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Using spatial characteristics of apex carnivore communication and reproductive behaviors to predict responses to future human development

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Abstract

A growing body of evidence has documented how wildlife alter their behavior in response to human encroachment. For carnivores, behaviors related to reproduction and communication are particularly sensitive to human disturbance and can provide an early warning indicator of development's negative impacts. Despite the important role carnivores play in an ecosystem, few tools have been developed to anticipate how future human development impacts these behaviors. We developed a set of models to understand spatial relationships between anthropogenic development and puma (*Puma concolor*) habitat selection for two critical reproductive behaviors: nursery habitat for raising young, and sites for communication with mates. Using geospatial location data from the Santa Cruz Mountains in California, USA, we found that female pumas use small nursery home ranges (9 km^2 ± 1.72 SE) of predominantly natural habitat, potentially with low levels of human development (< 1 housing unit per 40 acres), when supporting kittens < 8 weeks old. Areas immediately surrounding (≤ 600 m) puma communication sites were also almost entirely composed of undeveloped habitat or low-density development. When modeling projected human development compared to current land use, we found that increases in human development may eliminate 20% of current puma nursery habitat and nearly 50% of current communication site habitat. Future development will also increase the patchiness of suitable habitat, intensifying the difficulty of locating and accessing suitable areas for nurseries and communication. Focusing on the habitat needed to support reproductive and communication behaviors may be an effective way to prioritize conservation planning for pumas and other apex carnivores.

Keywords Anthropogenic development · Breeding habitat · Communication · Habitat loss · Habitat selection · *Puma concolor*

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Introduction

Early conservation efforts focused on setting aside large areas of land in order to preserve intact ecosystems, but conservation goals can no longer be accomplished by establishing protected areas alone (Wade and Theobald 2010; Wiersma and Sleep 2016; Kshettry et al. 2020). Increasing anthropogenic development necessitates creating viable conservation strategies that promote coexistence with wildlife across rapidly changing landscapes (Burdett et al. 2010; Visconti et al. 2016; Kshettry et al. 2020). Exurban development is the fastest growing land use type in the U.S, and currently occupies 25% of the lower 48 states (Theobald 2001; Theobald 2005). Within the next 25 years, exurban development is projected to increase by over 75%, with the highest rates of growth near coastal areas (Alig et al. 2004). Even modest growth in exurban areas may have large consequences for wildlife, making conservation planning for exurban areas critical (Burdett et al. 2010; Krausman et al. 2011; Wiersma and Sleep 2016). Our study seeks to evaluate how populations of a wide-ranging carnivore, *Puma concolor*, might respond to such exurban development. Specifically, we assess how two key behavioral characteristics, neonatal nursery sites and communication scrape sites, might be impacted by current and future development.

While some carnivore species may tolerate development (e.g. urban canids; Gehrt et al. 2010; Mueller et al. 2018), some species are displaced by areas with heavy human presence (Burdett et al. 2010; Wang et al. 2015; Vickers et al. 2015). Specifically focusing on pumas (*Puma concolor*), though they are not a wilderness-obligate species, there are no known urban puma populations (Gehrt et al. 2010). Further, suburban and even exurban development may present significant impediments to puma use (Burdett et al. 2010; Vickers et al. 2015; Benson et al. 2016). Pumas may live in open spaces adjacent to highly developed areas, however, they spend the majority of their time utilizing undeveloped parts of their home ranges. Previous research has shown that puma reproductive and communication behaviors are particularly sensitive to human activities (Beier et al. 1995; Burdett et al. 2010; Riley et al. 2014; Wilmers et al. 2013; Maletzke et al. 2017). Because nursery and communication site selection are essential for puma population persistence, their conservation is dependent on understanding how anthropogenic activity and development affects these behaviors.

When pumas are supporting neonate offspring, they transition from occupying large home ranges to localizing in a small area, adopting a central place foraging strategy as they make limited forays from their den or nursery site to secure food (Beier et al. 1995; Logan and Sweanor 2001). The areas surrounding nursery sites, or nursery home ranges, provide critical resources that directly affect survival of dependent young and population dynamics (Ross et al. 2010; Davies et al. 2016). Relative to other life stages, neonate mortality is often high, and neonates have high energetic demands. This makes selection of high-quality nursery habitat critical for reproduction and survival (Logan and Sweanor 2001; Laundré 2005). Understanding the specific habitat requirements during this restricted nursery home range period can help inform predictions of how development will impact future carnivore populations.

Communication sites are areas used for conspecific communication via scent marking and are important for selecting mates and defining territories (Allen et al. 2015). Males create communication sites, or scrapes, by using their hind feet to dig two shallow grooves with a mound of soil and duff at one end, and will sometimes urinate or defecate on the scraped mound of material (Allen et al. 2014). Male pumas communicate their presence to

competitors using scrapes (Allen et al. 2016), and advertise to females for breeding opportunities (Allen et al. 2015). Scrapes are often placed at prominent landscape locations, such as trail junctions, saddles, or under large trees. Communication sites are most frequently visited by males; however, these sites serve an important role to females as well (Allen et al. 2014, 2015). When a female is ready to breed, she will often linger at these locations and caterwaul to increase her chances of encountering a receptive mate (Logan and Sweanor 2001; Allen et al. 2015).

The Santa Cruz Mountains of California, USA, ranging from urban Silicon Valley to large areas of preserved open space, provided a backdrop for quantifying how varying levels of development affect puma behavior. Previous analyses conducted by Wilmers et al. (2013) suggested that anthropogenic development plays a key role in shaping habitat suitability for reproductive behaviors (i.e. communication and nursery sites), however that work did not assess the quality and characteristics of the habitat surrounding these sites. Here we extend that analysis by explicitly estimating habitat selection by females during their central place foraging phase (hereafter referred to as a nursery home range) and modeled current and future human development patterns. This allows us to more accurately model interactions between key puma behaviors and habitat availability in the context of human development. We hypothesized that pumas would avoid anthropogenic development, and anthropogenic development in our study would increase, thereby shrinking suitable habitat patches and increasing suboptimal matrix between patches.

Materials and methods

Study area

We conducted our study in the Santa Cruz Mountains of California, USA (Fig. 1). Our 1600 km^2 study area ranged from sea level to approximately 1155 m in elevation, with two distinct climactic zones: a cooler coastal climate on the west side, and warmer temperatures inland to the east. The climate was Mediterranean with hot, dry summers, and cool, wet winters; most of the annual precipitation occurs as rain between November and April. The study area encompassed a spectrum of human development and protected lands, creating a mosaic of land use where human density ranged from 0 to 40 housing units per acre (0 to 9884 housing units per km^2; see Table 1 for housing density categories and definitions). There were also large areas of preserved habitat managed by state, county, and city parks as well as private entities. In between were areas with human influence ranging from rural to urban development, as well as trails, fire roads, residential roads, and highways.

Field methods

We captured 45 free-ranging pumas from 2008 to 2014 with cage traps, leg hold snares, or trailing hounds as described in Wilmers et al. (2013). Puma capture, handling, and sampling protocols were approved by the Animal Care and Use Committee at the University of California, Santa Cruz (protocol #Wilmc1101), and the California Department of Fish and Wildlife. Individuals were tranquilized using Telezol (Fort Dodge Laboratories, Fort Dodge, IA, USA) and fitted with a GPS/VHF tracking collar (GPS PLUS, Vectronics
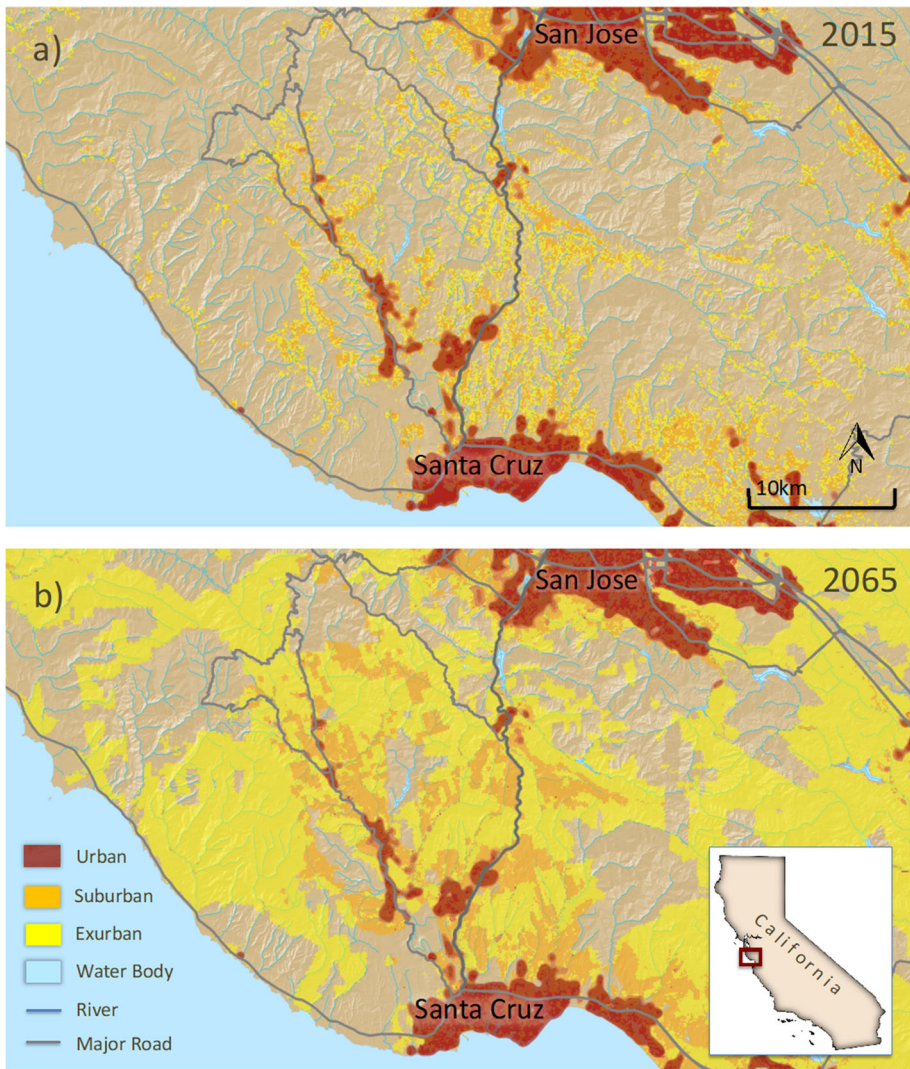
Fig. 1 Over the next 50 years, development is expected to greatly increase in the Santa Cruz Mountains, California, USA. The fastest growing projected land use change between 2015 (**a**) and 2065 (**b**) will be habitat shifting from lightly modified development to exurban development

Aerospace, Berlin, Germany). Collars were programmed to acquire a GPS location every 4 h, and the GPS data were remotely downloaded monthly via UHF, or transmitted via cellular phone towers every 1–3 days depending on collar program configuration and cell phone coverage.

We used female GPS collar data to locate potential nursery sites by searching for clusters of spatially aggregated GPS locations that persisted for > 1 week, and were characterized by repeated excursions by the female to and from the site. In one instance, the GPS collar failed and we used the collar's VHF signal to repeatedly triangulate the position of her nursery over the course of several days. We visited potential nursery GPS

Table 1 Recent (2015) and predicted (2065) land cover statistics of each development category, and the percent change from 2015 to 2065, for Santa Cruz, California, USA

Development category	Housing units per 100 km^2	Percent of study area		Percent change
		2015	2065	
Lightly modified (> 40 acres/house)	< 0.062	77.38	32.61	− 44.76
Exurban (2–40 acres/house)	0.062–1.236	6.43	49.23	+ 42.8
Suburban (0.25–1 acres/house)	1.236–9.884	11.07	12.63	+ 1.56
Urban (< 0.25 acres/house)	> 9.884	5.12	5.52	+ 0.4

clusters between 3 and 6 weeks of when the female first localized to confirm the site as a nursery by finding kittens or associated kitten sign. We then recorded the nursery coordinates using a handheld GPS unit, and subsequently monitored the female's movements in relation to the nursery as well as kitten fates.

We defined communication sites as frequently used scent marking areas containing ≥ 3 scrapes within 9 m^2 of one another (Allen et al. 2014). We located potential communication sites using an algorithm (described in full in Wilmers et al. 2013). The algorithm located sites within 300 m of previous locations in which males visited, with visits separated by > 7 days to eliminate feeding sites. Then we field-checked locations for scrapes and recorded site coordinates with handheld GPS units. We also located communication sites opportunistically during our extensive field activities, but sites identified by the algorithm comprised the vast majority of communication sites recorded.

Model variables

We used a digitized housing layer (described in Wilmers et al. 2013) to classify the current landscape into housing density categories as defined by Environmental Protection Agency Integrated Climate and Land-Use Scenarios (ICLUS) model (Bierwagen et al. 2009) (Table 1). We employed a spatially explicit regional growth model (SERGoM) developed by ICLUS (Bierwagen et al. 2009) to project future development in our study area (e.g. Burdett et al. 2010). SERGoM uses several categories of input to create projections, with special attention to exurban/low-density development (Bierwagen et al. 2009). For our analyses, we used the "base case" development projection as a conservative prediction of human development in Santa Cruz Mountains 50 years into the future (to the year 2065). This assumes a "business-as-usual" development pattern and the midline U.S. Census Bureau projection for population growth. For a detailed description of model assumptions, parameters, and alternative development patterns see Bierwagen et al. (2009). The SER-GoM model produces a 100 m resolution raster of housing development categories.

We quantified habitat data by extracting landscape attributes for each point or area. Prior to conducting statistical analyses, we used a correlation matrix to identify independent variable collinearity ($|r| < 0.50$). All variables met this criterion and were retained in the model. As a continuous variable, slope (x) was normalized as follows (Zuur et al. 2007),

$$x_i^{\mathrm{norm}} = (x_i - x^{\mathrm{mean}})/std$$

When modeling future selection, we could not adequately predict distance to the nearest road with the SERGoM model because the model output does not explicitly map road locations. However, the distance to roads had a marginal influence on site suitability, and the SERGoM does implicitly incorporate road density into their model output. This allowed our model to account for the influence of roads by including their effects as a component of development.

Statistical methods

We processed all spatial data in Geographical Information Systems program ArcGIS (v.10.1; ESRI, 2012) and R (v.2.1.3.1; R Development Core Team, 2010), and used R for our statistical analyses. We used two packages in R: the lme4 package (Bates et al. 2015) with a binomial link for model fitting, and the adehabitatHS package (Calenge 2006) for the compositional analysis. We also used the LoCoH (Getz et al. 2007) and SERGoM (Bierwagen et al. 2009) tools in ArcGIS.

Home ranges

We used 95% adaptive local convex hulls (LoCoH; Getz et al. 2007) to estimate an annual home range for each puma. We restricted our analyses to mature resident pumas because subadult pumas are seldom involved in reproductive behaviors. We excluded data for pumas monitored fewer than 12 continuous months. To avoid overestimating home range size due to shifts in territories, we used the first year of GPS data for individuals with data spanning longer than 1 year (n = 24).

Modeling suitability: potential nursery home ranges in 2015

We assessed selection and avoidance in nursery home range areas in a use-availability framework (Manly et al. 2002). This analysis considered the relationship between habitat selection within animals' home ranges (3rd order selection, *sensu* Johnson 1980) and landscape features. We compared habitat characteristics in areas surrounding nursery sites to similar areas within individual home ranges using a compositional analysis (Aebischer et al. 1993). By defining used areas as "nursery home ranges," or areas females utilized as a central place forager while she was bound to the nursery with young, immobile kittens, this analysis allowed us to incorporate kitten-rearing behavior in nursery site selection. To determine the effect of surrounding habitat, we compared nursery home ranges to comparably sized random areas selected within female home ranges. We modeled this behavior by creating a nursery 95% LoCoH home range (Getz et al. 2007) for each nursery site by using the GPS points collected while the female had kittens < 8 weeks old. We created comparable "available" nursery areas by placing a buffer around each random point. The buffer size was determined by sampling with replacement from a vector representing the size of all used nursery home ranges. We then compared the percent composition of each type of anthropogenic development (Table 1) in used nursery home ranges compared to similarly-sized available areas, drawing 5:1 available:used areas at random from within each female's home range (Manly et al. 2002).

Next, we used the results from the nursery home range compositional analysis to model landscape-level habitat suitability. Selected nursery home range habitat provided a metric for suitable conditions, which we used in a moving window analysis to identify preferred

nursery area habitat within the study area. Specifically, we measured the percent composition of each development category (lightly modified, exurban, suburban, or urban) in nursery home ranges, and used the mean ($\pm$ SE) amount of each type of development present to model suitable habitat across the study area. Positive t-values indicated a preference for the habitat type, and negative t-values indicated avoidance. For avoided development categories, we used the mean value, plus the standard error, as the maximum threshold for nursery home range suitability in our predictive model. For selected categories, we set the average value, minus the standard error, as the minimum threshold for modeling nursery home range selection. We used these mean values, plus or minus the standard error, to model habitat suitability across the study area, as well as project how suability will be influenced by development.

Modeling suitability: potential communication sites in 2015

Similar to the nursery analysis, we assessed selection and avoidance in communication sites in a use-availability framework (Manly et al. 2002). We performed two analyses that addressed selection at two different spatial scales—the first at the site, and the second at the area around each site. In each analysis, we defined "used" points or areas as locations in which we found communication sites, and drew "available" comparison locations at random from within each puma's home range (mapped using a 95% LoCoH) at a rate of 5:1 available:used (Manly et al. 2002).

For the first communication site selection analysis, we modeled site-level selection using a Resource Selection Function (RSF). The model variables were the four levels of development, as a categorical variable, and slope (the terrain steepness, calculated using a 3×3 cell moving window), as a continuous variable. These two habitat features were previously identified as the most important for predicting communication site selection (Wilmers et al. 2013).

For our second analysis, we compared development and slope in areas surrounding communication sites to equally-sized areas within individual home ranges. We quantified differences in used and available areas by placing a 600 m radius circle around each used and available communication site (Wilmers et al. 2013) and compared the slope and human development within used versus available areas using a compositional analysis (Aebischer et al. 1993). Originally modeled by Wilmers et al. (2013), the 600 m buffers represent the distance at which pumas are sensitive to human development when selecting communication sites.

Modeling future suitability: potential nursery and communication habitat in 2065

We mapped projected future housing density for the Santa Cruz Mountains for the year 2065 using the SERGoM GIS tool (Bierwagen et al. 2009). Using the tolerance/attraction thresholds generated from our compositional analysis (Table 2a), we created a moving window analysis to create binary (suitable/unsuitable) rasters for potential nursery home ranges and potential communication sites. In order to measure the distribution of suitable patches, we made a simulated puma home range grid with cell sizes the average size of a puma home range, and eliminated grid cells in urban areas, as these areas are unsuitable habitat for a puma.

Table 2 Human development in puma nursery and communication areas in the Santa Cruz Mountains, California, USA in 2015

Development category	Percent composition						
	a. Nursery areas	SE	Communication areas	SE	b. Female home ranges	SE	Study area
Lightly modified	94.0	4.0	97.6	0.4	85.5	1.4	75.9
Exurban	3.5	1.3	1.8	0.3	7.7	1.0	8.5
Suburban	2.5	1.9	0.6	0.2	5.5	0.87	12.3
Urban	0.1	0.0	0.1	0.01	1.3	0.02	3.3

Mean values for human development in nursery home ranges and within 600 m of communication sites (a), and mean values for female home ranges and the study area as a whole allow comparison between development levels in nursery areas (b)

Values are reported as percentages of each development category

We generated nursery LoCoHs, and used the mean size of successful nursery patches as a minimum area required to raise kittens to an age beyond the use of the first nursery site. In our analyses, we used binomial or quasibinomial regression to determine how projected development will affect the properties and distribution of suitable patches and sufficiently large patches and we incorporated slope into our modeled suitability using the estimated parameter coefficient. The ability of the model to discriminate between communication sites and non-communication sites was 'acceptable' as determined by an area of 0.79 under the receiver operator curve (Hosmer and Lemeshow 2004).

Results

We used GPS data from 15 female and 14 male pumas, which were monitored for a mean of 636 ± 102 SE and 428 ± 52 SE days respectively. We recorded 119,787 locations for a mean of 4130 ± 303 SE locations per animal. We documented 23 nursery home ranges for 12 female pumas (6 females had more than one nursery; Fig. 2). We also documented 299 communication sites from 13 males.

Nursery home range selection

The mean nursery home range area was $9 \text{ km}^2 \pm 1.72$ SE (Fig. 2). Though some nursery home range areas contained low levels of exurban, suburban, or urban development, each of the documented nursery sites themselves (n = 23) was located in the lightly modified human development habitat category (Table 2). When selecting nursery home ranges, female pumas preferred predominantly lightly modified habitat over any other housing density category (compositional analysis: $\text{mean}_{\text{nursery home range}} = 94\% \pm 4$ SE, $\text{mean}_{\text{female home range}} = 86\% \pm 1$ SE, $p < 0.01$). Urban development made up a very small portion of the areas utilized while supporting young kittens (compositional analysis: $\text{mean}_{\text{nursery home range}} = 0.0016\% \pm 0.0012$ SE, $\text{mean}_{\text{female home range}} = 1.3\% \pm 0.02$, $p < 0.01$, Table 2b).
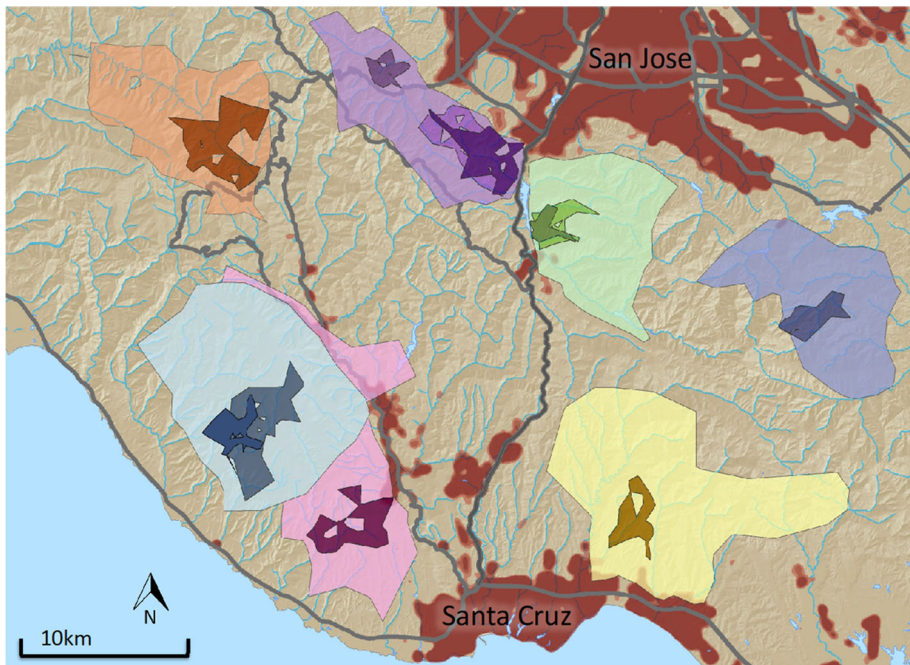
Fig. 2 Nursery home ranges in the Santa Cruz Mountains, California, USA between 2008 and 2014. An illustration of the difference between annual home ranges (translucent) and nursery home ranges (smaller opaque; area female utilized while maintaining a nursery), including urban and suburban areas in maroon. In cases where females had multiple nurseries, they are shown by different shades of the same color. For visual clarity, only a subset of the total 23 nurseries is shown

Communication site selection

Similar to nurseries, every communication site was located in lightly modified habitat (n = 299), and communication area composition was predominantly lightly modified habitat (Table 2). The RSF model suggested that male pumas significantly selected communication sites in undeveloped habitat ($\beta = 1.51 \pm 1.032$ SE) and relatively flat areas ($\beta = 0.03 \pm 0.124$ SE), and they selected against urban habitat ($\beta = -10.06 \pm 309.12$ SE; Table 3a). Similar to site-level conditions, males selected undeveloped habitat within communication areas as well (compositional analysis: mean$_{used}$ = 98% ± 0.35 SE, mean$_{random}$ = 88% $\pm$ 1.00 SE, t_{299} = $-$ 8.07, $p < 0.01$; Table 3b).

Future landscape for suitable nursery and communication sites

Over the next 50 years, models predict that high levels of lightly modified development will be converted to exurban development (Fig. 1). This shift would significantly reduce currently suitable habitat for communication sites and nursery home ranges (Fig. 3). In 2015, 75.9% of our study area was categorized as very lightly modified, the areas modeled as most suitable for nurseries and communicating, but by 2065 that number drops to 32.6% (Table 1). Every modeled female home range had sufficient nursery patches in 2015, or

Table 3 Models for puma communication site selection in 2015 in the Santa Cruz Mountains, California, USA

Habitat Variable	a	Communication RSF			b	Compositional analysis			
		Coefficient	SE	p		Mean percent		p	t
						Used	Available		
Slope		0.03	0.12	0.9					
Development category									
Lightly modified		1.51	1.03	< 0.01		97.59	88.35	< 0.01	− 8.07
Exurban		1.19	1.19	< 0.01		1.80	6.82	< 0.01	− 8.16
Suburban		0.98	1.02	< 0.01		0.62	4.64	< 0.01	− 6.28
Urban		− 10.06	309.12	0.7		0.01	0.15	0.5	− 1.77

(a) Resource selection function results comparing development at communication sites with available sites within male territories. (b) Compositional analysis results comparing the mean percent composition of each development category found within a 600 m radius of communication sites and areas of the same size randomly selected from male territories
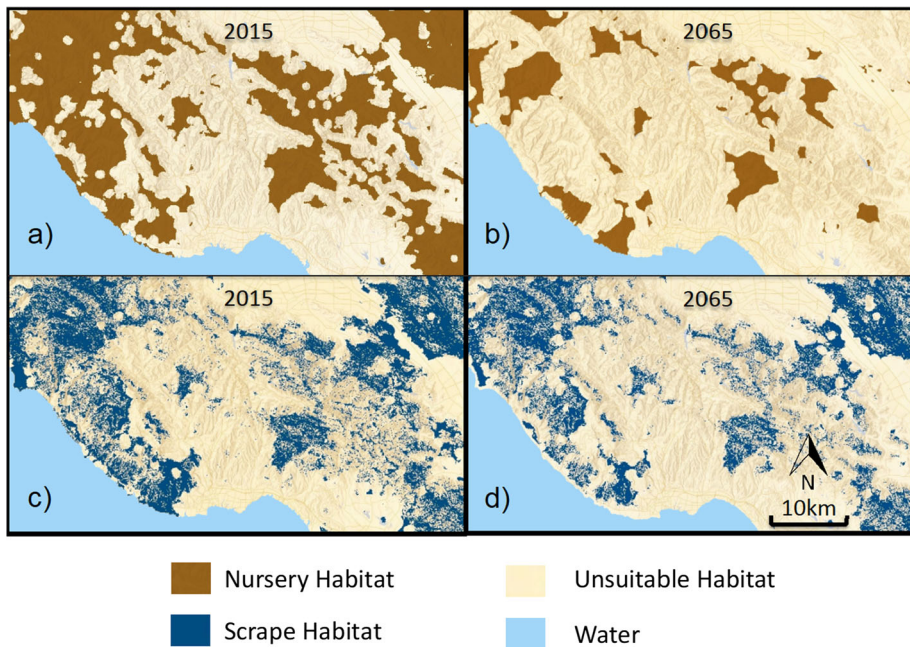

Fig. 3 Changes in puma nursery and communication habitat between 2015 and 2065 in the Santa Cruz Mountains, California, USA. The projected changes in spatial extent of suitable nursery habitat (in dark brown; panels **a** and **b**) and suitable communication habitat (in blue; panels **c** and **d**) habitat between 2015 and 2065. The matrix (tan) is a mix of habitat types, ranging from urban development to undeveloped natural habitats (namely mixed evergreen forest, redwood forest, oak savanna, chaparral, mixed oak forest, coastal prairie and coastal scrub, and sandhills). Future suitable habitat for each behavior is projected to shrink and become more fragmented

patches of continuous open habitat with low levels of urban, suburban, and exurban development, while only 77% had sufficient patches in 2065. Future suitable habitat patches are also projected to become farther apart (Fig. 3), with the average distance between sufficiently large nursery patches in 2065 projected to be three times the distance of 2015 (mean patch distance$_{2015}$: 787 m $\pm$ 117 SE, mean patch distance$_{2065}$: 2,749 m $\pm$ 260 SE; $p < 0.01$). A similar pattern was true for potential communication sites (Fig. 3). In 2015, 30% of the study area was considered suitable for communication sites, but our projections for 2065 reduced potential communication site area to 18%. Overall, remaining potential habitat is projected to shrink and became patchier, making suitable sites smaller and farther apart.

Discussion

We explored the relationship between anthropogenic development and puma nursery and communication habitat, and found habitat suitability for these behaviors were vulnerable to continued human development. Although suitable habitat may be utilized for only a short duration, pumas may breed at any time of year. Habitat suitable for breeding behaviors is likely to be disproportionately important for puma survival, making it important to consider these areas in conserve efforts (Boitani and Fuller 2000). Our future development projections suggest that nearly half of the lightly modified habitat that is key for these reproductive behaviors will be converted to exurban and suburban development by 2065. This would reduce available nursery habitat by 20% and potential communication habitat by nearly 50%, while making remaining habitat patchier and resulting in potential fitness costs for the population (Hinam and Clair 2008; Burdett et al. 2010; Gehrt et al. 2010). By explicitly modeling the spatial components of communication and nursery sites, we were able to predict how animals are likely to respond to increased development and fragmentation and help inform conservation efforts. Future studies on conservation planning may find it informative to explore spatial requirements for wildlife during sensitive periods (e.g., during the period of several weeks after giving birth when young are highly vulnerable). Focusing on the habitat requirements during infrequent, but highly important, activities may provide a critical tool for conservation planning efforts.

This study addresses female puma habitat use during the period in which they behave as central place foragers while raising immobile kittens, and highlights habitat with high conservation value with respect to puma reproduction. These areas require protective cover for kittens, as well as sufficient resources (prey, water, etc.) for the mother while supporting her growing young. When choosing nursery home ranges, female pumas avoided human development. Every documented nursery site was located in undeveloped habitat (< 1 housing unit per 100 acres), and females tolerated only small amounts of low-level human development in areas surrounding the nurseries. This strong preference for undeveloped habitat likely has fitness implications, as habitat near humans has elevated populations of synanthropic carnivores (Wang et al. 2015) that could injure or kill vulnerable kittens. Humans themselves may pose real risks, but even the perception of risk could become taxing to a mother (Suraci et al. 2019). For example, when a female is disturbed, she will often abandon kills she needs to feed her young, elevating energetic costs during a period that is already energetically expensive, and move her kittens to a new nursery site (Logan and Sweanor 2001).

Similar to females, males also selected lightly modified habitat at the site- and area-level in relatively flat areas when creating communication sites. Pumas appear to select sites that maximize their opportunities for communication between conspecifics (*sensu* Allen et al. 2014), while minimizing interaction with human disturbance. The cues left at communication sites are both chemical and physical (Allen et al. 2014), and vulnerable to human disruption. Hikers, cyclists, domestic dogs, and other recreationalists may trample, mark over, or otherwise disturb communication sites, making communication sites better suited to areas with little human impact. In the Santa Cruz Mountains, an aversion to precipitous slopes greatly narrows the habitat available for scraping, and selecting against human development reduces it further. Inadequate access to scrape habitat could generate fitness costs from lack of communication with conspecific competitors and potential mates.

Future habitat development will likely alter the landscape for reproductive and communication behaviors. The habitat loss and increasing habitat patchiness projected in 2065 could confer large energetic penalties to female pumas and potentially reduce fecundity. Habitat patchiness may leave some females without any access to optimal nursery habitat, which could create an ecological trap in which females try to raise young in adverse conditions. Similar to other carnivore species, neonate kittens experience a higher mortality rate than any other age group (Logan and Sweanor 2001). Nursing females are also unable to traverse long distances in search of prey because they need to make kills to feed themselves, and then quickly return to their young. Attempting to raise offspring in heavily modified habitat would likely increase neonate mortality and shorten the inter-birth interval. Pregnancy, lactation, and rearing young are energetically expensive, and the more often these behaviors need to occur, the higher the cost (Oftedal and Girrleman 1989).

In addition to needing resources close to nursery sites, moving in more heavily fragmented habitat imposes other potential costs to females with young. Roads present a dangerous direct and indirect challenge to wildlife in general (Bennett 2017), and pumas specifically (Ernest et al. 2003; Riley et al. 2014; Vickers et al. 2015; Benson et al. 2016). Reduced patch suitability and increased distance between patches in the future will likely result in pumas crossing roads more frequently, and losing some patches from uncrossable roads. In addition, living in close proximity to people, as predicted in model projections of the future, exposes puma populations to increased human-derived mortality sources (e.g. conflict with livestock or companion animals (Orlando 2008), anticoagulant rodenticide exposure (Moriarty et al. 2012).

For males, limited access to suitable scrape sites could cause a breakdown of territorial boundaries and effective communication, increasing male–male conflict (Chanchani et al. 2018). Resident male pumas patrol their territories to refresh communication sites every 2 to 3 weeks (Allen et al. 2016). Males use scrapes to establish dominance as well as define boundaries (Allen et al. 2015), allowing competing males to avoid physically confronting one another (Logan and Sweanor 2001). Intraspecific strife can be an important population driver (Rankin 2007), especially as isolation from other puma populations increases (Riley et al. 2014). The impacts could range from low cost outcomes, such as inefficient use of time or energy, to fitness costs including bodily harm or death.

Communication sites also serve as a way for males to advertise themselves to potential mates (Allen et al. 2014) and provide a location for females to communicate their receptivity to breeding (Allen et al. 2015). Without these sites, males and females could have a more difficult time finding mates, resulting in decreased reproductive success across the population (e.g., Slabbekoorn and Ripmeester 2008). Breeding success is correlated with territory maintenance, as kittens are generally sired by a territory-holding male (Logan and Sweanor 2001; Allen et al. 2015). Thus, the ability to secure and hold a

territory can have significant implications for reproductive success of a particular male, with broader population-level implications as well (Logan and Sweanor 2001).

Historically, pumas were widely distributed, occupying nearly every habitat in the Americas from the desert to tropical rain forests (Logan and Sweanor 2001), suggesting a high degree of adaptability. Our analyses did not take into account behavioral plasticity to an increasingly human-dominated landscape, and with diminished access to ideal sites, pumas may compensate to some degree by substituting less preferred sites. Pumas have demonstrated the ability to adapt and persist in urban- or suburban-adjacent areas (Burdett et al. 2010; Riley et al. 2014). However, evidence suggests they are less adaptable to persisting within more developed environments than many other carnivore species, such as coyotes or foxes (Gehrt et al. 2010); puma populations studied in areas adjacent to human development have suffered from inbreeding depression and population declines (Burdett et al. 2010; Vickers et al. 2015; Benson et al. 2016; Gustafson et al. 2019). Our study area is situated in an area already highly impacted by people; local puma population genetics show a relatively high degree of inbreeding and isolation (Gustafson et al. 2019), which could indicate that they are already living on the lower end of their acceptable spectrum. If they are currently subsisting in suboptimal habitat, further flexibility may not be possible. In addition, increased development will likely have additional negative implications for dispersal permeability and gene flow (Riley et al. 2014; Vickers et al. 2015; Gustafson et al. 2019) and overall habitat loss (Burdett et al. 2010; Visconti et al. 2016).

Our study highlights the need for regional planning to pay special attention to development patterns. In the next 50 years, 96% of the land use change is predicted to transform currently suitable habitat to lower quality, non-preferred exurban development (Table 1; Fig. 1). Redirecting some of this development into higher density, more efficient development in suburban or urban areas would allow space for humans and wildlife populations to coexist. The pervasiveness of habitat loss and transformation make it all the more important to carefully develop around remaining habitat (Burdett et al. 2010; Wang et al. 2015; Visconti et al. 20165; Maletzke et al. 2017). We modeled the relationship between pumas and human development in the Santa Cruz Mountains, but these dynamics are likely playing out across puma's large distribution and our findings are likely transferrable to other carnivore species as well. In addition, gaining a better understanding of how habitat modification influences wildlife can also help garner public support for sound conservation practices, and guide future development plans to ensure that wild populations can thrive alongside human development.

References

Aebischer NJ, Robertson PA, Kenward RE (1993) Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313–1325

Alig RJ, Kline JD, Lichtenstein M (2004) Urbanization on the US landscape: looking ahead in the 21st century. Landscape Urban Plan 69:219–234

Allen ML, Wittmer HU, Wilmers CC (2014) Puma communication behaviors: Understanding functional use and variation among sex and age classes. Behaviour 151:819–840

Allen ML, Wittmer HU, Houghtaling P, Smith J, Elbroch LM, Wilmers CC (2015) The role of scent marking in mate selection by female pumas (Puma concolor). PLoS ONE 10(10):e0139087

Allen ML, Yovovich V, Wilmers CC (2016) Evaluating the responses of a territorial solitary carnivore to potential mates and competitors. Sci Rep 6:e27257

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67(1):1–48

Beier P, Choate D, Barrett RH (1995) Movement patterns of mountain lions during different behaviors. J Mammal 76(4):1056–1070

Bennett VJ (2017) Effects of road density and pattern on the conservation of species and biodiversity. Curr Landsc Ecol Rep 2(1):1–11

Benson JF, Mahoney PJ, Sikich JA, Serieys LE, Pollinger JP, Ernest HB, Riley SP (2016) Interactions between demography, genetics, and landscape connectivity increase extinction probability for a small population of large carnivores in a major metropolitan area. Proc R Soc B 283(1837):20160957

Bierwagen B, Thomas J, Pyke C, Theobald DM, Choate A, Cohen J, Groth P (2009) Land-use scenarios: National-scale housing-density scenarios consistent with climate change storylines. Environmental Protection Agency

Boitani L, Fuller T (eds) (2000) Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York

Burdett CL, Crooks KR, Theobald DM, Wilson KR, Boydston EE, Lyren LM, Fisher RN, Vickers TW, Morrison SA, Boyce WM (2010) Interfacing models of wildlife habitat and human development to predict the future distribution of puma habitat. Ecosphere 1(1):1–21

Calenge C (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecol Model 197:516–519

Chanchani P, Gerber BD, Noon BR (2018) Elevated potential for intraspecific competition in territorial carnivores occupying fragmented landscapes. Biol Conserv 227:275–283

Davies AB, Marneweck DG, Druce DJ, Asner GP (2016) Den site selection, pack composition, and reproductive success in endangered African wild dogs. Behav Ecol 27:1869–1879

Ernest HB, Boyce WM, Bleich VC, May B, Stiver SJ, Torres SG (2003) Genetic structure of mountain lion (Puma concolor) populations in California. Conserv Genet 4(3):353–366

Gehrt SD, Riley SPD, Cypher BL (eds) (2010) Urban carnivores: ecology, conflict, conservation. John Hopkins University Press, Baltimore

Getz WM, Formann-Roe S, Cross PC, Lyons AJ, Ryan SJ, Wilmers CC (2007) LoCoH: nonparameteric kernel methods for constructing home ranges and utilization distributions. PLoS ONE 2(2):e207

Gustafson KD, Gagne RB, Vickers WT, Riley SP, Wilmers CC, Bleich VC, Pierce BM, Kenyon M, Drazenovich TL, Sikich JA, Boyce WM, Ernest HB (2019) Genetic source-sink dynamics among naturally structured and anthropogenically fragmented puma populations. Conserv Genet 20(2):215–227

Hinam HL, Clair CCS (2008) High levels of habitat loss and fragmentation limit reproductive success by reducing home range size and provisioning rates of Northern saw-whet owls. Biol Cons 141:524–535

Hosmer DW Jr, Lemeshow S (2004) Applied logistic regression. Wiley, Boca Raton

Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71

Krausman PR, Smith SM, Derbridge J, Merkle J (2011) The cumulative effects of suburban and exurban influences on wildlife. In: Cumulative effects in wildlife management: impact mitigation. CRC Press, Boca Raton, pp 135–192

Kshettry A, Vaidyanathan S, Sukumar R, Athreya V (2020) Looking beyond protected areas: Identifying conservation compatible landscapes in agro-forest mosaics in north-eastern India. Global Ecol Conserv e00905

Laundré JW (2005) Puma energetics: a recalculation. J Wildl Manag 69(2):723–732

Logan KA, Sweanor LL (2001) Desert Puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington, DC

Maletzke B, Kertson B, Swanson M, Koehler G, Beausoleil R, Wielgus R, Cooley H (2017) Cougar response to a gradient of human development. Ecosphere 8(7):e01828

Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2002) Resource selection by animals: statistical design and analysis for field studies. Kluwer Academic Publishers, Boston

Moriarty JG, Riley SP, Serieys LE, Sikich JA, Schoonmaker CM, Poppenga RH (2012) Exposure of wildlife to anticoagulant rodenticides at Santa Monica Mountains National Recreation Area: from mountain lions to rodents. In Proceedings of the Vertebrate Pest Conference (25)25

Mueller MM, Drake D, Allen ML (2018) Coexistence of coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) in an urban landscape. PLoS ONE 13:e0190971

Oftedal OT, Gittleman JL (1989) Patterns of energy output during reproduction in carnivores. Carnivore behavior, ecology, and evolution. Springer, Boston, pp 355–378

Orlando AM (2008) Impacts of rural development on puma ecology in California's Sierra Nevada. University of California, Davis, p 105

Rankin D (2007) Resolving the tragedy of the commons: the feedback between intraspecific conflict and population density. J Evol Biol 20:173–180

Riley SPD, Serieys LEK, Pollinger JP, Sikich JA, Dalbeck L, Wayne RK, Ernest HB (2014) Individual behaviors dominate the dynamics of an urban mountain lion population isolated by roads. Curr Biol 24:1989–1994

Ross S, Kamnitzer R, Munkhtsog B, Harris S (2010) Den-site selection is critical for Pallas's cats (*Otocolobus manul*). Can J Zool 88(9):905–913

Slabbekoorn H, Ripmeester E (2008) Birdsong and anthropogenic noise: implications and applications for conservation. Mol Ecol 17:72–83

Suraci JP, Clinchy M, Zanette LY, Wilmers CC (2019) Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. Ecol Lett 22(10):1578–1586

Theobald D (2001) Land-use dynamics beyond the American urban fringe. Geogr Rev 91(3):544–564

Theobald D (2005) Landscape patterns of exurban growth in the USA from 1980 to 2020. Ecol Soc 10(1):32

Vickers TW, Sanchez JN, Johnson CK, Morrison SA, Botta R, Smith T, Cohen BS, Huber PR, Ernest HB, Boyce WM (2015) Survival and mortality of pumas (*Puma concolor*) in a fragmented, urbanizing landscape. PLoS ONE 10(7):e0131490

Visconti P, Bakkenes M, Baisero D, Brooks T, Butchart SH, Joppa L, Alkemade R, Di Marco M, Santini L, Hoffmann M, Maiorano L (2016) Projecting global biodiversity indicators under future development scenarios. Conserv Lett 9(1):5–13

Wade AA, Theobald DM (2010) Residential development encroachment on US protected areas. Conserv Biol 24(1):151–161

Wang Y, Allen ML, Wilmers CC (2015) Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. Biol Cons 190:23–33

Wiersma YF, Sleep DJ (2016) A review of applications of the six-step method of systematic conservation planning. For Chronicle 92(3):322–335

Wilmers CC, Wang Y, Nickel B, Houghtaling P, Shakeri Y, Allen ML, Kermish-Wells J, Yovovich V, Williams T (2013) Scale dependent behavioral responses to human development by a large predator, the puma. PLoS ONE 8:4)e60590

Zuur AF, Ieno EN, Smith GM (2007) Analyzing ecological data. Springer, New York

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