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Scaling of rotational inertia in murine rodents and two species of lizard

Rebecca M. Walter* and David R. Carrier

Department of Biology, 201 South Biology Building, University of Utah, Salt Lake City, UT 84112, USA

*e-mail: walter@biology.utah.edu

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Summary

Because the force required to rotate a body about an axis is directly proportional to its rotational inertia about the axis, it is likely that animals with high rotational inertia would be constrained in their turning abilities. Given that rotational inertia scales with mass$^{1.67}$ in geometrically similar animals, whereas the ability to apply torque scales with mass$^{1.00}$, larger animals would be expected to have more difficulty turning than smaller animals of similar shape. To determine how rotational inertia scales with body mass, we used the fact that the period of a physical pendulum is proportional to its rotational inertia$^{0.50}$, and measured rotational inertia in two groups of vertebrates with greatly different body shapes: murine rodents (*Mus domesticus* and *Rattus norvegicus*) and lizards (*Iguana iguana* and *Varanus exanthematicus*). Rotational inertia did not deviate significantly from isometric scaling in the murine rodents as a group or in the varanid lizards, scaling with mass$^{1.63}$ and mass$^{1.59}$, respectively. Although rotational inertia did scale with negative allometry in iguanas and rats alone, with mass$^{1.56}$ and mass$^{1.42}$, respectively, it still increased much more quickly with increasing mass than the predicted ability to apply torque. This suggests either that these animals are not constrained by rotational inertia because of their relatively small size or that larger rodents and lizards are poorer turners than smaller ones. The murine rodents had a 3.0- to 4.9-fold lower rotational inertia than similarly sized lizards of either species. Given that the basal synapsids had body proportions and limb configurations similar to those of modern lizards, we suggest that the loss of the large muscular tail and elongated body form during the evolution of cynodonts and mammals reduced rotational inertia and probably improved turning ability.

Key words: agility, manoeuvrability, moment of inertia, locomotion, lizard, rat, mouse, *Mus domesticus*, *Rattus norvegicus*, *Iguana iguana*, *Varanus exanthematicus*.

Introduction

Terrestrial animals that are thought to be specialized for running possess a wide variety of body shapes and limb configurations. Consider the differences in body and limb configuration, as well as style of movement, between a fast iguanid lizard, such as *Callisaurus draconoides*, and a small galliform bird, such as a quail. Although the anatomical differences among running specialists can be dramatic, attempts to quantify locomotor performance suggest that differences in maximum running speed and in the energetic cost of running in similar-sized animals are usually quite small. For instance, maximum running speeds in cheetahs *Acinonyx jubatus* (110 km h^{-1}) and antelopes *Antilope cervicapra* (105 km h^{-1}) are remarkably similar, despite their large differences in body shape (Breland, 1963; Walker, 1976). The small lizard *Dipsosaurus dorsalis* achieves speeds (18.4 km h^{-1}) that are comparable with those of similar-sized mammals such as the sciurid *Ammospermophilus leucurus* (18.7 km h^{-1}) (Marsh and Bennett, 1985; Garland, 1983; Djawdan and Garland, 1988). Further, at low speeds, the cost of locomotion has been found to scale linearly with mass, seemingly independent of morphological variation. Taylor et al. (1974) found nearly identical costs of slow locomotion in similar-sized gazelles *Gazella gazella*, cheetahs *Acinonyx jubatus*, and goats *Capra hircus*, despite the obvious difference in body and limb morphology. Similarly, Bakker (1972) and John-Alder et al. (1986) found no difference in the cost of locomotion between mammals and lizards in spite of differences in limb proportions, limb posture and the use of the axial musculoskeletal system. If maximum speed and cost of transport are largely independent of variation in body configuration, what are the functional consequences of such dramatic morphological diversity?

A possible locomotor advantage of some body forms and limb configurations is an increase in the ability to turn sharply and to maneuver through non-uniform terrain. Turning is often important in predator–prey interactions, intraspecific competition and movements through the complex terrain that most animals inhabit, so it seems likely that selection would act to improve this parameter of locomotion. For example, Djawdan and Garland (1988) point out that the highly erratic zig-zagging predator-avoidance behavior of kangaroo rats *Dipodomys* might allow them to inhabit more open

microhabitats, where the enhanced risk of predation is prohibitive for similar species with more predictable escape behaviors. Although animals use different turning strategies depending on their body configuration (Eilam, 1994; Kafkafi and Golani, 1998; Jindrich and Full, 1999), certain phenotypes would probably result in greater turning performance.

One factor that has been shown to have a strong influence on turning ability is rotational inertia (Lee et al., 2001). Rotational inertia (I) is a body's resistance to rotation about an axis. It is defined as the differential elements of a body's mass (m) multiplied by the square of their distances from the rotational axis (r) ($I=\sum mr^2$) (Halliday et al., 1993). Because the distance of the mass from the rotational axis is squared, bodies whose mass is distributed far from the axis of rotation have very high rotational inertia. The torque (τ) required to achieve a given magnitude of rotational acceleration (α) about an axis is directly proportional to the body's rotational inertia ($\tau=I\alpha$) about the axis. Hence, one might expect natural selection to favor characters that reduce the mass of elements far from the axis of rotation or reposition body mass closer to the rotational axis. For example, the reduction in trunk and tail lengths that occurred during the evolution of basal synapsids to cynodonts and mammals clearly must have significantly reduced rotational inertia.

Although it is obvious that modern mammals have greatly reduced rotational inertia compared with basal synapsids (Fig. 1), the magnitude of this decrease is not clear. The present study attempts to estimate this reduction by comparing the rotational inertia of murine rodents (similar in body form to the early mammal *Megazostrodon*) with that of iguanid and varanid lizards (resembling basal synapsids such as pelycosaurs). Skeletal restorations of pelycosaurs such as caseids, ophiacodontids, edaphosaurids and sphenacodontids show 'lizard-like' body forms (Carroll, 1997; Fig. 1). These animals had a long trunk and tail and a sprawled limb posture. Although pelycosaurs were much larger than the lizards being used in this study, with some caseids approaching 3 m in length (Benton, 1997), this size difference can be addressed with the assumption of geometric similarity.

A further consideration of the present study is the scaling of angular acceleration with body size. If rotational inertia increases more quickly with body size than the ability to apply torque, then larger animals will be poorer turners than smaller animals. In geometrically similar animals, rotational inertia scales with mass$^{1.67}$ ($I=mr^2$, where r is a length along the body and scales with mass$^{0.33}$). The ability to apply torque, however, is directly proportional to mass ($\tau=Fd$, where muscle force, F, scales with mass$^{0.67}$ and distance of application, d, scales with mass$^{0.33}$). This means that, in geometrically similar animals, angular acceleration ($\alpha=\tau/I$) decreases with increasing mass ($\alpha\propto m^{-0.67}$), and one would expect poorer turning performance in larger geometrically similar animals than in smaller ones (Carrier et al., 2001). For this reason, one might expect natural selection to have resulted in lower rotational inertia in large species and growth stages than would be predicted by geometric similarity.

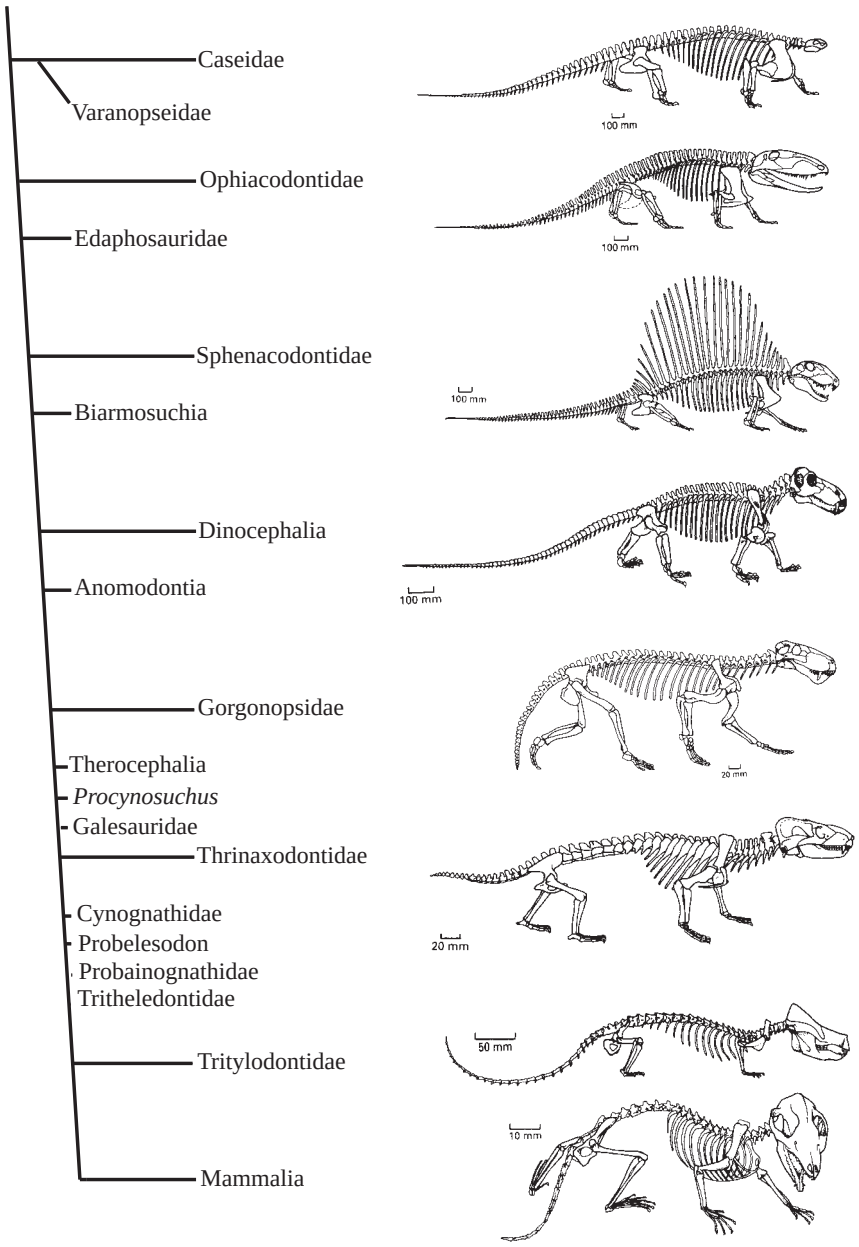

Fig. 1. Cladogram illustrating phylogenetic relationships and body shapes of representative synapsids. The phylogeny is compiled from Sidor and Hopson (1998), Sidor (1996), and Wilkinson (1999). Spacing along cladogram does not represent a timeline. Figures of body configuration are from Benton (1997).

Here, we test the hypothesis that rotational inertia exhibits negative allometry by measuring the rotational inertia of a size range of murine rodents (*Mus domesticus* and *Rattus norvegicus*) and lizards (*Iguana iguana* and *Varanus exanthematicus*). These measurements also allow us to estimate the decrease in rotational inertia that occurred during the evolution of mammals from the 'lizard-like' basal synapsids.

Materials and methods

Animals

To determine how rotational inertia varies with body size, we measured rotational inertia in size ranges of two species of lizard (*Iguana iguana* and *Varanus exanthematicus*) and murine rodent (*Mus domesticus* and *Rattus norvegicus*). While size ranges can be obtained through interspecific comparisons of adults or ontogenetic series, both have associated caveats. In an interspecific comparison, results might be biased by species with various specializations that increase rotational inertia (for example, the unusually high rotational inertia of ferrets). Results from an ontogenetic series that included altricial young, not subject to selection on locomotor performance, might also be biased because of developmental variation in body shape.

To obtain size ranges of iguanid and varanid lizards, we used ontogenetic series. This was performed mainly for practical reasons of specimen availability. However, given that these lizards must forage and escape predators independently from hatching, it is reasonable to expect selection on rotational inertia throughout ontogeny. In contrast, to obtain a size range of murine rodents, we used adult mice and late juvenile and adult rats. Being altricial, very young mice and rats do not actively forage or run from predators and, thus, are unlikely to experience similar selection for turning agility. Because the mice and rats are in the same sub-family (Murinae) and have similar life-styles and body morphologies, they were used to create a single scaling relationship, while the varanid and iguanid lizards were analyzed separately.

Rotational inertia was measured in 13 murine rodent carcasses ranging in mass from 25 to 546 g, including three adult mice and 10 juvenile and adult rats. For comparison, rotational inertia was measured in 17 green iguanas (*I. iguana*) ranging from 7.5 to 1664 g. Of these, 12 were carcasses, while five of the larger iguanas were anesthetized during measurements. Because small iguana specimens were readily available, rotational inertia values from two 9 g iguanas were averaged, as were those from four 10 g iguanas, to give a total of 13 data points. Rotational inertia was also measured in 11 savannah monitors (*V. exanthematicus*) ranging in mass from 18 to 2497 g. Three of the larger varanids were anesthetized with isoflurane; the others were frozen specimens.

Determination of center of mass and rotational inertia

Animals were weighed and then placed on a beam supported at one end by a metal stand and at the other by the scale.

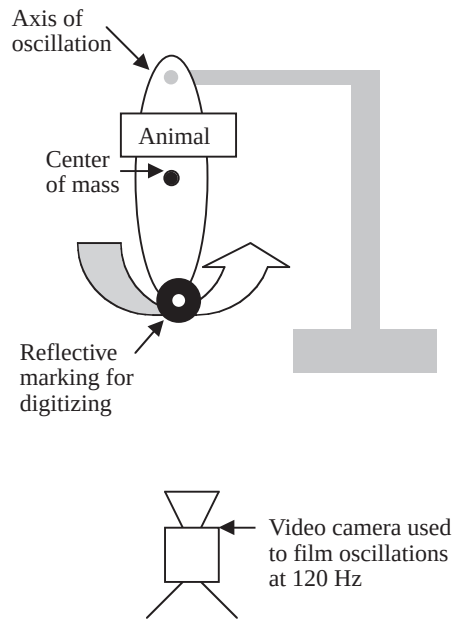

Fig. 2. Illustration of the arrangement for measuring rotational inertia. Animals were videotaped at 120 Hz while being oscillated as pendulums about each of two axes. Position data, obtained from digitizing a reflective marking on the animal, were used to determine the period of ocillation (see Materials and methods).

Knowing the distance between the scale and the metal stand (D_1), the scale reading (Sc) and the actual mass of the animal (m), we determined the distance of the animal's center of mass from the stand (D_2) and thereby its position on the animal (Nigg and Herzog, 1999):

$$D_2 = (Sc \times D_1)/m\,. \tag{1}$$

After the animals' centers of mass had been determined, their rotational inertias were measured using the following equation, relating the period of a physical pendulum to its rotational inertia (Manter, 1938):

$$I = (\tau/2\pi)^2 m\boldsymbol{g}h\,. \tag{2}$$

Here τ refers to the period of the pendulum, h is the distance from the swing point to the center of mass and $\boldsymbol{g}$ is the gravitational constant.

Murine rodent and lizard specimens were first frozen with their trunk and tail straight and their limbs in trotting postures, whereas live lizards were anesthetized during all measurements. This positioning with the trunk straight would tend slightly to overestimate the rotational inertia of a running animal because both lizards and rodents bend their trunk and tail during locomotion. Measurements consisted of locating the center of mass as described above and allowing specimens to oscillate as pendulums about two swing points (Fig. 2). Anesthetized lizards were weighed, and their center of mass was determined both before and after they had been braced in trotting postures using a light wooden support structure. The frame, to which the lizards were firmly taped (the tape peeled

off their scales easily without causing apparent damage), weighed 30 g. Its rotational inertia was measured by oscillating it separately and was subtracted from the total rotational inertia.

Swing points consisted of two holes drilled on a dorso-ventral axis through each animal or through the support for anesthetized animals. Holes were placed along the central axis in either the head or tail region so as to locate them as far as possible from the center of mass, thereby improving the pendulum's swing. Animals were then allowed to oscillate as a pendulum about an axle through each of the holes. A reflective marking was placed as far as possible from the axis about which the animal oscillated, and the position of this marker was videotaped at 120 Hz for several oscillations (Camera 007086 Peak Systems, Inc). These positional data were used to determine the period of oscillation and thereby the rotational inertia about the axis of oscillation (I_{OA}).

The parallel axis theorem (Halliday et al., 1993):

$$I_{CM} = I_{OA} - mh^2 , \quad (3)$$

where h is the distance from the axis of oscillation to the center of mass, was then used to calculate rotational inertia about the center of mass (I_{CM}).

Statistical analysis

Rotational inertia about the center of mass was computed separately for each of the two axes about which each animal oscillated, and the values were averaged. A similar method of calculating moment of inertia from oscillations about two axes, and averaging the moments for increased accuracy, was used by Fedak et al. (1982). In cases where the two values, which should theoretically be identical, differed by more than 10 %, measurements were repeated.

Possible error in the measurement of rotational inertia could result from friction about the axis of oscillation. We attempted to minimize this by spraying the axle with WD-40. Measurement error could also result from partial thawing of the narrow tail of the mice and smaller lizards during oscillations. We attempted to minimize this error by keeping animals in the freezer until just prior to measurement and refreezing them between the two measurements when thawing was apparent.

The averaged rotational inertia values and the subject's masses were $\log_{10}$-transformed. Allometric scaling relationships of mass *versus* rotational inertia were calculated using reduced major axis slopes (Sokal and Rohlf, 1997). To determine whether they differed significantly from geometric similarity or from one another, 95 % confidence intervals for both the slopes and the intercepts were computed.

Results

For the series of murine rodents, rotational inertia scaled with mass$^{1.63}$ and did not differ significantly from geometric similarity (Student's t-test; significance accepted at $P<0.05$) (Fig. 3). In the rats alone, rotational inertia scaled with significant negative allometry; mass$^{1.42}$. Rotational inertia scaled with mass$^{1.59}$ for savannah monitors and did not differ significantly from geometric similarity. For green iguanas, rotational inertia scaled with mass$^{1.56}$, which was a slight, but significant, departure from geometric similarity and the scaling of the murine rodents.

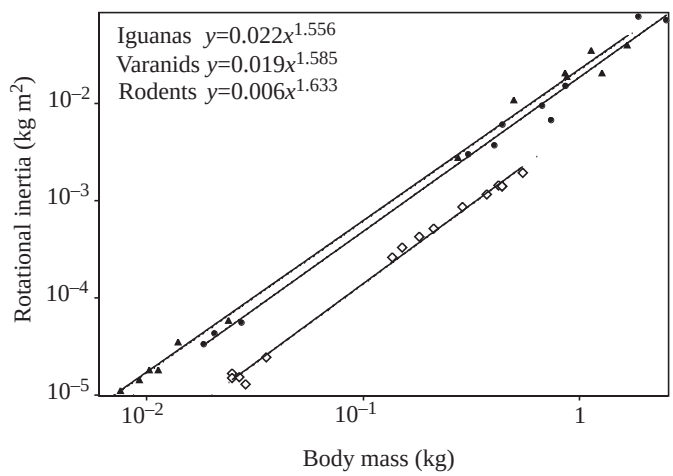

Fig. 3. Logarithmic plot of rotational inertia *versus* body mass for *Iguana iguana* (gray triangles), *Varanus exanthematicus* (filled circles) and murine rodents (open diamonds). Broken lines indicate extrapolation beyond the measured data set. The scaling relationships shown were determined from reduced major axis slopes. Rotational inertia values from two 9 g iguanas were averaged (mean $1.44\times10^{-5}\pm5.01\times10^{-7}$ kg m^2), as were those from four 10 g iguanas (mean $1.83\times10^{-5}\pm1.45\times10^{-6}$ kg m^2).

Over the size range measured, the murine rodents had a 3- to 4.9-fold lower rotational inertia than the either of the lizard species (Fig. 3). The igaunas had a 1.2- to 1.3-fold greater rotational inertia than the varanids.

Discussion

Scaling of rotational inertia in murine rodents

In the murine rodents, rotational inertia scaled with mass$^{1.63}$ and did not differ from geometric similarity. In the rats alone, rotational inertia did scale significantly lower than geometric similarity, with mass$^{1.42}$, but still increased with increasing mass much faster than the predicted ability to apply torque, which scales with mass$^{1.00}$ in geometrically similar animals. These findings predict that rotational acceleration would decrease as mass$^{-0.63}$ in the murine rodents and as mass$^{-0.42}$ in the rats alone. This prediction of decreasing agility with increased size is consistent with Djawdan's (1993) observation that smaller quadrupedal rodents made greater angle changes over a single stride than larger ones.

As the size range of rats represents an ontogenetic series, and mammals are known to exhibit allometric growth (Gould, 1977; Carrier, 1996), we would not necessarily expect to see geometric similarity in the scaling of either rotational inertia or torque production. Studies showing that juveniles of some

species have relatively longer limbs and greater acceleration than adults (e.g. Carrier, 1995, 1996) suggest relatively greater ability to produce torque in the juveniles of these species. Thus, using geometric scaling for ability to apply torque represents a conservative argument; angular acceleration may decrease more quickly with increased mass in some species than predicted above.

Given that agility and maneuverability on variable terrain often appear to be important for survival, we had originally expected rotational inertia to scale with significant negative allometry. Since body shape varies greatly among mammalian species, it seems unlikely that developmental constraints restrict murine rodents to geometric similarity in rotational inertia. Nevertheless, several explanations can be proposed for the higher-than-predicted scaling of rotational inertia in murine rodents. First, competing selective factors affecting body shape might prevent a negative departure from geometric similarity. For instance, as *R. norvegicus* originally inhabited burrows with long branching tunnels (Nowak and Paradiso, 1983), the need to maintain a low and narrow profile to move easily through these tunnels may have prevented the evolution of body allometries that reduce rotational inertia in larger individuals. Second, because the rodents used in this study were relatively small in comparison with many terrestrial mammals, rotational inertia may not increase enough over this size range to be a limiting factor in running turns. An animal's ability to turn sharply while running is dependent upon the rate at which it can decelerate in the direction of its initial heading and accelerate in the new direction and on the rate at which it can rotate to face a new direction (Jindrich and Full, 1999). It is not yet known which of these factors, linear acceleration and deceleration or rotational acceleration, limits turning performance in quadrupeds. Because angular acceleration is expected to decrease more quickly with increasing mass (scaling as $\text{mass}^{-2/3}$) than does linear acceleration (scaling as $\text{mass}^{-1/3}$), it seems likely that angular acceleration, and thus rotational inertia, would become more of a limiting factor in turning agility in larger animals. Even the largest rats measured were quite small compared with the full size range of terrestrial mammals. It may be that, in the measured size range, linear acceleration and deceleration abilities place stricter limitations on running turns than does rotational acceleration, while in much larger mammals, in which the exponential term has a greater impact on acceleration, angular acceleration acts as the limiting factor.

Scaling of rotational inertia in iguanid and varanid lizards

In lizards, scaling relationships have been calculated for a variety of morphometric parameters including snout–vent length, limb lengths and limb diameters (White and Anderson, 1994; Kramer, 1951; Marsh, 1988; Laerm, 1974; Dodson, 1975; Pounds et al., 1983; Christian and Garland, 1996). These studies show that, while lizards exhibit growth that is much more isometric than that of mammals, their growth is allometric. Therefore, it is not immediately apparent that rotational inertia should scale with geometric similarity. Further, these studies show much interspecific variation in scaling relationships even within families such as Iguanidae (Pounds et al., 1983).

While further experiments and modeling would be necessary to determine exactly how various reallocations of mass throughout growth would affect the scaling of rotational inertia, some predictions can be made. For instance, if muscle mass increased relative to trunk and appendage length during growth, then one might expect the decreased rotational inertia of the relatively shorter and stouter body forms of larger lizards to yield negative allometry. Longer or more massive forelimbs should increase rotational inertia about the lizards' relatively caudal center of mass, whereas increasing the length of the hindlimbs (which are much closer to the center of mass), as seen in larger species of *Sceloporus* and *Varanus* (Dodson, 1975; Christian and Garland, 1996), should have less effect on rotational inertia. Increasing hindlimb diameter (rather than locating the mass elsewhere), as in *Diposaurus dorsalis* and *Varanus* spp. (Marsh, 1988; Christian and Garland, 1996), might decrease rotational inertia.

Another possible effect of the scaling of limb lengths and diameters on the scaling of maximal angular acceleration is the relative ability of various limb morphologies to apply torque. Applied torque, which is equal to the force times the lever arm at which it is applied, would be relatively greater in larger lizards if both limb length and muscle cross-sectional area scaled with positive allometry. Christian and Garland (1996) found such positive allometry in a comparison of 22 species of adult varanid. Although savannah monitors have a relatively short and stout body form for a varanid lizard, if the ontogenetic scaling of their limb lengths and diameters were similar to the interspecific scaling in adult varanids, then angular acceleration would decrease much less dramatically with mass than predicted by geometric similarity.

Scaling relationships of hindlimb parameters vary among species of iguanid lizard. In groups such as *Diposaurus dorsalis* (Marsh, 1988) and in two species of *Basiliscus* (Laerm, 1974), in which hindlimb lengths scale with negative allometry, the ability to apply torque would scale much lower than in the varanids (closer to or less than $\text{mass}^{1.0}$). Thus, the increase in rotational inertia with increasing mass would not be partially compensated for by positive allometry in ability to apply torque. It is interesting that, in *I. iguana*, rotational inertia does scale with slight, but significant, negative allometry, unlike in *V. exanthematicus*. Still, a much greater negative allometry in the scaling of rotational inertia would be necessary to prevent a decrease in angular acceleration as iguanas increase in mass. Other factors could prevent modifications that reduce rotational inertia in larger iguanas. For instance, iguanas use their tail for swimming and as a weapon (Schmidt and Inger, 1957). Thus, while decreasing tail size would probably improve turning ability, it might have greater costs in other aspects of performance.

In summary, it seems that, although *V. exanthematicus* and *I. iguana* both deviate from isometric scaling in ways that ameliorate the expected reduction in angular acceleration with

increased size, they accomplish this quite differently. Varanids show positive allometry in torque production through positive allometry in limb length and muscle cross-sectional area (Christian and Garland, 1996), while iguanas show negative allometry in rotational inertia. However, both groups are still expected to show a decline in rotational acceleration with increasing mass. Therefore, we would predict that the agility of both groups will decrease with increasing size. While no scaling studies have been carried out on the turning abilities of iguanid or varanid lizards, White and Anderson (1994) noted that, in macroteiid lizards, the smaller *Callopistes flaviipunctatus* demonstrated greater agility in escape maneuvers than two species of *Tupinambis*, which were 1.3–7.8 times larger.

Evolutionary significance

Selection for improved turning performance may have contributed to the major tail reduction that occurred independently in the lineages that gave rise to birds (Carrier et al., 2001) and mammals, two groups known for their exceptional locomotor agility. This tail reduction is surprising when one considers the ancestral condition of these groups, in which the major hindlimb retractor muscle and, thus, the primary element of forward propulsion was located in the tail (Gatesy, 1990; Carroll, 1997). In fact, faster sprint speeds in lizards have been correlated with distal expansion of the caudofemoralis and a more distal break-point for caudal autotomy (Zani, 1996; Russell and Bauer, 1992). Much of the tail mass in lizards is composed of the caudofemoralis and the epaxial and hypaxial muscles necessary to brace the tail when the caudofemoralis contracts. Thus, associated with the tail reduction that occurred during the evolution of synapsids was a change in the muscles that retract the hindlimb from the caudofemoralis to the hamstrings. This seems disadvantageous energetically because it locates the hindlimb retractor mass in the thigh, where it must be accelerated and decelerated with each locomotor cycle. However, this change would improve turning abilities by greatly reducing the rotational inertia of the body and thereby increasing angular acceleration ($\alpha=\tau/I$).

The loss of the large and heavy tail may also have affected maneuverability by moving the center of mass cranially. Many quadrupedal mammals, including mice and dogs, perform high-speed galloping turns by planting their forelimbs and doing a semi-handstand while swinging the hindlimbs around. If the force applied by the forelimbs in this ‘handstand’ were directed in front of the center of mass, it would cause a pitching moment propelling the back end of the body downwards. Consequently, for this ‘handstand’ turn to work, the force applied by the forelimbs must be directed through or close to the center of mass. Although it is not known whether this ‘handstand’ turn increases maneuverability, it would probably have been facilitated by the cranial migration of the center of mass. In short, tail reduction in the synapsid lineage may have improved turning abilities both by reducing rotational inertia and, thus, the torque required to make the turn and by moving the center of mass cranially, making the mammalian ‘handstand’ turn possible during galloping.

Carroll (1997) describes the body configuration of pelycosaurs, early synapsids, as being best represented among extant taxa by varanid or iguanid lizards. The present study has shown that these lizards have a 3.0 to 4.9-fold greater rotational inertia than similar-sized mammals because of their elongated trunk and long heavy tail. In the evolution of therapsids and early mammals, loss of the large heavy tail and replacement of the caudofemoralis with the hamstrings as the major hindlimb retractor gave rise to animals with greatly reduced rotational inertia and, therefore, probably much greater agility.

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