

The search behaviour of terrestrial mammals

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Animals searching landscapes need to strike a balance between finding sufficient resources, while also minimizing encounter with predators. A key determinant of encounter rates is the average length scale over which ballistic motion is maintained, with ballistic movement leading to higher encounter rates than more diffusive movement. Using GPS data from 53 species, we show how the optimization of search strategies underpins broad patterns in the movement of terrestrial mammals. Ballistic length scales increase with body size, but predators maintained $\sim 250\text{m}$ longer ballistic length scales than similarly sized prey. These patterns emerge from a combination of bottom-up and top-down pressures, with individual deviations from the body-mass predictions being modulated by resource abundance. Our findings highlight the importance of encounter rates as a primary driver of mammalian movement.

As motile organisms move through landscapes in search of food and mates, they need to strike a balance between finding sufficient resources to grow and reproduce, while also minimizing the rate at which they encounter predators (1, 2). Because of the fitness consequences of foraging success (3, 4) and predator-prey dynamics (5–7), there should be strong selection pressure on movement strategies that optimize encounter rates. Although the exact movement processes that searching animals might take has been debated (8–11), the general consensus is that ballistic (i.e., directed) movement leads to higher encounter rates than more diffusive (i.e., tortuous) movement (2, 8–10, 12, 13). This occurs because individuals that exhibit diffusive movement will tend to repeatedly search over the same areas, whereas ballistic motion allows individuals to search over a larger area within the same amount of time. The average length scale over which ballistic motion is maintained, l_v (in m), is thus a key determinant of encounter rates (2, 14) and a potent trait on which natural selection may act.

Because ballistic movement is the more efficient search strategy, bottom-up pressure exerted by food needs will select for longer ballistic length scales. Importantly, however, increasing l_v will also increase the rate at which individuals encounter predators (1, 2). Top-down predation pressure thus selects for shorter ballistic length scales. Prey species searching for immobile vegetation must therefore optimize their movement against the opposing forces of their energetic requirements selecting for longer l_v , and predation pressure selecting for shorter l_v (2). Predatory species, in contrast, also benefit from maintaining longer ballistic length scales (2), but without the top-down predation pressure experienced by prey species. The combination of bottom-up and top-down regulation is thus expected to select for longer ballistic length scales in predators, versus relatively more diffusive movement in prey species, all else being equal (2) (Fig. 1).

Notably, ‘all else’ is rarely equal in ecological systems, and the relative importance of bottom-up versus top-down regulation is highly context specific. In resource poor ecosystems,

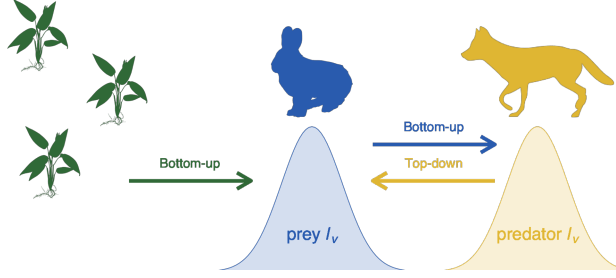


Figure 1: **Selection pressures on predator and prey ballistic length scales.** Schematic representation of bottom-up energetic requirements selecting for longer l_v , and top-down predation pressure selecting for shorter l_v .

individuals need to spend a significant amount of time searching for food (8, 15, 16). Because starvation is often a greater source of mortality than predation (17), the bottom-up driven need to find sufficient resources to survive should outweigh top-down pressure when resources are scarce. In productive environments, in contrast, bottom-up pressure on resource acquisition rates should be relaxed (3, 8, 18), allowing individuals to respond more directly to top-down pressure and maintain relatively more diffusive movement. These considerations lead to the expectation of a negative relationship between l_v and environmental productivity.

Although the importance of l_v in governing encounter rates is well recognised from a theoretical standpoint (2, 13, 14, 19), a generalized understanding of how bottom-up (i.e., resource availability) and top-down (predation pressure) factors shape general patterns in mammalian search strategies is lacking. The primary reason for this is that movement data have, historically, been sampled at too coarse of a resolution to quantify the average length scale over which ballistic motion is maintained for a broad range of species (20). To see this, consider that l_v is a function of the spatial variance of an animal's movement process (σ_p , in m^2 , proportional to the home-range area) and its positional and velocity autocorrelation timescales (τ_p and τ_v respectively, in sec), given by

$$l_v = \sqrt{\frac{\tau_v}{\tau_p} \sigma_p}. \quad (1)$$

While σ_p can be well estimated from coarse data (21), autocorrelation structures are only revealed when the time scale of measurement is less than or equal to the autocorrelation timescales (22). In particular, τ_v tends to be on the order of minutes to hours for terrestrial mammals (22–24).

Here, we leverage the rapid advances in the field of movement ecology (20, 25) that have enabled l_v to be estimated for a broad range of species. We annotated Global Positioning System (GPS) location data on 963 individuals from 53 species of terrestrial mammals (Fig. 3A) with mean adult body size (ranging from 0.4 to 4,000 kg), trophic group (herbivorous/frugivorous $n = 33$, and carnivorous $n = 20$). We restricted our analyses to range-resident animals and used continuous-time stochastic processes (26) to estimate l_v for each individual (Fig. 3B). We also annotated each data point with the mean Normalized Difference Vegetation Index (NDVI), a satellite-derived measure of resource abundance (27), to which each individual was exposed.

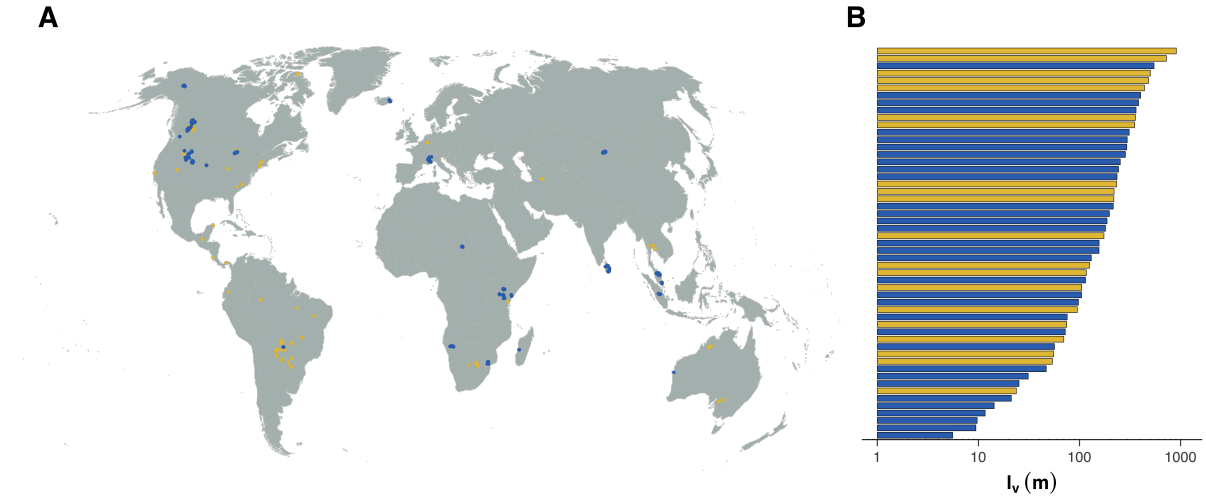


Figure 2: The distribution of mammalian movement data. In A, the GPS locations of 963 prey (blue) and predatory (yellow) mammals across 53 species are plotted on the global map; and B shows the median ballistic length scales, l_v , for each species.

These analyses revealed allometric scaling in both predator and prey ballistic length scales, with larger mammals tending to have longer l_v , all else being equal (Fig. 3A). The body mass

residuals followed theoretical predictions, with predator l_v being approximately 260m longer than that of comparably sized prey species (Fig. 3B). Least-squares regression also revealed a strong negative correlation between NDVI and the residuals of the allometric relationships in l_v for predators and prey (Fig. 3D). This was favoured over the null model of no relationship with NDVI by a ΔAIC_c of > 50 for predators and a ΔAIC_c of ~ 900 for prey. In other words, when resource abundance was ignored, predictions from the simple body-size relationships tended to underestimate observed l_v in low-productivity ecosystems, and over-estimate l_v in highly productive ecosystems. That bottom-up pressures appear to outweigh top-down pressure in resource scarce ecosystems is made all the more poignant when contrasted against patterns in trophic structure scaling. Resource poor environments tend to be more top heavy than productive ecosystems (28), effectively increasing individual level predation pressure.

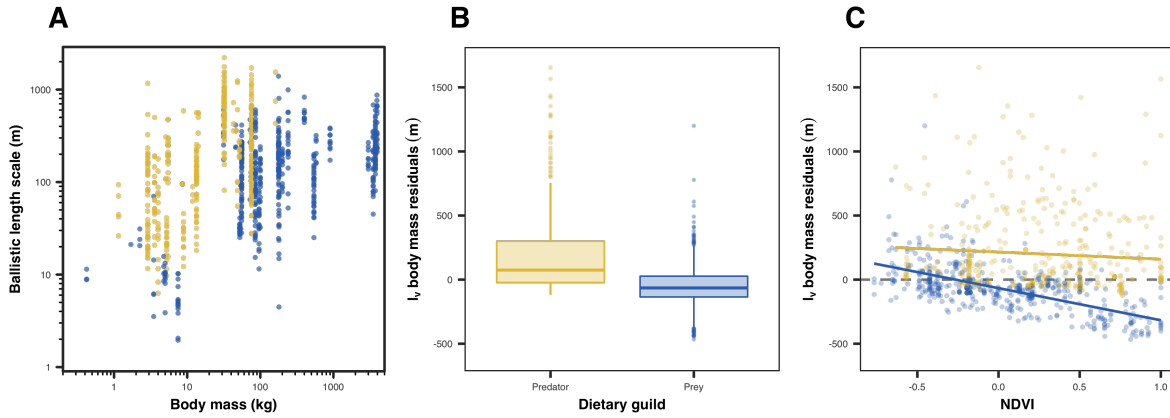


Figure 3: Trends in mammalian ballistic length scales. Mammalian l_v scales with body size, but predators exhibit more ballistic motion than prey species, and search behaviour is modulated by environmental productivity. The scatterplot in (A) show the allometric scaling of the ballistic length scale, l_v for prey (blue), as well as predatory (yellow) mammals. The boxplots in (B) show the residuals of the body mass scaling of l_v for predators and prey. When body size is accounted for, predatory species have significantly longer ballistic length scales on average (P value $< 10^{-15}$). The scatterplot in (C) show the body mass residuals as a function of the normalized difference vegetation index (NDVI), a measure of habitat productivity ranging on a scale between -1 and 1. The solid lines in C depict the fitted regression models.

An important question that arises from this work is ‘Why don’t predators have longer ballistic length scales?’. Without top-down regulation, there should be nothing preventing runaway selection in predator l_v . Nonetheless, we found that predator l_v was only $\sim 250\text{m}$ longer than that of comparably sized prey on average. There are three main reasons why predator ballistic length scales are not longer than we observed. The first is that individuals need to search over the area that they travel through and more directed motion does not necessarily imply an efficient search. Predators are thus limited by their perceptual range (2, 11). The second reason is that while many mammalian predators have few predators themselves, intra-guild and conspecific encounters can constrain predator movement (30). The third is that although local resource abundance will influence the relative importance of search times, it is not the only factor that will influence movement paths. Emerging empirical studies have found that the structure present in natural ecosystems can impact habitat permeability and the capacity for individuals to maintain directed motion (24, 31). We would therefore also expect to see a negative correlation between permeability and l_v . From our data, however, we found no support for a relationship between habitat structure and l_v for predators nor prey (supplementary material). Nonetheless, it is still possible that anthropogenic activities that introduce linear features, such as roads and edges, can permit predators to maintain unnaturally directed motion, leading to unnaturally high predation pressure on prey species (31).

Our findings highlight how the optimization of search strategies underpins broad patterns in the movement of terrestrial mammals. Predatory species searching for mobile prey have to maintain more directed motion than similarly sized prey species searching for immobile vegetation, with strong allometric patterns in mammalian ballistic length scales. Individual deviations from these allometries were influenced primarily by resource abundance rather than habitat structure. This points to the importance of encounter rates as a primary driver of mammalian movement strategies.

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Acknowledgments

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Supplementary materials

Materials and Methods

Supplementary Text

Figs. S1 to S3

Tables S1 to S4

References (4-10)

Materials and Methods

Empirical analyses

Tracking data analysis

To investigate pattern in the ballistic length scales, we compiled GPS tracking data on terrestrial mammals from the online animal tracking database Movebank (32), or from co-authors directly. Individual datasets were selected based on the criterion of range resident behavior, as evidenced by plots of the semi-variance in positions as a function of the time lag separating observations (i.e., variograms) with a clear asymptote at large lags (26, 33). All data from mi-

gratory, or dispersing periods were excluded as their measured movement strategies would not be representative of the normal foraging dynamics we aimed to describe. The visual verification of range-residency via variogram analysis (33) was conducted using the R package `ctmm` (26).

As noted in Eq. (1), the average length scale over which ballistic motion is maintained (l_v , in m) is a function of the spatial variance of an animal’s movement process (σ_{position} , in m^2) and its positional and velocity autocorrelation timescales (τ_{position} and τ_{velocity} respectively, in sec). Estimating l_v for these data thus first required estimating the autocorrelation structure in each of the individual tracking datasets. To do this, we fit a series of range-resident, continuous-time movement models to the data. The fitted models included the Independent and Identically Distributed IID process, which features uncorrelated positions and velocities; the Ornstein-Uhlenbeck (OU) process, which features correlated positions but uncorrelated velocities (34); and an OU-Foraging (OUF) process, featuring both correlated positions, and correlated velocities (33, 35). We then employed AICc based model selection to identify the best model for the data (35, 36), from which the positional autocorrelation timescale parameter, τ_p , was extracted. To fit and select the movement models, we used the R package `ctmm`, applying the workflow described by (26). Because only the OUF processes included information on all of the parameters required to estimate l_v , we further restricted our analyses to only those individuals for which the OUF model was selected. The final dataset included data from 53 species, comprising a total of 5,963,903 locations for 963 individuals. Finally, l_v was calculated from the parameter estimates for each of these individuals using Eq. (1).

Covariate data

For each of the species in our dataset we compiled covariate data on that species’ mean adult mass, in kilograms, and diet taken from the EltonTraits database (37). This dataset includes species with body masses covering 4 orders of magnitude (0.4 – 4000 kg). Dietary class was

then used to categorise species as being either a predator, or prey species. Predators were species that specialised primarily on mobile animal prey, whereas prey were herbivores and frugivores that specialised primarily on sessile vegetation. To assess ecological factors that may have influenced l_v , we also annotated each estimate with three satellite-derived metrics: i) mean Normalized Difference Vegetation Index (NDVI), a measure of resource abundance (27); ii) percent forest cover (38), a measure of habitat permeability. A summary of the dataset is shown in table 1

Assessing trends in l_v

The resulting dataset of ballistic length scales was then analysed to test for differences in l_v between predators and prey, and for any effects of NDVI or forest cover on l_v . Because l_v was correlated with body size (Fig. 3A), we controlled for mass by regressing l_v against body size on a \log_{10} - \log_{10} scale using generalised least-squares fitting with Gaussian distributed errors. Due to phylogenetic inertia (39), closely related species may exhibit similarities in movement due to common descent, requiring controlled comparisons (40). Accordingly, we did not treat species data records as independent, but rather corrected for this inertia by adjusting the variance-covariance matrix in our regression model based on the phylogenetic relationships using the R package `nlme` (44). Phylogenetic relationships between all of the 53 species in our dataset were obtained from the VertLife repository (42). We sampled 1,000 trees and estimated the consensus tree using the R package `phytools`, version 1.0-3 (43). The resulting tree is shown in figure 4.

The final step in our analyses was to determine whether individual deviations from the allometric relationships in l_v could be described by ecosystem productivity or permeability. We regressed the residuals of the phylogenetically controlled allometric models described above against NDVI and percent forest cover. Models were fitted for predators and prey separately.

Table 1: **Data summary.** Summary statistics on the empirical tracking data used in the analyses in the main text. Body mass is in kilograms and ballistic length scales, l_v , are in meters.

Binomial	n	Mass	Trophic Group	l_v
Acinonyx jubatus	3	46.7	Predator	357.6
Aepyceros melampus	20	52.50	Prey	31.1
Alces alces	33	541.46	Prey	97.6
Antilocapra marsupialis	10	31.5	Prey	362.7
Antilocapra americana	3	46.08	Prey	296.7
Beatragus hunteri	4	79.13	Prey	104.8
Brachylagus idahoensis	3	0.42	Prey	9.7
Canis latrans	49	13.41	Predator	125.8
Canis lupus	74	32.18	Predator	722.8
Capra ibex	39	85.17	Prey	75.6
Cerdocyon thous	19	5.24	Predator	23.7
Cervus canadensis	14	200	Prey	156.3
Chlorocebus pygerythrus	10	4.993	Prey	9.4
Connochaetes taurinus	35	180.00	Prey	156.0
Cuon alpinus	5	14.17	Predator	438.9
Elephas maximus indicus	24	3500	Prey	180.7
Elephas maximus maximus	51	3750	Prey	253.2
Elephas maximus sumatranus	9	3000	Prey	187.3
Equus hemionus hemionus	18	240	Prey	310.3
Equus quagga	9	400	Prey	546.3
Eulemur rufifrons	3	2.25	Prey	25.2
Euphractus sexcinctus	4	4.78	Prey	11.7
Felis catus	53	2.9	Predator	116.9
Felis silvestris	3	5.10	Predator	174.6
Giraffa camelopardalis reticulata	10	900.0	Prey	284.5
Hyaena brunnea	3	42.98	Predator	502.1
Lagostrophus fasciatus	1	1.7	Prey	21.2
Leopardus pardalis	3	11.90	Predator	74.6
Loxodonta africana	22	3940.03	Prey	402.9
Lycalopex culpaeus	8	8.62	Predator	95.2
Lynx rufus	13	8.9	Predator	70.0
Madoqua guentheri	15	7.50	Prey	5.6
Martes pennanti	17	4	Predator	54.0
Neogale vison	5	1.15	Predator	55.5
Odocoileus hemionus	5	54.21	Prey	72.4
Odocoileus virginianus	13	55.51	Prey	56.5
Oreamnos americanus	4	72.50	Prey	293.5
Oryx dammah	38	177.5	Prey	243.2
Ovis canadensis	3	74.64	Prey	114.8
Ovis dalli	66	55.65	Prey	197.6
Panthera leo	3	161.50	Predator	907.3
Panthera onca	105	75.7	Predator	350.7
Panthera pardus pardus	7	48.75	Predator	482.2
Panthera pardus saxicolor	6	52.04	Predator	218.9
Propithecus verreauxi	5	3.48	Prey	20.1
Puma concolor	2	51.60	Predator	233.1
Rangifer tarandus	19	86.03	Prey	215.9
Rangifer tarandus tarandus	8	86.03	Prey	384.1
Sus scrofa	23	96.12	Prey	46.9
Syncerus caffer	6	580.00	Prey	235.1
Ursus americanus	20	99.95	Prey	130.9
Vulpes lagopus	18	3.58	Predator	105.0
Vulpes vulpes	20	5.48	Predator	219.9

The relative support for these two models was then assessed by comparing the AICc value of the fitted models against intercept only models.

The R scripts used to produce the results presented in this work are openly available on GitHub at <https://github.com/NoonanM/BallisticMotion>.

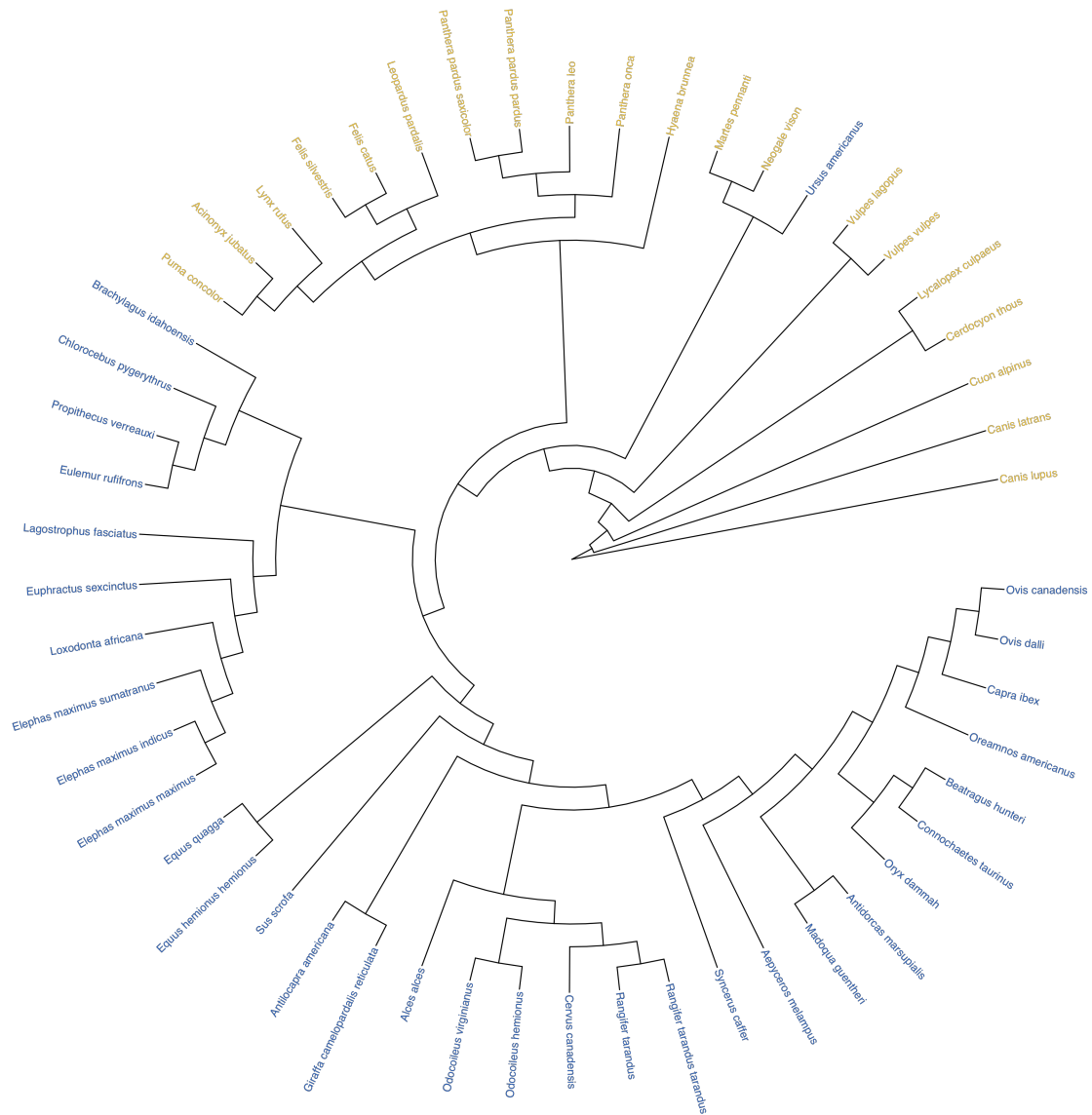


Figure 4: Phylogenetic relationships of the Mammalian species analysed in the main text with species labels coloured by trophic guild (prey in blue, predators in yellow).

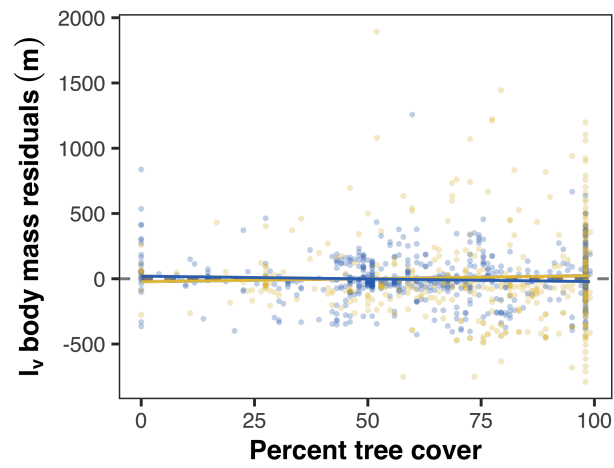


Figure 5: Residuals of the allometric scaling of the ballistic length scale, l_v for prey (blue), as well as predatory (yellow) mammals as a function of the percent tree cover. Each point is an individual ($n = 963$) representing 53 species.