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Effects of male targeted harvest regimes on prey switching by female mountain lions: Implications for apparent competition on declining secondary prey

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ABSTRACT

Apparent competition, or predator selection for rare secondary prey instead of abundant primary prey, is causing prey declines in many species worldwide. The causal mechanism for apparent competition is either lower intrinsic growth rate in the secondary prey or higher disproportionate predation by predators for secondary prey. Harvest regimes which target male carnivores are now widely accepted to result in increased sexually selected infanticide (SSI) because of rapid male turnover and immigration by non-sire males, and sexually segregated habitat use because of female avoidance of infanticidal males. If harvest regimes which target male mountain lions cause increased SSI and sexually segregated habitat use by females with young, it could also cause inverse prey switching by females with young or apparent competition in declining secondary prey. We tested for inverse prey switching by female mountain lions with young — from abundant increasing white-tailed deer at low elevations to declining mule deer at high elevations in a heavily hunted, sexually segregated population of mountain lions. The "no effect of targeted male harvest" hypothesis predicts that none or all sexes and reproductive classes of mountain lions will select for mule deer. The "targeted male harvest effect" hypothesis predicts that only females with young will select for declining mule deer. We rejected the "no effect of targeted male harvest" hypothesis and accepted the "targeted male harvest effect" hypothesis because only females with cubs selected for declining mule deer at high elevations and only during summer, when kittens were vulnerable to infanticide — other sex and reproductive classes selected for abundant increasing white-tailed deer at low elevations. We suggest that harvest regimes which focus on male harvest to reduce predation on declining secondary prey could be causing increased predation on declining secondary prey elsewhere.

1. Introduction

Traditional predator/prey dynamics theory is largely based on single predator/single prey systems that should show a Type 3 density dependent predation rate — whereby the predator functional (kills/predator), numerical (predators/area) and total (predation rate) responses decrease with decreasing prey density (Sinclair et al., 2006). Such a Type 3 response ensures that predation does not cause extirpation of prey. By contrast, Type 2 predation (inversely density dependent predation) increases as prey density decreases and could therefore cause extirpation of prey in the absence of prey refugia. Type 2 predation is rare in single predator/prey systems because the predator functional and numerical responses (hence total predation) must necessarily decrease with decreasing prey. However, apparent competition has been predicted and observed in multiple prey systems where the predator numerical response is determined by numbers of alternate primary, not secondary prey (Holt, 1977). In that case, predation can cause the secondary prey to decline in an inversely density dependent manner because the mortality rate of secondary prey increases as secondary prey density decreases (Allee et al., 1949).

In large mammal communities, apparent competition is the suspected or demonstrated cause of secondary prey declines in (at least) mountain caribou (*Rangifer tarandus*) (Seip, 1992; Kinley and Apps 2001; Wittmer et al., 2007; McLellan et al., 2010), porcupines (*Erethizon dorsatum*) (Sweitzer et al., 1997), roan antelope (*Hippotragus equinus*) (Harrington et al., 1999), mule deer (*Odocoileus hemionus*) (Robinson et al., 2002; Cooley et al., 2008), guanaco (*Lama guanico*) (Baldi et al., 2004; Novaro and Walker 2005), marmots (*Marmota vancouverensis*) (Bryant and Page, 2005), desert bighorn sheep (*Ovis canadensis*) (Gibson, 2006), Island fox (*Urocyon littoralis*) (Angulo et al., 2007), mountain bighorn sheep (*Ovis canadensis*) (Bourbeau-Lemieux et al., 2011), elk (*Cervus elaphus*) (Garrot et al., 2007), and Przewalski's horse (*Equus ferus*) (Van Duyne et al., 2009).

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In multiple prey systems apparent competition can occur if 1) Secondary prey cannot withstand proportional predation in sympatric prey communities because of lower intrinsic growth rate or 2) secondary prey are disproportionately preyed upon in both sympatric and allopatric prey communities (Holt, 1977; 1984; Holt et al., 1994). The ultimate cause of secondary prey decline is self-evident in the 1st case. Not so in the 2nd case. The question remains, why would relatively rare and declining secondary prey be preferentially selected by predators in the presence of abundant primary prey? The question is especially vexing when the secondary prey is allopatric (e.g., via elevation) to primary prey and shows no appreciable difference in vulnerability to predation (similar kill rate) or predation pay-off (similar biomass) — as it appears to be the case in our prey animal models: white-tailed deer (*Odocoilus virginianous*) and mule deer (Cooley et al., 2008; White et al., 2011).

The cause(s) of disproportionate selection usually remain unanswered (DeCesare et al., 2010), and the common management response is increased remedial hunting of predators (Ballard et al., 2001; Connoly, 1978; Logan et al., 1986; Ross and Jalkotzy, 1992; Lindzey et al., 1992, 1994; Almack 2000; Logan and Sweanor 2001; Lessard et al., 2005; Laundre and Clark, 2003; Laundre et al., 2007; Sanz-Aguilar et al., 2009; DeCesare et al., 2010). For example, a significant and steady decline in mule deer and corresponding increase in white-tailed deer has occurred throughout western North America over the last 40 years (Bleich & Taylor, 1998; Gill, 1999). In northeastern Washington, USA, and southeastern British Columbia, Canada; local populations of declining mule deer are now outnumbered by expanding white-tailed deer 4:1 (Robinson et al., 2002; Cooley et al., 2008). Robinson et al. (2002) found that selection for mule deer by mountain lion during summer in a sympatric mule deer and white-tailed deer community was the major factor in mule deer population decline in southeastern British Columbia. Cooley et al. (2008) also reported significant selection for mule deer and selection against sympatric white-tailed deer during summer in two other independent 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 mule deer during summer — increasing the encounter probability between predator and secondary prey (apparent competition hypothesis Holt, 1977). That suggests that mule deer may have been relatively easier to kill than more numerous sympatric white-tailed deer, but time between kills was similar between the two species, suggesting otherwise (Cooley et al., 2008). Regardless of the cause, sport hunting of mountain lion was further increased to mitigate mule deer declines in Idaho, British Columbia, and Washington (Lambert et al., 2006; Robinson et al., 2008; Cooley et al., 2009b).

Another possible hypothesis for disproportionate 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 differential habitat use (spatial segregation hypothesis). Cooley et al. (2009b) showed that increased remedial hunting of mountain lions to reduce predation on mule deer resulted in increased sexually selected infanticide (SSI) and sexually segregated habitat use — whereby females with cubs avoided numerous, potentially infanticidal immigrant males by selecting for high elevation areas (mule deer range) in summer, when kittens were vulnerable to infanticide. We now propose that increased remedial hunting may have actually exacerbated or caused apparent competition via sexual habitat segregation and prey switching by females with young — and that many other cases of apparent competition in other species may be exacerbated or caused by remedial hunting as well.

The goal of this investigation was to test the “apparent competition” or “no effect of hunting” and “spatial segregation” or “hunting effect” hypotheses for mountain lion selection of mule deer. The apparent competition hypothesis predicts that none or all sex/reproductive classes of mountain lion will select for mule deer, especially during summer, because of prey species overlap during that season. Further, elevations of mule deer and white-tailed deer kills should converge during summer as white-tailed deer move up into mule deer ranges. The spatial segregation or hunting effect hypothesis predicts that only females, and especially females with kittens, will select for mule deer during summer when most kittens are young and vulnerable to sexually selected infanticide. In addition, the elevation of mule deer kills will remain higher than those of white-tailed deer kills during summer as females with kittens maintain an elevation difference from potentially infanticidal males (Keehner et al., 2015).

2. Materials and methods

2.1. Study area

The study area is located in northeastern Washington, USA and southeastern British Columbia, Canada, and was defined by the sum polygon of all radio-marked female mountain lions. It covered 1312 km^2 of Northern Rocky Mountain Forest-Steppe–Coniferous Forest–Alpine Meadow (Bailey, 1995). 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 (*C. 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%/yr; female harvest = 16%/yr) to reduce predation on mule deer and reduce human/mountain lion conflicts. The population showed a pronounced (+16% per year) compensatory male immigration response to hunting (Robinson et al., 2008; Cooley et al., 2009a) and there was substantial evidence for sexually selected infanticide by those immigrant males (Cooley et al., 2009b), and sexually segregated habitat use (use of higher elevations) by females with cubs during summer (Keehner et al., 2015).

2.2. Animal capturing and monitoring

Mountain lion captures occurred during November through April of each year (2005–2008). The study area was searched for tracks and if found, hounds were released to tree mountain lions (Hornocker, 1970). Mountain lions were fitted with Lotek GPS4400S collars (Lotek Wireless, Newmarket, Ontario, Canada); 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 protocols.

Collars were programmed to attempt a location between 4 and 6 times per day. Individual mountain lions were assigned to one of three reproductive classes: female with kittens (FK); independent female (F) or independent male (M). Independent females were classified as female with kittens after kittens were discovered in the den. Females remained in that class so long as the kittens were still alive and accompanying the mother. Females with kittens reverted to independent female if kittens died or dispersed. Many females transitioned between both classes during the course of the study. Independent males were those animals that were independent of their mothers.

2.3. Prey availability

Prey availabilities were estimated for the entire study area (Neu et al., 1974; McCorquodale et al., 1986) but could not be estimated for each individual mountain lion's home range (Litvaitis et al., 1986). Prey availability within the study area was determined using two methods. The first method was based on aerial and ground count surveys conducted during 2003–2004 (Cooley et al., 2008). This method probably overestimated the proportion of white-tailed deer and underestimated the proportion of mule deer because female mountain lions (the primary predator of mule deer — see Results) declined at