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The allometry of locomotion

CARL S. CLOYED,[1,2,3,6] JOHN M. GRADY,[1] VAN M. SAVAGE,[4] JOSEF C. UYEDA,[5] AND ANTHONY I. DELL[1,2]

[1]*National Great Rivers Research and Education Center, East Alton, Illinois 62024 USA*
[2]*Department of Biology, Washington University of St. Louis, St. Louis, Missouri 63130 USA*
[3]*Dauphin Island Sea Lab, Dauphin Island, Alabama 36528 USA*
[4]*Department of Biomathematics, David Geffen School of Medicine, University of California, Los Angeles, California 90024 USA*
[5]*Department of Biological Sciences, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061 USA*

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Abstract. Organismal locomotion mediates ecological interactions and shapes community dynamics. Locomotion is constrained by intrinsic and environmental factors and integrating these factors should clarify how locomotion affects ecology across scales. We extended general theory based on metabolic scaling and biomechanics to predict the scaling of five locomotor performance traits: routine speed, maximum speed, maximum acceleration, minimum powered turn radius, and angular speed. To test these predictions, we used phylogenetically informed analyses of a new database with 884 species and found support for our quantitative predictions. Larger organisms were faster but less maneuverable than smaller organisms. Routine and maximum speeds scaled with body mass to 0.20 and 0.17 powers, respectively, and plateaued at higher body masses, especially for maximum speed. Acceleration was unaffected by body mass. Minimum turn radius scaled to a 0.19 power, and the 95% CI included our theoretical prediction, as we predicted. Maximum angular speed scaled higher than predicted but in the same direction. We observed universal scaling among locomotor modes for routine and maximum speeds but the intercepts varied; flying organisms were faster than those that swam or ran. Acceleration was independent of size in flying and aquatic taxa but decreased with body mass in land animals, possibly due to the risk of injury large, terrestrial organisms face at high speeds and accelerations. Terrestrial mammals inhabiting structurally simple habitats tended to be faster than those in complex habitats. Despite effects of body size, locomotor mode, and habitat complexity, universal scaling of locomotory performance reveals the general ways organisms move across Earth's complex environments.

Key words: acceleration; angular speed; animal movement; locomotor performance; maneuverability; predator–prey interactions; speed.

INTRODUCTION

Locomotion allows organisms to move through their environment and interact with each other, mediating behavior, species interactions, and biological processes across multiple levels of organization, from individuals to communities and even rates of speciation (Domenici 2001, Husak et al. 2006, Medina et al. 2018). For example, the relative speed and maneuverability of organisms is critical in determining the strength and outcome of competitive and trophic interactions that underlie population and community dynamics (Husak et al. 2006, Wilson et al. 2013, 2018, Grady et al. 2019). The locomotion of organisms also redistributes energy, nutrients, and genes across the landscape (Moore et al. 2007, Doughty et al. 2016, Medina et al. 2018). Many factors regulate locomotion, including energetic and biomechanical constraints of body size, the evolutionary history of the species, and the physical environment (Huey and Hertz 1982, Garland et al. 1988, Losos and Sinervo 1989, Domenici 2001, Van Damme and Vanhooydonck 2001, Vanhooydonck et al. 2015, Hirt et al. 2017*a*).

Body size constrains locomotion primarily through the metabolic and biomechanical properties of an organism (Peters 1983, Bonine and Garland 1999, Domenici 2001, Alerstam et al. 2007). Many studies have established that speed generally increases with body size (Garland 1983, Iriarte-Díaz 2002, Alerstam et al. 2007, Hurlbert et al. 2008, Hirt et al. 2017*a*), but a broad understanding of the allometry of organismal locomotion, which includes (1) multiple locomotor traits that characterize speed and maneuverability, (2) different modes of locomotion, and (3) spans the tree of life, is lacking. Previous studies on the allometry of locomotion focused on maximum body speed (Iriarte-Díaz 2002, Bejan and Marden 2006, Hirt et al. 2017*a*), which plays a central role in the outcome of trophic and competitive interactions (Table 1; Appendix S1: Fig. S1; Watkins

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[6] E-mail: ccloyed@disl.org

TABLE 1. Locomotor performance traits that are used in important ecological activities.

Locomotor performance trait	Ecological activities
Routine speed	foraging and other searching behaviors; dispersal; migration; most social activities and other behaviors
Maximum speed	escape and attack during predation events; courtship behaviors
Maximum acceleration	escape and attack during predation events
Minimum turning radius	out-maneuvering predators and/or prey courtship behaviors
Maximum angular speed	out-maneuvering predators and/or prey courtship behaviors

1996, Husak et al. 2006, Combes et al. 2012, Wilson et al. 2018). However, these studies ignore other aspects such as routine speed, acceleration, and maneuverability, which are also central to many species interactions (Appendix S1: Figs. S1–S3; Combes et al. 2012, Wilson et al. 2018). For example, routine speed (an organism's speed as it explores the landscape; Appendix S1: Fig. S2) is much lower than maximum speed and has been overlooked in recent syntheses. Most of the time that organisms spend moving is at routine speed, cutting the cost of transportation because lower speeds require less force (Biewener 2003, Claireaux et al. 2006, White et al. 2016) and allowing organisms to optimize home range sizes, dispersal, and migration (Table 1; Appendix S1: Fig. S2; Jetz et al. 2004, White et al. 2016). Furthermore, routine speed determines encounter rates between consumers and their resources, which helps shape population and community level processes (Appendix S1: Fig. S2; Shipley et al. 1996). Previous comparative work on the scaling of locomotion with size has also tended to overlook aspects of maneuverability, such as minimum turn radius and angular speed (but see Domenici 2001), which also plays an important role in predator–prey interactions (Table 1; Appendix S1: Fig. S3; Combes et al. 2012, Wilson et al. 2018). Finally, most prior work on the allometry of locomotion is often restricted to specific taxonomic groups (Alerstam et al. 2007, Hurlbert et al. 2008, Hirt et al. 2017*b*), habitats (Domenici 2001, Iriarte-Díaz 2002, Alerstam et al. 2007, Hurlbert et al. 2008, Hirt et al. 2017*b*), or modes of locomotion (flying, swimming, running; Domenici 2001, Iriarte-Díaz 2002, Hurlbert et al. 2008, Hirt et al. 2017*b*).

Other than body size, environmental medium and the complexity of the habitat through which organisms move also strongly affect locomotion (Bejan and Marden 2006, de Jager et al. 2011, Hirt et al. 2017*a*, Cloyed and Dell 2019). Different mediums (i.e., air, land, and water) place varying constraints on the physics of locomotion (Bejan and Marden 2006). Water, for example, requires more force to move through because of its greater viscosity than air (Biewener 2003, Bejan and Marden 2006), and swimming organisms move slower than those that fly (Bejan and Marden 2006, Hirt et al. 2017*a*). Flying organisms must overcome gravity, though, which is more energetically costly than swimming (Nespolo et al. 2008). Further, locomotion is generally faster and straighter in simpler habitats compared to more physically complex habitats (Sequeira et al. 2018, Cloyed and Dell 2019). These and other environmental constraints may affect the allometry of locomotion, affecting how organisms of varying sizes use habitats and how they have evolved to use those habitats (Brown and Maurer 1989, Losos 1990*b*, Van Damme and Vanhooydonck 2001, Scales and Butler 2016).

Organisms evolved to move in different environmental mediums and habitats, and this history can affect how each a species moves (Bergmann and Irschick 2010, Hirt et al. 2017*a*). Many distant groups have evolutionarily converged upon similar morphologies. Birds, bats, and insects have all evolved wings that produce lift in similar ways (Dickinson et al. 1999, Videler et al. 2004, Muijres et al. 2008). Likewise, tuna, lamnid sharks, and cetaceans have converged on similar morphological traits and locomotor patterns (Pabst 2000, Donley et al. 2004, Gleiss et al. 2011), despite being evolutionarily separated for hundreds of millions of years. The evolutionary length of time required to adapt to new locomotor modes in different environmental mediums is unknown, and groups that have more recently adopted a new locomotor mode may not move as efficiently as those that have used the mode for longer periods of time (Hirt et al. 2017*a*). For example, mammals have relatively recently colonization marine habitats, and they have slower size-normalized movement compared to fish, likely because they are not as adapted to moving through water as fish are (Hirt et al. 2017*a*). Integrating this phylogenetic history with body size, locomotor mode, and habitat across the tree of life should illuminate general patterns of locomotion.

The allometry of diverse locomotor traits that together characterize speed and maneuverability has not yet been synthesized into a single, empirically validated, quantitative framework across the tree of life. To address this gap, we extended current theory for the size dependence of both organismal speed and maneuverability by integrating energetic constraints with metabolic and biomechanical theory and principles (McMahon 1975, Peters 1983, Schmidt-Nielsen 1984, Brown et al. 2004, Pawar et al. 2012). To empirically validate our framework, we compiled and analyzed a new database of organismal locomotion that is unprecedented in size and breadth, comprising 884 species (Fig. 1) that span 23 orders of magnitude in body mass, from bacteria to whales, and includes five locomotor performance traits that are critical to the daily lives of many organisms: routine speed, maximum speed, maximum acceleration, minimum powered turn radius, and angular speed (Cloyed and Dell 2020). To explore how other factors affect locomotion, we extended our analysis beyond

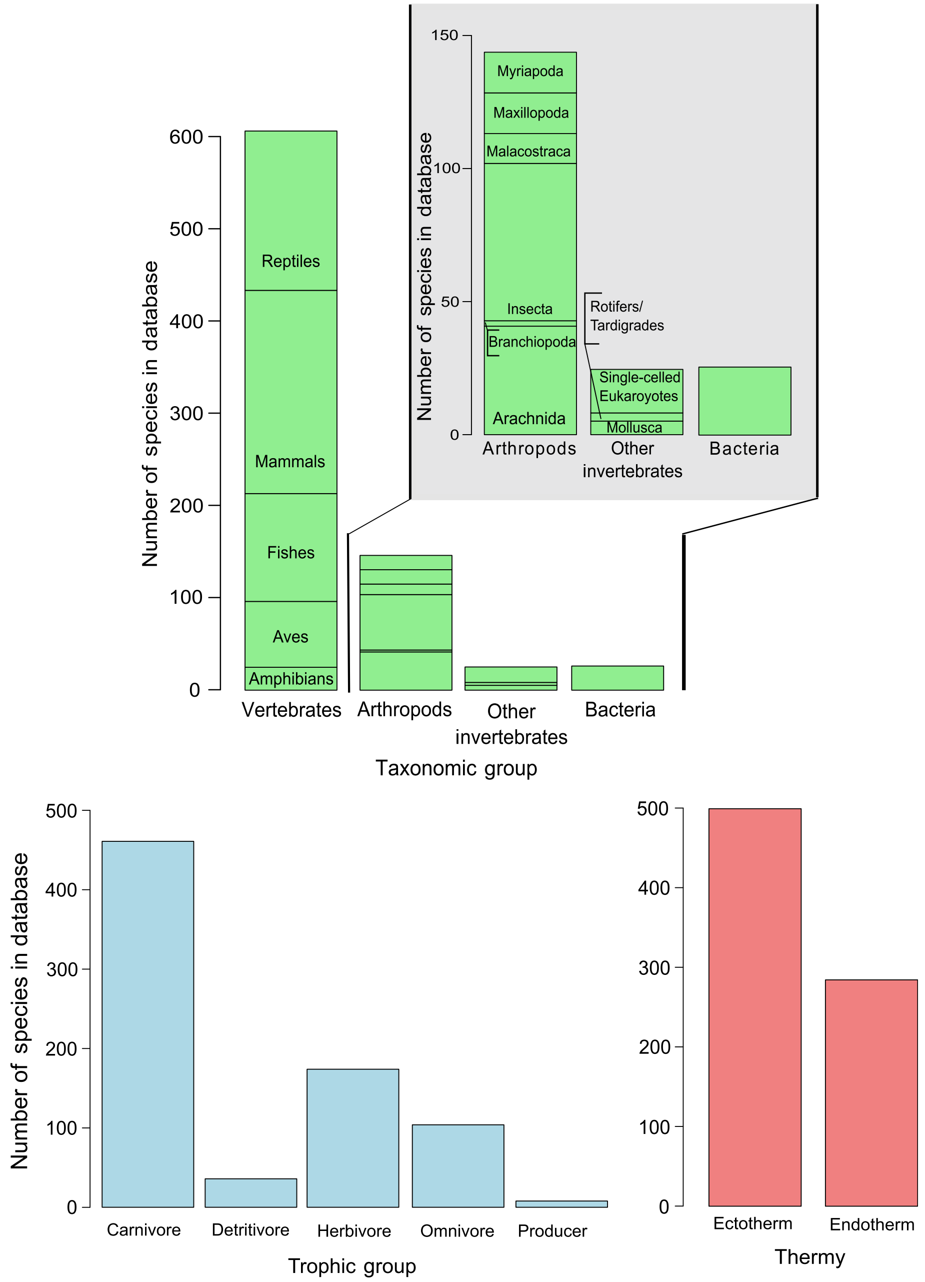

Fig. 1. Number and diversity of species in our analysis. Data are categorized by taxonomic (top), trophic (bottom left), and thermoregulatory (bottom right) groups.

body size to the effects of locomotor mode (flying, running, swimming), to estimate the evolutionary time it takes to optimize to different locomotor modes, and determine how habitat complexity shapes the speed of terrestrial mammals.

Theoretical Framework

Theory regarding the scaling of locomotor performance has focused on maximum speed and followed the classic allometric equation, $A = bM^x$, where A is the biological trait, b is a scaling coefficient, M is body mass, and x is the scaling exponent (McMahon 1975, Peters 1983, Calder 1984, Schmidt-Nielsen 1984). Variation in the predicted scaling exponent for speed arises because of assumptions about differences in small vs. large organisms and how these differences affect the scaling of stride length and frequency (McMahon 1975, Alexander and Jayes 1983, Peters 1983, Calder 1984, Schmidt-Nielsen 1984, Hurlbert et al. 2008). The earliest theoretical work assumed geometric similarity, where small and large organisms are considered geometrically scaled models of each other, and thus predicted no relationship between body size and speed so that the scaling exponent was 0 (Hill 1950, McMahon 1975). Later theory using elastic theory and static stress similarity assumed that limb structures of small and large organisms have similar buckling and breaking point in a way that is related to the ratio of the cross-sectional area and length of bone and muscle (McMahon 1975, Calder 1984). These assumptions were used to derive predicted scaling exponents of 0.25 and 0.40 for elastic and static stress similarity, respectively (McMahon 1975, Calder 1984). Finally, another theory based on dynamic similarity assumed geometric similarity but with associated forces and biological times that scale linearly such that small and large organisms face similar physical constraints, predicting an exponent of 0.17 (Alexander and Jayes 1983, Christiansen 2002, Hurlbert et al. 2008). Moreover, these dynamic similarity models have empirical support (Garland 1983, Christiansen 2002, Hurlbert et al. 2008), yet the relationship between maximum speed and body size is complicated by additional factors like injury, physical limitations, and power generated from metabolic processes (Biewener 1990, Iosilevskii and Weihs 2007, Dick and Clemente 2017, Hirt et al. 2017*a*). Metabolic powering had been associated with locomotor performance scaling (Peters 1983, Schmidt-Nielsen 1984), and metabolic theory has been applied to locomotor performance scaling to help further integrate external and internal forces along with biological times (Hurlbert et al. 2008, Pawar et al. 2012).

Organisms generate the force for locomotion by pushing some or all of their body onto an environmental medium, such as a leg onto ground, a wing onto air, or a torso or tail onto water (Fig. 2). Higher forces produce higher speeds and accelerations, and larger organisms can generate more force because of their larger muscles and longer appendages (Fig. 2). Although previous theory has incorporated metabolic powering (Peters 1983, Schmidt-Nielsen 1984, Hurlbert et al. 2008), which produces the power to exert force, the metabolic rates of an organism will vary among activities (Birt-Friesen et al. 1989, Glazier 2009, Auer et al. 2017). Pawar et al. (2012) incorporated a range of metabolic rates, from field to maximum, to produce a range of predicted exponents that encompasses a fuller theory of activities, interactions, and consumption rates (Jetz et al. 2004, Pawar et al. 2012). The relationship between metabolic rate (B) and body mass (M) is $B = B_0 M^{\beta}$, where B_0 is a coefficient accounting for taxon, metabolic state, and body temperature. The exponent β usually varies between 0.67 and 1.00 (Pawar et al. 2012). The power available for locomotion is described by the product of body velocity (v) and force (F) applied by an appendage, $B_0 M^{\beta} = v \times F$ (Pawar et al. 2012). If an organism devotes a proportion of its metabolic rate, B, to power locomotion, the equation can be solved as $v = B_0 M^{\beta}/F$. Importantly, force is dependent on the cross-section of appendage muscle, and force scales proportionally with body mass to an exponent of β_F, $F \propto M^{\beta_F}$, which typically varies

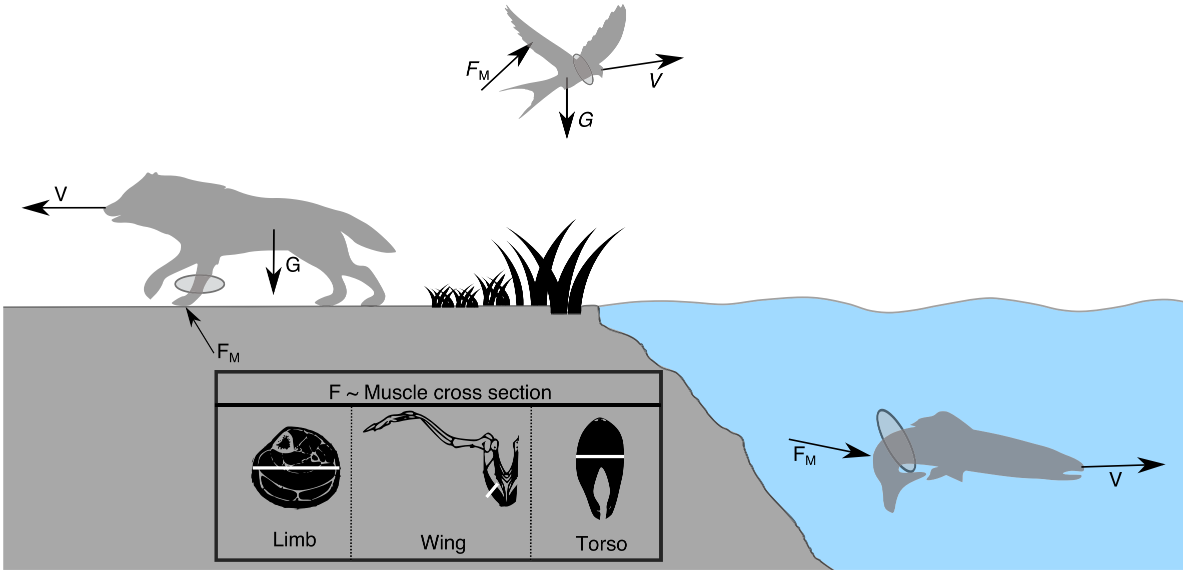

Fig. 2. A free-body diagram of the physical forces involved in the locomotion of aerial, terrestrial, and aquatic organisms. F_M, force individual exerts on environmental medium; G, gravity; and V, velocity. The force that an organism can exert on its surroundings is proportional to the cross-sectional area of the muscles in the limbs (terrestrial) or torso/tail (aerial, aquatic). Depending on how organisms exert F_M, V can represent forward motion (i.e., speed and acceleration) or maneuverability (i.e., minimum turn radius and angular speed).

between 0.50 and 0.67 (Peters 1983, Schmidt-Nielsen 1984, Savage et al. 2007). Pawar et al. (2012) then estimate velocity scales as

$$v = v_0 M^{\beta-\beta_F} \tag{1}$$

where v_0 is a constant that depends on locomotor mode (Bejan and Marden 2006). Field-to-maximum metabolic rate scales with an exponent between 0.80 and 0.90, and so v should scale with mass with an exponent between 0.13 ($\beta = 0.80$, $\beta_F = 0.67$) and 0.40 ($\beta = 0.90$, $\beta_F = 0.50$) (Pawar et al. 2012). Since maximum speed requires more force than routine speed and since force scales less than proportionally with body mass, we expect that maximum speed will scale at a slightly lower rate than routine speed.

We extended this theory for velocity to explain the allometry of body acceleration in the following way. The minimum time (t) it takes an organism to go from stationary to maximum velocity ($v_{\max}$) is defined as its maximum acceleration (a), $a = \Delta v/\Delta t$, where Δt is the change in time between a velocity of zero and $v_{\max}$, $a = (v_{\max} - 0)/\Delta t$. Velocity scales proportionally with mass to an exponent of x, $v_{\max} \propto M^x$. The time to reach maximum velocity scales as a typical biological time $\Delta t \propto M^x$ (Garland 1983, Alerstam et al. 2007, Hurlbert et al. 2008). The combined scaling of velocity (M^x) and time to maximum velocity (M^x) cancel one another so that acceleration is predicted to not vary with mass:

$$a = \frac{a_0 M^x}{M^x} = a_0 \tag{2}$$

where a_0 is a constant.

Theoretical derivations for the allometry of maneuverability are generally related to how body length scales with mass (Webb 1976, Blake et al. 1995). Minimum turn radius (r) is the shortest distance an organism uses to complete a 180° turn, and angular speed (as) is the rate at which it can spin to face a different direction. For minimum turn radius, any distance an organism can turn along the curve is an arc length (r), which is defined by the radius (R) of the circle and the angle (θ) associated with that arc length, $r = R \times \theta$. The radius of a turning organism is proportional to one-half a body length (L; Blake et al. 1995) so $r \propto (L/2) \times \theta$. The angle θ is mass independent, $\theta \propto M^0$, because the angle of the turn (180° for a u-turn) is the same for large and small organisms, and $r \propto (L/2) \times \theta$ becomes $r \propto L/2$ since θ is independent of body size. Body length scales with mass to a 1/3 power (Schmidt-Nielsen 1984, Hurlbert et al. 2008), and we predict that minimum turn radius scales with mass as

$$r = r_0 M^{\frac{1}{3}} \tag{3}$$

where r_0 is a constant.

Like minimum turn radius, the degree an organism rotates is size invariant. In order to rotate on the spot, organisms must travel along the circumference of the circle of rotation. The circumference of that circle is $2\pi R$, with the radius (R) being equal to $L/2$. Thus, angular speed should scale with body length (L), which scales with body mass to a 1/3 power (Schmidt-Nielsen 1984, Hurlbert et al. 2008). Since larger organisms have a greater circumference, they must travel further along that circumference to rotate a given number of degrees. It should therefore take larger organisms longer to rotate than smaller ones, and angular speed should scale as

$$as = as_0 M^{-\frac{1}{3}} \tag{4}$$

where as_0 is a constant.

MATERIALS AND METHODS

Data collection

To characterize the allometry of locomotion in organisms and test the assumptions and predictions from our theory (see Theoretical Framework), we performed a literature search on Web of Science and Google Scholar. The search included articles published before January 2019 and included combinations of the terms "body size," "mass," "length," "velocity," "speed," "acceleration," "turning radius," "turning speed," and "angular velocity." We found 287 sources from which we extracted the type and value of locomotion, the mass and/or length of the organism, habitat type (terrestrial, aquatic, or aerial) and temperature (body and/or environmental temperature). We also obtained information about the trophic level and thermoregulation of each species (e.g., endotherm vs. ectotherm). In total, we compiled data from 884 species (Fig. 1; Cloyed and Dell 2020). For maximum speed, we determined if the velocity was an escape or attack response, which has previously been suggested as being important for locomotor performance (Scales et al. 2009, Dell et al. 2011). For minimum turn radius, we only included data from powered (not unpowered) turns. When either length or mass was provided but not both, we used published length–weight regressions to determine the missing value. See Cloyed and Dell (2020) for the raw data and more detail about the methods.

Temperature correction

Temperature strongly impacts locomotor performance in ectotherms (Bennett 1990, Dell et al. 2011, Cloyed et al. 2019). Locomotor performance was measured at a variety of temperatures in the individual studies in our database. Many measurements were probably not made at the organism's optimal temperature, but we could not account for this because optimal temperatures are unknown for most species and can vary across populations (Elphick and Shine 1998, Richter-Boix et al. 2015). Additionally, our database includes both endotherms and ectotherms. Therefore, we used temperature corrections to account for studies performed at different temperatures (Brown et al. 2004, Schramski et al. 2015). We performed these corrections using the Boltzmann factor, $V_C = Ve^{E/kT}$, where V is the locomotion trait value (i.e., maximum speed, routine speed, acceleration, turning radius, angular velocity), E is the activation energy (eV), k is Boltzmann's constant, and T is temperature in Kelvin (Brown et al. 2004). We set the temperature correction to 15°C (288.15 K).

Phylogenetic analysis

We took the natural logarithm of Eqs. 1–4 to convert the exponents to coefficients and produce linear relationships. We then used phylogenetic least squares (PGLS) regression to estimate those coefficients and account for phylogenetic history. Taxonomic data were matched to the Timetree of Life (Hedges et al. 2015) with maximal overlap achieved by querying the Open Tree of Life taxonomy database and using the R package phyndr (Pennell et al. 2016), which swaps out taxa from the tree with taxa in the dataset if they have an equivalent phylogenetic position. We were able to include 613 species in these PGLS regressions. We also tested for curvature in routine and maximum speeds, as previous analyses have revealed that speed plateaus or may decrease at larger body sizes (Garland 1983, Chappell 1989, Iriarte-Díaz 2002, Hirt et al. 2017*a*). All PGLS analyses were conducted using the R package phylolm (Ho et al. 2018). Each trait was fit to models in combination with residual covariance structures following either Brownian Motion (BM), a Pagel's λ model (Pagel 1999), or an Ornstein-Uhlenbeck model with a fixed or random root (Grafen 1989, Hansen 1997). Models were fit using maximum likelihood and compared using Akaike's Information Criterion (AIC). To determine how long phylogenetic signals persist after accounting for adaptation to different locomotor modes, we used phylogenetic half-life from the OU model as our measure of phylogenetic signal, which measures in years how quickly phylogenetic covariance is erased by the evolutionary process. Half-life values less than a few million years indicate a model where no measurable covariance is explained by the phylogeny, and values nearing the height of the tree represent Brownian evolution and indicates models with strongly persistent phylogenetic covariance.

Non-PGLS analyses

In addition to performing PGLS regressions, we also performed the same analyses with ordinary least squares (OLS) regression to test the relationships between locomotor performance and body size. OLS regression does not account for phylogenetic history but allows us to test the allometry of locomotion across all 884 species in our database, instead of the 613 species with phylogenetic data. Our database had 17 species with sufficient data to test for intraspecific allometric patterns, and we used OLS regressions to test these relationships. Additionally, we used OLS regression to determine the scaling coefficients for different locomotor modes.

Habitat complexity

We determined whether and how habitat complexity affected the allometry of maximum speed of terrestrial mammals. We focused on maximum speed in terrestrial mammals because they were well represented in our database, the complexity of the habitats they primary used was relatively easy to classify, and a considerable amount of maximum speed data exists in the literature on this group. Using natural history information from the literature, we determined which habitat type each terrestrial mammal predominantly used: grasslands, savannahs, deserts, and tundra were considered "open" habitats; forests and thick scrublands were considered "closed" habitat; glades and park-like grasslands (i.e., grasslands with scattered trees) were considered "mixed" habitats, and mammals that used both open and closed habitats were considered to use mixed habitats; and "rocky" habitats were predominantly mountain and alpine environments. We used OLS regressions to test for different allometric relationships with maximum speed among habitats.

RESULTS

Our theory predicted that the slope between routine and maximum speed and mass would be between 0.13–0.4 (Eq. 1). Routine and maximum body speed both scaled as theoretically predicted in both linear and quadratic regressions (Fig. 3; Table 1; Appendix S1: Table S1), although quadratic regressions were a better fit than linear for routine and maximum speed (Appendix S1: Table S2). Speed plateaued at larger body sizes (~20–30 kg; Fig. 3a,b; Appendix S1: Table S2), which was more pronounced in maximum compared to routine speed (Fig. 3a,b). Our theory predicted that acceleration would not scale with mass, and PGLS regression on acceleration supported that prediction, though OLS regression had a positive allometric slope (Fig. 3c; Table 2; Appendix S1: Table S3). For maneuverability, our theory predicted that minimum turn radius would scale at 0.33 and angular speed would scale at −0.33. Minimum turn radius increased as predicted in both regression types, and our prediction was included in the 95% CIs for the PGLS (Fig. 3d; Table 2; Appendix S1: Table S3). Angular speed increased in the predicted direction, but our predicted value was not included in the 95% CI for the PGLS regression, but it was in the OLS regression (Fig. 3e; Table 2; Appendix S1: Table S3). We found similar, intraspecific allometric patterns of locomotion for 17 species in which we had data that spanned two or more orders of magnitude in mass (Fig. 4; Appendix S1: Table S4). Similarity between

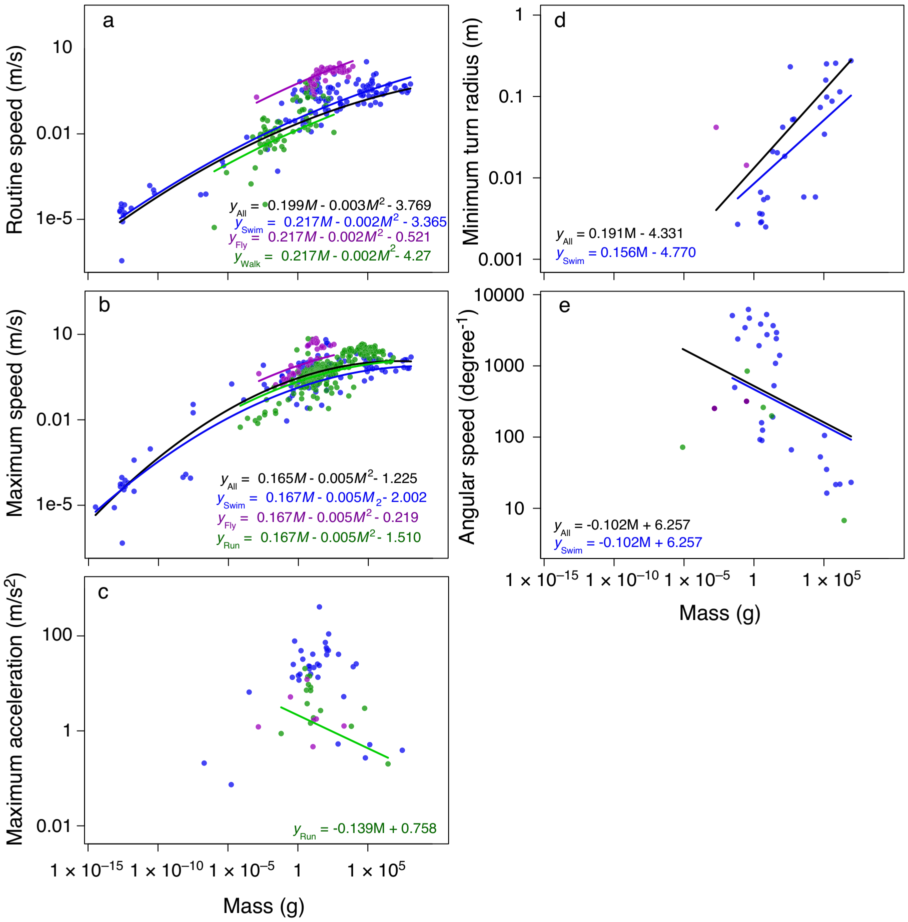

FIG. 3. The allometry of animal speed and maneuverability within (colored lines) and across (black lines) locomotor modes, including (a) routine speed, (b) maximum speed, (c) maximum acceleration, (d) minimum turn radius, and (e) angular speed. Blue lines/symbols indicate swimming organism, green indicates running organisms, and maroon indicates flying organisms. M is mass.

intra- and interspecific patterns provides evidence for the generality of allometric scaling in locomotion.

The allometric relationships among organisms that fly, swim, and run (i.e., locomotor modes) varied among the five traits. Routine and maximum speed both shared similar slopes and curvatures across modes, but flying organisms were faster than running and swimming organisms (Fig. 3a,b; Table 2; Appendix S1: Table S1). Acceleration decreased in large, terrestrial organisms (Fig. 3c; Table 2; Appendix S1: Table S3). We could not compare maneuverability among locomotor types as we only had sufficient data to test swimmers (Fig. 3d,e). The phylogenetic signals and half-lives (the expected time for a lineage to move from their ancestral value halfway to the typical phylogenetic value for the group and apparently erase its phylogenetic history) for routine speed, acceleration, and angular speed were high (341.25, 323.59, and 215.94 million years, respectively). Maximum speed had a weaker phylogenetic signal, with a lower half-life of 91.47 million years.

Maximum speed in terrestrial mammals varied with habitat complexity. The slopes between body size and maximum speed among habitats were statistically indistinguishable, but the intercept was highest for open habitats, followed by mixed, closed, and rocky habitats (Fig. 5; Table 3). The intercept for mammals in open habitats was significantly higher than for mammals in closed habitats (Fig. 5; Table 3), and mammals from simple habitats were faster than mammals from complex habitats.

DISCUSSION

We found broad theoretical and empirical support for a general trade-off in the allometry of locomotion: larger organisms are faster but less maneuverable than smaller organisms. Although previously recorded (Domenici 2001, Wilson et al. 2015), we provided a synthesis and theory for the scaling of locomotion that is wider than currently available, including species that span the tree of life and multiple locomotor traits that underpin the daily activities of many organisms (Husak et al. 2006, Combes et al. 2012, Wilson et al. 2018). Our results are

Table 2. Results of phylogenetic generalized least squares (PGLS) and ordinary least squares (OLS) regressions for all species and environments, including quadratic regressions for routine and maximum speed and linear regression on maximum acceleration, minimum turn radius, and angular speed.

		Slope			Curvature			
Locomotion type	*N*	Theoretically predicted	Mean (95% CI)	*P*	Mean (95% CI)	*P*	Intercept	log *L*
Routine body speed								
PGLS	246	0.13–0.40	0.200 (0.186–0.214)	<0.001	−0.003 (−0.002 to −0.004)	0.002	−3.796	−324.6
OLS	453	0.13–0.40	0.259 (0.239–0.279)	<0.001	−0.003 (−0.002 to −0.004)	<0.001	−2.244	−844.7
Maximum body speed								
PGLS	433	0.13–0.40	0.165 (0.130–0.198)	<0.001	−0.005 (−0.002 to −0.007)	<0.001	−1.225	−505.6
OLS	528	0.13–0.40	0.186 (0.173–0.199)	<0.001	−0.004 (−0.003 to −0.005)	<0.001	−1.204	−793.5
Maximum body acceleration								
PGLS	58	0	0.063 (−0.937 to 1.06)	0.208	NA	NA	0.651	−100.9
OLS	74	0	0.140 (0.09–0.20)	<0.001	NA	NA	1.240	−156.5
Minimum turn radius								
PGLS	29	0.33	0.191 (0.033–0.349)	0.020	NA	NA	−4.331	−51.8
OLS	30	0.33	0.205 (0.125–0.285)	<0.001	NA	NA	−5.063	−47.0
Angular speed								
PGLS	36	−0.33	−0.102 (−0.012 to −0.192)	0.042	NA	NA	6.260	−63.5
OLS	46	−0.33	−0.244 (−0.154 to −0.334)	<0.001	NA	NA	6.840	−77.7

Notes: *N* is number of species; NA is not available. Theoretically predicted slopes were generated from *Theoretical Framework*.

consistent with previous studies that indicate metabolic constraints play an important role in shaping locomotor performance (Garland 1983, Alerstam et al. 2007, Hurlbert et al. 2008). Our analyses included both routine and maximum speed and both had relatively small power exponents, but our calculated 95% CIs were bounded within our theoretical predictions. Furthermore, our scaling estimate for maximum speed (0.17) was similar to previous studies that found maximum speed scaled as 0.17 in terrestrial mammals (Garland 1983), between 0.14 and 0.34 among ant species (Hurlbert et al. 2008), and as 0.13 in aerial birds (Alerstam et al. 2007). The 95% CIs for maximum speed overlapped with a majority of these studies, and, although the Hurlbert et al. (2008) included some ant species with higher exponents, most were between 0.14 and 0.26 (Hurlbert et al. 2008). Our study has a much broader range of theoretically predicted scaling exponents for speed compared to other studies (Peters 1983, Calder 1984, Schmidt-Nielsen 1984), but our theoretical framework includes different types of metabolic power, such as resting, field, and maximum, with the latter two playing different roles in locomotion. Field metabolic rate likely plays an important role in routine speed while maximum metabolic rate likely controls maximum speed (Birt-Friesen et al. 1989, Glazier 2009, Auer et al. 2017). Consistent with these ideas and our theoretical expectations, the scaling of maximum speed was lower than routine speed. Empirical analysis also supported our prediction that acceleration does not scale with body size (or did so weakly in the OLS regression). Although comparatively little work has investigated the scaling of acceleration, studies that have looked over a broad range of species and/or body sizes have not found a relationship (Domenici 2001, Vanhooydonck et al. 2006), suggesting that body size itself does not shape acceleration but instead may be driven by factors such as the mass of specific muscles (Vanhooydonck et al. 2006). For turn radius, the PGLS estimate included the predicted 0.33 but the OLS did not. Although angular speed scaled in the predicted direction, the scaling exponent was lower than expected and neither the PGLS nor the OLS included 0.33 in the 95% CI. These results suggest that factors other than Euclidean biomechanics may shape maneuverability, such as metabolic powering (Hurlbert et al. 2008). The empirical validation of our theoretical framework implies that energetics and biomechanics together shape organismal locomotion.

The allometric patterns of routine and maximum speeds were consistent among locomotor modes and for maximum speed among terrestrial mammals from habitats that varied in their physical complexity (Van Damme and Vanhooydonck 2001). The consistent allometric scaling among locomotor modes indicates that the constraints body size places on locomotion—metabolic rate, appendage and body length, muscle size—are consistent among habitats (Van Damme and Vanhooydonck 2001, Hirt et al. 2017*a*). Previous studies have found significant differences in the scaling of maximum speed among locomotor modes. Both Bejan and Marden (2006) and Hirt et al (2017*a*) found that flying scaled at a lower rate than running and swimming, and Alerstam et al. (2007) found that birds scale at 0.13. However, these studies analyzed smaller datasets that were focused on specific taxonomic groups. Our dataset included flying birds, insects, and mammals, and so our results

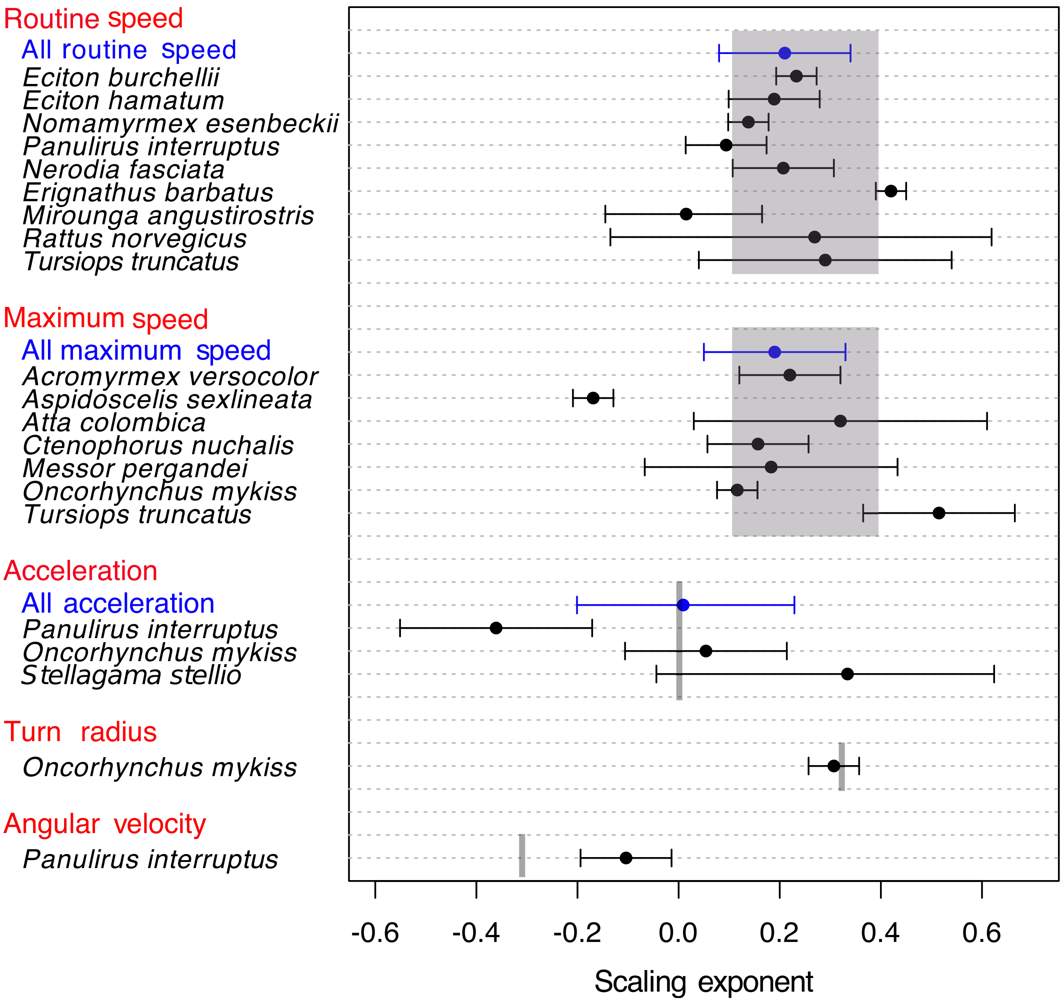

FIG. 4. The scaling exponents for the intraspecific analyses on locomotor performance and mass. Dots are estimated slopes and bars are 95% confidence intervals. Blue dots and lines are the averages of the intraspecific estimates and 95% CIs for each trait. Gray boxes represent theoretical predictions for routine and maximum speed and gray lines represent the theoretical predictions for maximum acceleration, minimum turn radius, and angular speed.

should provide a more robust test for how speed scales with body size across locomotor modes. Only the actual speed (i.e., the intercept) differed among organisms that use different modes or habitats that vary in complexity. For locomotor mode, flying organisms of a given size move faster through air than swimming organisms move through water as air is less resistant (Bejan and Marden 2006). Terrestrial organisms also move through air, but they do so via friction on a substrate and must decelerate and accelerate with each stride because of the impact on the substrate (Dickinson et al. 2000). The differences in speeds among flyers, swimmers, and runners may have a dramatic impact in predator–prey interactions: flying organisms have a large speed advantage over swimmers and runners that may favor flying organisms in many predator–prey interactions unless running and swimming organisms can evolve ways to overcome the asymmetry (e.g., ballistic tongues in frogs and chameleons that catch flying insects). We had too few data to compare maneuverability among locomotor modes, but it would be of great interest to know if allometric patterns of maneuverability are similar across locomotor modes. More research is needed that measures maneuverability in terrestrial and aerial organisms, as most studies have focused on speed.

Biologists have debated whether speed plateaus at larger body sizes, and, if so, why (Van Damme and Vanhooydonck 2001, Iriarte-Díaz 2002, Bejan and Marden 2006, Hirt et al. 2017*a*). We found strong support that speed plateaus in larger organisms. There are two likely explanations for this. The first, recently put forward by Hirt et al. (2017*a*), states that larger organisms cannot attain their true maximum speed because they cannot maintain acceleration long enough to reach that speed. This explanation assumes a negative relationship between acceleration and body size, especially in the

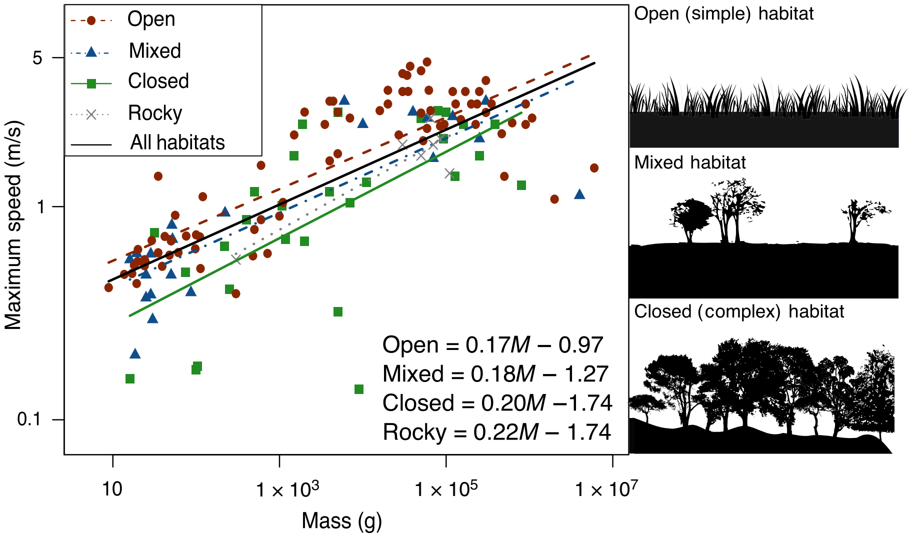

FIG. 5. The effects of habitat on maximum speed in terrestrial mammals. Slopes for different habitats are approximately the same but intercepts vary. The black line indicates the regression of maximum speed vs. mass across all habitats.

TABLE 3. Linear regression results for maximum speed scaled by body mass for terrestrial mammals in different habitat types.

Habitat type	*N*	Slope	Intercept
Open	79	0.17 (0.09–0.25)	−0.97 (−1.58 to −0.36)
Mixed	22	0.17 (0.09–0.25)	−1.27 (−1.69 to −0.58)
Closed	29	0.20 (0.14–0.26)	−1.74 (−2.29 to −1.19)
Rocky	7	0.19 (−0.03 to 0.41)	−1.74 (−3.90 to 0.42)

Notes: Values are means with 05% CI in parentheses. All the slopes are statistically indistinguishable from each other. Terrestrial mammals from rocky and closed habitats have nearly identical intercepts, whereas terrestrial mammals from open habitats have a significantly lower intercept than those from closed habitats. Terrestrial mammals from mixed habitats have an intercept that is intermediate between open and closed habitats and the 95% confidence intervals overlap with intercepts from both open and closed habitats.

largest organisms, a pattern not supported by our data. Instead, we found no relationship with the PGLS regression and a positive one with the OLS regression. However, we did find a negative relationship between acceleration and body size in terrestrial organisms. In addition, this explanation assumes that it is possible for very large organisms to obtain fast speeds without suffering from physical forces that would result in injury (Biewener 1990, Iosilevskii and Weihs 2007, Dick and Clemente 2017). Large organisms at high speeds have an increased chance of injury (Biewener 1990, Van Damme and Vanhooydonck 2001, Iosilevskii and Weihs 2007, Dick and Clemente 2017, Garland and Albuquerque 2017). Terrestrial mammals and reptiles can decrease the stress on their skeletal systems from impact at high speeds by increasing bone width and changing postures, but this is physically possible only up to a certain point, after which the only strategy to avoid skeletal fractures is to slow down (Biewener 1990, Dick and Clemente 2017). This may also explain the negative relationship between acceleration and body size in terrestrial organisms, as faster accelerations may place additional strain on the skeletal system. Likewise, for aquatic organisms, the viscosity of water results in cavitation at high speeds that can damage appendages and place an upper limit on speed in aquatic environments (Iosilevskii and Weihs 2007). Thus, the largest organisms are not the fastest. Indeed, many very large organisms rarely move at maximum speeds, as they are likely too large to be in danger of predation (Owen-Smith 1988). In contrast, routine speed can scale with body size at a higher exponent because it is more efficient for large organisms than it is for small ones. This combination of factors likely results in curvature in the allometric patterns of speed (Chappell 1989, Biewener 1990, Iosilevskii and Weihs 2007, Dick and Clemente 2017).

Energetic constraints and the sized-based trade-off between speed and maneuverability have important consequences for how large and small organisms interact with the environment and each other (Huey and Hertz 1984, Domenici 2001, Dial et al. 2008, Garland and Albuquerque 2017). Larger organisms, with higher routine speeds that translate into lower costs of transportation, can more efficiently maintain larger home ranges and migrate and disperse longer distances (Brown and Maurer 1989, Jetz et al. 2004, White et al. 2016) interacting with more species and habitats. Larger organisms may be better suited to being generalists than smaller organisms (Brown and Maurer 1989). Speed increases with size, and large predators (Brose et al. 2006) often exploit this fact during interactions (Huey and Hertz 1984, Combes et al. 2012, Wilson et al. 2018).

Conversely, the scaling of turn radius and angular speed means that smaller prey are maneuverable and can rely on quick changes of direction to escape predators (Patriquin and Barclay 2003, Combes et al. 2012, Wilson et al. 2018). From this pattern an important prediction arises; prey species may evolve protean behavior, where their movements include many random turns that are unpredictable to pursuing predators (Djawdan and Garland 1988, Jones et al. 2011, Moore and Biewener 2015). Given these biomechanical constraints, some larger organisms have evolved ways to increase the maneuverability of certain parts of their bodies. For example, sailfin fish (*Istiophorus albicans*) slash their elongated bills through schools of sardines (*Sardinella aurita*) and feed on the injured or disoriented fish that failed to escape (Domenici et al. 2014). These general and specific patterns of movement that emerge between different sized organisms may constrain the size ratios between predators and prey (Brose et al. 2006) and allow predators and prey to benefit from using different types of habitats.

Open habitats present fewer obstacles to forward motion and detection distance and may select for faster organisms (de Jager et al. 2011, Sequeira et al. 2018, Cloyed and Dell 2019). In our analysis, terrestrial mammals that inhabit grasslands and savannas had faster average body speeds than those that inhabited closed forests. Lack of refugia in open habitats may force prey to rely on high speeds to escape, which places them at a disadvantage because their smaller size makes them slower (Patriquin and Barclay 2003). In complex habitats, slower movements may favor smaller organisms and prey because prey can out-maneuver predators until they reach a refuge and hide (Pennings 1990, Buck et al. 2003, Patriquin and Barclay 2003). Thus, we would predict that the fastest organisms also use simple environments: cheetahs (*Acinonyx jubatus*) hunt in open grasslands, swordfish in pelagic waters (*Xiphias* spp.), and Peregrine Falcons (*Falco peregrinus*; the fastest birds when assisted by gravity) above physical obstructions. More research should focus on organismal speed and habitat use, because habitat use, predation and antipredation tactics, and maximum speed may have coevolved (Garland et al. 1988, Losos 1990*a*, Van Damme and Vanhooydonck 2001).

Our phylogenetic analyses revealed that a considerable amount of time is required to fully adapt locomotion once a group radiates into a different environmental medium (e.g., mammals to the ocean, bats to the air). Routine speed, acceleration, and maneuverability all had phylogenetic half-lives on the order of several hundred million years. Maximum speed had a much shorter phylogenetic half-life, and there may have been stronger selection on maximum speed than on other traits. For example, maximum speed often determines the outcome of predator–prey interactions, and many predator–prey pairs are engaged in evolutionary arms races regarding maximum speed (Irschick and Higham 2016, Wilson et al. 2018). Furthermore, the hundreds of millions of years it takes to evolve moving through a different environmental medium likely explains, in part, why convergent evolutionary groups—birds, bats, and insect as well as tunas and cetaceans—are evolutionarily separated by at least that length of time. The relatively long phylogenetic half-lives, even for maximum speed, and associated difficulty in fully adapting to a new locomotor mode may explain some of the residual variation in the allometric patterns of locomotion, as different species may be at different points in their evolutionary trajectories (Hirt et al. 2017*a*). Of course, different taxonomic groups bring different adaptations to new environments. For example, endothermic top predators in the world's oceans have body temperatures independent of ambient temperatures, and they can move much faster than comparably sized ectotherms in cold waters, leading to elevated richness in temperate habitats (Grady et al. 2019).

We show the allometry of organismal speed and maneuverability follows predictable scaling principles. Our general framework can be integrated with more detailed mechanical models of organismal locomotion across the various domains of life. Researchers can use our theoretical framework and empirical results to explore how speed and maneuverability affect food web and population models that use encounter and capture rate parameters to predict how and where energy and nutrients move through ecosystems. Overexploitation and land clearing have reduced organismal sizes in many systems with downstream effects on food web structure (Patriquin and Barclay 2003, Estes et al. 2011, Gómez-Campos et al. 2011). Accurate modeling of size effects on locomotion will help projections of community structure under human influence (Brose et al. 2006). Finally, because the scaling of movement reflects physical principles, scaling rules observed here may inform locomotory research in robotics and biomimetic technology.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3369/suppinfo

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Data used for analyses in this manuscript are freely available in a data paper published in *Ecology* (Cloyed and Dell 2020).