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### Factors Influencing Mountain Lion Kill Rates Across Three Ecosystems in the Americas

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Factors Influencing Mountain Lion Kill Rates Across Three Ecosystems in the Americas

By

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Undergraduate Thesis  
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## **Abstract**

Kill rate, defined as the number of prey killed per predator per unit time, is a key component to understanding predator-prey dynamics. A multitude of factors may affect kill rates, including, variation in age, sex, weight, or presence of offspring of either predator or prey species (intraspecific variation) and events such as the theft of a kill made by another animal (kleptoparasitism). These factors may influence the time a predator spends locating prey (search time) and the pursuing, killing, and consumption of prey (handling time). The sum of search time and handling time may be measured as the time between a subsequent kill, a metric I will use to make inferences on what affects mountain lion (*Puma concolor*) kill rates. Utilizing kill data obtained from Global Positioning System (GPS) collared mountain lions of Colorado, Wyoming, and Patagonia, I investigated the impacts of: 1) mountain lion sex, 2) mountain lion age, 3) accompaniment of offspring with mountain lion females, 4) prey weight, and 5) the presence of bears (habitual kleptoparasites) throughout study periods. Applying these factors, I determined the most parsimonious and biologically sound statistical model, best describing sources of variation in time between kills for mountain lions. Determinant factors were: age of a mountain lion, in which a juvenile (<2 years old) was predicted to be killed less often than an adult (>2 years old); presence of offspring, in which a female with accompanying offspring was predicted to kill more often than a mountain lion without; per kg of prey weight, in which time between kills was predicted to increase as the weight of a prey item increased; and based on bear activity, in which a mountain lion was predicted to kill more often when bears were active on the landscape than when they were not active. Further knowledge on this subject may be useful for harvest management of mountain lions regarding the lessening of impacts of predation on ungulate populations of concern, through age class and reproductive status targeting. Furthermore, I show some evidence of the indirect impacts of kleptoparasitism on ungulate populations, through the direct impacts on kill rates of predators such as the mountain lion from kleptoparasitic bear species.

## Introduction

Fundamental to understanding the impacts of predators on prey, is in the investigation of the impacts of predation, how predation is compensated by prey, and which individual prey are killed (Mills 2013). Predation itself is the product of the functional response and the numerical response of a predator in relation to a prey population. Put simply, the numerical response is the number of predators given the number of prey, while the functional response (also known as the kill rate), describes the numbers of prey killed per individual predator per unit time (Holling 1959 and Mills 2013). Adequate understanding of predator-prey systems and population dynamics relies in part on the knowledge of factors causing the kill rate of a predator to vary (Knopff et al. 2010). A multitude of factors may be influential to a predator's kill rate, including energetic requirements, interspecific competition, and intraspecific variation among both a predator and its prey regarding sex and age (Elbroch et al. 2014, Lima and Dill 1990, Miller et al 2014).

For enigmatic species, such as the mountain lion (*Puma concolor*), quantifying kill rates through field efforts in a natural habitat is extremely challenging. However, kill rates have been hypothesized to be driven by metabolic requirements (Ackerman et al. 1986). Thus, energetic models formed from basal metabolic rate and the energetic costs connected to activity, are utilized to estimate energetic requirements and the kill rates required to meet those energetic demands (Elbroch et al. 2014). However, estimated kill rates for the mountain lion rarely align with kill rates quantified through field observations (Elbroch et al. 2014 and Knopff et al. 2010). Many mountain lion studies have quantified empirical kill and consumption rates that were significantly greater than the rate predicted energetically (Elbroch et al. 2014 and Knopff et al. 2010). The discrepancy between predicted and observed kill rates could be the result of prevalent

energetic models relying solely on physiological values (e.g. mass and energy budgets) to estimate kill rates (Elbroch et al. 2014).

Mountain lions often experience interspecific competition and species interactions with those of the scavenger guild (Elbroch et al. 2015b and Elbroch et al. 2014). Studies suggest that mountain lions seem to abandon and/or increase frequency of kills in the face competition and harassment from scavengers and other predators (Knopff et al. 2010, Elbroch et al. 2015a, Elbroch et al. 2015b, Elbroch et al. 2013b). These forms of species interaction seem to significantly affect mountain lion fitness and foraging behavior (Elbroch et al. 2015a). Mountain lions of the Southern Greater Yellowstone Ecosystem experienced increased starvation, altered prey selection, and increased mortality due to competition from reintroduced gray wolves (Elbroch et al. 2015b). In both Colorado and northern California, mountain lions were found to increase the frequency of kills to compensate for kleptoparasitism by black bears (*Ursus americanus*) (Elbroch et al. 2015a). Mountain lions of Patagonia suffered kleptoparasitism by scavengers in the form of Andean condors (*Vultur gryphus*), resulting in reduced handling time at kills, abandonment of kills, and increased frequency of kills (Elbroch et al. 2013b). Similarly, ravens (*Corvus corax*) were revealed to scavenge up to 75% of the edible biomass of kills made by small grey wolf (*Canis lupus*) packs (2-3 individuals) in the Yukon, thereby increasing kill rates in those packs (Kaczensky et al. 2005). Mountain lions, being solitary ambush hunters, are seemingly limited in their ability to balance both the consumption and defense of kills from scavengers and kleptoparasites (Elbroch et al. 2015a, Elbroch et al. 2013b, Husseman et al. 2003). Thus, mountain lions may need to increase kill rates to counteract biomass acquisition loss. In contrast, Amur tigers (*Panthera tigris altaica*), a solitary felid who also ambushes prey, demonstrated higher empirical kill rates than energetically predicted despite little to no

interspecific competition (Miller et al. 2014). Amur tigers were thought to be using an optimal foraging strategy, in which tigers were actively minimizing risk of starvation instead of simply meeting daily basal energetic minimums. By increasing their kill rates (thereby increasing overall mean consumption rate (kg/day)), Amur tigers were thought to be reducing their chances of starvation over a given time (essentially killing as often as possible), thus prey encounter rate appeared to be a driving factor in determining kill rates (Miller et al. 2014). This coincides with the notion that solitary felids are random predators that kill prey as available within normal prey size limits (Husseman et al. 2003).

Mountain lion kill rates have been shown to be variable per age, sex, and reproductive status though the direction and magnitude of variation is inconsistent among various studies (Knopff et al. 2010 and Pierce et al. 2000). Females with kittens often have higher predation rates compared to solitary mountain lions due to higher energetic requirements as kittens grow (Knopff et al. 2010). Adult males often have higher kill rates than adult females, although Knopff et al. (2010) found that though males in their study had lower kill rates, prey size and consequently, biomass acquisition was higher. This may stem from the larger size of males allowing for the take of larger prey with less risk than smaller females (Sunquist and Sunquist 1989). Subadults usually kill less often and rely more on nonungulate prey items compared to adults, possibly due to lack of experience (Murphy 1998). Risk of injury for subadults during a predation event may lead to choosing prey that can be adequately handled (Pierce et al. 2000).

Utilizing kill data obtained from GPS-collared mountain lions of Colorado, Wyoming, and Patagonia, I investigated the impacts of: 1) mountain lion sex, 2) mountain lion age, 3) accompaniment of offspring with mountain lion females, 4) prey weight, and 5) the presence of bears (habitual kleptoparasites) throughout study periods. I predicted that time between kills

would decrease for: mountain lion males relative to females due to their larger size; mountain lion juveniles relative to adults due to their hunting inexperience forcing selection of smaller prey; mountain lion females with offspring relative to those without offspring due to increase energetic demands; and when bears were active on the landscape relative to when they were inactive due to kleptoparasitism. I also predicted that time between kills would increase as prey size increased, assuming that mountain lions would target larger prey thus being satiated for longer periods.

## **Methods**

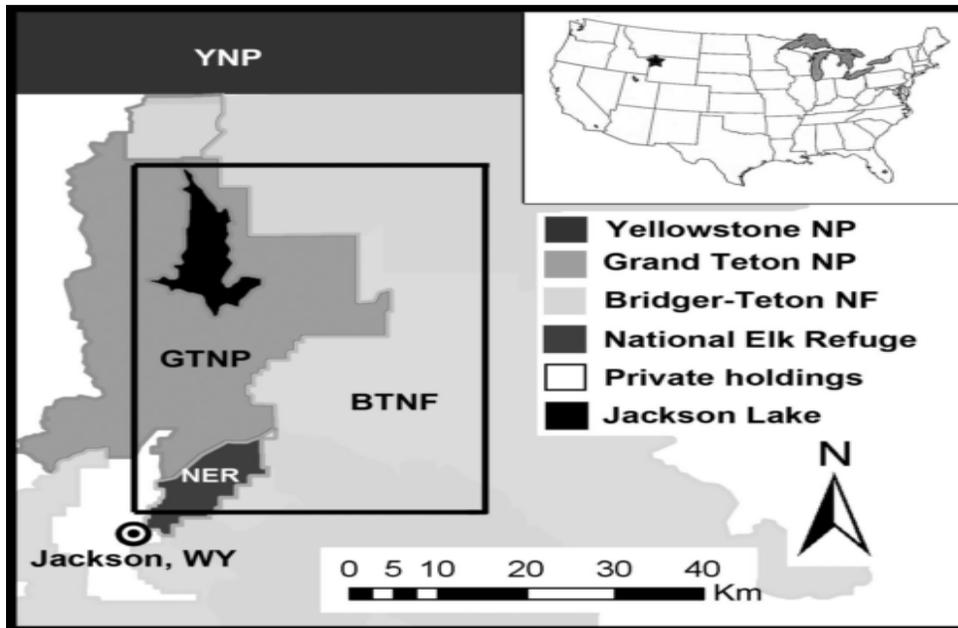
### *Study Areas*

The first study area was in western Colorado near the town of De Beque, and covered an area approximately 1100 km<sup>2</sup> (Elbroch et al. 2014). The study area supported two native ungulate species, elk (*Cervus canadensis*) and mule deer (*Odocoileus hemionus*), and large numbers of cattle (*Bos primigenius*). No predation on cattle occurred during the study period. Other common prey species included American beavers (*Castor canadensis*) and North American porcupines (*Erethizon dorsatum*), and competitive scavengers regularly detected at mountain lion kills included American black bears, coyotes (*Canis latrans*), Golden eagles (*Aquila chrysaetos*), and common gray foxes (*Urocyon cinereoargenteus*).

The second study area encompassed portions of the Southern Yellowstone Ecosystem (approximately 2,300 km<sup>2</sup>) (Fig. 1). These portions included Grand Teton National Park (United States Park Service), the National Elk Refuge (United States Fish and Wildlife Service), and the Bridger-Teton National Forest (United States Forest Service) north of the town of Jackson, Wyoming. The study area supported native ungulate species such as elk, mule deer, moose, bison (*Bison bison*), pronghorn, bighorn sheep, and a very small number of white-tailed deer

(*Odocoileus virginianus*). Other common prey species included American beavers and American porcupines among other small prey items. The study area also supported a diverse community of carnivores including wolves, black bears, grizzly bears (*Ursus arctos*), coyotes (*Canis latrans*), and red foxes (*Vulpes vulpes*).

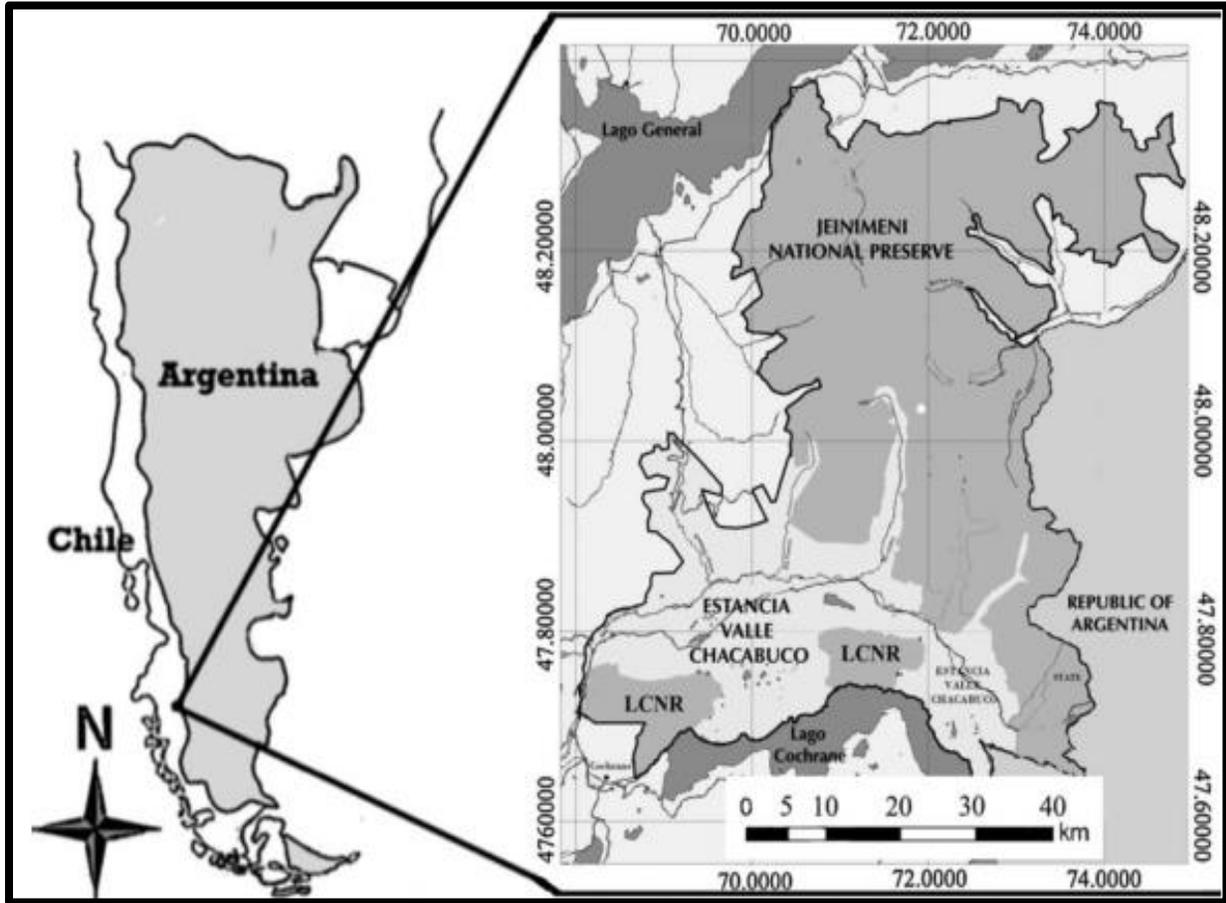
Figure 1. Map of Wyoming study area (Elbroch 2013a).



The third study area was in the southern portion of Chile's Aysén District, north of Lago Cochrane in central Chilean Patagonia (approximately 1,200 km<sup>2</sup>) (Fig. 2). The study area included the 69 km<sup>2</sup> Lago Cochrane National Reserve, the 690 km<sup>2</sup> private Estancia Valle Chacabuco, and approximately 440 of the 1611 km<sup>2</sup> Jeinimeni National Reserve. The study area supported two native ungulate species, guanacos (*Lama guanicoe*), huemul (*Hippocamelus bisulcus*). Other common prey included domestic exotic sheep (*Ovis aries*) and European hares (*Lepus europaeus*). Common scavengers included Culpeo foxes (*Lycalopex culpaeus*) and several birds, including Andean condors, southern (*Polyborus plancus*) and Chimango caracaras

(*Milvago chimango*), and black-chested buzzard eagles (*Geranoaetus melanoleucus*) (Elbroch et al. 2013b). Unlike Colorado and Wyoming, there are no bear species present on the landscape.

Figure 2. Map of Patagonia study area (Elbroch et al. 2012).



### Data Collection

Mountain lions of each study area were captured and fitted with GPS collars programmed to drop location data. In Colorado, 10 mountain lions were captured and studied, 7 in Patagonia, and 15 in Wyoming. GPS locations were investigated when a mountain lion had remained in place (within 150 m of subsequent GPS locations) for  $\geq 4$  hours in Colorado and Patagonia, and  $\geq 8$  hours in Wyoming. Subsequent field investigations were conducted by CyberTracker-certified field observers who systematically searched to locate and identify prey remains. For all three study areas, age-specific prey weight was estimated through known literature and growth

rates using simple linear regressions of weight and age (Elbroch et al. 2014). I did not utilize kill data in which the time between kills was greater than 35 days.

### *Analysis Methods*

Utilizing R statistical programming language, I performed multiple linear regression and model selection to find the most parsimonious and biologically sound model that best described sources of variation in time between kills for 2,236 mountain lions kills (R Core Team 2017). All factors investigated and used for analysis were categorical except for time between kills and prey weight which were continuous (kg). Time between kills was measured as the difference in days between the start of one kill and the start of the subsequent kill of a mountain lion. For sex, mountain lions were either male or female. For age, mountain lions were either adults ( $\geq 2$  years age) or juveniles ( $<2$  years age). For presence of offspring, mountain lions were either females with offspring or females without. For bear season, mountain lion kills were documented as either occurring during periods of bear activity on the landscape or not. Bear activity was defined as the first time in the year a bear species was present at a mountain lion kill and the last time in the year. In addition, I used study area as a factor to determine differences in time between kills and prey weights among Colorado, Wyoming, and Patagonia. Utilizing stepwise model selection methods, I ran univariate linear models for each factor with a cut-off p-value of 0.25 for inclusion into the final multivariate model. Individual mountain lions were included as a random effect in all univariate and multivariate modeling to account for variation in prey availability among mountain lions and for variable number of samples from different animals (Gillies et al. 2006). During final multivariate model selection, factors were omitted if p-values were greater than 0.05 when included among other factors. Final multivariate models were chosen based on a delta AIC scores within  $>2$  of one another. Univariate modeling was also performed to

investigate differences in prey weight among all factors. Prey species composition was also investigated. Further analysis was conducted to determine the effects of bear season within the study areas of Colorado and Wyoming where bear species are present, separate from Patagonia where bear species are not present. Additional analysis was conducted to determine the strength of effects

## **Results**

### *Kill and Consumption Rates*

A total of 32 mountain lions were observed and their kills recorded (Colorado = 10, Wyoming = 15, and Patagonia = 7). Kill rates were calculated as total number of prey killed per mountain lion per length of monitoring period and consumption rates were calculated as total kg of biomass of prey weight per mountain lion per length of monitoring period (see Appendix Table). A monitoring period was identified as a period of continuous observation of a mountain lion's kills, in which time between kills did not exceed 35 days. A total of 38 monitoring periods were recorded (Colorado = 10, Wyoming = 21, and Patagonia = 7). (The mean monitoring period length for mountain lions was 268 days in Colorado, 417 days in Wyoming, and 218 days in Patagonia. Mean kill rate (kill per day) for mountain lions was 0.17 in Colorado, 0.16 in Wyoming, and 0.22 in Patagonia. Mean consumption rate (Kg of prey per day) for mountain lions was 11.2 in Colorado, 14.9 in Wyoming, and 12 in Patagonia.

### *Time Between Kills*

Based on the established criterion I used for model selection, the 'best' model (Table 3, AIC = 13347.56,  $R^2 = 0.12$ ) included all factors except for mountain lion sex and the study areas of Wyoming and Colorado (Table 2). The random effect for individual mountain lions accounted

for approximately 10% of the explained variance (variance for the random effect = 2.4 and variance for the residual = 22). Despite the study area Patagonia having a p-value of 0.058, I decided to include it in the final model because of the closeness of its significance (p-value of 0.05). Time between kills between mountain lion sexes and the study areas of Colorado and Wyoming were found not to be significantly different for my analysis. Time between kills was reduced (-1.37 days) for mountain lion juveniles relative to adults, for females with offspring (-2.18 days) relative to those without, for mountain lions killing during bear season relative to not (-1.15 days), and for mountain lions in Patagonia (-1.48 days). Time between kills was found to be increased (+0.01 days) per kg of prey weight. For example, when only accounting for prey weight as a factor, the time between killing an adult male elk weighing approximately 700 kg and another prey item would be estimated at 7 days. In comparison, the time between killing an adult male mule deer weighing approximately 150 kg and another prey item would be estimated at 1.5 days, a difference of 5.5 days, based on the factor of prey weight.

Table 1. Data summary of univariate analysis sorted by AIC scores. Time between kills was measured as the difference in days between the start of one kill and the start of the subsequent kill of a mountain lion. For sex, mountain lions were either male or female, categorically described as 0 or 1 respectively. For age class, mountain lions were either adults (> 2 years age) or juveniles (<2 years age), categorically described as 0 or 1 respectively. For presence of offspring, mountain lions were either females without offspring or females with offspring, categorically described as 0 or 1 respectively. For bear season, mountain lion kills were documented as either occurring during periods of bears being vacant from the landscape or during periods of bears being present on the landscape, categorically described as 0 or 1

respectively. Bear activity was defined as the first time in the year a bear species was present at a mountain lion kill and the last time in the year.

Variable(s)	Est. Coeff.	Std. Error	P-value	AIC
Prey.Weight	0.01	0.001	2E-16	13392.87
Bear.Season	-1.50	0.25	2.25E-09	13430.74
Offspring	-1.58	0.38	0.0000311	13447.02
Cougar.AgeClass	1.29	0.61	0.0381	13459.08
PAT	-1.27	0.65	0.063	13459.97
StudyArea	-	-	-	13460.87
Cougar.Sex	0.68	0.62	0.283	13462.36
Null	-	-	-	13462.44
CO	0.64	0.62	0.314	13462.51
WY	0.28	0.58	0.635	13463.46

Table 2. Data summary of best multivariate model (Time Between Kills ~), AIC = 13347.56.

Time between kills was measured as the difference in days between the start of one kill and the start of the subsequent kill of a mountain lion. For age, juveniles (<2 years age) or mountain lions were either adults (> 2 years age), categorically described as 0 or 1 respectively. For presence of offspring, mountain lions were either females without offspring or females with offspring, categorically described as 0 or 1 respectively. For bear season, mountain lion kills were documented as either occurring during periods of bears being vacant from the landscape or during periods of bears being present on the landscape, categorically described as 0 or 1 respectively. Bear activity was defined as the first time in the year a bear species was present at a mountain lion kill and the last time in the year.

Variables	Est. Coeff.	Std. Error	P-value	Lower CI	Upper CI
Cougar.AgeClass	1.37	0.64	0.037	0.11	2.63
Offspring	-2.18	0.38	1.33882E-08	-2.92	-1.44
Prey.Weight	0.01	0.001	2E-15	0.01	0.01
PAT	-1.48	0.75	0.058	-2.96	-0.01
Bear.Season	-1.15	0.25	5.97945E-06	-1.65	-0.66

### *Prey Composition and Mean Weight*

Prey composition was conducted for all three study areas. For Colorado, mule deer were most preyed upon followed by elk, this relationship being vice versa for Wyoming. For Patagonia, guanaco was most preyed upon followed by introduced European hares. Prey composition percentages were also compiled for mountain lion juveniles. Ungulate adults (> 2 years age) were targeted less often by mountain lion juveniles, whose diet consisted more of ungulate juveniles (< 2 years age). Furthermore, almost half of the diet of mountain lion juveniles consisted of small prey items (0.44).

Differences in mean prey weight (kg) among factors were also estimated to investigate the potential for selectivity regarding prey items. Evidence was shown for difference in prey weight between Patagonia (Mean = 58.4, Standard Deviation = 13.45) and Wyoming (p-value = 0.01) but not Patagonia (Mean = 58.4, Standard Deviation = 13.45) and Colorado (Mean = 69.5, Standard Deviation = 14.55) (Figure 3). Some evidence was shown for difference in mean prey weight between Wyoming and Colorado (p-value = 0.06). There was no significant difference between prey weight for mountain lion sex (p-value = 0.36). However, there was evidence of difference in mean prey weight for mountain lion age (lower for juveniles at p-value = <0.05) (Figure 4), presence of offspring (higher with offspring at p-value = <0.05) (Figure 5), and bear season (lower during bear season at p-value = <0.05) (Figure 6).

Figure 3. Mean Prey Weight ~ Study Area with 95% CIs. Study areas included Colorado, Wyoming, and Patagonia.

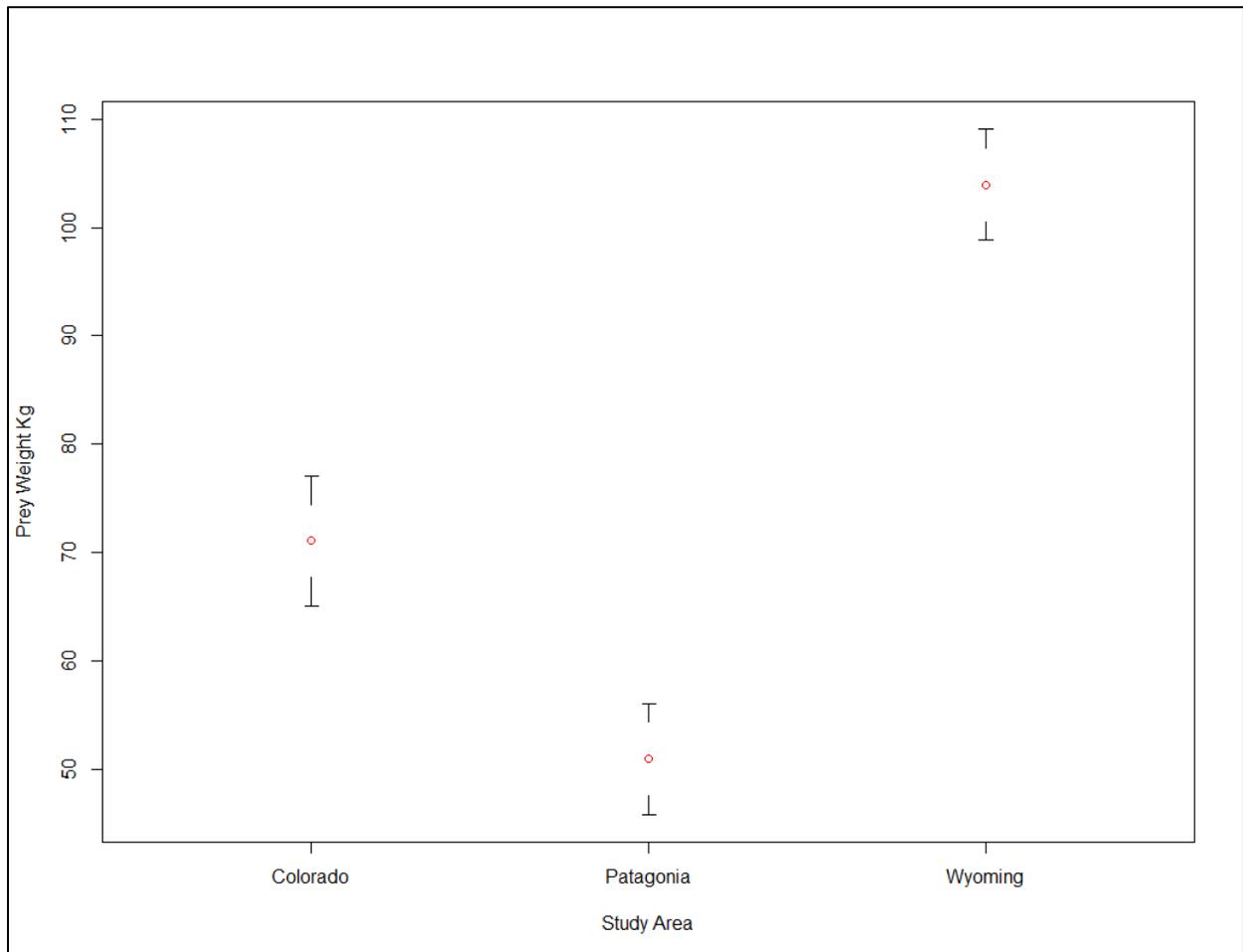


Figure 4. Mean prey weight ~ Mountain Lion age class with 95% CIs. For age, mountain lions were either adults (> 2 years age) or juveniles (<2 years age) and categorically described as 0 or 1 respectively.

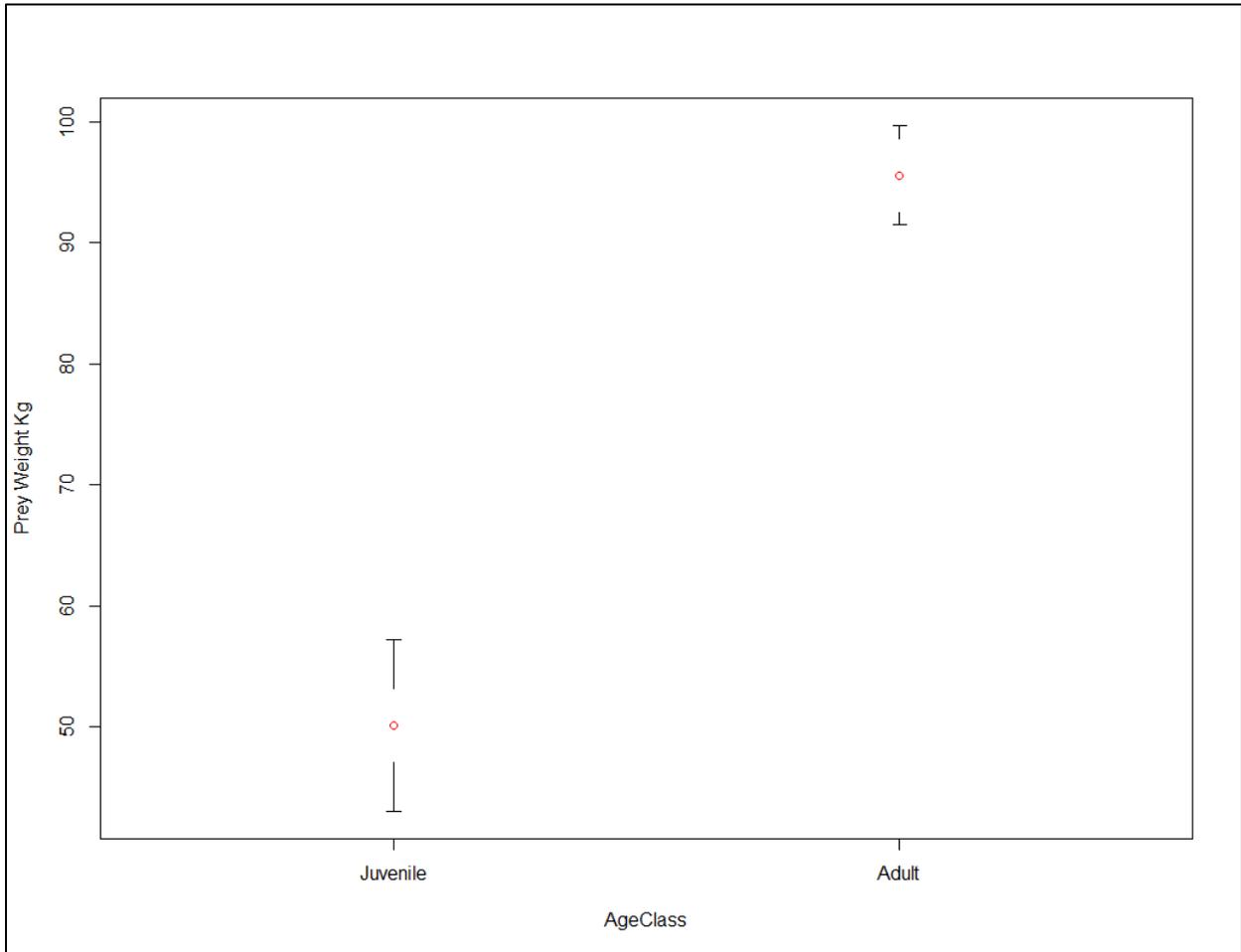
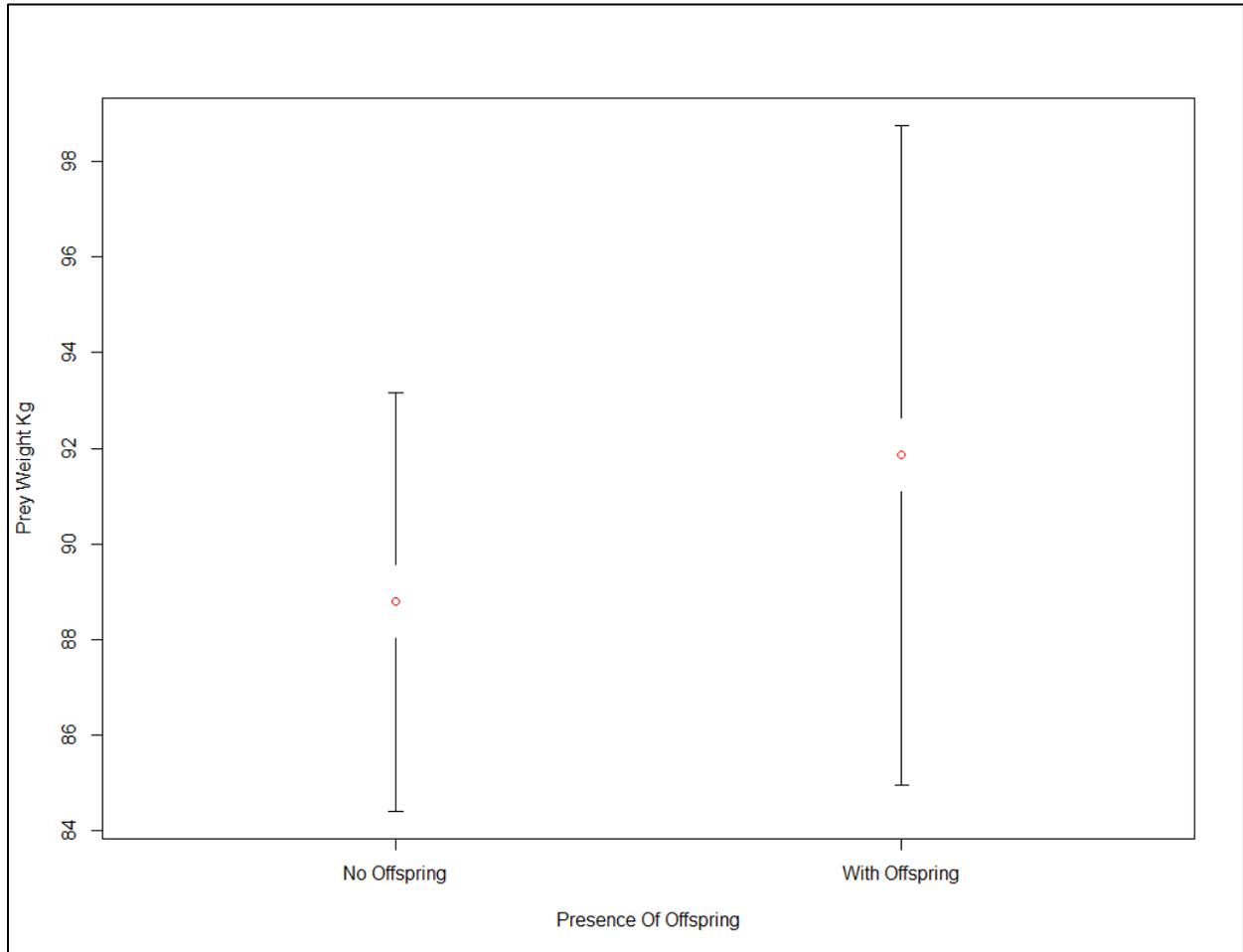


Figure 5. Mean prey weight ~ Presence of offspring with mountain lions with 95% CIs. For presence of offspring, mountain lions were either females without offspring or females with offspring, categorically described as 0 or 1 respectively.



### *Bear Season*

Separate analyses for Colorado and Wyoming were conducted to isolate the potential effect of kleptoparasitism because of bear presence. Although there is a documented kleptoparasite in Patagonia in the form of the Andean condor, the dataset provided was not adequate to determine their presence (Elbroch et al. 2013b). Time between kills was found to be significantly reduced in Colorado (-3.4 days) and Wyoming (-1.2 days) at p-values of <0.05 for both study areas during bear season. Mean prey weight was found to be significantly lower in both Colorado and Wyoming (p-value for both <0.05) for kills made during a bear season than otherwise (Figure 6). Excluding small prey items, prey composition percentages regarding ungulate age classes during bear season and no bear season were calculated (Table 4). In Colorado, ungulate juveniles were preyed upon more often during bear season (0.55) than during no bear season (0.43). In Wyoming, ungulate juveniles were preyed upon more so than adults regardless of bear presence, however, selection increased during bear season.

Table 3. Data summary for Time Between Kills ~ Bear Season in Colorado and Wyoming. Time between kills was measured as the difference in days between the start of one kill and the start of the subsequent kill of a mountain lion. For bear season, mountain lion kills were documented as either occurring during periods of bears being vacant from the landscape or during periods of bears being present on the landscape, categorically described as 0 or 1 respectively. Bear activity was defined as the first time in the year a bear species was present at a mountain lion kill and the last time in the year.

<b>Study Area</b>	<b>Est. Coeff.</b>	<b>Std. Error</b>	<b>P-value</b>
CO	-3.4	0.47	4.79E-12
WY	-1.2	0.32	0.000264

Figure 6. Mean Prey Weight ~ Bear Season in Colorado and Wyoming with 95% CI. For bear season, mountain lion kills were documented as either occurring during periods of bears being vacant from the landscape or during periods of bears being present on the landscape, categorically described as 0 or 1 respectively. Bear activity was defined as the first time in the year a bear species was present at a mountain lion kill and the last time in the year.

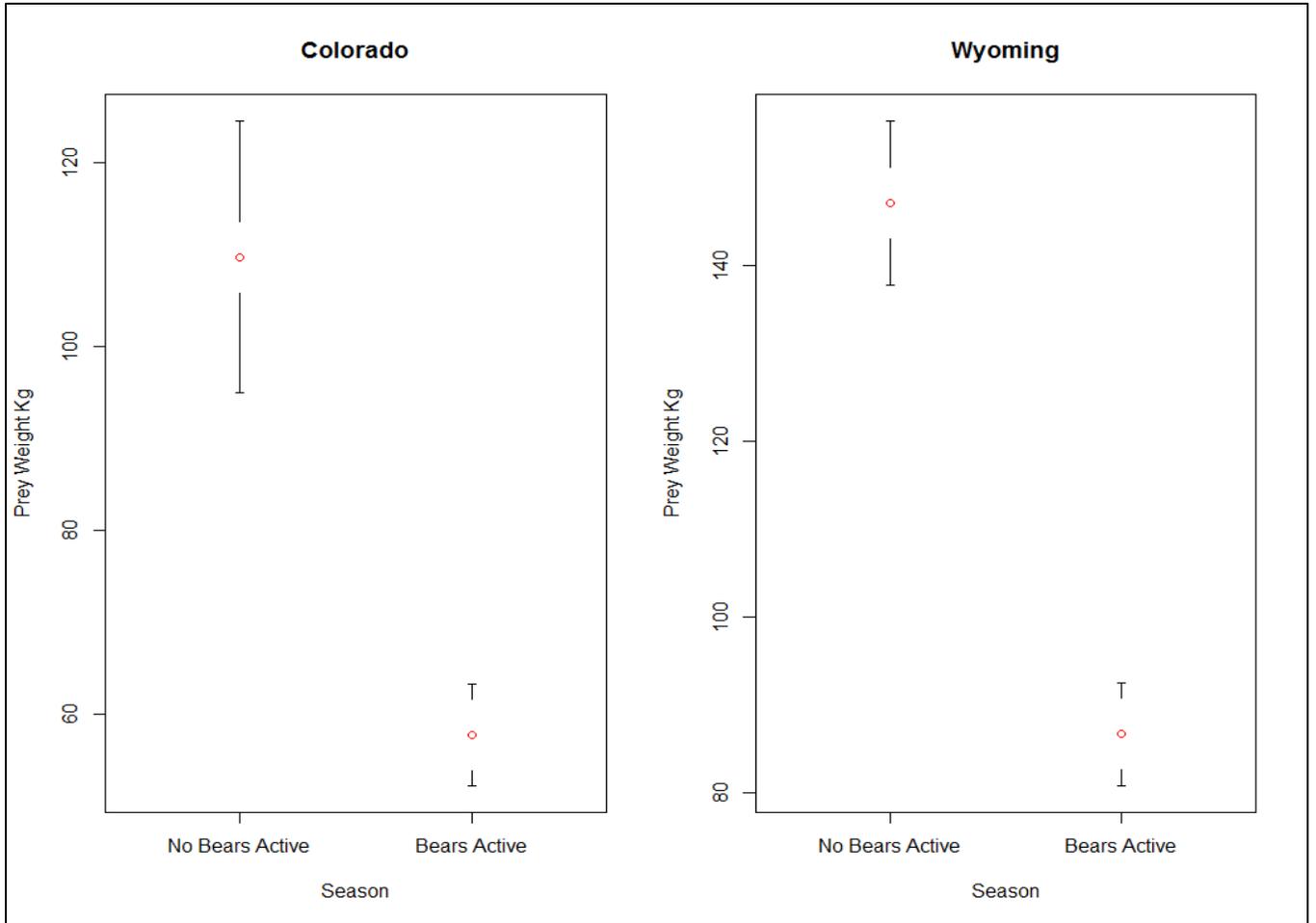


Table 4. Prey composition percentage for Bear Season and No Bear Season. For bear season, mountain lion kills were documented as either occurring during periods of bears being vacant from the landscape or during periods of bears being present on the landscape, categorically described as 0 or 1 respectively. Bear activity was defined as the first time in the year a bear species was present at a mountain lion kill and the last time in the year.

Study Area	Prey			%
CO Bear Season	Ungulate Juvenile			0.55
	Ungulate Adult			0.45
CO No Bear	Ungulate Juvenile			0.43
	Ungulate Adult			0.57
WY Bear Season	Ungulate Juvenile			0.62
	Ungulate Adult			0.38
WY No Bear	Ungulate Juvenile			0.58
	Ungulate Adult			0.42

*Top Model Effect Sizes*

For the effect of bear presence on the landscape, the effect of bear activity was much greater than that of no bear activity, with a much steeper slope (Figure 7). For the effect of accompaniment of offspring with mountain lion females, the effect of offspring was much greater than that of no offspring, with a steeper slope (Figure 8). For the effect of study area, the effects of Patagonia and Wyoming had similar slopes, with Colorado having a steeper slope (Figure 9). The effect size of Patagonia was greater than Colorado and Wyoming study areas. For the effect of mountain lion age, the effect of being a mountain lion juvenile was greater than that of being a mountain lion adult, with a steeper slope (Figure 10).

Figure 7. Effect size of presence of bears on the landscape or not on cougar kill rates. For bear season, mountain lion kills were documented as either occurring during periods of bears being vacant from the landscape or during periods of bears being present on the landscape, categorically described as 0 or 1 respectively. Bear activity was defined as the first time in the year a bear species was present at a mountain lion kill and the last time in the year.

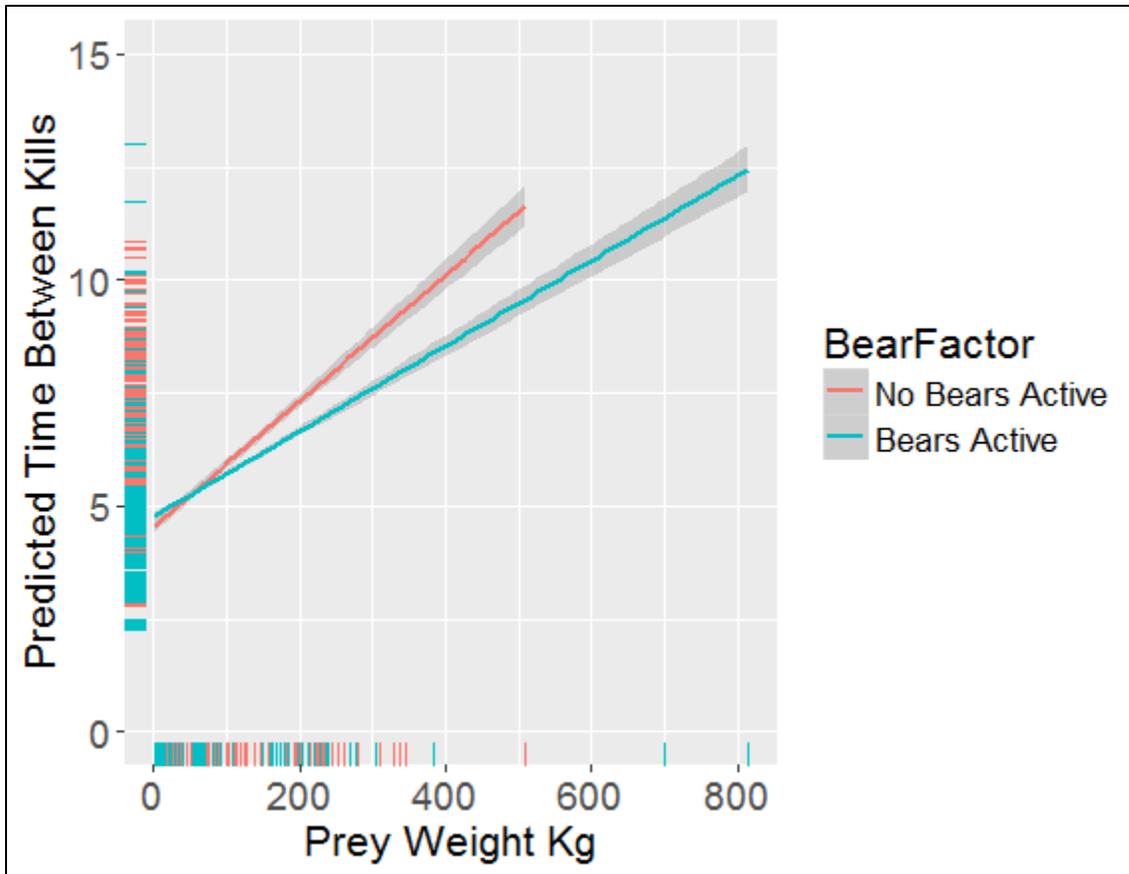


Figure 8. Effect size of accompaniment of offspring with mountain lion females on mountain lion kill rates. For presence of offspring, mountain lions were either females without offspring or females with offspring, categorically described as 0 or 1 respectively.

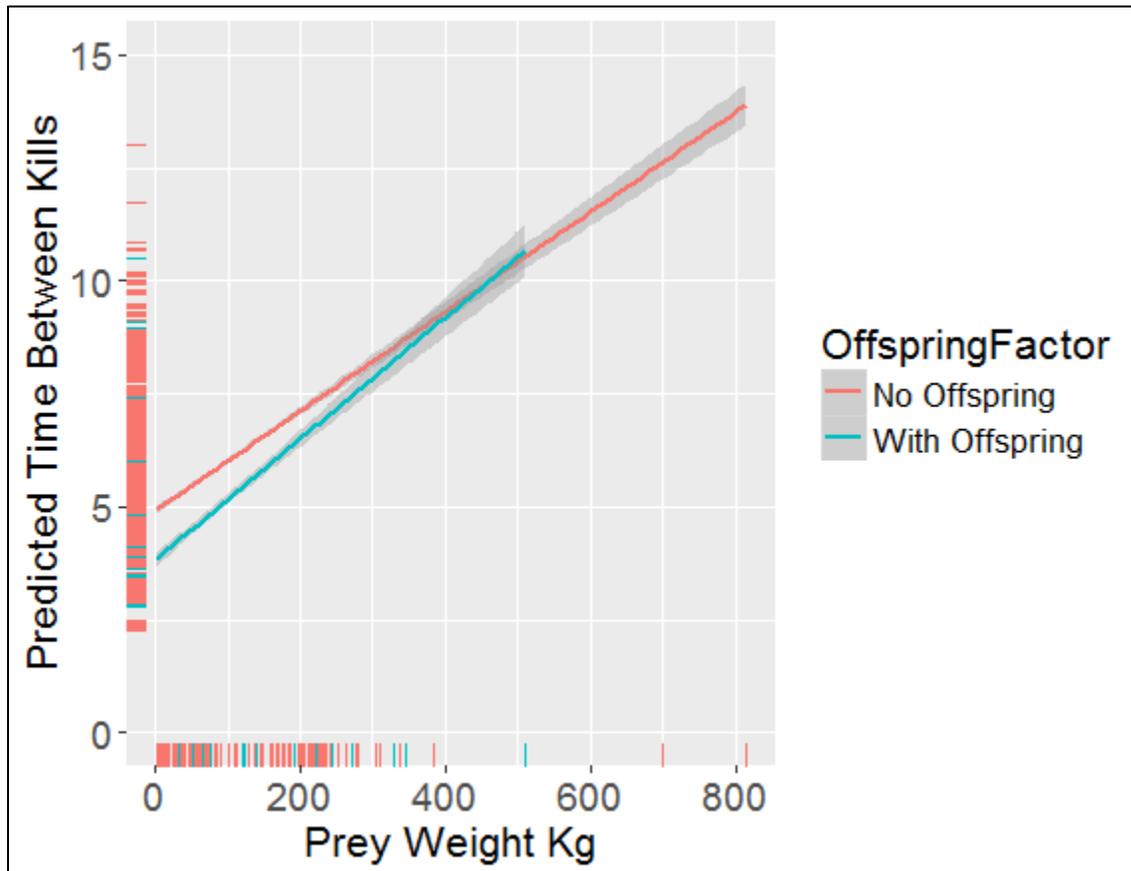


Figure 9. Effect size of study area on mountain lion kill rates. Study areas included Colorado, Wyoming, and Patagonia.

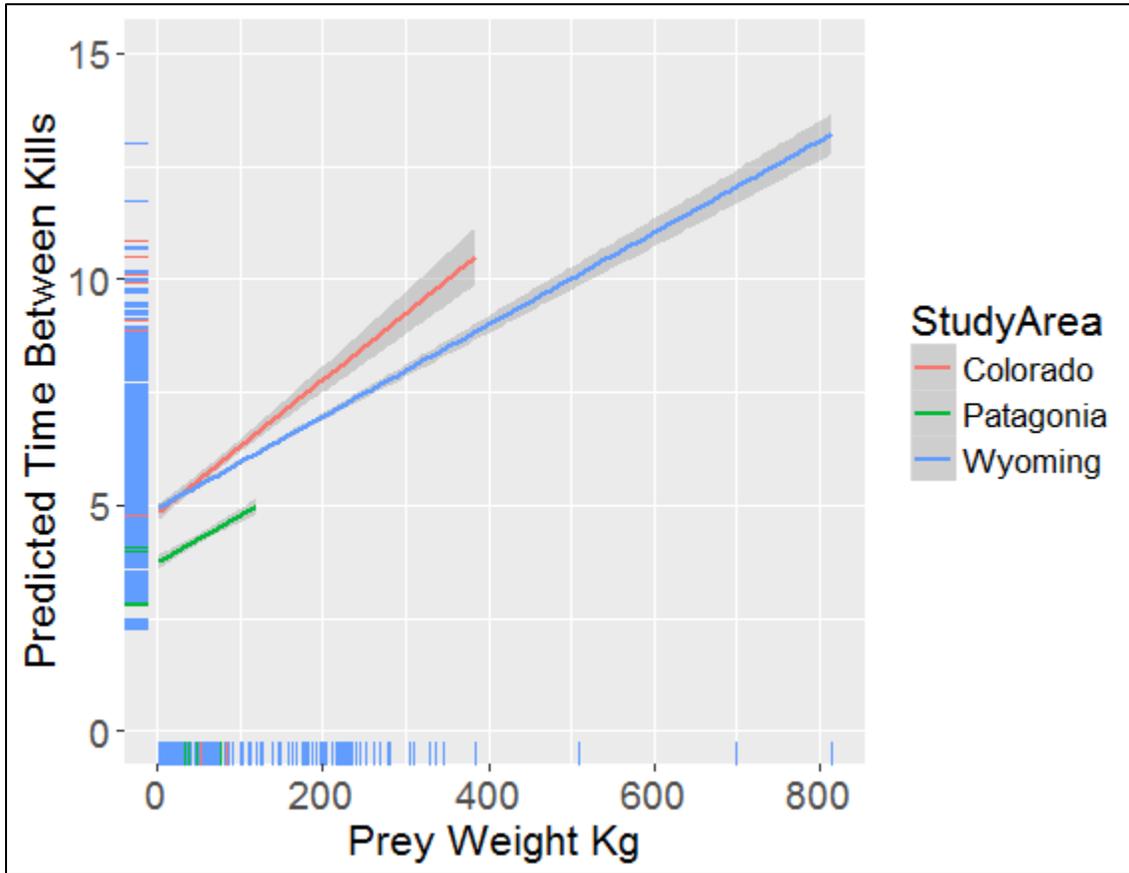
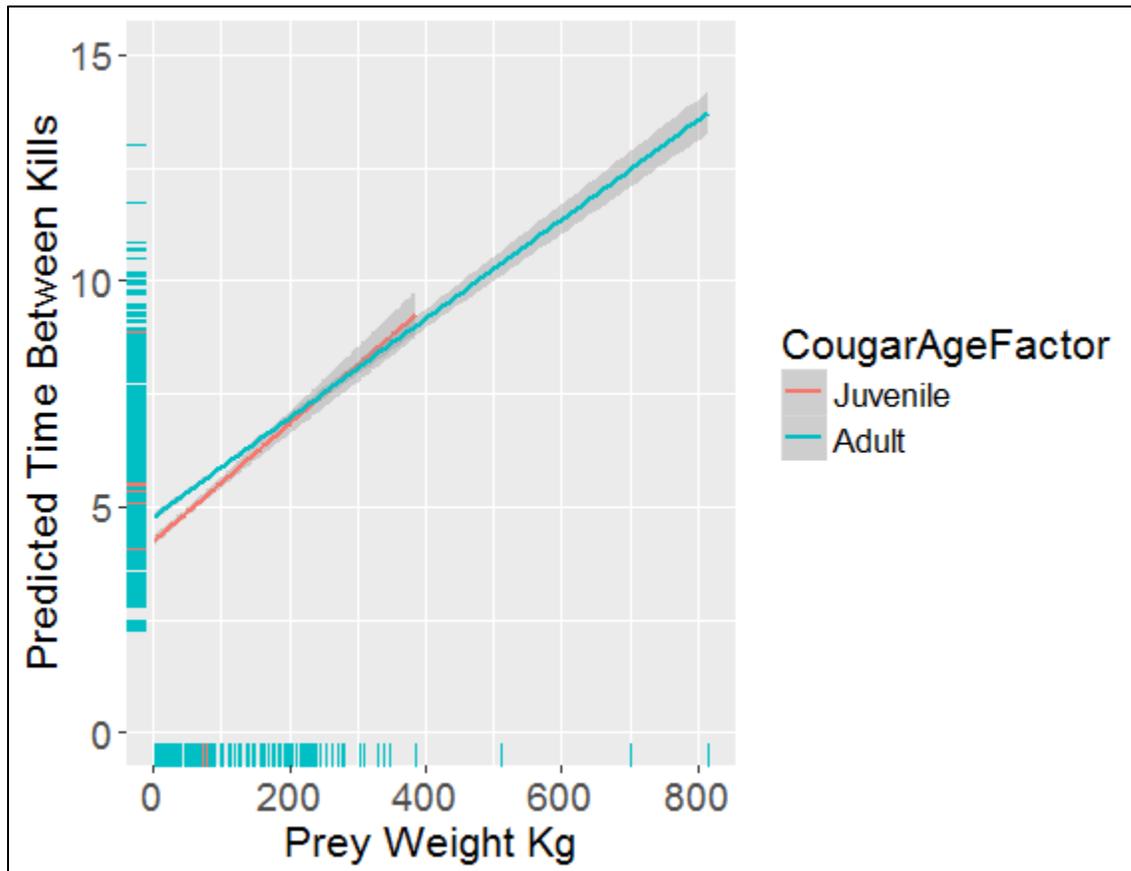


Figure 10. Effect size of mountain lion age class on mountain lion kill rate. For age, mountain lions were either adults (> 2 years age) or juveniles (<2 years age) and categorically described as 0 or 1 respectively.



## **Discussion**

### *Mountain Lion Intraspecific Variation*

Time between kills and mean prey weight were found to be not significantly different between mountain lion males and females. This seems to coincide with variation in reported kill rates between mountain lion sexes (Knopff et al. 2010). An important factor that I was not able to investigate with this study was weight of each individual mountain lion. Mountain lion weights may be an important determinant regarding size of prey killed, as larger individuals may be able to hunt larger prey and thus kill less often because of higher energetic intake per kill (Knopff et al. 2010). However, time between kills for mountain lion females with offspring was shorter while also having a higher mean prey weight than mountain lions with no offspring. This seems to lend credence to the notion that with increased family size, there is an increased need to kill more often and to perhaps target larger prey items to maximize energetic intake per kill. For this study, I did not evaluate the number offspring accompanied per females, inferring that results may be conservative and that the effect of numerous accompanying offspring is likely to be greater.

Mountain lion juveniles had both significantly shorter time between kills and mean prey weight relative to adults. Over 40% of prey composition of mountain lion juveniles consisted of small prey and over 60% of ungulate prey were juveniles. This appears to show evidence that mountain lion juveniles were actively hunting prey that were smaller in size and weight, and thus killing more frequently than adult mountain lions. This could perhaps coincide with the notion that less hunting experience lends to more limited prey on the menu for younger mountain lions.

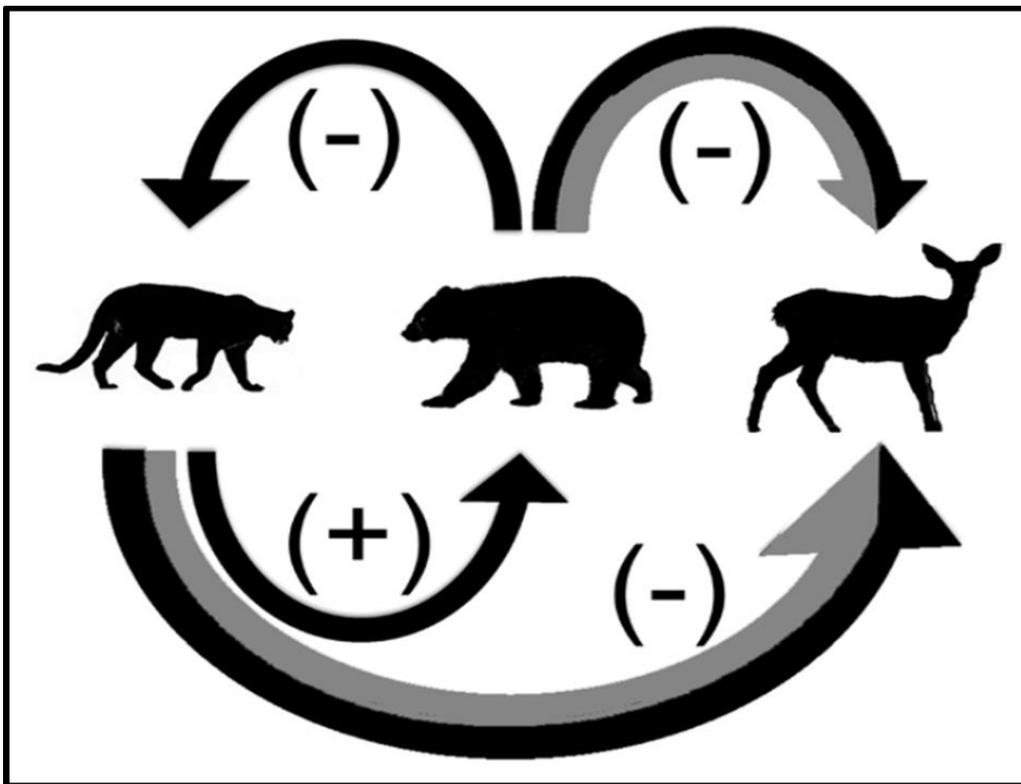
### *Bear Season*

Though bear presence on the landscape seems to have influence on mountain lion kill rates, there could be additional ecological occurrences that may equally explain the observed effect. Bear presence on the landscape is also correlated with the period of the year in which ungulate populations experience a birth pulse (Elbroch et al. 2015a, Lima and Dill 1990). The mean prey weight of kills made during a bear season in both Colorado and Wyoming were nearly half that of kills made during no bear season in those same study areas (Figure 6). Additionally, ungulate juveniles were increasingly targeted during bears seasons in both Colorado and Wyoming, although this relationship was less dramatic in Wyoming but more so in Colorado (Figure 6). From these results, it seems that seasonal patterns of predation may be linked to prey vulnerability and increased occurrence during temporal shifts in reproductive physiology and associated behavior (Lima and Dill 1990). Mountain lions may select for more ungulate juveniles (< 2 years age) during months when numbers of ungulate juveniles are at their highest proportion in the population (Molinari-Jobin et al. 2004). Knopff et al. (2010), found that mountain lions increased predation on smaller juvenile prey during the summer season. Due to the increase of available neonates and juveniles, predation on ungulate populations increased during the summer. This increase in kill rate may coincide with a decrease in time between kills (less biomass acquisition and satiation time) due to a higher predation of smaller prey item.

Despite this potentially confounding factor, bear species have been shown to negatively affect kill rates of mountain lions in other studies (Elbroch et al. 2015a). If results from this study are taken at face value, bear presence may impact kill rates of mountain lions where they are sympatric throughout their range. This relationship could indirectly impact prey populations in a negative manner, through the increased impact of predation by predators who must kill more to meet their energetic requirements not met because of kleptoparasitism (Fig. 11). Although no

bear species exist in Patagonia, there appears to be a kleptoparasitic relationship between mountain lions and Andean condors (Elbroch et al. 2013b). Unlike bear species who pose more of a seasonal threat, Andean condors occur year-round but are linked with specific habitat types (open vs. forested). Despite not accounting for kleptoparasitism in Patagonia for this analysis, there may be a relationship that exists, with current time between kill estimates being conservative.

Figure 11. Chart depicting the indirect effect of a scavenger on prey populations through competition with another predator. For Colorado and Wyoming, the scavenger could be a bear species, while in Patagonia, the scavenger could be the Andean condor.



*Management Implications*

This study shows some evidence that younger mountain lions and females with accompanying offspring seem to hunt in a selective manner. This knowledge may be applicable to mountain lion harvest management, where the impact of predation on certain ungulate populations are concerning. Shifts toward the harvesting of younger mountain lions or reducing the proportion of females with offspring in a population may reduce the impacts of predation. Additional to management considerations are the impacts of scavenger communities, in this case the impacts of bear species on mountain lion kill rates. Bears have a direct impact of predation on ungulates and may have an additional indirect impact as well, through the increasing of mountain lion kill rates because of bear kleptoparasitism (Elbroch et al. 2015a). Increasing bear harvest in areas where mountain lion and bear species occurrence is sympatric, may further reduce impacts of predation on an ungulate population.

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## **Appendix**

Data summary of Kill and Consumption Rates. A total of 32 mountain lions were observed and their kills recorded (Colorado = 10, Wyoming = 15, and Patagonia = 7). Kill rates were calculated as total number of prey killed per mountain lion per length of monitoring period and consumption rates were calculated as total kg of biomass of prey weight per mountain lion per length of monitoring period (see Appendix Table). A monitoring period was identified as a period of continuous observation of a mountain lion's kills, in which time between kills did not exceed 35 days. A total of 38 monitoring periods were recorded (Colorado = 10, Wyoming = 21, and Patagonia = 7). (The mean monitoring period length for mountain lions was 268 days in Colorado, 417 days in Wyoming, and 218 days in Patagonia. Mean kill rate (kill per day) for mountain lions was 0.17 in Colorado, 0.16 in Wyoming, and 0.22 in Patagonia. Mean consumption rate (Kg of prey per day) for mountain lions was 11.2 in Colorado, 14.9 in Wyoming, and 12 in Patagonia.

CatID	Sex	Study Area	Date of Monitoring Period	Length of Monitoring Period	# of Kills	Kills per Day	Kg of Prey	Kg of Prey per Day
P01	Male	Colorado	Mar 2011- Feb 2012	343	85	0.25	4901	14.3
P03	Male	Colorado	Mar 2011- Dec 2011	282	52	0.18	3449	12.2
P05	Male	Colorado	June 2011- July 2011	27	6	0.22	251	9.3
P06	Male	Colorado	June 2011- Nov 2011	139	28	0.20	1980	14.1
P07	Female	Colorado	Nov 2011- Apr 2013	511	71	0.14	8832	13.4
P08	Female	Colorado	Feb 2012- Dec 2012	313	39	0.12	3040	9.7
P09	Female	Colorado	Feb 2012- Mar 2013	393	57	0.15	4209	10.7
P10	Female	Colorado	Mar 2012- Nov 2012	240	51	0.21	2908	12.1
P12	Female	Colorado	Mar 2012- Aug 2012	165	16	0.10	962	5.8
P13	Male	Colorado	Mar 2012- Dec 2012	289	40	0.15	2759	10.3
F01	Female	Patagonia	Apr 2008- Oct 2008	202	39	0.19	2873	14.2
F02	Female	Patagonia	July 2009- Sept 2009	40	9	0.23	616	15.4
F03	Female	Patagonia	June 2009- Nov 2009	161	48	0.30	3496	21.7
F04	Female	Patagonia	Jun 2009- July 2010	414	108	0.26	4402	10.6
F05	Female	Patagonia	Sep 2009- Mar 2010	203	52	0.26	814	4.0
M02	Male	Patagonia	June 2009- Dec 2009	192	11	0.06	1265	6.6
M03	Male	Patagonia	June 2009- May 2010	318	71	0.22	3721	11.7
F109	Female	Wyoming	Apr 2012- July 2012	99	13	0.13	1241	12.5
F109	Female	Wyoming	Dec 2012- Dec 2013	376	57	0.15	8080	21.5
F109	Female	Wyoming	Nov 2014- Aug 2016	647	87	0.13	10911	16.9
F97	Female	Wyoming	Nov 2012- Mar 2013	127	27	0.21	1009	7.9
F99	Female	Wyoming	Sep 2014- Nov 2014	85	19	0.22	495	5.8
F47	Female	Wyoming	Dec 2012- Aug 2015	965	123	0.13	15018	15.6
F47	Female	Wyoming	Jan 2016- Nov 2016	304	65	0.21	5250	17.3
F49	Female	Wyoming	Mar 2013- Apr 2014	386	59	0.15	5004	13.0
F49	Female	Wyoming	Dec 2014- Oct 2016	659	111	0.17	7995	12.1
F51	Female	Wyoming	Mar 2012- Sep 2012	180	18	0.10	1272	7.1
F51	Female	Wyoming	Nov 2012- Mar 2014	499	83	0.17	10600	21.2
F57	Female	Wyoming	May 2012- June 2012	58	5	0.09	351	6.1
F61	Female	Wyoming	April 2012- May 2015	1137	214	0.19	25259	22.2
F61	Female	Wyoming	Dec 2015- Nov 2016	344	52	0.15	4273	12.4
F72	Female	Wyoming	Dec 2015- Oct 2016	301	86	0.29	6507	21.6
F90	Female	Wyoming	Mar 2016- Dec 2015	279	46	0.16	2613	9.4
F96	Female	Wyoming	Apr 2014- Nov 2015	574	82	0.14	5954	10.4
M29	Male	Wyoming	Nov 2012- Oct 2013	320	83	0.26	12213	38.2
M68	Male	Wyoming	Dec 2012- Sep 2013	253	43	0.17	3741	14.8
M62	Male	Wyoming	Apr 2012- Aug 2012	101	5	0.05	520	5.1
M85	Male	Wyoming	Dec 2013- Nov 2016	1078	184	0.17	23599	21.9

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