



Energetics and fear of humans constrain the spatial ecology of pumas

Barry A. Nickel^{a,1} , Justin P. Suraci^a , Anna C. Nisi^a , and Christopher C. Wilmers^a

^aCenter for Integrated Spatial Research, Environmental Studies Department, University of California, Santa Cruz, CA 95064

Edited by Alan Hastings, University of California, Davis, CA, and approved December 2, 2020 (received for review March 23, 2020)

Energetic demands and fear of predators are considered primary factors shaping animal behavior, and both are likely drivers of movement decisions that ultimately determine the spatial ecology of wildlife. Yet energetic constraints on movement imposed by the physical landscape have only been considered separately from those imposed by risk avoidance, limiting our understanding of how short-term movement decisions scale up to affect long-term space use. Here, we integrate the costs of both physical terrain and predation risk into a common currency, energy, and then quantify their effects on the short-term movement and long-term spatial ecology of a large carnivore living in a human-dominated landscape. Using high-resolution GPS and accelerometer data from collared pumas (*Puma concolor*), we calculated the short-term (i.e., 5-min) energetic costs of navigating both rugged physical terrain and a landscape of risk from humans (major sources of both mortality and fear for our study population). Both the physical and risk landscapes affected puma short-term movement costs, with risk having a relatively greater impact by inducing high-energy but low-efficiency movement behavior. The cumulative effects of short-term movement costs led to reductions of 29% to 68% in daily travel distances and total home range area. For male pumas, long-term patterns of space use were predominantly driven by the energetic costs of human-induced risk. This work demonstrates that, along with physical terrain, predation risk plays a primary role in shaping an animal's "energy landscape" and suggests that fear of humans may be a major factor affecting wildlife movements worldwide.

ecology of fear | energy landscape | movement ecology | large carnivore | accelerometry

Despite broad recognition that both energetic demands and avoidance of risk from predators shape animal decision-making across contexts, these factors have traditionally been examined separately when considering wildlife movement behavior and space use. Animal movement is an energetically expensive activity (1–3) that also plays a primary role in risk avoidance (4, 5). Yet the recently popularized “energy landscape,” which describes the effects of the physical environment on energetic costs of movement (6, 7), has yet to be integrated with the “landscape of fear,” defined as spatial variation in perceived risk from predators (8, 9). Combining fear and energetic costs of movement in a common currency across broad spatial scales may dramatically improve our ability to predict space use in free-living wildlife.

Integrating these two constraints on movement may be particularly crucial for understanding space use by large carnivores living in human-dominated landscapes. The cost of locomotion for these highly mobile species can be substantial, such that slight variations in the physical landscape can have profound impacts on movement costs and path choice (10–12). Large carnivores also face significant mortality risk from the human “super predator” (13), and resulting fear-based changes in space use (14–17) may also exert energetic costs by affecting the areas selected (e.g., for safety) and how carnivores move (e.g., travel speed, locomotion strategy) when in proximity to humans. At the smallest scales, movement reflects immediate behavioral responses to internal

states or external cues (18, 19), which, when integrated over longer time periods, lead to large-scale patterns of space use, including home range formation (20, 21). Thus, physical (e.g., topographic) and risk-based constraints on fine-scale movement may scale up to determine landscape-level patterns of large carnivore space use, including home range size (Fig. 1). However, the impacts of such physical vs. ecological constraints on large carnivore spatial ecology remain largely unknown.

As a far-ranging carnivore that often occupies rugged terrain and is known to fear humans (22), the puma (*Puma concolor*) provides a distinct opportunity to quantify how the energetic costs of the physical landscape and risk avoidance shape large-scale patterns of space use. Despite incurring large transport costs due to their natural history, large body size, and low aerobic capacity (11, 23, 24), pumas persist in what would appear to be energetically challenging habitats (11, 25), including areas dominated by humans (22, 26), whose presence may exacerbate the costs of challenging physical terrain. This study uses high temporal and spatial resolution GPS and triaxial accelerometer data to understand how the physical and risk landscapes interact to shape the movement ecology of free-ranging pumas through their effects on energy. We quantify the step-level energetic costs of travel attributable to landscape features and human-derived risk, and test whether these short-term energetic costs lead to impacts on the overall extent of puma space use at the landscape scale.

Results and Discussion

We deployed combined GPS/accelerometer collars on 13 adult pumas (5 females, 8 males; Fig. 2) living in the Santa Cruz Mountains of central California, a rugged, 1,700-km² study area

Significance

The physical landscape and the need to avoid predation risk both exert costs on animal movement. Yet how these fundamental factors interact to ultimately determine wildlife space use remains unknown, leaving open the question of how short-term movement costs drive long-term processes such as home range formation. We used data from collared pumas (*Puma concolor*) to integrate the costs of physical terrain and predation risk (from humans) in a common currency, energy. We show that both factors affect short-term movement costs and that, cumulatively, short-term costs constrain long-term space use (e.g., home range area). The relatively greater short- and long-term energetic cost of avoiding human-induced risk highlights the important role that risk plays in shaping an animal's "energy landscape."

Author contributions: B.A.N. and C.C.W. designed research; B.A.N. performed research; B.A.N. and J.P.S. analyzed data; and B.A.N., J.P.S., A.C.N., and C.C.W. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

Published under the PNAS license.

¹To whom correspondence may be addressed. Email: bnickel@ucsc.edu.

This article contains supporting information online at <https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2004592118/-DCSupplemental>.

Published January 25, 2021.

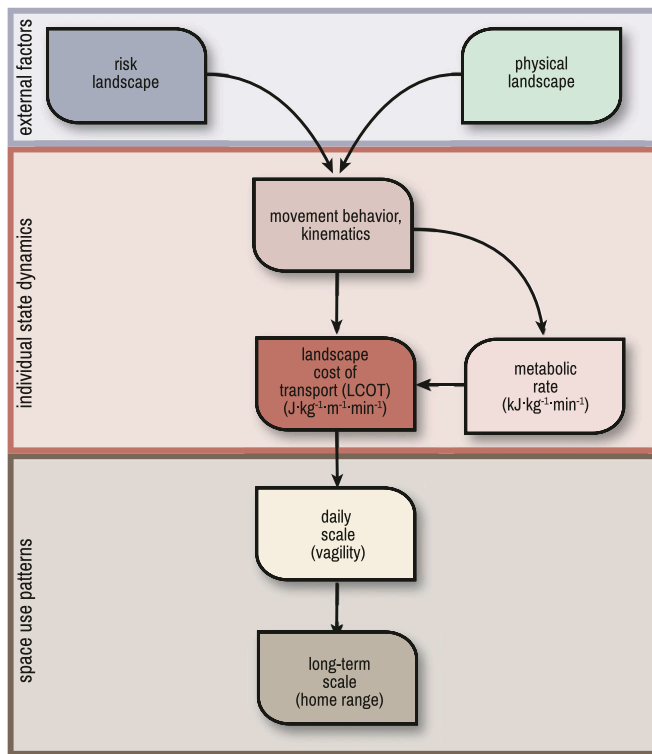


Fig. 1. A conceptual framework linking the physical and risk landscapes to patterns of space use in pumas. External factors including the physical characteristics of the landscape (e.g., terrain) and spatial variation in risk from humans interact to modify puma movement behavior and kinematics, which, in turn, determine an animal's metabolic rate. Metabolic rate and movement type (e.g., directed or meandering movements) together determine the LCOT, an estimate of the efficiency with which an animal moves between two points on the landscape (see text for details). The cumulative costs of moving across the landscape ultimately determine overall vagility (i.e., daily movement distances) and home range area, large-scale space use patterns that are constrained by short-term movement costs.

ranging from dense urban development to large tracts of relatively undisturbed native forest. We used high-resolution accelerometer data (collected at 16 Hz to 32 Hz) to calculate, for each 5-min interval between GPS fixes, the mean metabolic rate (kilojoules per minute) and the landscape cost of transport (LCOT; joules per kilogram per meter per minute) defined as the energetic cost of moving between two points on the landscape (in this case, separated by 5 min). LCOT is a metric distinguished from the commonly used “cost of transport” by the incorporation of time, which permits estimation of the efficiency with which an animal moves across the landscape. The LCOT of moving between two points on the landscape will tend to increase as efficiency decreases, that is, as an animal moves more slowly or with a less directed movement path. Importantly, although metabolic rate is used to calculate LCOT, these two quantities need not covary, as high metabolic rate activities may be associated with high-efficiency (e.g., directed) or low-efficiency (e.g., tortuous) movement across the landscape. Thus, the energetic costs of movement will depend on the specific movement behavior adopted (7), and we therefore classified all puma GPS locations corresponding to movement as either “meandering” or “directed” using a Hidden Markov Model (HMM) fit to GPS and accelerometer data (GPS locations classified as stationary were excluded from the analysis; see *Materials and Methods*).

We previously used experiments to show that pumas in our study area fear humans (22) and that this fear impacts puma movement behavior (27). Fear of humans may therefore exert an

energetic cost that varies with human-induced risk across the landscape, analogous to variation in costs of traversing rugged physical terrain (28, 29). We examined the energetic costs of moving through both the physical and risk landscapes (Fig. 1) by modeling puma metabolic rate and LCOT at short time scales (i.e., using values for each 5-min GPS location) using linear mixed effects models while accounting for movement behavior (meandering or directed movement) and individual puma ID with random effects (see *Materials and Methods*). Predictor variables included a suite of terrain characteristics that may influence the cost of travel, and housing density, which effectively captures spatial variation in human-induced risk for pumas (15, 26).

At the 5-min scale, puma movement costs were influenced by both physical terrain and risk from humans (Table 1). Overall, routes on less rugged, gently sloped terrain were found to be energetically cheaper per unit distance traveled and thus more efficient pathways on the landscape for free-ranging pumas. Metabolic rate and LCOT increased with increasing ruggedness ($\beta_{MR} = 0.0014$, 95% CI = [0.0009, 0.002]; $\beta_{LCOT} = 0.0036$, 95% CI = [0.002, 0.004]) and slope ($\beta_{MR} = 0.0018$ [0.001, 0.0022]; $\beta_{LCOT} = 0.003$ [0.002, 0.004]), while increasing topographic position (TPI; indicative of areas closer to local valleys or ridgelines; see *Materials and Methods*) led to increased metabolic rate ($\beta_{MR} = 0.0045$ [0.004, 0.005]) but decreased LCOT ($\beta_{LCOT} = -0.006$ [-0.007, -0.005]). This latter result indicates that travel speeds and thus efficiency of movement are highest along easy-to-traverse valleys and ridges, suggesting that previously observed selection by pumas for such topographic features (30, 31) is motivated by reduced locomotion costs.

Housing density also had a positive effect on both short-term metabolic rate ($\beta_{MR} = 0.015$ [0.006, 0.025]; Fig. 3A) and LCOT ($\beta_{LCOT} = 0.017$ [0.003, 0.033]; Fig. 3B), indicating that pumas experience increased energetic demands and decreased movement efficiency as their exposure to human development increases. Examination of random effects terms for puma movement behavior revealed that these impacts of human-induced risk are mediated by the type of movement in which pumas were engaged. Across individuals, housing density had a strong positive effect on metabolic rate regardless of whether pumas were meandering or moving directly (Fig. 3A), evidence that pumas are consistently engaging in more energetically demanding movements (i.e., moving more quickly, stopping less) in areas of higher perceived risk from humans. However, the positive effect of housing density on LCOT was only apparent when pumas were meandering (Fig. 3B), suggesting that, despite exerting more energy on sustained movements, pumas traverse the landscape less efficiently in human-dominated areas by taking more circuitous movement paths. Investigation of time allocation data indicates that pumas indeed spend a greater proportion of time meandering (relative to more efficient directed movements) when in areas with high housing density (*SI Appendix, Fig. S1*), resulting in increased energetic costs. For instance, pumas moving through identical physical terrain in moderately developed exurban habitat (i.e., 150 buildings per km²) would expend 13% more calories per 5-min period than if moving through the same terrain in wildland habitat (i.e., areas with zero housing density; see *Materials and Methods*).

Decreased movement efficiency near humans could be driven, in part, by increased hunting behavior in areas of high housing density if, for instance, risky areas near humans are also associated with greater prey availability or increased hunting success. However, we found no evidence that black-tailed deer (*Odocoileus hemionus columbianus*), the primary prey for pumas in our study area, are more likely to occur in areas of increased housing density, as determined by an occupancy model fit to deer detections on camera traps across the study area (*SI Appendix, Table S1*). Similarly, there is no evidence that pumas in our study system preferentially hunt in or near developed areas. The

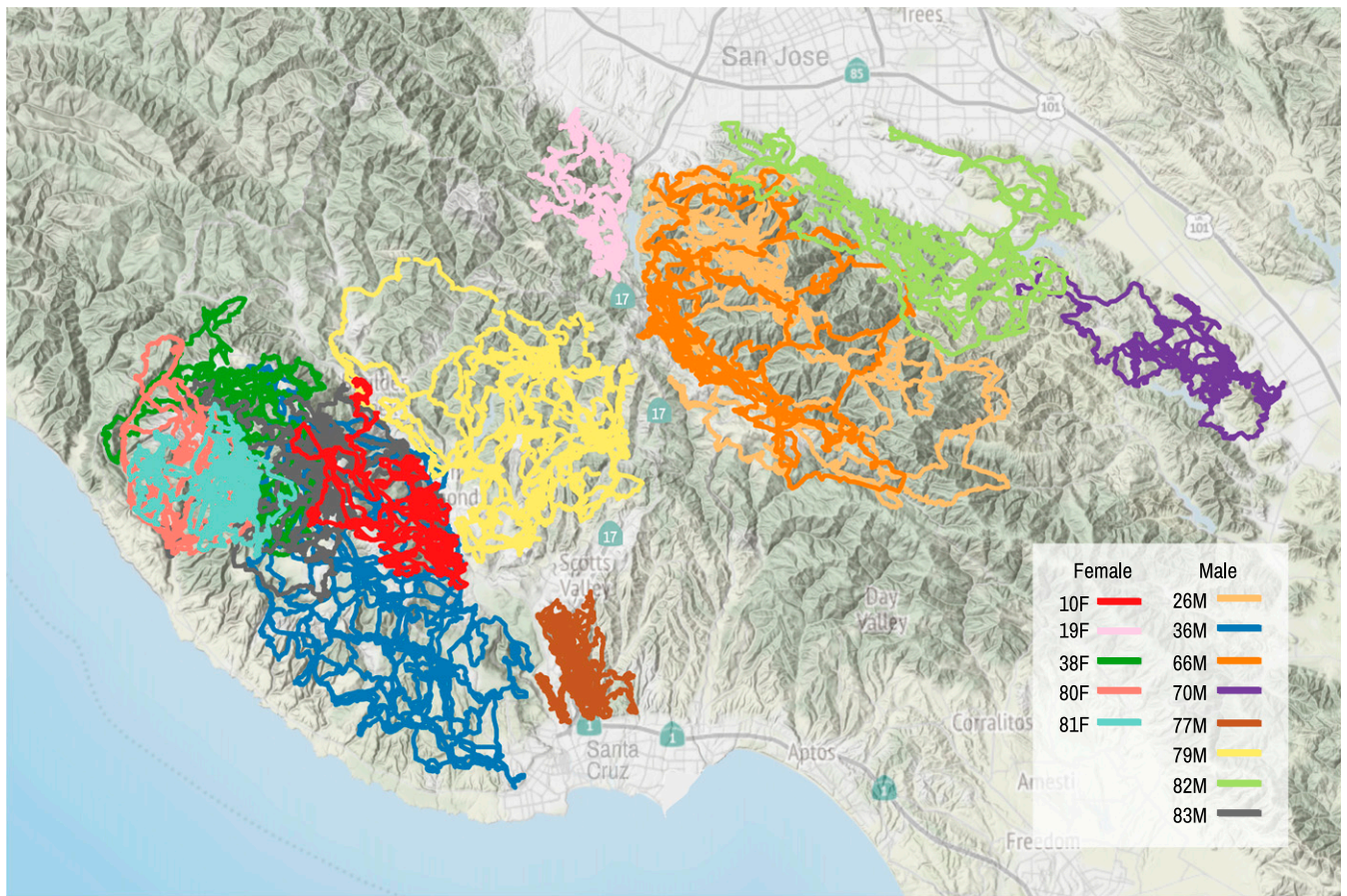


Fig. 2. Study area showing 5-min movement paths of 13 pumas.

majority of known puma kill sites in the Santa Cruz Mountains (72% of 731 kills) occurred in wildland areas, despite wildland only accounting for 63% of available habitat (*SI Appendix*). Pumas elsewhere have also been shown to strongly select against developed areas when hunting (32). Thus, it is unlikely that puma use of, or altered movement behavior in, areas of high human risk is driven by hunting. Use of high-risk areas, particularly by male pumas with large space requirements, may instead reflect the relatively limited availability of undeveloped habitat in the Santa Cruz Mountains. Some individual pumas may be displaced from higher-quality habitat by conspecifics, leading to increased use of developed areas, though further research is required to determine the degree to which space requirements and social interactions drive puma use of human-dominated landscapes.

Overall, the energetic costs of movement appear to rise more rapidly with increasing risk from humans than with increasing difficulty of the terrain (standardized effect sizes for housing density were 4 to 10 times greater than those for slope and ruggedness; Table 1), suggesting a greater impact of risk relative to physical landscape on puma movement at short time scales mediated by high-energy but low-efficiency movement behavior. Accelerometer-based estimates of energetic expenditure are known to integrate the costs of difficult terrain (33) insofar as increasing slope and ruggedness result in increased body movement. The potential for nonmovement energetic costs of difficult terrain preclude an exact comparison of the impacts of risk and physical landscape on puma energetic expenditure. However, any underestimate of the effect of terrain on energetics would need to be approximately an order of magnitude in size to reverse our conclusion that risk from humans has a greater effect

on puma movement costs than does the physical landscape (Table 1).

Despite considerable attention paid to the relationship between energetic physiology and space use across species (34–36), the degree to which energetic constraints drive differences in space use patterns within a species (i.e., at the individual level) remains unclear (37). We found that, for pumas, the short-term energetic costs of moving through the physical and/or risk

Table 1. Bayesian posterior estimates and associated 95% credible intervals for models of metabolic rate (\log_{10} [kilojoules per minute]) and LCOT (\log_{10} [joules per kilogram per meter per minute]) at the 5-min time scale

Model parameter	Posterior mean	95% credible interval
Metabolic rate		
TPI	0.0045	(0.0039, 0.0051)
Topographic ruggedness	0.0014	(0.0009, 0.0020)
Slope	0.0018	(0.0014, 0.0022)
Day (1)/night (0)	−0.008	(−0.009, −0.007)
Housing density	0.015	(0.0059, 0.0254)
TPI × slope	0.0022	(0.0018, 0.0027)
LCOT		
TPI	−0.006	(−0.007, −0.005)
Topographic ruggedness	0.0036	(0.0031, 0.0042)
Slope	0.0032	(0.0028, 0.0037)
Day (1)/night (0)	0.0061	(0.0051, 0.0069)
Housing density	0.0172	(0.0032, 0.0325)
TPI × slope	−0.001	(−0.0014, −0.0006)

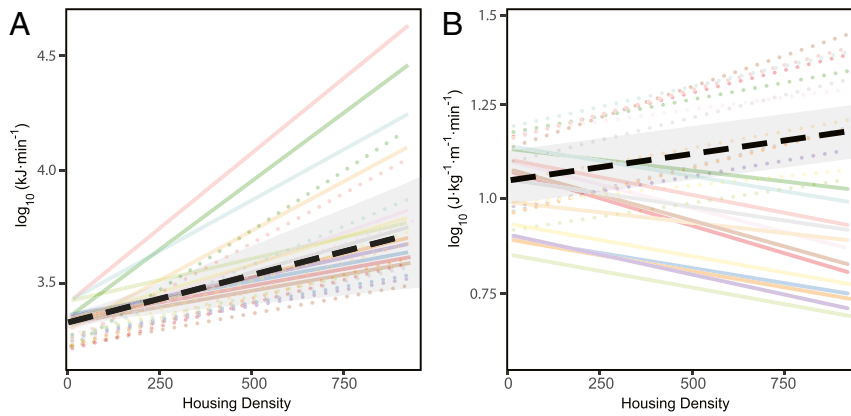


Fig. 3. Predicted effect of average housing density (200-m scale) experienced by pumas during each 5-min step on (A) metabolic rate (\log_{10} [kilojoules per minute]) and (B) LCOT (\log_{10} [joules per kilogram per meter per minute]). The black dashed line represents the posterior mean, estimated across individuals and movement types, with gray areas denoting the 95% credible interval. Random effects (colored lines) were included for each combination of movement type and individual, with solid lines indicating directed movement, dotted lines indicating meandering, and colors corresponding to individual pumas. Note that, for metabolic rate, all slopes are positive regardless of individual or movement type, while, for LCOT, positive slopes were only apparent when pumas were meandering.

landscapes scale up to impose metabolic constraints on long-term space use. For individual pumas of both sexes, the average distance traveled per day (Fig. 4A; $\beta = -0.95$ [$-1.28, -0.62$]) and home range area (Fig. 4B; $\beta = -20.13$ [$-27.3, -12.8$]) decreased sharply with increasing mean daily LCOT. Male and female pumas with the highest mean daily LCOT moved 48.4% and 28.9% (respectively) fewer kilometers per day and had 67.9% and 46.5% smaller home ranges than those animals of the same sex with the lowest daily LCOT, suggesting that pumas compensate for consistently high movement costs at the step level by reducing overall vagility and home range size (Fig. 1).

For male pumas, energetic constraints on daily and long-term (i.e., home range scale) space use appear to be driven predominantly by human-induced risk, consistent with the overall greater impact of risk on movement at short time scales. The average housing density experienced by an individual along its movement path was an important predictor of mean daily LCOT for males (Fig. 5A; $\beta = 0.02$ [$0.003, 0.042$]) and, correspondingly, had a strong, negative effect on both mean daily distance traveled (Fig. 5B; $\beta = -0.03$ [$-0.049, -0.007$]) and home range area (Fig. 5C; $\beta = -0.68$ [$-1.18, -0.23$]). Males experiencing the highest daily housing densities (186 km^{-2}) moved 61.6% fewer kilometers

per day and had 78.8% smaller home ranges than those individuals experiencing minimal housing density (i.e., 5 km^{-2}). Thus, the energetic costs associated with increasing risk from humans results in restricted space use by male pumas at both the daily and home range scales. Despite measurable costs of slope and ruggedness on short-term (5 min) movement (Table 1), we did not detect comparable effects of physical terrain on any longer-term (1 d to 60 d) measures of spatial ecology for male pumas (*SI Appendix, Table S2*), suggesting that any effects of physical terrain on space use at the landscape scale are overwhelmed by the costs of risk.

Female pumas did not exhibit a comparable relationship between housing density and longer-term space use patterns (mean daily LCOT: $\beta = 0.0007$ [$-0.06, 0.05$]; mean daily travel distance: $\beta = 0.003$ [$-0.06, 0.09$]; home range area: $\beta = -0.00008$ [$-0.86, 0.96$]; *SI Appendix, Table S2*), which could reflect the somewhat lower sample size for females in this study (five females vs. eight males), but may, in fact, be driven by real differences between males and females in the cumulative impacts of risk on space use. To maximize mating opportunities, male pumas must maintain large territories through near-constant patrolling, and thus often have home ranges that are several times the size of (and overlap with multiple) female home ranges (38). This requirement to

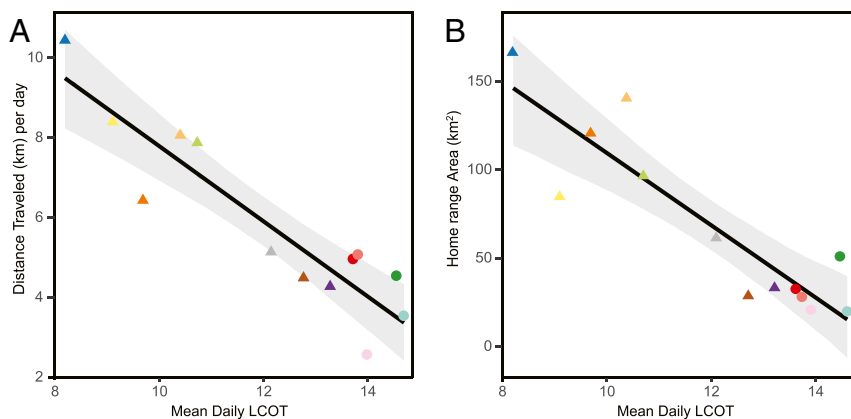


Fig. 4. The effect of average daily LCOT on (A) mean daily travel distance (kilometers) and (B) home range area (square kilometers). The data are symbolized by individual (color) and sex, i.e., female (circle) and male (triangle). Solid lines represent the posterior mean, and gray areas enclose the 95% credible interval of each regression.

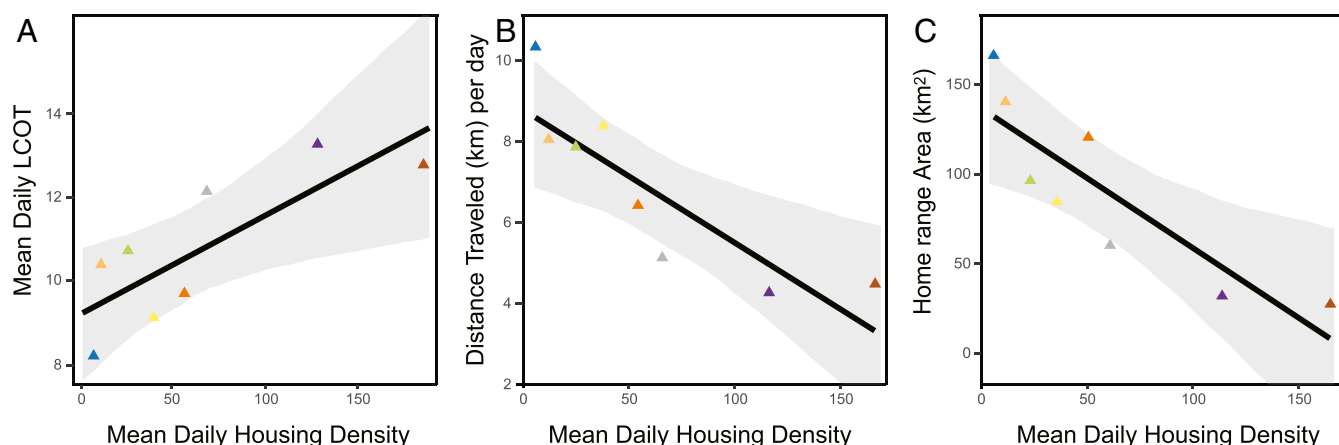


Fig. 5. Effect of mean daily housing density on (A) mean daily travel distance (kilometers), (B) home range area (square kilometers), and (C) mean daily LCOT for male pumas. Each individual puma is represented by a different color. Solid lines represent the posterior mean, and gray areas enclose the 95% credible interval of each regression. Female pumas showed no significant relationship between housing density and landscape-scale space use (SI Appendix, Table S2).

maintain large mating territories likely places a substantially higher premium on energetically efficient movement for male pumas than for females, whose home ranges only need to be large enough to provide sufficient hunting opportunities (39). The impact of human-induced risk on movement efficiency at short time scales (Fig. 3) may therefore result in greater cumulative costs for males at the landscape level, constraining space use where overlap with humans is high (Fig. 5).

By integrating the costs of both challenging physical terrain and risk from predators into a common currency (i.e., energy), our results reveal a framework linking step-level movement behavior to landscape-scale patterns of space use (Fig. 1). We show that the combination of the physical and risk landscapes drives short-term movement costs for pumas, and that such short-term costs, particularly those stemming from human-induced risk, scale up to influence long-term movement patterns, constricting overall space use by up to 78% for individuals experiencing consistently high costs at the step level (Fig. 1). This work provides an important extension of recent attempts to quantify the effects of the landscape on animal movement costs and pathways (6, 7) by highlighting that, without accounting for predation risk, such “energy landscapes” may overlook much of the energetic cost of navigating a complex environment.

Indeed, our results demonstrate that risk from humans plays a primary role in driving puma energetic costs, which, at least for males, must be compensated for by reduced vagility and space use at the landscape scale. A recent global analysis shows that a wide range of mammal species exhibit lower vagility with increasing human footprint on the landscape, which the authors attribute to movement barriers or changes in resource availability (17). We suggest that the energetic costs of avoiding risk from humans may itself lead to reduced long-term space use for many wildlife species living in human-dominated landscapes, potentially contributing to the global trend of diminished movements near people. Our findings demonstrate that behavioral changes induced by the fear of humans can substantially impact an animal’s energy budget, in this case, exacerbating the already high energetic demands of a large carnivore (11, 24, 40). Managing risk from people may therefore come at the cost of reductions in a range of other crucial behaviors, including long-range movements and territorial defense.

Materials and Methods

Study Area. This research was conducted in the Santa Cruz Mountains (37°10' N, 122°3' W), which lie in the Central Coast region of California (Fig. 1). In the study area, pumas primarily feed on black-tailed deer (*O. h. columbianus*) but occasionally on other species, including wild boar (*Sus scrofa*), raccoons

(*Procyon lotor*), and domestic cats (41). The 2,800 km² study area is bisected by a large freeway and is further crisscrossed by numerous smaller roads providing access to rural houses and developments. See Wilmers et al. (15) for further details on the study area.

Data Collection. Starting in 2015, we captured wild pumas, using trailing hounds or cage traps, as described in ref. 15. Each animal was tranquilized using Telazol and sexed, weighed, aged, and fitted with a combined GPS/accelerometer collar (Vectronics Aerospace GPS PLUS and GPS Vertex). Each collar was programmed to acquire a GPS fix every 5 min and triaxial acceleration at a frequency of 16 Hz to 32 Hz for a duration of 2 mo. The GPS sampling interval was chosen to maximize relocations while ensuring that each animal could traverse their home range multiple times before the collar battery died.

We recorded 247,110 GPS locations for 13 pumas (5 females, 8 males; see Fig. 2 for distribution) for a mean (\pm SE) of 19,009 (\pm 753) locations per animal. The mean (\pm SE) number of days that we recorded location data from each puma was 66 (\pm 3) days. The GPS fix success rate ranged from 98.2 to 99.9% with a mean (\pm SE) of 99.2% (\pm 0.2) across all collars.

Derivation of Energetic Cost. We calculated the energetic expenditure of wild collared pumas using previously derived relationships between triaxial accelerometer data and puma energetics from experimental trials of captive pumas moving on treadmills (11). The link between puma energetics and collar data are given by

$$\dot{V}_{O_2} = 3.52 + 58.42(\text{ODBA}) \quad [1]$$

$$(r^2 = 0.97),$$

where \dot{V}_{O_2} (milliliters of O₂ per kilogram per minute) is the amount of oxygen consumed over 1 min, and overall dynamic body acceleration (ODBA) is the sum of the absolute value of each accelerometer axis summed over 1 min (11). Oxygen consumption was then converted to kilojoules expended per minute as previously described (11, 42). We then estimated mean metabolic rate (kilojoules per minute) as the average of kilojoules expended per minute over each 5-min period between successive GPS locations. We also derived a metric, which we call the LCOT, calculated as the mean of 1-min increments of cost of transport (COT, as calculated in ref. 11) over each 5-min period. While COT has units of joules per kilogram per meter, LCOT has units of joules per kilogram per meter per minute. Because LCOT integrates across both space and time, it measures the average energetic cost of moving between two points on the landscape. As such, LCOT generally increases with the tortuosity of the movement path and the time taken to travel between two points.

It is important to note that collar-derived energetic values calculated from ODBA specifically reflect kinematic energetic expenditure associated with body movement but do not integrate nonmovement energetic costs such as those from thermoregulation or stress (43). For most terrestrial mammals, however, locomotion is known to account for the majority of energetic expenditure beyond that from baseline metabolism (1, 3, 43), so ODBA-derived

energetic estimates should therefore provide a reasonable estimate of the influence of landscape covariates on puma energetic outlays.

The degree to which ODBA captures, for a set speed, the increased metabolic costs of moving on an incline relative to moving on level ground has not been evaluated for pumas, and thus it remains possible that ODBA underestimates the total energetic costs that pumas experience when moving across a slope. However, underestimates of the energetic costs of slope are likely to be minimal for four reasons. 1) This question has been addressed in humans: Bidder et al. (33) showed that, at a given speed, ODBA is higher for humans walking on an incline relative to level ground, indicating that ODBA does capture increased metabolic costs associated with moving on an incline. 2) In captive pumas, the difference in metabolic costs (i.e., \dot{V}_{O_2}) between moving on an incline vs. level ground decreases with decreasing walking speed (44) such that, at speeds below $\sim 0.3 \text{ m}\cdot\text{s}^{-1}$, this difference becomes statistically indistinguishable. We observed a mean speed of $0.35 \text{ m}\cdot\text{s}^{-1}$ on slopes greater than zero in our dataset. 3) Recent research demonstrates that pumas in the wild alter their behavior to minimize the costs associated with steep terrain by both slowing down and selecting movement paths along contours that avoid steep angles (44), behavioral adjustments that are well captured by our ODBA-based methods. 4) Finally, we did not detect an effect of any terrain variable (slope, ruggedness, TPI) on long-term measures of puma space use (i.e., daily distance traveled and home range size; *SI Appendix, Table S2*). As these long-term space use measures are derived independently of our short-term energetic cost estimates, these results suggest that any cumulative costs of moving across difficult terrain are relatively minor.

Identifying Movement Behaviors. We identified movement modes from GPS and accelerometer data in order to account for differences in energetic expenditure between movement behaviors. We fit a three-state HMM using the combined GPS and accelerometer data to distinguish between three behavioral classes: stationary, meandering, and directed movement (42). The stationary state represents behaviors such as resting, feeding, and grooming, while the meandering and directed states are often associated with avoidance and foraging behaviors, or transit and territorial patrol, respectively (42).

Using the R package *momentuHMM* (45), the movement of each individual was classified into one of three underlying states by characterization of the distributions of travel distances, turning angles, and metabolic rate (kilojoules per minute) between consecutive locations. We calculated travel distance between successive 5-min GPS locations as the Euclidean distance between the locations (x_t, y_t) and (x_{t+1}, y_{t+1}) , and turning angle is calculated as the change in bearing ($b_t = \text{atan2}(y_{t+1} - y_t, (x_{t+1} - x_t))$) between the intervals $[t - 1, t]$ and $[t, t + 1]$. For this HMM, Gamma distributions were used to describe travel distances and metabolic rates, a von Mises distribution described the turning angles, and the Viterbi algorithm was used to estimate the most likely sequence of movement states to have generated the observations (46).

We began with the assumptions that resting behavior was characterized by very short travel distances, sharp turning angles, and low energy expenditure; meandering movement was characterized by moderate travel distances, sharp turning angles, and moderate energy expenditure; and directed movement was characterized by longer travel distances, small turning angles, and higher energy expenditure. Therefore, initial state-dependent probability distribution parameters for travel distance were set at $10 (\pm 5) \text{ m}$ when pumas were resting, $50 (\pm 25) \text{ m}$ when meandering, and $125 (\pm 50) \text{ m}$ when engaged in directed movement. Initial parameters for turn angles were set at $\pi/2$ radians when resting or meandering and 0 radians when directly moving. Angle concentration for each state was initially set at 1. For mean metabolic rate, initial parameters were approximated as $10 (\pm 5) \text{ kJ}\cdot\text{min}^{-1}$, $25 (\pm 5) \text{ kJ}\cdot\text{min}^{-1}$, and $35 (\pm 5) \text{ kJ}\cdot\text{min}^{-1}$ for resting, meandering, and directed movement, respectively (11, 42).

Data from periods of relative inactivity (e.g., resting) can appear similar to those from periods of meandering behavior, due to bias from GPS measurement error (47). Thus, to better distinguish between these behaviors, we also characterized clusters of GPS locations that were potential kill sites, day beds, or short-term stops during travel. We developed a custom program using the Python programming language (v. 2.7.9; Python Software Foundation) to define clusters as groups of three or more locations in which each location was within 25 m of the cluster centroid and 1 h of another GPS location of the same individual puma. Identified clusters representing resting behavior were then assigned as known states within the HMM framework. Results of the three-state movement model identified resting as the most common behavioral state for all animals, with only 20.7% (± 1.7) of the locations attributed to one of the movement-based behaviors—meandering

and directed. When engaged in movement-based behavior, both states were predicted at roughly equal proportions and occurred predominantly at night, with a mean ($\pm \text{SE}$) of 73.6% (± 1.7) of locations occurring between local sunrise and sunset. Because we were interested here in the energetic costs arising from locomotion, we excluded, from subsequent analysis, points identified as stationary behavior, focusing only on the predicted movement-based behaviors, meandering and directed travel.

Natural and Anthropogenic Landscape Covariates. To assess the roles that challenging terrain and potential risk from humans play in modulating puma energy costs, we included several topographic and risk-related covariates hypothesized to directly affect puma energetic expenditure. While other landscape variables such as land cover type (e.g., grassland vs. forest) are known to affect puma habitat use (15, 48), our interest here is on features of the landscape expected to have the greatest impact on locomotor costs (44). We therefore focused our analyses on topographic measures including local slope, terrain ruggedness, and TPI derived from a digital elevation model [DEM; (49)]. Local slope represents the magnitude of the steepest gradient in elevation at a location and was calculated using the average maximum technique (50). Ruggedness was calculated based on the vector ruggedness measure developed by ref. 51. TPI denotes position on the landscape relative to local ridges or valleys and was calculated as the absolute difference between elevation at a location and the mean elevation within a given distance away (52).

In order to test whether pumas experience increased energetic demands in close proximity to risky human-modified habitat, we used kernel density estimation to calculate a housing density surface as outlined in ref. 15 using a bandwidth of 200 m corresponding to the approximate scale at which pumas respond to human development when traveling (15). All covariates were rasterized with a $30 \times 30 \text{ m}$ pixel size, and mean values were calculated for each linear segment between consecutive GPS locations along an individual's movement path. All covariates were standardized (mean centered and scaled by 1 SD) to improve model convergence and to facilitate comparison of model coefficients among covariates (53). We also made sure that no covariates exhibited high levels of collinearity ($r > 0.7$).

Modeling Spatial Drivers of Step-Level Energetic Costs. To evaluate the local influence of the physical and risk landscapes on the relative energetic cost of movement, we regressed \log_{10} mean metabolic rate (kilojoules per minute) and \log_{10} LCOT (joules per kilogram per meter per minute) for each 5-min step against the terrain and risk covariates using linear mixed effects regression models (LMM), hereinafter referred to as the MR-LMM or LCOT-LMM model, respectively. To account for interindividual variation in energetic expenditure due to behavior-specific differences, we included movement mode (i.e., “meandering” or “directed”) nested within individual animal as a random intercept and also included a nested random slope on the effect of housing density (see below). As noted above, both metabolic rate and LCOT were derived from \dot{V}_{O_2} (transformed using known constant values), itself a model-derived quantity estimated (with associated error) from ODBA. We therefore propagated the uncertainty associated with each \dot{V}_{O_2} estimate into the MR-LMM and LCOT-LMM models using a Bayesian hierarchical approach. We first estimated the error associated with the conversion from ODBA to \dot{V}_{O_2} directly from the linear regression analysis described in ref. 11 and calculated the percent error of this relationship as the SD of the slope divided by the slope coefficient estimate. Following conventional error propagation procedures, we then used this percent error value to derive an observation error estimate, σ_o^2 , for each observed value of MR and LCOT by multiplying the observed value by the percent error. We incorporated this observation error into our analysis using the following model:

$$z_{ijk} = \beta_{0jk} + \beta_{1jk} HD_i + \beta \mathbf{X}_i + \epsilon_i$$

$$\epsilon_i \approx N(0, \sigma_p^2)$$

$$y_{ijk} \approx N(z_{ijk}, \sigma_o^2),$$

where z_{ijk} is the unobserved “true” value of MR or LCOT for observation i with movement mode j by puma k ; z_{ijk} is modeled as a linear function of housing density (HD) and other covariates (\mathbf{X} , including terrain and time of day) with residual error ϵ_i , which is normally distributed with mean zero and variance σ_p^2 . Our observed values of MR and LCOT, y_{ijk} , were then modeled as estimates of the true value with observation error σ_o^2 . β_{0jk} is a random

intercept, and β_{ijk} is the slope for HD , with each consisting of a random effect for movement mode j (meandering or directed) nested within puma k . The random intercept is given by

$$\beta_{0jk} \approx N(\beta_{0k}, \sigma_{\beta_{0k}}^2)$$

$$\beta_{ijk} \approx N(\mu_{\beta_{ijk}}, \sigma_{\beta_{ijk}}^2),$$

where $\sigma_{\beta_{0k}}^2$ is an error term describing the variance between movement modes for a given puma, and $\mu_{\beta_{ijk}}$ and $\sigma_{\beta_{ijk}}^2$ are hyperparameters common to all pumas. The random slope, β_{ijk} , was modeled in the same way.

Effects of Risk and Terrain on Spatial Ecology at the Landscape Scale. To assess whether the energetic costs of movement drive long-term patterns of space use, we examined the effects of LCOT, terrain, and housing density on daily travel distances and home range sizes. We calculated mean LCOT as the average of all 5-min LCOT values experienced by a puma over its collar deployment. Mean housing density, slope, ruggedness, and TPI were similarly calculated as the average across all 5-min steps for a given puma. We calculated mean daily travel distance (kilometers) by summing daily GPS-track distances for an individual puma and taking the average across all 24-h periods for the puma's collar deployment. Home range areas (square kilometers) were obtained using a fixed local convex hull (k-LOCOH; $\bar{k} = 115$) home range estimator fit to all locations for an individual puma, with the 95% isopleth representing the home range boundary (54, 55). Previous simulation efforts have revealed that k-LOCOH estimates of home ranges have error rates of ~9% (55). As such, to address uncertainty in our estimates of home range size, we incorporated this observation error into our analyses using a Bayesian approach (see below).

We regressed mean daily travel distance and home range area against each of the energetic (mean LCOT) and landscape variables (mean housing density, slope, ruggedness, and TPI) in separate Bayesian linear regression models, using individual pumas as the unit of replication. We also evaluated whether mean daily LCOT was influenced by the average housing density

experienced by an individual along its movement path. For models in which home range areas or mean daily LCOTs were used as response variables, we used an observation error model analogous to that presented above to propagate the error around these estimates through our analyses. All landscape scale models were run with data from both sexes pooled and also analyzed separately to account for any life history differences in space use (see *Results and Discussion* and *SI Appendix, Table S2*).

For all Bayesian models (i.e., step level and landscape level), we specified a Normal ($\mu = 0$, $\sigma = 1,000$) prior for coefficient estimates and a diffuse Uniform (0, 100) prior for SDs. Models were run with three chains for 2,000 iterations with 1,000 burn in iterations.

We confirmed model convergence via the Gelman–Rubin statistic (“R-hat” values < 1.1 for all parameters) (56). We tested model fit using Bayesian P values, which compare test statistics calculated from observed and expected (i.e., model-generated) data (57). As all models employed Gaussian distributions, we used the mean and coefficient of variation to calculate Bayesian P values (57). We found satisfactory fit between model and data for all models ($0.45 \leq P \leq 0.63$). We calculated the posterior means and 95% credible intervals for model coefficients and considered credible intervals that do not include zero to indicate a significant effect.

All statistical analyses were performed using the language R (v. 4.0.2; R Development Core Team, 2010), the rstan (58) package for interfacing with Stan (59), and the adehabitatHR (60) package for home range estimation.

Data Availability. Data have been deposited in <https://github.com/Center-for-Integrated-Spatial-Research/puma-energy-fear-landscape/>.

ACKNOWLEDGMENTS. We thank P. Houghtaling, R. King, C. Fust, S. McCain, and K. Briner for help in the field and many undergraduate volunteers for assistance with fieldwork. We thank the California Department of Fish and Wildlife, C. Wylie, D. Tichenor, B. Milsap, and T. Collinsworth for their assistance capturing pumas, and the many landowners that have allowed us access to their property. Funding was provided by the Gordon and Betty Moore Foundation and NSF (Grants 1255913 and 0963022 to C.C.W.). Portions of the paper were developed from the thesis of B.A.N.

1. T. J. Garland, Scaling the ecological cost of transport to body mass in terrestrial mammals. *Am. Nat.* **121**, 571–587 (1983).
2. C. R. Taylor, N. C. Heglund, G. M. Malooy, Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *J. Exp. Biol.* **97**, 1–21 (1982).
3. W. H. Karasov, Daily energy expenditure and the cost of activity in mammals. *Am. Zool.* **32**, 238–248 (1992).
4. A. T. Vanak *et al.*, Moving to stay in place: Behavioral mechanisms for coexistence of African large carnivores. *Ecology* **94**, 2619–2631 (2013).
5. J. P. Suraci *et al.*, Behavior-specific habitat selection by African lions may promote their persistence in a human-dominated landscape. *Ecology* **100**, e02644 (2019).
6. E. L. C. Shepard *et al.*, Energy landscapes shape animal movement ecology. *Am. Nat.* **182**, 298–312 (2013).
7. L. G. Halsey, Terrestrial movement energetics: Current knowledge and its application to the optimising animal. *J. Exp. Biol.* **219**, 1424–1431 (2016).
8. J. W. Laundré, L. Hernández, K. B. Altendorf, Wolves, elk, and bison: Reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. *Can. J. Zool.* **79**, 1401–1409 (2001).
9. K. M. Gaynor, J. S. Brown, A. D. Middleton, M. E. Power, J. S. Brashares, Landscapes of fear: Spatial patterns of risk perception and response. *Trends Ecol. Evol.* **34**, 355–368 (2019).
10. A. M. Pagano *et al.*, High-energy, high-fat lifestyle challenges an Arctic apex predator, the polar bear. *Science* **359**, 568–572 (2018).
11. T. M. Williams *et al.*, Instantaneous energetics of cougar kills reveals advantage of feline sneak attacks. *Science* **346**, 81–85 (2014).
12. M. L. Gorman, M. G. Mills, J. P. Raath, J. R. Speakman, High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. *Nature* **391**, 479–481 (1998).
13. C. T. Darimont, C. H. Fox, H. M. Bryan, T. E. Reimchen, The unique ecology of human predators. *Science* **349**, 858–861 (2015).
14. A. Oriol-Cotterill, D. W. Macdonald, M. Valeix, S. Ekwanga, L. G. Frank, Spatiotemporal patterns of lion space use in a human-dominated landscape. *Anim. Behav.* **101**, 27–39 (2015).
15. C. C. Wilmers *et al.*, Scale dependent behavioral responses to human development by a large predator, the puma. *PLoS One* **8**, e60590 (2013).
16. A. J. Loveridge, M. Valeix, N. B. Elliot, D. W. Macdonald, The landscape of anthropogenic mortality: How African lions respond to spatial variation in risk. *J. Appl. Ecol.* **54**, 815–825 (2017).
17. M. A. Tucker *et al.*, Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science* **359**, 466–469 (2018).
18. R. Nathan *et al.*, A movement ecology paradigm for unifying organismal movement research. *Proc. Natl. Acad. Sci. U.S.A.* **105**, 19052–19059 (2008).
19. J. M. Morales *et al.*, Building the bridge between animal movement and population dynamics. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **365**, 2289–2301 (2010).
20. B. Van Moorter, C. M. Rolandsen, M. Basille, J.-M. Gaillard, Movement is the glue connecting home ranges and habitat selection. *J. Anim. Ecol.* **85**, 21–31 (2016).
21. B. Van Moorter *et al.*, Memory keeps you at home: A mechanistic model for home range emergence. *Oikos* **118**, 641–652 (2009).
22. J. A. Smith *et al.*, Fear of the human ‘super predator’ reduces feeding time in large carnivores. *Proc. Biol. Sci.* **284**, 20170433 (2017).
23. C. M. Bryce, C. C. Wilmers, T. M. Williams, Energetics and evasion dynamics of large predators and prey: Pumas vs. hounds. *PeerJ* **5**, e3701 (2017).
24. C. Carbone, A. Teacher, J. M. Rowcliffe, The costs of carnivory. *PLoS Biol.* **5**, e22 (2007).
25. Y. Wang, J. A. Smith, C. C. Wilmers, Residential development alters behavior, movement, and energetics in an apex predator, the puma. *PLoS One* **12**, e0184687 (2017).
26. J. A. Smith, Y. Wang, C. C. Wilmers, Top carnivores increase their kill rates on prey as a response to human-induced fear. *Proc. Biol. Sci.* **282**, 20142711 (2015).
27. J. P. Suraci, M. Clinchy, L. Y. Zanette, C. C. Wilmers, Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecol. Lett.* **22**, 1578–1586 (2019).
28. J. Wall, I. Douglas-Hamilton, F. Vollrath, Elephants avoid costly mountaineering. *Curr. Biol.* **16**, R527–R529 (2006).
29. L. G. Halsey, C. R. White, A different angle: Comparative analyses of whole-animal transport costs when running uphill. *J. Exp. Biol.* **220**, 161–166 (2017).
30. B. G. Dickson, P. Beier, Quantifying the influence of topographic position on cougar (Puma concolor) movement in southern California, USA. *J. Zool. (Lond.)* **271**, 270–277 (2006).
31. B. Dickson, J. Jenness, P. Beier, Influence of vegetation, topography, and roads on cougar movement in southern California. *J. Wildl. Manage.* **69**, 264–276 (2005).
32. K. A. Blecha, R. B. Boone, M. W. Alldredge, Hunger mediates apex predator’s risk avoidance response in wildland-urban interface. *J. Anim. Ecol.* **87**, 609–622 (2018).
33. O. R. Bidder, L. A. Qasem, R. P. Wilson, On higher ground: How well can dynamic body acceleration determine speed in variable terrain? *PLoS One* **7**, e50556 (2012).
34. N. Tamburello, I. M. Côté, N. K. Dulvy, Energy and the scaling of animal space use. *Am. Nat.* **186**, 196–211 (2015).
35. W. Jetz, C. Carbone, J. Fulford, J. H. Brown, The scaling of animal space use. *Science* **306**, 266–268 (2004).
36. M. Reiss, Scaling of home range size: Body size, metabolic needs and ecology. *Trends Ecol. Evol.* **3**, 85–86 (1988).
37. C. M. Rosten, R. E. Gozlan, M. C. Lucas, Allometric scaling of intraspecific space use. *Biol. Lett.* **12**, 20150673 (2016).
38. B. G. Dickson, P. Beier, Home-range and habitat selection by adult cougars in Southern California. *J. Wildl. Manage.* **66**, 1235–1245 (2002).

39. B. Pierce, V. Bleich, R. Bowyer, Social organization of mountain lions: Does a land-tenure system regulate population size? *Ecology* **81**, 1533–1543 (2000).
40. C. Carbone, N. Pettorelli, P. A. Stephens, The bigger they come, the harder they fall: Body size and prey abundance influence predator-prey ratios. *Biol. Lett.* **7**, 312–315 (2011).
41. J. A. Smith, Y. Wang, C. C. Wilmers, Spatial characteristics of residential development shift large carnivore prey habits. *J. Wildl. Manage.* **80**, 1040–1048 (2016).
42. C. C. Wilmers, L. A. Isbell, J. P. Suraci, T. M. Williams, Energetics-informed behavioral states reveal the drive to kill in African leopards. *Ecosphere* **8**, e01850 (2017).
43. R. P. Wilson *et al.*, Estimates for energy expenditure in free-living animals using acceleration proxies: A reappraisal. *J. Anim. Ecol.* **89**, 161–172 (2020).
44. C. E. Dunford *et al.*, Surviving in steep terrain: A lab-to-field assessment of locomotor costs for wild mountain lions (*Puma concolor*). *Mov. Ecol.* **8**, 34 (2020).
45. B. T. McClintock, T. Michelot, momentuHMM: R package for generalized hidden Markov models of animal movement. *Methods Ecol. Evol.* **9**, 1518–1530 (2018).
46. R. Langrock *et al.*, Flexible and practical modeling of animal telemetry data: Hidden Markov models and extensions. *Ecology* **93**, 2336–2342 (2012).
47. A. Hurford, GPS measurement error gives rise to spurious 180 degree turning angles and strong directional biases in animal movement data. *PLoS One* **4**, e5632 (2009).
48. J. A. Dellinger *et al.*, Using mountain lion habitat selection in management. *J. Wildl. Manage.* **84**, 359–371 (2020).
49. D. Gesch, The National Elevation Dataset. *Photo. Eng. Remote Sensing* **68**, 5–11 (2002).
50. P. A. Burrough, R. A. McDonell, *Principles of Geographical Information Systems* (Oxford University Press, 1988).
51. J. M. Sappington, K. M. Longshore, D. B. Thompson, Quantifying landscape ruggedness for animal habitat analysis: A case study using bighorn sheep in the Mojave Desert. *J. Wildl. Manage.* **71**, 1419–1426 (2007).
52. J. P. Wilson, J. C. Gallant, Eds., *Digital Terrain Analysis in Terrain Analysis: Principles and Applications* (John Wiley, 2000).
53. B. M. Bolker *et al.*, Generalized linear mixed models: A practical guide for ecology and evolution. *Trends Ecol. Evol.* **24**, 127–135 (2009).
54. W. M. Getz, C. C. Wilmers, A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. *Ecography* **27**, 489–505 (2004).
55. W. M. Getz *et al.*, LoCoH: Nonparametric kernel methods for constructing home ranges and utilization distributions. *PLoS One* **2**, e207 (2007).
56. A. Gelman *et al.*, *Bayesian Data Analysis* (Chapman & Hall/CRC, ed. 1, 2006).
57. N. T. Hobbs, M. B. Hooten, *Bayesian Models: A Statistical Primer for Ecologists* (Princeton University Press, 2015).
58. Stan Development Team, RStan: The R interface to Stan (Stan Development Team, 2018).
59. B. Carpenter *et al.*, Stan: A probabilistic programming language. *J. Stat. Softw.* **76**, 1–32 (2017).
60. C. Calenge, The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecol. Modell.* **197**, 516–519 (2006).