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ECOLOGY AND CONSERVATION OF COUGARS IN THE EASTERN GREAT BASIN: EFFECTS OF URBANIZATION, HABITAT FRAGMENTATION, AND EXPLOITATION

by

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This research was designed to investigate cougar response to urbanization, habitat fragmentation, and exploitation from behavioral, demographic, and landscape perspectives. The source-sink model has been proposed as an alternative framework for the management of exploited cougar populations. I addressed the basic question of whether cougars conform behaviorally to the predictions of the source-sink model, and consequently, the applied question of whether the model could be used for the conservation of this species. To achieve this I evaluated three scale-specific questions using radio-telemetry and hunter-harvest data collected from 1996-2010. At the subpopulation scale, I tested the hypothesis that cougars are wildland obligates by measuring cougar response to a suite of anthropogenic land uses. At the meso scale I compared cougar dispersal patterns from two populations under different management. Lastly, at the statewide scale I examined the distribution of human-induced de facto
refugia and ecological traps in relation to the species range within Utah. Cougars show a strong proclivity for wildland over rural or suburban habitats, but all cougars used anthropogenic landscapes to some degree, and appear capable of surviving in highly disturbed, human-impacted environments. Cougar dispersal was correlated with maternal estrus; once young animals emigrated, natural and anthropogenic barriers directed movement into habitats marked by frequent human-caused mortality, with females selecting areas of lower conspecific density relative to males. Anthropogenic cougar mortality was disproportionately distributed in accessible, high quality habitats within the core of the species statewide range. Conversely, ecological traps were primarily situated within marginal habitats in remote settings on the periphery of the range. The source-sink model predicts that subordinate animals from saturated populations disperse to habitat with the highest suitability. Cougars of both sexes display behaviors that largely conform to these predictions. Based on the patchy but predictable distribution of cougar exploitation, Utah may already have a quasi source-sink system, which could be formalized through management action. In general, cougars are adaptable, behaviorally plastic, generalist carnivores, and as such defy broad habitat generalizations. These investigations have implications for sustainable hunting and long-term conservation of cougars in the multiple-use landscapes of the Intermountain West.
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David C. Stoner
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CHAPTER 1
INTRODUCTION AND LITERATURE REVIEW

BACKGROUND

Much of ecology is concerned with patterns in species distribution and abundance (Brown 1984). Animal populations reflect the distribution of their habitat, most readily modeled as the fundamental niche (sensu Hutchinson 1957). Within a species’ distribution, population density varies with the number and level of factors satisfied within its fundamental niche. The tolerance response curve represents the distribution of a species’ abundance around an optimum habitat quality (Cox and Moore 1993). The center of the curve represents the core of the species’ geographic range, where populations exhibit greater densities and lower amplitude dynamics (i.e. the realized niche most closely approximates the fundamental niche). Near the tails of the curve, one or more critical factors becomes limiting and populations exhibit lower abundance and greater variability. Here individuals may be incapable of reproduction and many of these populations are ephemeral. When habitats vary in quality over irregularly shaped or discontinuous geographic ranges, then the variation in a species’ abundance may behave like a metapopulation. Differential survival rates among habitat patches can influence the dynamics of the metapopulation by creating sources, sinks, or areas of relative stasis. The net result is a dynamic distribution that goes through episodes of expansion and contraction over ecological time.

Over the past millennia on six different continents and across an array of orders, large mammals from both terrestrial and marine ecosystems have experienced population
declines, range contractions, or extinctions (Woodroffe 2001, Inskip and Zimmerman 2009). Numerous mammalian species have suffered interacting detrimental effects from both the top down (exploitation), and the bottom up (habitat loss; Schipper et al. 2008). Large-bodied species occupying high trophic levels are particularly vulnerable to these threats because they are subject to disproportionately high levels of exploitation yet have slow life histories and occur at relatively low densities (Cardillo et al. 2005, Fritz et al. 2009). Worldwide, many carnivores have been extirpated from portions of their respective ranges (Woodroffe 2001, Cardillo et al. 2004, Laliberte and Ripple 2004), with modern extinctions in tandem with the human footprint (Channell and Lomolino 2000, Barnosky et al. 2011).

Ironically, in a review of factors contributing to extinction risk in mammals, Purvis et al. (2000) stated that the Carnivora were an enigma for conservation biology, as presently few threatened species come from this group, despite being faced with more threats than any other mammalian order. Nevertheless, either directly or indirectly anthropogenic factors are typically associated with species endangerment in the United States (Czech et al. 2000). Cougars (*Puma concolor*) seem to exemplify this paradox. Within a metapopulation context they can be declining or expanding simultaneously, depending on the scale of observation. It is not clear what extrinsic factors make them vulnerable to extirpation, nor those that intrinsically make them more resilient than other members of the Carnivora. The cougar therefore represents an ideal model organism to explore basic questions about the conservation biology of carnivores in a rapidly shrinking world.
Ecological niche, distribution, and status of *Puma concolor*

The cougar is a generalist predator that exhibits the widest latitudinal distribution of any terrestrial mammal in the western hemisphere, ranging from west-central Canada to Tierra del Fuego at the southern tip of Argentina (Pierce and Bleich 2003). The species occupies disparate biomes from temperate deserts to equatorial rainforests, and displays commensurately diverse dietary habits (Iriarte et al. 1990). Like most felids, cougars are obligate carnivores and their North American distribution is strongly correlated with various cervids (Pierce and Bleich 2003). In tropical Central and South America *Puma* demonstrates a much broader feeding niche (Emmons 1987, Monroy-Vilchis et al. 2009), but is still generally associated with cervids (Novack et al. 2005).

In North America cougars historically ranged from coast to coast. For most of the period following European colonization of the New World the species was widely persecuted as a pest (ca. 1620-1965). Efforts to eradicate cougars were largely successful in the eastern part of the continent. With the exception of a relict population in Florida, by 1930 overexploitation combined with habitat fragmentation and prey depletion (primarily white-tailed deer, *Odocoileus virginianus*) had rendered the species functionally extinct east of the Mississippi River (Maehr 1997). Despite increasingly conservative management, changing societal values (Murphy and Macdonald 2010), and the highly successful recovery of white-tailed deer, habitat fragmentation and Allee effects have largely precluded cougar recolonization of the eastern portion of their North American range. Cougars are now found primarily west of the continental divide,
exhibiting a patchy distribution among relatively mesic, mountainous landscapes capable of supporting ungulate prey.

Legal status of the species varies by jurisdiction and covers the spectrum of management classifications. During the 1960s and early 1970s most states with extant populations reclassified cougars from bountied predator to protected big game species (Pierce and Bleich 2003). At present, status of western cougars ranges from a state-listed Specially Protected Mammal in California, where no hunting is allowed, to vermin in Texas where killing is unregulated. Florida represents the other end of the management spectrum in which a relict population of the putative subspecies *P. c. coryi* is protected under the Endangered Species Act (Johnson et al. 2010). In the remaining western states, Canadian Provinces, and Mexico cougars are managed as a game animal with regulations on hunting opportunity, areas, seasons, and kill limits.

At the global scale the International Union for the Conservation of Nature (IUCN) gives *Puma concolor* a vulnerability ranking of Least Concern. The cougar ranks number 26 of 36 felids, and number 6 of 7 species of large felids (mean body mass > 40 kg) on the IUCN Red List. However, this varies by region with the Brazilian, Peruvian, Argentinean, and Columbian populations ranked as Near Threatened (Caso et al. 2008). In addition to *P. c. coryi*, within North America the eastern subspecies, *P. c. couguar* is also listed as Endangered under both the IUCN rankings and the Endangered Species Act in the United States. Although little evidence exists to indicate that beyond the Florida population cougars are extant in the eastern United States, *P. c. couguar*, along with two other subspecies (*P. c. coryi*, and *costaricensis*) are protected under Appendices I and II.
of the Convention on International Trade of Endangered Species (CITES; Nowell and Jackson 1996). Notably, recent DNA analyses suggest that all North American cougars are descended from a small group of founders and that the 15 *Puma* subspecies described by Young and Goldman (1946) should be lumped into a single subspecies, *P. c. couguar* (Culver et al. 2000). Consequently, these legal classifications may be reappraised in coming years.

Despite a long history of persecution, cougars have exhibited marked resiliency compared to other members of the *Felidae* (Chapron et al. 2008) and represent one of the last widely distributed large carnivores in North America. With the possible exception of the leopard (*Panthera pardus*), cougars inhabit a greater percentage of their historic range than any other large felid (Panthera 2007). Unlike many diurnally active, herding, or numerically abundant species there are no robust and widely accepted techniques for cougar enumeration (Choate et al. 2006). This characteristic makes the assessment of both local abundance and long-term population trends difficult. Conservation is further complicated by the steady rise in fatal attacks on humans over the past 35 years (CMGWG 2005), while the total habitat area remaining unaffected by some form of human activity has declined. The stochastic nature of cougar predation on humans and deterministic trends in habitat fragmentation raises questions about the continued social acceptance and ecological viability of cougars in parts of their current range.

**JUSTIFICATION**

In North America most of the largest members of the *Carnivora* have been extirpated
from portions of their historic ranges. Brown bears (*Ursus arctos*), wolves (*Canis lupus*), and jaguars (*Panthera onca*) exhibited severe range contractions following the implementation of federally subsidized predator eradication programs designed to benefit the livestock industry and big game populations (Young and Goldman 1946, Laliberte and Ripple 2004). Ranges did not contract from low to high quality habitat, as predicted by theory (Brown 1984), but along a human density / accessibility gradient (Laliberte and Ripple 2004). Cougars followed this same pattern, though not to the same extent.

Broadly, cougars seem to fit the “enigma” moniker of Purvis et al. (2000), though locally the species has demonstrated sensitivity to the effects of habitat loss, fragmentation, and overexploitation (Crooks 2002, Michalski and Peres 2005, Stoner et al. 2006). Both local and regional extirpations have been documented (Young and Goldman 1946, Beier 1996), and several populations have been isolated by urban encroachment (Beier 1996, Maehr 1997). In contrast, examples of long-distance dispersal (Stoner et al. 2008, Thompson and Jenks 2010), recolonization (Riley and Malecki 2001, Thompson et al. 2008), population expansion (Jung and Merchant 2005, Bacon and Boyce 2009, Wilson et al. 2010), and recovery from over-exploitation (Logan and Sweanor 2001, Anderson and Lindzey 2005, Robinson et al. 2008) abound. More broadly, ample evidence exists of large carnivores persisting and even recolonizing historic habitats when conservative management interacts with favorable environmental conditions (Linnell et al. 2001, Pyare et al. 2004, Ale et al. 2007).

Recent research has elucidated ecosystem-level effects of carnivore hunting and feeding behavior (e.g. Betscha and Ripple 2009). This influence has been assessed
directly through effects on prey abundance (McLaren and Peterson 1994, Sinclair et al. 2003) and behavior (Pierce et al. 2004, Creel et al. 2007, Laundré 2010), or indirectly via community composition (Crooks and Soulé 1999, Berger et al. 2001), animal biodiversity (Sergio et al. 2005, Ritchie and Johnson 2009), scavenger subsidies (Wilmers et al. 2003), and plant recruitment (Bump et al. 2009). Of particular interest are the results of Krumm et al. (2010), who found evidence that cougars prey disproportionately on diseased mule deer, adding support for the long debated “sanitation hypothesis” (Errington 1967). In a more subtle example, Choate (2009) determined that cougar recolonization of a palouse prairie ecosystem in northern Montana led to changes in feeding behavior and habitat selection of three ungulates that were commonly preyed on by cougars. Observed behavioral changes had fitness consequences, as individuals attempted to minimize predation risk by feeding on lower quality forage, or during diurnal hours when thermoregulation was more energetically expensive. In recent years, cougars have been documented expanding their current range or colonizing relatively unproductive ecosystems by incorporating exotic ungulates into their diet, such as feral horses and domestic sheep (Turner et al. 1992, Novaro et al. 2000, Bacon and Boyce 2009). In light of these findings and its role as a predator of mesocarnivores and large herbivores (Monroy-Vilchis 2009, Knopff et al. 2010), cougar abundance in, or absence from, a particular community may have ecosystem-level consequences for biodiversity (Sweitzer et al. 1997, Choate 2009, Donadio et al. 2010).
Patterns and consequences of anthropogenic activities

Humans and carnivores occupy overlapping niches and historically have competed for similar food resources. For example, Kruuk (2002) describes early hominids in African savannas appropriating kills from large carnivores, and conversely, fossil remains of ancient juvenile hominids display evidence of death by leopard predation. This suggests that some degree of coevolution has occurred between humans and certain carnivores. Competition is commonly manifested in the form of control actions implemented in response to marauding individuals that hunt livestock (i.e. kleptoparasitism), large-scale management actions aimed at reducing carnivore numbers as an attempt to minimize predation on native game species, and in response to attacks on humans (e.g. Packer et al. 2005). Based on this relationship one would predict that carnivore survival and distribution would be negatively correlated with some index of human abundance or activities (Woodroffe 2000). Yet a cursory glance at the literature does not provide unequivocal support for this hypothesis (Linnell et al. 2001, Karanth et al. 2004). Carnivores are still extant in many parts of the world with exceptionally high human densities, including Europe, south Asia, and North America, suggesting that some combination of behavioral and reproductive adaptations have allowed coexistence of these competitors. Nevertheless, conflicts are widespread and most carnivore extinctions have been associated with anthropogenic agency.

Urbanization and habitat degradation

In the western United States, urbanization adjacent to public lands has occasioned the juxtaposition of human communities and wildlife habitat, resulting in interface zones
defined by a mixture of homes and residual habitat patches (Hansen et al. 2005, Leu et al. 2008). Seasonal elevational migrations in response to snow accumulation and plant phenology, and landscaping with associated irrigation can bring ungulates into foothill regions, thereby attracting cougars to areas occupied by humans. A question of interest to both ecologists and wildlife managers is how cougars respond to anthropogenic landscapes, and further, do these habitats possess source or sink-like qualities within the greater metapopulation? Despite a growing body of literature describing the effects of human-caused mortality on cougar populations (Stoner et al. 2006, Robinson et al. 2008, Cooley et al. 2009, McKinney et al. 2009, Packer et al. 2009), little information exists on how individuals respond to non-lethal interactions with humans, or more generally on cougar behavior in urban-industrial landscapes. Indeed most research conducted on the species has been on legally protected populations, or those inhabiting remote areas (e.g. Hornocker 1970, Lindzey et al. 1994, Murphy 1998, Pierce et al. 2000, Logan and Swaanor 2001).

Globally, the human population is growing at a rate of 1.4% / year, and the United States at approximately 0.9% / year (U.S. Census Bureau). The West is the fastest growing region of the country, with Utah and four of its neighbors (Arizona, Colorado, Idaho, and Nevada) comprising five of the seven states with the highest growth rates (1.8-3.8%/yr). Commensurate with this growth is an expansion in housing and transportation infrastructure (Hansen et al. 2005). At the same time, traditional use of public lands for livestock grazing and hunting continues, alongside a growing interest in other forms of outdoor recreation. Although the magnitude of these impacts varies, there are few places
that remain completely isolated from the current trends in land-use change.

The Wasatch Front metropolitan area is home to approximately 1.7 million people and since 2000 has grown at an average annual rate of 1.6% (U.S. Census Bureau). Patterns in land ownership have created hard edges between exurban neighborhoods and wildlife habitat. Research indicates that animals living near urban areas are more likely to be killed on roads or in control actions (Beier et al. 2010). Moreover, some mammals may avoid urban areas altogether because of sensitivity to noise and light pollution (Beier 2006). Conversely, humans can provide allochthonous inputs to ecosystems of low or variable productivity, such as those found in the eastern Great Basin. Cougars may benefit from the presence of exotic and naïve prey such human commensals (pets, livestock), invasive generalists (e.g. raccoons, *Procyon lotor*; skunks, *Mephitis mephitis*), and feral domestics (e.g. house cats, *Felis catus*) that prosper in these environments (Prange and Ghert 2004, Randa and Yunger 2006). In arid climates perennial water can draw wild prey to predictable localities during summer (Tull and Krausman 2007). Mineshafts and culverts can serve as thermally constant cache, den, and rest sites, and road networks can provide predictable sources of carrion and winter travel routes. Thus, arguments can be made either way as to why cougars might be repulsed or attracted to areas of human activity.

Previous work examining human-cougar relationships has focused on human safety (Sweanor and Logan 2010), and the effects of habitat fragmentation on population dynamics (Beier 1996) or occupancy (Crooks 2002). Beier’s (1995, 1996) pioneering work also examined the effects of habitat isolation on population persistence on the
urban-wildland interface in southern California. A decade later on an adjacent study area, Sweanor and Logan (2010) examined cougar movement patterns in and around a popular state park surrounded by low-density housing. She and her colleagues used GPS telemetry to monitor movement patterns of 10 adult cougars to examine habitat use in relation to recreational activity. They found that cougars tended to avoid humans spatially or temporally. Orlando (2008) examined cougar movement patterns in one western Sierra Nevada ecosystem fragmented by small acre ranchettes. Her results demonstrated that low density development effectively fragmented habitat, increased cougar mortality, and exacerbated depredation problems. To date, these are the only published studies drawn from radio-marked animals living in near-urban settings. Beyond these efforts, several authors have hypothesized that cougars exhibit a negative behavioral response to non-lethal human activities (Van Dyke et al. 1986, Murphy 1998, Ripple and Betscha 2006). Overall though, it is unclear whether cougars display any pronounced or predictable behavioral responses to human-dominated landscapes.

Exploitation, habitat fragmentation, and source-sink dynamics

Many carnivores are exploited as part of regulated harvests (Packer et al. 2009), in response to agricultural damage (e.g. Kissling et al. 2009), or as part of the indigenous medicines trade (Nowell and Jackson 1996). Recent research has demonstrated demographic (Loveridge et al. 2007, Milner et al. 2007, Cooley et al. 2009), morphological (Coltman et al. 2003), and behavioral (Gobush et al. 2008) changes to some mammals resulting from exploitation. When sustained over long periods,
anthropogenic selective pressures can increase rates of change for certain phenotypic traits (Sasaki et al. 2009, Darimont et al. 2009). Direct exploitation is probably the single greatest factor affecting carnivore range dynamics (Laliberte and Ripple 2004), and has been commonly cited in reference to changes in the North American distribution of cougars (Young and Goldman 1946, Nowak 1976, Pierce and Bleich 2003).

In most North American jurisdictions cougars are subject to annual hunting programs. However, the difficulty in accurately assessing population abundance, trends, and recruitment on biologically meaningful scales impedes precise management (Choate et al. 2006). To work around these constraints a number of investigators have proposed a behavioral solution to managing exploited carnivores (Logan and Sweanor 2001, Laundré and Clark 2003, Nielson et al. 2006, Novaro et al. 2005, Stoner et al. 2006, Balme et al. 2010). This approach is predicated on a source-sink population structure, in which harvest pressure is applied in a spatially variable manner so that socially subordinate animals from productive source populations disperse to sinks. Source-sink models generally propose density-dependent dispersal as the behavior facilitating connectivity and persistence in populations defined by high mortality and / or low fecundity (Pulliam 1988). Two of the fundamental predictions inherent in the source-sink model are that: 1) lack of breeding opportunities prompts subadult emigration from more productive habitats, and 2) dispersers tend to settle in habitats with relatively low population densities. The second prediction implies that dispersers assess levels of resource abundance in different habitats and select the one in which fitness will be optimized, as indexed by intraspecific competition. Although a promising alternative to annual
population estimates, few efforts have been made to determine whether polygynous carnivores generally, or cougars specifically, conform to these predictions, and if so, under what environmental and demographic conditions (Mosser et al. 2009).

Dispersal is the primary behavioral mechanism facilitating numeric and demographic connectivity among sub-populations within a metapopulation framework. The behavior has been studied extensively in birds and mammals (Sutherland et al. 2000), but underlying cues, motivations, and mechanisms remain poorly understood and difficult to generalize. Much of the research on felid dispersal behavior has focused on sex biases in terms of frequency and distance traveled (Pusey and Packer 1987), potential effects on social organization (Smith 1993), estimating demographic parameters (Ferreras et al. 2004), and genetic legacies (Biek et al. 2006). Others have examined basic hypotheses about fitness benefits of various dispersal strategies (e.g. competition vs. inbreeding avoidance; Ronce 2007). Among mammals males usually disperse, whereas females tend to be philopatric. Cougars follow this general pattern, yet the role of territoriality and intrasexual competition has primarily been discussed in reference to a disperser’s decision to leave its natal range, and not on its decision to settle. Because of predominant male territoriality, cougar habitat selection approximates an Ideal Despotic Distribution (sensu Fretwell 1972). Although many researchers have documented the movement patterns of transient animals, few assessments have been made as to the relative roles of habitat fragmentation and intraspecific competition, and how widespread exploitation may modify source-sink dynamics of a territorial species with a complex social organization.
Little research has been conducted on cougar dispersal behavior. Beier (1995) followed the fates of 9 subadult cougars attempting to disperse from a small mountain range surrounded by urbanization in southern California. He determined that housing and transportation infrastructure were effectively isolating the population. Sweanor et al. (2000) presented the largest dataset yet compiled on this topic (n = 43), and argued that cougars in southern New Mexico exhibit a metapopulation-type structure due to the naturally patchy distribution of habitat in that area. In another study, Maehr et al. (2002) examined the dispersal patterns of 27 Florida panthers and found that natural and anthropogenic landscape features combined with natal population density were the best predictors of dispersal movements in that subspecies. Thompson and Jenks (2010) monitored dispersal patterns of cougars leaving a small, isolated habitat patch on the eastern edge of the species’ distribution. These investigators documented extraordinary distances and argued that for males, conspecific attraction and breeding opportunities were the driving factor prompting extended movements within the Great Plains. Each of these studies elucidated patterns in the behavior of the individual dispersers and their respective natal populations, but none of them provided information on the habitat quality or mortality rates in patches where dispersers settled. Because an individual’s decision or ability to settle an adult home range is predicated on both intrinsic (individual behavior) and extrinsic (social and environmental characteristics) factors (Ferraras et al. 2004), it is important to examine this behavior from both the social and landscape perspective. A number of critical questions remain unaddressed regarding cougar dispersal in ecosystems defined by high levels of natural and anthropogenic fragmentation, and
exploitation, including; how do males and females vary in their dispersal behavior; what landscape features facilitate or impede movement of these animals; and what social and habitat conditions prompt transients to settle? These questions are particularly pressing given the potential for crossing unpredictable demographic thresholds, and deterministic, longer-term climatically driven changes in habitat (Kokko and López-Sepulcre 2006).

Zoogeography, de facto refugia, and ecological traps

The _Puma_ lineage dates to the late Miocene (Johnson et al. 2006), with _P. concolor_ appearing in the fossil record > 300,000 years ago, well before the arrival of the first hominids to the New World (Culver et al. 2000, Gilbert et al. 2008). Based on mtDNA evidence, Culver et al. (2000) argued that _Puma_ is of South American origin and was lost from the North American fauna during the Pleistocene extinctions. Following glacial retreat, the species reinvaded North America from refugia in the tropics, while humans were colonizing North America from east Asia.

Biogeographic theory predicts that during periods of widespread population decline, a species range should contract from the edges inward, with the core acting as a stronghold (Brown 1984). Empirically this has been the case with some mammals (Lomolino and Channell 1995); however, in a review of recent extinctions and range contractions of 245 species, Channell and Lomolino (2000) found that ranges contracted from the point of contact with humans rather than from the periphery. Among both vertebrates and invertebrates 81% of North American species examined persisted along the edges or in remote sections of their ranges, and not in the core. Acting individually or in concert, range collapse resulted from habitat destruction, introduction of alien species, or over-
exploitation. Contraction spread like a contagion following the human footprint rather than along gradients in habitat quality. The authors argued that anthropogenically induced extinction superseded historical density patterns, and populations most likely to persist were those on undisturbed islands, range edges, or at high elevations. They concluded that remote or inaccessible regions may represent refugia for imperiled species (Channell and Lomolino 2000).

In North America the cougar’s present distribution is largely restricted to mountainous regions of the west as implied by the common name “mountain lion.” By default, behavioral and morphological adaptations for hunting ungulates in steep and broken terrain have allowed cougars to avoid extirpation by humans in these environments. At the continental scale, the North American case for *Puma* appears to follow the predictions of the Contagion Hypothesis, with range contraction expanding from the point of human contact (Morrison et al. 2007). Although there are no estimates of historical cougar abundance, eastern North America is generally more productive and homogenous than the West. Although the topographic complexity of the mountain West has provided a shelter for cougar populations, its highly seasonal climate means that cougars need more habitat to survive than they would in the East because of elevational migrations of their ungulate prey in response to winter snow accumulation. For example, based on a simple back-of-the-envelope calculation, Shaw (1989) estimated that > 26,000 km² of habitat would be required to sustain the estimated population size for minimum viability (~ 500 animals) in the western mountains. Even the largest nature reserves in North America are substantially smaller than this figure, indicating that successful conservation of this
species will have to include multiple-use lands. To date, no one has attempted a large-scale (e.g. statewide) analysis of cougar mortality patterns. Nor has anyone tried to correlate these patterns with landscape features to identify areas of vulnerability or sanctuary, irrespective of management status. Examining the distribution and relative intensity of human-caused mortality of a numerically rare carnivore may provide insights to spatial patterns of extinction, defining and delineating reserves for the conservation of large mammals, and the role of management actions in promoting or maintaining source and sink populations. These questions have direct relevance for the conservation of other mountain dwelling polygynous carnivores, particularly snow leopards (*Uncia uncia*), jaguars (*Panthera onca*), and brown bears (*Ursus arctos*). Collectively, these efforts may provide insights to why cougars have fared better than other large carnivores.

**Goal and Objectives**

The goal of this effort and is to understand the ecology and behavior of a widely distributed generalist predator, the cougar, in response to anthropogenic stressors and landscape characteristics within a source-sink context. Specifically, my objectives were three-fold: 1) to examine cougar behavioral response to anthropogenic landscapes and determine whether they are best characterized as synanthropic or wildland obligates; 2) investigate cougar dispersal behavior in relation to the basic predictions of the source-sink model of population dynamics; and 3) assess the relationship between anthropogenic cougar mortality and landscape heterogeneity within the context of the Contagion Hypothesis. Each of these objectives were investigated at a specific spatial scale.
Objective one was conducted at the scale of the individual study site (500 km²), objective two at the scale of two study sites (21,000 km²), and lastly objective three was investigated at the statewide scale (92,700 km²). Data for these objectives were drawn from a long-term monitoring project on cougar population dynamics and habitat use on two sites in Utah. This study is the first to intensively and simultaneously monitor two cougar populations under different management criteria for more than a decade. All analyses are retrospective.

Widespread exploitation and the rapidly expanding contact zone between urban areas and wildlands raise questions about the continued viability of cougars across some of the more productive portions of their current range. Given accelerating fragmentation combined with the inability to accurately quantify the abundance of this game species, an integrated analysis of cougar response to various human activities will be vital for conserving these animals and managing human-carnivore conflicts in multiple-use landscapes. Managers and conservationists have commonly stated that more information was needed on these aspects of cougar behavior and life history (CMGWG 2005). How cougars respond to both direct (e.g. hunting) and indirect (habitat fragmentation and degradation) interactions will have implications not just for cougar persistence, but also for population dynamics of key prey species, depredation control, ecosystem function, human safety, environmental aesthetics, and the conservation of imperilled carnivores.

**Literature Cited**


Orlando, A. M. 2008. Impacts of rural development on puma ecology in California’s Sierra Nevada. Dissertation, University of California, Davis, USA.


CHAPTER 2

BEHAVIORAL RESPONSE OF A LARGE, GENERALIST CARNIVORE TO ANTHROPOGENIC LANDSCAPES: FEAR, OPPORTUNITY, OR NONCHALANCE?

Abstract. Western North America has experienced remarkable human population growth and changes in land-use in recent decades. Habitat fragmentation and redistribution of resources have influenced carnivore behavior and population dynamics, resulting in increased conflicts with human interests. Developments in theoretical and applied research on carnivore habitat selection behavior have elucidated the tenuous balance between mortality risk and resource acquisition. Cougars (*Puma concolor*) are obligate carnivores extant over much of the West. Several investigators have hypothesized that cougars avoid landscapes associated with human activities. However, anthropogenic landscapes present cougars not only with survival costs, but with highly predictable foraging opportunities. We evaluated the hypothesis that cougars are wildland obligates by addressing three constituent questions: 1) how do cougars respond to human altered landscapes, 2) do cougars make trade-offs in habitat selection based on anthropogenic inputs, and 3) do near-urban cougar populations act as de facto sinks?

From 2002-2009 we employed Global Positioning Systems collars to study cougar movement and predation behavior in the Oquirrh Mountains near Salt Lake City, Utah. We instrumented 21 individuals and measured their response to four human land-use types comprising the urban-wildland interface (UWI) at two scales. At the landscape scale (500 km²), cougar response was defined by avoidance, as all individuals used
anthropogenic landscapes less than available. Within the UWI cougar response varied by demographic class and land-use type. Contrary to our predictions, maternal females did not make habitat selection trade-offs, but used risky habitats within the UWI at greater frequencies than their non-maternal counterparts. Human-caused mortality on the UWI disproportionately affected dispersing males and senescent females. Animals capitalizing on anthropogenic food resources tended to be inefficient hunters, exemplified by the very young and the very old. We argue that the cougar response to anthropogenic landscapes be described not as fear, but ambivalence. Cougars appear sufficiently flexible to exploit opportunities provided by human activity, but their nocturnal, reclusive, and non-gregarious behavior partially ameliorates potential conflicts. Rather than viewed as either a wildland obligate or synanthropic, cougars are best characterized as a behaviorally plastic, disturbance-adapted species.

**INTRODUCTION**

Habitat selection theory holds that animals tend to seek areas offering optimum fitness benefits, which can involve a trade-off between population density and habitat quality (Fretwell 1972). Recent theoretical developments have explored the role of behavior in habitat selection based on the balance between predation risk and food resources (Brown et al. 1999), and this has been evaluated for several large mammals (e.g. Bleich et al. 1997, Ben-David et al. 2004). Few investigators however, have examined these trade-offs in a human-carnivore system. Human activity presents animals with both costs and opportunities. For example, human caused mortality is almost universally cited in studies
of carnivores, even in remote or nominally protected areas (Woodroffe and Ginsburg 1998). Nevertheless humans can act as a source of allochthonous inputs, inadvertently creating highly predictable subsidies to ecosystems of low or variable productivity (Beckman and Berger 2003, Ruth et al. 2003). Human altered landscapes can offer an abundance of exotic and naïve prey such as human commensals (pets, livestock), or invasive generalists (e.g. skunks, *Mephitis mephitis*); and in arid climates irrigated landscaping can draw wild prey to predictable localities during summer (Tull and Krausman 2007). Within the bounds of extinction and domestication, most species will fall somewhere along the continuum ranging from wildland obligate to synanthropic. Wildland species are those with either a very low tolerance for human presence or activities, and/or very specific habitat needs, whereas synanthropic species can live among humans and benefit from anthropogenic activities.

Cougars (*Puma concolor*) are generalist predators widely distributed across the western hemisphere, occurring in disparate biomes such as temperate deserts and equatorial rainforests. This tremendous adaptability to climatic variation has led to commensurately diverse dietary habits (Iriarte et al. 1990), yet the species’ occurrence in a given community is generally associated with the presence of ungulate prey. Historically, cougars occurred over much of sub-boreal North America, but European colonization during the late 16\(^{th}\) century initiated widespread exploitation, prey depletion, and habitat alteration, with range contractions following settlement and associated economic activities (Pierce and Bleich 2003). Cougars are now largely relegated to the mountain West. With human-caused mortality playing a role in cougar abundance at the
continental scale, it follows that shy and reclusive individuals with an innate wariness of humans may have experienced greater survival.

The relationship between cougars and humans is complex and bi-directional. During the latter 20th century human population growth in the mountain West, accompanied by expansion of housing and transportation infrastructure led to increased conflicts between humans and cougars. Urbanization adjacent to public lands has resulted in a mixture of anthropogenic landscapes and relict habitat patches (Leu et al. 2008). This is pronounced in areas where ungulates exhibit elevational migrations between seasonal ranges in response to snow accumulation, which can inadvertently draw cougars closer to areas of human activity. Cougar management is complicated by simultaneous and sometimes incompatible directives focused on controlling problem individuals (e.g. human safety, property damage), while conserving larger populations that are vulnerable to extirpation because of anthropogenic fragmentation (Beier et al. 2010, Onorato et al. 2010).

Our scientific view of cougar behavior and habitat use has been shaped by studies conducted in remote regions of western North America, e.g. Seidensticker et al. (1973), Pierce et al. (2000), and Logan and Sweanor (2001). Little research has been conducted on these topics in near-urban environments. Previous work has focused on the effects of fragmentation on population dynamics (Beier 1995) or occupancy (Crooks 2002), but only recently has a greater effort been made to study cougar behavior in anthropogenic landscapes (e.g. Orlando 2008). Preliminary results have described cougar use of habitats adjacent to major metropolitan areas (Beier et al. 2010) while exhibiting a general aversion to human activities (e.g. Mattson 2007). Nevertheless, the frequency in pet
depredations, attacks on humans, and errant cougars within city limits have steadily increased since the 1970s (Torres et al. 1996). Aside from direct exploitation (Stoner et al. 2006, Robinson et al. 2008), debate exists on the sensitivity of cougars to non-lethal anthropogenic influences. Murphy et al. (1999) hypothesized that cougars may avoid disturbances such as mining, logging, or recreation if these activities are associated with a threatening human presence. They conceded, however that in the absence of strong negative consequences, cougars may continue to frequent areas of predictable human activity. Going further, Ripple and Beschta (2006) suggested that the mere presence of humans in large numbers, such as tourists in national parks, can render otherwise high quality habitat unsuitable for cougar use, cause home range abandonment, or reduce carrying capacity. Neither of these postulates were supported by field data, but clearly fall into the general hypothesis of cougar as a wildland obligate. In contrast, recent reviews by Beier et al. (2010) and Sweanor and Logan (2010) present a more nuanced view, suggesting that in near-urban populations, cougars exhibit individualistic responses to human activities even in the face of substantial human-caused mortality.

Our goal was to address the basic question of where cougars fall along the wildland-synanthropic continuum; and consequently the applied question of how to conserve this species in multiple-use landscapes. If cougars are wildland obligates, then they should exhibit a clear avoidance of human activities. Alternatively, if they have synanthropic tendencies, then we should see some level of attraction to these same activities. Within this context, we predicted that: 1) cougar space use would be better explained by variables related to prey acquisition (benefit) than by human activity (predation risk); and
2) negative responses to human landscapes would be weakest among males and strongest among females with kittens. We evaluated these predictions by measuring the behavioral response of resident cougars in different reproductive states to various forms of human activity in a highly disturbed urban-industrial landscape. We approached this question from both landscape and patch scales. We defined the landscape-scale as the study area (500 km²), and the patch-scale as that habitat within the “urban-wildland interface” or UWI (mean patch size = 0.1 ± 0.3 km²).

**METHODS**

**Study area**

The Oquirrh-Traverse Mountains form a boot-shaped complex (hereafter the Oquirrhs) in north-central Utah (40.5º N, 112.2º W) on the eastern edge of the Great Basin (Fig. 2-1). The ecoregion is defined by basin and range topography, in which mountains form islands of high productivity relative to the surrounding desert basins, and thus constitute the majority of cougar habitat in an area otherwise defined by aridity. The Oquirrhs measure > 950 km², but we focused fieldwork on 500 km² encompassing the northeastern slope on properties owned and managed by the Utah Army National Guard (Camp Williams) and the Kennecott Utah Copper Corporation. The site is bounded on the north by the Great Salt Lake and on the east by the Salt Lake Valley. Land ownership in the Oquirrhs is a patchwork of Federal (Bureau of Land Management), private grazing associations, and mining interests. Approximately 45% of the range is privately held. We selected this site for three primary reasons: 1) its proximity to the greater Wasatch Front
metropolitan area, 2) the diverse suite of human activities and associated land uses, and 3) the lack of public access.

Elevational relief (from lake level at 1,292 m to 3,200 m) is correlated with variation in moisture, vegetation, and animal diversity. Annual precipitation ranges from 30-40 cm in the Salt Lake and Tooele valleys to 100-130 cm on the highest ridges and peaks. Precipitation is bimodal, with most falling as snow from December-April, followed by a late summer monsoon. Mean monthly temperatures range from – 2.4°C in January to 22.2°C in July (Banner et al. 2009). This climatic regimen supports a variety of plant communities. Foothills are dominated by Gambel oak (*Quercus gambelii*), sagebrush (*Artemisia tridentata*), and Utah juniper (*Juniperus osteosperma*). Canyon maple (*Acer grandidentatum*) is prevalent in riparian zones at low elevations and across broader areas above 1,800 m. Mountain mahogany (*Cercocarpus spp.*) is common on ridges and well-drained soils. North facing slopes above 2,200 m support localized aspen (*Populus tremuloides*) and Douglas fir (*Pseudotsuga menziesii*) forests. The ungulate prey associated with these plant communities comprises mule deer (*Odocoileus hemionus*) and to a lesser extent elk (*Cervus elaphus*). However, a small number of pronghorn antelope (*Antilocapra americana*) and feral horses (*Equus caballus*) occur on the periphery of the site, and free-ranging livestock, including cattle (*Bos taurus*), sheep (*Ovis aries*), goats (*Capra hircus*), and horses are available from May-December. Potential competitors include coyotes (*Canis latrans*) and bobcats (*Lynx rufus*). Historically bighorn sheep (*Ovis canadensis*) and black bears (*Ursus americanus*) occurred in the Oquirrh Hills but were extirpated during the latter 19th century following the introduction of domestic sheep.
Both deer and elk are subject to limited annual hunts on Kennecott’s cooperative wildlife management unit. The study site is situated within the Oquirrh-Stansbury Cougar Management Unit, but both properties have been closed to the public and cougar hunting for > 15 years. Radio-instrumented cougars leaving those properties were legally protected as part of a parallel study.

Human activities on the Kennecott property are associated with mineral extraction operations. Attendant infrastructure stretched across 32 km with large tracts of intact habitat between. Operations included two pits, two concentrators, an in-pit crusher, an ore smelter, evaporation ponds, leach heaps, access roads, slurry and water lines, a tailings impoundment, and office buildings. All operations were continuously active, including 300-ton capacity haul trucks within the mine, various heavy equipment (dozers, front end loaders, track hoes), and light utility trucks. Most operational activities occurred within 200 m of infrastructure. Camp Williams is operated by the Army National Guard and was used for military training activities. During spring and summer the camp hosted large training units (battalion ≥ 300 soldiers) 4-6 times a year, and 4-8 artillery exercises annually. Bombardment exercises were focused on an impact zone on the west side of the installation. Various small arms ranges are used daily as weather permits. Prominent peaks on the site supported commercial radio and television transmitters with associated access roads used year-round. Based on 2000 census projections, human densities (residents / 100 km²) adjacent to the study area varied from 232 in rural Tooele County to 47,259 in urban Salt Lake County (U.S. Census Bureau). The three statistical metro areas that comprise the greater Wasatch Front; Salt Lake City, Provo-Orem, and Ogden-
Clearfield, were among the 100 fastest growing American metro areas during 2000-2006. The Salt Lake Valley is the economic hub of Utah and home to approximately 40% of the state’s population.

**Capture and application of radio-telemetry**

During winter (December to April) from February 1997 to April 2009 we conducted intensive capture efforts by trailing cougars into trees, culverts, cliffs, or mineshafts using trained hounds. Pursuit, immobilization, and aging techniques are detailed in Stoner et al. (2006). All adult (>2.5 yrs) and sub-adult (1.5-2.5 yrs) cougars were equipped with radio-collars (*Advanced Telemetry Solutions*, Isanti, MN). Each year we marked 3-4 animals with global positioning systems (GPS) collars (*Televilt Simplex* or *LoTek 4400S*) programmed to acquire 1 fix every 3 hrs beginning at midnight, allowing 120 seconds for each fix attempt. This schedule proved the best compromise between battery life (8-13 months) and monitoring circadian movements. With one exception, we only applied GPS collars to adult residents in order to minimize the potential loss of costly equipment. We tracked radio-collared cougars using aerial and ground-based telemetry techniques at approximately monthly intervals. We recaptured GPS instrumented animals annually to download data and replace collar batteries. Collars recorded a GPS coordinate (Universal Transverse Mercator, zone 12N, WGS 1984); an associated index of position accuracy, date, and time (Mountain Standard Time year-round). Methods for evaluating GPS position accuracy are detailed in Rieth (2010). For fieldwork we assumed an error radius of 100 m to account for errors induced by variation in canopy cover, terrain, and animal
behavior. We analyzed all geographic data in ArcGIS v. 9.2 (ESRI, Redlands, California). Animal handling procedures were conducted in accordance with Utah State University Institutional Animal Care and Use Committee standards (approval no. 937-R).

**Predictor variables**

*Sampling cougar space-use.*—All GPS locations were subsampled by time of day and season. We used time tables from the U. S. Naval Observatory to group hours into three categories based on the timing of sunset and sunrise at Salt Lake City during the winter and summer solstices (40.8° N, 111.9° W, December 21 sunrise: 0748, sunset: 1702; June 22 sunrise: 0456, sunset: 0202). We considered all points recorded between 0800-1600 hrs diurnal; 2000-0400 hrs nocturnal, and 0500-0700 and 1700-1900 hrs crepuscular. We used a 2-hr window to delineate crepuscular points because of seasonal shifts in photoperiod. Because prey distribution influences cougar behavior and habitat use (Pierce et al. 1999) we defined seasons based on ungulate movement patterns. Median mule deer migration dates in the eastern Great Basin occur in late October and mid-May, reflecting the timing of snow accumulation, melt-off, and plant phenology (McClure et al. 2005). Therefore we defined the seasonal calendar as: winter = December-April, spring = May, summer = June-October, and fall = November. When sample sizes were limiting we grouped spring with summer and fall with winter. Lastly, we used a 30-m digital elevation model (DEM) to quantify seasonal elevation shifts.

*Cougar predation, behavior, and habitat use.*—We attributed behaviors to all GPS position data based on the hour of the day, and whether or not the date corresponded to cougar localization around a cache site. We used the methods outlined by Anderson and
Lindzey (2003) to identify, locate, and separate cougar predation events from the data set. This consisted of isolating GPS location clusters comprised of ≥ 2 points within 100 m of each other collected between 2000-0400 hrs, indicative of a nocturnal feeding session. To calculate the number of days in association with a particular kill, we subtracted the time of the first point within 100 m of the cluster center from the last. All points in between these dates were considered temporally dependent on the cache site. We used movement correlates described by Beier et al. (1995) to attribute the following four behaviors to GPS data: 1) hunting (nocturnal fixes unassociated with a cache site), 2) cache site / feeding on a kill (≥ 6 nocturnal hrs in a given location), 3) travel (all crepuscular locations), and 4) resting (all diurnal locations).

Using the distribution of all putative cache sites extracted from the master data set, we delineated available cougar habitat within the study area. We created a fixed kernel 95% probability polygon around cache sites (Worton 1989, Rieth 2010) and subjectively selected an $h$-value of 1,500 m because it offered the best compromise between contouring animal use and minimizing the exclusion of outlying points. The $h$-value is the smoothing parameter, which for practical purposes represents the buffer width around the 95% probability polygon. Lastly, we buffered the layer by 100 m to account for GPS position errors. The resultant predictor variable “cougar habitat” was based on animal use patterns with fitness consequences (i.e. hunting and feeding), rather than on indirect predictors such as prey presence or preferred vegetation types, thereby minimizing the potential for confounding non-use with low habitat quality.

*Anthropogenic land-uses and the urban-wildland interface.*—We defined UWI broadly
to include any infrastructure or anthropogenic land use that disrupted surrounding native vegetation or terrain. Based on this definition we identified four general sub-categories of human land use, defined as: 1) “URBAN” (true urban in the form of residential, industrial, and commercial buildings and facilities indicating predictable human activity), 2) “MINE” (lands currently or historically used for open pit mining and associated tailings and leach heaps), 3) “AG” (all cultivated lands including farms, ranches, pasture, and unirrigated cropland), and 4) “DIST” (disturbed ground, including shooting ranges, junkyards, gravel pits, and water tanks). We used 5-m resolution color digital orthophoto quads collected August 2006 to digitize polygons around anthropogenic land-uses, and then buffered each polygon by 100 m to account for imagery error. We delineated the UWI geographically by calculating the intersection of the cougar habitat and land-use layers. We measured the proportion of the UWI comprised of the four sub-categories, which constituted the availability of these types within the cougar habitat layer, as defined by the distribution of cache sites.

*Prey habitat.*—Lacking a sample of marked animals our ability to predict ungulate presence was limited to the use of an index, which we compared against human variables. We focused on winter because ungulate migrations to low elevation ranges draw cougars closer to human activities. We assumed that the presence and abundance of deer during winter would be most predictable at low elevations with ephemeral snow cover. This assumption is based on extensive literature citing migration as a common strategy used by mule deer in mountainous terrain to cope with the food shortages and energetic demands associated with deep snow (Parker et al. 1984). Using a 30-m DEM and
Southwest ReGAP data (USGS 2004) we defined the DEER variable as southerly aspects (135°-270°) below 2,300 m comprised of mountain evergreen shrubs and piñon-juniper woodlands (Robinette et al. 1952).

**Distance measures and relative availability.**—We used the path distance function in ArcGIS combined with a 30-m DEM to index cougar response to selected predictor variables. This tool estimates the shortest distance between the edge of a polygon and the neighboring cell, while minimizing variation in elevation. The output was a set of grids in which each cell value represented a distance to the nearest variable of interest. We then overlaid cougar GPS locations on these grids and attributed cell values to each point. Predictor grids included URBAN, MINE, AG, DEER, and elevation. To estimate the background distribution of potential distances to each predictor variable we generated 2,000 random points from within the cougar habitat layer, with the stipulation that each point had to be > 100 m from any other. We attributed distance and elevation measures to each random point using the predictor grids. The distribution of distances represented the relative availability of these variables within the study area, which were then compared with animal use.

**Landscape-scale analyses**

*Cougar response to the UWI.*—At the scale of the study area we assessed the behavioral response of GPS monitored females and males to URBAN, MINE, AG, DIST, and DEER by measuring the distance between cache sites and each predictor variable. We define “response” as any statistically significant tendency indicating positive or negative selection of a given variable. These measures were then compared to their
relative availability.

**Patch-scale analyses**

*Cougar activity within the UWI.*—On the patch scale we assessed cougar use of the four human land-use types comprising the UWI from three perspectives. First, we plotted cache site distribution by land-use type (URBAN, MINE, AG, and DIST) based on their relative availability within the UWI. We examined patterns for males, non-maternal females, maternal females, and for the pooled sample. Secondly, based on the temporal signature of GPS locations we assessed differences in the proportion of time cougars spent engaged in hunting, feeding, traveling, and resting behaviors in UWI vs. wildland settings. We defined UWI points as those within 50 m of any human land-use anywhere within the Oquirrh Mountains, and wildland points as those ≥ 1,000 m from human land-uses. Third, we examined selection of land-use types for select behaviors by sex and reproductive status. In this case we evaluated the response of maternal females relative to males and non-maternal females. Those females for whom we had data during both reproductive phases, we compared their maternal selection to themselves when non-maternal.

*Analytical techniques.*—GPS data collected from mobile animals represents repeated measures on non-randomly selected individuals, and data are therefore auto-correlated. According to Manly (1992, p. 17), “an element of random selection of items must be maintained if valid statistical inferences are to be made.” Due to the unique characteristics of GPS-acquired data, we lacked a valid framework for statistical inference testing and refrained from conducting formal significance tests of differences
for the following reasons. First, our objective was to capture and collar every individual on the site, and on average we marked 83% of the estimated adult population (range = 57.1-100%). Our sample did not include animals we never detected or that were not susceptible to our capture methods, and therefore represented a non-probabilistic sample. Second, although not a true census of animal behavior, GPS data come close to providing a complete picture of a given individual’s activities (e.g. Knopf et al. 2010). That said, GPS instruments have their limitations, and are subject to acquisition bias resulting from terrain and animal posture. Because of these concerns we elected to present patch-scale results in descriptive form only. At the landscape-scale we evaluated cougar response to human variables based on a comparison of the frequency distributions of random points and animal use points using the Kolmogorov-Smirnov test. Landscape-scale comparisons were performed using SAS/STAT software in the SAS system for Windows (Version 9.2). We report all descriptive statistics as mean ± SD unless otherwise noted. The animals that contributed to the following analyses represent a subset of the population of interest, i.e. cougars in the northeastern Oquirrh Mountains. We have followed the recommendations of Schreuder et al. (2001) to clearly state the inferential limitations stemming from the sampling design.

**RESULTS**

Between 1997-2009 we marked 79 cougars during 146 capture events. Within this sample we conducted 36 GPS collar deployments on 24 animals (17 F, 7 M) from 2002-2009. Three of these individuals were censored because of early mortality (1 F) and
equipment failure (2 M), leaving 21 GPS instrumented cougars, representing 1,257 animal-weeks (1,043 F, 214 M), and 38,796 locations. Acquisition success varied from 19.7-86.1%, and averaged 56.5 ± 20.9% for resident females (n = 15), and 53.6 ± 15.7% for males (n = 5). From these data we identified 910 potential cache sites, of which 85% were field-truthed, resulting in the location of 449 kills. Sixty-one cache sites and 1,713 location points were identified within the UWI, and 2,226 points within 50 m of any human land use.

Circadian and seasonal movements

Cougars' elevational use varied both daily and seasonally. Within the day nocturnal positions averaged 65 m lower than diurnal positions (1,853 ± 94 m vs. 1,918 ± 102 m), and were consequently 118 m closer to human activities at night. This pattern did vary, most notably in that males tended to be closer to the UWI during the day than at night during summer, whereas females consistently displayed the opposite pattern during all seasons. Mean cougar elevational use was 205 m lower in winter than summer (1,885 ± 93 m vs. 2,090 ± 193 m), likely a result of snow-induced movements by their primary prey. This resulted in a mean lateral shift of 584 m (± 650 m) eastward and thereby closer to the UWI. For the pooled sample mean distance to the UWI was 1,717 ± 872 m during summer, decreasing to 1,191 ± 489 m in winter.

Landscape-scale: cougar response to urban, mining, agriculture, and deer

Cougar response to URBAN. During winter the distribution of cache sites within cougar habitat relative to urban differed from expected from habitat availability. Within
400 m of urban cougars used suitable habitat for caching prey items significantly less than its availability, whereas the opposite was true at distances > 400 m (Table 2-1). This pattern was driven by female selection, as males showed no statistical tendency to avoid this type \( (P = 0.84) \). In summer all cougars cached prey farther from urban than would be expected by chance, however this was largely a reflection of their preference for higher elevations during that season (Fig. 2-2).

**Cougar response to MINE.**—Mining activities were more widely distributed across the study area than the other two land-use types (mean elevation 1,734 ± 283 m). Female cache sites tended to be farther from mined lands during both winter \( (P < 0.005) \) and summer \( (P < 0.0001; \text{Table 2-1}) \). Males showed a non-significant \( (P = 0.15) \) tendency to cache prey closer to mined lands during summer, whereas winter caches were randomly distributed within 1,000 m of mining \( (P = 0.03; \text{Fig. 2-3}) \).

**Cougar response to AG.**—All cultivated lands on the study site were situated at relatively low elevations \( (\text{mean} = 1,632 \pm 32 \text{ m}) \), and so we limited our assessment to winter when cougars where most likely to encounter this land-use type. The distribution of cache sites relative to agriculture differed significantly \( (P < 0.001; \text{Table 2-1}) \), with both sexes demonstrating a subtle tendency to cache prey farther from agriculture when < 1,000 m, but closer to agriculture than available when beyond 1,000 m (Fig. 2-4).

**Cougar response to DEER.**—During winter cache sites were found significantly closer to low elevation southerly aspects than would be expected by chance alone \( (P < 0.001; \text{Table 2-1}) \). For both sexes, cache site distribution was significantly closer to deer winter range \( (< 500 \text{ m}) \) across all distance values (Fig. 2-5). During summer cougars used this
habitat type in proportion to availability.

**Patch-scale: cougar activity within the UWI**

*Demographic variation in cougar use of the UWI.*—Cougar use of anthropogenic landscapes was highly variable. Mined lands represented the largest land-use type within the UWI (44%), and all classes of cougars selected for it relative to other UWI land-use types. This pattern was strongest for maternal females and weakest for males (Fig. 2-6). Urban was the second most prevalent land-use type (28%), to which cougars exhibited a mixed response. Relative to availability, males selected for urban, females with kittens selected against it, and non-maternal females exhibited a neutral response. Agriculture represented 22% of the UWI and was consistently underused, with maternal females showing the weakest and non-maternal females the strongest, negative reaction to agriculture. Disturbed lands constituted 6% of the UWI and were used in proportion to availability among all demographic classes.

*Maternal female response to land-use type relative to other demographic classes.*—When all maternal females (n = 9) were compared against their non-maternal counterparts (5 M and a separate set of 5 F; Fig. 2-7A) the maternal group were notably more apt at procuring prey near agriculture and urban. Successful hunts, as indexed from feeding times, increased in all human land-use types, with urban, mined, and agriculture showing > 30% increases. Conversely, use of these types for resting decreased, with the largest declines in agriculture and disturbed areas, perhaps indicating that den and rendezvous sites were preferentially located in core wildland habitats. When we compared maternal females to themselves during periods without dependents (n = 6)
several patterns emerged, with the use of agriculture being noteworthy. Maternal females decreased their use of agriculture for hunting by > 40%, but increased their use of this type for feeding by almost 150% (Fig. 2-7B). The opposite pattern was true of mined lands. Maternal females increased their use of this type for hunting, but decreased time feeding there. Their use of urban and disturbed areas for hunting and feeding did not change appreciably from their non-maternal status.

Variation in cougar behavior in UWI vs. wildlands:—Within the UWI cougars spent the most time hunting (36%) and the least resting (12%), with feeding and traveling equally represented (25% and 27%, respectively). As a percentage of total time in a given environment, when in UWI settings cougars spent 66% more time feeding and 50% less time resting than they did when in wildland settings. When compared against their behavior in wildlands, cougars were traveling to and from the UWI during nocturnal hours for feeding opportunities (Fig. 2-8).

**DISCUSSION**

**Cougar response to anthropogenic landscapes**

On the landscape scale cougars selected against urban, mining, and agriculture relative to availability for killing and caching prey. This response varied by sex, with females showing consistently stronger avoidance of human land-uses than males, who used urban, mining, and agriculture (within 400 m) in proportion to availability. Cougars exhibited a threshold response to urban; habitat within 100 m was used far less than available for caching prey, but beyond this limit, use approximated availability. In contrast, the
strongest statistical patterns of cougar response were those to southerly aspects during winter with 80% of cache sites located within 250 m of these habitats. Reproductive state did not influence cougar response to human land uses; though within 1,000 m maternal females showed a consistent but non-significant tendency to be closer to urban, mining, and agriculture than non-maternal females. We found no evidence of resident animals habitually traveling through, or foraging in, urban settings. At this scale, our predictions that cougar space use would be better explained by variables related to prey than to human activities, and that males would exhibit a weaker negative response to human activities, were largely supported.

Although cougars selected against human landscapes at the landscape scale, none showed complete avoidance. Maternal females displayed a greater propensity to use mined and cultivated lands than males or non-maternal females, suggesting a balance between foraging constraints and perceived risks related to human activity. Despite the presence of prey in both land-use types, mining and associated reclamation activities most closely approximate the habitat features that cougars seek for hunting (Rieth 2010). Alternatively, mining activities are highly predictable, whereas human activity associated with urban and agriculture are highly variable and so cougar preference for mined lands may be as much a case of habituation as it is to habitat characteristics. The mixed response to urban may reflect the greater tolerance of males to hunt around noise or human activity, as urban was located primarily on low elevation deer winter ranges. When compared to their behavior in wildlands, cougars spent proportionately more time feeding, and less time resting within the UWI, suggesting a response to less cover and/or
higher human activity during daylight hours. Nevertheless, nocturnal forays into the UWI indicated that cougars were willing to exploit resources in that environment. On the patch scale cougar response to and behavior in, the UWI is best characterized as a habitat used sparingly during nocturnal hours in search of food.

When we examined maternal female response to human land-uses relative to males and non-maternal females, females with dependent kittens spent less time hunting in agricultural and urban lands, but more time feeding in these types. However, when compared to themselves without kittens, maternal females increased their hunting time in mined lands while decreasing their feeding time there. This pattern suggests either lower hunting success in mined lands, or use of an alternative small prey species that did not require extensive handling or feeding times, such as marmots (*Marmota flaviventris*). The opposite pattern associated with cultivated and urban land-uses suggests that either female cougars had higher hunting success there, or they exploited other foraging opportunities that did not require extensive search times. Seasonal ungulate use of agricultural lands is common in the Intermountain West (Thomas and Irby 1991), and in our study area most agricultural lands were bounded by paved roads connecting outlying suburbs to Salt Lake City. In winter commuter traffic is heaviest during crepuscular hours when deer are active. Some deer live near cultivated lands year-round, and 5 of 6 mortalities documented during a pilot deer study in the area were caused by vehicle collisions (Wolfe et al. unpublished). The effect of this coincidence is the predictable production of carrion in certain localities (Kassar and Bissonette 2005). Notably, we found 10 cache sites within 200 m of a highway or railroad.
Do maternal cougars exhibit a habitat trade-off?

As obligate carnivores and opportunistic scavengers (Bauer et al. 2005), cougars have probably evolved a sensitivity to the relative risks associated with various foraging strategies, and maternal females are the demographic class most likely to make trade-offs in habitat selection based on these risks. Two prominent causes of mortality in this population were injury resulting from struggles with ungulate prey and collision with vehicles, both comprising 23% of non-human and human causes, respectively. These factors have been reported in other cougar populations (Beier et al. 2010), and of the two, highway mortality represents an evolutionarily novel selection force. Five females died within the UWI; two of malnutrition and three by vehicle strikes. These animals ranged in age from 9-13 years old and ≥ 2 of them had dependent offspring at the time of death. Cougars canine teeth can diminish at a rate of 0.62 mm/yr from breakage and/or wear (Stoner and Wolfe, unpublished data), and roadside carcasses often have torn hides and extensive soft tissue damage, making them easier to locate and consume. Notably, road mortalities occurred in two distinct locations, each with an underpass. Based on tracking and telemetry data all three individuals had a history of using these underpasses (Wolfe and Stoner, unpublished data), both of which offered more cover than at-grade crossings. Moreover, both sites have been identified as “roadkill hotspots,” producing ≥ 6.1-17 carcasses / yr (Kassar and Bissonette 2005). This underscores the possibility that rather than simply crossing them, these animals were foraging along the roads themselves. The combination of increased energetic demands associated with maternity and extensive dental wear may have motivated these individuals to seek low-risk, manageable prey
items most readily available in the form of carrion. Older, maternal females may be exploiting easily accessible roadkill, while neglecting the risks associated with scavenging prey items from roadways, a strategy that proved to be much higher risk than these animals have yet evolved to adequately assess.

Female energetic demands vary with reproductive status, and many polygynous mammals (e.g. Bleich et al. 1997), including some carnivores (Bunnefeld et al. 2006, Rode et al. 2006) demonstrate a trade-off in habitat quality based on food abundance and predation risk. For example, Bunnefeld et al. (2006) studied the movements of Eurasian lynx (*Lynx lynx*) in Norway, and reported that anthropogenic landscapes were positively correlated with both lynx mortality and prey abundance. Lynx responded to these patterns individually, with maternal females selecting less productive habitats when their kittens were young, but shifting hunting activity closer to roads, farms, and towns as kitten energetic demands increased. Our data show a slightly different pattern; one in which maternal females exceeded other demographic classes in their use of all land-use types within the UWI for feeding, especially agricultural lands. Cougar kittens are weaned by 2-3 months, but do not disperse until ~ 12-18 months (Logan and Sweanor 2001), and studies examining cougar predation have consistently demonstrated that females with dependent young have higher kill rates than other demographic classes (e.g. Knopf et al. 2010). By using the UWI maternal cougars may have been capitalizing on scavenging opportunities or local variation in the vulnerability of resident mule deer (e.g. Farnsworth et al. 2005, Krumm et al. 2010). Maternal cougars on our site did not make habitat trade-offs in association with the threat of human-caused mortality and food acquisition; they
exhibited exactly the opposite pattern, in which even marginal, risky habitats heavily impacted by human activity were exploited in order to meet the increasing caloric needs of their offspring prior to dispersal. Thus, a trade-off between food acquisition and security for an obligate carnivore may only be apparent when juveniles are quite young. Alternatively, cougars may not be as fearful of abstract human activities as they are of the threat of intraspecific strife. If avoidance of other cougars is of primary importance, then the behavior of these animals can be interpreted as a habitat selection trade-off, as maternal females tended to exploit food resources where they were less likely to encounter other cougars.

**Are near-urban cougar populations de facto sinks?**

Human impacted landscapes have been identified as population sinks for some carnivores as a result of conflicts stemming from food attractants in the form of livestock or garbage (e.g. Mace and Waller 1998, Woodroffe and Ginsburg 1998). Our results offer a mixed view of this argument. Of the cache sites we located within the UWI, the proportion of non-ungulate prey, e.g. skunks, coyotes, feral house cats, raccoons, and wild turkeys, was twice that found in wildland habitats. To the extent that these species act as an attractant, cougars did exploit foraging opportunities on the margins of the human landscape. However, although humans accounted for one-third of documented mortalities, animals that died within the UWI were not a random subset of the population. The distribution of human-caused mortality was bi-modal, with young, transient males on one end, and old females on the other. All animals killed in control actions were subadult, dispersing males (n = 3); of which one was handicapped, one orphaned, and the other
malnourished. Females died almost exclusively of natural causes and most of those killed by humans (primarily roadkill) were ≥ 10 yrs old. Females between 3-8 yrs, the reproductive segment of the population exhibited high survival. All cougars killed by humans on the UWI in our sample were inefficient hunters, best exemplified by the very young and the very old. Despite the proximity of this population to one million people, most human caused mortalities were compensatory in nature. Therefore, this population did not fit the profile of an attractive sink (Delibes et al. 2001) or one unduly influenced by edge effects (Woodroffe and Ginsburg 1998, Woodroffe 2000), rather it better approximated the “stability phase” articulated by Linnell et al. (2000), in which regulatory mechanisms, in this case the exclusion of hunting or livestock depredation control within the study area, allowed this population to persist in the face of high human densities.

**Are cougars wildland obligates?**

On our study area cougars were primarily associated with wildland habitats but were able to acclimate to predictable human disturbances (Rieth 2010). We found no evidence of home range abandonment, nor did cougars completely avoid areas of human activity. Based on tracking evidence, cougars used a variety of human correlates, such as water developments and vacant buildings; they used culverts and mineshafts as den, rest, and cache sites, and hunted native prey near urban and agricultural areas. Despite this, domestic animals (free-ranging livestock) represented only 2% of >440 recovered kills, and no attacks on humans occurred. Response to humans was individualistic. For example, one female’s home range completely encircled the mine and included remnant
patches of habitat isolated by mine tailings, yet this individual showed the strongest avoidance of human activity within her home range (Stoner and Wolfe, unpublished data). Moreover, the cougars’ ability to acclimate to human activities, combined with the lack of an explicit analysis of deer numerical and behavioral response to these same factors, makes cougar presence in a given locality or response to land-use changes difficult to predict with any degree of precision. Thus, our work does not support the hypothesis that cougars avoid anthropogenic disturbances. That said, given their landscape-scale aversion to human activities, neither do they neatly fit the profile of a synanthropic species (e.g. Beckmann and Berger 2003, Gehrt and Riley 2010). Anthropogenic landscapes offered cougars a nuanced mix of attractants and deterrents, with their population-level response most accurately characterized as one of ambivalence. Based on our work in this system and under these conditions, cougars are best described as a disturbance-adapted species, that may preferentially persist in, but do not require, pristine or remote habitats. As noted elsewhere (Beier et al. 2010), regardless of proximity to urban areas, cougars essentially require only three ecological prerequisites: 1) the presence of vulnerable ungulate prey, 2) sufficient vegetative or topographic complexity to acquire said prey, and 3) conditions in which human-caused mortality is not additive to background sources.

Given the history of conflict between predators and agrarian societies, the ability of a large, potentially dangerous carnivore to persist on the periphery of a major American city is perplexing, and begs the question of what behavioral adaptations cougars possess that allow this (Cardillo et al. 2004). Simply put, it appears to be a combination of: 1)
seasonal and circadian activity patterns inversely correlated with those of humans, combined with a propensity to use heavy cover during daylight hours; 2) non-gregarious social behavior, 3) a malleable reproductive cycle, and 4) broad habitat requirements. Their wide latitudinal distribution and ability to exploit novel food resources (Turner et al. 1992), are evidence of the cougar’s ability to acclimate to heavily disturbed, post-industrial landscapes such as the one described here. Moreover, the strong attraction of cougars to high quality habitats defined by low survival caused by human exploitation (i.e. “attractive sinks”; Robinson et al. 2008, Chapter 3), makes it difficult for us to imagine the scenario hypothesized by Ripple and Beschta (2006) in which the predictable presence of humans, unaccompanied by dogs or lethal consequences, has the capacity to suppress densities or cause abandonment of areas that by every measure exemplify ideal cougar habitat. Indeed, our data suggest just the opposite; that individuals with physical maladies or during certain life stages may exploit foraging opportunities correlated with human activity.

Conservation and management

The lack of inferential statistics, unique configuration of human land-uses, and amount of private land on our study area make inference to other near-urban cougar populations questionable. That said, trends in urban growth, climate, and spatial variation in sport harvest suggest three aspects of our study that may be generalizable. First, based on patterns in land ownership and urban growth, the buffer between human land-uses and wildlife habitat will narrow, especially in western cities bounded by public lands. AS part of this trend the U.S. Forest Service uses forest thinning to reduce fuel buildup within a
2.4 km buffer of the UWI. In some pant communities this can attract ungulate prey. In conjunction with state restrictions on hunting and the discharge of firearms near areas of human habitation, much of the UWI may act as de facto refugia for cougars. Second, climate predictions for the Southwest indicate a drying trend associated with increased variability in precipitation (Seager et al. 2007), and consequently, heavy winters will continue to shape animal movements in the region. Third, in systems where hunting is either prohibited or constrained by land ownership patterns, such as the western Wasatch Mountains, cougars may reach advanced ages not seen in hunted populations. These conditions are not unique to our study area. Therefore, heavy, prolonged winters may result in high ungulate winter mortality and delayed upslope migrations; under these conditions the regular production of carrion on commuter highways has the potential to make the UWI attractive to cougars. This may precipitate increased cougar-human interactions and property damage. By retaining agricultural buffers around residential areas, proactive land-use planning and public education efforts targeting residents in high-risk areas might ameliorate some of these problems. For conservation, cougars appear capable of persisting in areas lacking wildland qualities, under the basic proviso that adequate protections can retain high female survival rates. Multiple use lands will be important for the conservation of both connectivity and source populations.

**Literature Cited**


Orlando, A. M. 2008. Impacts of rural development on puma ecology in California’s Sierra Nevada. Dissertation, University of California, Davis, USA.


USGS National Gap Analysis Program. 2004. Provisional digital land cover map for the southwestern United States. V. 1.0. RS/GIS Laboratory, College of Natural Resources, Utah State University.


TABLE 2-1. Results of the Kolmogorov-Smirnov test for differences in the distribution of cougar cache sites by sex and season, relative to four landscape factors of interest. We compared the distribution of the data against 2,000 randomly selected points within the habitat layer.

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</table>
Fig. 2-1. Oquirrh Mountains, Utah. The site was selected because of its proximity to the Wasatch Front metro area and lack of public access. The study was initiated in 1997, and GPS technology was introduced in 2002. Hatched area represents the Urban-Wildland Interface; comprised of four major land-use types, including urban, mining, agriculture, and disturbed areas.
Fig. 2-2. Cumulative frequency distributions of cougar cache sites (broken lines = use) relative to the distance from urban landscapes (solid line = availability). Here “urban” is defined as all residential, industrial, and commercial buildings. Use distributions below the random line indicate aversion, whereas those above it indicate selection for the factor of interest at that distance (see Table 2-2 for statistics).
Fig. 2-3. Cumulative frequency distributions of cougar cache sites (broken lines = use) relative to the distance from mined lands, year-round (solid line = availability). Use distributions below the random line indicate aversion, whereas those above it indicate selection for the factor of interest at that distance (see Table 2-2 for statistics).
Fig. 2-4. Cumulative frequency distributions of cougar cache sites (broken lines = use) relative to the distance from agricultural lands in winter (solid line = availability). Use distributions below the random line indicate aversion, whereas those above it indicate selection for the factor of interest at that distance (see Table 2-2 for statistics). “Agriculture” is defined here as all cultivated lands within the cougar habitat layer, including dry farming.
Fig. 2-5. Cumulative frequency distributions of cougar cache sites (broken lines = use) relative to the distance from southerly aspects (solid line = availability) for cougars during winter. Use distributions below the random line indicate aversion, whereas those above it indicate selection for the factor of interest at that distance (see Table 2-2 for statistics). Southerly aspects (135° SE to 270° W) hold less snow, support common browse plants, and are used here as an index of deer presence during winter.
Fig. 2-6. Demographic variation in cougar use of the UWI. Distribution of cougar cache sites (n = 61) by demographic class in relation to availability within anthropogenic landscapes. Analysis was based on a sample of 16 individual cougars (n = 12 F, 4 M), of which 7 were monitored solely during a reproductive phase (n = 21 cache sites) and 9 were monitored during both maternal and non-maternal states (n = 28 cache sites). The remaining 11 cache sites were from adult males. Urban and mining land-uses showed the highest and most consistent levels of human activity, whereas agriculture and disturbed landscapes showed highly variable amounts of human activity. See text for land-use definitions.
Fig. 2-7. Response of maternal females to land-use types within the UWI relative to other demographic classes. Use of UWI for 9 maternal females in relation to males (n = 5) and non-maternal females (n = 3; panel A). Use of UWI for 6 maternal females relative to their own use during non-maternal periods (panel B). Y-axis represents proportional change from other classes.
Fig. 2-8. A comparison of the proportion of time cougars spent engaged in four basic behaviors, between UWI and wildland habitats. Because of the disparity in the size of the data sets, we subsampled wildland data (n = 2,226) to approximately match the composition of the UWI data (n = 2,405), representing a mean of 106 points / animal. UWI points were those within 50 m of any type of human land-use for the total dataset.
CHAPTER 3

DISPERsal BEHAVIOR OF A POLYGYNous CARNIVORE: DO COUGARS FOLLOW SOURCE-SINK PREDICTIONS?

Abstract. The source-sink model of population dynamics predicts that competition in the natal deme drives emigration of subordinate animals to habitats offering lower competition for space and breeding opportunities. Cougars (*Puma concolor*) are top carnivores for which precise enumeration is untenable. Consequently, the source-sink model has been advanced as a potential framework for their conservation. Dispersal is a critical behavior for management based on this model, yet there is a dearth of knowledge on the landscape and social conditions that motivate cougar dispersal and settlement. We evaluated three predictions with respect to cougar dispersal behavior on two sites in Utah using radio-telemetry techniques: 1) maternal reproductive status prompts dispersal, 2) movement of dispersing animals is shaped by habitat configuration and permeability, and 3) dispersers preferentially settle in areas of high habitat quality and/or low conspecific density. Sites differed with respect to management status, the level of natural fragmentation, and distance to urban areas. We documented natal dispersal of 48 cougars and measured basic movement parameters including, sex and site-specific frequency, distance, seasonality, direction, and the habitat quality and mortality rates in areas where immigrants settled. Although males and females exhibited pronounced differences in dispersal frequency, we found few differences in distance traveled, season of departure, and direction moved. Dispersal distances tended to be longer in contiguous than
fragmented habitats. Seasonality was closely tied to the maternal estrus pulse. Natural and anthropogenic obstacles modified landscape permeability and therefore cougar movements. Relative to males, females dispersed into lower quality habitats with higher mean annual mortality rates. Cougars in this Great Basin ecosystem largely conformed to source-sink predictions. Female settlement was predicated on avoiding conspecifics, while male settlement suggested habitat selection based on mating opportunities. These findings have implications for population expansion and recolonization of habitats where female presence and Allee effects are limiting factors. Results can be used to parameterize source-sink models based on animal behavior and landscape permeability to conserve exploited cougar populations.

**INTRODUCTION**

Dispersal is the movement of an individual from its natal range to its adult range, and comprises three overlapping phases: emigration, transiency, and immigration (Ronce 2007). A number of factors have been proposed to explain the ultimate causes of mammalian dispersal patterns, including competition with close relatives and inbreeding avoidance (Bowler and Benton 2005). Natal population density, social stability, and parent-offspring relations, are also important proximate factors promoting dispersal, yet even under similar social and environmental conditions, not all individuals are equally likely to disperse (Cote et al. 2010). Among polygynous mammals male dispersal is near-obligatory, but female patterns are nuanced, showing a mixed strategy of dispersal and philopatry (Johnson 1986). Theory predicts that competition in the natal deme should
promote dispersal among young, subordinate animals to habitats that offer an optimal balance between intraspecific competition and resource availability (Fretwell 1972). By dispersing, these individuals should achieve higher fitness than they would as floaters in the natal deme. Indeed, this is the mechanism underlying the source-sink model of population dynamics as articulated by Pulliam (1988). Pulliam’s model assumes an Ideal Free Distribution (IFD, sensu Fretwell 1972), in which conspecific density is negatively correlated with habitat suitability (i.e. increasing density reduces quality), and thus, dispersers should settle in the closest suitable habitat. It also assumes that variation in vital rates is a product of disparities in habitat quality. Delibes et al. (2001) modified this model to account for anthropogenic influences on vital rates, unrelated to habitat quality. They argued that attractive sinks can be created when the most productive habitats are characterized by high rates of human-caused mortality.

Regulated exploitation can result in demographic changes to some carnivore populations (Stoner et al. 2006, Milner et al. 2007), yet the difficulty in accurately assessing population abundance, trends, and recruitment on biologically meaningful scales impedes precise management (Choate et al. 2006). To work around these constraints several investigators have proposed a behavioral solution for conserving exploited carnivores (Logan and Sweanor 2001, Laundré and Clark 2003, Novaro et al. 2005, Nielson et al. 2006, Balme et al. 2010). This approach is predicated on a source-sink population structure, in which harvest pressure is applied in a spatially variable manner so that subadults or socially subordinate animals from protected source populations disperse to harvest-induced sinks (Delibes et al. 2001, Robinson et al. 2008).
Source-sink models propose density-dependent dispersal as the behavioral mechanism facilitating connectivity and persistence in populations defined by high mortality and/or low fecundity (Pulliam 1988). The source-sink model predicts that: 1) lack of breeding opportunities prompt subadult emigration from the natal deme, and 2) dispersers generally settle in habitats with relatively low population densities. The second prediction implies that dispersers assess levels of resource abundance in different habitats and select the one in which fitness will be maximized, as indexed by intraspecific density. Although a promising alternative to costly annual population estimates, with few exceptions (Novaro et al. 2005), little effort has been made to determine whether polygynous carnivores conform behaviorally to the predictions of the source-sink model. Prior to the application of such a model several important questions need to be addressed, including; how males and females vary in their dispersal behavior; what landscape features facilitate or impede movement of dispersing animals; and what habitat and social conditions prompt immigration? Given that dispersal is a critical behavior for persistence of demes within a metapopulation context (Brown and Kodric-Brown 1977), effective conservation depends on a better understanding of the relationships between landscape permeability and animal behavior.

Cougars (*Puma concolor*) are one of the last widely distributed ungulate predators in many North American ecosystems. As an obligate carnivore they occur at low densities and exhibit variable dispersal strategies that are difficult to generalize, except that they seem to be influenced by landscape context and social dynamics (Maehr et al. 2002, Thompson and Jenks 2010). Little research has been conducted on cougar dispersal
directly, but of those studies, most were based on populations constrained by human activities or surrounded by unsuitable habitat. For example, Sweanor et al. (2000) studied cougar dispersal in southern New Mexico and described a source-sink type population resulting from the basin and range structure of the habitat. These authors noted that all males dispersed, but less than half of females, suggesting that female dispersal was at least partially density-dependent. Beier (1995) followed several subadult cougars attempting to disperse from a small habitat patch surrounded by urbanization in southern California. He argued that housing and transportation infrastructure were effectively isolating that sub-population, and in the absence of corridors was vulnerable to stochastic extinction. In another example from a near-urban population, Maehr et al. (2002) found that natural and anthropogenic landscape features combined with natal population density were the best predictors of dispersal movements in Florida panthers and argued that conspecific attraction and breeding opportunities seemed to motivate male settlement. Thompson and Jenks (2010) noted extraordinary dispersal movements stemming from the isolated location of their study population on the northern Great Plains. Each of these studies described the behavior of individual dispersers and their respective natal populations, but provided little information on habitat and social conditions in patches where dispersers settled. Because an individuals’ decision or ability to establish residency in an adult home range is predicated on both intrinsic (individual behavior) and extrinsic (social and environmental characteristics) factors, it is important to examine this behavior from both the social and landscape perspective.
Source-sink population dynamics are a probable outcome of heterogeneous patterns in habitat quality and mortality. Under these conditions it is important to ascertain whether a given subpopulation is acting as a source or a sink. Of equal importance is to determine from where a sink is likely to receive its immigrants; and conversely, where emigrants from a source population are likely to settle. Our primary question was whether cougars conform to the basic predictions of the source-sink model in a basin and range landscape.

We evaluated three predictions with respect to cougar dispersal behavior: 1) natal population density and maternal reproductive status prompt dispersal (density-dependent hypothesis), 2) dispersal patterns are non-random, being shaped by habitat fragmentation and connectivity (landscape permeability hypothesis), and 3) dispersers settle in areas of high habitat quality and/or low conspecific density (attractive sink hypothesis).

**METHODS**

**Study sites**

*Oquirrh Mountains: protected population, fragmented habitat, near-urban location.*—The Oquirrh-Traveler Mountains form a boot-shaped complex (hereafter the Oquirrh) in north-central Utah on the eastern edge of the Great Basin (40.5° N, 112.2° W; Fig. 3-1). The ecoregion is defined by naturally fragmented, basin and range topography, in which mountains form islands of high productivity relative to the surrounding desert basins. The Oquirrhs measure > 950 km², but we focused fieldwork on 500 km² encompassing the northeastern slope on properties owned and managed by the Utah Army National Guard (Camp Williams) and the Kennecott Utah Copper
Corporation. The site is bounded on the north by the Great Salt Lake and on the east by
the Salt Lake Valley. Approximately 55% of the range is under the jurisdiction of the
Bureau of Land Management (BLM), with the remainder privately held by individuals,
grazing associations, and mining companies. We selected this site because of the high
road densities, which facilitated fieldwork, combined with the lack of public access and
associated hunting pressure.

Elevations ranged from 1,292 m to 3,200 m, and were correlated with variation in
moisture, vegetation, and animal diversity. Annual precipitation ranged from 30-40 cm in
the Salt Lake and Tooele valleys to 100-130 cm on the highest ridges and peaks. Of this,
approximately 60% occurred as snow between December-April with the remainder
derived primarily from summer thunderstorms. Mean monthly temperatures ranged from
– 2.4°C in January to 22.2°C in July (Banner et al. 2009). This regimen supported a
variety of plant communities, with Gambel oak (*Quercus gambelii*), sagebrush (*Artemisia
tridentata*), and Utah juniper (*Juniperus osteosperma*) dominant on foothill sites, and
canyon maple (*Acer grandidentatum*) at mid-elevations. Mountain mahogany
(*Cercocarpus spp.*.) was common on ridges and well-drained soils. North facing slopes
above 2,200 m supported localized montane communities of aspen (*Populus tremuloides*)
and Douglas fir (*Pseudotsuga menziesii*). The ungulate prey base associated with these
plant communities was comprised primarily of mule deer (*Odocoileus hemionus*) and to a
lesser extent elk (*Cervus elaphus*). Free-ranging livestock, including cattle (*Bos taurus*),
sheep (*Ovis aries*), goats (*Capra hircus*), and horses (*Equus caballus*) were available
from May-December. Potential competitors included coyotes (*Canis latrans*) and bobcats
(Lynx rufus). Deer and elk were lightly hunted on the Kennecott portion of the site. The study area was situated within the Oquirrh-Stansbury Wildlife Management Unit, but both properties were closed to the public and cougar hunting was prohibited. Although radio-instrumented cougars leaving those properties were legally protected within the management unit, they were susceptible to poaching, damage control actions, trapping, and roadkill. In this sense the population was “quasi-protected.”

Monroe Mountain: exploited population, contiguous habitat, rural location.—The study site comprises part of the Sevier Plateau in the Southern Mountains ecoregion of south-central Utah (38.5º N, 112º W; Fig. 3-1). The site is a high volcanic plateau extending 75 km in along a north-south axis, and lies within a geologic transition from basin and range topography to the Colorado Plateau. The site is contiguous with other montane and subalpine habitats within the ecoregion. Hydrologically Monroe is part of the Great Basin, but climatically and biogeographically it is more closely associated with other massifs of the Colorado Plateau and southern Rocky Mountains. The study site measured ~1,300 km², and formed the central unit of the Fishlake National Forest, southeast of Richfield. Other landholders included the BLM, the State, and various private interests.

Elevations ranged from 1,600 m to 3,400 m with annual precipitation averaging 15-20 cm at lower elevations, increasing to 60-120 cm on the plateaus above 2,700 m. Precipitation was bimodally distributed with most falling as snow from January-February, followed by a late summer monsoon (Banner et al. 2009). Snowpack typically persisted until mid-June at elevations >3,000 m. Although vegetation was similar to the
reference site, there were notable differences in the proportions of each community, with the largest area (44%) dominated by piñon-juniper woodlands (*Pinus edulis*). Mixed conifer (*Abies concolor, Picea englemanii*) and aspen stands occurred across broad areas at higher elevations, with Gambel oak, mountain shrub patches, and mixed sagebrush-grassland meadows interspersed throughout. These plant communities supported a prey base of mule deer and elk. Other ungulates such as moose (*Alces alces*) and pronghorn antelope (*Antilocapra americana*) were occasionally observed on the site, but did not constitute important prey species. The study site falls within the Utah Division of Wildlife Resources’ (UDWR) Monroe Mountain Wildlife Management Unit, where deer, elk, and cougars were managed for sustainable hunting opportunities. From 1996 to 2009 the percentage of the estimated cougar population that was legally harvestable averaged 47 ± 35%. Other carnivores present included bobcats and coyotes which were both subject to trapping pressure. Resource use included livestock grazing (cattle, sheep), logging, fossil fuel exploration, and off highway vehicle recreation. Human densities around the site varied from 73 to 382 / 100 km², with most of the population distributed among small agricultural communities in the Sevier Valley on the northwestern boundary of the study site.

*Study design.*—This effort was part of a long-term monitoring project examining cougar population dynamics on two sites subjected to differing management objectives. We compared a protected cougar population to one with a history (>30 years) of annual, regulated harvests. The sites were also distinctive in terms of landscape context (naturally fragmented vs. contiguous) and human disturbance (near-urban vs. rural).
Capture, marking, and dispersal movements.—From January 1996 to April 2010 we conducted intensive capture efforts during winter (December to April). We used hounds to trail cougars of all age classes into trees, culverts, cliffs, or mineshafts. Pursuit and immobilization techniques are detailed in Stoner et al. (2006). We aged cougars using the tooth-wear criteria of Ashman et al. (1983); we used additional criteria for kittens by comparing body mass measures with those reported in Anderson (1983). Regardless of age, all animals captured were tattooed and all adults (>2.5 yrs) and subadults (1.0-2.5 yrs) were equipped with VHF radio-collars (Advanced Telemetry Solutions, Isanti, MN). Kittens were marked with an ear transmitter (ATS), ear tag, or a drop-off radio-collar. We considered subadults either yearling kittens still accompanying their mother, or transients initiating or in dispersal. We assumed subadults were resident progeny if the animals’ capture location and approximate age matched those of a resident female in the area detected during the prior winter with dependent offspring. Transient status was attributed to animals that were either >3 yrs upon capture, or tracking evidence indicated they had originated outside the study area boundaries. We radio tracked cougars using aerial and ground-based telemetry techniques at approximately monthly intervals. Although methods for detecting dispersal may be subject to some sampling bias they are comparable to other investigations on the topic. Animal handling procedures were conducted in accordance with Utah State University Institutional Animal Care and Use Committee standards (approval no. 937-R).

For the purposes of this study we defined dispersal as offspring independence from the mother and permanent departure from the natal home range. We defined philopatry as
offspring independence combined with a dispersal distance that resulted in continued use of some portion of the natal home range. We documented dispersal in two ways. First, as collared animals left their natal range we attempted to follow them by air until they established adult home ranges. Second, we monitored the annual harvest (November-June) for any marked animals. For collared individuals that we could not find on the study area we searched neighboring mountain ranges at semi-annual intervals. We analyzed all geographic data in ArcGIS v. 9.2 (ESRI, Redlands, California) using Universal Transverse Mercator (UTM) projection in datum NAD 83. All statistical analyses were conducted using SAS or Program R (for circular statistics). For proportional response variables we calculated the SE using procedures for generalized linear mixed models (PROC GLIMMIX). We provide p-values associated with all statistical analyses, but have avoided explicit definition of a significance level threshold (Hurlbert and Lombardi 2009).

Measurement and analysis of dispersal parameters

Frequency.—We compared dispersal frequency between sites using two datasets; one consisting solely of individuals < 12 months (“kittens”), and a larger dataset in which we grouped kittens of known origin with all subadults (“kittens and subadults”). The latter dataset introduced more uncertainty into the analysis because some subadults were transient upon capture. We defined dispersal frequency as the proportion of females of known fate that moved beyond their natal range. We compared proportions using a χ² test of homogeneity of proportions; significance was determined using an exact test based on Pearson’s χ² statistic.
Season.—Dispersal date was estimated using the mid-point of a range (date ± no. days), half way between the last telemetry location in the natal range and the first survey in which the individual was either not located, or located outside the natal range. For example, if a radio-collared animal was last located in the natal range on June 1, and the next survey flight occurred on July 16, then the estimated dispersal date was calculated as June 24 ± 23 days. In two instances (M15a, M15b) kittens were orphaned and so we used the date of the mother’s death as the dispersal date. Some dispersals were documented when kittens handled only one time were tattooed and subsequently recaptured in the harvest. In these cases we used the estimated the age of the kitten at the time of capture, and projected the season during which the individual would be 15 ± 3 months of age (the mean dispersal age for cougars in western North America; Anderson et al. 1992).

We identified three major seasons with ecological and evolutionary significance. Seasons corresponded to major events in cougar life history namely, maternal estrus, prey abundance, and mortality, all of which are reasonably predictable. Despite a broad mating season cougars are considered seasonally polyestrous. Young are born during every month of the year, but in western North America cougars display a pronounced birth mode from June-October (Laundré and Hernández 2007). Based on a 92-day gestation (Logan and Sweanor 2001), peak mating season occurs from March-June. Mule deer and elk show a tight birthing schedule in which most young are born between late-May and mid July (Robinette et al. 1977), with cougars exploiting this resource pulse well into autumn (Knopff et al. 2010). Sport hunting is the single largest mortality factor affecting cougar populations in the West (Logan and Sweanor 2001). In Utah the season spans
mid-November to early June, but approximately 90% of the kill takes place between November and February when persistent snow cover facilitates tracking with hounds. Therefore, we defined the dispersal seasons as estrus = March-June; prey abundance = July-October; and mortality = November-February. March, June, and November constituted periods of seasonal overlap, and so for animals dispersing during these months we split the datum between respective seasons. We made three comparisons using χ² tests of homogeneity of proportions and t-tests: 1) the distribution of dispersal season between sites (sexes pooled); 2) differences among seasons within sites, and 3) among seasons (sites pooled). When we pooled sites we compared dispersal proportions among seasons using generalized linear models with a multinomial distribution.

Distance.—Distance measures were based primarily on the locations of capture and mortality. The dispersal initiation point was either the capture site, the home range center (HRC) if the juvenile was instrumented, or the HRC of the mother, if collared. Both the natal and adult HRC were based on a mean UTM from telemetry data. In the absence of requisite telemetry data we used the actual (retrieval of a carcass) or estimated (hunter harvest report) mortality site to calculate the end point of the dispersal. Hunter-harvest reports were accurate to the drainage within a mountain range. Cougars do not typically make straight-line movements between their natal and adult home ranges, but in order to improve precision within our dataset and make comparisons with those in the literature we restricted our analysis to Euclidean measures. We compared dispersal distance between males and females by site, and for sites pooled using ANOVA in a two-way factorial (site, sex) in a completely randomized design.
**Direction.**—We report direction as the compass bearing connecting the natal HRC to the adult HRC. In two cases we had data on intermediate movements (M42, F31) and so used only the measure representing the first leg (departing the natal range). Previous research indicates that in remote areas cougars disperse in random directions (Sweanor et al. 2000), but directionally in constrained or urbanized environments (Maehr et al. 2002). To test this hypothesis we used Rayleigh’s $z$-test of uniformity (a goodness-of-fit test) to determine whether mean directions differed from a random distribution (Zar 1999); lastly we compared directional means between sites using one-way circular ANOVA (a circular analogue to a two-sample t-test).

**Habitat quality.**—Habitat quality for cougars is largely predicated on ungulate density (Rieth 2010), which tends to be associated with primary productivity. We developed a cougar habitat quality index by correlating estimates of deer and elk abundance (UDWR, unpublished data) collected at the scale of the management unit (mean area = 1,550 km² ± 1,170 km²), with 250-m grids of the Normalized Difference Vegetation Index, or NDVI (Spearman’s correlation coefficient, $r = 0.77$, $N = 52$, $P < 0.001$). NDVI is a satellite-derived index of photosynthetic activity that correlates strongly with primary productivity. NDVI grids were composite means based on measures from 7 seasons (2000-2006). We used NDVI measures for June to represent summer range (peak growing season) and April for winter range, when low elevation ranges are snow free and emergent spring grasses attract ungulates.

To sample NDVI grids and calculate mean values, we used circular approximations of home ranges by buffering our natal and adult home range point estimates. For natal and
adult home ranges of either sex, we used the mean home range areas for adult females from the Oquirrh site (Rieth 2010; mean = 69 km²; radius = 4.7 km). Circular home range estimators are gross approximations and tend to produce negatively biased estimates of home range quality. Therefore we used the smallest estimates for three reasons: 1) to minimize inclusion of unused area that would have been encompassed by larger circles (e.g. desert basins); 2) to better characterize habitat quality of the home range core, and 3) to maintain a consistent sampling frame among individuals.

To evaluate home range quality we subtracted mean NDVI values of the natal range from the adult home range. Negative values indicated a decline, positive an improvement, and those around zero indicated no difference between natal and adult home range habitats. We used a one-way ANOVA in a completely randomized design to make three comparisons: between study sites (sexes pooled); between sexes (sites pooled), and within group comparisons to determine if mean values differed from zero (i.e. post-dispersal habitat was not different from pre-dispersal). Within that ANOVA we used t-tests for within group comparisons.

*Mortality rates.*—Because we did not have population estimates in the watersheds where dispersing cougars settled, we used annual harvest data as an index of population status. We used 1:24,000 scale 12-digit hydrologic unit codes (HUC; NRCS 2007) as the sampling frame for calculating mortality rates in adult home ranges. Twelve-digit HUCs represented the best approximation of cougar home ranges in the absence of requisite telemetry data (mean area = 48 km² ± 30 km²; N = 1,932). Harvest data were compiled from 1996-2007 and included the sex-age class and approximate location of the mortality
We measured the response variable as the number of cougars killed / yr / 100 km² in watersheds where dispersing cougars settled or were last observed. We used all natal dispersers, including animals wearing radio-telemetry and those detected via harvest returns. Although this might bias the results (animals sampled from harvest should show up in watersheds with high harvest rates), we felt that any bias introduced by this method would be consistent between sexes. We square-root transformed data to meet requisite statistical assumptions and used a one-way ANOVA in a completely randomized design for comparisons.

RESULTS

Capture, marking, and dispersal movements.—On the Oquirrh site we conducted captures from February 1997 to March 2010, during which time we marked 26 kittens (11 F, 15 M) and 12 subadults (6 F, 6 M). Approximately 67% of subadults were local progeny, 17% were transients, and the remaining 16% were of uncertain origins. On Monroe we captured and marked 29 kittens (10 F, 19 M) and 25 subadults (10 F, 15 M) between January 1996 and April 2010. Among subadults 60% were local progeny, 28% were transients born elsewhere, and the remaining 12% were of uncertain origin. From the Oquirrh site we documented the fates of 23 animals post-independence (9 F, 14 M), of which 6 females dispersed and 3 were philopatric. All males dispersed, but 5 of 12 did not leave the Oquirrh Mountains and 2 died during dispersal. We observed movements of 26 post-independence animals from Monroe (10 F, 16 M); including 22 emigration events (6 F, 16 M) and 4 cases of female philopatry.
**Frequency.**—Oquirrh female dispersal frequency was 67% for kittens only (n = 9) and 73% for kittens and subadults (n = 11), whereas 33% and 60% of females dispersed from Monroe (n = 6 kittens; 10 kittens/subadults; Fig. 3-2). Although the pattern was consistent with expectations, in that female dispersal frequency was greater in the protected population, sample sizes were too low to detect differences in either dataset (kittens only: \( \chi^2 = 0.9, df = 1, P = 0.33 \); kittens and subadults: \( \chi^2 = 0.6, df = 1, P = 0.42 \)).

**Season.**—We determined the life-history season of dispersal for 23 and 25 animals from the Oquirrh and Monroe sites respectively (Fig. 3-3). Subadult cougars emigrated from both sites primarily during spring, coinciding with the estrus pulse (Oquirrh = 56.5%; Monroe = 48%). The second most frequent season differed between sites, with Oquirrh animals dispersing during the period of high prey abundance (23.9%), and Monroe animals leaving during the winter hunting season (32%). Seasonal distributions did not differ between sites (\( \chi^2 = 1.0, df = 2, P = 0.6 \)). Within sites, among season pairwise comparisons provided more support for estrus as the primary ecological factor prompting dispersal on the Oquirrh (estrus vs. human: \( t = -1.9, df = 21, P < 0.06 \); estrus vs. prey: \( t = -1.7, df = 21, P = 0.10 \)). Whereas all three seasons were statistically indistinguishable from each other on Monroe (estrus vs. human; \( t = -0.4, df = 23, P = 0.38 \); estrus vs. prey: \( t = -0.8, df = 23, P = 0.11 \); prey vs. human; \( t = 0.8, df = 23, P = 0.41 \)). When we pooled study sites and looked at among season differences, estrus was greater than either prey (\( t = -2.4, df = 46, P = 0.02 \)) or human (\( t = -2.0, df = 46, P = 0.05 \)); whereas prey and human did not differ from one another (\( t = 4.2, df = 46, P = 0.68 \)).
Distance.—Mean male dispersal distances were greater for Monroe than the Oquirrhs ($F_{1,27} = 5.6, P = 0.03$; Table 3-1). Within Monroe however, male distance did not differ from females ($F_{1,20} = 1.6, P = 0.22$). The small and highly skewed sample of Oquirrh females precluded statistical comparisons. This group was bi-modally distributed, being comprised of 3 short, within-range dispersals and two exceptional movements outside the Oquirrh Mountains.

Direction.—Mean dispersal direction for Oquirrh cougars was $247^\circ \pm 66^\circ$, as compared to $91^\circ \pm 75^\circ$ for those leaving Monroe (Fig. 3-4). Dispersal directions were not randomly distributed for either site (Oquirrhs, $n = 23$, $z = 0.5$, $P < 0.007$; Monroe, $n = 25$, $z = 0.4$, $P < 0.02$), and sites differed from one another ($F_{1,38} = 75.1$, $P < 0.001$). Oquirrh dispersers generally moved elsewhere within the range, with those leaving going to the Stansbury, Simpson, and Tintic Mountains. All northerly movements were initiated and completed within the study site. Monroe animals moved in all directions but there was an easterly tendency, with the primary recipients being the Fish Lake and Aquarius Plateaus (Fig. 3-5).

Habitat quality.—We compared the mean difference in April NDVI values between the natal and adult home range for each disperser (Fig. 3-6). During summer there was no difference between sites ($F_{1,37} = 0.02, P = 0.88$), but within sites values were slightly higher for adult home ranges (Oquirrhs: $t = 2.0$, $df = 37$, $P = 0.05$; Monroe: $t = 2.6$, $df = 37$, $P = 0.01$). However, Oquirrh dispersers moved into lower quality winter ranges compared to Monroe animals ($F_{1,37} = 5.4$, $P = 0.03$). Within sites Monroe dispersers settled into winter habitats of similar quality to their natal ranges whereas Oquirrh
animals moved into poorer winter habitats than their natal ranges (Oquirrh’s: \( t = -2.6, \text{df} = 37, P = 0.01 \); Monroe: \( t = 0.6, \text{df} = 37, P = 0.57 \)). When we pooled study sites we found no differences between sexes during summer (\( F_{1,37} = 0.7, P = 0.40 \)), but females moved into lower quality winter ranges than males (\( F_{1,37} = 3.3, P = 0.08 \)). Relative to their natal ranges, females moved into lower quality winter habitat than males (females: \( t = -2.2, \text{df} = 37, P = 0.03 \); males: \( t = -0.2, \text{df} = 37, P = 0.88 \)).

Mortality rates.—Seventy percent of females and 63% of males were followed into their adult home ranges using radio-telemetry, whereas the remaining 30 and 37% were detected from harvest returns. Despite low sample sizes (n = 10 F, 30 M), females dispersed to areas with greater mean annual mortality rates than males (Fig. 3-7; \( F_{1,38} = 2.9, P = 0.09 \)).

**DISCUSSION**

**Is cougar dispersal the result of density and maternal aggression?**

We found tentative support for the hypothesis that emigration is prompted by density and maternal reproductive status. Dispersal frequency was consistent for males (100%) but variable for females, suggesting the possibility of a density-dependent response (female dispersal frequency 67% vs. 33%). Thompson and Jenks (2010) argued that the 60% female emigration rate they observed was the result of intra-familial competition and inbreeding avoidance. Logan and Sweanor (2001) reported 43% of females dispersed from their protected study population, but hypothesized that as per-capita resources decline, female dispersal should increase in a density-dependent manner. Given our
sample size, we were not able to rigorously evaluate this hypothesis however, within the context of source-sink theory, dispersal was a commonly used strategy by females under a range of densities.

Seasonality data provided better support for the density-dependent hypothesis. Measures of this variable are scant in the literature and so difficult to generalize. Ross and Jalkotzy (1992) reported that all dispersals from their hunted population occurred between March and August, whereas Logan and Sweanor (2001) observed a later mode spanning July-October. Our results approximate this pattern. Both sites showed a pronounced spring dispersal pattern coinciding with modal cougar estrus (Laundré and Hernández 2007). Secondary seasons varied, with Monroe dispersers showing a distinct winter pulse that coincided with the period of high hunter-harvest mortality, which was not statistically distinguishable from estrus. Maternal identity of these animals was largely unknown, but 2 of 4 winter dispersers from the Oquirrhs were males orphaned after their mothers died of anthropogenic causes. The Monroe population was exploited during the entire study interval and kitten orphanage was a common artifact of this management regimen (Stoner et al. 2006). Winter dispersal may be an outcome of orphaning just prior to normal independence, a phenomenon we term “hard dispersal.” However, female cougars are not restricted to a discrete mating season and can enter estrus upon the loss of a litter. Alternatively, kitten mortality occurring throughout the year, potentially from infanticide following male immigration (Cooley et al. 2009), led to a wider mating season than was seen on the protected site, and thus a commensurately varied dispersal season. In either event, the prevalence of sport hunting during the winter
months suggests that winter dispersal may be common in exploited populations.

The role of maternal persuasion likely is important in the timing and frequency of dispersal. Beier et al. (1995) noted that prior to dispersal, cougar mothers abandoned kittens at kill sites near the edge of their home ranges. Presumably, this would be reinforced through agonistic responses by the mother toward the offspring upon further contact. Four of five philopatric females were orphaned at the approximate age of normal dispersal (~12-24 mos). Whether this influenced their ability to remain in their natal ranges is unknown. For males, dispersal is nearly ubiquitous and suggests a genetically fixed trait. Male fitness is highly variable compared to females (Chepko-Sade et al. 1987). If territorial males tend to kill subadult males, then a father killing his son is negatively impacting his own fitness. Moreover, if inbreeding avoidance is a factor in mammalian dispersal, then it is most likely to be expressed by mothers rejecting their sons. If this is the case, and fathers tend to kill same-sexed individuals, then a subadult male has essentially no choice but to disperse. Conversely, a mother may tolerate her daughter because of inclusive fitness benefits of sharing resources, while negating the survival costs associated with dispersal.

Prey abundance has been cited as an alternative to estrus in prompting emigration. Logan and Sweanor (2001) observed a dispersal pulse coinciding with the late-summer birthing season of desert mule deer, but postulated that maternal estrus was the most plausible ultimate explanation for the timing of offspring independence. Ungulates form the staple prey for cougars, but young individuals tend to exploit more non-ungulate prey than older ones (Knopf et al. 2010). Importantly, these hypotheses are not mutually
exclusive because of the overlap in season and the fact that some small and mid-sized mammals are giving birth during spring. Ferreras et al. (2004) noted that Iberian lynx (*Lynx pardinus*) breed when rabbit abundance is increasing, and this is when nearly all lynx disperse. Therefore, the non-ungulate food pulse coincides with estrus, and spring dispersal would benefit a young inexperienced hunter and its pregnant or lactating mother. This would tend to reinforce maternally mediated offspring dispersal sometime around estrus. If maternal impetus varies in response to conspecific density, then this could be interpreted as a density-dependent response.

**Is cougar movement influenced by landscape permeability?**

Our hypothesis that dispersal patterns should be shaped by landscape permeability were largely supported. During the transiency phase mean dispersal distances were similar between sexes. Oquirrh distances were generally shorter and bi-modally distributed compared to Monroe, reflecting the basin and range habitat. Animals that stayed in the Oquirrrhs had necessarily short distances, but those that chose to leave had to cross up to 25 km of unsuitable habitat. The small number of animals, particularly males, that left the Oquirrrhs, suggests that broad desert basins such as the Tooele and Rush Valleys may represent a psychological movement barrier to some individuals. Several of those that did leave used stepping-stone habitats to cross these valleys. Conversely, Monroe animals had relatively uninterrupted habitat to traverse and dispersal distances were unimodally distributed. Our results approximate the pattern of cougar dispersal elsewhere, in that our distances were longer in remote areas (Sweanor et al. 2000,
Thompson and Jenks 2010), and shorter in habitats constrained by anthropogenic barriers (Beier 1995, Maehr et al. 2002).

Dispersers from both sites exhibited directionality in their movements, with Oquirrh animals oriented southwest and Monroe animals tending easterly. Animals dispersing from the Oquirrhs were constrained from the north and east by the Great Salt Lake and the Wasatch Front metro area. Although cougars moved in all cardinal directions from Monroe Mountain, the site was well connected to habitats to the northeast and southeast by mid-elevation piñon-juniper forests and extensive willow-riparian systems. The lack of animals moving northwest suggests that the agricultural Sevier Valley, which is bisected by Interstate-70 may impede movement in that direction. Interestingly, a disperser who traveled south from the Oquirrhs turned northeast after hitting the Sevier Valley from the other side (Stoner et al. 2008).

The Wasatch Front metro area effectively hindered cougar movement between the Oquirrh and Wasatch Mountains. The incidence of cougars found within city limits suggests that animals do attempt to cross the valley, but the frequency with which they succeed is unknown. We documented only two attempts to cross this barrier. The first was an 8-month old animal who moved northeast ~ 8 km from his natal HRC after his mother was hit by a car. He traveled to an isolated ranch house where he was killed after attacking domestic animals. The second was also a male, who negotiated the Jordan River, Utah Lake, scattered subdivisions, and an 8-lane interstate to settle in the Wasatch Mountains. Based on satellite imagery, it is possible that if he followed variation in relative humidity or lighting, he could have found one of several riparian channels that
perforate the city. If so, then his movement would not have required extensive time in urban or agricultural settings. The only other animal to successfully disperse east of the Oquirrh was a female who circumvented the urban area by traveling 170 km south before turning north and east (detailed in Stoner et al. 2008). Beier et al. (2010) argued that urban areas are nearly impenetrable to cougar movement. Though not without exception, our results largely support the hypothesis that landscape configuration and permeability can direct cougar movement via habitat corridors and barriers (McRae et al. 2005).

**Do cougars disperse into attractive sinks?**

Our data support the “attractive sink hypothesis.” Relative to their natal ranges, females moved into lower quality winter habitat than males, a pattern that was more pronounced on the Oquirrh than Monroe. Dispersers followed the path of least resistance and for Oquirrh animals this led them into more xeric landscapes. The northeastern slope of the Oquirrh is impacted by a local “lake effect” in which storms coming from the northwest are recharged as they cross the relatively warm Great Salt Lake. The Wasatch and Oquirrh Mountains obstruct these storms, and so receive disproportionately greater precipitation than neighboring mountains to the west and south. Consequently, habitat quality follows a moisture gradient that decreases from the peaks of the Wasatch west into the Great Salt Lake Desert. The Oquirrh receive more moisture on their east slope than west and so animals deflected by the Wasatch Front urban barrier are pushed into less productive habitats. In contrast, no such gradient existed around Monroe and so animals dispersed into habitat of similar quality to their natal range.
Dispersing males established adult home ranges in areas with lower mortality rates, and hence turnover, than females, suggesting that conspecific attraction may play a more pronounced role in male habitat selection. This result was surprising given that male cougars are territorial, intolerant of other males, and strife is a common cause of mortality among subadult males (Logan and Sweanor 2001). In 15 years of intensive monitoring, males that successfully immigrated into our study populations tended to be older (≥ 4 yrs) and did so only after the death or departure of the prior resident. Younger and smaller males attempting to establish residency during the tenure of an adult male died in aggressive encounters within 6 months. That said, intraspecific strife was the most frequent cause of natural mortality on both sites, with females comprising 67 and 80% of the victims from the Oquirrh and Monroe, respectively (Stoner and Wolfe unpublished). This suggests that dispersing females may be actively avoiding conspecifics as they attempt to establish a home range. Female habitat selection may be focused on security and food, and therefore areas with high human-caused mortality, and consequently lower density, may be attractive when immigrating to a population of unrelated individuals.

Thompson and Jenks (2010) argued that male settlement was predicated on conspecific attraction and mating opportunities. Although males compete for territory, the dearth of females and therefore breeding opportunities may be a greater constraint on settlement than the presence of a dominant male. Both study populations were characterized by the continual presence of multiple resident females and annual to bi-annual resident male turnover. This hypothesis fits with the literature on sex-specific trade-offs in habitat selection, suggesting that females avoid conspecifics, and
consequently the more productive habitats that harbor higher cougar densities (Bunnefeld et al. 2006, Rode et al. 2006). Males selected habitats with lower mortality rates than those where females settled; nevertheless, dispersal from the Oquirrhs was generally oriented toward marginal habitats experiencing hunter-related mortality. The presence of a productive, protected population in the Oquirrhs, combined with natural and anthropogenic barriers to the north and east, effectively channeled dispersing animals into sink habitats. The overall pattern was an immigrant subsidy to exploited populations inhabiting lower quality habitat, in a classic example of source-sink dynamics.

**Do cougars behave according to source-sink predictions?**

An important assumption of the source-sink model is that females behave in a similar manner to males in order to obviate Allee effects. Notably, individual behavior tends to obfuscate density-dependence, particularly in small populations such as the ones detailed here. That said, cougars in this Great Basin ecosystem tended to conform to source-sink predictions, albeit in a loose and variable fashion. Females from a protected population dispersed at a slightly higher rate than those from an exploited one; they dispersed in similar directions and commensurate distances as males. Importantly, though female distances showed a bi-modal distribution, being clustered around very short, within natal mountain range, and longer, highly variable distances. For predictive management, the transient segment of the population will swell during late winter into summer and subpopulations adjacent to putative sources are more likely to receive female immigrants than those farther away; This general pattern is modified by landscape connectivity, the
effect of which is to constrain or promote movement in certain predictable directions (e.g. McRae et al. 2005). Female presence and density are the limiting resources in the recolonization of vacant habitats and our data show they may be attracted to harvest-induced sinks. These findings have implications for population expansion (Thatcher et al. 2009) and recolonization (Thompson and Jenks 2010) on the margins of the species range. These data can be used to parameterize behaviorally and spatially-explicit source-sink models to conserve cougars in the absence of precise population estimates.

**Literature Cited**


46:311-349.


Robinette, W. L., N. V. Hancock, and D. A. Jones. 1977. The Oak Creek mule deer herd
in Utah. Publication no. 77-15. Utah Division of Wildlife Resources, Salt Lake City, Utah, USA.


TABLE 3-1. Euclidean distances (in km) between natal and adult home range centers for all cougars dispersing from the Oquirrh and Monroe Mountain study sites, Utah, 1996-2010. One female outlier and all philopatric individuals or those that died in dispersal were excluded from calculations of the mean and SD.

<table>
<thead>
<tr>
<th>Study Site</th>
<th>Sex</th>
<th>n</th>
<th>Mean</th>
<th>SD</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oquirrh Mountains</td>
<td>Female</td>
<td>5</td>
<td>33.4</td>
<td>33.7</td>
<td>13-357</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>13</td>
<td>35.9</td>
<td>12.9</td>
<td>19-56</td>
</tr>
<tr>
<td>Monroe Mountain</td>
<td>Female</td>
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<td>40.1</td>
<td>19.5</td>
<td>11-62</td>
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<td></td>
<td>Male</td>
<td>16</td>
<td>51.3</td>
<td>19.1</td>
<td>15-92</td>
</tr>
</tbody>
</table>
Fig. 3-1. Oquirrh and Monroe Mountain study sites, Utah. The Oquirrh site was defined by protection from hunting, naturally fragmented habitat and proximity to a major urban area. Monroe was exploited, contiguous habitat, and located in a rural setting.
Fig. 3-2. Female dispersal frequency (± SE) for two datasets for Oquirrh (n = 9, 11) and Monroe (n = 6, 10) females, 1996-2010. “Kittens” refers to resident offspring only, whereas “kittens and subadults” is a pooled sample of resident offspring and subadult animals of uncertain origins that emigrated from the study site. Including these animals raised the sample size but introduced a positive bias by increasing dispersal frequency.
Fig. 3-3. Proportional distribution (± SE) of cougar dispersal season according to major life-history events (pooled over sex). The three season calendar correlates with pulses of breeding, resource abundance, and mortality risk in Utah cougars, 1996-2010.
Fig. 3-4. Dispersal directions for animals leaving the Oquirrh and Monroe study sites, Utah, 1996-2010. Mean azimuths (± SD) were 247° ± 66° for the Oquirrh, and 91° ± 75° for Monroe. Mean values incorporate within natal mountain range movements.
Fig. 3-5. Patterns in cougar dispersal from the Oquirrh (n = 4 F, 13 M) and Monroe (n = 6 F, 16 M) study sites, 1996-2010. Circles and stars represent end points only.
Fig. 3-6. The mean difference (± 95% CI) in winter range quality between natal and adult home ranges of dispersers as indexed by April NDVI values. Comparisons are between and within study sites pooled over sexes (Oquirrhs, n = 17; Monroe, n = 29; panel A), and between and within sexes, pooled over study sites (n = 10 F, 29 M; panel B), 1996-2010.
Fig. 3-7. Mean annual cougar mortality rates (± SE) in adult home ranges of dispersing cougars. Results derived from a sample of cougars marked in their natal ranges and followed into adult their home ranges with radio-telemetry (n = 7 F, 19 M), or recaptured after dispersal through harvest returns (n = 3 F, 11 M).
CHAPTER 4

BIOGEOGRAPHIC VARIATION IN COUGAR MORTALITY: ABUNDANCE, ACCESS, AND CONSERVATION OF AN EXPLOITED CARNIVORE

Abstract. Modern extirpations within the Carnivora have followed the human footprint. The contagion hypothesis predicts range contractions should occur along gradients in human activity leaving relict populations in range edges rather than in core. We evaluated this hypothesis for cougars (Puma concolor) in Utah using indices of remoteness and habitat quality in conjunction with multiple regression techniques to examine the distribution of hunter-harvested cougars. We used breakpoints derived from the literature and local field studies to predict areas of over-exploitation and those with sustainable harvest rates. We defined de facto refugia as watersheds open to sport hunting exhibiting mortality rates < 25% of the predicted population; conversely, watersheds that exceeded this value were considered "ecological traps." Within their geographic range in Utah, cougar mortality rates were greater in the core and lower along the periphery. The largest refugia were disproportionately represented in arid ecoregions with low human population densities. Patterns of cougar mortality followed the predictions of the contagion hypothesis, being spatially correlated with human access in high quality habitats. Ecological traps were well within mean cougar dispersal distances from refugia, suggesting the potential for source-sink dynamics. Our results indicate that habitats on the range margins are likely to harbor cougar populations in the event of widespread human-caused declines, and therefore may have greater conservation value than has previously been assumed. These methods have relevance for the conservation of other
exploited mountain-dwelling mammals that exhibit source-sink population dynamics. In the absence of robust enumeration techniques, resource managers may use the distribution of de facto refugia in conjunction with metapopulation theory to develop conservation strategies for this carnivore.

**INTRODUCTION**

The tolerance response curve uses the presence or absence of key variables influencing habitat quality to model the abundance of a species over its geographic range (Cox and Moore 1993). The center of the curve represents the range core, where populations exhibit higher densities and lower variability. Near the tails of the curve, one or more critical factors becomes limiting and populations exhibit lower abundance and greater variability, resulting in ephemeral occupancy. The correlation between habitat quality and population performance, may result in metapopulation dynamics, with differential survival and productivity among habitat patches creating sources, sinks, or areas of relative stasis. This produces a dynamic distribution exhibiting episodes of contraction and expansion over ecological time. When metapopulation dynamics are non-equilibrium, extinctions exceed recolonizations, resulting in widespread decline. During these periods the Melting Range Hypothesis (MRH) predicts that geographic ranges should contract from the edges inward, with the core acting as a stronghold (Lomolino et al. 2006). Although empirically some species conform to this prediction (Brown 1984), in a review of extinctions and range contractions of > 300 species from variety of taxa, Channell and Lomolino (2000) found, that rather than attenuating from the periphery into
the core, range contraction spread like a contagion from the point of contact with humans irrespective of habitat quality. Indeed, 81% of North American species examined persisted along the edges of their ranges, and not in the core. Acting individually or in concert, range collapse spread like a contagion, resulting from habitat destruction, introduction of alien species, or over-exploitation. The authors concluded that remote regions may represent refugia for species sensitive to anthropogenic disturbances.

Although secondary consumers tend to be at greater risk of extinction than primary consumers, *ceteris paribus*, modern extinctions within the *Carnivora* have been rare (Cardillo et al. 2005). However, the literature contains numerous descriptions of range contractions and extirpations (e.g. Laliberte and Ripple 2004, Morrison et al. 2007) with exploitation playing a significant role in these trends (Packer et al. 2009). Compared to other members of the Felidae, the geographic range of cougars (*Puma concolor*) remains relatively intact, yet the species exhibits both vulnerability and resilience to exploitation, depending on the scale of investigation. For example, in a global analysis of large mammals, Morrison et al. (2007) ranked the cougar number 17 out of 20 species exhibiting the greatest absolute range contractions, reflecting the extirpation of the species from most of eastern North America in the wake of European colonization. With the exception of a relict population in Florida, by 1930 predator control efforts combined with overexploitation of white-tailed deer (*Odocoileus virginianus*) rendered the species functionally extinct east of the Mississippi River (Anderson et al. 2010). Range contraction ended abruptly at the Continental Divide where they are still extant.

In western North America cougars currently exhibit a patchy distribution, occurring in
mountainous terrain with sufficient densities of ungulate prey. Ironically, at local scales cougars have demonstrated remarkable resilience to anthropogenic stressors such as hunting (Robinson et al. 2008) and habitat fragmentation (Sweanor et al. 2008). This is further evidenced by their continued presence on the periphery of numerous major American cities (Beier et al. 2010), expansion into former and novel habitats (Jung and Merchant 2005, Wilson et al. 2010), and their IUCN ranking as a species of “least concern” (Caso et al. 2008). However, in nearly all North American jurisdictions where extant, cougars are exploited at varying levels for recreational hunting, livestock protection, or human safety. Efforts to balance hunting opportunity with conservation are hindered by the lack of sensitive and robust trend estimators. Moreover, protected areas have limited utility as source populations because of the species’ wide-ranging habits, seasonal prey migrations, and high edge-to-area ratios. As a result, some protected carnivore populations are demographically indistinguishable from their hunted counterparts (Woodroffe and Ginsburg 1998, Balme et al. 2010).

Intrinsic factors associated with species’ declines have been well articulated (Davidson et al. 2009), but landscape correlates of population persistence are sparse. Several investigators have examined the role of refugia in conserving mammalian diversity as a function of legal protections (Woodroffe 2001), lack of human disturbance (Kerley et al. 2002), or as an artifact of patterns in human strife (Martin and Szuter 1999), yet scant research has been conducted to identify a priori where exploited or otherwise imperiled carnivores are likely to persist either locally, or within their global distributions (e.g. Naves et al. 2003, Rabinowitz and Zeller 2010). Our objectives were twofold: 1) to
evaluate the contagion hypothesis using cougars, a widespread, generalist carnivore subjected to regulated exploitation, and 2) to examine how variation in the quality of, and access by sport hunters to, habitat influences cougar mortality patterns in Utah. Importantly, within the study area cougars are still extant over most of their historic range, and our goal was not to measure contraction per se, but to predict contraction patterns in relation to habitat quality.

**METHODS**

**Study area**

Utah lies at the geographic center of the Intermountain West, straddling two major hydrologic basins. The Colorado Plateau drains the southern and western Rockies, and the Great Basin is a high elevation region with terminal drainage into the Great Salt Lake. The Wasatch-Uinta Mountains and Wasatch Plateau form the central cordillera of the state and the division between these drainage systems. Geologically, the Wasatch are considered the eastern extent of the basin and range faulting patterns that define Nevada and much of western Utah, whereas the High Uintas constitute an offshoot of the southern Rocky Mountains.

Climatically, Utah ranks as the second driest state in the U.S., with mean annual precipitation of 33 cm (range =13-150 cm). Precipitation comes principally during winter in the form of snow, but a strong latitudinal gradient of monsoonal moisture is apparent. Elevational range covers >3,400 m (550-4,150 m), with commensurate variation in plant communities, ranging from Mojave Desert alliances in the southwest to alpine tundra
along the crest of the High Uintas in the northeast (Banner et al. 2009).

Biogeographically the uplands of Utah are more closely allied with the Rocky Mountains than the Sierra Nevada.

Armstrong (1977) considered cougars and their principal prey species, mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) to be sufficiently widespread that they could not be associated with any particular biome or region of the state. Approximately 41% of Utah is occupied cougar habitat, which spans diverse communities ranging from semi-arid, piñon-juniper woodlands of the Great Basin and Colorado Plateau, to the mesic, aspen-conifer dominated forests of the Wasatch and Uinta Mountains (Cougar Discussion Group 2009). Habitat quality varies by ecoregion with the Colorado Plateau and Great Basin containing smaller, naturally fragmented habitats with lower cougar densities, and the mountain ecoregions comprised of large, relatively productive patches (Fig. 4-1).

**Study design**

Cougars are not amenable to precise enumeration and so are managed in a recursive manner. The hunt is regulated through the use of a model, which is informed by current hunt statistics (Cougar Discussion Group 2009), i.e. harvest data collected during year *t* are used to adjust opportunity for year *t+1*. Demographic and effort-based criteria derived from harvest indices are used to monitor population trends. For example, if hunter effort (catch-per-unit-effort), proportion of females in the kill, or mean age varies significantly from a pre-determined optimum, then opportunity is adjusted through a permit allocation system. Long-term hunt trends tend to reflect environmental
productivity, and therefore measures of opportunity are not independent of the response. We were interested in how factors beyond management prescriptions modified the distribution of human-caused cougar mortality. We therefore used hunter harvest data in ArcGIS (ESRI, Redlands, Ca.) to examine cougar mortality across a gradient in habitat quality and remoteness values. All spatial data and analyses were conducted using Universal Transverse Mercator projection (datum = NAD 83). Descriptive statistics are reported as the mean ± SD unless otherwise noted.

Habitat map

We used a map of predicted cougar occupancy developed by the Utah Division of Wildlife Resources (UDWR). The model uses the union of three variables to predict cougar presence: occupied mule deer and elk habitat, presence of woodland vegetation, and field evidence of cougar occurrence (confirmed mortalities, livestock depredation, or indirect sign). We restricted analyses to ungulate winter ranges where cougars were likely to occur during the period of greatest vulnerability. In mountainous regions mule deer and elk exhibit elevational migrations in response to the timing of snow accumulation and plant phenology (Pierce et al. 1999). Mule deer typically inhabit winter ranges between October and April (McClure et al. 2005) in localities where snowpack is < 46 cm (Gilbert et al. 1970). In Utah this varies from 1,540-2,300 m depending on winter severity, aspect, and other local factors. The cougar hunting season spans December to early June, but ~90% of the kill takes place between December and early March when snow cover facilitates tracking with hounds (UDWR unpublished data). To account for seasonal effects on habitat use we used an elevational cut-off to define the upper
boundary of winter habitat. Using radio-telemetry data from our on-going field studies, we calculated the mean winter elevation + 1 SD used by radio-instrumented cougars (Rieth 2010). This produced a ceiling of 2,615 m, which excluded most alpine and sub-alpine communities. Similarly, desert basins lack suitable stalking cover (Rieth 2010) and so we removed them based on landcover data (Utah ReGAP).

**Sampling units and cougar mortality rates**

We used UDWR defined cougar management units and subunits (heretofore CMU; Fig. 4-1) to assess coarse scale variation in cougar mortality and 1:24,000 scale watershed boundaries (12-digit hydrologic unit codes, HUC; NRCS 2007) to examine within and among CMU variation in cougar mortality. Mean habitat area within CMU boundaries (excluding non-habitat) was 1,550 km² ± 1,170 (N = 52; Fig. 4-1). Twelve-digit HUCs represented the best compromise between the spatial scale of animal behavior (cougar home ranges; Rieth 2010) and capturing within CMU variability (N = 1,932 watersheds; mean = 48 km² ± 30). We reasoned that watersheds offered a more ecologically meaningful sampling unit than administrative boundaries or grid cells, as cougar home range edges often coincide with ridgelines or other prominent topographic features (Rieth 2010). Watersheds also best approximated the scale and description of cougar mortality locations as recorded in annual harvest data.

To control for potentially confounding factors we subsampled the 1,932 watersheds into relatively homogenous groups. We censored all watersheds closed to the public or where cougar hunting was prohibited (industrial mines, military lands, and national parks, N = 64); or watersheds within jurisdictions for which we did not have data (Uintah-
Ouray, Navajo, and Goshute tribal lands, N = 91). We then dropped all watersheds without active deer/elk winter ranges or the presence of other ungulate prey species, such as bighorn sheep (Ovis canadensis) or feral horses (Equus caballus). Based on these criteria we dropped two CMUs that lacked suitable winter range (8a) and data (9a). Watersheds < 10 km² were added to the nearest neighbor with the greatest common boundary. Fourteen percent of the raw data fell outside the sample frame or were censored because of inadequate spatial information. Final sampling units represented the intersection of CMUs, predicted habitat, and watersheds, in which watersheds were nested within habitat, and habitat was nested within CMUs. Where watershed and CMU boundaries did not coincide we cut the watershed along the CMU boundary and attributed each part to the appropriate CMU.

Cougars have been classified as a game species in Utah since 1967, and as such hunters are required to submit carcasses to state personnel for the collection of biological and geographic data. These include the sex-age class and reproductive condition of the animal, and the date and location of kill. We compiled these data for cougars legally harvested between December 1996 and June 2007 (N = 4,507). Location data were accurate to the drainage within a CMU. Units with duplicate drainage names (e.g. “Cottonwood Canyon”) were segregated by county, and if duplicate names occurred within a county we censored both data points. We assigned each mortality to a watershed in the sample frame. Because watersheds varied in size we measured the response variable as a rate rather than as a count (no. cougars / year /100 km²). The mortality metric does not include natural or other human-caused mortalities such as poaching,
roadkill, or control actions (livestock depredation, human safety). The edited dataset comprised 1,626 watersheds, varying in size from 10-170 km² (mean = 45 km² ± 28), representing 4,217 individual animals.

**Remoteness index**

We ranked CMUs on the basis of five variables hypothesized to affect hunter access, or the relative amount of hunting pressure a given habitat patch might receive: 1) human population density, 2) distance to urban, 3) road density, 4) distance to nearest paved road, and 5) percent of habitat within private ownership. Measures for distance-to-urban, road density, and distance-to-paved-road were based on the mean of all watersheds within the habitat portion of the CMU. We measured distance from the geographic center of the watershed (a mean UTM) to the nearest urban area or paved road as the least-cost path. This method accounts for variation in elevation and provides a more realistic metric of how far a person would have to travel to arrive at the watershed center. On average, the least-cost path was 6% ± 2.8% greater than the Euclidean distance.

We defined human population density as the number of people per 100 km² living within a 1 km radius of the CMU boundary. Based on this definition, residents did not have to live in the habitat per se, but anywhere within 1 km of the CMU boundary. To calculate this metric we used the 2000 census numbers from TIGER line files (U.S. Census Bureau). We defined an urban area as any municipality with ≥ 500 permanent residents, excluding unincorporated areas and towns with < 500 residents. Urban demographic data were based upon 2000 census numbers and included towns in neighboring states within 1 km of the state boundary. Road density measures were
derived from 1:100,000 scale digital line graphs. We calculated road density as the total kilometers of unimproved road per 100 km² within a watershed. We limited our analysis to unpaved roads because hunters typically access habitat using all terrain vehicles or snowmobiles on unplowed roads. Distance to nearest paved road was calculated as the least-cost path from the watershed center to the nearest paved road. To calculate the percent of habitat comprised of private land each watershed was given a designation as “private” or “public” if > 50% of the area fell within a given category. We assumed that private land did not necessarily preclude access, but acted as a source of resistance. We acquired all spatially explicit demographic, road, and land ownership data from the Utah Automated Geographic Reference Center (AGRC 2007).

Cougar management units were ranked from 1-52 for each of these variables (weighted by human population density) with a rank of 1 indicating the least remote for a particular variable. We then summed the five ranks to create a score for each CMU. The total possible score was 260 (5 variables * 52 units), with the final scores ranging from 35-216. We used these scores to rank each unit in a linear fashion (discounting proportional differences) from lowest (1 = least remote) to highest (52 = most remote; Fig. 4-1, Table 4-1). The remoteness index applied only to CMUs and not to individual watersheds.

**Ungulate density**

Cougars are obligate carnivores and as such their habitat is defined by two factors: prey density and stalking cover. Of these, prey density is a more direct measure of habitat quality, and therefore a better predictor of cougar abundance (Pierce et al. 2000, Karanth
et al. 2004). The UDWR calculates indices of relative abundance for mule deer and elk on all CMUs. Annual surveys were designed to delineate winter ranges and estimate herd productivity for both species. Biologists conducted ground-based classification counts (number juveniles / adult female) from mid-November through December. Elk numbers are supplemented with aerial transects flown on triennial intervals conducted during January-February, subject to suitable counting conditions. Classification counts, hunter harvest data, and survival estimates from the literature are used to parameterize life-table analyses in deriving annual estimates of ungulate abundance for individual CMUs. We used these estimates to calculate winter range ungulate density as the total number of mule deer and elk per 100 km². Anticipating that the use of prey abundance to predict predator abundance might be confounded (i.e. higher cougar mortality may be causally related to ungulate abundance), we regressed estimates of ungulate abundance on an independent predictor variable, Normalized-Difference-Vegetation-Index for June (NDVI). Estimates of ungulate abundance correlated strongly with satellite derived indices of primary production (Spearman’s correlation coefficient, $r = 0.77$, $N = 52$, $P < 0.001$). Given these results, we felt confident that ungulate abundance was more likely a product of variation in primary productivity, rather than predator control efforts; and therefore prey density was suitable as a predictor of cougar mortality (Carbone and Gittleman 2002).

**Analytical techniques**

We conducted comparisons among both CMUs and individual watersheds (irrespective of CMU boundaries), at the statewide scale (213,772 km²). To analyze
relationships between remoteness, ungulate density, and their interaction on cougar mortality rates we used multiple linear regression. For between CMU comparisons, we used a square root transformation of ungulate density and cougar mortality rates to control excessive variance and to meet assumptions of normality. We categorized habitat quality using measures of ungulate density. We calculated the mean ± SD of transformed ungulate density and grouped all units within 0.5 SD of the mean as medium, and those either less than or greater than 0.5 SD from the mean as low or high quality habitats, respectively. Actual category divisions (high, medium, low) were based on the nearest breaks in the data. We then overlaid median prey density values for each habitat category on the regression. Statistical comparisons were made using SAS software (v. 9.2).

For among watershed comparisons we summarized the proportion of area within a habitat quality category comprised of de facto refugia and ecological traps. We defined a de facto refuge as an area of suitable habitat open to hunting but exhibiting negligible hunting mortality; conversely, an ecological trap was suitable habitat exhibiting high mortality levels (Delibes et al. 2001). We assumed that cougar density was homogenous across watersheds within a habitat category. Further, based the literature and local measures, we assumed that low, medium, and high quality habitats could harbor densities of 0.5, 1.5, and 2.5 independent cougars per 100 km² (Logan and Sweanor 2001 p. 167; Stoner et al. 2006), and could sustain annual mortality rates of 20-30% (Beck et al. 2005, Stoner et al. 2006). We used a hunting induced mortality rate of < 25% of predicted density to distinguish refugia from ecological traps (≥ 25%), and therefore a dichotomous categorization scheme in which every watershed was either a refuge or a trap. Although
the generality of this value is likely to vary with sex-age composition of the kill and level of immigration (Anderson and Lindzey 2005), we felt that it represented a practical cut-off for evaluating the relative impact of hunting mortality across a habitat gradient. Lastly, we calculated the percentage of area that fell above and below this threshold value.

Because carnivore home range area is negatively correlated with prey density (Herfindal et al. 2007), we predicted that a refuge would effectively protect individuals or subpopulations if the summed area of a watershed cluster (multiple watersheds with contiguous boundaries) was greater than the estimated mean male home range for a given habitat category. We reasoned that if male home ranges incorporate multiple female ranges (Logan and Sweanor 2001), then this metric would represent a suitable index for assessing the demographic value of a refuge. To calibrate this index we consulted the literature to determine male home range size over a variety of habitat types (Logan and Sweanor 2001). We considered all values ≤ 1 SD below the mean to be indicative of high quality male home ranges; within 1 SD of the mean to be medium, and ≥ 1 SD above the mean to be low quality habitats. Based on measures derived from 14 North American studies, mean male home range was 363 km² ± 185. We rounded these values to the nearest one-hundred and used 200, 400, and 600 km² to delineate refugia in high, medium, and low quality habitats, respectively. All single watersheds and clusters smaller than the habitat-specific cut-off value were dropped from the model to focus attention on the largest refugia and ecological traps. We used Hawth’s tools (Beyer 2004) to calculate mean distance between each ecological trap and the three nearest refugia.
RESULTS

Multiple regression analysis of among CMU mortality rates indicated that ungulate density and remoteness had significant relationships with cougar mortality (ungulate density $t_{47} = 3.18, P = 0.003$; remoteness $t_{47} = -2.29, P = 0.003$), with the full model explaining 41% of the variation in mortality ($F_{2,47} = 18.07, P < 0.001$, adj. $R^2 = 0.41$; Fig. 4-2). Ungulate density was positively correlated with hunting-induced cougar mortality (slope = 0.01228, SE = 0.00386), whereas remoteness had a negative effect (slope = -0.00533, SE = 0.00233). Together they acted in an additive manner, such that CMUs defined by low prey density and high remoteness exhibited the lowest mortality rates. We found evidence of an interaction between ungulate density and remoteness ($t_{46} = 2.11, P < 0.041$; model adj. $R^2 = 0.45$); however, this relationship was driven by a single low-mortality datum (no. 7), defined by high ungulate density and low remoteness. Given the influence of this outlier, we felt the model without the interaction provided a more parsimonious view of the relationship.

When we removed CMU boundaries and examined all watersheds solely on the basis of habitat quality, predicted winter habitat totaled 78,660 km², with low, medium, and high quality habitats comprising 50, 32, and 18% of the sum, respectively (Fig. 4-3). Across habitat categories, total refuge area (47,177 km²; $n = 1,039$ watersheds) exceeded that of ecological traps (31,483 km²; $n = 587$) by approximately 50%. The proportion of area classified as an ecological trap was positively related to habitat quality, though the difference between medium and high categories was marginal when compared to the
difference between medium-high and low quality habitats. Within habitat categories the area ratio of refugia to ecological traps varied from 1.25:1 in high quality habitats, to 1.75:1 in low quality habitats.

Major refugia (n = 31) and ecological traps (watershed clusters, n = 25) were distributed across all habitat categories and ecoregions (Fig. 4-4; Table 4-2). The most productive of these (high quality) were the Wasatch Front (no. 6) and the southeastern Wasatch Plateau (nos. 16-17). The seven largest refugia (>1,000 km²) were all comprised of low to medium quality habitats located in the Colorado Plateau ecoregion in the southeastern quarter of the state, of which two exceeded 3,300 km² (nos. 27, 30). Twenty-five ecological traps exceeded 200 km², and of these 80% were adjacent to a refuge. Mean Euclidean distance between ecological traps and the three nearest refugia was 56 km ± 29 and ranged from 26-136 km.

**DISCUSSION**

The Contagion Hypothesis predicts that remote habitats are more likely to harbor relict populations when range contractions are anthropogenically induced, regardless of habitat quality. Channell and Lomolino (2000) described populations of high conservation value as those living in marginal habitats, on undisturbed islands, or at high elevations. Our data suggest that hunting-induced cougar mortality rates were greatest in easily accessible habitats with high prey density; and conversely, lowest in remote areas with sparse ungulate prey, though this pattern did vary. For example, among prey rich habitats we documented remote areas with high mortality rates, identified here as
ecological traps (unit 8c), and proximate areas with virtually no mortality (unit 17a). If human behavior follows the law of diminishing returns, then sport hunters should select areas that offer both easy access and high encounter probabilities. If, in the most profitable areas either competition is high, or the resource has been depleted, poor habitats must be accessible (e.g. unit 19c), or remote habitats must be of high quality (unit 9c) to attract hunters. Mortality patterns suggest that in the event of anthropogenically induced range contractions, cougars in Utah are more likely to recede along a gradient in human population density rather than habitat quality. These results largely support the contagion hypothesis as outlined by Channell and Lomolino (2000).

Cougars in the Intermountain West exhibit a naturally fragmented distribution as a result of their association with basin and range, plateau, and volcanic topography. Differential survival among habitat patches can promote metapopulation-type dynamics. Recent research has elucidated patterns of source-sink dynamics in cougar populations derived from spatial variability in human-caused mortality (Stoner et al. 2006, Cooley et al. 2009). Immigration can subsidize local populations, or mask demographic changes. For example, Robinson et al. (2008) observed a cougar population that sustained 34% total annual mortality yet remained numerically stationary as a result of high immigration from nearby refugia. This may partially explain why certain areas, defined here as ecological traps (or “attractive sinks”) can sustain high mortality rates year after year. That said, it is unclear whether the refugia identified herein actually function as source populations. Perimeter-area ratios varied tremendously, and depending on actual animal movement patterns, edge effects might compromise the efficacy of some refugia.
Moreover, the patchy distribution of wintering ungulate herds and our liberal elevation cutoff beg for field surveys prior to any formal evaluation of these refugia or further modeling efforts. Given those caveats, mean distances between ecological traps and their three nearest refugia were well within the range of documented dispersal distances for both males and females (this volume). Although habitat quality of refugia was lower than in ecological traps, poor habitats may exhibit proportionally higher dispersal frequencies. Parallel field efforts have documented cougar reproduction in marginal habitats (R. Larsen, unpublished data), but it remains unclear whether young born in those habitats exhibit the philopatric behavior typically seen in higher quality habitats. If not, then these marginal habitats may act as a net exporter of dispersing subadults even if reproductive rates are relatively low. If so, remote, low quality habitats may have greater conservation value than has been previously assumed.

If high quality habitats have hidden survival costs, then exploitation may exert pressure on habitat selection behavior (Delibes et al. 2001). Over 95% of cougars taken in the hunt are captured with the aid of hounds trained to follow scent. Importantly, hounds are most effective when two environmental conditions are met: 1) frequent, persistent snowfall, which allows human observers to detect tracks and serves as a medium to hold scent, and 2) topographically benign habitats, as trail hounds have difficulty pursuing cougars through steep or broken terrain. Cougars that readily climb trees when pursued or inhabit relatively gentle terrain are being selected against with prevalent hunting methods. So long as hunting with the aid of hounds remains a predominant mortality factor for this species, individuals that can survive in marginal habitats, subsist on
alternative prey (e.g. bighorn sheep, feral livestock), winter at high elevations, or seek refuge in rocky escarpments rather than trees, are likely to exhibit higher survival and have an adaptive advantage over their counterparts in higher quality habitats. Thus, dry, poor quality refugia in southeastern Utah are likely to harbor cougars longer than in core habitats elsewhere in the state.

Importantly, the contagion hypothesis and its alternative, the melting range hypothesis (Lomolino et al. 2006) were derived empirically, and are not necessarily mutually exclusive. Direct anthropogenic impacts can operate concurrently with synoptic climatic effects. Forecasts for the southwestern United States suggest a warming and drying trend over the next century (Seager et al. 2007). Carnivores are sensitive to variation in the abundance of large herbivores and may be present in marginal habitats during relatively moist periods and abandoned when primary production drops below a level that can no longer support adequate prey. Large carnivores are most likely the first trophic level lost from these desert communities. Increased aridity could render marginal habitats unsuitable and therefore some of the refugia we identified in these already xeric habitats may be ephemeral (Table 4-2, nos. 2-5). Under these conditions, refugia in poor habitats might be rendered ineffective while those in high quality habitat would take on greater conservation value (refuge nos. 22, 28, 30). Thus human-caused range declines mean that refugia will primarily be located in remote and marginal habitats; if climatically driven, cougar populations should contract into moist habitats, and the interaction of these factors should leave relict populations in the few high quality habitats in remote locales.

Exploitation interacts with habitat fragmentation to drive carnivore range contractions
and extirpations. Establishment or use of protected areas has been proffered as a partial solution to this problem, but in the United States, even the largest protected areas (e.g. Yellowstone, Grand Canyon, Zion National Parks) are not sufficient to shelter viable populations of some wide ranging species (Woodroffe 2001, Minor and Lookingbill 2010). For example, Shaw (1989) estimated that ~ 26,000 km² would be required to sustain a viable population of cougars under prevalent habitat conditions in the Intermountain West. Few protected areas of this size exist anywhere in North America. Moreover, many park boundaries were defined by scenic qualities and may only represent summer habitat or have such high perimeter to area ratios as to be ineffective for conservation (Woodroffe and Ginsburg 1998). Therefore conservation of many of the largest and most mobile species will depend on the incorporation of, and connectivity between, private, multiple use lands, and other de facto wildlife refugia (Stein et al. 2008). Depending on habitat quality, refugia may act as source populations or at least be extinction resistant during periods of widespread human-caused declines. Given the mounting evidence demonstrating the ecological value of carnivores to ecosystem function (Bump et al. 2009), this research has important implications for the delineation of nature reserves and assessing large-scale connectivity.

**LITERATURE CITED**


Cougar Discussion Group. 2009. Utah cougar management plan V.2.0. Publication no. 09-15. Utah Division of Wildlife Resources, Salt Lake City, Utah, USA.


Associates, Sunderland, Massachusetts, USA.


### Table 4-1. Utah cougar management units and habitat characteristics (N = 52), 1996-2007.

<table>
<thead>
<tr>
<th>No.</th>
<th>Cougar Management Unit</th>
<th>Area (km²)</th>
<th>Remote Quality</th>
</tr>
</thead>
<tbody>
<tr>
<td>1a</td>
<td>Box Elder</td>
<td>2,286</td>
<td>20 med</td>
</tr>
<tr>
<td>1b</td>
<td>Box Elder, Pilot Mtn</td>
<td>150</td>
<td>38 low</td>
</tr>
<tr>
<td>2a</td>
<td>Cache, North</td>
<td>736</td>
<td>16 high</td>
</tr>
<tr>
<td>2b</td>
<td>Cache, South</td>
<td>1,294</td>
<td>12 high</td>
</tr>
<tr>
<td>3</td>
<td>Ogden</td>
<td>1,273</td>
<td>11 med</td>
</tr>
<tr>
<td>4</td>
<td>Morgan-Rich</td>
<td>1,744</td>
<td>32 med</td>
</tr>
<tr>
<td>5</td>
<td>East Canyon</td>
<td>1,138</td>
<td>8 med</td>
</tr>
<tr>
<td>6</td>
<td>Chalk Creek</td>
<td>842</td>
<td>30 high</td>
</tr>
<tr>
<td>7</td>
<td>Kamas</td>
<td>305</td>
<td>5 high</td>
</tr>
<tr>
<td>8a</td>
<td>North Slope, West Daggett</td>
<td>339</td>
<td>19 high</td>
</tr>
<tr>
<td>8c</td>
<td>North Slope, Three Corners</td>
<td>373</td>
<td>33 high</td>
</tr>
<tr>
<td>9a</td>
<td>South Slope, Vernal</td>
<td>937</td>
<td>25 high</td>
</tr>
<tr>
<td>9c</td>
<td>South Slope, Diamond Mtn</td>
<td>478</td>
<td>46 high</td>
</tr>
<tr>
<td>9d</td>
<td>South Slope, Bonanza</td>
<td>180</td>
<td>39 high</td>
</tr>
<tr>
<td>10a</td>
<td>Book Cliffs, Bitter Creek</td>
<td>2,669</td>
<td>50 low</td>
</tr>
<tr>
<td>10b</td>
<td>Book Cliffs, South</td>
<td>2,286</td>
<td>45 low</td>
</tr>
<tr>
<td>11a</td>
<td>Nine Mile, Anthro</td>
<td>998</td>
<td>49 low</td>
</tr>
<tr>
<td>11b</td>
<td>Nine Mile, Range Creek</td>
<td>3,186</td>
<td>41 low</td>
</tr>
<tr>
<td>12</td>
<td>San Rafael</td>
<td>3,470</td>
<td>44 low</td>
</tr>
<tr>
<td>13a</td>
<td>La Sal, La Sal Mtns</td>
<td>1,781</td>
<td>23 med</td>
</tr>
<tr>
<td>13b</td>
<td>La Sal, Dolores Triangle</td>
<td>287</td>
<td>37 med</td>
</tr>
<tr>
<td>14a</td>
<td>San Juan, Abajo Mtns</td>
<td>3,165</td>
<td>21 low</td>
</tr>
<tr>
<td>14b</td>
<td>San Juan, Elk Ridge</td>
<td>4,267</td>
<td>42 low</td>
</tr>
<tr>
<td>15</td>
<td>Henry Mtns</td>
<td>1,376</td>
<td>43 low</td>
</tr>
<tr>
<td>16a</td>
<td>Central Mtns, Nebo</td>
<td>2,339</td>
<td>17 med</td>
</tr>
<tr>
<td>16b</td>
<td>Central Mtns, Manti</td>
<td>3,718</td>
<td>9 high</td>
</tr>
<tr>
<td>17a</td>
<td>Wasatch Mtns, Salt Lake</td>
<td>290</td>
<td>3 high</td>
</tr>
<tr>
<td>17b</td>
<td>Wasatch Mtns, Heber</td>
<td>594</td>
<td>13 high</td>
</tr>
<tr>
<td>17c</td>
<td>Wasatch Mtns, Timpanogos</td>
<td>239</td>
<td>2 high</td>
</tr>
<tr>
<td>17d</td>
<td>Wasatch Mtns, Diamond Fork</td>
<td>1,198</td>
<td>14 high</td>
</tr>
<tr>
<td>17e</td>
<td>Wasatch Mtns, Avintaquin</td>
<td>1,976</td>
<td>36 med</td>
</tr>
<tr>
<td>18a</td>
<td>Oquirrh-Stansbury, Oquirrh</td>
<td>572</td>
<td>7 med</td>
</tr>
<tr>
<td>18b</td>
<td>Oquirrh-Stansbury, Stansbury</td>
<td>847</td>
<td>18 low</td>
</tr>
<tr>
<td>19a</td>
<td>West Desert, Deep Creek Mtns</td>
<td>1,523</td>
<td>47 low</td>
</tr>
<tr>
<td>19b</td>
<td>West Desert, Vernon</td>
<td>1,223</td>
<td>34 low</td>
</tr>
<tr>
<td>19c</td>
<td>West Desert, North Tintic</td>
<td>233</td>
<td>1 low</td>
</tr>
<tr>
<td>20</td>
<td>Southwest Desert</td>
<td>4,407</td>
<td>40 low</td>
</tr>
<tr>
<td>21a</td>
<td>Fillmore, Oak Creek</td>
<td>1,271</td>
<td>27 med</td>
</tr>
<tr>
<td>21b</td>
<td>Fillmore, Pahvant</td>
<td>1,735</td>
<td>4 med</td>
</tr>
<tr>
<td>25a</td>
<td>Plateau, Fish Lake</td>
<td>711</td>
<td>28 high</td>
</tr>
<tr>
<td>25b</td>
<td>Plateau, 1000 Lake</td>
<td>314</td>
<td>29 high</td>
</tr>
<tr>
<td>25c</td>
<td>Plateau, Boulder</td>
<td>2,318</td>
<td>35 med</td>
</tr>
<tr>
<td>22</td>
<td>Beaver</td>
<td>2,557</td>
<td>15 med</td>
</tr>
<tr>
<td>23</td>
<td>Monroe Mtn</td>
<td>726</td>
<td>10 high</td>
</tr>
<tr>
<td>24</td>
<td>Mount Dutton</td>
<td>851</td>
<td>24 med</td>
</tr>
<tr>
<td>26</td>
<td>Kaiparowitz</td>
<td>3,808</td>
<td>48 low</td>
</tr>
<tr>
<td>27</td>
<td>Paunsaugunt</td>
<td>3,161</td>
<td>31 low</td>
</tr>
<tr>
<td>28</td>
<td>Panguitch Lake</td>
<td>1,374</td>
<td>6 high</td>
</tr>
<tr>
<td>29</td>
<td>Zion</td>
<td>2,232</td>
<td>26 low</td>
</tr>
<tr>
<td>30</td>
<td>Pine Valley</td>
<td>2,899</td>
<td>22 med</td>
</tr>
</tbody>
</table>
**TABLE 4-2.** Largest watershed clusters forming *de facto* refugia for cougars in Utah, based on the distribution and level of human-caused mortality, 1996-2007 (n = 31).

Slashes indicate refuge straddles multiple cougar management units.

<table>
<thead>
<tr>
<th>Refuge no.</th>
<th>Cougar management unit, subunit</th>
<th>Refuge location or name</th>
<th>Habitat Quality</th>
<th>km²</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Zion / Paunsaugunt</td>
<td>Vermillion Cliffs, Moquith Mtns</td>
<td>low</td>
<td>617</td>
</tr>
<tr>
<td>2</td>
<td>Southwest Desert</td>
<td>Wah Wah Mtns</td>
<td>low</td>
<td>783</td>
</tr>
<tr>
<td>3</td>
<td>Nine Mile, Range Creek</td>
<td>Desolation Canyon</td>
<td>low</td>
<td>2,462</td>
</tr>
<tr>
<td>4</td>
<td>San Rafael</td>
<td>San Rafael Swell</td>
<td>low</td>
<td>2,525</td>
</tr>
<tr>
<td>5</td>
<td>San Juan, Elk Ridge</td>
<td>Dark Canyon Primitive Area</td>
<td>low</td>
<td>3,303</td>
</tr>
<tr>
<td>6</td>
<td>Plateau, Boulder / Kaiparowitz</td>
<td>Box Death Hollow Wilderness, GSENM¹</td>
<td>low-med</td>
<td>852</td>
</tr>
<tr>
<td>7</td>
<td>San Juan, Abajo / La Sal Mtn</td>
<td>Abajo Mtn (N), La Sal Mtn (S)</td>
<td>low-med</td>
<td>1,431</td>
</tr>
<tr>
<td>8</td>
<td>Kaiparowitz / Paunsaugunt / Plateau, Boulder</td>
<td>GSENM¹, Kaiparowitz Plateau</td>
<td>low-med</td>
<td>3,389</td>
</tr>
<tr>
<td>9</td>
<td>Pine Valley</td>
<td>Shoo and Little Pine Creek watersheds</td>
<td>med</td>
<td>423</td>
</tr>
<tr>
<td>10</td>
<td>Beaver</td>
<td>Black Mtns</td>
<td>med</td>
<td>519</td>
</tr>
<tr>
<td>11</td>
<td>Box Elder</td>
<td>Goose Creek Mtns</td>
<td>med</td>
<td>522</td>
</tr>
<tr>
<td>12</td>
<td>Fillmore, Oak Creek / W.Desert, Vernon</td>
<td>East Tintic Mtns</td>
<td>med</td>
<td>527</td>
</tr>
<tr>
<td>13</td>
<td>Wasatch, Avintaquin / Central Mtns, Manti</td>
<td>Price River watershed</td>
<td>med</td>
<td>538</td>
</tr>
<tr>
<td>14</td>
<td>Fillmore, Pahvant / Central Mtns, Nebo</td>
<td>Pahvant Mtns (NE), Valley Mtns</td>
<td>med</td>
<td>551</td>
</tr>
<tr>
<td>15</td>
<td>Beaver</td>
<td>Mineral Mtns</td>
<td>med</td>
<td>557</td>
</tr>
<tr>
<td>16</td>
<td>Morgan-Rich</td>
<td>Desert Ranch, Lost Creek watershed</td>
<td>med</td>
<td>616</td>
</tr>
<tr>
<td>17</td>
<td>Kaiparowitz / Plateau, Boulder</td>
<td>GSENM¹, Oak Creek watershed</td>
<td>med</td>
<td>1,052</td>
</tr>
<tr>
<td>18</td>
<td>La Sal Mtn, La Sal Dolores Triangle</td>
<td>La Sal Mtns (N), Dolores River watershed</td>
<td>med</td>
<td>1,052</td>
</tr>
<tr>
<td>19</td>
<td>Plateau, Thousand Lake, Boulder</td>
<td>Fremont River</td>
<td>med-high</td>
<td>264</td>
</tr>
<tr>
<td>20</td>
<td>Cache / Ogden</td>
<td>Wellsville Mtns, Willard Peak</td>
<td>med-high</td>
<td>358</td>
</tr>
<tr>
<td>21</td>
<td>Morgan-Rich / Chalk Creek</td>
<td>Echo Canyon, Chalk Creek watershed</td>
<td>med-high</td>
<td>362</td>
</tr>
<tr>
<td>22</td>
<td>Wasatch, Salt Lake / East Canyon</td>
<td>Wasatch Front</td>
<td>med-high</td>
<td>506</td>
</tr>
<tr>
<td>23</td>
<td>Cache / Ogden</td>
<td>Bear River Mtns (SE), Crawford Mtns (W)</td>
<td>med-high</td>
<td>721</td>
</tr>
<tr>
<td>24</td>
<td>Panguitch Lake</td>
<td>Panguitch Creek watershed</td>
<td>high</td>
<td>242</td>
</tr>
<tr>
<td>25</td>
<td>Central Mtns, Manti / Plateau, Fish Lake</td>
<td>Salina Canyon</td>
<td>high</td>
<td>275</td>
</tr>
<tr>
<td>26</td>
<td>Wasatch, Heber / Kamas</td>
<td>Upper Weber and Provo River watersheds</td>
<td>high</td>
<td>303</td>
</tr>
<tr>
<td>27</td>
<td>Panguitch Lake / Paunsaugunt</td>
<td>Mammoth Ridge, Sunset Cliffs</td>
<td>high</td>
<td>354</td>
</tr>
<tr>
<td>28</td>
<td>Central Mtns, Manti</td>
<td>Cottonwood, Huntington Creek watersheds</td>
<td>high</td>
<td>429</td>
</tr>
<tr>
<td>29</td>
<td>Wasatch, Diamond Fork</td>
<td>Diamond Fork (upper basin)</td>
<td>high</td>
<td>479</td>
</tr>
<tr>
<td>30</td>
<td>Central Mtns, Manti / Plateau, 1000 Lake</td>
<td>Quitchupah and Muddy Creek watersheds</td>
<td>high</td>
<td>480</td>
</tr>
<tr>
<td>31</td>
<td>South Slope, Vernal</td>
<td>Uinta Mtns (SE)</td>
<td>high</td>
<td>627</td>
</tr>
</tbody>
</table>

¹ GSENM, Grand Staircase-Escalante National Monument
Fig. 4-1. Utah cougar management units evaluated for remoteness, ungulate density, and cougar mortality, 1996-2007 (N = 52). Gray shading indicates predicted winter habitat for cougars and primary prey species. See Table 4-1 for details.
Fig. 4-2. The effect of remoteness on cougar mortality (controlling for variation in prey density). Regressions are presented as median values for high, medium, and low density prey.
Fig. 4-3. Proportional distribution and ratio of *de facto* refugia and ecological traps, by habitat quality category, Utah, 1996-2007.
Fig. 4-4. Statewide distribution of 31 major *de facto* refugia (mean annual mortality rates < 25%) and ecological traps (mean annual mortality rates ≥ 25%) for cougars in Utah, 1996-2007. “Major” connotes those watershed clusters comprising ≥ 200, 400, or 600 km² (for high, medium, and low quality habitats, respectively) of contiguous habitat.
My overarching goal was to determine how anthropogenic factors affect the behavior, movement, and distribution of cougars in Utah. The applied context for this was the question of whether the source-sink model of population dynamics could be used for the management of exploited cougar populations. To achieve this, I evaluated three broad questions, each with a specific spatial scale of investigation. First, at the local scale of a subpopulation, I examined cougar behavioral response to a suite of anthropogenic land uses. Second, I examined cougar movements at the meso scale using the mean dispersal radius around two subpopulations in central Utah, and compared transient behavior of animals from a protected, fragmented habitat near the Wasatch Front, to one that was exposed to ongoing hunting pressure, inhabiting a contiguous, wildland habitat. Lastly, at the statewide scale I calculated the number, size, and distribution of de facto refugia and ecological traps, as indexed by variation in annual hunter-harvest rates. These studies were drawn from a long-term monitoring project and all analyses were retrospective. Since the initiation of the project in 1996 we captured and marked > 200 animals on two study sites. In terms of duration, spatial extent, and number of animals marked, this project represents one of the largest datasets collected on this species, yet after making comparisons across management strategies, genders, reproductive classes, and age groups, it was a small sample from which to draw inference. Moreover, cougars show incredible behavioral plasticity in their response to environmental variability, which ultimately made the extraction of statistically rigorous conclusions difficult.
Nevertheless, these investigations have valuable implications for the development of plans for sustainable hunting and long-term conservation of cougars in the Intermountain West.

Notably, this species has a mixed reputation in the public eye, and economic and political concerns about its predatory nature can make effective, science-based management difficult to implement. Therefore, one of my primary goals was to measure variables critical for parameterizing ecologically relevant, behaviorally-driven management models (McPherson and DeStefano 2003). One of the most serious weaknesses in our ability to efficiently manage cougars is the lack of an economical, robust, and precise technique for measuring abundance. Along with the estimation of adult survival, this is the cornerstone of most wildlife management programs (Festa-Bianchet 2008), and yet, as of this writing nothing exists for cougars that meets these stringent criteria (Choate et al. 2006). As noted in Chapter 3, the source-sink model offers some promise as an alternative management strategy (Stoner et al. 2006). This method has been widely advocated for the management of cougars (Beck et al. 2005, Hornocker and Negri 2010, Cooley et al. 2011), and other species with similar behavioral constraints, such as grizzly bears (Ursus arctos; Nielson et al. 2006) and leopards (Panthera pardus; Balme et al. 2010). One of the primary benefits of this model is that it does not hinge on estimates of abundance, but it does require well-estimated behavioral parameters.

Despite some fairly direct efforts to outline a formula for managing cougars using the source-sink model (e.g. Logan and Sweanor 2001, Launrédé and Clark 2003), the method
remains largely conceptual. Prior to the development of a specific plan for cougars in Utah, several underlying assumptions of the model needed to be addressed. Chapters II-IV were just such an attempt. In the pages that follow, I have strived to reiterate the questions, discuss what my data show in response, and elucidate how these patterns might be used to develop a source-sink based management strategy for cougars in a region defined by pronounced gradients habitat quality, connectivity, and anthropogenic disturbances.

My first question was whether cougars are wildland obligates, or do they show synanthropic tendencies. On the basis of results herein, cougars are not wildland obligates and can survive and even thrive in highly disturbed, human-impacted environments, given adequate prey resources and, importantly some level of protection from exploitation. However, they do show a strong proclivity for wildland over rural or suburban environs. This is critical because the amount and configuration of habitat contained in protected areas such as national parks and military reservations is trivial relative to the spatial requirements of a viable cougar population (Shaw 1989). Moreover, as noted throughout the dissertation, seasonal prey migrations mean that entire cougar subpopulations are shifting in and out of the static boundaries of these few protected areas. These movements are marked by tremendous individual and temporal variation. This means two things for management. First, near-urban cougar populations are not necessarily de facto sinks, even if human-caused mortality occurs at some level; nor are prime-aged individuals habitually drawn to urban areas. This is also the downside, in that dispersing or senescent animals may be attracted to easily accessible roadkill or domestic
animals on the urban periphery. Management approaches for ameliorating potential conflicts can be implemented at two scales. On the local scale highway clean-up programs and proactive education campaigns targeting residents in vulnerable areas (i.e. the “urban-wildland interface”) are important for making these areas less attractive to cougars. Education should be focused on animal husbandry practices, removal of roadkill, and removal of potential attractants such deer-palatable landscaping. It is also important to consider land-use planning to extent possible. The maintenance of agricultural buffers between wildland habitats and areas of human occupation might provide a partial solution to this problem.

This study is the first attempt to evaluate the social conditions under which dispersing cougars settle. Hunter-harvest data were readily available and proved to be a reasonable index of sex-specific mortality rates at the watershed scale. My efforts to address the question of whether or not cougars conform to the predictions of the source-sink model were generally affirmative. Females did disperse at a higher frequency from a saturated population relative to one with lower cougar densities, but I could not demonstrate a statistically significant difference between the two. This was largely the result of small samples from which to perform the analysis. The fact remains that female dispersal was quite common, and the distances they traversed were commensurate with males. These movements were modified - both facilitated and redirected - by natural landscape features, such as stepping stone habitats, broad desert basins, and anthropogenic barriers, notably the Wasatch Front metro area and the Sevier Valley. There was no obvious bias in terms of gender response, although several data points and the literature suggest that
males may be more motivated to cross extensive areas of unsuitable habitat than females (Thompson and Jenks 2010). That said, 5 of 12 male dispersers eventually settled within the Oquirrh study area, while I observed no such behavior on Monroe despite its larger size. On the immigration side of the equation, the “attractive sink” hypothesis was borne out statistically. Both males and females immigrated into habitats subject to sustained human-caused mortality, but surprisingly, females selected areas of lower conspecific density (as indexed by hunter-harvest mortality) relative to males. In sum, cougars of both sexes display dispersal behaviors that appear conducive to source-sink management.

At this point I cannot address the question empirically, but my data suggest that cougars were repelled by the Wasatch Front metro area, which effectively pushed dispersing animals into desert regions. This small protected population appeared to provide a regular immigrant subsidy to less productive, exploited populations. Future applied research should be directed at modeling the source-sink relationship between the Oquirrhs and surrounding ranges. Specifically, there is a need to address the question of the extent to which cougar occupancy of the Tintic, Sheeprock, Simpson, Onaqui, or Stansbury Mountains depend on dispersal from the Oquirrhs? Part and parcel of this analysis should be an evaluation of the implications of the loss of this source, either due to isolation or changes in cougar management at Kennecott.

Notwithstanding the fact that this is the largest dispersal dataset yet compiled for this species, my estimates of dispersal parameters were based on small sample sizes and beg for continued basic research on the topic. That said, these estimates can provide a reasonable baseline from which to initiate modeling connectivity and dispersal rates
between adjacent subpopulations. Measures of primary productivity and hunter-harvest data (as detailed in Chapter 4) can be used in conjunction with landscape models identifying major obstacles to movement or paths of least-resistance (McRae and Beier 2007). These models can be used to develop experimental management units where fieldwork can be focused on measuring occupancy, density, productivity, and movement. For example, I detected a notable demographic connection between Monroe and the plateau units to east, and the Tushar Mountains to the west. Marking animals and adjusting hunter-opportunity to create steep mortality gradients between neighboring units would be a reasonable means of determining whether the source-sink relationships between neighbors are reciprocal or not. The pattern could then be reversed in a rest-rotation type schedule, and combined with ancillary management experiments of deer population response to changes in cougar abundance. This also would serve to field-validate the movement predictions made in this thesis.

One of the primary questions of this thesis was to what extent do exploited cougar populations adhere to the predictions of the contagion hypothesis (Channell and Lomolino 2000)? This idea predicts that when range contractions are anthropogenic in nature, then relict populations should be found in remote areas irrespective of habitat quality. If the pattern of cougar harvest does fit this hypothesis, then it offers managers greater predictive ability about where, and to what degree, certain management objectives may be achievable. Anthropogenic cougar mortality in Utah did indeed fit the predictions of the contagion hypothesis. Within my defined study area human-caused mortality was most pronounced in easily accessible and productive habitats in the core of the
geographic range; whereas poor habitats on the range periphery were subjected to less hunting pressure, even after controlling for the effects of prey density and access. Refugia were larger relative to sink habitats but disproportionately located in desert ecoregions. Conversely, ecological traps were primarily found in high quality habitats. On the basis of my spatial analysis of cougar mortality, Utah may already have a quasi source-sink system, which could be formalized through management action.

The relevance of these results for management is twofold: first, from a population perspective, cougars in marginal desert habitats are likely to be the most resistant to anthropogenic extirpations. Population reductions in these areas will be difficult to achieve using sport hunting. Cougar hunters are drawn to accessible areas that maintain consistent snow cover and portend high encounter rates. By and large desert mountains are too dry and steep to efficiently and economically pursue cougars with dogs. Although cougar density in most refugia is likely low, animals from these areas may serve as a source for outlying ecological traps. Second, one of the primary management concerns in desert regions is survival of bighorn sheep. Cougars can be effective predators of this prized game species, and in prey depauperate ranges bighorn may constitute an attractant to some individual cougars. Use of these results for management could be comprised of two steps. First, the three model parameters would need to be calibrated to better fit local scale measures (e.g. management units). For example, an accurate, site-specific winter habitat ceiling could be incorporated to fit each mountain range in the model over a range of winter severities (i.e. dry vs. wet years), and then simulations could be run varying the assumed densities and sustainable harvest rates. Second, a monitoring program could be
designed to field-truth putative refugia at regular intervals using tracking or camera surveys to verify cougar, or at least prey occupancy of those watersheds (Nichols and Williams 2006). The effective size of a refuge or a trap can be modified directly using actions such as road closures, or indirectly through manipulation of season dates and opportunity levels.

Wildlife management and conservation is predicated on the implicit assumption that animals behave in stereotypic ways and population dynamics are largely deterministic. Yet, animals respond to the pressures of their environment in diverse and unique ways, with natural selection molding broad patterns based on the relative success or failure of various strategies. While the study of animal behavior starts from an individual standpoint, wildlife management is firmly rooted in the population perspective. This perspective is adequate when populations are large enough to garner the requisite sample sizes and therefore meet rigorous statistical assumptions. However, in a fragmented world, large continuous populations can be subdivided into small constituents that comprise anthropogenically derived “metapopulations,” reducing the validity of predictions drawn from this perspective. This is particularly true for large carnivores for reasons enumerated throughout this thesis. Small, isolated remnant populations may exhibit variable dynamics not simply because of the mathematics of their intrinsic rates of increase, but also because of the prominent role that individual behavioral idiosyncrasies play on the system as a whole. In small populations background “noise” or residual variation can emerge as the driver of the systems dynamics.

For economic and logistical reasons many of our research and management practices
are focused on subpopulations that because of their size, do not reflect the scale at which the population of interest is operating (e.g. du Toit 2010). Management priorities dictate a research agenda focused on population level inquiries, but sampled at what amounts to a collection of a few individuals, whose behavior may or may not be typical within the population of interest, nor provide inference to others (e.g. Stoner et al. 2008). Although feasibly matching the scale of the question to the scale of sample is not simple, the hidden cost is a loss of both accuracy and precision and eventually the long-term predictive abilities for management. One might argue that we should endeavor to not only match the scale of the sample to the scale of the question, but conversely, match the scale of the question to the feasibly attainable sample. Therefore, samples of idiosyncratic individuals are best used to estimate system bounds and parameterize behavioral models. These models could then be used in conjunction with standard demographic models to simulate the dynamics of the population of interest. However, stochasticity is an integral component of all natural systems, as are thresholds, time lags, and alternative stable states (Ludwig et al. 1993, Beisner et al. 2003). Therefore, modeled results should be interpreted cautiously, updated regularly, and integral assumptions should be evaluated through continued basic research.

**Literature Cited**


