

**EFFECTS OF REPRODUCTIVE STATUS OF MOUNTAIN LIONS ON PREY
SELECTION OF MULE DEER AND WHITE-TAILED DEER IN
NORTHEASTERN WASHINGTON**

By

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ABSTRACT

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A significant and steady decline in mule deer and corresponding increase in white-tailed deer has occurred during the last 20 years throughout western North America. In northeastern Washington, disproportionate selection for mule deer by mountain lion during summer is the major limiting factor of mule deer population growth. One hypothesis predicts that mountain lions select for declining mule deer during summer because their primary prey (white-tailed deer) moved up in elevation and become sympatric with higher elevation mule deer –increasing the encounter probability between predator and prey (apparent competition). Another hypothesis predicts that only females, and especially females with kittens will select for mule deer during summer when most kittens are vulnerable to sexually selected infanticide (sexual segregation). I calculated prey use and estimated prey availability to test whether mountain lions selected for mule deer as a result of apparent competition or sexual segregation. When pooled into a single group, mountain lions selected for mule deer annually, in winter and in summer. However, the

most pronounced selection for mule deer was by females with kittens and occurred during summer. My results suggest disproportionate selection of mule deer by mountain lions is most pronounced by females with kittens and may be a result of sexual segregation by females with kittens to avoid potentially infanticidal immigrant males. Further, hunting regimes focusing on male harvest may exacerbate disproportionate selection for mule deer by causing females to move into higher elevation, low density prey areas.

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INTRODUCTION

A significant and steady decline in mule deer (*Odocoileus hemionus*) and corresponding increase in white-tailed deer (*Odocoileus virginianus*) has occurred throughout western North America over the last 40 years (Bleich & Taylor 1998; Gill 1999). In northeastern Washington, USA, local populations of mule deer are now outnumbered by white-tailed deer 4:1 (Robinson et al. 2002; Cooley et al. 2008), because of disproportionate selection by mountain lion (*Puma concolor*) for mule deer. Reducing the impacts of predation through sport hunting of carnivores like mountain lion, has been employed to mitigate prey population declines (Ballard et al. 2001; Connolly 1978). Robinson et al. (2002) found that selection for mule deer by mountain lion in a mule deer and white-tailed deer community was the major factor in mule deer population decline in southeastern British Columbia and northeastern Washington. Cooley et al. (2008) also reported significant selection for mule deer and selection against white-tailed deer during summer months in 2 other nearby study areas of northeastern Washington.

Both Robinson et al. (2002) and Cooley et al. (2008) proposed that mountain lions selected for declining mule deer during summer because their primary prey (white-tailed deer) moved up in elevation and became sympatric with higher elevation mule deer during summer – increasing the encounter probability between predator and prey (apparent competition hypothesis Holt 1977). This suggests mule deer may be relatively easier to kill than sympatric white-tailed

deer. In both cases sample sizes were too small to test for possible prey selection differences among sex and reproductive classes of mountain lions.

Another possible hypothesis for mountain lion selection of mule deer is that certain sex/reproductive classes of mountain lions (i.e. females with kittens) select for less numerous mule deer at higher elevations because of sexually segregated habitat use (sexual segregation hypothesis). For example, Wielgus & Bunnell (1994; 1995) found that female grizzly bears (*Ursus arctos*) with cubs avoided potentially infanticidal immigrant males and selected for high elevation food poor habitats as a counter strategy to sexually selected infanticide (Wielgus & Bunnell 2000; Wielgus et al. 2001). Perhaps the same phenomenon accounts for selection of mule deer in heavily hunted mountain lion populations in northeastern Washington where immigrant males are abundant. Lambert et al. (2006); Robinson et al. (2008); Cooley et al. (2009a, 2009b) found that mountain lion population losses from heavy hunting of mostly male lions was compensated for by increased male immigration. If females with kittens avoid such potentially infanticidal males, heavy hunting could exacerbate rather than alleviate predation on declining prey such as mule deer.

The goal of this investigation was to test the “apparent competition” and “sexual segregation” hypotheses for mountain lion selection of mule deer. The apparent competition hypothesis predicts that all sex/reproductive classes of mountain lion will select for mule deer, especially during summer because of prey species overlap. The apparent competition hypothesis further predicts elevations of mule deer and white-tailed deer kills will converge during summer (as white-tailed deer move up into mule deer ranges). The sexual segregation hypothesis predicts that only females, and especially females with kittens, will select for mule deer during summer when most kittens are vulnerable to sexually selected infanticide. The sexual segregation

hypothesis also predicts that elevation of mule deer kills will remain higher than those of white-tailed deer kills during summer (as females with kittens maintain an elevational difference from potentially infanticidal males).

Determining the causes for selection by mountain lion of declining mule deer and other sensitive species can help managers recover those species. For example, if apparent competition appears causal, increased hunting of predators (mountain lion) could result in reduced predation on declining secondary prey (mule deer) (Robinson et al. 2002; Lambert et al. 2006; Cooley et al. 2008). By contrast, if sexual segregation is causal, increased hunting of male predators could actually exacerbate predation on declining, secondary prey by causing females with kittens to segregate into higher elevations to avoid potentially infanticidal juvenile immigrant males.

STUDY AREA

The study area is located in northeastern Washington, USA and southeastern British Columbia, Canada, (Fig. 1.1) and was defined by the sum polygon of all marked female mountain lions. It covered 1312 km² of Northern Rocky Mountain Forest-Steppe-Coniferous Forest-Alpine Meadow (Bailey 1995). The portion of the study area found within Washington (Game Management Unit 105) is located just north of Kettle Falls, WA. The northern (British Columbia) portion of the study is just south of Castlegar, British Columbia.

Elevations range between >400 m along the riverbanks, to >2000 m in montane areas in the north. Precipitation averages between 51 cm and 102 cm annually (Bailey 1995). Tree and plant communities include ponderosa pine (*Pinus ponderosa*) on the lower elevation south and west facing slopes; western red cedar (*Thuja plicata*) in moist lower elevation valleys; Douglas-fir (*Pseudotsuga menziesii*) interspersed throughout much of the mid elevations; and western larch (*Larix occidentalis*); subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) at higher elevations. Land use includes recreation (mostly hunting), timber harvest, and ranching. Carnivore species include mountain lions, black bears (*Ursus americanus*), bobcats (*Felis rufus*) and coyotes (*Canis latrans*). White-tailed deer and mule deer are the most common ungulates in the study area (Cooley et al. 2008). Elk (*Cervus elaphus*), moose (*Alces alces*), and mountain goats (*Oreamnos americanus*) are rare but present. Hunting of mountain lions (especially males) was very heavy in this area (male harvest = 35 %) to reduce predation on mule deer and reduce human/mountain lion conflicts. The population showed a pronounced (+16% per year) compensatory male immigration response (Robinson et al. 2008; Cooley et al.

2009a) and there was substantial evidence of sexually selected infanticide by immigrant males (Cooley et al. 2009b).

METHODS

Mountain lion capture and monitoring

Mountain lion captures occurred during November through April of each year (2005-2008). The study area was searched for tracks and hounds were released to tree mountain lions (Hornocker 1970). A dosage of 0.4 mL per 10kg of body mass of ketamine hydrochloride (200mg/mL) and xylazine hydrochloride (20 mg/mL) was injected into the hindquarter of treed mountain lions via a projectile dart (Ross & Jalkotzy 1992; Spreadbury et al. 1996). Mountain lions were fitted with Lotek GPS4400S collars, monitored for condition and released. All animals were handled in accordance with Washington State University Animal Care permit #3133 and Animal Welfare Assurance Committee permit A3485-01. Collars were programmed to attempt a location fix between 4 and 6 times per day. During denning periods, some collars were remotely programmed to turn on 24-48 times per day to aid in finding den sites. Animals were recaptured once per year (when possible) and collars refitted with new batteries.

Individual mountain lions were assigned to one of three reproductive classes: female with kittens (FK); independent female (F) or independent male (M). Independent females moved into the females with kittens class after kittens were discovered in the den. Females remained in the class as long as the kittens were still alive and accompanying the mother. Females with kittens reverted to independent female if kittens were discovered dead. In cases where the kittens successfully reached dispersal age and were collared, the female was moved from female with kittens back into independent female as soon as the last remaining sub-adult kitten dispersed. Many females transitioned between both classes on multiple occasions. Independent males were those animals that were independent of their mothers.

Prey use and availability

Prey availabilities were estimated using 2 methods. First, prey availability within the study area was based upon aerial surveys conducted during 2004 and ground count surveys conducted during 2003-2004 -the same method as used by Cooley et al. (2008). Availabilities were estimated for the entire study area (Neu et al. 1974; McCorquodale et al. 1986) but not for each individual's home range (Litvaitis et al. 1986). Availabilities were assumed to remain constant throughout the study period. Aerial and ground surveys to estimate availability in 2007-2008 were not conducted because of a lack of funding. Second, prey availabilities were assumed to be equivalent to the observed overall kill ratios during the study (36% mule deer and 64% white-tailed deer); in case prey availabilities changed from 2004 to 2008.

Prey use was defined as the proportion of each deer species (white-tailed deer or mule deer) discovered at kill sites. I assumed the individual mountain lion whose point locations clustered around the kill was responsible for killing the prey. Kill site clusters were identified using a modified Anderson & Lindzey (2003) method with Arc GIS 9.2 software. GPS clusters containing more than 2 points within 50 meters and within a temporal distance of 36 hours were marked for investigation. Winter (W) kills were defined as those occurring between November 1 and April 30 and summer (S) kills as May 1 through October 31 to coincide with snowfall and the elevational shifts of prey. Mule deer tend to migrate out of the higher elevations beginning in November and begin to move up (locally) in May. Most snow falls in the study area during the mid November to mid-April period. Seasons also correlated to periods of kitten vulnerability immediately after birth; more than 90% of kittens were born during the summer season (Cooley et al. 2008). I calculated the annual date for each kill and plotted them by reproductive class to

ensure that kill distributions were more or less evenly distributed throughout the year for all sex/reproductive classes (Fig. 1.2).

Kill sites were investigated in person during cougar capture activities in winter 2005 and winter 2006; as well as between May and August of 2007 and 2008. Coordinates from putative kill sites were input to a handheld GPS device (Garmin GPSMap 60 CSX) and physically examined. Searches were conducted in the immediate area of the clusters outward to a distance of 50-60 m until evidence of a kill was discovered. Evidence included piles of hair, bones, bone fragments, teeth, jaw bones and hooves. I recorded the position of kill on slope, orientation, vegetation cover, canopy cover and elevation. When field identification was possible, species of prey was recorded. In cases where prey species could not be readily identified, DNA samples of prey were collected and stored in 120 ml sealed sample cups along with 5ml of silica gel beads to reduce sample degradation from moisture. Hair, teeth, bone, bone marrow, skin and tissue were collected if available. Samples were subsequently stored at -2° C from field collection (approx. 2-3 months) until archiving at -80° C (approx 3-36 months). DNA samples were delivered to the Washington Department of Fish and Wildlife (WDFW) genetics laboratory (Olympia, WA) for genetic analysis and species identification. Samples were assigned a catalog number and species identifications were reported as mule deer (MD); white-tailed deer (WT); elk, moose, coyote, black bear, mountain lion or no identification possible.

Prey selection

I tested for both first and second order selection of prey species (Thomas & Taylor 1990; Thomas & Taylor 2006). Design type I (Thomas & Taylor 1990) increases the power to detect selection with relatively small sample sizes (compared to type II, III or IV). For first order

selection of prey, data from individuals were pooled into reproductive classes [(FK); (F) and (M)] and season [(W) and (S)]; availability of prey was assumed identical across the study area. In order to control the experimentwise Type I error rate I also used Bonferroni's correction method (Kuehl 2000.) when making multiple comparisons.

First order selection

I used 2 methods to test for first order prey selection. First, I used the log-likelihood Chi-square goodness of fit test (Manley et al. 2002) to test if each reproductive class used a prey species disproportionately to their availability on the landscape.

$$\chi^2 = 2 \sum_{j=1}^n \sum_{I=1}^I \mu_{ij} \log_e(\mu_{ij} / E\{\mu_{ij}\})$$

(Manley et al. 2002 Equation 4.27)

Where $df = n(I-1)$, I is the number of prey categories, and where $E(\mu_{ij})$ is the expected number of prey type i used by the j th mountain lion if use is proportional to availability. A significant result indicates non-random selection by at least some individuals.

Second, I calculated selection ratios for each reproductive class using Manley et al. (2002).

$$\omega_i = (\mu_{ij} / \mu_{+j}) / \pi_i$$

(Manley et al. 2002 Equation 4.28)

Where ω_i = the selection ratio for the j th animal and the i th type of resource; (μ_{ij} / μ_{+j}) = the ratio of the observed proportion of type i resource used by the j th animal; and π_i = the known proportion of resource i available to the population.

I then tested for significant differences in selection ratios of each species using:

$$\chi^2 = (\omega_{i_{WT}} - \omega_{i_{MD}})^2 / \text{var}(\omega_{i_{WT}} - \omega_{i_{MD}})$$

(Manley et al. 2002 Equation 4.18)

Where $df = 1$; $\omega_{i_{WT}}$ = selection ratio of white-tailed deer; $\omega_{i_{MD}}$ = selection ratio of mule deer.

Second order selection

For second order selection, prey use by each individual in each class was compared to availability; availability was assumed identical for each individual across the study area (Design type II). In both cases landscape availabilities were believed appropriate because the home ranges were very large relative to the study area size. As with any study where data are pooled, one individual in a pool may strongly influence the mean of the entire pool enough to incorrectly infer a population effect where none exists (Chesson 1978). Because each individual's selection is evenly weighted, this design lowers the probability of inferring selection upon a population when none exists (Type II errors); but at the cost of increased sampling effort or Type I error. The individual mountain lions in this design are the sample units rather than the individual kills. I used the same methods and equations for 2nd order selection as 1st order selection for those individuals that had the minimum required sample size $N \geq 5$ (Knoke & Burke 1980).

Segregation by elevation

I used analysis of variance (ANOVA) to test for differences in elevation of kills of mule deer and white-tailed deer by reproductive classes and season. Data were tested for normality using Anderson-Darling method and equal variances using Levene's test. Elevations were recorded using a handheld GPS during kill site inspections and cross referenced with a digital elevation map (DEM) of the study area.

RESULTS

Mountain lion capture and monitoring

I examined 312 clusters from 15 cougars from 2004 through 2008; (6 solitary males; 8 solitary females and 5 females with kittens). The sum of individuals of each reproductive class exceeds total sample size because females moved from one reproductive class into another on multiple occasions. Of those, 298 clusters contained evidence of kills and 226 were identified to species.

Prey use and availability

Sightability-corrected aerial surveys and ground counts estimated prey availability within the study area at 82% white-tailed deer (n=1130) and 18% mule deer (n=255) (Cooley et al. 2008). Observed kill ratios yielded an estimated prey availability of 64% white-tailed deer (n=144) and 36% mule deer (n=82).

Annually, females with kittens (FK) killed 49% mule deer (n=36) and 51% white-tailed deer (n=38). During winter, they killed 40% mule deer (n=17) and 60% white-tailed deer (n=26). During summer, they killed 61% mule deer (n=19) and 39% white-tailed deer (n=12).

Females (F) killed 30% mule deer (n=23) and 70% white-tailed deer (n=53) annually. During winter, they killed 31% mule deer (n=14) and 69% white-tailed deer (n=31). In summer, they killed 29% (n=9) mule deer and 71% white-tailed deer (n=22).

Males (M) killed 30% mule deer (n=23) and 70% white-tailed deer (n=53). During winter, they killed 33% mule deer (n=14) and 67% white-tailed deer (n=29). During summer, they killed 27% mule deer (n=9) and 73% white-tailed deer (n=24).

Prey Selection

Design type I

Annually, all pooled individuals selected for mule deer ($\chi^2 = 40.05$, d.f. = 1, $p < 0.01$). Females with kittens showed the strongest selection ($\chi^2 = 34.77$, d.f. = 1, $p < 0.01$) followed by females ($\chi^2 = 6.22$, d.f. = 1, $p < 0.01$) and males ($\chi^2 = 6.22$, d.f. = 1, $p < 0.01$). Bonferroni's correction (for 3 classes $p = 0.017$) yielded no change in results.

During summer, only females with kittens strongly selected for mule deer ($\chi^2 = 27.81$, d.f. = 1, $p < 0.01$). Neither females ($\chi^2 = 2.06$, d.f. = 1, $p = 0.15$) nor males ($\chi^2 = 1.55$, d.f. = 1, $p = 0.21$) selected for mule deer. Bonferroni's correction yielded no change in results.

During winter, all reproductive classes selected for mule deer but selection was strongest by females with kittens ($\chi^2 = 10.40$, d.f. = 1, $p < 0.01$) followed by males ($\chi^2 = 4.92$, d.f. = 1, $p = 0.03$) and then females ($\chi^2 = 4.20$, d.f. = 1, $p = 0.04$). Using Bonferroni's correction, only females with kittens selected for mule deer; females and males did not. (Table 1.1).

Annually, the selection ratio of all pooled individuals favored mule deer (1.97 MD vs. 0.78 WT, $p < 0.01$). Selection was strongest again for females with kittens (2.64 MD vs. 0.63WT, $p < 0.01$). (Table 1.2). Bonferroni's correction yielded no change in results.

During summer, females with kittens showed the strongest selection ratio for mule deer (3.33 MD vs. 0.47 WT; $p < 0.01$); followed by females (1.58 MD vs. 0.87 WT; $p = 0.04$). However, the male selection ratio did not significantly favor one species over the other (1.48 MD vs. 0.89 WT; $p = 0.07$). Using Bonferroni's correction, only females with kittens selected for mule deer.

During winter selection ratios for all classes were significantly stronger for mule deer; beginning with females with kittens (2.15 MD vs. 0.74 WT; $p < 0.01$); and followed by females

(1.69 MD vs. 0.84 WT; $p < 0.01$) and males (1.77 MD vs. 0.83 WT; $p < 0.01$) Bonferroni's correction yielded no change in results.

Design type II

Annually, 4 of 5 females with kittens; 1 of 6 females and 1 of 6 males selected for mule deer (Table 1.3). Using Bonferroni's correction, 3 of 5 females with kittens; 1 of 6 females and 0 of 6 males select for mule deer.

During summer, 3 of 4 females with kittens; 1 of 3 females and 0 of 3 males selected for mule deer (Table 1.4). Using Bonferroni's correction, 2 of 4 females with kittens, 0 of 3 females and 0 of 3 males selected form mule deer.

In winter, 2 of 4 female with kittens; 1 of 5 females and 1 of 5 males selected for mule deer (Table 1.5). Using Bonferroni's correction, 1 of 4 females with kittens, 1 of 5 females and 0 of 5 males selected form mule deer.

Selection ratios

Annually, selection ratios were strongest for mule deer among females with kittens (4 of 5); followed by females (2 of 6) and males (2 of 6) (Table 1.6). Using Bonferroni's correction, male selection decreased to 1 of 6.

During summer, females with kittens showed the strongest selection ratios for mule deer (3 of 4); followed by females (1 of 3) and males (1 of 3) (Table 1.7). Using Bonferroni's correction, 2 of 4 females with kittens; 1 of 3 females and 0 of 3 males selected for mule deer.

During winter, selection ratios were strongest for mule deer among females with kittens (2 of 4); followed by males (2 of 5) and females (1 of 5) (Table 1.8). Using Bonferroni's correction, male selection decreased to 1 of 5.

Changing availabilities to 34% mule deer and 64% white-tailed deer resulted in only females with kittens selecting for mule deer annually ($\chi^2 = 5.79$, d.f. = 1, $p = 0.01$) and during summer ($\chi^2 = 8.85$, d.f. = 1, $p < 0.01$) using 1st order selection. (Table 1.9). No other classes selected for mule deer during any season.

Segregation by elevation

All data were normally distributed and the null hypotheses of unequal variances were rejected in all cases. In summer, females with kittens ($\bar{x} = 1048\text{m}$, $\text{SE} = 34.7\text{m}$) killed prey at significantly higher ($p < 0.01$) elevations than females ($\bar{x} = 888\text{m}$, $\text{SE} = 42.1\text{m}$) or males ($\bar{x} = 930\text{m}$, $\text{SE} = 37.6\text{m}$), as predicted by the sexual segregation hypothesis. During winter, no differences ($p=0.70$) in mean elevation of kill sites were detected between reproductive classes [females with kittens ($\bar{x} = 846\text{m}$, $\text{SE} = 29.6\text{m}$); females ($\bar{x} = 817\text{m}$, $\text{SE} = 37.7\text{m}$) and males ($\bar{x} = 809\text{m}$, $\text{SE} = 30.8\text{m}$)].

Mule deer ($\bar{x} = 1014\text{m}$, $\text{SE} = 36.7\text{m}$) kill sites were significantly higher ($p=0.03$) than white-tailed deer ($\bar{x} = 914\text{m}$, $\text{SE} = 28.5\text{m}$) kill sites during summer and during winter ($p<0.01$) [MD ($\bar{x} = 914\text{m}$, $\text{SE} = 34.5\text{m}$); WT ($\bar{x} = 782\text{m}$, $\text{SE} = 21.0\text{m}$)]. Elevation of mule deer and white-tailed deer kills did not converge during summer as predicted by the apparent competition hypothesis.

DISCUSSION

My results confirm the findings of Robinson et al. (2002) and Cooley et al. (2008) whereby mountain lion disproportionately selected for mule deer, especially during summer. Mule deer were killed twice as often as their availability (36% vs. 18%). Conversely, white-tailed deer made up 82% of the available deer but only 64% of the kills. Prey selection ratios further indicate that mule deer are being preyed upon nearly twice as much as would be expected if they were killed as available on the landscape. The best explanation for the disproportionate selection of mule deer appears to be elevational segregation by females with kittens (sexual segregation hypothesis).

The sexual segregation hypothesis predicted females with kittens would segregate themselves from potentially infanticidal males during summer months when kittens were vulnerable. Segregation to higher elevations to avoid infanticidal males as has been suggested in other carnivore species (Wielgus et al. 2001). Robinson et al. (2008) showed an influx of immigrant males into the study area during 2002-2005, as adult resident males were harvested. When females with kittens are segregated by elevation from males, mule deer selection should be more pronounced because relative mule deer densities increase with elevation. If this scenario were true, I would expect to see a significant increase in elevation of kills by females with kittens relative to solitary females and males during summer (when most kittens were born and more vulnerable). Results from summer showed exactly that; significantly higher mean elevations of kills by females with kittens than solitary males or females. This suggests the best explanation for pronounced selection of mule deer by females with kittens is the result of segregating into higher elevations, shifting the relative available prey density towards mule deer (Fig. 1.3).

Further, both Type I and Type II designs showed that females with kittens selected for mule deer during summer much more than either of the other reproductive classes. Corresponding prey selection ratios confirmed these trends. In fact, many of the same females did not select for mule deer when alone, but did when accompanied by kittens. Selection differences between reproductive classes were even more pronounced when availability estimates were changed to reflect overall observed kill proportions. In that case, only females with kittens selected for mule deer, annually and (very strongly) during summer; all other reproductive classes during both summer and winter, did not. Finally, when experimentwise Type I error rates were reduced using Bonferroni's method, females with kittens were selecting for mule deer while females and males did not.

These results run counter to the apparent competition hypothesis prediction that no differences in selection would be evident between reproductive classes. In addition, the apparent competition hypothesis predicted that during summer months, white-tailed deer would move up into mule deer range and mountain lions would simply follow their primary prey (white-tailed deer) up in elevation and encounter more secondary prey (mule deer). In this case, I would have expected to see a significant difference in winter elevations between white-tailed deer (lower elevations) and mule deer (higher elevations) followed by a convergence in elevation during summer (mule deer and white-tailed deer at similar elevations). Results from this study support elevational segregation of mule deer and white-tailed deer during winter, but (contrary to the apparent competition hypothesis) show prey segregation continued during summer. White-tailed deer moved up in elevation, but mule deer also increased in elevation during summer, thus mule deer were killed at significantly higher elevations than white-tailed deer. It does not appear mule deer predation is exacerbated by an increase in overlap with white-tailed deer (Table 1.11).

Management implications

These results call into question the continued justification of hunting male mountain lions where the underlying assumption is that predation impacts on mule deer do not differ by reproductive status. Based on this assumption, males are emphasized in harvest regimes because hunting of male mountain lions is believed to have the same impact on mule deer predation as does hunting of females and females with kittens. Further, because harvesting males is believed to have the least impact on mountain lion populations, an emphasis on males appears to offer the most efficient trade-off between maximizing the effects of predator reduction on prey species (mule deer) and minimizing the effects of predator reduction on predator (mountain lion) populations themselves. However, my results suggest, the greatest impact of predator reduction on prey populations should come from harvest of females with kittens. Further, the hunting of male mountain lions to reduce predation on declining mule deer in Robinson et al. (2002) and declining endangered mountain caribou (*Rangifer tarandus*) in Lambert et al. (2006) may have exacerbated predation in those cases by precipitating a compensatory male immigration response resulting in sexual segregation by females with kittens to high elevation, low density prey areas. I realize my findings and interpretations may be highly controversial and I encourage others to replicate this experiment and test for sexually segregated prey selection in other areas and predator/prey systems.

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Table 1.1 Observed and expected values of mule deer and white-tailed deer kills for three reproductive classes of mountain lion in northeastern Washington from 2005-2008. Log-likelihood X^2 results are shown, $\alpha = .05$.

Group	Prey	Obs ^a	Expect ^b	x^2LL^e	<i>P</i>
Annual (All)	WT ^f	144	184	40.05	<0.01
	MD ^g	82	42		
Annual (F) ^h	WT	53	62	6.22	0.01
	MD	23	14		
Annual (FK)	WT	38	60	34.77	<0.01
	MD	36	14		
Annual (M) ^h	WT	53	62	6.22	0.01
	MD	23	14		
Winter (F)	WT	31	37	4.20	0.04
	MD	14	8		
Summer (F)	WT	22	25	2.06	0.15
	MD	9	6		
Winter (FK)	WT	26	35	10.40	<0.01
	MD	17	8		
Summer (FK)	WT	12	25	27.81	<.001
	MD	19	6		
Winter (M)	WT	29	35	4.92	0.02
	MD	14	8		
Summer (M)	WT	24	27	1.55	0.21
	MD	9	6		

a Observed kills

b Expected kills (total kills x estimated proportion available)

e X^2 log-likelihood statistic

f White-tailed deer

g Mule deer

h Not a 'typo' – (F) and (M) results identical

Table 1.2 Selection ratios for three reproductive classes of mountain lion in northeastern Washington from 2005-2008. Log-likelihood X^2 results are shown, $\alpha = .05$.

Group	Prey	ω_i^c	β_i^d	SE(ω_i)	CI		LLx^{2e}	P
					lower	CI upper		
Annual (All)	WT ^f	0.78	0.28	0.04	0.70	0.86	51.39	<0.01
	MD ^g	1.97	0.72	0.21	1.57	2.38		
Annual (F)	WT	0.85	0.34	0.07	0.73	0.98	11.23	<0.01
	MD	1.64	0.66	0.30	1.05	2.23		
Annual (FK)	WT	0.63	0.19	0.07	0.49	0.77	52.61	<0.01
	MD	2.64	0.81	0.35	1.96	3.33		
Annual (M)	WT	0.85	0.34	0.07	0.73	0.98	11.23	<0.01
	MD	1.64	0.66	0.30	1.05	2.23		
Winter (F)	WT	0.84	0.33	0.09	0.68	1.01	7.86	<0.01
	MD	1.69	0.67	0.39	0.93	2.45		
Summer (F)	WT	0.87	0.36	0.10	0.67	1.07	4.05	0.04
	MD	1.58	0.64	0.45	0.69	2.46		
Winter (FK)	WT	0.74	0.26	0.09	0.56	0.92	18.06	<0.01
	MD	2.15	0.74	0.42	1.32	2.98		
Summer (FK)	WT	0.47	0.12	0.11	0.26	0.68	49.99	<0.01
	MD	3.33	0.88	0.51	2.33	4.33		
Winter (M)	WT	0.83	0.32	0.09	0.65	1.00	9.08	<0.01
	MD	1.77	0.68	0.40	0.98	2.55		
Summer (M)	WT	0.89	0.38	0.10	0.70	1.08	3.13	0.08
	MD	1.48	0.62	0.43	0.64	2.32		

c Selection index (Manley et al. 2002)

d Standardized selection index

e X^2 statistic

f White-tailed deer

g Mule deer

Table 1.3 Observed and expected values of mule deer and white-tailed deer kills for individual mountain lion in northeastern Washington from 2005-2008. Observed and expected values are given for each species. Log-likelihood X^2 results are shown, $\alpha = .05$.

ANNUAL Class	Individual Mountain lion	Prey	Obs ^a	Expected ^b	LLX^{2e}	P
F	30	WT ^f	6	11.42	10.40	<0.01
		MD ^g	8	2.58		
F	32	WT	18	17.13	0.25	0.61
		MD	3	3.87		
F	37	WT	6	7.34	1.14	0.28
		MD	3	1.66		
F	44	WT	6	6.53	0.21	0.64
		MD	2	1.47		
F	45	WT	7	6.53	0.20	0.65
		MD	1	1.47		
F	47	WT	6	7.34	1.14	0.28
		MD	3	1.66		
FK	30	WT	11	19.58	15.37	<0.01
		MD	13	4.42		
FK	32	WT	12	17.13	6.66	0.01
		MD	9	3.87		
FK	37	WT	3	4.08	1.26	0.26
		MD	2	0.92		
FK	44	WT	6	10.61	8.19	<0.01
		MD	7	2.39		
FK	46	WT	6	8.97	4.21	0.04
		MD	5	2.03		
M	23	WT	5	4.90	0.01	0.91
		MD	1	1.10		
M	25	WT	3	5.71	5.20	0.02
		MD	4	1.29		
M	42	WT	13	14.69	0.94	0.33
		MD	5	3.31		
M	48	WT	13	15.50	1.90	0.16
		MD	6	3.50		
M	49	WT	13	14.69	0.94	0.33
		MD	5	3.31		
M	50	WT	6	6.53	0.21	0.64
		MD	2	1.47		

a Observed kills
b Expected kills (total kills x estimated proportion available)
e X^2 log-likelihood statistic
f White-tailed deer
g Mule deer

Table 1.4 Observed and expected values of mule deer and white-tailed deer kills for individual mountain lion in northeastern Washington from 2005-2008. Observed and expected values are given for each prey species. Log-likelihood X^2 results are shown, $\alpha = .05$.

SUMMER							
Class	Mountain lion	Prey	Obs ^a	Expected ^b	LLX^{2e}	P value	
F	30	WT ^f	4	6.53	4.08	0.04	
		MD ^g	4	1.47			
F	32	WT	5	4.90	0.01	0.91	
		MD	1	1.10			
F	45	WT	6	5.71	0.08	0.77	
		MD	1	1.29			
FK	30	WT	3	8.16	12.69	<0.01	
		MD	7	1.84			
FK	32	WT	0	4.90	23.69	<0.01	
		MD	6	1.10			
FK	37	WT	3	4.08	1.26	0.26	
		MD	2	0.92			
FK	46	WT	3	4.90	3.06	0.08	
		MD	3	1.10			
M	42	WT	7	8.97	1.97	0.16	
		MD	4	2.03			
M	48	WT	7	7.34	0.08	0.77	
		MD	2	1.66			
M	49	WT	7	7.34	0.08	0.77	
		MD	2	1.66			

a Observed kills

b Expected kills (total kills x estimated proportion available)

e X^2 statistic

f White-tailed deer

g Mule deer

Table 1.5 Observed and expected values of mule deer and white-tailed deer kills for individual mountain lion in northeastern Washington during WINTER from 2005-2008. Observed and expected values are given for each species. Log-likelihood X^2 results are shown, $\alpha = .05$.

WINTER Class	Mountain lion	Prev	Obs ^a	Expected ^b	LLX^{2e}	P value
F	30	WT ^f	2	4.90	6.71	0.01
		MD ^g	4	1.10		
F	32	WT	13	12.24	0.28	0.59
		MD	2	2.76		
F	37	WT	3	4.08	1.26	0.26
		MD	2	0.92		
F	44	WT	5	5.71	0.43	0.51
		MD	2	1.29		
F	47	WT	3	4.08	1.26	0.26
		MD	2	0.92		
FK	30	WT	8	11.42	4.44	0.03
		MD	6	2.58		
FK	32	WT	12	12.24	0.02	0.87
		MD	3	2.76		
FK	44	WT	3	7.34	10.07	<0.01
		MD	6	1.66		
FK	46	WT	3	4.08	1.26	0.26
		MD	2	0.92		
M	23	WT	5	4.90	0.01	0.91
		MD	1	1.10		
M	25	WT	3	5.71	5.20	0.02
		MD	4	1.29		
M	42	WT	6	5.71	0.08	0.77
		MD	1	1.29		
M	48	WT	6	8.16	2.52	0.11
		MD	4	1.84		
M	49	WT	6	7.34	1.14	0.28
		MD	3	1.66		

a Observed kills

b Expected kills (total kills x estimated proportion available)

e X^2 statistic

f White-tailed deer

g Mule deer

Table 1.6 Annual selection ratios for individuals in each reproductive class of mountain lion in northeastern Washington from 2005-2008. Log-likelihood X^2 results are shown. $\alpha = .05$.

ANNUAL Class	Mountain	Prey	ω_i^c	β_i^d	SE(ω_i)	CI	CI	LLX^{2e}	P value
F	30	WT ^f	0.53	0.14	0.162	0.21	0.84	19.95	<0.01
		MD ^g	3.10	0.86	0.739	1.65	4.55		
F	32	WT	1.05	0.58	0.095	0.87	1.24	0.73	0.39
		MD	0.78	0.42	0.417	0.00	1.59		
F	37	WT	0.82	0.31	0.193	0.44	1.20	2.22	0.13
		MD	1.81	0.69	0.860	0.13	3.50		
F	44	WT	0.92	0.40	0.188	0.55	1.29	0.46	0.49
		MD	1.36	0.60	0.835	0.00	2.99		
F	45	WT	1.07	0.61	0.144	0.79	1.35	7.47	<0.01
		MD	0.68	0.39	0.000	0.68	0.68		
F	47	WT	0.82	0.31	0.193	0.44	1.20	2.22	0.13
		MD	1.81	0.69	0.860	0.13	3.50		
FK	30	WT	0.56	0.16	0.125	0.32	0.81	27.72	<0.01
		MD	2.94	0.84	0.577	1.81	4.07		
FK	32	WT	0.70	0.23	0.133	0.44	0.96	12.07	<0.01
		MD	2.33	0.77	0.601	1.15	3.51		
FK	37	WT	0.74	0.25	0.269	0.21	1.26	2.40	0.12
		MD	2.17	0.75	1.196	0.00	4.52		
FK	44	WT	0.57	0.16	0.170	0.23	0.90	15.49	<0.01
		MD	2.92	0.84	0.769	1.42	4.43		
FK	46	WT	0.67	0.21	0.184	0.31	1.03	7.84	<0.01
		MD	2.47	0.79	0.827	0.85	4.09		
M	23	WT	1.02	0.53	0.187	0.65	1.39	0.03	0.85
		MD	0.91	0.47	0.828	0.00	2.53		
M	25	WT	0.53	0.14	0.229	0.08	0.97	10.35	<0.01
		MD	3.10	0.86	1.031	1.08	5.12		
M	42	WT	0.89	0.37	0.130	0.63	1.14	1.92	0.16
		MD	1.51	0.63	0.580	0.37	2.64		
M	48	WT	0.84	0.33	0.131	0.58	1.10	3.69	0.06
		MD	1.72	0.67	0.587	0.56	2.87		
M	49	WT	0.89	0.37	0.130	0.63	1.14	1.92	0.16
		MD	1.51	0.63	0.580	0.37	1.51		
M	50	WT	0.92	0.40	0.188	0.55	1.29	5.44	0.02
		MD	1.36	0.60	0.000	1.36	1.36		

c Selection index (Manley et al. 2002)

d Standardized selection index

e X^2 statistic

f White-tailed deer

g Mule deer

Table 1.7 Summer selection ratios for individuals in each reproductive class of mountain lion during SUMMER in northeastern Washington from 2005-2008. Log-likelihood X^2 results are shown. $\alpha = .05$.

SUMMER Class	Individual Mountain lion	Prey	ω_i^c	β_i^d	SE(ω_i)	CI Lower	CI upper	x^{2e}	P value
F	30	WT ^f	0.61	0.18	0.217	0.19	1.04	7.75	<0.01
		MD ^g	2.72	0.82	0.972	0.81	4.62		
F	32	WT	1.02	0.53	0.187	0.65	1.39	0.03	0.85
		MD	0.91	0.47	0.828	0.00	2.53		
F	45	WT	1.05	0.58	0.163	0.73	1.37	2.85	0.09
		MD	0.78	0.42	0.000	0.78	0.78		
FK	30	WT	0.37	0.09	0.178	0.02	0.72	28.95	<0.01
		MD	3.80	0.91	0.816	2.20	5.40		
FK	32	WT	0.00	0.00	0.000	0.00	0.00	312.54	<0.01
		MD	5.43	1.00	0.307	4.83	6.03		
FK	37	WT	0.74	0.25	0.269	0.21	1.26	2.40	0.12
		MD	2.17	0.75	1.196	0.00	4.52		
FK	46	WT	0.61	0.18	0.250	0.12	1.10	5.86	0.02
		MD	2.72	0.82	1.119	0.52	4.91		
M	42	WT	0.78	0.28	0.178	0.43	1.13	3.74	0.05
		MD	1.98	0.72	0.796	0.42	3.53		
M	48	WT	0.95	0.44	0.170	0.62	1.29	0.19	0.66
		MD	1.21	0.56	0.756	0.00	2.69		
M	49	WT	0.95	0.44	0.170	0.62	1.29	0.19	0.66
		MD	1.21	0.56	0.756	0.00	1.21		

c Selection index (Manley et al. 2002)

d Standardized selection index

e X^2 statistic

f White-tailed deer

g Mule deer

Table 1.8 Winter selection ratios for individuals in each reproductive class of mountain lion during WINTER in northeastern Washington from 2005-2008. Log-likelihood X^2 results are shown. $\alpha = .05$.

WINTER Class	Individual Mountain lion	Prey	ω_i^c	β_i^d	SE(ω_i)	CI Lower	CI upper	LLx^{2e}	P value
F	30	WT ^f	0.41	0.10	0.236	-0.05	0.87	15.01	<0.01
		MD ^g	3.62	0.90	1.065	1.53	5.71		
F	32	WT	1.06	0.59	0.108	0.85	1.27	0.83	0.36
		MD	0.72	0.41	0.478	0.00	1.66		
F	37	WT	0.74	0.25	0.269	0.21	1.26	2.40	0.12
		MD	2.17	0.75	1.196	0.00	4.52		
F	44	WT	0.88	0.36	0.210	0.46	1.29	0.88	0.34
		MD	1.55	0.64	0.932	0.00	3.38		
F	47	WT	0.74	0.25	0.269	0.21	1.26	2.40	0.12
		MD	2.17	0.75	1.196	0.00	4.52		
FK	30	WT	0.70	0.23	0.162	0.38	1.02	8.21	<0.01
		MD	2.33	0.77	0.730	0.90	3.76		
FK	32	WT	0.98	0.47	0.127	0.73	1.23	0.06	0.80
		MD	1.09	0.53	0.564	0.00	2.19		
FK	44	WT	0.41	0.10	0.193	0.03	0.79	21.99	<0.01
		MD	3.62	0.90	0.878	1.90	5.34		
FK	46	WT	0.74	0.25	0.269	0.21	1.26	2.40	0.12
		MD	2.17	0.75	1.196	0.00	4.52		
M	23	WT	1.02	0.53	0.187	0.65	1.39	0.03	0.85
		MD	0.91	0.47	0.828	0.00	2.53		
M	25	WT	0.53	0.14	0.229	0.08	0.97	10.35	<0.01
		MD	3.10	0.86	1.031	1.08	5.12		
M	42	WT	1.05	0.58	0.163	0.73	1.37	0.24	0.62
		MD	0.78	0.42	0.720	0.00	2.19		
M	48	WT	0.74	0.25	0.190	0.36	1.11	4.74	0.03
		MD	2.17	0.75	0.850	0.51	3.84		
M	49	WT	0.82	0.31	0.193	0.44	1.20	2.22	0.13
		MD	1.81	0.69	0.860	0.13	1.81		

c Selection index (Manley et al. 2002)

d Standardized selection index

e X^2 statistic

f White-tailed deer

g Mule

Table 1.9 Alternative first order selection results assuming availabilities: 34%% mule deer and 64% white-tailed deer. Log-likelihood X^2 results are shown. $\alpha = .05$.

Group	Prey	Obs ^a	Expect ^b	χ^2 LL ^e	<i>P</i>
Annual (All)	WT ^f	144	147	0.16	0.68
	MD ^g	82	79		
Annual (F)	WT	53	49	0.77	0.38
	MD	23	27		
Annual (FK)	WT	38	48	5.79	0.01
	MD	36	26		
Annual (M)	WT	53	49	0.77	0.38
	MD	23	27		
Winter (F)	WT	31	29	0.30	0.58
	MD	14	16		
Summer (F)	WT	22	20	0.50	0.47
	MD	9	11		
Winter (FK)	WT	26	28	0.38	0.53
	MD	17	15		
Summer (FK)	WT	12	20	8.85	<0.01
	MD	19	11		
Winter (M)	WT	29	28	0.11	0.73
	MD	14	15		
Summer (M)	WT	24	21	0.90	0.34
	MD	9	12		

Figure 1.1 Study Area –This figure shows the study area in northeastern Washington, USA and southeastern British Columbia, Canada.

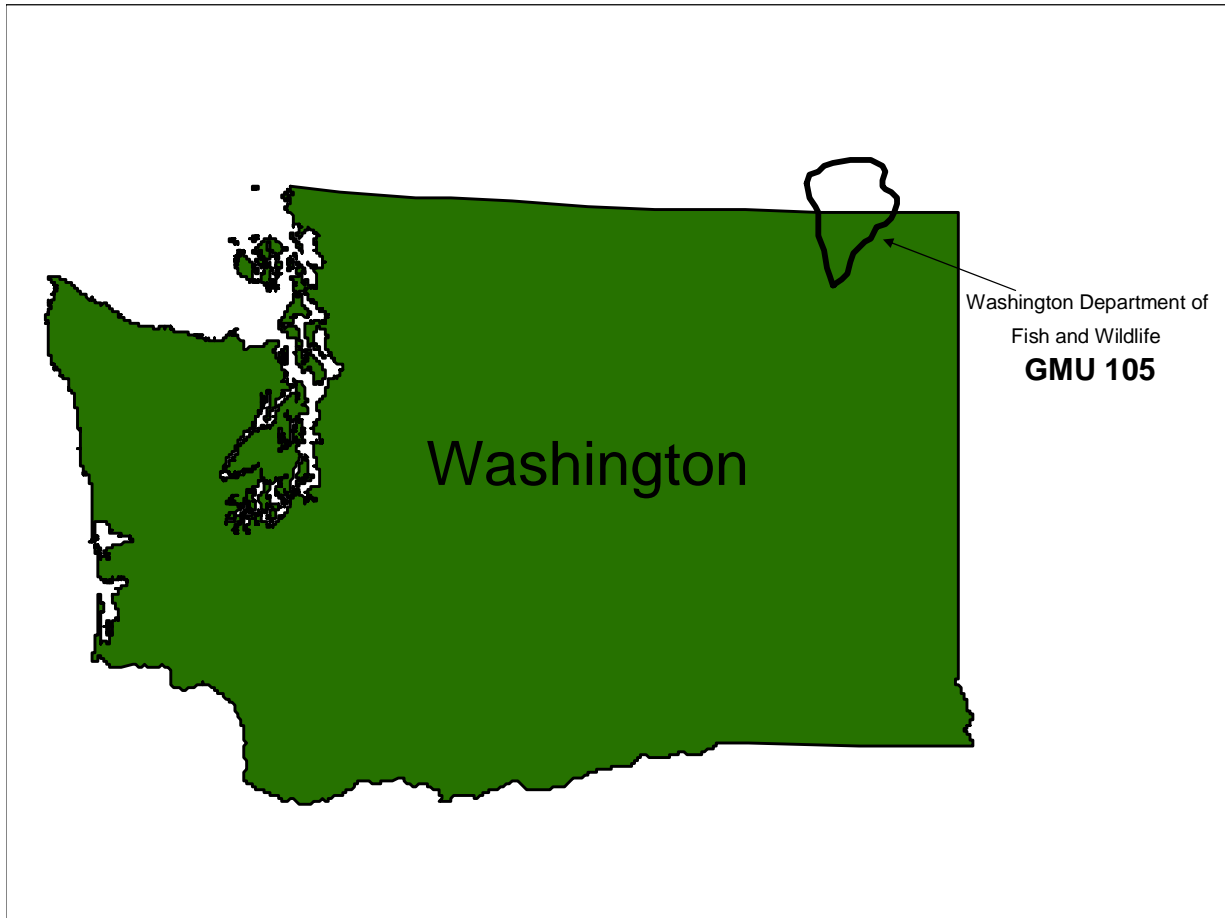


Figure 1.2: Annual sampling distribution of each reproductive class. Each line represents at least one kill on the corresponding day. Winter = Nov.1 to Apr. 30; summer = May 1 to Oct. 31.

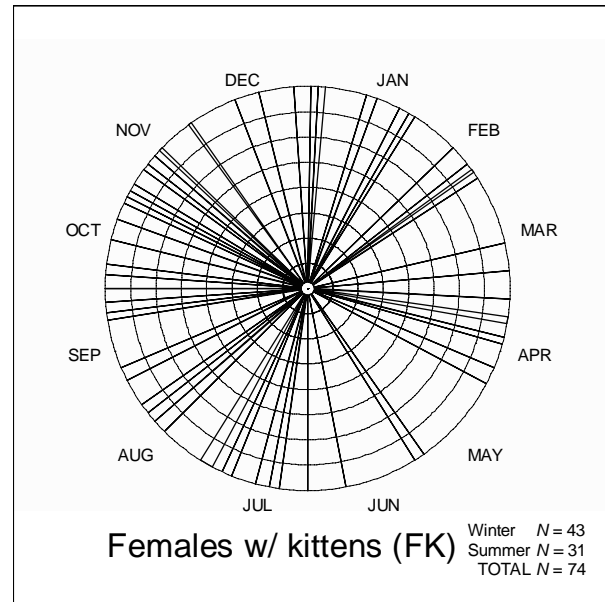
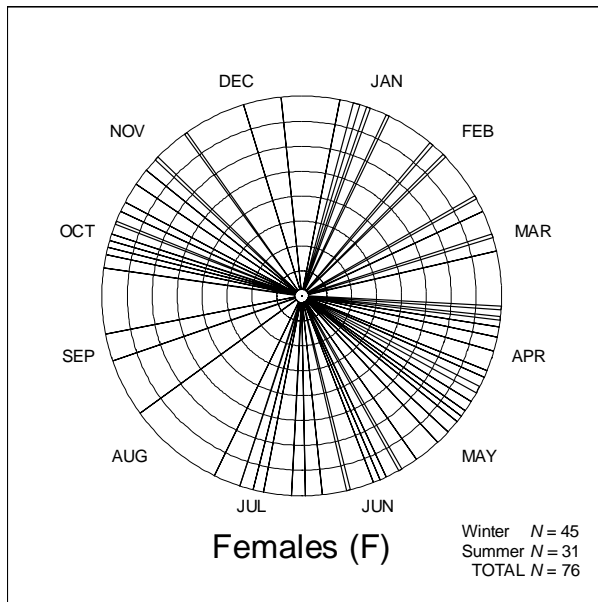
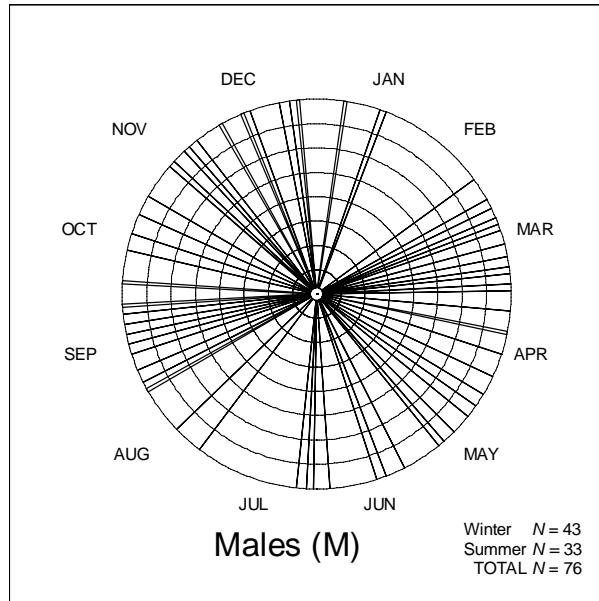


Figure 1.3 Relative Prey Densities

