could probably be explained by both

species selecting more natural environments. All of the factors investigated had a stronger effect on deer activity compared to coyotes, except for canopy cover.

This chapter explores the possibility of mammals becoming acclimated to novel environments. This was observed in the avoidance of higher housing areas and in the increased affiliation of areas with high canopy cover in the highly urbanized landscape of the Chicago metropolitan area. Understanding wildlife plasticity and acclimation to human-dominated environments is an important aspect to conservation that is only recently being realized with the Urban Ecology program. Urban habitats are at the forefront of human-wildlife interactions. Understanding wildlife behavior in this habitat is key to successful conservation.

1.6   The start of the next leg of the journey

I started this program with hopes of gaining ecological knowledge to successfully do conservation work. Even though I am now starting a Master in Education program this does not mean my goal has changed, it just finally crystalized. When I would tell friends, family, and colleagues that I wanted to do conservation work, I would inevitably get questioned on what I thought was the most effective way to do conservation. I would always answer, through education. I believe that education is the most sustainable mechanism for inspiring conservation. So I have finally listened to myself. I leave this program with a sound ecological knowledge base and hopes of inspiring young kids about the world around them.

"It is a better thing to travel hopefully than it is to arrive."

- R. L. Stevenson

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2. Coexistence of Pumas (*Puma concolor*) and Jaguars (*Panthera onca*): Agile and Fragile versus Hulky and Bulky

2.1 <u>Introduction</u>

Interspecific competition is a major driving force limiting the coexistence of species (Brown 1971, Di Bitetti *et al*. 2010). Competition of similar sympatric species can result in competitive exclusion of one of the species (Hardin 1960). However, species are able to avoid interspecific competition through morphological, physiological, or behavioral tradeoffs, which in turn, will lead to differences in resource use (Tilman 1987).

One way to examine potential mechanisms of coexistence among animals is to examine differences in diet and habitat use among co-occurring species. For example, carnivores of varying size coexist by consuming prey items that correlate to their size leading to resource partitioning via prey choice (Rosenzweig 1966). Species of similar size may also coexist via resource partitioning by differing their pursuit strategies that optimize success on different prey (Rosenzweig 1966). For example, canines are more apt to run down their prey whereas felines stalk (Rosenzweig 1966). Thus, members of the Canidae and Felidae families are capable of sympatric coexistence due to their different pursuit styles that lead to different resource use and therefore minimize competition. Finally, co-occurrence is a prerequisite for competition to occur, and species may avoid interspecific competition through temporal or spatial separation (MacArthur and Levins 1964, Rosenzweig 1966, Roughgarden 1974). These are all fairly clear and obvious ways species may coexist: if species do not co-occur in time or space, or they do not share resources they will not compete and therefore they can

coexist. However, there are several examples of similarly sized species that coexist

spatiotemporally and appear to have overlapping diets. These counter examples, while

rare, may be important for understanding the limits to coexistence, and for testing classic

ideas about species coexistence.

Here we are interested in this peculiar situation where similar sized carnivores co-

occur in time and space, and contain similar species in their diets. How do these species

coexist? We hypothesize a mechanism of coexistence based on tradeoffs between the

agility to catch elusive and agile prey items and the strength to subdue more dangerous

prey without incurring debilitating injury. Agile yet fragile predators such as cheetahs

(*Acinonyx* jubatus) have a high rate of capture per attempt (Frame 1999, Hayward *et al*.

2006), but do not attack dangerous prey and are susceptible to interference competition

from larger predators (Schaller 1972). Hulky yet bulky predators such as African lions

(Panthera leo) can subdue more dangerous prey, but are not well suited for hunting down

the agile prey items. Thus, this mechanism of coexistence takes the form of fine scale

character displacement resulting in subtle difference in diet profiles among competitors.

The predator prey system of pumas (*Puma concolor*) and jaguars (*Panthera onca*)

combined with the small and agile members of the deer family (*Cervidae*) and the hulky

and dangerous members of the peccary family (*Tayassuidae*) are an ideal system to test

these ideas. The two carnivores share similar morphological features (jaguars are slightly

larger than pumas), habitat use, activity patterns, and their diet consists of similar sets of

species (Sunquist and Sunquist 2002). Further, the two cats are sympatric throughout

much of the jaguar's range. In areas where jaguars and pumas coexist, both carnivores

feed on deer and peccaries (Aranda 1994). We hypothesize that the puma represents the

agile yet fragile species that are more apt at subduing elusive, hard to catch prey (e.g. deer), however are less capable of safely subduing dangerous prey (e.g. peccary). Also, we hypothesize that the jaguar represents the hulky yet bulky species that are more apt at subduing dangerous prey safely however are less capable of catching elusive and more agile prey items.

In this paper we explore the proposed tradeoff between the agility and strength of a carnivore coupled with the elusiveness and dangerousness of a prey as a mechanism of coexistence. We explore this hypothesis using pumas and jaguars as our model system. Additionally, we present a simple consumer resource model to demonstrate that agility and dangerousness of a prey and associated adaptations of predators alone can permit coexistence in paired carnivore systems. We hypothesize that, while pumas and jaguars exhibit diet overlap, there are key prey species at the extremes of the elusive-dangerous spectrum, which are critical to puma-jaguar coexistence and may limit the range of each carnivore. We approach this problem in three distinct ways. (1) We describe a simple model of a two predator-two prey system containing a tradeoff between predator agility and strength coupled with elusiveness and dangerousness of a prey as a mechanism of coexistence. Here we ask whether differences in agility and dangerousness of prey alone can promote coexistence of predator species. (2) We present a meta-analysis of diet profile data collected from the literature from regions where pumas and jaguars coexist. From this profile we investigate deer and peccary consumption, but also expand this to investigate a more general relationship between agile and dangerous prey. We hypothesized that pumas will consume significantly more deer compared to jaguars, while jaguars will consume significantly more peccary compared to pumas. Further, we

hypothesized that, an *a priori* assessment of the agility or dangerous of prey would reveal a similar diet specialization. (3) We compare historic range overlap among pumas, jaguars, and their main prey species. We hypothesized that prey specialization might have limited the range of each cat to co-occur with it's target prey. Bringing these three threads together, we argue that two species can coexist through subtle tradeoffs in terms of agility and strength. We also argue that pumas and jaguars are an example of this situation.

2.2 <u>Methods</u>

2.2.1 <u>Model description and analysis</u>

We build upon the MacArthur (1972) consumer-resource model with a two prey-two predator system of deer and peccaries and pumas and jaguars. The novel aspect of our model is that the prey species are represented by a spectrum of risk and the predator chooses what level of risk they are willing to accept. This risk, through predator choice, influences effective encounter rates between predator and prey (H_{ij}).

The distribution of risk within a prey population is given by a line (equation 1).

$$F_{ij}(R) = b_{ij} - \frac{b_{ij}^2}{2} R \tag{1}$$

Let R be the risk of the prey to the predator and let b_{ij} determine the shape of the distribution for taxa i depredating taxa j. b_{ij} is the fraction of the prey species that represent zero risk to the predator species. The largest b_{ij} represents the hardiest predator attacking the least risky prey (e.g. jaguar on deer). The smallest b_{ij} represents the weakest predator attacking the riskiest prey (e.g. puma on peccary).

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We incorporate this risk of predation into a standard predator-prey model. The following represents the growth equations for prey populations (equation 2) and predator populations (equation 3).

$$\frac{dR_i}{dt} = R_i \left[r_i \left(1 - \frac{R_i}{K_i} \right) - \sum_{j=1}^{2} H_{ij} N_j \right] \tag{2}$$

$$\frac{dN_j}{dt} = N_j \left[\sum_{i=A}^{B} e_{ij} H_{ij} R_i - \left(d + \sum_{i=A}^{B} \omega_{ij} H_{ij} R_i \right) \right] \tag{3}$$

We allow the predator to choose the probability of attacking an encountered prey item (p_{ij}). This probability is based on the largest risk the predator is willing to accept (θ_{ij}) and the fraction of the prey species that represent zero risk to the predator species (b_{ij}) (see appendix B). This gives rise to the effective encounter rate (H_{ij}). The product of predator choice and encounter rate gives effective encounter rate.

The average risk of harm from a prey species on a predator species is ω. ω depends on θ_{ij} and b_{ij} (see appendix B). We derive the average prey risk for a predator based on the prey risk distribution and maximum risk the predator is willing to accept (see appendix B).

Parameters are defined in Table 1 and the values that were utilized in the model are also given. We chose encounter rates to have the opposite pattern of b_{ij}. This ensures that coexistence is possible (Vincent *et al.* 1996). The highest encounter rate occurs between the pairing of the most agile predator (puma) and the least agile prey (peccary). Whereas, the lowest encounter rate occurs with jaguars and deer.

We explored the parameter space by increasing each value parameter by 50% to test the sensitivity of the analysis to ensure the model was robust.

Table 1: Parameter definitions and values in simulation of consumer-resource model.

Parameter	Definition	Value in simulation
a_{A1}	Encounter of puma on deer	0.03
a_{A2}	Encounter of jaguar on deer	0.009
a_{B1}	Encounter of puma on peccary	0.05
a_{B2}	Encounter of jaguar on peccary	0.03
b_{A1}	Fraction of deer that represent zero risk to pumas	0.3
b_{A2}	Fraction of deer that represent zero risk to jaguars	0.7
b_{B1}	Fraction of peccaries that represent zero risk to pumas	0.1
b_{B2}	Fraction of peccaries that represent zero risk to jaguars	0.4
θ_{A1}	Maximum risk puma is willing to accept with deer	0.09
θ_{A2}	Maximum risk jaguar is willing to accept with deer	0.08
θ_{B1}	Maximum risk puma is willing to accept with peccary	0.08

θ_{B2}	Maximum risk jaguar is willing to accept with peccary	0.07
H_{A1}	Effective encounter rate of puma on deer	8.05E-4
H_{A2}	Effective encounter rate of jaguar on deer	4.97E-4
H_{B1}	Effective encounter rate of puma on peccary	3.99E-4
H_{B2}	Effective encounter rate of jaguar on peccary	8.34E-4
d_1	Death rate of pumas	0.01
d_2	Death rate of jaguars	0.01
r_A	Growth rate of deer	0.1
r_B	Growth rate of peccaries	0.1

2.2.2 Diet data collection

An extensive literature review was performed to find all diet profiles studies on sympatric pumas and jaguars, but we limited data collection to those studies that had reported diets from regions where pumas and jaguars co-occur. We also limited diet data collection to articles that report diets in relative biomass. Some of the papers contained multiple surveys at different geographic locations, and in our analysis we treated each individual survey as a separate data point. The meta-analysis resulted in 10 puma and jaguar diet profiles from geographic locations where they co-occur (Taber *et al*. 1997, Nunez *et al*. 2000, Scognamillo *et al*. 2003, Novack *et al*. 2005, De Azevedo 2008,

Rosas-Rosas *et al*. 2008, Foster *et al*. 2010). From these data we compiled a list of all potential prey species for both cats and performed two ANOVAs to determine: (i) whether pumas and jaguars differ in relative amounts of deer or peccary consumed and (ii) whether pumas and jaguars differ in the relative amounts of agile or dangerous prey consumed.

First, we analyzed relative amounts of only deer or peccary consumed by each cat as above. Deer are considered to be agile, and peccary are considered to be dangerous by our definitions (see below). To determine if pumas and jaguars consumed a significantly different amount of prey type (deer or peccary) a two-way ANOVA and Fisher's Exact test were performed on relative biomass for each group. Data were transformed for normality by taking the arcsine square root proportion of all the relative biomasses.

Second, we were interested in whether the broader set of prey items captured by pumas and jaguars significantly differed in their agility or dangerousness. To avoid bias in designating prey we used a double-blind procedure. Specifically, the diet data were collected from the literature by LSS and compiled into a list of species. Subsequently, each prey species was independently assigned to a prey type by JSB. Our goal was to avoid any bias in the designation of agile or dangerous prey types and instead designate each prey item as agile or dangerous completely independently from information concerning puma or jaguar diets. JSB had no knowledge of the relative amounts of any prey eaten, which cat had consumed them, or the geographic locations the diets had come from. JSB had only a list of prey and information about the morphology and behavior of each prey.

Thus, prey items from the species list were ranked as agile, dangerous, or neither based on reports from literature and professional judgment. Agile is defined as prey that is relatively difficult to pursue and has a relatively low potential to cause harm to the predator during pursuit and capture. Alternatively, dangerous was defined as a prey species that is relatively easy to pursue but has a relatively high potential to cause harm to the predator during pursuit and capture. Prey that were not likely to cause harm to a predator, did not require agility to catch, or might have been opportunistically consumed were categorized as neither. These might be prey such as fish, or small rodents that are occasionally eaten as incidental prey, but do not require feats of agility to pursue nor are they particularly dangerous.

Once the data were categorized as agile, dangerous, or neither, the list was returned to LSS. From the relative biomass data proportions of agile and dangerous prey were summed for pumas and jaguars separately in terms of biomass of the diet of each cat and in each prey category. To determine if pumas and jaguars consumed a significantly different amount of prey type (agile or dangerous) a two-way ANOVA and Fisher's Exact test was performed on relative biomass data for each group, as above. Data were transformed for normality by taking the arcsine square root proportion of all the relative biomasses. We used an alpha of .05 for all statistical tests. All analyses were performed with SYSTAT version 13.

2.2.3 Range data collection

If puma are adapted to capture relatively agile prey this might limit their range to co-occur with agile prey. Similarly, if jaguars are adapted to capture relatively dangerous prey, this might limit their historic ranges to co-occur with dangerous prey. To examine

these ideas about range limits, historic North American range data were collected from a mammal guide (Hall and Kelson 1959) and combined with data for North and South America collected from NatureServe's Digital Distribution Maps of the Mammals of the Western Hemisphere, Version 3.0 (Patterson *et al*. 2003, NatureServe 2012). It was impossible to determine if the South American distributions were current or historical, but North American ranges were known to be historic (Hall and Kelson 1959). The South American maps used are believed to be the most accurate available. From these data, all deer species were included into one deer range map, this included: white-tailed deer (*Odocoileus virginanus*), mule deer (*Odocoileus hemionus*), red-brocket deer (*Mazama Americana*), and South American brown-brocket deer (*Mazama gouazoubira*). The guanaco (*Lama guanicoe*) was also included in the range map because of their morphological similarity to deer. Similarly, all peccary species were included into one peccary range map, this included: collared peccaries (*Pecari tajacu*), white-lipped peccaries (*Tayassu pecari*), and chacoan peccaries (*Catagonus wagneri*). Four maps were constructed (puma, jaguar, deer/guanaco, and peccary) and the maps were overlaid with one another to calculate percent overlap of all pairwise combinations of predators and prey in ArcGIS ver. 10 (ESRI 2011).

We also constructed range maps for all prey designated as either agile or dangerous (Appendix A). Remarkably, the agile prey range map was nearly identical to the deer/guanaco map, and the dangerous prey range maps were nearly identical to the peccary range map. Thus, we present these data in the appendix (Appendix C).

2.3 <u>Results</u>

    2.3.1 <u>Model</u>

Figure 1 illustrates the Zero Net Growth Isoclines (ZNGI) of pumas and jaguars. A ZNGI depicts all combinations of resource 1 and resource 2 such that a consumer's population growth is zero (Tilman 1982). Pumas always have a higher encounter probability and jaguars always have a higher attack probability. However, due to behavioral differences between the predators, pumas have a higher effective encounter probability on deer and jaguars have a higher effective encounter probability on peccaries. Because of the larger effective encounter rate, pumas can subsist on a smaller population of deer than jaguars. Likewise, jaguars can subsist on a smaller population of peccaries than pumas. Coexistence of the predators further requires that each predator consume more of the prey species that they are most limited by (i.e. pumas need to consume more deer and jaguars need to consume more peccaries). This ensures intraspecific competition is greater than interspecific competition.

Figure 1 shows that with a high enough carrying capacity of both deer and peccaries, pumas and jaguars coexist. If the carrying capacity of deer is too low then jaguars will outcompete pumas and vice versa for peccary carrying capacity. If the carrying capacity of both deer and peccary are too low than both predators go extinct.
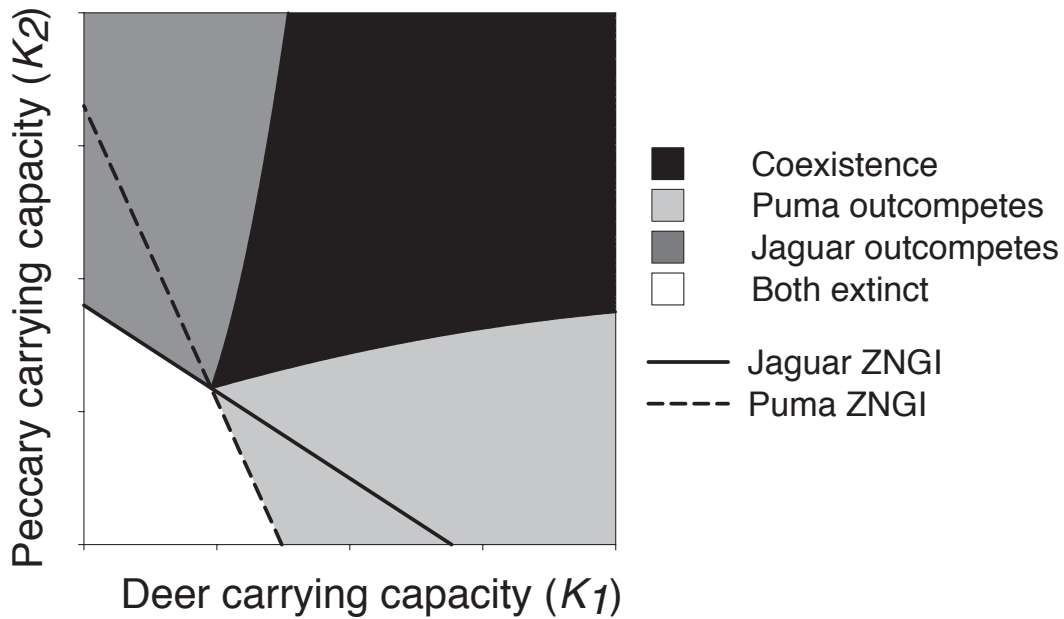
Fig. 1: Coexistence of jaguars and pumas as a function of prey carrying capacity. Lines represent zero net growth isoclines (ZNGI) for jaguars (solid) and pumas (dashed) that differ in their ability to exploit the two resources, peccary and deer.

2.3.2 <u>Diets – Deer and peccary</u>

To investigate relative amounts of just deer or peccary that were consumed, a 2-way ANOVA was performed on the transformed data with a dependent variable of relative biomass consumed and factors of predator type (puma or jaguar) and prey species (deer and peccary) (Table 2). There was a trend suggesting that pumas consume more deer biomass than jaguars and jaguars consumed more peccary biomass than pumas (Fig. 2a), however the result was only marginally significant ($P = .053$, Table 2).

Table 2: 2-way ANOVA table with dependent variable of species biomass (arcsine square root of proportion of deer and peccary) and factors of predator type and species type (deer and peccary).

Source	df	Mean square	*F-ratio*	*P-value*
Predator	1	0.012	0.313	0.579
Prey Species	1	0.155	4.109	0.050
Predator x Prey	1	0.151	4.001	0.053
Error	36	0.038		

Because the non-transformed data were non-parametric data, a Fisher's Exact Test was performed on a 2x2 contingency table. The Fisher's Exact Test was performed to determine if pumas consumed a significantly greater amount of deer species than jaguars and if jaguars consumed a significantly greater amount of peccary species compared to pumas.

The numbers in the data cells of the Fisher's Exact Test represents each time one predator consumed more of the prey species represented by the row than the other predator. Out of ten studies, pumas consumed more deer than jaguars in nine of the studies and jaguars consumed more peccaries than pumas in seven studies. The results lead to the rejection of the null hypothesis that there is no association between predator type and species type consumed ($P < .01$).

2.3.3 Diets – Agile and dangerous prey

To investigate differences in the amount of either agile or dangerous prey consumed by each predator, a 2-way ANOVA was performed with the dependent variable of relative biomass consumed and a factorial combination of predator type (puma or jaguar) and prey type (agile or dangerous) (Table 3).

Table 3: 2-way ANOVA table with dependent variable of prey biomass (arcsine square root of proportion) and factors of predator type and prey type (agile or dangerous).

Source	df	Mean square	*F-ratio*	*P-value*
Predator	1	0.102	1.750	0.194
Prey Type	1	0.657	11.292	0.002
Predator x Prey	1	0.460	7.904	0.008
Error	36	0.058		

Pumas consumed a larger proportion of agile prey compared to jaguars (Fig. 2b) and jaguars consume a significantly larger proportion of dangerous prey compared to pumas (Fig. 2b). Pumas clearly consumed a greater amount of agile prey compared to dangerous prey (Fig. 2b). However, though jaguars consumed more dangerous prey then pumas, jaguars did not consume different amounts of dangerous prey relative to agile prey (Fig. 2b).
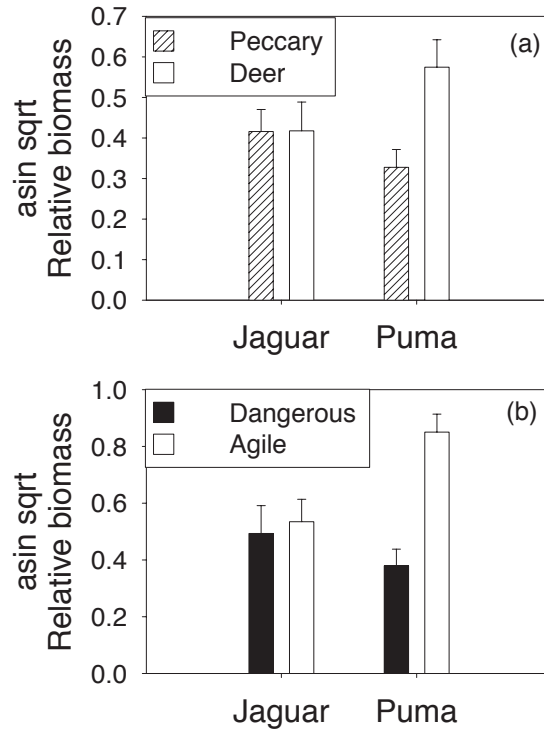
Fig. 2: Means of arcsine square root transformed relative biomass consumed by jaguars and pumas on (a) peccaries (hatched bars) and deer (open bars) or (b) total amount of all dangerous prey (black bars) and agile prey (open bars). A list of dangerous and agile prey are given in Appendix A. One standard error is shown.

With the non-parametric data a Fisher's Exact Test was performed on a 2x2 contingency table. It was performed to determine if pumas consumed a significantly greater amount of agile prey than jaguars and if jaguars consumed a significantly greater amount of dangerous prey compared to pumas.

The Fisher's Exact test was performed in the same manner as the previous. Out of ten studies jaguars consumed more dangerous prey that pumas in seven studies and pumas consumed more agile prey than jaguars in eight of the studies. The resulting one-tailed *P*-value of .03 leads to rejection of the null hypothesis that there is no association

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between predator type (pumas and jaguars) and consumption amount of prey type (agile and dangerous).

2.3.4 Range overlap

Four maps were produced to represent jaguar and peccary range overlap (Fig 3a) and puma and deer/guanaco range overlap (Fig. 3b). Percent range overlap was calculated for all possible pairwise combinations of species by overlaying each map in all pairwise combinations.
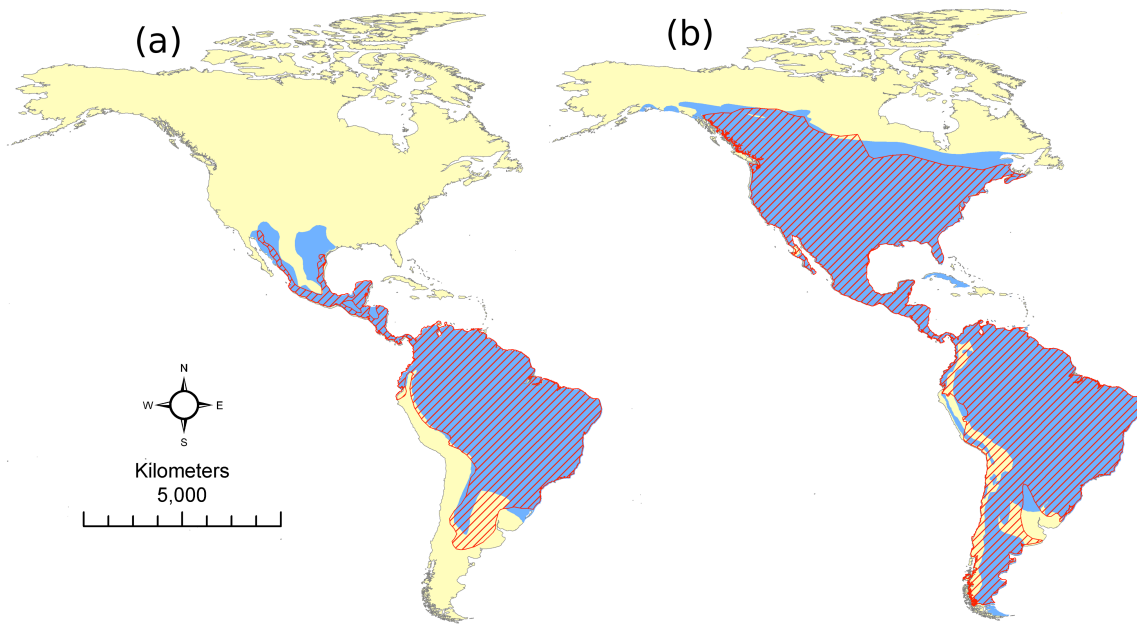
Fig. 3: Overlaid range maps of (a) jaguar and peccary and (b) puma and deer. In both panels, prey ranges (peccary or deer) are filled with blue, while predator ranges (jaguar or puma) are hatched in red. Maps adapted from Hall (1959) and NatureServe's Digitial Distribution Maps of the Mammals of the Western Hemisphere, Version 3.0 (Patterson et al. 2003). Range maps for dangerous and agile prey are given in Appendix C, but are nearly identical to these such that dangerous = peccary and deer = agile.

The historic range of puma (Fig. 3b) overlaps 95%, 93%, and 97% with jaguar, deer, and peccary ranges, respectively. The range of jaguar (Fig. 3a) overlaps 44%, 42%, and 89% with puma, deer, and peccary ranges, respectively. The deer range (Fig. 3a) overlaps, 92%, 91%, and 94% with puma, jaguar, and peccary ranges, respectively. The peccary range (Fig. 3b) overlaps 46%, 91%, and 45% with puma, jaguar, and deer ranges, respectively. These overlaps are consistent with our hypothesis that prey might limit predator ranges. Though puma range over most of the two continents (Fig. 3b), jaguars are much more limited and almost perfectly co-occur with the range of the peccary (Fig. 3a).

We examined range maps for the entire set of either agile or dangerous prey as well. Given that deer range almost completely throughout North and South America, it was not surprising that the agile map was identical to the deer/guanaco map (i.e. all other agile prey ranges were contained within the deer/guanaco range Fig. 3b). However, it was striking that the range map for dangerous prey was also contained within the peccary range map (Fig. 3a). Given that these range maps are nearly identical to those in Fig. 3, they are given in appendix C.

2.4 <u>Discussion</u>

We proposed a new mechanism of coexistence in predators that results in fine scale difference in diet profiles. We proposed that there is a tradeoff between agility and strength in a predator. A predator that is agile enough to consume elusive, hard to catch prey will be too fragile to safely subdue dangerous prey. Likewise, a predator that is hulky enough to safely subdue a dangerous prey will be too bulky to catch agile prey. We found: (1) Differences in agility and dangerousness of prey alone can promote

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coexistence of predator species. (2a) Pumas consume more deer compared to jaguars, while jaguars consume more peccaries compared to pumas. (2b) An *a prioiri* assessment of the agility or dangerousness of prey revealed that pumas consumed significantly more agile prey compared to jaguars and jaguars consume significantly more dangerous prey compared to pumas. (3) Prey specialization might have limited the range of each cat to co-occur with its target prey as evident in the range maps.

2.4.1 Model

We theoretically examined coexistence of pumas and jaguars as a function prey type carrying capacity. We found that given a high enough deer and peccary population, pumas and jaguars will coexist. However, pumas will outcompete jaguars if the carrying capacity of peccaries is too low. Jaguars will outcompete pumas if the carrying capacity of deer is too low (Fig. 1). This is consistent with our hypothesis of coexistence in an agile yet fragile and hulky yet bulky carnivore system. Vincent and collaborators (1996) showed that for coexistence to occur there has to be a tradeoff in effective encounter probability between two substitutable resources (Vincent *et al*. 1996). In the puma-jaguar system pumas have a higher effective encounter probability on deer and jaguars have a higher effective encounter probability on peccaries due to their decisions to accept a particular prey type.

2.4.2 Diets – Deer and peccary

Deer and peccary species are good representatives of opposite ends of the prey spectrum. Peccaries posses tusks and travel in large herds, whereas deer do not possess tusks and only the males have antlers. Furthermore, there are accounts of peccaries attacking and killing jaguars (Perry 1970, Scognamillo 2001). Throughout the region

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where jaguars and pumas occur sympatrically, they both consume peccaries and deer. Aranda (1994) showed that jaguars will consume a greater proportion of peccaries and pumas will consume a greater proportion of deer. In addition, jaguars and peccaries share a historic range overlap, which may represent an evolutionary link between the two (Aranda 1994). However, another study showed that both pumas and jaguars primarily rely on deer species (Nunez *et al*. 2000) while another showed that pumas selected collared peccaries (Scognamillo *et al*. 2003). The diet profiles of sympatric pumas and jaguars analyzed with the Fisher's Exact Test in this paper support the theory of diet partitioning along the deer-peccary gradient with pumas consuming more deer species than jaguars and jaguars consuming more peccary species than pumas. The random effect of study may have contributed error to the ANOVA (table 1) and lead to an overly conservative test. The Fisher's Exact Test, on the other hand removes the effect of study. Field studies are greatly limited in the geographical scope. The novel aspect of our study was analyzing diet profiles over a much larger geographic area from Mexico to South America to gain a greater scope of coexistence for pumas and jaguars.

2.4.3 Diet – Agile and dangerous prey

Our meta-analysis of sympatric puma and jaguar diet studies supports our hypothesis. Pumas consume more agile prey, whereas jaguars consume more dangerous prey (Table 3 and Fisher's Exact Test). A tradeoff in morphometrics becomes apparent when comparing pumas and jaguars. Pumas have relatively long limbs, slim, lanky bodies, and a rounded head. Furthermore, they have been classified as an animal that is more likely to flee than to fight (Hornocker and Quigley 1987, Seidensticker 1991). On the other hand, jaguars lack the grace possessed by other members in the *Panthera* genus

and instead have unusually short sturdy limbs and a deep-chest (Gonyea 1976). In addition, the jaguars' canines are larger and more powerful then other big cats (Werdelin 1983, Kiltie 1984, Valkenburgh and Ruff 1987). Examining these descriptions of pumas and jaguars, the morphological evidence is consistent with our hypothesis that pumas are more capable of catching agile, hard to catch prey but are less capable of safely subduing dangerous prey. Jaguars are more apt at safely subduing dangerous prey items but are not as able to catch agile, hard to catch prey.

2.4.4 <u>Range overlap</u>

We visually examined with GIS the hypothesis that pumas primarily prey upon deer and deer like species and jaguars primarily prey on peccaries by developing range maps for the Americas. Our results weakly support this hypothesis. Deer occur in 92% of the range of pumas, whereas peccaries only occur in 46% of the range. Peccaries occur in 91% of the range of the jaguar and deer occur in 91% of the range. However, our results should be interpreted with caution. Range maps are displayed in a continuous manner when in reality this is not the case. Even though our analysis shows that deer occur throughout the entire range of the puma, there may be pockets where this is not true. Furthermore, density of an individual species is not homogenous throughout its range. The actual range overlap for all of our maps is most likely less than the percentages we calculated thus reducing the geographic relationships among species.

Why is fragility an important concern for carnivores? Predators rely on peak performance to subdue prey (Brown and Kotler 2004). Any serious injury to a predator greatly reduces its chance of survival (Sunquist and Sunquist 1997). A predator's pursuit of prey may result in injuries which may be as minor as an unsuccessful attempt

(Hayward and Kerley 2005). However, some prey species will actively defend themselves against an attack (Makacha and Schaller 1969, Ruggiero 1991, Berger and Cunningham 1994) that may lead to severe injury of the predator or even death (Mangani 1962, Beyers 1964, Eloff 1964). Even minor injuries to a predator that relies on peak performance to subdue prey may be life threatening (Brown and Kotler 2004). Predators are aware of this risk of injury when they are foraging (Berger-Tal *et al*. 2009). Some prey species are more dangerous than others, and a predator's diet selection should reflect this (Brown and Kotler 2004).

Traditional theories suggest coexistence via partitioning resources along axes of diet, space, and time, thus avoiding conspecifics. Species are able to coexist by having morphological, physiological, or behavioral tradeoffs, which in turn, will lead to large enough differences in resource or niche use (Tilman 1987). However, most theories on mechanisms of coexistence stop short of explaining why the divisions in diet profiles are such. For example, differences in diet profiles have been observed and suggested as a mechanism of coexistence in sympatric jaguars and pumas, where on average jaguars consume larger prey than pumas (Taber *et al*. 1997, Nunez *et al*. 2000, Scognamillo *et al*. 2003, De Azevedo 2008). This is consistent with our hypothesis once the risk of injury to the predator is factored into the prey types. Following Tilman (1987), we suggested a tradeoff in the ability to catch agile and dangerous prey.

The tradeoff between agility and strength as a mechanism of coexistence can be observed in multiple predator species pairs. One such pair is the cheetah and the African lion. Adult cheetahs weigh on average between 30 and 72 kg (Stuart and Stuart 2000) and they are known to avoid prey items that may result in injury. They select prey items

that are small but frequently very agile (Hayward *et al*. 2006). Whereas, some lions will

hunt buffalo almost exclusively (Makacha and Schaller 1969, Funston *et al*. 1998) even

though they are considered very risky (Mangani 1962, Hayward and Kerley 2005).

Another pair example can be observed in the *Buteo* genus of hawks between red-tailed

hawks (*Buteo jamaicensis*) and ferruginous hawks (*Buteo regalis*). Ferruginous hawks

are the largest species in the *Buteo* genus (Woffinden and Murphy 1989). Their diet is

mainly composed of jackrabbits, ground squirrels, or pocket gophers (Olendorff 1993).

Whereas, red-tailed hawks consume a larger proportion of birds in comparison to

ferruginous (Restani 1991). Capturing birds requires great agility from the red-tailed

hawk whereas, subduing small to medium size rodents require greater strength from the

ferruginous hawk.

Diet selection along an agile-dangerous gradient is analogous to the concept of

centrifugal community organization, which Rosenzweig and Abramsky (1986) used to

explain habitation selection. The centrifugal community organization concept states

when two species occur sympatrically in low densities they will use the same preferred

habitat that yields the highest fitness outcome. However, as the density of the species

increases, the species will move to utilizing peripheral habitats in opposite directions

(Rosenzweig and Abramsky 1986). This same concept may apply to diet selection in

sympatric species.

To further test this mechanism we should observe greater overlap in diet profiles

of allopatric pumas and jaguars. Furthermore, agile prey should be in higher abundances

with pumas, and dangerous prey should be in higher abundance in areas with jaguars.

The tradeoff in predator agility and strength may be applicable to many predator systems

and should be further investigated. This mechanism explains in greater detail the reason

differences in diet profiles are observed in numerous predator species pairs.

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Appendix A

Agile Prey: White-tailed deer (adult and juvenile), Red-brocket deer, South American brown-brocket deer, Brocket deer (sp.), Paca, Agouti, Azara's Agouti, Rabbits, Eastern cottontail, and Chacoan mara.
Dangerous Prey: White-lipped peccary (adult and juvenile), Collared peccary (adult and juvenile), Peccary (sp. adult and juvenile), Giant anteater, Mexican porcupine, Cabybara, and Caiman crocodiles.
Incidental Prey or Neither Agile nor Dangerous Prey: Livestock (>15kg), Domestic Cattle, Sheep, Dog, Northern tamandua, Northern raccoon, Crab-eating raccoon, Raccoon, Nine-banded armadillo, Armadillo (sp.), Iguana, Coati (sp.), White-nosed coati, South American coati, Kinkajou, Skunk, Grey fox, Greater grison, Virginia/common opossum, Spiny pocket mouse, Freshwater crustacean, Mexican spiny-tailed iguana, Grayish mouse-opossum, Rodent (sp.), Snake (sp.), Lizard (sp.), Bird (sp.), Monkey (sp.), Sonoran mud turtle, White-eared opossum, Opossum (sp.), Tufted capuchin, Common yellow-toothed cavy, Reptiles (sp.), Ring-tailed cat, Jaguar, Puma, Tapeti, Black tegu, and Long-tailed weasel.

Appendix B

The probability of accepting prey i is equal to the fraction of prey in the risk distribution below theta or the area under the risk distribution curve from 0 to theta. The average risk of prey i is a function of b and theta.

$$p_{ij}(\theta_{ij}) = \int_0^{\theta_{ij}} b_{ij} - b_{ij}^2 R/2 \ dR = b_{ij}\theta_{ij} - b_{ij}^2\theta_{ij}^2/4$$

$$\omega_{ij} = \int_0^{\theta_{ij}} \left(b_{ij} - b_{ij}^2 R/2\right) R \ dR = b_{ij}\theta_{ij}^2/2 - b_{ij}^2\theta_{ij}^3/6$$
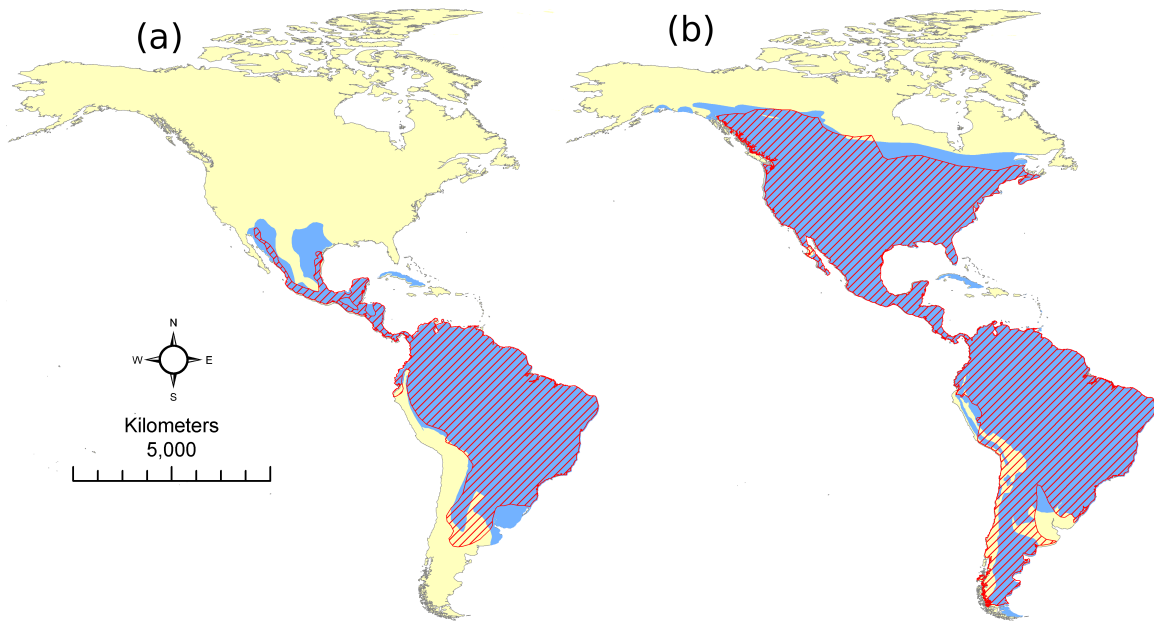
Fig. 4: Overlaid range maps of (a) jaguar and dangerous prey and (b) puma and agile prey. In both panels, prey ranges (dangerous or agile) are filled with blue, while predator ranges (jaguar or puma) are hatched in red. Maps adapted from Hall (1959) and NatureServe's Digitial Distribution Maps of the Mammals of the Western Hemisphere, Version 3.0 (Patterson et al. 2003). Range maps for dangerous and agile prey are nearly identical to these such that dangerous = peccary and deer = agile.

3. Negative human - puma (*Puma concolor*) interactions: A landscape perspective

3.1 <u>Introduction</u>

  Carnivore attacks on humans are a concern for wildlife managers and conservationists alike. Suggested reasons for attacks on humans have included: high human populations (Langley 2005, Herrero *et al*. 2011) carnivore habituation to humans (McCullough 1982) decrease in prey availability (Packer *et al*. 2005, Valeix *et al*. 2012) and acute injuries to the carnivore (Patterson 2004). However, evidence is usually lacking for sound conclusions on what causes an attack (Loe and Roskaft 2004).

  Negative human-puma (*Puma concolor*) encounters have been on the rise since the 1970s (Mattson 2007). The majority of research investigating negative puma-human interactions have focused on fine-scale characteristics of the attacks (Fitzhugh 1988, Beier 1991). Previous research has thoroughly investigated factors such as victim demographics (Coss *et al*. 2009) victim activity, and season at the time of attack (Beier 1991, 1992, Coss *et al*. 2009). In addition, Beier (1991) examined the demographics and health status of the attacking pumas, as well as a full summary of human actions that can prevent the occurrence of attacks (Fitzhugh 1988, Beier 1991, Fitzhugh and Fjelline 1997). Mattson *et al*. (2011) calculated the probability of a human encountering a puma and, given an encounter, the probability that it becomes aggressive. Research to date has yet to examine, on a landscape scale, factors driving the increase in puma attacks. Understanding the landscape factors will allow for more informed land management techniques that could help reduce the likelihood of an attack. We examine the effects of

human population density, livestock density, and sport hunting on the propensity for negative puma-human interactions.

Puma attacks on people are very rare when compared to other fatal and non-fatal wildlife conflicts, such as venomous snake bites (Weiss 1990) lions, bears, and leopards (Loe and Roskaft 2004). However, negative human-puma encounters have been on the rise since the 1970s and 1990s (Mattson 2007). This increase has lead to multiple publications from the Mountain Lion Workshops (Fitzhugh 1988, Fitzhugh and Fjelline 1997, Fitzhugh *et al*. 2003) along with a unified guideline for wildlife managers (CMGWG 2005). Landscape level research is needed to identify potential hotspots and drivers of negative human-puma encounters at a population level; this knowledge will help create land management practices that may, in turn, reduce conflict (Arundel *et al*. 2007, Sweanor and Logan 2010). Reducing puma-human conflict will lessen public fear as well as help conserve puma populations (Sweanor and Logan 2010).

Negative human-wildlife interactions increase with the rise of human population (Torres *et al*. 1996, Woodroffe 2000) and human populations are increasing throughout the U.S. Furthermore, in the 1990s, the mountainous western region of the U.S. had the fastest growing population in the country with a decadal growth rate of 25.4% (Hansen *et al*. 2002). Many rural counties in the U.S. have a greater increase in populations compared to urban counties (Theobald 2000). Some pumas incorporate proportions of exurban (low housing density in natural environments) and rural habitat into their home-ranges, thus increasing the risk of human-puma encounters (Burdett *et al*. 2010). Furthermore, in the 1980s, puma population numbers were increasing in several areas, including California (Mansfield 1986), Colorado (Anderson and Tully 1989), Nevada

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(Stiver 1989), Texas (Russ 1989), Wyoming (Shorma 1989), and British Columbia (Herbert 1989), though it should be noted that estimates from other states are not currently available. However, puma populations throughout the West probably increased from 1965 to 1980 when their classification switched from a bountied predator to a game species, and puma hunting became regulated. The switch occurred nation-wide, except in California, where pumas are protected (Beier 1991) and Texas, where they are classified as a non-game animal with unregulated hunting. The known historic increase in human population, along with a likely increase in puma population may contribute to the increase in puma attacks on people.

An injured or an inexperienced predator should become more willing to take higher-risk prey or bolder hunting tactics that may increase their probabilities of making a kill but also incurring an injury (Brown and Kolter 2007). When dominant prey is unavailable, livestock may be a suitable alternative (Valeix *et al*. 2012). Domesticated livestock are easier to catch compared to wild species of similar size because they have lost virtually all of their ancestors' natural predator avoidance behavior (Linnell *et al*. 1999), yet they may be riskier because of their association with humans. Very often landowners retaliate against livestock depredation by opportunistically killing the assumed predator (Quigley and Crawshaw Jr 1992, Conforti and de Azevedo 2003). These alternative prey items can be classified as "sink prey," which we define as prey that if solely consumed by the predator, results in negative fitness for the predator. For a puma, its diet is dominated by deer species (Ackerman 1982). However, when a puma is injured or inexperienced, a deer may be too difficult for it to catch and it instead may hunt livestock. We classify livestock as a sink prey type for pumas because of the high

risk of mortality associated with livestock depredation. With unhealthy young male and female pumas more likely to be involved in a negative puma-human interaction than any other age or health status class (Mattson *et al*. 2011) a decrease in available sink prey, such as livestock, may cause an increase in puma attacks on people.

In a system with humans hunting pumas, the human is the predator and the puma is the prey. Predator presence can exhibit both lethal (Taylor 1984) and nonlethal effects on the prey (Lima 1998). In some instances the nonlethal effects play a larger role in the prey population compared to the lethal effects (Brown *et al*. 1999). Prey respond to the presence of predators by increasing their vigilance and avoiding areas with predators (Brown *et al*. 1999). With that, we take an ecology of fear approach to examine the relationship between humans and pumas. Part of ecology of fear examines how the hunting behavior of the predator and the antipredatory behavior of the prey determines the predator-prey interactions (Brown 2010). The presence of human hunters has been shown to alter activity patterns in some mammals (Kilgo *et al*. 1998, Kitchen *et al*. 2000) suggesting human avoidance behavior, but this has yet to be examined in pumas. As predation risk decreases (i.e. human hunting) prey should reduce their apprehension of the predator (Brown *et al*. 1999). Thus, the decrease in both the number of pumas killed (lethal effect) and the numbers of hunters (nonlethal effect) resulting from the change in legal status of pumas may have decreased the pumas' fear of humans and led to an increase in puma attacks.

Our goal is to analyze attacks where it appears that pumas possibly viewed humans as potential prey rather than a defensive attack. We have developed three, non-mutually exclusive alternative hypotheses to explain puma attacks on people. 1. Increase

in human population. An increase in the number of humans in puma inhabited states will increase the probability of an attack. 2. Lack of sink prey. Attacks occur out of desperation of the puma, either from being ill, injured, or being a young and inexperienced transient individual. A decrease in sink prey, especially cattle and sheep, will lead to desperate pumas to attack humans instead of livestock. 3. Lack of fear. A decrease in hunting or a lack of hunting in areas will cause pumas to decrease their fear of humans, thus increasing the possibility of an attack.

In this paper, we analyze changes in human population density, livestock (cattle and sheep) density, and human hunting patterns on pumas to explain occurrences of puma attacks on people. This is the first paper, to the knowledge of the authors, which has examined puma attacks on a broader landscape scale.

3.2 <u>Methods</u>

3.2.1 <u>Data collection: Livestock and human census</u>

Cattle and calves and sheep and lamb (hereafter livestock) abundances were obtained for each state at state level when available from 1910 to 2007. Pre 1910 and post 2007 data were not available. Livestock data were retrieved from the National Agricultural Statistics Service, USDA (www.nass.usda.gov/Data_and_Statistics).

Human population estimates were obtained for each state for the time period of 1890 to 2010 from the U.S. Census Bureau (www.census.gov). Data points for human and livestock populations between census reports were estimated by using a straight-line interpolation. All state census estimates were converted to state densities using the 2010 land areas available from the U.S. Census Bureau.

3.2.2 <u>Data collection: Attacks</u>

Incidents of human-puma encounters from 1890 to 2010 were compiled.

Following previous publications (Mattson *et al*. 2011) we compiled attack incidents from

five sources: (1) attack records from Beier (1991), (2) attack records from Etling (2001),

(3) official state records, (4) news reports, and (5) attack record by L. Lewis on

cougarinfo.org (Lewis 2011). All attack records were read for validity by considering

confirmation from state Fish and Wildlife officials and account by the victim. We are

only interested in encounters between puma and humans that appear to be caused by

pumas viewing humans as potential prey. Thus, we included only encounters where

evidence suggests that the puma initiated the interaction with the human, direct contact

was made from puma to human, and the human was the primary target (i.e. we did not

include if a human intervened in a puma attacking another animal or a person).

Encounters were removed if the human was riding a horse because it was impossible to

determine if the horse or the human was the intended target. Further, if two or more

people were injured from an attack, the attack counted as a single attack to avoid pseudo-

replication.

3.2.3 <u>Data collection: hunting</u>

Sport hunting statistics were compiled from 1980 to 2000 in five year bins for the

following states: Arizona, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon,

Utah, Washington, and Wyoming (Dawn 2002). Texas does not require reporting of

successful kills of pumas so numbers are unavailable for Texas. California does not

allow sport hunting of pumas, but depredation statistics from 1972 to 2009 are available

from the California Department of Fish and Game. It should be noted that the kill data

represents raw numbers. Proportions of puma populations harvested annually cannot be extrapolated from the numbers due to the unreliable and inconsistent puma population estimates.

3.2.4 Analysis

Human population estimates and the attack reports were restricted to 1910 to 2007 to match available livestock numbers, resulting in an analysis of 78 attacks. A binary logistic regression analysis (generalized linear model) with a logit link was performed with human and livestock density on attack data. For each state and year the state was classified as having an attack occur (1) or the absence of an attack (0). If there were multiple attacks in a single year in a single state it was still classified as a single occurrence. The two models with the lowest AIC_c value was selected and then tested against one another with a log-likelihood ratio test to determine if one was significantly better than another (Crawley 2005). The selected model was then tested against the null model with a log-likelihood test (e.g. Crawley 2005).

Due to the lack of information on hunting statistics only descriptive statistics could be performed. We followed Mattson *et al*. (2011) and used an alpha level of .10 for all statistical tests to reduce the possibility of a type II error. Committing a type II error may lead to ignoring potential drivers of an attack (Mattson *et al*. 2011). All analyses were conducted using R (2011).

3.3 Results

3.3.1 Historic and geographic attack distribution

Previous investigations have reported a rapid increase in number of attacks since the 1970s to 1990s (Mattson 2007). To examine this, frequency distributions both in time

and space were constructed. Changes in attack rate frequency (number of attacks) since 1891 in both the U.S. and Canada were examined (Fig. 1). Attacks were grouped in 10-year bins for the U.S., Canada, and U.S. and Canada combined. This resulted in a total of 166 attacks, 90 in the U.S. and 76 in Canada.
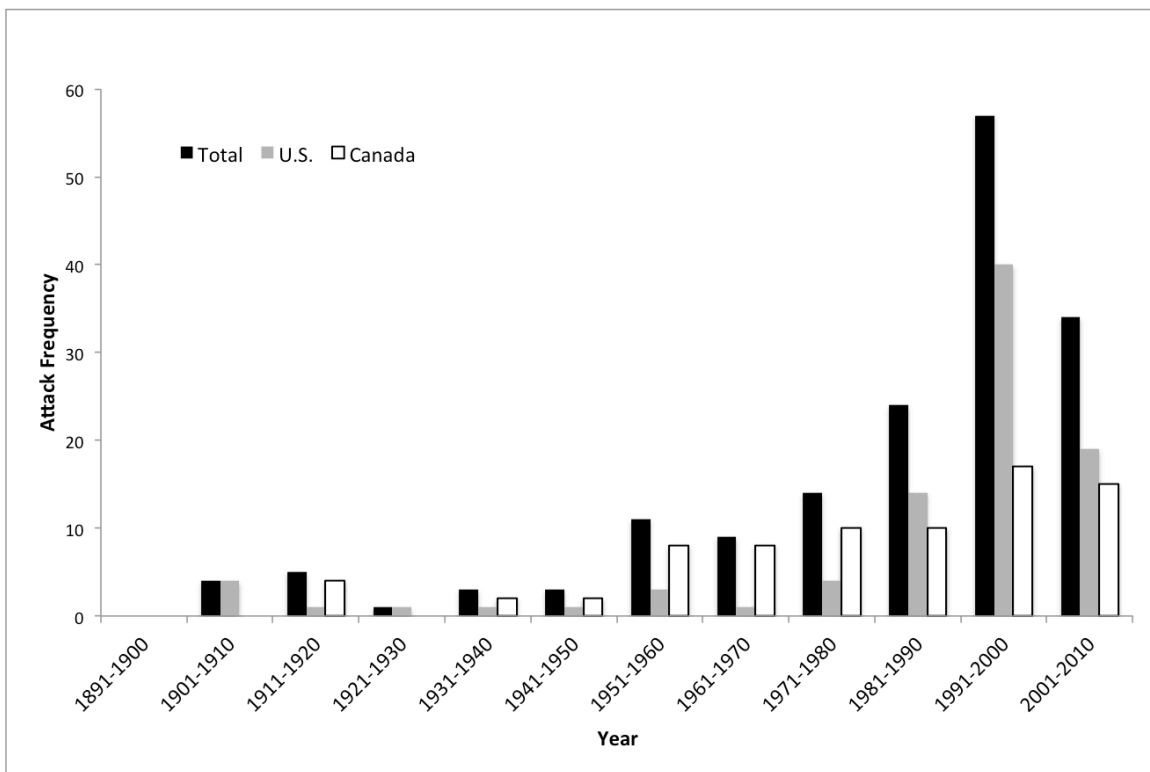
Figure 1: Frequency distribution of puma attacks on humans grouped in 10-year bins. Data represents number of attacks. Black bars indicate attacks in the U.S. and Canada, gray bars indicate attacks in the U.S. only, and white bars indicate attacks in the Canada only.

Attacks increased significantly in both the U.S. and Canada from 1891 - 1990 to 1991-2010 ($P < .001$ for both U.S. and Canada). However there was a greater increase in

attack rates in the U.S. from 1891 - 1990 to 1991 - 2010 than in Canada ($P < .01$, $X^2 =$ 8.93).

We examined geographic patterns of puma attacks within the United States. Attacks were binned in either the 1891 - 1990 (100 year interval) or the 1991 - 2010 (20 year interval) to examine the potential increase in attacks. Attack rates were calculated by determining the arithmetic mean of attacks per year in each state (Fig. 2).
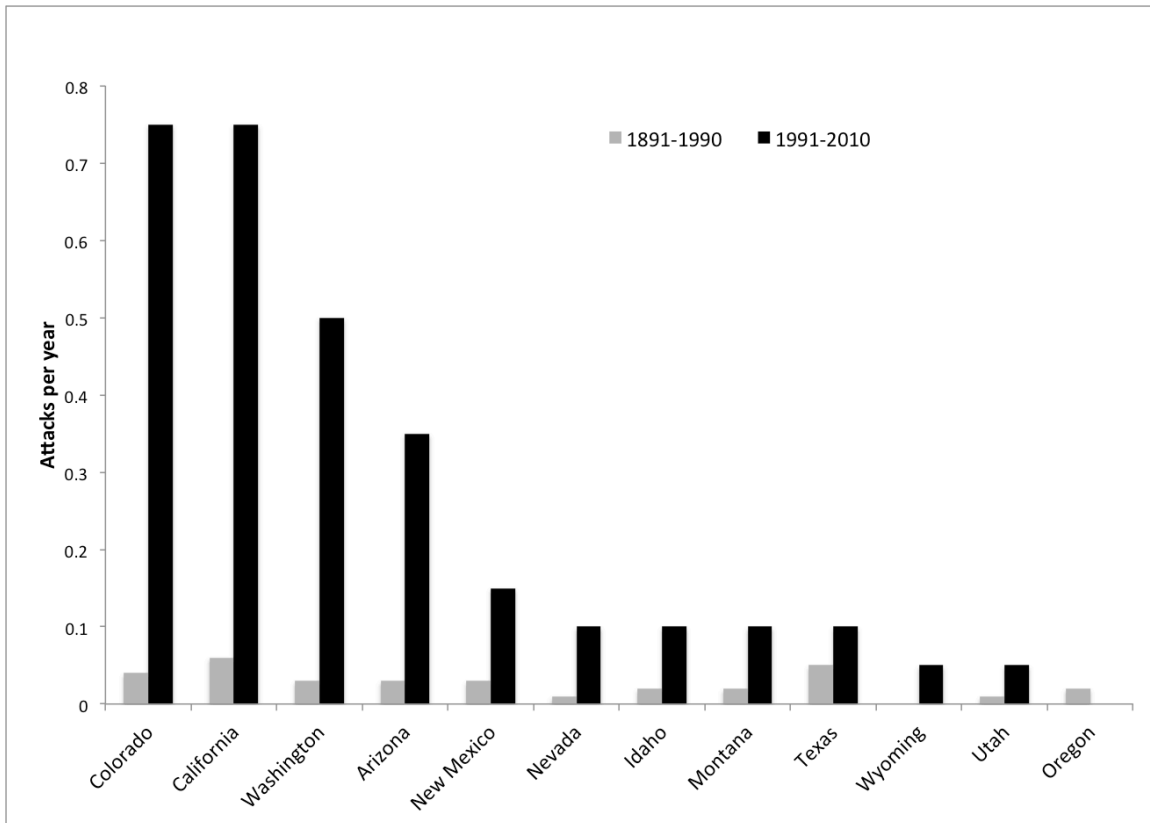
Figure 2: Frequency distribution of puma attacks on humans per year grouped in 100-year bins (gray bars) and 20-year bins (black bars) by state. Attacks rates were calculated by determining the arithmetic mean of attacks per year in each state.

Colorado, California, and Washington had the highest increase in attack rates

(0.71, 0.69, and 0.47, respectively). States were grouped as having either high rates of

attacks, more than 10 attacks from 1991 - 2010 (Colorado, California, and Washington)

or low rates of attacks with fewer than 5 attacks from 1991 - 2010 (New Mexico, Nevada,

Idaho, Montana, Texas, Wyoming, Utah, and Oregon). Arizona, with 7 attacks from

1991 - 2010 was not included to be conservative about our analysis. A contingency

analysis was performed comparing the high attack rate states in 1891 - 1990 and 1991 -

2010 with the low attack rate states in 1891 - 1990 and 1991 - 2010. The high attack rate

states had a significant increase in attacks compared to the low attack rate states ($P < .05$,

$X^2 = 5.01$).

3.3.2 Human and livestock density

We used a binary logistic regression (generalized linear model) to determine the

relationship between attacks, human density, livestock density, and the interaction

between human and livestock density (Table 1).

Table 1: The results of the binary logistic regression (GLM) performed on all possible factor combinations. Both terms, Livestock and Human represent densities. Significant levels: * = $P < 0.1$, ** = $P < .05$, *** = $P < .01$, **** = $P < .001$, ***** = $P < .0001$

| Model name	AICc	Factors	Estimate	Standard error	Z	P
Full model	422.32	Intercept +	-4.503	0.57	-7.895	*****
		Human +	131.376	33.618	3.908	*****
		Livestock +	76.025	46.69	1.628	.1035
		Human*Livestock	-6505.965	2425.032	-2.683	***
No interaction	427.32	Intercept +	-3.406	0.3404	-10.005	*****
		Human +	42.515	5.967	7.126	*****
		Livestock	-14.784	30.238	-0.489	0.625
Interaction	434.99	Intercept +	-3.414	0.171	-19.944	*****
		Human*Livestock	2497.291	368.989	6.768	*****
Human and interaction	**422.96**	**Intercept +**	**-3.665**	**0.194**	**-18.878**	*****
		Human +	**94.09**	**25.07**	**3.753**	****
		Human*Livestock	**-3607.446**	**1682.914**	**-2.144**	**
Livestock and interaction	434.92	Intercept +	-2.989	0.335	-8.911	*****
		Livestock +	-44.51	31.686	-1.405	0.16
		Human*Livestock	2819.799	434.322	6.492	*****
Human	425.56	Intercept +	-3.55	0.180	-19.715	*****
		Human	41.45	5.54	7.483	*****
Livestock	469.80	Intercept +	-3.371	0.32	-10.552	*****
		Livestock	39.652	25.656	1.546	0.122

A log-likelihood ratio test was performed between the full model (AICc = 422.32) and the Human and interaction model (AICc = 422.96) to determine if was one significantly better than either because of their similar AICcs. The more complex model is not significantly better ($P = .1037$), so the more parsimonious model (Human and interaction) was accepted.

A log-likelihood ratio test was used to determine the significance of the selected model compared to the null. Human density has a significant affect on the probability of an attack ($P < .0001$). There is a significant interaction between human density and

livestock intensity and the probability of an attack ($P < .05$). Thus, according to the

model (Table 1) and the log-likelihood ratio test, there is a significant positive

relationship between attacks and human density and a significant negative relationship

between the interaction of human and livestock density and attacks.

A contour plot was constructed illustrating the model fit of the selected model

(Fig. 3). The plot represents possibility of an attack based on human density and

livestock density.
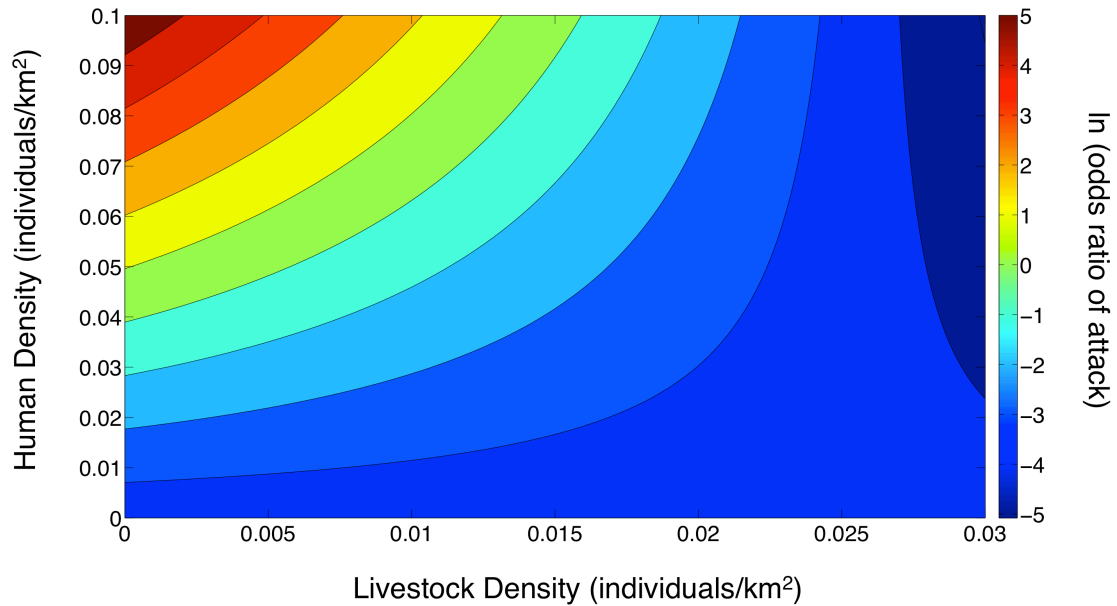
Figure 3: Contour plot illustrating model fit from the selected model. X-axis represents livestock density per km^2. Y-axis represents human density per km^2. Z-axis represents the ln of odds ratio of attack (the probability of attack divided by the probability of no attack).

Given puma presence, the highest possibility of an attack occurs under high

human population and no livestock. As human density decreases so does the possibility

of an attack. Livestock alone does not affect the possibility of an attack. However, the

presence of livestock can reduce the affect human density has on the possibility of an

attack (Fig. 3).

3.3.3 <u>Hunting</u>

A frequency distribution of puma harvests in all states of concern except Texas

was graphed in five-year bins (Fig. 4). Bins represent average harvest per year in 5-year

increments.
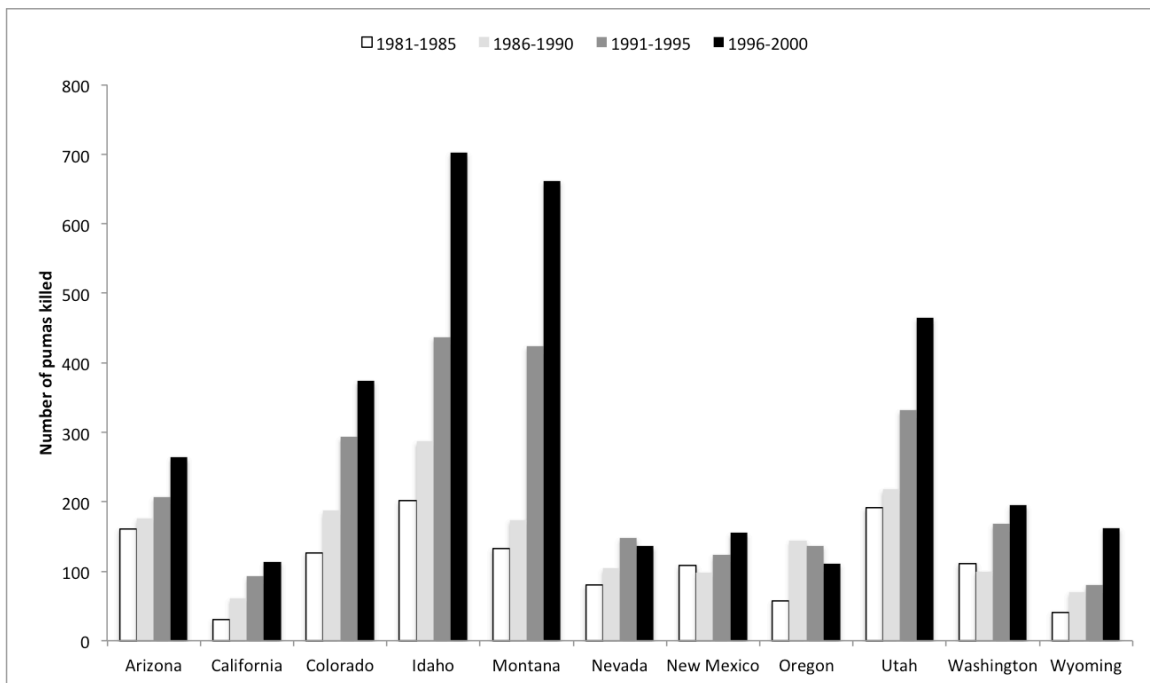
Figure 4: Frequency distribution of yearly average of pumas killed in 5-year bins. All state harvest data obtained from Dawn (2002) except California that came from California Fish and Wildlife.

Due to the lack of historic hunting records and lack of reliable and consistent

puma population numbers, no statistical tests can be performed on the data. Oregon had

the lowest attack rate (Fig. 2) and had one of the lowest harvest rates (Fig. 4). Whereas, California had one of the highest attack rates (Fig. 2) and had one of the lower harvest rates (Fig. 4). Puma harvest increases with time, but no clear correlation with attacks, spatially or temporally can be made.

3.4 <u>Discussion</u>

We have developed three, non-mutually exclusive alternative hypotheses to explain puma attacks on people. We found that puma attacks are significantly positively associated with an increase in human population density. Livestock density alone is not a good indicator of puma attacks, however puma attacks are significantly negatively associated with the interaction between human and livestock density. Patterns in sport hunting alone are not good indicators of puma attacks.

Understanding the specific driving force behind puma attacks is essential for effective management options. Our three hypotheses, if taken independently of one another, would result in different management guidelines. A significant positive relationship between human density and puma attacks suggests separation of human activity in puma habitat. A significant negative relationship between livestock density and puma attacks suggests increasing available sink prey items for pumas to reduce attacks. Finally, a significant negative relationship between sport hunting and attacks would suggest guidelines to allow for sport hunting or depredation management of pumas to reduce attacks. However, only human density and the interaction between human and livestock density were significant indicators of the likelihood of a puma attack.

3.4.1 <u>Increase in human population</u>

Puma attacks have been on the rise since the 1970s and 1990s (Mattson 2007). An increase in human population was highly significant ($P < .0001$) and the strongest correlate to puma attacks on humans (Table 1). An increase in human population has been suggested as a possible reason for the increase in attacks (Beier 1991). This result is consistent with black bear (*Ursus americanus*) attacks on humans (Herrero *et al*. 2011). However, when examining the proportion of individuals attacked per decade by pumas (number of attacked victims in a decade / population total for the 12 Western states in a decade) in the 1890s compared to 1980s, 1990s, and 2000s, they are all on the same order of magnitude, 1 in 10 million. The probability of a puma attack has not changed in order of magnitude since the 1890s. The increase in human population has provided the illusion that puma attacks are on the rise. This indicates that, at least so far, an increase in human density does not increase the probability of an individual being attacked.

3.4.2 <u>Lack of sink prey - Livestock</u>

There was a significant negative interaction between human and livestock density on the probability of an attack (Table 1). The interaction term is determined via a multiplicative operation. Thus, this suggests that the more human density increases, the greater the negative effect livestock density has on attacks. However, our best model excluded livestock density alone as a predictor of puma attacks. The density of livestock may be a poor indicator of attack probability, however livestock husbandry practices may be a better indicator. Worldwide, livestock is the greatest user of land, however over time the husbandry practices have shifted from grazing to feedlots (Naylor *et al*. 2005). This implies that the accessibility of livestock as prey may have declined over time due to

changes in husbandry practices. Livestock association with human structures, such as cattle-posts in Botswana, has shown a reduced likelihood of depredation by African lions (*Panthera leo*) (Valeix *et al*. 2012). Depredation rates also decrease with livestock association of human presence and activity (Mazzolli *et al*. 2002, Ogada *et al*. 2003).

Furthermore, livestock is not the only possible sink prey for pumas. Sink prey may also include smaller species that are known to occasionally occur in puma diets such as, beavers, Virginia opossums, porcupines, and cottontail rabbits. Female pumas are found to have a more diverse prey base that varies greater in size compared to male pumas (Mattson *et al*. 2007). With female pumas having the greatest likelihood of attacking humans, a reduction in small, varied prey may be increasing the probability of an attack. An examination of small wild prey availability via species census in relation to puma attack hotspot locations should be examined.

3.4.3 Lack of fear - Hunting

Human avoidance is observed in populations of hunted coyotes (*Canis latrans*) (Kitchen *et al*. 2000) and white-tailed deer (*Odocoileus virginianus*) (Kilgo *et al*. 1998). However, with the limited data available on puma harvest no observable trends in attack propensity can be gleaned. Hunting populations of pumas significantly decreases the mean age of the population (Stoner *et al*. 2006, Robinson *et al*. 2008, Cooley *et al*. 2009), furthermore females are significantly younger in a hunted population as opposed to a protected population (Stoner *et al*. 2006). Studies show that young female pumas are the most likely demographic to be involved in a negative human-puma encounter (Mattson *et al*. 2011). With no evidence from our limited data showing that hunting may lead to pumas avoiding humans, further studies should examine if hunting may actually lead to

an increase in the likelihood of an attack in some populations by reducing the mean age of the puma population.

The significant negative interaction between human and livestock density on attacks may have useful implications for the management of human-puma conflict. Under high human density, livestock availability becomes important for decreasing attacks on humans. Livestock may represent a sink prey item for pumas. With high human density, other possible natural sink prey may not be available. However, livestock depredation is another source of human-wildlife conflict. In light of our results, we suggest taking a Win-Win Ecology approach (Rosenzweig 2003) and providing habitat for natural sink prey items, such as beavers and porcupines, within human habitation, to decrease negative human-puma interactions.

3.5 <u>Literature cited</u>

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4. Distribution of coyote (*Canis latrans*) and white-tailed deer (*Odocoileus virginianus*) in the Chicago metropolitan area through time and space

4.1 Introduction

Many animals exhibit plasticity to minimize energy costs and the potential for death (Van Dyke *et al*. 1986, Drew and Bissonette 1997). In particular, wildlife shift their temporal and spatial distributions to maximize gains and minimize risks from the environment (Kitchen *et al*. 2000). Temporal and spatial variation can arise due to avoidance of predation (Festa-Bianchet 1988), prey abundance (Karanth *et al*. 2004), vegetation, season (Beier and McCullough 1990), and human activity (Van Dyke *et al*. 1986, Arundel *et al*. 2007). We can group these factors as interspecific interactions, habitat, or human presence. Using camera-trap data, we examined how these factors influence the presence and absence of coyotes (*Canis latrans*) and white-tailed deer (*Odocoileus virginianus*, hereafter deer) in the Chicago metropolitan area.

Housing density and traffic likely alter distributions of mammalian wildlife. For some species, increases in housing density decreases suitable habitat by changing both abiotic and biotic factors (Odell and Knight 2001). Housing development often decreases or at least alters the presence of native vegetation, which may alter the presence of some wildlife species (Theobald *et al*. 1997). Chace and Walsh (2006) found urban areas that maintained more native vegetation maintained more species of native birds compared to urban areas that did not. Structural barriers that are often associated with housing development, such as fencing, likely restrict movement of some animal species (Theobald *et al*. 1997). Mammalian avoidance is also observed in high traffic areas. Roads impose high mortality (Forman and Alexander 1998). However, at the same time,

both coyotes (Quinn 1997, Grinder and Krausman 2001, Gehrt 2007) and deer (Quinn 1997, Grinder and Krausman 2001, Grund *et al*. 2002, Porter *et al*. 2004, Gehrt 2007) can be found in close proximity to human establishments.

Compared to urban environments, food, water and shelter all positively contribute to an animal's fitness (Rothley 2002). Canopy cover and access to water thus influence distributions of large mammal species. Adequate canopy cover can provide both food resources (Quinn 1995) and protection from predation (Mysterud and Òstbye 1999). Many mammal species need access to a water source. Both coyotes and deer select habitats with adequate vegetation cover (Pollock *et al*. 1994, Quinn 1995, 1997). However, deer may be more selective for vegetation cover because they are browsers and they are dependent on reliable digestible fiber (Pauley *et al*. 1993).

Interspecific interactions among wildlife can alter distributions. This is especially true when considering predator-prey relationships. The relationship among coyote and deer in the Chicago metropolitan area may be best examined through the ecology of fear (Brown *et al.* 1999). Experimental studies show that foragers alter habitat use to reduce the risk of mortality from a predator even at the cost of their foraging rate (Dill and Fraser 1984, Lima *et al*. 1985). Potential predators do not need to actively hunt a prey species to alter their distribution. Prey altering their habitat use and distribution in response to predator presence is an example of the nonlethal effect that a predator can have on a prey (Lima 1998). The fitness of the forager can be maximized by choosing habitats that minimize the risk to reward ratio (Gilliam and Fraser 1987). Predators should optimize their foraging efficiency by biasing their time in areas with the highest concentration of potential prey (MacArthur and Pianka 1966). Deer are an important

food source for coyotes in the Chicago metropolitan area (Morey *et al.* 2007), however deer consumptions often comes in the form of carrion for coyotes (Ozoga and Harger 1966, Nellis and Keith 1976). For some populations of deer, traffic collisions are the main source of mortality (Porter *et al.* 2004) and in Chicago, carrion from road-killed deer is available year-round (Morey *et al.* 2007).

In collaboration with the Lincoln Park Zoo's Urban Wildlife Institute and their existing biodiversity monitoring project, we take a correlative approach to interpret spatial and temporal distribution of coyotes and deer in the Chicago metropolitan area. Our primary objective is to determine the relationship among human activity, habitat characteristics, and coyote and deer spatial and temporal distribution through generalized linear models. We use quantifiable variables that represent habitat and human factors that may alter the distribution and activity density of coyote and deer in the Chicago metropolitan area. We hypothesize that: 1) There will be a negative association for both coyote and deer presence in relation to human activity. Furthermore, deer and coyote detections will decrease with an increase in housing density and road length and decrease with distance to urban center. These negative effects of human activity will be stronger for coyotes than for deer. 2) There will be a positive association for both coyote and deer in relation to natural habitat. Hence, coyote and deer detections will increase with proximity to water and with canopy cover. The positive association with natural habitats will be a stronger for deer than for coyotes. 3) There will be a negative association for deer in relation to coyotes in either space or timing of their behaviors within the same space.

4.1.1 <u>Conceptual framework</u>

We developed a conceptual framework to analyze the presence and absence of coyotes and deer in the Chicago metropolitan area (Fig. 1). We chose the following variables to examine: housing density, road lengths, distance to urban center, canopy cover, distance to water, and coyote presence. We grouped our variables of interests into three different factors: human activity, habitat characteristics, and interspecific interactions. The human factor was represented by housing density, road length, and distance to urban center. Canopy cover and distance to water represented the habitat factor. To simplify our model we only examined how human and habitat factors may affect coyote and deer abundance and not the feedback loop between human and habitat.
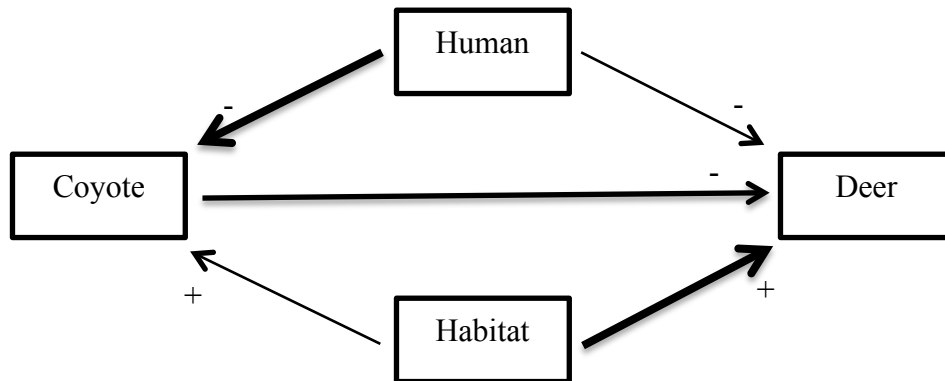
Fig. 1. Conceptual framework suggesting the sign and magnitude (thickness of the arrows) of correlative relationships between coyote and deer in human-dominated habitats. "Human" encompasses distance to urban center, average housing density, and road length. "Habitat" represents distance to water and canopy cover. Bold lines represent a stronger relationship and fine lines represent a weaker relationship.

We hypothesized that deer will exhibit a negative association with both human activity and the presence of coyotes, while coyotes will exhibit a stronger negative association with human activity. Additionally, coyotes and deer are known to avoid residential and urban areas that are commonly associated with human activity (Storm *et al*. 2007, Gehrt *et al*. 2009, Gehrt *et al*. 2011). Thus, an increase in housing density and traffic and a decrease in distance to urban center is likely to reduce use of the habitat by deer and coyotes in order to avoid humans (Douglass and Ernst 1985, Storm *et al*. 2007, Grubbs and Krausman 2009). Additionally, since carrion deer is a major resource for coyotes in the Chicago metropolitan area (Ozoga and Harger 1966, Nellis and Keith 1976, Morey *et al*. 2007) coyotes may have a nonlethal effect on deer distribution but deer may not affect coyote distribution. Thus, deer may exhibit negative association with coyote presence.

We hypothesized that both coyotes and deer will exhibit a positive association with habitat, represented by canopy cover and water. Both vegetation and water provide needed resources for coyotes and deer. Therefore, a limited amount of canopy cover area and decreased access to water is likely to reduce coyote and deer presence. Both deer and coyotes will incorporate urban areas within their home ranges, however some urban coyotes have home ranges completely lacking natural areas (Grund *et al*. 2002, Gehrt *et al*. 2009). Thus, the habitat characteristics may have a greater effect on deer compared to coyotes due to the deer's requirement as a browser and need for digestible fiber (Pauley *et al*. 1993).

4.2 <u>Methods</u>

     The Lincoln Park Zoo's Urban Wildlife Institute (UWI hereafter) has an ongoing project, "Monitoring Urban Wildlife". Their goal is to use remotely triggered cameras to assess biodiversity in the Chicago Metropolitan area. Their mission is to improve conservation strategies along with understanding the ecology and behavior of urban wildlife in the Chicago metropolitan area with the use of camera data. This paper is in collaboration with the UWI and their existing camera data.

     UWI developed a transect design for camera data collection (Fig. 2). Each transect was approximately 50km in length and radiated out from Chicago's urban center, represented as the center of the "Loop" that constitutes the boundaries of downtown. Each transect was divided into 10 sections of 5km each. A maximum of four cameras were placed in each section, with each camera a minimum of 1km from all others. All cameras were placed in either a golf course, cemetery, park, or forest preserve. Due to this design, not all cameras were placed equidistant from one another. Additionally, because the three transects radiate out from a central location within Chicago, the first sections of each transect were too close to one another to allow placement of 12 cameras, thus only four cameras were placed in the first section, across all transects. During the time period covered by this study, there were a total of 93 active monitoring stations. The stations closest to the urban center were located in Clybourne Park, Seward Park, Skinner Park, and Lake Meadows Park. The three transects terminated in Mettawa in Lake County, Lockport in Will County, and Fermilab in Kane County.
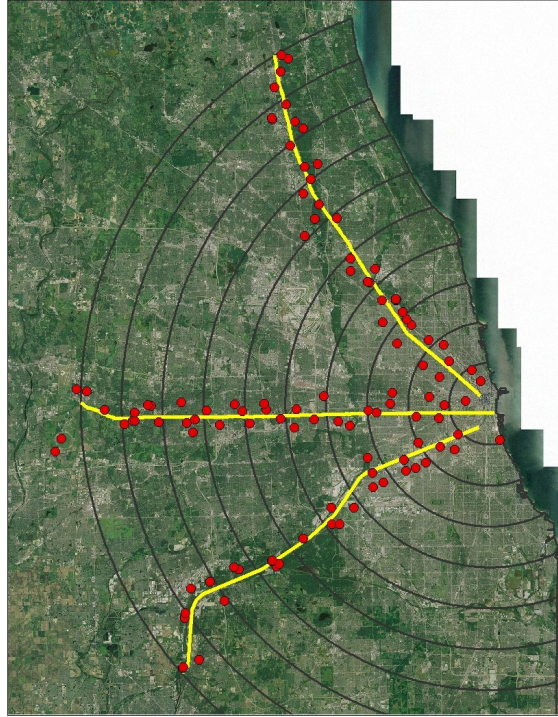
Fig. 2: Transect design developed and implemented by UWI.
Yellow lines represent the three transects radiating 50km out from the
"Loop" with each red circle representing a camera. Each concentric black
line represents 5km.

UWI deployed cameras in the fall, winter, spring, and summer in 2010 and 2011.

Cameras were deployed for approximately four weeks at a time. However, due to camera

malfunction, vandalism, and theft the average number of camera nights per camera for

2010 and 2011 combined was 27.5 days (range = 1 - 125 days, SD = 14.3). Cameras

were baited with fatty-acid lures and liquid scent lures.

Within a 500m buffer around each monitoring station, UWI quantified the

following variables with ArcGIS ver. 9.3 (ESRI 2009): average housing density, total

road length (excluding local roads), and average percent canopy cover. UWI also

calculated distance to water, and distance to urban center for each camera.

Photo data were divided into four, four-hour time blocks centered around sunset, sunrise, noon, and midnight. However, around summer and winter solstices there are fewer than 8 hours of night and day, respectively. To resolve this issue we used midpoints between dawn and dusk as "realized noon and "realized midnight". The number of photos containing deer and coyotes along with presence-absence data (species detected or not detected) were tallied for each camera in each time block. The photo data represent activity density, not actual density of coyotes and deer. Photo data will capture movement of individual species, however actual density cannot be determined from photo data alone. Photo data may be skewed to represent many individuals moving through the habitat or it may represent a few individuals moving through the habitat frequently. However, the presence-absence data used in the analysis does not have this limitation.

Presence-absence photo data were analyzed with two binary generalized linear models (GLM) with a logit link. A separate binary GLM was conducted for each species. We used an alpha level of .05. All analyses were conducted using R (2011).

4.3 <u>Results</u>

A total of 4,679 and 1,055 photos of deer and coyote, respectively, were obtained from the camera data. Out of 93 functioning cameras, 52 and 24 cameras never captured deer and coyotes, respectively. 22 out of the 93 cameras were never triggered by either deer or coyotes.

A histogram was produced representing the total number of photos of coyotes and deer throughout all cameras divided into two-hour blocks (Fig. 3). Deer exhibited crepuscular activity, whereas coyote exhibited nocturnal activity.
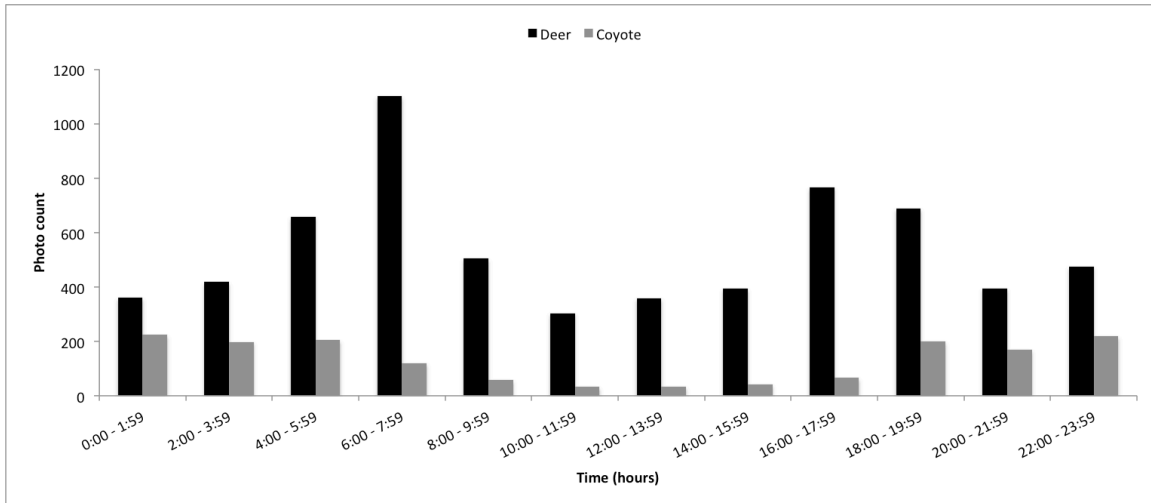
Fig. 3: Histogram of coyote and deer activity density distribution through time. Black bars represent deer and gray bars represent coyotes.

Deer had their two highest activity densities between 6:00 and 7:59 with 1,102 photos and between 16:00 and 17:59 with 767 photos. Deer had their two lowest activity densities between 10:00 and 11:59 with 304 photos and between 12:00 and 13:59 with 359 photos. Coyotes had their two highest activity densities between 0:00 and 1:59 with 224 photos and between 22:00 and 23:59 with 219 photos. Coyotes had their two lowest activity densities between 10:00 and 11:59 with 33 photos and 12:00 and 13:59 with 34 photos.

Temporal histograms based on seasons (fall, winter, spring, and summer) similar to Fig. 3 were produced for both coyotes (Fig. 4) and deer (Fig. 5). Histograms represented proportion of photos, at any 2-hour time block, based on season.

Coyotes exhibited nocturnal behavior regardless of the season. Coyotes exhibited the greatest peak in activity between 18:00 and 23:59 (Fig. 4).
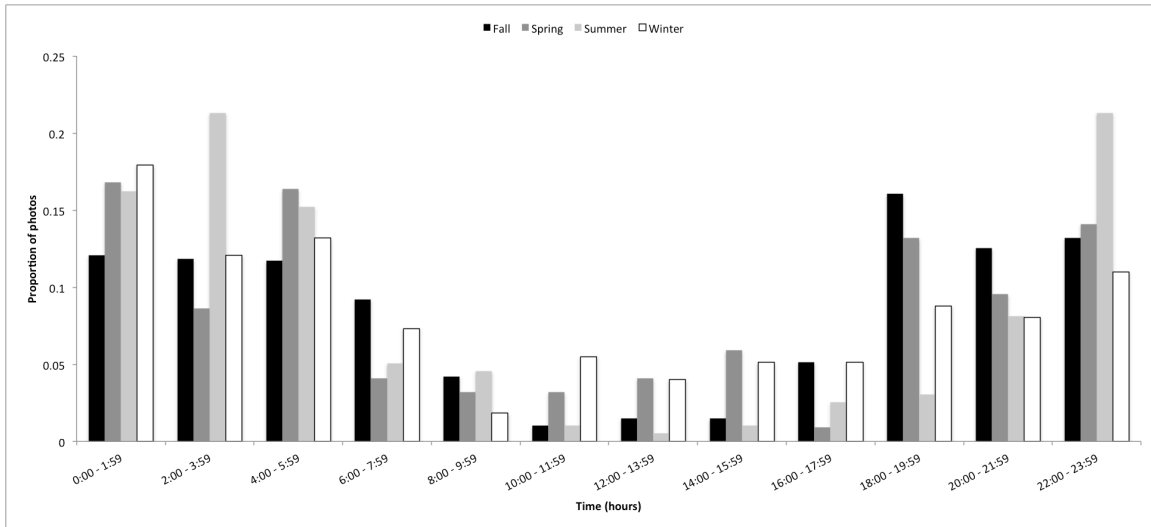
Fig. 4: Histogram of proportion of coyote photos based on seasons: fall, spring, summer, and winter.

Deer exhibited crepuscular activity regardless of season. Deer exhibited the greatest peak in activity from 4:00 to 7:59 and from 16:00 to 19:59 (Fig. 5).
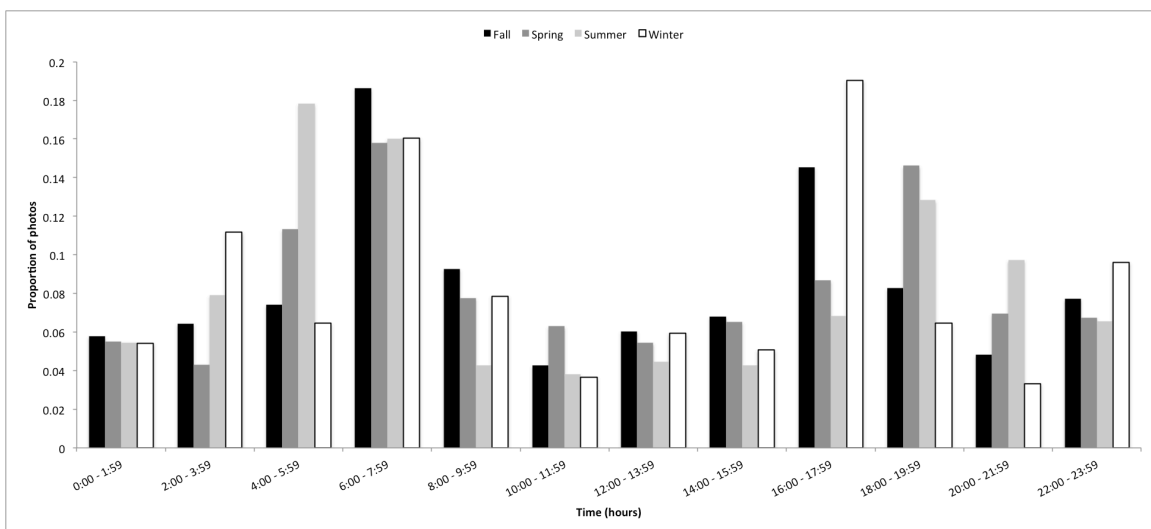
Fig. 5: Histogram of proportion of deer photos based on seasons: fall, spring, summer, and winter.

A binary GLM was analyzed on the presence-absence data. The following

independent variables: distance to urban center, distance to water, road length, average

housing density, percent canopy cover and time with a single dependent variable of

presence-absence was analyzed. Four-hour time blocks around sunset, sunrise, and noon

blocks were compared against the midnight block as discrete independent categorical

variables. The deer analysis had an additional independent variable of coyote presence.

Table 1: Binary GLM output of coyote presence-absence data. Significant levels: $* = P < .05$, $** = P < .01$, and $*** = P < .001$

	Estimate	Std. Error	Z	P
Distance to Urban Center	6.905e-6	1.420e-5	0.486	0.626648
House Average	-5.850e-4	2.434e-4	-2.404	0.016223*
Road Length	-9.037e-3	6.540e-3	-1.382	0.167040
Distance to Water	-3.041e-4	1.617e-4	-1.881	0.059953
Canopy Cover	4.375e-2	1.066e-2	4.103	4.08e-5***
Noon	-2.594	4.184e-1	-6.201	5.61e-10***
Sunrise	-1.159	3.807e-1	-3.044	0.002338**
Sunset	-1.483	3.850e-1	-3.853	0.000117***

Table 1 represents the binary GLM output for the coyote analysis. Coyotes are

negatively associated with housing density ($P < .05$) and positively associated with

canopy cover ($P < .0001$). An increase in distance to water decreased the likelihood of

coyotes, however the result was only marginally significant ($P = .0599$). Additionally,

there were significantly fewer photos in the noon ($P < .0001$), sunrise ($P < .01$), and

sunset ($P < .0001$) time blocks compared to the midnight time block. Distance to urban

center and road length did not significantly predict coyote photos.

Table 2: Binary GLM output of deer presence-absence data. Significant levels: $* = P < .05$, $** = P < .01$, and $*** = P < .001$

	Estimate	Std. Error	Z	P
Distance to Urban Center	-3.611e-5	1.861e-5	-1.940	0.052378
House Average	-2.428e-3	6.425e-4	-3.779	0.000158***
Road Length	-1.180e-2	9.672e-3	-1.220	0.222469
Distance to Water	-1.938e-3	5.075e-4	-3.818	0.000134***
Canopy Cover	6.527e-2	1.507e-2	4.332	1.48e-5***
Noon	2.132e-1	5.342e-1	0.399	0.689888
Sunrise	8.767e-1	5.123e-1	1.711	0.087022
Sunset	7.898e-1	5.195e-1	1.520	0.128445
Coyote	1.583	4.103e-1	3.858	0.000114***

Table 2 represents the binary GLM output for the deer analysis. An increase in

housing density significantly decreases deer photos ($P < .001$). There was a significant

decrease in photos of deer with an increase in distance to water ($P < .001$). An increase

in canopy cover significantly increases deer photos ($P < .0001$). Deer were positively

associated with the presence of coyotes ($P < .001$). Distance to urban center and road

length did not significantly predict deer photos. Temporal distributions of photos were

not significantly different from the midnight photos.

A linear regression was analyzed for the total number of photos of coyotes against deer throughout all cameras divided into two-hour blocks (Fig. 4).
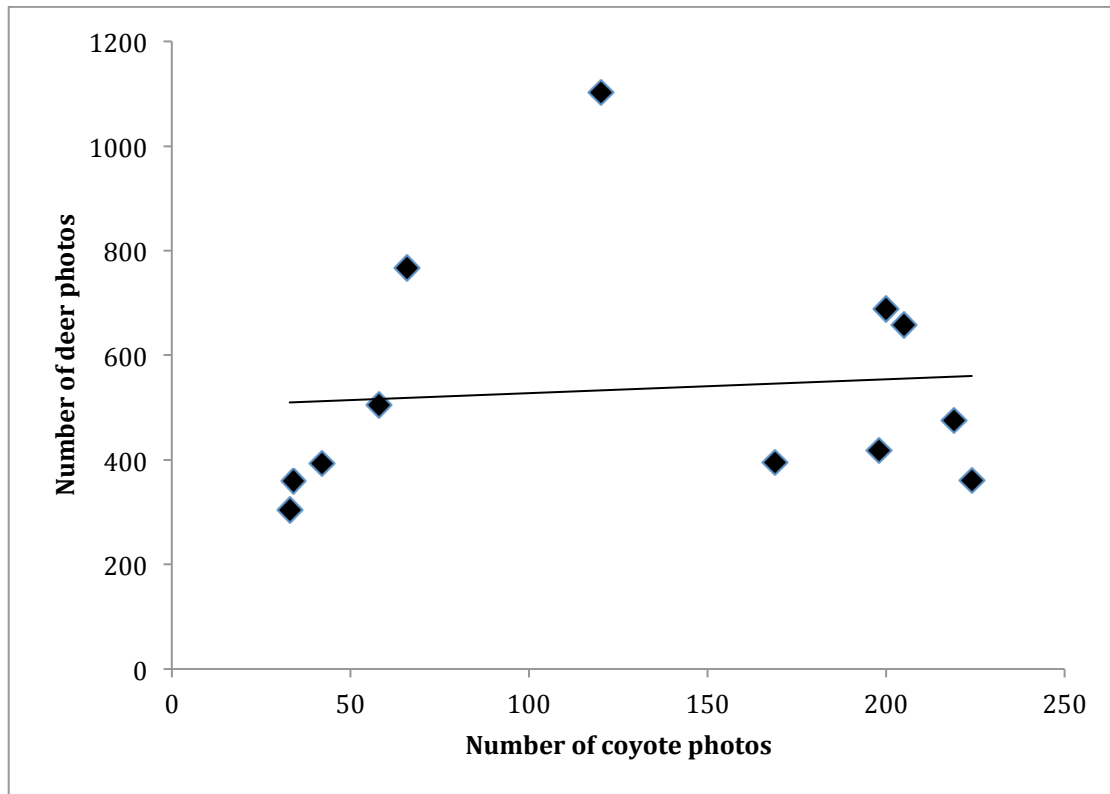
Fig. 6: Linear regression of total number of photos of coyotes and deer totaled across all cameras in two-hour time blocks. R^2 of 0.00828 illustrates no relationship between number of photos of coyote and deer totaled across Chicago Metropolitan area based on time.

The linear regression (Fig. 6) illustrates no relationship between coyotes and deer based on two-hour time blocks across all cameras ($R^2 = .00828$).

4.4 Discussion

All of the factors analyzed had a stronger effect on deer photos compared to coyotes based on the larger estimate values for deer, except for canopy cover (Table 1

and 2). Our hypothesis that both deer and coyote would have a strong selection for habitat was supported both by findings for distance to water and canopy cover (Table 1 and 2). However, distance to water had a stronger effect on deer and canopy cover had a stronger effect on coyotes (Table 1 and 2). Both deer ($P < .001$) and coyotes ($P < .05$) have a significant negative association with an increase in housing density, suggesting an avoidance of human activity. However, our hypothesis that human activity would have a stronger negative affect on coyotes than deer was not observed in our results (Table 1 and 2). There was no significant effect of distance to urban center and road length on deer or coyotes. Additionally, the binary GLM data suggests that there was a positive association between deer and coyotes ($P < .0001$). However, the linear regression indicates no relationship between coyotes and deer when examined at a finer temporal scale (Fig. 6). Thus, the GLM results may be an artifact due to the similar significant habitat selection observed by both species (Table 1 and 2).

The histogram suggests that coyotes are more nocturnal and deer appear to be more crepuscular (Fig. 3). Peak deer activity during sunset and sunrise is consistent with other studies (Beier and McCullough 1990). Also, peak nocturnal activity for coyotes is consistent with other studies of urban coyotes (Grinder and Krausman 2001, McClennen *et al.* 2001) including telemetry studies in Chicago metropolitan area (Gehrt *et al.* 2011). The increased nocturnal photo data of coyotes could suggest avoidance of humans, which has been suggested by Gehrt (2007). Additionally, Kitchen *et al.* (2000) examined differences in activity patterns in a population of coyotes while they were being hunted (1983-1988) and 8 years after hunting had ceased (1996-1997). Kitchen *et al.* (2000) found no difference in total overall movement of coyotes and no difference in the activity

patterns of mammalian prey for the coyote. However, Kitchen *et al*. (2000) did find that after hunting had stopped, coyotes were significantly more active during daytime hours. Kitchen *et al*. (2000) concludes that coyotes shifted to more nocturnal patterns while they were hunted to avoid humans and after the hunting had stopped the coyotes shifted to more diurnal activity patterns. Kitchen's conclusion is supported by the fact that coyote's visual system is more adapted for diurnal or crepuscular activity and not nocturnal activity (Kavanau and Ramos 1975).

Seasonal variation may play a role in the distribution of coyotes and deer in the Chicago metropolitan area. In winter, access to shelter may be more important and in the summer, access to food may be more important (Dexter 1998). We pooled data across all four seasons. Separating data based on season may shed light on possible variation in distribution of deer and coyotes. Change in habitat type use based on snow depth has been observed in deer (Beier and McCullough 1990). Deer select against closed forests, open woodland, and grasslands with increase in snow depth (Beier and McCullough 1990). The linear regression (Fig. 3) and GLM (Table 2) suggest contradictory relationships among coyotes and deer, however seasonal variation may play a role in the interspecific interactions. The primary source of deer in a coyote diet comes from carrion (Ozoga and Harger 1966, Nellis and Keith 1976), however coyotes are most successful at killing deer during the winter months. During this time deer are usually in their poorest physical condition and the increased snow depth favors coyotes in the hunt (Ozoga and Harger 1966).

Additionally, species composition and level of disturbance of the canopy may alter distribution patterns of coyotes and deer. We analyzed data at a 500m scale and

found a positive association for both coyote and deer in relation to canopy cover. However, we suggest exploring finer grain canopy cover data as an indicator of distribution. Using percent canopy cover independent of species for the distribution of deer may not address the possibility of an inedible forest for deer. Also vegetation structure, such as disturbed versus mature forests and tree species has been shown to be more important for determining presence of coyote instead of open versus cover (Kays *et al*. 2008, Kelly and Holub 2008).

Our results suggest no effect of distance to urban center and road length on coyotes. However, other studies on urban coyotes have illustrated an avoidance of developed areas (Quinn 1997, Riley *et al*. 2003), however coyotes may increase use of developed habitat during night hours (Tigas *et al*. 2002). Thus, additional studies should be performed to determine if coyotes in the Chicago Metropolitan area demonstrate a temporal avoidance in relation to the urban center and roads.

The use of cameras to determine presence and habitat selection has both benefits and limitations, especially when compared to telemetry. The use of cameras allows for an investigation within highly urbanized city limits. Radio collaring in highly urbanized areas depend on opportunistic trapping thus making extensive trapping efforts not feasible due to safety concerns for both people and the trapped animal (Gehrt *et al*. 2009). Another benefit that occurs with camera use instead of radio collaring is the ability, at no additional cost, to interpret data for interspecific interactions. Radio collaring for determining interspecific interactions potentially requires doubling collaring efforts or decreasing sampling size.

However, camera data does have limitations. One thousand trap nights has been suggested as the minimum number of nights to determine if an animal is truly absent from an area (Carbone *et al*. 2001). When considering battery life and camera malfunction, a total of 1,000 trapping nights becomes extremely intensive to determine absence. Furthermore, abundance data cannot be accurately determined by solely camera trapping for monochromatic animals. However, abundance estimates from camera data has been used for jaguars in Belize and Bolivia (Silver *et al*. 2004), tigers in India (Karanth 1995), and ocelots in Brazil (Trolle and Kery 2003) using capture-recapture models based on pelage patterns.

We analyzed housing density, road lengths, and distance to urban center to represent factors associated with humans and canopy cover and water to represent factors associated with habitat as variables that may alter the distribution of coyote and deer in the Chicago Metropolitan area. The use of these factors have been widely used to explore habitat selection in both coyotes and deer (Vogel 1989, Kilpatrick and Spohr 2000, Grinder and Krausman 2001, Grund *et al*. 2002, Atwood *et al*. 2004, Storm *et al*. 2007, Kays *et al*. 2008, Gehrt *et al*. 2009, Ordenana *et al*. 2010). While other studies obtain significant association or disassociation with these variables the restricted information that is obtained from presence-absence data may explain the lack of significant results obtained from some of our factors. However, the strong uniqueness of this study is the true urban setting. While telemetry studies allow for fine-scale data, this study was able to obtain data from a high-density urban center that has not been accomplished in Chicago before with telemetry.

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