

Linking resource selection and mortality modeling for population estimation of mountain lions in Montana



Hugh S. Robinson^{a,b,*}, Toni Ruth^c, Justin A. Gude^d, David Choate^e, Rich DeSimone^d, Mark Hebblewhite^f, Kyran Kunkel^g, Marc R. Matchett^h, Michael S. Mitchellⁱ, Kerry Murphy^j, Jim Williams^k

^a Panthera, New York, NY 10018, USA

^b College of Forestry and Conservation, University of Montana, Missoula, MT 59812, USA

^c Hornocker Wildlife Institute/Wildlife Conservation Society, Salmon, ID 83467, USA

^d Montana Fish Wildlife and Parks, Helena, MT 59620, USA

^e Ecology Center and Berryman Institute, Utah State University, Logan, UT, USA

^f Wildlife Biology Program, University of Montana, Missoula, MT 59812, USA

^g University of Montana, Missoula, MT 59812, USA

^h U.S. Fish and Wildlife Service, Charles M. Russell Wildlife Refuge, Lewiston, MT, USA

ⁱ US Geological Survey, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT 59812, USA

^j Hornocker Wildlife Institute/Wildlife Conservation Society, Jackson, WY, USA

^k Montana Fish Wildlife and Parks, Kalispell, MT 59901, USA

ARTICLE INFO

Article history:

Received 20 November 2014

Received in revised form 8 May 2015

Accepted 11 May 2015

Keywords:

Harvest

Leslie matrix

Metapopulation

Montana

Puma concolor

ABSTRACT

To be most effective, the scale of wildlife management practices should match the range of a particular species' movements. For this reason, combined with our inability to rigorously or regularly census mountain lion populations, several authors have suggested that mountain lions be managed in a source-sink or metapopulation framework. We used a combination of resource selection functions, mortality estimation, and dispersal modeling to estimate cougar population levels in Montana statewide and potential population level effects of planned harvest levels. Between 1980 and 2012, 236 independent mountain lions were collared and monitored for research in Montana. From these data we used 18,695 GPS locations collected during winter from 85 animals to develop a resource selection function (RSF), and 11,726 VHF and GPS locations from 142 animals along with the locations of 6343 mountain lions harvested from 1988–2011 to validate the RSF model. Our RSF model validated well in all portions of the State, although it appeared to perform better in Montana Fish, Wildlife and Parks (MFWP) Regions 1, 2, 4 and 6, than in Regions 3, 5, and 7. Our mean RSF based population estimate for the total population (kittens, juveniles, and adults) of mountain lions in Montana in 2005 was 3926, with almost 25% of the entire population in MFWP Region 1. Estimates based on a high and low reference population estimates produce a possible range of 2784 to 5156 mountain lions statewide. Based on a range of possible survival rates we estimated the mountain lion population in Montana to be stable to slightly increasing between 2005 and 2010 with lambda ranging from 0.999 (SD = 0.05) to 1.02 (SD = 0.03). We believe these population growth rates to be a conservative estimate of true population growth. Our model suggests that proposed changes to female harvest quotas for 2013–2015 will result in an annual statewide population decline of 3% and shows that, due to reduced dispersal, changes to harvest in one management unit may affect population growth in neighboring units where smaller or even no changes were made. Uncertainty regarding dispersal levels and initial population density may have a significant effect on predictions at a management unit scale (i.e. 2000 km²), while at a regional scale (i.e. 50,000 km²) large differences in initial population density result in relatively small changes in population growth rate, and uncertainty about dispersal may not be as influential. Doubling the presumed initial density from a low estimation of 2.19 total animals per 100 km² resulted in a difference in annual population growth rate of only 2.6% statewide when

* Corresponding author at: Panthera, 8 West 40th Street, 18th Floor, New York, NY 10018, USA. Tel.: +1 646 786 0409; fax: +1 646 786 0401.
E-mail address: hrobinson@panthera.org (H.S. Robinson).

compared to high density of 4.04 total animals per 100 km² (low initial population estimate $\lambda = 0.99$, while high initial population estimate $\lambda = 1.03$). We suggest modeling tools such as this may be useful in harvest planning at a regional and statewide level.

© 2015 Elsevier B.V. All rights reserved.

1. Introduction

In North America, the mountain lion (*Puma concolor*) is hunted throughout much of its range. Wildlife managers generally apply 1 of 3 models in the harvest of mountain lions: general season (unlimited numbers of either sex may be harvested), limited entry (harvest is limited by restricting the number of licenses sold), and quota system (harvest is limited by season closure once a prescribed number of animals are taken). A fourth “zone management” (Logan and Sweanor, 2001) or “metapopulation” model (Laundre and Clark, 2003) has been proposed but has seen limited application to date. These harvest strategies are thought to reduce the risk of overharvest by ensuring a sustainable loss of the total population (limited entry), reduction of female mortality (quota system), or preservation of source populations that sustain hunted areas (metapopulation model).

To be effective in conserving mountain lion populations, both the limited entry and quota systems require managers have some knowledge of the true mountain lion population level or its possible range. Overestimation of total population, and therefore quotas or tags issued, can quickly lead to overkill and a rapidly declining population (Lambert et al., 2006). Conversely, underestimation of the true population may lead to unnecessary limitations of public recreational opportunities. To date, no accurate method exists to broadly estimate mountain lion populations (Choate et al., 2006). Intensive collaring programs have been employed to estimate density; however these techniques are labor intensive, costly, and impractical for estimation of populations at broad geographic scales. As a result, most jurisdictions rely on hunter effort and harvest trends, expert opinion, hunter testimony, or other indices to determine population and harvest levels (Anderson and Lindzey, 2005; McBride et al., 2008). The metapopulation model requires no estimation of population level, but does require knowledge of immigration rates between hunted and unhunted areas, with the number of new emigrants representing the sustainable harvest (Cougar Management Guidelines Working Group, 2005). Few studies have rigorously estimated immigration rates between hunted and unhunted areas however, and as a result the efficacy of the metapopulation model approach to harvest remains untested.

In Montana a combination of limited entry and quotas are used by the Montana Fish Wildlife and Parks (MFWP) to allow recreational opportunities for the public, while maintaining viable mountain lion populations, thus creating a need for accurate and defensible population estimates. MFWP has proposed basing population estimates on mean densities from past research, extrapolated to forested areas in the western portion of the state. This method seems preferable to relying simply on opinion or public perception, which can run contrary to true density or trend (Freddy et al., 2004; Lambert et al., 2006). However, it does not take into account the variation in populations caused by resource availability, local mortality factors, and levels of immigration and emigration, which may ultimately control mountain lion density (Cooley et al., 2009b; Robinson et al., 2014).

Like most long lived vertebrate species, mountain lion population growth is sensitive to changes in adult female survival, and harvest-induced mortality of adult females is additive (Cooley et al., 2011; Robinson et al., 2014). The effect of any harvest program is dependent on its resultant mortality rate (i.e. animals harvested/animals available), yet the size of most lion

populations is unknown. In fact, after more than 40 years of research, a method to estimate the size or trend of lion populations is still the most pressing research need for mountain lion management (McKinney, 2011). Mountain lion densities observed in field-based census projects, where researchers have tried to capture or otherwise account for every individual, have tended to range from approximately 1 to 2 adults and/or 2 to 4 total animals per 100 km² (Quigley and Hornocker, 2010).

Both male and female juvenile cougars are capable of long distance dispersals (Stoner et al., 2008; Elbroch et al., 2009), with noteworthy accounts of individuals traveling >1000 km (Thompson and Jenks, 2005; Abhat, 2011). In Montana, mean male and female dispersal distances were recently found to be 43 km and 24 km, respectively (Newby, 2011). Cooley et al. (2009b) showed that dispersal may have a dampening effect on population change induced by harvest; reducing population growth in lightly hunted areas through emigration, and increasing population growth in heavily hunted areas do to immigration. While harvest can induce source-sink dynamics by altering local demographic rates (Dias, 1996; Novaro et al., 2005; Andreasen et al., 2012), the innate ability of mountain lions to disperse long distances may frustrate management goals of population reduction, may lead to unexpected impacts of harvest in neighboring management units, or even provide a level of cushion or margin of error causing population growth in a particular area to tend toward 1.0 regardless of management programs.

While survival and dispersal are known to have large effects on mountain lion populations, much uncertainty remains about their effects in a harvest management context. The functional form of dispersal effects on mountain lion populations is not entirely clear and as such has been largely ignored in harvest planning. Whether connectivity among management units is best modeled as a function of distance or needs to include a measure of habitat quality (i.e. ecological distance or friction) is unclear in a population modeling context, let alone in a harvest management context. Most mountain lion harvest strategies do not directly account for dispersal among management units.

Here we use a combination of resource selection functions (RSFs), mortality estimation, and dispersal modeling to develop a cougar metapopulation model for Montana. This model incorporates available data, our current state of knowledge regarding mountain lion habitat selection and population dynamics, and explicitly considers major uncertainties including unknown population sizes and various possible functional forms of dispersal among management units (including no dispersal). We demonstrate how predictions from this model might be used to inform decisions about harvest management programs by predicting the effects of lion hunting regulations implemented in Montana.

2. Materials and methods

2.1. Study area

Our study area was the state of Montana (381,154 km²), the 4th largest and 3rd least populated state (behind only Wyoming and Alaska) in the USA. The state is bisected by the continental divide, approximately 1/3rd of the way across the state from the western

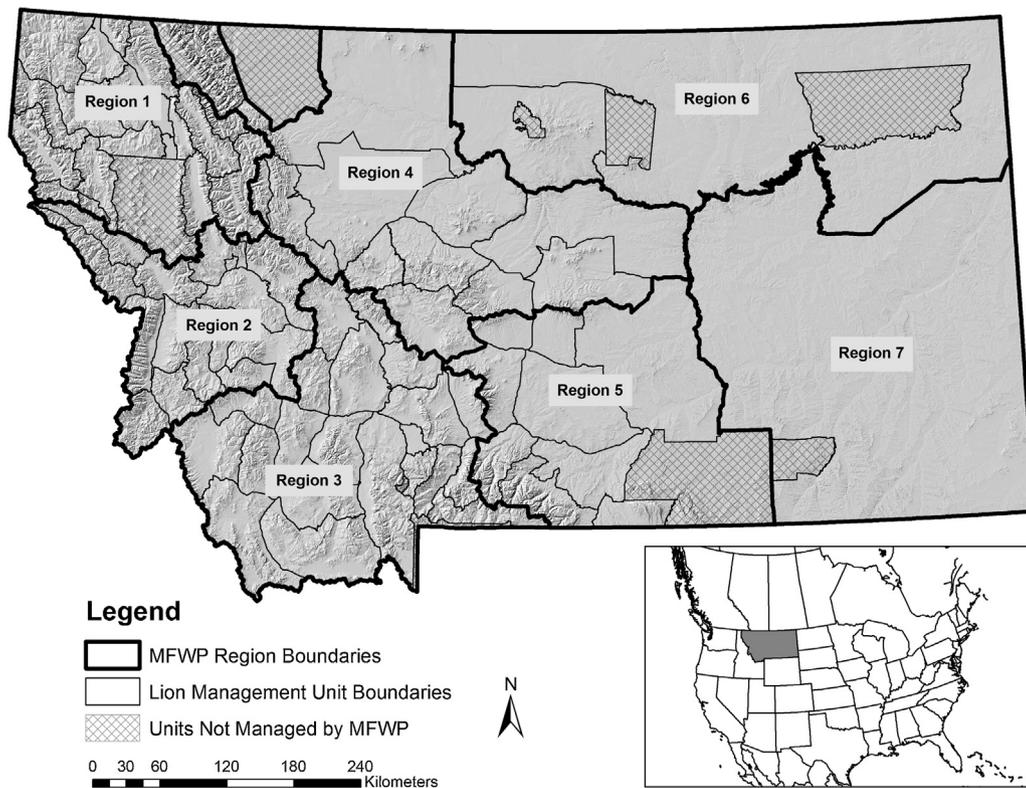


Fig. 1. Study area, the state of Montana showing MFWP wildlife management region boundaries, and nested mountain lion management unit boundaries.

border. The divide and the size of the state contribute to considerable variation in elevation, vegetation and climate from west to east. The northwest is characterized by dense, inland maritime forested mountains, which progress to montane forests, and intermountain grassland and foothill habitats in western, southwestern and central Montana (MFWP, 2005). Eastern Montana is more arid, and is characterized by plains forests, grasslands, and shrub-steppe habitats (MFWP, 2005). Riparian complexes are located throughout the state (MFWP, 2005).

MFWP divides the state into 7 administrative regions for wildlife management, and each region is further divided into hunting districts specific to each game species (Fig. 1). The number and size of management units within each region varies considerably. For instance Region 1 contains 18 units ranging in size from 340 km² to 3600 km², while all of Region 7 (77,000 km²) is a single management unit. Staff in each region are responsible for proposing harvest limits and/or quotas for the management units within that region, and a politically-appointed Commission is ultimately responsible for making decisions about harvest for all game species. Quota levels for cougars are set to achieve a variety of management goals by the Commission, with input and support from MFWP staff and the public. Additionally, private landowners and National Wildlife Refuges can limit access and place more restrictions on hunters than regulations set by the Commission. National Parks are responsible for wildlife management within their borders, as are Native American Reservations.

2.2. Model structure

To explore the potential metapopulation effects of current and planned harvest on cougar populations in Montana we combined empirical data collected within the state over the past 3 decades in 5 steps. First we developed a winter resource selection function (RSF) for cougars in Montana (Manly et al., 2002). Next we extrapolated a

range of known minimum population estimates from a small area in the center of the state to all cougar habitat in Montana based on the relationship of population to resource availability (Boyce and McDonald, 1999). Third we assumed human harvest to be an additive form of mortality in cougar populations and following this assumption estimated survival and fecundity rates for each game management unit in Montana based on harvest level from 2005 to 2010. Fourth we constructed a single metapopulation model for the state by combining, through dispersal, dual sex Leslie population matrices for each management unit. Finally to demonstrate the use of this model, we predicted the possible population level effects of proposed lion harvest changes in 2013 (Fig. 2).

2.3. Model parameters

2.3.1. Telemetry data collection

From 1980 to 2012, 9 telemetry based mountain lion projects were conducted in Montana (Table 1). These combined data provide a thorough representation of mountain lion habitats across the state (Fig. 3) (see individual studies for specific information regarding radio collars and collaring methods). We compiled VHF and GPS telemetry data from all 9 studies, screening to ensure only independent animals were represented. Original location intervals (e.g., 4 h in the case of GPS data or weekly in the case of VHF data) were maintained, but addressed statistically (see model training below).

2.3.2. Resource selection function (RSF)

RSF model training – We divided the data by study area and to a great extent telemetry method. We used data from projects that were predominantly based on GPS collars for model training and reserved data from projects based on VHF data for model validation (Table 1). GPS data collected in Eastern Montana were the exception. Of 3 GPS based studies in Eastern Montana we used data from 1 study area for model training and 2 for validation (Table 1

Table 1
Mountain lion telemetry studies conducted in Montana 1980 to 2012 and used in this study.

Study	Location	Years	N	Telemetry Method	Locations	Use in this study
Murphy (1983)	Fish Creek	1979–1982	9 (6F, 3M)	VHF	127	RSF validation
Williams (1992)	Sun River	1991–1992	24 (15F, 9M)	VHF	104	RSF validation
Murphy (1998)	Yellowstone National Park	1987–1995	41 (29F, 12M)	VHF	1335	RSF validation
Ruth (2004a)	North Fork	1993–1997	38 (28F, 8M)	VHF	692	RSF validation
Ruth and Buotte (2007)	Yellowstone National Park	1986–2006	39 (21F, 18M)	VHF and GPS	2782	RSF model training
Choate (2009)	National Bison Range	2000–2003	8 (7F, 1M)	VHF	576	RSF validation
Robinson and DeSimone (2011)	Garnet Range	1998–2006	39 (31F, 8M)	VHF and GPS	14,127	RSF model training. Reference population density
Kunkel et al. (2012)	Rocky Boys	2006–2009	6 (2F, 4M)	GPS	1786	RSF model training
Kunkel et al. (2012)	Fort Belknap	2008–2010	3 (2F, 1M)	GPS	84	RSF validation
Matchett (2012)	Missouri Breaks	2011–2012	2 (2M)	GPS	209	RSF validation

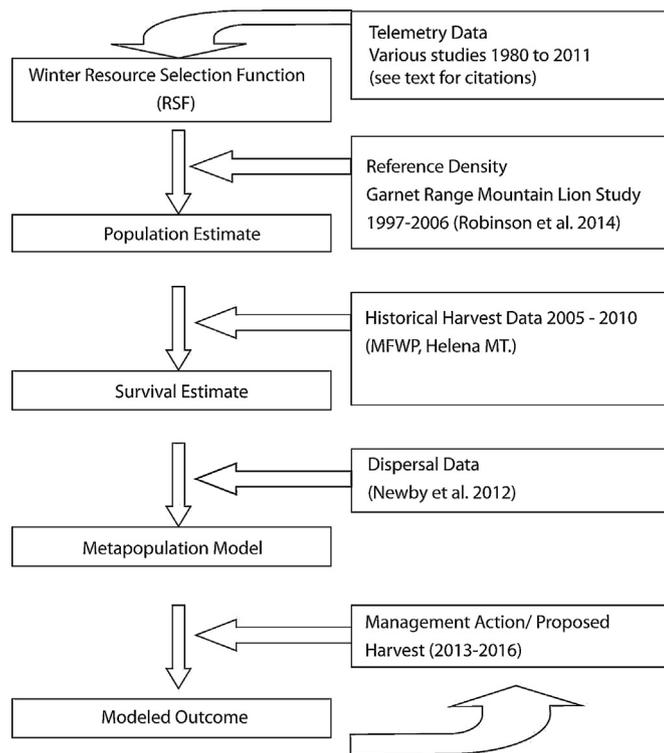


Fig. 2. Our 4 part modeling process utilizing past and current mountain lion research conducted in Montana 1980–2012.

and Fig. 2). Model training was based on the most recently collected and most accurate data (i.e., predominantly GPS). Model validation was based on a completely independent data set (i.e., no data, VHF or GPS, from any single study was used in both the model building and validation). We developed a winter resource selection function model (RSF) following Manly et al. (2002) for male and female mountain lions combined. RSFs evaluate resource selection by comparing the proportionate use of resources relative to their availability under a logistic regression framework. In a telemetry based study such as this, the used resources are determined using the collected telemetry locations, however the use of logistic regression makes the selection of available habitat instrumental in proper model parameterization (Hosmer and Lemeshow, 2000, Manly et al., 2002; Keating and Cherry, 2004). We wanted to develop a homerange level or second-order habitat selection model (i.e., selection of home range resources within the regional

landscape sensu Johnson, 1980). Therefore we measured availability by randomly distributing unused locations within a 99% adaptive home range kernel (href) based on the combined locations of all animals within a specific study area. Random locations were matched with used locations from the same study area at a 1 to 1 ratio.

We used 3-level generalized linear mixed-effects modeling (GLLMM in Stata) to account for unbalanced sample size between individual radiocollared animals, varying resource availability between population segments, and to account for the individual animal as the most appropriate sample unit (Gillies et al., 2006; Bolker et al., 2009). The form for a GLLMM for location i , animal j , and study area k , with a random intercept is:

$$\text{Logit} \{ \Pr(y_{ijk} = 1 | x_{ijk}, \zeta_{jk}) \} = \beta_1 + \beta_2 x_{2j} + \beta_3 x_{3ij} + \zeta_{jk} + \varepsilon_{ijk} \quad (1)$$

where β_1 to β_3 are the fixed effects, and ζ_{jk} is the random variation in the intercept at the animal and study area levels, ε_{ijk} is unexplained residual variation. The ε_{ijk} are independent across locations, individuals, and study areas, while the ζ_{jk} are independent across study areas and animals (Rabe-Hesketh et al., 2008). Only winter RSFs, December 1st to April 15th, were developed as population estimates below were based on a winter collaring program.

We considered a suite of spatial resource or ‘habitat’ covariates in the development of our RSF model. Habitat variables could be loosely categorized as land cover (e.g., dominant vegetation) or topographical (e.g. elevation, Table 2). Land cover categories were based on Gap Analysis Program level 1 (US Geological Survey Gap Analysis Program, 2010). We overlaid mountain lion telemetry data and random locations on a suite of raster layers (30 meter resolution) in a geographic information system (GIS) to quantify the underlying habitat associated with each used and available location.

We used a manual stepwise model building method described by Hosmer and Lemeshow (2000) to create “best” models that described the resource selection of cougars. This model building approach best reflects the balance between prediction and mechanism as achieved through regression-type models (Stephens et al., 2005). Candidate variables were considered if biologically relevant, ecologically plausible, and uncorrelated at a correlation coefficient of $|r| < 0.5$ (Hosmer and Lemeshow, 2000). We considered both linear and non-linear (quadratic) responses to continuous variables and used a combination of graphical and information criteria (AIC) based methods to determine how a response was best modeled. First, frequency histograms of used and available locations were plotted then compared to the predicted values of a univariate model to graphically depict mountain lion response. Secondly, the AIC

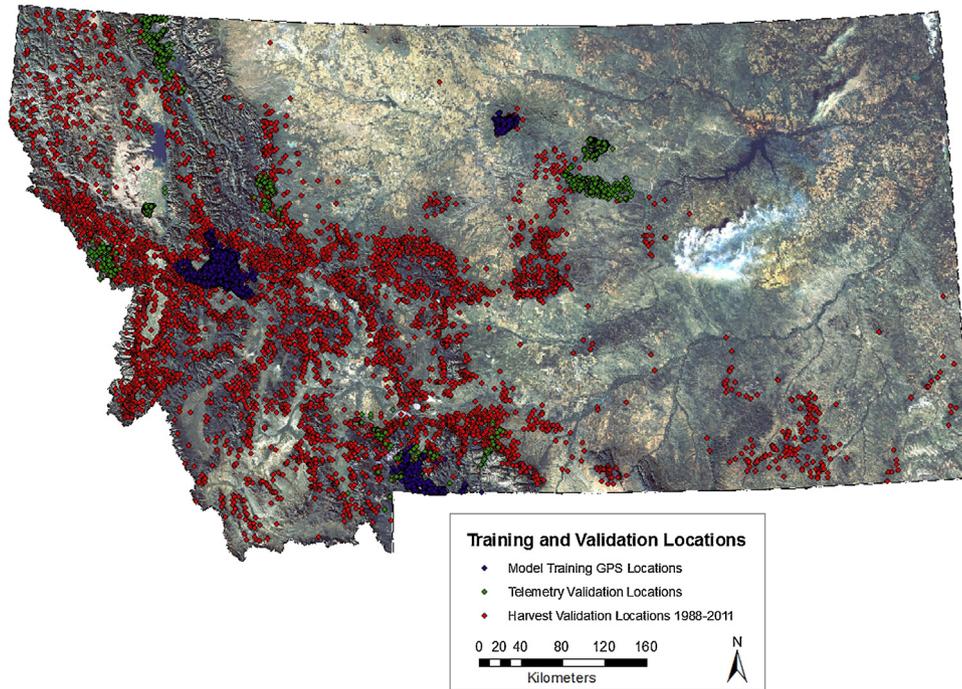


Fig. 3. Winter mountain lion resource selection function (RSF) model training and validation locations, Montana 1980–2012.

values of univariate models fit as a linear and quadratic response were compared in order to gauge if modeling as a quadratic improved fit (Burnham and Anderson, 1998). We followed the same procedure for all continuous covariates in which we expected potential non-linear resource selection patterns (i.e., selection for intermediate levels), including elevation, slope, distance to human activity, and distance to forest.

RSF model validation – The most important measure of model fit for habitat or resource selection models is predictive capacity, or how well the model predicts the observed locations of animals (Boyce et al., 2002). This was especially true for this project as we hoped to make inference to all of cougar range in the State of Montana. We used both within-sample and out-of-sample validation techniques to test the predictive ability of our models. Within-sample validation first consisted of standard logistic regression

diagnostics and goodness-of-fit measures (Fielding and Bell, 1997). We tested our models for multicollinearity using variance inflation factors (VIFs). Individual variables that are completely uncorrelated have VIF values of 1. Individual parameters with VIF scores greater than 10 were removed as candidate variables, and all models were tested to ensure that mean scores were not considerably larger than 1.0 (Hosmer and Lemeshow, 2000). We used classification tables to assess the model's ability to correctly cross-classify locations as used (sensitivity) or available (specificity). Area under the receiver operating characteristic (ROC) curve was calculated for each model. Generally ROC scores of >0.7 are considered acceptable levels of discrimination between locations while scores >0.8 are considered excellent (Hosmer and Lemeshow, 2000). We used k-fold cross-validation, where 5-random subsets of the data were validated with a model built from the remaining 80% of the data.

Table 2

Terrain and land cover GIS layers (candidate variables) used in predictive RSF models for mountain lions in Montana.

Variable	Variable type	Range of values	Description
Topography			
North	Categorical	0.1	North aspects from 315° to 45°
South	Categorical	0.1	South aspects from 135° to 225°
East	Categorical	0.1	East aspects from 45° to 135°
West	Categorical	0.1	West aspects from 225° to 315°
Flat	Categorical	0.1	No aspect (slope = 0)
Slope	Continuous	0–1100	Percent slope
Elevation	Continuous	201–3897 m	Elevation in meters
Land cover			
Agriculture	Categorical	0.1	Pasture and cultivated crops
Barren	Categorical	0.1	Disturbed barren land
Developed	Categorical	0.1	Human development of varying intensity
Forest	Categorical	0.1	Deciduous and coniferous forest
High montane	Categorical	0.1	Alpine areas above treeline
Introduced veg	Categorical	0.1	Introduced vegetation
Semi desert	Categorical	0.1	Semi-desert scrub and dry grassland
Shrubland	Categorical	0.1	Grassland and shrubland
Transitional vegetation	Categorical	0.1	Recently burned, logged, and regenerating areas.
Water	Categorical	0.1	Water
Distance to forest cover	Continuous	0–9555	Linear distance to forested land cover
Distance to development	Continuous	0–49059	Linear distance to developed land cover

Within k-fold cross-validation, if the RSF model predicts habitat use well, there should be a strong Spearman's rank correlation (ρ) between predicted use and ranked habitat categories (e.g., from 1 to 10). A Spearman's rank correlation of >0.64 indicates that the model has good predictive ability (Fielding and Bell, 1997; Boyce et al., 2002).

The amount of data we obtained afforded an out of sample validation, which arguably provides the best measure of a model's ability to predict resource use correctly (Fielding and Bell, 1997). We reserved all data from 7 of 10 study areas across the State for as an out of sample data set (i.e., not used in model training; Table 1). The reserved data set contained all projects based solely on VHF data and as well as locations from 2 study areas in eastern Montana where GPS collars were used. We believed that using a validation set composed primarily of older, less accurate (i.e., VHF) data was the most conservative method of validating our model. Our reasoning was that using VHF locations from the 1980s and 1990s to validate an RSF model based on, among other variables, a 2010 landcover classification (US Geological Survey Gap Analysis Program, 2010) and 2000–2012 telemetry locations would be expected to validate poorly because of habitat changes since the VHF data were collected (e.g., what was forest in 1980 and possibly selected for by mountain lions at the time the location was collected may now be cleared or developed and would thus have a low RSF value). Further, using the VHF based telemetry studies along with GPS data collected in eastern Montana provided greater geographical extent of our validation set.

We evaluated the predictive ability of our model using a method similar to that proposed by Johnson et al. (2006) where reserved out of sample locations are overlaid onto the projected RSF model that we binned into equal quantiles (10 bins of equal areas). We measured the performance of our model using a Spearman rank correlation between the frequency of out of sample locations and ranked habitat categories (Boyce et al., 2002). Finally, as we were predicting resource use across the entire state including areas where no telemetry data had ever been collected, we used locations of lions harvested between 1988 and 2011 in Montana as a second form of out of sample validation (Fig. 2). We used a Spearman rank correlation to test the relation between the number of harvest locations and our predicted ranked habitat categories across the state.

2.3.3. Population estimation

From 1997 to 2006, MFWP conducted an intensive mountain lion collaring program in the Blackfoot river watershed of west central Montana. Each year, staff from that project calculated a minimum population estimate for the core Garnet study area based on collared and uncollared but harvested animals (Robinson and DeSimone, 2011). The estimate was made for December 1st of each year, prior to the start of the hound hunting season. Due to varying hunting pressure, and associated survival, the Garnet population declined from 1998 to 2000 before recovering by 2006 to levels approaching those at the start of the study (Table 3). Cougar densities over the span of the study were in line with those reported elsewhere including unharvested populations. Quigley and Hornocker (2010) summarized total densities from 10 cougar studies conducted across North America between 1973 and 2006 and found mean total mountain lion densities of 2.00–3.24 per 100 km².

Following the method of Boyce and McDonald (1999) we extrapolated the Garnet reference density to the rest of the state at three levels; the mean density over the study period (3.08/100 km²), as well as high (4.04/100 km²) and low (2.19/100 km²) extremes (Table 3). Boyce and McDonald's (1999) method assumes that the relationship between available resources (i.e., total RSF value) and population level remains constant both spatially and temporally; the fixed ratio of animals to resource selection function in the

reference population is extrapolated to the remainder of the study area. Our RSF did not explicitly take into account prey availability, which is known to affect predator density (Carbone and Gittleman, 2002). Rather prey density, or availability, is assumed to be represented in the landcover categories used in our RSF. In a harvested population, the actual population level may diverge significantly from that set by available resources (i.e., carrying capacity) (Sinclair et al., 2006). Ultimately our survival and fecundity estimates, used below in population modeling, are directly related to what we assumed the population to be each year. By extrapolating separate estimates based on a range of population levels we hoped to quantify our uncertainty regarding the true population level in any particular management unit, the effect that this uncertainty has on estimates of survival and fecundity, and therefore the associated uncertainty in our population models.

2.3.4. Population parameter estimation

Survival – To estimate survival rates we combined our RSF based population estimates for each mountain lion management unit with harvest data from 2005 to 2010. Hunting mortality in mountain lions has been shown to be additive (Cooley et al., 2009b; Robinson et al., 2014). Robinson and DeSimone (2011) used competing risks analysis (Pintilie, 2006) to calculate cause-specific natural mortality rates in mountain lions, in the presence of hunting. Non-hunting mortality rates (i.e., all non-harvest related mortality) in central Montana were 0.10 (SE = 0.02) for adult females, 0.15 (SE = 0.10) for adult males, 0.09 for juveniles (SE = 0.04) and 0.17 (SE = 0.06) for kittens (Robinson and DeSimone, 2011, unpublished data). These values were used as baseline mortality rates in the calculation of total mortality rates in this study.

For adult mountain lions, to account for the additive nature of natural and hunting mortality, we calculated survival as:

$$S_A = 1 - \left(\text{baseline mortality}_A + \left(\text{harvest} \frac{N_{ij}}{\hat{N}_{kij}} \right) \right) \quad (2)$$

where baseline mortality_A is the adult cause specific mortality rate for all causes besides hunting, harvest N_{ij} is the sex specific number of harvested animals for management unit i in year j , and \hat{N}_{kij} is the k th sex specific adult population estimate (mean, high, or low) for the i th management unit in year j .

To account for the additive nature of hunting on kitten survival, we calculated kitten survival as:

$$S_K = (1 - \text{baseline mortality}_K) \times S_{Af} \quad (3)$$

where baseline mortality_K is the kitten cumulative incidence function for all forms of mortality besides hunting, and S_{Af} is adult female survival.

These estimates of annual survival are clearly dependent on year and management unit specific hunting pressure. Because we could not be certain of the true population level, and therefore survival rate, we calculated 3 survival rates for each lion management unit, in each year from 2006 to 2011. Rates were again based on the low, mean, and high starting population estimates for each lion management unit extrapolated from the Garnet reference population. Variation across these 15 estimates of annual survival were used to estimate variability in survival within hunting units and this was used in a standard deviation matrix to estimate stochastic population growth rates (Caswell, 2001).

Calculating juvenile survival created a specific problem as animals in the juvenile age class (animals 13–24 months) spend part of the year still traveling with their mother, and part as independent animals (Sweaner et al., 2000). During independence they are undoubtedly harvested as adults and thus would contribute to the total harvest causing us to underestimate adult survival. However, they cannot be classified as kittens as most over the age of

Table 3

Annual minimum population estimates from the Garnet Range Mountain Lion Study. These population estimates were used as reference population levels extrapolated to each management unit across the state.

Year	Total pop.	Adult females	Adult males	Total density (/100 km ²)	Adult density (/100 km ²)
1997	37	14	7	4.04	2.30
1998	27	11	6	2.95	1.86
1999	20	10	5	2.19	1.64
2000	21	8	4	2.30	1.31
2001	25	8	3	2.73	1.20
2002	24	9	3	2.62	1.31
2003	30	11	3	3.28	1.53
2004	32	11	3	3.50	1.53
2005	33	11	4	3.61	1.64
2006	33	10	2	3.61	1.31
Mean	28	10	4	3.08	1.56

12–14 months would likely survive if abandoned following harvest of their mother. In the end we used a fixed rate of 0.592 for juvenile survival and associated standard deviation (Robinson et al., 2014). These telemetry based juvenile survival rate and variance estimates combine all causes of mortality, including harvest, from a marked sample of 69 individuals under a range of hunting pressure and population levels and thus are a reasonable estimate that captures uncertainty associated with the effect of harvest on juvenile survival.

Fecundity – We calculated birth pulse fecundity as:

$$F = S_{Af} \times M \quad (4)$$

where M is the mean annual maternity rate and S_{Af} is annual adult female survival. Although mountain lions can give birth year round the majority of their births occur during the summer months. Modeling mountain lions as birth pulse vs. birth flow may lower population growth rates as F will include an entire year of adult survival rather than survival to the midpoint of the year as would be the form for birth flow. We used a constant annual maternity rate of 1.29 kittens/female observed in the Garnet study area of Montana (Robinson et al., 2014). This maternity rate would roughly equate to each female >24 months of age having an average litter of 2.5 kittens every 2 years.

2.3.5. Metapopulation modeling

We constructed stage-based (kitten, juvenile, and adult), dual sex Leslie matrix models in program RAMAS GIS (Applied Biomathematics, Setauket NY) for each management unit and populated each matrix with the survival and fecundity parameters (as well as the population estimates) described above (Leslie, 1945; Caswell, 2001). All models were started assuming a stable age distribution. To date, in most models of cougar populations the role of dispersal has been alluded to but not modeled explicitly (but see Beier, 1993). Despite direct evidence of the important role dispersal appears to play in cougar population dynamics most models have assumed closed populations or that emigration and immigration are equal and can therefore be ignored (Cooley et al., 2009a). Similarly, while some studies have measured dispersal distance and direction (e.g., Sweanor et al., 2000) few have been able to quantify the environmental characteristics that help shape dispersal patterns (but see Newby, 2011).

We created a single metapopulation model for the entire state within RAMAS by treating each mountain lion management unit as a separate population joined through juvenile dispersal. In this sense our definition of a metapopulation differs from the traditional view of a series of patches separated by unsuitable habitat. In our model patches are for the most part artificial with boundaries being jurisdictional rather than structural. While it is fairly well established that male mountain lion dispersal is intrinsic or density-independent, it is unclear how natal population density affects female dispersal (Logan and Sweanor, 2010). We based

dispersal rates and distances on recent research conducted in Montana. Robinson and DeSimone (2011) calculated juvenile dispersal rates as the total number of dispersing juveniles divided by the total number of radio collared juveniles surviving to dispersal age in each year. They found that 100% of males, and 50% of juvenile females displayed dispersal behavior; defined as juveniles establishing a home range with <5% overlap of their natal home range.

Dispersal between populations – We modeled dispersal between populations in 3 ways; no dispersal, a high or purely distance based dispersal and a lower or ecological distance based dispersal between units. For our no dispersal model we set the dispersal function between units to 0. This can be viewed as treating each mountain lion management unit as a closed population, or making the assumption that immigration and emigration are equal for each specific unit and therefore can be ignored. Our high or Euclidean distance based dispersal probability was based on the negative exponential function (Kitching, 1971):

$$m_{ij} = \exp\left(\frac{-D_{ij}}{b}\right) \quad (5)$$

where m_{ij} is the proportion of dispersal eligible individuals that move from patch i to patch j , D_{ij} is the distance between patches, and b is the average dispersal distance. In our case each management unit (Fig. 1) is considered a single “patch” with distance measured from center of the management unit to the edge of the neighboring unit (see below). Newby et al. (2013) quantified dispersal of 81 juvenile cougars in Montana and the Yellowstone ecosystem and found a mean distance of 52.76 km and maximum of 171 km. Dispersal distance differed between males and females in a hunted population (male $\bar{x} = 42.6$, female $\bar{x} = 24.2$) but not in a protected system (male $\bar{x} = 62$, female $\bar{x} = 67.4$). Based on Newby et al.’s (2013) findings we used a mean dispersal distance of 53 km and a maximum distance of 200 km for both males and females. We modeled 50% juvenile female dispersal and 100% male juvenile dispersal. For a lower dispersal rate we used an ecological distance, where juveniles move between populations as a function of distance and habitat quality. We used the inverse of our combined population RSF as a dispersal “friction layer” (Chetkiewicz and Boyce, 2009). We then calculated ecological distance within RAMAS by combining this friction layer with our Euclidean distance dispersal function. Whereas the distance based dispersal model does not take into account any landscape or habitat features, ecological distance works to increase the functional distance between 2 management units that are connected by poor habitat and thus takes into account dispersal barriers.

In both our Euclidean distance and ecological distance dispersal layers, distance between patches was measured as center to edge (i.e., center of the focal patch to edge of each neighboring patch). The use of this distance measure has the effect of creating asymmetric dispersal between large and small patches (i.e., juveniles are more

likely to leave small patches than large due to the shorter distance to edge). In RAMAS dispersal occurs after survival and reproduction, therefore the number of animals that move between populations is a function of how many animals survive to the end of their second year. Where dispersers end up, or if they leave at all, is a random process; we modeled dispersal as a combination of the number of animals that survive to dispersal age and distance they travel based on Eq. (5).

Density dependence and carrying capacity – We used ceiling density dependence to represent territoriality in adult mountain lions and to limit population growth within each management unit to a biologically reasonable level (Root, 2004). Quigley and Hornocker (2010), in a survey of 17 mountain lion studies from across North America, maximum adult densities ranging from 0.63 to 7.3/100 km² however 16 of these estimates were <3.0 (the outlier being a single study from Vancouver Island). We based our ceiling density on a liberal estimate of 3 adults per 100 km². In RAMAS we set density dependence to affect survival of adults only. This has the effect of allowing normal reproduction and survival of kittens and juveniles based on the survival matrix, and therefore emigration is not affected. We calculated the RSF requirements of 3 adult mountain lions per 100 km² in our Garnet reference population and then projected this density to each management unit. We did not restrict the ratio of males to females however a ratio of approximately 1.5–2 females per male would normally result from the disparate survival of males and females and the resultant stable age distribution.

Uncertainty in initial density and dispersal – Two major uncertainties in this modeling process were the initial abundance of animals in each management unit and how to model dispersal between units. We used a two-way factorial analysis of variance (ANOVA) to test for the significance of initial abundance (low, mean, or high) and dispersal type (none, friction, and distance) on modeled annual growth rates (λ).

2.3.6. Metapopulation contribution

We calculated a relative contribution index for each management unit based on its production of dispersers and size, or:

$$c = \frac{n_{i(t-1)}(\Delta\lambda)}{N_t} \quad (6)$$

where N_t is the statewide population estimate, $n_{i(t-1)}$ is the population estimate for management unit i at the start of the model period (i.e., 2005), $\Delta\lambda$ is the difference in modeled management unit growth rate between 2005 and 2010 modeled with dispersal (i.e., juveniles moving between management units based on their survival and the distance function) and without dispersal (i.e., the dispersal term in the model set to 0 mimicking all closed populations). This index increases and is positive when a district represents a large relative proportion of the statewide population and when growth is lowered by dispersal (i.e., it is a net contributor or source). The index is negative when dispersal increases the population growth rate of a unit (i.e., sink). Values approaching 0 may occur where there is little difference between model outputs, or if the total population of a particular unit is very small relative to the population size for the state (i.e., neutral).

2.3.7. Management application

In the spring of 2012, the MFWP Commission heard proposals regarding changes to 2013 mountain lion harvest levels. MFWP Region 1 proposed increases in female harvest quotas in some management units toward a goal of reducing the lion populations in those specific areas, while maintaining stable harvest to achieve lion population stability in other units. These quotas were based on previous research results concerning harvest rates and harvest mortality levels required to produce population declines in lions

(Robinson and DeSimone, 2011). These research results were used as conceptual rules of thumb to predict the outcome of the proposed quotas but did not account for dispersal among units.

To demonstrate the utility of our population modeling framework to inform decisions about harvest quotas, we modeled the possible population outcome of proposed 2012–13 harvest changes in Montana. We recalculated survival and fecundity rates for the affected units using Eqs. (2)–(4) above, but based on our current modeled high population estimates (i.e., the modeled outputs from above). We based our projection of the impact of the new quotas on our high density estimates as Region 1 had been criticized for not harvesting enough mountain lions to have the desired reduction in population. Our intention was to calculate a high or maximum growth rate for the management units of Region 1, given the new quota levels, in order to determine if in fact they were likely to show a desired reduction. Adult female harvest rates were projected to be 75% of the full female subquota. We then ran these management models for 3 years, as the proposed harvest levels are to be maintained at these levels until 2015.

3. Results

3.1. Captures and monitoring

Between 1980 and 2012, 236 independent mountain lions were collared and monitored for research in Montana. From these data we used 18,695 GPS and VHF locations collected during winter from 85 animals in 3 study areas to develop our resource selection functions. We used 11,726 VHF and GPS locations from 142 animals from 7 study areas and the locations of 6343 harvested lions to validate our models (Table 1 and Fig. 3).

3.2. Resource selection functions

Our statewide resource selection model showed a general trend of high to low habitat quality from west to east (Fig. 4). Our stepwise model selection left 9 variables in the model as significant (Table 4). The influences of elevation and slope on use were best modeled as quadratic functions with mountain lions selecting for intermediate elevations and slopes.

Validation – Our top model explained approximately 13% of the variation in lion resource selection. The within sample goodness-of-fit statistics provide a mixed picture of the model's performance. Sensitivity was 0.75 suggesting a 75% probability of the model correctly classifying a location as used. Specificity was poorer, demonstrating a 55% ability to classify a location as available. The model had a ROC score of 0.71, just above an acceptable level. K-fold cross validation revealed excellent predictive capacity to model training data (Spearman rank correlation $\rho = 1.0$). Both out of sample validation data sets showed the models correctly predicted relative presence of cougars in Montana. The male out of sample locations did not fit the model as well as female locations across the 7 study areas with an over representation of locations at midlevel RSF values (Fig. 5), but both male and females locations had high and significant Spearman rank correlation values (Male $\rho = 0.84$, Female $\rho = 1.0$). The harvest data also showed excellent agreement between the occurrence of harvest locations and our predicted probability of cougar use in all 7 administrative regions of Montana (i.e., ρ scores range from 0.84 to 1.00). Despite the high ρ -scores, our model appears to perform better in Regions 1, 2, 4 and 6, than in Regions 3, 5, and 7 (Fig. 6). In Regions 3 and 5 especially, there appear to be more animals harvested in low quality areas than we would expect if our RSF model was predicting mountain lion spatial use well in those areas. This suggests more quality habitat in those regions than our model

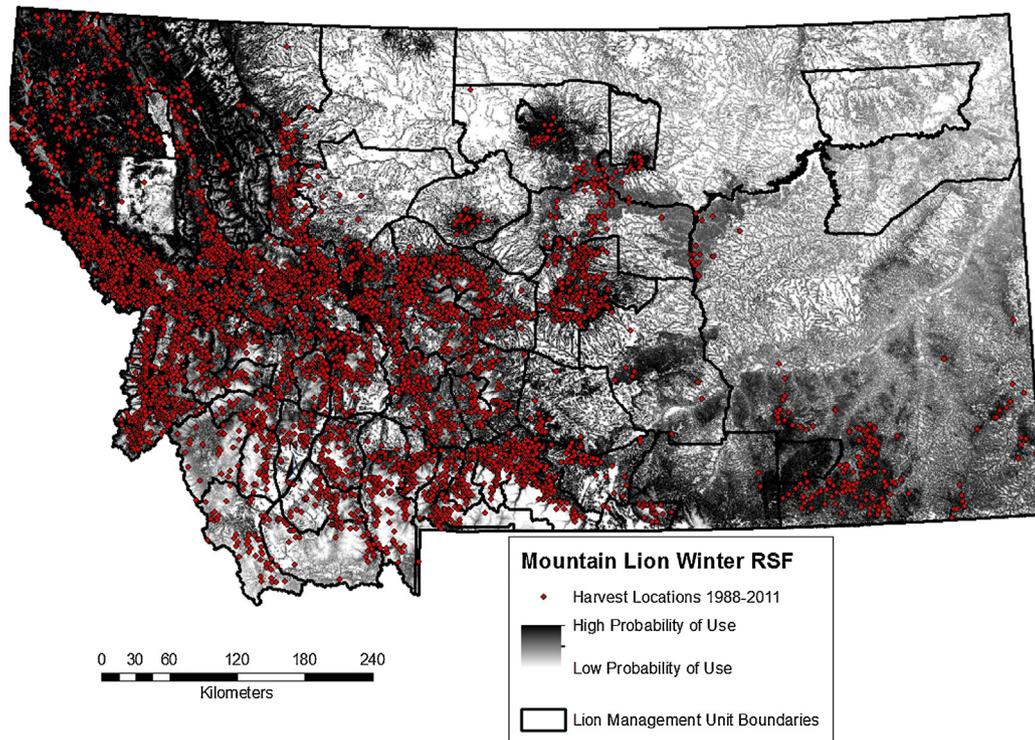


Fig. 4. Statewide mountain lion winter resource selection function (RSF) and hunting locations used in model validation (for presentation purposes only 1000 randomly chosen locations of the total 6343 used are shown).

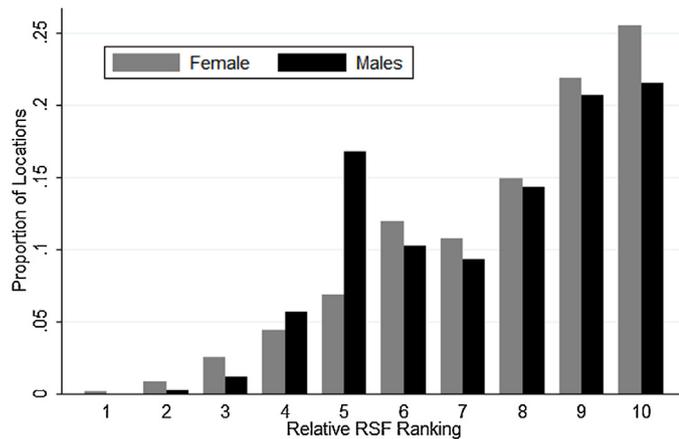


Fig. 5. Telemetry based out of sample validation of our resource selection function model by sex. Bar height represents the proportion of reserved telemetry locations and associated RSF value (see also Fig. 3).

predicts, which has important implications for our population projections as it would lead to underestimation of the populations in those areas.

3.3. Population estimation

Our mean RSF based population estimate for the total population (kittens, juveniles, and adults) of mountain lions in Montana was 3926, with almost 1/3rd of the entire population in MFWP Region 1 (Table 5). Estimates based on the high and low Garnet population estimates produce a possible range of 2784–5156 mountain lions.

3.4. Uncertainty in initial density and dispersal

The interaction of initial population estimate and dispersal was non-significant in both models. Two-way analysis of variance showed that our predicted growth rates at the unit level were affected by both dispersal and initial population estimate (Table 6). At the regional level however, how dispersal was modeled, if at all, had no effect on modeled annual growth rate (Table 6).

3.5. Metapopulation growth and contribution

Using 3 varying starting population density estimates, and 3 different levels of dispersal we estimated the mountain lion population in Montana to be stable to slightly increasing between 2005 and 2010 (Tables 7–9). Our contribution metric suggested that the largest source populations in the state were unit 100 (Region 1) in the extreme NW corner of the state, unit 202 (Region 2) along the Montana Idaho border, the Crow Reservation in the south central portion of the state, and Glacier National Park. All but Glacier are hunted areas but with relatively large populations (i.e., >130 individuals), high connectivity, and adult female survival rates ≥ 0.80 . Conversely units 132 (Region 1) and 560 (Region 5) appear to be the strongest sinks with intermediate population levels (i.e., 23 and 44 individuals respectively), good connectivity and low adult female survival (i.e., approximately 0.65) (Fig. 7).

3.6. Management application

If the season changes implemented by the Commission for 2012–2013 are continued through 2015, we expect the mountain lion population in Region 1 to decline by approximately 5% annually, matching management goals. We project the annual reduction in the population in Region 1 will be somewhat evenly distributed across the region (Table 10). Of note are model projections for units 102, 123, and 124, where small increases in the proposed harvest

Table 4
Male and female combined mountain lion winter resource selection function (RSF) showing variable, beta coefficient, standard error, Z score and Wald chi-square p-value. For categorical variables (see Table 2 those not in the model are included in the constant term. For distance variables a positive coefficient shows avoidance (i.e. use increases with distance) while negative coefficients show selection (i.e. use decreases with distance). Squared variables are quadratic terms and reveal a selection for intermediate values.

Covariate	Coefficient	Standard Error	Z	P > Z
South aspect	0.3181	0.0274	11.6	0
High montane	-1.3883	0.3093	-4.49	0
Agriculture	-1.9151	0.1512	-12.66	0
Developed	-0.6110	0.1706	-3.58	0
Transitional vegetation	-0.7200	0.0453	-15.89	0
Elevation	0.0191	0.0002	72.32	0
Elevation ²	-0.000006	8.67E-08	-77.5	0
Percent slope	0.02648	0.0017	15.45	0
Percent slope ²	-0.00015	1.96E-05	-8.06	0
Distance from forest	-0.0078	0.0002	-33.71	0
Constant	-14.9483	0.2250	-66.43	0

Table 5
Mean population level (2005) and parameter estimates (standard deviation) for mountain lions in Montana, 2005–2010 based on Garnet reference population estimates (Table 3).

Region	Initial population 2005	Adult female survival	Adult male survival	Juvenile survival	Kitten survival	Fecundity
1	1101	0.81 (0.07)	0.45 (0.19)	0.59 (0.09)	0.66 (0.06)	0.52 (0.04)
2	675	0.86 (0.05)	0.41 (0.23)	0.58 (0.09)	0.70 (0.03)	0.55 (0.03)
3	380	0.73 (0.13)	0.21 (0.13)	0.58 (0.09)	0.60 (0.11)	0.47 (0.08)
4	650	0.79 (0.06)	0.45 (0.17)	0.58 (0.09)	0.64 (0.05)	0.50 (0.03)
5	537	0.79 (0.08)	0.47 (0.19)	0.58 (0.09)	0.64 (0.06)	0.50 (0.04)
6	135	0.86 (0.09)	0.73 (0.17)	0.58 (0.09)	0.70 (0.07)	0.55 (0.05)
7	448	0.86 (0.03)	0.64 (0.13)	0.58 (0.09)	0.70 (0.02)	0.55 (0.01)
Total	3926	0.80 (0.08)	0.40 (0.18)	0.58 (0.09)	0.65 (0.06)	0.51 (0.05)

Table 6
Analysis of variance results for the effect of initial abundance estimation and dispersal type on modeled annual population growth at the unit (88 management units modeled 9 ways – 24 runs dropped when starting population estimates where 0) and regional scale (7 regions modeled 9 way).

Scale	Source	Partial SS	df	MS	F	P-value
Unit	Model	1.125	4	0.281	16.6	<0.01
	Initial population	0.312	2	0.156	9.26	<0.01
	Dispersal	0.812	2	0.406	24.05	<0.01
	Residual	12.887	763	0.016		
	Total	14.012	767	0.018		
Region	Model	0.006	4	0.001	1.89	0.12
	Initial population	0.005	2	0.002	3.2	0.04
	Dispersal	0.001	2	0.001	0.59	0.55
	Residual	0.049	58	0.001		
	Total	0.056	62	0.001		

Table 7
Estimated population growth rates 2005–2010 by MFWP management region (see Fig. 1) based on mean population levels and survival estimates.

Region	No Dispersal (SD)	Low/Friction Based Dispersal (SD)	High/Distance Based Dispersal (SD)
1	1.01 (0.04)	1.02 (0.04)	1.01 (0.04)
2	1.05 (0.04)	1.02 (0.04)	1.03 (0.04)
3	0.98 (0.07)	0.97 (0.07)	1.00 (0.06)
4	0.99 (0.05)	0.98 (0.05)	0.97 (0.04)
5	1.03 (0.04)	1.03 (0.04)	1.02 (0.04)
6	1.06 (0.04)	1.03 (0.04)	1.04 (0.04)
7	1.05 (0.02)	1.05 (0.02)	1.05 (0.02)
Total	1.02 (0.03)	1.02 (0.03)	1.01 (0.03)

Table 8
Estimated population growth rates 2005–2010 by MFWP management region (see Fig. 1) based on low population levels and survival estimates.

Region	No dispersal (SD)	Low/friction based dispersal (SD)	High/distance based dispersal (SD)
1	0.99 (0.05)	1.00 (0.05)	0.99 (0.05)
2	1.02 (0.06)	1.00 (0.06)	1.00 (0.05)
3	0.93 (0.09)	0.92 (0.08)	0.96 (0.08)
4	0.97 (0.06)	0.95 (0.06)	0.95 (0.05)
5	1.03 (0.05)	1.03 (0.06)	1.01 (0.05)
6	1.05 (0.05)	1.02 (0.06)	1.03 (0.06)
7	1.04 (0.03)	1.04 (0.03)	1.04 (0.03)
Total	1.00 (0.05)	1.00 (0.05)	0.99 (0.05)

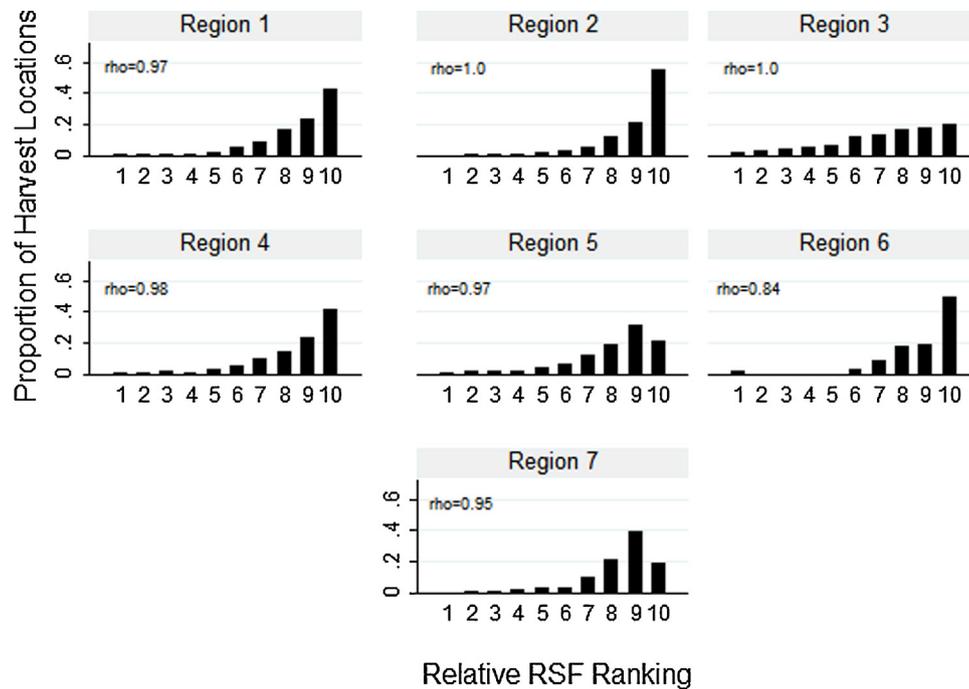


Fig. 6. Resource selection function (RSF value) and associated proportion of harvest locations by MFWP region (rho scores from Spearman rank correlations provided for each region).

Table 9
Estimated population growth rates 2005–2010 by MFWP management region (see Figure 1) based on high population levels and survival estimates.

Region	No dispersal (SD)	Low/friction based dispersal (SD)	High/distance based dispersal (SD)
1	1.02 (0.04)	1.03 (0.03)	1.02 (0.03)
2	1.05 (0.03)	1.03 (0.03)	1.03 (0.03)
3	1.00 (0.05)	0.99 (0.05)	1.02 (0.04)
4	1.00 (0.04)	0.99 (0.04)	0.99 (0.04)
5	1.02 (0.03)	1.02 (0.03)	1.02 (0.03)
6	1.04 (0.02)	1.02 (0.03)	1.03 (0.03)
7	1.03 (0.01)	1.03 (0.01)	1.03 (0.01)
Total	1.03 (0.03)	1.02 (0.03)	1.02 (0.03)

(i.e., 1 additional adult female) result in relatively large reductions in annual growth. As these units contain more than 24, 12, and 6 adult females respectively, the reductions in population growth are due primarily to reduced dispersal from more heavily hunted areas rather than direct mortality of adult females.

4. Discussion

The objective of wildlife management programs, including mountain lion sport-hunting programs, is to increase, decrease, or maintain populations (Sinclair et al., 2006). Once these objectives

Table 10
Montana Fish Wildlife and Parks Region 1 female mountain lion harvest quotas 2012 and 2013 (see also Fig. 1) and resultant change in population growth estimates.

Mountain lion management unit	Mean female harvest 2005–2010	Female subquota 2012	Proposed 2013 female subquota	Modeled annual population growth rate 2005–2010 (SD)	Modeled annual population growth rate 2013–2015 (SD)
100	5.16	6	12	1.00 (0.04)	0.91 (0.07)
101	1.66	3	6	1.00 (0.04)	0.88 (0.07)
102	1.88	4	5	1.02 (0.04)	0.92 (0.07)
103	1.50	3	5	1.04 (0.03)	0.97 (0.05)
104	1.83	2	5	1.02 (0.03)	0.96 (0.05)
109	1.33	3	5	0.97 (0.07)	0.72 (0.12)
110	2.16	2	4	0.99 (0.04)	0.95 (0.06)
120	1.33	2	4	1.02 (0.04)	0.95 (0.07)
121	6.33	6	8	1.01 (0.04)	1.00 (0.05)
122	1.50	0	6	1.03 (0.04)	0.94 (0.06)
123	1.16	1	2	0.99 (0.05)	0.94 (0.09)
124	0.66	1	1	1.09 (0.04)	0.98 (0.08)
130	2.16	4	6	0.98 (0.05)	0.85 (0.08)
132	2.16	4	10	1.06 (0.06)	0.77 (0.07)
140	1.66	1	6	1.07 (0.02)	0.98 (0.04)
141	0	0	6	1.08 (0.02)	0.86 (0.05)
150	0.33	0	7	1.06 (0.01)	0.90 (0.03)
170	0	0	0	1.18 (0.06)	0.97 (0.11)

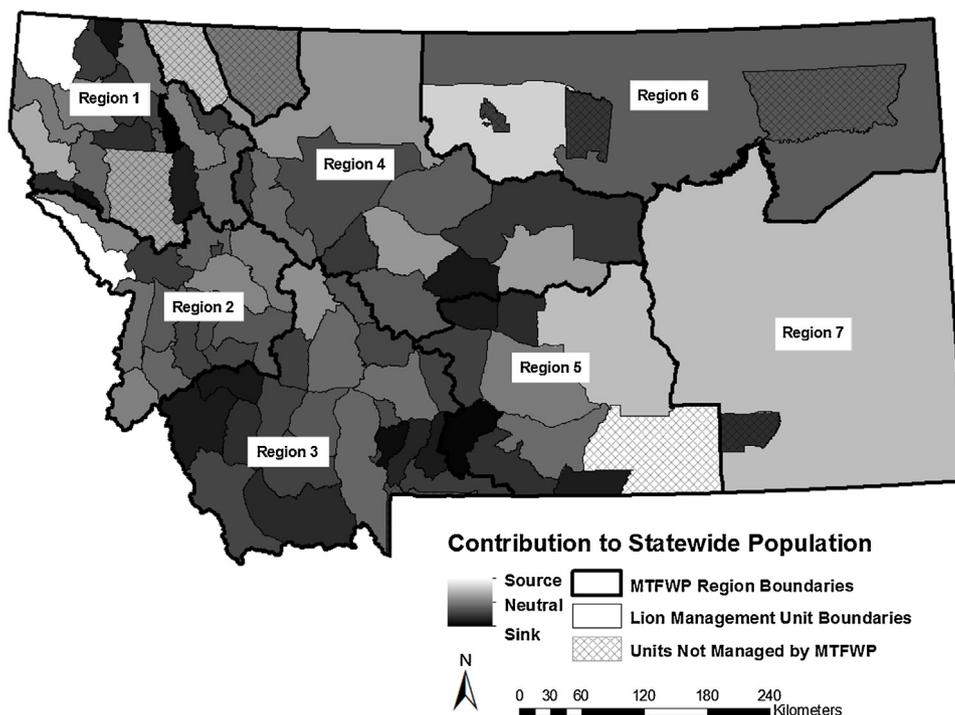


Fig. 7. The relative contribution of each mountain lion management unit to Montana's statewide population, 2005–2010.

are made clear adaptive management principles may be applied to frame a management program and possible management actions (Walters, 1986). Adaptive management can make use of models to predict the possible effects of management actions on resources, relative to objectives (Williams et al., 2007). Depending on the level of knowledge about a particular issue, predictive models can be quantitative and should represent uncertainty about the effects of management actions on resources, in this case lion population dynamics. This project is a first attempt at modeling a mountain lion metapopulation at a regional or statewide scale, incorporating all available information and being explicit regarding key uncertainties, toward a goal of informing mountain lion harvest management. We based our metapopulation model on an empirically developed and validated model of mountain lion habitat, our current understanding of how harvest effects survival, and accounted for management units that are small in scale relative to the dispersal capabilities of mountain lions. Use of this model in an adaptive management framework will help to clear up key uncertainties about the effects of harvest on large-scale mountain lion population dynamics such that management objectives can be achieved with greater frequency. We believe this project is therefore a step forward on several pressing research needs for mountain lions (McKinney, 2011).

4.1. Population estimation

Although our model is based on our best available knowledge, it consists of many steps (Fig. 2) at each of which error is no doubt introduced. These errors and uncertainties are compounded at each step of the modeling process, and we were cognizant of this throughout the project. Our reference population estimates are based on minimum counts over an 8-year study in the Garnet Mountain range. Knowing we could not ultimately estimate the precise number of mountain lions in Montana we made a conscious decision to maintain this negative direction bias so that our final results might be viewed also as conservative estimates of population growth. We regarded this result to be most useful to managers.

Our use of minimum starting densities, resultant low survival estimates, an assumption of no compensatory response in survival to harvest, and the use of sample variance rather than process variance in our stochastic population models all produce results biased low.

4.2. Resource selection

Our top mountain lion winter RSF model indicates that mountain lions select habitat types that offer cover, forest edges, intermediate elevations, moderate slopes, and generally avoided anthropogenic development and habitat types without cover (such as agricultural and high mountain areas). These model covariates are very similar to the findings of other studies documenting mountain lion dispersal and resident habitat (Newby, 2011).

Out of sample validation of our top model indicated predictive accuracy in areas relatively similar to model training areas (i.e., Regions 1, 2, 4 and 6), however we likely underestimated mountain lion habitat in Region 3 and possibly 5 (Fig. 1) as evidenced by a high number of harvested animals in low RSF categories (Fig. 6). Out of sample validation is the best measure of regression model predictive accuracy, because in-sample validation procedures can be overly optimistic or misleading (Harrell, 2001). By using a single RSF model as a basis for our metapopulation model, we assumed that the relationship of our RSF to the underlying population level would remain constant both temporally and spatially. While this assumption seems supported by the predictive accuracy of our model and the similarity of our RSF results to other studies, it should be further evaluated.

Our model training data sets were collected in the Greater Yellowstone after wolf reintroduction, however wolves were not present in the Garnet and Rocky Boys study areas. Similarly, our out of sample validation data sets contained a mixture of study areas with wolves (i.e. North Fork; Ruth, 2004a) and without (i.e. Yellowstone prior to 1996; Murphy, 1998). Today wolves have expanded their range to most suitable habitat in the State, overlapping with mountain lions in all but the most eastern portion of the State (Rich

et al., 2013). The presence of wolves may affect both mountain lion spatial use and prey abundance ultimately lowering mountain lion density (Ruth, 2004b; Kortello et al., 2007; Elbroch et al., in press).

4.3. Model uncertainty

Sensitivity analysis of past mountain lion population models has shown that female survival is the most important parameter in determining population growth rates (Lambert et al., 2006). In a hunted population the variation in female survival can account for up to 40% of total population growth (Robinson et al., 2014). Our single RSF validated better for adult females than males (Fig. 5). Although we cannot validate our modeled population growth rates against true growth, we feel that the models based on our mean and high reference starting population estimates in particular should resemble actual growth trends.

4.3.1. Effects of dispersal method vs. starting density

We modeled dispersal 3 ways including an assumption of no dispersal among units, Euclidean distance, and through a combination of habitat quality and distance (friction). Due to the size of the area we were modeling, computing limitation made it necessary to increase the pixel size of our friction (i.e., resource selection) layer from 0.09 ha to 36 ha in our population model simulations. This may have unduly restricted our quantification of dispersal in areas dominated by poor habitat quality or areas where high quality habitat was limited to thin linear features (i.e., riparian areas). In other ongoing studies, GPS collared mountain lions in eastern Montana especially, have been observed using much narrower pathways of higher quality habitat depicted by our RSF model. Studies of mountain lion dispersal have demonstrated that mountain lions follow habitat peninsulas (Beier, 1995), and that dispersing mountain lions use similar habitats as residents (Newby, 2011), and therefore connectivity is likely a function of habitat quality and not distance alone. An increased ability to model fine scale habitat use in a population modeling/dispersal framework should provide more accurate results than those presented here.

Analysis of our metapopulation model revealed that between the two major uncertainties in our model, true dispersal pattern vs. true starting population level, knowledge of mountain lion population size may be more informative than knowledge regarding dispersal patterns or rates. When population level was held constant (i.e., either high, mean, or low) and only dispersal was allowed to vary there was an average absolute difference of 1.4% between no dispersal and high or Euclidean distance based dispersal (Tables 7–9). It is noteworthy that the predicted effect on population growth was only 2.6% at a statewide scale, given the high starting population was almost double the low starting population (total density of 4.04/100 km² vs. 2.19/100 km²), (Tables 8 and 9). Two recent DNA mark recapture studies in Montana have suggested that densities of mountain may be higher than those presented here, perhaps as high as 6.7 mountain lions per 100 km² compared to our high density of 4.04/100 km² (Russell et al., 2012; Proffitt et al., in review). Unfortunately neither of these studies produced population estimates of resident adults which are needed to estimate survival in our Eq. (2). Our results suggest that models based on such higher estimates of density would decrease management unit specific estimates of growth but change estimates of growth little at a regional or statewide scale.

The effects of uncertainty in population size or dispersal on model outputs is reduced by increases in scale as evidenced by our two way analysis of variance results. Starting population level was a significant factor on modeled lambda at both the unit and regional scale, whereas dispersal level was only a significant factor on modeled lambda at the unit scale. We take this to suggest that managers may have greater latitude in initial density assumptions

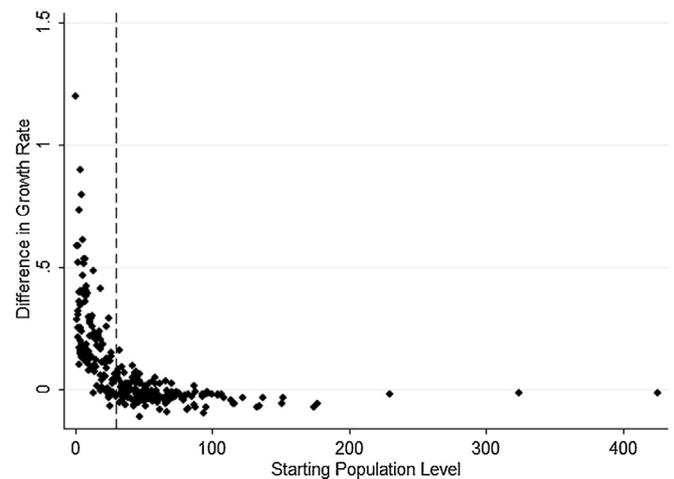


Fig. 8. Difference in individual hunting unit growth rate between models assuming distance-based dispersal and no dispersal (data points are 88 Montana hunting units at 3 starting densities, reference line = 30, values below 0 represent source sites where population growth is lowered by dispersal, while values above 0 represent sinks).

than earlier thought if management is approached at larger scales, adding further support for metapopulation or source sink management conducted at a regional scale (Logan and Sweanor, 2001).

Our RSF model predicts that MFWP Region 1 is characterized by near-ubiquitous high quality mountain lion habitat and this region used a permit system to regulate female harvest to relatively low levels during 2005–2010. Conversely FWP Region 3 has smaller, more linear patches of lion habitat interspersed with larger areas less suitable for lions (Figs. 1 and 4), and used a quota system to achieve relatively higher levels of female harvest in 2005–2010. The effect of our uncertainty regarding population level and dispersal rate was greater in MFWP Region 3 than MFWP Region 1. The difference between modeled growth rates based on low and high starting density estimates averaged 7% for units in Region 1 and 16% for Region 3. A regression of differences in growth due to dispersal at varying starting population levels illustrates this issue of scale further. Populations of less than 30 individuals benefit most from dispersal in our model (Fig. 8). Depending on the management objective (most predictions were for increasing populations in MFWP Regions 1 and 2, and for a declining population in MFWP Region 3, during 2005–10 regardless of assumptions), such findings can help to quantify the value of reducing these different uncertainties for achieving management objectives (e.g. Runge et al., 2011).

4.3.2. Effects of jurisdictional boundaries

Use of our model for informing decisions about lion harvest is currently hampered by a couple of deficiencies. First, mountain lion populations clearly operate across political boundaries, but our model currently only includes information about management units within the state of Montana. Every neighboring jurisdiction has substantial lion populations and corresponding lion management programs (Anderson et al., 2010). Dispersal and connectivity of mountain lion populations to and from neighboring jurisdictions has been documented in recent years (Thompson and Jenks, 2010; Andreasen et al., 2012). However, our model does not account for this connectivity to neighboring areas, creating a false edge effect in our predictions. Population growth and size predictions for management units adjacent to the state boundaries are likely to be biased because dispersal from adjacent management units in neighboring states is not accounted for.

4.4. Management implications

The use of a metapopulation model such as this to predict the effects of various harvest regulations on lion populations is only part of an adaptive mountain lion harvest management program. In adaptive management, predictions about the effects of harvest must be paired with monitoring to evaluate those predictions and the effects of the management action (Nichols and Williams, 2006). Although existing methods for estimating lion population size and trend are cost- and time-prohibitive for widespread use (McKinney, 2011), new developments in the use of genetic identification of individuals in a spatial mark-recapture framework offer promise (Russell et al., 2012). These methods allow for the estimation of population size using samples from one season, and are far cheaper than other alternatives. However, they are sufficiently expensive such that they are unlikely to be routinely used every year. Recognizing cost will be a limitation to implementation of monitoring methods, we believe that such monitoring techniques could be paired with predictions from our model in a thoughtful manner by focusing on a subset of sites chosen to represent the variation necessary to address key uncertainties in predictions (Walters and Holling, 1990; Conroy et al., 2012). Designing a management program in this manner will help resolve key uncertainties, improve predictions about the effects of harvest on mountain lion populations, and improve the success of management decisions at meeting population objectives.

Acknowledgements

Project funding and support were provided by the sale of hunting and fishing licenses in Montana and Montana Fish, Wildlife and Parks (FWP) Federal Aid in Wildlife Restoration grants, and the University of Montana. This manuscript and the modeling process it describes were greatly improved by feedback and discussions with MFWP wildlife biologists. In particular we would like to thank Jay Kolbe and Adam Grove for their interest and input. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

- Abhat, D., 2011. State of wildlife: northeast. *Wildl. Prof.* 5, 18.
- Anderson, C.R., Lindzey, F.G., 2005. Experimental evaluation of population trend and harvest composition in a Wyoming cougar population. *Wildl. Soc. Bull.* 33, 179–188.
- Anderson, C.R., Lindzey, F.G., Knopff, K.H., Jalkotzy, M.G., Boyce, M.S., 2010. Cougar management in North America. In: Hornocker, M.G., Negri, S. (Eds.), *Cougar Ecology and Conservation*. University of Chicago Press, Chicago, IL.
- Andreasen, A.M., Stewart, K.M., Longland, W.S., Beckmann, J.P., Forister, M.L., 2012. Identification of source-sink dynamics in mountain lions of the Great Basin. *Mol. Ecol.* 21, 5689–5701.
- Beier, P., 1993. Determining minimum habitat areas and habitat corridors for cougars. *Conserv. Biol.* 7, 94–108.
- Beier, P., 1995. Dispersal of juvenile cougars in fragmented habitat. *J. Wildl. Manage.* 59, 228–237.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.-S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* 24, 127–135.
- Boyce, M.S., McDonald, L.L., 1999. Relating populations to habitats using resource selection functions. *Tree* 14, 268–272.
- Boyce, M.S., Vernier, P.R., Nielsen, S.E., Schmiegelow, F.K.A., 2002. Evaluating resource selection functions. *Ecol. Model.* 157, 281–300.
- Burnham, K.P., Anderson, D.R., 1998. *Model Selection and Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York.
- Carbone, C., Gittleman, J.L., 2002. A common rule for the scaling of carnivore density. *Science* 295, 2273–2276.
- Caswell, H., 2001. *Matrix Population Models: Construction, Analysis, and Interpretation*. Sinauer Associates, Sunderland, MA, USA.
- Chetkiewicz, C.L.B., Boyce, M.S., 2009. Use of resource selection functions to identify conservation corridors. *J. Appl. Ecol.* 46, 1036–1047.
- Choate, D.M., 2009. Cougar-induced Behavioral Plasticity: Ungulate Behavior Under the Risk of Predation on the National Bison Range, Biological Sciences. University of Notre Dame, Notre Dame, IN, pp. 281.
- Choate, D.M., Wolfe, M.L., Stoner, D.C., 2006. Evaluation of cougar population estimators in Utah. *Wildl. Soc. Bull.* 34, 782–799.
- Conroy, M.J., Stodola, K.W., Cooper, R.J., 2012. Effective use of data from monitoring programs and field studies for conservation decision making: predictions, designs and models working together. *J. Ornithol.* 152, S325–S338.
- Cooley, H.S., Wielgus, R.B., Koehler, G., Maletzke, B., 2009a. Source populations in carnivore management: cougar demography and emigration in a lightly hunted population. *Anim. Conserv.* 12, 321–328.
- Cooley, H.S., Wielgus, R.B., Koehler, G.M., Robinson, H.S., Maletzke, B.T., 2009b. Does hunting regulate cougar populations? A test of the compensatory mortality hypothesis. *Ecology* 90, 2913–2921.
- Cooley, H.S., Bunnell, K.D., Stoner, D.C., Wolfe, M.L., 2011. Population management: cougar hunting. In: Jenks, J.A., Cooley, H.S., Conover, M.R. (Eds.), *Managing Cougars in North America*. Jack H. Berryman Institute, Utah State University, Logan, UT, pp. 111–133.
- Cougar Management Guidelines Working Group, 2005. *Cougar Management Guidelines*. WildFutures, Bainbridge Island, WA.
- Dias, P.C., 1996. Sources and sinks in population biology. *TREE* 11, 326–330.
- Elbroch, M., Wittmer, H.U., Saucedo, C., Corti, P., 2009. Long-distance dispersal of a male puma (*Puma concolor puma*) in Patagonia. *Rev. Chilena Hist. Nat.* 82, 459–461.
- Elbroch, M., Lendrum, P.E., Newby, J., Quigley, Thompson, D.J., 2015. Recolonizing wolves influence the realized niche of resident cougars. *Zool. Stud.* 54, 2–11.
- Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* 24, 38–49.
- Freddy, D.J., White, G.C., Kneeland, M.C., Kahn, R.H., Unsworth, J.W., deVergie, W.J., Graham, V.K., Ellenberger, J.R., Wagner, C.H., 2004. How many mule deer are there? Challenges of credibility in Colorado. *Wildl. Soc. Bull.* 32, 916–927.
- Gillies, C.S., Hebblewhite, M., Nielsen, S.E., Krawchuk, M.A., Aldridge, C.L., Frair, J.L., Safer, D.J., Stevens, C.E., Jerde, C.L., 2006. Application of random effects to the study of resource selection by animals. *J. Anim. Ecol.* 75, 887–898.
- Harrell, F.E., 2001. *Regression Modeling Strategies: With Applications to Linear Models, Logistic Regression, and Survival Analysis*. Springer, New York.
- Hosmer, D.W., Lemeshow, S., 2000. *Applied Logistic Regression*, 2nd ed. Wiley, New York, NY, USA.
- Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61, 65–71.
- Johnson, C.J., Nielsen, S.E., Merrill, E.H., McDonald, T.L., Boyce, M.S., 2006. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. *J. Wildl. Manage.* 70, 347–357.
- Keating, K.A., Cherry, S., 2004. Use and interpretation of logistic regression in habitat selection studies. *J. Wildl. Manage.* 68, 774–789.
- Kitching, R., 1971. Simple simulation model of dispersal of animals among units of discrete habitats. *Oecologia* 7, 95–116.
- Kortello, A.D., Hurd, T.E., Murray, D.L., 2007. Interactions between cougars (*Puma concolor*) and gray wolves (*Canis lupus*) in Banff National Park, Alberta. *Ecoscience* 14, 214–222.
- Kunkel, K., Vosburgh, T., Robinson, H., 2012. Ecology of cougars (*Puma concolor*) in north-central Montana. Final report to the US fish and wildlife service. In: Program. W.W.F.N.G.P., Bozeman, MT.
- Lambert, C.M.S., Wielgus, R.B., Robinson, H.S., Katnik, D.D., Cruickshank, H.S., Clarke, R., Almack, J., 2006. Cougar population dynamics and viability in the Pacific Northwest. *J. Wildl. Manage.* 70, 246–254.
- Laundre, J., Clark, T.W., 2003. Managing puma hunting in the western United States: through a metapopulation approach. *Anim. Conserv.* 6, 159–170.
- Leslie, P.H., 1945. On the use of matrices in certain population mathematics. *Biometrika* 33, 183–222.
- Logan, K.A., Sweanor, L.L., 2001. *Desert Puma: Evolutionary Ecology and Conservation of an Enduring Carnivore*. Island Press, Washington, DC.
- Logan, K.A., Sweanor, L.L., 2010. Behavior and social organization of a solitary carnivore. In: Hornocker, M.G., Negri, S. (Eds.), *Cougar Ecology and Conservation*. University of Chicago Press, Chicago, IL, pp. 105–117.
- Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., Erickson, W.P., 2002. *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*, 2nd ed. Kluwer Academic Publishers, Dordrecht/Boston.
- Matchett, R., 2012. Mountain Lion Research in the Missouri River Breaks. US Fish and Wildlife Service, Charles M. Russell National Wildlife Refuge, Lewiston, MT.
- McBride, R.T., McBride, R.T., McBride, R.M., McBride, C.E., 2008. Counting pumas by categorizing physical evidence. *Southeast. Nat.* 7, 381–400.
- McKinney, T.D., 2011. Cougar research and management needs. In: Jenks, J.A., Cooley, H.S., Conover, M.R. (Eds.), *Managing Cougars in North America*. Jack H. Berryman Institute Press, Utah State University, Logan, Utah, pp. 189–200.
- Montana Department of Fish Wildlife and Parks, 2005. *Montana's Comprehensive Fish and Wildlife Conservation Strategy*. Helena, MT.
- Murphy, K., 1983. Relationships Between a Mountain Lion Population and Hunting Pressure in Western Montana. University of Montana, pp. 48.
- Murphy, K., 1998. The ecology of the cougar (*Puma concolor*) in the northern Yellowstone ecosystem: interactions with prey, bears, and humans. In: *Forestry, Wildlife, and Range Sciences*. University of Idaho, Moscow, ID, pp. 147.
- Newby, J.R., 2011. Puma Dispersal Ecology in the Central Rocky Mountains. University of Montana, Missoula, MT.
- Newby, J.R., Mills, L.S., Ruth, T.K., Pletscher, D.H., Mitchell, M.S., Quigley, H.B., Murphy, K.M., DeSimone, R., 2013. Human-caused mortality influences spatial population dynamics: pumas in landscapes with varying mortality risks. *Biol. Conserv.* 159, 230–239.

- Nichols, J.D., Williams, B.K., 2006. Monitoring for conservation. *Trends Ecol. Evol.* 21, 668–673.
- Novaro, A.J., Funes, M.C., Walker, R.S., 2005. An empirical test of source-sink dynamics induced by hunting. *J. Appl. Ecol.* 42, 910–920.
- Pintilie, M., 2006. *Competing Risks: A Practical Perspective*. John Wiley & Sons, Chichester, England/Hoboken, NJ.
- Proffitt, K., Goldberg, J.F., Hebblewhite, M., Russell, R., Jimenez, B., Robinson, H.S., Pilgrim, K., Schwartz, M.K., 2015. Integrating resource selection and harvest into a spatial capture-recapture models for large carnivores. *Ecol. Appl.* (submitted for publication).
- Quigley, H., Hornocker, M.G., 2010. Cougar population dynamics. In: Hornocker, M.G., Negri, S. (Eds.), *Cougar: Ecology and Conservation*. The University of Chicago Press, Chicago, IL, USA, pp. 59–75.
- Rabe-Hesketh, S., Skrondal, A., Skrondal, A., 2008. *Multilevel and Longitudinal Modeling Using Stata, 2nd ed.* Stata Press Publication, College Station, TX.
- Rich, L.N., Russell, R.E., Glenn, E.M., Mitchell, M.S., Gude, J.A., Podruzny, K.M., Sime, C.A., Laudon, K., Ausband, D.E., Nichols, J.D., 2013. Estimating occupancy and predicting numbers of gray wolf packs in Montana using hunter surveys. *J. Wildl. Manage.* 77, 1280–1289.
- Robinson, H.S., DeSimone, R.M., 2011. The garnet range mountain lion study: characteristics of a hunted population in west-central Montana. In: *Federal Aid in Wildlife Restoration Project W-154-R*, Helena, MT.
- Robinson, H.S., Desimone, R., Hartway, C., Gude, J.A., Thompson, M.J., Mitchell, M.S., Hebblewhite, M., 2014. A test of the compensatory mortality hypothesis in mountain lions: a management experiment in west central Montana. *J. Wildl. Manage.* 78, 791–807.
- Root, K.V., 2004. Florida panther: using models to guide recovery efforts. In: Akcakaya, H.R., Burgman, M.A., Kindvall, O., Wood, C.C., Sjogren-Gulve, P., Hatfield, J.S. (Eds.), *Species Conservation and Management: Case Studies*. Oxford University Press, New York, NY, USA, pp. 491–504.
- Runge, M.C., Converse, S.J., Lyons, J.E., 2011. Which uncertainty? Using expert elicitation and expected value of information to design an adaptive program. *Biol. Conserv.* 144, 1214–1223.
- Russell, R.E., Royle, J.A., Desimone, R., Schwartz, M.K., Edwards, V.L., Pilgrim, K.P., McKelvey, K.S., 2012. Estimating abundance of mountain lions from unstructured spatial sampling. *J. Wildl. Manage.* 76, 1551–1561.
- Ruth, T.K., 2004a. Patterns of Resource Use Among Cougars and Wolves in Northwestern Montana and Southeastern British Columbia. University of Idaho, Moscow, ID, pp. 122.
- Ruth, T.K., 2004b. Ghost of the Rockies: the Yellowstone cougar project. *Yellowstone Sci.* 12, 13–24.
- Ruth, T.K., Buotte, P.C., 2007. Cougar ecology and cougar-carnivore interactions in Yellowstone National Park. In: *Final Technical Report*. Society, H.W.I.W.C., Bozeman, MT.
- Sinclair, A.R.E., Fryxell, J.M., Caughley, G., 2006. *Wildlife Ecology, Conservation, and Management, 2nd ed.* Blackwell Pub., Malden, MA/Oxford.
- Stephens, P.A., Buskirk, S.W., Hayward, G.D., Martinez del Rio, C., 2005. Information theory and hypothesis testing: a call for pluralism. *J. Appl. Ecol.* 42, 4–12.
- Stoner, D.C., Rieth, W.R., Wolfe, M.L., Mecham, M.B., Neville, A., 2008. Long-distance dispersal of a female cougar in a basin and range landscape. *J. Wildl. Manage.* 72, 933–939.
- Swenar, L.L., Logan, K.A., Hornocker, M.G., 2000. Cougar dispersal patterns, metapopulation dynamics, and conservation. *Conserv. Biol.* 14, 798–808.
- Thompson, D.J., Jenks, J.A., 2005. Long-distance dispersal by a subadult male cougar from the Black Hills, South Dakota. *J. Wildl. Manage.* 69, 818–820.
- Thompson, D.J., Jenks, J.A., 2010. Dispersal movements of subadult cougars from the Black Hills: the notions of range expansion and recolonization. *Ecosphere* 1, 1–11.
- US Geological Survey Gap Analysis Program, 2010. Northwest Gap Analysis Project Land Cover Data. University of Idaho <http://gap.uidaho.edu/index.php/landcover>
- Walters, C.J., 1986. *Adaptive Management of Renewable Resources*. Macmillan/Collier Macmillan, New York.
- Walters, C.J., Holling, C.S., 1990. Large-scale management experiments and learning by doing. *Ecology* 71, 2060–2068.
- Williams, J., 1992. *Ecology of Mountain Lions in the Sun River area of Northern Montana*. Montana State University, Bozeman, MT, pp. 109.
- Williams, B.K., Szaro, R.C., Shapiro, C.D., 2007. *Adaptive Management: The U.S. Department of the Interior Technical Guide*. U.S. Department of the Interior, Washington, DC.