



Research Article

# A Test of the Compensatory Mortality Hypothesis in Mountain Lions: A Management Experiment in West-Central Montana

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**ABSTRACT** Mountain lions (*Puma concolor*) are widely hunted for recreation, population control, and to reduce conflict with humans, but much is still unknown regarding the effects of harvest on mountain lion population dynamics. Whether human hunting mortality on mountain lions is additive or compensatory is debated. Our primary objective was to investigate population effects of harvest on mountain lions. We addressed this objective with a management experiment of 3 years of intensive harvest followed by a 6-year recovery period. In December 2000, after 3 years of hunting, approximately 66% of a single game management unit within the Blackfoot River watershed in Montana was closed to lion hunting, effectively creating a refuge representing approximately 12% (915 km<sup>2</sup>) of the total study area (7,908 km<sup>2</sup>). Hunting continued in the remainder of the study area, but harvest levels declined from approximately 9/1,000 km<sup>2</sup> in 2001 to 2/1,000 km<sup>2</sup> in 2006 as a result of the protected area and reduced quotas outside. We radiocollared 117 mountain lions from 1998 to 2006. We recorded known fates for 63 animals, and right-censored the remainder. Although hunting directly reduced survival, parameters such as litter size, birth interval, maternity, age at dispersal, and age of first reproduction were not significantly affected. Sensitivity analysis showed that female survival and maternity were most influential on population growth. Life-stage simulation analysis (LSA) demonstrated the effect of hunting on the population dynamics of mountain lions. In our non-hunted population, reproduction (kitten survival and maternity) accounted for approximately 62% of the variation in growth rate, whereas adult female survival accounted for 30%. Hunting reversed this, increasing the reliance of population growth on adult female survival (45% of the variation in population growth), and away from reproduction (12%). Our research showed that harvest at the levels implemented in this study did not affect population productivity (i.e., maternity), but had an additive effect on mountain lion mortality, and therefore population growth. Through harvest, wildlife managers have the ability to control mountain lion populations. Published 2014. This article is a U.S. Government work and is in the public domain in the USA.

**KEY WORDS** additive mortality, carnivore, compensatory mortality, cougar, hunting, life-stage simulation analysis, Montana, population dynamics, *Puma concolor*, survival.

Errington (1956) coined the term “doomed surplus” to describe animals that would die by other natural causes if not killed by predators. Many hunting programs assume a similar relationship to human harvest, namely, density-dependent compensatory mortality. Modern wildlife management and hunting programs are premised on the idea of sustainable yield, and the concept of a harvestable surplus

due to compensatory mortality (Larkin 1977). Under the compensatory mortality hypothesis, harvest mortalities are compensated by reductions in non-harvest mortality (compensatory mortality), increases in reproduction (compensatory natality), or immigration (Boyce et al. 1999, Williams et al. 2002, Turgeon and Kramer 2012). Evidence of compensation has been shown in a variety of species including game birds (Burnham and Anderson 1984, Sandercock et al. 2011), ungulates (Bartmann et al. 1992, Simard et al. 2013), and carnivores (Sterling et al. 1983, Sparkman et al. 2011). All mortality is not compensatory, however, as evidenced by the numerous populations that

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have been threatened or driven to extinction by overharvest (e.g., Baker and Clapham 2004, McGlone 2012). Managers would benefit from a better understanding of the life-history traits and harvest levels where mortality moves from compensatory to additive in many exploited populations (Sandercock et al. 2011, Peron 2013).

Carnivores are hunted for both sport, where population stability is desired, and population control, where mortality must be additive to achieve reduced population levels. In North America, perhaps because of their conflict with humans, a great deal of early research into the effect of harvest on a carnivore species focused on coyotes (*Canis latrans*). This work suggested that harvest mortality was largely compensatory through immigration and density-dependent or compensatory natality (Knowlton 1972, Todd and Keith 1983, Knowlton et al. 1999). These early findings, combined with a reluctance to study other disturbed or hunted populations of large carnivores, shaped management perceptions through the 1970s and 1980s (Frank and Woodroffe 2001). Recent research has suggested that hunting mortality in other carnivores may be almost perfectly additive (Creel and Rotella 2010, Murray et al. 2010).

Evidence of the additive nature of hunting to mountain lion mortality and population growth has been shown in past studies where populations were reduced through hunting, and/or increased once harvest level was reduced (Lindzey et al. 1992, Ross and Jalkotzy 1992, Lambert et al. 2006). Conversely, non-hunted populations often show high levels of intraspecific strife and mortality, leading some to speculate that hunting may be compensatory (Quigley and Hornocker 2010). The effect of harvest on a population is dependent on total harvest rate, age, and sex classes being harvested, and compensation for harvest by increases in survival or other vital rates such as maternity and immigration (Mills 2007).

The combined effects of harvest and dispersal include changes to age and social structure that may cascade through a hunted population, magnifying or reducing the effects of harvest. Mountain lions display high levels of juvenile dispersal (Chepko-Sade et al. 1987, Sweanor et al. 2000, Zimmermann et al. 2005). Males disperse to avoid inbreeding regardless of population density (intrinsic dispersal), whereas females disperse, albeit at much lower levels than males, to avoid intraspecific competition (Greenwood 1980, Logan and Sweanor 2001). Hunting can therefore skew the sex and age ratio of a population towards younger males as harvested males are quickly replaced through juvenile immigration (Robinson et al. 2008). Vertebrate species have adapted to specific age and sex population structures. Males, in general, reach sexual maturity more quickly than females because of reduced life spans (Jones et al. 2008, Ricklefs 2008). Deviations from “natural” population age and demographic structure could reduce productivity (Nussey et al. 2009). Reproductive senescence is common in mammalian females as they age (Packer et al. 1998, Berube et al. 1999). Hostetler et al. (2012) found reduced litter production in female mountain lions (Florida panthers) >9 years. Maternity of

mountain lions may be reduced in hunted populations if younger males do not breed successfully, or if female recruitment is restricted and kitten production is reduced as females senesce (Berube et al. 1999), both additive effects. Conversely, harvest may reduce direct resource competition among females, resulting in increased litter sizes or maternity rates (Ordiz et al. 2008), a compensatory effect.

Logan et al. (1986) and Logan and Sweanor (2001) suggested that removal of male mountain lions from a population may decrease survival of remaining resident males by disrupting social organization and increasing direct or exploitative competition for mates and territory. Also, the loss of dominant, territorial males may increase instances of infanticide, an unexpected additive form of mortality (Logan and Sweanor 2001). Male mountain lions may kill kittens to induce their mothers into estrous, thus increasing breeding opportunities (Packer et al. 2009). However, the role played by infanticide in shaping kitten survival remains unclear. Harvest programs can induce immigration of new males, thereby increasing infanticide rates and limiting population growth (Swenson et al. 1997). A high level of male turnover resulted in increased levels of infanticide in African felids (Whitman et al. 2004, Balme et al. 2010).

Unlike ungulate species that give birth in a single “birth pulse” in early spring, mountain lions give birth year-round. In the United States, mountain lions are most heavily hunted from September to March (Cooley et al. 2011), which exposes dependent kittens to the risk of starvation due to abandonment following harvest of their mothers, perhaps increasing their naturally high mortality (Logan and Sweanor 2001). Similar to the effects of hunting on adult mortality, however, how this source of mortality is compensated for by decreases in other natural mortality is not well understood.

Ultimately, the compensatory or additive effects of harvest are best measured at the population level in terms of population growth. Matrix population models are a widely used tool for exploring the relationship of various population parameters, or vital rates, on population growth (Getz and Haight 1989, Caswell 2001). Ecologists have used matrix models and the quantifiable properties of sensitivity and elasticity to mathematically describe the consequences of varying vital rates of several species with differing life strategies. Evolutionary theory suggests that natural selection will favor low levels of variation in population parameters that contribute most to population growth (Pfister 1998). In long-lived vertebrates, and other K-selected species, adult female survival normally has the highest demographic elasticity (Gaillard et al. 1998, 2000); that is, small changes in female survival will result in the largest proportional changes in population growth rate.

Although sensitivity analysis will reveal which vital rates have the greatest effect on population growth, those same vital rates may have such low natural variability that they functionally account for little variation in population growth between years. If K-selected species have adapted life strategies where the most important vital rates have the lowest degree of variability, hunting may disrupt this adaptive

**Table 1.** Predictions of how mountain lion population vital rates should respond to harvest under the compensatory and additive mortality hypothesis.

Vital rate	Compensatory mortality hypothesis	Additive mortality hypothesis
Reproduction		
Litter size	Increase	No effect or reduce
Maternity	Increase	No effect or reduce
Survival	No effect	Reduce
Dispersal		
Male emigration	Reduce	No effect
Female emigration	Reduce	No effect
Male immigration	Increase	No effect
Female immigration	Increase	No effect
Population growth	No effect	Reduce

strategy by increasing their variance. Wisdom et al. (2000) developed an extension of elasticity analysis called life-stage simulation analysis (LSA), which measures the direct effects of annual variance in vital rates on population growth.

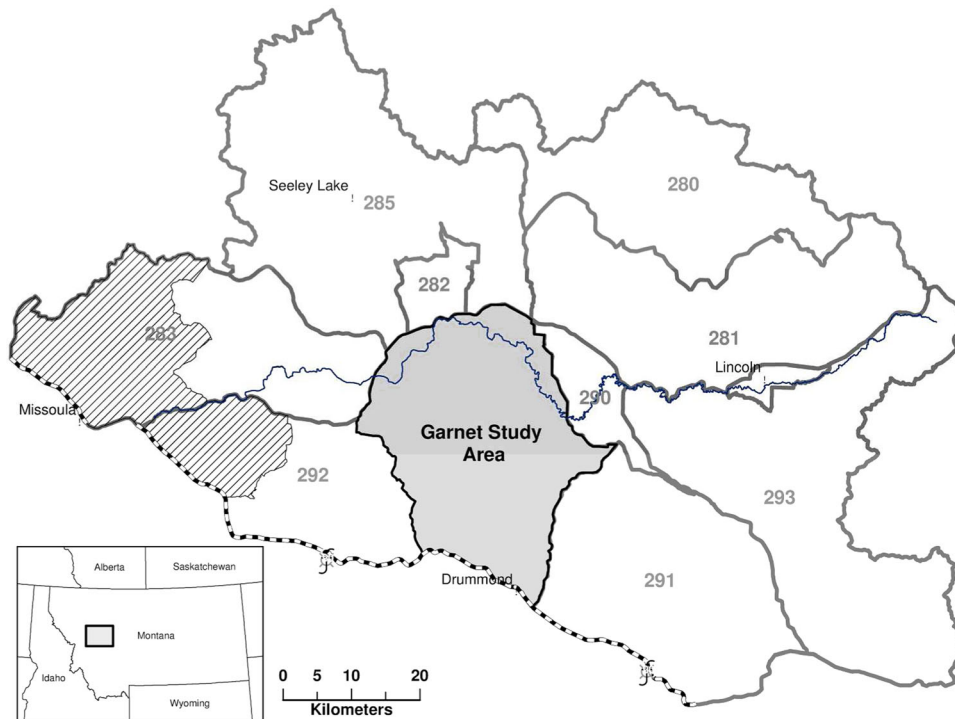
We used temporal and spatial variation in harvest structure to test the compensatory mortality hypothesis by directly comparing population parameters (i.e., survival, maternity, etc.), population structure (i.e., mean age of independent males), and population growth between hunted and non-hunted segments of a mountain lion population. Specifically, if harvest mortality was compensatory, we expected population growth to tend toward stability regardless of harvest level because of compensatory reductions in other mortality sources, or through increases in reproduction and recruitment (Table 1). If harvest mortality was additive, we

expected population growth to decline with increased harvest because of reduced survival accompanied by no change in reproduction or recruitment (Table 1). We also used matrix population modeling, sensitivity analysis, and LSA to quantify how harvest affects the natural variability of vital rates, and how those changes are reflected in annual population growth.

## STUDY AREA

We conducted the study in the Blackfoot River watershed (7,908 km<sup>2</sup>) in Powell, Granite, Lewis and Clark, and Missoula counties in West-Central Montana. Hunting district 292 served as our refuge area, hereafter referred to as the Garnet study area (915 km<sup>2</sup>). This area was protected from hunting for 6 years of the 9-year study (Fig. 1). The entire watershed is characterized by relatively moderate rolling topography, with gentle to moderate slopes dissected by steep limestone canyon areas along drainages (Brainerd 1985). This area is representative of much of western Montana, a mountainous mix of private (i.e., Plum Creek Timber Company and private land owners) and public lands (i.e., Bureau of Land Management, Helena and Lolo National Forests) with elevations ranging from 1,160 m to 2,156 m (Montana Department of Fish, Wildlife and Parks 2004). Daily mean temperatures range from -8.7°C in January to 16.5°C in July with annual precipitation ranging from 19 cm to 33 cm, occurring primarily from December to June (Western Regional Climate Center, Ovando, MT).

Dominant land cover varies from high-elevation mixed lodgepole pine (*Pinus contorta*)-subalpine fir (*Abies lasiocarpa*)



**Figure 1.** The Garnet study area (915 km<sup>2</sup>), and greater Blackfoot River watershed (7,908 km<sup>2</sup>) in western Montana. Numbers (i.e., 292) represent Montana Fish, Wildlife and Parks regional mountain lion management unit designations.

stands, to more mesic Douglas-fir (*Pseudotsuga menziesii*)-western larch (*Larix occidentalis*) stands at mid-elevations, and Douglas fir, ponderosa pine (*P. ponderosa*), and aspen (*Populus tremuloides*) at low elevations. Valley bottoms consist of a mixture of irrigated and dry land agriculture, cattle rangelands, and native bunchgrass-sagebrush (*Artemisia* spp.)-juniper (*Juniperus scopulorum*) communities (Lehmkuhl 1981). The majority of the low to mid-elevation forests have been logged in the past 50 years (Raithel 2005).

Ungulate prey species present in the area included elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), and moose (*Alces alces*). Elk populations were stable over the course of the study (Montana Department of Fish, Wildlife and Parks 2004), whereas deer populations may have been recovering from the El Niño-induced severe winter of 1996–1997 (Montana Department of Fish, Wildlife and Parks 2006). Cattle grazing occurred on private and public lands, however, cattle and other livestock depredations by mountain lions were rare. Carnivores besides mountain lions included black bear (*Ursus americanus*) and grizzly bear (*Ursus arctos*). Smaller predators included bobcat (*Lynx rufus*), Canada lynx (*Lynx canadensis*), coyote (*C. latrans*), wolverine (*Gulo gulo*), pine marten (*Martes americana*), and long-tailed weasel (*Mustela frenata*). Wolf (*Canis lupus*) had not recovered during the study period; the first confirmed pack established in 2006, the last year of our study (Montana Department of Fish, Wildlife and Parks 2006).

## METHODS

In December 2000, following 3 years of heavy harvest, approximately 66% of a single hunting district was closed to mountain lion hunting, effectively creating a refuge representing approximately 12% (915 km<sup>2</sup>) of the greater Blackfoot watershed (7,908 km<sup>2</sup>) in West-Central Montana (Fig. 1). Hunting continued in the remainder of the watershed, but harvest levels declined between 2001 and 2006 as quotas were reduced (Table 2).

### Capture and Monitoring

From 1997 to 2000, we applied capture efforts approximately equally across the entire watershed (Fig. 1). Following protection of the Garnet study area, we focused most capture efforts there, towards the goal of capturing all resident individuals (i.e., census). In the remainder of the Blackfoot,

we continued to monitor radioed lions marked during the first 3 years of the study including re-instrumenting individuals when their radiocollar's battery life was spent. In addition, we monitored animals that either dispersed from the Garnet or had home ranges overlapping the boundary between the 2 areas.

We used trained hounds to tree mountain lions when we located fresh tracks in the snow. We darted treed animals and drugged them with a 0.06 ml/kg estimated weight mixture of ketamine hydrochloride and xylazine hydrochloride (1.45 ml xylazine to 10 ml ketamine) delivered using a Pneu-Dart Model 193SS cartridge fired rifle with disposable darts (Pneu-Dart, Inc., Williamsport, PA). We gave animals the antagonist yohimbine hydrochloride to counteract the xylazine before release.

We estimated age of captured mountain lions by tooth replacement, wear, gum recession, and cementum age analysis (Ashman et al. 1983, Laundre et al. 2000). We fitted radiocollars (Telonics, Mesa, AZ) depending on the size and age of the individual: an expandable (20–34 cm) kitten collar equipped with either a Mod-073 or Mod-305 transmitter, or an adult collar equipped with a Mod-500 transmitter. We located collared animals from fixed-wing aircraft approximately twice per week. Beginning in 2001, we fitted Telonics global positioning system (GPS) collars programmed to acquire a location every 5 hours to newly collared animals and replaced very high frequency (VHF) collars on already marked animals as opportunity allowed.

We collared both newborn kittens at the den, and those traveling with newly collared adult females. We collared newborn kittens without chemical immobilization approximately 1 month from the time the mother localized at a den site. When we located kittens outside the den (from 3 to 12 months) we treed and immobilized them as with adults. Expandable Mod-073 collars remained on kittens up to 7 months of age; mod-305 collars remained on kittens up to 10 months of age; and a mod-500 adult collar was worn by the animal through adulthood. Capture and handling protocols were approved by Montana Fish, Wildlife and Parks and conducted by their staff (Montana Department of Fish, Wildlife and Parks 2007).

### Population Characteristics

*Sex and age structure.*—We calculated a minimum population for the Garnet study area each year by back-

**Table 2.** Mountain lion harvest, quotas (harvest/quota), and harvest density (animals/1,000 km<sup>2</sup>) for the Blackfoot River watershed in West-Central Montana, 1998–2006. Beginning in December 2000, the Garnet was managed separately from the remainder of the Blackfoot watershed.

Area	Sex	1998	1999	2000	2001	2002	2003	2004	2005	2006
Garnet	Female	8 <sup>a</sup>	8 <sup>a</sup>	8 <sup>a</sup>	0	0	0	0/1 <sup>b</sup>	0	0
	Harvest density	8.74	8.74	8.74						
	Male	5 <sup>a</sup>	6 <sup>a</sup>	6 <sup>a</sup>	0	0	0	1/1 <sup>b</sup>	1/1	1/1
	Harvest density	5.46	6.55	6.55				1.09	1.09	1.09
Black-foot	Female	35/30	42/41	30/30	15/15	10/9	4/3	4/3	0/0	1/0
	Harvest density	4.42	5.31	3.79	1.89	1.26	0.5	0.5	0	0.12
	Male	41/40	30/33	27/29	19/21	12/9	8/7	7/7	6/7	8/7
	Harvest density	9.61	9.10	7.20	4.29	2.78	1.51	1.39	0.75	1.13

<sup>a</sup> Garnet managed as part of the Blackfoot watershed.

<sup>b</sup> One either-sex permit issued in 2004.

calculating the lifespan of all mountain lions known to have been present in the study area including collared and harvested animals (Logan and Sweanor 2001, Stoner et al. 2006, Robinson et al. 2008). This technique assumes that animals collared or harvested without being collared at time  $t$  were present within the watershed but undetected at time  $t - 1$  (specific to each animal's age and sex); as such, this method may underestimate population levels towards the end of the study period because of fewer sampling occasions. We assumed that all males were immigrants, whereas all females were recruited from within the population. Therefore, we backdated males to 24 months of age, immigrating into the population after their second birthday. We assumed females were philopatric and were likely born inside the Blackfoot watershed; however, we could not be sure if they were born inside or outside the protected Garnet study area. Therefore, we backdated females to 12 months, accounting for our philopatric assumption without biasing further any total population estimate of the Garnet study area. We used a Z-test to compare mean ages and proportion of the population consisting of adults of each sex between the hunted and non-hunted populations (Zar 1999). We hypothesized that harvest would reduce the mean age of males while increasing their proportion in the population because of a compensatory immigration response to harvest, whereas harvest would increase the mean age of adult females in the population while reducing their proportion in the population because of reduced recruitment (i.e., high juvenile mortality and/or low immigration) as resident animals aged.

**Reproduction.**—We estimated maternity, the mean number of young born per reproductive female per year (Caswell 2001), and its component, litter size, based on females of reproductive age within the Garnet study area only. We felt monitoring effort was sufficient within the Garnet that no litters born to, or traveling with, collared females would be missed, but logistical constraints prevented this level of monitoring in the larger watershed. We estimated average litter size based on kittens observed at den sites (i.e., <7 weeks), which assumes no kitten mortality had occurred prior to observation. The compensatory mortality hypothesis predicts that litter size will increase in a hunted population because of increased available resources (Table 1). The additive mortality hypothesis predicts that litter size will be unaffected or decline with harvest because of the age structure of females (Table 1). We tested the effect of harvest on litter size (as observed at den sites when kittens were <7 weeks) using a repeated-measures analysis of variance (ANOVA) comparing litter size within the Garnet study area during hunting and non-hunting periods. We used a repeated-measures ANOVA as the sample consisted of females with multiple litters (Zar 1999).

We observed age at dispersal and, for animals that did not leave the study area, first reproduction by radiocollaring dependent kittens and juveniles. As some hunted populations have a population skewed towards older females, we also tested how or if female age affected litter size. Using a repeated-measures ANOVA, we tested for an age effect on litter size in the females that we monitored (Zar 1999).

Reduced fertility in older females could be an additive effect of harvest (Table 1).

Some researchers have used litter size, mean birth interval, and proportion of females traveling with young as surrogate measures of maternity (e.g., Lambert et al. 2006); however, these measures may introduce a bias by excluding females that fail to reproduce. We estimated maternity rate based on the total number of kittens born to all radiocollared females of reproductive age (>24 months) monitored, thus including the proportion of non-reproductive females in the population. As with litter size, the compensatory mortality hypothesis predicts that maternity rate will increase in the hunted population because of reduced competition and increased resource availability, whereas the additive mortality hypothesis predicts that maternity will be reduced or unchanged between hunted and non-hunted periods (Table 1). We tested for a hunting effect on maternity rate using a Z-test to compare the mean annual maternity rate within the Garnet study area during hunting and following protection (Zar 1999).

**Dispersal.**—We defined dispersal as a juvenile establishing a home range with <5% overlap of its natal home range, whereas we considered juveniles establishing home ranges with >5% overlap to be philopatric (Logan and Sweanor 2001). Dispersal rate was based on the number of independent juveniles in each year that moved outside their natal home range compared to the number monitored. We modeled juvenile dispersal as a binomial function of the estimated total population size for males and females separately (i.e., we used a generalized linear model specifying a logit link and binomial family; Hardin and Hilbe 2007). The additive mortality hypothesis predicts density-independent dispersal, whereas the compensatory mortality hypothesis suggests reduced dispersal of both sexes in the hunted population (Table 1).

### Survival and Mortality

We examined mountain lion mortality in 3 ways: survival modeling, survival rate analysis, and cause-specific mortality analysis. We used survival modeling to examine the effect of independent variables (i.e., sex, age, geographic location, and hunting pressure as dictated by quota levels) on mountain lion survival and to objectively determine the best method of breaking the population into segments or cohorts with similar survival experiences. We used survival analysis to calculate and compare the survival probabilities of animals within those cohorts. Finally, we calculated and compared cause-specific mortality rates.

We derived a spatially explicit encounter history from telemetry data for each individual mountain lion to estimate survival rates and test hypotheses about factors influencing survival. We removed duplicate same-day locations from GPS collar data and combined them with VHF data to create a continuous record based on calendar time for each animal (Fieberg and DelGiudice 2009). We censored (interval truncated) animals not located for >61 days until relocated (Winterstein et al. 2001). During the first 4 years of the study, before we began to deploy GPS collars, we scheduled

telemetry flights twice a week. During some periods, most notably the winter and spring of 2001, we could conduct flights only once a month because of weather, financial, and logistical constraints. We began deploying GPS collars in October 2001 and aerial telemetry flights were again limited during short periods for the remainder of the study. The 61-day period allowed some animals to be missed on 2 consecutive flights during these times of infrequent aerial telemetry. If not located after 61 days, we right-censored animals at the date of their last location in the study area.

We modeled factors influencing mountain lion survival using a combination of manual backward stepwise and best-subsets model selection (Hosmer et al. 2008). First, we conducted a univariate analysis using Cox regression (Cox 1972) to test the significance of sex, age, and hunting quota on mountain lion survival. We coded sex as an indicator variable with females coded as 1 and males coded as 0. We coded age and quota level as continuous variables, with age estimated in months and quota based on the annual-, sex-, and location-specific quotas as set by Montana Fish, Wildlife and Parks (Table 2).

We modeled mountain lion survival on the landscape by constructing 12 spatiotemporal a priori models, each suggesting a different hypothesized response in survival of the population to our experimental harvest design. We discuss 4 of these models in detail here (see online Supplementary Material for graphical depiction and explanation of all 12). For instance, the single-population (1-segment) model tested the hypothesis of total compensatory mortality by modeling survival as constant across the landscape and study period; equivalent to a null model relative to management (Fig. S1). The other 3 models represented different ways in which hunting mortality might be manifest. The management model tested the hypothesis that survival responded to small incremental changes in management or quota level, thus dividing the population into 6 segments, equivalent to a global model relative to management (Fig. S2, see also Table 2). The 3-segment population model grouped animals across the drainage between 1998 and 2000 (segment 1), then divided the population into 2 segments (segments 2 and 3) based on the protection of the Garnet study area following 2000, while hunting continued in the remainder of the Blackfoot drainage (Fig. S3). Under the compensatory mortality hypothesis, hunting replaces other forms of mortality, causing survival to remain relatively constant. Therefore, this model would not be supported if the compensatory hypothesis were true because survival between segments 2 and 3 would not differ. The 4-segment model (Fig. S4) tested the hypothesis that survival before protection of the Garnet study area differed between the watershed and the Garnet although management was the same for both areas, and that survival increased significantly outside the protected area once female quotas were set to 0. We used Akaike's Information Criterion for small sample sizes ( $AIC_c$ ) to select among competing models to evaluate the strength of evidence for each hypothesis regarding the relationship of survival to temporal and geographical quota levels, as well as

age and sex (Burnham and Anderson 1998, Hosmer et al. 2008).

We modeled survival time using a parametric Weibull distribution (Hosmer et al. 2008):

$$\ln(T) = \beta_0 + \beta_1 x + \sigma \times \varepsilon \quad (1)$$

where  $T$  is survival time,  $\beta_0$  the model intercept,  $\beta_1$  the covariate,  $\sigma$  a parameter estimating the shape of the hazard function based on the data, and  $\varepsilon$  the error term. We checked model specification using a link test (Cleves et al. 2004).

We calculated annual survival rates for 3 age classes of mountain lions: kitten (1–12 months), juvenile (13–24 months), and adult (>25 months) for each population model segment (as delineated by our a priori model selection, see above) using the Nelson–Aalen estimator (Nelson 1972, Aalen 1978). Because kittens were first collared at a range of ages (1–12 months) rather than only at the den (i.e., within the first 7 weeks), our estimate of kitten survival is biased high. We based survival rates on a biological year (1 Dec–30 Nov) reflecting the start of the hound-hunting season on 1 December. We raised the cumulative hazard estimate for each segment to the power of  $1/t$ , where  $t$  represents the length of that period in years, to calculate a mean annual survival rate across that period. To test for differences in survival between the various segments of the population, we used a Peto–Prentice test (Peto and Peto 1972, Prentice 1978, Hosmer et al. 2008). The compensatory mortality hypothesis predicts no difference in survival between hunted and non-hunted segments of the population. Conversely, reduced survival in the hunted population would indicate additive mortality.

We calculated cause-specific mortality rates using cumulative incidence functions (CIFs; Kalbfleisch and Prentice 1980, Heisey and Patterson 2006). These functions allow the estimation of mortality rates in the presence of competing risks, which are defined as >1 mutually exclusive, cause of death (Pintilie 2006). Unlike the modified Mayfield or Heisey–Fuller (Mayfield 1961, Heisey and Fuller 1985) methods of mortality estimation, which assume a normal or constant distribution of mortality risk, CIFs are non-parametric and make no assumption regarding the underlying hazard distribution.

We grouped mortalities by 6 causes. We classified animals that were harvested as part of a legal hunt, or kittens that were orphaned and starved after their mothers were shot as hunting mortality. Illegal mortality included animals killed in snares or otherwise killed out of season. We classified animals that died naturally because of starvation, disease, or intraspecific strife (including cases of infanticide) as natural mortalities. The category depredation included animals shot because of conflict with humans (i.e., livestock depredation permits, and self-defense). The final 2 categories were vehicle collisions and unknown, where a clear cause of death could not be determined.

We used cause-specific mortality rates to test the compensatory mortality hypothesis in 2 ways. First, we regressed survival of juvenile and adult mountain lions against hunting mortality. We omitted kittens because of

their non-independence from adult females. We included juveniles because they spend approximately half of their juvenile year independent of their mothers and, unlike kittens, no juveniles starved after being orphaned by hunting. If hunting were compensatory, we would expect survival to remain constant as hunting mortality increased (Table 1). Conversely if hunting mortality were additive, we would expect a monotonic decrease in survival with an increase in hunting mortality (Williams et al. 2002). This regression used survival and hunting mortality probabilities based on the management model population structure (i.e., 6 population segments based on varying hunting quota levels, see Fig. S2). A similar analysis could have been conducted on annual survival and mortality values (e.g., Murray et al. 2010). However, because the management goal during the first 3 years of the study was to reduce the population, almost ensuring additive mortality, using annual rates may have biased our analysis towards inferring additivity of hunting mortality. We assumed this structure was less biased than an annual model towards an additive finding because the first 3 years of mortality are captured in a single data point and the model contains both hunting and natural mortality based on the protected and hunted portions of the Blackfoot watershed following December 2000.

We also tested the compensatory mortality hypothesis in adult and kitten survival by comparing the CIF for hunting and all other mortality sources between the hunted and non-hunted periods. Pepe and Mori (1993) provided a method for comparing the CIF of a main mortality source and competing risks simultaneously between 2 groups. This method tests the hypothesis of equality in the CIF of a main event (i.e., hunting mortality) while also testing for equality in the remaining competing risks (Pintilie 2006). If hunting mortality were additive, we would expect an increase in the hunting mortality rate, whereas the CIF for competing risks would be constant (i.e., no compensatory decrease in other mortality sources in the presence of hunting). Conversely, if hunting mortality were compensatory, we would expect an increase in the hunting CIF, with a concurrent reduction in the CIF for competing risks in the hunted population.

### Population Modeling and Growth

Methods described thus far examined how harvest affected individual population parameters (i.e., survival, maternity, etc.). Ultimately, we were interested in how changes in these parameters combined to affect population growth. To quantify the population effects of harvest, we constructed a stage-based, 2-site, dual-sex Leslie matrix model (Leslie 1945) in MATLAB<sup>®</sup> (The MathWorks, Natick, MA). The model consisted of 2 transition matrices joined by juvenile dispersal terms and was based on the 2 top survival models using the estimated survival and fecundity parameters described below. We calculated stochastic growth rates and associated standard deviations by running 10,000 2- to 6-year iterations (dependent on population segment, see Supplementary Material).

*Vital rates.*—We used age- and sex-specific survival rates previously discussed, estimated using the Nelson–Aalen

estimator. We estimated variance of the Nelson–Aalen survival estimator following Anderson et al. (1997):

$$\text{Var}(\hat{S}(t)) = (\hat{S}(t))^2 V^2(t) \quad (2)$$

and

$$V^2(t) = \sum_{(i:t_i < t)} \frac{d_i(r_i - d_i)}{r_i^3} \quad (3)$$

where  $\hat{S}(t)$  is the survival estimate to time  $t$ ,  $d_i$  is the number of deaths at time  $t_i$ , and  $r$  is the number at risk at time  $t_i$ . We then used White's method to remove sampling variance from annual estimations of survival variance, and included this value of process variance in a beta-distributed variance vector in each matrix model (White 2000).

We assumed that females did not breed until becoming adults (>24 months; Root 2004, Robinson et al. 2008, Treves 2009). We also assumed an equal ratio of male and female kittens (total fecundity divided equally between sexes; Logan and Sweanor 2001). We modeled variance in maternity using a stretched beta distribution with a maximum value of 2.5 annually, or maximum litter size of 5 every 2 years (Morris and Doak 2002). We modeled fecundity as a birth-pulse post-breeding process. Kittens entered the matrix as newborns and fecundity was the product of adult female survival ( $S_a$ ) and average annual maternity ( $M_a$ ; Morris and Doak 2002):

$$F = S_a \times M_a \quad (4)$$

We calculated a dispersal rate based on the number of independent juveniles in each year that moved between the Garnet study area and the remainder of the Blackfoot drainage compared to the number monitored. In this sense, our modeling definition of dispersal does not match the more traditional definition (reported above), where juveniles that establish home ranges with >5% overlap of their maternal home range are considered to be philopatric rather than dispersers (Logan and Sweanor 2001). Our model assumed a closed system consisting only of 2 populations, the Garnet study area and the remainder of the Blackfoot watershed. Therefore, for parameterization of our population models, an animal could have established a home range adjacent or overlapping with its mother's (philopatry) but still be classified as a disperser if its new home range was primarily (>50%) outside its maternal area (the Garnet area or the remainder of the drainage). We did not consider juveniles that dispersed out of the Blackfoot watershed completely to be dispersers because they were effectively lost to this system and population model and we therefore censored them.

*Initial abundance and density dependence.*—We set initial 1998 abundances at 37 total animals (i.e., kittens, juveniles, and adults) for the Garnet study area based on a minimum population back-calculated using known-aged animals, and 283 total individuals in the remainder of the Blackfoot drainage, extrapolating a similar total density (4.0 mountain lions/100 km<sup>2</sup>) to the remainder of the watershed. We started all models in 1998 at a stable age distribution, then the mean modeled age distribution for further projections.

For instance, we started the 3-segment population model in 1998 with a stable age distribution and projected for 3 years, when survival rates changed or diverged between the Garnet and remainder of the Blackfoot. We projected a second period from 2001 to 2007 based on the age distribution outputs from the 1998 to 2000 model.

We applied a ceiling density dependence to stochastic models that affected survival of adults only (>24 months; Root 2004). We set a ceiling density of 27 adults for the Garnet study area and 210 adults for the remainder of the Blackfoot drainage based on an average density of 3 adults per 100 km<sup>2</sup>. This liberal estimate of maximum adult density was commensurate with observed levels of 2.92 mountain lions/100 km<sup>2</sup> in Wyoming (Anderson and Lindzey 2005) and 2.58 mountain lions/100 km<sup>2</sup> in northeastern Washington (Robinson et al. 2008) both hunted populations.

*Sensitivity and life-stage simulation analysis.*—If harvest is additive, its effect on total population growth should vary based on which population parameter is affected in an additive manner and how reliant population growth is on that parameter. We tested the effect of each population parameter on population growth rate through perturbation. The sensitivity of lambda to each vital rate (i.e., survival, maternity, and dispersal) was calculated by individually reducing each rate by 0.10 and recalculating lambda for each population as well as the total population combined (Caswell 2001). The inclusion of lower-level parameters (maternity and female survival combined to calculate fecundity) in our matrix model negated the use of elasticities (Caswell 2001). We conducted an LSA to quantify the effects of variance on population growth within the Garnet study area separately during the hunted period (1998–2000), and the non-hunted period (2001–2006), comparing the  $r^2$  values for each vital rate, for each period (Wisdom et al. 2000). We conducted sensitivity analysis using the 3-segment population model. Because we were only interested in the effect of harvest on vital rate variability and population growth, we conducted LSA on only the Garnet portion of the 3-segment population model pre- and post-harvest (i.e., segment 1 vs. segment 2, see Fig. S3).

Finally, given the results of our sensitivity and LSA analysis, we constructed a deterministic population model to quantify how varying levels of maternity, female kitten survival, and adult female survival combine to affect population growth. In this model, we fixed all male survival rates as well as juvenile female survival at the average levels observed for the entire study population, but ran successive simulations in which we incrementally increased kitten and adult female survival from 0.01 to 1.0, at 3 levels of maternity (1.08, 1.29, and 1.40; maternity during the hunting period, mean maternity across the study period, and maternity during the non-hunting period, respectively). We used standard matrix analysis techniques (Caswell 2001) to calculate the projected long-term population growth rate ( $\lambda$ ) for each possible parameter combination. The probability of a kitten surviving to become a juvenile was the combined function of kitten and adult survival (i.e., kitten survival  $\times$  adult survival) to mimic the effect of kitten abandonment

following an adult's death. We modeled fecundity levels as in the other population models.

## RESULTS

### Harvest, Capture, and Monitoring

From 1998 to 2006, 299 mountain lions (158 M and 141 F) were harvested from the Blackfoot watershed, with 41 (18 M, 23 F) harvested from the Garnet study area. Mean age of harvested animals was 2.88 years (M  $\bar{x}$  = 2.64 yr and F  $\bar{x}$  = 3.16 yr). A female quota existed in all but the last 2 years of the study in the Blackfoot watershed. This quota was filled or exceeded in each year (i.e., 100–133% quota), and females composed 37% of the animals harvested (Table 2).

We captured 121 individual mountain lions 152 times between January 1998 and December 2006, including 82 kittens, 8 juveniles, and 31 adults. Of these, we collared 117 individuals and monitored them for habitat use and survival. We monitored animals for an average of 502 days (range: 7–3,231 days) with males remaining on the air for shorter periods ( $\bar{x}$  = 284 days) than females ( $\bar{x}$  = 658 days). We recorded known fates for 63 animals, and right-censored the remainder. We used right-censored animals in analysis until loss due to collar failure ( $n$  = 16), dispersal from the Blackfoot River drainage ( $n$  = 7), or survival to the end of the study ( $n$  = 31).

### Population Characteristics

*Sex and age structure.*—The minimum total population count for the Garnet study area ranged from 37 mountain lions (4.0/100 km<sup>2</sup>) in 1997 to a low of 20 (2.2/100 km<sup>2</sup>) in 1999, before recovering to 33 (3.6/100 km<sup>2</sup>) in 2006 (Table 3). The average age of adult females increased from 3.53 years during the hunted period to 4.83 in the non-hunted population, although this difference was not significant ( $Z$  = -1.47,  $P$  = 0.14). Similarly, the average age of adult males increased from 2.73 to 3.53, also a non-significant increase ( $Z$  = -1.46,  $P$  = 0.14). The oldest radiocollared female monitored during the study was 10 years old and the oldest male was 6 years old.

From 1997 to 2006, the Garnet population averaged 37% adult females, 15% adult males, 17% juveniles, and 30% kittens. Although the proportion of adult females in the population remained relatively constant between the hunted and non-hunted phases ( $Z$  = 1.20,  $P$  = 0.22), the proportion of adult males in the hunted population was higher (21%) than in the non-hunted (10%;  $Z$  = 2.87,  $P$  < 0.01; Table 3.).

*Reproduction.*—Mean total litter size of litters visited early in the den (<7 weeks) was 2.92 ( $n$  = 24, 95% CI: 2.70–3.13). Litter size was not affected by hunting ( $F_{1,11}$  = 0.27,  $P$  = 0.61). Of 32 litters where birth month could be confirmed, mountain lions gave birth in all months but December, February, and March. Most litters were produced from July to October. The mean age of sires in our population was 35 months (Onorato et al. 2011). Fourteen known-aged females gave birth to their first litter at a mean age of 31.4 months (range: 23–37 months). We found no effect of female age on litter size ( $F_{6,6}$  = 1.39,  $P$  = 0.35). Average birth interval was 602.6 days (95% CI: 503–702



**Table 3.** Minimum total mountain lion population (including kittens, juveniles, and adults), mean adult age, and proportion of total population consisting of adult male and female mountain lions censused on 1 December, 1997–2006, Garnet study area, western Montana.

Year	Minimum total population	Mean adult age (yr)		Adult proportion of total population	
		Male	Female	Male	Female
1997	37	2.29	3.79	0.189	0.378
1998	27	2.83	3.91	0.222	0.407
1999	20	2.8	3.7	0.25	0.5
2000	21	3	2.75	0.19	0.381
Hunted mean		2.73	3.53	0.21	0.42
2001	25	3.67	3.75	0.12	0.32
2002	24	3	4.44	0.125	0.375
2003	30	4	4.82	0.1	0.367
2004	32	3	4.91	0.094	0.344
2005	33	3.5	5.27	0.121	0.333
2006	33	4	5.8	0.061	0.303
Non-hunted mean		3.53	4.83	0.10	0.34

days) or 19.8 months. Approximately 58% of females  $\geq 24$  months gave birth each year, and 89% of females were traveling with dependent young.

The mean maternity rate across the study period was 1.29 ( $n=9$ , 95% CI: 0.84–1.76) kittens per female per year. Although maternity was lower during the hunting period ( $\bar{x}=1.08$ ,  $n=3$ , 95% CI: 0–3.59) compared to the protected population ( $\bar{x}=1.40$ ,  $n=6$ , 95% CI: 1.02–1.78), this difference was not significant ( $Z=-0.53$ ,  $P=0.59$ ). In 1999, we documented no litters born to collared females; however, because of heavy harvest pressure, we monitored only 2 adult females.

**Dispersal.**—We monitored 66 mountain lions (39 F and 27 M) during their juvenile year (13–24 months of age) during 1998–2006. Of these 66 individuals, 47 survived to independence. Mean age of dispersal was 15 months ( $n=33$ , range: 11–23 months). Dispersal was severely constrained in the hunted population before 2001. During the first 3 years of study when harvest level was high, only 2 of 12 juvenile females survived to independence. One dispersed out of the Blackfoot drainage, and 1 established a philopatric home range inside the Garnet study area. Between 2001 and 2006, during protection of the Garnet from hunting, we monitored 54 juvenile mountain lions, 45 of which survived to independence. In total, female juveniles showed essentially equal levels of dispersal ( $n=12$ ) and philopatric behavior ( $n=14$ ). We found no relationship between population level and dispersal rate of juvenile females ( $Z_5=0.60$ ,  $P=0.55$ ). We did not document any philopatric behavior in radiocollared juvenile males ( $n=19$ ; 100% dispersal).

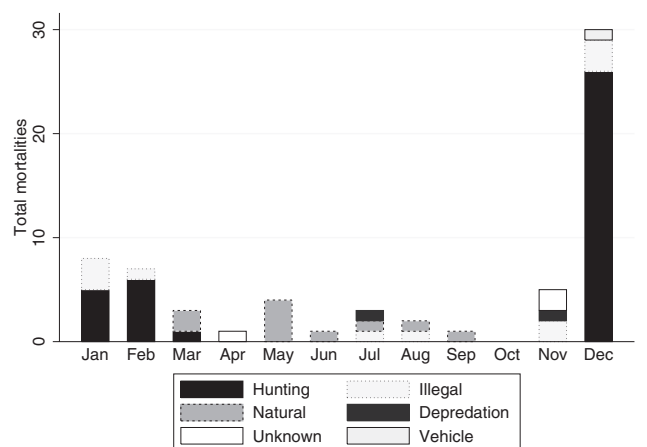
### Survival and Mortality

We recorded mortalities in every month but October, with the majority coinciding with the start of the hound-hunting season in December (Fig. 2). Sex was the best predictor of mountain lion survival followed by quota and age. Females were 73% less likely than males to die (hazard ratio [HR] = 0.27,  $Z=-4.79$ ,  $P<0.01$ ), with risk of mortality increasing 10% with each numerical increase in quotas (HR = 1.10,  $Z=2.77$ ,  $P<0.01$ ). Risk of mortality was highest for kittens, declining by 1% for each month survived

(HR = 0.99,  $Z=-1.52$ ,  $P=0.11$ ). Although age was not a significant model covariate at the 0.05 level, Hosmer and Lemeshow (2000) recommend retaining variables with a probability of significance of 20% ( $P=0.2$ ) for inclusion in further modeling following univariate analysis. This recommendation, coupled with our desire to create age-based population models as the next phase of our research, led to inclusion of all 3 variables in our subset models, with age broken into 3 categories.

Two models, 3-segment and 4-segment, including 3 age classes and sex, were the top models (Table 4; Figs. S3 and S4). The management model, which we thought best fit the actual quota levels, was the seventh ranked model (Table 4). A linktest showed that both the 3-segment ( $Z=-0.51$ ,  $P=0.61$ ) and the 4-segment ( $Z=-0.58$ ,  $P=0.56$ ) models were properly parameterized.

Mean annual survival, pooling all individuals across all years, was 0.651 (SD = 0.03). Survival of kittens ( $\bar{x}=0.785$ , SD = 0.05) and juveniles ( $\bar{x}=0.592$ , SD = 0.09) did not vary by sex (kitten:  $\chi^2_1=0.14$ ,  $P=0.70$ ; juvenile:  $\chi^2_1=0.18$ ,  $P=0.66$ ). Among adults, female survival ( $\bar{x}=0.786$ ,



**Figure 2.** Timing and cause of 63 radiocollared mountain lion mortalities, 1998–2006, in the Blackfoot River watershed, Montana.

**Table 4.** Top models in best-fit analysis of mountain lion survival patterns in Blackfoot watershed Montana, 1998–2006. Null model log likelihood (LL) was –54.2168 (8 remaining models in Table S1).

Rank	Model	LL	df	AIC <sub>c</sub>	ΔAIC <sub>c</sub>
1	3-Segment	–36.1078	7	87.1115	0
2	4-Segment	–35.5328	8	88.2269	1.1154
–					
7	Management	–35.4528	10	92.7088	5.5973
–					
10	1-Segment	–44.1786	5	98.8296	11.7181

SD = 0.05) was higher than males ( $\bar{x} = 0.515$ , SD = 0.12;  $\chi^2_1 = 5.04$ ,  $P = 0.02$ ).

Adult survival (F:  $n = 13$ , M:  $n = 3$ ) was similar between the Garnet study area and the remainder of the Blackfoot drainage before December 2000 ( $\chi^2_1 = 0.45$ ,  $P = 0.50$ ), but differed once hunting was halted in the Garnet ( $\chi^2_1 = 17.62$ ,  $P < 0.01$ ; F:  $n = 38$ , M:  $n = 17$ ; Table 5), consistent with the additive mortality hypothesis. Once adult female quotas were reduced to 0 outside the Garnet study area (segment 4 of the 4-segment population model, see Fig. S4), adult survival increased from 0.60 to 0.87 ( $\chi^2_1 = 3.08$ ,  $P = 0.08$ ) compared to survival before quota reduction (population segment 2). The marginal significance in total adult survival is explained by an increase in adult female survival while adult male survival remained relatively constant (Table 5).

**Table 5.** Mean annual survival rates of radiocollared mountain lions broken into population segments according to our 3- and 4-segment model structures 1998–2006, western Montana. Sample sizes ( $n$ ) include animals that were counted in the risk pool of more than 1 model segment. The 3-segment model assumes that survival was similar across the watershed prior to protection of the Garnet (combined hunted), but differed after December 2000 when hunting ceased in the Garnet (Garnet protected and Blackfoot hunted). The 4-segment model assumes survival differed among 4 groups: 1) Garnet study area before December 2000 (Garnet hunted), 2) Garnet study area after hunting ceased in the area (Garnet protected), 3) Blackfoot watershed before 2005 (Blackfoot hunted), and 4) Blackfoot watershed during the last 2 years of the study when female quotas were reduced to 0 (Blackfoot hunted reduced). Survival of kittens and juveniles did not vary by sex; therefore, we present pooled estimates.

Model and segment	Area (yr)	Age and sex	$n$	Mean survival	SD
3-segment 1	Combined hunted (1998–2000)	Kitten	24	0.6566	0.09
		Juvenile	12	0.3117	0.12
		Female adult	13	0.6737	0.09
		Male adult	3	0.7167	0.21
3-Segment 2	Garnet protected (2001–2006)	Kitten	60	0.8505	0.06
		Juvenile	43	1.0	
		Female adult	25	0.9654	0.03
		Male adult	10	0.7788	0.15
3-Segment 3	Blackfoot hunted (2001–2006)	Kitten	29	0.9672	0.05
		Juvenile	44	0.6920	0.08
		Female adult	31	0.7130	0.08
		Male adult	16	0.4699	0.13
4-Segment 1	Garnet hunted (1998–2000)	Kitten	16	0.7281	0.11
		Juvenile	10	0.2326	0.13
		Female adult	9	0.5740	0.13
		Male adult	3	1.0	
4-Segment 2	Blackfoot hunted (1998–2004)	Kitten	34	0.5352	0.15
		Juvenile	32	0.2735	0.13
		Female adult	29	0.5985	0.11
		Male adult	7	0.5387	0.13
4-Segment 3	Garnet protected (2001–2006)	Kitten	60	0.6151	0.12
		Juvenile	43	1.0	
		Female adult	25	0.9654	0.03
		Male adult	10	0.7788	0.15
4-Segment 4	Blackfoot hunted reduced (2005–2006)	Kitten	9	0.9048	0.12
		Juvenile	21	0.6218	0.14
		Female adult	17	0.8746	0.09
		Male adult	10	0.5488	0.21

Hunting was the main cause of mortality for all age and sex classes across the study period, accounting for 36 of 63 mortalities documented. Additional factors were illegal mortalities, natural, unknown, depredation, and vehicle collision (Table 6). Across the study period, mountain lions in the Blackfoot watershed had a 22% annual probability of mortality due to hunting. Regression analysis of hunting-caused mortality and survival of juveniles and adults showed a significant negative slope of  $-0.97$  ( $F_{1,4} = 21.97$ ,  $P = 0.01$ ), consistent with the additive-hunting mortality hypothesis and suggesting hunting mortality is completely additive (Fig. 3). For adults and juveniles, PepeMori tests of equality in cause-specific mortality rates were significant (hunting mortality  $\chi^2 = 31.18$ ,  $P < 0.01$ ; all other mortality  $\chi^2 = 3.58$ ,  $P = 0.06$ ). The difference in other mortality sources between hunted and non-hunted populations was due to higher mortality in the hunted populations, supporting the additive-hunting mortality hypothesis.

During the heavy hunting period before closure of the Garnet study area, 6 kittens died of starvation following the harvest of their mothers, leading to a kitten cause-specific mortality rate of 0.41 (SE = 0.14). During the same period, no kittens died of natural mortality; however, following closure of the Garnet study area, 6 kittens died of natural causes including cannibalism or infanticide, a cause-specific mortality rate of 0.16 (SE = 0.06). Kitten mortality

**Table 6.** Number of cause-specific mortalities and associated mortality rates (cumulative incidence function, CIF) of radiocollared mountain lions in 1998–2006 in western Montana.

Age class	Sex	Hunting	Illegal	Natural	Depredation	Unknown	Vehicle
Kitten	Male	2		5	1		1
	Female	4		2			
Juvenile	Male	9	2		1		
	Female	4	1			1	
Adult	Male	8	2				
	Female	9	6	3		2	
Total		36	11	10	2	3	1
CIFs		0.221	0.055	0.038	0.007	0.011	0.006
SE		0.03	0.01	0.01	0.006	0.006	0.006

attributed to hunting was higher during the 3-year period of heavy hunting than in the 6 years following protection of the Garnet study area ( $\chi^2 = 7.58, P = 0.01$ ). However, we found no change in all other sources of mortality between the 2 periods ( $\chi^2 = 0.49, P = 0.48$ ), supporting the additive mortality hypothesis.

### Population Modeling and Growth

We monitored 47 kittens until independence from their mothers. One female and 6 males dispersed out of the watershed completely and were censored from dispersal rate calculations. Dispersal rates of juveniles from the Garnet study area to the Blackfoot was 0 prior to the cessation of hunting, but increased to  $0.82 \pm 0.19$  per year for females and  $0.71 \pm 0.39$  per year for males once the Garnet was closed to hunting. No radiocollared juveniles immigrated into the Garnet study area from the remainder of the Blackfoot watershed, where hunting was allowed, although low juvenile survival reduced the number of independent juveniles in our Blackfoot sample to 4 (3 F and 1 M), all of which remained in the hunted area.

Our population models indicated that the mountain lion population in the Blackfoot watershed declined by approximately 11–12% per year between 1998 and 2000 (Table 7). With cessation of hunting in the Garnet study area in 2001, the 3-segment model predicted recovery beginning immedi-

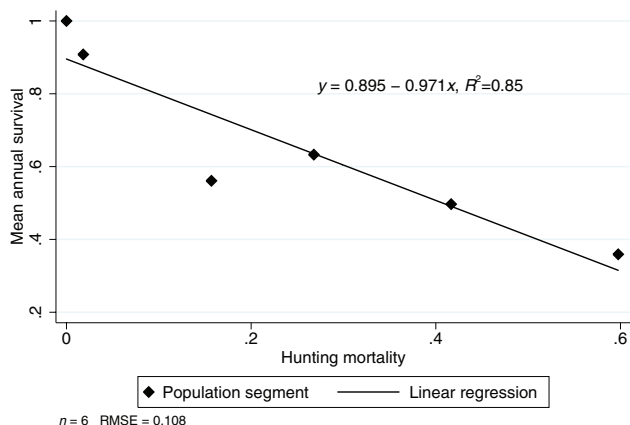
ately, with the watershed population growing at approximately 3% annually (Table 7). The 4-segment model indicated that mountain lion numbers in the watershed were still slightly declining between 2001 and 2004, before climbing rapidly following reductions in quotas outside the Garnet in 2005 (Table 7). Both models predicted a watershed-wide population level in January 2007 slightly below 1998 levels (Fig. 4). Both models also predicted final abundances in the Garnet study area of approximately 28 individuals, 9 fewer than at the start of the study. The trend in watershed-wide estimates from both modeled populations matches the minimum count for the Garnet based on backdating (Fig. 4); however, both models predicted a slower recovery within the Garnet study area than the minimum count for the number of animals based on backdating (Fig. 4).

The growth rate of the watershed-wide, mountain lion population was most sensitive to changes in adult female survival followed by juvenile and kitten female survival and maternity (Fig. 5). Negative sensitivities of dispersal from the Garnet to the hunted area of the watershed following 2001 attest to the lower survival probability of adults in the hunted area compared to the protected Garnet. LSA showed that hunting increased the importance of adult female survival to population growth by 50%, while reducing the significance of kitten survival and maternity (Fig. 6). The sum of adult female survival, female kitten survival, and maternity accounted for 92% and 57% of the variability in annual population growth of non-hunted and hunted populations, respectively. In general, adult female survival levels below 0.80 should lead to declining population levels (Fig. 7).

## DISCUSSION

### Population Characteristics

Hunting directly reduced population size from 37 to 20 animals between 1997 and 2000, but population parameters such as litter size, birth interval, maternity, age at dispersal, and age at first breeding were not significantly affected. Increased harvest increased the proportion of adult males in the population, while reducing the average age of both adult males and females, likely because of a compensatory immigration response into vacated home ranges (Cooley et al. 2009). We had hypothesized that female recruitment would be reduced by harvest, perhaps more greatly than



**Figure 3.** Regression of the relationship of hunting mortality and survival of independent mountain lions, 1998–2006, in the Blackfoot River watershed, Montana based on the management model population breakdown (see also Fig. S2).

**Table 7.** Modeled population growth rate ( $\lambda$ ;  $\pm$ SD) based on the 3- and 4-segment population models in western Montana, 1998–2006.

Study area	Model	1998–2000 ( $\lambda$ )	2001–2004 ( $\lambda$ )	2005–2006 ( $\lambda$ )
Garnet	3-Segment	0.8686 (0.08)	1.024 (0.06)	1.024 (0.06)
	4-Segment	0.9352 (0.11)	0.9855 (0.05)	1.016 (0.09)
Blackfoot	3-Segment	0.8797 (0.08)	1.033 (0.06)	1.033 (0.06)
	4-Segment	0.8829 (0.12)	0.9375 (0.11)	1.176 (0.10)
Combined	3-Segment	0.8795 (0.08)	1.034 (0.05)	1.034 (0.05)
	4-Segment	0.8928 (0.11)	0.9475 (0.09)	1.155 (0.09)

males because of shorter female dispersal distance and reduced juvenile survival, resulting in an increased adult female age structure. Both female and male immigration were likely occurring during the heavy harvest period despite very low juvenile survival in the study area. The change in age structure of the population to a greater proportion of males did not affect productivity.

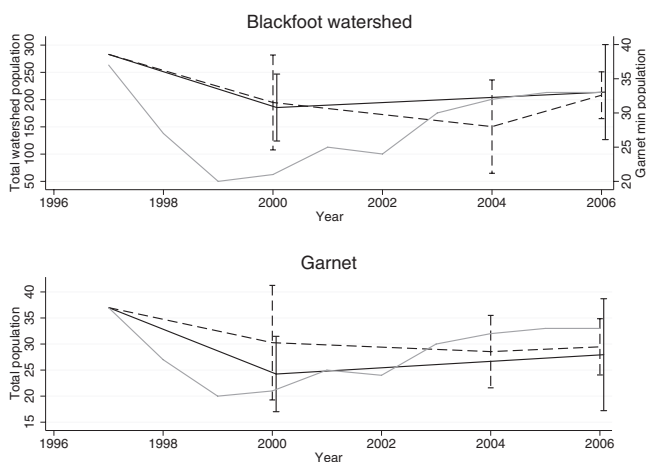
We estimated a mean litter size of 2.92 (measured at the den <7 weeks); however, this did not differ between hunted and unhunted periods. Estimates of litter size have ranged from a low of 1.9 in Florida (Maehr and Caddick 1995) to a high of 3.1 in southeastern British Columbia (Spreadbury et al. 1996), with most averaging around 2.5 (Logan and Sweanor 2001). Logan and Sweanor (2001), Cooley et al. (2009), and most recently Hostetler et al. (2012) have likely produced the least biased estimates of litter size by visiting den sites within the first month of birth, producing means of 3.0 ( $n=53$ ), 2.55 ( $n=33$ ), and 2.6 ( $n=94$ ), respectively. Similarly, our estimated birth interval of 19.8 months closely matched others in the literature, including 17.4 in New Mexico (Logan and Sweanor 2001), 19.7 in Alberta (Ross and Jalkotzy 1992), and 24.3 in Utah (Lindzey et al. 1994).

We found no effect of hunting on maternity rates, and the mean maternity rate of 1.29 was also similar to other published rates (e.g., New Mexico ranged from 1.3 to 1.6 kittens/F/yr [Logan and Sweanor 2001], whereas

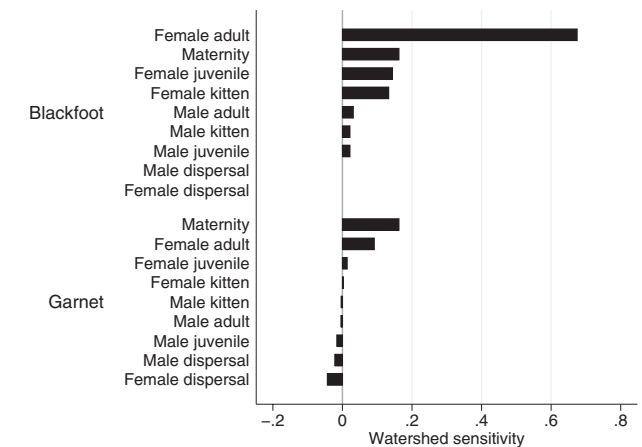
Robinson et al. [2008] and Cooley et al. [2009] reported maternity rates in hunted populations of 1.2 and 1.1 kittens/F/yr. Onorato et al. (2011) found the mean age of sires in our population, 35 months (range: 15–57 months), was younger than reported elsewhere. For instance, Logan and Sweanor (2001) found that 71% of litters in their non-hunted population were sired by males 35–88 months of age. However, as indicated above, the younger age structure of the male population during the hunted period did not affect kitten production.

Mean age at dispersal in our study population was similar to other mountain lion studies, where dispersal occurred between 10 and 33 months (Sweanor et al. 2000). Levels of philopatry were also similar to non-hunted populations. Sweanor et al. (2000) found that 68% of female recruits came from the local population, compared to a 50% philopatry rate in juvenile females in our work. We documented 100% male juvenile dispersal following protection from hunting.

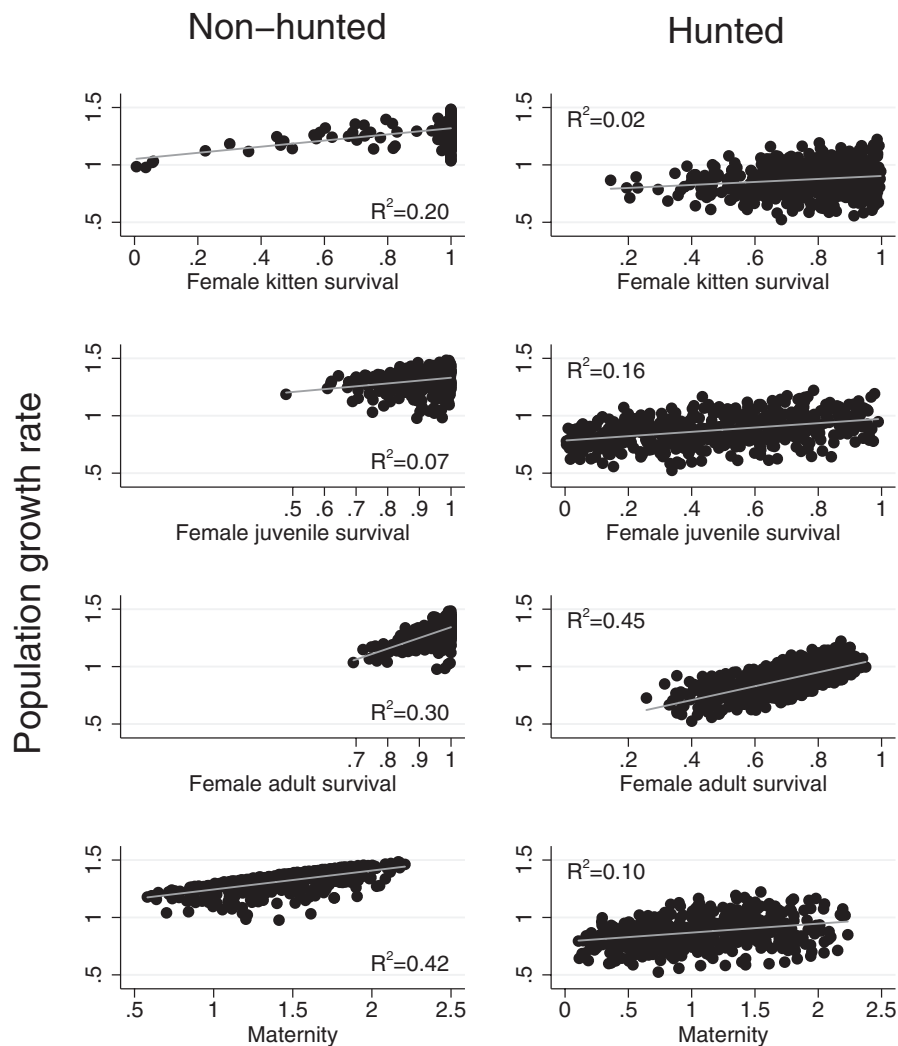
Perhaps our most striking finding of the effects of hunting on the characteristics of this mountain lion population was the elimination of emigration during the heavy harvest period. Although this result may suggest a compensatory response (i.e., increased philopatry) of juveniles to reduced conspecific densities, juvenile survival was reduced to a level such that only 2 females and no males survived to dispersal



**Figure 4.** Projected population levels ( $\pm 1$  SD) for the entire Blackfoot watershed and Garnet study area based on the top population models: 3-segment model (solid black line) and 4-segment model (dashed line). The minimum population for the Garnet study area, based on backdating known-aged animals, is included for comparison (solid gray line).



**Figure 5.** Sensitivities of mountain lion population growth to matrix vital rates of the 3-segment population model, 2001–2006. Maternity sensitivity is for both the Garnet and Blackfoot hunted area subpopulations in western Montana. For ease of interpretation, we present only sensitivities of the entire watershed population based on the 3-segment model 2001–2006; the sensitivities for all population segments from other population models were similar.



**Figure 6.** Life-stage simulation analysis (LSA) for mountain lions in the Garnet study area in West-Central Montana during the hunted and protected periods from 1998–2006. The  $R^2$  value describes the proportion of the variation in population growth explained by variation in the vital rate. We omitted values for males because their survival rates and associated variances had little effect on population growth.

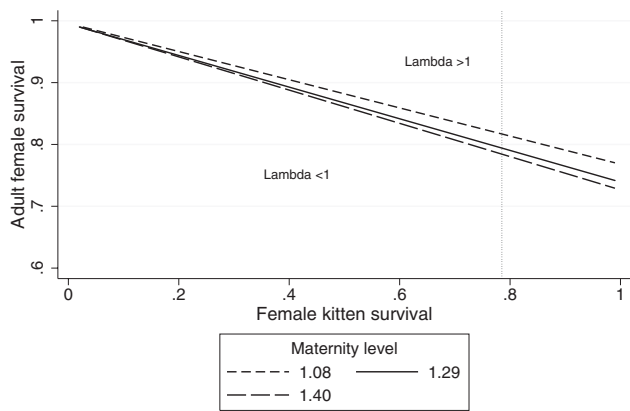
age (Table 5). Metapopulation dynamics are an increasingly important focus of mountain lion management and immigration, and emigration can play a major role in balancing hunted and non-hunted mountain lion populations (Beier 1993, Robinson et al. 2008, Cooley et al. 2009). Harvest levels equivalent to those recorded during the first 3 years of our study may severely reduce a population’s ability to act as a source of immigration to other areas, affecting not only the focal population level, but also those populations surrounding it (Liu et al. 2011).

### Survival and Mortality

Human-caused mortality shaped the survival of mountain lions in our study area, with hunting being the leading cause of mortality. The compensatory mortality hypothesis posits that harvest reduces the probability of animals experiencing other sources of mortality, thus allowing survival rates to remain relatively constant. We found an almost perfectly linear decrease in total survival of adults and juveniles with increased hunting mortality. We also found that mortality

due to all other causes (i.e., illegal, natural, depredation, vehicle, and unknown) was actually lower in the non-hunted population when compared to the hunted population. Both of these findings support the additive mortality hypothesis. The 3-segment model demonstrated the distinct difference between harvest pressures and resultant survival within the Garnet study area and remainder of the Blackfoot following the restriction of hunting in 2001. We interpret the relatively poor performance of the management model as evidence that the small incremental reductions in quotas following 2000 (Table 1) did not result in significant differences in population-level survival rates.

We believe an important mechanism rendering the effects of harvest as additive is kitten mortality due to starvation following harvest of adult females. We found an essentially equal number of kitten mortalities due to the direct effects of hunting through abandonment and natural mortality following closure of the Garnet to hunting. However, because of the timing of hunting mortalities (early in the biological yr), and the longer period of monitoring and



**Figure 7.** The relationship between mountain lion female kitten survival, adult female survival, and population growth at maternity rates of 1.08, 1.29, and 1.4. Areas above the lines represent possible lambda values greater than 1.0 and areas below represent survival levels that may lead to a decline in population. The dotted reference line represents our kitten survival estimate of 0.785 from 1998 to 2006 in the Blackfoot River watershed, Montana.

sample size following closure of the Garnet to hunting, estimated mortality rates due to hunting were significantly higher. The main influence of hunting on kitten survival may be starvation due to abandonment, not infanticide, and reductions in natural mortality do not compensate for hunting losses of kittens. Our results regarding the additive nature of hunting mortality in mountain lion populations build on Cooley et al. (2009). The additive effects of harvest, not only on adults but also through the orphaning of kittens, suggests that hunting, especially of adult females, shapes survival in hunted populations and has the potential to quickly reduce population levels.

Logan and Sweanor (2001) described the “sledgehammer approach,” where hunting quotas are set mainly by the previous season’s hunter success rate. As success rates decline, quotas may be reduced. However, because of a lack of inexpensive and reliable methods for tracking populations, even reduced quotas may not match existing population levels leading to further declines (Fryxell et al. 2010). Our survival modeling suggested that incremental reductions in quotas outside the protected Garnet study area did not result in significant increases in adult survival until female quotas were reduced to 0, possibly because of a mismatch between quota levels and existing population levels.

### Population Modeling and Growth

Matrix population models based on the structure of our 2 top survival models resulted in similar predicted population-level outcomes. They suggested that the mountain lion population in the greater Blackfoot watershed was declining annually between 11% and 12% before protection of the Garnet study area in 2001, but recovered to levels slightly below 1998 by the end of the study in 2007. This was due to protection of the Garnet area, dispersal out of the protected Garnet, and reduced quotas in the remainder of the watershed beginning in 2004. Differences in the predicted level of decline, and the speed and level of the recovery is the result of slightly different estimated survival rates for the various survival

model segments. Our estimates of kitten survival were biased high because of inclusion of kittens first marked as late as 12 months. However, even with this optimistic estimate of kitten survival, both population models predict declining populations in response to the heaviest harvest levels. If our kitten sample was based purely on animals marked at the den, our estimate of survival would most certainly be lower as would our estimate of population growth, thus strengthening our conclusion of harvest being additive.

Our sensitivity analyses showed that maternity was second in importance to female survival rates in influencing population growth rates. Sensitivity analysis does not account for annual variability, as the LSA does. Although maternity rate was held constant for all models at 1.29 kittens per female per year, fecundity is a function of maternity and adult female survival. Differences in fecundity also partially explain the different performance of each model segment.

Sensitivity analysis also showed that dispersal of both juvenile males and females from the protected Garnet into the hunted Blackfoot watershed had a strong negative effect on Garnet population growth and a weak negative effect on growth in the watershed as a whole. The population demonstrated a negative sensitivity of dispersal from the Garnet to the Blackfoot (Fig. 5), which is due to the lower survival rates in the unprotected portion of the Watershed. The matrix model suggested that juveniles would be better off remaining where their probability of survival and reproduction were higher (i.e., inside the Garnet).

Our LSA clearly demonstrated the effect of hunting on the normal population dynamics of mountain lions. In the non-hunted population, adult female survival accounted for approximately 30% of the variation in population growth between years, whereas reproduction (kitten survival and maternity) accounted for approximately 62%. Hunting reversed this balance, shifting the reliance of population growth towards adult survival (45% of the variation in growth), and away from reproduction (12%). In general, we found little effect of male survival on population growth. In the non-hunted segment of our population, male survival accounted for less than 1% of the variability in annual population growth; this level increased to 5% in the hunted population.

By varying 3 important vital rates to population growth (adult female survival, female kitten survival, and maternity) in a deterministic matrix model, we showed that adult female survival rates  $>0.80$  (depending on kitten survival) are required for population growth (Fig. 7). However, kitten survival estimated with minimal bias due to delayed marking (e.g., Cooley et al. 2009, Hostetler et al. 2010) suggests that rates may rarely be  $>0.50$  (see also Logan and Sweanor 2001). At that level, adult female survival  $<0.85$  will likely result in population reduction (Fig. 7). Consistent with these results, Lambert et al. (2006) modeled broad mountain lion population declines in British Columbia, Washington, and Idaho with adult female survival rates of 0.77. Our estimates of mean kitten survival may have been biased high as the average age of a kitten when first marked was 4.7 months. As a result, our population models may slightly overestimate

true growth. However, the predictions of our deterministic model regarding the relationship of kitten survival, adult female survival, maternity, and population growth (Fig. 7) are not affected by our measure of kitten survival.

Immigration and emigration have dramatic effects on real population growth rates when compared to modeled rates that do not account for dispersal. Our population models assumed a closed system consisting of only 2 populations, the Garnet and the remainder of the Blackfoot drainage. We found no juvenile dispersal from the Blackfoot back into the Garnet and therefore could not model the effect of immigration into the Garnet. We found a difference of approximately 8 animals between our modeled population estimates, and our minimum count for the Garnet. This small difference over a 9-year period could be explained by as few as 3 litters that were born inside the Garnet and were not accounted for by our estimate of mean maternity rates. However, immigration into the Garnet was likely occurring, but from outside the Blackfoot watershed. Accounting for immigration and emigration, Cooley et al. (2009) showed real population decline ( $\lambda = 0.91$ ) in a heavily hunted area with adult female survival estimated at 0.66. Without immigration, population growth would have been significantly lower, that is,  $\lambda = 0.78$ . That same study found an essentially stable real population growth rate ( $\lambda = 0.98$ ) in a lightly hunted population with adult female survival of 0.87, with emigration reducing modeled growth from 1.10.

## MANAGEMENT IMPLICATIONS

Our research indicates that mountain lion populations are affected by human harvest through additive effects on survival of all age classes and a resultant disruption of juvenile dispersal. We found no effect of harvest on reproductive parameters (i.e., litter size, birth interval, maternity, age at dispersal, and age at first breeding). The consistency in litter size and associated birth interval and maternity rate observed by several studies with varying levels of protection suggests that mountain lions do not possess the ability to respond to harvest through increased reproduction. This lack of elasticity in reproduction and therefore recruitment increases the need for connectivity to facilitate immigration into hunted populations. The high reliance on adult female survival for population growth should dictate very conservative female harvest unless population reduction is the stated management goal. Our results show the strong effect of harvest on targeted populations through shaping survival, and perhaps on neighboring untargeted populations by affecting dispersal patterns. Given the limitations of techniques of abundance estimation currently available and the effect of harvest on mountain lion populations, we recommend lion population objectives and harvest strategies that account for this lack of precision. A source-sink or zone management strategy, as proposed by Logan and Sweaner (2001) would protect the biological integrity of mountain lion populations, while providing public harvest opportunity and flexibility to managers in addressing management concerns.

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