Landscape and Urban Planning 183 (2019) 50–58

Contents lists available at ScienceDirect

Landscape and Urban Planning

journal homepage: www.elsevier.com/locate/landurbplan

Research Paper

Moving through the matrix: Promoting permeability for large carnivores in a human-dominated landscape

Justine A. Smith[a,b,*], Timothy P. Duane[b], Christopher C. Wilmers[b]

[a] Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA 94720, USA
[b] Environmental Studies Department, University of California, Santa Cruz, CA 95064, USA

ARTICLE INFO

Keywords:
Connectivity
Conservation planning
Habitat fragmentation
Puma concolor
Residential development
Step-selection function

ABSTRACT

Landscape connectivity for wildlife populations is declining globally due to increasing development and habitat fragmentation. However, outside of full protection of undeveloped wildlife corridors, conservation planners have limited tools to identify the appropriate level of densification such that landscape permeability for wildlife is maintained. Here we sought to determine the development characteristics that contribute to movement potential in an exurban landscape for a large carnivore, the puma. We first fit a piecewise step-selection function from movement paths from 28 male pumas to identify threshold levels of development that produce barriers to movement. We then applied this threshold to projected housing densities of existing parcels under a full General Plan buildout scenario in Santa Cruz County to illustrate how parcels at risk of increasing above the puma movement threshold can be identified. Finally, we tested the relative importance of characteristics associated with parcels and the surrounding area on relative puma movement. We found that pumas exhibit avoidance of housing density that saturates at a threshold, and that puma utilization of parcels at risk of densification above this threshold is predicted by parcel area and the housing density and area of surrounding parcels. Our work suggests that maintaining permeability in developing landscapes is likely contingent on preventing densification and parcel subdivision in exurban areas. We discuss how our findings and approach can be used by conservation planners to promote landscape permeability in already partially developed landscapes.

1. Introduction

Land use change contributes to the loss of biodiversity and ecosystem services, in part due to habitat fragmentation and restriction of animal movement (Crooks, Burdett, Theobald, Rondinini, & Boitani, 2011; Dobson et al., 2006; Wilcove, Rothstein, Dubow, Phillips, & Losos, 1998). Terrestrial large carnivores (and the ecosystem services they provide) are particularly vulnerable to fragmentation, as they often have large home ranges and exhibit long dispersal distances (Crooks et al., 2011; Dobson et al., 2006). Large carnivores have been examined as conservation umbrellas for large-scale connectivity planning due to their large spatial requirements (Beier, Majka, & Spencer, 2008; Thorne, Cameron, & Quinn, 2006). Maintaining connectivity between and within carnivore populations has therefore been a major focus of conservation research, with the intent of identifying and preserving movement corridors through landscapes that face ongoing development pressure (Clark, Laufenberg, Davidson, & Murrow, 2015; Fattebert, Robinson, Balme, Slotow, & Hunter, 2015; Morrison & Boyce, 2008; Rabinowitz & Zeller, 2010).

Connectivity for large carnivores is often assessed by least-cost path and resistance surface analyses, which have proved to be useful tools for identification of movement corridors for wildlife, particularly between populations. However, least-cost path and resistance surface analyses are limited by data inputs and assumptions about animal movement (Sawyer, Epps, & Brashares, 2011; Zeller, McGarigal, & Whiteley, 2012). Movement decisions inferred from step- or path-selection functions are almost entirely absent from resistance surface analyses (Zeller et al., 2012) and the behavioral state of the animal is rarely considered (Abrahms et al., 2017, but see Wilmers et al., 2013). Step-selection functions and path-selection functions of animals in a state of directed travel provide the most mechanistic approach to understand how animals make movement decisions, and have potential to vastly improve connectivity analyses (Abrahms et al., 2017; Cushman & Lewis, 2010; Zeller et al., 2012, 2016).

One of the most important limitations of least-cost path approaches is that they assume that there is only one or few potential paths an

* Corresponding author at: Department of Environmental Sciences, Policy and Management, Mulford Hall, University of California, Berkeley, Berkeley, CA 94720, USA.

E-mail addresses: jsmith5@berkeley.edu (J.A. Smith), tpduane@ucsc.edu (T.P. Duane), cwilmers@ucsc.edu (C.C. Wilmers).

https://doi.org/10.1016/j.landurbplan.2018.11.003
Received 12 August 2017; Received in revised form 24 September 2018; Accepted 19 November 2018

animal will take. However, many large carnivores are generalist species and can tolerate moderate levels of human disturbance. In human-dominated landscapes, these species might experience instantaneous disturbances that influence their decision-making and movement processes due to fear responses (Smith et al., 2017), resulting in use of suboptimal paths through modified areas. Even when resistance surfaces incorporate measures of the human footprint (e.g. Baldwin, Perkl, Trombulak, & Burwell, 2010), these variables are often treated as linear and continuous, despite evidence that animals do not respond linearly to disturbance (Hebblewhite & Merrill, 2008). A combination approach that uses more mechanistic habitat selection models and a broader interpretation of sufficient environmental conditions might more appropriately characterize animal movement potential in semi-permeable landscapes.

Current tools used to determine connectivity potential favor undeveloped corridors, impeding the incorporation of semi-permeable areas into conservation priorities. Connectivity planning at large spatial scales often promotes the preservation of open space with corridors of maximum permeability connecting them (Jongman, 1995). Approaches to preserving corridors and reducing sprawl can include clustering development in a few target areas that minimize impacts of low-density residential development by disrupting less total land area (Dale, Archer, Chang, & Ojima, 2005; Radeloff, Hammer, & Stewart, 2005; Sushinsky, Rhodes, Possingham, Gill, & Fuller, 2013). However, if not planned and developed in ways that maintains ecological connectivity, prioritizing denser development can prevent movement of wildlife and reduce gene flow (Hilty, Lidicker, & Merenlender, 2006). Alternative approaches may be necessary for conservation planning in regions that are already heavily impacted by low-density development and are a mosaic of private and public lands. In some cases, undeveloped private landholdings may increase the permeability, or relative probability of animal movement, of low-density development that lies between public lands or protected areas and can be essential to the conservation of wildlife because of its role in maintaining connectivity between said protected areas.

Restricting further development in moderately developed areas can thus be a complementary approach to corridor preservation, so as to maintain a greater net potential for animal movement between protected areas. For many species, certain levels of housing density may act as only a filter to animal movement, characterized by moderate resistance to movement with some functional permeability (Burdett, Crooks, Theobald, & Wilson, 2010; Hebblewhite & Merrill, 2008). These regions of low-density development may be vital to landscape connectivity if they serve as a permeable or semi-permeable matrix, which allows for some animal movement despite not maintaining full movement potential (Sawyer et al., 2013). However, above this density threshold, housing may act as a barrier; although wildlife are capable of moving through housing at this density, they may do so only very rarely because of behavioral avoidance strategies (Wilmers et al., 2013). Hence allowing areas with existing low-density development to increase in density can reduce their functional permeability until they are no longer viable areas for animal movement. Because housing development is more likely to occur where infrastructure already exists, existing low-housing-density areas are particularly at risk of becoming barriers to animal movement, and undeveloped private landholdings in these regions might pose nontraditional conservation opportunities. The strategic prevention of housing densification in low-density residential areas can therefore help to maintain connectivity at the scale of a wildlife population if disturbed landscapes provide moderate movement potential (Way, Ortega, & Strauss, 2004; Wilmers et al., 2013).

Our primary goal was to understand patterns of movement of a generalist large carnivore, the puma (*Puma concolor*), through low-density development to inform connectivity approaches in developing landscapes. In particular, we sought to (1) measure the shape of the relationship between individual puma movement decisions and housing density and (2) determine the relative influence of parcel characteristics on the degree of use by pumas. Based on the first objective, we hypothesized that pumas would exhibit nonlinear avoidance of housing density, whereby semi-permeable low-density development becomes impermeable at some threshold level. We predicted that puma avoidance of housing density would be accelerating (i.e. grow stronger with increased housing density) rather than saturating (i.e. high initially and approach an asymptote) due to documented use of residential areas while hunting (Smith, Wang, & Wilmers, 2015, 2016; Wilmers et al., 2013). Based on the second objective, we hypothesized that the characteristics of a focal parcel and its surrounding parcels would influence the propensity for pumas to move through a parcel. We predicted that focal parcel size, the size of surrounding parcels, and the housing density of surrounding parcels would impact puma use of parcels that are at risk of development. Our approach determines puma movement potential throughout the landscape rather than identifying high-quality corridors.

2. Methods

2.1. Study system

We conducted this work in a developing region of the western United States. Low-density residential development comprises 25% of land use the United States (Bierwagen et al., 2010; Theobald, 2005) and has widely restructured biotic communities due to reductions in biodiversity and resilience (Hansen, Knight, & Marzluff, 2005; Lumpkin & Pearson, 2013; McKinney, 2002; Merenlender, Reed, & Heise, 2009). Regions in the western United States have been disproportionately impacted by low-density residential growth, with rates two to three times the national average (Hammer, Stewart, & Radeloff, 2009; Theobald, 2003). Much of this low-density development abuts or intersects with wildlands, creating challenges for conservation. Of all development types in the western United States, residential development is the primary cause of expansion of the wildland-urban interface (WUI; Theobald & Romme, 2007), and 12.3 million WUI units are projected to be added in the western United States from 2000 to 2030 (Hammer et al., 2009). California holds the largest number of housing units in the WUI of any state (Radeloff et al., 2005) due to 65 years of sustained population growth and extensive immigration to pristine areas with low population sizes (Duane, 1996, 1999; Fulton & Shigley, 2005). The vast majority of land in the WUI in the USA is privately owned, exacerbating challenges to wildlife management in these sensitive areas (Theobald & Romme, 2007). The risks posed to wildlife in regions experiencing high growth rates of low-density development in the WUI include increased human-caused mortality, habitat loss, conflict with non-native species, and habitat fragmentation (Hansen et al., 2005).

Our research took place in Santa Cruz County, California. Santa Cruz County exemplifies developing regions around the globe that are experiencing rapid expansion and growth and urgently require targeted conservation efforts to retain ecological function. Santa Cruz County is one of three counties that make up the Santa Cruz Mountains, an isolated mountain range in the Central Coast region of California. In the next 50 years, Santa Cruz County is projected to grow by 18% and its neighboring counties, Santa Clara County and San Mateo County (which are the heart of Silicon Valley), will grow by 23% and 29% respectively (California State Department of Finance, 2013). How future growth affects current habitat in the Santa Cruz Mountains will likely be markedly different among counties based on their urban to rural ratio. Currently, San Mateo and Santa Clara counties are both less than 2% rural, whereas Santa Cruz County is 12% rural (United States Census Bureau, 2010). Part of this pattern may be attributed to the many open space parks and county parks that line the outskirts of the Bay Area on its southwest side, preventing extensive rural development. The General Plan of Santa Cruz County also designates the majority of the county's unincorporated land for Rural Residential use, which has the potential to be converted to low-density residential development (Santa Cruz County, California, Municipal Code, 1994). Within the unincorporated areas of the Santa Cruz Mountains, Santa Cruz County has the highest projected development increase among the three counties projected from 2010 to 2100, and its growth rate is within the top 10% of counties nationwide (United States Environmental Protection Agency, 2014).

We chose the puma as our study species because of its large space requirements, long dispersal paths, and preference for undeveloped habitat (Smith et al., 2015; Sweanor, Logan, & Hornocker, 2000; Wilmers et al., 2013). Although pumas avoid high-density developments, they show less aversion to low-density development, making them an ideal species for which to study thresholds of avoidance to human development (Gray, Wilmers, Reed, & Merenlender, 2016). Because the puma's habitat generality regularly exposes it to human development in other regions throughout its range (Benson et al., 2016; Land et al., 2008; Lewis et al., 2015; Moss, Alldredge, & Pauli, 2015), our use of the puma as a study organism is pertinent to other areas where wildlife coexist with low-density residential expansion. Our approach is also applicable to other large and medium sized carnivores that live in the WUI such as bobcats, caracals, and leopards.

2.2. Puma selection of movement steps

To determine the housing density most likely to deter movement by pumas, we applied a step-selection function (SSF) to puma location data from GPS collars (methods regarding puma capture and tagging can be found in Wilmers et al. (2013); IACUC no. WILMC1011). We chose to focus on male pumas in this analysis because they are the primary disperser in this species, they have greater daily movement distances than females, and their home ranges are three times the size of the average female home range (Smith et al., 2015). We used a step interval of four hours and only included steps equal to or greater than 500 m because our goal was to capture directed travel (which is often a more appropriate behavioral state for which to examine connectivity; Abrahms et al., 2017; Wilmers, Isbell, Suraci, & Williams, 2017), while ensuring a fine enough resolution to capture important details of the behavioral process (Thurfjell, Ciuti, & Boyce, 2014). Male pumas commonly move up to 500 m from their kill sites while they are still feeding on a kill (Wilmers unpubl. data).

Step-selection function models require that each known path (e.g. the line between each successive movement location) be paired with a sample of available paths (i.e. paths that the animal could have taken). To calculate these available paths, we empirically determined the distribution of puma step lengths and turn angles between 4-h GPS locations using logspline density estimation (Kooperberg & Stone, 1991). We then took random draws from these distributions to generate five random paths from each puma location. We also checked to ensure that step length and turn angle were not correlated ($r > 0.7$) at our scale of analysis. We then projected the random and real steps in a geographic information system (GIS; ArcMap 10.1) and eliminated simulated steps that overlapped the ocean. Using a housing layer, manually digitized from high resolution (30 cm) satellite imagery (Transverse Mercator, WGS 84 UTM Zone 10; Esri, 2009), we extracted the number of houses within a 150-m buffer of each step and calculated the housing density (houses/km^2) within that buffer. We used a 150-m buffer because this was the distance at which pumas in our study area were found to respond negatively to residential development (Wilmers et al., 2013).

SSFs take an exponential form and are commonly fit using conditional logistic regression (Forester, Im, & Rathouz, 2009; Fortin et al., 2005; Thurfjell et al., 2014). To estimate covariates for the SSF, we used the clogit command in the *survival* package in R (Therneau & Grambsch, 2000; Therneau, 2015), stratified by step starting location (i.e. the location from which each set of real and random paths originate) with housing density as the predictor variable. We included an interaction effect between housing density and the average housing density for paired real and simulated steps to control for availability-specific responses. We used robust standard errors following Fortin et al. (2005), which account for inter-cluster correlation in assessing variation. To test for the presence of a threshold effect, we used piecewise regression to fit a two-segmented model that split housing density into two covariates with different slopes on either side of a breakpoint (Kohl et al., 2018). We used a grid search approach to determine the best location of the breakpoint by comparing the quasi-likelihood under independence criterion (QIC) values of candidate spline models, which are more conservative than AIC and allow for clusters of observations to have independent correlation structures (Basille et al., 2015; Kohl et al., 2018; Pan, 2001). The optimal breakpoint was determined to two decimal places by conducting three rounds of model selection from candidate splines, where the best model was that with the lowest QIC score. First, we used integers between minimum and maximum standardized housing density (centered and normalized) as the candidate breakpoints. Between the two best-supported integer breakpoints, we ran candidate models of standardized housing density every 0.1. Finally, we ran candidate models every 0.01 between the two best models from the previous model selection. We compared the best segmented model to a model with a continuous response variable of housing density to test if the piecewise model better fit the data.

Importantly, we recognize that the presence of a breakpoint can imply very different relationships to housing, depending on if the curve shows accelerating or saturating avoidance. An accelerating avoidance curve would indicate that pumas do not strongly avoid housing until a certain density, and then increasingly avoid housing above the threshold value. A saturating avoidance curve would indicate that pumas increasingly avoid housing density even at low levels (i.e. a filter), but after a certain point relative probability of use is so low that the curve flattens out (i.e. a barrier). A breakpoint in either of these two curve shapes could be applied as a development density threshold, but the implications for pumas' relationship to development are very different. For an accelerating curve, development should not hinder puma movement until it reaches the threshold, when it would then decrease probability of use as housing increases. For a saturating curve, any development should be avoided, but development above the threshold is likely to become a barrier to movement, where development densities allow little movement potential.

2.3. Parcels at risk of reducing permeability

We constructed a buildout analysis of all potential new development allowed under the Santa Cruz County General Plan (Santa Cruz County, California, Municipal Code, 1994). We used a database of parcels with the potential of incurring new development and subdivisions developed for the Conservation Blueprint for Santa Cruz County (Mackenzie, McGraw, & Freeman, 2011). This database was constructed by locating vacant underutilized parcels within and outside the urban services line (USL; Santa Cruz County, California, Municipal Code, 1994), a boundary that dictates infrastructure and services provided to residential units by the county. For properties within the USL, one housing unit was assigned for each potential parcel or new housing site. For rural properties outside the USL, new housing was limited by General Plan restrictions on development with regard to slope, distance to water bodies, riparian woodland areas, fault zones, agriculture and mineral resource lands, floodways, and FEMA Zone A (floodplain management). Further constraints on parcel size due to Least Disturbed Watershed coverage, Water Quality Constraints coverage, Water Supply Watershed coverage, and Groundwater Recharge Area coverage were applied to eliminate undevelopable parcels. Parcels not excluded as undevelopable were assigned new residential units based on vacancy status (i.e. if the land is undeveloped) and potential lot splits according to allowable densities specified by land-use category designations in the General Plan (Santa Cruz County, California, Municipal Code, 1994).

To assess current housing density, we digitized all buildings in Santa Cruz County from high resolution satellite imagery and derived housing density within a 150-m buffer of the parcel boundaries. We used a 150-m buffer to stay consistent with the scale of the SSF analysis. We added potential new units in developable parcels according to the buildout analysis and amended them to the digitized buildings dataset to recalculate housing density at full buildout. We identified parcels whose maximum housing density was both (1) below the puma movement threshold prior to buildout and (2) above the threshold post-buildout. The subset of parcels that determined to be above the post-buildout threshold (hereafter, "threshold parcels") are those that, if developed in accordance with the Santa Cruz General Plan, would increasingly impede puma movement after such development. All other parcels are either already impeding such movement or would not substantially impede puma movement even if they are developed to densities allowed under the General Plan.

2.4. Parcel characteristics and puma utilization

We tested the importance of threshold parcel features on relative puma use. Relative puma use was defined as the proportion of puma steps that crossed into a threshold parcel of all steps within 150 m of the parcel boundary. We excluded parcels for which there were no puma steps within 150 m. We constructed a linear regression model with the proportion of puma steps that pass though the focal threshold parcel as the dependent variable and features of the parcel as the independent variables. Parcel features included the area of the focal parcel, the mean area of the surrounding parcels, and the mean housing density of the surrounding parcels. We calculated Pearson correlation coefficients for each pair of covariates to ensure that collinearity would not obscure covariate coefficient estimates. The three parcel features were not correlated with one another ($R < 0.5$), therefore we included all covariates in the model. We scaled and centered each covariate to allow for comparisons of coefficient values. We then determined the best model of all combinations of covariates by comparing the AIC values of all candidate models and choosing the model with the lowest AIC score and highest Akaike weight. Models with a ΔAIC of less than 2 were considered plausible best models.

3. Results

We used 11,765 total steps from 28 male pumas in our puma SSF analysis. Pumas were monitored for 537 ± 4 SE days (range: 41–1678). On average, used steps had a housing density of 19.68 ± 0.51 SE houses/km^2 and available steps had a housing density of 27.89 ± 0.31 SE houses/km^2. The linear model with a single housing density covariate (QIC = 41479.68, ΔQIC = 178.76) did not fit the data as well as the best linear spline model (QIC = 41300.92, ΔQIC = 0), supporting the presence of a response threshold. The model with only the housing density covariate had a stronger fit than the model that also had an interaction term with average housing density at paired points (QIC = 41371.68, ΔQIC = 70.76). The best-fit linear spline model had a knot at housing density of 41 houses/km^2 (1 house per 6 acres). The shape of the relationship between puma probability of use and housing density indicated saturating avoidance, whereby pumas showed a steep decline in probability of use until the housing density threshold, followed by consistently low probability of use above the threshold (Fig. 1). This relationship suggests that low levels of housing density act as a filter to puma movement, while relative probability of use saturates at the threshold to create a relative barrier to movement. Although relative probability of use above the threshold is greater than zero, pumas are less likely to choose to move through areas at these higher housing densities.

Of the 96,828 parcels in Santa Cruz County, 11,175 were determined to have the potential for further development. Developable parcels currently have 552.79 ± 5.77 SE houses/km^2 but are projected to increase their average housing density to 736.16 ± 7.31 SE houses/km^2 at buildout (Fig. 2). The subset of developable parcels that lie outside the USL had considerably lower current housing densities (131.38 ± 2.44 SE houses/km^2) and buildout housing densities (187.14 ± 2.97 SE houses/km^2). Most developable parcels (78%) and developable parcels outside the USL (60%) were already above the puma movement threshold at current housing density levels, yet after buildout the proportion increased to 85% of all developable parcels and 72% of developable parcels outside the USL. Of developable parcels, 753 were identified as threshold parcels, or parcels at risk of increasing from below to above the puma movement threshold of 41 houses/km^2, therefore their conservation could assist in maintaining permeability (Fig. 3). Before buildout, threshold parcels had an average housing density of 22.73 ± 0.48 SE houses/km^2, whereas the average housing density in a parcel after buildout was 92.26 ± 3.18 SE houses/km^2. Of threshold parcels, only 43 were within the USL (35 of which were part of a single complex in Santa Cruz owned by the University of California), and one was within the RSL (rural services line). Therefore, nearly all parcels at risk of increasing to above the puma movement threshold fall outside of both USL and the RSL.

All three examined parcel covariates predicted relative puma use of threshold parcels, as the best model was the global model with all three covariates (Table 1). Mean housing density of surrounding parcels, mean area of surrounding parcels, and area of the focal threshold parcel were each positively correlated with proportion of puma steps that fell within the parcel to the total steps within 150 m of the parcel boundary (Table 1). Area of the focal threshold parcel was the strongest predictor of puma use, followed by mean housing density of surrounding parcels (Table 1).

4. Discussion

We found evidence for a puma movement threshold, although our prediction that the threshold would indicate accelerating avoidance to housing density was not supported. Instead, pumas exhibited a saturating avoidance of housing density, suggesting that pumas avoid housing even at low densities but that avoidance asymptotes at a threshold of housing density. Therefore, the construction of any development will limit habitat connectivity for pumas, but housing development above the threshold causes a change in landscape permeability from a filter to a barrier constraining puma movement, whereby avoidance levels off at moderate housing densities. Our prediction that spatial and development characteristics of parcels influence relative puma use was supported. Parcels identified to be at risk of reducing puma movement permeability in the case of full buildout experienced greater utilization by pumas when the area of the parcel was larger, the area of nearby parcels were larger, and the housing density of nearby parcels was higher.

In our application of an SSF to identify parcels of concern in our buildout analysis, we were able to utilize animal behavior to inform conservation priorities. Our threshold-based approach can help prevent further functional fragmentation of landscapes by avoiding the development of barriers in landscapes where ideal conditions of larger, fully-permeable movement corridors are already absent. Our work builds on existing studies showing that pumas use rural and exurban areas (Burdett et al., 2010; Lewis et al., 2015; Smith et al., 2015, 2016) but generally avoid areas of high housing density (Burdett et al., 2010; Wilmers et al., 2013). We expand on this previous work by exploring how pumas choose specific pathways of movement, thus making our work particularly relevant for assessing connectivity. The limitation of our approach is that it prioritizes movement without considering other necessary measures needed to maintain healthy populations of pumas, such as protecting large core areas for denning and communication (Wilmers et al., 2013). We emphasize that this analysis solely focuses on maintaining landscape connectivity within a population for the purposes of movement and dispersal. Connectivity is only one

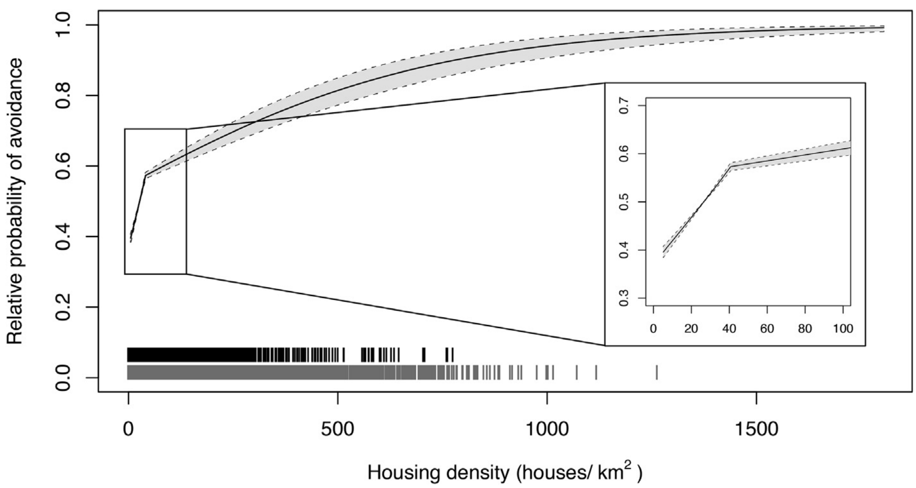

Fig. 1. Puma relative probability of avoidance of housing density on movement paths, calculated as the difference between 1 and the relative probability of use. Puma probability of avoidance increases steeply with increasing housing density until approximately 41 houses/km^2, then remains at high probability of avoidance beyond that threshold. The inset highlights the change in relative probability of use at the threshold location. Black vertical lines along the x-axis represent housing densities of puma paths used in the analysis, with a maximum of 775 houses/km^2. Grey vertical lines represent housing densities of simulated paths.

important component of population viability, and other information on demographic processes are needed to make holistic conservation plans for wide-ranging species such as the puma.

Our results are most relevant to highly developed and isolated regions where pumas or other wide-ranging species are forced to navigate human-dominated landscapes. Although there is no evidence for a functional response to housing density in our study area in regard to space use (Wilmers et al., 2013), high overall anthropogenic disturbance throughout the region does not allow for complete avoidance of residential areas. Puma populations with ample natural habitat may show a stronger aversion to housing than those in this study due to lack of pressure to use marginal habitats. Puma avoidance of housing is also likely related to the level of human-caused mortality in the population and prey availability in human-dominated areas. Agencies seeking to apply our method should obtain a population- and species-specific estimates of local movement thresholds. Jurisdictions without the capacity or resources to collar animals may be able to approximate thresholds using camera trap data through nonlinear estimates of relative activity or occupancy (George & Crooks, 2006; Rich, Miller, Robinson, McNutt, & Kelly, 2017).

Our work suggests that maintaining permeability for large, wide-ranging carnivores may require preventing development of key parcels that are at risk of densification in exurban landscapes, particularly for parcels that are large and situated within an area of higher relative housing density. Preventing the subdivision of large parcels may help to promote movement through exurban areas. Perhaps counterintuitively, higher proportional use of parcels by pumas in high housing density areas supports that densification should be limited in even marginal puma habitat, provided that the general area is accessible by moving pumas. We emphasize that we do not promote the further expansion of exurban sprawl or the development of low-density housing as an alternative to clustered development, and we explicitly warn against misinterpreting our results to justify building up to the threshold housing density presented here. Low-density and exurban developments can cause ecological breakdowns, and often do not serve as habitats in which wildlife can live (Hansen et al., 2005; Merenlender et al., 2009; Odell & Knight, 2001). We present a method to prevent further fragmentation of landscapes that occurs as housing density increases and decreased permeability hinders wildlife movement. Of course, *a priori* designs built on principles of smart growth and conservation planning are preferred in areas not yet developed or fragmented (Daniels & Lapping, 2005; Underwood, Francis, & Gerber, 2011). Our approach acknowledges that many landscapes are already impacted by anthropogenic development, and that the remaining conservation potential of these areas should be maintained whenever possible.

Challenges to conservation in habitats with low-density development are primarily intrinsic to their spatial arrangement on the landscape. General Plan designations and zoning regulations for conservation purposes in the United States have been used to decrease housing density, yet these measures have been criticized as resulting in greater environmental degradation by causing more extensive land development and increased vehicle miles travelled (Hansen et al., 2005; Merenlender, 2007; Robinson, Newell, & Marzluff, 2005). We suggest that, although the best way to prevent impacts of low-density development is to prevent it (Dale et al., 2005), efforts to curb increasing housing density in critical locations important to puma permeability can still provide conservation value. Solely promoting denser development plans carries with it its own ecological dangers and is often insufficient to address historical development patterns. For example, Santa Cruz County has enacted measures to curtail development in rural areas, including restricting services to properties outside the USL and RSL (Santa Cruz County, California, Municipal Code, 1994), yet the majority of developable parcels outside of the USL and RSL are already above the puma movement threshold. Service restrictions alone have been overcome due to the high economic value of the land for housing development, so landowners have provided on-site infrastructure (e.g., wells for water and septic systems rather than sewers connected to wastewater treatment plants) to develop their properties (Duane, 1999). Biological data on species responses to development, as we present here, can improve county efforts to maintain ecological processes as development pressure increases in the shadow of Silicon Valley. Our approach can complement efforts targeted at maintaining core habitats and high-quality movement corridors by identifying where further densification is likely to create barriers to animal movement.

Planners and land use regulators can use our approach to identify threshold parcels and then apply appropriate regulatory tools to conserve them at development levels below the threshold. More conservative planning for connectivity could employ a level of acceptable housing density below this threshold to retain a higher relative probability of use. Conservation planning and land use regulation to achieve conservation objectives vary widely internationally, but among the tools available to planners and regulators are infrastructure extension concurrency policies (e.g., for sewer and water services, as Santa Cruz County has already implemented), urban growth boundaries (UGBs [Knapp & Nelson, 1992; Nelson, 1992]), existing-use zoning (Duane, 1999), transferable development rights (TDRs [Nelson, Pruetz, & Woodruff, 2011]), and conservation easements (Byers & Ponte, 2005; Pidot, 2005; Wright & Czerniak, 2000). As our case study illustrates, restrictions on service extensions have limited impact when land and housing market dynamics make it worthwhile to invest in on-site infrastructure to allow development. UGBs are also unlikely to prevent relatively low-density development that may still push a parcel over the

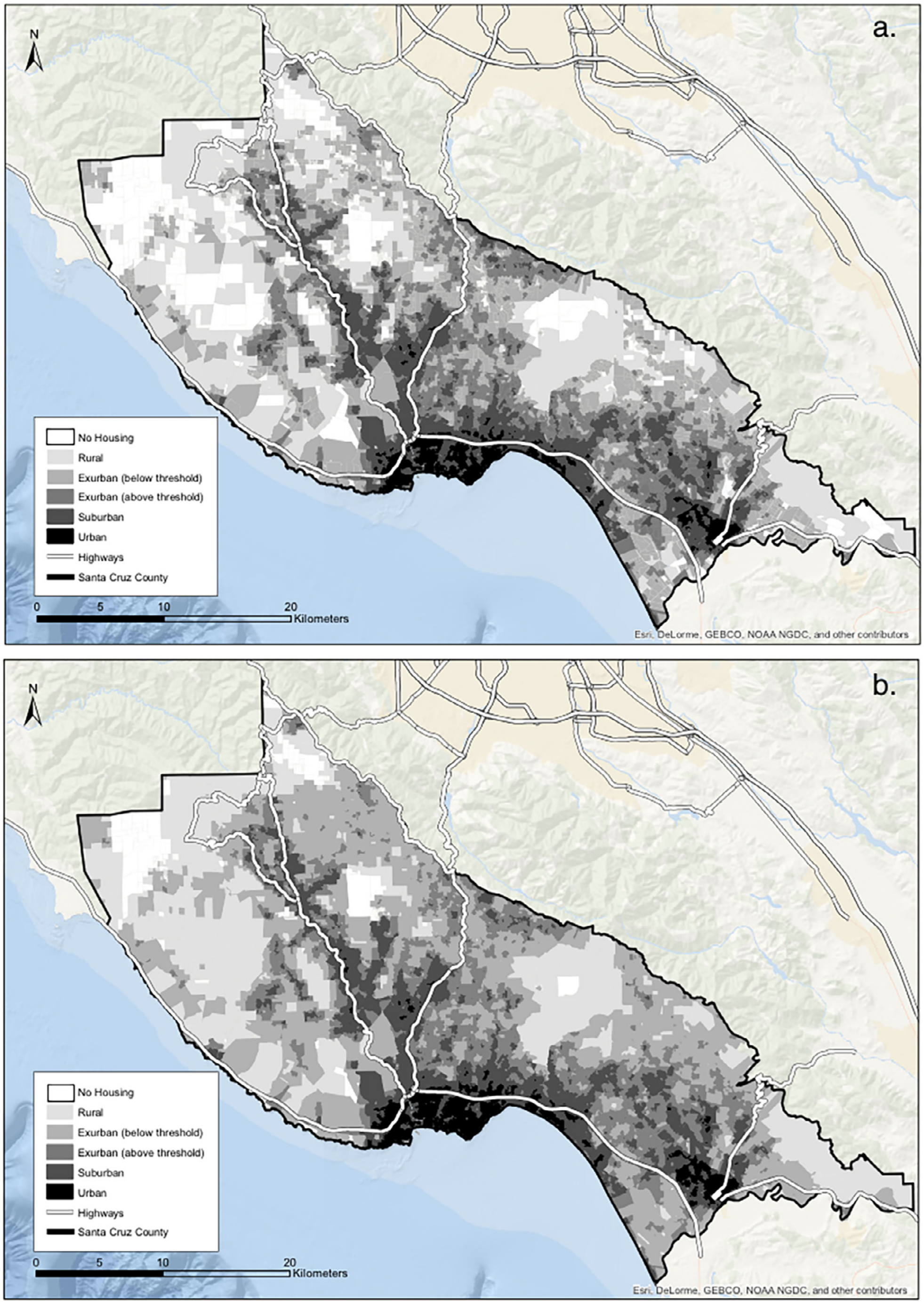

Fig. 2. Housing density class (no housing, rural, exurban, suburban, or urban; United States Environmental Protection Agency, 2010) in Santa Cruz County by parcel for (a) current housing and (b) housing at buildout. The exurban category is split into housing densities above and below the threshold at which puma relative probability of avoidance saturates.

threshold density (Knapp & Nelson, 1992; Nelson, 1992). It may therefore be necessary to use some combination of existing-use zoning, TDRs, and conservation easements to provide protections against development that would cross the threshold density. These tools can redirect development that is currently allowed under the General Plan and Zoning designations toward locations that are more appropriate for higher density (Arendt, 1996; Duane, 1999). The resulting development pattern would then be more likely to maintain existing levels of permeability across the threshold parcels identified in our analysis.

5. Conclusions

Habitat loss, modification, and conversion are the most significant contributors to species loss and declines worldwide (Dirzo & Raven, 2003). Although low-density development can reduce the functionality of wildlife habitat, it can sometimes provide move-through habitat for wildlife. One risk low-density housing poses to connectivity is that it is more likely to be developed than areas with no existing development due to infrastructure access (e.g. roads; Hawbaker, Radeloff, Clayton, Hammer, & Gonzalez-Abraham, 2006). Our results support that although all housing development reduces puma movement, avoidance

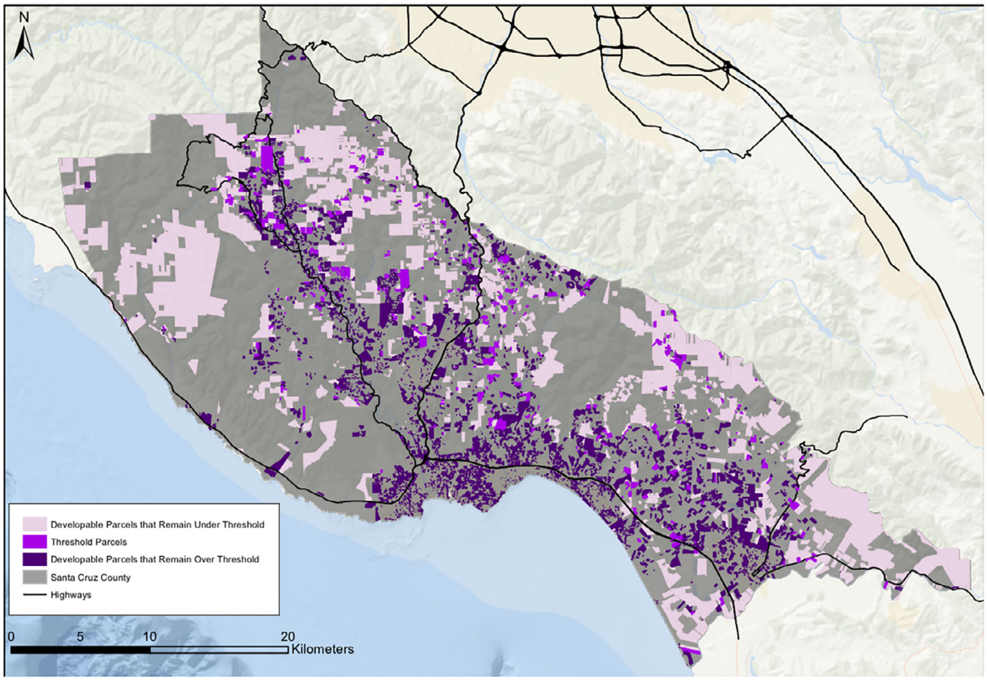

Fig. 3. Developable parcels in Santa Cruz County according to the county General Plan. Parcels in light purple are currently under the housing density threshold at which puma relative probability of avoidance saturates and remain under the threshold at buildout. Parcels in dark purple are already above the puma movement threshold at current housing densities. Parcels in bright purple are classified as threshold parcels; they are currently under the movement threshold but are at risk of increasing above the movement threshold at buildout. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Results of model selection to predict proportion of puma movement paths that intersect a focal threshold parcel (i.e. parcels at risk of developing over a housing density threshold in a full buildout scenario) in relation to surrounding parcels within 150 m. The threshold used is defined as the housing density at which puma relative probability of avoidance saturates. All covariates are scaled and centered. Parcel area is a measure of the focal parcel area. Surrounding parcel area is a measure of the mean area of parcels within 150 m of the boundary of the focal parcel. Mean housing density is a measure of the mean housing density of parcels within 150 m of the boundary of the focal parcel.

Model rank	AIC	ΔAIC	Akaike weight	Covariates	Coefficient	SE
1	−289.86	0.00	0.747	Parcel area	0.0632	0.0079
				Surrounding parcel area	0.0153	0.0075
				Mean housing density	0.0307	0.0079
				Intercept	0.1534	0.0075
2	−287.68	2.18	0.251	Parcel area	0.0634	0.0079
				Mean housing density	0.0309	0.0079
				Intercept	0.1534	0.0075
3	− 276.81	13.05	0.001	Parcel area	0.0727	0.0076
				Surrounding parcel area	0.0156	0.0076
				Intercept	0.1534	0.0076
4	−274.57	15.29	0.000	Parcel area	0.0731	0.0076
				Intercept	0.1534	0.0076
5	−230.55	59.31	0.000	Surrounding parcel area	0.0164	0.0079
				Mean housing density	0.0504	0.0079
				Intercept	0.1534	0.0079
6	−228.20	61.66	0.000	Mean housing density	0.0507	0.0079
				Intercept	0.1534	0.0079
7	−192.47	97.39	0.000	Surrounding parcel area	0.0172	0.0081
				Intercept	0.1534	0.0081

saturates at a threshold of housing density. Increasing development densities in these areas beyond threshold densities therefore risks establishing barriers to animal movement. Maintenance of landscape permeability may require prevention of development on large, undeveloped parcels in areas already impacted by residential development. Future conservation planning work should continue to expand approaches to landscape connectivity and broaden the contexts in which lands are considered valuable for conservation.

Acknowledgements

This work was supported by National Science Foundation grant #1255913, the Gordon and Betty Moore Foundation, and the American Association of University Women. We thank Michel Kohl, John Benson, and Pete Mahoney for their guidance on statistical analysis. We thank the Land Trust of Santa Cruz County for their contribution of developable parcels in Santa Cruz County. We thank P. Houghtaling, Y. Shakiri, V. Yovovich, Y. Wang, J. Kermish-Wells, C. Fust, S. McCain, R. King, K. Briner, and many undergraduate volunteers for assistance with field work. We thank the California Department of Fish and Wildlife, C. Wylie, D. Tichenor, B. Milsap, and T. Collinsworth for their capturing pumas. We thank the two anonymous reviewers for their constructive comments on the manuscript.

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