



# Effects of male targeted harvest regime on sexual segregation in mountain lion



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## ABSTRACT

Male targeted harvest regimes of carnivores are now widely accepted to result in increased sexually selected infanticide (SSI). Male targeted harvest regimes of males should therefore result in increased sexually segregated habitat use in infanticidal carnivores. We tested the effects of low and high levels of male hunting mortality and associated SSI on sexually segregated habitat use in mountain lions. The “no effect of hunting” hypothesis predicts that no sexual segregation would occur or that all female mountain lions would segregate from males because of sexual dimorphism. The “hunting effect” hypothesis predicts that females with kittens would segregate from younger immigrant males in the heavily hunted population during summer when kittens are vulnerable to SSI. We rejected the “no effect” hypothesis and accepted the “hunting effect” hypothesis for mountain lions. Females with kittens avoided immigrant males in the heavily hunted population during summer—others did not. This sexual segregation corresponded with females with kittens selecting for food-poor, high elevations in the heavily hunted population but not in the lightly hunted population. Avoidance of males and selection for high elevations resulted in prey switching by females with kittens from abundant primary prey in lower elevations to rare, sensitive and threatened secondary prey at higher elevations. It appears that remedial sport hunting of mountain lions to reduce predation on declining prey actually caused sexual segregation and increased predation on declining prey. We suggest that excess mortality of male carnivores could result in unanticipated cascade effects including sexual segregation and prey switching to declining prey.

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## 1. Introduction

Sport hunting in a wide variety of male carnivores can induce sexually selected infanticide (SSI) by causing rapid turnover of breeding males (see Wielgus and Bunnell, 1994a, 2000; Wielgus et al., 2001, for North American grizzly bears *Ursus arctos*; Swenson et al., 1997; Swenson, 2003, for European brown bears *U. arctos*; Packer et al., 2009, 2011, for African lions *Panthera leo*; and Balme et al., 2012a, 2012b, for African leopards *Panthera pardus*). In our animal model (mountain lions, *Puma concolor*), high male mortality (35%) resulted in a shift in the sex/age structure towards numerous, younger, potentially infanticidal, immigrant males (Robinson et al., 2008). Lower male mortality (15%) resulted in less numerous, but older resident males (Cooley et al., 2009a). The higher male mortality corresponded with higher mortality rates of kittens (69% vs. 42%, Cooley et al., 2009b) and higher rates of plausible infanticide (27% vs. 0%, Wielgus et al., 2013).

Females should respond behaviorally to SSI by separating from and avoiding potentially infanticidal, immigrant males. For example, in a heavily hunted North American grizzly bear population (30% older male

mortality, Wielgus and Bunnell, 1994a), females with cubs segregated into high elevation, xeric, food-poor environments where the numerous younger immigrant males were rare (Wielgus and Bunnell, 1994b). In a nearby lightly hunted population (19% younger male mortality, Wielgus et al., 1994) females with cubs did not segregate from older resident males in food-rich environments (Wielgus and Bunnell, 1995). Those behavioral differences (sexual segregation) corresponded with reproductive strategies where the elasticity of cub survival was greater than the elasticity of litter size which maximized fitness (Wielgus and Bunnell, 2000, Wielgus et al., 2001). Steyaert et al. (2013) also found that European female brown bears with cubs in a heavily hunted population segregated into different habitats than males during the potentially infanticidal breeding season. However, those papers demonstrated sexually segregated differences in habitat use and selection for *U. arctos*, not avoidance of males per se. It is still possible, though highly unlikely, that those sexual differences in habitat use could have been due to intrinsic differences in habitat selection between the sexes (habitat segregation: Clutton-Brock et al., 1982, Villaret and Bon, 1995, Main and Coblenz, 1996, Conradt, 1999, Ruckstuhl and Neuhaus, 2005) not actual avoidance of males because of SSI (social segregation: Swenson, 2003, Rode et al., 2006).

In this paper, we compare sexually segregated spatial distribution in a lightly and heavily hunted population of another species (mountain

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lions) to test for generality to other carnivores. We also directly test the social segregation hypothesis (females with cubs avoid immigrant males in a heavily hunted population but do not avoid resident males in a lightly hunted population) by examining differences in spatial distribution between reproductive classes. We use the same two study areas (northeastern Washington and central Washington) and same two heavily and lightly hunted mountain lion populations as extensively reported in Cooley et al. (2008), Robinson et al. (2008), Cooley et al. (2009a), Cooley et al. (2009b), White et al. (2011), and Wielgus et al. (2013)—to test if hunting has an effect on sexual segregation.

If sexual segregation were driven by intrinsic sexual differences in body size and energetics (hunting has no effect)—the habitat segregation hypothesis makes four basic predictions based on reproductive class, area, season, and their combined effects. 1) Reproductive classes: the higher energy demands of females with kittens should be more similar to larger, sexually dimorphic males than that for lone females (Ruckstuhl and Neuhaus, 2002), therefore sexual segregation should be less pronounced for females with kittens. 2) Areas: males in the lightly hunted area selected for larger prey (elk *Cervus elaphus* vs. mule deer *Odocoileus hemionus*) than females (White et al., 2011), but elk were not available in the heavily hunted area (Cooley et al., 2008, Wielgus et al., 2013)—therefore sexual segregation should be more pronounced in the lightly hunted area where sexually dimorphic use of prey was already apparent. Furthermore, home range size, male to male home range overlap, and female to female home range overlap were greater in the heavily hunted area (Maletzke, 2010)—so spatial sexual segregation should be less pronounced there because of greater shared area among conspecifics. 3) Seasons: spatial expansion of home range size occurred during summer and male to male and female to female home range overlaps increased with increasing home range size (Maletzke, 2010)—so spatial sexual segregation which is driven by landscape factors, rather than risk avoidance, should be less pronounced during summer because of greater shared area among conspecifics (Terborgh et al., 1999). 4) The additive effects of reproductive class, area, and season: sexual segregation should be most pronounced for solitary females in the lightly hunted area during winter and should be least pronounced for females with kittens in the heavily hunted area during summer.

If segregation was driven by social avoidance of males by females because of the threat of SSI (hunting has an effect) the reproductive class, area, and season predictions are exactly the opposite. 1) Reproductive classes: sexual segregation from males for females with kittens should be higher than for solitary females. 2) Areas: Sexual segregation should be more pronounced in the heavily hunted area because of the abundance of younger potentially infanticidal males. 3) Seasons: Goodrich et al. (2008) found that tiger (*Panthera tigris*) cubs were most vulnerable to infanticide during the first 6 months of life. Almost all mountain lion births occurred during the summer and all six cases of plausible infanticide within the heavily hunted area appeared to occur during the summer months (Cooley et al., 2009b)—so sexual segregation should be more pronounced during the summer. 4) Additive effects: sexual segregation should be most pronounced for females with kittens in the heavily hunted area during summer and should be least pronounced for solitary females in the lightly hunted area during winter.

## 2. Materials and methods

### 2.1. Study areas

The two areas selected for use in this study reflect different intensities of human hunting mortality on mountain lions (Fig. 1). The heavily hunted study area (HH) in northeastern Washington covered 1476 km<sup>2</sup>. Hound hunting and boot hunting (incidental harvest of mountain lions while hunting deer or elk) were encouraged in the area to alleviate human–mountain lion conflicts (Lambert et al., 2006) and to relieve predation on declining mule deer (Robinson et al., 2002, 2008; Cooley et al., 2008). There was no established quota on harvest of male

mountain lions and bag limits were limited to one cougar per hunter per year. It is comprised of Northern Rocky Mountain Forest–Steppe–Coniferous Forest–Alpine Meadow (Bailey, 1995) and includes Washington Game Management unit 105. Elevations ranged from <400 m along the riverbanks, to >1400 m in montane forest. Precipitation ranges between 51 cm and 102 cm annually, falling mostly in the form of snow (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 included recreation (mostly hunting), timber harvest, and cattle ranching. Carnivore species included mountain lions, black bears (*Ursus americanus*), bobcats (*Felis rufus*) and coyotes (*Canis latrans*). White-tailed deer (*Odocoileus virginianus*) and mule deer were the most common ungulates in the study area (Cooley et al., 2008). Elk, moose (*Alces alces*), and mountain goats (*Oreamnos americanus*) were very rare.

The lightly hunted study area (LH) encompasses the western half of Kittitas County in central Washington and covers 1652 km<sup>2</sup>. There was no established quota on harvest of male mountain lions and bag limits were limited to one cougar per hunter per year. Hound hunting of mountain lion was prohibited during the period of the study although, “boot hunting” was allowed. It is classified as Northern Cascade Mixed Forest (Bailey, 1995) and includes Washington Game Management Units 335 (Teaaway) and 336 (Taneum). Ponderosa pine and Douglas fir communities were intermixed with agricultural lands in the lower elevations (550 m). Sub-alpine fir, Engelmann spruce, Pacific silver fir (*Abies amabilis*) and western hemlock (*Tsuga heterophylla*) dominated the mid and upper elevations (1550 m). The majority of precipitation falls during winter as snow; the average winter snowfall is 160 cm (Cooley et al., 2009a). Elk and mule deer are the most numerous ungulates. White-tailed deer are absent or extremely rare in the area. Other common carnivores include black bear, bobcat and coyote.

### 2.2. Demographic comparisons of heavily hunted (HH) and lightly hunted (LH) areas

The heavily hunted (HH) area had an overall hunting mortality rate of 0.24 and a male hunting mortality rate of 0.35. The survival-fecundity growth rate was 0.78, with a net immigration rate (mostly males) of 0.13—resulting in an overall observed growth rate of 0.91. Density was stable (at equilibrium) over 5 years at 3.46 mountain lions/100 km<sup>2</sup>. The mean age of males was 24 months (Cooley et al., 2009b). The mean home range size of females was 240 km<sup>2</sup> and males was 752 km<sup>2</sup> (Maletzke, 2010). Six of 11 kitten deaths reported in Cooley et al. (2009b) were believed to have been caused by male mountain lions via infanticide.

The lightly hunted area (LH) had an overall hunting mortality rate of 0.11 and male hunting mortality rate of 0.16. The survival-fecundity growth rate was 1.10 with a net emigration rate of 0.12 (mostly males) resulting in an annual observed growth rate of 0.98. Density was stable over the period of the study at 3.62 mountain lions/100 km<sup>2</sup>. The mean age of males was 41 months (Cooley et al., 2009b). The mean home range size of females was 199 km<sup>2</sup> and males was 348 km<sup>2</sup>. Zero of five kitten deaths were reported in Cooley et al. (2009b) as infanticides although some may have occurred and not been detected.

### 2.3. Capturing and handling

All animals were handled in accordance with Washington State University Animal Care Permit #3133 and Animal Welfare Assurance Committee Permit A3485-01. Mountain lion captures were conducted during winters 2002–2008. The study areas were searched for tracks and hounds were released to tree mountain lions (Hornocker, 1970).

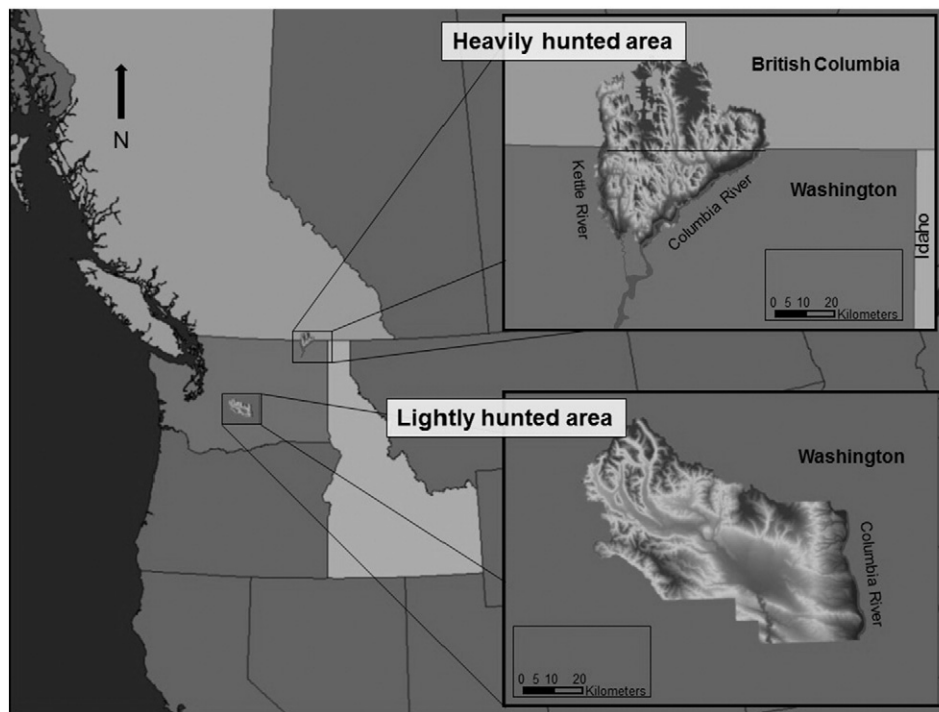


Fig. 1. Heavily hunted and lightly hunted study areas in Washington and British Columbia.

A dosage of 0.4 ml per 10 kg of body mass of ketamine hydrochloride (200 mg/ml) and xylazine hydrochloride (20 mg/ml) was injected into the hindquarter of treed mountain lions via a projectile dart (Ross and Jalkotzy, 1992). Mountain lions were fitted with Lotek GPS4400S collars (Lotek Wireless, Newmarket, Ontario, Canada), examined for sex, age, and condition, and released. Collars were programmed to attempt a location between four and six times per day. Animals were recaptured once per year (when possible) to assess condition and refit the collars with new batteries. For details see Cooley et al. (2009a) and Robinson et al. (2008).

#### 2.4. Reproductive classes and seasons

Individual mountain lions were assigned to one of three reproductive classes: females with kittens (FK); solitary females (F) or independent males (M). Independent females were classified as “females with kittens” after kittens were discovered in the den. Females remained in that class as long as their kittens were alive accompanying the mother. Females with kittens reverted to “solitary females” if kittens died or dispersed. Many females transitioned between both classes during the course of the study. Independent males were those sexually mature animals that no longer accompanied their mothers. Winter was between November 1 and April 30 and summer was May 1 through October 31—to coincide with periods of snowfall and kitten vulnerability (Cooley et al., 2009b). More than 90% of kittens were born during the summer (Cooley et al., 2009b).

#### 2.5. Sexual segregation

We first studied the three-dimensional home range overlap between the sexes and then further compared the selection of elevation between the sexes.

#### 2.6. Utilization distribution overlap index

We first calculated 95% kernel density estimates using Hawth's Analysis Tools for ArcGIS (Beyer, 2004) to estimate summer and winter

home ranges for individuals in all reproductive classes. We then calculated seasonal utilization distribution overlap indices (UDOI-Fieberg and Kochanny, 2005) for adjacent male and female mountain lions showing at least 1% overlap of their home ranges during the study, using a script written for the R environment for statistical programming (R Development Core Team, 2009). 3-d utilization distribution overlap differs from 2-d home range overlap by including a temporal component to calculate the probability that two individuals used the same space (Fieberg and Kochanny, 2005). Index values range from 0.0 (no overlap) to 2.0 (complete overlap). All references in this study to UDOI are between females with kittens and males, and solitary females and males. We calculated the mean UDOI value for each female by summing the UDOI values of each overlapping male and dividing by the number of overlapping males (Maletzke, 2010). We tested for differences in mean UDOI values for reproductive class, area, season, and their interactions using factorial analysis of variance (ANOVA) and Tukey's Honestly Significant Test. We compared the additive effects of reproductive class, area, and season by constructing 95% confidence intervals around the mean UDOI for individuals within each class, area, and season combination.

#### 2.7. Use versus availability of elevation

If segregation occurs at a finer (within home range) scale than the UDOI is able to detect, it may still be influenced by social or habitat factors *within* the home range (Neu et al., 1974). If such differences are occurring *within* home ranges, comparing UDOI values may fail to capture these fine scale differences if the variation occurs *within* the home range scale rather than at a landscape scale. Therefore, we also compared the use/availability of elevation (same as Wielgus and Bunnell, 1994b) by mountain lions in the heavily hunted population to that of the lightly hunted population to determine if segregation by elevation was occurring at the finer, within home range scale.

We compared the use of available elevation by FK, F and M within study areas and within seasons using Type II and Type III parametric ANOVA study designs (Thomas and Taylor, 1990). We also tested for differences in the distribution of used and available elevation using



non-parametric Kolmogorov–Smirnov tests. First, we calculated the availability of elevation for each individual using the mean of all 30 m × 30 m pixels contained within the 95% kernel density estimator home ranges calculated for use in the UDOI analysis. We then calculated use of elevation for each individual using the mean of all GPS point location coordinates for that individual. To determine if individuals were using elevation differently than was available to them (Type III; Thomas and Taylor, 1990, 2006), we used paired t-tests (SYSTAT) to test for differences in the mean elevation of used, versus available points of elevation for each individual.

Next, to determine if mean use was different than mean availability for each reproductive class, we calculated the means for all individuals within each reproductive class by study area and season and tested for differences in mean use and mean availability for reproductive classes (Type II; Thomas and Taylor, 1990) within each area and season using paired t-tests. To determine if the differences in use and availability within each reproductive class were different between reproductive classes, we used analysis of variance (Type II; Thomas and Taylor, 1990).

### 2.8. Kolmogorov–Smirnov tests

Last, because animal locations may be bimodal distributed with respect to elevation, we compared the actual distribution of points across the elevation gradient in the kernel home range with the available elevation. An individual may use elevation much higher, as well as much lower than the mean but have very little use near the mean (and therefore the mean may not accurately reflect the use of elevation within the home range). We calculated the mean difference in use versus availability for each reproductive class, by study area and season, and we tested for differences using the Kolmogorov–Smirnov test (SYSTAT). This was a non-parametric analog to our Type II ANOVA test.

## 3. Results

### 3.1. Utilization distribution overlap index

We captured, radio-monitored, and analyzed spatial data from 42 mountain lions in the two study areas: 22 total lions (13 males and 9 females) in the lightly hunted area and 20 total lions (7 males and 13 females) in the heavily hunted area. Each lion had  $760 \pm 418$  (95% CI) GPS telemetry acquisitions per year.

UDOI differed among the main effects of reproductive class, area, and season in that order, but their interactions were not significant (Table 1). FK (UDOI = 0.25) overlapped less with males than F (UDOI = 0.47). The heavily hunted area (UDOI = 0.25) had less overlap with males than the lightly hunted area (UDOI = 0.46) and summer (UDOI = 0.26) had less overlap than winter (UDOI = 0.45).

The additive effects showed that the lowest UDOI with males was for FK in heavily hunted area during SUMMER (0.08) and the highest UDOI (0.66) was for F in lightly hunted area during WINTER (Fig. 2).

**Table 1**

Analysis of variance results for effect of reproductive class, area and season on Utilization Distribution Overlap Indices of mountain lions 2005–2008.

Source	Type III SS	Df	Mean squares	F-ratio	P
Reproductive class	0.482	1	0.482	8.952	<b>0.005</b>
Area	0.432	1	0.432	8.012	<b>0.008</b>
Season	0.385	1	0.385	7.141	<b>0.011</b>
Season × Area	0.006	1	0.006	0.103	0.750
Reproductive class × Area	0.024	1	0.024	0.454	0.505
Reproductive class × Season	0.026	1	0.026	0.474	0.496
Reproductive class × Season × Area	0.019	1	0.019	0.345	0.561
Error	1.885	35			

Bold indicates a significant P value.

### 3.2. Use versus availability of elevation

In the lightly hunted area no reproductive classes used elevation differently from availability during summer, nor were any reproductive classes different from each other (Table 2). During winter, all reproductive classes used elevations lower than were available but no reproductive classes were different than any other.

In the heavily hunted area during summer, females with kittens selected for elevations + 31.15 m higher than available, solitary females used elevation at availability, and males selected for elevations – 38.76 m lower than availability (Table 2). The overall difference in use versus availability of elevations between females with kittens and males was 69.91 m. During winter, only males selected for lower elevation than availability (– 29.13 m) and there were no differences between reproductive classes (Table 2).

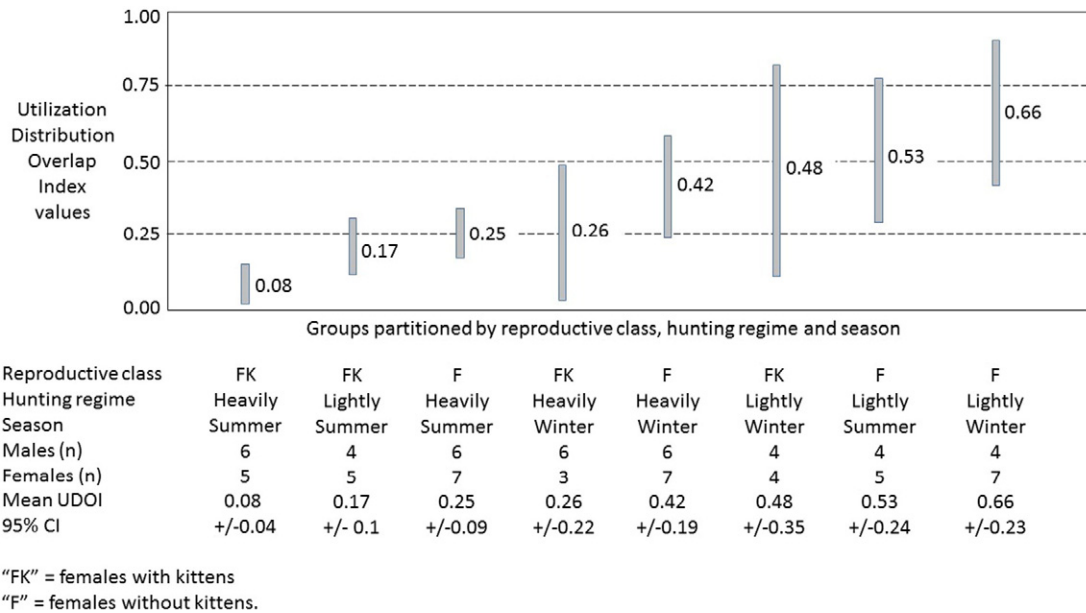
Results from the Kolmogorov–Smirnov tests showed similar but more conservative results. The only difference in use vs. availability using the Kolmogorov–Smirnov test was between females with kittens and males in the heavily hunted area during summer. (Table 3).

## 4. Discussion

Our results show that trophy hunting of male carnivores exacerbates sexual segregation in mountain lions because of SSI, as it does in North American grizzly bears (Wielgus and Bunnell, 1995) and appears to do in European brown bears (Steyaert et al., 2013). Our results do not support the “no effect of hunting” or habitat segregation hypothesis of sexual segregation in mountain lions because: 1) Sexual segregation (differences in UDOI and differences in selection of elevation) was less pronounced for solitary females with dissimilar energetic requirements than males and more pronounced for females with offspring with similar energetic requirements. 2) Sexual segregation was less pronounced in the lightly hunted area where sexually dimorphic prey use was already observed and was more pronounced in the heavily hunted area where intra-sexual spatial overlap and shared space was already greater. 3) Sexual segregation was less pronounced during winter and was more pronounced during the summer when intra-sexual spatial overlap and shared space was already higher. The increased overlap between reproductive classes during winter is similar to results from a mountain lion population in Wyoming where associations appeared to be driven by snow depth and prey distribution (Elbroch et al., 2014).

Our results support the “hunting effect” social segregation hypothesis of sexual segregation in mountain lions because females with offspring avoided males (lower UDOI) and selected for higher elevations than males, especially in the heavily hunted area (with more infanticidal immigrant males), and during the summer when kittens are more vulnerable to infanticide. Differences in UDOI were not apparent in either study area during winter, suggesting avoidance of males may be due to the higher vulnerability of offspring to infanticide when kittens are younger. Most kittens were born during summer months; as a result, the mean age of kittens was lower during summer than during winter. During winter their larger size and cumulative effect of learned behaviors may increase their chances of survival when encountering males. Goodrich et al. (2008) reported similar behavior in tigers where most incidents of infanticide occurred when tiger kittens were less than 6 months old. The same occurred for infanticide in European brown bears with younger cubs of the year (<1 year old) bearing the brunt (Swenson et al., 1997, 2001a, 2001b) and females with young cubs segregating from males (Steyaert et al., 2013). Sexual segregation in North American grizzly bears was also greatest during the summer for females with cubs of the year (Wielgus et al., 1994; Wielgus and Bunnell, 1995) and for black bears with cubs of the year (Collins et al., 2002).

The mean UDOI values for each reproductive class by season by area show a clear pattern supporting the main effects. First, females with kittens appear to have lower UDOI values than solitary females. Second,



**Fig. 2.** 95% CI of mean UDUI values of mountain lions in northeastern and South Central Cascades partitioned into groups by reproductive class, hunting regime and season. A value of 0.0 indicates no overlap and a value of 2.0 indicates complete overlap.

the heavily hunted area has lower UDUI than the lightly hunted and finally, summer showed lower UDUI values than winter. The additive effects showed that the lowest overlap was between females with kittens in the heavily hunted area during summer, and the greatest overlap was by females in the lightly hunted area during winter.

Differences in how females with kittens used elevation within their home ranges relative to males appeared very pronounced in the heavily hunted area; and no differences between these classes were evident in the lightly hunted area. In the heavily hunted area, females with kittens used elevation on average 31.15 m higher than was available to them; males used elevations 38.76 m lower than was available to them; solitary females used nearly exactly what was available (−3.19 m). The net difference in use of elevation versus availability between females with kittens and males during the summer in the heavily hunted was 69.91 m. The biological effect of 69.91 m can be compared to results from Husseman et al. (2003). They modeled differences in kill site attributes between wolves (*Canis lupus*) and mountain lions and found a mean difference in kill elevations between the species of 82 m (1688 m and 1608 m respectively). The difference in elevation observed

here for females with cubs and males is similar to that observed for two different species of predator.

These results are consistent with the observed differences in prey use by different reproductive classes in the heavily hunted area during summer. Females with kittens selected for low density, declining secondary prey (mule deer) at higher elevations during summer, but males and solitary females selected for high density, primary prey (white-tailed deer) at low elevations throughout the year (Keehner et al., unpublished results). Such prey switching from abundant to rare prey (all else being equal) runs counter to all standard energetic models of rational predator/prey dynamics (Case, 2000, Sinclair et al., 2006).

These results and the results of Robinson et al. (2008), Cooley et al. (2009a, 2009b), and Maletzke (2010), indicate that spatial segregation between reproductive classes of mountain lion is occurring in the heavily hunted study area and may be the result of heavy male harvest of mountain lions. Furthermore, this segregation appears to be influencing predator selection for low density, declining, mule deer (Robinson et al., 2002; Cooley et al., 2008; Keehner et al., unpublished results). For yet another example, declines in the last remaining threatened Selkirk Mountain caribou (*Rangifer tarandus*) population in the lower US (Wittmer et al., 2005) also appears due to social segregation and prey switching by female mountain lions. In that case, very heavy hunting of males (66%, Lambert et al., 2006) corresponds with female use of high elevation caribou range and male use of low elevation white-tailed deer range (Wielgus, unpublished results). It appears that hunting of mountain lions to reduce predation on sensitive mule deer and

**Table 2**

Differences in use versus availability of elevation within (paired t-test) and between (ANOVA) reproductive class(es) in lightly hunted and heavily hunted populations of mountain lions in Washington 2002–2008.

Season	Class	Used	Available	U-A	P	P (between classes)
<i>Lightly hunted</i>						
Summer	FK	966.69	976.23	−9.54	0.18	0.87
	F	934.55	937.77	−3.22	0.31	
	M	1058.78	1068.20	−9.42	0.22	
Winter	FK	805.82	829.49	−23.67	<0.01	0.36
	F	830.99	855.56	−24.56	<0.01	
	M	871.22	909.79	−38.56	<0.01	
<i>Heavily hunted</i>						
Summer	FK	1078.57	1047.42	31.15	0.01	0.04
	F	994.29	997.47	−3.19	0.43	
	M	975.22	1013.98	−38.76	0.11	
Winter	FK	836.85	836.90	−0.05	0.50	0.53
	F	845.95	858.64	−12.69	0.18	
	M	802.86	831.98	−29.13	0.09	

Bold indicates a significant difference in use versus availability of elevation.

**Table 3**

Results of Kolmogorov–Smirnov of differences in use versus availability of elevation between reproductive classes of mountain lion in lightly hunted and heavily hunted populations of mountain lions in Washington 2002–2008.

<i>Lightly hunted</i>					<i>Heavily hunted</i>			
	Class	FK	F	M		FK	F	M
Summer	FK	1	–	–	FK	1	–	–
	F	0.844	1	–	F	0.222	1	–
	M	0.958	0.735	1	M	<b>0.016</b>	0.236	1
Winter	FK	1	–	–	FK	1	–	–
	F	0.844	1	–	F	0.859	1	–
	M	0.707	0.971	1	M	0.188	0.313	1

threatened mountain caribou may have actually precipitated and caused the mule deer and caribou declines.

## 5. Conclusion

So far, the unanticipated cascade effects of male trophy hunting in mountain lions includes: 1) female mountain lion population decline (Lambert et al., 2006, Robinson et al., 2008, Cooley et al., 2009b, Wielgus et al., 2013), 2) increased sexual segregation (this paper), and 3) prey switching to declining secondary prey (Keehner et al., unpublished results, Wielgus, unpublished results). Similarly, Davidson et al., 2011 found socio-spatial behavior in African lions (*P. leo*) was negatively affected by trophy hunting in Africa. Johansson et al., 2015 found that retaliatory killing of snow leopards (*Panthera uncia*) may disproportionately increase male snow leopard mortality as male snow leopards are more likely to prey upon domestic livestock than females or young males. Historically, carnivore management has seemingly concluded that the removal of males from the population is simply compensatory in nature. Recent studies have demonstrated very clearly, that the numerical response of carnivore populations is not the only consideration managers should take into account when setting hunting seasons, methods, bag-limits or quotas. Socio-spatial behaviors, including the effects of segregation also affect valuable prey species. We encourage others to conduct similar studies in other potentially infanticidal carnivores such as grizzly bears, brown bears, black bears, leopards, jaguars, and tigers to see if adult male mortality has similar negative effects worldwide.

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