Dispersal behaviour of a polygynous carnivore: do cougars Puma concolor follow source-sink predictions?

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Original article

Dispersal behaviour of a polygynous carnivore: do cougars *Puma concolor* follow source-sink predictions?

David C. Stoner, Michael L. Wolfe, Clint Mecham, McLain B. Mecham, Susan L. Durham & David M. Choate

The source-sink model of population dynamics predicts that density drives emigration of subordinate animals to habitats offering lower competition for resources. Several authors have suggested use of this model as a potential framework for conservation of exploited carnivores when precise enumeration is unfeasible. Dispersal is a critical behavioural mechanism for management based on this model, yet there is a lack of knowledge on the habitat and social conditions that motivate carnivore emigration and settlement. The cougar *Puma concolor* is a widely distributed and heavily exploited carnivore, indigenous to the western hemisphere. We evaluated patterns in cougar dispersal behaviour from two sites in Utah, differing in terms of management and the level of natural and anthropogenic habitat fragmentation. We used our results to evaluate three predictions with respect to cougar dispersal behaviour: 1) natal population density and maternal reproductive status prompt emigration, 2) movement of dispersing cougars is shaped by habitat configuration and permeability, and 3) dispersers preferentially settle in areas of high habitat quality and low conspecific density. We documented the emigration of 62 individuals and measured movement variables, including sex and site-specific frequency, distance, seasonality, direction and the habitat quality and harvest rates characterizing 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 occurred most frequently during spring, coinciding with the estrus pulse. Natural and anthropogenic obstacles modified landscape permeability, and therefore dispersal distances were shorter in fragmented habitats than in contiguous ones. Relative to males, females dispersed into habitats of lower productivity with higher mean annual harvest rates. Patterns in male settlement suggested habitat selection based on mating opportunities, whereas female settlement was predicated on avoiding conspecifics. Cougars in this Great Basin ecosystem largely conformed to source-sink predictions. Results can be used to parameterize source-sink models based on animal behaviour and landscape permeability to conserve exploited carnivores, under conditions of population expansion or recolonization of habitats where Allee effects are a limiting factor.

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Few carnivore populations are insulated from anthropogenic stressors, including habitat fragmentation and exploitation (Packer et al. 2009). Regulated harvest can result in demographic changes to carnivore populations (Stoner et al. 2006, Milner et al. 2007), yet the difficulty in 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 behavioural solution for conserving exploited carnivores (Logan & Sweanor 2001, Laundré & 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 animals from protected source populations disperse to harvest-induced sinks (Leopold 1933, Delibes et al. 2001, Robinson et al. 2008).

Recent research suggests that the decision of whether or not to disperse is multi-factorial, context-dependent and highly individualistic (Cote et al. 2010). However, on the population scale, there are some general patterns. For polygynous mammals, male dispersal is near-obligatory, whereas female dispersal 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 of both sexes to habitats offering 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. This is the mechanism underlying the source-sink model of population dynamics as articulated by Pulliam (1988). Pulliam's model proposed density-dependent dispersal as the behavioural mechanism facilitating connectivity and persistence in populations defined by high mortality and/or low fecundity. This model assumes that variation in vital rates is a product of disparities in habitat quality, but Delibes et al. (2001) argued that otherwise productive habitats can become 'attractive sinks' when they are characterized by low density stemming from high rates of human-caused mortality.

Although a promising alternative, little effort has been made to determine whether polygynous carnivores conform behaviourally to the predictions of the source-sink model (see Novaro et al. 2005). Prior to the application of such a model, several questions need to be addressed, including 1) how males and females vary in their dispersal behaviour, 2) what landscape features facilitate or impede movement of dispersers, and 3) what habitat and social conditions prompt immigration. Dispersal is a critical behaviour for persistence of demes within a metapopulation context (Brown & Kodric-Brown 1977), and therefore effective conservation depends on a better understanding of the relationships between animal behaviour and landscape permeability.

The cougar *Puma concolor* is one of the last widely-distributed ungulate predators in many North American ecosystems. They occur at low densities and exhibit variable dispersal strategies that seem to be influenced by landscape context and social dynamics (Maehr et al. 2002, Thompson & 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, Beier (1995) monitored cougars dispersing from a small habitat patch surrounded by urbanization in southern California. He argued that housing and transportation infrastructure were effectively isolating that population and, in the absence of connections with surrounding habitat, it was vulnerable to stochastic extinction. Sweanor et al. (2000) studied cougar dispersal in southern New Mexico and postulated a source-sink type population resulting from the basin and range structure of the habitat. Similarly, Maehr et al. (2002) noted that the best predictors of dispersal movements in Florida panthers were natal population density and movement barriers. Lastly, Thompson & Jenks (2010) argued that conspecific attraction and breeding opportunities seemed to motivate or preclude male settlement.

Each of these studies described the behaviour of individual dispersers and their respective natal populations, but provided little information on habitat or social conditions in patches where dispersers settled. Because an individuals' ability to establish a home range in a new population is predicated on both environmental and demographic factors, examination of this behaviour from both landscape and social perspectives should lead to greater predictive management abilities. 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 behaviour: 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 exhibiting relatively high turnover rates (attractive sink hypothesis).

Material and methods

Study design

This effort was part of a long-term monitoring project examining cougar population dynamics on two sites subjected to differing management objectives (Stoner et al. 2006). From 1996-2012, we compared dispersal patterns of individuals originating from a semi-protected population to one with a > 30 year history of annual harvests. The sites were also distinctive in terms of landscape context (naturally fragmented vs contiguous) and human disturbance (near-urban vs rural). Importantly, habitat and management regime were correlated and so the interaction of these factors on observed movement patterns cannot be evaluated here.

Study sites

Oquirrh Mountains: protected population, fragmented habitat, near-urban location

The Oquirrh Mountains are located in north-central Utah on the eastern edge of the Great Basin (40.5°N, 112.2°W; Fig. 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 km^2, but we focused our fieldwork on 500 km^2 encompassing the northeastern slope, on properties owned and managed by the Utah Army National Guard (Camp Williams) and Kennecott Utah Copper. The site is bounded on the north by the Great Salt Lake and on the east by the Wasatch Front metro area. 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. Human density adjoining the study area varied from 232 inhabitants/100 km^2 in rural Tooele County to 47,259/100 km^2 in urban Salt Lake County (U.S. Census Bureau).

Elevations ranged from 1,292 to 3,200 m a.s.l. and correlated with variation in moisture, vegetation and faunal diversity. Annual precipitation ranged from 300-400 mm in the Salt Lake and Tooele valleys to 1,000-1,300 mm on the highest ridges and peaks. Of this, approximately 60% occurred as snow between December and 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 climatic 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. North facing slopes > 2,200 m a.s.l. supported localized montane communities of aspen *Populus tremuloides* and Douglas fir *Pseudotsuga menziesii*. The ungulate prey base associated with these plant communities was composed 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 to December. Deer and elk were lightly hunted on the Kennecott portion of the site. Our 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 semi-protected.

Monroe Mountain: exploited population, contiguous habitat, rural location

Monroe Mountain is located in the Southern Mountains ecoregion of south-central Utah (38.5°N, 112°W; see Fig. 1). The site is a high volcanic plateau, extending 75 km along a north-south axis, and lies within a geologic transition from basin and range topography to the Colorado Plateau. Monroe is contiguous with other montane and subalpine habitats within the ecoregion. Hydrologically, Monroe Mountain drains into 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 km^2, and formed the central unit of the Fishlake National Forest. Other landholders included the BLM, the State of Utah and various private interests.

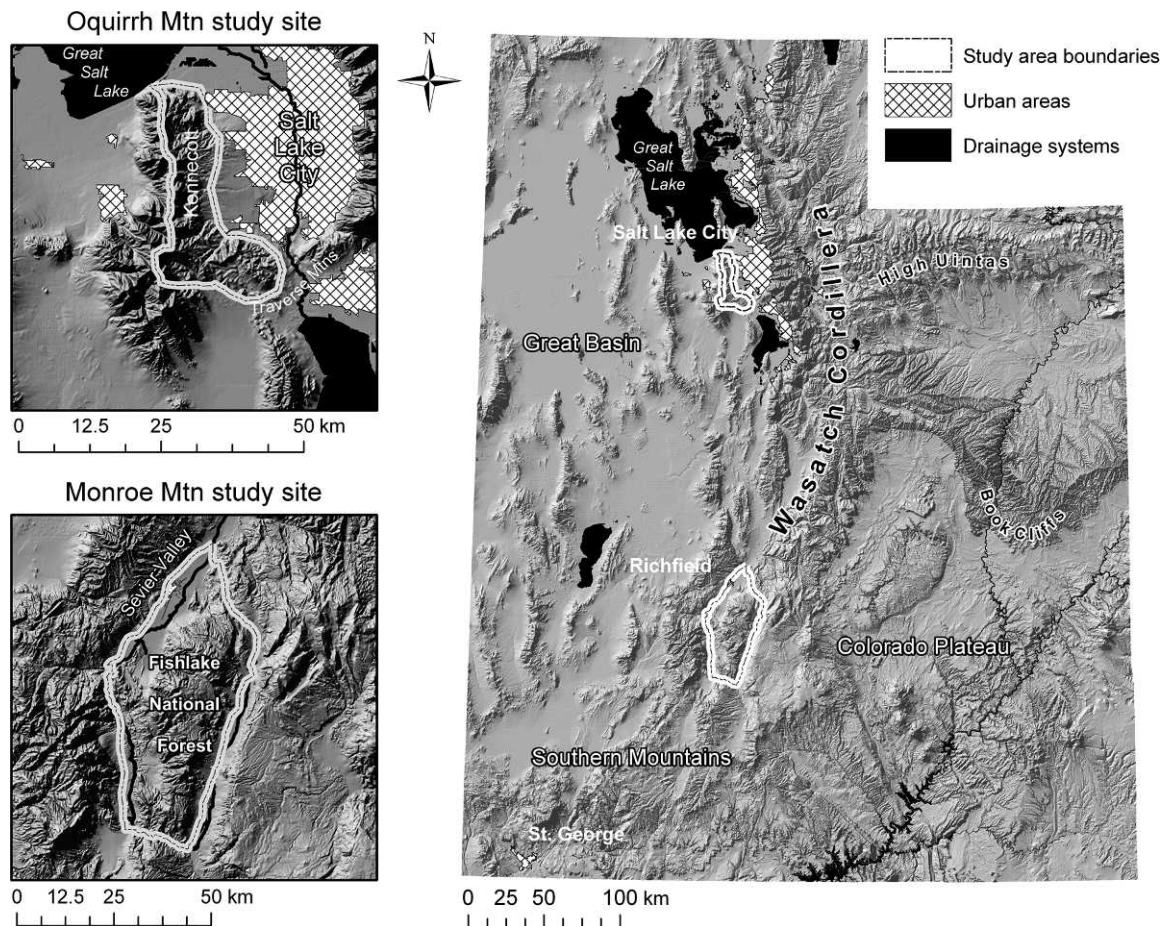Elevations ranged from 1,600 to 3,400 m a.s.l. with

Figure 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, whereas the Monroe population was exploited and occupied contiguous habitat in a rural setting.

annual precipitation averaging 150-200 mm at lower elevations, increasing to 600-1,200 mm on the plateaus > 2,700 m a.s.l. Precipitation was bimodally distributed with most falling as snow from January-February, followed by a late summer monsoon (Banner et al. 2009). Although vegetation was similar to the Oquirrhs, there were notable differences in the proportions of each community, with the largest area (44%) dominated by piñon-juniper woodlands *Pinus edulis*. Mixed conifer (white fir *Abies concolor* and Engelmann spruce *Picea englemanii*) and aspen occurred across broad areas at higher elevations, with Gambel oak, mountain shrub 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 is part of the Utah Division of Wildlife Resources' (UDWR) Monroe Mountain Wildlife Management Unit, where deer, elk and cougars were managed for hunting opportunity. From 1996 to 2012, the number of cougar hunting permits issued represented an average of 46 ± 34% (SD) of the adult population, but hunter success rates averaged 64 ± 19%. Resource use included livestock grazing (cattle and sheep), logging, fossil fuel extraction and off-road vehicle recreation. Human densities around the site varied from 73 to 382 inhabitants/100 km^2, with most of the population distributed among small agricultural communities in the Sevier Valley on the northwestern boundary of the study site.

Capture, marking and dispersal movements

From 1996 to 2011, we conducted captures of cougars during winter (December-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 and weight criteria reported by Ashman et al. (1983) and Laundré & Hernández (2002). All animals captured were tattooed and all adults (> 2.5 years) and subadults (1.0-2.5 years) were equipped with VHF radio-transmitters (Advanced Telemetry Solutions, Isanti, Minnesota). Kittens were marked with an ear transmitter, ear tag or a drop-off radio-collar. We considered subadults either yearling kittens still accompanying their mother or transients 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 years upon capture, or those which tracking evidence indicated had originated outside the study area boundaries. We radio-tracked cougars using aerial and ground-based telemetry techniques at approximately monthly intervals. Animal handling procedures were conducted in accordance with Utah State University Institutional Animal Care and Use Committee standards (approval no. 937-R).

We defined dispersal as the permanent departure from the natal home range to an independent home range for the purposes of reproduction. We defined philopatry as offspring independence combined with continued use of some portion of the natal home range. We documented dispersal movements by tracking collared animals until they established adult home ranges, or through monitoring the annual harvest for marked animals (November-June). When we could not find collared individuals on the study area, we searched neighbouring mountain ranges at semi-annual intervals.

We analyzed all geographic data in ArcGIS v. 9.2 (ESRI, Redlands, California, USA) using Universal Transverse Mercator (UTM) projection in datum NAD 83. We used Program R for circular statistics (R Development Core Team 2012) and the FREQ or GLIMMIX procedures in SAS v. 9.3 for all other statistical analyses. For proportional response variables, we calculated the SE using procedures for generalized linear mixed models; all other descriptive statistics are reported as the mean ± SD. We provide P-values associated with all statistical analyses, but have avoided explicit definition of a significance level threshold (Hurlbert & Lombardi 2009).

Measurement and analysis of dispersal patterns

Frequency
We defined dispersal frequency as the proportion of males and females of known fate that moved beyond their natal range. We compared dispersal frequency between sites using only individuals of known residency status captured when still associating with their mothers (< 12 months old). We compared proportions using an ANOVA Type III test of fixed effects.

Timing
To evaluate hypotheses about dispersal timing, we estimated departure date using the mid-point of a range (date ± number of 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 instances in which kittens were orphaned, we used the mother's death as the date of independence. Some dispersals were documented when kittens handled one time were tattooed and subsequently recaptured in the harvest. In these cases, we used the estimated age of the kitten at the time of capture, and projected the season during which the individual would be 15 ± 3 months of age (mean dispersal age for cougars in western North America; Anderson et al. 1992). For sibling groups, we used only one datum for dispersal season.

We divided the year into three broad seasons corresponding to major life-history phenomena for cougars. These were modal periods of estrus (breeding season), abrupt increases in prey abundance (fawning/calving season) and increased mortality risk (cougar hunting season). In western North America, cougars display a pronounced birth mode from June to October (Laundré & Hernández 2007), and based on a 92-day gestation (Logan & Sweanor 2001), peak mating season occurs from March to 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 into autumn (Knopff et al. 2010). Sport hunting is the single largest mortality factor affecting cougar populations in most western states (Packer et al. 2009). In Utah, the hunting 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. Based

on these patterns, we divided the year into three seasons that corresponded to pulses in estrus and breeding activities (March-June), prey abundance (July-October) and mortality risk (November-February). All of these phenomena are reasonably predictable. Nevertheless, March, June and November constituted periods of seasonal overlap, and so we split the datum between respective seasons for animals dispersing during these months.

We made two comparisons using χ^2 tests of homogeneity of proportions with weighted counts, in which weights were allocation proportions: 1) the distribution of dispersal seasons between sites (sexes pooled), and 2) differences among seasons with sites pooled. For the latter analysis, we conducted pairwise comparisons among seasons using a generalized linear model with a multinomial distribution and a generalized logit link.

Distance

We considered the dispersal initiation point as either the capture site or the home range center (HRC) of the juvenile or mother, if instrumented. 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 (Stoner et al. 2013). In order to improve precision within our dataset and make comparisons with those in the literature, we restricted our analyses to Euclidean measures. We compared dispersal distances between sites with sexes pooled, between sexes with sites pooled and sex*site interactions using a two-way factorial ANOVA in a completely randomized design. Distances were square-root transformed to meet distributional assumptions.

Direction

We report direction as the azimuth connecting the natal HRC to the adult HRC or mortality site. Previous research indicates that in remote areas cougars disperse in random directions (Sweanor et al. 2000), but they disperse directionally in environments constrained by urbanization (Maehr et al. 2002). To evaluate whether mean directions differed from a random distribution under both of these conditions, we used Rayleigh's z-test of uniformity (a goodness of fit test; Zar 1999). Lastly, we compared directional means between sites using one-way circular ANOVA.

Habitat quality

Habitat quality for large carnivores is largely predicated on prey density (Carbone & Gittleman 2002), which is positively correlated with primary productivity (Pettorelli et al. 2009). We developed a statewide cougar habitat quality index using late winter and early summer measures of the Normalized Difference Vegetation Index (NDVI; detailed in Stoner et al. 2013) to evaluate the relative differences in habitat quality between natal and adult home ranges.

To sample NDVI grids, 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 as a proxy (mean $= 69$ km^2, radius $= 4.7$ km; Rieth 2009). Circular home-range estimators are gross approximations and tend to produce negatively biased estimates of home-range quality. However, we chose this measure for three reasons: 1) to minimize inclusion of unused areas, such as desert basins, which would have been encompassed by larger circles, 2) to better characterize habitat quality of the putative home-range core, and 3) to maintain a consistent sampling frame among individuals.

To evaluate differences in home-range quality, we subtracted NDVI$_{natal}$ from NDVI$_{adult}$, with negative values indicating a decline and positive values an improvement from natal range quality. We used a two-way factorial ANOVA in a completely randomized design to examine differences between study sites (sexes pooled) and sexes (sites pooled), and within groups to determine if mean values differed from zero (i.e. were pre- and post-dispersal habitats different). We used t-tests for within group comparisons.

Harvest 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 turnover. We used 1:24,000 scale 12-digit hydrologic unit codes (HUC; NRCS 2007) as the sampling frame for calculating harvest rates in adult home ranges. Twelve-digit HUCs represented the best approximation of cougar home ranges in the absence of requisite telemetry data (mean watershed area $= 48$ km^2 $\pm$ 30 km^2, N $= 1,932$). Harvest data were compiled from

1996-2007 and included the sex-age class and approximate location of the mortality (Stoner et al. 2013). We measured the response variable as the number of cougars killed/year/100 km^2 in watersheds where dispersing cougars settled or were last observed. We used all natal dispersers, including animals wearing radio-telemetry collars and those detected via harvest returns. Although this potentially produces a biased result, in that animals sampled from harvest could show up in watersheds with high harvest rates, we reasoned that any bias 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 between-sex comparisons.

Results

Capture, marking and dispersal movements
On the Oquirrh site, we conducted captures from February 1997 to April 2011, during which time we marked 31 kittens (14 females and 17 males) and 12 subadults (six females and six males). Approximately 67% of subadults were local progeny, 17% were transients and the remaining 16% were of uncertain origins. On Monroe, we captured and marked 33 kittens (13 females and 20 males) and 29 subadults (12 females and 17 males) between January 1996 and April 2011. Among subadults, 60% were local progeny, 28% were transients born elsewhere and the remaining 12% were of uncertain origin. On the Oquirrh site, we documented the fates of 26 animals post-independence (10 females and 16 males), of which six females dispersed and four were philopatric. All males dispersed, but seven of 12 did not leave the Oquirrh Mountains and two died during dispersal. From Monroe, we observed movements of 36 animals post-independence (15 females and 21 males), including 31 dispersal events (10 females and 21 males) and five cases of female philopatry. We monitored dispersal movements through May 2012.

Frequency
All males dispersed from their natal ranges, whereas female dispersal frequency was 60% from the Oquirrhs (N = 10) and 44.4% from Monroe (N = 9). Although female dispersal frequency was slightly higher in the protected population, statistical power was too low to detect differences between sites ($F_{1,17} = 0.46$, $P = 0.51$).
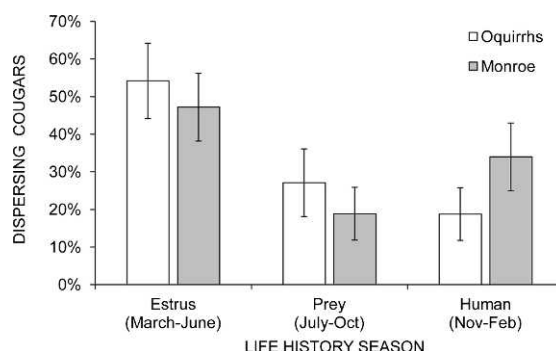

Figure 2. Proportional distribution ($\pm$ SE) of cougar dispersal season according to major life-history events (pooled over sex). The three-season calendar correlates with pulses of breeding (Estrus), food abundance (Prey) and hunting pressure (Human) in Utah cougars, 1996-2012.

Timing
We determined the life-history season of dispersal for 24 and 27 animals from the Oquirrh and Monroe sites, respectively (Fig. 2). Subadult cougars emigrated from both sites primarily during spring, coinciding with the estrus pulse (Oquirrhs = 54.2%, Monroe = 47.2%). The second most frequent season varied between sites, with Oquirrh animals dispersing during summer, the period of high prey abundance (27.1%), and Monroe animals during the winter hunting season (34%). However, seasonal distributions did not differ between sites ($\chi^2 = 1.8$, df = 2, P = 0.4). When we pooled our study sites and looked at among-season differences, more dispersals occurred during the season of estrus than either high prey abundance (t = -2.2, df = 59, P < 0.03) or human-caused mortality (t = -1.8, df = 59, P = 0.07); whereas the seasons of prey abundance and human-caused mortality were statistically indistinguishable from one another (t = 0.4, df = 59, P = 0.6).

Distance
Dispersal distances from Monroe tended to be slightly greater than those from the Oquirrhs (sexes pooled: $F_{1,12.5} = 4.3$, P < 0.06), but there were no differences between sexes when sites were pooled ($F_{1,12.5} = 0.01$, P = 0.91). Monroe males dispersed farther than Oquirrh males ($F_{1,31} = 8.1$, P < 0.008; Table 1), but within Monroe, male and female distances did not differ ($F_{1,9.8} = 0.4$, P = 0.52). The small and skewed sample of Oquirrh females precluded their inclusion in statistical comparisons.

Direction
Mean dispersal direction for Oquirrh cougars was

Table 1. Euclidean distances (km) between natal and adult home-range centers for cougars dispersing from the Oquirrh and Monroe Mountain study sites, Utah, 1996-2012. One female outlier and all philopatric individuals or those that died in dispersal are included in the ranges, but excluded from calculations of the mean (SD).

Study site	Sex	N	Mean	SD	Range
Oquirrh Mountains	Female	4	33	34	13-357
	Male	16	31	16	6-56
Monroe Mountain	Female	9	65	57	11-179
	Male	19	52	23	15-103

$236° \pm 67°$, as compared to $83° \pm 81°$ for those leaving Monroe. Directions were not randomly distributed for either site (Oquirrhs: $N = 20$, $z = 0.5$, $P < 0.005$, Monroe: $N = 27$, $z = 0.4$, $P < 0.02$), and sites differed from one another ($F_{1,45} = 73.9$, $P < 0.001$). Oquirrh dispersers generally moved elsewhere within the range, with those leaving going to the Stansbury, Simpson and Tintic Mountains (Fig. 3). All northerly movements were initiated and completed within the Oquirrh Mountains. Monroe animals moved in all directions but oriented northeast and southeast, with the primary destinations being the Fishlake and Aquarius Plateaus (see Fig. 3).

Habitat quality

We compared the mean differences in the winter and summer range NDVI values between natal and adult home ranges for each disperser. Adult summer ranges did not differ between sites ($F_{1,41} = 0.01$, $P =$
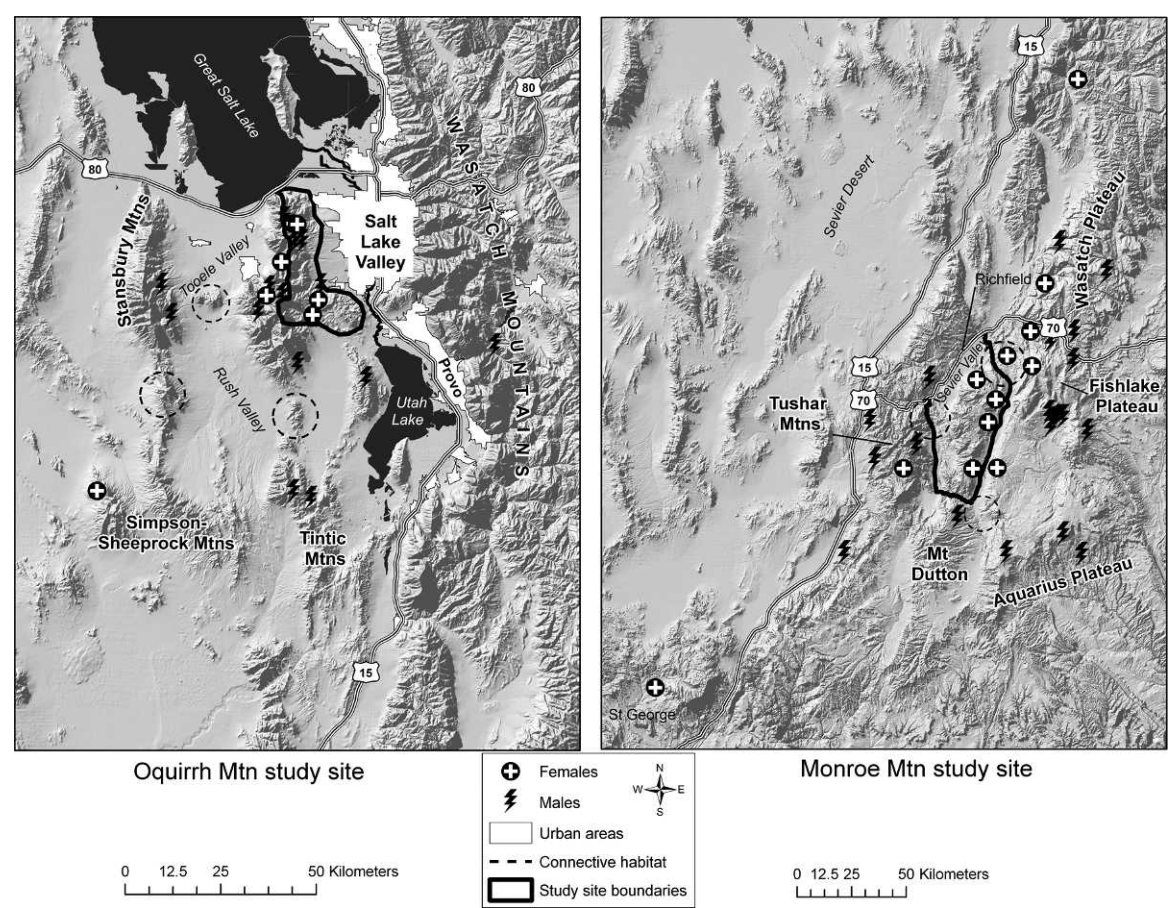

Figure 3. Patterns in cougar dispersal from the Oquirrh (N = seven females and 16 males) and Monroe (N = 13 females and 22 males) study sites, 1996-2012. One Oquirrh female left the state and is not pictured (detailed in Stoner et al. 2008). Symbols represent end points only.
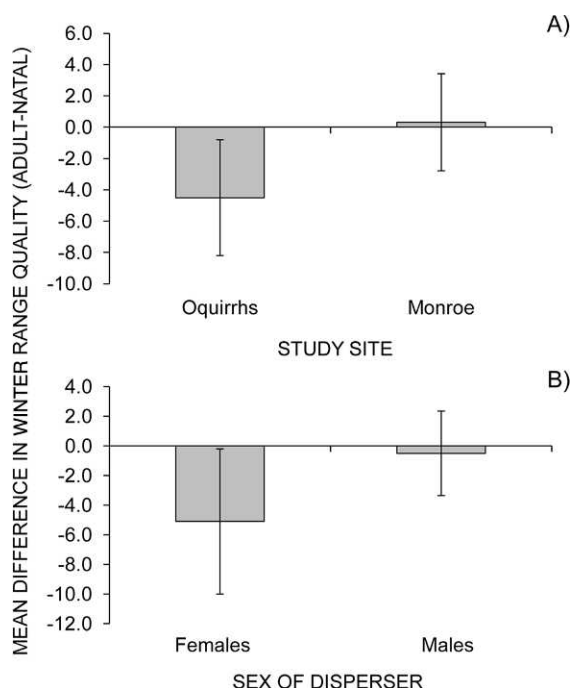
Figure 4. The mean difference (± 95% CI) in winter-range quality between natal and adult home ranges of dispersers as indexed by April NDVI values. Comparisons are between and within study sites pooled over sexes (Oquirrhs: N=19, Monroe: N=24; panel A), and between and within sexes, pooled over study sites (N = 11 females and 32 males; panel B), 1996-2012.
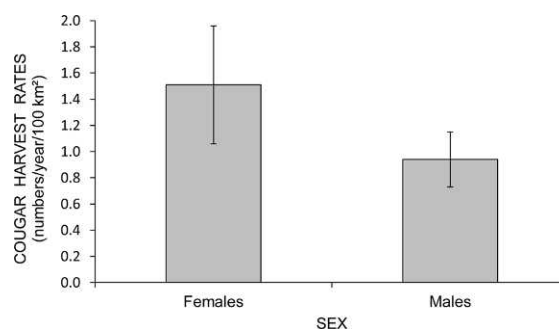

Figure 5. Mean annual cougar harvest rates (± 95% CI) in adult home ranges of dispersing cougars, 1996-2012. Results derived from a sample of cougars marked in their natal ranges and followed into adult their home ranges with radio-telemetry (N = 9 females and 21 males), or recaptured after dispersal through harvest returns (N= five females and 13 males).

for 48 dispersers (13 females and 35 males), of which, 62% were followed using radio-telemetry and 38% were detected via harvest returns. Harvest rates in watersheds where dispersing cougars settled varied by sex (Fig. 5), with females immigrating to areas reflecting greater mean annual harvest rates than males (1.51 ± 0.83 vs 0.94 ± 0.64 cougars/year/100 km^2; $F_{1,46} = 5.6$, $P = 0.02$).

0.94), but within sites, values were slightly higher for adult home ranges on Monroe, but not for the Oquirrhs (Oquirrhs: t = 1.6, df = 41, P = 0.11, Monroe: t = 1.9, df = 41, P < 0.06). However, Oquirrh dispersers tended to move into lower quality winter ranges than Monroe animals ($F_{1,41}=3.6$, P < 0.07; Fig. 4A). Within sites, Oquirrh animals moved into poorer winter habitats than their natal ranges, whereas Monroe dispersers moved into winter habitats of similar quality to their natal ranges (sexes pooled, Oquirrhs: t=-2.4, df=41, P=0.02, Monroe: t=0.2, df=41, P=0.87; see Fig. 4A). After pooling our study sites, we found no differences in quality of summer ranges between sexes ($F_{1,41}=0.07$, P=0.79), but females tended to occupy lower-quality winter ranges than males ($F_{1,41}=3.1$, P=0.08; see Fig. 4B). Relative to their natal ranges, females tended to move into lower quality winter habitat, whereas males showed no pronounced difference (females: t=-2.2, df=41, P < 0.03, males: t=-0.4, df=41, P= 0.71; see Fig. 4B).

Harvest rates
We estimated turnover rates in the adult home ranges

Discussion

Is cougar dispersal the result of natal population density and maternal estrus?
We found no evidence for density as a predictor of dispersal frequency for either sex. Logan & Sweanor (2001) reported that 43% of females dispersed from their protected study population, postulating that as *per capita* resources decline, female dispersal should increase in a density-dependent manner. More recently, Logan & Sweanor (2010) hypothesized that if intrasexual competition drives male dispersal, then dispersal rates should decline with increasing turnover of resident males (e.g. harvested populations). We found no support for either of these hypotheses. Male dispersal rates were consistent between sites (100%), showing no relationship with density or management regime. Female dispersal rates did vary between sites but these differences were not statistically distinguishable. Although small sample sizes precluded a rigorous evaluation of the former hypothesis, within the context of source-sink theory, dispersal was a common strategy used by females under a range of densities.

Data on departure dates provided support for

estrus as a factor influencing the timing of subadult dispersal. Measures of this variable are scant in the literature and so difficult to generalize. Ross & Jalkotzy (1992) reported that all dispersals from their hunted population occurred between March and August, whereas Logan & Sweanor (2001) observed a later mode spanning July-October. Our results were intermediate, with both sites showing a pronounced spring dispersal pattern coinciding with modal cougar estrus (March-June; Laundré & Hernández 2007). Secondary seasons varied between sites, with Monroe dispersers exhibiting a winter pulse that corresponded with the period of high hunter-harvest mortality. Kitten orphanage was a common artifact of this management regimen (Stoner et al. 2006), and so winter dispersal may be an outcome of orphaning just prior to normal independence; i.e. a phenomenon we term 'hard dispersal'. Alternatively, high male turnover may have resulted in a higher incidence of infanticide (Cooley et al. 2009). One result of low kitten survival might be a wider mating season, and therefore greater variation in the timing of dispersal. In either case, the prevalence of sport hunting during the winter months suggests that winter dispersal may be common in exploited populations.

The role of parent-offspring conflict is an important factor in the timing and frequency of dispersal (Liberg & von Schantz 1985). Beier et al. (1995) noted that prior to dispersal, maternal cougars abandoned kittens near the edges of their home ranges. On Monroe, four of five philopatric females were orphaned at the approximate age of normal dispersal (~ 12-20 months), suggesting that maternal persuasion may play a role in female dispersal. For males, dispersal is nearly ubiquitous and indicates a genetically fixed trait. Among males, competition for reproductive opportunities results in high levels of aggression, including father-son conflict. Moreover, if inbreeding avoidance is a factor in mammalian dispersal, then it is likely to be expressed by mothers rejecting their sons because of sex-specific disparities in reproductive costs (Liberg & von Schantz 1985). Under these conditions, subadult males have little choice but to disperse. Conversely, female offspring do not compete reproductively with either parent, and so mothers may show greater tolerance toward their daughters, thereby minimizing the potential for agonistic encounters with unrelated individuals while dispersing through unfamiliar terrain.

Prey abundance has been cited as an alternative to estrus in prompting emigration. Logan & Sweanor (2001) hypothesized that maternal estrus was the most plausible ultimate explanation for the timing of offspring independence, but observed a dispersal pulse coinciding with the late-summer birthing season of desert mule deer. Ungulates are the staple prey for cougars, but subadults tend to exploit more non-ungulate prey than adults (Knopf et al. 2010). Importantly, these hypotheses are not mutually exclusive because of the overlap in season and the fact that many small mammals give 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 dispersal sometime around estrus when food abundance is generally increasing.

Is cougar movement influenced by landscape permeability?

Our hypothesis, that dispersal patterns should be shaped by landscape permeability, was largely supported. Mean dispersal distances were similar between sexes, with Oquirrh distances being shorter compared to Monroe, reflecting the surrounding basin and range structure of the habitat. Animals that stayed in the Oquirrhs were limited to short distances, but those that left had to cross up to 25 km of unsuitable habitat. Only 36% of dispersers left the Oquirrhs, suggesting that broad desert basins may represent psychological movement barriers to some individuals. In contrast, Monroe animals had relatively uninterrupted habitat to traverse. Our results approximate the pattern of cougar dispersal elsewhere, in that distances were longer in remote areas (Sweanor et al. 2000, Thompson & Jenks 2010), and shorter in habitats constrained by anthropogenic barriers (Beier 1995, Maehr et al. 2002). However, our results contrast with others (Logan & Sweanor 2010), in that we found no sex differences in dispersal distance; indeed, our three longest movements were all made by females.

Dispersers from both sites exhibited directionality in their movements, with Oquirrh animals oriented southwest and Monroe animals tending easterly. Oquirrh dispersers were constrained by the Great Salt Lake and the Wasatch Front metro area (see Fig. 3). We documented only one successful crossing of

this urban area and so our results largely support the view that landscape configuration and permeability can channel cougar movement in certain predictable directions (Beier et al. 2010).

Although cougars moved in all directions from Monroe Mountain, the site was well connected to neighbouring habitats by mid-elevation piñon-juniper forests and willow *Salix* spp.-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. Although barriers act as impediments, seasonal prey migrations may interact with landscape connectivity to attract dispersing cougars. In a parallel study of mule deer on Monroe Mountain (N = 65), approximately 14% of wintering deer migrated to summer ranges on adjacent plateaus (UDWR, unpubl. data). These movements matched the destinations of several spring-dispersing male cougars, underscoring prey migration routes as potential predictors of cougar dispersal directions (Pierce et al. 1999).

Do cougars disperse into attractive sinks?
Delibes et al. (2001) argued that attractive sinks are productive sites in which anthropogenic mortality reduces density, making them highly suitable to immigrants (e.g. Robinson et al. 2008). Although our results generally support this concept, settlement patterns differed as a function of productivity gradients characterizing the ecoregions in which our study areas were located. Monroe dispersers showed no differences in habitat quality between their natal and adult home ranges, whereas animals dispersing from the Oquirrhs generally moved into areas of lower productivity. The northeastern slope of the Oquirrhs is impacted by a local 'lake effect' in which northwestern storms pick up moisture as they cross the Great Salt Lake. The Oquirrh Mountains obstruct these fronts, and so receive disproportionately greater precipitation than neighbouring mountains to the west and south. Consequently, habitat quality follows a moisture gradient that decreases from the peaks of the Oquirrhs, west into the Great Salt Lake Desert. Thus, animals deflected by the Wasatch Front urban barrier were directed into less productive habitats. Conversely, no such gradient existed around Monroe and so animals dispersed into habitat of similar quality to their natal range.

Regardless of study area, dispersers moved into areas of high turnover. This pattern varied by sex, with males settling in areas defined by lower harvest rates and higher quality winter ranges relative to females. Although males compete for territories, the relative scarcity of females, and therefore breeding opportunities, may be a greater hindrance to settlement than the presence of a dominant male (Thompson & Jenks 2010). Conversely, female mammals often make habitat selection trade-offs in which they avoid more productive sites if predators or male conspecifics are likely to be encountered (Bleich et al. 1997, Bunnefeld et al. 2006, Rode et al. 2006). Predation risk for cougars is associated with humans and conspecifics. Intraspecific aggression was the most frequent cause of natural mortality on both sites, with females comprising 67 and 80% of the victims from the Oquirrhs and Monroe, respectively (M. Wolfe & D. Stoner, unpubl. data). If selection of an adult home range is predicated on reproductive impulses, then dispersing females may place a higher priority on minimizing predation risk than on maximizing foraging opportunities when immigrating to a population of unrelated individuals. The presence of a saturated population in the Oquirrhs, combined with natural and anthropogenic barriers to the north and east, effectively channelled dispersing cougars of both sexes into marginal habitats experiencing harvest-related turnover. 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?
Despite discrepancies in frequency, habitat quality and population turnover, cougars in this Great Basin ecosystem largely conformed to source-sink predictions. If source-sink models are to be used to inform harvest management, two broad patterns should be considered. First, the transient segment of the population will swell during spring and summer, coinciding with peak recreation and livestock production on public lands. Second, subpopulations adjacent and connected to putative sources are more likely to receive immigrants than those farther away (e.g. McRae et al. 2005). That said, dispersing cougars do not necessarily follow the path of least resistance, and so to improve the accuracy of applied source-sink models, prey migration routes should be incorporated to the extent possible.

These findings have implications for population expansion on the margins of the species' range (Thatcher et al. 2009, LaRue et al. 2012). Cougar recolonization of vacant habitats is hindered by Allee

effects, and measures presented here may be useful for parameterizing models predicting the sources and potential colonizing routes of cougars (e.g. Andersen et al. 2004). The behavioural phenomena described above may have relevance for the management of other polygynous carnivores distributed as meta-populations that exhibit behaviours such as male territoriality, intraspecific aggression and infanticide.

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