Habitat preference and use by the Cougar (*Puma concolor)*

by

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Abstract

Cougars (*Puma concolor*) are widespread in the western US, penetrating even into the edges of inhabited and developed areas. Despite their widespread distribution, many aspects of their lives remain unquantified and poorly studied. To explain the factors that influence cougar behavior, I adapted methods used for the African Lion and field data and movement metrics from USGS to designate behavioral states of cougars to GPS locations. Fitting a Bayesian multinomial model, I explain cougar behavior based on vegetation and visibility – the amount of visible area at a point, accounting for the amount of daylight – as well as elevation and land cover. The model explains a third of the variation in the data, but considerable individual variation makes differentiating between behaviors difficult. Visibility likely plays a role in cougar behavior, but additional research is necessary to fully identify all the factors that drive cougar behavior.

Introduction

Understanding large carnivore behavior and habitat use is critical for their management and conservation. Cougars (*Puma concolor*) affect prey populations and are a source of human-wildlife conflict, so their management influences the entire animal community and local economies (Blake & Gese, 2016; D. J. Mattson, Logan, & Sweanor, 2011). Like many other large carnivores, cougars are critical for helping to keep herbivore numbers in check and maintaining the current ecosystem balance, particularly for ensuring deer numbers do not skyrocket. However, most management plans prioritize public safety, which has increasingly regarded cougars as a threat due to increased attacks in previous decades, though this is also affected by the human behavior in the encounters (D. J. Mattson et al., 2011). Nonetheless, a better understanding of cougar behavior in these situations is critical and can also prevent unnecessary management killings.

Currently cougars are listed as a species of Least Concern by IUCN, in part because their actual population numbers are unknown and despite the fact that their low population density makes them susceptible to localized extinction (Crooks, 2002; Rieth, 2010). Cougars are fairly widespread worldwide with their range extending into and through South America, although they have been extirpated in eastern North America, except for a small, isolated endangered population in southern Florida. The uncertainty in their status and the risk of habitat fragmentation reinforces the need for a better understanding of cougars and their habitat use (Montana Fish Wildlife & Parks, 2018).

Multiple studies demonstrate that cougars prefer to hunt in areas of rugged terrain and/or complex vegetation structure conducive for stalking and ambushing prey (Atwood, Gese, & Kunkel, 2009; Elbroch & Wittmer, 2012; Husseman et al., 2003; Kunkel et al., 2013). Modelling and studying such environmental elements can be difficult though, due to the complexity and relatively small scales at play. Topography and terrain ruggedness can be easily characterized, but fine-scale variation, such as minor gullies and depressions, can counteract any broad predictions of terrain suitability for cougars. Topography is also stable and rarely undergoes major alterations. Vegetation, on the other hand, is variable and susceptible to change: wildfires and controlled burns, for example, can change the vegetation structure as well as the herbivore forage. Burned landscapes can increase the carrying-capacity and individual health of herbivores due to the regrowth of high quality forage, with effects lasting for years (Hobbs & Spowart, 1984; Mellars, 1976). Changes in prey abundance and distribution will influence use of the habitat by cougars, in addition to, or perhaps contrary to, the direct effects of habitat modification (Smallwood, 1994).

Mountain lions are primarily ambush hunters, which means that vegetative cover is important for hunting (Rieth, 2010). Given their small stature, with females and males averaging 100 and 140 pounds, they also take advantage of topography and slope to maximize hunting success. Field investigations report instances when cougars on steep slopes attack and kill much larger prey, including 600 pound adult elk. While studies have investigated the importance of slope and terrain ruggedness, the importance of vegetation and visibility on cougar habitat use and activity has been less well quantified and their effects less conclusively described (Bishop, Unsworth, Garton, & Ransom, 2005; Ironside et al., 2018; Pierce, Bowyer, Bleich, & Krausman, 2004).

A better understanding of the importance of fine-scale vegetation and terrain can improve our ability to manage cougars and their prey. Using fine-scale LIDAR, Loarie et al. (2013) quantified the visibility in the landscape at the level of an individual lion, enabling the description of different habitats preferred by males or females depending on their activity (e.g. hunting, resting) (Loarie, Tambling, & Asner, 2013). These methods have the potential to be adapted to cougars in the Americas. By describing the vegetation structure of cougar kill sites with great precision, we can refine current definitions of cougar habitat, and particularly "high-quality" habitat. Using line-of-sight distance measurements at 1-m elevation in 5° increments to simulate visibility at the height of a lion's head, Loarie et al. (2013) defined the landscape as either obstructed or visible. Expanding on this, I calculate viewsheds, the area visible from any point, to quantify visibility of a location. In part, this expansion is based on the fact that visibility and viewsheds have the potential to more accurately describe habitat and terrain (Ironside et al., 2018).

Many studies, indeed the majority, across the US that focus on cougars and cougar habitat are largely based on expert opinion, due to the paucity of actual tracking and GPS data (Beausoleil, Dawn, Martorello, & Morgan, 2008; LaRue & Nielsen, 2011, 2016; O. Neil, Rahn, & Bump, 2014). The ability to use high quality tracking data greatly improves knowledge and models, but is difficult due to logistics and expense (Mansfield, 2007). The U.S. Geological Survey (USGS) Colorado Plateau Research Center, in conjunction with National Park Service (NPS) and Department of Energy (DoE) biologists, has studied more than 20 cougars since 2003 in the southwest US and has collected tracking data from GPS collars, descriptions of kill sites and regional data on fires (David J. Mattson, 2007). Here, I use this unique dataset to examine how the behavioral patterns of mountain lions are influenced by vegetation structure and visibility, and to ultimately better describe cougar habitat use.

Methods

To determine the drivers of cougar behavior, I assembled information on potential explanatory factors, including visibility, vegetation, elevation, gender, and season. To quantify visibility for each cougar GPS location, I made a fine-resolution surface of the study area and calculated the area of the viewshed, considering the availability of daylight with which to see. Using the cougar locations themselves, I classified behavioral states based on spatial movement patterns. I further differentiated behavior by comparing field investigations of activity sites. A multinomial model was generated to look at the effect of visibility on cougar behavior, accounting for group-level and individual effects.

Study area

The study area covered northern Arizona and southern Utah, which is largely part of the Colorado Plateau ecoregion. This area is topographically diverse ranging from 300 meters by the Colorado River and low-lying areas up to mountain peaks at 4000 meters in elevation, largely dominated by plateaus intersected and separated by steep canyons, although with a variety of volcanoes and mountains in the region. Predominant vegetation in the area included sagebrush (*Artemisia tridentata*), blackbrush (*Coleogyne ramosissima*), saltbush (*Atriplex* spp.), piñon-juniper woodland (*Pinus edulis - Juniperus monosperma/osteosperma*), Ponderosa pine (*Pinus ponderosa*), Gambel oak (*Quercus gambelii*), Douglas fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*), creosote (*Larrea tridentata*), and mixed conifers. Grasses included galleta grass (*Hilaria jamesii*), Indian ricegrass (*Achnatherum hymenoides*), and blue grama (*Bouteloua gracilis*), among others. The conifer and pine forested areas were primarily in higher elevation areas, while creosote and saltbush flats dominated the scrubland and valleys.

Cougar movement and environmental data

I obtained data on cougar locations and field visits from United States Geological Survey (USGS), National Park Service (NPS), and Bureau of Land Management (BLM) studies at Grand Canyon National Park, Zion National Park, Grand Staircase-Escalante National Monument, and Capitol Reef National Park (Figure 1). Cougars there have been captured, GPS collared, and released as part of on-going studies since 2003[1], in part to study cougar land-use, movement, and activity in the region. The original dataset consisted of 18679 locations for 15 different cougars, recorded at 4 hour intervals for a total of 6 fixes per day per animal. The location data

[1] (Northern Arizona University IACUC Protocol # 02–082–R4)

came from multiple studies in the region, but through federal agencies using similar collection methods, data quality, and the same southwestern ecosystem – all of which allowed their consolidation and comparison. Field visits had been made to clusters of GPS points, where kills or bed sites were suspected to occur. These field visits looked for evidence of the activity that occurred, and included time and environmental information on those locations.

I obtained LiDAR data for a section of the North Rim of the Grand Canyon from USGS that had originally been collected to assess tree mortality, along with publicly available LiDAR data and a digital elevation model (DEM) from The National Map (U. S. Geological Survey, 2017; Watershed Sciences, 2007). Land use and land cover (LULC) data were obtained from the 2011 National Land Cover Dataset (NLCD) (Multi-Resolution Land Characteristics Consortium (U.S.), 2011). All geospatial data were imported into ArcGIS Pro and re-projected into NAD83 UTM Zone 12 N which covers the study area.

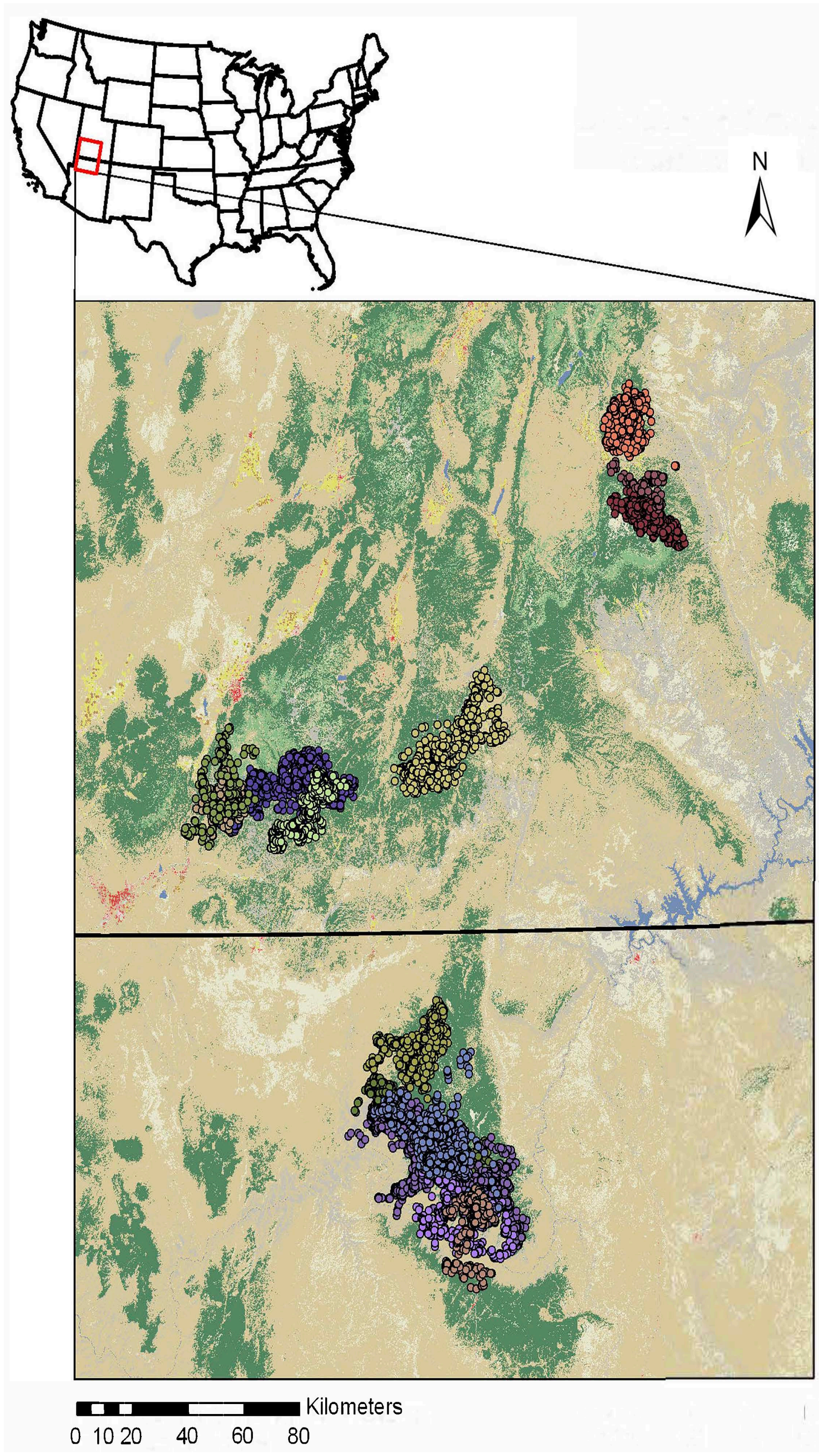

Figure 1. Location of study area and data points in and near the Grand Canyon NP, Zion NP, and Grand Staircase-Escalante NM in Utah and Arizona. Locations for each cougar are denoted in separate colors.

Path analysis and behavioral classification

Based on the methodology of Ironside et al. (2017), I calculated a Path Identification Index (PII) for every cougar location using R (R Core Team, 2018). The PII evaluates consecutive cougar locations and calculates four statistics: the turn-angle for the initial point, the speed (step-length per time) for that point, a tortuosity index and site fidelity. Tortuosity measures the curviness of a path: the ratio of total distance traveled to net displacement. This was calculated as the combined distance from the previous location to the next location (total distance actually travelled) divided by the direct distance from the previous location to the following location skipping the current location (the direct distance or net displacement), and then standardized from 0 to 1. A low value means the cougar moved in a straight line (no tortuosity), while a high value means that the cougar moved strongly in a direction orthogonal to the net displacement (high tortuosity). Site fidelity is particularly relevant for cougars that cache kills and return to them several times to feed, or that stay in one location to rest. For each location, site fidelity was calculated as the number of points within 100m and as a ratio of points within a temporal window ±8 weeks. Each of these four statistics is standardized on a 0-1 scale and added together to produce a 0-4 index. The PII is useful for identifying changes in behavior between area-restricted searching and directed persistence, with low index values related to fast, directed movement and high values related to slower, wandering movement in a frequently-visited area (K. E. Ironside et al., 2017). Comparing PII values with visits to kill sites determines basic thresholds to categorize each point into a behavior: cache/rest, searching, or directed movement (Ironside, personal communication).

Separation of stationary location behaviors

I also used the data on kill site visits to help distinguish between feeding and resting sites. Both feeding and resting behavior have similar geospatial movement signatures, and thus have nearly identical PII values. Using the field visits, I created both a multinomial and a binomial model to predict large/small/no kill or kill/no kill based on cluster duration and time of cluster initiation, as these two variables were comparable between the field data and the location data. I tuned the binomial model using a Receiver Operating Characteristics (ROC) curve from the *ROCR* package to maximize the sum of True Positive and True Negative classifications (Sing, Sander, Beerenwinkel, & Lengauer, 2005). Comparison of the multinomial and the tuned binomial model revealed >1% different classification accuracy, showing that both models were almost equally accurate; therefore, I used the multinomial model to predict feeding/resting status for the GPS collar locations. Based on the PII and this model, I defined four behavioral states to classify all locations: feeding, directed movement, searching, or resting.

Visibility and Viewsheds

I used visibility as a metric and proxy for vegetation structure. This was predicated on the interpolation of LiDAR points to create a Digital Surface Model (DSM) fine-scale enough to retain shapes and bumps from plants and trees, in addition to larger geological landforms. Most of the LiDAR point clouds had point spacing of 0.28-0.58m, density of >6 points/m^2, and accuracy of ~30cm horizontally. Given this data quality, I was able to build a DSM with a resolution of 1.5m. However, the LiDAR data covered only a small fraction of the study area, therefore I subsetted all of the animal movement locations keeping only those that overlapped the DSM. Using the DSM, I estimated the ability of an individual cougar to view its surroundings by calculating the visible area (i.e. viewshed) for each subset location.

The position of the cougar locations varied across the DSM, but to avoid systematically reducing the viewshed area in points near the edge of the DSM, I buffered the DSM by 10 km. To do this, I downloaded multiple DEM rasters from The National Map and mosaiced them together into a single 10m-resolution raster. This raster was then resampled to 1.5m to be consistent with the DSM. I chose a 10km buffer based on visible distance: at sea level the horizon appears 5 km away to the average person. Doubling this 5km distance allowed for local high points, while also keeping the buffer small enough that viewshed calculations could be calculated. Even with this buffer limited to 10km, large viewsheds of tens of thousands of meters should still be clearly distinguishable from small ones (~25m^2), and the difference between large viewsheds (e.g. 1,000,000 m^2) and immense ones (e.g. 100,000,000 m^2) is not of interest here. I used a DEM that extended beyond the DSM because at far distances the landforms will affect visibility more than vegetation, and the inclusion of nearby vegetation from the DSM would maintain that information.

I calculated viewsheds, the area a cougar can see at a single point, for each of the 770 cougar locations that overlapped the DSM areas. This overlap meant that data for visibility analyses were from 15 individuals, 6 males and 9 females. In addition to vegetation, another critical component of visibility is light. To account for this, I also retrieved the time of day for each location to include in the model (adjusted from GST to local time), along with month (to account for seasonal variation). Elevation and generic land cover types were also extracted from the NLCD land cover and DEM elevation rasters for each cougar location. I examined the correlation between all explanatory variables (viewshed, DEM, landcover, month, and time of day) for multicollinearity higher than 0.7 (Dormann et al., 2013). Data exploration revealed no strong multicollinearity between variables (see Appendix, Figure S1).

Home range and land cover use

The number of points in each land cover class for each individual was also calculated from the data. With the locations for each individual, I used the *ctmm* package in R to create autocorrelated kernel-density estimate (AKDE) home ranges based on time-weighted Ornstein-Uhlenbeck processes (Fleming & Calabrese, 2019). To investigate habitat use within the home range, I calculated the distribution of land cover habitat types within each individual home range. Finally, I visually inspected how well the GPS locations represented the habitat and calculated a Pearson product moment correlation of used habitat with available home range habitat.

Multinomial model

Given the set of environmental variables and the calculated behavioral states of the cougars, I built a multinomial model to test the importance of visibility on predicting behavior. Model fitting was primarily done using the *brms* package, which uses the Stan programming language and a Bayesian framework with a Hamiltonian Monte Carlo sampling algorithm (Bürkner, 2017). I fit a simple multinomial logistic regression model to the data, with the behavioral state as the response variable and the main effects of viewshed size and time of day and their interaction as explanatory variables, including random effects for individual animal, gender, and month. For each Bayesian model I ran 4 chains, with 2000 iterations each (with 1000 iteration burn-in) giving 4000 iterations total per model run, which appeared sufficient and allowed all chains to converge with $\hat{R} \cong 1$ (Bürkner, 2017). In the *brms* Bayesian framework, the addition of additional predictor variables of land cover and elevation caused instability in the model and failure to converge. For lack of a prior-defined reference state, the model took directed movement as the base state for probability comparisons.

To help with model verification, interpretation, and communication of results to audiences, I also ran in parallel a frequentist multinomial model in the *nnet* package (Venables & Ripley, 2002). This framework allowed for both a simple model of viewshed and time of day, as well as a more complex model integrating land cover and elevation. Unfortunately, *nnet* does not easily allow for random effects, so animal ID, gender, and month were included simply as fixed effects to contain part of the variance inherent in those variables. The Bayesian models were post-processed for accuracy and parsimony using a WAIC (Watanabe-Akaike Information Criteria), Leave-One-Out (LOO) test, and a Pareto smoothed importance sampling test. The frequentist models were compared using simple AIC and deviance. For both model frameworks, I manually selected the terms to include in the models based on the lowest AIC score while also retaining the visibility term because it was of primary interest to this study. Based on the AIC scores, I determined that the most parsimonious model did not include elevation or land cover type variables. After selecting the best model, I assessed the frequentist models for statistical significance using an ANOVA likelihood-ratio χ^2 test and used pseudo-R^2 to estimate the proportion of explained variance. I calculated a suite of Maximum Likelihood, McFadden, Adjusted McFadden, Cragg Uhler, Count, and Adjusted Count R^2 values to assess several of the best models to evaluate model performance; selecting the model with the lowest AIC also had the effect of choosing the model with the highest R^2 measures.

Behavior model and classification verification

Transition rates between the four “observed” behavioral states were calculated from the data and modelled between four underlying hidden latent states using a Hidden Markov Model (HMM) for all 19000+ points, using only the simplified DEM and LULC as predictor variables. The resulting model produced a transition probability matrix, along with measures of emission probability rates for each latent state. The intersection of LiDAR data and the location tracks broke up the tracks and the time-series, preventing the HMM model from being run on the smaller dataset and/or using the visibility information as a predictor. I used these model outputs to help understand and verify the classification of behaviors, and thus to help ensure that the overall results were sound. All calculations for the HMM were done using the *seqHMM* package in R (Helske & Helske, 2019). A 4-state model was supported by previous research, although the use of HMM versus a Hidden Semi-Markov Model (HSMM) allows for less flexibility in analysis (van de Kerk et al., 2015).

Results

Cougar behavior summary

Based on the data, the cougars on average spent 35.0% (±9.0) of their time in directed movement, 8.5% (±17.1) of their time feeding, 12.3% (±5.1) resting, and 44.2% (±8.5) searching – although this could underestimate time resting and feeding due to poor GPS location fixes during these behaviors (Kirsten E. Ironside et al., 2017). The proportion of time spent on each behavior varied highly among individuals. The calculated viewshed for the points ranged from 27m^2 up to more than 150km^2, spanning several orders of magnitude. The median viewshed size was 13000m^2; which is a more appropriate than the mean (2.9km^2±9.6) given the presence of extreme values. Movement step-length and speed were nearly identical, and both appeared to have an exponential distribution; the log-step-length had a distinct bimodal distribution (Ashman's D=2.51), with means of 3.74±1.39 log(m) and 7.22±0.84 log(m) (Ashman, Bird, & Zepf, 1994).

Bayesian Model: Effect of habitat visibility on movement behavior

The Bayesian model showed that the visibility metric followed the expected trends, with directed movement and resting increasing with greater visibility, while cover-associated activities such as feeding and searching decrease with greater visibility (Figure 2). However, the differences between the reference state (directed movement) and other behaviors was not always statistically significant (i.e. not different from 0; Figure 5, appendix Table S6). The

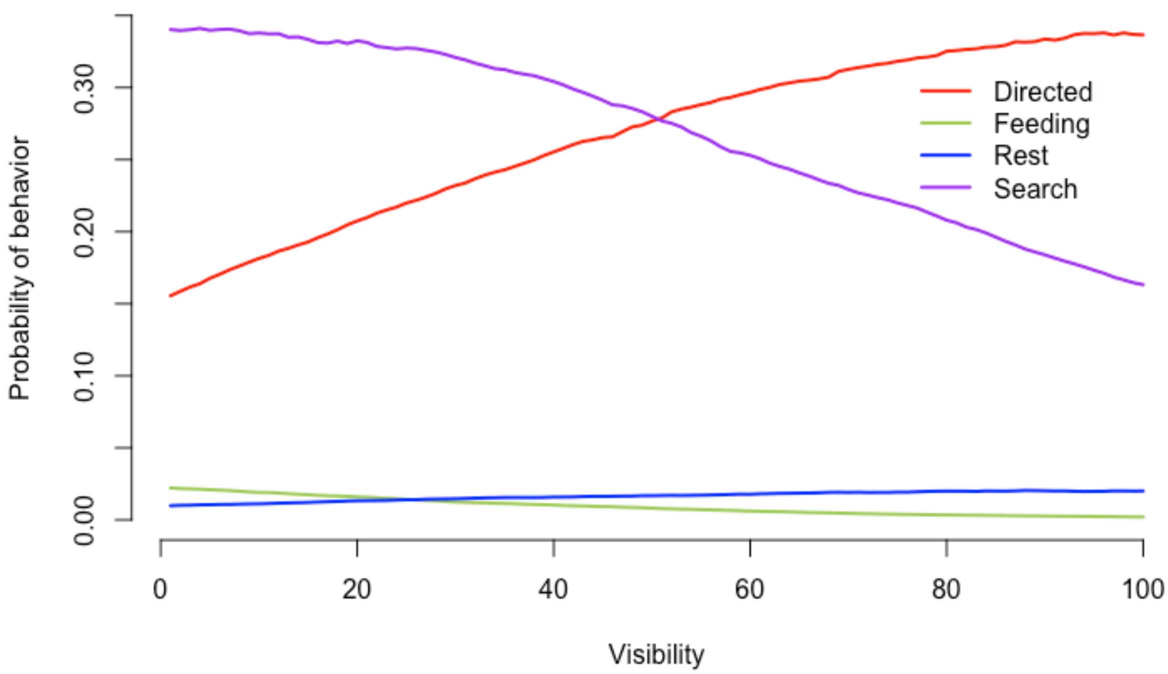

Figure 2. Marginal effects of visibility from 0 (low) to 100 (high) on the relative probability of behaviors in mountain lions.

credible intervals for the random effect intercept of individual was always statistically significant and did not include zero, suggesting individuals display distinct behavioral patterns.

Frequentist Model: Effect of habitat visibility on movement behavior

In the frequentist multinomial model, the overall model structure was significant ($p<0.01$) and explained roughly 42% of the variance in the data. In this model, visibility was significant, although the χ^2 test of significance showed a slight decrease in deviance explained by the term with the addition of the time-of-day variable and more with elevation. Adding other variables to the model demonstrated that visibility and time of day were highly important, while individual animal effects, gender, and season also played important explanatory roles. Land cover and elevation were less important predictors in the full model (Appendix Table S7).

The frequentist model predicted the original data with 56% accuracy (Appendix Table S4). The amount of time spent in each land cover type varied strongly among individuals, but was 80% correlated ($p<0.01$) with the proportional representation of each land cover type within home ranges – although with an apparent preference for forests and areas with vegetative structure (Figure 3).

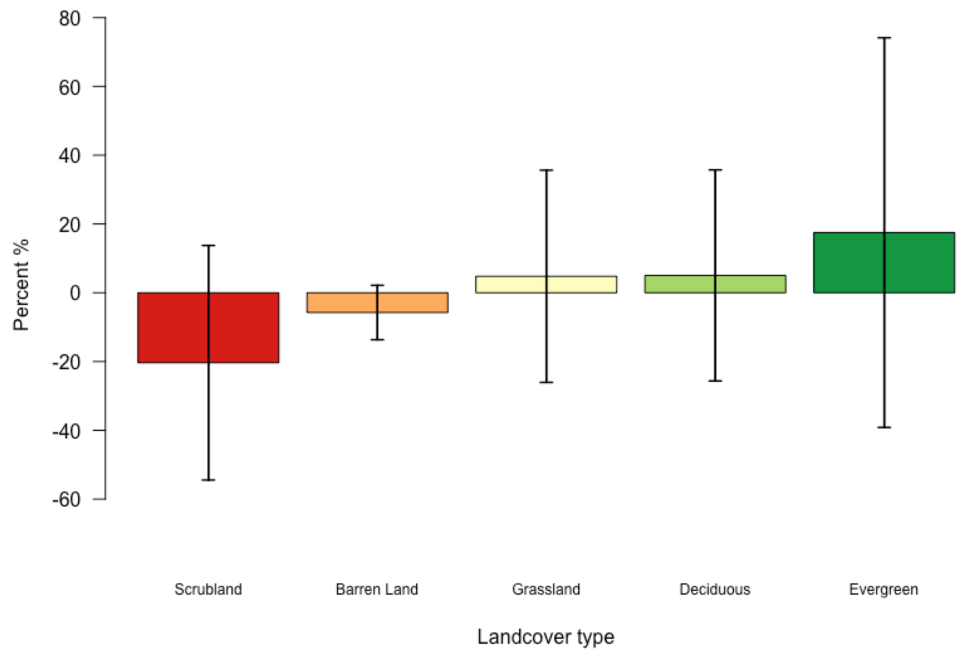

Figure 3. Difference of cougar habitat use between GPS locations and habitat types within modelled home ranges. Although not statistially significant, there is a visible preference for forests and grasslands; habitat types with change <1% not plotted here.

Behavior modelling of hidden states

There was some autocorrelation or behavioral "momentum" visible in the transition probabilities, as seen by the tendency to maintain behaviors (except for resting behavior). The emission probabilities from the HMM are the probability that a cougar in any given state will emit or be detected in an observed state. The emission probabilities exist for each of a set of hidden states – which is to say, that it is impossible to know exactly which behavior a cougar is engaging in. The true behavior, or state, of the cougar is hidden, but the probability of the hidden state can be estimated from the visible observed states. The emission probabilities from the HMM suggested that for most of the hidden states there tends to be a fairly clear observed state, altough undefined behaviors tend to be classified as resting state, which also corresponds with the model having the lowest success in back-predicting that class onto the original data (Table 1).

Table 1. Emission probabilities of hidden states, showing the probability of observing a behavior based on the current behavioral state. Colored cells highlight large probability of observed behavior for each hidden states.

Hidden State	Observed Behavior: Feeding	Directed	Rest	Search
State 1	0.544	0.186	0.029	0.240
State 2	0.047	0.790	0.018	0.146
State 3	0.110	0.263	0.287	0.340
State 4	0.039	0.094	0.015	0.852

Discussion

Cougars have complex behavioral patterns, with vegetation and visibility playing important roles in determining their behavioral state. In this study, cougars are preferentially hunting and searching in areas of dense vegetation and use open, high visibility areas for resting or directed movements. It is therefore possible to predict likelihoods of cougar behavior in an area based on the vegetation structure and visibility.

Vegetation structure was a significant predictor of behavior, but interacted with several other variables, including: vegetation and daylight, gender and season, and individual cougars (Figure 4). This complexity, along with strong individual differences among cougars, results in high levels of variation in the data (Figure 5). To fully tease apart the nuances of behavior and account for high levels of variation, a higher sample size of GPS-collared cougars is necessary. Similarly, while the frequentist approach shows the importance of the overall model – which includes fixed effects of visibility and daytime (interacting), animal ID, month, and gender – differentiating between probabilities of precise behavioral states is difficult.

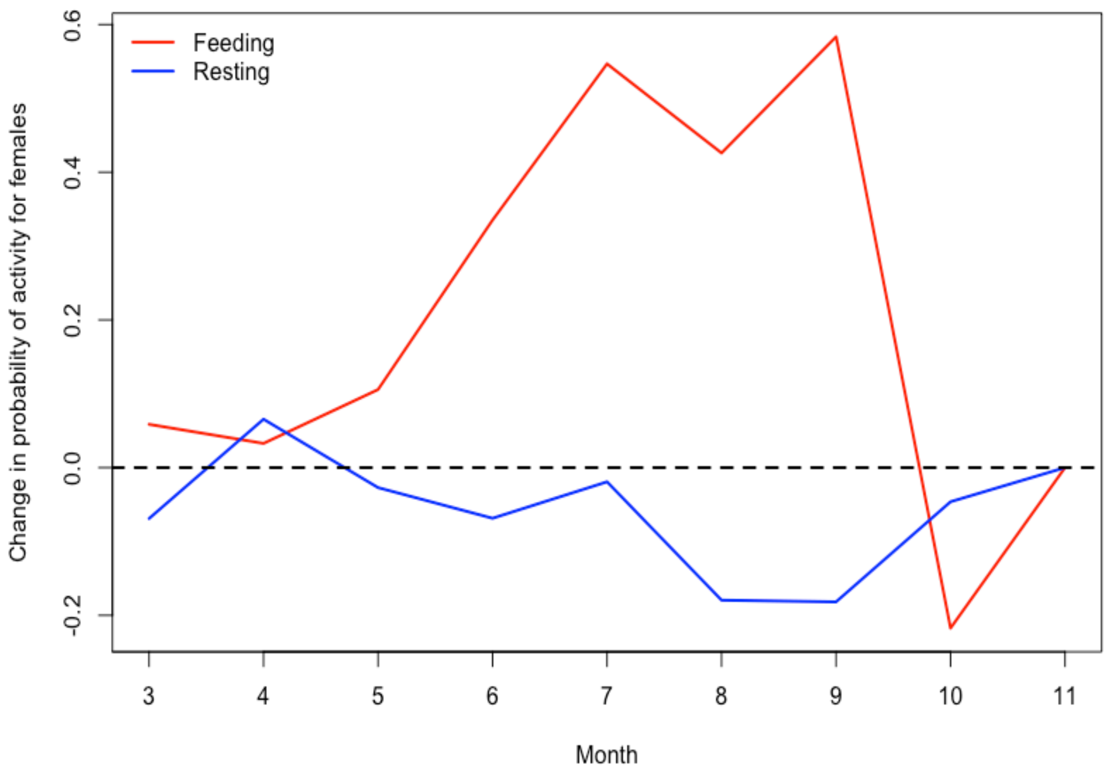

Figure 4. Interaction effects between gender and season. The dashed line represents no difference in probability of behavior for males and females. When the curve is negative, males are more likely to engage in an activity than females; positive values, females are more likely.The difference between feeding and resting behavior in late summer illustrates the likelihood of females to be hunting and feeding for kittens.

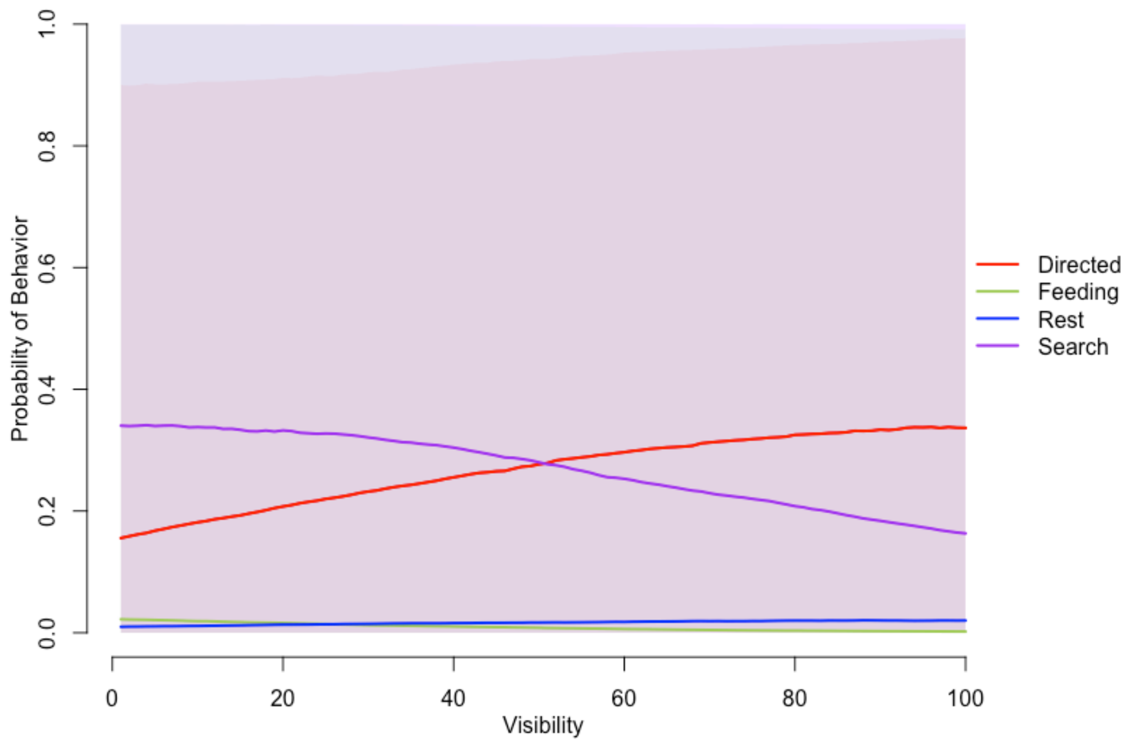

Figure 5. Marginal effects of visibility on behavior type, including error and uncertainty as shaded regions.

Cougars tended to select for forested areas despite the presence of shrubland and barren areas in their habitat, suggesting they select for vegetation structure (Figure 3). These overall preferences agree strongly with existing knowledge and models of cougar habitat which show a strong trend to forest or forest-classified land covers (Burdett et al., 2010; Dickson & Beier, 2002; K. L. Nicholson, Krausman, Smith, Ballard, & McKinney, 2015). Forest land cover includes various biome-specific habitat types, namely chaparral which is coded as forest in the National Land Cover Database, and some riparian and woodland types. Selection of forested habitat corresponds with typically good habitat for cougar prey species, including mule deer (*Odocoileus hemionus*), elk (*Cervus canadensis*), and bighorn sheep (*Ovis canadensis*) (Collins & Urness, 1983; Grover & Thompson, 1986; M. C. Nicholson, Bowyer, & Kie, 1997). Conducting a comparison of selected land covers within the home range versus the larger study area, or perhaps a comparative habitat/non-habitat analysis with pseudo-absence points, could reveal the importance of vegetation structure to cougars on a broader scale, as opposed to the behavioral analysis done here.

Viewsheds contain a great deal of useful information, and appear to be a viable and important element in quantifying visibility. Previously, visibility could only be estimated with qualitative field estimates, which can be strongly influenced by observer bias. In this study, fine-scale LiDAR information made it possible to remotely and systematically measure a visible area. My method of estimating viewsheds, while it needs further refinement, is a promising advancement in understanding the behavior of cougars, and other species as well. The transferrability of the analysis between African lions and mountain lions suggests it may be possible to extend it to other species whose behavior is affected by vegetation structure.

Time of day strongly affected the behavior of cougars. Although it recognized that time of day influences activities, and that cougars are largely crepscular, I included the term mainly for the effect it could have on visibility (Rieth, 2010). Ideally, additional terms would be used to model lunar light, but such information was not included here. Nevertheless, the probabilities of behaviors occurring at different times of the day correspond well with expectations: cougars are slightly more likely to be hunting or feeding around dusk and dawn, with an increase in resting towards midnight, and direct movement during daylight hours (Figure 6). The results indicate that the cougars also spend a majority of their time moving, either as directed movement or as searching and hunting movement.

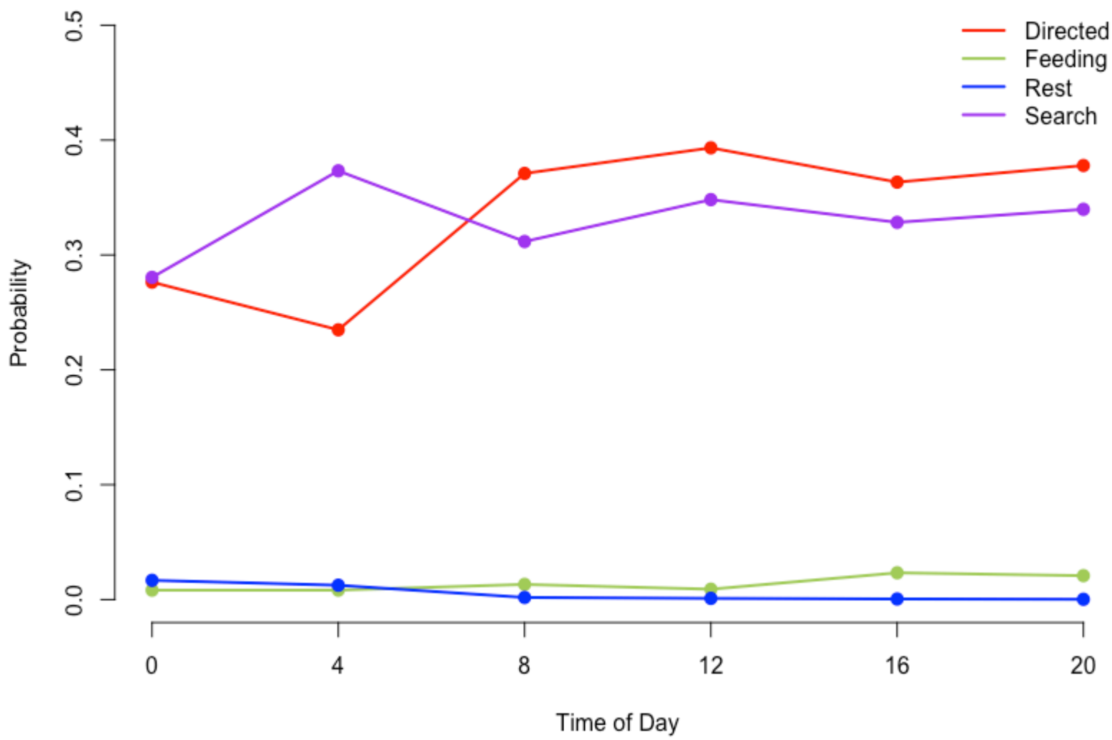

Figure 6. The marginal effect of time of day on cougar behaviors.

The cougars had an average home range size of 840 km^2 (±770), which is larger than other estimates of home range size for cougars. Some studies have already noted that variance in home range size depends on location and habitat, as well as the width of confidence intervals employed (Dickson & Beier, 2002). The choice of 95% confidence intervals for the kernel estimate of home range was chosen in part because it gives a higher estimate that buffers the points to allow for possible area usage with the coarse temporal resolution of the fixes.

Improvements and future avenues of work

In this study, GPS locations of cougars were recorded every 4 hours, which limited the ability to detect fine resolution interactions with the environment and relate behavior to environmental variables. By comparison, Loarie et al. (2013) used hourly GPS fixes to describe and predict behavior in African lions, which likely facilitated the ability to detect differences among behavioral states. To take advantage of the growing collection and use of fine-scaled

LiDAR data, the data on animals and their behaviors also need to be fine-scaled. I recommend that to study cougar behavior, future collaring efforts record locations hourly, or even every 15 minutes. More frequent GPS transmission of location will reduce battery life, and so the goal of collaring programs – the study of behavior or the quantification of long-term movements or home ranges – needs to be clearly defined at the start of the campaign.

Estimation of visibility might be improved by using locally relative measures of visibility. For example, on an open plain the few existing trees would provide high cover relative to the otherwise open space. By comparison, with the absolute scale of viewshed used here, the trees would be classified as high visibility points. To scale the visibility metric to the local average would be useful, although technically challenging. Estimates of visibility could be further refined by improving the quantification of realistic visiblity as well. Both Loarie et al.'s (2013) method and my method employed a simple binary classification of visible/not visible. This technique does not allow for partial visibility and visual penetration (Murgoitio, Shrestha, Glenn, & Spaete, 2014). In essence, when a cougar looks at a tree, it can often see partially through the branches, or depending on the height of the canopy, can see under the tree – this allows for partial visibility and visual penetration through the vegetation. Such aspects of visibility could be included by using standardized LiDAR return densities at different heights above ground, although this would be computationally intensive and not perfectly reflect cougar visibility.

Determing the drivers of animal behaviors is complicated, but as the quality and resolution of movement and environmental data improves we will be able to develop more nuanced models with a fuller suite of behaviors – which we know exist in cougars. Being able to differentiate more behaviors can further refine and improve our ability to predict, manage, and live with cougars.

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Citations

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Appendix

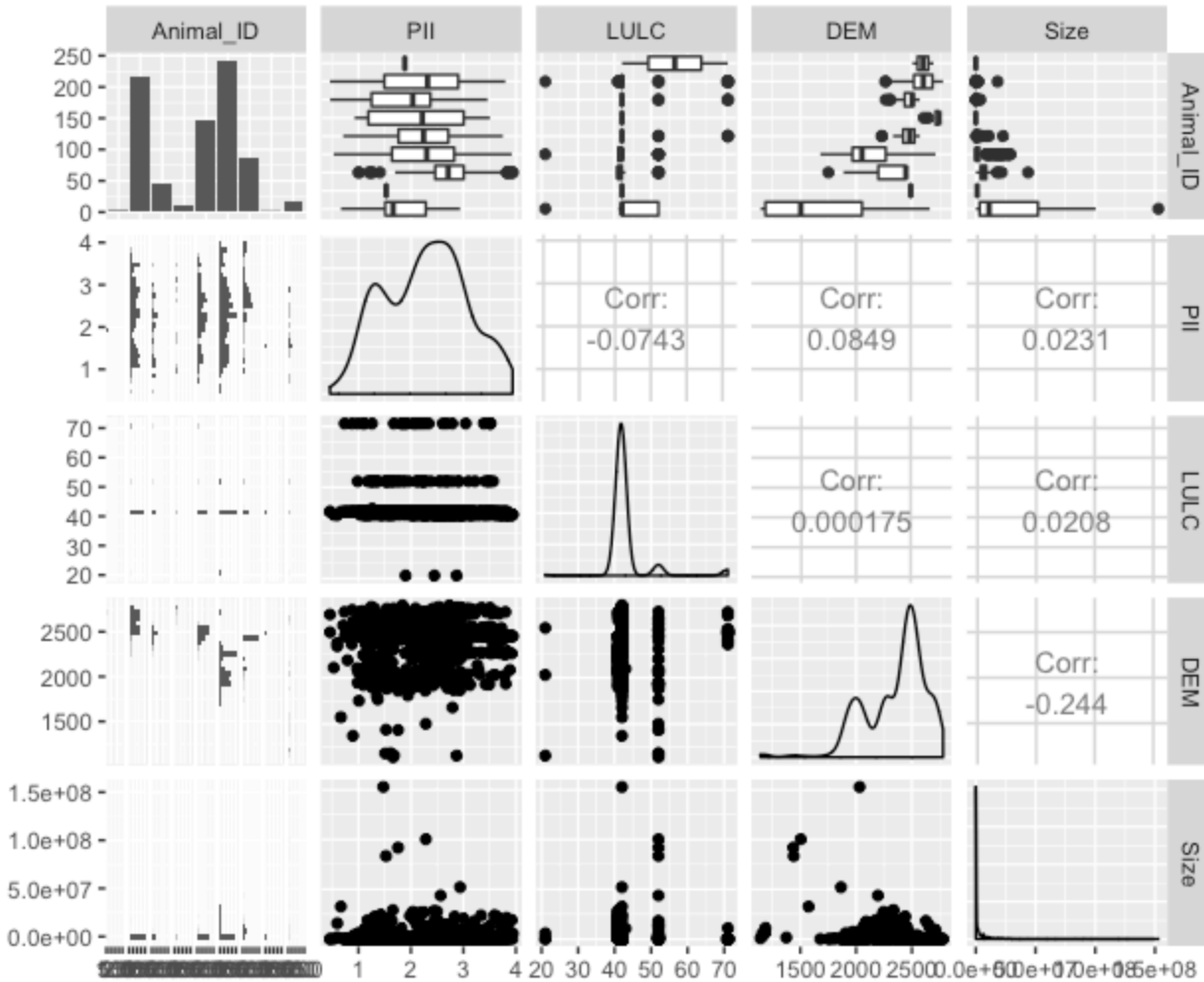

Figure S1. Correlation values and data distributions for the raw variables.

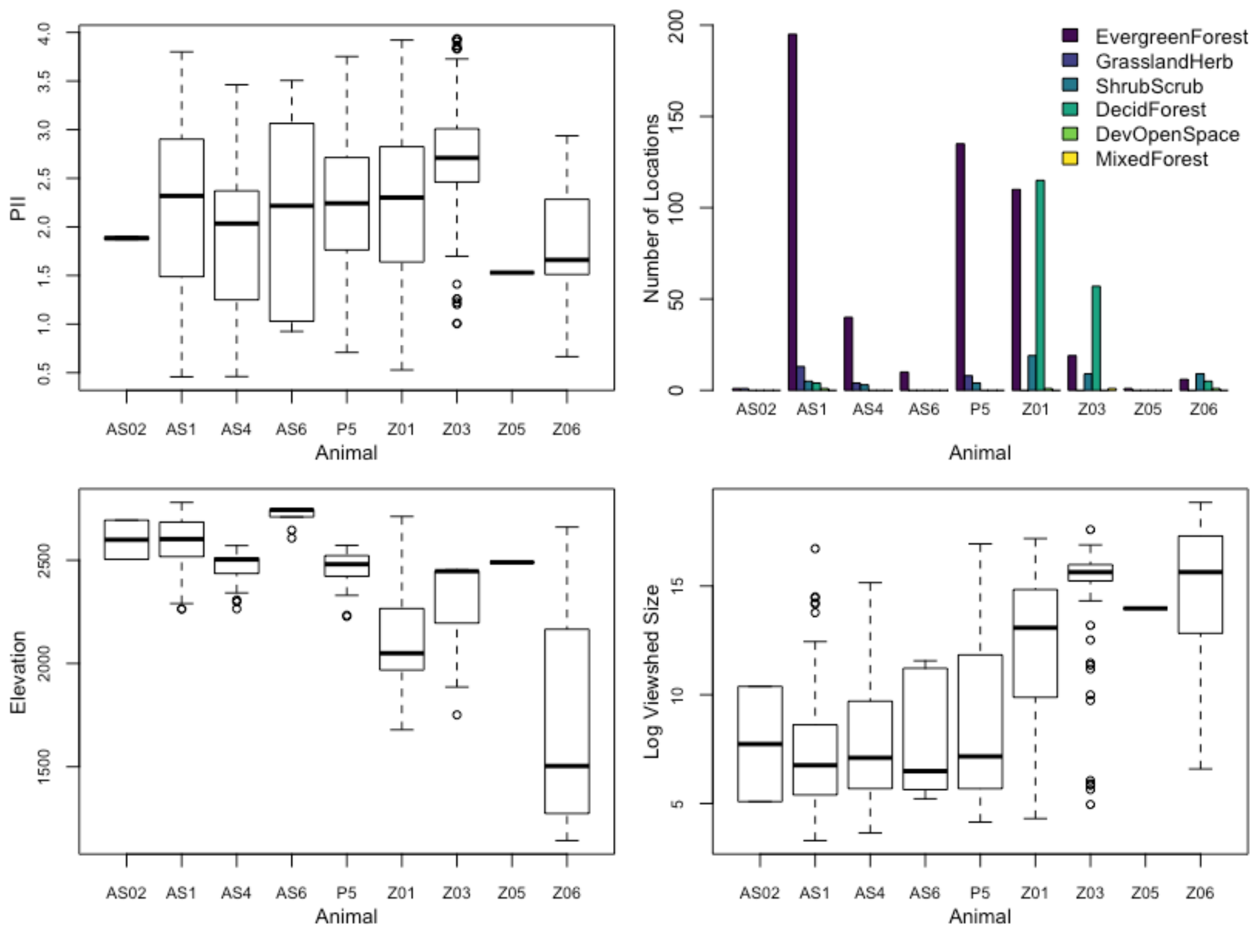

Figure S2. Distribution of animal locations by movement type (as PII value), land cover preference, elevation, and log viewshed size. High levels of individual variation and habitat discrepancy are visible, although all the cougars showed a preference for forest land cover (either evergreen or deciduous).

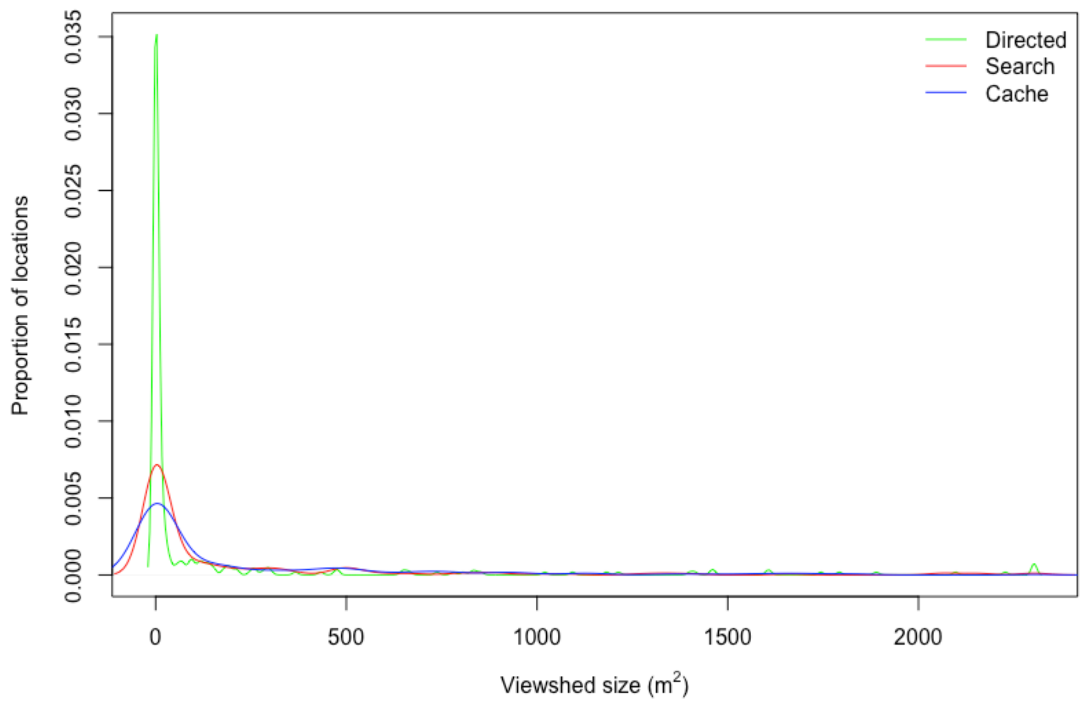

Figure S3. Relative proportion of viewshed sizes for each PII behavior mode. Viewshed size seemed to display a logarithmic distribution, with a cluster around somewhat low-visibility areas, and a long tail with several outliers at extremely large viewshed sizes.

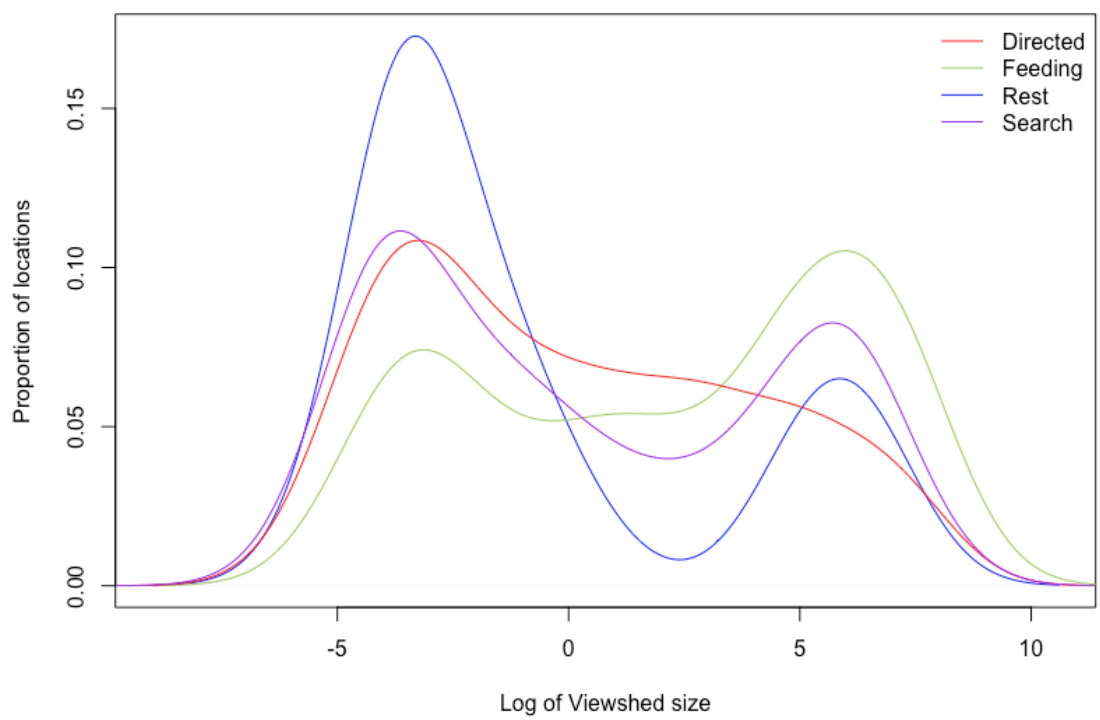

Figure S4. Relative proportion of the log of viewshed area, for each behavior. The distribution forms an interesting bimodal shape for almost all behaviors. Note use here of 4 behavior types.

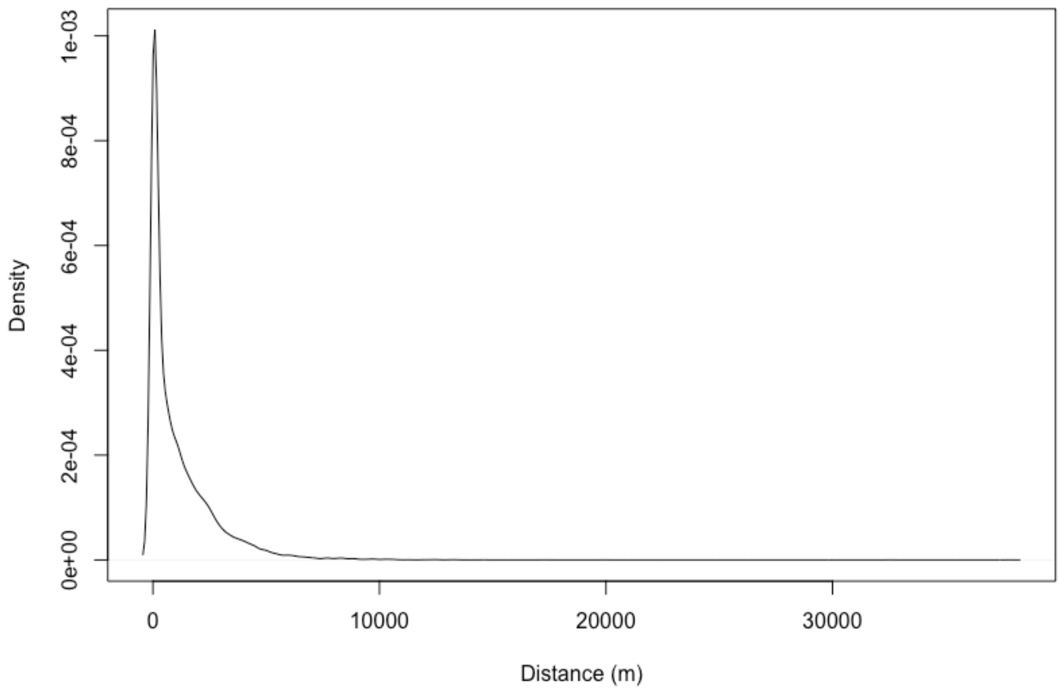

Figure S5. Distribution of step-lengths for points; the step-length is the distance travelled from one point to the next, and can also be used as a proxy for speed. As before, there is an apparent logarithmic distribution.

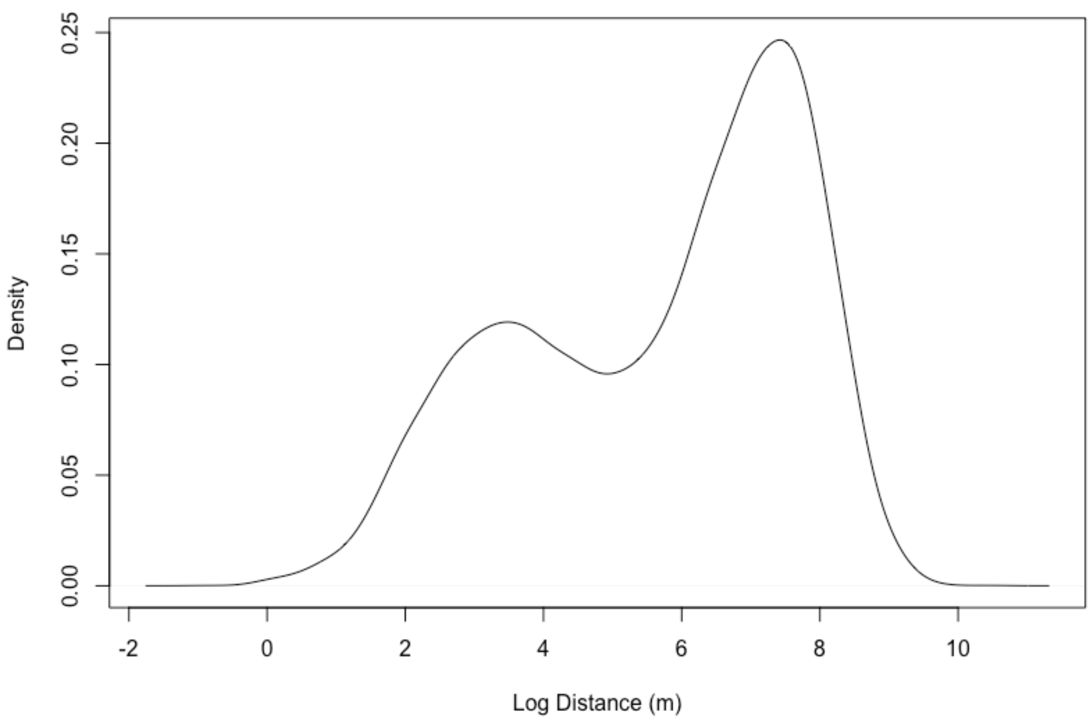

Figure S6. Density of step-length as log-meters. Here, taking the logarithm of the step-length between points condenses the distribution, and shows a bimodal curve now.

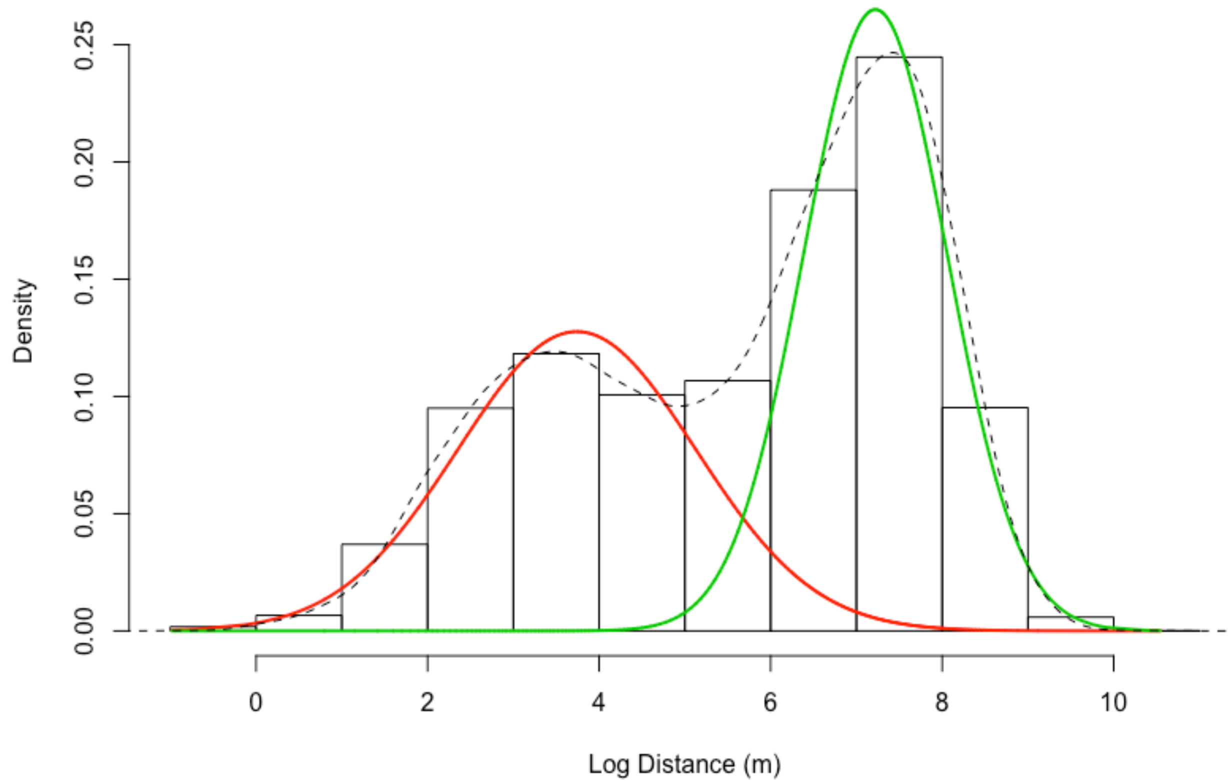

Figure S7. Mixture model of underlying uni-modal elements for log step-length curves. This appears to show two distinct movement modes.

Table S4. Confusion matrix and accuracy statistics for the Bayesian multinomial model.

Confusion Matrix and Statistics (Frequentist)

		Reference			
		Feeding	**Directed**	**Rest**	**Search**
Prediction	**Feeding**	112	22	8	61
	Directed	40	107	0	28
	Rest	7	1	5	8
	Search	96	46	25	204

Overall Statistics:

Accuracy:	0.5558
95% CI:	(0.5199, 0.5913)
No Information Rate	0.3909
P-Value [Acc > NIR]:	<0.01
Kappa:	0.3381
Mcnemar's Test P-Value:	0.000131

Statistics by Class:

	Feeding	**Directed**	**Rest**	**Search**
Sensitivity	0.439	0.608	0.132	0.678
Specificity	0.823	0.886	0.978	0.644
Pos Pred Value	0.552	0.611	0.238	0.550
Neg Pred Value	0.748	0.884	0.956	0.757
Prevalence	0.229	0.049	0.391	
Detection Rate	0.146	0.139	0.006	0.265
Detection Prevalence	0.264	0.227	0.027	0.482
Balanced Accuracy	0.631	0.747	0.555	0.661

Table S5. Transition probabilities between behavioral modes

		End Behavior			
		Directed	**Search**	**Rest**	**Feeding**
Starting Behavior	**Directed**	0.601	0.345	0.015	0.04
	Search	0.267	0.514	0.068	0.151
	Rest	0.101	0.562	0.337	0
	Feeding	0.08	0.404	0.001	0.516

Table S6. The output summary of the Bayesian model, showing Credible Intervals and estimated error.

Table S6. *brms* output for model

Family:	Categorical
Links:	muFeeding = identity; muRest = identity; muSearch = identity
Formula:	Btype ~ SizeStd * Daytimegrp + (1 | Animal_ID) + (1 | Gender) + (1 | Month)
Data:	fdata (Number of observations: 770)
Samples:	4 chains, each with iter = 2000; warmup = 1000; thin = 1; total post-warmup samples = 4000

Group-Level Effects:	***~Animal_ID (Number of levels: 9)***					
	Estimate	**Est.Error**	**l-95% CI**	**u-95% CI**	**Eff.Sample**	**Rhat**
sd(muFeeding_Intercept)	3.8	2.43	1.28	9.96	2411	1
sd(muRest_Intercept)	4.2	2.87	0.95	11.49	2329	1
sd(muSearch_Intercept)	1.34	0.73	0.49	3.09	1948	1
	~Gender (Number of levels: 2)					
	Estimate	**Est.Error**	**l-95% CI**	**u-95% CI**	**Eff.Sample**	**Rhat**
sd(muFeeding_Intercept)	5.14	6.66	0.12	22.83	866	1.01
sd(muRest_Intercept)	5.93	6.29	0.16	22.84	2154	1
sd(muSearch_Intercept)	4.28	5.34	0.1	18.57	1600	1
	~Month (Number of levels: 11)					
	Estimate	**Est.Error**	**l-95% CI**	**u-95% CI**	**Eff.Sample**	**Rhat**
sd(muFeeding_Intercept)	2.07	0.82	1	4.05	1658	1
sd(muRest_Intercept)	1.2	0.71	0.15	2.9	1198	1
sd(muSearch_Intercept)	0.61	0.26	0.23	1.24	1371	1
Population-Level Effects:						
	Estimate	**Est.Error**	**l-95% CI**	**u-95% CI**	**Eff.Sample**	**Rhat**
muFeeding_Intercept	-2.36	6.83	-17.79	8.74	465	1.02
muRest_Intercept	-2.8	6.44	-17.63	9.89	1734	1
muSearch_Intercept	0.51	4.7	-8.97	10.68	929	1
muFeeding_SizeStd	-2.8	3.1	-9.29	3.17	949	1
muFeeding_Daytimegrp4	-1.04	1.4	-3.84	1.65	1399	1
muFeeding_Daytimegrp8	-1.84	1.1	-3.91	0.36	1173	1

muFeeding_Daytimegrp12	-0.37	1.23	-2.84	2.02	1315	1
muFeeding_Daytimegrp16	0.1	1.13	-2.05	2.35	1101	1
muFeeding_Daytimegrp20	-0.48	1.15	-2.72	1.82	1056	1
muFeeding_SizeStd:Daytimegrp4	2.41	3.69	-4.54	9.82	1146	1
muFeeding_SizeStd:Daytimegrp8	4.09	3.16	-1.82	10.75	955	1
muFeeding_SizeStd:Daytimegrp12	0.13	3.58	-6.72	7.3	1120	1
muFeeding_SizeStd:Daytimegrp16	1.15	3.36	-5.32	8.03	1037	1
muFeeding_SizeStd:Daytimegrp20	1.86	3.39	-4.6	8.74	987	1
muRest_SizeStd	-0.06	2.15	-4.34	4.05	1162	1
muRest_Daytimegrp4	0.76	1.02	-1.25	2.78	1514	1
muRest_Daytimegrp8	-2.15	1.21	-4.57	0.17	1940	1
muRest_Daytimegrp12	-1.79	1.46	-4.92	0.83	2201	1
muRest_Daytimegrp16	-2.86	1.96	-7.12	0.37	2342	1
muRest_Daytimegrp20	-1.19	1.66	-4.62	2.17	1711	1
muRest_SizeStd:Daytimegrp4	-1.84	2.66	-7.18	3.28	1331	1
muRest_SizeStd:Daytimegrp8	-0.21	2.73	-5.64	5.14	1392	1
muRest_SizeStd:Daytimegrp12	-2.19	3.27	-8.54	4.23	1648	1
muRest_SizeStd:Daytimegrp16	-1.24	3.67	-8.37	6.02	1770	1
muRest_SizeStd:Daytimegrp20	-6.26	5.14	-18.66	2.06	1802	1
muSearch_SizeStd	-1.21	1.51	-4.17	1.78	873	1
muSearch_Daytimegrp4	0.25	0.77	-1.27	1.75	1243	1
muSearch_Daytimegrp8	-1.12	0.65	-2.38	0.15	1062	1
muSearch_Daytimegrp12	-0.2	0.72	-1.61	1.19	1236	1
muSearch_Daytimegrp16	-0.43	0.7	-1.78	0.93	1143	1
muSearch_Daytimegrp20	-0.62	0.69	-1.99	0.75	1098	1
muSearch_SizeStd:Daytimegrp4	0.28	1.89	-3.4	4.05	1065	1
muSearch_SizeStd:Daytimegrp8	2.02	1.62	-1.22	5.15	919	1
muSearch_SizeStd:Daytimegrp12	0.19	1.76	-3.28	3.68	1002	1
muSearch_SizeStd:Daytimegrp16	0.72	1.74	-2.72	4.1	973	1
muSearch_SizeStd:Daytimegrp20	1.06	1.75	-2.35	4.44	973	1

Samples were drawn using sampling(NUTS). For each parameter, Eff.Sample is a crude measure of effective sample size, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

Table S7. Chi-squared test output, and coefficients of frequentist model.

Analysis of Deviance Table (Type II tests)

Response: Behavior

Variable	*Likelihood Ratio* (χ^2)	*Degrees of freedom*	*P-value*
SizeStd	1.084	3	0.78
Daytimegrp	40.681	15	<0.01
Animal_ID	88.235	24	<0.01
Gender	0	3	1.00
Month	129.754	30	<0.01
SizeStd:Daytimegrp	12.109	15	0.67

	Feeding	**Rest**	**Search**
(Intercept)	-41.53	-35.54	-86.73
SizeStd	-2.49	0.47	-1.13
Daytimegrp4	-0.96	0.81	0.28
Daytimegrp8	-1.86	-1.95	-1.11
Daytimegrp12	-0.42	-1.57	-0.25
Daytimegrp16	0.10	-2.16	-0.41
Daytimegrp20	-0.47	-1.20	-0.60
Animal_IDAS1	41.15	35.25	-10.00
Animal_IDAS4	-30.29	23.60	23.91
Animal_IDAS6	-37.24	-84.89	53.32
Animal_IDP5	31.50	24.91	24.71
Animal_IDZ01	32.19	10.72	23.77
Animal_IDZ03	8.04	5.08	54.04
Animal_IDZ05	-23.28	0.07	-45.05
Animal_IDZ06	-60.81	-50.67	-10.00
GenderM	-11.62	-10.35	34.03
Month2	48.51	45.21	2.48
Month3	79.29	74.63	33.09
Month4	7.93	9.96	62.33
Month5	9.87	10.02	63.29
Month6	11.46	10.47	63.77
Month7	12.08	8.66	63.58
Month8	10.50	10.51	62.53
Month9	11.82	11.39	63.50
Month10	12.76	10.10	63.78
Month11	-36.22	-39.86	62.21
SizeStd:Daytimegrp4	2.04	-2.33	-0.10
SizeStd:Daytimegrp8	3.76	-0.41	1.95
SizeStd:Daytimegrp12	0.17	-2.13	0.28
SizeStd:Daytimegrp16	0.72	-1.98	0.56
SizeStd:Daytimegrp20	1.39	-4.55	0.86

Figure S8. Transition and emission probabilities from the Hidden Markov Model. Transition probabilities are shown as the numbers on the lines between states; emission probabilities are the pie charts for each state.

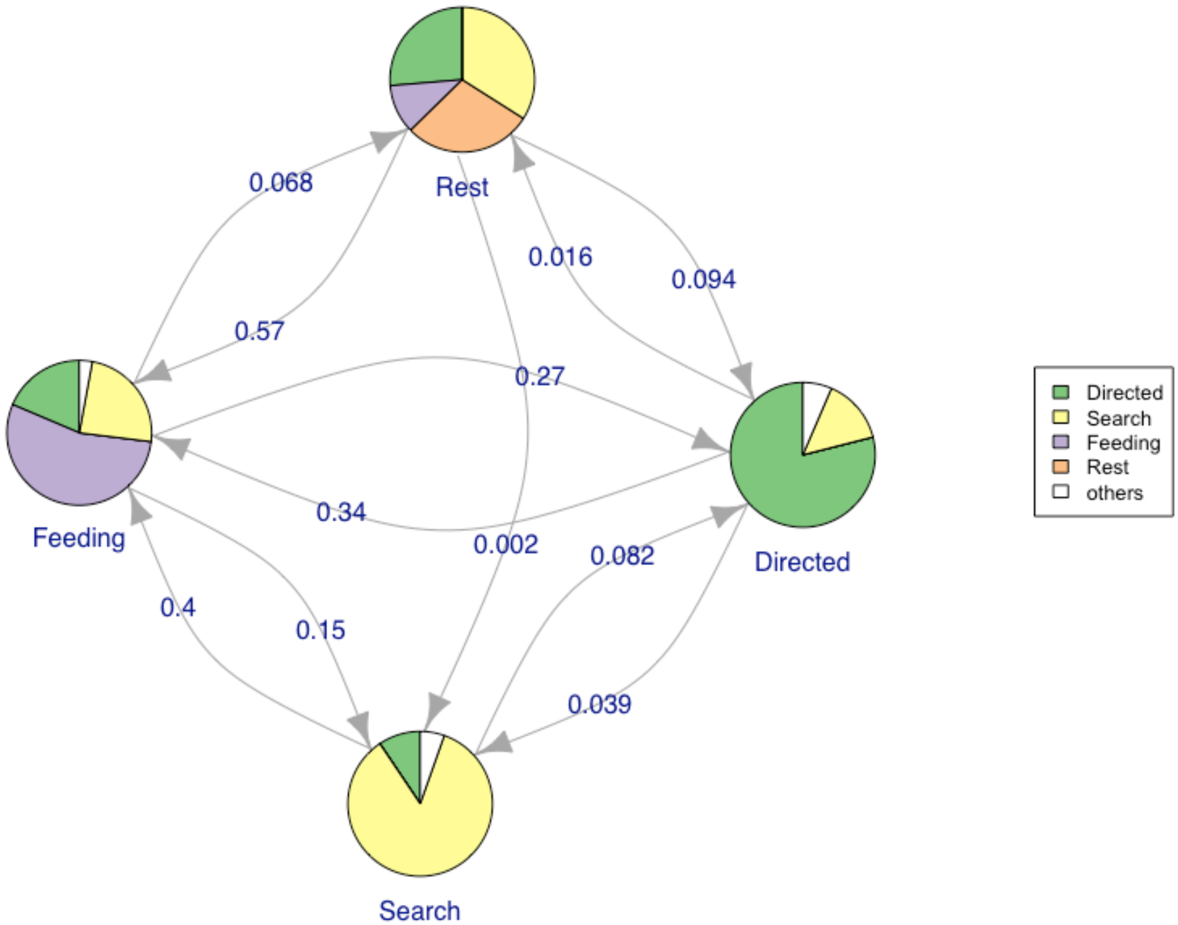

Table S8. Changes in percentages of land covers in animals home ranges to land cover used by GPS locations. A general trend of locations to favor forest habitat is visible.

	Evergreen Forest	Grassland Herbaceous	Shrubland/Scrub	Deciduous Forest	Developed Open Space	Mixed Forest
AS02	1.3%	44.7%	-37.4%	-0.1%	-0.1%	0.0%
AS1	42.3%	0.4%	-34.2%	1.7%	0.3%	0.0%
AS4	42.3%	5.6%	-36.2%	0.0%	-0.2%	0.0%
AS6	20.7%	-8.6%	-10.4%	0.0%	-0.1%	0.0%
P5	40.5%	2.2%	-32.6%	0.0%	-0.5%	0.0%
Z01	5.2%	-0.1%	-17.7%	18.4%	-0.7%	-1.0%
Z03	-30.9%	-0.1%	-1.5%	37.7%	-1.0%	-3.1%
Z05	48.8%	-0.2%	-24.0%	-17.8%	-0.8%	-1.1%
Z06	-12.7%	-1.0%	10.8%	5.5%	3.4%	-1.3%

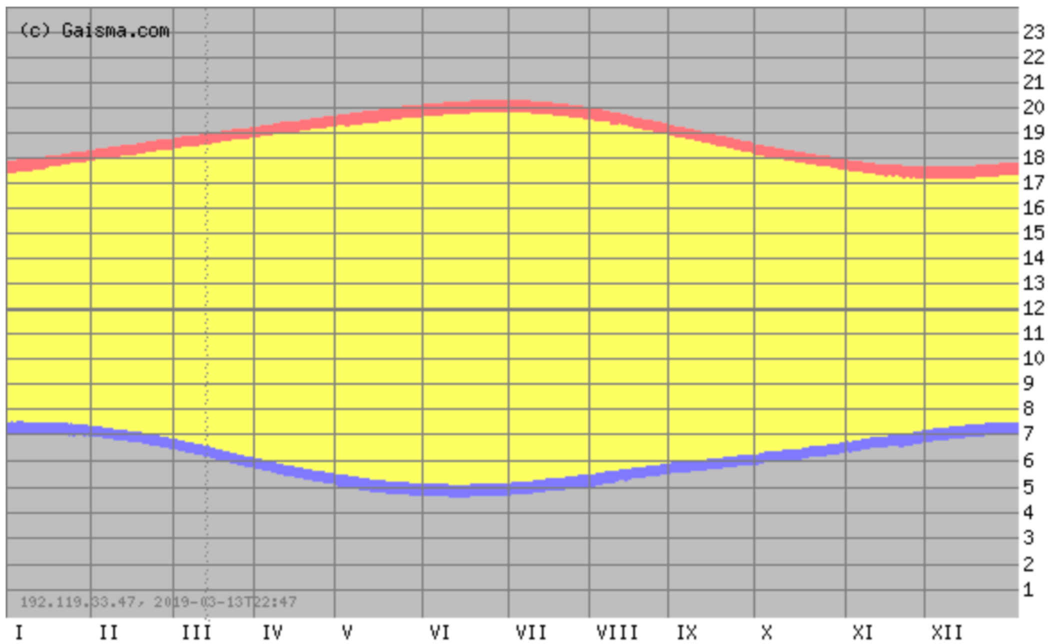

Figure S9. Daylight times for the southern part of the study area, at the Grand Canyon in Arizona. Gray areas are dark nighttime, blue is dawn, yellow is daytime, and red is dusk. Months are on x-axis, military time on the y-axis. Image adapted from Gaisma.com

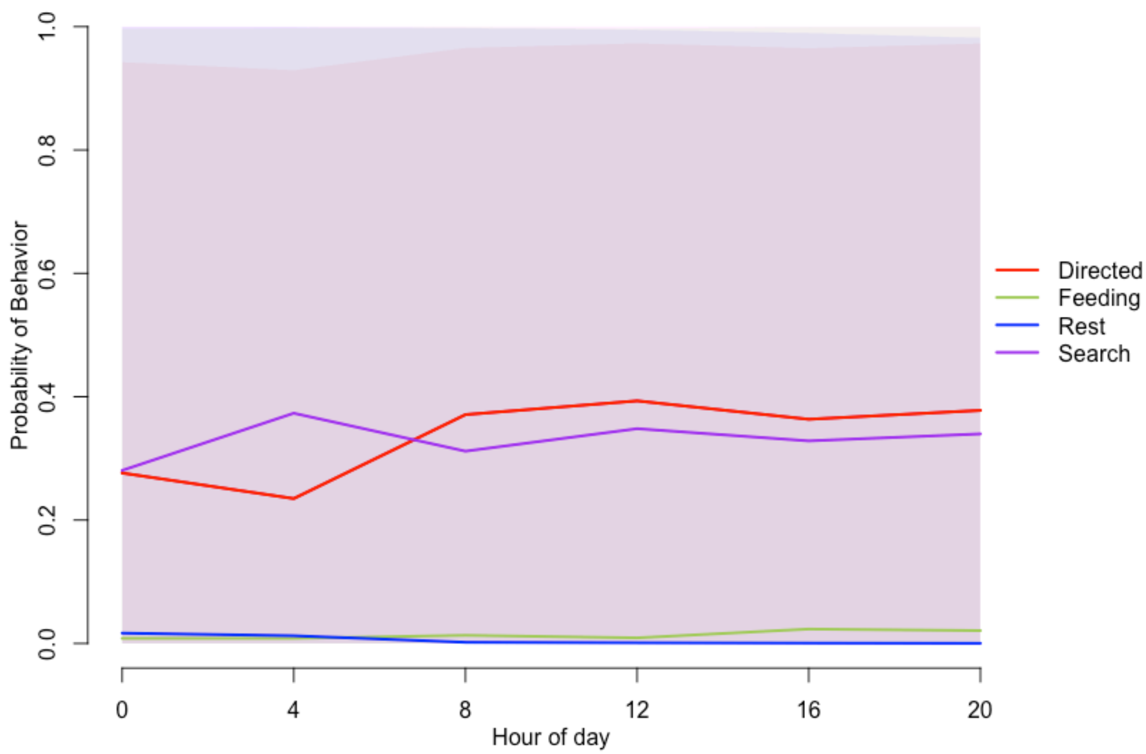

Figure S10. The marginal effects of time of day on behavior, with 95% credible intervals marked by the extent of the shading.

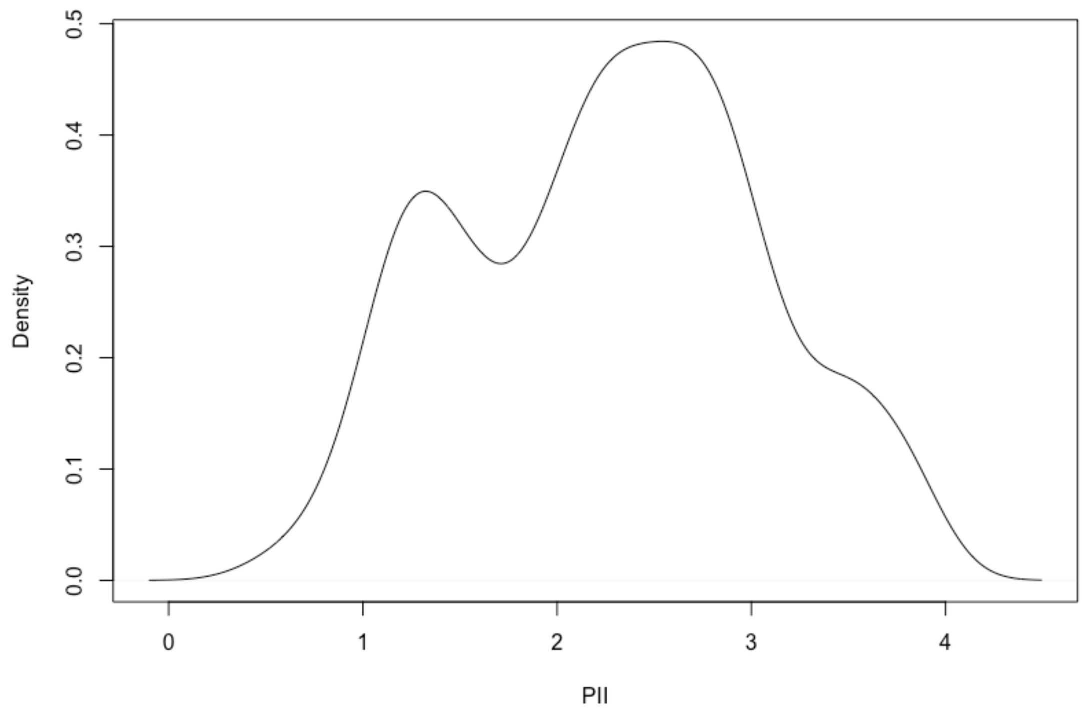

Figure S11. Density curve of PII values for dataset; note the multi-modal form, potentially relating to the 3 movement types identified in the project.

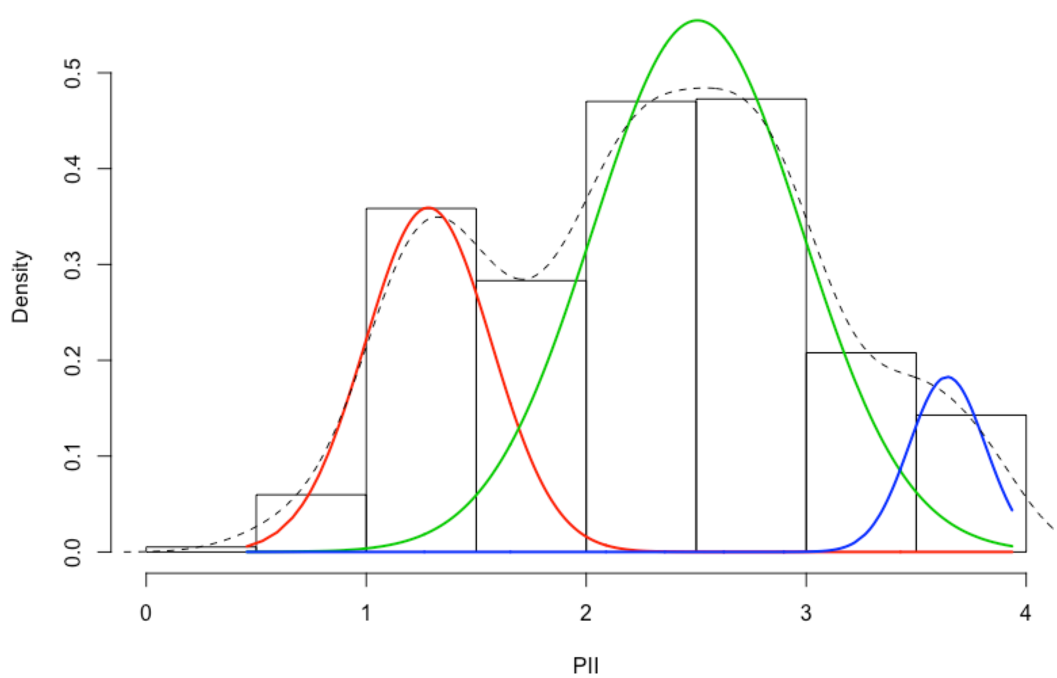

Figure S12. Mixture model of unimodal curves for the PII values. This breaks the PII density curve into a combination of underlying unimodal curves. Colors of unimodal curves are arbitrary, to simply differentiate curves.

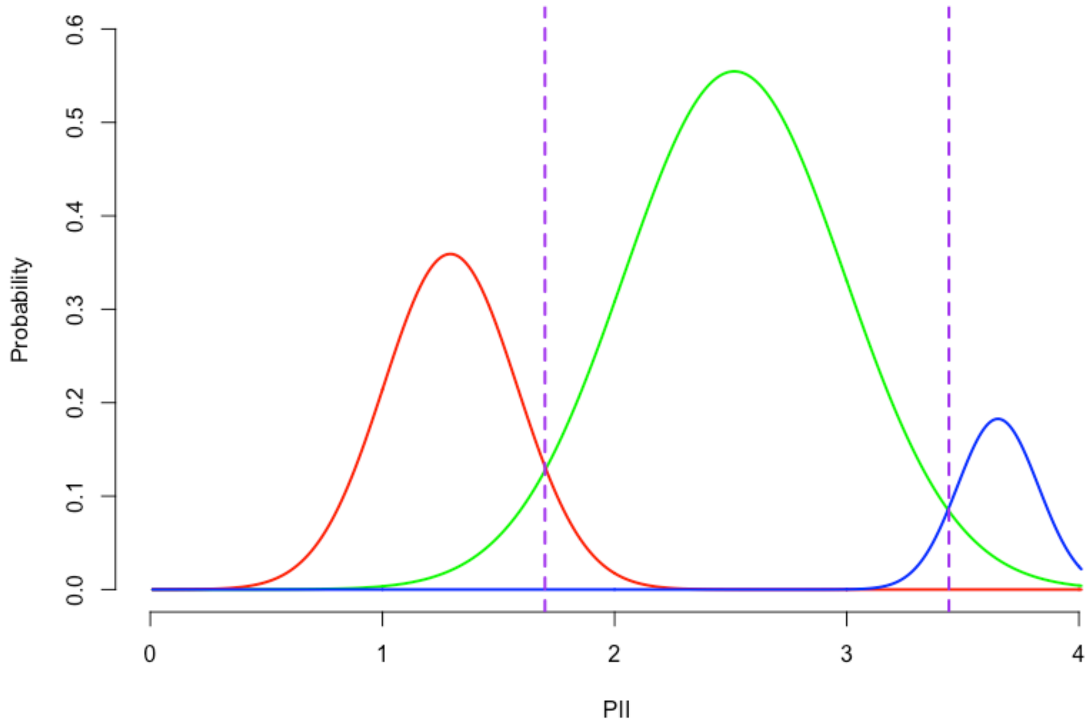

Figure S13. Intersect thresholds for the unimodal PII curves. Using the unimodal curves calculated by the mixture model, intersection points were calculated.
NOTE: all models were re-run using these threshold values, to compare to the field site-verified thresholds. No major differences were noted in model accuracy or predictive ability.

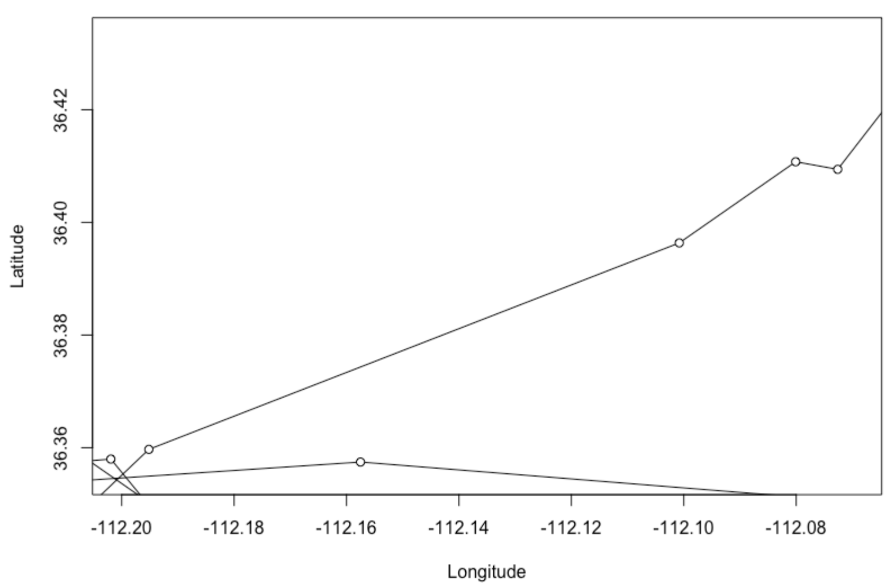

Figure S14. An example of directed movement locations, with locations showing fairly fast, straight movement pattern.

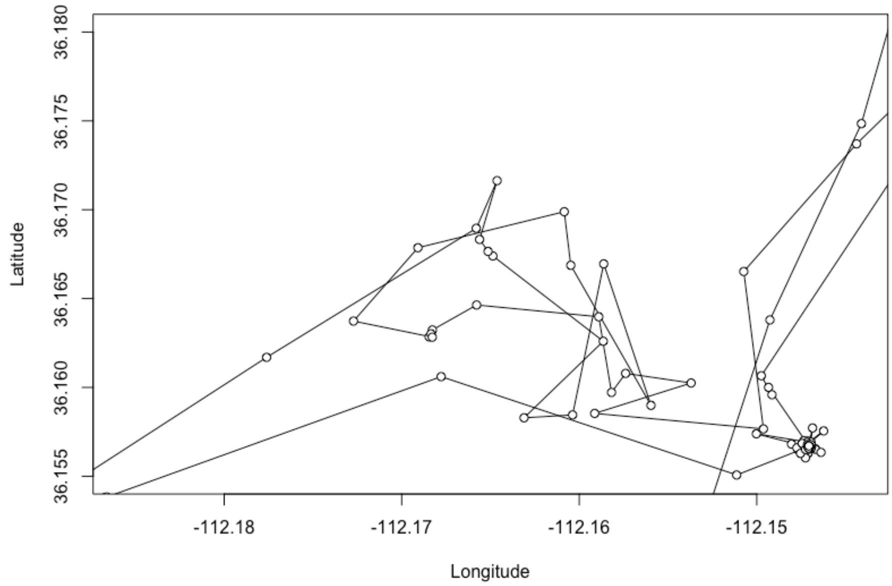

Figure S15. An example of searching locations, with locations showing slower, zigzagging and circuling movement patterns.

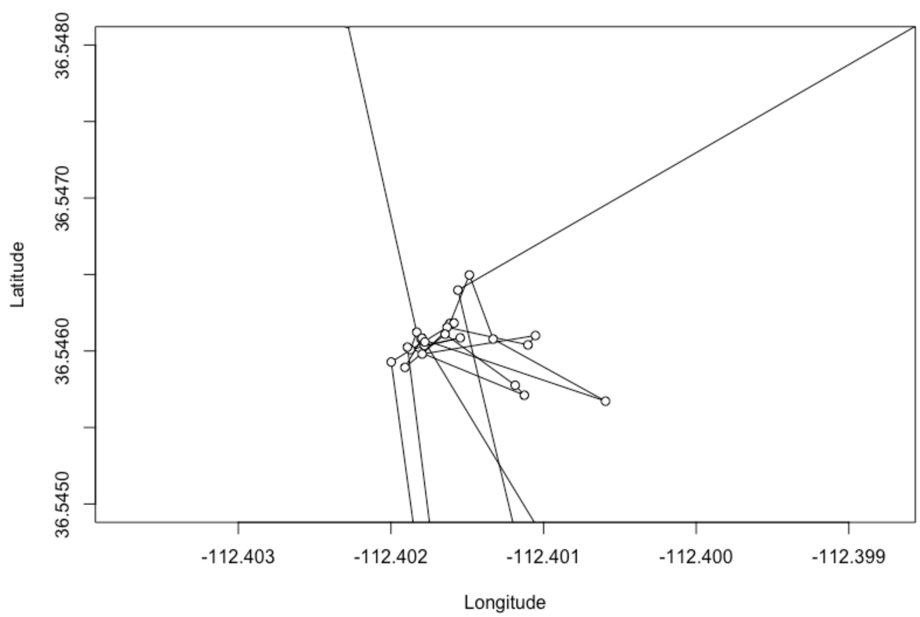

Figure S16. An example of stationary locations, with locations overlapping on top of one another and showing little movement.

Table S9. Summary statistics of home range size (km^2) for each cougar, along with average amount of each land cover in each home range.

	Individual ID								
Viewshed	**AS02**	**AS1**	**AS4**	**AS6**	**P5**	**Z01**	**Z03**	**Z05**	**Z06**
Mean	1.62E-02	1.27E-01	2.00E-01	2.68E-02	6.25E-01	3.92E+00	6.81E+00	1.17E+00	3.40E+01
Variance	5.15E+02	1.58E+06	4.14E+05	1.78E+03	5.31E+06	5.12E+07	3.56E+07	NA	2.10E+09
Median	1.62E-02	8.62E-04	1.21E-03	6.63E-04	1.29E-03	4.90E-01	6.18E+00	1.17E+00	1.11E+01

	Landcover Type					
Viewshed	**Deciduous Forest**	**Developed Open Space**	**Evergreen Forest**	**Grassland & Herbaceous**	**Mixed Forest**	**Shrubland/Scrub**
Mean	6.72E+00	1.92E+00	1.05E+00	4.60E-01	1.05E+01	1.01E+01
Variance	5.77E+07	1.11E+07	5.70E+07	4.56E+06	NA	5.29E+08
Median	4.14E+00	7.51E-03	2.26E-03	2.78E-03	1.05E+01	1.52E+00