



Road-crossings, vegetative cover, land use and poisons interact to influence corridor effectiveness

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ABSTRACT

Landscape connectivity is essential to conserving resilient wildlife populations in the Anthropocene. Maintaining connectivity requires preserving or restoring patches of habitat, accounting for the behavioral factors that determine movement between patches and mitigating threats. We measured natural and anthropogenic features that influence movement and mortality for bobcats (*Lynx rufus*) in a system threatened with complete isolation by urbanization. Our overarching objective was to inform local land acquisition and restoration to maintain two last-chance wildlife corridors. We collected five-minute movement data from 36 bobcats in central California to assess features of road-crossing hotspots and model habitat selection, including functional responses to housing densities and vegetation. We collected opportunistic mortalities and assessed rat poison exposure to evaluate edge effects as acute threats. Bobcats strongly selected for natural vegetation, evident at the level of a single tree or shrub. Individuals selected low-density housing (<5 houses/ha) yet avoided high-density housing development and monoculture agriculture. Narrow (<25 m wide) riparian strips were critical to connectivity. Bobcats successfully crossed the busiest highway in the landscape but frequently died when crossing a less-trafficked road with a high median barrier. Vehicles and disease were dominant sources of mortality, while 94% of bobcats were exposed to rat poisons despite California's 2014 regulations implemented to reduced wildlife exposure. Maintaining landscape connectivity requires conserving key habitats, mitigating the effects of infrastructure, and sustaining populations of highly mobile, healthy individuals. Our findings have driven conservation action through land acquisition. We demonstrate how robust, rapid data collection can facilitate real-world conservation outcomes.

1. Introduction

The movement of individuals and their genes across landscapes is vital to population persistence (Fletcher et al., 2016), the adaptability of species to environmental change (Thomas et al., 2004), and ecosystem resilience (Sgrò et al., 2011). Landscape connectivity is a fundamental underpinning of diverse ecological processes including predator-prey interactions, nutrient cycling, and disease dynamics (Fletcher et al., 2016). The global expansion of human populations, however, is drastically changing the ability of organisms to move across landscapes. Seventy-five percent of the planet's terrestrial surface is impacted by numerous anthropogenic activities collectively referred to as the "human footprint" (Sanderson et al., 2002). This footprint has reduced terrestrial mammal vagility by 30–50% (Tucker et al., 2018) and correlates with anthropogenic mortality (Hill et al., 2019). Understanding

factors that influence animal vagility and associated risk is increasingly elemental to biodiversity conservation in the Anthropocene (Fletcher et al., 2016).

Humans transform landscapes and inhibit wildlife movement in two fundamental ways. First, destruction of natural habitat fragments landscapes and reduces connectivity (Foley et al., 2005). Second, humans create infrastructure and linear barriers when building cities, paving roads, erecting fences, or damming rivers. Yet the effects of infrastructure and barriers can be complex and sometimes counterintuitive. Roads, for example, may facilitate movement in areas with low human footprint (Whittington et al., 2011) while in areas with high human footprint, roads can act as a critical impediment to movement (Riley et al., 2014a). Overall, however, roads may act as an important source of mortality (Hill et al., 2019) and suppress animal population abundance (Fahrig and Rytwinski, 2009) irrespective of their effects on

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animal movement.

Edge effects around habitat also disrupt population dynamics and persistence (Benson et al., 2016; Fagan et al., 1999; Watling et al., 2011). Thus, the qualities of matrices (i.e., developed portions of the landscape in which habitat patches are embedded) themselves can fundamentally influence ecological connectivity (Watling et al., 2011). For example, dispersal routes obstructed by human infrastructure can increase mortality, especially for subadult individuals, and isolate populations (Riley et al., 2014b; Kramer-Schadt et al., 2004). Isolation erodes genetic variation (Benson et al., 2016), increasing vulnerability to other stressors (Keller and Waller, 2002). Disease dynamics can shift in transformed landscapes while pesticide exposure kills wildlife, may increase disease susceptibility (Riley et al., 2014c), and can cause population declines (Riley et al., 2007). When retaining or restoring connectivity, an appraisal of the acute edge effect threats to populations is essential to implementing robust mitigation measures.

Corridors that facilitate wildlife movement between habitat patches can mitigate barriers caused by fragmentation (Beier, 2018; Beier et al., 2008). Identifying effective corridors is challenging because landscape connectivity is a complex combination of structural features and functional processes, and consequently, corridors based on expert opinion can substantially deviate from animal-defined corridors (LaPoint et al., 2013). Structural connectivity, the presence of habitat linking sub-populations, may be a function of a suite of variables including land cover type, patch size, isolation, mortality risk, and whether linear features facilitate or disrupt movement (Fletcher et al., 2016). Functional connectivity is assessed via the behavioral response of individuals to those landscape features and other factors and movement rates between sub-populations (Carvalho et al., 2016; Kramer-Schadt et al., 2004). Because observing functional movement is difficult due to the need to monitor select individuals at precise times moving long distances, structural connectivity often becomes a proxy for functional movement. Yet, accounting for actual behavior, and in particular varying choice among individuals, provides essential insight into how animals move through the landscape (LaPoint et al., 2013).

Fortunately, we have entered a “golden age” of bio-logging with technological advances that can record extremely fine-grain movement of tagged animals (Wilmers et al., 2015). Using high-resolution data to define movement corridors is more reliable than expert-opinion and cost-based models that ignore unique interactions between animal behaviors and structural features (Abouelezz et al., 2018; LaPoint et al., 2013). Technological advancements improve rapid assessments to inform mitigation and restoration measures via land acquisition and retro-fitting infrastructure to reduce barrier effects (e.g., Serieys and Wilmers, 2019). Additionally, we can pair precise animal locations with high-resolution remote monitoring of extensive landscapes to better match fine-scale movement with fine-scale landscape features down to individual trees.

Here, we use high-resolution movement (5 min) and remote sensing (0.6 m [0.36 m² pixels]) data to determine the presence of two “last-chance” wildlife linkages (the only remaining corridors that connect habitat patches) in landscapes threatened by imminent anthropogenic development in central California. We used a landscape-species approach (Sanderson et al., 2002) to identify natural and human-derived features that influence connectivity. Additionally, we wanted to understand factors that reduce functional connectivity by increasing mortality. We chose a mesocarnivore, the bobcat (*Lynx rufus*), because its scale of movement is congruous with the scale of the study areas, while their resource requirements translate into an inherent need to navigate hostile matrices to move among habitat patches (Crooks, 2002). As a mammalian carnivore, bobcats exist at low densities and are thus genetically sensitive to habitat fragmentation and inbreeding (Ruiz-López et al., 2012). Their trophic status leaves them vulnerable to the bioaccumulation of urban pathogens and pesticides (Carver et al., 2016; Serieys et al., 2015). Overall, these ecological traits make them intrinsically vulnerable to extinction associated with habitat degradation

(Cardillo et al., 2005), and excellent proxies for sympatric species (e.g. puma, *Puma concolor*; badger, *Taxidea taxus*; coyote, *Canis latrans*) that have similar extinction risk (Cardillo et al., 2005) and may also contribute to ecosystem processes (Zavaleta et al., 2009) in the study areas.

Our overarching goal was to make management recommendations to local conservation agencies before more extensive habitat loss leads to irreversible population fragmentation and decline. Our specific objectives included: i) intensive monitoring of bobcat movement complemented with movement-explicit step selection functions to identify the relative importance of natural and human-modified landscape features that influence bobcat movement through the last-chance corridors; ii) evaluate the barrier and mortality effects of roads to characterize safe and dangerous road-crossing hotspots so that potentially needed retrofitting of roads can facilitate connectivity and mitigate threats; and iii) assess the role of vehicles, ubiquitous rat poisons, and an urban-associated disease (notoedric mange, *Notoedres cati*; Serieys et al., 2015) in driving bobcat mortality thereby potentially inhibiting functional connectivity. Given the severity of fragmentation in the region, these high-resolution data are essential to designing mitigation measures to preserve and restore landscape connectivity amidst ongoing development and habitat loss.

2. Methods

2.1. Study area

We conducted this study within the San Francisco Bay Region and adjacent southern counties (Fig. 1) in the California Floristic Province, the sixth most important biodiverse conservation region within the U.S. (Stein et al., 2000). The region is characterized by a series of mountain ranges with anthropogenic development concentrated in the interlinking valleys.

Our study sites comprised two stretches of fragmented habitat that remain as the only two viable linkages between the Santa Cruz Mountains and the eastern ranges — the Coyote Valley to the east, and the Aromas Hills to the southeast. Local conservation stakeholders describe these areas as the “last-chance” wildlife corridors for Santa Cruz Mountains faunal populations because they constitute the last remaining potential linkages between the Santa Cruz Mountains and adjacent mountain ranges (Fig. 1, Supplemental Fig. S1). Both areas are imminently threatened by intense commercial development. Conservation organizations seek mitigation measures that would preserve remaining natural habitat of greatest importance to wildlife and maintain biological connectivity between the mountain ranges (Serieys and Wilmers, 2019).

Each study area encompasses roughly 30 km² (Supplemental Fig. S1). Land uses include orchards, row crops, commercial development, residential neighborhoods, and altered open areas (i.e., golf courses and school yards). Remaining natural areas are a mix of riparian strips, mixed oak and shrub savannah, and serpentine grassland.

2.2. Sampling, movement, and mortality data

We used standard cage-trapping techniques to capture bobcats during three trapping sessions between June 2017 and December 2018. In Coyote Valley, dry season trapping occurred June 1–July 30, 2017 while wet season trapping occurred November 10, 2017–February 28, 2018 because one on-the-ground objective in Coyote Valley was to test for potential seasonal differences in bobcat habitat selection. In Aromas Hills, we trapped during one trapping session between June 1, 2018 and December 31, 2018. We used cage traps (Tru-catch traps, Bell Fourche, South Dakota or CamTrip cages, Caging Bobcats, Barstow, California) that were checked a minimum of every 12 h. Individuals were chemically immobilized with a mixture of ketamine HCl (5 mg/kg) and medetomidine HCl (0.1 mg/kg). We recorded age class, sex, weight, and

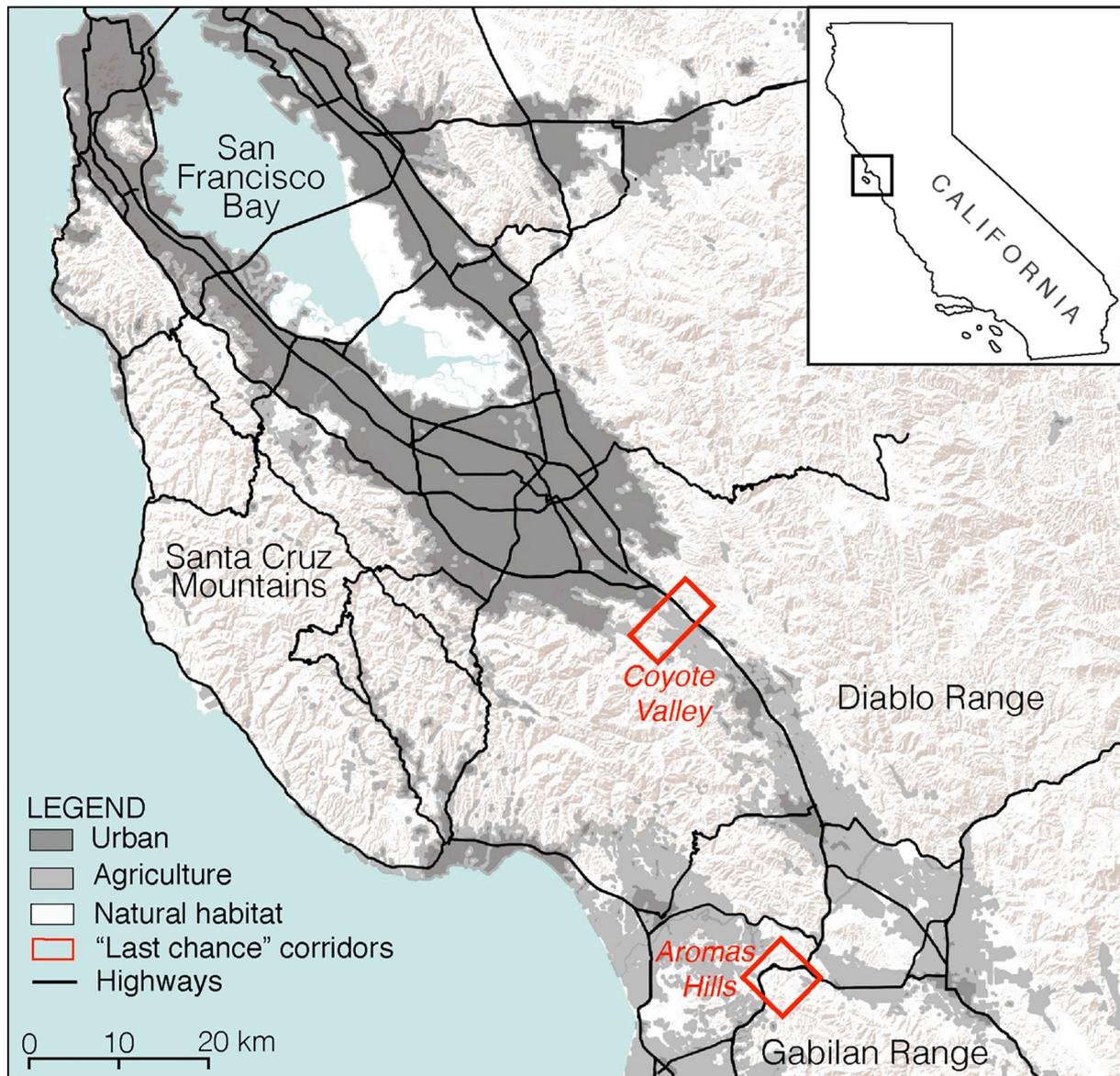


Fig. 1. A map of the Santa Cruz Mountains and neighboring ranges.

morphological measurements. We classified as juveniles (<2 years) or adults (≥ 2 years) based on body size, weight, tooth wear and eruption, and reproductive status (Serieys et al., 2015).

Individuals were collared, and their movements monitored using GPS and triaxial accelerometers (Eobs GmbH; Grünwald, Germany) that sampled locations at 5-min intervals when the animal was moving, and at 3-h intervals when the animal was at rest (Supplemental Methods 1, collar programming file). Collars were set to record data for a minimum of three-months for each individual.

We performed mortality surveys for GPS-collared individuals on a weekly-monthly basis, depending on the ease of locating each individual, particularly given that we were unable to obtain entry access to various regions of the study areas. We opportunistically collected carcasses from untagged bobcats to increase our understanding of factors contributing to mortality in the study areas. We necropsied all carcasses and recorded cause of mortality, collection date and location, sex, age class, and presence of notoedric mange (*Notoedres cati*; Riley et al., 2007).

All animal capture, handling, collaring, and sample collection was approved by the Institutional Animal Care and Use Committee (IACUC) of the authors' institution (Protocol numbers). Scientific collecting

permits were authorized by the California Department of Fish and Wildlife (Aromas, SCP-11968; Coyote Valley, SCP-13565).

2.3. Anticoagulant rodenticide exposure

To further assess contributors to mortality, we tested for a standard panel of commercially available anticoagulant rodenticide (AR) compounds (brodifacoum, bromadiolone, difethialone, difenacoum, chlorophacinone, diphacinone, warfarin, and coumachlor) when it was possible to recover the liver of animals that died. The detection of ARs in liver reflects the history of exposure for the individual (Serieys et al., 2015). We assessed the presence and concentrations of each compound using HPLC and LCMS/MS as has been previously described (e.g. Serieys et al., 2015). The threshold of detection required for quantitation by LCMS/MS for our panel of ARs was 0.05 ppm for brodifacoum, chlorophacinone, and diphacinone, and 0.02 ppm for bromadiolone, coumachlor, difethialone, warfarin, and difenacoum. When compounds were detected by HPLC, but at concentrations too low to be quantitated by LCMS/MS, we report the compound as "level of detection" (LOD). For compounds that were LOD, when calculating mean concentrations across individuals, we assigned the smallest non-zero value (0.01) given

our level of detection precision.

2.4. Landscape covariates

We tested the influence of topography (SLOPE), vegetation (TREES, SHRUBS, GRASS, EUCALYPTUS), distance from water (streams, lakes, ponds; WATER), monoculture agriculture (CROPS, ORCHARDS), and anthropogenic landscape features including distance from arterial roads (ROADS) and housing density within a 100-meter radius around each GPS location (HOUSE; see Section 2.6 below for radius selection) on bobcat movement. For additional GIS layer source details, see Supplemental Table S1.

To assess the influence of vegetation on bobcat movement across the study areas, we first conducted a supervised maximum likelihood land cover classification in ArcGIS 10.5 (ESRI, Redlands, CA) from US Department of Agriculture National Agricultural Imagery Program high-resolution (0.6 m [0.36 m² pixels]) remotely sensed imagery (USDA 2016) recorded at spectral bands corresponding to blue, green, red, and near-infrared wavelengths. We classified land cover as trees, shrubs, grass, non-vegetation (i.e., urban or rock), and water (Supplemental Table S1). We resampled the land cover raster at 1.2 m resolution to account for errant pixels. We subsequently used the California Department of Conservation agricultural layers for Santa Clara, Monterey, San Benito, and Santa Cruz Counties (California Department of Conservation; consrv.ca.gov) to identify monoculture agricultural areas that we classified as either row crops or orchard. Informal quality assessment showed high correspondence between the agricultural layers and row crops and orchards visible in the NAIP imagery. However, informal quality assessment revealed shaded vegetation classified as water; we corrected for this by masking out water bodies using the USGS Natural Hydrography Dataset (NHDH_CA_92v200; usgs.gov) and reclassifying remaining water pixels (initially classified as water) as TREES. We transformed bobcat locations from WGS84 into the 1983 North American Datum and reprojected them into the Universal Transverse Mercator Zone 10 N coordinate reference system. For each location, we sampled the presence or absence of trees, shrubs, grass, row crops, and orchards such that each category had a binary designation of 0 or 1. To account for GPS error in observed locations, points were classified as trees and shrubs if trees or shrubs were within a 5-meter radius of each location and, if either class was present within the buffer, assumed the true location of the bobcat was within the nearer of the two vegetation classes (though such instances were rare).

We estimated other natural landscape features including the minimum distance from the nearest stream, pond, or reservoir (WATER; USGS Natural Hydrography Dataset [NHDH_CA_92v200]; usgs.gov) and topographical features, elevation (ELEVATION) and slope (SLOPE), extracted from the USGS 1/9 arc-second Digital Elevation Model (sciencebase.gov).

We measured four types of disturbed landscapes on bobcat movement—monoculture agriculture, eucalyptus, housing density, and roads. We identified locations within monoculture agricultural areas that included orchards and row crops (ORCHARDS or CROPS, California Department of Conservation; consrv.ca.gov). To determine the effect of a dense 4 km² eucalyptus grove (in Aromas Hills) on bobcat movement and habitat selection, we used QGIS (QGIS Development Team, 2019) to manually map the eucalyptus grove from the high-resolution NAIP imagery. We tested the effect of housing density within a 100-meter buffer (see ‘Section 2.6. Housing density scale’ below for more details about buffer size determination) surrounding each location (HOUSE, based on Microsoft’s Building Footprints; Open Data Commons Database License). Finally, we calculated the distance of each location from the nearest arterial (primary or secondary) road (ROADS; ESRI Roads [DataMaps10.2]). Primary arterial roads are highways or freeways with high traffic volumes, while secondary arterial roads comprise smaller, less-trafficked roads that feed directly into primary roads (Riley et al., 2014a). Arterial roads in our study included US Route 101 found in both

study areas, as well as six secondary roads of particular interest in the study areas (described further below, Section 2.8).

2.5. Movement-explicit habitat selection

We analyzed movement-explicit habitat selection using step-selection functions (SSFs; Thurfjell et al., 2014) because we wanted to characterize habitat that specifically influenced decision-making while individuals were moving across the landscape. Because the collars collected both 5-min movement, and 3-hour resting locations, we isolated movement locations by removing resting locations. We implemented a standard 1:20 match-case control empirical design by creating strata where each individual’s end ‘used’ location (t) was paired with 20 ‘available’ locations (Duchesne et al., 2010; Fortin et al., 2005). We investigated selection in response to topography, vegetation, streams and lakes, monoculture agriculture, distance from arterial roads and housing density.

Habitat selection analyses are sensitive to the spatiotemporal scale at which available habitat is characterized (Boyce, 2006; Wilmers et al., 2015; Thurfjell et al., 2014; Suraci et al., 2019) and fix intervals determine the strength and order of habitat selection (Thurfjell et al., 2014; Suraci et al., 2019). For example, at fine temporal scales (<20 min), movement decisions reflect options within a maximum of several hundred meters (Thurfjell et al., 2014; Suraci et al., 2019). Thus, at fine scales, the selection for natural vegetation within an individual’s immediate vicinity will obscure potential avoidance of risky anthropogenic features on the landscape (e.g. Suraci et al., 2019). A primary objective of this study was to assess the relative influence of both anthropogenic and natural landscape features on movement decision making. Therefore, we subsampled our 5-min movement data to an intermediate (3 h) fix interval following Suraci et al. (2019). At intermediate fix intervals, the relative importance of anthropogenic landscape features is best captured in SSF habitat selection studies in human-dominated landscapes (Suraci et al., 2019).

We simulated ‘available’ locations to match each observed location t by sampling, with replacement, random vectors originating from the immediately preceding ‘used’ location (i.e., location $t-1$). Random vectors were drawn based on the empirical distribution of turn angles and step lengths between consecutive locations derived from data on all individuals that were the same sex as the focal individual. However, while drawing the random vectors, we excluded the focal individual’s data to avoid circularity (Fortin et al., 2005). We included three resource-independent behavioral parameters in the models to control for inherent biases in animal movement that may also affect habitat use. Step length (STEP, calculated between t and $t-1$) and log-transformed step length (LOG.STEP) controlled for potential habitat selection biases arising from the ability of individuals to travel to available locations (Forester et al., 2009; Nicosia et al., 2017). Directional persistence (DIR.PERSIST) controlled for the inherent tendency of individuals to move in a constant direction and was calculated between t , $t-1$, and $t-2$ (following (Duchesne et al., 2010; Nicosia et al., 2017; Suraci et al., 2019) as:

$$\cos(\theta_t - \theta_{t-1})$$

where θ_t is the absolute (angle relative to North) of the vector resulting in the current step t , and θ_{t-1} is the absolute angle of the preceding vector resulting in step $t-1$.

We estimated selection (β) coefficients using conditional logistic regression (CLR) via cox proportional hazards models in package ‘survival’ 2.43-3 (Therneau, 2018) for R statistics software (R Core Team, 2019). Successive strata were not independent due to temporal autocorrelation (Craiu et al., 2008), thus deflating standard errors associated with β coefficients. Therefore, we calculated robust standard errors using generalized estimating equations (GEE; Prima et al., 2017) by specifying intra-group (‘cluster’) correlation. We classified clusters by collaring events following a recommendation to use one cluster per

individual when the number of individuals exceeds 30 (Prima et al., 2017). Two individuals were opportunistically recollared in Coyote Valley. Clusters represented 38 collaring events across 36 bobcat individuals (total $n_{strata} = 35,701$).

Next, we modeled the relative probability of a bobcat selecting a particular location as a function of all natural and disturbance landscape variables described above. All covariates were standardized (mean = 0, standard deviation = 2; Gelman and Hill, 2007). We performed pairwise Pearson correlations to ensure that covariates were not strongly collinear ($|r| \leq 0.40$ for all pairwise relationships). We first independently modeled the two topographic covariates (ELEVATION, SLOPE) to determine which covariate performed best. We identified the best fit topographical model as that with the lowest quasi-likelihood under independence (QIC) score, a criterion indicated by Craiu et al., 2008 for use in GEE-based analyses. SLOPE performed best, and thus was included in all downstream modeling. Next, we fit a set of 20 candidate models (Supplemental Table S2) representing hypotheses regarding the potential influence of 10 landscape covariates (SLOPE, CROPS, ORCHARD, GRASS, TREES, SHRUBS, EUCALYPTUS, WATER, ROADS, and HOUSE) on bobcat movement. We selected the top model as that with the lowest QIC. We provide parameter estimates and 95% confidence intervals (derived from robust standard errors) on the logit scale, as estimated by CLR.

2.6. Housing density scale

To assess the scale at which housing density exerted the strongest influence on bobcat habitat selection, we calculated housing density individually at 16 different scales between 50 and 1000 m radius (at 50–100 m increments) buffers surrounding each used and available location. We tested the relative effects of these 16 different buffer sizes individually while controlling for directional persistence and step length using the CCLR framework. We identified the most parsimonious model (100 m buffer size) by comparing the QIC as described above.

2.7. Functional responses: housing density and vegetation cover

We wanted to determine whether bobcats exhibit a functional response to changes in low- to medium-housing density. We considered a functional response for both study areas collectively, but we also considered distinct functional responses within Aromas Hills and Coyote Valley because the two study areas have differing spectra of housing densities. In Aromas Hills, bobcats regularly moved through low-density neighborhoods (<5 houses/ha). In contrast, Coyote Valley residential development is largely high-density (>5 houses/ha) that bobcats rarely permeated. We tested for functional responses using a piecewise linear spline regression model that split housing density into two or three covariates with different slopes on either side of a breakpoint (Kohl et al., 2018; Smith et al., 2019b). We selected optimal breakpoints using a grid search approach of the breakpoint by comparing the QIC values of candidate spline models against models with a simple linear effect (on the log link scale) for housing density.

Next, because land acquisition, primarily of agricultural parcels, is active in both study sites, we considered a functional response to varying degrees of composite vegetation cover (i.e., trees and shrubs). Our aim was to calculate recommended vegetation restoration guidelines for parcels. We specifically tested for the functional response on the scale of one acre (a common management unit) by extracting the composite value for proportion cover by trees and shrubs in a one-acre circular buffer around each location. We performed the same grid search method described above.

2.8. Road crossings

We used 5-minute relocation data to identify the date, time, and location of road-crossing events for each individual that crossed one of

seven arterial primary or secondary roads. We focused this analysis only on major arterial roads with noted high traffic volume and road mortalities in the study areas (e.g. Serieys and Wilmers, 2019). Highway 101 was the only primary road in both study areas and is an 8–10 lane freeway with numerous culverts and underpasses. Average daily traffic is roughly 84,000 vehicles/day in Coyote Valley, and 52,000 vehicles/day in Aromas Hills (dot.ca.gov). All other roads were secondary (Supplemental Fig. S1) and average all daily average traffic volumes exceeded 2000 vehicles/day (Monterey Road: 9000; Route 129: 10,200; Route 25: 2400; Route 156: 3100; Bailey Road: 5525; Santa Theresa Road: 7500 vehicles/day). We defined a road-crossing location as any intersection of a line segment between two consecutive 5-minute bobcat locations and a line feature representing the arterial road. These locations were thus rough approximations of actual crossing locations. We classified road-crossings as occurring during the day or night based on local sunrise and sunset times.

We calculated the expected number of road crossings per hectare using a two-dimensional kernel density estimator (KDE) with a 250 m search radius of identified road-crossings in ArcGIS 10.3. The expected number of crossings ranged from 0 to 11.31, which we reclassified according to easily interpretable categories of areas of infrequent crossings (<1/ha), regular crossing areas (1–2/ha), and road-crossing hotspots (>2/ha).

3. Results

3.1. Movement sampling

We captured 38 bobcats (22 adults, 16 juveniles; 21 males, 17 females; Supplemental Table S3) across both study areas (Coyote Valley: 26; Aromas Hills: 12). One juvenile's collar fell off within two days, and we did not collar one juvenile. Therefore, we collected 652,700 5-min GPS-collar locations from 36 individuals (22 adults, 14 juveniles; 20 males, 16 females; Supplementary Table S3) filtered to 32,373 three-hour observations for habitat selection analyses. We monitored GPS-collared bobcats for an average of 143.8 tracking days (range: 16–369; median = 131 days).

3.2. Movement-explicit habitat selection

Both natural and anthropogenic landscape features strongly influenced bobcat habitat selection while individuals were moving (Table 1). Alternative models exhibited $\Delta QIC > 17$ (Supplemental Table S2). Their

Table 1

The top habitat selection model comprising landscape covariates and three resource-independent behavioral parameters. Water is measured as the distance from the nearest water source, and thus a negative selection coefficient represents a positive association. Behavioral parameters controlled for inherent biases in animal movement that influence habitat use. Directional persistence (DIR.PERSIST) controlled for the inherent tendency of individuals to move in a constant direction. Step length (STEP) and log-transformed step length (LOG.STEP) controlled for the habitat selection biases arising from the ability of individuals to travel to available locations.

Covariate	Assoc.	β estimate	Robust SE	Lower 95% CI	Upper 95% CI	p- Value
TREE	+	1.43	0.08	1.27	1.60	<0.001
SHRUB	+	1.30	0.10	1.09	1.51	<0.001
CROP	–	–0.55	0.08	–0.71	–0.40	<0.001
ORCHARD	–	–0.15	0.03	–0.21	–0.09	<0.001
HOUSE	–	–0.18	0.04	–0.25	–0.10	<0.001
EUCALYPTUS	–	–0.26	0.07	–0.41	–0.12	<0.001
WATER	+	–0.49	0.19	–0.87	–0.12	0.010
SLOPE	+	0.18	0.06	0.07	0.28	0.002
DIR.PERSIST		0.15	0.05	0.05	0.24	0.003
STEP		–0.07	0.18	–0.43	0.30	0.724
LOG(STEP)		0.40	0.13	0.14	0.65	0.003

strong selection for trees ($\beta = 1.43$) and shrubs ($\beta = 1.30$) was remarkably apparent even when mapping each individuals' movement data over satellite imagery (Fig. 2). Bobcats strongly avoided highly transformed landscapes — even those that remained largely vegetated. Specifically, bobcats avoided row crops ($\beta = -0.55$), eucalyptus ($\beta = -0.26$), and orchards ($\beta = -0.15$). Bobcats selected for proximity to

water ($\beta = -0.49$ [the coefficient is negative because the covariate is calculated as the distance from water]) and steeper slopes ($\beta = 0.18$). Bobcats selected against high density housing (≥ 5 houses/ha; $\beta = -0.18$).

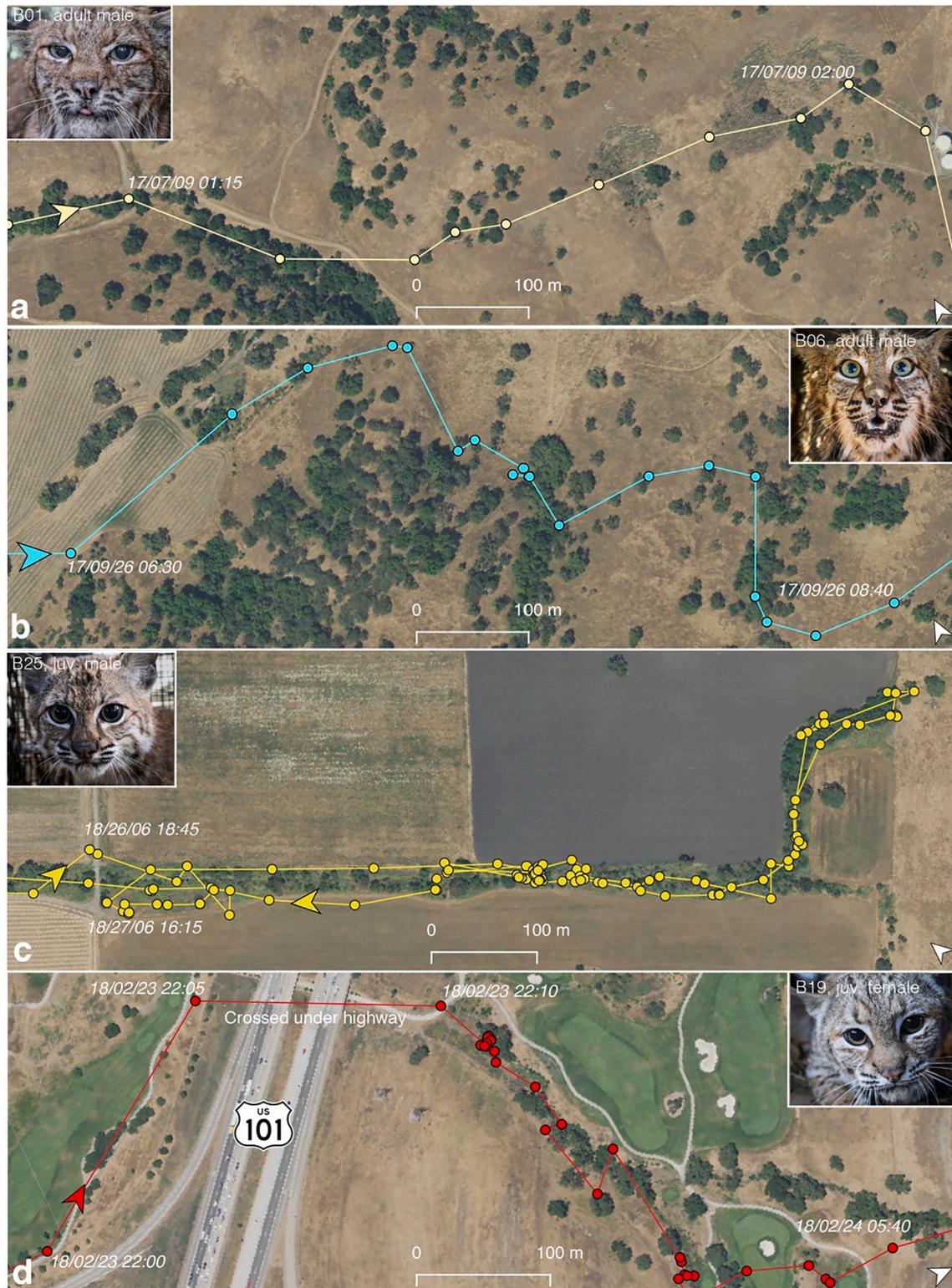


Fig. 2. Bobcat movement is evident at the scale of a single tree or shrub. A–B) Approximately 1 h of 5-min interval data for adult males. C) Approximately 22 h of 5-min data for a juvenile male. D) Juvenile female crosses under Highway 101 following sparse vegetation.

3.3. Functional responses: housing and vegetation

For the combined study areas, and for Coyote Valley specifically, we found no support for a functional response to housing. Coyote Valley's dense, multifamily residential development was impermeable to bobcats with the exception of three juveniles that took single forays into these areas. In Aromas Hills, a clear functional response emerged (Fig. 3a). Probability of selection increased from 0 to 0.95 houses/ha (i.e. between 2 and 3 houses within 100 m; knot = 0.4 standard deviations above the mean; Δ QIC of -8.15), after which the probability of avoidance increased as housing density increased.

Bobcats across both study areas exhibited a strong functional response to vegetation (Δ QIC = -1216.0 ; Fig. 3b). The relative probability of selection increased for vegetation cover (on the scale of one acre) as the proportion of vegetation increased, saturating at 69% (0.47 standard deviations above the mean), and thereafter, declining gently.

3.4. Roads: permeability and features of hotspots and barriers

We documented 29 bobcats (22 adults, 13 juveniles, 19 males, 16 females) cross arterial roads 3333 times (Supplemental Tables S4–S5). The majority (80%) of crossings occurred at night. Adults crossed more frequently than juveniles (adults: 0.85 crossings/day; juveniles: 0.52 crossings/day), while females crossed more frequently than males (females: 0.86 crossings/day; males: 0.58 crossings/day). Seventy-nine percent of crossings were across secondary roads, while 21% were across Highway 101. We did not detect road avoidance using habitat selection models. We identified 14 road-crossing hotspots: 10 in Coyote Valley and four in Aromas Hills. Five hotspots crossed Highway 101. Nine crossed secondary roads. All crossing hotspots (Fig. 4a–c) shared certain features. They were in topographical depressions, often in drainages or stream beds (12/14), and in every case, trees or shrubs flanked both sides of the road. Four crossing hotspots across Highway 101 were characterized by extensive overpasses across riparian areas (that bobcats could cross under). In the remaining hotspot, a large culvert was present.

While biologists did not specifically record whether cats passed under or over roads, we assume animals used this infrastructure in the majority of cases (e.g. Fig. 2d). Along stretches of Highway 101 that did not have crossing infrastructure, particularly an 8 km stretch in Aromas Hills, we did not document attempted crossings by collared bobcats and rarely road mortalities. Two Aromas Hills bobcats moved directly adjacent to the highway along the stretch absent of crossing infrastructure, but the highway delineated the boundary of their movements.

The deadliest and least-crossed arterial road was Monterey Road

(Fig. 4d) although this road had only 10.7% the average daily traffic volume as the adjacent primary road, Highway 101. However, Monterey Road characterized by a lack of potential crossing infrastructure, frequent wildlife road mortalities, and a prominent concrete median topped with mesh wire fencing (~ 1.5 m tall). Crossing Monterey Road accounted for only 1.6% of total successful crossing events, but seven of thirteen road mortalities in Coyote Valley. Of the twenty-five Coyote Valley bobcats, all were captured < 3.2 km from Monterey Road (median = 792 m). Yet we observed only five individuals successfully cross the road, three of which were eventually killed on the road. Unexpectedly, Monterey Road formed a stronger movement barrier for bobcats than Highway 101.

3.5. Mortality and poisons

We documented 28 bobcat mortalities (18 Coyote Valley, 10 Aromas Hills; 9 GPS-collared, 19 opportunistic; Supplemental Tables S3, S5). Of the nine GPS-collared bobcats, four were hit by cars, two died of notoedric mange, two were predated, and one was attacked by domestic dogs. Of the opportunistic mortalities, 13 were hit by cars and four died of mange. Although the majority (68%) of the mortalities were detected opportunistically (and thus source of mortality potentially skewed by detection bias), in Coyote Valley, vehicle collision was the leading source of mortality ($n = 12$) while in Aromas Hills, mange was the leading source of mortality ($n = 5$).

Bobcat death due to notoedric mange has previously been linked with secondary anticoagulant rodenticide (AR) exposure (Riley et al., 2007). Therefore, we assessed AR exposure in bobcats when possible. We recovered livers from 18 individuals and detected exposure to ARs in 17 (94.4%) of these individuals tested. Bobcats, like other predatory species, are secondarily exposed to these globally ubiquitous poisons via consuming poisoned prey (Hindmarch et al., 2018; Riley et al., 2007; Serieys et al., 2015). Five different commercial compounds were detected — second-generation brodifacoum, bromadiolone, and difethialone, and first-generation diphacinone and chlorophacinone. Individuals were exposed to 1–5 compounds (median = 3.5; Supplementary Table S4), indicating repeat exposure events because AR baits are formulated with single compounds. The total concentrations detected ranged from “level of detection” (LOD)—1.82 ppm, with a mean concentration of 0.37 ppm (median = 0.15, SD = 0.52). In contrast to previous liver-based bobcat studies (Riley et al., 2007; Serieys et al., 2015), we most frequently detected first-generation compounds diphacinone and chlorophacinone, and diphacinone specifically was present in every AR-positive bobcat, while chlorophacinone was detected in 78% of individuals ($n = 14$; mean = 0.02 ppm). The mean concentration

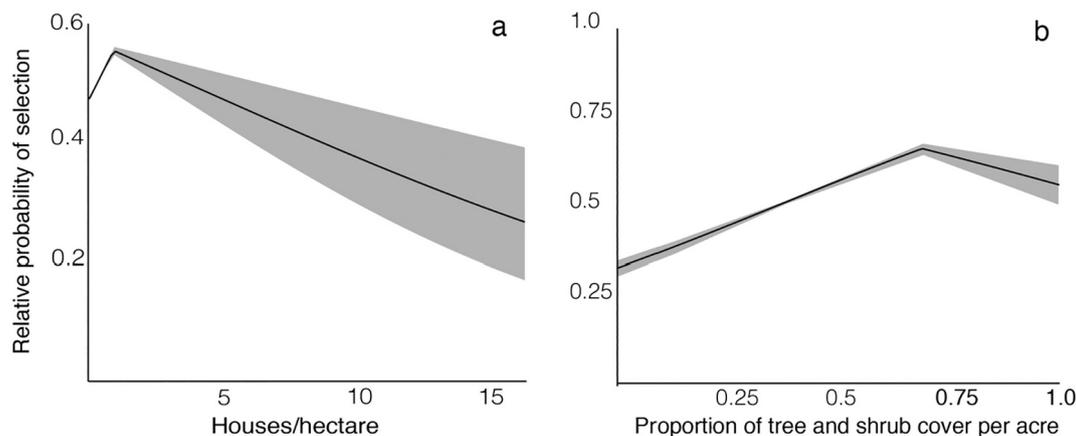


Fig. 3. Functional responses to housing density and vegetation. a) Relative probability of selecting low housing density increases steeply up to one house/ha. The relative probability of selecting for areas without housing is approximately equivalent to the relative probability of selecting for housing densities of 5 houses/ha. b) Relative probability of selecting habitat with cover (composite tree and shrub) increases as vegetation increases.

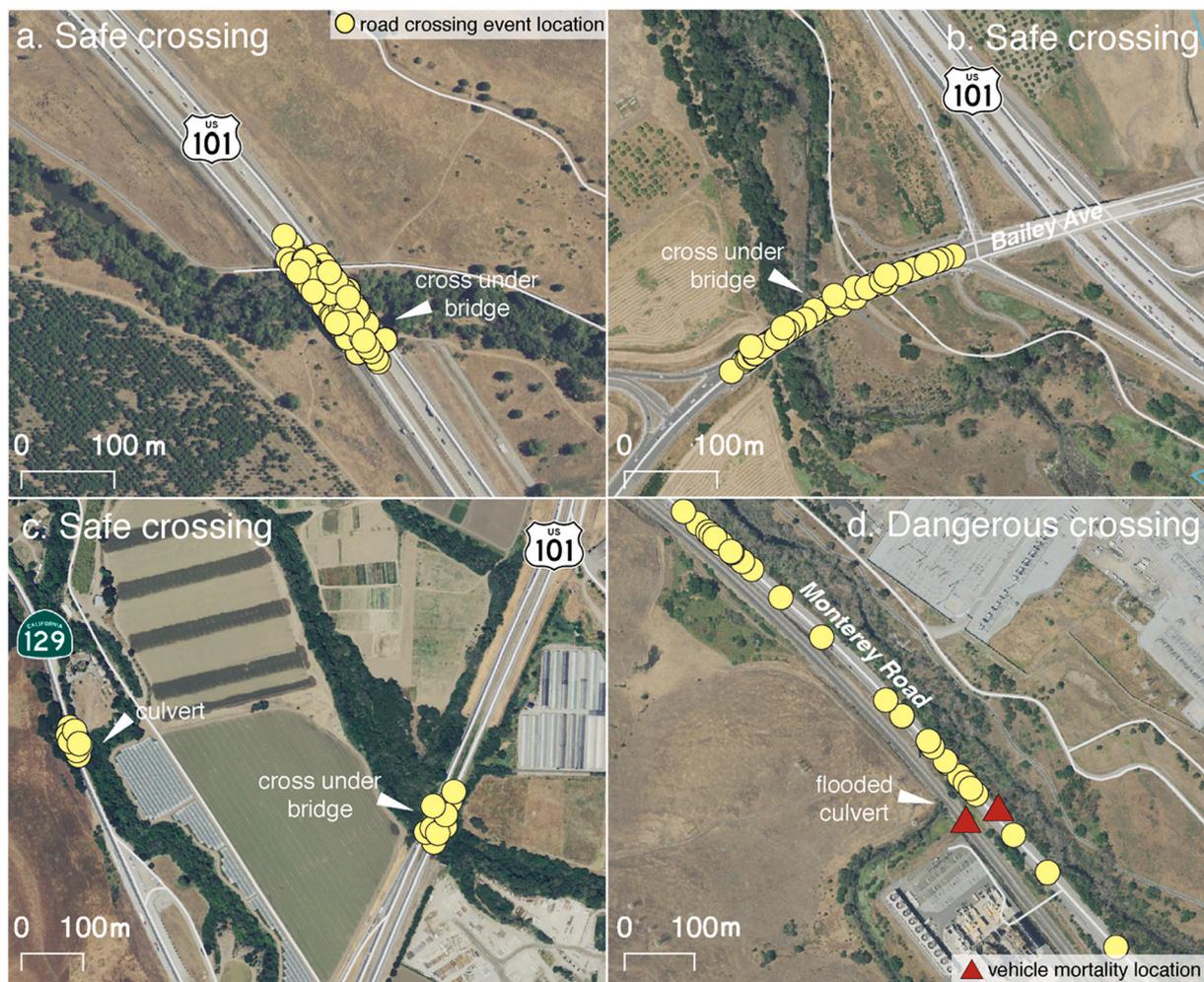


Fig. 4. Road-crossing hotspots (a–c) and Monterey Road (d). Individual road-crossing events documented from unique bobcats are represented by a yellow circle. High resolution (5-min) relocation data were used to identify the date, time, and location of road-crossing events for each individual that crossed arterial roads. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

of diphacinone (mean = 0.15 ppm) was also relatively high compared with other compounds. With respect to second-generation compounds, 11 bobcats were exposed to brodifacoum (mean = 0.03 ppm), nine to bromadiolone (mean = 0.17 ppm), and three to difethialone (all 'LOD'). For six bobcats that died of mange, we detected 36% greater total concentration of ARs (mean = 0.42 ppm) as for bobcats that died of other causes (mean = 0.31 ppm).

4. Discussion

We used advanced bio-logging technology to collect high-resolution bobcat movement observations in a human-modified landscape to provide rapid data-based recommendations for preserving “last-chance” corridors linking the Santa Cruz Mountains wildlife community with those in adjacent ranges. By using both 5-min and 3-h resolution movement data, we identified unexpected trends, such as the critical importance of individual trees and shrubs in promoting structural connectivity, whether within habitat patches or over roads. We observed varying degrees of permeability in matrices in the study area, where, for example, high-density housing development was impermeable and avoided, while low-density housing was not only permeable to bobcats, but even attractive and positively selected. Yet, complementing our movement data with mortality data demonstrated a pervasive, but an easily overlooked edge effect—nontarget rat poison exposure. Indiscriminate poisoning of nontarget wildlife is likely important

impediment to functional connectivity for numerous species beyond our focal bobcats. By integrating these diverse data on habitat selection, road interactions, and edge effects, this study reinforces that the maintenance of structural connectivity alone is insufficient for preserving corridors that abet wildlife conservation in fragmented landscapes.

4.1. Selection for complex vegetation

In coastal sage scrub and oak woodland savannah habitat, native vegetation that adds complexity to the landscape was the most critical natural component of structural connectivity. Bobcat selection for natural vegetation was evident at the scale of a single tree or shrub. As previously observed in bobcats (Abouelezz et al., 2018; Litvaitis et al., 2015; Reed et al., 2016) and other ecologically-similar carnivores such as Eurasian lynx (*Lynx lynx*; Bouyer et al., 2015), leopards (*Panthera pardus*; Fattedbert et al., 2015), and pumas (*Puma concolor*; Burdett et al., 2010), bobcats strongly avoided areas simplified by monoculture (row crops and orchards) and opted instead for the more complex structure of natural vegetation. More complex vegetation offers better cover for stalking prey (Hopcraft et al., 2005; Smith et al., 2019a). Unexpectedly, vegetated riparian corridors <25 m wide provided sufficient cover for bobcats (of all demographics) to move through otherwise barren, row crop fields, an essential element to landscape connectivity in the fragmented landscape. We detected multiple juveniles residing exclusively in these narrow swaths of vegetation (Fig. 2c), suggesting that these

linear sections of vegetation are important to functional connectivity.

4.2. Contrasting permeability of matrix infrastructure

Studies have repeatedly found that large felids will move through low-density housing (Burdett et al., 2010; Lewis et al., 2015; Smith et al., 2019b) but in Aromas Hills, such conditions actually proved preferential to bobcats. In contrast, high-density residential areas were impermeable with exception to three juveniles that took single forays into densely developed areas. Possible explanations for selection of low-density residential areas could be that landscaping creates more complex, better-irrigated habitat, or that bobcats are attracted to synanthropic prey near houses. In southern California, bobcats selected urban areas for nighttime foraging of rabbits (*Sylvilagus* spp.; Dunagan et al., 2019). While low-density residential areas can offer increased resources, these areas may represent ecological traps (Battin, 2004) because bobcats are more likely to be exposed to rodenticides in residential areas than in unaltered habitat (Serieys et al., 2015). The characteristics of matrices can thus have dichotomous effects on habitat selection with repercussions for functional connectivity if the resources bobcats seek are poisoned.

The influence of roads revealed the nuanced effects of matrix infrastructure versus activity in mediating connectivity. Roads are ubiquitous and affect the ability of all wildlife species to live and move within human-dominated landscapes (Clark et al., 2015; Kramer-Schadt et al., 2004; Poessel et al., 2014). However, it is often impossible to disentangle the barrier effects of the structural features of roads from those associated with traffic on those roads (Riley et al., 2014a). We found that crossing hotspots occurred where complex vegetation (trees or shrubs) intersected the road rather than where traffic was light. Highway 101 was a strong impediment to movement in Aromas Hills (particularly along an 8 km stretch that did not have any available safe-crossing infrastructure) while Coyote Valley bobcats readily crossed the freeway. In Aromas Hills, only two collared individuals found two safe-crossing areas. In Coyote Valley, 11 bobcats found at least nine culverts or underpasses that provided safe-crossing locations (three of which were crossing hotspots) without encountering vehicles. The Highway 101 bridges and culverts in Coyote Valley typically occur where riparian strips intersect the highway, such that natural vegetation funneled bobcats toward features that offer safe crossing for numerous species (Grilo et al., 2008; Smith et al., 2015).

In contrast, Monterey Road bears substantially less traffic but was a stronger barrier to movement and killed more bobcats. We identified a single culvert that was always flooded, which discourages carnivores from passing through (Tigas et al., 2002). When wildlife attempt to cross over the road, they encounter a concrete median topped with chain-link fencing. The combination of forcing bobcats to cross through traffic and erecting an obstacle half-way across proved particularly deadly.

4.3. Edge effects as threats to functional connectivity

The impacts of habitat fragmentation extend beyond the boundaries of anthropogenic development and can cryptically reduce fitness (Flesch, 2017) and increase mortality (Benson et al., 2019) thereby constraining functional connectivity. As previously documented elsewhere for bobcats and wildlife in North America generally, human activities, and specifically vehicles, were the predominant source of mortality we documented (Hill et al., 2019; Serieys et al., 2015). Secondly, notoedric mange, which has been linked with AR exposure in 99% of investigated cases in California bobcats (Serieys et al., 2015), was another prominent source of mortality; in Aromas Hills, it even eclipsed vehicle collisions as the leading source of mortality. We were unable to statistically model cause-specific mortality and survival on our mortality data given that: i) our sample size of tagged mortalities was low, and ii) untagged opportunistic mortalities may bias our findings.

Bobcat deaths from vehicles and mange in our study areas attest to

the multiple harmful edge effects wildlife experience in human-dominated landscapes (Hill et al., 2019). The prevalence of mortality due to notoedric mange associated with rodenticide exposure was unexpected and demonstrates that in vulnerable landscapes, cryptic threats to functional connectivity cannot be overlooked. The deadly spillover of common pesticides into natural populations is more prevalent than frequently recognized because it can easily go undetected (Berny, 2007). Rodenticide exposure for sampled bobcats was high (94%) even though the California Department of Pesticide Regulation restricted the use of second-generation anticoagulant rodenticides in 2014 to reduce harm to wildlife (section 6471, Title 3, California Code of Regulations, www.cdpr.ca.gov). The observed prevalence was consistent with that found in a more extensive study of bobcats (88% of livers, n = 172) in southern California prior to these new regulations (Serieys et al., 2015). Clearly, these restrictions were insufficient to protect our study population from ongoing harm. While overall exposure rates were similar between the two studies, one critical difference is that we detected first-generation ARs (diphacinone) in every sample while the prior study recorded first-generation ARs in fewer than half of all exposed bobcats. This suggests that end users reacted to the new regulations not by reducing the use of ARs but by substituting first-generation ARs for the restricted ones. Exposure was likely higher in Aromas Hills than in Coyote Valley due to intensive application of ARs in agricultural areas, which are far more extensive in the former. Even if bobcats avoid crop fields and orchards areas specifically, poisoned prey can travel to adjacent natural areas or riparian corridors that bobcats favor.

Anticoagulants, and diphacinone in particular, have been linked with immune dysfunction and altered gene expression in bobcats (Fraser et al., 2018; Serieys et al., 2018), and these consequences explain increased mange vulnerability. The altered immune function and gene expression associated with ARs highlights the complex nature of edge effects, and that certain edge effects can indirectly kill wildlife through altered immunity and disease dynamics. Yet negative effects of ARs are not limited to bobcats. Just in California, ARs have directly killed predators that include bobcats, pumas (Benson et al., 2019), coyotes (Riley et al., 2003), gray foxes (*Urocyon cinereoargenteus*, Riley, NPS Unpubl. data), San Joaquin kit foxes (*Vulpes macrotis*; Cypher et al., 2014), fishers (*Pekania pennanti*; Gabriel et al., 2012), barn owls (*Tyto alba*), Cooper's hawks (*Accipiter cooperii*), great horned owls (*Bubo virginianus*), red-shouldered hawks (*Buteo lineatus*), striped skunks (*Mephitis mephitis*), and Turkey vultures (*Cathartes aura*; California Fish and Wildlife Unpubl. data). Wildlife exposure to pesticides demands intervention if managers want to maintain or restore ecological connectivity near the wildland-urban or wildland-agricultural interface.

4.4. Conservation and management implications

Our movement data have already guided parcel acquisition of a key habitat patch in Coyote Valley, thus successfully aiding in restoring one "last-chance" corridor. Our functional response and habitat selection analyses for vegetation indicates that in barren agricultural fields that undergo rehabilitation, faster growing shrubs (as opposed to slow-growing oak trees) can be used to more quickly add complex vegetation to the landscape and thus rapidly restore a matrix component to natural habitat. Our study thus offers a compelling example of how rigorous data collection and analysis of animal behavior can focus highly targeted conservation actions. Moving forward, by recognizing the effects of vegetation and infrastructure on connectivity, considerable capacity exists to reduce mortality and to restore and preserve movement corridors, and corresponding gene flow within Coyote Valley and Aromas Hills. The lessons learned here apply more broadly to bobcats and other highly mobile terrestrial predators across the urban-wildland interface of North America.

The findings that anthropogenic and natural landscape features can exert strong influence on bobcat movement are a cause for both concern and optimism. Although matrix components that include crops, roads,

and medium-high-density housing impede bobcat movement, culverts, low-density housing, and the restoration of trees and shrubs can mitigate these effects even in broadly-transformed landscapes. Corridors can be very narrow so long as they contain shrubs and trees in addition to grass. Yet preserving structural connectivity alone will not conserve Santa Cruz Mountains wildlife. Functional connectivity requires healthy, abundant populations to generate fit dispersers (Pulliam, 1988). Exposure to people is poisoning wildlife and bobcat preferential selection of low-density housing and narrow corridors in agricultural fields is potentially luring them into toxic ecological traps. We investigated AR exposure in a single species, but repeatedly, research has found that where one species is affected, others are too (Gabriel et al., 2018; Riley et al., 2007). Further, these poisons threaten numerous endangered species (Benson et al., 2019; Cypher et al., 2014; Gabriel et al., 2012, 2018). Ongoing monitoring, local outreach to encourage reduced AR use, and alternative interventions, such as integrated pest management approaches, are needed to maintain functional connectivity for Santa Cruz Mountains wildlife populations.

Similarly, more must be done to reduce vehicle collisions. Our hotspot analyses elucidate where road-crossing attempts are most likely, facilitating a targeted mitigation approach when prioritizing which culverts to retrofit or maintain as viable crossing structures. Retrofitting or maintaining culverts to prevent standing water could be a relatively simple solution to mitigate mortality. High median barriers were associated with increased mortality; the same barriers on the freeway edges could funnel animals toward available culverts. By bookending “safe-crossing” culverts with natural vegetation, some species may be encouraged to use them (Smith et al., 2015) while clearing vegetation along the roadside at dangerous crossing locations could deter crossing attempts.

Overall, we found substantial scope to reduce edge effects and preserve connectivity between the Santa Cruz Mountains and neighboring ranges even in the face of ongoing development. Specific actions to preserve these links beyond restoration of “last-chance” corridors are needed however; passivity will not succeed.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Tracking data are available via the Movebank Data Repository (<http://www.movebank.org>).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2020.108930>.

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