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## Invited Perspectives in Physiological Zoology

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### Ontogenetic Limits on Locomotor Performance

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#### Abstract

*For most vertebrates, locomotor activity begins at the time of hatching or birth. Although handicapped by small size, rapidly growing tissues, and naïveté, juveniles of most species must maneuver in the same environment and avoid the same predators as adults. Thus, it is not surprising that some ectothermic and precocial endothermic tetrapods undergo ontogenetic changes that allow juveniles to sprint almost as fast and jump almost as far as adults. Allometric changes that have been shown or suggested to enhance performance in juveniles include relatively longer limbs, relatively greater muscular forces and contractile velocities, and higher muscular mechanical advantage. Compensation for rapid growth has been shown to occur in the bones of precocial birds and mammals. The limb bones of these animals have relatively greater cross-sectional diameters and areas than those of adults. This maintains a parity of bone and muscular strength during periods of rapid growth, when bones are composed of weaker, more flexible tissue. In contrast to their sprinting and jumping performance, young animals appear to have significantly less locomotor stamina and agility than adults. The lower stamina may, in large part, simply be a consequence of juveniles being smaller than their parents. The awkwardness of youth appears to result from a conflict between the process of growth and the effective integration of the sensory, neural control, and motor systems. Because juveniles often suffer higher rates of mortality from predation, selection for improved locomotor performance is likely to be strong. Consequently, as a possible result of ontogenetic canalization, the adult phenotype may be determined as much or more by selection on the locomotor performance of juveniles as by direct selection on the locomotor abilities of adults.*

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## Introduction

Humans are among the most altricial species on the planet. We begin life totally dependent on our parents, and our dependency continues for years. This altricial condition is probably most apparent in our locomotor abilities. Young of our species do not begin to walk until almost a year after birth, and it is 15–20 yr before juveniles can match adult locomotor performance. In a practical sense, human locomotion is a behavior of adults. This aspect of our biology may contribute a set of biases that influence the questions that we ask as physiologists. Perhaps it is a consequence of our altricial nature that the vast majority of studies of locomotor function are directed exclusively toward the goal of understanding the adult life stage. Generally little attention is given to locomotor function in young animals.

This focus on the locomotion of adults may be misleading. In the vast majority of vertebrates, locomotor activity begins at the time of hatching or birth. Most juveniles must maneuver in the same environment and avoid the same predators as adults. But, juveniles tend to be slower, have less stamina, and are less agile than their parents. They are handicapped by small size, growing tissues, and naïveté about the environment in which they find themselves. Consequently, juveniles are captured with less effort and suffer higher rates of mortality from predation than do adults (Williams 1966; Estes 1976; Wassersug and Sperry 1977; Arnold and Wassersug 1978). I believe it is exactly this attention by predators that should draw the focus of physiologists studying locomotion. Because of higher mortality from predation, selection for improved locomotor performance is likely to be strong in juveniles. If this is true, then as a possible result of ontogenetic canalization (Frazzetta 1975), the locomotor phenotype of adults may be more a reflection of the demands placed on juveniles than of direct selection on adults.

There are at least three general questions that can be asked about the ontogeny of locomotor function. First, what factors limit the locomotor performance of young animals? We know that juveniles tend to be less adept than adults, but we do not understand why. Second, are there adaptations that overcome ontogenetic limitations on locomotion and improve the performance of juveniles? Answering this question will require an understanding of how ontogeny limits locomotion as well as a knowledge of the evolutionary history of developmental stages. Third, has natural selection acting on the locomotor performance of juveniles influenced the adult phenotype? In general, we think of selection as acting primarily on adult life stages. However, selection acting at any level of development can influence the mature state (Frazzetta 1975; Burggren 1992).

We know surprisingly little about any of these topics. This article focuses on the first question, What limits locomotor performance in juveniles? An understanding of the limitations imposed by ontogeny is necessary before we can address potential adaptations and any impact on the adult phenotype. To illustrate how selection on the performance of juveniles might influence later stages of life, this article ends with a speculative discussion of wing growth in birds.

### **Ontogenetic Limits on Locomotion**

There are at least two ways in which ontogeny can be expected to limit locomotor performance. First, young animals are smaller than adults. Size has been shown to influence the locomotion of adults in many ways (for review and synthesis, see Pedley [1977]; McMahon [1984]; Schmidt-Nielson [1984]). The extent to which these scaling effects influence locomotion during ontogeny has received relatively less attention from physiologists (Emerson 1978; Huey and Hertz 1982; Carrier 1983; Cavagna et al. 1983; Garland 1984; Gabriel 1985; Marsh 1988; Carrier and Leon 1990; Queathem 1991; Katz and Gosline 1992, 1993; Biewener and Bertram 1993, 1994). Second, there may be conflicts between locomotor function and the process of growth. Ricklefs (1979) has suggested that the process of growth may interfere with mature function. In an attempt to explain why posthatching growth of precocial birds is three to four times slower than that of altricial species of the same body size, he suggested that the tissues of a growing animal are apportioned between embryonic (growth) and mature (maintenance) functions. He suggested the functional capacities of the young animal are directly related to the proportion of its tissue that is differentiated, whereas its rate of growth is directly related to the remaining proportion of tissue that is undifferentiated and therefore nonfunctional. For the purposes of this discussion, the question becomes, To what extent can a particular tissue or organ grow and simultaneously function in locomotion? To address how scaling and ontogenetic limitations may influence the locomotion of young animals, I consider the development of three aspects of locomotor performance in terrestrial vertebrates: acceleration, stamina, and agility.

#### *Acceleration*

The ability to accelerate is the aspect of locomotor ontogeny that has received the most attention from vertebrate biologists (Table 1). From these studies, two distinct developmental patterns can be discerned. First, the young of

TABLE 1

*Studies measuring the ontogeny of sprinting and jumping performance*

|                                   | Performance Improves with Maturation                                           | Young Are Equivalent to Adults      |
|-----------------------------------|--------------------------------------------------------------------------------|-------------------------------------|
| Sprint speed of lizards . . . . . | Huey 1982; Huey and Hertz 1982; Garland 1985;<br>Losos et al. 1989; Losos 1990 | Huey 1982; Garland 1984; Marsh 1988 |
| Sprint speed of snakes . . . . .  |                                                                                | Jayne and Bennett 1990              |
| Sprint speed of humans . . . . .  | Ruskin 1978                                                                    |                                     |
| Jumping of frogs . . . . .        | Emerson 1978 (distance); Zug 1978                                              | Emerson 1978 (acceleration)         |
| Jumping of humans . . . . .       | Ruskin 1978                                                                    |                                     |
| Jumping of jackrabbits . . . . .  |                                                                                | Carrier (1995)                      |

most species start out with a poor capacity to accelerate compared with that of adults, and their ability improves steadily as they grow. This presumably reflects both scaling effects and ontogenetic limitations on the functional capacities of the bones and muscles (Close 1972; Goldspink 1980; Currey 1984). However, the specific limitations have not yet been sorted out for any species. Second, there are a number of species in which juveniles can accelerate as rapidly as adults. In this group, there are species that initially have lower performance but reach adult levels at a relatively small size (Fig. 1) and other species that appear to have adult performance very soon after hatching or birth. A few studies have successfully related precocial locomotor performance to ontogeny of the musculoskeletal system. One notable example is a study by Marsh (1988) on the lizard *Dipsosaurus dorsalis*, in which an early capacity for rapid acceleration and high sprint speeds was shown to be correlated with allometric changes in limb dimensions and changes in the time course of force generation by the skeletal muscles. Here I consider aspects of mammalian ontogeny that allow young jackrabbits to accelerate as rapidly as adults.

Hares provide an illustration of both ontogenetic limitations on the early ability to accelerate and ways in which these limitations may be overcome.

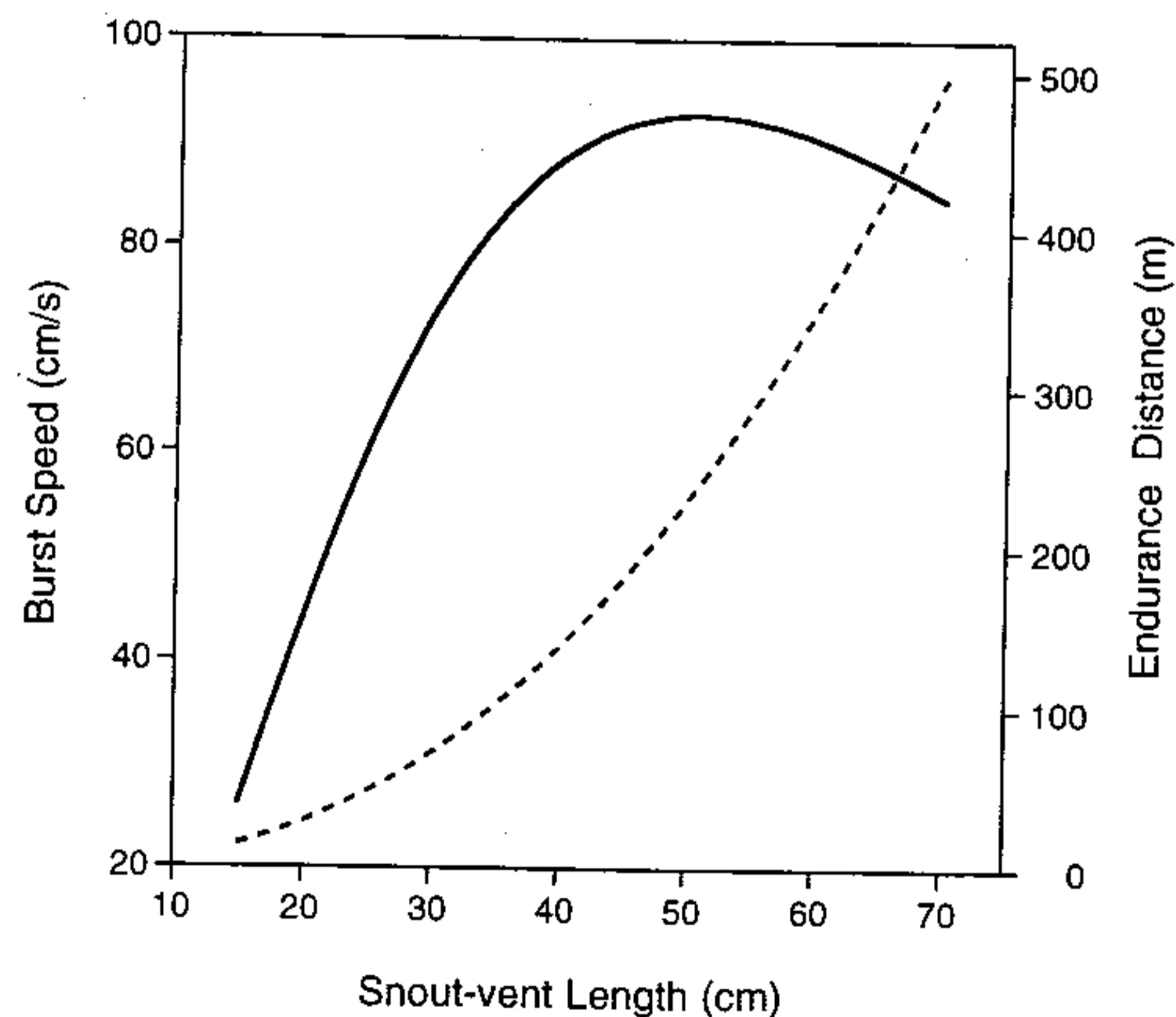


Fig. 1. Burst speed (solid line) and endurance distance (dashed line) vs. snout-vent length for a growth series of the garter snake (*Thamnophis sirtalis*). Lines are least squares regressions from a sample of 497 individuals. Individuals of intermediate body length achieve the same burst speeds as larger individuals but are not able to travel as far. Modified from Jayne and Bennett (1990).

During the period when young black-tailed jackrabbits (*Lepus californicus*) are growing at their highest rate and are only 25%–30% of adult body mass ( $M_b$ ), they are able to achieve takeoff velocity from a standing jump equivalent to that achieved by adults (Fig. 2). They do this by accelerating more rapidly than adults (Carrier 1995). How is this possible?

To accelerate more rapidly than adults, young hares must be relatively stronger. Ontogeny of the isometric contractile properties of the gastrocnemius muscles of black-tailed jackrabbits suggests that this is true (Carrier 1983). The force that this muscle generates during isometric tetanic contractions scales to  $M_b^{0.956}$  (Fig. 3A). This exponent is not significantly different from one, indicating that isometry of muscle strength is maintained during

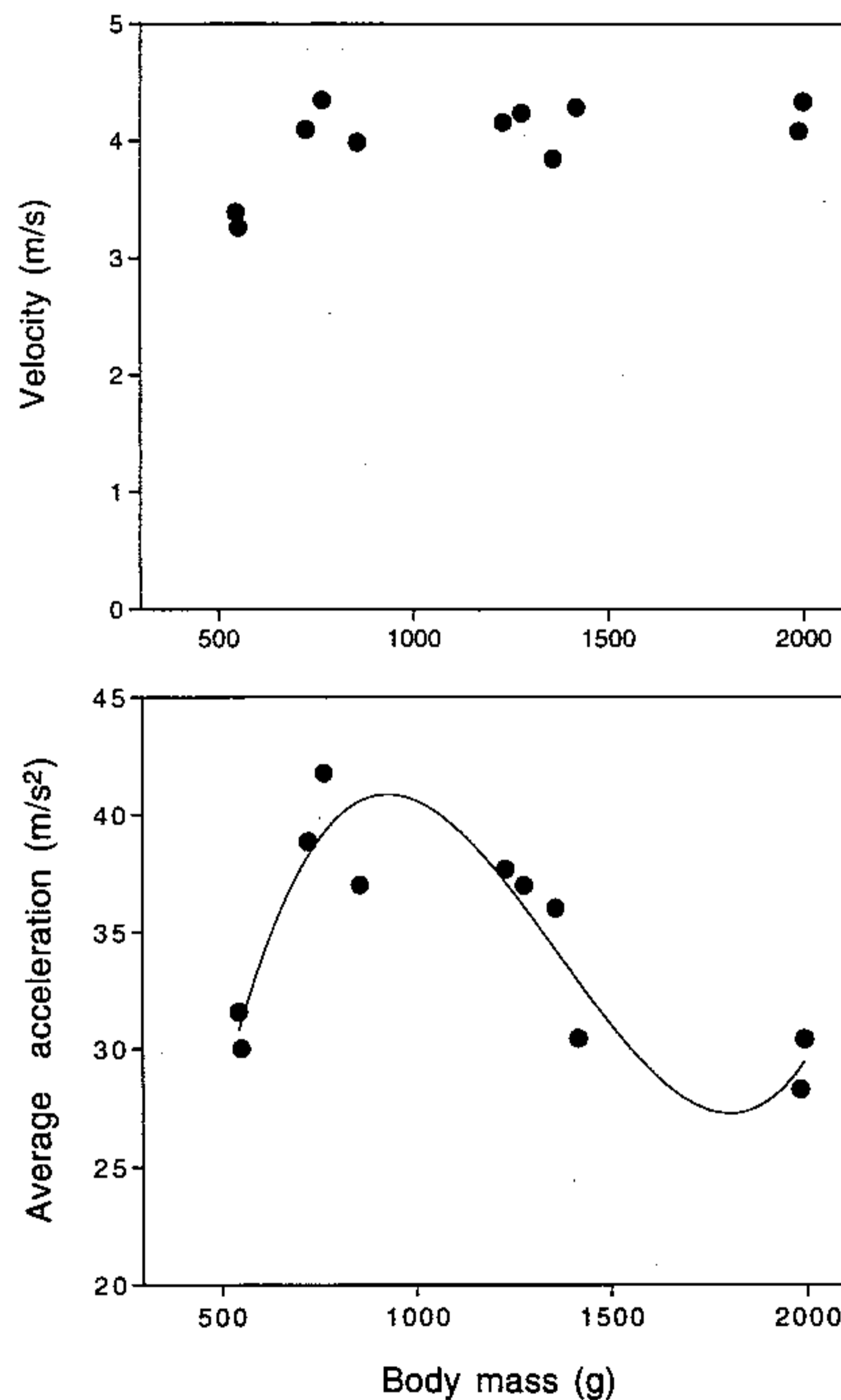


Fig. 2. Takeoff velocity (A) and average acceleration (B) during a standing jump versus  $M_b$  for a growth series of black-tailed jackrabbits (*Lepus californicus*). The line for average acceleration is a third-order polynomial least squares regression. From Carrier (1995).

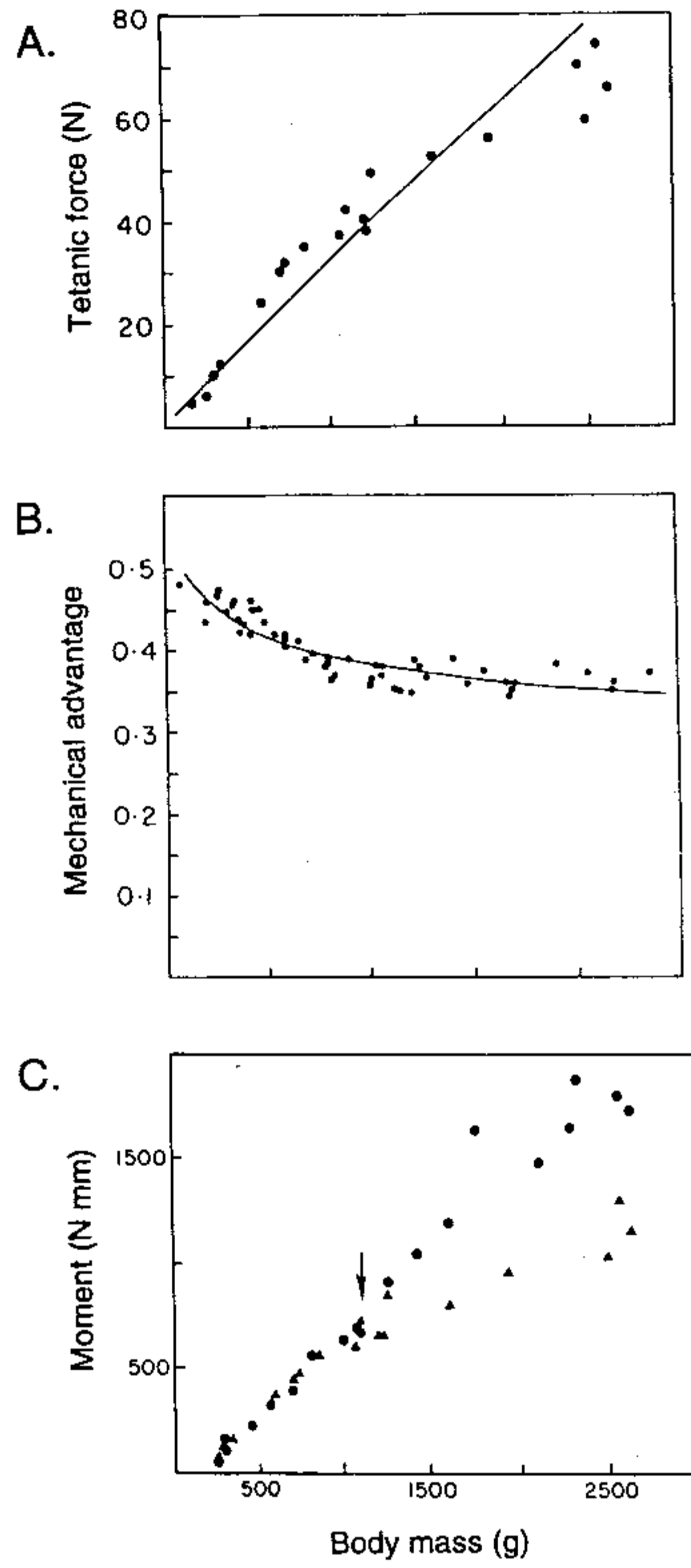


Fig. 3. Ontogenetic changes in the musculoskeletal system of black-tailed jackrabbits (*Lepus californicus*). A, Maximum isometric tetanic force of the gastrocnemius muscle. B, Mechanical advantage of the gastrocnemius muscle (i.e., calcaneum length/third metatarsal length) around the ankle joint. C, Comparison of the moment required to break the third metatarsal (dots) to the moment imposed on all four metatarsal bones by the gastrocnemius muscle (triangles). Arrow indicates (1,100 g) point at which the two moments begin to diverge. Modified from Carrier (1983).

growth. However, a power equation does a poor job of describing the data. The youngest individuals fall on the line, but juveniles lie above the line and adults fall below the line. Thus, for their size, hares in the range of 600–1500 g have stronger gastrocnemius muscles than adults. Young hares also have greater mechanical advantage around their joints than adults (Fig. 3B). Greater muscular strength in relation to their  $M_b$  combined with greater mechanical advantage around their joints makes it possible for young hares to exert relatively greater forces on the ground, and this allows them to accelerate more rapidly than adults when they jump.

The pattern of bone growth in endothermic tetrapods leads one to the suggestion that young hares should not be able to accelerate as rapidly as adults. The limb bones of both birds (Carrier and Leon 1990) and mammals (Currey 1970; Currey and Butler 1975; Carrier 1983) are initially composed of weak, flexible tissue. This appears to be a consequence of a high growth rate (Currey 1984). Limited time and/or nutrients may simply make it impossible to deposit dense lamellar tissue when bones are growing rapidly. In any case, bones composed of weak tissue could be expected to limit a young animal's ability to apply force to the substrate. However, young jackrabbits are able to compensate for the weak tissue by having relatively thicker bones with a greater cross-sectional second moment of area (Carrier 1983). The allometry of bone cross-sectional dimensions makes it possible for young hares to maintain a tight parity between bone and muscle strength during the period when they are growing at the highest rate and the strength of the bone tissue is changing rapidly (Fig. 3C). Thus, during postnatal ontogeny in jackrabbits, neither bone nor muscle appear to be limiting for acceleration.

The allometric changes in bone and muscle that make it possible for young jackrabbits to accelerate more rapidly than adults are very different from the allometric changes that maintain locomotor function with increases in size in interspecific comparisons of adults. Interspecific increases in size are associated with a relative loss of whole-muscle strength (Alexander et al. 1981), positive allometry of muscle mechanical advantage (Goldstein 1972; Alexander 1977; Alexander et al. 1979), and isometry or slight positive allometry of bone diameter (McMahon 1973; Alexander 1977; Biewener 1983, 1989). Ontogenetic trends in *Lepus californicus* are the reverse. The strength of muscles initially increases with positive allometry, while the mechanical advantage of muscles and the diameter of bones exhibit negative allometry. The different allometric patterns of bone diameter reflect the need to maintain locomotor function with bones composed of very different material. Among adult mammals, the strength of bone tissue is independent of body size (Currey 1970; Alexander 1977; Biewener 1982). Consequently,



to maintain equivalent skeletal function, two changes have been observed to occur as body size increases. As already mentioned, an increase in size in adult mammals is often associated with a slight positive allometry of bone diameter. However, this change is not sufficient to maintain similar safety factors against breakage, so there is also a compensatory change in posture of the limbs, to a more erect stance (Biewener 1989). This results in greater muscle mechanical advantage in larger mammals and allows different-sized adults to maintain similar stress levels in their bones. In contrast, during postnatal ontogeny in birds (Carrier and Leon 1990) and mammals (Carrier 1983), the strength of bone tissue increases two to eight times. Thus, to maintain equivalent skeletal function, young birds and mammals must have relatively thicker bones. How postural adjustments during growth affect musculoskeletal integrity has yet to be addressed.

### *Stamina*

With very few exceptions, young animals have less stamina than adults (Ruskin [1978]; Garland [1994]; for exceptions see Taigen and Pough [1981]; Pough and Kamel [1984]). This may largely be a consequence of the fact that juveniles are smaller than their parents. Size is likely to influence stamina for a variety of reasons. For instance, smaller animals may have smaller reserves of energy relative to their metabolic rate (Lindsey 1966). Among adults, metabolic energy storage can be expected to scale to the first power of  $M_b$  or higher (Lindstedt and Boyce 1985), whereas metabolic rate scales to  $M_b^{0.75}$ . Because endurance is likely to be a function of the ratio of metabolic rate and energy reserves, it should scale to the 0.25 or greater power of  $M_b$ . This argument has been made for endurance to starvation (Schmidt-Nielson 1984; Lindstedt and Boyce 1985; Millar and Hickling 1990). However, the same reasoning, with somewhat different exponents, should hold for locomotor stamina.

In addition to having smaller energy reserves, it is more costly for small animals to run. The mass-specific cost of running in mammals has been found to be proportional to  $M_b^{-0.316}$  (Taylor et al. 1982). Thus, as size increases, less energy is required per unit  $M_b$  to run a given distance. This relationship is due to at least two factors. First, because small animals have higher stride frequencies when they run, their muscles must develop force more rapidly than the muscles of larger animals. This requires that smaller animals have muscle fibers with more rapid rates of actin-myosin cross-bridge cycling, and because each cross-bridge cycle consumes a unit of energy, more energy will be consumed by a smaller animal to run a given distance (Heglund et al. 1982; Heglund and Taylor 1988; Kram and Taylor

1990). Second, smaller mammals have a lower capacity to store energy elastically in their tendons during running (Biewener et al. 1981; Pollock and Shadwick 1994). Thus, more muscular work is required for small animals to run. In addition to the higher cost of running, small animals also appear to be limited in the running speeds that they can sustain because they reach maximum rates of oxygen consumption at lower speeds (Taylor et al. 1980). All of these observations come from interspecific comparisons of adults. There is very little information available to indicate what the patterns might be during ontogeny. However, there are no obvious reasons why the effects of scaling that influence endurance among adults would not also affect young animals during ontogeny. Thus, young animals can be expected to have less stamina than their parents because their energy reserves are likely to be smaller relative to their metabolic rate, their mass-specific cost to travel a given distance will be higher, and the speed at which they reach maximum rates of oxygen consumption will be lower.

If body size does place limits on the endurance of small animals, it may not be possible for young animals to achieve adult levels of stamina. In their analysis of the ontogeny of locomotor performance of garter snakes, Jayne and Bennett (1990) found that although juveniles could reach the same burst speeds as adults, endurance performance was always lower in the smaller (i.e., younger) animals (Fig. 1). This hints that locomotor stamina may be more tightly constrained during ontogeny than is acceleration performance. If this were true, adaptations for greater acceleration early in ontogeny might be fairly common. The greater muscular strength and mechanical advantage of young hares suggests that they may, in fact, be specialized for acceleration to the detriment of their ability to sustain locomotion (Carrier 1995).

In addition to the effects of changing body size, the process of growth may limit the endurance of young animals. First, because young animals are growing, they have higher resting metabolic rates. This could adversely influence the amount of energy they can hold in reserve and might therefore limit locomotor stamina. Second, the mass of limb bones may be relatively greater during periods of rapid growth (see the discussion of bone strength). This would increase the energy necessary to move the limbs (i.e., increase the internal work of locomotion). Third, ontogenetic changes in metabolic capacity might also influence endurance.

In humans, anaerobic threshold, maximum rate of oxygen consumption, work efficiency, and response time for oxygen uptake are all independent of body size throughout much of the growth period (Cooper et al. 1984). Thus, at intermediate levels of exertion, the cardiorespiratory system of children is equivalent to that of adults. However, several studies indicate

that children have a lower capacity for anaerobic metabolism than adults. The oxygen cost of high-intensity exercise, normalized to the actual work done, is higher in children than in adults (Zanconato et al. 1991). After vigorous exercise, blood and muscle lactate concentrations are lower and serum pH is higher in children (Eriksson et al. 1973; Paterson et al. 1986). In addition, during high-intensity exercise, the ratio of concentration of muscle phosphate to phosphocreatine increases to a lesser extent than in adults (Zanconato et al. 1993).

In contrast to humans, the aerobic, but not anaerobic, metabolism of growing ectothermic tetrapods may be limited. During the ontogeny of garter snakes, lactic acid concentrations at exhaustion increase 1.5 times, while the oxygen-carrying capacity of the blood increases three times (Pough 1977). This suggests a greater ontogenetic increase in aerobic than in anaerobic capacity. American toads display a similar pattern (Taigen and Pough 1981). Following metamorphosis the mass-specific rate of oxygen consumption and aerobic scope increases more than twofold in juvenile toads, whereas anaerobic scope and whole-body lactate levels after vigorous exercise are independent of body size following metamorphosis. In these two species, juveniles have near adult levels of anaerobic metabolism at an early age but have a limited aerobic capacity that improves as they mature.

One factor that may improve the stamina of juveniles in many species is the presence of relatively long limbs (Fig. 4). Because of the pendulum-like transfer between potential and kinetic energy during walking, there is a speed at which the cost to travel a given distance is minimized (Cavagna et al. 1977). In humans the most efficient walking speed is low in young children but reaches adult values by the time a child is 12 yr of age (Cavagna et al. 1983). Although 12-yr-olds weigh only half of what adults weigh, their legs are approximately as long as those of adults. The relatively long legs of young humans give them stride lengths that closely approach those of adults. Consequently, in both adults and 12-yr-olds the most efficient transfer of kinetic and potential energy occurs at the same stride frequency and same speed.

### *Agility*

Young animals are often awkward and clumsy. Agility is something that is difficult to quantify, and I am not aware of any attempts to study it during postnatal development. However, we know from personal experience and anecdotal observations that very young animals are not as graceful as their parents. They make locomotor mistakes: misplacing feet, leaping in the

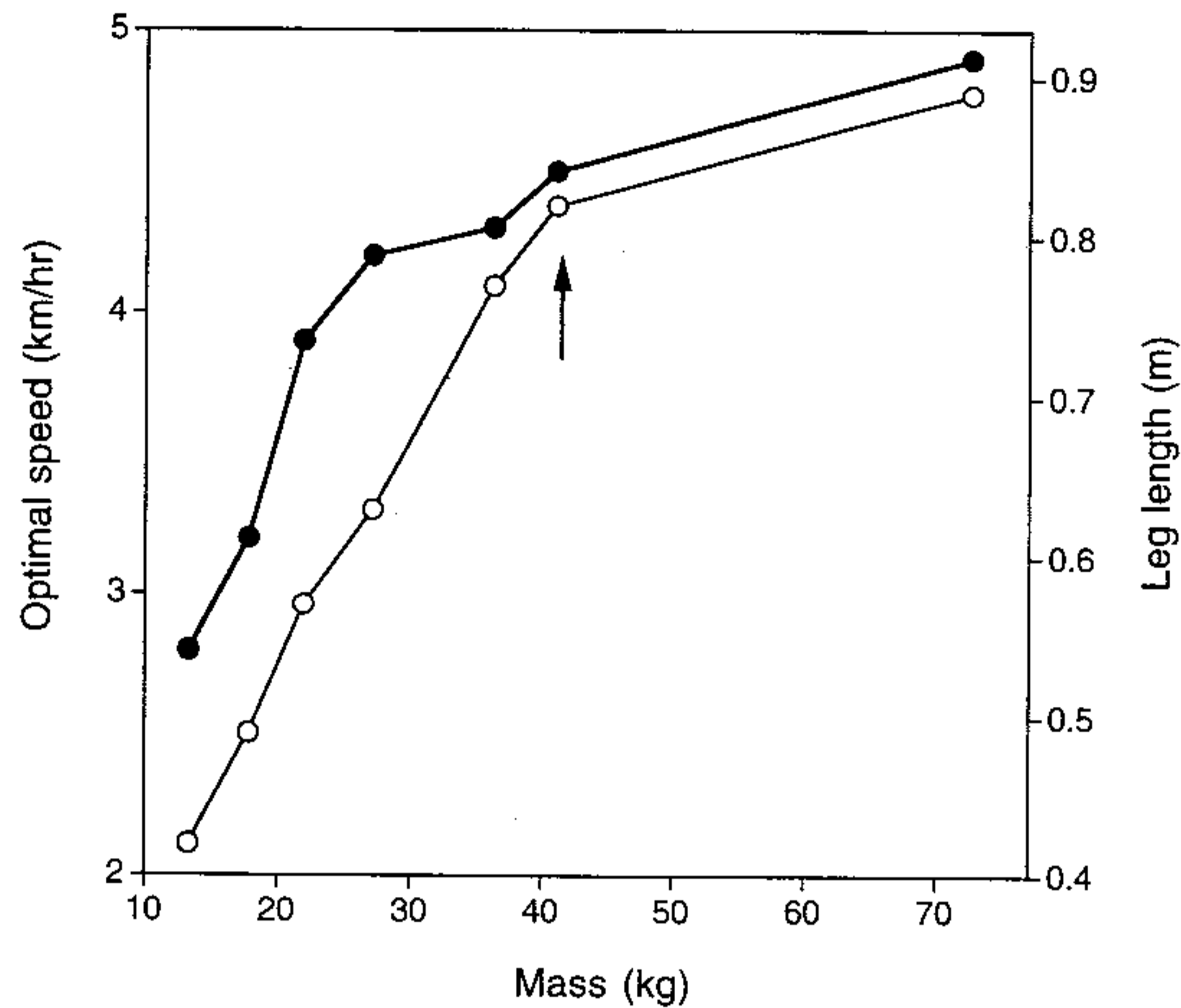


Fig. 4. Optimal walking speed (solid dots) and leg length (open dots) versus  $M_b$  for a growth series of human children (2–12 yr old) and adults. The optimal walking speed is the speed at which the weight-specific work to move the center of mass a given distance is minimized. The arrow points to data from 12-yr-olds. Modified from Cavagna et al. (1983).

wrong direction, or tripping and collapsing when they should be sprinting forward or turning.

The clumsiness of young animals has traditionally been attributed to an immaturity of the nervous system. In addition, the development of early locomotor skills has been shown to be associated with maturation of the nervous system (Peters 1983). However, two observations suggest that neural development, by itself, may not explain the ontogenetic attainment of effective and graceful locomotion. First, many tetrapods display well-coordinated movements shortly after hatching or birth, indicating that the nervous system can be functional throughout postnatal development and growth. An early adeptness at sophisticated movements is most apparent in ectothermic tetrapods and precocial mammals and birds. Second, by studying the kinematics of early movements and the patterns of electrical activity of the skeletal muscles, developmental neurobiologists have shown that central pattern generators and peripheral nerves are in place and functional before the appearance of specific locomotor behavior (Bekoff and Lau 1980; Provine 1981; Stehouwer and Farel 1985; Bekoff 1986; Bradley and Smith 1988).

These observations indicate that the nervous system can be up and running at an early stage and does not necessarily limit well-coordinated movements in young animals. If this is true, why do young mammals and birds not move with the grace and skill of their parents?

Much of the awkwardness of youth may be due to an animal's lack of experience with the environment and with the capabilities of its own motor system. Also, if an ability to adapt movement to a changing environment and circumstances is ultimately advantageous, then learning may be required (Bekoff and Byers 1981; Fagen 1981). However, growth can be expected to pose two problems for effective neural control. First, during growth the size and shape of sensory fields, both special sensory (Knudsen and Knudsen 1985) and somatic sensory, are continuously altered. This may pose problems for correct perception, leading to mistakes in judging distance, size, and position and in the control of balance and position. Consider the problem that growth poses for proprioception. If an animal is growing rapidly and allometrically, the anatomical location of a particular part of its body, such as the tip of its toes, changes continuously relative to the rest of its body. Second, changes in body proportions and functional capacities of the musculoskeletal system will produce changes in motor output. These ontogenetic changes may lead to a conflict between the process of growth and the effective integration of sensory perception, neural control, and motor output. Continuous integration of these systems during growth would require constant modifications of neural control pathways, and this may not be practical or possible.

A number of researchers have suggested that there may be a conflict between growth and the integration of sensory input, neural control, and motor output (Bradley and Bekoff [1989]; Stehouwer [1992]; Assaiante and Amblard [1993]; see Thelen [1989] for a consideration of how integration of the locomotor system may be a self-organizing process during postnatal ontogeny). However, I know of only one example that illustrates the conflict. This comes from the work of Thelen and her collaborators on the disappearance of the stepping response in human infants. When newborn infants are held upright with their trunks tilted slightly forward and their feet resting on a stable surface, they often perform stepping movements that resemble mature walking. Evidence that this response is related to mature walking comes from the observation that, in both infant stepping and mature walking, increased stepping rates are associated with a proportional decrease in stance phase duration and a swing phase of constant duration (Thelen et al. 1981). In human infants the stepping response appears to peak at about 1 wk of age. After 1 wk there is a dramatic decline in the number of steps taken, and by 5–6 wk it is difficult to elicit the stepping response. The disappearance

of stepping has been attributed solely to development of higher cortical centers that inhibit this presumably spinal response. However, during the period when stepping naturally disappears, infants are gaining weight rapidly by adding adipose tissue in disproportion to muscle. Thelen and Fisher (1982) proposed that it is this rapid addition of fat that is responsible for the decrease in stepping. The legs simply become too heavy for the relatively small muscles to lift. Support for this suggestion comes from the observation that when 4-wk-old infants were submerged to chest level in water, stepping increased in rate and amplitude (Thelen et al. 1984). Thus, the human stepping response is an example in which the integration of neural control and motor output breaks down as a result of growth.

If growth can lead to a disruption of the integration of sensory input, neural control, and motor output, the degree to which an individual lacks coordination would be more a function of its rate of growth than its age or experience. Animals would be most awkward during those periods when they were growing rapidly. The undocumented awkwardness of adolescence in our own species is often said to be related to a growth spurt. Furthermore, clumsiness could be expected to be less of a problem for ectothermic than endothermic tetrapods because ectotherms grow, on average, 10 times more slowly (Case 1978). Similarly, precocial mammals and birds (Ricklefs 1979) would be more agile than altricial species that grow more rapidly.

### **Selection Acting on Juveniles and the Adult Phenotype**

Comparative physiology assumes that organisms are adapted to the environment in which they live. In studies of locomotor performance and function, physiologists have focused almost exclusively on mature individuals. However, the adult is not the only life stage where natural selection is acting. Because of higher predation pressure on juveniles, the locomotor phenotype of adults may, in some cases, be more a reflection of selection acting on the performance of juveniles than a direct result of selection acting on the adults. Although one can imagine adaptations for locomotor performance at an early ontogenetic stage that would change the adult phenotype, I know of no examples where this can be argued to have occurred. A potentially more common phenomenon, or at least one that might be more easily studied, is a situation in which vulnerability to predation would lead to selection for accelerated development.

Williams (1966) has suggested that when the risk of mortality varies ontogenetically, natural selection can be expected to accelerate development through those stages in which mortality is high. The generality of this prin-

ciple has been supported by observations on a number of species in which mortality rates are the highest during the shortest stage of their life cycle (King and Dawson 1972; Stein 1975; Wassersug and Sperry 1977; Pomeroy 1990). In many cases, a greater rate of mortality in a particular developmental stage results from susceptibility to predation resulting from ontogenetic limitations on locomotor performance. Selection acting to accelerate development through these periods of locomotor ineptitude could have a dramatic impact on the morphological configuration of the adult. One easily envisioned possible outcome is an earlier termination of growth resulting in reduced body size. Because many species experience allometric growth, this might also produce changes in shape and proportion of the locomotor system (Alberch et al. 1979).

Growth of the avian wing provides several examples that illustrate how selection for accelerated development might influence the locomotor phenotype of the adult. During posthatching growth in California gulls, the length of the bones of the hind limb scale approximately isometrically with  $M_b$ , but the length of the wing bones increases with strong positive allometry (Carrier and Leon 1990). Consequently, a termination of growth that produced a 25% decrease in  $M_b$  of adult gulls would, in theory, result in a 12.5% decrease in length of the hind limb skeleton but a 29% decrease in length of the wing skeleton.

Such changes in the relative length of the wing are a likely result of accelerated development because bone growth appears to be an important rate-limiting factor in the growth of the wing as a whole. Two observations suggest that birds may be approaching a maximum limit on the rate of linear growth of long bones. First, during posthatching growth in California gulls, the bones of the wing grow rapidly and continuously in length, while other aspects of the wing, such as bone diameter and bending strength, muscle mass, and feather surface area, do not undergo significant growth until shortly before fledging (Carrier and Leon 1990). Second, species that have long wing bones relative to their body size tend to have longer fledging periods than species with shorter bones (Carrier and Auriemma 1992). Both of these observations suggest that for some species the period from hatching to first flight may be determined by the rate at which bones can increase in length. Thus, selection for earlier fledging might result in a reduction in wing length before it leads to a reduction in adult body size.

As a further example of how predation pressure might influence the adult phenotype, consider the group of birds with the longest fledging periods. For their body size, the various species of albatrosses have both the longest fledging periods and the longest wing skeletons. For example, the fledging period of the wandering albatross is 278 d (Tickell 1968). The traditional

explanation for such a long period between hatching and first flight is that the chicks are energy limited as a result of their parents' nesting on remote islands in regions that have sparse resources (Lack 1968; Case 1978). However, the observation that fledging period may be partially determined by the time required to grow wing bones leads to an alternative explanation. In this scenario, growth of exceptionally long wings requires an extensive period from hatching to first flight. This in turn requires that adults nest in remote locations so that their chicks are removed and protected from predators. From this perspective, the long wings, and therefore the mode of flight and unique life history, of albatrosses may be viewed as a consequence of relaxed selection acting on the locomotor performance of juveniles. In other words, a long fledging period may be possible because albatross chicks suffer low mortality from predation, and this makes adults that have long wings a possibility.

## Conclusions

Given the high rates of predation on juveniles, we can expect strong selection acting on the locomotor performance of the early life stages of many species. Although this selection is likely to have been important in determining the evolutionary pathways that organisms have taken, very little is known about the ontogeny of locomotion. We need to ask several questions. What limits locomotor function during growth and development? Are the same locomotor behaviors of equal importance to juveniles and adults? Has natural selection resulted in adaptations that circumvent ontogenetic limitations in a way that improves the performance of juveniles? And to what extent has selection acting on juveniles influenced the adult phenotype?

In this article, I have tried to illustrate ways in which growth and development may limit locomotor performance, by considering the ontogeny of three aspects of performance. Contrary to intuition, bone and muscle strength are not necessarily limiting to acceleration during postnatal ontogeny. The young of several species of tetrapods have been shown to jump as far and sprint as fast as adults. Because young animals are smaller and have shorter limbs, these precocial juveniles must accelerate more rapidly than their parents. Allometric growth of bone diameter, muscle strength, and mechanical advantage make these higher rates of acceleration possible in black-tailed jackrabbits. In contrast to acceleration performance, young animals do have less stamina than adults, and this appears to be a consequence of the fact that young animals are smaller than their parents. Young animals also tend to be less graceful than adults. This may result from a conflict



between rapid growth and the effective integration of sensory perception, neural control, and motor output. Consequently, these three aspects of performance provide examples in which both scaling effects and direct conflicts between growth and mature function (Ricklefs 1979) limit the locomotor abilities of young animals.

However, if we are to gain even preliminary answers to the three questions posed at the beginning of this article, significant gaps in our knowledge need to be filled. To address the first two questions, what limits performance during ontogeny and whether there are adaptations that circumvent some of these limitations, will require a clearer understanding of (1) how locomotor performance varies ontogenetically and (2) how particular components of the locomotor system change during growth. At this point, much less is known about locomotor performance during growth in endothermic than in ectothermic tetrapods. There is also less information concerning the ontogeny of maximum running speed and the development of coordinated movements than the ability to accelerate and sustain locomotion. Most studies that have quantified ontogenetic changes in stamina have compared different growth stages moving at the same absolute speed. Because of size effects, it would also be useful to quantify ontogenetic changes in stamina at metabolically equivalent speeds, such as the speed at which 50% or 100% of the maximum rate of oxygen consumption is reached.

The ontogeny of different components of the locomotor system have been studied to varying degrees. The contractile properties of locomotor muscles have been monitored during growth in only a few ectothermic and endothermic species. Changes in the mechanical properties of bone during ontogeny has been studied in mammals but not in other groups. Even less is known about how metabolic capacity changes during growth. To gain an understanding of why stamina tends to be lower in young animals, it would be helpful to know how the maximum rate of oxygen consumption and the running speed at this maximum rate of metabolism change during ontogeny.

The third question, the extent to which selection acting on the locomotor performance of juveniles has influenced the configuration of adults and the evolutionary pathways adopted by organisms, is difficult and complex. To begin to address this, we need a better understanding of developmental limitations on locomotion and knowledge of the evolutionary history of locomotor phenotypes at different developmental stages. That is, we need to know the ancestral configuration of juveniles. This information will not be available until the ontogeny of locomotion has been studied in many more species.

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