RESEARCH ARTICLE

Fine-scale movement decisions by a large carnivore inform conservation planning in human-dominated landscapes

Justin P. Suraci · **Barry A. Nickel** · **Christopher C. Wilmers**

Abstract

Context Developed landscapes are increasingly important movement habitat for many large carnivore populations, despite fragmentation and heightened anthropogenic risks. The availability of vegetation cover is a key factor mediating carnivore use of human-dominated landscapes. Restoring or modifying networks of vegetation patches may therefore provide an important tool for enhancing the connectivity value of developed areas, but requires understanding how vegetation patch networks are functionally linked by carnivore movement decisions, which occur at scales considerably finer than those typically addressed by connectivity analyses.

Objectives We investigated the factors driving fine-scale movement decisions by pumas (*Puma concolor*) in fragmented habitats and applied our results to enhancing puma connectivity through human-dominated landscapes.

Methods We used high-resolution data on vegetation cover and puma locations from central California to model puma habitat selection at the scale of individual movements between vegetation patches. These results informed network-based connectivity models comparing the benefits of specific wildlife corridor restoration actions (e.g., revegetation).

Results Puma movements between vegetation patches were driven by patch size, vegetation type, and spatial arrangement relative to sources of anthropogenic risk (buildings). Pumas avoided buildings but accepted higher building densities as patch area increased or inter-patch travel distances decreased. Connectivity modeling revealed that the strategic placement of vegetation patches can substantially reduce resistance to puma movement across an otherwise high resistance developed landscape by diversifying movement options.

Conclusion Our results reveal the factors mediating large carnivore use of human-dominated landscapes and provide a generalizable tool for increasing movement potential via the manipulation of vegetation cover.

J. P. Suraci (✉) · B. A. Nickel · C. C. Wilmers
Center for Integrated Spatial Research, Environmental Studies Department, University of California, Santa Cruz, CA 95064, USA
e-mail: justin.suraci@gmail.com

Introduction

Habitat fragmentation and increased urbanization are primary threats to many wildlife species, impeding animal movement, degrading habitat quality, and isolating populations (Fahrig 2003; Crooks et al. 2017). Increasing development poses particular challenges for large carnivores given their substantial space requirements and long history of conflict with people (Ripple et al. 2014; Chapron and López-Bao 2016). Yet, many carnivore populations nonetheless occur in or near human-dominated landscapes (Chapron et al. 2014; Benson et al. 2016; Gehr et al. 2017; Smith et al. 2019b), and such areas are predicted to be increasingly important for large carnivore persistence and connectivity as the human footprint continues to expand (Carter and Linnell 2016; Rio-Maior et al. 2019). Maintaining or enhancing moderately developed areas to facilitate their use by carnivores is therefore a critical conservation goal, and one which requires an understanding of the drivers of carnivore movement decisions when navigating these marginal habitats.

For many large carnivore populations, the avoidance of anthropogenic risk may be a major factor motivating movement decisions in human-dominated landscapes. Human-caused mortality is widespread among carnivores (Oriol-Cotterill et al. 2015), and fear of humans has correspondingly been shown to alter large carnivore movement and habitat selection (Wilmers et al. 2013; Gehr et al. 2017; Suraci et al. 2019a, b). Promoting carnivore use of developed areas therefore requires maintaining or restoring habitat features that reduced perceived risk from humans while increasing overall habitat quality (Oriol-Cotterill et al. 2015; Rio-Maior et al. 2019). Vegetation cover is one such feature, providing concealment from humans (Suraci et al. 2019b) and, for some species (e.g., felid ambush predators), increasing hunting success (Holmes and Laundré 2006; Smith et al. 2019a). Several studies have correspondingly documented increased use of human-dominated landscapes by large carnivores as cover availability increases (Boydston et al. 2003; Ordiz et al. 2011; Llaneza et al. 2016; Suraci et al. 2019b; Nickel et al. 2020). However, availability may be only part of the story, as the value of any individual vegetation patch will likely depend not only on the amount of cover it provides, but also on its spatial arrangement relative to other vegetation patches and to sources of anthropogenic risk (e.g., buildings and roads). Thus, understanding how networks of cover patches across developed landscapes are functionally linked by carnivore movements may provide key insights into managing and restoring these areas.

Enhancing linkages between large carnivore populations is an important conservation objective, particularly for populations living near urbanized regions where major highways or developments represent substantial barriers to movement (Benson et al. 2016; Di Minin et al. 2016; Gustafson et al. 2019). Regional connectivity analyses covering large spatial extents (e.g., several thousand square kilometers) (Dickson et al. 2013; Zeller et al. 2016; Rio-Maior et al. 2019) have been valuable in identifying potential corridors through human-dominated landscapes. However, the necessarily coarse scale of these regional studies often provides only limited insight into how best to enhance a particular corridor to increase its use by carnivores. Given the role of vegetation cover in mediating carnivore use of developed areas, the restoration or manipulation of vegetation patch networks may provide a valuable tool for increasing the effectiveness of otherwise degraded corridors, particularly when paired with the creation of highway crossing structures [e.g., wildlife underpasses; (Gloyne and Clevenger 2001; Ng et al. 2004)] to both increase habitat permeability and direct animals along relatively safe movement routes. Network-based approaches to connectivity modeling highlight the importance of maintaining a diversity of movement pathways between target areas to increase overall connectivity (McRae et al. 2008; Rayfield et al. 2011). However, identifying optimal network structures for vegetation patches and highway crossings that will maximize carnivore use (within the constraints set by limited restoration funding) remains a challenge, requiring both fine-scale information on carnivore movement across vegetation patch networks and planning tools to compare alternative restoration scenarios.

Here we examine fine-scale movement decisions by pumas (*Puma concolor*), a species which exemplifies several of the major challenges facing large carnivores in human-dominated landscapes. Throughout western North America, pumas are frequently found in close proximity to developed areas (Wilmers et al. 2013; Benson et al. 2016), yet perceived risk from humans has been shown to strongly affect puma behavior

(Smith et al. 2017; Suraci et al. 2019a), leading to avoidance of anthropogenic features on the landscape such as buildings and roads (Wilmers et al. 2013; Knopff et al. 2014; Zeller et al. 2016). Habitat fragmentation and the resulting loss of connectivity are primary threats to pumas, particularly in coastal California (Benson et al. 2016; Saremi et al. 2019), where populations occur in relatively isolated areas of low to moderate development separated by major roads and urban centers (Gustafson et al. 2019). As cover dependent carnivores (Holmes and Laundré 2006; Smith et al. 2019a), pumas consistently select for tree or shrub cover over open habitats (Knopff et al. 2010; Wilmers et al. 2013; Dellinger et al. 2020) and elsewhere have been shown to readily use highway crossing structures, including underpasses and culverts (Foster and Humphrey 1995; Gloyne and Clevenger 2001). Thus, the availability of vegetative cover and the spatial arrangement of cover patches relative to sources of anthropogenic risk and safe road crossings are likely to be key variables affecting puma use of human-dominated landscapes and the value of such landscapes as connectivity corridors.

In this study we address two research objectives. We first examine how networks of vegetation patches in otherwise open landscapes are functionally linked by puma movement decisions (Dancose et al. 2011) using high-resolution data on puma locations and vegetation cover. We hypothesize that aspects of cover patches themselves (e.g., vegetation type, size, isolation from neighboring patches) will interact with sources of anthropogenic risk to determine the sequence of patches visited by a puma navigating through a human-dominated landscape. Secondly, we apply our results on fine-scale habitat selection to the enhancement of puma connectivity in coastal California by developing a network-based connectivity model that quantifies the effects of specific restoration actions (e.g., addition of new cover patches and highway crossing structures) on puma dispersal probability. We use this model to compare multiple restoration scenarios for a previously identified corridor, allowing us to assess which combination of management actions will have the greatest potential to increase puma connectivity.

Methods

Study area

The Santa Cruz Mountains of central California (SCM) is an approximately 1700-km^2 mosaic of open space lands and exurban and suburban development bordered by urban areas (e.g., the cities of Santa Cruz and San Jose). Building density across the SCM study area ranged from 0 (wildlands) to > 1500 (urban fringe) buildings km^{-2}, with the average ($\pm$ SD) building density across the region being 55 ($\pm$ 155) buildings km^{-2} (Fig. 1a). Human disturbance is high throughout the region, including in undeveloped areas, which experience substantial recreational activity (Nickel et al. 2020). SCM consists of redwood (*Sequoia sempervirens*) and Douglas fir (*Pseudotsuga menziesii*) forests fringed by more open habitat types (grasslands, live oak (*Quercus* spp.) savannah, and coastal scrub). We focused our analysis of puma movement decisions on three focal areas within SCM (Fig. 1a) determined by (1) habitat type and (2) data availability. Focal areas were characterized by open, moderately developed habitat (i.e., > 35% total grassland and developed areas) with patches of tree or shrub cover at the margins of the contiguous forests that represent core puma habitat in the region. Each focal area was occasionally used by one or more pumas during high resolution GPS sampling (see below). The sizes of the three focal areas were 73, 113, and 170 km^2, with average building densities within each focal area being 12.9, 21.7, and 44.9 buildings km^{-2}, respectively (Fig. 1a). We defined cover patches within the three focal areas (Fig. 1b) as remnant patches of tree or shrub vegetation that ranged in size from 20 m^2 to 410 ha (median = 83 m^2) and were on average 1.9 km ($\pm$ 2.6 km) from the edge of the core forest.

The Coyote Valley (CV), an approximately 5-km wide valley lying between SCM and the larger Diablo Range (Fig. 1a), has been identified as an "essential connectivity area" (Spencer et al. 2010) for regional wildlife in general and represents among the only potential dispersal corridors for pumas migrating into or out of SCM. However, no successful dispersal events out of SCM by GPS collared pumas (n = 69 adult and juvenile animals collared to date) have been detected since monitoring began in 2008 (CCW, unpublished data), suggesting that, under current
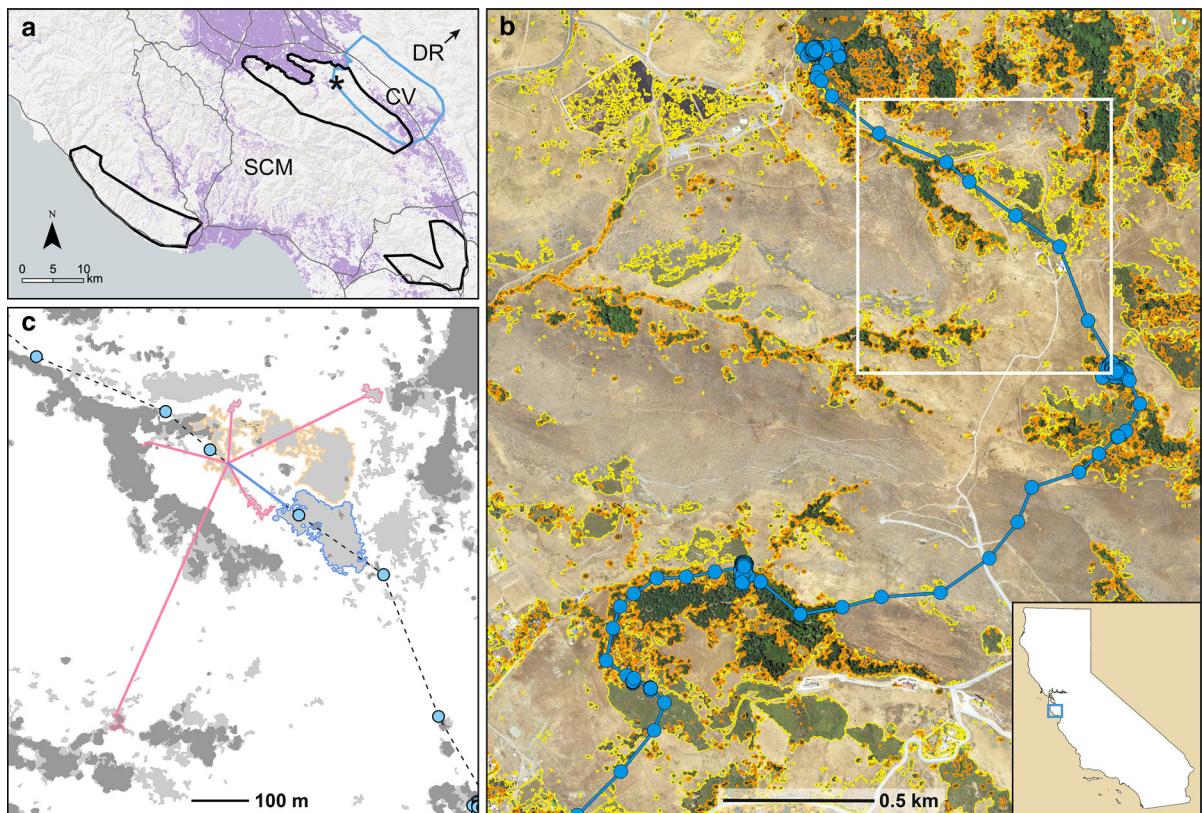
Fig. 1 Details of the study area and puma patch selection analyses. (**a**) Map of the Santa Cruz Mountains (SCM) and Coyote Valley (CV), highlighting the three SCM focal areas (black polygons) within which puma habitat selection was analyzed, and the CV corridor (blue polygon) connecting SCM and the Diablo Range (DR). Locations of buildings are shown in purple. Thin grey lines denote major highways. (**b**) Detail from one focal area (corresponding to the asterisk in (a)) showing aerial imagery habitat classification results for patches of trees (orange outline) and shrubs (yellow outline). An example movement track (five-minute GPS locations) from a male puma, are shown in blue. (**c**) Detail of boxed region in (b) illustrating the methodology for comparing used and available cover patches in patch selection analyses. Tree (dark grey) and shrub (light grey) cover patches are shown, along with puma locations (blue points) and movement path (dotted line). For a single movement event between a source (yellow outline) and target (blue outline) cover patch, the used edge is shown as a blue line along with randomly generated available edges (pink lines) to patches the puma could have visited (outlined in pink). For clarity, only five of the ten randomly generated available edges are shown. The inset in panel (b) shows the location of the study area (blue rectangle) within California, USA

conditions, the suitability of CV as a puma dispersal corridor is limited. CV consists of agricultural lands and residential and commercial development interspersed with small remnant patches of protective cover, with an average ($\pm$ SD) building density of 66 ($\pm$ 162) buildings km^{-2} (Fig. 1a). CV is bisected by two major highways, which are thought to present substantial barriers to puma movement. Highway crossing opportunities are likely limited to three underpasses under one highway and a single culvert under the other (see below and Online Appendix S1 for further details). No puma movement data currently exists for CV to inform corridor restoration decisions.

Thus, as described in detail below, we apply insights gained from quantifying puma movement decisions in SCM to model the effects of proposed restoration scenarios on puma connectivity across CV. We justify this approach by (1) using cross validation to ensure that our models of puma habitat use in SCM have good out-of-sample predicative power and (2) confirming that the range of habitat covariates on which the models are trained (i.e., those in SCM) overlap with the range observed in CV. Analogous approaches are commonly used in species distribution modeling, where species presence or absence across a broader

region is inferred from species detections in a subset of the landscape (Elith and Leathwick 2009).

Characterizing puma movement and habitat cover at fine spatial scales

We collected data on puma movement in the three SCM focal areas from 12 adult pumas (five females and seven males) fit with GPS collars (GPS Plus, Vectronics Aerospace, Berlin, Germany) sampling at 5-min intervals. We captured pumas using trailing hounds or cage traps following procedures described by Wilmers et al. (2013) and with approval by the Institutional Animal Care and Use Committee of the University of California, Santa Cruz (Protocol WilmC1612) and the California Department of Fish and Wildlife (Permit SC-11968). GPS location error ranged between approximately 0 and 15 m. All puma location data used here were collected between 15 May 2015 and 22 August 2017 and represent data from between 2 and 145 days for a given puma (mean ± SD = 49.3 ± 44.6 days) depending on how much time each individual spent within the focal areas (we address sample size differences between animals below).

Quantifying puma use of relatively small patches of protective cover requires characterizing habitat at a sufficiently fine spatial scale. We used high-resolution aerial imagery of our three SCM focal areas and the Coyote Valley from the US Department of Agriculture's National Agriculture Imagery Program (NAIP). We acquired 4-band, 0.6 m spatial resolution NAIP imagery collected in 2016, as this year approximates the mid-point of all puma location data used here. We used a supervised maximum likelihood classifier to classify each 0.36 m^2 pixel of NAIP imagery as either "tree" or "shrub" (or one of a suite of non-focal habitat types: grasslands, water bodies, built environment) and converted contiguous clusters of pixels classed as "tree" or "shrub" into individual polygon features representing patches of habitat cover (Fig. 1b). All tree polygons that were contiguous with the core forest of the SCM study area were reclassified as "core" to distinguish them from patches of tree cover separated by areas of open habitat. Habitat classification analyses were performed in ArcGIS (v10.5, ESRI, 2017), and are described in detail in Online Appendix S2: Habitat classification from aerial imagery.

Puma movement decisions in fragmented landscapes

We focused our analysis of puma habitat selection on occasions when an individual moved from one (source) patch of vegetation cover to another (target) patch across open habitat, hereafter referred to as a "movement event" (Fig. 1c). Puma locations within the three SCM focal areas were assigned to an individual tree or shrub patch if they were either completely within the patch or < 10 m from the patch border. All other GPS locations were considered to be in open areas between patches. We included events in which a puma moved from core forest to a tree or shrub target patch but excluded events in which a puma moved in the opposite direction (i.e., from a patch to core forest). In keeping with the network approach to analyzing habitat connectivity outlined below, we quantified the habitat between source and target patches along the straight-line edge between patches, defined as the line between the approximate location at which the puma left the source patch (hereafter the "exit point") and the approximate location at which it entered the target patch. The edge was determined by drawing a line between the last puma GPS location in the source patch and the first location in the target patch and then removing the portions of that line that fell within the source and target patch polygons (Fig. 1c). We restricted our analyses to only edges > 10 m in length to minimize noise from GPS location error, resulting in a median edge length of 72.8 m (range 10.0 to 1012.7 m; Online Appendix S2: Fig S1). The edge between patches differed from the actual movement path only when the GPS locations in the source and target patches were separated by one or more locations in open habitat (i.e., when the animal took longer than five minutes to move between patches), which was the case for 18.3% of movement events (mean ± SD number of locations between patches for all movement events = 0.4 ± 1.3; max = 23). To ensure that our edge-based approach provided accurate estimates of puma habitat selection, we also performed habitat selection analyses based on the actual paths traveled by pumas during movement events (see below).

We used a case–control study design to compare each movement event to a used target patch with 10 possible movement events to available patches (Dancose et al. 2011). Rather than selecting available

patches completely at random from the area surrounding a source patch, we developed a method based on the empirical distribution of edge lengths between patches that pumas were actually observed to use. This method (described in detail in Online Appendix S2: Specifying available edges) prevented more distant patches from being overrepresented in the available patch data set relative to their actual availability to pumas, a situation which would lead to an overestimation of the importance of distance in driving puma movements between patches. Once available patches were identified, we specified available edges as the straight line between the exit point of the source patch and the closest border of the available patch polygon.

For each used and available movement event, we extracted several covariates describing properties of both the target patches and the habitat along edges between patches. These covariates represent factors known to affect puma habitat selection [e.g., habitat type, anthropogenic features; (Wilmers et al. 2013; Knopff et al. 2014; Zeller et al. 2016)] as well as aspects of cover patches themselves that may determine their perceived value to pumas. All patch and edge covariates are summarized in Table 1 and described in detail in Online Appendix S2: Model

covariates. We natural log transformed right skewed covariates (AREA, PROX, and LENGTH) and centered and scaled (by 1 SD) all continuous covariates prior to modeling. We tested all pairs of covariates for collinearity by examining Pearson correlation coefficients (r_p), only including covariates in the same model if $r_p < 0.6$. All spatial analyses of patches and edges were performed using the *sp*, *sf*, *rgdal*, *rgeos*, and *raster* packages in R (v3.5.3, R Core Team 2019).

We analyzed resource selection functions (RSFs; Manly et al. 2002) under a step selection function design (Thurfjell et al. 2014; Suraci et al. 2019b) by fitting conditional logistic regression (CLR) models to our matched case–control data on movement events where each matched set of used and available events constituted a single stratum. We fit CLR models using the coxph function from the *survival* package in R (R Core Team 2019). To account for autocorrelation in the data, we estimated robust standard errors for all CLR models via generalized estimating equations (GEE) using independent clusters of puma movement evets (Prima et al. 2017). To create clusters, we took advantage of the fact that pumas typically visited our three focal areas of marginal habitat (Fig. 1a) only occasionally, with long breaks separating visits, and

Table 1 Summary of all covariates estimated for patches and edges used in the resource selection function analyses

Variable name	Explanation
Patch	
TYPE	Patch vegetation type (Tree or Shrub)
AREA	Area (m²) of the cover patch
NEIGHBOR	Distance (m) to nearest neighboring patch
PROX	Proximity of other patches. Estimates amount of local vegetation cover
COMPACT	Estimate of how closely a patch resembles a perfect circle
BUILD_DIST	Average distance (m) between the patch and the 25 nearest buildings
Edge	
LENGTH	Edge length
ELEV	Elevation (m, average w/in 30 m buffer)
SLOPE	Slope (degree, average w/in 30 m buffer)
TPI	Topographic position (absolute value, average w/in 30 m buffer), ranging from hillside (low) to ridge or valley (high)
WATER	Proportion of 30 m buffer consisting of water bodies or wetlands
AG	Proportion of 30 m buffer consisting of agricultural fields
BUILD_DEN	Average kernel density (200 m kernel width) of buildings w/in 30 m buffer
ROAD_DIST	Distance to nearest road (m)
ROAD_CROSS	Categorical; whether the edge crossed a road

See Online Appendix S2: Model covariates for additional details

grouped all movement events by an individual puma separated by more than seven days into separate clusters (Prima et al. 2017; Suraci et al. 2019b). This resulted in a total of 34 data clusters (mean ± SD number of clusters per individual = 2.8 ± 1.3, range 1 to 6).

We analyzed data from all pumas combined (hereafter, the all-data model), and also analyzed subsets of data representing factors that might affect puma movement and habitat use in human-dominated landscapes. We considered sexes separately, as differences in life history lead to differences in the ways that male and female pumas use space [e.g., males maintain substantially larger home ranges than females; (Dickson and Beier 2002)] and may also influence their sensitivity to anthropogenic disturbance. We also separated data into diurnal and nocturnal subsets by coding whether or not each movement event occurred between local sunrise and sunset (based on the time that the puma left the source patch). Pumas are typically nocturnal and may perceive less risk from humans at night when overall human activity is lower (Knopff et al. 2014; Nickel et al. 2020). For each dataset (all data, females only, males only, diurnal, nocturnal) we fit a set of 23 candidate models representing hypotheses regarding the effects of edge and patch attributes on puma movement decisions and consisting of combinations of the covariates presented in Table 1, as well as several interactions (see Online Appendix S1: Table S1). We identified the best fit model for each data set as that with the lowest quasi-likelihood under independence (QIC) score (Craiu et al. 2008). Where QIC model selection identified several models with comparable support (ΔQIC < 2), we selected the most parsimonious model (i.e., that with the fewest coefficients) for further analysis. "Top" models presented below are the most parsimonious for a given data set (Online Appendix S1: Table S1). To confirm whether our approach, based on habitat along the straight line edges between vegetation patches, accurately captures puma habitat use, we used identical methods to extract habitat covariates along actual puma movement paths and reran the all-data analysis using path-based covariates. We then compared top model coefficient estimates between the edge- and path-based models (Online Appendix S2: Path-based habitat selection modeling). Finally, we refit the top all-data model using only data from pumas with at least 10 days of

data and at least 40 movement events (n = 9 pumas) to test whether low sample sizes for some pumas affected our results.

Following Manly et al. (2002), we used the top CLR model coefficients β to calculate values of the relative probability of selection w for habitat covariate x via the exponential model

$$w(\mathbf{x}) = \exp(\beta_1 x_1 + \ldots + \beta_n x_n).$$

We evaluated the robustness of all top models using k-fold cross validation for case–control designs (Fortin et al. 2009; Dancose et al. 2011), as described in Online Appendix S2: Cross validation.

Connectivity analysis of fine-scale restoration scenarios

We assessed the effects of proposed restoration actions (revegetation and creation of new highway crossings, see below) on connectivity for pumas across the Coyote Valley (CV) using circuit theory-based connectivity modeling and a network design (McRae et al. 2008). Tree and shrub vegetation patches in CV (n = 25,730) were treated as nodes in a network, with edges between nodes representing possible movements that a dispersing puma could make between vegetation patches. We defined neighboring patches (i.e., those potentially linked by puma interpatch movements) using the Gabriel neighbor rule (Dale and Fortin 2014) in which two nodes A and B are considered neighbors as long as a circle with diameter AB does not contain any other nodes. We then defined edges between all pairs of patch neighbors as the shortest straight line between boundaries of the two patches, resulting in 47,619 edges across CV (Online Appendix S1: Fig. S1). The advantage of using the Gabriel rule to define neighboring patches, rather than examining all possible movement events across CV, was that this approach resulted in a moderately dense network of movement events while remaining computationally tractable. However, our approach could be used with any graph- or distance-based neighbor rule (Dale and Fortin 2014).

To calculate resistance estimates for each potential movement event between patches in CV, we extracted the same set of patch- and edge-level covariates as described above (Table 1) for each CV movement event and used parameter estimates from the top all-data CLR model to calculate the relative probability of

use (i.e., $w(\mathbf{x})$ score) for each event. Values of all patch- and edge-level covariates overlapped substantially between SCM and CV (Online Appendix S1: Table S2). Because pumas could potentially move in either direction between neighbor patches, we calculated $w(\mathbf{x})$ twice for each neighbor pair, iteratively treating each patch in the pair as the target patch. We then took the average of the two $w(\mathbf{x})$ values and used the inverse of this average relative probability of use value as the resistance estimate for each edge in the network (Zeller et al. 2012; Rio-Maior et al. 2019).

We modeled connectivity under present conditions as well as under several restoration scenarios developed in consultation with regional conservation partners, Peninsula Open Space Trust, to inform their habitat restoration efforts in CV. Restoration scenarios involve both the addition of patches of vegetation in key locations as well as the installation of additional crossing points across one of the two major highways bisecting CV (see Online Appendix S2: Fig. S3). We considered six scenarios: no new vegetation and no additional crossing points (NV−, i.e., current conditions); no new vegetation with new highway crossing points (NV+); moderate revegetation without (RV1−) and with (RV1+) new crossing points; and extensive revegetation without (RV2−) and with (RV2+) new crossing points. Full details of the six restoration scenarios are given in Online Appendix S2: Coyote Valley connectivity analysis.

We analyzed connectivity under each of the six scenarios using circuit theory (McRae et al. 2008) via Circuitscape software (v 4.0, www.circuitscape.org). For each restoration scenario, we calculated the average resistance distance for a puma moving across CV (see Online Appendix S2: Coyote valley connectivity analysis). Resistance distance is an estimate of total resistance between two nodes across all nodes in the network (McRae et al. 2008), and in this context provides a relative estimate of how isolated the two sides of CV are from each other, with lower resistance distance values indicating greater relative connectivity. We also calculated current flow for all edges, which is proportional to the expected net movement of pumas (McRae et al. 2008), and thus how concentrated puma movement is predicted to be along a given edge.

Results

Puma movement decisions in fragmented landscapes

We recorded 2600 movement events by pumas between source and target patches (mean ± SD events per individual = 216.7 ± 310.2, range 7 to 990). K-fold cross validation indicated excellent predictive power for all top RSF models (Online Appendix S1: Table S3). We found strong correspondence between the results of our edge-based and path-based RSF analyses, indicating that the edge-based approach accurately reflects puma movement across networks of vegetation patches (Online Appendix S1: Fig. S2). Finally, refitting the all-data top model excluding data from pumas with low sample sizes had negligible effects on our results (< 5% change in the value of all coefficient estimates relative to the model fit with the full data set), and we therefore included all puma data in the analyses presented below.

Our top all-data model indicates that AREA and LENGTH were primary drivers of whether a puma moved to a given target patch. Pumas were substantially more likely to move to a target patch as patch area increased or edge length decreased (Fig. 2a; Online Appendix S1: Table S4), and the interaction between these two factors suggests that, as target patch area increase, pumas are more willing to undertake longer movement distances (Fig. 3a). Patch type also had a strong effect on selection, with pumas being more likely to move to shrub over tree patches (Fig. 2a). The proximity of the target patch to other patches interacted with patch area in its effect on puma selection. Pumas tended to prefer patches surrounded by relatively little other vegetative cover (i.e., low PROX), and this preference increased with increasing target patch area (Fig. 3b). The positive effect of neighboring patch distance (NEIGHBOR, Fig. 2a) on relative probability of use similarly indicates that pumas preferred patches that were somewhat isolated from surrounding vegetation. Finally, pumas selected edges characterized by low SLOPE and high TPI (the latter corresponding to areas along ridgelines or valleys; Table 1), indicating a preference for movement paths with relatively low energetic costs (Fig. 2a).

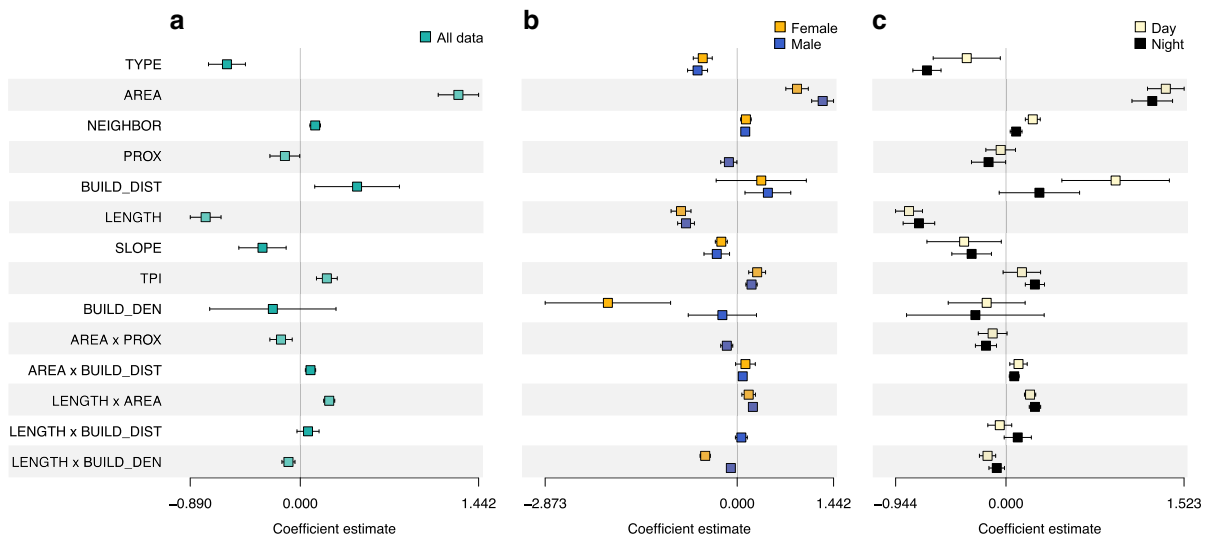The intensity of human development was a major driver of puma movement decisions. Pumas exhibiting

Fig. 2 Coefficient estimates and 95% confidence intervals from the top RSF models predicting the relative probability of a puma moving to an available cover patch. Coefficient estimates and CIs are shown on the logit scale (as estimated by conditional logistic regression) and covariate names are defined in Table 1. Top model results are shown for (**a**) all puma location data,

(**b**) female (orange) and male (blue) pumas separately, and (**c**) diurnal (beige) and nocturnal (black) locations separately. Coefficient estimates are only shown for those covariates included in the top model for a given data set. For all models, the reference condition for vegetation type (TYPE) is "shrub"
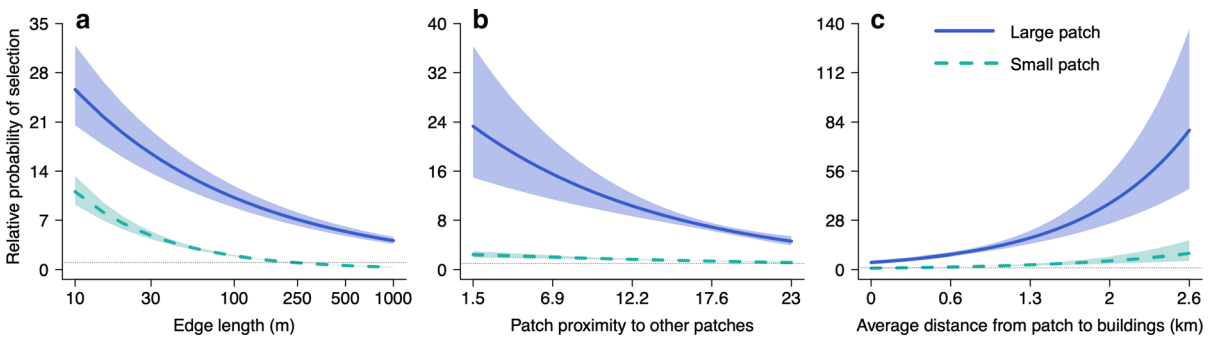

Fig. 3 Interactions between target patch area and other covariates in their effects on puma cover patch selection estimated by the top all-puma RSF model. Patch area interacts with (**a**) the length of the edge between source and target patches, (**b**) patch proximity to other patches (a unitless index (Gustafson and Parker 1992)) and (**c**) average distance between the target patch and the 25 nearest buildings. Predicted relative probability of selection (i.e., $w(\mathbf{x})$; see main text) is shown for small (285 m^2; dashed blue line) and large (4040 m^2; solid blue line) target patches, representing the 33% and 66% quantiles, respectively, of all used target patch sizes in our data set. Error lines are $\pm$ 1 SE. Note that the x-axis in panel **a** is plotted on the log scale

increased selection for patches as the average distance to buildings (BUILD_DIST) increased and as building density along the edge (BUILD_DEN) decreased, though with considerable uncertainty around the effect of BUILD_DEN (Fig. 2a). However, these effects were mediated by the amount and spatial arrangement of cover patches. Avoidance of patches close to buildings decreased as patch area increased (Fig. 3c),

and decreasing travel distance between patches similarly moderated the negative effect of both BUILD_-DIST and BUILD_DEN on puma selection probability (Fig. 4a, b). Due to collinearity (see Online Appendix 2), ROAD_DIST and BUILD_DIST were never included in the same model, and model selection suggested that BUILD_DIST was a better predictor of puma movement. ROAD_CROSS was also dropped
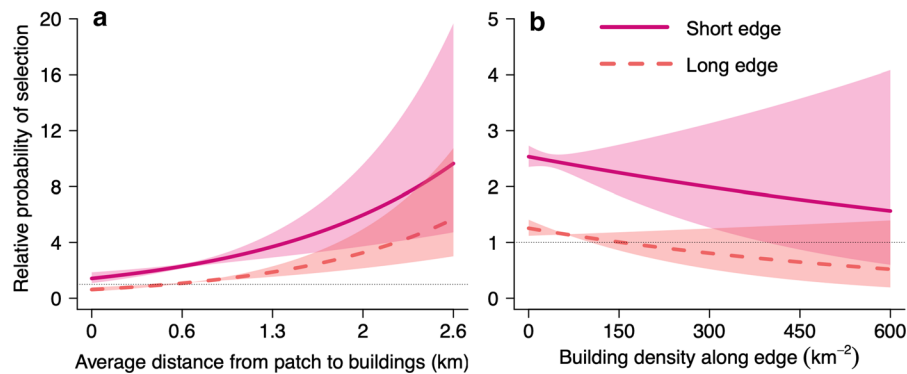
Fig. 4 Interactions between edge length and other covariates in their effects on puma cover patch selection estimated by the top all-puma RSF model. The length of the edge between source and target patches interacts with (**a**) the average distance between the target patch and the 25 nearest buildings and (**b**) average building density along the edge. Predicted relative probability of selection (i.e., $w(\mathbf{x})$; see main text) is shown for short (46 m; solid red line) and long (113 m; dashed red line) edge lengths, representing the 33% and 66% quantiles, respectively, of all used edge lengths in our data set. Error lines are $\pm$ SE

from the top all-puma model (Online Appendix S1: Tables S1 and S4), however, the weak effect of ROAD_CROSS should be interpreted with caution given that only a small proportion (5.2%) of used and available movement events in our data set crossed roads (see Online Appendix S2: Model covariates).

Puma sex and time of day (i.e., diurnal or nocturnal) had relatively modest effects on puma selection for vegetation patches. Our dataset contained 780 movement events by female pumas and 1820 by males. Top female-only and male-only RSF models revealed similar sex-specific patterns of habitat selection but suggested that female movement decisions in patchy habitats are somewhat more strongly influenced by anthropogenic disturbance than are those of males (Fig. 2b; Online Appendix S1: Tables S5 and S6). For females, BUILD_DENS had the largest effect size of any covariate (Online Appendix S1: Table S5), with females avoiding target patches with high building density along the intervening edge. For males, our model predicted larger effect sizes for several non-anthropogenic factors (e.g., AREA, LENGTH, TYPE) than for building density (Online Appendix S1: Table S6). When considering data from all animals, puma habitat preferences were also largely consistent across diurnal and nocturnal periods (Fig. 2c; Online Appendix S1: Tables S7 and S8). Only 25.8% of puma movement events occurred during daylight hours. During the day, pumas tended to be less selective of target patch vegetation type (TYPE) and avoided patches near buildings more strongly than at night (as estimated from relative effect sizes). However, 95%

CIs for all covariates overlapped between day and night, with the sole exception of NEIGHBOR (Fig. 2c).

Connectivity analysis of fine-scale restoration scenarios

Connectivity analyses indicated that, by increasing puma movement options, both the addition of revegetation plots and the creation of new highway crossing points would lead to increased puma connectivity across CV (Fig. 5a). The predicted effects of each of the six proposed restoration scenarios on cumulative resistance to puma movement (i.e., resistance distance) are presented in Table 2. Under current conditions (scenario NV-), the model predicts that few highway crossing options and limited vegetation in the vicinity of crossing points may create a bottleneck effect, concentrating puma movement options along a small number of highly important edges (Fig. 5b). The addition of three new highway crossing points without any revegetation (scenario NV +) is predicted to help alleviate this bottleneck by increasing the number of low resistance movement options available (Fig. 5c; percent reduction in resistance distance relative to current conditions: NV+ = −21.2%; Table 2). Our models predicted that revegetation in the absence of new crossing points can increase connectivity when the number of revegetation patches is sufficiently high and when patches are strategically placed near existing crossing points (Fig. 5d; RV2− = −16.8%), but that less thorough revegetation would be of little value on
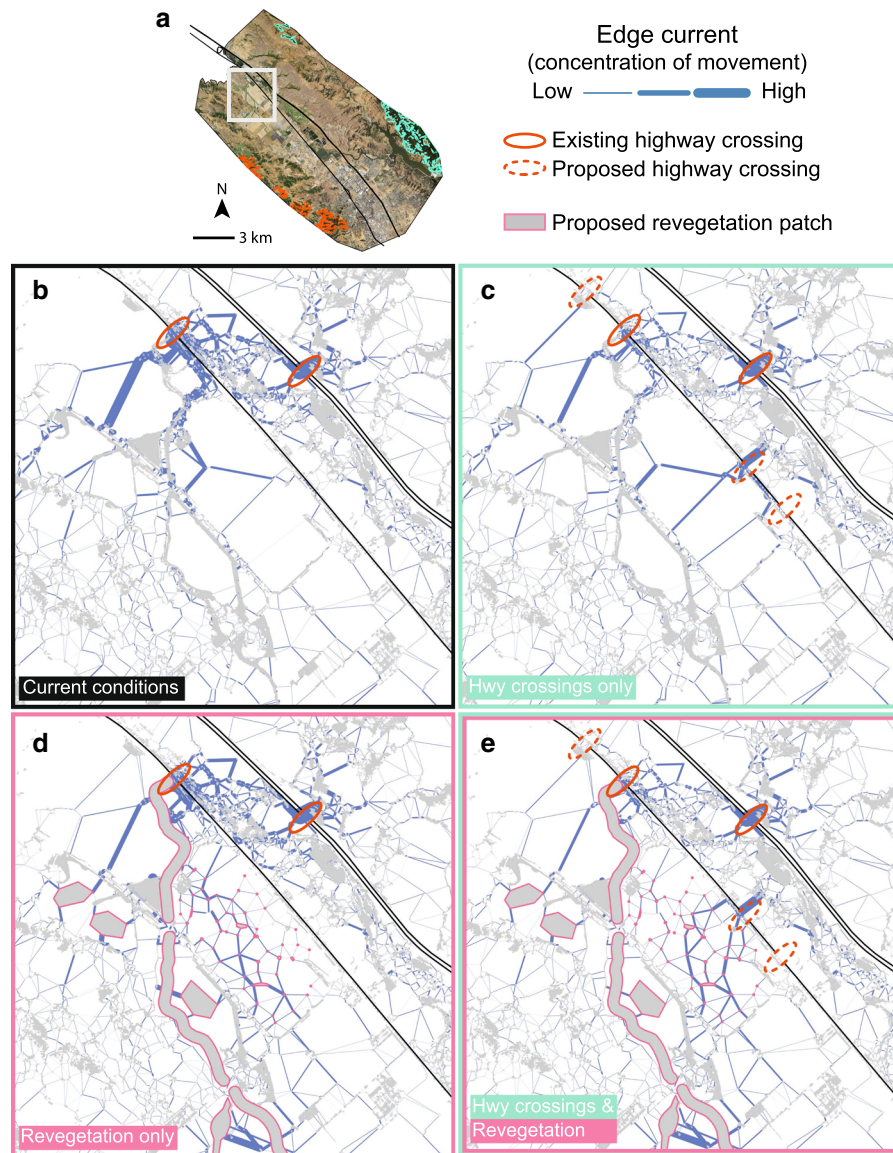
Fig. 5 Circuit theory-based current flow maps of Coyote Valley (CV) comparing proposed restoration scenarios for puma connectivity. (**a**) Map of CV illustrating the two major highways bisecting the study area (black lines) and the large (> 19 ha) vegetation patches that served as current start (blue outline) and end points (red outline) for circuit theory modeling (for broader geographic context of CV, see Fig. 1a). The grey box highlights the area of most intensive proposed restoration, detailed in all other plots. (**b-e**) Edge current values (width of blue lines), representing the relative concentration of puma movement along an individual edge, are mapped for present conditions (**b**, scenario NV1−), the addition of new highway crossing points only (**c**, NV +), extensive revegetation only (**d**, RV2-), and the addition of new crossing points plus extensive revegetation (**e**, RV2 +). Cover patches are shown as grey polygons, with proposed revegetation patches outlined in pink. Existing (solid red oval) and proposed (dashed red oval) highway crossing points are shown. Comparing maps **c-e** with map **b** highlights the benefits of restoration actions in terms of providing increased puma movement options and thereby reducing current flow through any one edge

its own (RV1− = 3.4%). The greatest decrease in cumulative resistance is achieved through a combination of new highway crossings and revegetation (RV1+ = −23.4%, RV2+ = −30.8%), which is predicted to substantially decrease puma reliance on any single movement path (Fig. 5e).

Table 2 Comparison of circuit theory-based connectivity modeling results for each of the six Coyote Valley restoration scenarios

Restoration scenario	Resistance distance[a]	Change in resistance[b]
NV−	161.63 (16.48)	–
NV+	127.42 (16.17)	− 21.2%
RV1−	167.08 (16.47)	3.4%
RV1+	123.80 (16.11)	− 23.4%
RV2−	134.41 (16.42)	− 16.8%
RV2+	111.81 (16.12)	− 30.8%

[a]Mean (SD) across all combinations of start (northeast Coyote Valley) and end (southwest Coyote Valley) patches

[b]Percent change in resistance distance relative to NV1− (current conditions). More negative resistance distance indicates greater connectivity

Discussion

Our habitat selection modeling revealed that the size and spatial arrangement of remnant vegetation patches interacts with the anthropogenic footprint on the landscape to shape puma movement decisions in fragmented habitats. The presence of buildings negatively affected puma selection for vegetation patches, but pumas were more willing to accept high building densities as patch area increased or inter-patch travel distance decreased. By integrating these inferences into connectivity models, we found that strategic placement of vegetation patches can substantially reduce resistance to puma movement across an otherwise high resistance landscape by diversifying movement options, particularly when paired with road crossing enhancements.

The area of target patches and the travel distances required to reach them were major drivers of puma selection for vegetation patches, a result that was consistent across sexes and diel periods (Fig. 2). These factors are analogous to the concepts of area and isolation of habitat fragments or islands, which form the basis of metapopulation theory (Hanski 1998). Indeed, at the regional scale, the size of and distance between habitat patches are common predictors of patch colonization rates and inter-patch connectivity for species across a wide range of taxa (e.g., Opdam et al. 1985; Rodríguez and Andrén 1999; Andersson and Bodin 2009). Thus, the primary factors determining whether two patches are connected at the fine scale of puma movement decisions correspond to those known to drive connectivity between populations at regional scales.

Functionally, this preference for larger and closer patches likely stems from their increased detectability and from selection against long movements through open habitats, which pumas have previously been shown to avoid (Dickson and Beier 2002; Wilmers et al. 2013; Knopff et al. 2014). Larger patches may also be inherently more valuable by providing more protective cover and/or better hunting opportunities. In a similar analysis of functional connectivity at fine spatial scales, Dancose et al. (2011) found that plains bison (*Bison bison*) navigating a complex of meadows in a forest matrix also preferentially moved to larger and closer meadows, which these authors note may be expected by chance alone. However, we detected an interaction between patch size and edge length, indicating that pumas were willing to move farther to access larger patches (Fig. 3a). This result suggests that selection for large patches is driven at least in part by their perceived value rather than likelihood of random encounter alone.

Part of the value of large patches may also lie in the amount of edge habitat they provide. (Note that here we use "edge" to refer to the border between two habitat types, i.e., the forest edge, rather than links between nodes in a network.) Puma hunting success for ungulate prey has been suggested to be highest along forest edges (Holmes and Laundré 2006), and previous studies have found consistent selection by pumas for edge habitat (Holmes and Laundré 2006; Knopff et al. 2014). This preference for edge habitat may explain our finding that pumas were more likely to move to target patches with relatively low amounts of other vegetation cover in the immediate vicinity (i.e., positive effect of NEIGHBOR and negative effect of PROX on patch selection; Fig. 2a),

particularly as target patch size increased (Fig. 3b). Pumas in our study area also showed a marked preference for shrub over tree patches (TYPE, Fig. 2a), which is consistent with findings from other puma populations (e.g., Knopff et al. 2014) and potentially reflects the greater protective cover provided by shrubs as compared to stands of trees with relatively open understory.

Our results indicate that the human footprint on the landscape plays a major role in influencing puma movement decisions, but as predicted, the effect of human disturbance was mediated by the amount and spatial arrangement of protective cover. We found that pumas consistently selected for patches that were farther from buildings (Fig. 2a), and that female pumas strongly preferred relatively low building density along movement routes between patches (Fig. 2b). However, avoidance of these anthropogenic features decreased with increasing target patch area and decreasing edge lenght (Figs. 3, 4). Thus, sufficient cover availability and the existence of travel routes that require only modest movements across open habitat can mitigate the negative effects of development on puma movement. Previous studies have identified the availability of protective cover as a key factor facilitating large carnivore use of human-dominated landscapes (Boydston et al. 2003; Ordiz et al. 2011), allowing carnivores to engage in essential activities such as resting (Llaneza et al. 2016) and feeding (Suraci et al. 2019b) while avoiding risk from humans. Our results indicate that, by facilitating movement through moderately developed areas, vegetation cover is also critical to maintaining or restoring linkages between large carnivore populations.

Mitigating the impacts of connectivity loss on puma populations in coastal California (Benson et al. 2016; Gustafson et al. 2019) will require enhancing movement potential through the heavily modified landscapes currently separating puma core areas. Our assessment of multiple restoration scenarios for the Coyote Valley corridor indicates that the strategic placement of revegetation patches has the potential to substantially increase the likelihood of puma movement across this moderately developed area (Fig. 5). However, revegetation per se will not necessarily enhance connectivity (Table 2); the predicted benefits of some revegetation actions (e.g., RV2−) over others (e.g., RV1−) stem from their capacity to increase the number of available movement options for dispersing

pumas, reducing puma reliance on a small number of high-value routes. This finding is in agreement with previous work in our study system demonstrating that maintaining sufficient movement routes for pumas through partially developed habitat is a key consideration when attempting to limit the impacts of new development on puma habitat (Smith et al. 2019b). More broadly, this work accords with general insights from network-based connectivity modeling highlighting the importance of multiple, redundant pathways between areas of high quality habitat to increase the probability of successful dispersal by any target species (McRae et al. 2008; Rayfield et al. 2011).

Our connectivity results also highlight the central importance of highway crossing enhancements in facilitating puma connectivity (Fig. 5). Previous research indicates that pumas and other carnivore species are inclined to use crossing structures underneath roadways (i.e., underpasses and culverts) such as those currently in existence in CV (Foster and Humphrey 1995; Ng et al. 2004), and that the presence of vegetative cover in the immediate vicinity of such crossing structures may increase their use by carnivores (Gloyne and Clevenger 2001). The restoration strategies outlined here, i.e., combining targeted revegetation with additional crossing structures, can be used both to increase overall habitat permeability and to direct carnivores to safe road crossing points by increasing cover availability near crossing structures.

The analyses presented above treated all puma movements between patches of vegetation cover similarly regardless of the behavioral motivations behind individual movement decisions. We considered this general approach to be a necessary first step given the range of factors likely motivating large carnivore use of human-dominated landscapes when, e.g., moving across a corridor or exploring marginal habitat on the periphery of a home range. However, large carnivore coexistence within human dominated landscapes requires that these landscapes provide more than just opportunities for movement. Prey availability and hunting success will be primary factors determining coexistence potential (Gehr et al. 2017) and may be important drivers of vegetation patch selection, particularly for ambush predators such as pumas. Characteristics of vegetation patches may also determine their suitability for non-movement behaviors such as resting and feeding (Llaneza et al. 2016), which previous research indicates are highly

sensitive to human disturbance (Smith et al. 2017; Suraci et al. 2019b). The framework developed here can be readily extended to incorporate information on large carnivore behavioral state (e.g., from movement and other biologging data), allowing researchers to test whether vegetation patch selection depends on the behavior in which an animal is engaged (e.g., travel, hunting, resting etc.). Individual animals may also exhibit consistent variation in habitat selection (Leclerc et al. 2016) and such personality effects may play a significant role in driving carnivore use of human-dominated landscapes, an important are for future research.

Despite substantial anthropogenic risks, several large carnivore populations have demonstrated the ability to persist and expand in moderately developed landscapes in close proximity to people (e.g., Wilmers et al. 2013; Chapron et al. 2014; Rio-Maior et al. 2019). In many cases, these areas are increasingly critical to large carnivore population viability (Carter and Linnell 2016), requiring an understanding of how such habitats should best be managed to facilitate carnivore use. Maintaining or enhancing functional connectivity for carnivores navigating human-dominated landscapes is critical to this effort. We suggest that an increased focus on functional connectivity at the fine scale of large carnivore movement decisions will provide a valuable compliment to regional scale conservation planning when designing landscapes that support human-carnivore coexistence.

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