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Wild canids and felids differ in their reliance on reused travel routeways

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Diverse factors, including environmental features and cognitive processes, can drive animals' movements and space use, with far-reaching implications. For example, repeated use of individual-level travel routeways (directionally constrained but imperfectly aligned routes), which results in spatial concentration of activity, can shape encounter-based processes including predation, mate finding, and disease transmission. However, how much variation in routeway usage exists across species remains unknown. By analyzing GPS movement tracks for 1,239 range-resident mammalian carnivores—representing 16 canid and 18 felid species from six continents—we found strong evidence of a clade-level difference in species' reliance on repeatedly used travel routeways. Across the global dataset, tracked canids had a 15% (± 7 CI) greater density of routeways within their home ranges than did felids, rising to 33% (± 16 CI) greater in landscapes shared with tracked felids. Moreover, comparisons within species across landscapes revealed broadly similar home range routeway densities despite habitat differences. On average, canids also reused their travel routeways more intensively than did felids, with hunting strategies and spatial contexts also contributing to the intensity of routeway usage. Collectively, our results suggest that key aspects of carnivore routeway-usage have an evolutionary component. Striking interspecific and clade-level differences in carnivores' reliance on reused travel routeways within home ranges identify important ways in which the movement patterns of real-world predators depart from classical assumptions of predator-prey theory. Because such departures can drive key aspects of human-wildlife interactions and other encounter-based processes, continued investigations of the relationships between movement mechanisms and space use are critical.

Carnivora | home range | movement ecology | probability ridges | spatial ecology

The authors declare no competing interest.

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Issues of space use by moving animals are foundational to diverse research topics at the interface of evolution, ecology, and behavior, including the evolution of territoriality, range residency, and migration (1, 2) as well as the ecology of foraging and predator–prey interactions (3, 4). Classically, many key theoretical results in these fields have required strong assumptions about the homogeneity of space use, with studies that allow for spatial heterogeneity often yielding strikingly different predictions (5–7). Despite the mathematical complications that spatial heterogeneity engenders, such considerations are often highly warranted from a biological perspective. For example, reliance on well-traveled routes (8–14) constitutes a specific way in which the movement of wild animals can depart radically from the ideal gas dynamics that provide the mathematical foundations of encounter-based processes in ecology (e.g., predation, mate finding, disease transmission) (15–18).

Depending on spatial scale, understanding when, where, and how strongly individual animals rely on repeatedly used travel routes through their landscapes can help identify foraging strategies (19), delineate conservation priorities for migrating species (20), and provide information about how learning and memory shape movements (10, 21–23). Among range-resident predators, repeated use of travel routes may emerge as animals navigate among preferred feeding regions (e.g., waterholes, rabbit warrens) or as animals use particular routes for both relocation and foraging (23–25). Questions about reliance on travel routes differ fundamentally from investigations of repeated site visitation, which, by emphasizing destinations and residency time, can be studied using periodograms and repeatability analyses (14, 26, 27). Given the operational demands of field research, however, studies of route-usage in wild species on large scales have typically involved only one or a few species instead of being broadly comparative. Consequently, a robust, cross-species understanding of (dis)similarities in route-usage and the spatial heterogeneity it engenders is lacking. However, increasing opportunities to combine GPS tracking data with publicly accessible remote sensing data mean that large-scale comparative analyses of space use by wild animals are now possible in rigorous and unprecedented ways (28–30).

Studies exploring repeated usage of particular travel routes for terrestrial species—variously discussed in terms of traplines (8, 11), trails (18), recursive paths (12, 13), hunt paths (14, 31), and other terms—focus on similarities in the spatial trajectories of animal movements over time, with recognition that both environmental factors (e.g., valleys, roads, cliff faces) and cognitive processes (e.g., perception, learning, memory) may underlie the emergence of particular reused routes (10, 14, 23–25, 32). The various terms used in the literature to characterize spatial consistency in animal movement often differ in connotation. For example, a “game trail” connotes a very narrow track wherein individuals are often stepping in one another’s footsteps, even to the point of creating a bare-earth path through vegetation. In contrast, a “corridor” implies a passageway for migration or other movement through favorable habitat bounded by more hostile areas; corridor width is not restricted by definition, but is often interpreted as being narrow relative to the scale of animal movement (20, 25). A movement “route” is similarly not formally defined with regard to width, but a degree of narrowness is often implied (10, 12). No term in current usage seems to capture the idea that bundled sets of narrow routes with similar orientations may exist as animals traverse a given region of their home range repeatedly but with imperfect consistency. Recognizing that some would reserve the term route for use exclusively with narrow channels for movement, we introduce the term “routeway” to characterize cases where travel is directionally constrained but imperfectly aligned. Below, we introduce statistical methods for identifying routeways from GPS tracking data. We emphasize that routeways exhibit a heightened degree of directional persistence of motion and would be distinct from movement networks that can be characterized by the potential for changes in direction at intersection points.

Mammalian carnivores have long been subjects of space-use research because of their diverse environments and ecological niches, and their association with critical conservation issues (33–35). Within the order Carnivora, the dog and cat families (Canidae and Felidae, respectively) are members of two highly divergent lineages (respectively, the suborders Caniformia and Feliformia) that last shared a common ancestor 41 (36) to 51 Mya (37). The Canidae and Felidae constitute obvious choices for comparative research on predator space use because each family represents a substantial evolutionary radiation, and each includes diverse species whose movements in nature have been studied extensively by researchers worldwide via GPS tracking (29, 38). Collectively, canids and felids tend to be home range resident species (34, 39–41). Their strategies for locating food involve stereotyped movement behaviors (e.g., cursorial pursuit, patient stalking), which in turn reflect important evolutionary differences in biomechanics, physiology, and preferred resources

Significance

Animals’ space-use patterns are central to eco-evolutionary theories of territoriality and foraging and to resource management practices, all of which can entail assumptions of spatial homogeneity. We found evidence for species- and clade-level variation in mammalian carnivores’ reliance on re-used travel routeways within their home ranges, with canids having, on average, both a greater density of travel routeways and a greater probability of routeway usage than felids. Such marked variation in the heterogeneity of species’ space-use patterns is important because it provides a strong empirical contrast to long-standing assumptions of mathematical models of predator-prey dynamics and, more broadly, highlights key issues of space use that are relevant for the conservation and management of at-risk mammalian carnivores globally.

(42–46). These strategies vary among carnivore species, but can also depend on prey species, habitats, and local conditions (39–41, 43, 44, 46). In addition, relationships between carnivores' movement behaviors and space use patterns can depend on cognitive processes such as perception and memory (13, 14, 21, 31, 33, 47–49), which also have an evolutionary basis (49–51). Overall, canids and felids share and even compete for many environments and food types, and present similar spatial planning challenges related to conservation and human–wildlife interactions (34, 52, 53), providing a broad context for comparative analyses.

We examined whether the many evolutionary, behavioral, and ecological dissimilarities among canid and felid species would translate into systematic differences in their use of space within their home ranges, particularly with regard to species' reliance on reused travel routeways. We focused on two aspects of routeway usage: the density of routeways within individuals' home ranges and the intensity with which individuals reused those routeways. If we found strong differences in the density, or use intensity, of routeways across wild carnivore species, it would suggest that at least one mechanistic (nonrandom) driver was at work. Absent such a driver, widespread variation in home range location and composition across taxa and landscapes would be expected to homogenize routeway usage across taxa, or at least obscure weak effects. Variation in routeway usage could arise mechanistically from behavioral differences in movement strategy while foraging, and relatedly, speed, both of which can be investigated in conjunction with GPS tracks. Diverse environmental features such as habitat structure, seasonality, topography, and human infrastructure might also contribute to variation in routeway usage, and such influences can be evaluated through investigations that link remote sensing and movement data. Through detailed analyses of a large database of GPS tracks representing diverse wild felid and canid species, we found evidence that differences in behavior and environmental factors are in fact important predictors of these carnivores' reliance on reused travel routeways. More intriguingly, however, we found robust support for the existence of clade-level differences in routeway density and routeway usage within home ranges. These differences, in which canids systematically exceed felids in their reliance on travel routeways, have important implications for both our understanding of predator–prey interactions and conservation planning.

Results

After leveraging an established workflow for estimating a home range distribution for an individual animal from its GPS track (Fig. 1 *A–C*), we characterized the location of reused routeways within the home range via statistical features called “probability ridges” (Fig. 1*D*). A ridge is a spatially contiguous curve of heightened probability in a smooth 2-D probability density function and is mathematically unsigned, indicating movement can progress “in both directions” along the ridge. Within a home range, probability ridges will emerge when an animal repeatedly traverses a region using similar trajectories. In this way, ridges delineate the center of a routeway along its length (*SI Appendix, SI Detailed Methods*).

To facilitate comparisons across individuals and species whose home range sizes vary widely, we adopted the nondimensional measure of ‘ridge density’, which scales total ridge length by home range size (*SI Appendix, SI Detailed Methods*). Furthermore, adding spatial buffers to identified probability ridges allowed us to then calculate ‘ridge-associated probability mass’ as the proportion of the probability mass in an individual's home range distribution that was ridge-associated for each of several buffer widths. Thus, we use ridge density to quantify the existence of routeways, and

likewise, we use ‘ridge-associated probability mass’ to quantify the intensity of routeway usage. After establishing the performance of our routeway estimation methods via detailed simulation studies (*SI Appendix, Figs. S11–S13 and Tables S5 and S6*), we analyzed ridge densities and ridge-associated probability masses within and across clades, controlling for home range size, phylogeny, habitat types, GPS data quality, and other potentially explanatory (or confounding) covariates.

Clade-Level Effects for Ridge Density. Across all models, ridge density was significantly higher for canids than felids. The phylogenetically controlled mixed model revealed a 15% (± 7 CI) ($P < 10^{-5}$) increase in ridge density among canids compared with felids when using the full dataset of 1,239 GPS tracks. This canid-felid clade-level difference is readily apparent when plotted on a phylogenetic tree, both for the empirical means and the predicted values (Fig. 2). We also extracted five subdatasets to assess potentially confounding effects associated with our aggregation of multispecies, multisite GPS track data. These subdatasets allowed us to address any effects of 1) data preprocessing, 2) animals' instantaneous speeds, 3) unknown phenological effects stemming from GPS tracks of duration < 1 y, 4) unmodeled spatial variation arising from individuals' heterogeneous landscapes, and 5) phylogenetic uncertainty. Analyses of these subdatasets yielded results that were broadly similar, with canids' heightened ridge density increasing from the above-mentioned results for the full-dataset to 33% (± 16 CI) ($P < 10^{-5}$) for the “shared landscapes” subdataset (consisting of the GPS tracks from a set of nine landscapes in which one or more canid species and one or more felid species were studied together) (Fig. 3*B*). Collectively, these consistent clade-level effects indicate that the difference in ridge density between canids and felids is a robust feature that is not sensitive to the details of individual GPS tracks, species, or landscapes (*SI Appendix, Table S1*), nor to phylogenetic uncertainty (*SI Appendix, SI Detailed Methods, Phylogenetic Considerations*).

Predictive Model Fits for Ridge Density. To quantify the importance of the canid-felid clade effect relative to other possible sources of variation, we used statistical models that included a battery of terms as fixed and random effects within a phylogenetically controlled generalized linear mixed modeling framework (*SI Appendix, SI Detailed Methods, Statistical Analyses*). For the full dataset, predictions of ridge density reflected significant effects of home range size ($P < 10^{-4}$), terrain roughness ($P < 0.05$), and movement strategy while hunting (represented by the indicator variable slow walking; $P < 0.05$), but no other variables were significant predictors. Specifically, animals engaging in slow-walking behavioral strategies and possessing large home ranges featuring greater terrain roughness exhibited lower ridge density beyond the clade-level effect for the full dataset; effect size plots appear in Fig. 3*A*. Outside of the full dataset, tree cover was a significant predictor for the “year or longer” dataset ($P < 0.01$), and terrain roughness was a significant predictor for all datasets except the year or longer and shared landscapes datasets. Effects of movement strategies were not significant except for the slow-walking indicator variable in the “no-preprocessing” dataset ($P < 0.02$). Average instantaneous speed of travel was not a significant term in the model for the “including speed” dataset ($P > 0.8$), suggesting individual-level variation in speed is not contributing to the observed clade-level differences in ridge density. Effect size plots for the including speed subdataset and all other subdatasets appear in *SI Appendix, Fig. S1*.

Across the nine shared landscapes (which included temperate and tropical forests, temperate and tropical savannas, plus deserts

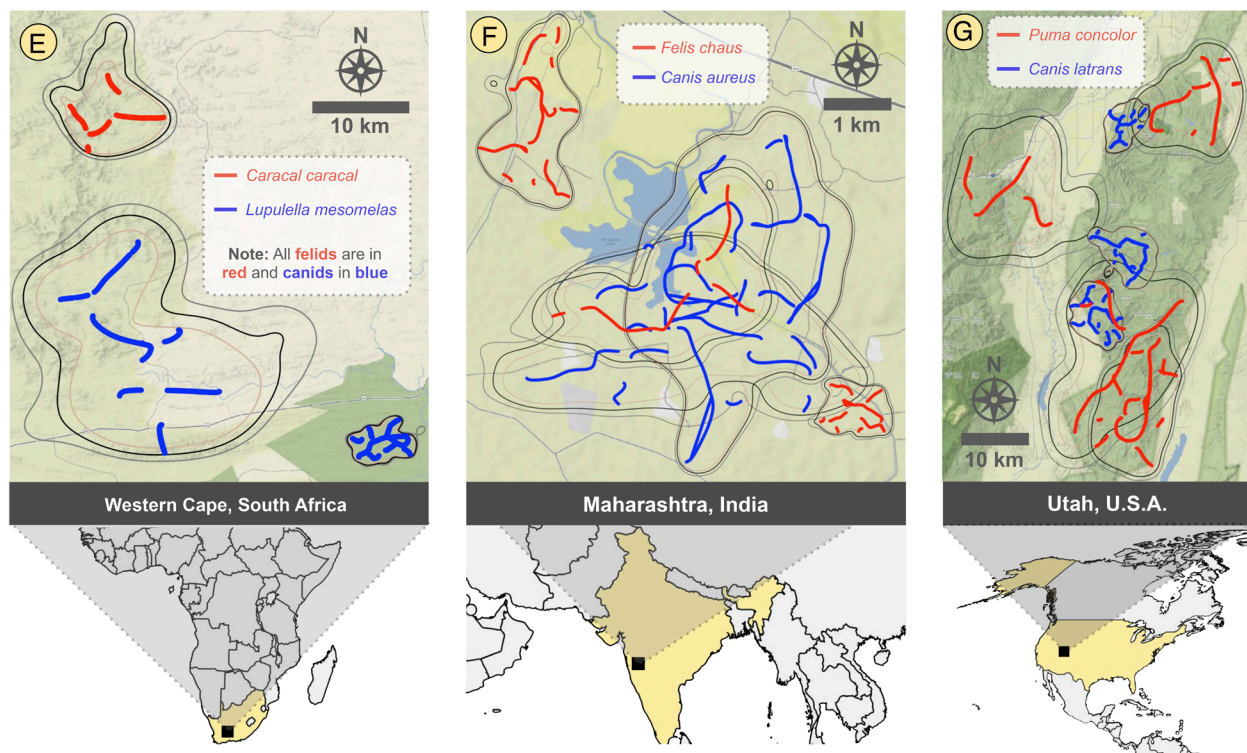
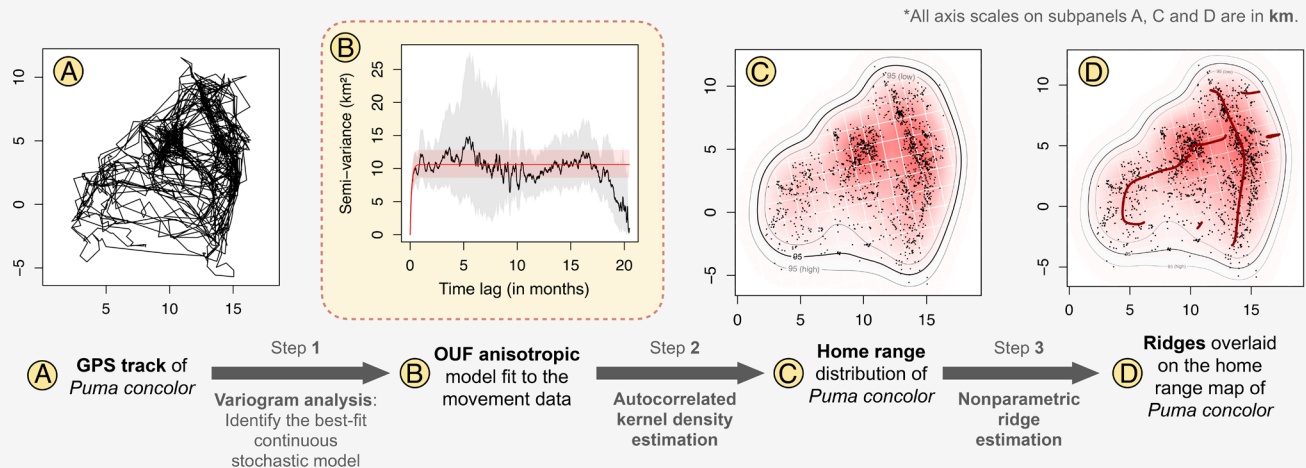


Fig. 1. Diagram of analysis workflow building maps of probability ridges from GPS tracking data (A–D) and sample maps showing home ranges and probability ridges overlaid on landscapes (E–G). Panel A shows the original movement track data for cougar F70 (*Puma concolor*) from Utah, USA (54). Panel B shows the empirical semivariance (black) for F70's movement track, together with 95% confidence limits (gray shading) and the best-fit variogram (red) and its 95% confidence limits (pale red shading) corresponding to an anisotropic version of the OUF continuous-time stochastic process (SI Appendix, SI Detailed Methods). As in geostatistical analyses involving semivariograms, large lags involve the fewest datapoints and have little influence on model fit. Panel C depicts the cougar's estimated home range distribution including its boundary (black curve) and corresponding 95% confidence limits (gray curves), probability density surface (red hashing), and SD of the AKDEc bandwidth kernels (white grid lines). Original movement trajectories are represented as black dots for clarity. Panel D identifies the calculated probability ridges that indicate routeways of repeated usage (red curves) overlaid on the home range distribution. Note: Panels A, C, and D are mappable objects, but B is not. In Panels E–G, plots show mean home ranges (black contours), outer and inner 95% confidence bounds on the home ranges (gray and plum contours, respectively), and the location of probability ridges (red- and blue-colored curves) for individuals from six species in landscapes in which movements of both canids and felids were studied [Panels E: (55); F: (56); and G: (54)]. Backgrounds depict topographical relief and landcover type, ranging from arid (tan) to mesic (green) (Stadia Maps: <https://stadia.com/attribution/>). Variograms, home ranges, and probability ridges were calculated via the R package *ctmm* as detailed under Materials and Methods. Cougar F70 appears in the Upper Right of panel G. Panels D–G show ridges calculated via the accurate but computationally inefficient *ks* algorithm (SI Appendix).

and xeric scrublands), mean ridge densities of canid species were routinely higher than those of felid species inhabiting the same landscapes (Fig. 4), providing additional support for the robustness of the clade-level differences. Similarly, for the 11 species with GPS tracks in three or more landscapes, we found remarkable consistency in mean ridge density within species across landscapes after controlling for other factors (SI Appendix, Fig. S2).

Nine of the 11 species showed no significant differences in ridge density across landscapes, whereas only two species, *Lynx rufus* and *Felis silvestris*, exhibited any significant heterogeneity. Only one of seven landscapes differed from the others for *L. rufus*, and only one of four landscapes differed from the others for *F. silvestris* (SI Appendix, Fig. S2). This high degree of consistency within species across diverse landscapes suggests a strong role for

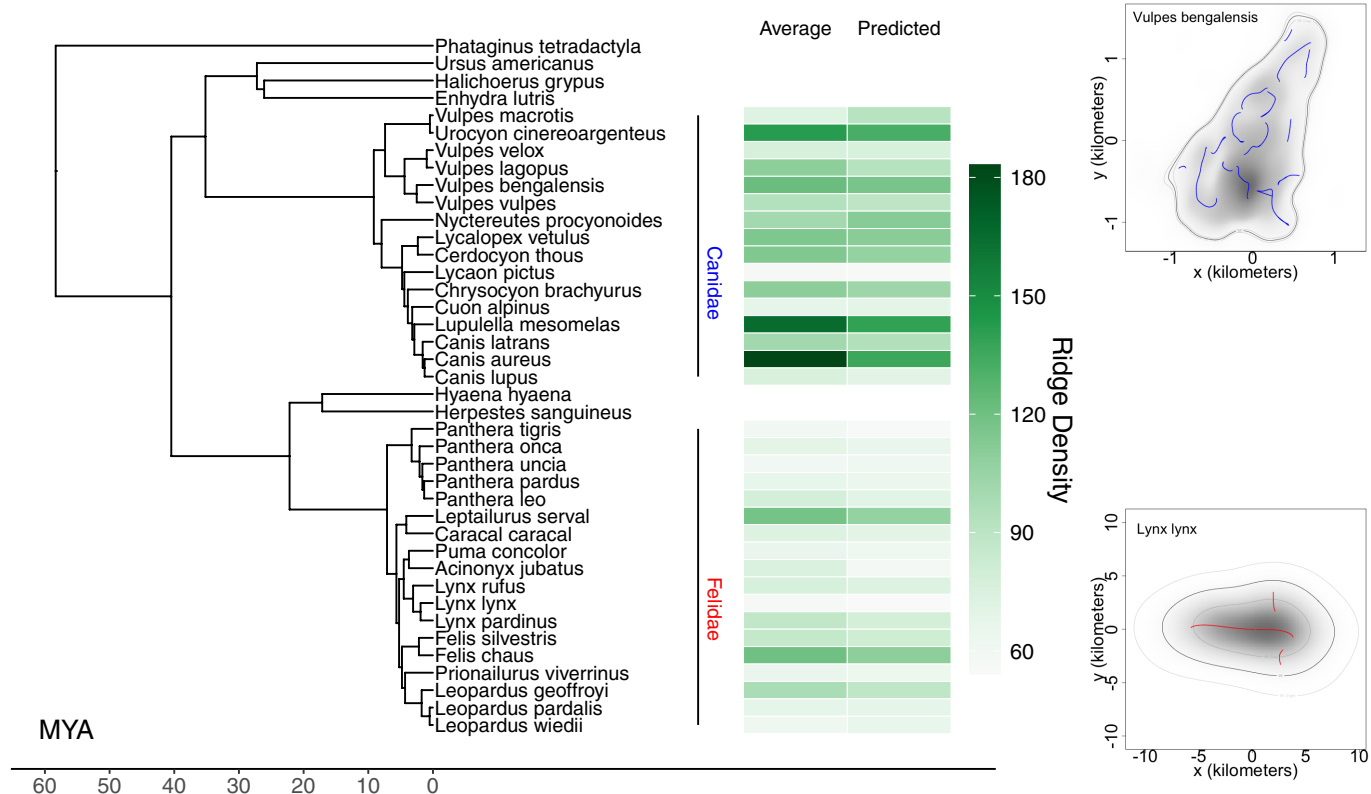


Fig. 2. Mean empirical ridge density for 34 species of canids and felids and the corresponding model-predicted mean values for the full dataset of 1,239 tracks (Dataset S1). Example plots for individuals whose home ranges feature very high ridge density [*Canis aureus*; “Jackal 08” (56)] and very low ridge density [*Lynx lynx*; “Kars” (57)] are shown next to the color key. Ridges appear as blue and red curves for the canid and felid exemplars, respectively, and the background gray shading indicates probability density of space use with each home range. The phylogenetic tree includes outgroup and ingroup species (without movement data) used only to help structure the phylogenetic distance matrix and visualize the phylogenetic tree; these species were truncated from the phylogenetic distance matrix prior to statistical analyses. Ridges plotted were calculated via the accurate but computationally inefficient *ks* algorithm (SI Appendix).

biological species-level features in driving the pronounced clade-level effects (Fig. 3). Species-level mean ridge densities predicted by the model for the full dataset fell well within the empirical ranges for all species except the raccoon dog (*Nyctereutes procyonoides*), for which only two GPS tracks could be analyzed (SI Appendix, Fig. S3).

Separate analyses of the canid and felid groups were broadly similar, revealing few differences in the predictive models that could be interpreted as evidence of strong interaction effects (SI Appendix, Fig. S4). Engaging in the disruptive fast hunting movement strategy was associated with higher ridge density in canids, but with lower ridge density in felids. Other exceptions were that increasing terrain roughness decreased ridge density for felids ($P < 0.03$) but not for canids and that increases in seasonality (quantified by a measure of primary productivity, Var DHI GDP, see SI Appendix, Table S1) decreased ridge density for canids ($P < 0.02$) but not felids (SI Appendix, Fig. S4).

Ridge-Associated Probability Mass. By surrounding each ridge with a series of spatial buffers (Materials and Methods), we quantified the proportion of the probability mass in each individual’s home range that was ridge-associated. Overall, the ridge-associated probability mass in an individual’s home range roughly correlated with its ridge density. For narrowly defined ridge tops (i.e., probability ridges with 10 or 50 m fixed-width buffers on either side), canids had, on average, significantly more ridge-associated probability mass in their home range distributions than did felids (7.1 to 20.2% more for 10-m buffers and 5.3 to 14.9% more for 50-m buffers using the full dataset; SI Appendix, Fig. S5).

At the species level, ridge-associated probability mass varied widely, with diverse taxa, including several species of foxes and some forest-dwelling cats, averaging 20 to 40% of their probability mass associated with probability ridge tops, indicating a strong concentration of activity along those routeways (SI Appendix, Fig. S6). Individuals with larger home range sizes consistently had lower ridge-associated probability mass, regardless of buffer width (SI Appendix, Fig. S7). For 50-m buffers, increasing percent tree cover and human footprint index, plus the use of the pursuit and slow-walking strategies were all significant predictors of reduced ridge-associated probability mass (SI Appendix, Fig. S7A). As was true for ridge density (Fig. 3B), we found even larger interclade differences for ridge-associated probability mass when focusing on the shared landscapes dataset; in this case, the interclade differences were highly significant for buffer widths ranging from 10 m (95% CI: 17 to 42% more for canids) to 200 m (95% CI: 5 to 19% more) (SI Appendix, Figs. S5 and S7F). More broadly, the interclade differences in ridge-associated probability mass were a robust result evident across all subdatasets for narrowly defined ridge tops (≤ 50 m buffer width; SI Appendix, Fig. S7).

Discussion

Drawing on a dataset of 1,239 carnivore GPS tracks, representing 16 canid and 18 felid species across six continents, we found that on average, canid home ranges feature substantially greater densities of reused travel routeways (quantified as probability ridges, Figs. 1 and 3) compared to felid home ranges. Moreover, canids used these routeways more extensively than did felids, as quantified

A

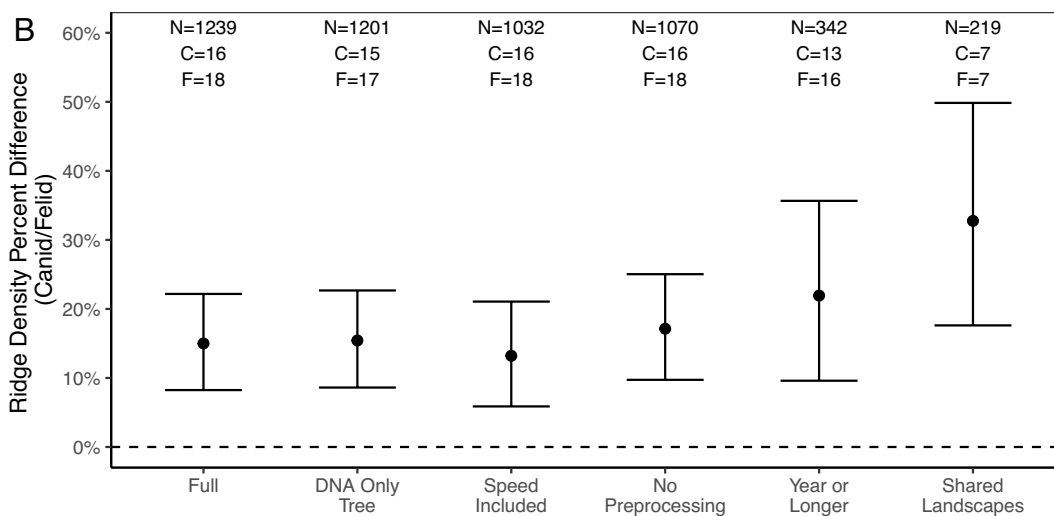
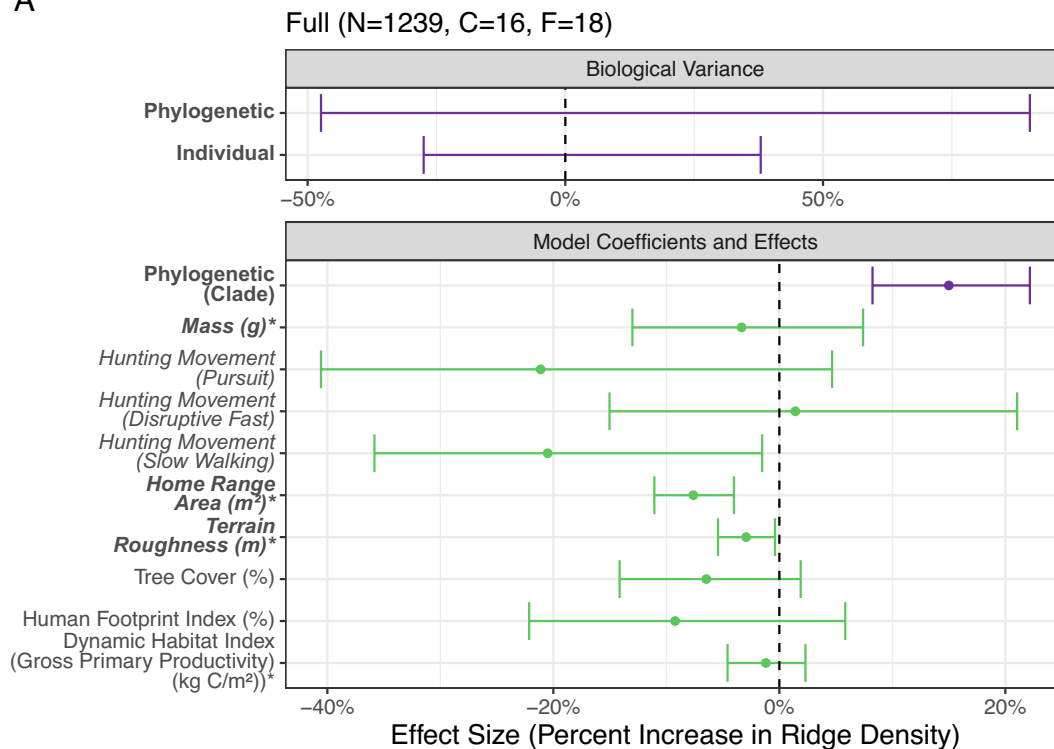


Fig. 3. Effect size plots for ridge density for the full dataset (A) and mean ($\pm 95\%$ CI) clade-level percent differences from models for all datasets (B). In (A), continuous variables were standardized so that the effect size corresponds to 1 SD of the predictor, whereas for a variable expressed as a percentage, the effect size corresponds to the full effect of that predictor at 100%. Predictors in bold font and purple plotting represent biological variation, and the plots labeled Phylogenetic and Individual are prediction intervals. The plotting labeled Phylogenetic (Clade) is part of the overall phylogenetic variation, but it is expressed as a mean and CI alongside other model coefficients. Model covariates are in green, including indicator variables (italics), variables log transformed for analysis (bold-italics), and standardized variables (asterisk). In (B), clade effects are plotted as canids minus felids, with $y = 0.0$ indicating no difference between clades and positive values indicating increased ridge density in canids. Clade effects are highly significant ($P < 0.0003$) in each of the six datasets). N, C, and F are the number of individuals, canid species, and felid species, respectively.

by the greater ridge-associated probability mass in their home ranges (*SI Appendix, Figs. S5–S7*). These results, which control for variation in home range size, contrasting hunting strategies and landscape characteristics, as well as variation in the quantity and quality of movement track data, identify striking differences in carnivores' space use with regard to reliance on reused travel routeways and the resulting internal heterogeneity of their home ranges. The magnitude and consistency of these differences are remarkable given the diverse challenges of collecting and working with field data across so many different species and landscapes.

Collectively, clade-level differences in carnivore movement and space use, together with species-level variation attributable in part to different hunting strategies and landscape contexts (*SI Appendix, Figs. S3 and S6*), have a variety of implications, with connections to such diverse topics as the mathematical modeling of predator–prey interactions and the practical implementation of conservation plans. Canids' higher average ridge densities (Fig. 3B) and higher average ridge-associated probability masses (*SI Appendix, Fig. S5*) serve to concentrate their activities along particular routeways within their home ranges, which will influence the pace and pattern

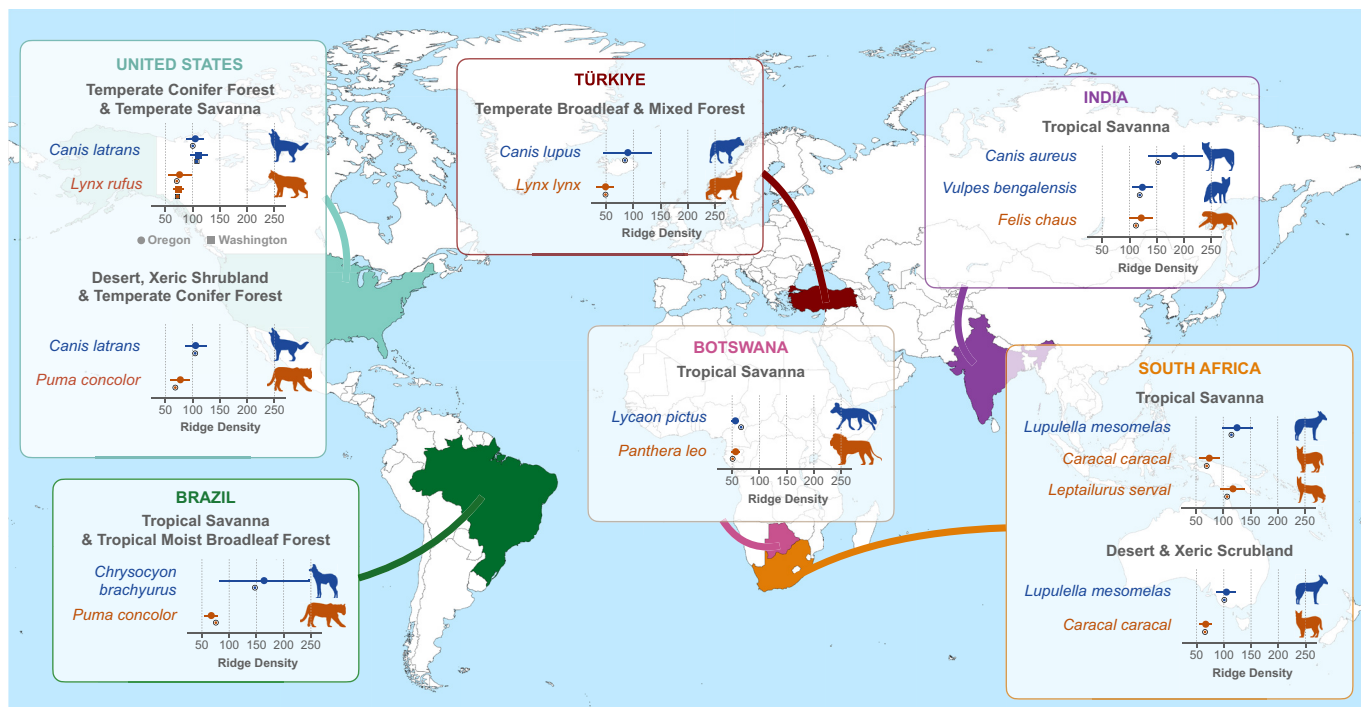


Fig. 4. Ridge densities for canids and felids for the nine landscapes in which at least one species from each clade was tracked together (the shared landscapes dataset; $n = 219$ individuals total). Solid symbols are empirical means ($\pm 95\%$ CI), whereas black-bordered, open symbols (offset lower) indicate means predicted by the statistical model for this dataset (*SI Appendix, Table S3*). At the clade level, canid ridge densities are on average $33\% (\pm 16\text{ CI})$ higher than felids across the shared landscapes dataset (Fig. 3B).

of their encounters with conspecifics and with prey (58–60). Such concentrations of movement and activity represent striking departures from the dynamics of ideal gases, which have long provided the theoretical foundations of predator–prey dynamics, mate finding, and other encounter-based processes in ecology, but which are increasingly challenged by models with alternative reaction kinetics (15–17, 61, 62). For example, interclade differences in reliance on travel routeways could mean that the linkages between animal movement and disease transmission operate quite differently across taxa (63, 64), as species that concentrate movement along well-traveled routeways would have different exposure profiles for depositing or acquiring infective agents than would species whose movements were not so spatially constrained. Variation in carnivores' reliance on travel routeways could also have important trophic consequences via impacts on the spatial distribution of prey species, which often avoid areas of heightened predator activity (65, 66).

Another consequence of carnivores' differential reliance on well-traveled movement routeways pertains to the risks associated with human interactions. For example, stricter adherence to reused routeways could reduce hunting efficiency as travel routeways are compromised through development or through increased contact with humans when established travel routeways overlap with new areas of human activity (67). Similarly, poaching with snares or traps along predictably reused travel routeways would be a greater threat to those species with greater ridge-associated probability mass (*SI Appendix, Fig. S6*). Of course, one potential benefit of some species' greater affinities for routeway-attuned travel is that negative interactions with human infrastructure might be more easily addressed for such species, such as through construction of highway wildlife crossing structures at key locations (53, 68).

What Drives Variation in Carnivore Routeway Usage? The phylogenetically structured variation in routeway usage among carnivores could derive from several sources, including database

artifacts, biases in our statistical modeling, environmental factors, and biological processes. The first possibility—that the differences we report between canids and felids are simple statistical artifacts—seems unlikely. Throughout our analyses, we have controlled for the effects of a diverse array of factors at the individual-, species-, and landscape levels that could affect the formation of travel routeways (*SI Appendix, Tables S1 and S2*), and our results still indicate the existence of strong phylogenetic structure. For example, when canids and felids occupied the same landscapes (reducing the potential for unmodeled spatial variables to affect the clade-level difference), ridge density for canids exceeded that of felids by $33\% (\pm 16\% \text{ CI})$; Figs. 3B and 4) with a concomitant 10 to 30% mean increase in the intensity of ridge use (*SI Appendix, Fig. S5*). Nevertheless, we recognize that other factors, such as unmodeled environmental variables, unmodeled clade- or species-specific behaviors (e.g., site fidelity), and unknown differences among the particular populations of carnivores to which the GPS-tracked individuals belonged, could all contribute to the observed clade-level differences in route usage if those other factors occurred across individuals or taxa in just the right way (see *SI Appendix* for further discussion of potential sources of bias).

Moving beyond statistical artifacts and biases, environmental features constitute a key alternative explanation for routeway-following behavior in home ranges (23), and features like creek valleys, forest roads, and cliff faces are known to shape carnivores' routeway-like movements in particular settings (25, 68, 69). However, the identity and importance of physical landscape features capable of creating or refining animals' travel routeways will vary strongly across biomes, habitats, and even individual home ranges (23), and additional variation will emerge due to species- and individual-level sensitivities and behavioral reactions to those features (47, 60, 66, 70, 71). With so many factors at play, the ways by which diverse environmental contexts (and individuals' heterogeneous responses to environmental features) could scale

up to yield the observed clade-level differences in ridge density and ridge-associated probability mass are unclear.

Potential biological drivers of the clade-level difference in routeway usage include issues of morphology, perception, and cognition. The skeletal architectures of canids and felids differ in key ways, including major differences in shoulder joints, hind limbs, and orbital morphology, and these differences have been previously interpreted with regard to both movement and hunting strategies (42, 44, 45, 72, 73). For example, felids have “floating” clavicles that may increase their maneuverability relative to canids, whereas canids have a rigid shoulder structure restricting lateral limb movement and encouraging straightforward linear travel (74). Whether phylogenetic differences in joint morphology or visual perceptual fields could scale up to influence travel patterns within carnivore home ranges remains unclear.

Canids’ increased reliance on movement routeways could also be mediated by their greater capabilities for olfactory perception (75). Although canids, felids, and indeed other carnivores routinely scent mark for purposes of social communication and identification, canids’ enhanced abilities to detect scents (76) could reinforce movement along particular routeways, as modeled in ref. 77. Differences in diet may also play a role, in that all felids are carnivores, but many canids can be omnivorous, exploiting a wider range of resources depending on availability. Successful foraging via the latter, more generalized strategy could rely more heavily on memory, particularly when resources, or access to them, varies seasonally (19, 24, 78).

A Link to Cognition? Given our phylogenetic modeling, and our finding that ridge densities are generally consistent within species across landscapes and biomes (*SI Appendix, Fig. S2*), it seems plausible that the observed clade-level differences in ridge density and ridge-associated probability mass have a biological, perhaps cognitive, component. In this context, clade-level differences in species’ reliance on routeways for navigation could be linked to different cognitive strategies, with canids using routeways more heavily and felids exhibiting more flexible, less repetitive, or more random movement. Routeway-based movement allows for easier and more efficient movement for some species and environmental contexts (10, 12, 18, 28) and is widely considered a hallmark of the cognitive maps that some species employ for navigation (19, 21). The development of animals’ travel routeways can hinge on experiential learning and memory (79–81), which have been experimentally demonstrated to drive the establishment of home ranges in pheasants and deer (82, 83).

As for a specific mechanism, one speculative possibility emerges from the animal cognition literature, where laboratory experiments suggest that domestic dogs (*Canis lupus familiaris*) have four to eight times longer working memory plus stronger spatial cognition and object permanence skills compared to domestic cats (*F. silvestris catus*) (84–86). Methodological concerns regarding the breeds and sources of animals used in those laboratory studies limit the extension of these ideas to wild animals. However, in humans, greater working memory is believed to be associated with memory retrieval structures that facilitate quick and accurate retrieval of large amounts of information from long-term memory (87, 88), and greater working memory predicts improved performance on navigational tasks (89, 90). Crucially, controlled search processes are believed to be regulated by working memory and executive control (91). Laboratory studies of rodents that examined relations between prefrontal and hippocampal function also suggest a tight coupling between prefrontal-regulated working memory processes and hippocampal-mediated long-term spatial memories (92, 93).

Future Directions. Additional understanding of the observed phylogenetic signals in routeway usage could perhaps be gained through targeted analyses of species not studied here. That is, are space-use patterns typical of other mammalian carnivore groups predictable from their relationships with canids and felids? For example, hyaenas, which have been studied extensively in the context of cognition (49), present an interesting case study for future work because they are behaviorally canid-like in many ways, but evolutionarily far closer to felids (34). The predictions are that hyaena species should have greater ridge density and greater ridge-associated probability mass than other members of the Feliformia, after controlling for other factors. Another testable hypothesis is that clade-level differences in routeway usage may map onto differential success in rebuilding carnivore populations via translocations and/or the release of captive-bred animals (52, 83, 94). In such settings, naïve carnivores must gain proficiency in spatial navigation as they establish home ranges in new landscapes, creating excellent opportunities for understanding how animals learn (80, 95–97).

Conclusion. We found that mammalian carnivores vary widely in their reliance on reused travel routeways within their home ranges and that this variation is predictable as a function of phylogeny, behavioral hunting strategies, and environmental context. Further efforts to delineate (and statistically associate) the location of probability ridges in real landscapes with specific, species-relevant landscape features should provide insight into the relative importance of anthropogenic features (e.g., roads, fences) versus natural features (e.g., forest edges, creek valleys, cliffs) in shaping animals’ preferred travel routeways (25, 69, 98). Spatial concordance (or lack thereof) between an individual’s probability ridges and the landscape features in its home range should also inform understanding of the relative biological and physical bases of least-cost movement paths inferred from energetics modeling (99–101). Putative cognitive differences between canids and felids suggest one possible mechanism behind the robust clade-level differences in routeway usage we quantified, but available methods do not allow for easy, en masse discrimination of routeway-based movements driven by cognition versus those deriving from physical constraints (23). Regardless of its source, however, pronounced heterogeneity in carnivores’ use of travel routeways has a variety of far-reaching implications. Among other possibilities, these findings provide empirical justification for new approaches to mathematical modeling of encounter processes in wildlife ecology (e.g., disease dynamics, mate finding, consumer–resource interactions) and also suggest avenues by which improved understanding of animals’ spatial behavior may benefit practical conservation efforts.

Materials and Methods

Collectively, the full dataset of 1,239 tracks entailed almost 4.60 million GPS fixes, with 2.24 million fixes for canids, and 2.35 million for felids. Durations of individual tracks ranged from 4.14 and 4.28 wk (canids and felids, respectively) to 163 wk and 516 wk (again, respectively). Nominal sampling rates ranged from 1/min to ~1/d for both carnivore families. See [Dataset S1](#) for detailed track-level information on fixes, durations, fix rates, and other measures. We emphasize, however, that these data on the number of fixes, durations, and fix rates per track are potentially beguiling, as it is not these numbers themselves that determine data sufficiency for home range analysis, but rather the effective sample size (ESS) values, with sufficiency for $ESS \geq 5$ [(38, 102); also see *SI Appendix, SI Detailed Methods*]. For canids, ESS values ranged from 5.1 to 6,728 with a mean of 412, whereas for felids, ESS ranged from 5.0 to 6,891 with a mean of 170. As detailed in *SI Appendix*, we control for track-level variation in ESS in all of our statistical analyses.

Delineation of an animal's reused travel routeways necessitates identification of its home range [i.e., the region where the animal spends its time; (81, 102)] and the intensity with which it uses space within that home range. As explained in *SI Appendix, SI Detailed Methods*, we made these determinations using an established workflow that delineates an animal's home range distribution from GPS tracking data as a 2-D probability density function (hereafter, 2-D PDF) (102, 103) together with an implementation of a recently developed statistical method for identifying so-called probability ridges in a 2-D PDF (104). All spatial statistical analyses involving home ranges and probability ridges were conducted using the R package *ctmm* (102, 103), which advantageously allows processing of highly heterogeneous GPS tracks and avoids any subjective postprocessing.

With analogies to landscape ridges in geomorphology, a probability ridge represents a spatially contiguous curve with heightened probability relative to other, adjacent areas within a PDF (104). That is, a probability ridge is a 1-D feature interpretable as a spatially extended mode. Whereas a simple statistical mode occurs at a point where probability density is maximal in all directions, ridge points occur where probability density is maximal in the direction perpendicular to the tangent of a ridge curve while density along the curve is not constrained. A sequence of adjacent ridge points need not be in a straight line, and a ridge curve will emerge as a function of curvature present in the 2-D PDF. Note that for a 2-D PDF that is not related to a movement process, probability ridges will not necessarily correspond to specific movement routes, as such ridges would merely indicate areas of heightened probability. In contrast, for a 2-D PDF derived from animal movement data, ridges will correspond to route-like structures because movement is constrained to be (mathematically) continuous and movement through regions of high probability is favored. Thus, biologically speaking, a probability ridge curve will emerge when an animal repeatedly uses similar, spatially localized routes to navigate a given region within its home range. Animals do not necessarily (and indeed, are unlikely to) exactly move along a probability ridge. Instead, probability ridges merely provide spatial summaries for the orientation of movement in particular portions of an animal's home range.

However, as in geomorphology where ridgelines can occur in geographical regions of either high or low average elevation, the existence of a probability ridge in a region of a home range does not characterize the overall probability mass in that region. To quantify the extent to which individuals used the probability ridges in their home ranges, we spatially "buffered" each ridge curve by several specific widths (10, 50, 100, and 200 m) to transform each one-dimensional ridge curve into a series of two-dimensional features. From those features, we then calculated a double integral (across the buffered ridge width and along the ridge) to estimate the probability mass encompassed by a particular buffered ridge. Summing the probability mass across all of an individual's ridges (but eliminating any double-counting of probability mass in areas where buffered ridges intersect within a home range), we obtained a total ridge-associated probability mass for each individual for each buffer width. These ridge-associated probability mass values (out of a maximum possible of 1.0 total probability mass for each home range) provide a measure of how intensively a given animal is moving via its set of routeways relative to the nonrouteway portions of its home range.

We thus focused our analyses on two measures of animal routeway usage within a home range: 1) ridge density (ranging from 0 upward, and quantifying how extensive the set of probability ridges is within a home range) and 2) ridge-associated probability mass (ranging from 0 to 1, and quantifying how intensively an individual travels along the ridges in its home range) (*SI Appendix, SI Detailed Methods*).

The flow diagram (Fig. 1 A–D) illustrates how the steps of our analyses work together to yield maps of probability ridges as reused travel routeways. After all processing, 1,239 tracks across 34 species (16 canids, 18 felids) were usable for comparative analysis of the density of probability ridges in each animal's home range via phylogenetically controlled generalized mixed effects modeling (*SI Appendix, SI Detailed Methods*). Our statistical approach allowed us to test for the existence of a clade-level difference in the density of probability ridges while also controlling for, and testing the potential importance of, a broad suite of individual-, species-, and landscape-level covariates, including those that provided alternative explanations for observed clade-level differences in ridge density and ridge-associated probability mass (*SI Appendix, Tables S1 and S2*). To evaluate

the robustness of our findings, we also analyzed several subdatasets drawn from within the full dataset of 1,239 usable tracks (*SI Appendix, SI Detailed Methods*).

Because our ridge-based methods for delineating routeways rely on the asymptotic properties of continuous stochastic processes (*SI Appendix, SI Detailed Methods*), our methods are insensitive to the marked variation in "sampling schedules" that results from discontinuous GPS fixes, which can vary greatly across individuals, taxa, and landscapes. In contrast, existing methods for estimating high-traffic areas such as corridors, routes, and path networks for individual taxa, such as types of Brownian bridges (105, 106) and network analyses (23), yield metrics with inherent scale dependencies that would muddle and compromise comparisons across our highly heterogeneous multispecies data (107–111). For example, spatial thresholds necessary to define route networks (i.e., what specific network nodes are interconnected) could not remain consistent across diverse sampling schedules and movement behaviors without tremendous loss of information due to data coarsening to a common schedule. Indeed, coarsening all our tracks to a minimum common sampling frequency of 1/d would require discarding 93.4% of our 4.60 million datapoints.

Simulation studies (*SI Appendix*) make clear that, subject to minor errors stemming from the vagaries of finite sampling effort, our methods do not falsely identify probability ridges when they should not exist (*SI Appendix, Fig. S11*) and accurately identify both the location and length of probability ridges when they are known to exist analytically (*SI Appendix, Fig. S12*). Both the lengths and densities of probability ridges estimated for empirical tracking datasets far exceed the false positive errors expected from finite sampling effort in null models (*SI Appendix, Fig. S13 and Tables S5 and S6*).

Data, Materials, and Software Availability. Code for all analyses have been deposited in Zenodo (<https://zenodo.org/records/16172335>). Spatially anonymized versions of all movement tracks have been deposited in Zenodo (<https://doi.org/10.5281/zenodo.11159169>). **Dataset S2** presents detailed information regarding the original sources of animal tracking data, the movement tracks used in this analysis (including their sources and availability), animal care and permit authorizations, and funding acknowledgements. As detailed in **Dataset S2**, many of the movement tracks we analyzed are already publicly available as supplemental material associated with previous species-specific publications or through the ecological repository <https://www.movebank.org>; such datasets are either openly accessible or available through communication with the data holders. Other datasets are, however, not publicly available in raw form because they are protected by national or state laws that prohibit their public release or because they detail the movements of endangered species. To facilitate further analyses, spatially anonymized versions of all movement tracks are available at <https://doi.org/10.5281/zenodo.11159169>. The anonymization process preserves the internal integrity of the track, but obscures the animals' locations inside parks and sanctuaries or with respect to landscape features. Such anonymization has no effect on the calculation of ridge density or ridge-associated probability mass within an animal's home range. Together with the summary of track-level information available in **Dataset S1**, these anonymized tracks will allow users to recreate the same or similar hypothesis tests that we report, and also conduct future analyses of some or all of the movement tracks and their pre-summarized environmental contexts. Collaborations with the original data holders detailed in **Dataset S2** are generally encouraged, and in cases where data are held by Indigenous groups or institutions from regions that are under-represented in the global science community, collaboration may be required to ensure inclusion. Previously published data were used for this work [Some movement data is available on online repository Movebank (indicated in spreadsheet "Cat_Dog Data Analyzed.AnimalCare.Acknowledgements.csv"). Movement data associated with a publication includes refs. 112–114].

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