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De facto refugia, ecological traps and the biogeography of anthropogenic cougar mortality in Utah

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ABSTRACT

Aim Modern extirpations within the *Carnivora* have generally followed the human footprint. The contagion hypothesis predicts that range contractions should occur along gradients in human activity, leaving relict populations in remote areas at range edges. We evaluated this hypothesis for cougars (*Puma concolor*), a widely distributed and heavily exploited North American carnivore.

Location Colorado Plateau and Great Basin ecoregions within Utah, USA.

Methods We examined the spatial distribution of anthropogenic cougar mortality ($n = 4217$) using indices of remoteness and habitat quality within a GIS/multiple-regression analytical framework. To identify areas of disproportionately high or low exploitation rates, we used break-points from the literature and local field studies. We defined *de facto* refugia as watersheds with mean annual harvest rates $\leq$ 24% of the predicted population, whereas ecological traps were those watersheds that exceeded this value.

Results Cougar harvest rates were greater in the core and lower along the periphery of their statewide geographic range. The largest refugia were overrepresented in arid ecoregions with low human population densities, whereas ecological traps were concentrated in areas of low remoteness. Ecological traps were within mean cougar dispersal distances from refugia, highlighting the potential for source-sink dynamics. Patterns of anthropogenic cougar mortality generally followed the predictions of the contagion hypothesis, being spatially correlated with human access in high-quality habitats.

Main conclusions Low-quality habitats on the range margins are likely to harbour carnivore populations in the event of widespread human-caused declines, and therefore may have greater conservation value than has previously been assumed. Resource managers may consider using the distribution of *de facto* refugia and ecological traps within a source-sink context to develop conservation strategies for cougars and other wide-ranging, low-density carnivores with high dispersal tendencies.

Keywords

Colorado Plateau, ecological trap, exploitation, Great Basin, *Puma concolor*, range contraction, refuge.

INTRODUCTION

During periods of synoptic environmental change, the melting-range hypothesis predicts that species' distributions should contract inward from low-quality, marginal habitats along the range edges to the most productive habitats in the range core (Brown, 1984; Lomolino *et al.*, 2006). Despite substantial empirical support for this hypothesis, in a review of modern extinctions and range contractions, Channell & 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. The authors concluded that remote regions may represent refugia for species sensitive to anthropogenic disturbances.

The singular and combined effects of exploitation, habitat fragmentation and prey depletion have played an important role in carnivore range contractions across the western hemisphere (Laliberte & Ripple, 2004; Cardillo *et al.*, 2005; De Angelo *et al.*, 2011). Importantly, patterns in population persistence have shown tremendous spatial heterogeneity. For example, cougars (*Puma concolor*) are a widely distributed, habitat generalist historically found across both American continents. The species was extirpated from most of eastern North America following European colonization (Morrison *et al.*, 2007), but the westward contraction of cougar range ended abruptly at the Rocky Mountain front. Their current range within the Intermountain West is characterized by dramatic variations in aridity, topography, prey abundance and human population density. Taken together, this suggests that cougar behavioural and morphological adaptations to steep, rugged terrain have conferred some protection to individuals in remote areas where human access is constrained.

In nearly all North American jurisdictions where extant, cougar populations are exploited for sport harvest, livestock protection or human safety (Packer *et al.*, 2009). Ironically, despite continental-scale range contractions, locally the species has 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 & Merchant, 2005; Wilson *et al.*, 2010), and their IUCN ranking as a species of 'least concern' (Caso *et al.*, 2008). Over most of their current range, cougars are simultaneously managed to minimize predation impacts on ungulate populations, and for sustainable sport hunting opportunities (Cooley *et al.*, 2011). These often conflicting objectives are complicated by the lack of robust population trend estimators, which has led to a greater focus on the identification of potential source populations (Choate *et al.*, 2006). If protected areas are large relative to a species' spatial requirements, then they may serve as unexploited refugia. However, delineation of protected area boundaries is often based on socio-economic factors, rather than ecologically meaningful criteria. In these cases, the efficacy of parks as buffers against over-exploitation may be compromised if the focal species strays beyond the boundaries as a result of ranging habits, high edge-to-area ratios or seasonal prey migrations (e.g. Ruth *et al.*, 2011). These phenomena may attract hunters to reserve boundaries (Tolon *et al.*, 2012), and consequently, some carnivore populations inhabiting protected reserves are demographically indistinguishable from their counterparts in unprotected areas (Balme *et al.*, 2010a; Loveridge *et al.*, 2010). As a result of these constraints, research over the past decade has emphasized use of the source–sink model for managing cougars and

other large carnivores (Sweanor *et al.*, 2000; Balme *et al.*, 2010b; Cooley *et al.*, 2011).

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 artefact of patterns in human strife (Martin & Szuter, 1999), yet scant research has been conducted to identify *a priori* where exploited carnivores are likely to persist either locally or within their global distributions (e.g. Naves *et al.*, 2003; Rabinowitz & Zeller, 2010). Here, we used the distribution of regulated cougar exploitation in Utah to test two predictions from the contagion hypothesis: (1) that anthropogenic mortality would be positively correlated with human access, but uncorrelated with habitat quality; and that (2) refugia would be disproportionately located in marginal habitats within a defined portion of the species' range. We then mapped these results to identify areas of both disproportionately low and high harvest rates, which we qualitatively refer to as *de facto* refugia and ecological traps.

METHODS

Study area

Utah lies at the geographic centre of the Intermountain West, straddling the Colorado Plateau and Great Basin ecoregions. The Uinta-Wasatch Mountains and Plateaus form the central cordillera of the state and the division between these drainage systems. Moisture comes principally during winter in the form of snow, but the southern half of the state experiences a second mode derived from monsoonal rainstorms. Precipitation is strongly correlated with elevation and varies from 13 to 150 cm annually. Elevations extend from 550 to 4150 m, with commensurate variation in plant communities, ranging from Mojave Desert to alpine tundra ecosystems (Banner *et al.*, 2009).

Within North America, cougar distribution is predicated on the availability of ungulate prey, particularly mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*; Beck *et al.*, 2005). In Utah, cougars exhibit a broad habitat tolerance, occurring from the semi-arid, low-elevation piñon-juniper (*Pinus edulis*, *Juniperus* sp.) belt, to the mesic, aspen (*Populus tremuloides*) and conifer dominated forests of the higher mountains and plateaus (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 relatively large, mesic patches (Fig. 1).

Study design

Cougars are not amenable to precise enumeration at large scales and so are managed in a recursive manner using har-
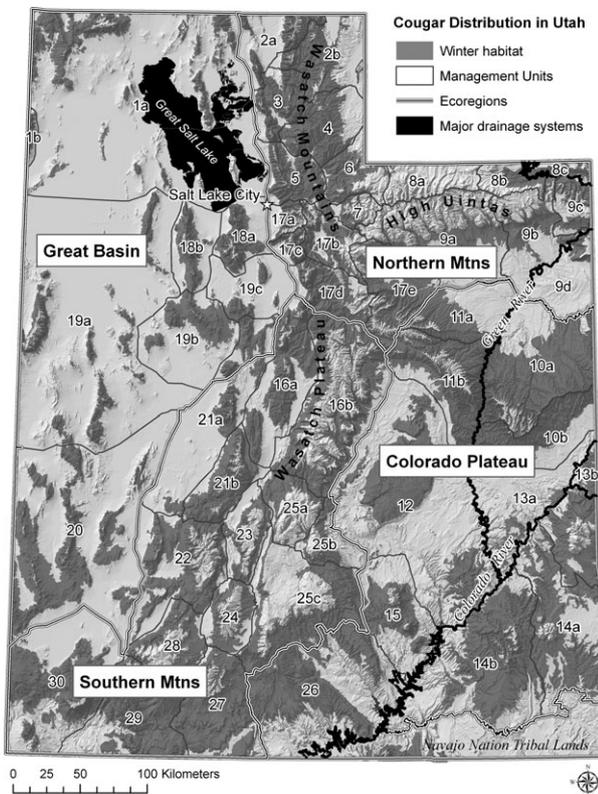
Figure 1 Utah cougar management units evaluated for remoteness, prey density, and cougar harvest, 1996–2007 ($N = 52$). Gray shading indicates predicted winter habitat for cougars and primary prey species. See Table 1 for details.

vest indices. Permit numbers are regulated through the use of a model in which demographic (proportion of the kill comprised of adult females) and catch/unit-effort (mean number of days required to catch a cougar) data collected during year t are used to adjust opportunity for year $t + 1$. Actual harvest strategies and permit numbers are predicated on local or regional priorities such as ungulate population trends, conflicts over livestock production or quality hunting experiences for a limited number of licensed hunters (detailed in Cooley et al., 2011). Despite inter-annual variation in permit numbers, long-term harvest trends tend to reflect environmental productivity, and therefore, measures of opportunity are not independent of actual harvest rates (Cougar Discussion Group, 2009).

We were interested in how factors beyond management prescriptions modified the distribution of hunter harvest after controlling for differences in habitat quality. To achieve this, we used spatially explicit harvest data in ArcGIS (ESRI, Redlands, CA, USA) to examine how cougar harvest rates varied in relation to remoteness and habitat quality. All spatial data were recorded in Universal Transverse Mercator projection (datum = NAD 83). Statistical comparisons were made using SAS software (version 9.2), and descriptive statistics are reported as the mean ± SD unless otherwise noted.

Habitat map

Our base explanatory variable was a map of predicted cougar distribution developed by the Utah Division of Wildlife Resources (UDWR). This model uses the union of three variables to delineate cougar habitat: presence of mule deer or elk, 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 to human-caused mortality. In mountainous regions, mule deer and elk exhibit elevational migrations in response to the timing of snow accumulation and plant phenology (Monteith et al., 2011). 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 zone occurs between 1540 and 2300 m depending on winter severity, aspect and other site-specific factors. The cougar hunting season spans mid-November through early June, but ~ 90% of the kill occurs between December and early March when snow cover facilitates tracking with hounds. To account for seasonal effects on cougar habitat use, we used an elevational cut-off to define the upper boundary of winter habitat. Using radio-telemetry data from 76 cougars monitored during our long-term field studies, we calculated the mean winter elevation + 1 SD used by marked animals (Stoner et al., 2006; Rieth, 2009). This produced a ceiling of 2615 m, which excluded most alpine and subalpine communities. Similarly, we removed desert basins where we assumed cougar presence was itinerant due to the lack of sufficient cover and prey resources (Sweanor et al., 2000).

Sampling units and cougar harvest rates

We used UDWR defined cougar management units and subunits (heretofore CMUs; Fig. 1) to assess coarse-scale variation in cougar harvest. Mean habitat area within CMU boundaries was 1550 km² ± 1170 ($N = 52$). To examine within and among CMU variation, we used 1:24,000 scale watershed boundaries (12-digit hydrologic unit codes, HUC; Natural Resources Conservation Service, 2007). Twelve digit HUCs represented the best compromise between the spatial scale of animal behaviour (cougar home ranges; Rieth, 2009) and capturing within CMU variability ($N = 1932$ watersheds; mean area = 48 ± 30 km²). 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, 2009). Watersheds also best approximated the scale and description of cougar mortality locations as recorded in annual harvest data.

To control for confounding factors, we subsampled the 1932 watersheds into reasonably homogenous groups. We censored all watersheds closed to the public or where cougar hunting was prohibited (industrial mines, military lands and

national parks, $N = 64$). Although these areas likely qualify as refugia, they did not meet our criteria that the habitat was open to hunting, and therefore could not inform us about the statistical relationship between harvest rates and remoteness. We also censored 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*). Watersheds were nested within predicted habitat, which was nested within CMUs, with the final sampling units representing the intersection of these three variables.

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 spatial data, including the sex, age 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 ($N = 4,507$). Hunter harvest represents the single greatest cause of cougar mortality systematically quantified at the statewide scale (> 90%). Although other natural (intraspecific strife, malnutrition) and human (poaching, roadkill and control actions) causes can be locally important to cougar populations, we excluded these data because of their relative scarcity and poor precision. Harvest location data were accurate to the drainage within a CMU, but some CMUs contained drainages with duplicate names. In these cases, we segregated drainages 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 and measured the response variable as a density, where harvest rate was defined as the number cougars killed per year 100 per km². The edited dataset comprised 1626 watersheds, varying in size from 10 to 170 km² (mean = 45 ± 28 km²), representing 4217 animals.

Remoteness index

We ranked CMUs on the basis of five variables hypothesized to affect the relative amount of hunting pressure a given habitat patch might receive, including human population density, distance to urban area, road density, distance to nearest paved road and per cent of habitat in 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 centre of the watershed (a mean UTM) to the nearest urban area or paved road as the least-cost path.

We defined population density as the number of people per 100 km² living within a 1 km radius 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 $\geq$ 500 permanent residents. Road density measures derived from 1:100,000

scale digital line graphs were calculated as the total kilometres of unimproved road per 100 km² within a watershed. We limited our analysis to unpaved roads because hunters typically access habitat using off-highway vehicles on unplowed roads. Distance to nearest paved road was calculated as the least-cost-path from the watershed centre to the nearest paved road (in km). To calculate the per cent 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 (Automated Geographic Reference Center, 2007).

Cougar management units were ranked from 1 to 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 summed the five ranks to create a score for each CMU and ranked each unit in a linear fashion (discounting proportional differences; Fig. 1, Table 1).

Ungulate density

Cougars are obligate carnivores and as such their habitat is defined by prey density and stalking cover (Beck *et al.*, 2005). Of these, prey density is a more direct measure of habitat quality, and therefore a better predictor of potential cougar abundance (Pierce *et al.*, 2000; Carbone & Gittleman, 2002). The UDWR calculates indices of relative abundance for mule deer and elk on all CMUs. Annual surveys were designed to estimate herd productivity and delineate winter ranges for both species. State wildlife managers conducted ground-based classification counts (number juveniles/adult female) from mid-November through December. Elk estimates were supplemented with aerial transects flown on triennial intervals conducted during January–February. 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 expected 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 harvest may be causally related to ungulate abundance), we regressed estimates of ungulate abundance on an independent predictor variable, June Normalized-Difference-Vegetation-Index (NDVI; Pettorelli *et al.*, 2011). Abundance estimates correlated strongly with satellite-derived indices of primary production (Spearman's correlation coefficient, $r = 0.77$, $N = 52$, $P < 0.001$), suggesting that patterns in ungulate abundance were more likely a product of variation in primary productivity than cougar harvest rates, and therefore, ungulate density was suitable as a predictor of potential cougar density (but see Basille *et al.*, 2009 for a discussion of variation in this general pattern).

Analytical techniques

At the statewide scale (213,772 km²), we conducted comparisons among both individual watersheds and CMUs. We used multiple linear regression techniques to analyse putative effects of remoteness and ungulate density on cougar harvest rates. For among CMU comparisons, we used a square root transformation of ungulate density and cougar harvest to control excessive variance and to meet assumptions of normality. 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. We then overlaid median ungulate density values for each habitat category on the regression.

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 predicted habitat open to hunting that exhibited relatively low hunting mortality rates; and conversely, ecological traps were those habitats exhibiting relatively high harvest levels. We assumed that cougar density was homogenous across watersheds within a habitat category. Further, based on radio-telemetry studies conducted locally (Stoner *et al.*, 2006) and over a range of habitat types in North America (tabulated in Logan & Sweanor, 2001), we assumed that low-, medium- and high-quality habitats could harbour mean densities of 0.5, 1.5 and 2.5 non-juvenile cougars per 100 km² and could remain stationary under annual harvest rates of ≤ 24% of predicted density (Anderson & Lindzey, 2005; Beck *et al.*, 2005; Robinson *et al.*, 2008). Logan & Sweanor (2001) postulated that when hunting mortality is strongly compensatory, harvest rates would have to exceed 28% of the population in order to cause declines, but when harvest is additive to natural mortality, declines could result at rates as low as 12%. We used the 24% value to distinguish refugia from ecological traps, and therefore, a dichotomous categorization scheme in which every watershed fell into one category or the other. We then calculated the percentage of area that fell above and below this threshold. Although the generality of this value is debatable (Logan & Sweanor, 2001; Anderson & Lindzey, 2005), given currently available estimates in the literature, we felt it represented a practical break-point for distinguishing the relative differences in hunting mortality among heterogeneous habitats.

Carnivore home range size is negatively correlated with prey density (Herfindal *et al.*, 2007), and we expected a refuge could effectively protect individuals or subpopulations if the 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 & Sweanor, 2001), then this metric would represent a suitable index for assessing the demographic value of a refuge. We consulted the literature to determine male home range size over a variety of habitat types and 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 (tabulated in Logan & Sweanor, 2001), mean male home range was 363 ± 185 km². 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, and therefore most demographically meaningful, refugia and traps. We then calculated the effective harvest rate for all watershed clusters (both refugia and ecological traps) as the mean harvest rate (no. cougars per year 100 km^{-2}) with respect to the predicted habitat-specific density. This metric provided an index of the proportion of the predicted population removed annually through harvest. Lastly, we calculated the mean distance between each ecological trap and its three nearest refugia.

RESULTS

Among CMUs, remoteness and ungulate density were significant predictors of cougar harvest (remoteness $t_{47} = -2.29$, $P = 0.03$; ungulate density $t_{47} = 3.18$, $P = 0.003$) as was the full model ($F_{2,47} = 18.07$, $P < 0.001$, adj. $R^2 = 0.41$; Fig. 2). Remoteness was negatively correlated with cougar harvest (slope = −0.005, SE = 0.002), whereas ungulate density had a positive effect (slope = 0.012, SE = 0.004). Together they acted in an additive manner, such that CMUs defined by high remoteness and low ungulate density exhibited the lowest harvest rates.

After removing CMU boundaries and examining watersheds solely on the basis of habitat quality, predicted winter habitat totalled 78,660 km², with low-, medium-, and high-quality habitats comprising 50, 32, and 18% of the sum, respectively. Based on criteria defined above, total refuge area (47,177 km²; $n = 1039$ watersheds) exceeded that of ecological traps (31,483 km²; $n = 587$) by approximately 50%. The proportion of area classified as ecological traps was positively related to habitat quality, although the difference between medium and high categories was small when those categories were compared to low quality habitats (Fig. 3).

Watershed clusters constituting major refugia ($N = 31$) and ecological traps ($N = 25$) were distributed across all habitat categories and ecoregions (Fig. 4; Table 2). The most productive refugia were the Wasatch Front (no. 6) and the southeastern Wasatch Plateau (nos. 16-17). The seven largest refugia (> 1000 km²) were all comprised of low- to medium-quality habitats located in the Colorado Plateau ecoregion, of which two exceeded 3300 km² (nos. 27, 30). Mean annual harvest rates among major refugia were 6.0 ± 3.7% (range = 0–15.4%) of the predicted population, of which two had no recorded harvest mortalities during the 12-year

Table 1 Habitat characteristics of cougar management units in Utah (*N* = 52), 1996–2007. Remoteness scores in column four are ranked from 1 to 52, with 1 being the least remote. Subunits 8a and 9a were dropped from the model due to the lack of winter habitat and occurrence of cougar harvest data.

Cougar Management Unit		Habitat		
No.	Name	Area (km²)	Remote	Quality
1a	Box Elder	2286	20	Med
1b	Box Elder, Pilot Mtn	150	38	Low
2a	Cache, North	736	16	High
2b	Cache, South	1294	12	High
3	Ogden	1273	11	Med
4	Morgan-Rich	1744	32	Med
5	East Canyon	1138	8	Med
6	Chalk Creek	842	30	High
7	Kamas	305	5	High
8b	North Slope, West Daggett	339	19	High
8c	North Slope, Three Corners	373	33	High
9b	South Slope, Vernal	937	25	High
9c	South Slope, Diamond Mtn	478	46	High
9d	South Slope, Bonanza	180	39	High
10a	Book Cliffs, Bitter Creek	2669	50	Low
10b	Book Cliffs, South	2286	45	Low
11a	Nine Mile, Anthro	998	49	Low
11b	Nine Mile, Range Creek	3186	41	Low
12	San Rafael	3470	44	Low
13a	La Sal, La Sal Mtns	1781	23	Med
13b	La Sal, Dolores Triangle	287	37	Med
14a	San Juan, Abajo Mtns	3165	21	Low
14b	San Juan, Elk Ridge	4267	42	Low
15	Henry Mtns	1376	43	Low
16a	Central Mtns, Nebo	2339	17	Med
16b	Central Mtns, Manti	3718	9	High
17a	Wasatch Mtns, Salt Lake	290	3	High
17b	Wasatch Mtns, Heber	594	13	High
17c	Wasatch Mtns, Timpanogos	239	2	High
17d	Wasatch Mtns, Diamond Fork	1198	14	High
17e	Wasatch Mtns, Avintaquin	1976	36	Med
18a	Oquirrh-Stansbury, Oquirrh	572	7	Med
18b	Oquirrh-Stansbury, Stansbury	847	18	Low
19a	West Desert, Deep Creek Mtns	1523	47	Low
19b	West Desert, Vernon	1223	34	Low
19c	West Desert, North Tintic	233	1	Low
20	Southwest Desert	4407	40	Low
21a	Fillmore, Oak Creek	1271	27	Med
21b	Fillmore, Pahvant	1735	4	Med
25a	Plateau, Fish Lake	711	28	High
25b	Plateau, 1000 Lake	314	29	High
25c	Plateau, Boulder	2318	35	Med
22	Beaver	2557	15	Med
23	Monroe Mtn	726	10	High
24	Mount Dutton	851	24	Med
26	Kaiparowitz	3808	48	Low
27	Paunsaugunt	3161	31	Low
28	Panguitch Lake	1374	6	High

Table 1 Continued.

Cougar Management Unit		Habitat		
No.	Name	Area (km²)	Remote	Quality
29	Zion	2232	26	Low
30	Pine Valley	2899	22	Med

sampling period (nos. 2 and 6). Twenty-five ecological traps exceeded 200 km², and of these 80% were adjacent to a refuge. Mean annual harvest rates among major ecological traps were 90.2 ± 48.5% of the predicted population (range = 40.5–260.4%). Euclidean distances between ecological traps and the three nearest refugia averaged 56 ± 29 km (range = 26–136 km).

DISCUSSION

The contagion hypothesis predicts that remote habitats are more likely to harbour relict populations when range contractions are anthropogenically driven, regardless of habitat quality. Our data largely support this argument. Hunting-induced mortality rates were greatest in easily accessible habitats with high prey density; and conversely, lowest in remote areas with sparse ungulate prey. However, the correlation between harvest and habitat quality was positive rather than neutral reflecting the association of towns with mesic sites. In support of our second prediction, the largest refugia were primarily situated in remote habitats on the margins of the species' statewide range. This pattern also varied, as among prey-rich habitats, we documented both remote areas with high harvest rates, that is, ecological traps (unit 8c) and near-urban areas with no harvest (unit 17a). If hunter behaviour follows the law of diminishing returns, then these patterns are best explained as sport
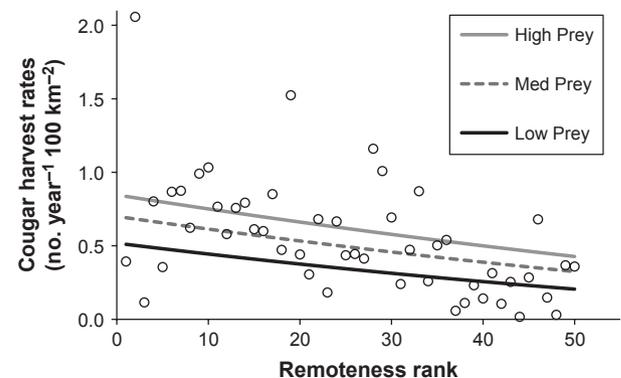

Figure 2 The effect of remoteness on the distribution of cougar harvest (controlling for variation in prey density). Regressions are presented as median values for high, medium, and low prey densities.
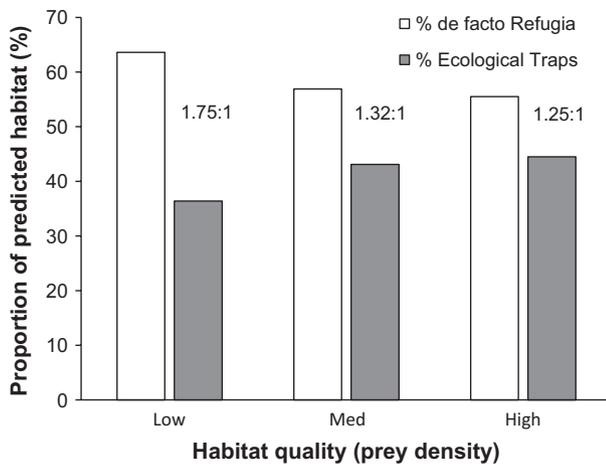
Figure 3 Proportional distribution and ratio of *de facto* refugia to ecological traps, by habitat quality category (as indexed by prey density), Utah, 1996–2007.

hunters selecting accessible areas defined by 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. Harvest 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 than habitat quality *per se*.

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 source–sink dynamics. Recent research has postulated or documented source–sink dynamics in cougar populations resulting from spatial variability in human-caused mortality (Sweanor *et al.*, 2000; Stoner *et al.*, 2006; Cooley *et al.*, 2009; Ruth *et al.*, 2011), with dispersal from more productive or unexploited populations acting as a subsidy to demes characterized by high mortality. In our analysis, effective harvest rates in refugia averaged 6%, whereas in 8 of 25 ecological traps this metric exceeded 100% of the predicted population. Maximum cougar densities measured in two Utah populations undergoing little to no exploitation were 3.2 independent animals per 100 km² (M. Wolfe & D. Stoner, unpublished data), suggesting that, rather than using unusually conservative density estimates, harvest in these areas was heavily subsidized by transient animals from outside the focal area. Similarly, Robinson *et al.* (2008) reported stationary cougar densities on a small study site (< 1000 km²) subjected to annual harvest rates of ~ 24%, even though modelling of survival and reproductive parameters predicted a declining trend. The authors attributed this pattern to obligatory male dispersal and high immigration rates from surrounding areas subject to lower human-offtake. That said, it is unclear whether the refugia identified herein actually function as source populations. High perimeter–area ratios and animal
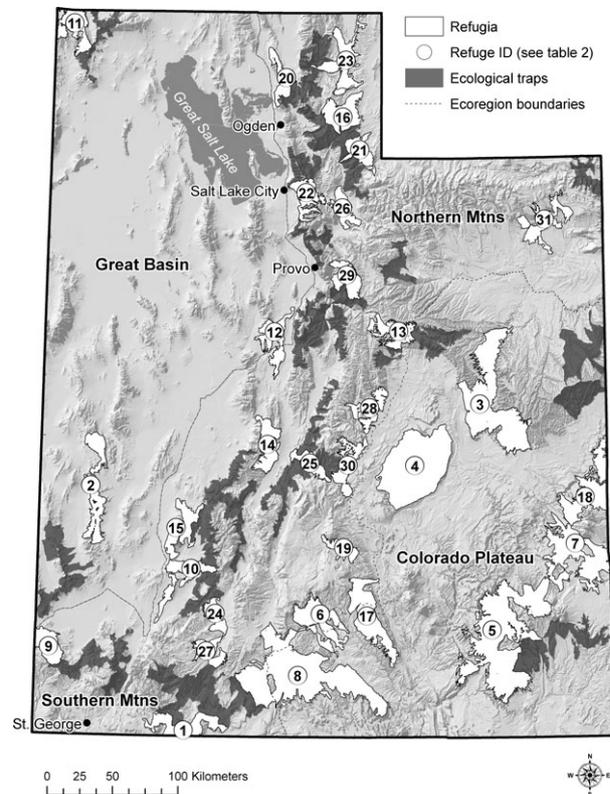

Figure 4 Statewide distribution of 31 major *de facto* refugia (mean annual harvest rates ≤ 24%) and ecological traps (mean annual harvest rates > 24%) for cougars in Utah, 1996–2007. 'Major' connotes those watershed clusters comprising ≥ 200, 400, or 600 km² (for high, medium, and low quality habitats, respectively) of contiguous habitat.

movement patterns indicate that edge effects could compromise the efficacy of some unhunted habitats as refugia. Moreover, the patchy distribution of wintering ungulate herds and our liberal parameter values (winter elevations, harvest rates) beg for field evaluation of putative refugia prior to the implementation of predictive modelling efforts or management prescriptions.

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 (Stoner, 2011). If subadult dispersal is proportionately higher from poor habitats as a result of lower carrying capacity, then these marginal areas may act as net exporters of dispersers even if reproductive rates are relatively low (Andreasen *et al.*, 2012). Parallel field efforts have documented cougar occupancy and reproduction in arid and insular mountain ranges in the Sonoran (Naidu *et al.*, 2011), Mojave (K. Longshore & D. Choate, unpublished data) and Great Basin Deserts (R. Larsen, unpublished data). Coarse-scale modelling efforts such as the one we present here could be supplemented with formal track and camera-trap surveys, offering a means of evaluating cougar occupancy in areas exhibiting relatively low harvest rates. Our results suggest

Table 2 Largest watershed clusters forming *de facto* refugia for cougars in Utah, based on the distribution and level of hunting mortality, 1996–2007 (*N* = 31).

Refuge no.	Management unit, subunit	Refuge location or name	Habitat Quality	km²	Effective harvest rate (%)
1	Zion/Paunsaugunt	Vermillion Cliffs, Moquith Mtns	Low	617	2.7
2	Southwest Desert	Wah Wah Mtns	Low	783	0.0
3	Nine Mile, Range Creek	Desolation Canyon	Low	2462	1.4
4	San Rafael	San Rafael Swell	Low	2525	0.7
5	San Juan, Elk Ridge	Dark Canyon Primitive Area	Low	3303	4.0
6	Plateau, Boulder/Kaiparowitz	Box Death Hollow Wilderness, GSENM[1]	Low-med	852	5.9
7	San Juan, Abajo/La Sal Mtn	Abajo Mtn (N), La Sal Mtn (S)	Low-med	1431	7.6
8	Kaiparowitz/Paunsaugunt/Plateau, Boulder	GSENM*, Kaiparowitz Plateau	Low-med	3389	3.6
9	Pine Valley	Shoal Creek, Little Pine Creek watersheds	Med	423	9.2
10	Beaver	Black Mtns	Med	519	8.6
11	Box Elder	Goose Creek Mtns	Med	522	4.3
12	Fillmore, Oak Creek/W.Desert, Vernon	East Tintic Mtns	Med	527	3.2
13	Wasatch, Avintaquin/Central Mtns, Manti	Price River watershed	Med	538	7.2
14	Fillmore, Pahvant/Central Mtns, Nebo	Pahvant Mtns (NE), Valley Mtns	Med	551	7.1
15	Beaver	Mineral Mtns	Med	557	10.0
16	Morgan-Rich	Deseret Ranch, Lost Creek watershed	Med	616	8.1
17	Kaiparowitz/Plateau, Boulder	GSENM*, Oak Creek watershed	Med	1052	3.7
18	La Sal, La Sal Mtn, Dolores Triangle	La Sal Mtns (N), Dolores River watershed	Med	1052	4.8
19	Plateau, Thousand Lake, Boulder	Fremont River	Med-high	265	11.0
20	Cache/Ogden	Wellsville Mtns, Willard Peak	Med-high	358	7.5
21	Morgan-Rich/Chalk Creek	Echo Canyon, Chalk Creek watershed	Med-high	362	15.4
22	Wasatch, Salt Lake/East Canyon	Wasatch Front	Med-high	506	0.0
23	Cache/Ogden	Bear River Mtns (SE), Crawford Mtns (W)	Med-high	721	5.8
24	Panguitch Lake	Panguitch Creek watershed	High	242	9.7
25	Central Mtns, Manti/Plateau, Fish Lake	Salina Canyon	High	275	13.3
26	Wasatch, Heber/Kamas	Upper Weber/Provo River watersheds	High	303	5.5
27	Panguitch Lake/Paunsaugunt	Mammoth Ridge, Sunset Cliffs	High	354	2.8
28	Central Mtns, Manti	Cottonwood, Huntington Creeks watersheds	High	429	4.7
29	Wasatch, Diamond Fork	Diamond Fork (upper)	High	479	9.0
30	Central Mtns, Manti/Plateau, 1000 Lake	Quitchupah and Muddy Creek watersheds	High	480	4.2
31	South Slope, Vernal	Uinta Mtns (SE)	High	627	4.3

Slashes indicate refuge straddles multiple cougar management units. Effective harvest rate is defined as the mean annual proportion of the predicted population removed by hunter harvest.

*GSENM, Grand Staircase-Escalante National Monument.

that 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 behaviour (Delibes *et al.*, 2001). Over 95% of harvested cougars are captured with the aid of hounds trained to follow scent. Importantly, hounds are most effective on snow-covered, moderate slopes. Snow allows human observers to detect tracks and serves as a medium to hold scent, while gentle terrain enables trail hounds to efficiently pursue cougars. So long as hunting with the aid of hounds remains the predominant mortality factor for cougars in exploited populations (as opposed to other techniques), individuals that can survive in xeric habitats, subsist on alternative prey (e.g. bighorn sheep, feral livestock) or winter at high elevations, are likely to exhibit higher sur-

vival and have an adaptive advantage over conspecifics in habitats without these qualities. Dry, low-quality refugia in southeastern Utah are likely to harbour cougars longer than more productive habitats within the core of the statewide range.

Direct anthropogenic impacts can operate concurrently with synoptic climatic effects, and so, the contagion and melting-range hypotheses are not mutually exclusive. Forecasts for the southwestern United States predict a warming and drying trend over the next century (Seager *et al.*, 2007). Carnivores are sensitive to variation in the abundance of their prey (Pierce *et al.*, 2012) and may only occupy marginal habitats during relatively moist periods. Tertiary consumers are likely the first to be lost from desert communities when primary production drops below a level that can no longer support adequate prey, and therefore, some of the

refugia we identified in these already arid ecosystems may be ephemeral (Table 2, nos. 2–5). Consequently, refugia in poor habitats might become ineffective, while high-quality refugia would take on greater conservation value (Table 2, nos. 22, 28, 30). When cougar range declines stem from direct human causes, refugia will primarily be located in remote and marginal habitats; conversely, if climatically driven, 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.

Channell & Lomolino (2000) described populations of high conservation value as those occupying undisturbed islands, marginal habitats or living at high elevations. Beyond these *de facto* refugia, establishment of protected areas has been proffered as a partial solution to the threat of overexploitation and extirpation (Logan & Sweanor, 2001; Laundré & Clark, 2003). Indeed, spatial or temporal regulation of what Leopold termed the 'hunting factor' constitutes the most primitive form of wildlife management (see Leopold, 1933; and references therein). Yet, few examples exist of protected areas large enough to shelter viable populations of large, wide-ranging mammals (Woodroffe, 2001; Minor & Lookingbill, 2010), and the static boundaries of protected areas may only represent seasonal habitats or have such high perimeter–area ratios that they fail to confer survival benefits to resident animals (Woodroffe & Ginsburg, 1998). Therefore, resource managers may consider using the distribution of *de facto* refugia and ecological traps within a source–sink framework to develop conservation strategies for cougars and other widespread, but elusive mammals that exhibit high dispersal tendencies (Lindzey, 1987; Logan & Sweanor, 2001; Cooley *et al.*, 2011). Long-term conservation of large and mobile species will depend on the incorporation and maintenance of connectivity between, private, multiple-use and other protected or semi-protected lands (e.g. Stein *et al.*, 2008), which may harbour local populations during periods of widespread human-caused declines.

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