Impacts of Rural Development on Puma Ecology in California's Sierra Nevada

By

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To Reba, Ellie, Missy, Cleo, Pearl and Cotton,

your incredible effort and unflagging enthusiasm was a constant inspiration.

and

To the pumas,

knowing you was a rare and wonderful opportunity.

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Abstract

In Western North America, many rural areas are being converted to ranchette-style residential development (2-16$^+$-ha plots), potentially degrading habitat for large carnivores including pumas (*Puma concolor*), and impacting ecosystem integrity. In a rapidly developing rural region of California's Western Sierra Nevada, I studied the impacts of low-density development on puma habitat utility, behavioral ecology, mortality, and viability. I characterized properties experiencing puma depredation, a major puma mortality cause in the study region, and compared attributes of properties that had, and had not, experienced depredation. Most depredations (67%) occurred on ranchette-sized parcels and hobby farms, while 3 professional ranches (2.9% of properties experiencing puma depredations) accounted for a disproportionate share (17%) of depredations and pumas killed (23%). Numbers and densities of goats and sheep most strongly predicted puma depredation on a property, followed by geographic features including high slope and elevation, brushy cover, and proximity to rivers and national forests. I then investigated whether rural development reduced puma habitat utility by examining habitat use and movement parameters from GPS-collared pumas in undeveloped and developed rural areas of the same ecosystem. Development appeared to limit habitat utility, with pumas in the developed zone occupying smaller, less round home ranges than undeveloped zone animals. Unlike undeveloped zone pumas, developed zone animals avoided roads and appeared to use riparian areas as movement corridors, and steep-sided canyons bordering residential areas for rest and feeding cover. Finally, I examined whether rural development functionally fragmented puma habitat at the population, landscape, and individual scales. Dispersal and survival parameters, including a high developed zone mortality rate (42.9%), suggested a “source-sink” population structure. Pumas crossed highways 7.9 times less and housing developments 3.7 times less than expected, and these obstacles threatened to disrupt landscape connectivity. Within their home ranges, pumas avoided developed areas (≤20-acre parcels) and preferentially used less developed areas (>40-acre parcels), especially during the day. Low-density rural development exacerbated puma depredation and mortality, constrained habitat utility, and fragmented habitat. Conserving pumas and associated wildlife communities will require efforts to reduce human-caused mortality, protect corridors, retain open spaces, preserve source populations, and limit anthropogenic obstacles to landscape connectivity.

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Introduction

Pumas (*Puma concolor*) are large carnivores that impact predator-prey dynamics, ecological energy flow, and stability of mammalian carnivore and herbivore communities (Terbough et al. 1999, Logan and Sweanor 2001). Pumas occur at low densities, require extensive habitats and healthy prey populations to remain viable and, thus, present a useful focal species for conservation planning and efforts to avert landscape-level habitat fragmentation (Noss et al. 1996, Crooks 2002). Yet, pumas are relatively resilient and behaviorally plastic (Weaver et al. 1996, Cougar Management Guidelines 2005). The species occupies the broadest geographic distribution of any terrestrial mammal in the western hemisphere besides humans, and a wide range of environments, including human-dominated rural areas (Logan and Sweanor 2001). Residential development, particularly ranchette style subdivision of open spaces into 2- to 16^+-ha (5- to 40^+-acre) plots, is rapidly expanding in rural western North America (Theobald 2005), encroaching upon available habitats for large mammals. Puma sightings and depredations on pets and livestock indicate pumas use developed rural areas (CDFG 2006), but the habitat value of these areas to puma populations is questionable. To conserve pumas and associated biodiversity, we must understand how to identify high quality habitat, and how pumas respond to habitat alteration at the individual and population levels.

In a rapidly developing rural region of California's Western Sierra Nevada, I investigated the factors influencing puma depredation, individual spatial and behavioral responses of pumas to rural development, and whether rural development fragmented puma habitat at

the individual, population, and landscape scales. In Chapter 1, I sought to understand the dynamics of and potential for minimizing puma depredations, an important source of human-caused puma mortality in the study area. I characterized the size of properties experiencing depredation and the types of properties hosting a disproportionate share of the incidents. I then measured and compared attributes of properties that had, and had not, experienced puma depredation, and identified features most related to risk at the property and landscape levels.

In Chapter 2, I investigated puma responses to rural development at the individual level to identify constraints on movement patterns or habitat utility. I compared home range size and shape; within-home range movement parameters; habitat attributes associated with travel and rest or feeding bouts; and within-home range habitat selection, between GPS-collared pumas living in undeveloped versus developed rural zones of the same ecosystem. In the third chapter, I examined whether low-density rural development functionally fragmented habitat for pumas. At the population level, I analyzed whether mortality and dispersal parameters of GPS-collared pumas indicated a "source-sink" condition (Pulliam 1988) between the undeveloped and developed zones of the study area. I tested whether anthropogenic and natural barriers impeded puma movements and thus connectivity within landscapes. Within pumas' home range areas, I determined whether the animals preferentially used or avoided diminishing size classes of residential property parcels, and whether use of parcels by size differed between day and night. I offer recommendations for conserving pumas in the face of rural development.

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CHAPTER 1

Assessing puma depredation risk factors in California's Sierra Nevada

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Assessing puma depredation risk factors in California's Sierra Nevada

Abstract:

California has experienced consistently high levels of puma depredation on pets and livestock, and potential for depredation rises as Californians increasingly reside in puma habitat. We characterized properties experiencing puma depredations in a rapidly developing rural region, and then visited geographically similar properties that had, and had not, experienced puma depredations. Logistic regression and classification tree analysis were used to identify geographic, domestic animal, and animal management features predictive of puma depredation risk at the property and landscape levels. Most depredations (67%) occurred on ranchette-sized (2.0-16.2 ha) parcels and hobby farms, while 3 professional ranches (2.9% of properties experiencing depredations) accounted for a disproportionately large share (17%) of depredations and pumas killed (23%). High numbers and densities of goats and sheep most strongly predicted depredation on a property. Geographic features including high slope and elevation, brushy cover, and proximity to rivers and national forest lands, contributed to depredation risk.

Key words: *cougar, depredation, hobby farm, livestock, mountain lion, ranchette, rural development, wildlife-human conflict*

Introduction

Throughout much of Western North America, pumas (*Puma concolor)* are the only remaining large predator occurring in healthy populations. Changes in land use, landscapes, and management have brought humans and pumas into increasing contact, resulting in threats to human safety and depredations on pets and livestock (Beier 1991, Torres et al. 1996, Cougar Management Guidelines Working Group, 2005:7, 63-66). Removal due to conflicts with humans is a major source of human-induced puma mortality in California, where the species is not hunted. When a puma kills or damages pets or livestock (depredation), the affected party may contact California Department of Fish and Game (CDFG) and request a permit for removal of the puma by his/herself or by a wildlife control officer (Updike 2005).

In California, incidents of puma depredation increased fairly steadily during 1972-2000 (Figure 1-1). This increase was coincident with factors including cessation of puma hunting, recovery of puma population from suppression, human expansion, land use changes, and fluctuations in mule deer numbers *(Odocoileus hemionus)*, the pumas' main prey source. State policy from 1907-1963 aimed to increase deer populations and minimize depredation on livestock by suppressing the puma population through a bounty (Mansfield 1986, Torres *et al.* 1996). By 1963, puma depredations were rare and deer abundant or overpopulated, so bounties were ended (Mansfield 1986). Since 1972, California's pumas have been managed solely through removal in response to human safety threats or depredation on domestic animals (Updike 2005), a change from preemptive to reactive management. Depredation-related killing has favored take of young male pumas (Torres *et al.* 1996), producing less relative potential for population suppression than the preceding bounty program which favored female take.

The number of pumas killed due to depredation in California rose from 0 in 1972 to a high of 146 in 2000, then fell to 70 pumas removed in 2006 (Figure 1-1). Cessation of the policy of puma population suppression may have driven the initial increase in depredations (Torres et al. 1996). Human expansion into puma habitat, fluctuations in deer numbers, and changes in land use, including a transition from larger scale ranching to hobby farm subdivisions have all likely influenced depredation levels through the duration of the policy. Torres *et al.* (2004) provided data indicating that the mean number of pumas removed annually in California decreased 843% between the final decade of bounties (1951-1960, $\mu = 153.5$ removals/yr) and the first decade of conflict-related puma removal (1971-1980, $\mu = 18.2$ removals/yr). Statewide and regional censuses and research projects indicated that puma numbers and range increased from the 1960's through the 1980's (Weaver 1976, Clark 1985, Mansfield 1986, Updike 2005), while the population likely stabilized in recent years, fluctuating with deer population (Updike 2005). Torres *et al.* (1996) suggested that increases in depredation on pets were related to increases in new home development and human activity in puma habitat, while increases in livestock depredations were related to regional increases in puma distribution and abundance.

Puma depredation is a topic of concern to many in California and elsewhere, as residents lose their animals and pumas face mortality risks that could threaten population viability where development intensifies (Beier 1993). Because potential for puma-human conflict rises as people increasingly reside in and use natural areas, we asked whether depredation risk factors could be identified and potentially mitigated. We characterized the size of properties that had experienced puma depredations, and the types of properties hosting a disproportionate share of these incidents, in a rapidly developing rural region affected by frequent depredation during 2000-2004. We then visited properties that had, and had not, experienced puma depredation and measured geographic, domestic animal, and animal management attributes during site visits and using remote geographical information system (GIS) spatial analysis methods. We compared attributes between properties that had, and had not, encountered depredation, and identified features most related to risk at the property and landscape levels. Several organizations offer pamphlets containing recommendations for minimizing puma depredation risk (CDFG 2006, Wildlife Health Center 2006, Mountain Lion Foundation 2006), but systematic, region-specific study is valuable for identifying the importance of risk factors, and testing the effectiveness of protective measures.

Study area

We conducted this study in Placer, El Dorado and Amador counties in California's Western Sierra Nevada mountains and foothills. This rural region had experienced high numbers of puma depredations in recent years. The western portion of these adjoining rural counties borders the flat, agricultural Central Valley and the Sacramento metropolitan area. Elevation ranges from sea level in the west to over 2500 m at the Sierra Nevada crest. Most private and residential lands are in the western foothills, characterized by oak (*Quercus sp.*) dominated woodlands and chaparral shrublands. Eastward, vegetation transitions with rising elevation to conifer forests. The eastern portion of these counties is dominated by non-residential timberlands, networked by logging roads. Depredations occurred almost entirely in the western study area. Most of these counties' areas provide puma habitat, excluding only valley agricultural lands, urban areas, and the high elevation zones of the Sierra crest.

The area supports populations of mule deer *(Odocoileus hemionus)*, black bear *(Ursus americana)* and puma, but represents a region of ecological concern. Large foothill tracts have been converted to ranchette style settlement, or other uses such as vineyards and orchards. The area is intersected north-south by high-traffic interstate highways US I-50 and US I-80, which serve as corridors for development emanating from the Sacramento metropolitan area. Placer County had the fastest growing human population in California, with an estimated 27.6% increase from 2000 to 2005 (US Census Bureau 2006). Human population increased by 9.6% in Amador County and 13.1% in El Dorado County during the same period. Over 60% of El Dorado County's undeveloped private land has been zoned for residential (0.4-8 ha (1-20 acre)) or exurban (8-16 ha (20-40 acre)) development (Stoms 2004). In Placer County, 93% of the foothills are privately owned, of which over 50% have been zoned for rural residential or urban land use (Stralberg & Williams 2001).

Methods

We used the CDFG puma depredation database to identify study area properties that had experienced depredations (CDFG 2007). This database and supplemental files contained all puma kill permits issued by the department from 1972 onward, provided the number and species of domestic animals killed, address where depredation occurred, acreage, and indicated whether the puma was killed. To characterize the current problem we calculated descriptive parameters for all properties experiencing puma depredations in the study area during 2000-2004, using JMP 5® statistical software (SAS Institute, Cary, N.C.). We determined the mean, median, and standard deviation of parcel sizes, and the number and proportion of puma depredations and removals occurring at each address, to identify properties with a disproportionate share of depredations or pumas killed. Local wildlife damage control agents who had responded to puma depredation complaints helped us characterize the animals raised and the status (professional vs. hobby) of properties of interest.

During 2004-2005, we sampled sets of properties that either had or had not experienced puma depredations in the preceding 5-year period (2000-2004), to identify factors predicting depredation risk. We inputted information from all puma depredation permits issued in the study area during 2000-2004 to an ArcGIS® 9.x (ESRI, Redlands, CA, USA) GIS. We plotted property locations for each permit using county parcel GIS files obtained from Amador, El Dorado, and Placer counties, and GPS locations recorded on site using handheld Garmin® GPS units. Hawth’s Tools v.3.26 (Beyer 2004) extension for ArcGIS 9.x® was used to randomly select a set of these properties that had experienced depredations (hereafter, *depredation properties*) for attribute sampling. Properties experiencing multiple depredations were excluded from being chosen twice but were more likely to be selected due to greater representation in the permit files.

We then selected properties for sampling that had not experienced a depredation (hereafter, *non-depredation properties*), as a control group. We created a residential parcels file in ArcGIS® 9.1 by selecting only properties containing residences from the county parcel layers. To minimize geographic variation between the comparison groups, we built a 10 km buffer around depredation properties, and selected non-depredation properties from residential parcels situated within the depredation properties' buffer zones. To avoid spatial bias toward either dense urban areas or large parcels, we chose non-depredation properties from 6 parcel size classes matched to the selected depredation properties' size classes (Table 1-1). We selected a random set of these residential parcels for sampling as non-depredation properties using Hawth's Tools' "generate random selection". Properties were included in the non-depredation sample only if interviews with residents confirmed that: no puma depredation had taken place within the previous 10 years; domestic animals lived on the land and were kept primarily outdoors; and neither the composition of animals nor animal management practices had changed substantially in the previous two years.

We consulted with professionals who respond to depredation incidents (primarily USDA APHIS Wildlife Services) to generate a list of property characteristics potentially associated with puma depredation risk. This list included a range of geographic, domestic animal, and animal management features that we measured for each sampled property using onsite interviews, onsite measurements, or GIS methods (Table 1-2). All GIS layers used were downloaded from the California Spatial Information Library website (http://gis.ca.gov), except for property parcel layers, which were obtained from the counties. We visited the selected depredation properties and conducted sampling if occupied by the same residents that had experienced the depredation. Only selected non-depredation properties that had outdoor domestic animals were included in sampling. Residents of depredation properties were asked for information on property characteristics at the time the depredation occurred, while residents of non-depredation properties provided information on current conditions. Additionally, we asked residents whether they had been aware that pumas posed a significant depredation threat in their area, before experiencing a depredation or before our visit.

Using the listed site visit or GIS methods (Table 1-2), we recorded the following geographic features from the central point of each property: distance to nearest public land tract >100 km^2 (entirely national forest lands); distance to nearest major river; distance to nearest riparian area, including low order streams; slope; aspect; elevation; and primary vegetation type on property (not at central point). We measured thickness of horizontal cover *in situ* at the brushiest corner of the animal pasture experiencing depredation or the primary animal pasture (for non-depredation properties), by taking readings of distance to cover at each 60° of arc with a laser rangefinder held 1 m above the ground. Domestic animal features documented were species, numbers and density of domestic animals (#/pen size (ha)), and number of goats, sheep, and goats and/or sheep. We recorded animal management features: presence of one or more dogs trained to guard animals (hereafter, *guard dogs*); any type of outdoor dog; electric fence; deterrent lighting, noisemakers, or other deterrents; fence height; availability of shelter for animals; and whether animals were enclosed at night.

To characterize features potentially predictive of depredation, we calculated the percent occurrence, or the mean, median and standard deviation of each factor measured for the depredation and non-depredation properties, using JMP 5®. We tested for differences between means of each variable from the depredation versus non-depredation properties using 2-sample Student's *t*-tests for continuous variables, and contingency tables with the Pearson chi-square statistic for categorical variables, with confidence levels of $\alpha = 0.10$ due to the low proportion of some features in the samples. Several variables were logarithmically transformed to approximate normal distributions.

We next tested the ability of the significant variables identified in univariate analyses to predict puma depredation, using logistic regression with binomial outcome on R® statistical software (R-project 2004). We excluded variables showing no relationship to depredation occurrence in initial univariate analyses. The importance of each variable to predicting depredation occurrence on a property was inferred using hierarchical partitioning statistical analysis (Mac Nally 2000, 2002). Hierarchical partitioning analyzed all possible models, determining the contribution of each variable to explaining variance in depredation occurrence independently of, and jointly with the other explanatory variables. We conducted this analysis using the hier.part contributed package in the $R^{®}$ statistical software (R-project 2004, Walsh and Mac Nally 2005).

To rank the factors predicting depredation risk, we ran a nonparametric multivariate classification tree analysis (Breiman *et al.* 1984) following the method outlined by Maindonald and Braun (2007) using the rpart contributed in the $R^{®}$ statistical software. Classification trees represent a dichotomous key, with splits or branches chosen to minimize model error. The tree displays the importance levels of subordinate depredation risk factors given threshold values of primary risk factors.

Results

Examination of depredation permits issued during 2000-2004 (n = 161) revealed that 3 properties accounted for 16.5% of all permits issued and 23.3% of all pumas killed, while representing only 2.9% of properties experiencing depredations. All 3 properties were professional ranches over 40.5 ha (100 acres) in size, grazing goats and sheep widely on extensive pastures. Properties experiencing depredations during 2000-2004 ranged from 0.2 to 427.0 ha (0.5 to 1055.0 acres), with mean 18.9 ha (48.7 acres), median 7.3 ha (18.0 acres) and standard deviation 64.6 ha (159.6 acres). Sixty-seven percent of properties for which depredation permits were issued were 2.0-16.2 ha (5-40 acres) in area, representing ranchette parcel sizes typical of exurban style development.

We evaluated potential risk factors on 43 depredation properties and 42 non-depredation properties (Tables 1-3 and 1-4). Univariate analyses revealed that depredation properties were significantly closer to large public land segments (>100 km^2), major rivers, and riparian areas, than were non-depredation properties. Depredation properties had higher mean slope, elevation, animal number, animal density, more horizontal cover, and were more likely to have goats or sheep and to be in conifer forest than non-depredation properties. More non-depredation properties occurred in urban or agricultural vegetation types, had outdoor dogs of any type, and enclosed animals at night. Four depredation property residents stated that their animals were normally enclosed at night but had not been enclosed on the date of the depredation. Depredation properties were more often south-facing and less often east-facing than non-depredation properties.

There was no difference in the presence of guard dogs between depredation and non-depredation properties ($t = 1.147$, $p = 0.257$), but non-depredation properties also had significantly fewer goats and sheep, animals for which guard dogs are typically kept. Guard dogs were present on 27.2% (3 of 11) of the non-depredation properties that contained goats or sheep and 14.3% (6 of 42) of non-depredation properties overall. Five (12.8%) of the 39 depredation properties with goats or sheep, and 14.0% of all depredation properties had guard dogs. Although some cattle occurred in the study area and calves appeared infrequently in depredation records (2 records in 2000-2004), none of the depredations investigated involved cattle. Several residents raising goats or sheep stated that they had been encouraged by neighbors or resource managers to keep these animals to reduce the relatively high risk of fire on their properties. Nearly all interviewees expressed interest in recommendations for reducing depredation risk for their animals. Thirty-seven of the 85 interviewees (31.5%) stated they been unaware of the significant threat of puma depredation in their area prior to our interview or to experiencing a depredation.

We determined the relative contributions of each of property attribute to depredation risk by including significant variables identified in univariate analyses in our multivariate analyses. We combined presence of goats and presence of sheep in one category because these animals comprised similar proportions of species killed in our depredation sample (46.5% goats, 48.8% sheep), often occurred together, and were managed similarly. Goats and/or sheep were present on 90.7% of sampled depredation properties. We included only southerly aspect, which displayed the only positive relationship to depredation risk among aspect classes.

Figure 1-2 displays results of multiple regression with hierarchical partitioning analyses, depicting the ability of property features to predict depredation independently, jointly, and total (independent and joint). Presence of goats or sheep on a property explained more of the variance in depredation occurrence than any other factor (20.1% total). Greater numbers of animals and density of animals on a property followed in importance to predicting depredation (14.1% total and 9.4% total, respectively). Subordinate factors positively contributing to depredation occurrence were less distance to horizontal cover (more cover in or near animal pens; 5.5% total), less distance to public land (5.0% total), greater slope (3.9% total), and southerly aspect (3.9% total). Presence of an outdoor dog lowered depredation risk (3.8% total).

When tested for their contribution to depredation independent of the other factors, the variables of primary importance retained their order of importance (goats/sheep present, 6.5%; animal number, 4.7%; animal density, 3.1%), while secondary factors, distance to public land (2.1%), presence of a dog (2.1%), and horizontal cover (2.1%), had similar predictive value. Analysis of the contribution of each factor jointly with the other factors also upheld the primary importance of goats/sheep present (18.6%), animal number (13.0%), and animal density (8.6%). Among subordinate factors, only southerly aspect (3.6%) gained slightly in importance over presence of any dog (2.6%), and slope (3.1%).

Classification tree analysis ranked property features' contributions to depredation risk, contingent upon the other features' values (Figure 1-3). Again, presence of goats or sheep was the primary factor predicting depredation risk. If a property did not have goats or sheep, number of animals > 12.5 predicted depredation risk, with no other significant factors. Properties containing goats or sheep and located above 346 m (1135 ft) elevation faced increased risk of depredation. For properties with goats or sheep lower than 346 m elevation, depredation was less likely unless animal density exceeded 8.0/ha^2 (19.8/acre^2). If animal density for these lower elevation properties with goats or sheep exceeded 8.0/ha^2, then proximity to a river predicted risk of depredation. In this case, properties closer than 7.2 km to a river faced depredation risk. If these properties were further from a river, depredation was less likely.

Discussion

Patterns of puma depredation occurrence in the Western Sierra Nevada reflected the region's mix of rural and suburban development, forests and ranchlands. Three large goat/sheep ranches experienced repeated depredations, and were responsible for 23.3% of puma removals and 16.5% of permits issued, while comprising only 2.9% of properties with depredations overall. However, depredations occurred on a wide range of property sizes (0.2 ha to 427 ha (0.5-1055 acres)), impacting hobby farmers, suburban residents, and ranchers, with a substantial majority of depredations (67%) taking place on ranchette-sizedparcels of 2.0-16.2 ha (5-40 acres). Ranchettes were often used as horse properties or hobby farms with traditional barnyard animals or exotic species (*e.g.*. emus, peacocks, exotic goats and sheep, llama).

Other studies of large predator depredation, including lynx (*Lynx sp.)*, puma, and gray wolves (*Canis lupus*), have examined ranching systems interspersed with forested areas (Mech et al. 2000, Mazzolli et al. 2002, Stahl 2002, Musiani et al. 2003, Polisar et al. 2003, Bradley and Pletscher 2005, Michalski et al. 2006), or free-range forest grazing systems (Ciucci and Boitani 1998, Mazzolli et al. 2002, Odden et al. 2002), but did not focus on developing rural areas. These studies found a combination of geographic and animal management features related to increased depredation risk, including proximity to or proportion of forested area, proximity to a deep river canyon or forested riparian corridor, more vegetative cover, and greater livestock numbers or densities (Ciucci and Boitani 1998, Mazzolli et al. 2002, Stahl et al. 2002, Bradley and Pletscher 2005, Michalski et al. 2006). Corralling and keeping animals closer to residences, which sometimes kept dogs nearby, were found to significantly reduce depredations (Ciucci and Boitani 1998, Mech et al. 2000, Mazzolli et al. 2002, Stahl et al. 2002, Bradley and Pletscher 2005, Michalski et al. 2006). Consistent findings that animal management factors affect depredation risk indicate that adjusting management methods may reduce depredations and thus predator removals.

Similar to studies in ranching and open range systems, we found proximity to public lands (national forests), rivers and riparian areas, greater slope and vegetative cover, and greater animal density, all increased depredation risk for properties with goats or sheep, while dogs had a protective influence. In effect, brushy, sloped, high elevation sheep or goat pastures with creeks or near river canyons and forests, faced higher puma depredation risk. Landscape features positively associated with depredation were related to more rugged or natural environments, generally considered good puma habitat for their ability to provide stalking and security cover, and ungulate prey (Cougar Management Guidelines Working Group, 2005:3, 25). Large numbers of animals on a property led to high depredation risk for that property even without goats or sheep.

Other depredation studies found significant losses of goats and sheep to predators, with fewer losses of cattle, comprised mostly of calves (Ciucci and Boitani 1998, Mazzolli et al. 2002, Odden et al. 2002, Musiani et al. 2003). These studies did not evaluate developing environments or depredation on hobby animals and pets. The strong influence of geographic features and domestic animal characteristics on depredation risk may have impeded our ability to detect significant effects of some animal management features, such as protective fencing, enclosure of animals, shelter, and guard dogs, which were present on relatively few sampled properties. In contrast, dogs of any type were present on many properties and were found to reduce the threat of puma depredation, similar to other studies where guard dogs reduced depredation on sheep and goats (Smith et al. 2000, Andelt 2004). The fact that several depredation properties had typically enclosed animals, but not on the date of depredation, suggested consistency of enclosing animals could be important for avoiding depredation.

Ranchette-style development is common across western North America and puma research and management must address this growing form of land use. Depredation risk factors and effective prevention will differ between hobby farms and professional livestock producers, necessitating different management strategies. Culling pumas is an ineffective solution unless accompanied by other risk reduction measures, given the wide dispersion of development in puma range, pumas' ability to travel long distances (Weaver et al. 1996, Theobald 1997), and the incidence of repeated puma removals from some properties. Long-term control of puma depredations will likely require both ranchers and hobby farmers to adapt protective animal management methods.

Management Implications

We believe that efforts to educate residents about depredation and prevention methods could reduce the numbers of domestic animals and pumas killed, because many interviewees expressed interest in recommendations for reducing risk, and because a large proportion of residents had been unaware of the degree of depredation threat in their area. Residents who are encouraged to raise sheep and goats to minimize fire danger in brushy landscapes should also receive information on how to reduce puma depredation threat. On ranches with a disproportionately large share of depredations, resource managers should work with ranchers to implement protective animal management methods, which may include dogs and will likely be site and operation specific. Hobby farmers and suburban residents should be encouraged to keep dogs and guard or enclose goats, sheep, and other smallstock at night, or avoid keeping these animals, especially in rugged habitat near riparian areas that are likely frequented by pumas. Evaluation of the effectiveness of puma depredation deterrent measures focused specifically on ranchette-sized hobby farms with goats and sheep could yield valuable insights for minimizing puma depredations.

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Tables and Figures

Table 1-1. Number of properties sampled with and without puma depredation by parcel size class in California's Western Sierra Nevada, 2000-2005.

Size in Hectares	0.30-2	2^+-4	4^+-8	8^+-16	16^+-40	40^+-223
Size in Acres	0.75-5	5^+-10	10^+-20	20^+-40	40^+-100	100^+-550
Depredation Properties	8	9	11	6	6	3
Non-depredation properties	8	9	10	6	6	3

Table 1-2. Features evaluated and methods used to assess puma depredation risk for properties with and without puma depredation in California's Western Sierra Nevada, 2000-2005.

Feature Type	Feature	Description	Measurement
Geographic	Distance to public land	Min. distance (km): property center to public land >100 km^2	ArcGIS®, CDFG Public, Conservation & Trust Lands layer
	Distance to river	Min. distance (km): property center to river	ArcGIS®, USEPA River Reach layer, CA Hydrography
	Distance to riparian area	Min. distance (km): property center to riparian area	ArcGIS®, USDA Forest Service Riparian layer
	Slope	Degree slope: property center	ArcGIS® Spatial Analyst slope tool, USGS 1:24k DEM
	Aspect	Cardinal aspect: property center; N, S, E or W	ArcGIS® Spatial Analyst aspect tool, USGS 1:24k DEM
	Elevation	Meters, at property center	ArcGIS®, USGS 1:24k DEM
	Vegetation type	Primary vegetation type	ArcGIS®, CDF-FRAP Multi-Source Land Cover layer
	Horizontal cover	Min. distance (m) to horizontal cover 1 m above ground: brushiest edge of pen or pasture	Site visit; mean of 6 laser rangefinder measurements to nearest cover, taken each 60° from fixed position 1 m high
Domestic Animal	Species	Presence of goat, sheep, dog, or other animals; analyzed individually	Onsite interview
	Number	No. domestic animals kept primarily outside	Onsite interview
	Density	No. domestic animals/ primary pen size (ha)	Onsite interview
Animal Management	Guard dog(s)	≥1 dog trained to guard animals	Onsite interview
	High fence	Main pen fence ≥1.8 m tall	Onsite measurement
	Electric fence	Main pen fence with electrified wires	Onsite interview

Table 1-2 Continued.

Feature Type	Feature	Description	Measurement
Animal Management	Other deterrent	Noisemakers, lighting, llamas, mules	Onsite interview
	Fence height	Main pen mean fence height (m)	Onsite measurement
	Shelter available	Any roofed shelter available to all animals	Onsite interview
	Enclosed at night	Animals enclosed in 4-walled building nightly	Onsite interview

Table 1-3. Central tendency values and mean comparisons for features of properties with and without puma depredations in California's Western Sierra Nevada, 2000-2005. Mean values shown with 95% confidence limits.

	Depredation properties (n = 43)		Non-depredation properties (n = 42)			
	Mean	Median	Mean	Median	*t*-statistic	p-value
Dist. to public land (km)[a]	7.29 ±1.72	5.23	11.00 ±2.00	9.99	3.12	0.003*
Dist. to river (km)[a]	5.32 ±1.33	4.40	7.25 ±1.42	6.90	2.00	0.048*
Dist. to riparian area (km)[a]	0.46 ±0.12	0.38	0.60 ±0.15	0.42	2.04	0.044*
Slope (deg)	10.1 ±1.4	9.2	7.3 ±1.4	7.1	2.84	0.006*
Elevation (m)	558 ±78	597	445 ±79	364	2.11	0.038*
Dist. to horiz. cover (m)[a]	11.9 ±2.8	9.0	24.3 ±6.0	16.5	3.42	0.001*
Animal number[a]	71.4 ±69.7	20.0	8.4 ±2.9	6.0	5.54	<0.001*
Animal density (no./km^2)	0.81 ±0.24	0.40	0.19 ±0.25	0.05	3.53	0.001*
Fence height (m)	1.40 ±0.11	1.22	1.34 ±0.11	1.22	0.81	0.422

*Difference in feature value between properties with and without depredation, two-sample independent Student's t-test, $\alpha = 0.10$.

[a] Natural log (ln) transformation used in analysis.

Table 1-4. Comparison of geographic, domestic animal, and animal management features for properties with and without puma depredations in California's Western Sierra Nevada, 2000-2005.

	Depredation properties (n=43)	Non-depredation properties (n=42)		
	%	%	χ^2	p-value
Vegetation type				
Urban/agriculture	2.3	16.7	5.125	0.024*
Grassland/open woodland	27.9	40.5	1.493	0.222
Chaparral	11.6	4.8	1.325	0.250
Conifer forest	16.3	4.8	2.977	0.085*
Montane hardwood	39.5	31.0	0.685	0.408
Aspect				
North	18.6	31.0	1.741	0.187
South	9.3	26.2	4.170	0.041*
East	44.2	16.7	7.579	0.006*
West	27.9	26.2	0.134	0.714
Goats present	46.5	19.0	7.255	0.007*
Sheep present	48.8	21.4	6.989	0.008*
Goats or sheep	90.7	26.2	36.50	<0.001*
Any dog	62.8	88.1	7.314	0.007*
Guard dog(s)	14.0	14.3	0.002	0.965
High fence	9.3	14.3	0.508	0.476
Electric fence	20.9	23.8	0.101	0.750
Any deterrent	58.1	57.1	0.009	0.926
Shelter available	65.1	76.2	1.255	0.262
Enclosed at night	30.2	47.6	2.704	0.100*

*Difference in feature value between properties with and without depredation, Pearson's chi-square test, $\alpha = 0.10$.

Figure 1-1. Numbers of puma depredation permits issued and numbers of pumas killed for depredation in California during 1972-2006.

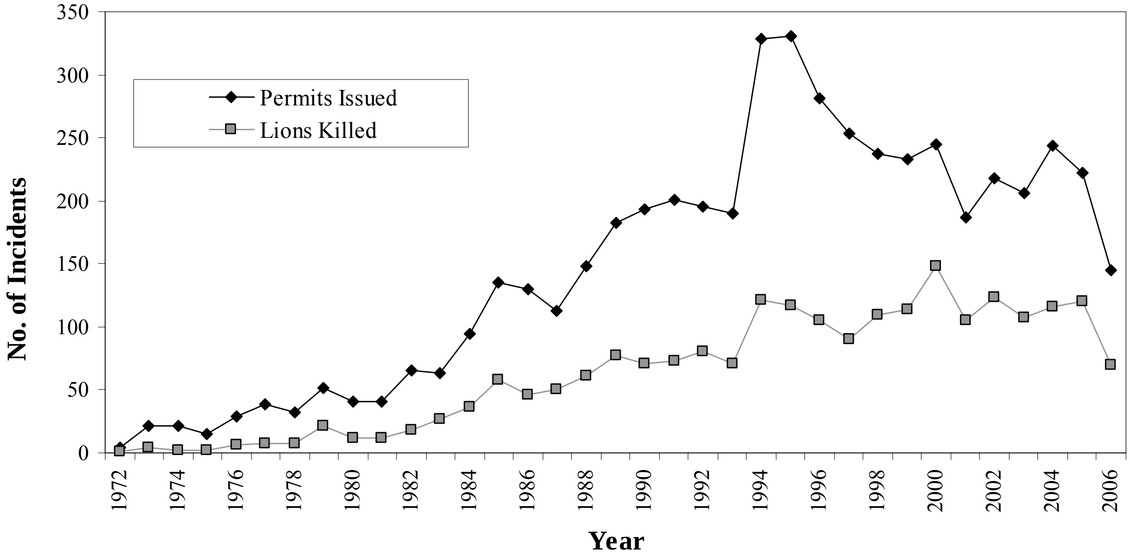


Figure 1-2. Influence of property features on depredation risk for properties with and without puma depredations in California's Western Sierra Nevada, 2000-2005, using hierarchical partitioning analysis.

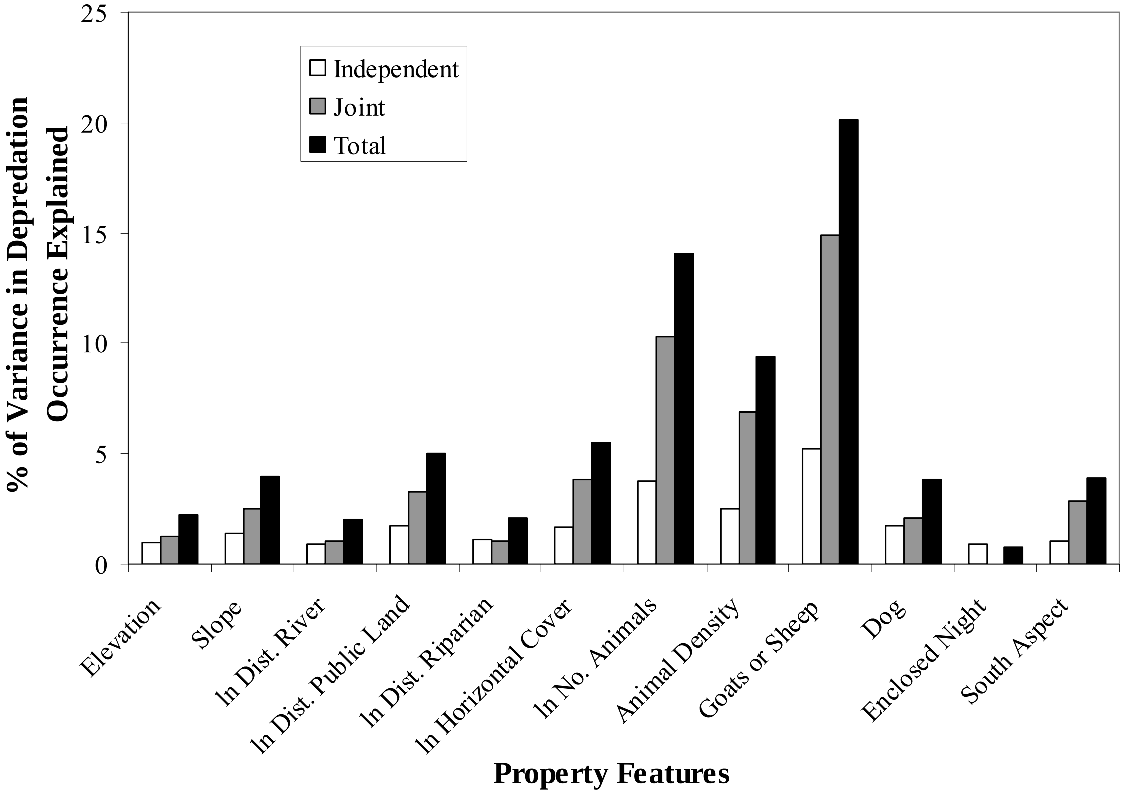
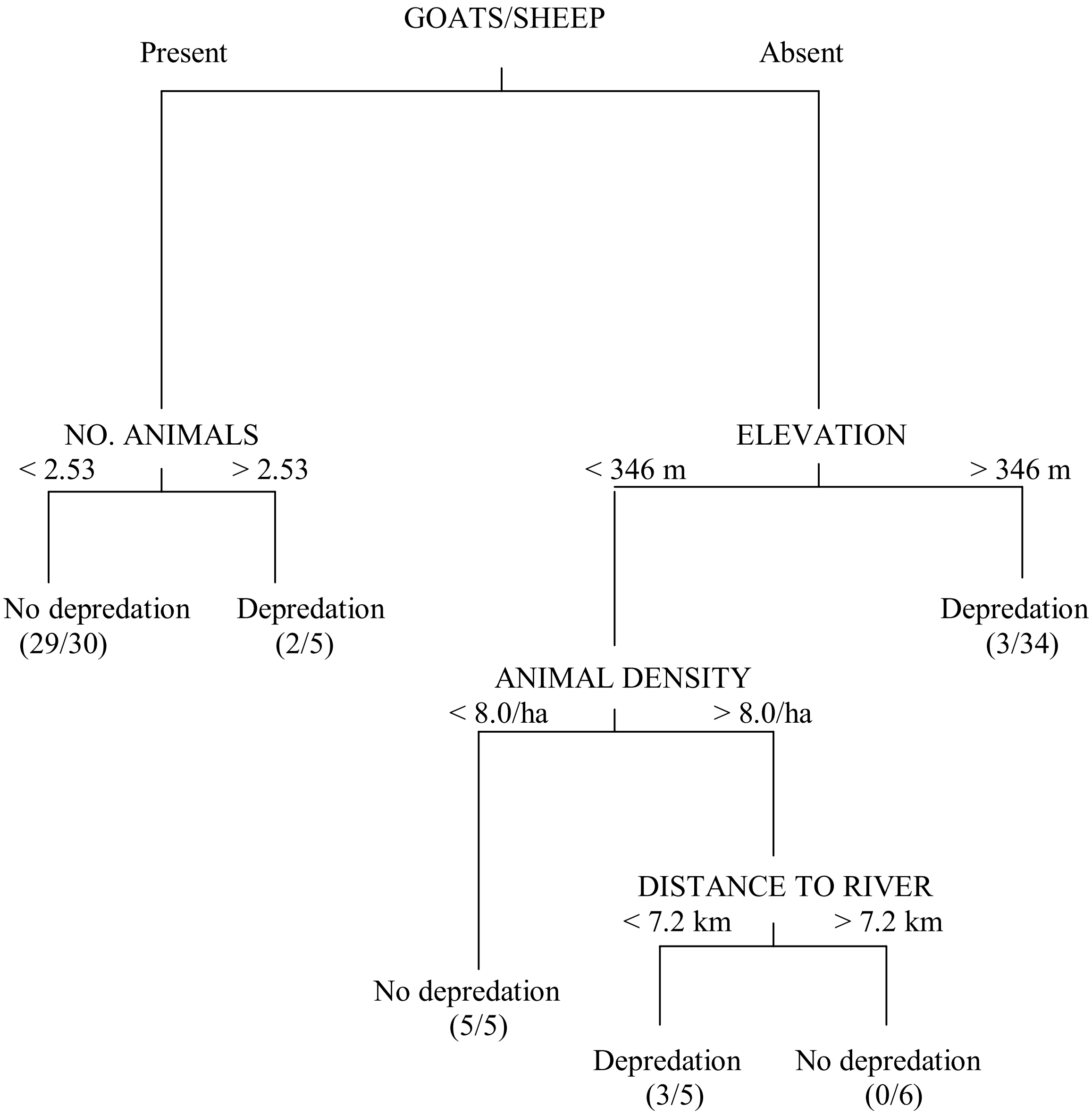


Figure 1-3. Classification tree displaying contingent contributions of property features to puma depredation risk in California's Western Sierra Nevada, measured from properties with (n = 43) and without depredation (n = 42), 2000-2005. Parentheses contain no. of properties containing feature/no. properties overall in each category.



CHAPTER 2

Effects of rural development on puma habitat use

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Effects of rural development on puma habitat use

Abstract:

Rural residential development may reduce habitat utility for large carnivores, potentially impacting population stability and ecosystem integrity. We tested whether ranchette style development constrained habitat use or altered movement patterns of pumas in California's Western Sierra Nevada. GPS collars were used to track pumas in developing rural areas and in undeveloped timberlands of the same ecosystem. We asked whether development affected home range size or shape; movements within home ranges; habitats used for travel or rest/feeding; and pumas' selection of habitats in their home range areas. We assessed the same relationships for subadult versus adult pumas, and males versus females. Development appeared to limit habitat utility. Developed area home ranges were smaller and less round than those in the undeveloped zone. Subadult male home range sizes were similar to those of females and often located along the urban interface. Developed zone pumas used lower slopes, lower elevations, and used riparian areas more often, for travel than for rest or feeding. Undeveloped zone animals used only low-traffic road zones more for travel than for rest or feeding. Selection of habitats within home range areas was influenced by aspect and vegetation type for undeveloped zone animals. In contrast, developed zone pumas avoided roads, and exhibited preference for riparian areas, high slopes, low elevations and large parcel sizes within their home range areas. Developed zone pumas appeared to use riparian areas as movement corridors, and steep-sided canyons bordering residential areas for rest and feeding cover. Movement parameters differed with sex but not development zone.

Key words: *cougar, rural development, GPS collars, habitat use, habitat utility, home range, mountain lion, movement, ranchette*

Introduction

Pumas are relatively resilient large carnivores, behaviorally plastic in their ability to occupy a range of habitats given adequate stalking cover, and utilize various prey in times of scarcity (Anderson 1983, Karr and Freemark 1985, Weaver et al. 1996). In large expanses of rural western North America, pumas persist where open spaces are being converted to low-density, "ranchette" style development, characterized by 2- to 16^{+}-hectare (5- to 40^{+}-acre) residential subdivisions (Duane 1996). Rural development could alter behavior and habitat value for wide-ranging carnivores, undermining resiliency mechanisms and threatening persistence and ecological integrity (Noss et al. 1996, Weaver et al. 1996). We investigated the impacts of rural residential development on puma behavioral ecology at the individual level.

Rural development may increase large mammal mortality including by vehicle collisions, legal or illegal killing, removal of animals threatening humans or property, disease transmission, or accidental poisoning (Harris and Gallagher 1989, Noss et al. 1996, Forman and Alexander 1998, Sweanor et al. 2004, Cougar Management Guidelines Working Group 2005). Cumulative effects of highways, fencing, horticulture or residential developments may limit the routes available for carnivores to search for food and mates, and degrade interior habitat security and prey population stability or abundance (Theobald et al. 1997). Obstacles and residences can limit home range placement and size, or cause large carnivores to range more widely for adequate resource access (Van Dyke et al. 1986, Weaver et al. 1996, Riley et al. 2003). Habitats used for travel could be limited, and poor habitats and obstacles could force animals to travel more or move greater distances (Tigas et al. 2002, Dickson et al. 2005). Large carnivores may avoid areas associated with roads or housing developments, and alter selection of habitats within their home ranges in response to development (Weaver et al. 1996, Jalkotzy et al. 1997).

To identify possible constraints to puma habitat utility posed by rural development, we compared habitat use patterns between GPS-collared pumas in adjacent undeveloped forests (*hereafter, undeveloped* zone) and rural developed areas (*hereafter, developed zone*), as well as between puma sexes and age classes. We asked whether puma home range sizes or shapes differed between these groups. We tested whether development zone, age, or sex related to differences in short-term distances moved by pumas, turn angles along estimated movement paths, or overall proportions of time spent traveling versus resting or feeding. We identified differences in habitats associated with travel bouts versus rest/feeding bouts for each puma group. Finally, we asked whether pumas' third-order selection of habitat elements (Aebischer et al. 1993) differed from the availability of those elements in individuals' home range areas, for each sex, age class, and development zone. Results indicate alterations of puma spatial and behavioral ecology at the individual level associated with low-density rural development.

Study area

We conducted this study in Sierra, Nevada, Placer, El Dorado and Amador counties, in California's Western Sierra Nevada mountains and foothills. The western portion of these adjoining rural counties borders the flat, agricultural Central Valley and the Sacramento metropolitan area. Elevation ranges from sea level in the west to over 2500 m at the Sierra Nevada crest. River canyons running roughly east-west separate mountain ridges in the higher elevations. Most private and residential lands are in the western foothills, characterized by oak (*Quercus sp.*) dominated woodlands and chaparral shrublands. Eastward, vegetation transitions with rising elevation to conifer forests. The eastern portion of these counties is dominated by non-residential timberlands, networked by logging roads. An urban/wildland interface corresponding to housing density on private versus public lands, typically national forests, transected our study area and was used to define the "developed zone" versus the "undeveloped zone" (Figure 2-1). Most of the counties' areas provided puma habitat, excluding only valley agricultural lands, urban areas, and the high elevation zones of the Sierra crest. Past monitoring by California Department of Fish and Game (CDFG) found the Western Sierra puma population distinct from pumas in the Eastern Sierra (pers. comm. Jeff Finn, Eric Loft, CDFG), and our study did not include that region.

The area supports populations of mule deer *(Odocoileus hemionus)*, black bear *(Ursus americana)* and puma, but represents a region of ecological concern. Large foothill tracts have been converted to ranchette style settlement, or other uses such as vineyards and orchards. The area is intersected north-south by high-traffic highways US Route-50 and

I-80, which serve as corridors for development emanating from the Sacramento metropolitan area. Placer County had the fastest growing human population in California, with a projected 27.6% increase from 2000 to 2005 (US Census Bureau 2006). Population increased by 9.6%, 13.1%, and 6.9% in Amador, El Dorado, and Nevada Counties respectively, during the same period. In Nevada County, the amount of undeveloped land zoned for residential or commercial development was 3.5 times the county's developed land area (Walker et al. 2003). Over 60% of El Dorado County's undeveloped private land has been zoned for residential (0.4-8-ha (1-20-acre)) or exurban (8-16-ha (20-40-acre)) development (Stoms 2004). In Placer County, 93% of the foothills are privately owned, of which over 50% have been zoned for rural residential or urban land use (Stralberg & Williams 2001).

Methods

GPS collars

During January 2002 to May 2005, we deployed GPS collars on 19 pumas. Eight Televilt PosRec C600 collars (TVP Positioning AB, Sweden) with GPS fix intervals of either 1 or 2 hours were fitted on pumas. We deployed 2 Televilt PosRec C300 collars with 12-hour fix intervals on juveniles. After the first year of study, we used Telonics (Mesa, AZ) GPS collars with ARGOS (Advanced Research and Global Observations Satellite) uplink, and 3-hour fix intervals. Nine Telonics ARGOS collars were deployed on pumas. These collars were programmed to transmit the 6 most recently stored locations once every 2 weeks for internet download, allowing tracking of pumas in lieu of aerial telemetry as needed. All collars were equipped with VHF transmitter beacons, mortality sensors, and automatic drop-off mechanisms, and detached at pre-programmed dates. Upon collar retrieval, we downloaded all stored GPS locations to database files. We worked to deploy collars on male and female pumas, adults and subadults, and pumas living in the undeveloped forested zone and the developed zone mosaic of foothill ranches, ranchettes, and housing developments. We considered male pumas > 30 months old and females > 24 months old adults, due to potential for reproductive activity (Logan et al. 1996), and pumas younger to be subadults.

To capture pumas, teams of houndsmen and biologists conducted extensive track surveys on unpaved roads in national forests, private timberlands, recreation areas, state, federal and private reserves, and on private ranches. We documented the GPS locations of all puma scratches and tracks observed, as well as track age, width of front and rear heel pad, and notes on the suspected individual. When we discovered fresh puma sign, trained hound dogs were set on the track. Pumas were treed and chemically immobilized with Capture-All 5 (5 parts ketamine hydrochloride to 1 part xylazine hydrochloride) or Telazol (tiletamine and zolazepam (100 mg/mL solution); Fort Dodge Animal Health, Fort Dodge, Iowa) at dosages in accordance with the CDFG Wildlife Restraint Handbook (2000). Drug was delivered using Pneu-Dart guns and darts (Pneu-Dart Inc., Williamsport, PA). We took blood and hair samples, body measurements, notes on condition, determined age from tooth wear and gumline recession, and fitted pumas with ear tags and collars, following CDFG animal welfare protocols (CDFG 2000).

Pumas were then tracked using ground-based VHF telemetry and monthly or semi-monthly telemetry flights. Pumas wearing ARGOS-enabled collars were also monitored using satellite transmitted GPS fixes. When mortality signals were transmitted, we located the collar and investigated the cause of puma death or collar detachment.

We estimated the precision of GPS collar location fixes before collar deployment. We activated the collars and left them for periods of several days in fixed locations, occasionally agitating collars to avoid GPS shut-off. We documented highly accurate stationary collar locations using a Trimble GeoXT GPS system (Trimble Navigation, Sunnyvale, CA). We considered fixes "high quality" if location points for stationary collars were within 30 m of each other in more than 95% of cases, and locational error more than 100 m occurred less than 1% of the time. The "2D" and "3D" locations from all Telonics collars were considered high quality and both types were used in analyses. Only the "3D" data from Televilt collars met these criteria and were analyzed.

Home range

We constructed 95% kernel home ranges (Worton 1987) for each puma from which a GPS collar download was obtained, and recorded the area of each home range in square kilometers using Hawth's Tools v.3.26 extension (Beyer 2004) for ArcGIS 9.x® (ESRI, Redlands, CA). We included the entire period of GPS collar locations collected for each puma in home range calculations, up to 12 consecutive months. For subadults that dispersed, we used only post-dispersal locations. We used the ArcGIS 9.2® measurement tool to measure mean length (km) and width (km) of each home range, and calculated the ratio of length/width to compare home range shapes.

We tested whether home range sizes and shapes could be accurately compared between puma zone, age, and sex groups, using JMP 5® statistical software (SAS Institute, Cary, N.C.). Two sample Student's *t*-tests were used to determine whether pumas in each group to be compared wore collars for comparable numbers of days. We used Pearson's chi-square tests to assess whether puma groups wore collars during the same seasons, tabulating each month of the year that a collar collected data, with locations from November through April considered "wet season" locations, and those from May through October categorized as "dry-season" locations.

We tested for differences in home range area and shape between zones, sexes, ages, and between divisions of groups that initial analyses suggested as important. Juvenile male JM150 was included in zone comparisons but not sex or age class comparisons, because his home range likely represented that of his mother, not an independent subadult male.

Movement behavior

We used all high quality GPS collar locations to calculate movement behavior parameters and travel or rest/feeding habitat associations for each puma. To resolve differences in fix intervals (1, 2, or 3 hours for different collars) and fix success rates among collars, we standardized data to include only locations recorded at 6-hour intervals. We excluded subadult female, SF901, from this analysis due to a 12-hour fix interval. For subadults that had gained independence and dispersed from natal ranges, we analyzed only data collected after the animal had established an independent home range, i.e. moved repeatedly within the same area and ceased long-distance (> 1 home range area) linear movements. Dependent juvenile male JM150 was excluded from sex and age group comparisons.

For each puma's 6-hour interval locations, we created point and path shapefiles in ArcGIS 9.2®. We used Hawth's Tools to calculate the Euclidean distances moved between consecutive location pairs, and turn angles for each set of three consecutive locations. We calculated mean 6-hour distance moved and mean turn angle for each puma using JMP 5®. We created new data files for each puma, containing only locations representing periods when the puma was traveling, and only locations when the animal was resting or feeding. The first location of a consecutive pair was labeled a "travel location" if the points were separated by 1500 m or more, indicating the animal had moved a minimum of 1500 m during that 6-hour period. This distance was roughly 50% greater than the mean 6-hour movement distance for all pumas. Initial fixes in consecutive pairs of locations separated by less than 500 m from each other were classified as "rest/feeding locations", representing periods when the puma moved approximately 50% less than the mean 6-hour movement distances for all pumas sampled.

For each animal, we calculated percent travel as the ratio of the individual's travel locations to total locations. Percent rest/feeding was calculated as the ratio of rest/feeding locations to all locations for each animal. We used Student's *t*-tests in JMP 5® to determine whether percent travel locations, percent rest/feeding locations, mean distance moved, or mean turn angle differed for pumas by zone, sex, age, males by age class, males by zone, or females by zone. Sample sizes did not allow for comparisons of other subgroups.

We then examined habitat attributes associated with puma travel or rest/feeding. To compare the proportions of travel and rest/feeding locations associated with roads, we separated USGS Digital Line Graph county road layers into high-traffic roads (state and interstate highways) and low-traffic roads (remaining roads, paved and unpaved) in ArcGIS 9.2®. We constructed 100 m buffer zones on each side of all roads, creating "high-traffic road zones" and "low-traffic road zones". Hawth's Tools''s "intersect point tool" was used to create separate data columns of travel and rest/feeding locations that intersected high-traffic or low-traffic road zones, for each puma.

We used the "intersect point tool" to document slope (degrees), elevation (m), property parcel size (ha), and presence of riparian zones at each travel and rest/feeding location for all pumas, and calculated mean values of these attributes for each animal. USGS National Hydrography Dataset CA SWRCB files were used to identify, and construct 50 m buffer zones around, all waterways, indicating "riparian zones". We obtained elevation measurements from USGS 1:24000 DEM raster files, and built slope and aspect layers from these files using ArcGIS 9.2® Spatial Analyst extension. We used digital county parcel maps from Amador, El Dorado, Placer and Nevada counties to document property parcel size at each puma location point. We did not obtain a parcel map for Sierra County and did not include juvenile male JM150 in parcel size comparisons.

Paired *t*-tests were conducted to determine whether mean slope, elevation, parcel size, and presence of high-traffic roads, low-traffic roads or riparian zones differed between travel and rest/feeding locations for all pumas. We repeated these comparisons for pumas by zone, sex and age class.

Habitat use

We compared geographic attributes at documented puma location points versus at large numbers of random points in the animals' home range areas, to characterize and compare habitat use patterns by puma group. We constructed 95% kernel home ranges for each individual, using all high quality GPS locations for the duration of each animal's GPS collar dataset. We then constructed a "home range area" for each puma, by creating a 1 km buffer surrounding each animal's kernel home range and merging this area to the home range, in ArcGIS 9.2®. The buffer was added to include areas that were potentially accessible to pumas, but may have contained features that pumas avoided, which we wished to identify.

For each point in a puma GPS location file, we documented the associated elevation, slope, parcel size, and intersections with high-traffic road zone, low-traffic road zone, and riparian zone, using Hawth's Tools''s "intersect point tool" and the GIS map layers for each attribute. We used "intersect point tool" to document the aspect and vegetation type at each point. We created a GIS aspect layer using the USGS 1:24000 DEM raster file and the ArcGIS 9.2® Spatial Analyst extension aspect tool. The 2000 CDF CALVEG (Fveg2.02) GIS map layer was used to identify vegetation types. We classified aspect values as North, South, East, or West, and vegetation types as montane hardwood/montane hardwood-conifer (montane hardwood), annual grassland or open oak woodland (grassland/oak woodland), conifer forest, or chaparral. Points rarely occurred in other vegetation types and those were not included in analysis. We calculated the mean of each geographic attribute value associated with puma locations for each animal. For vegetation type and aspect, we calculated the percentage of points intersecting each of the 4 vegetation types and the 4 aspect classes. For high-traffic road, low-traffic road, and riparian zones, we calculated the percentage of each animal's locations occurring within those zones.

To compare puma habitat use with the general distribution of geographic attributes within each animal's home range area, we created a set of 400 random points in each home range area using Hawth's Tools. We documented values for slope, elevation, aspect, parcel size, vegetation type, and presence of high-traffic road zone, low-traffic road zone, and riparian zone, for each random point in pumas' home range areas. We calculated the mean values or percent occurrences of each geographic attribute for each home range area's random point dataset.

Paired *t*-tests were conducted to identify within group differences between attribute mean values and percent occurrences at actual puma locations versus in the animals' general home range areas. We conducted these comparisons for all pumas pooled, and for each zone, sex, and age class. Slope, elevation, and parcel size values, were logarithmically (ln) transformed to approximate normal distributions.

Results

GPS collars

We deployed 22 GPS collars on 19 pumas during 2002-2005, and tracked animals by collar during 2002-2006. Fourteen collars yielded downloads, representing all GPS fix data collected by collars on 13 pumas. Table 2-1 displays the zone, age class, sex, collar type, number of fixes collected, fix interval, and total data period for each collared puma from which downloads were obtained. Three of the downloaded collars were worn by adult males, 6 by adult females (one female was collared twice), 1 by a subadult female, 3 by subadult males, and 1 by a dependent juvenile male. Seven of the pumas from which downloads were obtained had occupied the developed zone, while 6 undeveloped zone pumas provided collar downloads. All collared subadults lived in the developed zone. The subadult female was collared in her developed zone natal range, while 2 of 3 subadult males were collared pre-dispersal in the undeveloped zone and subsequently moved to establish developed zone home ranges.

One developed zone puma resided in an area of timberlands and residential development bordering a busy highway. The other developed zone pumas occupied foothill and mountainous areas characterized by a mix of ranchette-style subdivisions, ranches, and occasional residential developments. The undeveloped zone pumas all lived within extensive areas of forest with few or no residences and light human activity, mainly forestry and recreation.

By 2007, 5 of 7 pumas collared in the developed zone from which downloads were obtained were known to have died, including 3 of 4 subadults. Three pumas were killed in response to depredation on sheep or goats, 1 by vehicle collision, and 1 by another puma. One undeveloped zone adult male was known to have died, possibly hurt by another puma.

Home range

Home range areas for each puma, covering a maximum of 12 months or the duration of data collection if less than 12 months, are displayed in Table 2-1. The mean number of days and the months of year that pumas wore collars did not differ significantly between any of the zone, sex or age groups for which we wished to compare home range sizes and shapes (Table 2-2). Results of home range size and shape comparisons by puma group are presented in Table 2-3. Mean ≤ 12-month home range area for adult male pumas (n = 3) was 402.6 km^2. This area was 229% larger than mean adult female home range size (n = 4), 176.04 km^2, and 346% larger than the mean ≤ 12-month home range size for subadult males (n = 3), 116.5 km^2. Mean ≤12-month home range size for adult males that were tracked more than 6 months was 539.6 km^2 (n = 2). This area was 272% larger than the mean home range size of adult female pumas tracked for more than 6 months (n = 4), 198.6 km^2.

Developed zone home ranges were smaller than undeveloped zone home ranges (*t* = 2.831, df =11, p = 0.016), but home range sizes did not differ significantly for males and females overall (*t* = 0.920, df = 10, p = 0.379) or for adult males and adult females (*t* = 1.816, df = 6, p = 0.119), possibly due to small sample size and migratory movements by 2 females. Two undeveloped zone adult females appeared to migrate, using separate ranges during the wet and dry seasons, resulting in particularly large and oblong home range areas. Developed zone home range area remained smaller than undeveloped zone home range area when migrating animals in the undeveloped zone were excluded from analysis (*t* = 2.602, df = 9, p = 0.029). Home range area in the developed zone also remained smaller than undeveloped zone home range area when the 2 undeveloped zone adult males with the largest home ranges in our sample were excluded (*t* = 3.390, df = 9, p = 0.008). Small sample sizes (3 to 5 animals per category) and uneven distribution of age classes by zone may have inhibited identification of potential differences between more exclusive subgroups.

Home range shape (length/width km) was less round in the developed zone than the undeveloped zone when migratory animals were excluded (*t* = 2.285, df = 9, p = 0.048). Shape did not differ between any other groups. Two subadult males had particularly long, narrow home ranges (23.6 km x 4.6 km, and 18.1 km x 4.7 km) stretched along busy highways in the developed zone. Two developed zone adult female home ranges bordered on residential developments and highways and appeared irregularly shaped. Although some undeveloped zone puma home ranges were bordered or intersected by a highway or major river, these home ranges appeared more broadly round, with length/width ratios of 1.1 km to 3.0 km.

Movement behavior

Table 2-4 displays the mean percent travel locations, mean percent rest/feeding locations, 6-hour movement distances, and turn angles for all pumas pooled and for each sex, age class, and zone. Results of group comparisons are indicated. Percentage of travel locations was greater for male pumas than females ($t = 2.306$, df = 9, p = 0.047), while females had a greater percentage of rest/feeding locations than males ($t = 3.653$, df = 9, p = 0.005). Males moved greater mean distances than females per 6-hour interval ($t = 2.262$, df = 9, p = 0.050), while turn angles were greater for females than male pumas ($t = 3.713$, df = 9, p = 0.005). Subadult males moved shorter mean distances than adult males ($t = 3.129$, df = 4, p = 0.035).

Table 2-5 displays mean parcel size, slope, elevation, and percent of locations intersecting riparian, high-traffic road, and low-traffic road zones for puma travel versus rest/feeding locations. Values are presented for all animals, and for zone, sex, and age groups, with differences between travel and rest/feeding habitat attributes indicated for each group. For all pumas pooled, travel locations occurred on lower mean slopes than rest/feeding locations ($t = 3.380$, df = 12, p = 0.006). Both high-traffic and low-traffic roads were more often associated with travel than rest/feeding locations ($t = 2.608$, df = 12, p = 0.023; $t = 3.654$, df = 12, p = 0.003).

Travel locations for developed zone pumas occurred at lower slopes (*t* = 7.290, df = 6, p = 0.001) and elevations (*t* = 3.237, df = 6, p = 0.018), and were more likely to occur along high-traffic roads, than rest/feeding locations (*t* = 2.579, df = 6, p = 0.042). Developed zone puma travel locations also occurred more often in riparian zones than rest/feeding locations (*t* = 2.981, df = 6, p = 0.025). Pumas in the undeveloped zone displayed none of these relationships, but had more travel locations along low-traffic roads than rest/feeding locations (*t* = 6.199, df = 5, p = 0.002). Tracking indicated that pumas often walked along low-traffic roads for distances up to 5 km, between dusk and dawn.

Male travel locations occurred on lower mean slopes (*t* = 3.537, df = 5, p = 0.017) and more often along low-traffic roads than male rest/feeding locations (*t* = 2.665, df = 5, p = 0.045). Female puma travel locations occurred at lower mean elevations than female rest/feeding locations (*t* = 5.187, df = 5, p = 0.004), with no other differences identified. Subadult pumas, which were sampled only in the developed zone, used significantly lower slopes (*t* = 13.501, df = 3, $p < 0.001$) and elevations for travel than rest/feeding (*t* = 5.865, df = 3, p = 0.010). Subadult puma travel locations were more often along high-traffic roads than rest/feeding locations (*t* = 5.095, df = 3, p = 0.015). Adult puma travel locations occurred more often along low-traffic roads than adult rest/feeding locations (*t* = 2.667, df = 7, p = 0.032).

Habitat Use

Table 2-6 displays geographic attribute values and significant differences at actual puma locations (observed values), versus in puma home range areas (expected values), for all pumas and each group. For all pumas pooled, actual collar locations were more often in montane hardwood (*t* = 4.276, df = 12, p = 0.001) and chaparral vegetation types (*t* = 3.116, df = 12, p = 0.009), and less often in conifer forest (*t* = 3.689, df = 12, p = 0.003) than the occurrence of those types in puma home range areas. All animals pooled used lower elevations (*t* = 3.279, df = 12, p = 0.003), and used high-traffic (*t* = 4.010, df =12, p = 0.001) and low-traffic road zones (*t* = 2.246, df = 12, p = 0.022) less than expected by non-selective use of home range areas. All pumas used northerly aspects less (*t* = 3.918, df = 12, p = 0.002) and southerly aspects more often (*t* = 3.793, df = 12, p = 0.003) than expected.

Pumas in both development zones used montane hardwood more frequently than expected by non-selective use of home range areas (*t* = 3.764, df = 6, p = 0.009; *t* = 2.859, df = 5, p = 0.035). Developed zone pumas used larger parcels (*t* = 2.594, df = 6, p = 0.021), greater slopes (*t* = 3.061, df = 6, p = 0.011), and lower elevations (*t* = 2.843, df = 6, p = 0.015) than expected. Developed zone pumas also used riparian zones more (*t* = 3.281, df = 6, p = 0.008), and low-traffic and high-traffic road zones less (*t* = 3.624, df = 6, p = 0.006; *t* = 4.787, df = 6, p = 0.002) than expected by non-selective home range area use. Undeveloped zone animals used northerly aspects (*t* = 5.610, df = 5, p = 0.001) and conifer forests less (*t* = 4.287, df = 5, p = 0.008), and southerly aspects (*t* = 3.627, df = 5, p = 0.015) and chaparral more often than expected (*t* = 2.731, df = 5, p = 0.041).

Male pumas used chaparral (t = 2.666; df = 5; p = 0.045) and southerly aspects (t = 3.568, df = 5, p = 0.008) more, and high-traffic road zones (t = 2.879, df = 5, p = 0.017) and northerly aspects (t = 2.893, df = 5, p = 0.034) less than expected, but did not show selection for other attributes. Female pumas used montane hardwood (t = 3.498, df = 5, p = 0.009) more, and both high-traffic road (t = 2.910, df = 5, p = 0.017) and low-traffic road zones less (t = 2.839, df = 5, p = 0.018) than expected by non-selective use of their home range areas.

Our sample included 4 subadult pumas, all in the developed zone. Subadults used high-traffic road zones (t = 15.597, df =3, p < 0.001) less often than expected. Like all pumas pooled, the 8 adults sampled used montane hardwood (t = 4.130, df = 7, p = 0.004), chaparral (t = 2.860, df = 7, p = 0.024), and southerly aspects more (t = 4.111, df = 7, p = 0.005), and conifer forests (t = 2.713, df = 7, p = 0.015), northerly aspects (t = 4.000, df = 7, p = 0.005) and low-traffic road zones less (t = 2.466, df = 7, p = 0.043) than expected.

Discussion

Pumas responded to the presence of rural development by adjusting spatial patterns of habitat use, including home range patterns, selectivity of habitats used for travel and resting or feeding, and selection of habitats within their home range areas. Sex, and not development presence, affected movement parameters including short-term movement distances, turn angles, and proportions of time spent traveling and resting/feeding.

Pumas in the developed zone occupied smaller home ranges than those in the undeveloped zone, even when adult males or migratory animals in the undeveloped zone were excluded from analysis. Smaller home ranges could have resulted from various factors, such as puma avoidance of obstacles or poor habitat, or conversely, greater abundance of prey in developed areas. Male pumas have been found to occupy home ranges 1.5 to 5 times as large as those of females in the same populations (Logan and Sweanor 2001), and subadult males commonly use smaller home ranges than adult males (Hemker 1984, Beier 1995, Logan and Sweanor 2001), patterns supported by our findings. When migratory females were excluded from analysis, subadult male home range sizes ($\mu = 120$ km^2) were similar to those of females ($\mu = 116$ km^2). Home range sizes of independent subadult males likely reflected energetic demands, as is typical of female large carnivores (Lindstedt et al. 1986), and not the mate-searching behavior practiced by adult males. Subadult male pumas can be expected to attempt establishment of larger home range areas in prime habitats as they mature and become better able to compete with adult males.

Developed zone home ranges were more irregularly shaped than those in the undeveloped zone when migratory animals were excluded. Home range shape did not differ for any other groups. Puma occupation, especially by subadult males, of urban interface borders may have caused irregular developed zone home range shapes. Beier (1995) found that subadult male pumas in a developing area dispersed to the urban-wildland edge and established small, temporary home ranges stretched along that interface. Similarly, all 3 subadult males we sampled resided in developed areas, and established smaller, more irregularly shaped home ranges than those of adult males, 2 of which were stretched along major highways. Female developed zone home ranges bordered highways and residential areas, likely related to the irregular home range shapes observed.

All movement parameters differed with sex, while development zone and age were not related to any movement parameter differences besides adult males moving greater distances than subadult males. Female pumas' shorter movement distances and greater turn angles than males suggested more intensive use of smaller home ranges than adult male pumas that are driven to range widely searching for mates in addition to prey. Subadult male movement distances also likely reflected a focus on prey searching rather than mate searching. Koehler & Maletzke (2005) and Sweanor (1990) found male pumas covered greater daily distances within larger home ranges than females, while female pumas used smaller home ranges, turned at greater angles, or moved less linearly. Dependent young may limit female movement distances and increase the time females must spend hunting. Care for young kittens may have contributed to female's relatively high proportion of rest/feeding bouts.

Developed zone pumas displayed greater selectivity of habitats for travel versus rest or feeding than any other group. Undeveloped zone animals used only low-traffic road zones, typically lightly used logging roads, more often for travel than for rest/feeding. A mean 44% of undeveloped zone puma travel locations were in low-traffic road zones. Developed zone animals did not appear to select low-traffic roads for travel, but instead used lower slopes and elevations, and high-traffic road zones and riparian zones more for travel than for rest/feeding. In developing areas, low-traffic roads were likely less secure for puma travel, coinciding with human activities and residences. Locations in high-traffic road zones were minimal (0.8% of travel locations), and could have reflected associated topographic features that were conducive to travel. Travel versus rest/feeding habitat selection displayed by subadults reflected that of all developed zone animals, while few differences were identified within other groups.

Puma selectivity of habitats within their home range areas also corresponded more strongly to zone than to sex or age class. Developed zone pumas' avoidance of low- and high-traffic road zones in their home range areas, and selection for riparian areas and large property parcels, suggest the animals avoided patches of residential development or greater human activity. The developed zone was characterized by a mosaic of ranches, ranchettes and dispersed housing developments, often bordering steep river canyons, and transected by creek drainages with riparian vegetation. Developed zone animals' selection for riparian areas, and greater slopes and lower elevations than in their home range areas suggests the pumas relied upon river canyons and riparian drainages that ran through developed areas.

Developed zone pumas likely used canyons and riparian drainages for stalking cover, gentle travel terrain, and secure rest or feeding cover. Dickson and Beier (2006) found pumas to use canyon bottoms particularly for travel, and speculated these areas offered low energetic cost travel paths and abundant prey. Dickson et al. (2005) found pumas used travel paths with lower slopes than alternative paths. Developed zone animals may have selected rugged, sloped habitats such as ravines and canyon walls for rest, hunting or feeding cover, while preferring canyon bottoms and low slopes for travel. Studies relying on diurnal puma locations that found pumas to select steep habitats at higher elevations than surrounding areas (Logan and Irwin 1985, Laing 1988), may have described puma rest/feeding habitats. The finding of Orlando et al. (2008a) that properties in this study area with steep slopes, higher brushy cover, and near rivers or creeks faced heightened puma depredation risk, likely resulted from the apparent third-order selection of developed zone pumas for river canyons and riparian areas.

Puma habitat use in the undeveloped zone was not affected by anthropogenic and topographic features like developed zone habitat use, although the zones were geographically similar. Undeveloped zone pumas' habitat use related only to vegetation types and aspect. GPS collars have sometimes been less able to record locations in steep, rugged terrain, and at north or east aspects with dense closed canopy vegetation (Friar 1994, D'Eon et al. 2002, Graves and Waller 2006). These effects could have influenced our results, although undeveloped zone pumas may have also preferred south-facing slopes and more open vegetation types. Southerly aspects had experienced extensive burning in a large portion of the study area, and may have been well used by deer. GPS fix biases would have inhibited detection of pumas' use of the low elevations, high slopes, and riparian areas within canyons. However, we found all pumas pooled and developed zone pumas to use lower mean elevations, and developed zone animals to select higher slopes and use riparian areas more often than expected.

Although pumas were able to live in areas of rural low-density development, behaviors relating to habitat use were altered. Development appeared to constrain home range size and shape, and cause increased selectivity of habitats for specific activities and within animals' home range areas, suggesting degradation of overall habitat utility at the level of individual home ranges.

Management implications

Pumas can and do use areas of rural development, but habitat use is apparently constrained and these areas may not constitute quality habitats. Riparian areas such as creek drainages and river canyons likely function as important corridors and cover, aiding persistence of pumas in developing regions. Low-density residential development of rural landscapes adjoining wild areas can be expected to negatively impact large carnivores, by decreasing habitat utility for individuals, and potentially increasing mortality rates through conflicts with humans, legal and illegal killing, and vehicle collisions. These effects could destabilize existing ecological communities. Conservation of contiguous riparian zones, landscape networks of refugia (Fahrig 1988) consisting of undeveloped high quality habitats, and efforts to minimize human-carnivore conflicts are likely necessary to sustain large carnivores in rural areas.

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Tables and Figures

Table 2-1. GPS collar and puma home range parameters for collared pumas in California's Western Sierra Nevada, 2002-2006. Puma ID: S = sub-adult, A = adult, J = juvenile; M = male, F = female. Collar type: TA = Telonics Argos, TP = Televilt PosRec.

Puma ID, Zone	Collar Type	No. 2D & 3D fixes	Fix interval (hrs)	Total data period (days)	Home range area ≤ 12 mos (km^2)
Developed Zone					
SM119	TA	1197	3	211	157.3[2]
SM130	TA	2055	3	478	119.1[3]
AM852a	TP	1240	1	69	128.6
SM852b	TP	1131	2	180	73.2
AF200	TA	1114	3	454	112.6
AF797	TP	445	2	224	85.8
SF901	TP	146	12	270	128.1
Undeveloped Zone					
JM150	TA	484	3	95	176.0
AM160	TA	1521	3	287	417.3
AM190	TA	2285	3	492	661.9
AF180	TA	3014	3	463	136.5
AF819	TP	830	2	230	283.1
AF868[c]	TP	1047	1	105	262.2[1]
AF829[c]	TP	1549	2	250	262.2[1]

[1] Collars AF868 & AF829 were worn successively by the same puma.
[2] Home range area calculated for post-dispersal locations only: 8 mo. period.
[3] Home range area calculated for post-dispersal locations only: 6 mo. period.

Table 2-2. Comparison of number of days and months of year GPS collars were worn between puma groups in California's Western Sierra Nevada, 2002-2006. No. of days comparison: two-sample independent Student's t-test, no differences at α = 0.05. Months of year comparison: grouped into wet and dry season; Pearson's chi-square test, no differences at α = 0.05.

Group	No. Days				Months of year		
	Means	t	df	P-value	$\chi 2$	df	P-value
Developed/ undeveloped zone	269.4/320.3	0.617	11	0.550	0.682	1	0.409
Male/female	286.2/332.7	0.567	10	0.583	1.658	1	0.198
Adult/subadult	321.8/284.8	0.422	10	0.682	0.525	1	0.469
Developed/ undeveloped zone w/o adult males	269.4/285.8	0.172	9	0.867	0.500	1	0.480
Developed/ undeveloped zone nonmigratory	269.4/334.3	0.644	9	0.536	0.331	1	0.565
Developed zone female/undeveloped zone female	316.0/349.3	0.343	4	0.749	0.306	1	0.580
Adult male/adult female	282.7/345.2	0.554	6	0.600	0.392	1	0.531
Adult male/subadult male	282.7/289.7	0.045	4	0.996	0.277	1	0.599
Subadult male/ non-migratory female	234.5/352.8	1.111	6	0.309	2.596	1	0.107

Table 2-3. Home range area and shape comparisons for collared pumas in California's Western Sierra Nevada, 2002-2006, by development zone, sex, and age. Home ranges use 95% kernel density estimator method, representing ≤12 months of puma locations.

Puma group	n	≤ 12-month home range area (km^2)	Length/ width (km^2)
Developed zone	7	115.0*	2.74
Undeveloped zone	6	322.8*	1.73
Male	6	259.6	2.70
Female	6	168.1	2.06
Adult	8	261.0*	1.96
Sub-adult	4	119.4*	3.23
Developed zone	7	115.0*	2.74
Undeveloped zone w/o adult males	4	214.5*	1.87
Developed zone	7	115.0*	2.74*
Undeveloped zone non-migratory	4	347.9*	1.26*
Developed zone female	3	108.8	1.97
Undeveloped zone female	3	227.3	2.14
Adult male	3	402.6	1.73
Adult female	5	176.0	2.09
Adult male	3	402.6	1.73
Sub-adult male	3	116.5	3.67
Subadult male	4	119.6	3.33
Non-migratory female	4	115.8	1.75

*Difference between puma groups at $\alpha = 0.05$ using two-sample independent Student's t-test.

Table 2-4. Comparisons of mean movement parameter values at 6-hour location intervals, for GPS-collared pumas by group in California's Western Sierra Nevada, 2002-2006.

Puma group	% travel locations	% rest/ feeding locations	Movement distance (m)	Turn angle	N
All	21.8	34.3	943.7	113	12
Developed zone	20.4	33.6	886.3	115	6
Undeveloped zone	23.1	35.0	1012.6	111	6
Male	24.7*	32.1*	1072.3*	104*	5
Female	18.5*	36.2*	789.4*	123*	6
Adult	21.6	34.5	957.1	114.0	8
Subadult	22.9	32.1	908.0	109.2	3
Adult: male	26.6	32.1	1236.7*	99.2	3
Subadult: male	22.9	32.1	908.0*	109.2	3
Developed: male	21.9	32.6	939.3	108.4	4
Undeveloped: male	30.4	33.3	1098.3	102.4	2
Developed: female	17.8	35.6	780.5	128.4	3
Undeveloped: female	19.0	36.6	795.3	119.4	2

*Difference between puma groups at $\alpha = 0.05$ using two-sample independent Student's t-test.

Table 2-5. Comparison of habitat attributes associated with travel (T) vs. rest/feeding (R/F) for collared puma groups in California's Western Sierra Nevada, 2002-2006.

Puma group	n	Mean parcel size[1] (acres)		Mean slope[1] (deg)		Mean elevation[1] (m)		High-traffic road %		Low-traffic road %		% Riparian	
		T	R/F	T	R/F	T	R/F	T	R/F	T	R/F	T	R/F
All	12	248.3	220.0	14.2*	16.4*	994	1053	0.522*	0.064*	33.7*	20.9*	19.1	17.3
Developed	7	214.6	186.1	13.3*	17.3*	663*	756*	0.828*	0.115*	24.8	21.6	22.2*	19.0*
Undeveloped	5	483.6	458.0	15.2	15.3	1381	1400	0.165	0.017	44.0*	20.1*	12.8	12.4
Male	6	259.1	255.3	14.1*	16.4*	1039	1059	0.669	0.083	35.1*	20.8*	20.1	17.6
Female	5	230.2	161.4	14.3	16.3	943*	1027*	0.351	0.056	28.5	19.7	19.7	18.1
Adult	8	295.1	248.4	14.9	16.2	1082	1102	0.418	0.054	31.0*	17.3*	18.0	16.2
Subadult	3	201.4	191.8	12.4*	16.6*	809*	928*	0.862*	0.100*	44.1	39.3	23.6	21.0

*Difference at $\alpha = 0.05$ between travel and rest/feeding locations within puma group, using paired Student's t-test.

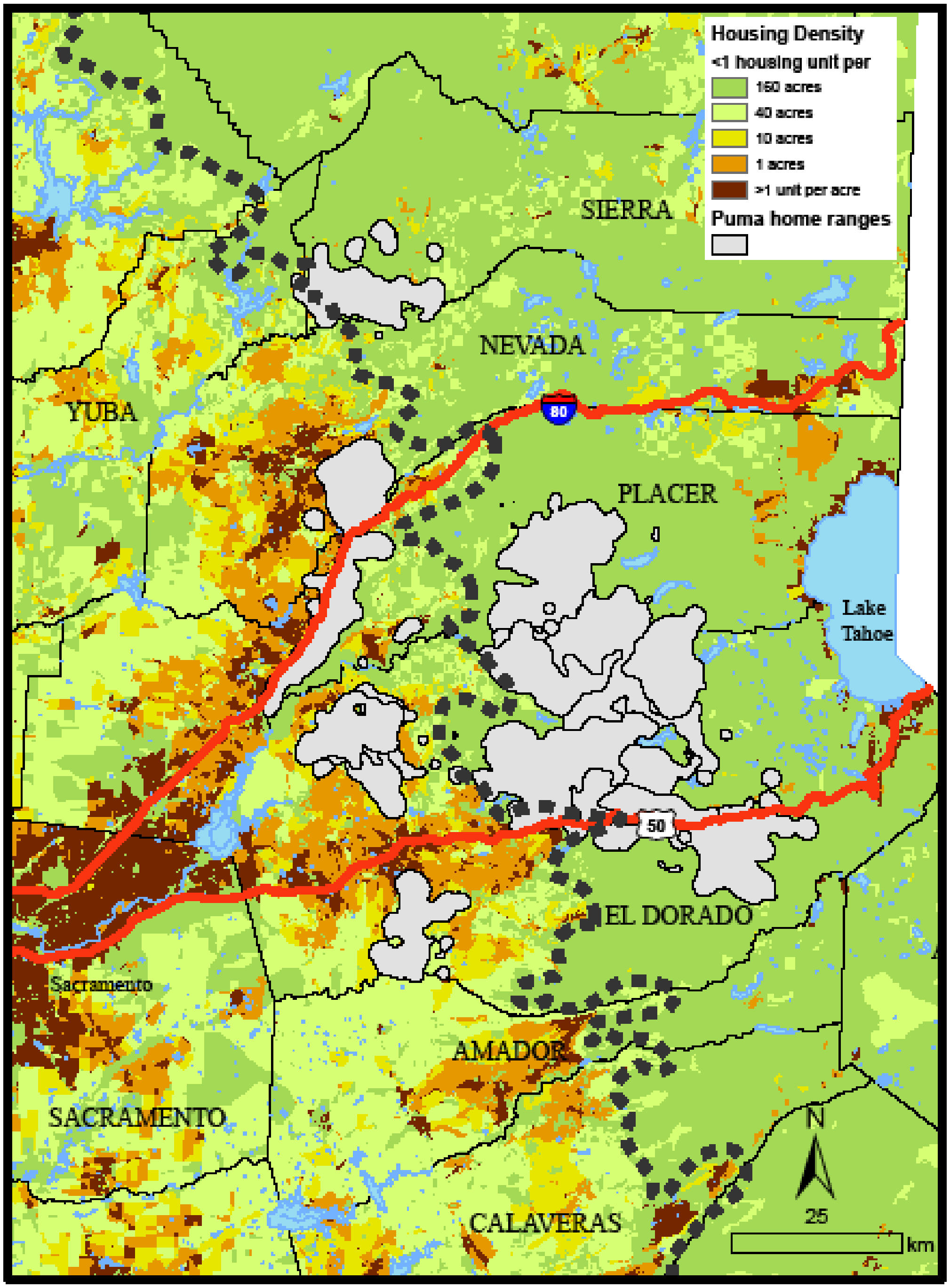
[1] Transformation (ln) of value used in analyses.

Table 2-6. Observed vs. expected geographic attribute values of habitats used by GPS-collared pumas in California's Western Sierra Nevada, 2002-2006, by puma zone, sex, and age group. Values presented as observed/expected. Observed: mean attribute values at locations from puma GPS collars. Expected: mean attribute values at 400 random locations in each pumas' home range area.

Geographic attributes	All pumas	Developing zone	Undeveloped zone	Male	Female	Sub-adult	Adult
n	13	6	7	6	6	4	8
% Montane hardwood	34.7/27.9*	50.0/40.8*	16.8/12.8*	33.7/27.7	38.7/30.4*	37.8/31.2	35.4/27.9*
% Grassland/oak woodland	6.9/10.2	12.2/18.6	0.7/0.1	2.9/6.6	11.8/15.1	7.1/9.6	7.5/11.5
% Conifer forest	39.4/47.2*	19.8/25.3	62.3/72.9*	41.0/50.3	34.2/40.7	30.2/39.4	41.3/48.5*
% Chaparral	16.2/9.6*	14.7/9.4	18.0/9.9*	18.9/10.4*	13.8/9.1	18.8/13.0	15.1/8.1*
Parcel size[1] (acres)	248/227	156/129*	475/500	235/210	262/244	195/180	351/355
Slope[1] (deg)	15.2/14.4	14.8/12.8*	15.4/15.8	15.0/14.1	14.9/13.5	15.0/13.8	15.1/14.1
Elevation[1] (m)	1006/1027*	628/652*	1375/1396	930/953	842/865	843/866	1073/1092
% North-facing	14.6/22.2*	13.7/19.2	15.8/25.8*	13.7/21.9*	16.1/21.9	11.9/18.7	16.4/23.5*
% East-facing	19.0/21.0	19.3/23.2	18.8/18.4	19.1/21.7	18.3/20.2	19.5/22.7	18.3/20.0
% South-facing	36.2/26.8*	34.7/25.8	38.0/28.0*	39.4/26.7*	33.1/27.0	38.6/26.8	36.1/26.9*
% West-facing	30.1/30.0	32.4/31.9	27.4/27.9	27.8/29.8	32.5/30.0	28.0/31.7	31.3/29.6
% High-traffic road zones	0.43/2.20*	0.57/3.21*	0.28/1.04	0.48/2.00*	0.35/2.63*	0.62/3.19*	0.31/1.88
% Low-traffic road zones	29.9/35.1*	30.4/38.8*	29.3/30.7	35.2/39.0	23.1/32.2*	39.6/43.8	24.0/31.5*
% Riparian zones	10.2/9.5	18.3/10.1*	9.7/9.2	9.8/9.3	10.8/10.0	11.1/9.7	9.9/9.6

*Difference between observed and expected within puma group at $\alpha = 0.05$, using two-sample paired Student's t-test.

Figure 2-1. Approximate urban-wildland interface dividing developed and undeveloped zones of puma study area in California's Western Sierra Nevada, 2002-2006. Housing densities are from California Dept. of Forestry and Fire Protection dataset CEN00BLM03_1. Kernel density home ranges of 13 collared pumas are shown.



CHAPTER 3

Does rural development fragment puma habitat?

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Does rural development fragment puma habitat?

Abstract:

We examined whether exurban development fragmented puma habitat at three ecological scales. We investigated whether rural development produced a "source-sink" population structure by analyzing puma survival and dispersal in undeveloped and developed zones of a rapidly exurbanizing region. We tested whether anthropogenic or natural barriers degraded landscape connectivity by impeding puma movements. In individual home ranges, we investigated whether rural development created preferred and non-preferred habitat patches by testing whether pumas preferentially used or avoided diminishing size classes of residential property parcels. Dispersal and survival parameters including frequent dispersal and establishment of home ranges in the developed zone, and particularly high 12-month mortality in that zone (42.9%), suggested a source-sink, or source-pseudo-sink, rather than a habitat-limited or unfragmented population structure. Pumas crossed highways 7.9 times less, housing developments 3.7 times less, and major rivers 4.3 times less than expected, indicating these structures impeded puma movements and could threaten landscape connectivity. Within their home range areas, pumas used smaller (≤20 acres) property parcels less than expected and more often at night, and larger (>40-acres) parcels more than expected, and more often during the day. To sustain puma populations in the face of rural development, we recommend protection of source populations from development, maintenance of movement corridors and 40$^+$-acre parcel sizes, and efforts to reduce puma-human conflict in developed rural areas.

Keywords: *cougar, connectivity, development, dispersal, GPS collars, habitat fragmentation, mountain lion, puma, ranchette, survival*

Introduction

In Western North America, human population has been increasing and many rural areas rapidly urbanizing (Theobald 2005, U.S. Census Bureau 2006), encroaching upon available habitats for large mammals. Highways, agricultural, and suburban development threaten to fragment quality habitat and undermine the viability of wildlife populations (Andren 1994, Noss et al. 1996, Crooks 2002). Many rural areas have been transformed by low-density "exurban" development, characterized by 2- to 16^{+}-ha (5- to 40^{+}-acre) residential subdivisions (Duane 1996, Theobald 2005). Puma (*Puma concolor*) sightings and depredations on pets and livestock indicate pumas use developed rural areas (CDFG 2006), but the habitat value of these areas is questionable.

Habitat fragmentation may occur at different hierarchical scales, potentially creating patches of low quality habitat within individuals' home ranges (Andren 1994), producing a "source-sink" condition at the population level, or disrupting landscape-level connectivity, which is essential for sustaining fragmented subpopulations (Hansson 1991). In a source-sink system, excess offspring produced in quality, "source" areas disperse into "sink" areas of mixed or low quality habitat associated with high mortality or inadequate resources, which are unable to independently support populations (Pulliam 1988). Areas of coastal southern California have reached a critical point of fragmentation in which remaining high quality source areas are too small to sustain viable puma populations, and have become separated by dense development and highway systems (Hunter et al. 2003, Riley et al. 2005, Beier et al. 2006).

We initiated a study in a rapidly developing rural region to examine whether low-density rural development functionally fragmented puma habitat. We asked whether rural development was likely to create demographic sinks by analyzing puma survival and dispersal in undeveloped timberlands (*hereafter, undeveloped zone)* versus exurbanizing rural areas (*hereafter, developed zone)* of the same region. We tested whether anthropogenic and natural barriers impeded puma movements and thus connectivity within landscapes. Finally, we examined whether developed zone pumas preferentially used or avoided diminishing size classes of residential property parcels within animals' home range areas. We asked whether pumas' use of parcels by size differed between day and night, suggesting responses to human activity levels. We focused on this wide ranging species to identify threats to habitat connectivity likely to impact local wildlife communities (Terborgh et al. 1999, Noss et al. 1996), and to facilitate regional conservation planning.

Study area

We conducted this study in Sierra, Nevada, Placer, El Dorado and Amador counties, in California's Western Sierra Nevada mountains and foothills. The western portion of these adjoining rural counties borders the agricultural Central Valley and the Sacramento metropolitan area. Elevation ranges from sea level in the west to over 2500 m at the Sierra Nevada crest. River canyons running roughly east-west separate mountain ridges in the higher elevations. The western foothills are characterized by oak (*Quercus sp.*) dominated woodlands and chaparral. Eastward, vegetation transitions with rising elevation to conifer forests. This area is primarily non-residential timberlands, networked by logging roads. An urban/wildland interface corresponding to housing density on private versus public lands, typically national forests, transected our study area and was used to define the “developed zone” versus the “undeveloped zone” (Figure 3-1). Most of the counties’ areas provide puma habitat, excluding only valley agricultural lands, urban areas, and the high elevation zones of the Sierra crest.

The area supports populations of mule deer *(Odocoileus hemionus)*, black bear *(Ursus americana)* and puma, but represents a region of ecological concern. Large, contiguous regions at high elevations are protected from land conversion as national forests, wilderness and other public land designations, while other areas are privately managed timberlands. In contrast, the western foothills are largely privately owned and increasingly residential. Traditional grazing land is being converted to ranchette style settlement, or other uses such as vineyards and orchards. The area is intersected north-south by high-traffic highways US Route-50 and I-80, which serve as corridors for development emanating from the Sacramento metropolitan area.

Placer County had the fastest growing human population in California, with a projected 27.6% increase from 2000 to 2005 (US Census Bureau 2006). Population increased by 9.6%, 13.1%, and 6.9% in Amador, El Dorado, and Nevada Counties respectively, during the same period. In Nevada County, the amount of undeveloped land zoned for residential or commercial development was 3.5 times the county's developed land area (Walker et al. 2003). Over 60% of El Dorado County's undeveloped private land was zoned for residential (0.4- to 8-ha (1- to 20-acre)) or exurban (8- to 16-ha (20- to 40-acre)) development (Stoms 2004). In Placer County, 93% of the foothills were privately owned, of which over 50% were zoned for rural residential or urban land use (Stralberg & Williams 2001).

Methods

GPS collars and capture

During 2002- 2005, we deployed GPS collars on 19 pumas. Eight Televilt PosRec C600 collars (TVP Positioning AB, Sweden) with 1- or 2-hour GPS fix intervals were fitted on pumas, and 2 PosRec C300 collars with 12-hour fix intervals were placed on juveniles. After the first year of study, we used Telonics (Mesa, AZ) GPS collars with ARGOS (Advanced Research and Global Observations Satellite) uplink, and 3-hour fix intervals. Nine Telonics ARGOS collars were deployed on pumas, which transmitted their 6 most recently stored locations a maximum of once every 2 weeks for internet download, allowing limited tracking in lieu of aerial telemetry. All collars were equipped with VHF beacons, mortality sensors, and automatic drop-off mechanisms, and detached at pre-programmed dates. We downloaded all stored GPS locations from retrieved collars to database files.

To capture pumas, we conducted extensive track surveys on unpaved roads on public and private lands. We recorded GPS locations of all puma sign, track age, width of front and rear heel pad, and notes on the suspected individual. Pumas were treed by trained hounds and chemically immobilized with Capture-All 5 (5 parts ketamine hydrochloride to 1 part xylazine hydrochloride) or Telazol (tiletamine and zolazepam (100 mg/mL solution); Fort Dodge Animal Health, Fort Dodge, Iowa) at dosages in accordance with the CDFG Wildlife Restraint Handbook (2000). Drug was delivered using Pneu-Dart guns and darts (Pneu-Dart Inc., Williamsport, PA). We took blood and hair samples, body measurements, notes on condition, determined age from tooth wear and gumline recession, and fitted pumas with ear tags and collars, following CDFG animal welfare protocols (CDFG 2000). We considered male pumas > 30 months old, and females > 24 months old to be adults, due to potential for reproductive activity (Logan et al. 1996), and younger pumas to be subadults. Collared pumas were tracked using ground-based VHF telemetry and monthly or semi-monthly telemetry flights. Pumas wearing ARGOS-enabled collars were also monitored using satellite transmitted GPS fixes.

We estimated the precision of GPS collar location fixes before deployment. We left activated collars in fixed locations for 3-4 days, occasionally agitating collars to avoid GPS system shut-off. We documented highly accurate stationary collar locations using a Trimble GeoXT GPS system (Trimble Navigation, Sunnyvale, CA). We considered fixes “high quality” if fixes for stationary collars were within 30 m of each other in more than 95% of cases, and error exceeded 100 m less than 1% of the time. The “2D” and “3D” location fixes from all Telonics collars were considered high quality and both types were used in analyses. Only the “3D” data from Televilt collars met these criteria and were analyzed.

Survival

We asked whether puma mortality differed between the developed and undeveloped zones. We documented survival or mortality of each puma during the period of monitoring, beginning at capture and ending with the puma's last documented location. When collars transmitted mortality signals, we located the collar and investigated the cause of puma death or collar detachment. We calculated percent mortality during the study for all collared pumas as well as for pumas by zone, sex, and age class. We conducted two-sample independent Student's *t*-tests in JMP 5® statistical software (SAS Institute, Cary, N.C.) to determine whether pumas in each zone, sex, and age class were monitored for similar periods of time, allowing valid comparisons of mortality rates.

We used Pearson's chi-square tests to determine whether the proportion of pumas known to have died to pumas alive at the end of monitoring differed between zone, sex, or age classes. We recorded mortality and cause of death for pumas after collar drop-off through spring 2007, in the case that ear tag numbers on carcasses were reported to CDFG. We did not include puma deaths occurring after the expected date of collar retrieval in analyses, because developed zone pumas often died due to depredation. These deaths were more likely to become known to us post-collar drop-off than were undeveloped zone puma mortalities, which were less likely to result from depredation. To facilitate comparison of survival with other studies, we also calculated mortality rates within 1 year of collaring (12-month mortality rates), including only pumas that were monitored for at least one year, or died within in less than 12 months of monitoring.

Dispersal

We analyzed subadult dispersal patterns in combination with survival, to determine whether the population conformed to a habitat-limited structure, a source-sink structure, or an unfragmented population structure. We expected that a large proportion of subadults in a habitat-limited environment, such as that of the Florida panther (Maehr 2002), would disperse long summed distances or durations compared to other populations, potentially at young ages, but fail to establish independent home ranges. We expected relatively short Euclidean dispersal distances for those animals successfully establishing home ranges, indicating a lack of available habitat elsewhere. This pattern could be represented by "frustrated dispersal" (Lidicker 1975), in which animals disperse long total distances, fail to find suitable habitat for a home range, and frequently return to their natal regions. In a source-sink population structure, we expected a large proportion of subadults to disperse and establish independent home ranges, but to experience high mortality or low chance of reproductive success in their new home ranges (Pulliam 1988). In an unfragmented structure, we expected dispersal frequency, establishment of independent home ranges, and survival rates to be similar to other puma populations in relatively undisturbed areas that were not heavily hunted.

We documented dispersal parameters for collared subadults that gained independence from their mothers during the study period. We used GPS collar locations from downloaded collars, as well as capture and mortality locations taken with handheld Garmin® (Garmin Ltd.) GPS units. If we did not obtain a GPS collar download from a puma, we calculated dispersal parameters using locations from collars' ARGOS uplink systems, aerial and ground VHF telemetry, or puma capture and recapture. We created databases and map layers containing locations for each puma in an ArcGIS 9.2® (ESRI Institute, Redlands, CA) Geographic Information System.

We documented puma age at capture (±1 month) and noted whether the animal was still traveling with its mother as indicated by capturing the mother or by analyzing tracks in the area. We determined age at independence (±6 weeks, inclusive) as the age when a puma stopped traveling with its mother as documented by track surveys or location data from collared mother and offspring. Age at dispersal (±1 month) was determined from collar location data and indicated by movements leaving and not re-entering a subadult puma's natal home range.

We used high quality GPS collar locations to construct 95% kernel home ranges (Worton 1989) for each puma's pre-dispersal locations (natal home range) and post-dispersal locations (post-dispersal home range) with Hawth's Tools extension (Beyer 2004) in ArcGIS 9.2®. Hawth's Tools was used to create linear "dispersal paths" between consecutive locations for each puma. We considered dispersal to begin with the first location exiting and not returning to the natal home range, and to end when long-range (5^{+} km) directional movements ceased and pumas began to revisit territory, indicating home range establishment. We measured linear dispersal distance as the Euclidean distance (km) between the center of a puma's natal range and the center of the animal's post-dispersal home range, using the ArcGIS® measurement tool.

Because pumas sometimes changed dispersal directions, we also estimated the distance traveled during dispersal (summed dispersal distance). We measured and summed the minimum Euclidean distances between location points taken 2 weeks apart for the duration of dispersal movements. We recorded the duration of dispersal (days), predominant direction of movements including major direction changes for each animal, and whether dispersal began from and terminated in the undeveloped or developed zone. We also documented whether each dispersal-aged puma died or lived to the end of the monitoring period, and cause of death.

Obstacles to movement

We tested whether pumas avoided crossing rivers, highways or residential housing developments in their home range areas to determine whether these features posed obstacles to puma movements, and to compare the severity of obstacle presented by natural versus anthropogenic features. We used all high quality locations from puma GPS collars that yielded data downloads to construct 95% kernel home ranges for each puma using Hawth's Tools in ArcGIS 9.2®. We merged a 1 km buffer zone around each kernel home range to create the "home range area" for each puma. The 1 km buffer, a small area relative to puma movement distances, allowed us to investigate potential obstacles forming puma home range borders.

Using ArcGIS 9.2®, we created polyline shapefiles for major highways from USGS DLG digital road map layers, and for major rivers from USGS National Hydrography Dataset digital map layers. We created a “residential housing development” polygon shapefile containing only areas of adjoining residential parcels smaller than 2.0 acres (0.8 ha), and extending >1 km in any direction. Because highways, major rivers, and residential areas sometimes occurred in association, we removed the portions of these layers that occurred within 300 m of each other, and only analyzed potential obstacles in areas where they did not coincide with the other 2 features.

Puma data files were filtered to include only locations that occurred at a 6-hour interval from the next location. We did not include subadult female 901 in these analyses due to lack of location points. We used a query to create files of locations for each puma that occurred within 300 m of highways, rivers, and residential developments. We included only locations on the side of the potential obstacle containing most of the puma’s ranging area, to determine whether pumas were crossing features from one side to the other.

We used the Hawth’s Tools to construct unique path lines between each set of consecutive 6-hour interval locations occurring within potential obstacles’ buffer zones. For each puma we recorded the number of estimated puma paths that crossed rivers, highways, and residential developments. We then determined the expected frequency of potential obstacle crossings for each animal, based on the individual’s movement data. Hawth’s Tools was used to generate a list of distances (steplength) and turn angles between all successive 6-hour interval locations in each puma’s GPS collar dataset. We filtered non-successive location points from these tables. We calculated the likelihood of feature crossings within 6 hours for each puma location point that occurred in the highway, river or residential development buffer, on the side of most of the animal's home range area. For each puma, we used Hawth's Tools' "conditional point sampling tool", to generate 1000 points around each collar location occurring in a potential obstacle 300 m buffer zone, based on the steplength and turnangle distributions recorded for the given puma. We thus created predictions of the puma's expected next movement based on its own movement data.

We created a large (5000 m) buffer to display areas opposite the potential obstacle from the puma location points analyzed. The "intersect point tool" was used to generate a count of the number of newly generated points that fell within this zone, indicating an expected crossing of the obstacle feature. We calculated the percentage of all generated points that lay across potential obstacles to determine the expected probability of each puma crossing each feature. Paired Student's t-tests were used in JMP 5®, to compare the percent of expected crossings to the percent of observed crossings of each highway, river, and residential development for all pumas, to determine whether pumas avoided crossing these features. We used a query to calculate the percentage of observed puma paths crossing highways, that occurred within 300 m of a creek or river that passed beneath the roadway, to investigate whether pumas may use underpasses. We also noted whether we saw puma sign in these riparian underpasses during tracking.

Parcel size use

For developed zone pumas, we asked whether the animals preferentially used or avoided property parcel size classes in their home range areas representative of various types of rural development including ranches, ranchettes, and suburban style housing development. For each developed zone puma's collar dataset, we used Hawth's "intersect point tool" in ArcGIS 9.2® to generate a data field displaying the areas (acres) of all property parcels containing a puma location point. Because smaller parcel size classes tended to be located in groups of like-sized parcels, the small spatial error associated with GPS collar locations was not expected to cause an underestimate of puma use of small parcel size classes. We calculated the percentage of each puma's locations occurring in each of 6 parcel size classes, chosen for relevance to development planning designations: 0.10 to 5.00 acres (0.04 to 2.02 ha), 5.01 to 10.00 acres (2.03 to 4.05 ha), 10.01 to 20.00 acres (4.05 to 8.09 ha), 20.01 to 40.00 acres (8.10 ha to 16.19 ha), 40.01 to 100.00 acres (16.19 to 40.47 ha), and 100^+ acres (40.47^+ ha).

We next estimated the spatial coverage of each parcel size class within each puma's home range area. We used Hawth's Tools to create random points within each puma's home range area, equal to the number of high quality locations collected for each puma. We used "home range areas" to include areas bordering home ranges that pumas might avoid, which we wished to identify. For each home range area, we documented the property parcel sizes associated with each randomly generated point using the "intersect point tool", and calculated the percentages of random points falling within each parcel size class. Paired Student's t-tests were used in JMP 5® to test for differences between use of each parcel size class by pumas (observed use) and the spatial coverage of those parcel classes in home range areas (expected use).

We then asked whether puma use of parcel classes differed between day and nighttime. We designated all location points occurring between 09:00 hrs and 17:00 hrs PST as daytime locations, and all points occurring between 21:00 hrs and 05:00 hrs PST as nighttime locations. Day and night location files were created for each puma, including the parcel sizes associated with each location point. We calculated the percentage of locations in each of the 6 parcel size classes for the day and nighttime locations of each puma. Paired Student's t-tests were used in JMP 5® to identify diel differences in puma use of the parcel size classes.

Results

GPS collars and capture

We deployed GPS collars on 19 pumas during 2002-2005, with one animal collared twice. Pumas were tracked by collar during 2002-2006. Fourteen of these collars yielded successful downloads, representing all data collected by GPS collars on 13 individuals. Table 3-1 displays age class; sex; development zone; collar type; number of location fixes used in analyses; fix interval; duration of data for each puma; and mortality occurrence and cause of death. We used only high quality fixes in analyses for pumas from which collar downloads were obtained. Pumas whose GPS collars failed were only included in survival and dispersal analyses, using ARGOS transmitted GPS collar locations, aerial and ground VHF locations, and capture and carcass locations, as noted (Table 3-1).

We collared 4 adult male pumas, 4 subadult males, 1 juvenile male (dependent), 7 adult females, and 3 subadult females. Nine collared pumas occupied the developed zone while 10 of the animals lived in the undeveloped zone. Subadult pumas collared in the undeveloped zone that moved to developing rural areas after independence were classified as developed zone pumas. Developed zone pumas lived in a mosaic of ranches, ranchettes, public lands and residential developments networked by highways. Undeveloped zone pumas occupied a mix of national forest and private timberlands with few or no residential properties.

Survival

Table 3-1 displays the number of days that each puma was monitored from first observation (typically, capture date) through the animal's last documented location. Survival or mortality at the end of each animal's monitoring period is noted, as well as cause of death.

Six of 9 pumas (66.7%) collared in the developed zone were known to have died between 10 weeks and 26 months after capture, while 1 of 10 pumas (10%) died in the developed zone, 10 months post-capture. Because the death of subadult female 901 was documented long after collar retrieval (26 months post-capture), we included in analyses only the 10-month period during which this female was tracked by collar, in order to compare survival between groups monitored for comparable periods. Pumas were monitored for a mean 296 days with standard deviation of 164 days. Two-sample independent Student's t-tests found the number of days pumas were monitored did not differ between sexes (t =

1.300, df = 17, p = 0.212), ages (t = 0.078, df = 17, p = 0.939), development zone (t = 0.088, df = 17, p = 0.931) or for animals documented to have survived versus those that died (t = 0.273, df = 17, p = 0.788). Thus, we were able to compare puma mortality proportions between groups using fates documented within the periods that animals were monitored.

Table 3-2 displays the mean percent mortality for each puma group within the time of monitoring, excluding the death of SF901, 26 months post-capture. Developed zone pumas were more likely to die (55.6%) than undeveloped zone pumas (10%; $\chi^2 = 4.550$, p = 0.033). Mortality rates did not differ between males and females ($\chi^2 = 1.310$, p = 0.252) or between subadult and adult pumas ($\chi^2 = 0.224$, p = 0.636).

We also calculated 12-month puma mortality rates (Table 3-2) including only pumas that were tracked for a year or more, or died within the first 12 months of being monitored. Overall, 30.8% of pumas (4 of 13) died within a year of collaring. Adult mortality was 25.0% (2 of 8), while 40.0% (2 of 5) of subadults died. All pumas killed within their first 12 months of being monitored were male, and 3 of 4 occupied the developed zone. The developed zone 12-month mortality rate was 42.9% (3 of 7) and the undeveloped zone rate was 16.7% (1 of 6).

Adult male AM160 was the only undeveloped zone puma that died while tracked by collar. The body was intact but cause was unknown. GPS collar data indicated AM160 and adult male AM190 were proximate to each other for several hours 14 days before

AM160’s death, after which AM160’s movements shortened, but no recent external wounds were apparent.

In the developed zone, tracks and wounds indicated subadult male SM119 was killed by an adult male puma, 7 months after collaring. SM119 was in thin, poor condition when killed. Subadult male 852b was killed on a busy multi-lane highway, 6 months post-capture. AM852a, a 4-year old adult male, was killed due to depredation on sheep 10 weeks after capture. Adult female AF200 was killed 16 months after capture due to depredation on goats newly introduced to a large ranch. Developed zone subadult females SM901 and SM889 were collared as dependent juveniles, and both were killed post-independence for depredation on Barbados sheep on ranchette properties. Subadult female SF889 was in thin, poor condition at time of death.

Dispersal

Five subadults were collared as dependent juveniles, and an additional subadult was collared while already dispersing, at 13 ±1 months old. Dispersal parameter values are displayed in Table 3-3, including number of dispersal location fixes; minimum age of independence; age of dispersal; duration of dispersal movements; linear distance dispersed; summed distance traveled, direction moved; natal zone; zone where dispersal was completed; and puma fate. The collar of subadult female SF889 failed prior to independence from its collared mother, with only carcass location indicating dispersal, and age of independence and dispersal unknown.

All pumas gained independence between 11 and 13 months of age, with a mean of 12 months (n = 5; margin of error, 1.5 months). Five of 6 independence-aged animals dispersed, including all 3 males and 2 of 3 females. Documented dispersal age for 4 subadults ranged from 13 to 14 months with a mean of 13.5 months (margin of error, 1 month). Dispersal movements were documented to proceed for 56 to 147 days, although the male that moved for 147 days was still dispersing when its collar signal was lost. Collar locations indicated that sibling males SM170 and SM130 associated during dispersal for 42 ±7 days.

All 5 pumas that dispersed were collared in undeveloped zone natal ranges, and all but one female dispersed into the developed zone. The only puma that remained philopatric with its mother was female SF901, the only individual collared in a developed zone natal range. The 3 dispersing males all initially moved southwest, toward lower elevations and developed areas, and 2 eventually changed directions. The female that remained in the undeveloped zone dispersed south-southeast. Female SF889, from which only pre- and post-dispersal locations are known, moved west overall from the undeveloped zone to the developed zone.

Collar location data indicated that all dispersing animals crossed the home ranges of other collared pumas, and dispersal paths traversed all major sectors of the study area. All dispersing males crossed major highways, rivers and rural residential areas, and traveled from 86.3 km to 194.0 km, measured as the sum of linear distances traveled every two weeks during dispersal. Males dispersed Euclidean distances 23.2 km to 141.1 km (μ =

67.6 km) away from their natal ranges. Female subadult SF881 traveled 31.5 km summed distance, and dispersed 27.2 km Euclidean distance from its natal range, while female SF889 dispersed 16.2 km Euclidean distance from its natal range.

Male SM170 moved more than 80 km into the Auburn city limits, then across more than one hundred kilometers of rugged, mountainous terrain before collar signal cessation. Male SM119 briefly occupied a commercial area of the city of Placerville, before moving north to establish a long, narrow home range straddling multi-lane highway I-80, and being killed by another puma. Additionally, independent subadult male SM852b had already occupied a long, narrow home range stretched along highway I-50, at the time of collaring. SM852b was killed by a vehicle on the highway. Overall, 57.1% of the subadult animals (4 of 7) were known to have died during our study, all in the developed zone. Two of these were in thin, poor condition at time of death.

Obstacles to movement

Table 3-4 displays the expected and observed percentages of puma that crossed highways, rivers, and dense residential developments. Highways occurred in the home range areas of all 6 developed zone pumas and 4 of 6 undeveloped zone pumas, for which collar downloads were obtained. Three developed zone puma home range areas and all undeveloped zone home range areas contained major rivers. Dense residential developments occurred in the home range areas of 5 developed zone pumas and 1 undeveloped zone puma.

Pumas crossed potential obstacle features far less often than predicted from paths generated using that animal's movement data. Paired t-tests indicated that pumas crossed highways ($t = 50.661$, $df = 9$, $p < 0.001$), rivers ($t = 11.873$, $df = 7$, $p < 0.001$), and residential developments ($t = 7.612$ $df = 5$, $p < 0.001$) significantly less than expected. Paths derived from puma movement patterns predicted that pumas would cross highways 785% more often, rivers 430% more often, and dense residential developments 373% more often, than was documented. A majority (67.8%) of puma paths that crossed highways were within 300 m of creeks or rivers and associated highway bridges, and we occasionally noted puma tracks passing beneath these bridges.

Parcel size use

For developed zone animals, Table 3-5 and Figure 3-2 display the percentage of puma locations in each property parcel size class, versus the percent land coverage of those parcel classes in the animals' home range areas. Paired t-tests indicated that pumas used the smaller parcel size classes of 0.10 to 5.00 acres (0.04 to 2.02 ha), 5.01 to 10.00 acres (2.03 to 4.05 ha), and 10.01 to 20.00 acres (4.05 to 8.09 ha), less than the land coverage of those parcel classes in the pumas' home range areas ($t = 3.688$, $df = 5$, $p = 0.014$; $t = 4.466$, $df = 5$, $p = 0.006$; $t = 2.612$, $df = 5$, $p = 0.048$). Puma use of the 20.01- to 40.00-acre (8.10- to 16.19-ha) parcel class did not differ from the spatial coverage of this class in the animals' home range areas ($t = 1.216$, $df = 5$, $p = 0.278$). The larger parcel size classes, 40.01 to 100.00 acres (16.19 to 40.47 ha) and 100.00^+ acres (40.47^+ ha), contained a greater percentage of puma locations than the representation of these parcels in puma home range areas ($t = 2.603$, $df = 5$, $p = 0.048$; $t = 2.766$, $df = 5$, $p = 0.040$).

Table 3-6 and Figure 3-3 display the percentage of puma locations in each parcel size class for daytime versus nighttime locations. Paired Student's t-tests indicated that nighttime puma locations (21:00 hrs to 05:00 hrs PST) occurred more often in the smaller parcel size classes, 0 to 5.00 acres, 5.01 to 10.00 acres, and 10.01 to 20.00 acres, than did daytime locations (09:00 hrs to 17:00 hrs PST) ($t = 2.657$, $df = 5$, $p = 0.045$; $t = 3.719$, $df = 5$, $p = 0.014$; $t = 4.604$, $df = 5$, $p = 0.006$). Nighttime locations occurred less often in the 2 largest parcel size classes, 40.01 to 100.00 acres and 100.00^{+} acres, than did daytime puma locations ($t = 6.482$, $df = 5$, $p = 0.001$; $t = 4.795$, $df = 5$, $p = 0.005$). Puma use of 20.01-acre to 40.00-acre parcels did not differ between day and night ($t = 1.387$, $df = 5$, $p = 0.224$).

Discussion

We found evidence that low-density rural development, with associated highways and dense housing developments, fragmented puma habitat. Our results were consistent with attributes of a source-sink population structure, disrupted connectivity of landscapes for pumas, and the creation of habitat patches that pumas avoided in their developed zone home range areas.

Survival and dispersal parameters were obtained from a small sample, but were consistent with a source-sink population and differed from our expectations for a habitat-limited, or an unfragmented population structure. The 12-month mortality rate for all pumas in our sample, 31%, was greater than annual mortality rates from unhunted populations in other western states of 12% to 28% (Lindzey et al. 1988, Anderson et al. 1992, Beier and Barrett 1993, Logan and Sweanor 2001). Mortality for the Western Sierra pumas was comparable to the higher mortality figures from hunted puma populations, reported as 27%, 0% to 27%, and 32% (Ashman et al. 1983, Robinette et al. 1997). Our subadult puma 12-month mortality rate, 40%, was also considerably greater than the 24% annual mortality rate reported from an expanding population in New Mexico (Sweanor et al. 2000), and the 26% rate from a habitat-limited population in Florida (Maehr et al. 2002).

However, 12-month mortality in the undeveloped zone, 16.7%, was among the lowest reported in the literature, while the 42.9% mortality rate in the developed zone exceeded even mortality from a heavily exploited puma population in Arizona, in which pumas were culled for depredation control (Cunningham et al. 2001). Cunningham et al. (2001) contended that their study population, with a 38% mortality rate, represented a demographic sink. Jalkotzy et al. (1992) projected that a puma population could sustain an overall mortality rate of about 15%, of which 5% would be from natural causes. Further, 3 of 4 collared females in the developed zone died within 26 months of collar deployment, all at breeding age. High levels of mortality among breeding-aged females can significantly impact large carnivore population viability (Lindzey et al. 1992, Gittleman 1993).

If the puma population were habitat-limited, we expected frequent failure of dispersing subadults to establish independent home ranges; long summed dispersal distances and durations compared to other populations, but short Euclidean dispersal distances for animals that eventually established home ranges; and potentially, young ages of independence and dispersal. In contrast, all dispersing subadults successfully established home ranges, except SM170 whose outcome was not known. Age of independence of juvenile pumas ($\mu = 12 \pm 1.5$ months) was low compared to mean ranges from other studies (13.7 ±1.6 months, Sweanor et al. 2000; 15.2 ±3.0 months, Ross and Jalkotzy 1992). Mean dispersal age, 13.5 ±1 months, was less than the means of 15.2 ±1.6 months, 16.0 months, 17.9 ±4 months, 18.0 ±2.8 months, and 16-19 months, reported from pumas in other North American populations (Sweanor et al. 2000, Ross and Jalkotzy 1992, Maehr et al. 1991, Beier 1995, Hemker et al. 1984).

The sample of puma dispersal distances suggested that habitats containing adequate food resources, or at least, that were free of competitive adult males, were sometimes available to pumas in developed areas near the undeveloped zone. Euclidean dispersal distances ($23\text{-}142^{+}$ km for males and 16-27 km for females) appeared similar to or less than dispersal distances documented in other populations (Sweanor et al. 2000: 67-176 km, males, 2-96 km, females; Anderson et al. 1992: 29-247 km, males, 9-140 km, females; Ross and Jalkotzy 1992: 30-155 km, all pumas). Mean Euclidean dispersal distance for habitat-limited Florida panthers eventually establishing home ranges was only 37 km for males, and 11 km for females (Maehr 2002). The summed dispersal distances (86.3-194.0 km males, 31.5 km female) of our sampled subadults were not particularly long compared to Euclidean distances, in contrast to a frustrated dispersal model (Lidicker

1975). Duration of dispersal (1.9-4.9$^+$ months) was far less than for Florida panthers (7.0 months for females, 9.6 months for males, Maehr 2002).

In an unfragmented population structure, we expected occurrence of dispersal, establishment of independent home ranges, and survival rates to be similar to puma populations in relatively undisturbed areas that were not heavily hunted. Survival rates, notably in the developed zone, appeared considerably lower than in other puma populations, including hunted populations. Like in unfragmented populations, all subadult males dispersed and most or all established independent home ranges (Seidensticker et al. 1973, Hemker et al. 1974, Anderson et al. 1992, Ross and Jalkotzy 1992). Two of 3 subadult females dispersed, including both those collared in the undeveloped zone, although female dispersal typically appears rare (Laing and Lindzey 1993, Sweanor 2000). Logan and Sweanor (2001) postulated that female puma dispersal, unlike male dispersal, is partly density dependent and is driven by a shortage of per capita food resources in a puma’s natal region.

Consistent with expectations for a source-sink population structure, most subadults dispersed and established home ranges, but experienced high mortality in their new home ranges (Pulliam 1988). Notably, 4 of 5 dispersers moved from undeveloped zone natal ranges, ostensibly a demographic source area, into the developed zone, potentially a sink area. The only subadult failing to disperse was the only animal with a natal range in the developed zone. Instead of constituting a true sink, some or all of the developed zone could have functioned as a “pseudo-sink” (Watkinson and Sutherland 1995), an area able to independently sustain a small population but where high immigration raises the number of individuals beyond that which the area can support.

The developed zone may have offered habitat availability due to sufficient resources coupled with a high turnover of pumas driven by high mortality. However, 2 of 4 developed zone subadults died in poor, thin condition. Young pumas trying to obtain food and gain adequate hunting skills while avoiding interactions with adult males, often the main cause of puma mortality in unhunted populations (Logan and Sweanor 2001), may effectively have been pushed into marginal urban interface habitats. For example, two subadult males established long, narrow home ranges along major highways before their deaths. The male portion of this population may conform to Pulliam and Danielson's (1991) "ideal preemptive distribution", in which young, subordinate animals move from a high quality source area into a low quality sink until they are ready to challenge older males occupying source areas. In contrast, young pumas in particular could have been attracted to these interface areas by the presence of roadkill, suburban deer, or domestic animals, which may have been relatively easy to obtain.

Highway and housing construction threatened to fragment puma habitat by disrupting landscape connectivity for pumas. Animals crossed highways in their home range areas 7.9 times less than expected if movements were not impeded. Puma home ranges tended to border rather than include highways. Pumas crossed 4- to 8-lane highways rarely, likely by passing under bridges along riparian areas, and one puma was killed crossing a highway. Highways ≥ 6 lanes have been documented to seriously fragment puma populations and cause significant mortality (Beier 1995, Beier and Barrett 1993, Logan and Sweanor 2001). Increasing traffic or further highway expansion could increase mortality and disconnect puma habitats in our region. Housing developments (parcels ≤ 2 acres (0.8 ha)) disrupted puma movements similar to the effects of major rivers, with pumas crossing both features about four times less than expected. Dense housing developments not only threaten to increase human-caused puma mortality, but may degrade landscape connectivity. Noss et al. (2002) contended that for large carnivores, connectivity mainly involves circumventing barriers such as highways and developed areas, and minimizing human causes of mortality.

Subdivision of property parcels to 20 acres or less decreased pumas' use of these parcels within their home range areas, and created patches of preferred (≥40-acre (16.2-ha) parcels) and non-preferred habitat (≤20-acre (8.1-ha) parcels). Patterns of habitat avoidance and preference by parcel size were similar for all developed zone pumas sampled, with each animal using the 20^+-to 40-acre size class in a neutral manner. Yet these mid-sized parcels also presented heightened mortality risks from human-caused sources such as vehicle collisions or depredation on pets and livestock. Orlando et al. (2008a) found depredations, the primary cause of puma death in our study, to occur on a mean property parcel size of 48.7 acres (18.9 ha), and median parcel size of 18.0 acres (7.3 ha) in the Western Sierra study area. All pumas preferred ≥40-acre parcels more strongly during the day, and avoided ≤20-acre parcels more strongly during the day. Pumas may have been avoiding use of human dominated environments during times of high human activity, but still relying partly on these areas for hunting.

Rural development created preferred and non-preferred/high-risk habitat patches at the individual level (third-order selection (Aebischer et al. 1993); disrupted functional connectivity at the landscape level; and created a source-sink or source-pseudo-sink condition at the population level for pumas. Source-sink population structures are not necessarily unsustainable or uncommon among wide-ranging large carnivores (Howe et al. 1991, Dias 1999, Noss et al. 1996, Pulliam 1988). Howe et al. (1991) found that a large but finite proportion of a metapopulation can exist in non-sustaining subpopulations, and these demographic sinks may connect source populations, aiding overall viability. In a source-sink or -pseudo-sink condition, protection of large demographic source areas, interconnectedness between sources, and protection of buffer areas supporting sink populations is vital to maintain long-term viability (Hansson 1991, Howe et al. 1991, Roberts 1998). The status of population subunits must be carefully monitored.

Management Implications

Conservation of the pumas in developing rural areas mandates concern regarding housing and highway expansion as a threat to source area connectivity, and residential development as a threat to puma habitat utility in buffer and source areas. Most undeveloped foothill land in our study region is already slated for residential development in parcel sizes of 40 acres or less (Strahlberg and Williams 1991, Stoms 2004, Walker et al. 2003). Although the higher elevation undeveloped zone of the Western Sierra may continue to support pumas, this zone spanned only about 1.4 times the average home range width of an adult male puma in our study population (Orlando et al. 2008b). We expect further foothill development to constrict remaining source areas, threaten connectivity, degrade marginal area habitats for pumas, and result in an overall decline in numbers of pumas.

To conserve pumas and associated biodiversity, source areas, in our case the undeveloped national forests and timberlands of the Western Sierra, should be managed for minimum puma mortality risk from conflict with humans and livestock, and for healthy populations of ungulate prey. Rural developed areas in puma habitat, even those representing population sinks, should be managed as buffer zones and for connectivity between source areas. State and county planning should aim to limit habitat fragmentation from major road development or expansion, and maintain habitat linkages and property parcel sizes greater than 40 acres. Measures to limit human-caused mortality are essential, including educating residents on depredation threats and prevention, and providing wildlife-friendly highway crossings along movement corridors.

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Tables and Figures

Table 3-1. Collar performance, time monitored by collar, and puma fates, by development zone for GPS-collared pumas in California's Western Sierra Nevada, 2002-2007. TA = Telonics Argos collar. TP = Televilt PosRec Collar. Puma ID: S = Subadult, A = Adult, J = Juvenile; M = Male, F = Female.

Puma ID	Collar type	No. High quality fixes	Fix interval (hrs)	Days monitored by collar	Mortality	Cause of death
Developed zone						
SM119	TA	1197	3	211	Y	puma
SM130	TA	2055	3	478	N	
SM170	TA	72[1]	NA	236	N	
AF200	TA	1114	3	454	Y	depredation
AF797	TP	445	2	224	N	
AM852a	TP	1240	1	68	Y	depredation
SM852b	TP	1131	2	171	Y	vehicle
SF889	TP	22[2]	NA	521	Y	depredation
SF901	TP	146	12	270	Y[4]	depredation
Undeveloped zone						
AM110	TA	7[1]	NA	172	N	
JM150	TA	484	3	95	N	
AM160	TA	1521	3	286	Y	unknown
AF180	TA	3014	3	677	N	
AM190	TA	2285	3	492	N	
AF809	TP	163	2	317	N	
AF819	TP	830	2	230	N	
AF838	TP	12[1]	NA	82	N	
AF868/ 829[3]	TP	2596	2, 1	355	N	
SF881	TP	34[1]	NA	288	N	

[1] Argos uplink, aerial, and ground locations only; no GPS collar download.

[2] Aerial and ground locations only; no GPS collar download.

[3] Adult female collared twice consecutively.

[4] Puma killed 16 mos. after collar detachment, mortality not used in analyses.

Table 3-2. Mortality of GPS-collared pumas by group during time of monitoring and during first 12 months of monitoring, in California's Western Sierra Nevada, 2002-2006.

Puma Group	Total mortality		12-month mortality	
	n	%	n	%
All	19	31.6	13	30.8
Developed Zone	9	55.6*	7	42.9
Undeveloped Zone	10	10.0*	6	16.7
Male	9	44.4	7	57.1
Female	10	20.0	6	0.0
Adult	11	27.3	8	25.0
Subadult	8	37.5	5	40.0

*Pearson's chi-square test indicates mortality difference between groups, $\alpha = 0.05$.

Table 3-3. Dispersal parameters for GPS-collared subadult pumas in California's Western Sierra Nevada, 2002-2006. Puma ID: S = subadult, M = male, F = female. Zone: U = undeveloped, D = Developed. NA = Not applicable, puma did not disperse.

Dispersal Parameter	SM119	SM130	SM170	SF881	SF889	SF901
Age of independence (mos, ±6 wks)	13[1]	12	12	12	unknown	11
Age at dispersal (mos, ±1 month)	13	14	14	13	unknown	NA
Dispersal period (days)	108	124	147[2]	56	unknown	NA
Euclidean distance dispersed (km)	23.2	38.4	141.1	27.2	16.2	0
Summed distance traveled (km)	138.7	86.3	194.0	31.5	unknown	0
Movement direction	SW, N	SW	SW, SE	SSE	W	NA
Natal zone	U	U	U	U	U	D
Dispersal zone	D	D	D	D	D	D
Mortality: reason	Y: puma	N	N	N	Y: depredation	Y: depredation

[1] Puma already independent when captured at 13 mos. of age.
[2] Collar failed during dispersal.

Table 3-4. Percent puma paths crossing potential obstacles in California's Western Sierra Nevada; projected from GPS collar data 2002-2006. Puma ID: S = subadult, A = adult, J = juvenile, M = male, F = female. Expected crossings calculated as the percentage of 1000 points randomly generated using each puma's movement parameter distribution, situated across the potential obstacle from an actual puma location point within a highway, river, or residential area buffer zone.

Puma ID	% Highway crossings		% River crossings		% Residential area crossings	
	Expected	Observed	Expected	Observed	Expected	Observed
Developed Zone						
SM119	37.1	7.6	36.1	3.3	32.9	16.4
SM130	31.0	4.5	31.8	5.8	28.6	3.9
AM852a	31.3	0.0	31.8	0.0	27.0	9.6
SM852b	29.8	0.2	NA	NA	NA	NA
AF200	30.7	3.4	NA	NA	24.2	7.2
AF797	31.8	5.1	NA	NA	26.7	8.5
Undeveloped Zone						
JM150	33.5	3.7	32.2	11.4	NA	NA
AM160	36.8	7.3	36.7	12.6	NA	NA
AM190	40.0	10.0	41.1	14.1	34.9	1.1
AF180	26.2	0.0	NA	NA	NA	NA
AF819	NA	NA	30.6	16.0	NA	NA
AF868	NA	NA	31.3	0.0	NA	NA
Mean % difference expected/observed		785.2*		429.7*		373.2*

*Difference between observed and expected values for all pumas pooled using paired Student's t-test, $\alpha = 0.05$.

Table 3-6. Percent day vs. night use of property parcel size classes by GPS-collared pumas in developed rural zone of California's Western Sierra Nevada, 2002-2006. Values presented as percent day/percent night use. Day use: percent puma collar locations in parcel size class during 09:00 hrs-17:00 hrs. Night use: percent puma collar locations in parcel size class during 21:00 hrs-05:00 hrs.

Puma ID	0.10-5 acres	5.01-10 acres	10.01-20 acres	20.01-40 acres	40.01-100 acres	100.01+ acres
SM119	6.9/20.8	5.3/9.0	10.9/13.2	13.0/10.1	23.3/16.9	40.5/29.7
SM130	0.0/0.0	0.0/0.0	4.4/8.9	9.7/12.9	34.8/30.7	51.1/47.6
AF200	0.5/3.3	2.9/7.1	6.4/9.7	15.7/15.1	25.7/20.9	48.8/44.0
AF797	2.2/7.1	3.0/7.8	10.0/11.2	15.4/16.8	23.9/16.8	45.2/40.1
AM852a	0.2/3.1	1.0/2.2	3.1/7.8	15.7/20.3	37.1/26.8	43.0/39.9
SF901	2.8/9.8	4.4/7.4	9.1/10.4	18.5/23.0	26.2/15.6	38.8/33.5
Mean	2.1/7.4*	2.8/5.6*	7.3/10.2*	14.7/16.4	28.5/21.3*	44.6/39.1*

*Difference between mean daytime and mean nighttime use of parcel size class, paired Students *t*-test, $\alpha = 0.05$.

Figure 3-1. Approximate urban-wildland interface dividing developed and undeveloped zones of puma study area in California's Western Sierra Nevada, 2002-2006. Housing densities are from California Dept. of Forestry and Fire Protection dataset CEN00BLM03_1. Kernel density home ranges of 13 collared pumas are shown.

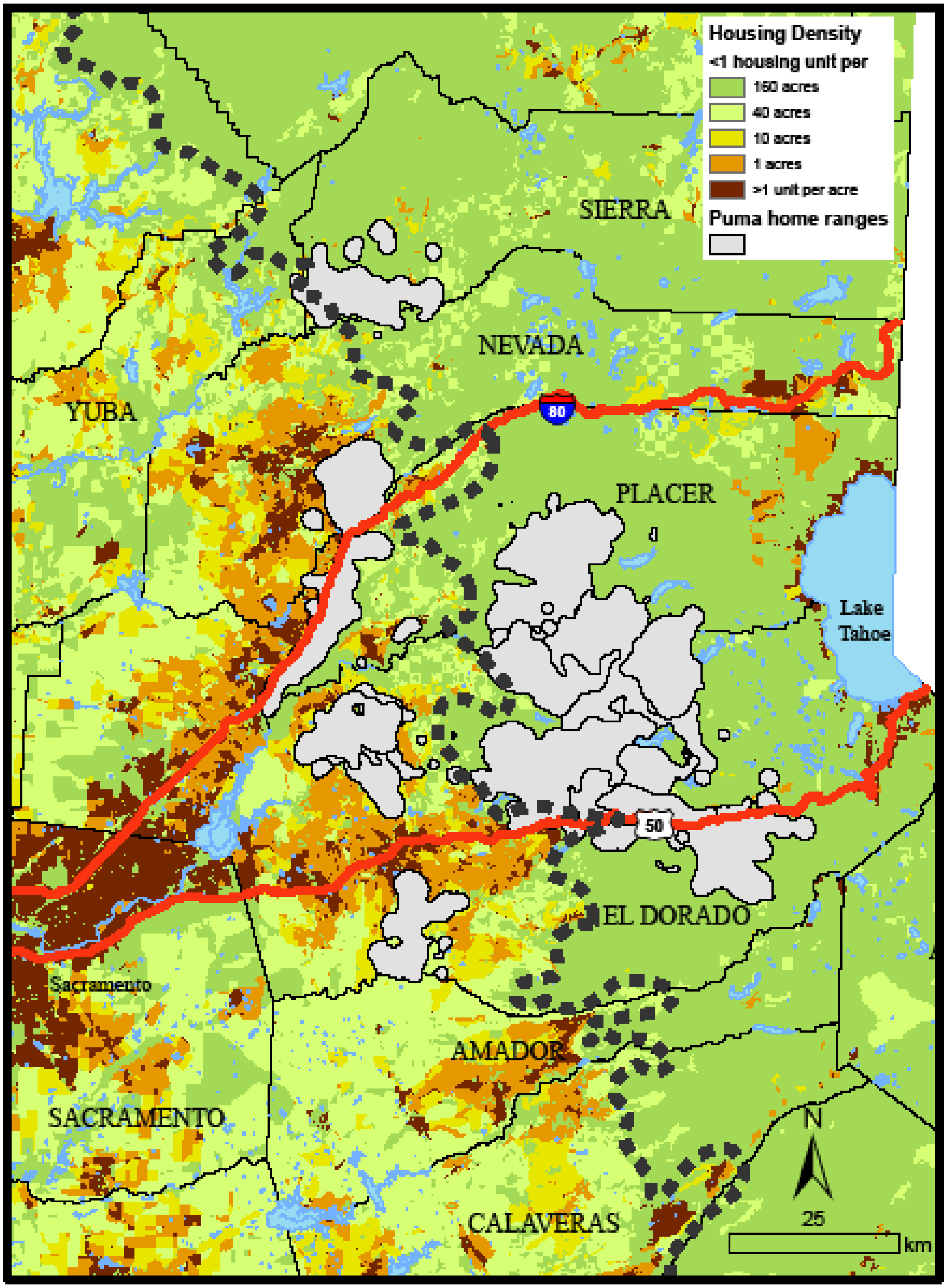

Figure 3-2. Percent puma use by property parcel size class vs. percent land coverage of parcel size classes in puma home range areas (95% kernel home range and 1 km buffer), for GPS collared pumas in developed rural zone of California's Western Sierra Nevada, 2002-2006.

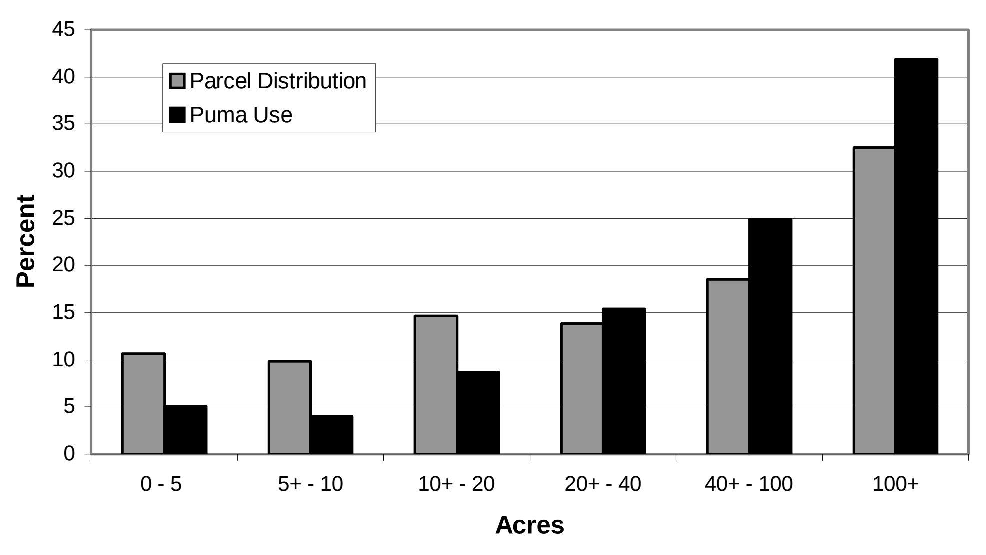

Figure 3-3. Percent use by property parcel size class, day vs. night, for GPS collared pumas in rural developed zone of California's Western Sierra Nevada, 2002-2006.