

Sensitivity of landscape resistance estimates based on point selection functions to scale and behavioral state: pumas as a case study

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Abstract Estimating landscape resistance to animal movement is the foundation for connectivity modeling, and resource selection functions based on point data are commonly used to empirically estimate resistance. In this study, we used GPS data points acquired at 5-min intervals from radiocollared pumas in southern California to model context-dependent point selection functions. We used mixed-effects conditional logistic regression models that incorporate a paired used/available design to examine the sensitivity of point

selection functions to the scale of available habitat and to the behavioral state of individual animals. We compared parameter estimates, model performance, and resistance estimates across 37 scales of available habitat, from 250 to 10,000 m, and two behavioral states, resource use and movement. Point selection functions and resistance estimates were sensitive to the chosen scale of the analysis. Multiple characteristic scales were found across our predictor variables, indicating that pumas in the study area are responding at different scales to different landscape features and that multi-scale models may be more appropriate. Additionally, point selection functions and resistance estimates were sensitive to behavioral state; specifically, pumas engaged in resource use behavior had an opposite selection response to some land cover types than pumas engaged in movement behavior. We recommend examining a continuum of scales and behavioral states when using point selection functions to estimate resistance.

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Introduction

Estimating landscape resistance to animal movement is the foundation for connectivity modeling and the identification of conservation corridors. In this

context, ‘resistance’ represents the willingness of an organism to cross a particular environment, the physiological cost of moving through a particular environment, the reduction in survival moving through a particular environment, or an integration of all these factors. As reviewed in Zeller et al. (2012), methods for empirically estimating resistance to movement use either point locations collected independently or extracted from telemetry data, steps or paths derived from telemetry data, or genetic markers. Typically, when points, steps, or paths are employed, a resource selection function is developed and then used to predict probability of use across the area of interest. The inverse of this probability is then used as an estimate of resistance. The assumption here is that low resistance areas are preferred while high resistance areas are avoided.

Resource selection functions based on points, or point selection functions (PSFs), are widely used to analyze wildlife-habitat relationships (Boyce et al. 2002) and, although PSFs do not explicitly represent movement, they are one of the most common ways to empirically estimate resistance to movement for a species (Zeller et al. 2012). At the core of any PSF, and resource selection functions in general, is a ‘used’ versus ‘available’ design where ‘preferred’ habitats are used in greater proportions than their availability and vice versa (Manly et al. 2002). Use of PSFs in ecology have traditionally been based on one or two scales of analysis (Wheatley and Johnson 2009), and inferences are made across all data points regardless of the behavioral state of an individual. However, PSFs, particularly those based on GPS telemetry data, have the potential for examining a range of scales and behavioral states to model increasingly realistic relationships between individuals and their environments through ‘context-dependent’ modeling.

Context-dependent modeling acknowledges that an animal’s interaction with its environment depends on its location, its surroundings, and its behavioral state (Dalziel et al. 2008), and thus accounts for the landscape and behavioral context of an individual. A simple, but effective way to model context-dependent PSFs is to use conditional logistic regression. Conditional logistic regression, also called case-controlled or paired logistic regression, pairs each used point or area with a relevant available area (Compton et al. 2002). The available area is often defined based on the acquisition interval of GPS

collars. For example, with a 1-h acquisition interval, the extent of the available area is defined as some upper quantile of the distribution of step lengths at 1-h (Boyce 2006). However, in conditional logistic regression, the chosen extent of available habitat also determines the scale of the analysis (ignoring grain size), and the collar acquisition interval is rarely chosen with a priori knowledge of the scales at which a species responds most strongly to its environment (following Holland et al. (2004), we use the term ‘characteristic scale’ to reference this strongest scale of response). Furthermore, there may be different characteristic scales for each habitat type or landscape feature. Therefore, using a single scale may result in inaccurate estimates of selection and resistance (Wheatley 2010; Norththrup et al. 2013) and a continuum of scales should be examined so as to capture the true characteristic scale(s). If multiple characteristic scales are found, a multi-scale model may be more appropriate to model context-dependent resource selection (Meyer and Thuiller 2006; DeCesare et al. 2012; Martin and Fahrig 2012).

Historically, PSFs were modeled using all data points, regardless of the behavior of the animal at the time the points were collected. However, it is reasonable to assume that selection of habitat for feeding or denning, for example, may be different than selection of habitat for movement between resource patches. Combining data from different behavioral states in a single analysis almost certainly biases inferences about resource selection and estimates of landscape resistance. Fortunately, the availability of high resolution GPS data now allows for approaches that incorporate different behavioral states. Distance, or rate of movement, and turning angle have been the primary criteria used to discern between two main behavioral states, variously defined as active versus resting (Squires et al. 2013), or static versus traveling (Dickson et al. 2005). While a few studies have begun to compare resource selection during different behavioral states (e.g. Dickson et al. 2005; Squires et al. 2013), there are no comparative studies on how behavior influences resistance estimates.

We investigated the influence of scale and behavioral state on context-dependent PSFs and the resistance estimates derived from these PSFs using GPS collar data from pumas (*Puma concolor*) in southern California. The GPS collars were programmed at a

high sampling intensity (5-min intervals), allowing us to empirically examine a continuum of scales, from a very fine scale to the scale of a typical home range for a puma in the region (Dickson and Beier 2002). First, we hypothesized that PSF inference would be sensitive to the extent of available habitat and that pumas would have different characteristic scales for different land cover types. Second, we hypothesized that using all data points or partitioning points based on behavioral state (resource use versus movement) would influence interpretation of how pumas were responding to their environment. Third, we hypothesized that resistance estimates based on context-dependent PSFs would be sensitive to both scale and behavioral state. Fourth, we hypothesized that a multi-scale model would be more appropriate for modeling resistance to movement than a single-scale model. Lastly, we hypothesized that results from a context-independent model would differ from the results of our context-dependent models, both in model performance and estimates of resistance.

Methods

Study area and data collection

The study area encompassed 4,089 km² in the Santa Ana Mountains and surrounding lowlands in southern California, including portions of Orange County, Riverside County and San Diego County. The Santa Ana mountains are a coastal range with elevation ranging from sea level to 1,734 m and a Mediterranean climate defined by hot dry summers and mild wetter winters.

Eight pumas (five female and three male) were collared between October 2011 and February 2012 and were fit with Lotek 4400 S GPS collars programmed to acquire locational fixes every 5 min (Lotek Wireless Inc., Canada). Collar duration ranged from 12 to 71 days (median = 24). Long-term collar accuracy from manufacturer tests is 5 to 10 m, though vegetation types and topographical conditions may decrease accuracy (Chang, personal communication). Therefore, two-dimensional fixes with a PDOP > 5 were removed to avoid the use of data that may have large spatial errors, as recommended by Lewis et al. (2007), resulting in a mean data loss of 2.96 %. Missed fixes from failure of the collar to record a GPS location resulted in a mean data loss of 15.87 %, bringing our total mean data loss to

18.83 %. Citing various studies, Frair et al. (2010) have cautioned that coefficients of selection become statistically different when there is a 10–25 % loss of data from positional or habitat bias. However, our losses were relatively consistent across individuals and if biases were introduced, they were likely uniform in nature. The final data set consisted of 61,115 fixes across the eight individuals (range 1,650–20,433; median = 5,846). Due to the low number of individuals, sexes were pooled in the analyses, and a mixed-effects model was used to account for inter-individual differences (see “[Statistical analysis](#)” section).

We used land cover types from the California Wildlife Habitat Relationship database as independent variables in our PSFs. The Wildlife Habitat Relationship data were obtained from the CalVeg geospatial data set (USDA Forest Service 2007) in vector format at the 1:24,000 scale, which we rasterized at a 30-m resolution. There were 25 mapped land cover types present in the study area, but many types had very low occurrence (<1 %). In order to avoid issues with data sufficiency, we aggregated these 25 types into nine classes based on provided descriptions from the California Department of Fish and Game (1988). The final land cover classes and their percentages of the study area were as follows: chaparral (45 %), urban (19 %), coastal scrub (14 %), annual grassland (6 %), coastal oak woodlands (5 %), agriculture (5 %), riparian areas (3 %), perennial grassland (2 %), and naturally barren or open areas (1 %).

Used and available habitat

All data analysis was performed using R software (R Core Team 2013). Our used and available habitat were defined in a paired design to allow for the use of conditional logistic regression (Compton et al. 2002). For each telemetry point, we designated ‘used’ habitat as a 30-m fixed-width buffer around the pixel where a point was located. We calculated the proportions of land cover types across these nine pixels. This definition of used habitat allowed us to meet two goals: (1) it provided a buffer that helped to account for small locational errors in the telemetry points (Rettie and McLoughlin 1999), and (2) it allowed us to incorporate the immediate environment around each point into the area of used habitat. The latter goal was based on the assumption that an individual may not only be selecting habitat at the used pixel, but may be

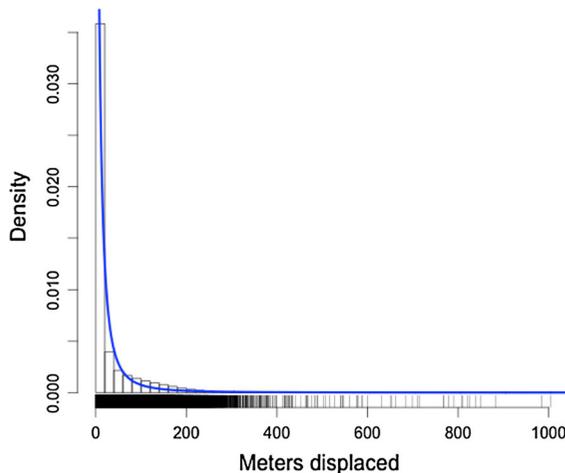


Fig. 1 Distribution of displacement distances and fitted Pareto distribution (*blue line*) at the 5-min acquisition interval. Displacement distances were calculated as the *straight-line* distance between consecutive points. Pareto distributions were fit to the data at each of our 37 acquisition intervals. (Color figure online)

selecting a particular pixel because of its immediate surroundings. This may be especially important for puma that are known to utilize edge habitats (Laundré and Hernández 2003; Laundré and Loxterman 2007).

‘Available’ habitat for each used point was defined as follows. We calculated the straight-line distances between consecutive points, which gave us a distribution of displacement distances. Breaks in the data due to poor fixes or missing fixes were taken into account in the calculation of these distances. We then fit a generalized Pareto distribution to the empirical distribution of displacement distances using the POT package (Ribetet 2012). The Pareto distribution fit the empirical distribution well due to its characteristic steep curve and long right tail (Fig. 1). We then placed a Pareto kernel over each used point, thresholded this kernel at the 97.5 percentile of the Pareto distribution or the maximum observed displacement distance, whichever was smaller, calculated the intensity of each land cover type, and converted these intensities to proportions. Our approach allowed us to census the entirety of land cover types within the available area in their correct proportions, as opposed to what is commonly done in PSFs where a random sample of points are selected within the available area. This alleviates issues with selecting a sample size for available points and associated biases in inference (Norththrup et al. 2013). In addition, the use of the

Pareto kernel allowed us to weight land cover within an ecological neighborhood (*sensu* Addicott et al. 1987) around each used point based on probability of use.

To explore the effect of acquisition interval and associated extent of available habitat on PSF inference and estimates of resistance, we implemented 36 additional extents as defined by acquisition intervals from 10- to 360-min at 10-min intervals. For each new acquisition interval, we calculated the displacement distances by subsetting the 5-min data at that interval and calculating the straight-line distance between consecutive points. We then fit a new Pareto distribution to each empirical distribution, defined a maximum threshold and calculated the proportion of available habitat within the Pareto kernel as described above (online Appendix 1). It is important to note here that all of the original 5-min points were used in the PSF analyses for each of our 37 scales; the subsetting of points was performed only to acquire the distributions of displacement distances for the additional 36 scales.

GPS collars programmed at a high sampling intensity produce data that are autocorrelated, making it difficult to meet the independence assumption inherent to logistic regression. When this assumption is violated, the standard errors of the parameter estimates may be deflated resulting in inflated type 1 error rates (Legendre 1993) and the parameter estimates themselves may or may not be biased (Dormann et al. 2007; Hawkins et al. 2007). However, because we were primarily concerned with the predictive ability of the models, and were not testing the significance of the parameters in a traditional hypothesis testing framework, we opted not to alter our data structure or our models to account for autocorrelation in our data (though see “Behavioral states” section where some correlation may be addressed in our parameterization of resource use points).

Behavioral states

We distinguished between two behavioral states: (1) resource use, and (2) movement. A static or slow and tortuous trajectory more likely reflected resource use, such as acquiring food and seeking and using day beds, than a faster and more direct trajectory, which more likely reflected purposeful movement through the landscape between resource use patches. Because we did not know, a priori, if a telemetry point was

Table 1 Behavioral states, alternative definitions of behavioral states, and associated attributes used in the PSF analyses

behavioral state	Alternative definition	Distance threshold (m)	Number of data points	Number of clusters
All behaviors		0	61,115	–
Movement	M1	12.5	17,614	–
	M2	25	12,436	–
	M3	50	8,800	–
	M4	100	4,212	–
	M5	200	507	–
Resource use	RU1	200	60,608	268
	RU2	100	56,903	1,382
	RU3	50	52,315	1,933
	RU4	25	48,679	2,381
	RU5	12.5	43,501	3,892

Consecutive resource use points at or below the threshold distance were assigned to the same resource use cluster, and the points within each cluster were down-weighted so that each cluster received an effective weight of one. Movement points were any points above the threshold distance and each point had a weight of one

recorded during a movement or resource use behavior, we used a range of definitions for each behavioral state based on the distances between locations. Distance thresholds were defined along a geometric progression from 12.5 to 200 m with a common ratio of two (Table 1). The largest distance threshold was capped at 200 m due to an insufficient number of data points beyond this distance. At the 12.5 m distance threshold, any point 12.5 m or closer to the previous point was identified as a resource use point and any point further than 12.5 m from the previous point was identified as a movement point. Consecutive resource use points within the 12.5-m threshold distance of each other were considered part of the same resource use cluster. This same procedure was performed for each distance threshold.

Our range of definitions for each behavioral state ran the continuum from least conservative to most conservative. The 12.5-m distance threshold required resource use points to be very close to one another and the definition of resource use at this threshold likely did not include any true movement points. Therefore, this was considered our most conservative definition of resource use. Conversely, the 12.5-m distance

threshold was considered our least conservative definition for movement since there were likely many true resource use points included with the designated movement points. At the opposite end of our continuum, 200 m, the movement points were considered to be relatively pure. For the remainder of the paper we will refer to resource use and movement points along this continuum as follows: RU1 and M1 are the resource use and movement points, respectively, based on the least conservative definition for each behavioral state (RU = 200 m; M = 12.5 m), whereas RU5 and M5 are based on the most conservative definitions (RU = 12.5 m; M = 200 m).

Statistical analysis

At each scale and for all definitions of each behavioral state, as well as for all points regardless of behavioral state, we conducted a conditional mixed-effects logistic regression with individual cat as a random effect. We performed both simple regressions for each land cover type and multiple regressions including all land cover types. For the multiple regressions, we used the land cover type with the weakest effect in the simple regressions as the reference class. In conditional logistic regression, there is no model intercept, therefore the reference land cover type was simply omitted from the analysis. We confirmed that correlation among our predictor variables was relatively low prior to performing the multiple regressions (maximum Pearson correlation coefficient = -0.48). We also created a multi-scale model using the characteristic scale for each land cover type as identified from the simple regressions (see below).

We used the `lmer` (or `glmer`) function in the `lme4` package (v. 0.999999-2, Bates et al. 2013) for performing conditional mixed-effects logistic regression in R. The use of `lme4` requires the differences between the used and available for each variable to be calculated at each point prior to analysis and that the response variable equals one for each data point [as described in Agresti (2002)]. The full model specification in R is provided in online Appendix 2. Online Appendix 2 also provides a discussion of other options for conditional mixed-effects logistic regression in R along with an example of the R code used to conduct this analysis.

For the movement data, each point was given equal weight in our models. For the resource use data, each

point in a cluster was down-weighted by its proportional contribution to that cluster. For example, in a cluster with 10 points, each point was assigned a weight of 0.1 and thus each cluster, regardless of the number of points, received an effective weight of one.

We defined the characteristic scale for each land cover type as the scale with the largest absolute regression coefficient and/or largest deviation from an odds ratio of one. To evaluate the predictive performance of the models, we performed a tenfold cross-validation using the methods recommended by Johnson et al. (2006). These methods are based on the Hosmer–Lemeshow approach, but are adapted for use with RSFs. For each model, we calculated the utilization value for each RSF bin using the Pareto kernel that corresponded to the extent of available for that model (results were similar when we used a uniform kernel). We quantified predictive performance of the models using Lin's (1989) concordance correlation coefficient (CCC). For a good model, the predicted observations should fall close to the expected observations on a line originating at 0 with a slope of 1 (Johnson et al. 2006). The CCC statistic measures how correlated two points are based on their deviance from this 45-degree line. We based the interpretation of results on the square of the CCC statistic.

To determine if results from context-dependent models differ from context-independent models, we focused on the multi-scale models since we assumed they might be more appropriate than the single-scale models. To derive the context-independent model, we ran a mixed-effects logistic regression in an unpaired framework using lmer with all data points. We compared model performance amongst our context-dependent multi-scale models and the context-independent multi-scale model.

Estimation of resistance

Resistance estimates from PSFs are typically calculated by taking the inverse of the predicted probability of presence. These estimates are often truncated at some upper value or re-scaled to a range, say from 1 to 10 or 1 to 100 (e.g., Ferreras 2001; Pullinger and Johnson 2010). Truncation and rescaling may alter the relative relationships between resistance estimates by introducing unnecessary subjectivity. To avoid this subjectivity, we used the inverse of the predicted probability of presence as our resistance estimates

without any data standardizations. Because estimating a complete resistance surface for the full factorial of models was computationally prohibitive, we generated 20,000 random points across the study area, predicted the probability of presence across these points, and used the inverse of these values as our estimates of resistance.

To determine how sensitive resistance estimates were to the choice of scale, we calculated the absolute proportional difference in resistance estimated at each scale from that estimated at the 5-min/250-m scale. Similarly, to determine how sensitive resistance estimates were to behavioral state, we calculated, at each scale, the absolute proportional difference in resistance estimates based on the most conservative definition of each behavioral state (RU5 and M5) from that estimated based on all points and from each other. We explored how different the single-scale estimates of resistance were from the multi-scale estimates by calculating the absolute proportional differences in resistance estimated by each single-scale model from that estimated by the multi-scale model. Finally, we calculated the absolute proportional difference in resistance estimates between our multi-scale context-independent model and our context-dependent models.

Results

Characteristic scales

The simple conditional mixed-effects logistic regression models revealed different characteristic scales among land cover types, including four general patterns of response: (1) a fine-scaled response where the strongest response occurred at the finest scale(s) (e.g., Fig. 2a); (2) a unimodal response where the strongest response occurred at an intermediate scale (e.g., Fig. 2c); (3) an asymptotic threshold response, where the response was weak at fine scales, and became stronger and eventually reached an asymptote as scale increased (e.g., Fig. 2h); and (4) a coarse-scaled response where the strength of response increased with scale without reaching an asymptote (e.g., resource-use curves, Fig. 2e). This last pattern may be due to the true characteristic scale being at a coarser scale than we examined. The multiple regression models showed the same patterns.

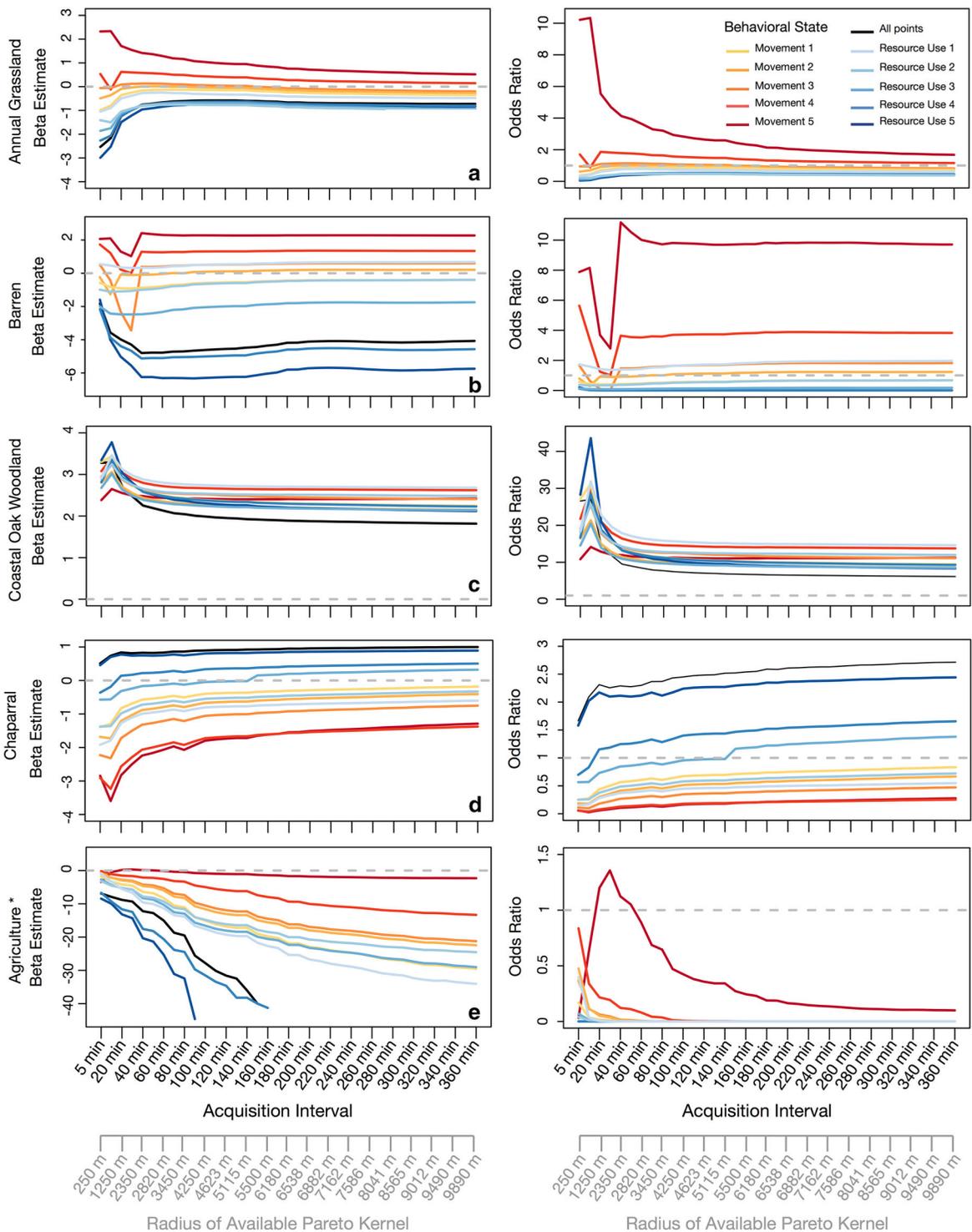


Fig. 2 Beta estimates and odds ratios from simple conditional mixed-effects logistic regressions for each land cover type across scales and behavioral states. Movement and resource use 1 were the least conservative definitions of those behavioral

states and movement and resource use 5 were the most conservative. * For some behavioral states at coarser scales, complete separation was reached in the model solution, which prevented us from estimating beta coefficients and odds ratios

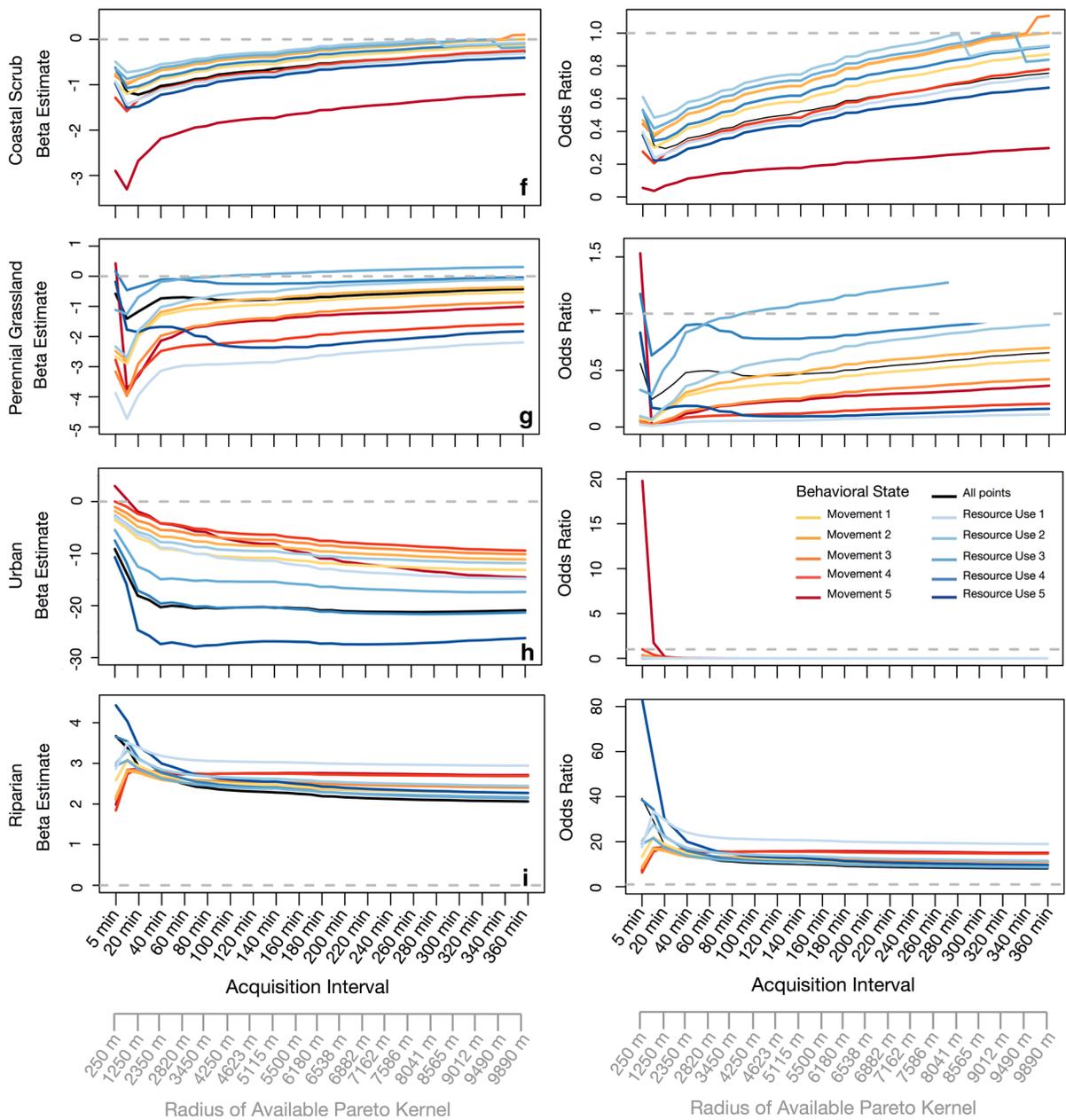


Fig. 2 continued

Despite pronounced differences in effect size, characteristic scale, regardless of preference or avoidance, remained relatively consistent across behavioral states for several land cover types (Fig. 2). For example, across most definitions of each behavioral state, grassland had its strongest effect at the 5-min/250-m scale (Fig. 2a); coastal oak woodland, coastal scrub, and perennial grassland types had their

strongest effects at the 10-min/530-m scale (Fig. 2c, f, g, respectively); barren had its strongest effect at the 40-min/2,350-m scale (Fig. 2b); and agriculture had its strongest effect at the 360-min/9,890-m scale (Fig. 2e). In contrast, some cover types exhibited marked differences in characteristic scale between behavioral states. For example, chaparral exhibited a fine-scale response for all movement states, but an

increasingly coarse-scale response for the more conservative resource use states (Fig. 2d). Conversely, riparian exhibited a fine-scale response for all resource use states, whereas the response was weakest at the finest scales for all movement states (Fig. 2i).

Behavioral states

Behavioral state had a strong but variable influence on the magnitude and nature of the effect attributed to each land cover type. In some cases, the effect was consistently positive (i.e., exhibiting selection for the land cover type) or negative (i.e., exhibiting selection against the land cover type), but the magnitude of effect (i.e., effect size) varied markedly between definitions of the two behavioral states. For example, with agriculture and urban, there was a consistent negative effect and the effect size was greater for the resource use state compared to movement, but the effect size generally increased as the definition of the resource use state became more conservative, whereas it generally decreased as the definition of the movement state became more conservative (Fig. 2e, h). In other cases, the effect was relatively similar across behavioral states (e.g., coastal oak woodland, Fig. 2c, and riparian, Fig. 2i), indicating that selection for or against some land cover types may not be that sensitive to choice of behavioral state. Importantly, in some cases, using movement points versus resource use points led to opposite conclusions regarding habitat selection. For example, with annual grassland, the strength of effect weakened but remained negative as the behavioral state moved along the continuum from the most conservative definition of resource use (RU5) to the least conservative (RU1)(Fig. 2a). However, for the movement states, the response was still weakly negative for the least conservative definitions, but became increasingly positive for the most conservative definitions. We observed a similar pattern of reversal in habitat selection between behavioral states for barren and chaparral land cover types (Fig. 2b, d).

Lastly, models based on all data points (i.e., that did not distinguish between behavioral states) tended to reflect the average relationship observed across the continuum of definitions of the resource use behavioral state (Fig. 2). This was perhaps not too surprising given the disproportionate sample sizes attributed to

resource use versus movement (Table 1), but it has serious implications for the development of resistance surfaces intended to reflect resistance to movement for purposes of connectivity modeling.

Model performance

Regardless of scale or behavioral state, all the models performed reasonably well (Fig. 3). The lowest squared CCC was 0.39, or a CCC of 0.62. In general, the resource use models performed better (mean squared CCC of 0.924) than the movement models (mean squared CCC of 0.820). We also observed an increase in model performance with scale, such that at the coarsest scale all the models (across all behavioral states) had a squared CCC > 0.75. However, both trends were not entirely consistent.

The multi-scale model generally performed as well or better than any single-scale model in modeling selection during resource use or both behaviors combined; however, for movement data, the single-scale models at coarser scales tended to perform better than the multi-scale model (Fig. 3). The squared CCC for the context-independent multi-scale model was 0.564. Therefore, the context-dependent multi-scale models clearly outperformed the context-independent model for all points and all definitions of each behavioral state with the exception of M5, where model performance was roughly equivalent (squared CCC of 0.527).

Sensitivity of resistance estimates

Resistance estimates were highly sensitive to scale. Holding behavioral state constant, proportional differences in resistance ranged from 0 to 245 (or 24,500 %) across scales (Fig. 4). In Fig. 4, each plot represents either all points or a subset of the points selected to represent a particular behavioral state. Within each plot (i.e., holding behavioral state constant), the x-axis represents the extent of available habitat assessed (representing the data acquisition interval and corresponding extent of available) and the y-axis represents various percentiles of the distribution of absolute proportional difference in resistance values between the reference surface (the 5-min/250-m scale as an arbitrary reference) and the surface estimated at each of the remaining scales. The color intensity in each cell represents the magnitude of the

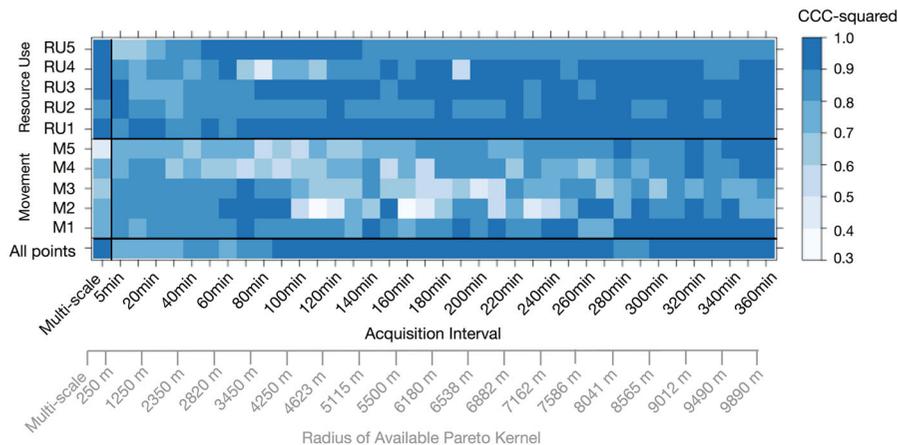


Fig. 3 Squared CCC across scales and behavioral states. A high *squared CCC* indicates good model performance

absolute proportional difference (on a natural log scale) between each surface and the reference surface. This figure reveals two important patterns. First, regardless of scale and behavioral state, the extreme differences in resistance were in the upper 20 % of the distribution, meaning that a relatively small portion of the landscape was most sensitive to the choice of scale. Second, estimates of resistance based on the most conservative definitions of each behavioral state were somewhat more sensitive than those based on the least conservative definitions. Thus, restricting the data to points clearly representing either movement or resource use resulted in estimates of resistance that were highly sensitive to scale.

Resistance estimates were also highly sensitive to behavioral state. Holding scale constant, proportional differences in resistance ranged from 0 to 245 (or 24,500 %) between behavioral states (Fig. 5). The interpretation of Fig. 5 is similar to Fig. 4, but the reference surface is either all points (Fig. 5a, b) or M5 (Fig. 5c). Figure 5 indicates that, across all scales, estimates of resistance differed more between all points and movement points than between all points and resource use points, and in both cases the sensitivity was greatest at the upper quantiles. Also, estimates of resistance based on the most conservative definitions of the two behavioral states were more different from each other than either one was from all points. This pattern was generally consistent across all scales and most evident at the upper quantiles. Considering both scale and behavioral state, we found resistance estimates to be slightly more sensitive to scale than behavioral state.

Given the results from the regression analyses, it seemed intuitive that the multi-scale model would be more appropriate for the PSFs and, thus, for the resistance estimates. Therefore, we evaluated the sensitivity of resistance to the choice of multi-scale versus single-scale models for all points and the data subsets based on the most conservative definitions of movement (M5) and resource use (RU5). As expected, resistance estimates were sensitive to the choice of single- versus multi-scale modeling approaches regardless of data subset (Fig. 6). The greatest differences in estimates of resistance were between the multi-scale model and the finer single-scale models and at the upper quantiles. In addition, estimates of resistance for the movement points were more sensitive than either all points or the resource use points.

Lastly, we compared resistance estimates between the multi-scale context-independent model and the multi-scale context-dependent model for all points, M5 and RU5, and observed that resistance estimates were sensitive to whether context-dependent or -independent inference was used. As seen in the other resistance results, differences in resistance estimates between the two methods were greatest at the upper quantiles of the resistance distributions (online Appendix 3).

Discussion

Our findings highlight the utility of context-dependent modeling for PSFs and resistance estimation. With such modeling, both scale (spatial and temporal) and

Fig. 4 Log proportional differences in resistance estimates as measured from the smallest scale (5 min/250 m) for models using all points and Movement 1, Movement 5, Resource Use 1, and Resource Use 5 points. The *y-axis* represents a range of percentiles for the distribution of proportional differences. *The legend* represents the log proportional differences. *Warmer colors* indicate larger differences. Please refer to “Sensitivity of resistance estimates” section for an in-depth description of this plot. (Color figure online)

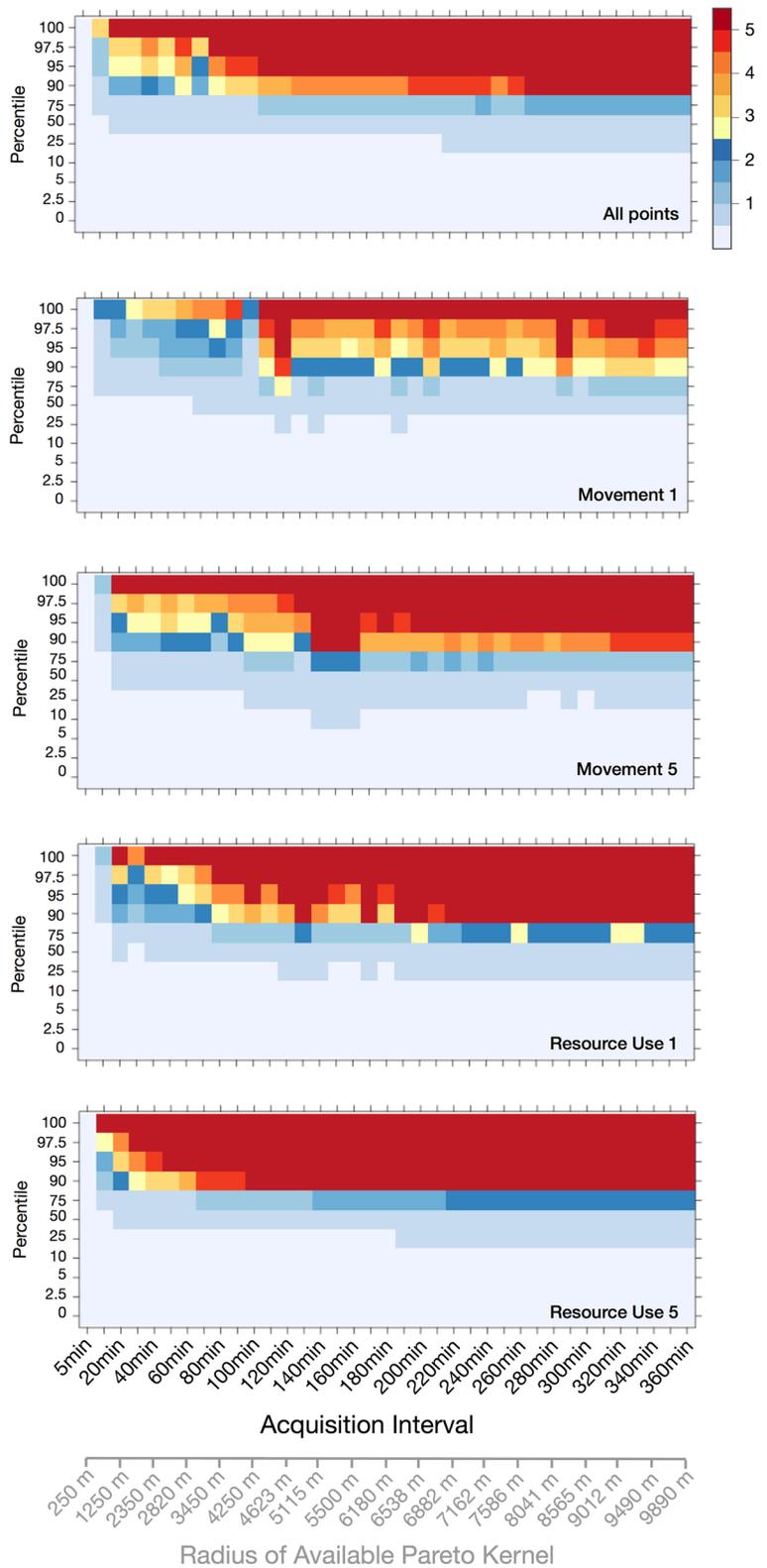
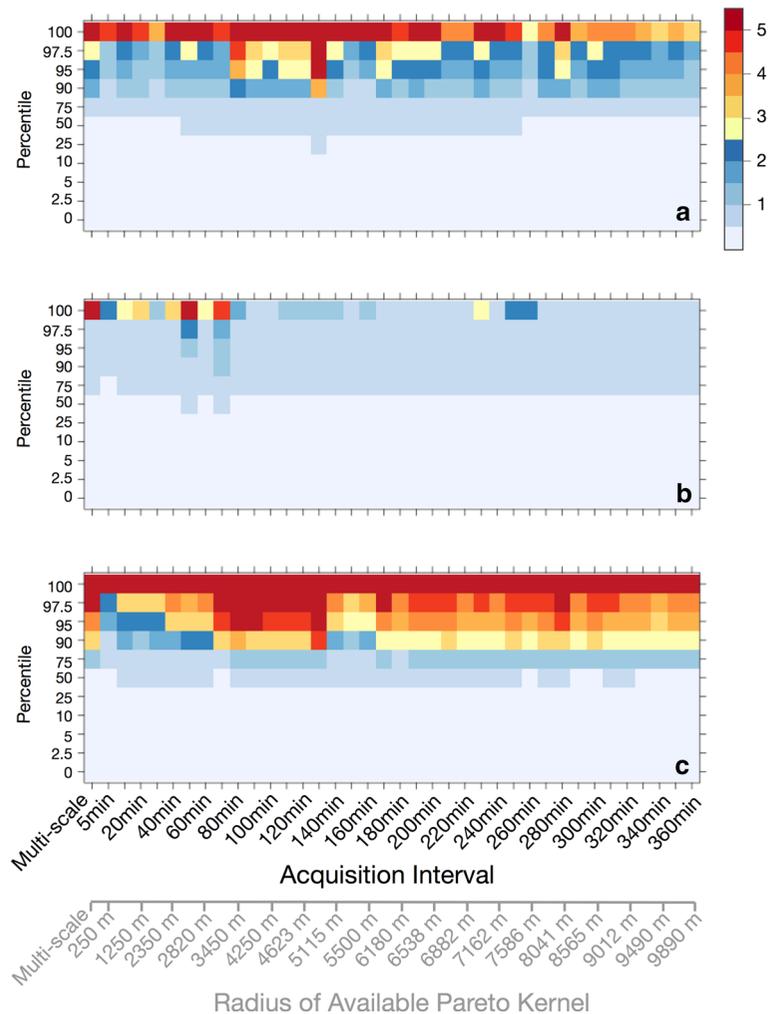


Fig. 5 Log proportional differences in resistance at each scale between models using **a** all points and Movement 5, **b** all points and Resource Use 5, and **c** Movement 5 and Resource Use 5. The *y-axis* represents a range of percentiles for the distribution of proportional differences. *The legend* represents the log proportional differences. *Warmer colors* indicate larger differences. Please refer to “Sensitivity of resistance estimates” section for an in-depth description of this plot. (Color figure online)

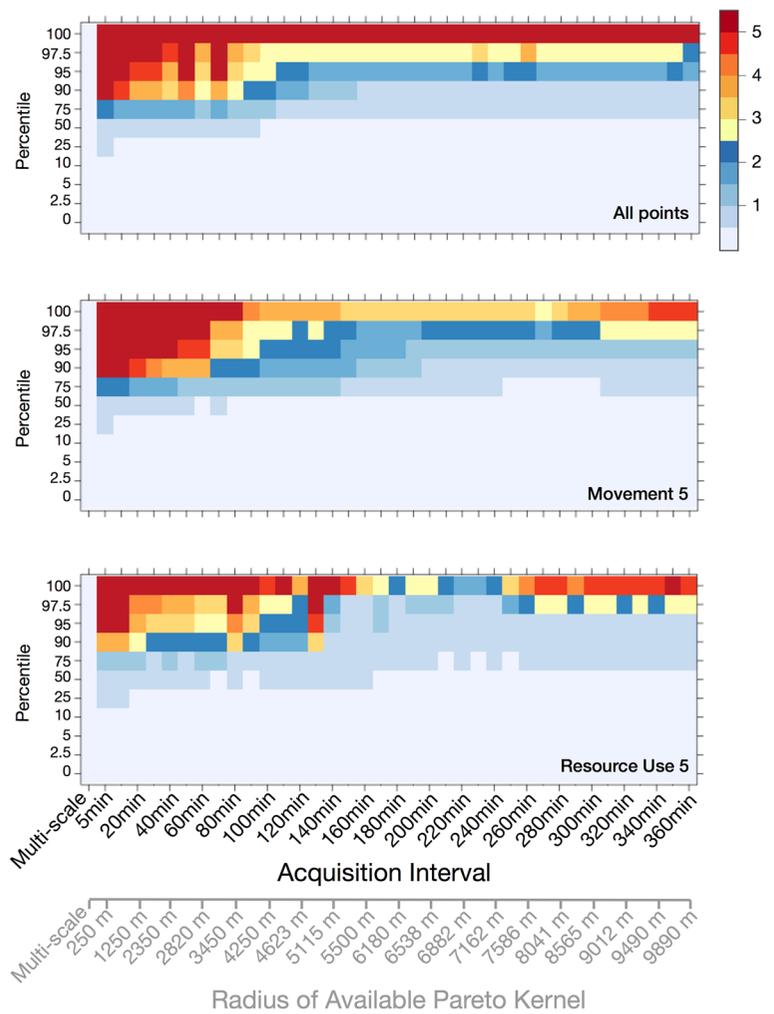


behavioral state (e.g. resource use versus movement) can be used to produce a more detailed, context-dependent estimation of resource selection and resistance to movement (Dalziel et al. 2008). It has long been recognized that species respond to their environment at different scales and that no single scale can capture the relationship between a species and its environment (reviewed in Levin 1992). Instead, it is more realistic to assume there are multiple characteristic scales along the continuum from feeding site to species range, and that adopting Wien’s (1989) ‘domains of scale’ concept allows for more flexibility in modeling the true scales at which a species responds to its environment. By examining a range of scales, we found multiple characteristic scales across land cover types. For example, pumas in the study area responded

more strongly to annual and perennial grassland, coastal oak woodland, coastal scrub and riparian areas at fine scales (250–530 m), to barren areas at mid scales (2 km), and to agricultural and urban areas at coarse scales (7.6–9.9 km). This suggests a mostly bimodal scale of habitat selection; pumas appear to be selecting certain land cover types in their immediate perceptual range, while avoiding large agricultural and urban areas, reflecting what has been published in the literature on puma resource selection in coastal mountain habitat of California (Dickson and Beier 2002; Sweanor et al. 2008; Burdett et al. 2010; Wilmers et al. 2013).

In addition to identifying a single characteristic scale for each land cover type, we observed a dramatic effect of scale on the effect size (i.e., the magnitude of

Fig. 6 Log proportional differences in resistance between the multi-scale model and each single scale model for models using all points, Movement 5 and Resource Use 5 points. The y-axis represents a range of percentiles for the distribution of proportional differences. The legend represents the log proportional differences. Warmer colors indicate larger differences. Please refer to “Sensitivity of resistance estimates” section for an in-depth description of this plot. (Color figure online)



the regression coefficient and corresponding odds ratio) for most land cover types. For example, based on the simple regression model using data representing the most conservative definition of movement (M5), the odds ratio for annual grassland was roughly 10 when the scale was 10 min/530 m and decreased to roughly 2 when the scale was 360 min/9,890 m (Fig. 2a). Thus, the inferred preference for annual grassland during movement was dramatically greater at finer scales than coarser scales. This has implications for estimating resistance (and modeling connectivity), since this would translate into dramatically lower resistance to movement if the resistance surface were derived from finer-scale data than if it were derived from coarser-scale data. Similar sensitivities to scale were observed for most land cover types.

One of our more startling findings was a reversal from preference to avoidance of some land cover types as the scale varied. For example, based on a simple regression using data representing the most conservative definition of movement (M5), the odds ratio for agriculture was close to zero (indicating strong avoidance) at the finest scales, increased to roughly 1.3 (indicating a weak preference) at the 30-min/1,590-m scale, but then decreased to less than one (indicating avoidance) at scales beyond 60 min/2,820 m (Fig. 2e). These results have important implications for inferences regarding habitat selection (preferred vs. avoided), and, by extension, estimates of resistance.

Given the above findings, we suggest that context-dependent modeling should involve an exploration of

multiple scales, echoing previous recommendations by Wheatley (2010) and Martin and Fahrig (2012). Though many GPS collar studies may not be intensive enough to acquire an empirical distribution of movement distances at the 5-min sampling intervals we had in our study, it should not prevent the examination of multiple scales. Whether the scales are empirically-derived or not, a continuum of scales should be used to approximate the true characteristic scale of response.

Though our definitions of behavioral state were relatively simplistic, since they relied solely on displacement distances, our findings provide evidence that resource use and movement behaviors are likely to be confounded in most PSF studies. For our study animals, this appeared to be less of an issue for resource use inference than movement inference since, when all points were used, results were often similar to those obtained via resource use points only. However, differences were readily apparent when evaluating movement behavior. This has ramifications when modeling resistance to movement since, if all points are used, it may be concluded that a species routinely avoids a habitat type, when in fact that type may be tolerated, or even preferred, during movement events. This may lead to artificially inflated or deflated resistance estimates for certain land cover types. By decoupling resource use from movement, we found that pumas had notably different responses to annual grassland, barren and chaparral land cover types depending on their behavioral state. For example, pumas had a negative response to annual grassland and barren areas during resource use behaviors, but had a positive relationship to these land cover types with our most conservative definitions of movement. Published RSF studies on pumas have shown only that they avoid these two habitat types (e.g., Dickson and Beier 2002). The opposite trend was observed for chaparral, where for our two most conservative definitions of resource use, chaparral was preferred, likely due to its use for day beds, but it was strongly avoided for our two most conservative definitions of movement. Chaparral habitat is notoriously difficult for humans to travel through and it is not unrealistic to assume the same difficulty would be faced by a puma. Our results based on resource use points may be biased toward day bed locations, especially for models based on RU5 points. Parsing out daybed locations, from resource use, from movement may reveal further important puma-habitat relationships. Though we removed GPS points that are

prone to large spatial errors, small errors may have introduced some bias in our behavioral state definitions, particularly for RU5.

Regardless of behavioral state, we found that our study animals largely avoided agricultural and urban areas. However, these areas were avoided more strongly during resource use behavior than movement behavior. As in previous studies, we found that pumas preferred coastal oak woodland and riparian areas and avoided coastal scrub (Burdett et al. 2010; Wilmers et al. 2013), and the use of these three land cover types did not appear to be sensitive to the choice of behavioral state. In the same study area, Dickson et al. (2005) compared resource selection functions for pumas between static points and travel points and found that although there were no statistical differences in habitat selection between the two behavioral states, that chaparral and riparian vegetation types were used more often as resting locations than during travel. Our results reflect these behavioral differences across all scales for chaparral and across fine scales for riparian habitat. Though many of our findings regarding behavioral state are intuitive, they demonstrate that resource selection depends on the behavioral state of the study animal. Our findings point to a need for more attention to be paid to the behavioral context of study animals for future PSF and resistance analyses.

Failing to use the appropriate behavioral state for the question at hand may be due to the paucity of empirical definitions for different behavioral states. Knowing when an individual is using resources or moving, or simply moving slowly to acquire resources, may mostly be guesswork, so there is a need for methods that will aid in the identification of different behavioral states. Previous studies have modeled moving versus resting or resource use states based on movement distance and turning angles (Morales et al. 2004; Squires et al. 2013) or fractal dimensions (Fritz et al. 2003). State space models, as described in Patterson et al. 2008 have also been used to distinguish behavioral states. For pumas in particular, there have been studies that have attempted to identify states of predation and feeding (Ruth et al. 2010; Wilmers et al. 2013) and denning and communication behaviors (Wilmers et al. 2013) through cluster sampling. Though these studies are highly informative, more research on this topic is needed. The increased use of accelerometers on GPS collars may aid greatly in this effort (Brown et al. 2012).

We found resistance estimates were also sensitive to scale and behavioral state. This sensitivity was especially evident at the upper quantiles of the differences in resistance values, indicating that choice of scale and behavioral state has the largest effect on ~20 % of the landscape. In addition, estimates of resistance were more sensitive when attempting to decouple movement points from all points than when decoupling resource use points from all points. These results have important implications for modeling connectivity, because in most cases the objective is to estimate resistance to movement rather than resource use.

Though our results are specific only to pumas in southern California, we believe the lessons learned herein can be applied to other species and study areas. Context-dependent models allow for habitat selection and resistance to be estimated at each cell across the study landscape based on its location, surrounding environment, and the behavioral state of the individual. Thus, the resistance assigned to a particular cover type will vary across the landscape depending on the local context. Most current methods for estimating resistance are context-independent and resistance estimates are static for each landscape feature (e.g. land cover type), regardless of its landscape context. Using context-dependent models to estimate a resistance surface is more computationally intensive than context-independent methods since they require a unique resistance value to be calculated for each grid cell in a landscape. Our results provide empirical evidence that context-dependent models generally outperform context-independent models indicating the extra computational time is warranted. For future habitat selection and resistance models based on PSFs, we recommend context-dependent models that explore a continuum of scales and consider using the appropriate behavioral state for the question at hand.

Step or path data may be more appropriate than point data for modeling resistance since it explicitly represents animal movement. Resource selection functions from these data would likely be sensitive to scale and behavioral state as well. However, further research is needed into this topic to determine the degree of sensitivity. A further concern with step and path data is the GPS collar acquisition interval. Step and path data incorporate information along the straight line between consecutive telemetry points. Short intervals may be adequate to represent resource

use for an individual, but as intervals increase, the straight line between points may be too coarse to truthfully reflect resource use during movement. We are currently exploring these questions and the utility of step and path data for estimating resistance.

In closing, although our findings indicate that inferences regarding habitat selection and landscape resistance derived from PSFs are highly sensitive to both the choice of scale for assessing availability of habitat and the choice of data filters for decoupling behavioral states, the following challenges remain regarding the implications of these findings for modeling connectivity. First, while we can confirm that estimates of habitat selection and landscape resistance derived from PSFs vary among scales and behavioral states, it is unclear how best to determine which scale(s) and/or behavioral state is the most ecologically meaningful for purposes of modeling connectivity, since it will undoubtedly depend on the objective and method of modeling connectivity. However, it seems likely that decoupling movement from resource use will be important in most applications, since the former is typically the focus for connectivity modeling, and that adopting a multi-scale approach will lead to the most robust inferences. Second, our findings indicate that while most of the landscape exhibits some sensitivity to the choice of scale and behavior, only a relatively small portion of the landscape exhibits extreme sensitivity, and it is unknown how this will affect measured connectivity given the differences among methods such as least-cost path modeling to identify corridors between a set of well-defined nodes and a more synoptic modeling approach based on resistant kernels in which connectivity is evaluated from every location to every other location. Lastly, our results were based on a single categorical predictor (land cover) at a single resolution. Choice of thematic content and resolution and the spatial grain of the predictor variables will likely also have a large effect on PSF inference and resistance estimates.

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