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PUMA DISPERSAL ECOLOGY IN THE CENTRAL ROCKY MOUNTAINS

By

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Puma Dispersal Ecology in the Central Rocky Mountains

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The structuring of populations within a metapopulation, connected through dispersal, is important to basic and applied ecology. However, a considerable gap exists in our knowledge of the influence landscape heterogeneity has on dispersal and its consequences. We examined landscape effects on dispersal and its consequences for puma (*Puma concolor*) populations using data from three separate populations in the Central Rocky Mountains including the Northern Greater Yellowstone Ecosystem (NGYE), the Southern Greater Yellowstone Ecosystem (SGYE) and the Garnet Mountains of Montana.

We found human-induced mortality reduced inter-population vital rates with population consequences. The NGYE population was dependent largely on immigration for its own growth and emigration for its overall contribution to the metapopulation. The Garnet population, subject to high human induced mortality, was a population sink until a 915 km^2 area was closed to hunting, after which that area became a source, largely from a 16x emigration increase. Human-induced mortality affected emigration, dispersal distance, and establishment success. Effective dispersal of subadult males (n=59) was reduced primarily through direct mortality, whereas females (n=67) were more influenced by indirect effects reflected in reduced emigration and dispersal distances.

We further examined dispersal-landscape relationships through disperser habitat preferences. Generalized linear mixed-effects models were constructed from *a priori* models of disperser habitat to test the importance of forest cover, topographic cover, suitable hunting habitat, and anthropogenic disturbance. Models were fit to location data from GPS-marked (n=11) and VHF-marked (n=123) dispersers from all three study areas. Model selection, using Akaike's Information Criterion, found landscape characteristics associated with successful hunting of ungulate prey combined with anthropogenic disturbance parsimoniously explained locations of GPS-marked individuals. For VHF-marked dispersers the hunting habitat model ranked highest with the combined hunting habitat and anthropogenic disturbance model second. Model fitting from both datasets indicate habitat characteristics important to dispersers is similar to resident adults. A resource selection function estimated from the top GPS model was highly predictive of disperser locations from the independent VHF dataset. This model can identify areas important to dispersing individuals and suggests adult habitat is a useful surrogate for landscape connectivity.

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Dr. Toni Ruth provided the original foundation for the following work. Her work is an exemplar of rigorously conducted field science. Along with Toni several other people led field projects involved in this thesis including Dr. Howard Quigley, Dr. Kerry Murphy and Rich DeSimone. I am very grateful for their generosity with their research efforts and their support and advice.

I owe much appreciation to Dr. Daniel Pletscher and Dr. Michael Mitchell for their instruction and guidance throughout my graduate education and research endeavors.

To my field mates on the Northern Yellowstone Cougar Project including Polly Buotte, Michael Sawaya and Daniel Stahler, I offer my thanks for the best of times and friendship through the worst. My co-workers on the Teton Cougar Project, Peter Alexander and Marylin Cuthill, have shown remarkable patience and support during the writing process.

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Of all people, my wife Tasha is the one that I owe the deepest gratitude. I will ever appreciate and admire her love, and willingness to sacrifice so much in this process.

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PREFACE

Gathering empirical data on the large and unpredictable movements made by dispersing organisms has proven difficult, and this is especially true for large carnivores. The work I present here was only possible through the collaboration of multiple long-term research projects independently examining puma populations. I am indebted to the biologists that conducted these studies and their generosity in allowing me to participate in their research.

Dr. Kerry Murphy, under the direction of Maurice Hornocker, initiated an intensive study of the northern Yellowstone puma population in 1987 which continued through 1993. This research examined the ecology of the re-establishing puma population in the northern Yellowstone area and its interactions with prey, grizzly (*Ursus arctos*) and black (*Ursus americanus*) bears, and humans. Fieldwork was resumed in 1998 by Dr. Toni Ruth with the Hornocker Wildlife Institute/Wildlife Conservation Society and continued through 2005. The 1995 reintroduction of wolves into Yellowstone gave impetus for this study, as it allowed the ecology of pumas to be examined in the presence of wolves and compared to the former body of work on northern Yellowstone pumas.

The Hornocker Wildlife Institute began puma research in the southern Greater Yellowstone Area in 2000 as a sister project to the northern Greater Yellowstone Area puma project. Similarly to the northern study, this research was designed to examine basic puma ecology and the influence of wolves and other carnivores. In 2003 the study was reorganized under Craighead Beringia South, with Dr. Howard Quigley remaining as the principle investigator along with Derek Craighead.

Rich DeSimone, with Montana Fish Wildlife and Parks, initiated an intensive study on the puma population in the Garnet Mountains of western Montana beginning in 1997, which continued through 2006. Objectives of the MTFWP research were to document population characteristics and examine the effectiveness of various survey techniques as population indexes.

The following thesis was founded upon the long-term research on these puma populations and the cooperation of their principal investigators. I have presented this thesis in the form of two manuscripts for subsequent publication in peer-reviewed journals. Given the cooperation necessary to this research, I have included the co-authors at the beginning of both manuscripts and use the pronoun “we”, to reflect multiple authorship.

CHAPTER I

INTRODUCTION

The heterogeneity of landscapes explains why the distribution and abundance of species are patchy (Hanski & Gilpin 1991; Jacobson & Peres-Neto 2010). Because the overarching theme of ecological studies is the distribution and abundance of organisms, a realistic view of ecology cannot ignore the dynamics of spatially structured populations (Fahrig & Merriam 1994; Krebs 1994). Dispersal is fundamental to this spatially explicit understanding of ecology because it determines both the dynamics of spatially structured populations and the scale over which they occur (Clobert 2001; Kareiva 1990; Mills 2007).

One of the ways in which dispersal influences population dynamics is through supplying genetic variation, essential to the fitness of individuals in the short-term and the evolutionary potential of species in the long-term (Hogg *et al.* 2006; Mills 2007; Mills & Allendorf 1996). In a well-known example, a small isolated population of Florida panther (*Puma concolor coryi*) displayed signs of inbreeding and low fitness leading to a population decline and an imminent threat of extinction (Land *et al.* 2004; Maehr 1995; Rolke *et al.* 1993). Population performance improved only after 8 female pumas from Texas (*P. c. stanleyana*) where introduced for the purposes of genetic introgression (Johnson *et al.* 2010).

Along with the importance of dispersal to population genetics, ecologists have long recognized dispersal is essential at the demographic level. Since Levins (Levins 1969) proposed populations may interact within a metapopulation, the heterogeneity of populations and their interactions on the landscape has become a major focus of basic and applied ecology (Baguette & Stevens 2003; Hanski & Gilpin 1991; Harrison 1991). For many species, the among population interactions (i.e., emigration and immigration) can play a greater role in its demography and persistence than within population vital rates (i.e., birth and death) (Blaustein 1981). Metapopulation persistent often depends on these interpopulation movements because they allow productive local populations to balance losses from other local populations (e.g., source-sink dynamics) as well as provide colonizers to populations that have gone extinctions (Brown & Kodric-Brown 1977; Pulliam 1988; Schreiber 2006; Stacy & Taper 1992). Indeed, dispersal occurring at adequate levels over a large number of populations can allow metapopulations to persist, even if they embraces only populations which exhibit negative growth in the absence of immigration (Schreiber 2006).

Given the genetic and demographic importance of interpopulation movements, efforts are increasingly made to explicitly consider the interactions of multiple populations in conservation (Baguette & Stevens 2003; Chepko-Sade & Halpin 1987; Clobert 2001; Crooks & Sanjyan 2006; Kareiva 1990; Mortelliti *et al.* 2010; Schwartz *et al.* 2002; Waser *et al.* 2001; Weins 2001). As a result of anthropogenic habitat change and human-induced mortality, some species have become ever more reliant on refuges where populations are insulated from human-induced vital rate declines. Populations outside these areas may persist as sinks that are reliant on immigrants from population sources, such as refuges.

Managing for effective dispersal from sources to maintain sinks has become a cornerstone of wildlife and fisheries management (Bennet 1990; Botsford *et al.* 2009; Figueira & Crowder 2006; Joshi & Gadgil 1991; Kramer-Schadt *et al.* 2004; Labonte *et* *al.* 1998; McCoy *et al.* 1999; McCullough 1996; Naranjo & Bodmer 2007; Revilla *et al.* 2004; Sladek Nowlis 2000; Zimmermann 2004) . Furthermore, effective dispersal may also be essential to maintain source populations which may themselves require immigrants for their own growth; such populations have been dubbed a “dependent sources” (Franklin *et al.* 2004; Hixon *et al.* 2002). This situation may require the maintenance of multiple well-connected source populations for conservation.

Large carnivores exhibit many characteristics that may make it especially important to maintain multiple, interacting populations. For example carnivores occupy a high trophic level, occur at low densities, and are prone to conflicts and persecution by humans, all of which results in their dependence on large landscapes for maintaining populations. Conservation for these species will depend on the identification and maintenance of source populations and dispersal pathways, as well as an understanding of how these are affected by humans and the landscape (Balme 2009; Morrison 2008; Novaro *et al.* 2005; Smith *et al.* 2010; Smith 1993; Zimmermann *et al.* 2007).

Pumas are top predators, occur at low density, require large landscapes, are prone to human-induced mortality, and exhibit dispersal characteristics similar to many other large carnivores. For example, pumas exhibit high rates of natal dispersal, where subadult individuals - independent of their mother, yet too young to have established adult breeding territories - leave their natal range to establish an adult breeding range in a new area (Howard 1960). Dispersal among males is considered to be innate with virtually all males emigrating from their natal range and often travel large distances, up to several hundred kilometers (Laundre & Hernandez 2003b). Female dispersal appears to be more flexible with many remaining philopatric, and although female dispersers are capable of extensive movements, dispersal tends to occur over smaller spatial scales (Stoner *et al.* 2008).

Genetic analysis of puma populations have mostly confirmed these patterns, indicating genetic exchange over large, heterogeneous landscapes and little differentiation between puma populations Yet, they have supplied some, albeit mixed, evidence for genetic structuring due to distance and prominent linear barriers such as highways, rivers, and desert basins (Anderson 2004; Culver *et al.* 2000; Ernest *et al.* 2000; McRae 2005; Sinclair *et al.* 2001). Although informative, genetic techniques are limited in their ability to assess specific landscape effects on dispersal. Genetic measures of connectivity (such as F_{st} values and assignment tests) are generally unable to distinguish between historical and recent population exchange and/or may not be accurate under high levels of population exchange expected for species with strong dispersal tendencies (Jacobson & Peres-Neto 2010; Williamson 2004; Wolff 1997). In addition, such genetic measures generally cannot provide information on emigration rates of source populations, rates of survival and establishment of dispersers, and habitat use of dispersing individuals (Lowe & Allendorf 2010).

The high rates of dispersal naturally occurring in puma populations suggest population persistence and growth is largely determined by emigration and immigration (Hemker *et al.* 1984; Laing & Lindzey 1993; Logan *et al.* 1986; Ross & Jalkotzy 1992; Spreadbury 1996; Stoner *et al.* 2006; Sweanor *et al.* 2000). Puma populations subject to hunting generally exist within a network of sources and sinks (Cooley *et al.* 2009; Quigley & Hornocker 2010; Robinson *et al.* 2008). Source-sink dynamics likely allowed the historic persistence of pumas in the western U.S., where populations in remote, inaccessible areas acted as sources to persecuted sink populations, and provided individuals that re-established extirpated populations (Laundre & Clark 2003). The recognition that source-sink dynamics are important to puma populations has led to calls for explicit consideration of source-sink dynamics in puma management efforts (Cougar Managment Guidlines Working Group 2005; Logan & Sweanor 2001; Wyoming Game and Fish Department 2006). Still largely missing, however, is information elucidating how these spatial processes are shaped by the landscape.

Our objective was to determine how landscape characteristics influence dispersal patterns such as emigration, dispersal distances, habitat use during dispersal, and survival to become established adults. In addition, we examined how these dispersal components determined the contribution of local populations to the region and how this contribution changed temporally under different demographic contexts.

We gathered information on both puma demography and dispersal movements through a collaborative effort of four long-term (6-9 yrs), intensive puma population studies that examined three separate areas (see Appendix: A). Two of the studies were conducted in the northern Greater Yellowstone Area, primarily on the northern range of Yellowstone National Park and the adjacent area. The objective of the first of these studies (1987-1993) was to examine puma ecology as the population recovered from historic persecution. The second study (1998-2005) examined population characteristics in the presence of reintroduced wolves. A third study in the southern Greater Yellowstone Area (2001-present) was initiated as a sister study to that in the north, and likewise examined puma ecology in the presence of wolves. The fourth study focused on a puma population in the Garnet Mountains of western Montana (1997-2006), which differed from the other study populations in its greater exposure to human-induced mortality, as well as its lack of wolf and grizzly bear populations. Levels of human hunting pressure varied in the Garnet system over the study period. Heavy hunting was ubiquitous through the study area from 1997-2000, after which a small (915 km^2) section of the study area was experimentally closed to hunting, though hunting pressure remained high in the surrounding area. All four of these studies involved large samples of marked pumas (ranging from 82-123 animals over the course of the studies) which allowed us to examine the influence of landscape characteristics on dispersal patterns from well-documented populations.

In chapter II we used data gathered in these field projects to examine the influence of human-induced mortality on dispersal characteristics for both male and female dispersers. We compared the dispersal characteristics of the Garnet Mountain population, exposed to a landscape with high risk of anthropogenic mortality, to pumas on the northern range of Yellowstone National Park, relatively more insulated from anthropogenic risks. In addition to the spatial variation in anthropogenic risk, the levels of human-induced mortality changed over time, providing further opportunities to examine the effects of mortality context on dispersal. We examined how this mortality context affected major dispersal components: emigration, dispersal distances, and survival of dispersers to successful immigration. In addition, we incorporated dispersal information, along with observed population growth and immigration rates to quantitatively estimate the annual per capita contribution of local populations to their region (Runge *et al.* 2006). This allowed us to operationally categorize the populations as sources or sinks, and determine how their contribution changed temporally under different demographic contexts.

Chapter III details our examination of landscape use by pumas during dispersal. The landscape matrix surrounding populations can significantly influence dispersal movements for some species (Revilla *et al.* 2004; Ricketts 2001). Efforts to delineate landscape connectivity for pumas, and other species typically assume resident adult habitat is a appropriate surrogate for suitable dispersal habitat (Kautz *et al.* 2006; LaRue 2008; Thatcher *et al.* 2009). However, habitat requirements may differ depending on the life history stage of the individual (Selonen & Hanski 2006; Stamps *et al.* 2005). For example, dispersing individuals may use the landscape differently than residents as dispersers need to explore unknown and potentially dangerous areas while prospecting for a breeding territory.

We used Global Positioning System (GPS) and Very High Frequency (VHF) radio-telemetry locations from dispersing pumas in the three different study areas to identify habitat preferences for dispersing pumas. We developed *a priori* models of disperser habitat use based on ecological mechanisms hypothesized to influence dispersers' use of the landscape (Beier 1995; Beier 2002; Comiskey *et al.* 2002; Dickson *et al.* 2005; Hemker *et al.* 1984; Land *et al.* 2008; LaRue 2008; Laundre & Hernandez 2003a; Laundre & Loxterman 2007; Logan *et al.* 1986; Maehr *et al.* 2002; Seidensticker 1977; Stoner *et al.* 2008; Sweanor *et al.* 2000; Thatcher *et al.* 2009; Williams *et al.* 1995; Woodruff 2006). By testing competing models of habitat use based on ecological relationships from data derived from multiple study systems, we could generate more robust inferences on disperser habitat use (Garshelis 2000). Location data from dispersing pumas was used to fit generalized linear mixed effects models, with fixed effects based on landscape characteristics predicted to be important to dispersal. The advantage of generalized linear mixed effects models is the ability to include a random term for the individual sampled, accounting for the diverse landscapes encountered by dispersers. In addition, random terms based on study area, sex, and time of year could be included to examine their significance in altering a disperser's use of the landscape.

Within all three study areas locations from GPS and VHF marked individuals provided two distinct datasets. This allowed us to compare the results of model testing from the two independent data sets. Finally, we used the best performing model derived from GPS collared individuals to build a resource selection function (RSF) for dispersing puma habitat use. We then validated the RSF using the independent VHF location database. This provided a model of varying levels of habitat preference which could be applied to the heterogeneous landscape of the Central Rocky Mountains (Mortelliti *et al.* 2010; Stoddard 2010).

Strong dispersal capacity is an important asset in the conservation of a species (Noss *et al.* 1996). It is likely that this ability has been historically important in allowing puma populations to persist in the face of exploitation and persecution. However, interpopulation movements may have thresholds at which excessive habitat fragmentation or mortality prohibits connectivity. A better understanding of interpopulation processes and these populations' responses to changing landscapes, along with the will to protect these processes, is likely to become increasingly essential to conservation.

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CHAPTER II

LANDSCAPE CONTEXT INFLUENCES SPATIAL POPULATION DYNAMICS: PUMAS UNDER VARYING LEVELS OF HUMAN-INDUCED MORTALITY

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ABSTRACT

An understanding of how stressors affect both individual disperser attributes and the contribution of single populations to multi-population dynamics are of immediate value to basic and applied ecology. Pumas (*Puma concolor*) are wide-ranging carnivores expected to be influenced by inter-population movements and susceptible to human-induced source-sink dynamics. We quantified the contributive roles of two populations using long-term, detailed data from the Garnet Mountains of western Montana, where human-induced mortality was high, and a relatively secure landscape in the Northern Greater Yellowstone Ecosystem (NGYE). The NGYE puma population depended on inter-population movements for its own growth as well as its ability to make a net contribution to the larger region. The Garnet area under heavy hunting pressure was a sink with a declining population until hunting was eliminated within a 915 km^{2}core area, at which point it became a source with positive intrinsic growth and a 16x increase in emigration. We also examined the spatial and temporal landscape effects on individual dispersal attributes (emigration, dispersal distance, establishment success) of subadult pumas (N=126) in both systems. Human-induced mortality regimes modulated all three dispersal components, reducing inter-population vital rates for males and females in different ways. Male inter-population exchange was reduced directly through elevated pre- and post-emigration mortality. Indirect effects were more evident for females, which displayed reduced emigration propensity and dispersal distance in high-risk landscapes. Human-induced mortality is known to powerfully influence within-population vital rates. In addition, human-induced mortality, acting on inter-population vital rates, will determine the ability of local populations to contribute to the larger region. Given the importance of interpopulation movements at the local and regional level these effects may have profound impacts on populations. In spatially structured management approaches it will be especially important to consider the impacts of human-induced mortality on both within- and between-population vital rates.

INTRODUCTION

Although the general importance of spatial structure is deeply appreciated in both basic and applied ecology, the interacting influences of dispersal and mortality across landscapes are still poorly understood. In single population studies of long-lived vertebrates adult survival, when amenable to change, is known to contribute strongly to population growth (Gaillard *et al.* 2000; Hostetler *et al.* 2009; Oli & Dobson 2003; Saether & Bakke 2000). In multi-population systems elevated mortality may be have more complicated influences, because mortality may also affect dispersal characteristics.

Natal dispersal involves three distinct components: emigration from the natal area, movement between natal and target areas, and successful establishment into a new breeding site (Bowler & Benton 2005; Howard 1960). Due to the large and unpredictable movements of dispersers, estimating these components of dispersal is difficult. Even more challenging is replicating estimates across different landscapes or mortality contexts (Cooper *et al.* 2008; Koenig *et al.* 1996; Morrison & Wood 2009). If among and within-population vital rates can be derived from the field, however, the role of a local population within the multi-population context can be quantified and source and sink areas operationally identified (Griffin & Mills 2009; Runge *et al.* 2006).

In applied ecology, an understanding of how human-induced mortality affects dispersal characteristics and the role of local populations on the landscape is of immediate value. Recognizing that populations occur under naturally and artificially heterogeneous environments across which they interact (Revilla *et al.* 2004; Small *et al.* 1991; Thomas & Kunin 1999), management agencies are increasingly incorporating population spatial structure into wildlife and fisheries management (McCullough 1996); Cougar Management Guidelines 2005; Botsford et al. 2008). For harvested species, identifying and managing source populations is considered an efficient spatially explicit approach, as it requires less detailed information and precise monitoring compared to managing a population for a target size or mortality level (Joshi & Gadgil 1991; McCullough 1996). Spatial approaches are especially applicable to highly vagile and cryptic species like large carnivores which depend on refuges, such as National Parks and Wilderness areas, in the face of habitat loss, habitat fragmentation, and high human-induced mortality (Karanth & Chellam 2009). These refuges can act as sources for neighboring population sinks where persistence would otherwise be precluded (Balme 2009; McCullough 1996; Novaro *et al.* 2005; Weaver *et al.* 1996; Woodroffe & Ginsberg 1998). Important to these spatial management approaches is the accurate assessment of the role of local populations in the region, the effectiveness of dispersal movements across the landscape, and how these may be modulated by human-induced mortality.

Pumas range widely across North America and are of high interest as both a harvested species and species of concern (Cougar Managment Guidlines Working Group 2005; Montana Fish Wildlife and Parks 1996; Wyoming Game and Fish Department 2006). Puma populations can exhibit source-sink dynamics induced by human-caused mortality (Laing & Lindzey 1993; Logan *et al.* 1986; Ruth *et al.* 2010, in press; Stoner *et al.* 2006). For example, a heavily hunted puma population in Washington remained numerically stable over time due to immigration, despite survival and reproductive rates insufficient for population maintenance (Robinson *et al.* 2008). In contrast, a lightly hunted population also remained stable despite birth and death rates indicating a growing population, apparently due to high levels of emigration (Cooley *et al.* 2009).

We took advantage of detailed long-term, large-scale demographic data from two puma populations with different amounts of human-induced mortality to describe how landscape effects modulate spatial population dynamics. Specifically, we operationally defined the populations as sources and sinks based on within-population growth and between population exchange, and determined how these varied temporally. Additionally, we examined the components of dispersal – amount of emigration, dispersal movement, and establishment success – and their sex specific spatial and temporal variation under differing human-induced mortality contexts.

The puma population in the Northern Greater Yellowstone Ecosystem (NGYE) was largely insulated from anthropogenic risks. We used NGYE puma data from 2 periods. From 1987-1993 (hereafter called "Phase I"), the puma population was growing after their former reduction due to control efforts within Yellowstone National Park (early 20th century) and persecution as a predator in surrounding areas (up to 1971) (Murphy *et al.* 1999). During Phase II (1998-2005) of NGYE research, the puma population reached higher densities than in phase one and remained relatively stable (Ruth *et al.* 2008a; Ruth & Buotte 2007; Ruth *et al.* 2010, in press). The second study phase differed importantly from the first in that wolves (*Canis lupus*) had been reintroduced into the area. Wolves often dominate pumas in competitive interactions and can cause direct mortality, loss of kills, and alter puma space use (Ballard *et al.* 2003; Kortello *et al.* 2007; Ruth 2004; Ruth & Buotte 2007; Ruth & Murphy 2010).

In contrast to the more protected and largely inaccessible NGYE study population, puma in the Garnet Mountains of Montana were exposed to higher human induced mortality through heavier hunting pressure, greater human access via roads and off road vehicles, and more private lands. In the first 3 years of Garnet research (1997-2000), the puma population was heavily hunted throughout the study area, but in subsequent years of Garnet research (2001-2006) hunting was restricted (DeSimone & Semmens 2005). However, human-induced mortality remained high compared to the NGYE over all years of Garnet research (MDFWP hunt reports 1997-2006). We predicted that after puma hunting was restricted in the Garnet area, the population's per capita contribution to the region would increase in part due to higher levels of dispersal into surrounding subpopulations.

To help interpret changes in source-sink dynamics, we also investigated how landscape-level human-caused mortality affected proximate drivers of dispersal characteristics (emigration, dispersal movements, and establishment). First, we predicted pumas in the higher harvest Garnet area would have lower emigration rates than the NGYE due to greater human-induced mortality and population turnover. Second, we predicted that high turnover due to heavy harvest in the Garnet area would open territories for settlement (Ausband & Moehrenschlager 2009; Fonseca & Hart 1996; Kluyver & Tinbergen 1970; Waser 1985) and lead to shorter dispersal distances and settlement closer to natal areas. Third, we predicted that direct mortality from human sources would result in fewer Garnet dispersers successfully surviving dispersal to establish adult home ranges. Finally, we considered the influence of density and sex-specific differences on dispersal characteristics.

We expected sex specific differences would manifest themselves in more males emigrating from the study areas (Maehr *et al.* 2002; Stoner *et al.* 2006) and dispersing further (Laundre & Hernandez 2003b; Sweanor *et al.* 2000), however, higher rates of mortality for dispersing male pumas would likely limit their ability to successfully immigrate (Logan & Sweanor 2010). Pumas are a trophy game species through out much of the west, and males are especially targeted as trophy animals (Lambert *et al.* 2006); Robinson et al. 2008; Ruth et al. 2010), and are prone to mortality from lethal encounters with other males (Murphy 1998); but see Logan and Sweanor 2001 for unhunted population). Therefore, we hypothesized that females would be more likely to survive the dispersal process and establish adult home ranges compared to males.

STUDY AREAS

Northern Greater Yellowstone Ecosystem (NGYE)

The primary study area covered 3,779 km^2, including the northern range of Yellowstone National Park and the surrounding area of the Absorka-Beartooth Wilderness and private and public lands in the Gardner basin (Murphy 1998; Ruth *et al.* in press). Terrain is mountainous with steep broken canyons along the Yellowstone River and with elevations ranging from 1,500 – 2,900 meters. Documentation of dispersal movements extended out 200 kilometers from the study area across the Greater Yellowstone Ecosystem.

Pumas preyed primarily on elk (*Cervus elaphus)* and mule deer (*Odocoileus hemionus)*. Other ungulate prey included bighorn sheep (*Ovis canadensis*), pronghorn antelope (*Antilocapra americana*), moose (*Alces alces*), mountain goats (*Oreamnos hemionus*), and a small number of white-tailed deer (*O. virginianus*). Carnivore species included coyotes (*Canis latrans*), grizzly bears (*Ursus arctos*), and black bears (*U. americanus*). Both bear species commonly usurped puma kills especially in spring and early summer (Murphy 1998; Ruth & Buotte 2007). Wolves (*Canis lupus*) were reintroduced to Yellowstone's northern range in 1995 and increased over much of the Phase II study (Smith *et al.* 2010). Pumas were displaced from their kills by wolves and on occasion wolves killed kittens and adult cats (Ruth 2004; Ruth *et al.* in press).

Pumas occupy the northern range of Yellowstone National Park year round but in winter the surrounding population is restricted to low elevation elk wintering range, making puma space use highly seasonal. Minimum estimated annual density of independent adult and subadult pumas ranged from 3.0 – 10.7/1000km^2 over the study years, based on annual number observed via capture, telemetry and snow tracking for the extent of area covered by all estimated adult home ranges combined. The average home range size, estimated using 95% fixed kernel, for adult male pumas was 922 km^2 (SE=192 km^2) and 378 km^2 (SE=48 km^2) for adult females (Ruth & Buotte 2007; Ruth *et al.* 2010).

Approximately 58% of the study area (2,224 km^2) was within park boundaries where hunting of pumas is not allowed, and 26% (974 km^2) was within Wilderness areas inaccessible to hunters from which no pumas were harvested. (Ruth *et al.* in press). As pumas dispersed they encountered primarily public lands, in Yellowstone and Grand

Teton National Parks and National Forests and Wilderness (84.2% public land; SE=0.09%) and road densities of 0.36 km/km^2 (SE=0.02) (Tiger/line files, Census 2000).

Garnet Mountains, Montana

The study area was situated in 2,500 km^2 of the mountainous Blackfoot River Drainage, with elevations from 1160 - 2156 meters. Large-ungulate prey species included elk, mule deer, white-tailed deer, and moose. Large carnivores included coyotes and black bears, with grizzly bears and wolves occurring very rarely.

In the Garnet Mountain core study area, liberal hunting of pumas was permitted from 1997 to 2000 (pre-closure). Hunting was then prohibited in a 915-km^2 area until 2006 (closure), but continued throughout the surrounding Blackfoot Drainage. Densities of independent pumas over the Garnet study area were estimated to be 4.8 – 11.7/1000 km^2. Home ranges were less seasonal than in the NGYE. Average 95% fixed kernel home range size of adult male pumas was 400 km^2 (SE=191 km^2); female home ranges averaged 237 km^2 (SE=31 km^2) (DeSimone, R., unpublished data).

Dispersal of individuals from the core Garnet study area extended the study area by 80 kilometers throughout the greater Blackfoot drainage. The Blackfoot drainage was largely comprised of private lands (48%, SE=1.3%) and average road densities were 0.78 km/km^2 (SE=0.02).

Overall human-induced mortality was higher in the Garnet system than in NGYE even after hunting was restricted in the Garnets. Legal harvest removals of pumas in the hunt districts overlapping the Garnet study area were 3X greater annually than those overlapping the NGYE study area (range 1.2 to 4.69X greater in Garnets than NGYE; MDFWP hunt reports 1987-2006). In addition most of the NGYE study area (58%) was within the boundaries of Yellowstone National Park and not exposed to any hunting. Garnet individuals were also exposed to higher levels of other forms of human-induced mortality including poaching, snaring and depredation removals (see Appendix B).

METHODS

Field Sampling

Pumas >3 months of age were captured and immobilized using trained hounds. Kittens were captured in the den by hand at 5-8 weeks old, or with hounds in the following winter. Pumas were marked in one ear with unique numbered ear tags, tattooed in the opposite ear, and fitted with a VHF or GPS radio-collar equipped with mortality switches (Murphy 1998; Ruth *et al.* 2008b). VHF collared individuals were relocated at 1 – 14 day intervals from the ground and the air. A subset of adult and subadult individuals were fitted with GPS collars beginning in 2001.

Minimum number of adult and subadult pumas were documented annually. Annual estimates provided close to a complete census through a combination of having nearly all individuals in the population telemetry marked and extensive snow track transects (1,200 to 2,850 km/winter) to detect unmarked individuals (DeSimone & Semmens 2005; Murphy 1998; Ruth *et al.* in press). Additional documentation of pumas on the study areas was gathered from resource management personnel, hound hunters, and state harvest records. Despite the nearly complete census of the study populations annual estimates should be considered population minimums, because undocumented pumas may have used areas overlapping the study areas and we did not formally estimate detection probability (DeSimone & Semmens 2005; Murphy 1998; Ruth *et al.* in press).

Disperser Attributes: Emigration, Dispersal Distance, and Disperser Success

Emigration.– From the telemetry data we estimated dispersal characteristics including emigration versus philopatry rates, dispersal distance, and disperser success. Dispersers are subadults, independent from their mothers but not yet established as breeding adults at approximately 24 months of age (Cooley *et al.* 2009; Logan & Sweanor 2001; Murphy 1998). We censored from the dataset subadult pumas that died within their natal home ranges before 24 months old, and classified remaining subadults born in the study area as emigrants or philopatric. Emigrants were those that left their natal home range without returning. Philopatric individuals were those that survived to 24 months old and whose movements overlapped their natal range by 5% or more (95% fixed kernel home range estimates).

We quantified the annual total number of emigrants and the rate of emigration as the proportion of subadults born on the study area that emigrated. We used Mann-Whitney U-tests to evaluate differences in numbers of male and female emigrants (for the 13 years of the NGYE data and the 9 years of the Garnet data), and emigrant numbers in the years that the Garnet study area had full hunting (3 years) versus limited hunting (5 years). Differences in the proportion of subadults emigrating between the sexes and study areas were tested using Fisher's exact tests. We assessed the influence of annual density on emigration versus philopatry of female subadults in the same year and also the influence of the previous year's density. We performed a simple linear regression of the proportion of emigrating females in a year (t), against annual minimum density estimates for the same year (t) as well as the previous year (t-1).

Dispersal Distance.-Post-emigration monitoring was conducted opportunistically through aerial telemetry, with flights ranging up to 200 kilometers from the primary study area. We also relied on reports of puma hunters for relocations and fates of individuals. Hunter tag returns do not share the spatial and temporal restrictions of radio-telemetry and allowed documentation of individuals in some cases years after they were last radio tracked. This provided information for estimating dispersal distances and individual's fates.

Dispersal distance was measured as the Euclidean distance between a disperser's origin and final dispersal location (D_e). We fixed the origin of the dispersal event as the median location of the emigrant's natal range prior to dispersal. In the absence of adequate relocation data to establish a natal range, the individuals pre-dispersal capture site was considered the origin. The final dispersal location was the median location of the individual's established adult home range, when data on movements after they had completed dispersal were available. In the absence of successful establishment or adequate relocation data, the individual's mortality site was used. In cases of lost contact, we used the last location obtained for the individual as a final dispersal location. Inclusion of dispersal distances from lost individuals was included in analysis, because dispersal distances for these individuals were comparable to known fate individuals and did not reduce distance estimates. Estimates of dispersal distance should be considered a minimum, because not all movements could be detected which tends to bias long range dispersal distances downward (Cooper *et al.* 2008; Koenig *et al.* 1996)

Differences in dispersal distance between study areas may reflect differences in the distribution of resources, conspecific and other competitors, all which may act on disperser space use. Therefore a second measure of dispersal distance was used which scales dispersal distance based on average home range diameter, which is also expected to vary with resources and conspecifics (Buechner 1987; Labonte *et al.* 1998; Murphy 1998; Ruth & Buotte 2007; Trewhella *et al.* 1988; Waser 1985). Adult lifetime home ranges for each sex in both study areas were estimated using a 95% fixed kernel and converted to represent an equivalently sized circular home range:

$$2(\sqrt{(\text{home range area})/\pi})$$

Linear dispersal distances were then divided by this diameter to determine number of average home ranges traversed (D_{hrd}) .

Dispersal distances of male and female pumas in the two study areas were compared using both the absolute Euclidean distance (D_e) and distance scaled by home range size (D_{hrd}). First, pairwise comparisons of dispersal distances between the sexes and studies were made using two-tailed t-tests. Next, we modeled covariate effects on dispersal distance using linear regression. Models included terms for study area, sex, an interaction term for study area and sex, and the fate of the individual. The fate of the disperser, whether it was killed during dispersal or survived, was included as early mortality would be expected to shorten dispersal movements. The global model included the following:

$$\text{Distance} = \beta0 + \beta(\text{Area}) + \beta(\text{Sex}) + \beta(\text{Sex*Area}) + \beta(\text{Fate}) \text{ (equation 1).}$$

The best model was selected using Aikake's Information Criterion corrected for small sample sizes (AICc) (Burnham & Anderson 1998).

Disperser success.-Each disperser was classified as successfully establishing a home range, mortality while transient, or as contact lost. Because female pumas typically establish an adult home ranges by 24 months old (Cooley *et al.* 2009; Logan & Sweanor 2001; Murphy 1998), we assumed successful dispersal of radio-collared females when movement localized and remained stable until they were > 24 months old. For cats that could not be reliably relocated using radio-telemetry, but were later relocated from tag returns, we assessed successful dispersal based on age. Females were assumed to have successfully dispersed if they were at least 24 months at the time of the tag return data.

The completion of male dispersal was complicated by a tendency to restrict movements during their first winter after leaving their natal range, and then abandoning these temporary home ranges to continue dispersal (Beier 1995). Therefore, males were not assumed to have ended their transient movements until the beginning of autumn (September 23rd) following their first winter independent from their mothers. Evidence of localization (via radio-telemetry) and tag returns occurring after this period were assumed to indicate the male had established.

Dispersers that died before reaching the age of adulthood were considered dispersal mortalities and to have failed to successfully establish. Individuals which emigrated and for which relocation information was not available beyond establishment age or death were classified as loss of contact while transient. Finally, disperser success was defined as the proportion of male and female dispersers that likely survived to establish adult home ranges. We used a Fisher's exact test to evaluate sex differences in survival as well as differences between study systems. All data summations and statistical analysis were performed in the R programming environment, version 2.9.1 (The R Foundation for Statistical Computing, 2009).

Population Contribution

The annual per capita contribution of each population to metapopulation growth was estimated using a contribution index (Runge et al. 2000). The index includes the contribution made by the study populations own annual population growth from philopatric individuals, or the “self-recruitment rate”, as well as recruits it provides to other subpopulations via successful emigration. The self-recruitment rate (R) of the local population (r), was estimated by the observed growth rate (minus immigration), in the independent age class over ‘t’ time steps. Thus,

$$R^r = \lambda^r - I^r \qquad \text{(equation 2)}$$

where λ^r is the geometric mean growth rate of independent pumas between the first study year (N_0) to the last year (N_t).The term I^r denotes the annual per capita rate of immigration into the population. Estimates of growth rate and immigration were derived from annual population surveys of the independent puma populations on the study area. Surveys did not allow estimation of sampling variance in population or immigration estimates, therefore all variance is assumed to reflect a mixture of sample and process variance.

We estimated the contribution made by the local population via successful emigration to other subpopulations, (E^r) with:

$$E^r = \varepsilon_j^r * \Sigma\Phi_j^{rs} \qquad \text{(equation 3)}$$

where ε_j^r is the average proportion of independent pumas emigrating from the study area (r) annually and Φ_j^{rs} is the successful immigration of a disperser from (r) into subpopulations (s). The subscript j denotes that individuals are independent subadults (the dispersal age class). Average emigration was obtained through radio-telemetry and tag return data on the number of individuals emigrating from their natal range divided by the number of independent pumas estimated to be in the population in that year. Some individuals emigrated from their natal range, but remained within the study area. In such cases they were not counted as emigrants to avoid double counting. Successful immigration was estimated based on the proportion of all emigrants from the study area that appeared to have survived to establish an adult home range outside the study area.

The annual per capita contribution C^r of a population was thus estimated:

$$\begin{aligned} C^r &= (\lambda^r - I^r) + \varepsilon_j^r * \Sigma\Phi_j^{rs} \\ &= R^r + \varepsilon_j^r * \Sigma\Phi_j^{rs} \\ &= R^r + E^r \qquad \text{(equation 4)} \end{aligned}$$

Annual $C^r > 1$ indicates that the local population is a net contributor to the metapopulation and acting as a source, while a $C^r < 1$ indicates the area is a population sink (Runge *et al.* 2006). Note if the self-recruitment rate shows a local population is not supporting itself ($R^r < 1$), the area can still be acting as a source to other subpopulations via dispersal.

The contribution of the NGYE was estimated separately for phase I (1987-1992), while the population was expanding, and in phase II (1999-2003) after wolves were reintroduced and the puma population plateaued (Ruth *et al.* 2008a). The contribution of the Garnet study area was also examined over two time periods, when hunting was permitted in the core of the study area (no protection: 1997-2000) and after hunting was restricted to areas outside of the core study area (protection: 2000-2006).

RESULTS

Field Sampling

Dependent kittens marked during research totaled 200 (NGYE N=116; Garnet N=84) and 113 of these kittens were monitored to subadult age (NGYE N=61; Garnet N=52). Additional pumas born on the study areas initially captured as subadults increased the total number of marked subadults to 126 (NGYE N=68; Garnet N=58). Of these marked individuals 104 (83%) were monitored until their fate (death or successful establishment as adults) could be determined (NGYE N=53; Garnet N=51).

Disperser Attributes: Emigration, Dispersal Distance and Disperser Success

Emigration.– No sex bias was apparent in the median absolute number of male and female pumas emigrating annually in either study area [NGYE: 2/year (male range=0-6; female range=0-5); Garnet: 1/year (male =0-6; female=0-5)].

Expressed as proportions of subadult males and females emigrating versus remaining philopatric (Table 1), no sex difference was seen in NGYE for immigration rate of males (81.8%;SE=18.2%) versus females (74.3%,SE=25.7%). In the Garnet system a significantly higher proportion of males (73.1%; SE=8.7%) than females (43.8%; SE=8.8%) emigrated (Fisher's exact test, p=0.038). While none of the 26 Garnet males displayed philopatry, 15 of 32 females did (Table 1).

While a higher proportion of males than females emigrated in the Garnet study overall, this pattern was reversed when hunting was permitted in the core area. In these years, 1 of the 4 subadult females monitored in the population emigrated, and none of the 4 subadult males did so. Males during this time may have showed emigration behavior eventually, but all were killed immediately after becoming independent from their mother.

Differences in the level of human-induced mortality in the 2 study areas was reflected in female emigration rate but not males. A significantly higher proportion of females in the NGYE emigrated than in the Garnet area (Fisher's exact test, $p=0.013$). In addition, changes in hunting pressure on the Garnet landscape affected emigration. Only one female (and no males) was documented emigrating during the years the pumas were hunted in the core study area (Table 1). When hunting was restricted (2001-2006) annual emigration increased to 2 to 8 per year (Mann-Whitney U-test, $p=0.0007$).

Annual emigration rate of female pumas did not appear positively or negatively correlated with the density of independent pumas in the same year ($\text{Emigration}_t \sim \text{Density}_t$) or the previous year ($\text{Emigration}_t \sim \text{Density}_{t-1}$). (all $p>0.23$).

Dispersal distance.– Our two measures of dispersal distance gave mixed evidence of sex bias in dispersal distance in the NGYE. Mean Euclidean dispersal distance (D_e) was similar for males (62 km SE=7.1, N=25) and females (67.4 km; SE=3.9, N=24) (Fig. 1). In terms of home ranges, females dispersed further (3.08 D_{hrd}; SE=0.43) than males (1.81 D_{hrd};SE=0.21) (two-tailed t-test, $p=0.012$) (Fig. 2).

The Garnet area showed a sex bias towards longer male dispersal distances in both D_e (two-tailed t-test, $p=0.0003$) and D_{hrd} (two-tailed t-test, $p=0.04$) (Fig. 1,2). Mean D_e of males in the Garnet study area was 42.6km (SE=2.6, N=18) and 1.89 D_{hrd}(SE=0.17) and females 24.2 km (SE=2.6, N=14) or 1.4 D_{hrd} (SE=0.15). Males in the NGYE dispersed farther (D_e) than males in the Garnet system (two-tailed t-test, $p=0.011$); however, not after scaling for home range sizes (D_{hrd}) (two-tailed t-test, $p=0.766$). Female dispersal distances responded more strongly to the landscape context for both measures of dispersal distance. Females D_e in the NGYE were greater than that of Garnet females (two-tailed t-test, p=0.00008) and also Garnet males (two-tailed t-test, p-0.02). NGYE female's D_{hrd} were greater than any other group, while D_{hrd} observed for Garnet females was less than all other groups.

Additional support for the influence of the landscape on dispersal distances was found in modeled effects of mortality, sex, and study area on dispersal distance (Appendix C). The top model retained the effects of mortality and study area on D_e, NGYE emigrants dispersed further than their Garnet counterparts after accounting for the effect of mortality in reducing dispersal distance (AIC weight=0.265). Three alternative models of D_e were within 2 ΔAICc of the top model and study area emigrated from was the only variable retained in all these models (AIC weights of top 4 models=0.809).

Modeled effects on D_{hrd} evidenced the influence of the landscape, but also how males and females responded to the landscape differently. The top model of D_{hrd} included study area, disperser's sex, mortality, and an interaction between study area and sex (AIC weight=0.441). After accounting for differences in home range sizes, individual's sex and mortality, NGYE dispersers were still found to disperse farther than Garnet emigrants. Only one model was within 2 ΔAICc of the best model and it included emigration area, disperser's sex, and an interaction between area and sex, but not mortality (AIC weight=0.248).

In examining temporal changes in dispersal distances of NGYE pumas, we found no evident change in male dispersal between phases, but females appeared to respond to changing conditions. Female D_e increased from an average of 49.1 km (SE=10.7, N=11) in phase I to 83 km (SE=13.6, N=13) in phase II (Mann-Whitney U test, p=0.08). We were unable to assess temporal differences in the Garnets between years before protection in the core area and after. Low recruitment and high mortality in the first three years of Garnet research resulted in too few documented dispersers to make dispersal distance comparisons in this system.

Disperser success.– We found support for the expectation females would exceed males in the probability of successfully surviving dispersal to establish an adult home range (Fig 3). In the NGYE effect sizes were limited [(female success=72.2% (SE=10.6%), male success=47.6% (SE=10.9%) (Fisher's exact test, p=0.193)]. Differences between sexes in the Garnets were large [(female success=55.6% (SE=16.6%), male success=11.8% (SE=7.8%) (Fisher's exact test, p=0.028)]. Male emigrants in the NGYE were significantly more successful than Garnet males (Fisher's exact test, p=0.034). NGYE females also tended to be more successful than their Garnet counterparts, but differences were not statistically significant (Fisher's exact test, p=0.423).

Dispersing females tended to survive to greater ages than males and individuals in the NGYE tended to survive longer than their same-sex counterparts in the Garnets. Median age at death for females after they dispersed was 55.8 and 30.8 months in the NGYE and Garnet areas, respectively. For male dispersers' the median age at death was 30.5 and 21.6 months, in the NGYE and Garnets respectively.

In the Garnet system all known mortalities of dispersing males (17 mortalities) and females (6 mortalities) were from anthropogenic sources. Legal harvest was the primary mortality source for males (13 total), with an additional 2 poached, 1 killed after a livestock depredation, and 1 killed by a hunter claiming self-defense. Among the 6 female mortalities recorded in the Garnets: 4 were legally harvested, 1 was poached, and 1 died due to unknown causes.

Of the 21 documented mortalities of males dispersing from the NGYE study area hunters killed 16. Of the remaining 5, 2 were killed in fights with adult male puma and 3 died from infections, possibly associated with injuries. Among female dispersers in the NGYE 8 deaths were human caused, 7 from legal hunting and 1 snared. Another 5 deaths were recorded for females: 2 by conspecifics and 2 from infections.

Population Contributions

The estimated annual stochastic growth rate of the NGYE independent puma population during Phase I (from 1987–1992) was $\lambda = 1.104$ (95% CI 1.02-1.18; Table 2), following expectations that it was increasing in the area. Much of this growth was attributable to a high per capita annual immigration rate of 0.137 (SE=0.032). Removing the population growth attributable to immigration provided a mean annual self-recruitment rate of R = 0.967, with high variance (95% CI= 0.88-1.78). After accounting for subadults emigrating from the NGYE (ε=0.170, SE=0.067) and the probability of surviving to establish in a new area ($\Sigma\Phi_j^{rs} = 0.590$, SE=0.079), the net annual contribution rate of the NGYE was C = 1.067 (95% CI 0.848-1.286). This indicates NGYE tended to act as a source in Phase I. In Phase II of NGYE research (1999-2003) puma population growth appeared to be stationary to slightly negative, $\lambda = 0.949$ (95% CI 0.837-1.06), with less than half the per capita immigration rate than during phase I (Table 2). However, the per capita emigration rate remained high (ε=0.231, SE=0.052) and after accounting for disperser success ($\Sigma\Phi_j^{rs}$=0.590, SE=0.079) the population still appeared to act as a source, C = 1.036 (95% CI 0.835-1.237).

During the first three years (1997-2000) of Garnet research, with hunting imposed, minimum population estimates indicated a declining puma population, λ = 0.745 (95% CI 0.457-1.034). Little emigration from the study area occurred during this period (ε=0.011, SE=0.011) and disperser survival was low ($\Sigma\Phi_j^{rs}$=0.269, SE=0.087), resulting in a population sink, C = 0.748 (95% CI 0.51-0.986). However, between 2000 and 2006 (when hunting was restricted) the Garnet puma population appeared to grow, λ = 1.106 (95% CI 0.891-1.322). Per capita emigration rate increased (ε=0.269, SE=0.087), and after accounting for disperser survival ($\Sigma\Phi_j^{rs}$=0.269, SE=0.087), the population appeared to act as a source (C = 1.178;95% CI 0.900-1.455).

There were no confirmed immigrations into the Garnet population during the years the population was studied. It cannot be determined with certainty that no immigration occurred, however, and undetected immigrations would positively bias estimates of contribution as increases would be attributed to self-recruitment. However, undetected immigrants were unlikely to have qualitatively changed the post-hunting Garnet source designation, because to cause C<1 would require an unlikely undetected immigration rate (I>0.18).

DISCUSSION

We took advantage of extensive field datasets from 2 study areas to quantify puma dispersal characteristics and explore the landscape-level effects of human-induced mortality on these characteristics. Furthermore, we used estimates of inter-population vital rates, coupled with estimated within-population growth, to quantify each population's contribution to their respective region and operationally define them as sources or sinks.

In both study areas we found that inter-population movements largely modulated both within population growth as well as the populations contribution to the surrounding region. For example, population growth in the NGYE was largely due to immigration, in the absence of which the population would have negative growth. Despite this, the population could be a net source by consistently exporting large numbers of recruits to other subpopulations. This illustrates how a failure to account for dispersal can lead to faulty conclusions as to the role a population plays in the regional context (Aebischer *et al.* 2010; Figueira & Crowder 2006; Griffin & Mills 2009; Gundersen *et al.* 2001; Watkinson & Sutherland 1995). In the case of the NGYE ignoring the contribution via dispersal would suggest the population was not acting as a source. While not accounting for immigration would fail to show its own dependence on immigration for its maintenance and growth. Indeed, the NGYE may be a "dependent source"; suggesting it may be advisable to retain multiple, mutually supportive source areas, especially when annual contribution is variable as in our study populations (Franklin *et al.* 2004; Hixon *et al.* 2002).

Elevated mortality from anthropogenic sources has well appreciated effects on within-population vital rates. Our results indicate that human-induced mortality can also impact interpopulation vital rates with consequences for local and regional populations. The Garnet population illustrates the impact of human-induced mortality acting on both within- and between-population vital rates (Novaro *et al.* 2005). Under heavy hunting pressure, the Garnet puma population was a sink with a declining population and little or no emigration. After the creation of a small refuge (915 km^2), and reduced hunting in the surrounding area, it quickly became a source. The increased contribution was due to both population growth and an increase in per capita emigration leading to a 16-fold increase in absolute number of emigrants/year. These findings are corroborated by deterministic models of the Garnet population which found the 915-km^2 refuge area was a sink before hunting closure and a source for the surrounding after the closure (Robinson *et al.* in press).

Interpopulation dynamics, and their determination of population contribution, will depend on the characteristics of dispersal including emigration, dispersal distance, and establishment success (Bowler & Benton 2005; Howard 1960). Contrasting these three dispersal components under varying levels of anthropogenic risk showed all three were reduced by human-induced mortality.

Emigration of males in the NGYE and Garnet landscapes occurred at similarly high rates; however, female emigration differed greatly under different mortality contexts. While females in the more secure NGYE emigrated at high rates, comparable to the males; females in the higher mortality Garnets had much lower emigration rates and were more philopatric (Table 2). High population turnover appeared to provide available territories near the natal area, which indirectly reduced female emigration rates by encouraging philopatric establishment (Matthysen 2005; Sutherland *et al.* 2002; Wolff 1997).

In addition, to this spatial contrast, comparisons within the Garnet study area pre- and post-hunting closure showed marked differences in the amount of emigration. There was very little female emigration and no male emigration under heavy hunting, however, both increased substantially after the hunting closure. Collectively, these results point to effects of landscape contexts – specifically human hunting – influencing emigration rates.

While emigration rate showed a response to high mortality, we did not find a linear relationship between population density and emigration in the NGYE or Garnets. For various species emigration has been shown to correlate both positively and negatively with density in different studies (Fonseca & Hart 1996; Frank & Woodroffe 2001; Lambin *et al.* 2001; MacDonald & Johnson 2001; Stoen *et al.* 2006; Sutherland *et al.* 2002; VanderWaal 2009; Wolff 1997). Failure to find a linear relationship between density and emigration shouldn't suggest that density does not influence puma dispersal. We did find NGYE female emigration rates were somewhat higher during Phase II when the population had reached high density and removals of individuals was associated with lower emigration in the Garnets. The exact relationship between density and emigration is likely non-linear and will most likely depend on where density is in relation to carrying capacity given the current availability of resources and competitors (Kluyver & Tinbergen 1970; Matthysen 2005; Mills 2007; Waser 1985).

The second dispersal component examined, dispersal distance, was also found to be influenced by human-induced mortality. In the NGYE both sexes dispersed similar absolute distances (D_e), which were significantly greater than Garnet dispersers. Dispersal distances of pumas in the Garnet study were male biased, but males in this system dispersed much shorter distances than either sex in the NGYE.

While differences in dispersal distance (D_e) may in part be due to human-induced mortality levels, other landscape effects may be at play. Therefore, to make study area comparisons we accounted for ecological differences between the sites by scaling dispersal distance to average home range diameter (D_{hrd}) (Bowman 2003; Bowman *et al.* 2002; Buechner 1987; Trewhella *et al.* 1988; Waser 1985). We found D_{hrd} dispersed by males in the NGYE and Garnet system was very similar. However, female pumas in the NGYE dispersed significantly greater D_{hrd} than males in either study and females in Garnet, indicating NGYE females could substantially contributed to population exchange over an extensive area. These results complement independent findings based on genetic studies that female pumas in and around the NGYE study area exhibited unexpectedly low relatedness, suggesting high levels of population interchange (Biek *et al.* 2006). In contrast, Garnet females dispersed significantly less D_{hrd} than any other group, thus indicating limited capacity for interpopulation exchange among females in landscapes with high population turnover.

High population turnover could reducing dispersal distance by removing dominant adults and other competitors, especially among territorial species (Sutherland *et al.* 2002). Evidence for this is seen in the Garnet system where high population turnover likely opened territories encouraging settlement near dispersers' natal range (Cooley *et al.* 2009; Gundersen *et al.* 2002; Robinson *et al.* 2008; Smith 1993; Stoner *et al.* 2006; Wielgus *et al.* 2001). In contrast the more stable NGYE population may have encouraged continued prospecting by dispersing individuals to more distant areas.

Along with competition from conspecifics, dispersal movements can also be shaped by competition from other members of their ecological guild (Williamson 2004). Pumas in the NGYE faced competition from wolves after their 1994-1995 reintroduction and subsequent expansion, which may have influenced puma dispersal movements.

After the reintroduction of wolves to the NGYE, pumas altered their space use towards more steep, rugged terrain such as canyon areas (Ruth & Buotte 2007). Wolves could also have impacted movements of dispersing pumas. Average dispersal distances of female pumas in the NGYE increased from 49.1 km (SE=10.7) prior to 1995, to 83 km (SE=13.6) after wolves were in the system. Possibly dispersing pumas responded to the presence of wolves and the additional constraints they may have put on resources or puma spatial patterning. However the increase in female dispersal distance may reflect other, unobserved, changes on the landscape independent of wolf effects such as changes in puma densities or prey resources in the surrounding landscape.

Finally, we examined how successful establishment, the final component of dispersal, may also be subject to human-induced mortality. High susceptibility to mortality during dispersal is thought to limit successful immigration for many species including pumas (Boyd & Pletscher 1999; Fuller *et al.* 2003; Quigley & Hornocker 2010). We found male pumas dispersing from both study areas had low survival, but differences between high and low risk landscapes were striking, with only an estimated 11.8% of Garnet males successfully completing dispersal, compared to 47.6% of NGYE males. Following the same trend, 55.6% of Garnet females survived to establish home range compared to 72.2% of NGYE females.

Quigley and Hornocker (2010) observed that subadult pumas are often killed by humans just prior to establishing breeding territories. Our results support this observation in both study systems, and it was especially evident in the Garnet system where all documented mortalities were human caused. Median ages of death for male emigrants from both study areas along with Garnet females were all less than 31 months. At this age few individuals are likely to have provided a genetic contribution to the population (Logan & Sweanor 2001; Murphy 1998; Ross & Jalkotzy 1992).

Overall these results indicate landscapes with high human-induced mortality can show reduced dispersal, with effects manifest upon each component of dispersal (emigration, dispersal distance, and establishment). These effects were manifest different for males and females. Males were more directly affected by elevated pre- and post-emigration mortality. In the Garnets under heavy hunting no males dispersed and even after a hunting closure only 2 of 19 dispersers likely survived to establish an adult home range over the 9 year study. Females were more sensitive to indirect effects of high population turnover, responding with reduced emigration rates, greater philopatry, and shorter dispersal distances reducing the extent of interpopulation exchange.

Interestingly, though the rate and extent of dispersal is generally considered male biased in pumas, we found female dispersal in the relatively secure NGYE to be comparable to males (Anderson 2004; Beier 1995; Biek *et al.* 2006; Dobson 1982; Laing & Lindzey 1993; Logan & Sweanor 2010; Pusey & Packer 1987; Ross & Jalkotzy 1992; Sweanor *et al.* 2000). Given the lower survival rates for male dispersers in our study areas, this may indicate that females could contribute more to interpopulation exchange than males in some hunted populations.

While comparisons between the NGYE and Garnet systems indicate the influence of human-induced mortality on dispersal, we could not fully account for the influence of other habitat differences between the two landscapes. For example, the greater amount of anthropogenic fragmentation in and around the Garnet study area may have discouraged dispersal movements. However, the temporal variations observed in the study area confirm the important influence of high population turnover on dispersal.

In spatially structured populations the effects of human-induced turnover will have important consequences, especially for source-sink dynamics. The contribution of a source population is fundamentally tied to surrounding areas. As our study populations illustrate, human induced mortality within and around a potential source can limit the amount and spatial extent of a local population's contribution via dispersal. This supports previous observations that high mortality landscapes around refuges may create a "fence-effect", limiting dispersal and the refuge's ability to act as a source (Revilla *et al.* 2001; Woodroffe & Ginsberg 1998). Spatially structured management approaches relying on source populations should therefore explicitly consider the effects of human-induced mortality on interpopulation movements.

Table 1. Number of marked subadult pumas from the Northern Greater Yellowstone and Garnet Mountain areas during research period. Garnet study divided into years in which the entire study area was open to hunting and after the 915-km2 core area was protected. Marked subadults classified by dispersal behavior including those that emigrated, those that established home ranges philopatrically, and those that died before their status could be determined.

Study	**Years**	**Emigrant**		**Philopatric**		**Died pre-dispersal**		**Total Subadults**	
		Female	male	Female	male	female	male	female	male
Northern Greater Yellowstone	1988-1993, 1999-2005	26	27	8	2	1	4	35	33
Garnet Mountain (no protection)	1998-2000	1	0	1	0	2	4	4	4
Garnet Mountain (protection)	2001-2006	13	19	14	0	1	3	28	22

Table 2. Estimated annual per capita contribution of the Northern Greater Yellowstone and the Garnet Mountain study areas. The contribution metric incorporates the puma population's self-recruitment rate (observed growth rate, λ, minus the proportion of growth attributed to immigration), as well as the recruits provided to neighboring subpopulations through dispersal (Emigration* Disperser survival). The Northern Greater Yellowstone study is divided into an earlier study (phase I, 1988-1993) when the population was recently re-colonizing the area and expanding, and a later study (phase II, 1999-2005) when puma densities reached a plateau and post-wolf reintroduction. The Garnet study was divided into years when hunting was permitted throughout the study area (no protection, 1997-2000) and after pumas were protected in the 915-km2 core of the study area (protection, 2001-2006).

	Λ	**Immigration rate**		**Emigration rate**		**Disperser survival**		**Contribution**	
Study		mean	SE	mean	SE	mean	SE	Mean	SE
NGYE (phase I)	1.104	0.137	0.032	0.170	0.067	0.590	0.079	1.067	0.108
NGYE (phase II)	0.949	0.048	0.020	0.231	0.052	0.590	0.079	1.036	0.096
Garnet (no protection)	0.745	0.000	0.000	0.011	0.011	0.269	0.087	0.748	0.088
Garnet (protection)	1.106	0.000	0.000	0.265	0.074	0.269	0.087	1.178	0.114

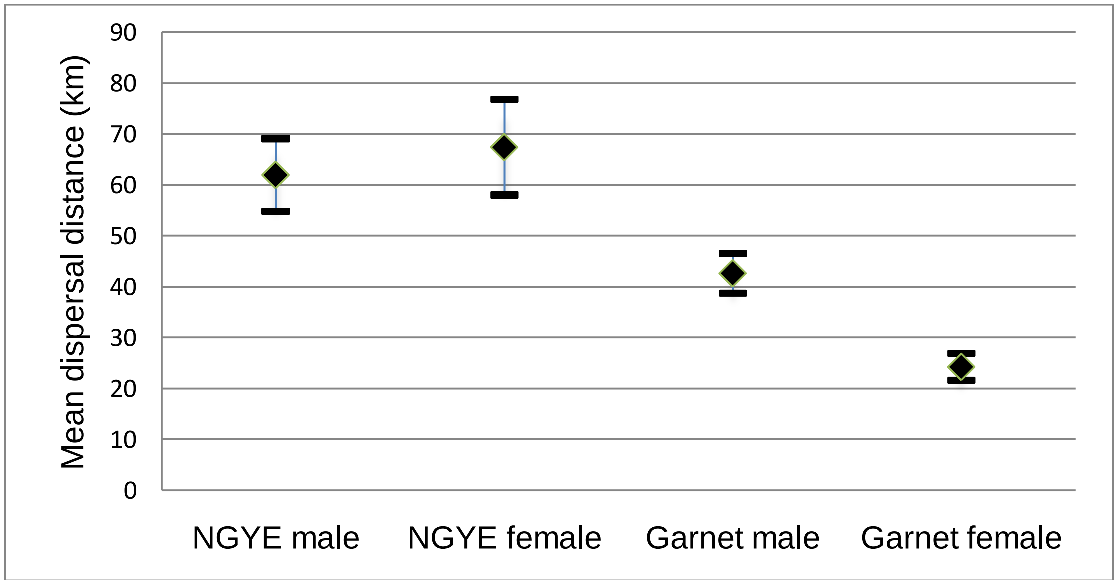

Figure 1. Mean Euclidean distance dispersed from center of natal range to final location for 81 dispersing pumas, with standard error bars. Both male and female dispersers from the more secure Northern Greater Yellowstone Ecosystem (NGYE) showed greater dispersal distances than individuals in the high turnover Garnet system. While there was a male bias in dispersal distance observed in the Garnets, females dispersed as far as males in the NGYE.

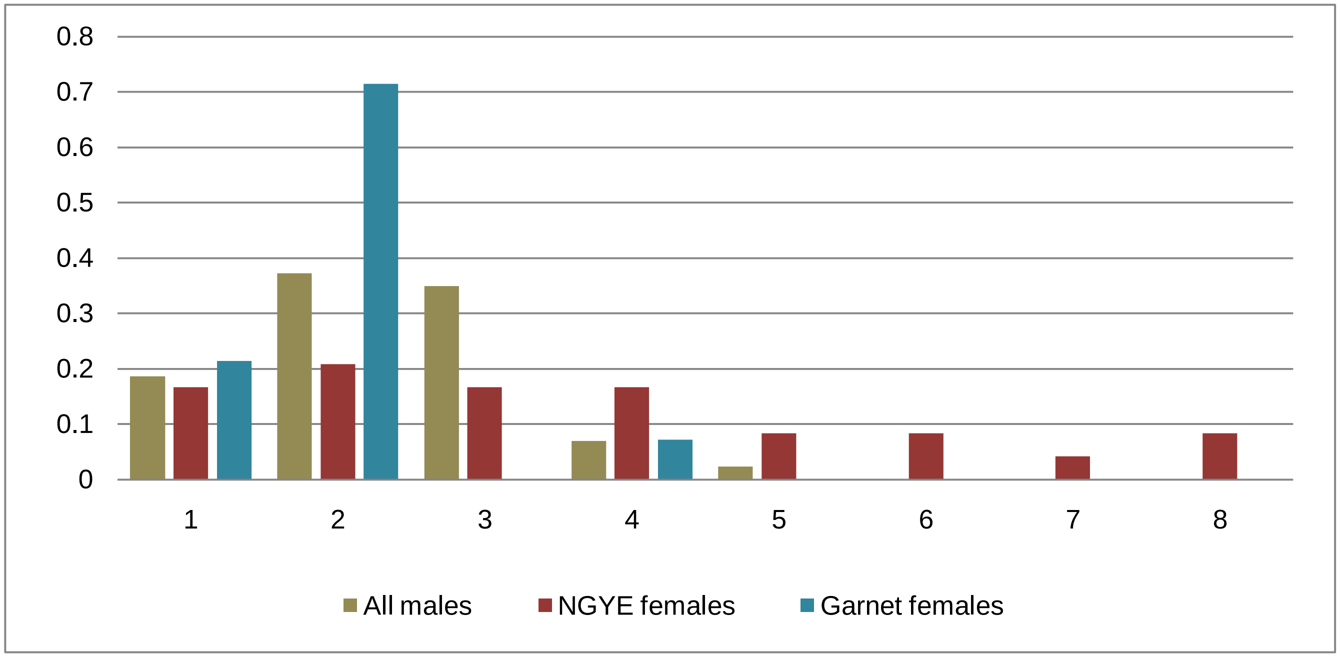

Figure 2. Proportion of final locations within a given home range diameter of natal ranges for dispersing pumas in the Northern Greater Yellowstone (NGYE) and Garnet studies. Final location taken as mortality site, center of established adult territory, or last known location. Home range diameters estimated separately for male and female adult pumas in both study areas using mean 95% fixed kernel estimated home range. Males from the NGYE and Garnet studies were pooled, due to similarity in number of home ranges traversed. Females dispersing from the NGYE and Garnet studies differed significantly in home ranges traversed ($p<0.001$) and are reported separately.

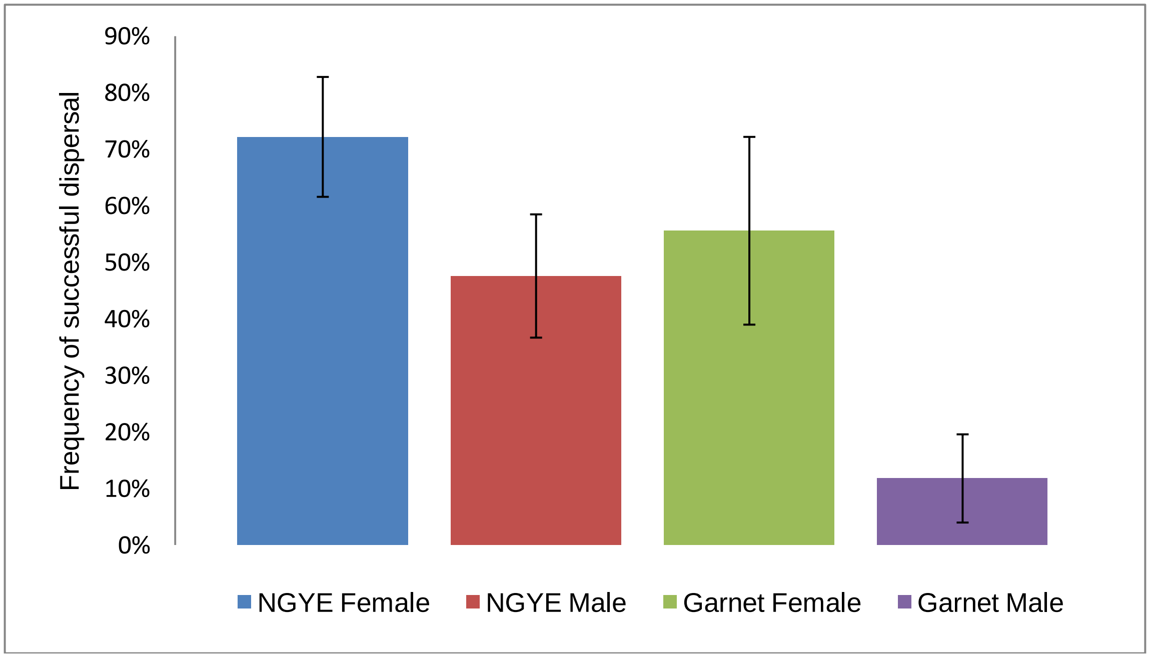

Figure 3. Proportion of dispersing male and female subadult pumas from the Northern Greater Yellowstone (NGYE) and Garnet Mountain study areas that successfully survived dispersal to establish territories. Individuals that reached the adult age class were assumed to have established. Proportions of dispersers that either died during dispersal or were known to have survived to adulthood. Individuals with unknown fates omitted. Error bars represent standard error.

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CHAPTER III

HABITAT USE OF PUMAS DURING DISPERSAL IN THE CENTRAL ROCKY MOUNTAINS

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ABSTRACT

Dispersal movements through heterogeneous landscapes are foundational to species' evolution, ecology and conservation. Habitat use during dispersal is expected to be especially significant for populations strongly influenced by inter-population processes. We examined habitat use of dispersing pumas (*Puma concolor*) in three separate study populations in the Central Rocky Mountains using location data from GPS (n = 11) and VHF (n = 123) radio-collared individuals, providing two independent datasets from all three study areas. Hypotheses for landscape features preferred during dispersal were tested with *a priori* models centered on forest cover, topographic cover, hunting habitat, and anthropogenic disturbance. Model selection found the model combining suitable hunting habitat and anthropogenic disturbance ranked best for GPS marked dispersers and ranked second, after the hunting habitat model, for the VHF dataset. Tests of competing *a priori* models indicate dispersing pumas prefer habitats similar to resident adult pumas. A resource selection function (RSF) developed using results obtained from the best performing GPS model and validated with an independent dataset (VHF locations) proved to be highly predictive of disperser space use. Collectively, the tested hypotheses and the validated RSF model indicated that landscape linkages of suitable hunting habitat and minimized anthropogenic development in these areas will assist conservation of puma populations and inter-population connectivity.

INTRODUCTION

Despite the demonstrated importance of understanding dispersal in a heterogeneous landscape, the large and unpredictable movements of individuals away from study sites limits comprehensive assessments of interpopulation movements (Bowler & Benton 2005; Williamson 2004). Specifically, researchers lack information on how landscape attributes enhance or restrict dispersal movements (Harrison 1992; Revilla *et al.* 2004; Stamps *et al.* 2005). Given such deficiencies in knowledge, assessments of connectivity habitat often rely on expert opinion and simplified assumptions of habitat relationships, including the assumption that habitat use of resident animals is a suitable proxy for dispersal habitat (Harrison 1992; La Rue 2008). However, habitat requirements may be life stage dependent and dispersers may be subject to unique habitat requirements (Beyer *et al.* 2010; Palomares *et al.* 1999; Rueda 2008).

Disperser habitat selection is expected to influence population connectivity and therefore is especially important to conservation efforts when population dynamics are dominated by interpopulation movements, through high dispersal rates or source-sink dynamics (Andereassen *et al.* 2002; Greene 2003; Lima & Zollner 1996). When human induced dispersal mortality or fragmentation further affects interpopulation processes, habitat selection during dispersal may become even more important to persistence (Franklin *et al.* 2004). Because large carnivore populations are often structured by interpopulation processes and are susceptible to negative anthropogenic effects, maintaining adequate connectivity habitat on the landscape is of special concern for these species (Boyd & Pletscher 1999; Fuller *et al.* 2003; Howard 1960; Kindal & Van Manen 2007; Noss *et al.* 1996; Novaro *et al.* 2005; Smith 1993).

Pumas are characteristic of many large carnivores with relatively extensive stable home ranges, high levels of innate long-range dispersal, and potential for source-sink population structure and conflict with humans (Logan & Sweanor 2001; Quigley & Hornocker 2010; Robinson *et al.* 2008; Stoner *et al.* 2008; Sweanor *et al.* 2000). Pumas are also typical in that interpopulation exchange occurs through natal dispersal where most subadults (individuals independent from their mother but not yet breeding age) leave their natal ranges to establish breeding territories in a new area (Howard 1960; Logan & Sweanor 2010).

In the face of rapid development, the relationship between dispersal movements and human disturbance is of particular importance. Dispersing subadults are the individuals most likely to come into conflict with humans, and human caused mortality from sport hunting or puma-human conflicts is often the leading cause of puma mortality (Aune 1991; Quigley & Hornocker 2010; Ruth *et al.* 2011; Sweanor & Logan 2010) A better understanding of dispersal movements in relation to anthropogenic development could help identify potential conflict areas and assist in efforts to preserve interpopulation connectivity.

Whereas past research has described movements of dispersing pumas and highlighted their importance to population dynamics, information on habitat preferences of dispersing pumas is limited (Cooley *et al.* 2009; Maehr *et al.* 2002; Robinson *et al.* 2008; Ross & Jalkotzy 1992; Stoner 2008; Sweanor *et al.* 2000; Thompson & Jenks

2005). The one study directly examining puma dispersal movements in relation to landscape characteristics comes from Southern California where movements were found to be constrained by intense anthropogenic development (Beier 1995). To date no formal examination of disperser habitat preference has been made in a relatively intact matrix, where intense fragmentation has not constrained or even frustrated dispersal movements (Beier 1995; Maehr *et al.* 2002).

We drew on well-established natural history and ecological knowledge of pumas to develop and test four *a priori* hypotheses driving dispersal (Table 1). Pumas are habitat generalists which survive in diverse biomes; however, three resources are essential: adequate stalking and security cover, a prey base including large ungulates, and landscapes relatively free from anthropogenic disturbance (Beier 2010; Seidensticker 1977). We used these essential habitat requirements as a foundation for our hypotheses concerning disperser habitat use and to develop models to test these hypotheses. Models, including combinations of multiple hypotheses, were fit to disperser location data from 3 large-scale studies spanning 30 years and including 134 dispersing cougars in western Montana and the Greater Yellowstone Ecosystem.

The first hypothesis tested was that dispersing pumas would select forested landscapes. Past efforts to delineate puma dispersal corridors have assumed forested landcover underlies dispersal habitat because it supplies hiding cover, however this assumption has yet to be tested (Beier 1995; LaRue 2008; Logan 1986; Maehr 2002; Murphy 1998; Ruth *et al.* 2003).

Our second hypothesis focused on topographic cover, with the prediction that dispersing pumas would prefer steep, rugged terrain. Similar to forest cover, steep, rugged terrain provides security and stalking cover for pumas (Murphy 1998; Ruth & Buotte 2007), potentially directing disperser movements to remain in topographically complex areas (Beier 1995; Stoner *et al.* 2008; Sweanor *et al.* 2000). Whereas topographically complex areas supply security cover, less steep and rugged terrain may facilitate travel (Dickson *et al.* 2005). Therefore, we also evaluated the hypothesis that pumas would use relatively gentle terrain during dispersal movements.

Our third hypothesis was that dispersing pumas would maximize use of areas with high access to ungulate prey. Under this hypothesis locations of dispersing pumas were predicted to occur disproportionately in areas associated with successful hunting of ungulate prey (Table 1) (Husseman 2002; Laundre & Hernandez 2003a; Williams *et al.* 1995). Habitat use of resident adult pumas is closely tied to suitable hunting habitat which must include both large ungulate prey and appropriate stalking cover (Logan & Sweanor 2001; Seidensticker 1977). Therefore, this hypothesis proposes disperser habitat use would correspond to that of resident adult animals.

The same habitat characteristics may supply the needs of resident animals and dispersers; for example, suitable hunting habitat could provide dispersers with immediate foraging needs, as well as prospecting sites for potential home ranges and information on conspecifics (Ackerman *et al.* 1986; Clobert *et al.* 2009; Laundre 2005; Ruth 2004; Stamps *et al.* 2005). Alternatively, dispersers may use marginal habitats, poorly suited for permanent residence, as resident animals may discourage the presence of dispersers. Conflicts with resident adults can be deadly for both sexes and especially for young males, which are often killed when they intrude into an adult male territory. Therefore, we proposed a variant hypothesis that dispersers would use marginal habitat, in order to avoid occupied territories and potential conflicts with residence.

Testing the use of suitable adult habitat by dispersers was further motivated by the widespread practice of using resident habitat use as a surrogate for dispersal habitat, an assumption commonly made in assessing connectivity and delineating corridors for many species including pumas (Belden & Hagedorn 1993; McRae & Beier 2007; Morrison 2008; Thatcher *et al.* 2009). While this simplifying assumption is often necessary in the face of sparse data, it is in need of empirical tests based on field data (Harrison 1992; Selonen & Hanski 2006; Stamps *et al.* 2005).

Our final hypothesis evaluated if dispersal movements of pumas would be constrained by anthropogenic influences. We predicted that dispersing pumas– similar to other carnivores – would preferentially use areas relatively free from anthropogenic development for recreational, residential or commercial purposes and with relatively low road density, indicative of human activity (Beier 1995; Belden & Hagedorn 1993; Hebblewhite & Merrill 2008; Mace *et al.* 1996; Maehr 2002; Maehr *et al.* 2002; Van Dyke 1986).

In order to model habitat use we used location data collected on dispersing pumas collared with Global Positioning System (GPS) and Very High Frequency (VHF) transmitters within three separate puma study populations. Pumas dispersing in the three different study areas faced varying conditions including different climactic and physiographic conditions, conspecific populations and social structure, prey and competitor species assemblages, and levels of human disturbance and hunting.

Using data from GPS collared individuals, we developed a resource selection function (RSF) based on parameter estimates from the model that most parsimoniously explained disperser habitat preference. As the ultimate utility of an RSF lies in its ability to predict use by the target organism (Boyce *et al.* 2002; Wiens *et al.* 2008), we tested our predictive model against the independent data set obtained from VHF collared individuals. Our intention was to develop a predictive model of areas likely to be used by dispersing pumas in the Central Rockies that could be used to assess landscape connectivity and potential dispersal pathways.

STUDY AREAS

We used data from three long-term puma studies in the Garnet Mountains of western Montana (2,500 km^2), and two regions of the Greater Yellowstone Ecosystem (GYE). The northern GYE study (NGYE) centered on the northern range of Yellowstone National Park and neighboring areas (3,779 km^2), while the southern GYE study (SGYE) included the Teton and Gros Ventre Mountains of Idaho and Wyoming (2,300 km^2). Long-range dispersal movements of marked individuals extended the geographic area of the study up to 180 km beyond the primary study areas.

Research was conducted primarily in mountainous terrain and included high, rugged mountains reaching approximately 3,600 meters elevation to broad river valley bottoms at 1,040 meters. Most of the NGYE and SGYE areas are at higher elevation, and cooler, than the Garnet study area. Mean daily temperatures in the study areas range from -10.48C in January at Tower Falls, Yellowstone National Park to 18.9C in July at the in the Garnet study area (Western Regional Climate Center, Ovando, MT; (Despain 1991;

Houston 1982). Precipitation, largely in the form of snow, is greatest January to June across all study areas. Precipitation tends to be lowest in the Garnet area (19-33cm) and highest in the SGYE (420-464cm) (Coughenour 1996; Woodruff 2006).

For all three study areas landcover in higher elevation mountains is dominated by lodgepole pine (*Pinus contorta*) and Engelman spruce (*Picea engelmanni*). Douglas-fir (*Psuedotsuga menzeseii*) dominates the middle and lower elevations, and occasional aspen (*Populus tremuloides*) stands occur at mountain bases and foothills. A distinct ecotone is often present along mountain bases where steep forested terrain abuts open valley bottoms. Broad valley bottoms are primarily comprised of native bunch grasses (*Pseudoegneria* spp. and *Festucca* spp.) and sagebrush (*Artemisia* spp.), along with pasture and cropland. Gallery forests of black cottonwood (*P. balsamifera*) are common along watercourses in valley bottoms (Despain 1991; Houston 1982; Lehmkuhl 1981).

Across the three study areas ungulate prey include elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), and moose (*Alces alces*). Western Montana has relatively more white-tailed deer compared to the GYE where mule deer are more widely distributed (DeSimone & Semmens 2005; Mackie *et al.* 1998; Murphy 1998). The GYE also has greater amounts of alternative prey species including pronghorn (*Antilocapra americana*) and bighorn (*Ovis canadensis*) populations, and a small number of mountain goat (*Oreamnos hemionus*) (Murphy 1998; Ruth *et al.* 2008a).

In the Garnet area black bears (*Ursus americanus*) and coyotes (*Canis latrans*) are common (Harris 2007). Along with these species, grizzly bears (*U. arctos*) are present in the GYE (Schwartz *et al.* 2010). Wolves (*C. lupus)* were reintroduced into the GYE in

1995 and rapidly expanded from their initial release in Yellowstone National Park to areas throughout the GYE (Smith *et al.* 2010).

Research areas cover a wide range of land ownerships and uses including: National Parks, USFS Wilderness and Forests, BLM lands, state lands, municipalities, corporately owned lands with timber and mining extraction, and private properties used for grazing, agriculture and residential areas. The study areas differ greatly in the amount of anthropogenic development and human activity. The GYE contains National Parks and larger tracts of wilderness areas. In contrast, the Garnet study area contains relatively more anthropogenically dominated landscapes, with more privately held lands and higher road densities. The Garnet study area also had higher puma harvest quotas than in the GYE and this combined with easier access for humans resulted in the Garnet puma population incurring more human caused mortalities than GYE populations (MTFWP, mountain lion hunt district records 1988-2006).

METHODS

Field Sampling

For all 3 field studies, movement data were acquired by capture and marking of individuals with telemetry devices. Captures occurred primarily during winter using hounds to tree pumas, and followed immobilization and handling procedures detailed in Logan et al. (1986) and (Quigley 2000).

Age of captured pumas were estimated based on size, tooth-wear and pelage characteristics (Anderson & Lindzey 2000; Ashman 1983). Animals considered subadults (12-30 months old) were typically fitted with padded VHF collars with canvas expansion splices to allow for growth. Kittens 5-8 weeks old were captured by hand in the den and fit with an expandable VHF collar (MOD 125 Telonics, Inc). Dependent kittens not captured at dens were captured using hounds the winter following their birth.

Movements of dispersal aged (subadult) pumas were recorded via ground and aerial telemetry. VHF telemetry error quantified in the NGYE was 33 meters (SD=81, n=81) for ground based telemetry and 156.8 meters (SD=121.1, n=21) for aerial telemetry (Murphy 1998; Ruth *et al.* 2008b). A subset of individuals were fitted with GPS collars, providing more accurate and finer scaled movement data throughout the day and night (Beier *et al.* 2006; Comiskey *et al.* 2002).

Subadults were considered actively dispersing after they permanently left the boundaries of their natal range and prior to their establishment in a permanent breeding territory. Natal ranges were estimated with a 95% fixed kernel using locations of individuals while they were still dependent kittens traveling with their mother. In the absence of information on the target individual's natal locations, natal range estimates were obtained from same litter sibling or the individual's mother.

Dispersers were considered to have established when individuals showed site fidelity or upon reaching an age of assumed adulthood. Females were considered to be adults at 24 months if relocation data did not indicate earlier establishment (Cooley *et al.* 2009; Murphy 1998). Males tend to restrict movements during their first winter after leaving their natal range and then abandon these temporary home ranges to continue dispersing (Beier 1995). Therefore, males were assumed to have ended their transient movements at the beginning of autumn (September 22) following their first winter independent from their mothers.

Site fidelity based on movement data was determined in cases where relocation data was obtained at a resolution of > 1 location/month throughout the period of establishment. In these cases, individuals were considered to have finished dispersing if they localized in an area for one month without subsequently abandoning the area or the individual reached the adult age class, which ever came first.

In most cases it was not possible to ascertain precisely when an individual may have terminated dispersal movements and established an adult home range. Therefore, some post-dispersal locations may have been inadvertently included in the analysis of dispersal habitat use. However, contamination from post-dispersal locations was likely minimal and of more concern for VHF marked animals, because sparse VHF relocation data often did not provide clear evidence of establishment of a home range. Even for the VHF dataset few post-dispersal locations were expected because location rates were much higher immediately after the individuals emigrated and were still relatively near their natal range. After this period continued dispersal movements often resulted in the individual eluding relocation before it was killed or established an adult home range.

Habitat Analysis

Landscape variables were measured within a 300 meter radius of locations and habitat preference was measured using a use-availability design (Manly *et al.* 1993). Dispersing individuals present unique difficulties in defining availability, as actively dispersing individuals are transient and have no fixed home range (Beyer *et al.* 2010; Mitchell & Powell 2003). In addition individuals are traveling through widely diverse landscapes, and the number of locations between individuals is unbalanced.

The special challenges of defining availability for dispersers were addressed by drawing availability from the landscape along the route each individual disperser traveled. Each individual's locations were buffered by the average distance between successive locations (3.7 km) and random points, equal in number to observed locations, distributed throughout this buffered area. While it is unlikely that all points were equally available to an individual, they were theoretically accessible in terms of the movement capacity of pumas.

Observed locations were compared to availability in order to test competing models of dispersing puma habitat use (Table 1). As more than one of the these hypothesized ecological mechanisms could contribute to disperser habitat preference, additive combinations of the candidate models were also examined. In order to reduce unnecessary assumptions and aid in interpretability, interaction terms were not included within the models as there were no clear *a priori* relationships between variables. Combining the hunting habitat and anthropogenic model provided the global model, as it included all 3 habitat characteristics considered essential to pumas (i.e., adequate ungulate prey; cover for stalking, hiding, and escape; freedom from anthropogenic disturbance).

Variables used to construct habitat models were selected using the following criteria: (1) variables were guided by biologically reasonable associations between landscape characteristics and puma ecology; (2) variable measurements were relatively reliable and static to minimize error and temporal mismatches between variable measurements and puma locations; (3) information used in models would be readily available for management applications (Aarts *et al.* 2008; Hirzel & Le Lay 2008; Mitchell *et al.* 2001).

Landscape data were gathered from widely available topographic, landcover, and land use GIS data layers. Landcover data was taken from Landsat imagery acquired in 1999-2001 depicted at a 1:100,000-scale (30 meter resolution) (GAP Ecological Systems, USGS Mapping Zone 19 and 21). Hydrographic data was taken from the high resolution, 1:24,000/1:12,000-scale USGS, National Hydrography Dataset. Topographic variables were derived from the 1:100,000-scale National Elevation Dataset (DEM). Road data was obtained from 1:100,000/1:24,000-scale TIGER/Line files (Census 2000).

Exploratory analysis of variables included testing for correlations among independent variables in order to ensure no independent variables showed ≥ 0.7 correlation with one another (Wiens *et al.* 2008). Potential non-linearity in the shape of the response curve was examined by fitting landscape variables to location data using smoothing splines in generalized additive models (GAMs) (Klar 2008). When model tests indicated a potentially significant non-parametric term, variable transformations were explored guided by inspection of residual plots.

Models were fit to GPS and VHF datasets using restricted maximum likelihood estimates in generalized linear mixed-effects models (GLMM) with a logistic link function and assuming a binomial error structure. To account for autocorrelation in individuals locations and the unbalanced number of locations per individual a random intercept for individual puma's id was included in models, assuming marked individuals were a random sample of the disperser population (Gillies *et al.* 2006; Hebblewhite & Merrill 2008; Klar 2008)

Models including all fixed effect variables were fit with and without a second random intercept for disperser's sex (Koper & Manseau 2009; McLoughlin *et al.* 2009). Lack of improvement in log likelihood estimates were taken to indicate male and female dispersers could be included within the same model.

Habitat use may show functional responses under different spatial and temporal contexts. Potential structure in the data due to differences in habitat use between study areas was examined similarly to sex differences, with a second random intercept for study areas. Seasonal difference in habitat use was assessed by adding a random intercept for winter (November 1-April 30) and summer (May 1-October 31), and differences due to time of day with a random intercept for day time and night time locations.

The global model performance for both VHF and GPS datasets were evaluated initially by the area under the receiver operator curve (AUC). All fitted a priori models of habitat preference (Table 1) were tested against the null model, which included a random intercept for individual only, using a likelihood ratio test (Hosmer & Lemeshow 2000). Competing models were then compared using Akaike's information criterion corrected for small sample sizes (AICc) (Burnham & Anderson 1998). Model comparisons and ranking were conducted separately for VHF and GPS datasets which allowed assessment of the constancy of results from two independent datasets (Garshelis 2000).

A resource selection function (RSF) was developed to provide a predictive model of habitat use for dispersing pumas, which could be used in assessing the relative importance of landscapes in facilitating dispersal. The RSF was estimated using parameter estimates from the best a priori model for disperser habitat based on GPS collared individual's locations and took the form:

$$w^*(x) = \exp(\beta_0 + \beta_1 x_1 + \ldots \beta_n x_n + \text{ų}^{puma}) \text{ (equation 1)}$$

where $w^*(x)$ is the approximated probability of use, β_0 is the estimated intercept, $\beta_n x_n$ are the fixed parameter estimates, and ų^{puma} the random intercept for puma id.

The best measure of a RSFs performance is its ability to predict use in an independent data set (Pearce & Ferrier 2000). Therefore, we tested the GPS-telemetry based RSF against the VHF-telemetry dataset to compare the proportion of use observed against that expected under the RSF model. Following (Wiens 2008) all VHF locations and random (available) locations were scored based on the RSF and separated into ordinal bins by their probability of use.

Probability cut points for bins were initially assigned such that available area (number of random locations) were equal in all bins (Hosmer & Lemeshow 2000). Cut points were then recalculated using a moving window average in order to smooth across bin selection and account for unevenness in RSF scores across the landscape (Hirzel *et al.* 2006).

In order to adjust the expected probability of use by the available area on the landscape for RSF bin categories, the mid-point value of the bin was multiplied by the number of random locations it contained (Johnson *et al.* 2006). The proportion of locations observed in separate RSF bins were then regressed to the area adjusted expected probability of use. Regression results with a high R^2 value, a slope not different from 1, and an intercept that did not differ from 0, were considered to indicate a good model fit (Doherty *et al.* 2008; Johnson *et al.* 2006). The models ability to predict dispersal use was then tested using a Spearman's-rank correlation between observed and area-adjusted expected values.

RESULTS

Field Sampling

A total of 134 subadult pumas were marked and successfully monitored via telemetry while dispersing. A total of 123 VHF collars were deployed in the Garnet (n=48), NGYE (n=58), and SGYE (n=15) study areas and tracking efforts produced a total of 2383 locations of adequate accuracy to be included in analysis. GPS collars were deployed on 11 individuals, 5 of which were in the Garnet system and 3 in each of the GYE studies resulting in a total of 4767 locations.

Exploratory Analysis

Initial univariate exploration of GPS and VHF locations found that used locations differed significantly from random in several respects (Table 2). Both GPS and VHF locations showed greater use of steep slopes, rugged terrain, and forested areas. Locations from both datasets were at lower elevation, had lower amounts of anthropogenic development, and lower edge density (km/km^2), but were closer to forest edge than random locations. GPS locations also showed higher use of shrub cover and closer proximity to water, while VHF locations did not. VHF locations occurred at lower road densities (km/km^2) than random locations, but no difference was evident for GPS locations.

No correlations between variables were observed greater than r=0.67. Inspection of GAMs and residuals from univariate regression indicated the assumption of linearity was appropriate for variables, except for elevation, which was log-transformed.

Inclusion of a second random intercept for sex, study area, or time of day did not improve likelihood estimates for the GPS or VHF global models, indicating differences due to these factors were insignificant after accounting for individual variability. Similarly, for the VHF dataset, likelihood estimates for the global model without a random intercept for season were higher than likelihood estimates with season effects included. However, seasonal effects appeared to influence habitat use in the GPS dataset.

For the GPS global model the inclusion of a seasonal effect improved likelihood estimates (likelihood ratio test, G = 40 (df1), p=0.0001). However, the inclusion of a season random effect did not change any of the fixed effect parameter estimates significantly and separately constructed winter and summer models were qualitatively similar. Nevertheless we compared *a priori* models for GPS marked individuals‘ summer and winter locations separately, as well as year round.

Testing of Hypothesized Models

For the GPS data set the global model fit predictions of use reasonably well with observations (AUC = 0.902). The global model was most parsimonious for explaining space use of GPS collared dispersing pumas (AIC weight=1.00), performing significantly better than the null model with only a random intercept for individual (likelihood ratio test, G = 3138(df=10) p<0.00001). The second best model fitted with data from GPS collared cats was the prey access model, but it was not competitive with the global model (ΔAIC=40.99, AIC weight=0.00); all other models were considerably worse (Table 3). Model comparisons made separately for winter and summer GPS locations were very similar to each other, and the year round model, and showed the same ranking in top models.

The global model also performed well with the VHF dataset (AUC = 0.952). Among VHF collared individuals prey availability best explained disperser use (AIC weight=0.82) (Table 3). The global model did rank high compared to other models (ΔAIC=3.02, AIC weight=0.18). Both the hunting habitat and global model performed significantly better than the null, random intercept only model (likelihood ratio test, G=738, $p<0.00001$; and G=740, $p<0.00001$, respectively). The topographic cover model, and models incorporating topography, consistently outperformed models based on forest cover and anthropogenic disturbance alone.

Model comparisons against location data from two independent datasets found variables associated with prey availability were consistently related to disperser space use. Parameter estimates for these variables were qualitatively similar for both GPS and VHF data (Table 4). For both final models puma locations were positively associated with forest, shrub cover, and steep slopes; while they were negatively correlated with high edge density, ruggedness, elevation, distance to edge and distance to water.

Resource Selection Function

The RSF, based on the global GPS model (Table 4), was used to score relative probability of use (range 0-1) for locations and random sites in the VHF dataset. Regression outputs for observed and area-adjusted expected values suggested the RSF model was reasonable as indicated by having an intercept not different from 0 (intercept estimate=-4.08; 95% CI: (-265.16, 257.46)), and a slope which differed from 0, but not 1 (slope estimate=1.01; 95% CI: (0.3, 1.73) (Fig. 1). However, model fit was relatively weak (R^2=0.67) indicating some RSF bins differed from that expected if the model was proportional to the probability of use (Johnson *et al.* 2006).

Observations of individual bins found an unexpected large number of observed locations fell into the highest RSF bin category (RSF=0.844 – 1). After adjusting for the area available, the expected number of locations in the highest bin class was 25.6%, but 40% of observed locations fell into this class. Similarly, a relatively large number of observed locations were in the lowest RSF class (RSF=0 – 0.07) where 0.4% were expected, but 2.4% observed.

Overall, despite the unexpected differences in particular probability classes, the GPS based global model was highly predictive of disperser space use in the independent VHF dataset. Ranked observed locations were perfectly correlated with those predicted (Spearman’s $\rho=1$, $p<0.00001$; Fig. 2).

DISCUSSION

Landscape heterogeneity can act on metapopulation dynamics through effects on dispersal rates and pathways (Ricketts 2001). We determined some of the ecological influences shaping disperser habitat preference and landscape characteristics predictive dispersing puma use. Ideally habitat characteristics would be tied to vital rates (Griffin & Mills 2009; Mitchell *et al.* 2001; Mitchell & Powell 2003). However, as is typical, data were inadequate to tie habitat directly to vital rates, in this case disperser’s survival and immigration success (Crooks & Sanjyan 2006). Therefore, we attempted to find matrix characteristics supplying structural connectivity with the assumption that dispersing pumas prefer landscapes that facilitate success (Garshelis 2000; Mitchell & Powell 2003; Mortelliti *et al.* 2010).

Space use of resident adult pumas is strongly tied to hunting of ungulate prey and we found hunting habitat is a similarly important mechanism modulating disperser space use. Locations for both GPS and VHF marked dispersing pumas, from 3 different study areas, were best explained by models incorporating habitat characteristics associated with good hunting habitat (Table 3). Specifically use was found to be positively related to (1) steep slopes, (2) forest, and (3) shrub cover; and negatively related to (4) elevation, (5) terrain ruggedness, (6) distance to water, (7) distance to forest edge, and (8) edge density. Areas with these characteristics are expected to provide pumas with presence of ungulate prey, along with visibility to locate prey and cover for stalking (Houston 1982; Laundre & Loxterman 2007; Lehmkuhl 1981; Long *et al.* 2009; Mackie *et al.* 1998; Murphy & Ruth 2010; Toweill & Thomas 2002; Williams *et al.* 1995). These areas also provide essential security and escape cover for puma (Murphy 1998; Ruth & Buotte 2007; Seidensticker 1977) .

The preference of dispersing puma for areas with good prey availability supports Stoner *et al.'s* (2008) observation of a GPS collared dispersing puma in Utah using areas favored by mule deer. Similar results have been found for dispersing Iberian lynx (*Lynx pardinus*) which prefer areas associated with high rabbit densities, their primary prey (Palomares 2001; Palomares *et al.* 1999).

Coincident with the preference of dispersing pumas for suitable hunting habitat is the similarity to resident adult puma habitat. Prior research has repeatedly indicated access to prey is the primary determinant of space use by resident adult pumas (Laundre & Hernandez 2003a; Logan & Sweanor 2001; MTFWP 1996; Pierce *et al.* 2000; Seidensticker 1977; Williams *et al.* 1995). For example, an RSF for adult female puma winter use in Wyoming highlighted the importance of ambush sites near ungulate foraging areas (Anderson *et al.* unpublished data). Habitat characteristics used by dispersers in our three study areas were very similar to those identified in this model. In the Central Rocky Mountains these landscape characteristics are typical at the ecotone along mountain bases and foothills where well-forested hillsides meet open valley bottoms. Dispersing pumas may be attracted to such areas by the presence of ungulates. These areas are also attractive to humans for agriculture, residence and recreation. Such areas may be hotspots for puma conservation and management of human/puma conflict.

Our model of puma dispersal habitat may assist managers in identifying areas important for population connectivity and human/puma conflict in the Central Rockies. More generally, the similarity we found between dispersing and resident animals habitat use is promising for efforts to delineate connectivity habitat in other systems. Studies of other dispersing predators' habitat selection in relation to resident habitat have provided mixed results. Some species, for example coyotes (*Canis latrans*), select similar habitats as dispersers and residents, while others such as spotted owls (*Strix occidentalis*) and tigers (*Panthera tigris*) use marginal habitats (unsuitable for permanent residence) during dispersal (Miller *et al.* 1997; Roy & Dorrance 1985; Smith 1993). Connectivity assessments often use resident habitat as a surrogate for disperser habitat, and our findings suggest that this may be reasonable, at least for puma (Chetkiewicz & Boyce 2009; Cushman *et al.* 2009; Jacobson & Peres-Neto 2010; McRae & Beier 2007; Pe'er & Kramer-Schadt 2008; Pullinger & Johnson 2010; Thatcher *et al.* 2009).

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Use of suitable resident habitat may be important to dispersers in successfully gathering information and prospecting for a breeding territory. (Chepko-Sade & Halpin 1987) (Bowler & Benton 2005; Clobert *et al.* 2009; Morales *et al.* 2010; Stamps *et al.* 2005). In addition, pumas have been known to establish temporary home ranges during dispersal and these areas may be selected to meet security and foraging needs supplied by suitable hunting habitat (Beier 1995; Sweanor *et al.* 2000).

Along with the importance of hunting habitat to dispersers, we found evidence that anthropogenic development can affect disperser use. The inclusion of the anthropogenic disturbance model along with the hunting habitat model greatly improved model performance among GPS marked dispersers. This global model also had the highest likelihood for the VHF dataset; however, the reduced, hunting habitat alone, model was more parsimonious (Table 3).

Parameter estimates from both global models consistently showed disperser use was negatively associated with anthropogenic development. Closer inspection of our human development index found that even the lowest levels of development, such as recreational open spaces (e.g., urban interface hiking trails, golf courses, ski runs) were avoided by dispersing pumas.

While use was negatively associated with the anthropogenic development index, we found no significant relationship between use and road density. Pumas may use secondary roads in more remote settings (Dickson *et al.* 2005). However, major freeways have been associated with genetic structuring of puma populations indicating they reduced gene flow (Ernest *et al.* 2000; McRae 2005). It is possible puma use roaded areas, if roads receive little traffic, while avoiding primary roads such as freeways. Our study areas had relatively low primary road densities, which provided little opportunity for detecting such an effect. Though secondary roads may not be avoided, it should be noted they can improve human access and reduce puma survival (Ruth *et al.* in press)

Past research supports our findings that anthropogenic development could discourage use by dispersing pumas. For example, Florida panther research found intensification of human activity compelled resident pumas to abandon their home ranges and anthropogenic development may have curtailed natural dispersal (Maehr *et al.* 2002; Thatcher *et al.* 2009). Anthropogenic development was also avoided by translocated pumas in New Mexico and dispersing pumas in southern California and Florida (Beier 1995; Maehr *et al.* 2002; Ruth *et al.* 1998).

(Harrison 1992) suggested landscape linkages for carnivores should include suitable habitat of adequate width to allow permanent residence and be buffered from potentially deleterious human disturbances. Empirical examination of puma dispersal habitat use in our three study areas suggests implementing this rule of thumb would likely be an effective approach to maintaining connectivity. While dispersal may occur across less favorable landscapes, these conservative linkages would preserve habitats with a high probability of use by potential dispersers.

In addition to exploring the ecological mechanisms underlying habitat preference of dispersing pumas, we tested the predictive ability of the best performing model. Based on GPS collared individual, parameter estimates from the top model were used to develop a resource selection function. We validated the RSF model of dispersing puma habitat use with the independent dataset obtained from locations of VHF collared individuals. Model validation showed the RSF was predictive of dispersing puma use. After adjusting estimated probability of use for the area available on the landscape, we found the relative amount of observed VHF locations to be highly correlated with those predicted (Fig. 2).

Although the RSF was a good predictor of use overall, it tended to underestimate use in sites with the very highest and lowest probability of use. Such discrepancies between observed and expected locations may not be surprising when applying the RSF to an independent data set. Pumas are highly vagile and are likely able to sample a wide suite of potential areas. In addition as generalist carnivores they tolerate of a wide range of conditions (Young 1946). Dispersing pumas are likely to be especially plastic in their use of the landscape, due to the necessity of extensive travel through unfamiliar areas and inherent behavioral plasticity (Cougar Management Guidelines 2005; Stoner *et al.* 2008; Thompson & Jenks 2005).

While important connectivity sites for pumas may correspond to high quality habitat for residence, this does not negate the importance of marginal areas in maintaining connectivity. Our examination of puma dispersal habitat had limited ability to evaluate the potential importance of marginal habitats. However, marginal areas may facilitate puma population connectivity in a non-trivial manner, especially when it borders high quality habitat (Gustafson & Gardner 1996). Marginal habitats separating more suitable habitats may be traversed. For example, dispersing pumas have been shown to travel through inhospitable open desert basins and dispersing pumas from the Black Hills have been found far into the mid-west (Stoner *et al.* 2008; Sweanor *et al.* 2000; Thompson & Jenks 2005).

While marginal habitats may not preclude dispersal movements, neither does the presence of high quality dispersal habitat ensure interpopulation connectivity. The presence of high quality habitat may not be sufficient for connectivity, especially if mortality is high. However, the identification and conservation of good dispersal habitat will be important to management of spatially structured populations; especially when the number of individuals dispersing annually is small and variable.

Pumas and other large carnivores have relatively slow life history strategy and occur at low population densities. Therefore, the numbers of individuals available for population exchange will be necessarily small and stochastic. While the annual number of dispersers from a given population is limited, puma populations largely rely upon immigration (Logan & Sweanor 2001; Quigley & Hornocker 2010; Robinson *et al.* 2008; Ross & Jalkotzy 1992). Thus, a prudent approach to puma conservation would identify and maintain high quality dispersal habitat over a large region connecting multiple populations, while limiting human-induced mortality. The RSF we developed may be useful for these efforts in the Central Rockies. More generally, our results suggest adult habitat is a useful surrogate for connectivity habitat and minimizing human development in these habitats would help conserve dispersal movement.

Table 1. Hypotheses and predictions of landscape characteristics modulating habitat preferences of dispersing pumas in the Central Rocky Mountains.

Landscape characteristics	**Hypothesis and associated models**	**References**
Forest cover	Dispersing pumas prefer forested areas, which supply security cover. $w^*(x)= \exp(\beta_0 + \beta_{\mathrm{Forest}} + \text{ų}^{\mathrm{puma}})$ Forest=amount of forest cover within 300 meter buffer of location	(Beier 1995; Holmes 2006; LaRue 2008; Logan *et al.* 1986; Maehr *et al.* 2002; Seidensticker 1977; Williams *et al.* 1995)
Topographic cover (a,b)	a) Dispersing pumas prefer topographically complex terrain, which supplies cover. b) Dispersing pumas prefer gentle terrain, which facilitates travel. $w^*(x)= \exp(\beta_0 + \beta_{\mathrm{Slope}} + \beta_{\mathrm{Rugged}} + \text{ų}^{\mathrm{puma}})$ Slope=degree slope from 30m DEM Rugged=vector based change in aspect derived from 30m DEM (Sappington 2007)	(Dickson *et al.* 2005; Katnik 2002; Logan *et al.* 1986; Murphy 1998; Seidensticker 1977)
Foraging habitat (a,b)	a) Dispersing pumas prefer areas associated with high quality hunting habitat. b) Dispersing pumas use areas of marginal hunting habitat due to conspecific pressure. $w^*(x)= \exp(\beta_0 + \beta_{\mathrm{Forest}} + \beta_{\mathrm{Shrub}} + \beta_{\mathrm{Edge}} + \beta_{\mathrm{Edgedist}} + \beta_{\mathrm{H2Odist}} + \beta_{\mathrm{Elevation}} + \beta_{\mathrm{Slope}} + \beta_{\mathrm{Rugged}} + \text{ų}^{\mathrm{puma}})$ Shrub=amount of shrub cover w/in300m Edge=density forest/non-forest edge (km/km2) Edgedist=distance (m) to forest/non-forest edge Elevation= in meters from 30m DEM	(Husseman 2002; Logan *et al.* 1986; Logan & Sweanor 2001; Murphy 1998; Seidensticker 1977; Stoner *et al.* 2008; Williams *et al.* 1995)
Anthropogenic development	Dispersing pumas avoid areas with anthropogenic development. $w^*(x)= \exp(\beta_0 + \beta_{\mathrm{Develop}} + \beta_{\mathrm{Road}} + \text{ų}^{\mathrm{puma}})$ Develop=amount of developed areas ranging from recreational open space with <20% constructed material to residential and urban areas Road=density of secondary and primary roads (km/km2)	(Beier 1995; Maehr *et al.* 2002)

$w^*(x)$ represents probability of use

β_0 represents the slope intercept

ų^{puma} represents a random intercept for puma id

Table 2. Landscape variables used in *a priori* models of dispersing puma habitat use. Attributes measured for observed locations (n=7150) and random (7204) sites in a 300-meter buffer.

	Variable description	**GPS**		**VHF**	
		Puma Loc Mean (95%CI)	Random Loc Mean (95% CI)	Puma Loc Mean (95% CI)	Random Loc Mean (95% CI)
Slope[2,3]	Mean slope in degrees	14.6 deg. (14.3-14.8)	8.5 deg. (8.4-8.8)	17.6 deg. (17.2-17.9)	13.1 deg. (12.7-13.4)
Rugged[2,3]	Mean physiographic vector ruggedness measure (VRM)	0.0048 vrm (0.0047-0.0049)	0.0035 vrm (0.0034-0.0036)	0.0053 vrm (0.0051-0.0055)	0.0042 vrm (0.0041-0.0044)
Forest[1,3]	Percent of area dominated in forest	55.7% (54.9-56.6%)	47.9% (47-48.9%)	55.0% (53.8-56.1%)	49.8% (48.5-51.1%)
Shrub[3]	Percent of area dominated by shrub	6.1% (5.8-6.4%)	4.6% (4.4-4.9%)	3.6% (3.3-3.8%)	3.6% (3.3-3.9%)
Edge[3]	Length of forest/non-forest edge per km^2	3.07km/km^2 (2.99-3.16)	4.81km/km^2 (4.67-4.95)	3.95km/km^2 (3.8-4.09)	4.7km/km^2 (4.5-4.9)
EdgeDist[3]	Distance to nearest edge in meters	1279 m (1231-1328)	1945 m (1871-201.9)	1616 m (1468-1765)	1951 m (1789-2113)
H2ODist[3]	Distance to nearest perennial water in meters	212.8 m (207.8-217.8)	224.8 m (219.3-230.4)	267.8 m (258.3-277.3)	268.0 m (258.9-277.1)
Elevation[3]	Mean elevation in meters	1751 m (1738-1764)	1796 m (1782-1811)	1995 m (1978-2012)	2022 m (2004-2041)
Develop[4]	Percent of area dominated by human development*	0.25% (0.18-0.32%)	0.77% (0.66-0.88%)	0.18% (0.12-0.23%)	0.39% (0.31-0.49%)
Road[4]	Length of secondary and primary roads per km^2	0.72km/km^2 (0.68-0.75)	0.73km/km^2 (0.69-0.76)	0.39km/km^2 (0.35-0.43)	0.49km/km^2 (0.44-0.53)

Parameter estimates in table represent pooled locations across study animals.

* - Includes all levels of anthropogenic development from recreational open space to residential/commercial areas.
1 - Variable associated with hypothesis of forest cover use.
2 - Variables associated with hypothesis of topographic cover use.
3 - Variables associated with hypothesis of hunting habitat use.
4 - Variables associated with hypothesis of avoidance of anthropogenic development

Table 3. Candidate models of environmental factors potentially influencing habitat use of dispersing pumas including: forest cover, topographic cover, selection of quality foraging habitat, and avoidance of anthropogenic development. Models fit to locations from GPS (n=11) and VHF (n=123) collared pumas independently and ranked according to AIC values. Models of foraging habitat and foraging habitat plus anthropogenic factors performed best for VHF and GPS datasets respectively.

Ranked models for GPS data	**K**	**Log-likelihood**	**AICc**	**ΔAICc**	**AIC wgt**
Foraging + Anthro. dev.	12	-3736	7496	0.00	1.00
Foraging	10	-3758	7537	40.99	0.00
Forest + Topo. + Anthro. dev.	7	-4372	8758	1261.98	0.00
Topo. + Anthro. dev.	6	-4377	8766	1269.98	0.00
Forest + Topo.	5	-4381	8772	1275.97	0.00
Topo.	4	-4385	8778	1281.97	0.00
Forest + Anthro. dev.	5	-5253	10515	3018.97	0.00
Anthro. dev.	4	-5267	10543	3046.97	0.00
Forest	3	-5282	10570	3073.97	0.00
Null (random intercept only)	2	-5305	10615	3118.97	0.00

Ranked models for VHF data	**K**	**Log-likelihood**	**AICc**	**ΔAICc**	**AIC wgt**
Foraging	10	-1508	3035	0.00	0.88
Foraging + Anthro. dev.	12	-1507	3039	4.02	0.12
Topo.	4	-1661	3331	191.96	0.00
Forest + Topo.	5	-1660	3331	191.97	0.00
Topo. + Anthro. dev.	6	-1661	3334	194.97	0.00
Forest + Topo. + Anthro. dev.	7	-1660	3334	194.98	0.00
Forest	3	-1859	3725	585.96	0.00
Forest + Anthro. dev.	5	-1857	3725	585.97	0.00
Anthro. dev.	4	-1873	3754	614.96	0.00
Null (random intercept only)	2	-1877	3758	618.96	0.00

Table 4. Coefficient estimates and standard error for variables in best GPS and VHF based models of dispersing puma habitat. The best approximating model based on locations from GPS marked individuals (n=11) included variables associated with high quality foraging habitat and anthropogenic development. The best approximating model based on locations for VHF marked individuals (n=123) included only high quality foraging areas.

Variables	**GPS model estimates**	**VHF model estimates**
(intercept)	40.3 ±3.20***	27.1 ± 3.734***
Slope	0.25 ± 0.008***	0.17± 0.011***
Rugged	-141.1 ± 10.37***	-119.2 ± 18.46***
Forest	0.0019 ± 0.00036***	0.0025 ± 0.00060***
Shrub	0.0075 ± 0.00119***	0.0048 ± 0.00210***
Edge	-0.24 ± 0.010***	-0.21 ± 0.0158***
Dist Edge	-0.0036± 0.00021***	-0.0032± 0.00035***
Dist Water	-0.0009 ± 0.00019***	-0.0002 ± 0.00027
(log) Elevation	-5.46 ± 0.318***	-3.68 ± 0.497***
Develop	-0.02461 ± 0.004357***	
Road	0.0235 ± 0.0254	

** - (p<0.001)

*** - (p<0.0001)

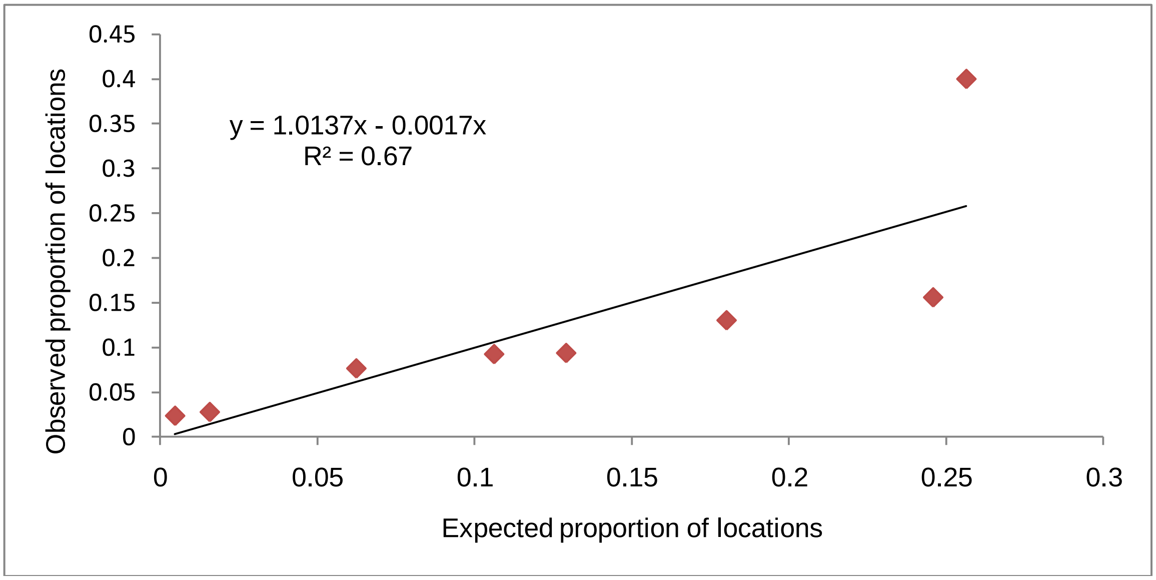

Figure 1. Fitted regression between the proportion of observed (n=2038) and expected dispersing puma locations. Observed and available locations scored using RSF from independent dataset of GPS collared dispersing pumas. A well-fit model would have an intercept not differing from 0, a slope of 1, and a high R^2. While the above model meets slope and intercept criteria the R^2 value is lower than expected for a model proportional to probability of use.

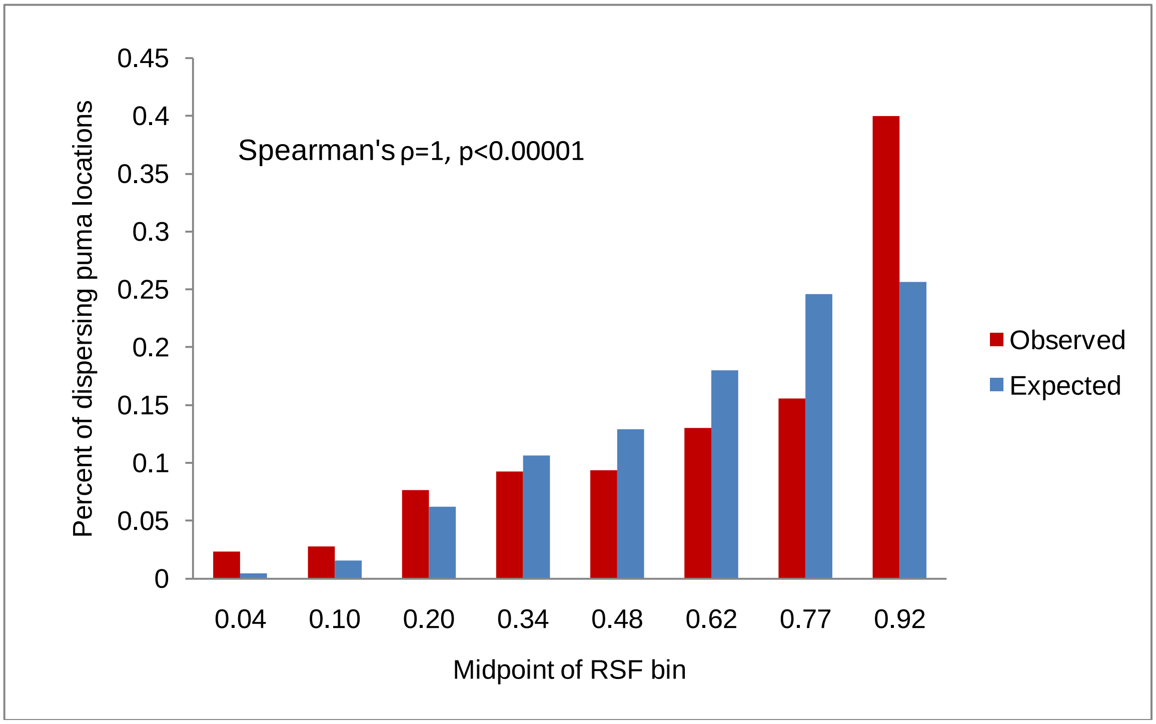

Figure 2. Observed (n=2038) and expected frequency of VHF collared dispersing puma locations in eight ordinal resource selection function (RSF) bins. Rank correlation indicates the RSF effectively predicted dispersal locations. A large number of dispersal locations occurred in the highest and lowest RSF classes relative to that expected.

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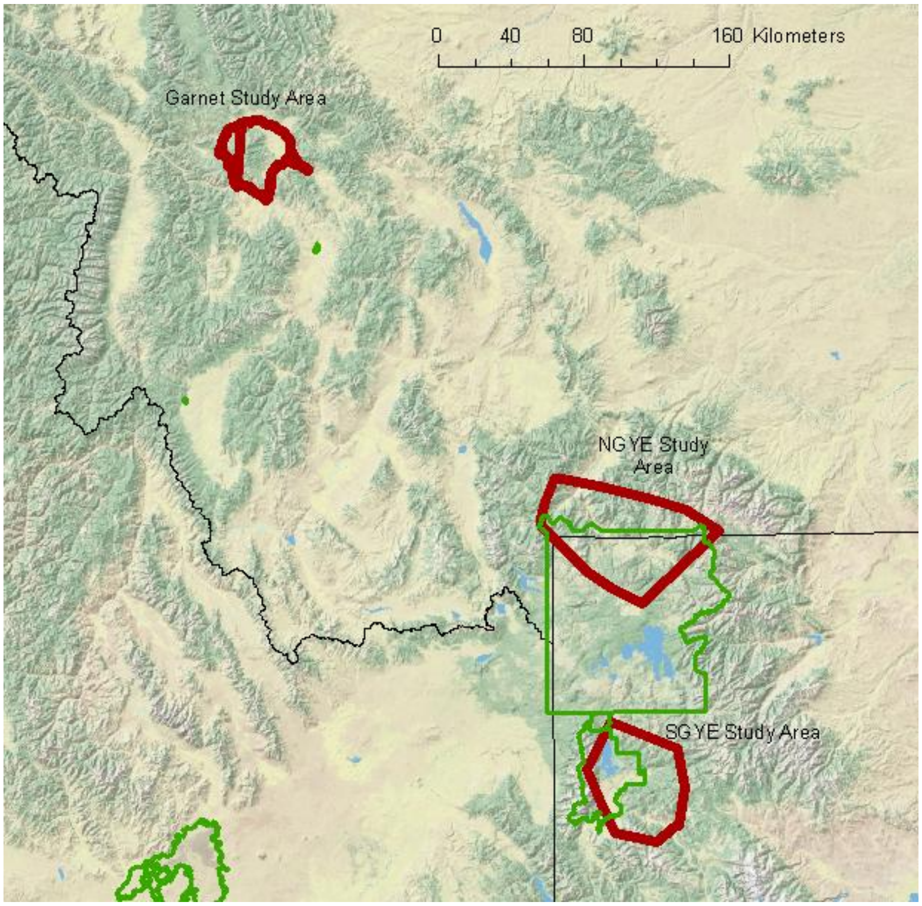
APPENDICES

APPENDIX A

STUDY AREA MAP



Puma dispersal characteristics were examined using long-term research in three separate study areas. Study systems included the Garnet mountains of western Montana (9 years) and the Northern Greater Yellowstone Ecosystem (NGYE; 13 years) and the Southern Greater Yellowstone Ecosystem (SGYE; 9 years). The study areas are demarcated in red and Yellowstone National Park is shown in green.

PPENDIX B

CONTRAST BETWEEN GARNET AND NGYE STUDY AREAS

Comparison between Northern Greater Yellowstone (NGYE) and Garnet Mountain study areas. Descriptive statistics for landscape characteristics associated with security habitat for pumas and exposure to human induced mortality. Areas of higher elevation, topographic and vegetative cover are typically associated with puma security habitat. Landscapes that have high road densities, and large amounts of agricultural and privately held lands are associated with increased puma mortality.

	Northern Greater Yellowstone		**Garnet Mountains**	
Landscape Characteristic	Mean	95% CI	mean	95% CI
Elevation^a	2269 meters	2257 – 2282 meters	1575 meters	1560 – 1590 meters
Slope^a	15.5%	15.3 – 15.8%	13.3%	13 – 13.7%
Terrain ruggedness^a	0.0043	0.0042 – 0.0044	0.0036	0.0034 – 0.0037
Percent forest cover^a	71%	69.9 – 72.1%	56.8%	54.9 – 58.7%
Percent open/agricultural^a	14.30%	13.5 – 15.1%	27%	25.5 – 28.5%
Percent urban^a	0.01%	0 – 0.028%	0.04%	0.018 – 0.056%
Road density^a	0.37 km/km^2	0.35 – 0.4 km/km^2	0.77 km/km^2	0.74 – 0.81 km/km^2
Percent of privately held land^a	12%	10.9 – 13%	49.4%	46.7 – 52.1%
Area protected from hunting^b	9,467 km^2		915 km^2	
	median^d	range^d	median^e	range^e
Annual harvest rate^c	2.3 puma/1000km^2	1.1 – 4 puma/1000km^2	5.1 puma/1000km^2	0.8-12.5puma/1000km^2

a – Values taken from random point along travel routes of dispersers from the two study areas (n=2547 NGYE, n=876 Garnet).

b – Protected areas includes only places mountain lion hunting is prohibited. In the NGYE this includes Yellowstone National Park and Grand Teton National Park. In the Garnet Mountains the protected area includes the core of the study area, which was protected in 5 out of the 9 years research was conducted.

c – Includes estimated annual removal of pumas due to hunting in the primary study areas and the hunting districts immediately adjacent to these study areas.

d – Legal harvest in districts adjacent to the northern range of Yellowstone National Parks. Pumas harvested per area does not include the majority of the puma study population inside Yellowstone National Park where they were protected from hunting.

e – Legal harvest throughout the Blackfoot Drainage inclusive of area where hunting was prohibited

APPENDIX C

AIC RESULTS FOR CHAPTER II DISPERSAL DISTANCE MODELS

Models fit for 62 dispersing pumas from the Northern Greater Yellowstone and Garnet Mountain study areas examining influences on dispersal distance. The first table examines the effects on observed Euclidean dispersal distance (D_e) and the second on the number of home ranges traversed (D_{hrd}). Models ranked by relative differences in AICc values (ΔAICc) and weights (ωAICc). Home ranges traversed estimated by dividing straight-line dispersal distance from point of origin to final dispersal location by mean adult home range diameter. Final locations are mortality sites or, if the individual survived to establish a territory, the center of its adult home range. Modeled effects include categorical variables for dispersal mortality, study area emigrated from, sex, and an interaction term between individual's sex and study area. Home range diameters calculated for adults of each sex in each study area using 95% fixed kernel.

Models for Euclidean Dispersal Distance (D_e)	**ΔAICc**	**ωAICc**	**No. of parameters**
1. Study area; mortality	0.000	0.265	3
2. Study area	0.505	0.206	2
3. Study area; sex; study area x sex; mortality	0.702	0.186	5
4. Study area; sex; mortality	1.105	0.152	4
5. Study area; sex	2.573	0.073	3
6. Study area; sex; study area x sex	2.649	0.070	4
7. Mortality	4.622	0.026	2
8. Study area; sex	5.654	0.016	3
9. Null	8.373	0.004	1
10. Sex	10.508	0.001	2

Models for Home Range Diameters Dispersed (D_{hrd})	**ΔAICc**	**AICc weights**	**No. of parameters**
1. Study area; sex; study area x sex; mortality	0.000	0.441	5
2. Study area; sex; study area x sex	1.151	0.248	4
3. Mortality	3.153	0.091	2
4. Study area; mortality	3.861	0.064	3
5. Sex; mortality	4.551	0.045	3
6. Study area; sex; mortality	5.265	0.032	4
7. Study area; sex	5.562	0.027	3
8. Study area	5.961	0.022	2
9. Sex	6.461	0.017	2
10. Null	7.392	0.011	1