



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 km². 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 km². 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 (Teaway) 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 km². The mean age of males was 24 months (Cooley et al., 2009b). The mean home range size of females was 240 km² and males was 752 km² (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 km². The mean age of males was 41 months (Cooley et al., 2009b). The mean home range size of females was 199 km² and males were 348 km². 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).

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