

# Postnatal ontogeny of the musculo-skeletal system in the Black-tailed jack rabbit (*Lepus californicus*)

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(Accepted 8 February 1983)

(With 10 figures in the text)

The ontogeny of 23 postcranial skeletal dimensions, mechanical properties of the third metatarsal and the femur, and the isometric contractile properties of the gastrocnemius muscle were measured in a complete postnatal growth series of the highly cursorial hare *Lepus californicus*. Newborn hares are handicapped by short limbs, relatively weak muscles and bone tissue, and shorter muscular contractile distances. However, during growth these deficiencies are rapidly overcome. Hind limb length and gastrocnemius contractile distance undergo positive allometry, scaling as (body mass)<sup>0.39</sup> and (body mass)<sup>0.41</sup>, respectively. The mechanical advantage of the gastrocnemius lever system experiences negative allometry ( $\alpha(\text{body mass})^{-0.12}$ ), giving young hares larger advantage around their joints. This, combined with initial positive allometry of gastrocnemius contractile force ( $\alpha(\text{body mass})^{1.23}$ ) and subsequent negative allometry of contractile force ( $\alpha(\text{body mass})^{0.61}$ ), results in the production of relatively greater propulsive forces transmitted from the foot to the ground in juveniles than in adults. In addition, the second moment of area of the metatarsal is relatively large in younger animals, and scales in such a way that during the first half of postnatal growth mechanical similarity is maintained between the breaking moment of the bone ( $\alpha(\text{body mass})^{1.50}$ ) and the moment imposed on the bone by the gastrocnemius ( $\alpha(\text{body mass})^{1.54}$ ). These ontogenetic changes contribute to the development of a locomotor system which is effective at escape by the time the young hare is only 20% of adult body size, and must forage independently. Differences between the ontogenetic allometry of *Lepus*, the interspecific allometry of mammals and the ontogenetic allometry of reptiles are noted and considered in a phylogenetic context.

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## Introduction

The muscles and bones of the vertebrate body interact to provide support and movement. During ontogeny the mechanical and physiological properties of the muscles and bones are continually altered as the two systems progress through a sequence of growth and developmental changes. As a result of growth, bones change their linear dimensions and proportions, increase in density (Trotter & Pearson, 1970) and mineral content (Currey & Butler, 1975), and multiply the number of secondary osteons per unit area (Torzilli, Takebe, Burstein, Zika *et al.*, 1982). Muscles, on the other hand, begin as a collection of weak, slow-twitching unspecialized myotubes, that differentiate into several distinct types of muscle fibres each possessing specific contractile and metabolic characters (see Close, 1972; Goldspink, G., 1980). These fibres display differential radial growth (Swatland, 1981; Goldspink & Ward, 1979), and experience a relative increase in protein content (Goldspink, D. F., 1980). The muscles undergo a relative increase in mass (Goldspink, D. F., 1980) and change their points of attachment along the length of the bones (Dodson, 1975; Grant & Hawes, 1977). For most vertebrates the bones and muscles must interact to maintain locomotor function throughout much of this dynamic period.

Over the years considerable attention has been focussed on the growth and development of various mechanical and physiological properties of the vertebrate muscular and skeletal systems. The contractile properties of muscles during growth have been measured in cats (Close & Hoh, 1967; Hammarberg & Kellerth, 1975*a,b*), mice (Close, 1965*a*) and rats (Buller & Lewis, 1965; Close, 1964; Brown, 1973). Developmental changes have also been investigated in the strength and mechanical properties of bone in dogs (Torzilli *et al.*, 1982; Torzilli *et al.*, 1981), domestic rabbits (Bonfield & Clark, 1973) and humans (Currey, 1979*a*; Currey & Butler, 1975). Most of this research has dealt either with bone or with muscle; few studies have examined the ontogeny of one system in the context of the other. Consequently, an unnatural gap exists between these two areas of study. Compounding the isolation of the two fields is a lack of consideration of the effects of ontogeny on locomotor function. Although much can be learned by careful evaluation of specific aspects of the ontogeny of each system, there is clearly a need to understand the functional integration of the bone-muscle system during growth and locomotor development.

This study follows the ontogeny of the musculo-skeletal system in one species of mammal, *Lepus californicus*, the Blacktailed jackrabbit. A mammal was chosen for this study because mammals have determinate growth, which is rapid and restricted to a relatively short portion of the animals' life (Case, 1978). Rapid determinate growth is also present in birds and can be contrasted with the slow indeterminate growth of many ectotherms (Haines, 1969). Among mammals, *Lepus californicus* is an ideal choice for a number of reasons. First, hares are precocial (Case, 1978), developing locomotor ability early in ontogeny. Second, leporids are highly modified for the cursorial habit (Gambaryan, 1974; Bramble & Carrier, 1979;

Carrier & Bramble, 1980). These first two conditions should augment the need for functional integration of the musculo-skeletal system during growth. Third, hares are wild rather than domesticated animals. Their life history, morphology, physiology and behaviour are controlled by the physical and biological environment in which they live. Finally, hares are of small enough size to facilitate measurement of contractile properties of muscle and mechanical properties of bone.

### Materials and methods

The collection of *Lepus californicus* used in this study came from 2 separate localities. The majority of the hares utilised for morphometric analysis were collected in Curlew Valley (Box Elder Co.) in extreme northern Utah by Drs Charles L. Stoddart and Frederick Knowlton. The animals were donated to this study in an eviscerated condition. Consequently, data obtained from these hares is presented as a function of eviscerated mass instead of full body mass. Fortunately, full body mass scales isometrically with eviscerated mass (Table II), making both equal measures of body size.

Animals used in the analysis of the contractile properties of muscle and the mechanical properties of bone were collected from Little Sahara Recreational Area, Juab County, in central Utah. Hares from both localities belong to a single subspecies, (*Lepus californicus deserticola*; Hall, 1951). Both localities are subject to similar climatic conditions and are characterized by the Northern Desert Shrub Biome (Fautin, 1946). These environmental similarities make it unlikely that hares from the 2 localities differ significantly in growth. Specimens used in the analysis of skeletal morphometrics and mechanical properties of bone were collected at night with a spotlight and gun. Those used to determine the contractile properties of the gastrocnemius were also spotlighted, but were pursued on foot and captured alive in a large trout net.

### Morphometrics

Fifty-eight hares including individuals of both sexes were weighed cleaned of excess tissue and placed in a dermestid beetle colony to obtain cleaned skeletons. The eviscerated mass of these hares ranged from 79 to 2375 g. The series represents the entire postnatal growth series, from animals only a few hours old to fully mature adults. From the postnatal skeletons a total of 24 length measurements were taken (to the nearest 0.1 mm) with dial calipers. These measurements were chosen because of their relevance to locomotion (i.e. body proportions, muscle lever systems and bone strength). Due to damage from shooting, not all skeletons are complete. The sample size for most measurements is therefore below 54 (*N* in Table II). Table I and Fig. 1 describe the measurements taken.

To provide a basis for comparison, certain measurements were also taken from a growth series of the domestic cat. Measurements 9, 12, 13, 17 and 18 of Table I were recorded from 10 cats ranging in size from 251 to 4445 g full body mass.

### Contractile properties of the gastrocnemius

Isometric twitch and tetanic contractions of a single muscle were recorded *in vivo* from 19 hares, ranging in size from 125 to 2642 g full body mass. The gastrocnemius was the obvious choice as it is accessible and easy to instrument. The animals were tested within 12–48 h of capture. The lateral and medial heads of the gastrocnemius were measured together as a single muscle, as the two cannot be separated without damage to the muscle.

TABLE I  
Explanation of skeletal measurements

## A. Lengths

- (1) Skull, anterior premaxillary to nuchal crest
- (2) Cervical vertebra, anterior centrum of atlas to posterior epiphysis of 7th cervical
- (3) Thoracic vertebra, anterior epiphysis of first thoracic to posterior epiphysis of 12th thoracic
- (4) Lumbar vertebra, anterior epiphysis of first lumbar to posterior epiphysis of 7th lumbar
- (5) Axial skeleton, sum of measurements 2, 3 and 4
- (6) Pelvis, anterior crest of ilium to ischial tuberosity
- (7) Femur, depression for Ligamentum Teres on head to distal surface of medial condyle
- (8) Tibia, proximal surface of medial condyle to facet of medial malleolus
- (9) Third metatarsal, articulation with ext. cuneiform to articulation with phalange
- (10) Hind limb, sum of measurements 7, 8 and 9
- (11) Humerus, proximal surface of head to distal surface of trochlea
- (12) Radius, articulation with humerus to articulation with semilunar
- (13) Third metacarpal, articulation with Os magnum to articulation with phalange
- (14) Front limb, sum of measurements 11, 12 and 13
- (15) Scapula, vertebral border at spine to glenoid fossa
- (16) Pisiform, articulation with cuneiform to insertion of Flexor carpi ulnaris (Fig. 1)
- (17) Calcaneum tuber, anterior notch of fibular condyle to insertion of gastrocnemius (Fig. 1)
- (18) Olecranon, centre of trochlear notch to insertion of triceps (Fig. 1)
- (19) Greater trochanter, depression for Ligamentum Teres on head to dorsal insertion of gluteus (Fig. 1)
- (20) Third trochanter, depression for Ligamentum Teres on head to insertion of psoas (Fig. 1)

## B. Mechanical advantage of muscles

- (21) Triceps at elbow, measurement 18 divided by the sum of measurement 12 and 13
- (22) Gastrocnemius at ankle, measurement 17 divided by measurement 9
- (23) Flexor carpi ulnaris at wrist, measurement 16 divided by measurement 13
- (24) Gluteus at hip, measurement 19 divided by measurement 10
- (25) Psoas at hip, measurement 20 divided by measurement 10

## C. Diameters

- (26) Humerus, midshaft diameter in parasagittal plane
- (27) Femur, midshaft diameter in parasagittal plane
- (28) Tibia, midshaft diameter in parasagittal plane
- (29) Third metatarsal, midshaft diameter in parasagittal plane

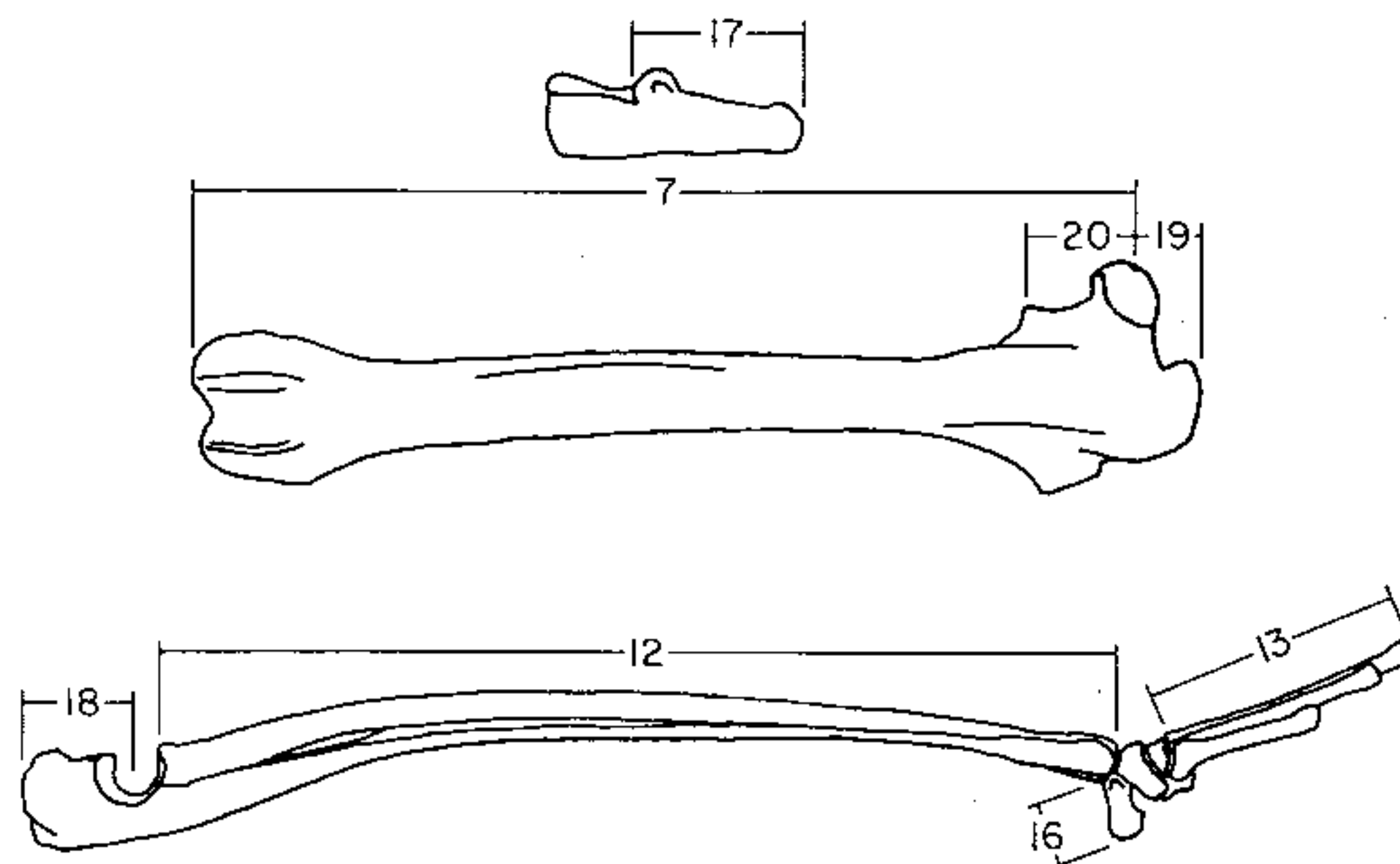


FIG. 1. Illustration of certain skeletal measurements of *Lepus californicus* described in Table I.



Hares were anaesthetized initially with 40 mg sodium pentobarbital/kg body mass, injected intravenously, followed by 10–20% of the initial dose every 30–60 min. Animals less than 300 g body mass received 20 mg sodium pentobarbital/kg body mass, intravenously or intraperitoneally. The distal insertion of the gastrocnemius was separated from the tendon of the plantaris and isolated by cutting the tip of the calcaneal tuber. The muscle itself was not exposed. The sciatic nerve was isolated by dissection of the lateral thigh and cut centrally. During the recording session, the nerve was kept moist with Ringer's solution. All animals were fixed in the prone position and the tibia was secured in a steel-screw clamp, such that the long axis of the gastrocnemius was oriented vertically.

The recording apparatus consisted of a Grass (FT10C) force-displacement transducer (maximum working range 10 kg) connected via a Beckman (9853A) amplifier to a Beckman (R511A) chart recorder. The distal end of the gastrocnemius tendon was attached to the transducer with a short (1–2 inches) double link of 30 lb test polyfilament nylon fishing line. Since the tendon stretches, measurement of force at its distal end will underestimate the strength of the muscle. However, measurement here instead of the distal end of the muscle more accurately measures the actual forces delivered to the tip of the calcaneal tuber. The gastrocnemius was stimulated indirectly through the sciatic nerve using supramaximal square electrical pulses of 25 ms for single (twitch) contractions and 1 ms at 200 pulses/s for tetanic contractions. The body temperature of the hare was maintained at 36–39°C with an electric heating pad.

To determine tension, the muscle was put under tension at approximately resting length, and stimulated with pulses of increasing voltage until the supramaximal voltage was established. The optimal length (that at which the muscle contracts with maximum force) of the muscle was then determined by raising and lowering the stage holding the animal, and stimulating the muscle at different lengths. Once the optimal length had been determined the muscle was stimulated with single pulses to record twitch force as well as the time from the initiation of the contraction to peak force (twitch time). Tetanic force was next determined. The change in contractile strength due to change in muscle length was then determined by stretching the muscle to the length at which it produced roughly 50% maximum twitch force, and then, in intervals, releasing the tension on the muscle and recording its twitch force at each interval. At the completion of the test the hares were killed with an overdose of sodium pentobarbital. The apparatus was then calibrated with standard brass weights.

In instances, such as this, where the forces exerted by intact muscles are measured, one can never be sure that the whole muscle is activated. However, the large forces that were obtained (see Results), suggest that the muscles were almost, if not fully, activated.

### *Mechanical properties of bone*

The right and left third metatarsals from 19 hares and the left femurs from 12 hares, ranging in size from 257 to 2642 g full body mass were loaded under 3 point static bending (Currey, 1970). The bones were removed from the animals and stored frozen until the time of testing. Sedlin & Hirsch (1966) found no important changes in the mechanical properties of bone that had been stored for extended periods below 0°C. Care was taken not to allow the bone to desiccate prior to testing. All testing was conducted at room temperature, about 20°C.

Bending was done on an Instron table machine. The deflection of the bone at the point of loading occurred at a rate of 1.27 mm/min, producing failure of the bone in 30–60 s. Static loading of this

kind produces values for stress and modulus of elasticity that are lower than those generated at higher and more realistic loading rates (Currey, 1975; McElhaney, 1966). However, static loading is more easily controlled, thus facilitating between group comparison, as was required in this study. The loaded length of the bone included the length of the whole diaphysis and so varied for each animal. The load was applied perpendicular to the long axis of the bone, in the parasagittal plane.

The breaking load is a measure of the strength of the bone as a whole. In order to determine the breaking stress (force/unit area) and the modulus of elasticity, the second moment of area of the bone's cross-section was determined. The bones were assumed to be annular ellipses of constant dimensions. Cross-sectional dimensions were measured with dial calipers from enlarged (10×) photographs of the cross-sections. The outer and inner diameters were measured in the direction of bending and at right angles to this direction. This allowed calculation of the second moment of area ( $I$ ) from the relation;

$$I = 3.14 (BA^3 - ba^3)/64,$$

where  $B$  = external width at load point,  $b$  = internal width at load point,  $A$  = external depth at load point,  $a$  = internal depth at load point (Vose & Kubala, 1959).

Breaking and yield stress was then calculated from the relation;

$$\text{Stress} = FLA/8I$$

where,  $F$  = force applied to the bone,  $L$  = distance between supports (length of diaphysis)  $A$  = external depth at load point (Vose & Kubala, 1959).

The elastic modulus ( $E$ ) was calculated from

$$E = FL^3/48ID$$

where,  $F$  = yield force,  $D$  = deflection distance of bone (Nash, 1972).

Mineralization of femur cortical bone was determined by ashing (Currey, 1969). Twenty per cent of the bone length was removed from the centre of the diaphysis, cleaned of marrow, degreased by soaking in chloroform for 1 week and ashed in an oven at 600°C for 24 h.

### *Quantitative techniques*

All data are presented in the form of the allometric equation  $Y = a\chi^b$ , where, in most cases,  $\chi$  is body mass. Body mass or weight is the measure of size which has the most relevance to locomotor function (Schmidt-Nielsen, 1977). Equations were fitted by least squares regression, after the data had been log transformed. Although use of the regression method has been criticized because of the assumption of independent and dependent variables (Kermack & Haldane, 1950; Sacher, 1970), alternative methods that do not require this assumption (i.e. reduced major axis) would produce only slightly different equations, due to the high correlation coefficients of most of the regressions (Misra & Reeve, 1964).

Power equations of the general form  $Y = a\chi^b$  have long been used as an analytical tool in allometric studies (see Huxley, 1932; Gould, 1966). The usefulness of the power equation is that the exponent  $b$  shows whether the parameter  $Y$  is increasing at a greater rate (positive allometry), a lower rate (negative allometry) or the same rate (isometry) as parameter  $\chi$ . The numerical value of the exponent that indicates isometry depends on the units of  $X$  and  $Y$ , and on the type of comparison being made (e.g. shape, mechanical function). If the units of  $X$  and  $Y$  are the same, as is the case when a length  $L$  is compared to another length  $L$ , isometry is denoted by an exponent of one. If, on the other hand,  $X$  is a volume  $L^3$  and  $Y$  is a length  $L$  isometry is indicated by  $b = 3$  (see Gould, 1966 for discussion). If changes in the compared parameters,  $Y$  and  $X$ , do not alter the shape of the animal, "geometric similarity" is maintained. If the changes do not alter the mechanical function (as would be the case if muscular force increased at the same rate as body mass,  $b = 1$ ) then "mechanical similarity" is maintained.

TABLE II

Allometric equations of the form  $y=am^b$ , where  $m$  is eviscerated body mass in grams, fitted to the morphometric data obtained from an ontogenetic series of *Lepus californicus*

Dependent variable <i>Y</i>	<i>N</i>	<i>r</i>	<i>F</i>	Factor <i>a</i>	Exponent, <i>b</i> and 95% confidence limits
Lengths of bones (mm)					
(1) Skull	42	0.988	1695.89	13.450	$0.252 \pm 0.026$
(2) Cervical vert.	39	0.986	1292.118	3.215	$0.405 \pm 0.011$
(3) Thoracic vert.	43	0.987	1649.756	5.900	$0.404 \pm 0.018$
(4) Lumbar vert.	41	0.978	885.642	4.216	$0.455 \pm 0.015$
(5) Axial skeleton (2+3+4)	30	0.983	842.813	13.791	$0.417 \pm 0.019$
(6) Pelvis	51	0.980	1231.763	3.401	$0.434 \pm 0.022$
(7) Femur	53	0.974	968.026	5.063	$0.407 \pm 0.026$
(8) Tibia	55	0.983	1505.320	4.187	$0.460 \pm 0.028$
(9) metatarsal	53	0.967	734.167	4.208	$0.328 \pm 0.018$
(10) Hind limb (7+8+9)	49	0.981	1249.243	15.379	$0.388 \pm 0.029$
(11) Humerus	49	0.984	1492.895	5.618	$0.362 \pm 0.026$
(12) Radius	50	0.987	1897.779	5.114	$0.397 \pm 0.022$
(13) Metacarpal	49	0.948	418.554	3.568	$0.275 \pm 0.017$
(14) Front limb (11+12+13)	44	0.988	1783.181	15.029	$0.353 \pm 0.025$
(15) Scapula	50	0.989	2146.881	2.915	$0.420 \pm 0.018$
(16) Pisiform	49	0.908	221.441	1.296	$0.225 \pm 0.009$
(17) Calcaneum tuber	55	0.914	271.233	3.773	$0.206 \pm 0.020$
(18) Olecranon process	49	0.967	683.420	1.894	$0.267 \pm 0.007$
(19) Greater trochanter	44	0.940	319.707	0.224	$0.479 \pm 0.017$
(20) Third trochanter	42	0.875	131.581	1.055	$0.307 \pm 0.009$
Mechanical advantages of muscles					
(21) Triceps at elbow (18/(12+13))	48	0.861	132.310	0.239	$-0.16 \pm 0.073$
(22) Gastrocnemius at ankle (17/9)	53	0.889	194.115	0.885	$-0.121 \pm 0.117$
(23) Flexor carpi ulnaris at wrist (16/13)	49	0.495	15.269	0.363	$-0.051 \pm 0.108$
(24) Gluteus at hip (19/10)	44	0.579	21.185	0.012	$0.114 \pm 0.050$
(25) Psoas at hip (20/10)	42	0.308	4.214	0.060	$-0.064 \pm 0.058$
Bone diameter (mm)					
(26) Humerus	49	0.974	878.590	0.558	$0.314 \pm 0.011$
(27) Femur	49	0.958	531.081	0.678	$0.306 \pm 0.008$
(28) Tibia	51	0.954	499.389	0.420	$0.355 \pm 0.014$
(29) Metatarsal	20	0.947	157.015	0.639	$0.225 \pm 0.038$
Masses					
(30) Full body (g)	55	0.997	8979.931	1.270	$1.000 \pm 0.021$
(31) Heart (g)	24	0.985	724.705	0.004	$1.148 \pm 0.088$
(32) Gastrocnemius (desiccated (mg))	19	0.995	1743.990	0.220	$1.236 \pm 0.062$
(33) Plantaris (desiccated (mg))	19	0.996	2217.860	0.034	$1.408 \pm 0.063$
(34) Triceps (desiccated (mg))	19	0.990	908.949	0.478	$1.134 \pm 0.021$

$N$ =number of specimens,  $R$ =correlation coefficient,  $F$ =Fisher  $F$  distribution statistic.



Ideally a plot of the data should form a uniform cloud around the curve generated by the power equation, indicating that the rate of increase in  $Y$  relative to  $X$  stays constant. If, however, the trend of the data diverges at some point from the power curve, differential growth is still occurring but the rate of relative growth (exponent of the power equation) is changing. Changes in the exponent during postnatal growth are common in this and other studies (Gould, 1966; Shea, 1981). They can have important functional implications, but do complicate statistical description. For this reason, in this study many of the data are graphed with the regression line of the power equation, providing a means of visual examination. In some instances where the power equation is clearly an inadequate description, the data were divided into 2 sets, above and below 1100 g body mass before calculating regressions. This technique of applying more than one line to a set of data has been criticized (see Gould, 1966), as it artificially amplifies differences in the exponent, however, it does provide a closer description of the allometry during specific portions of ontogeny.

### Morphometric analysis

Allometric equations of the initial morphometric analysis are given in Table II. If *Lepus* was to maintain geometric similarity throughout ontogeny, bone lengths and diameters would scale as (body mass)<sup>0.33</sup>, muscle mass as (body mass)<sup>1.00</sup> and muscle mechanical advantage as (body mass)<sup>0.00</sup>. The allometric coefficients (exponents) in Table II clearly show that *Lepus* does not maintain geometric similarity during ontogeny. In general, bone lengths and muscle masses tend to show positive allometry, while bone diameters and muscle mechanical advantages show negative allometry.

The length of the limbs and of the axial skeleton show positive allometry. This has the effect of converting the shape of the animal from that of a stout infant, into a lean and lanky adult. Such changes of shape are typical of altricial groups, such as Capuchin monkeys (Jungers & Fleagle, 1980), mice (Green & Fekete, 1933), House wrens (Huggins, 1941) and chickens (Lerner, 1941). In contrast, other precocial cursors such as the larger perissodactyls and artiodactyls seem to begin life with relatively long legs, which their bodies then grow into. This apparent difference between *Lepus* and precocial ungulates suggests that, although *Lepus* can run within a few hours after birth (pers. obs.), there may be a greater discrepancy between the locomotor ability of the newborn and adult hare than between the newborn and adult ungulate.

The length of the axial skeleton, which is proportional to (body mass)<sup>0.42</sup>, increases at a greater rate than the length of the limbs. The hind limb increases in length more rapidly than the front limb, scaling as (body mass)<sup>0.39</sup> and (body mass)<sup>0.35</sup>, respectively (exponents statistically different by Student's  $t$ -test  $P < 0.05$ ). Comparison of the individual axial and limb segments also reveals marked allometry. The lumbar region of the vertebral column increases in length at a greater rate than do either the cervical or thoracic regions. The middle limb segments (tibia and radius) increase in length more rapidly than the proximal or distal segments. The distal segments (metatarsals and metacarpals) increase in length at the lowest rate, being relatively long in young individuals. The tendency for juveniles to possess relatively large feet has been observed in other groups of mammals, with good examples among primates (see Jungers & Fleagle, 1980) and heteromyid rodents (J. Nikolai, pers. comm.).

### Scaling of lever systems

The scaling of the lever arms of limb muscles is of particular importance to locomotor



function. A high value for the ratio of the in-lever/out-lever (mechanical advantage) leads to a relatively large propulsive force applied at the point of contact with the ground due to the contraction of the muscle. Conversely, a low mechanical advantage results in a relatively small propulsive force. However, lever systems with low advantage elicit a greater angular excursion of the limb when the muscle shortens through a given length. Accordingly, high mechanical advantage tends to increase an animal's ability to accelerate and decelerate rapidly, while low mechanical advantage is superior when speed is more important than acceleration. The allometry of the mechanical advantages of the lever systems of *Lepus* is significantly negative (exponent  $< 0$ ,  $P < 0.05$ ) in three of the five lever systems measured (Table II), illustrating that young individuals have greater absolute mechanical advantage at certain key limb joints than do adults.

Decreasing mechanical advantage with increasing size, as seen in the growth of *Lepus*, is the reverse of what is found in interspecific comparisons of adult mammals (Alexander, 1977; Goldstein, 1972), adult birds (Maloiy *et al.*, 1979) and in the ontogeny of *Alligator* (Dodson, 1975). However, an analysis of two lever systems during the ontogeny of the domestic cat revealed scaling relationships similar to those of *Lepus* (Table III). This similarity, in light of the fact that cats are altricial, suggests that a loss of mechanical advantage during growth may be the general condition for mammalian cursors and possibly all mammals.

A plot of the measured mechanical advantages vs body mass (Fig. 2) shows that in general the most pronounced decline in advantage occurs during the first half of postnatal growth. Looking more specifically at the relationship between the advantage of the gastrocnemius and body mass it is found that the most dramatic change in slope occurs at approximately 900 g eviscerated body mass (i.e. 1100 g full body mass). Below this size mechanical advantage decreases as  $(\text{body mass})^{-0.126}$ , while above 900 g, mechanical advantage does not change appreciably, scaling as  $(\text{body mass})^{-0.026}$ , (Table IV). The drop in mechanical advantage during early postnatal growth will change locomotor ability, decreasing accelerational potential, unless there is a corresponding increase in the contractile strength of the gastrocnemius. If the ability to accelerate is to be maintained or improved during early postnatal growth, the scaling of the lever systems predicts that the locomotor muscles should become relatively stronger as the animal matures.

TABLE III  
Allometric equations of the form  $Y = aM^b$ , where  $M$  is full body mass in grams, for the skeletal dimensions of the domestic cat. Data were log transformed and equations were fit by least squares regression

Dependent variable $Y$	$N$	$r$	$F$	Factor $a$	Exponent, $b$ and 95% confidence limits
Lengths of bones (mm)					
(1) Metatarsal	10	0.980	201.764	1.795	$0.415 \pm 0.067$
(2) Calcaneum	10	0.957	87.772	1.679	$0.300 \pm 0.074$
(3) Metacarpal	10	0.983	228.461	2.028	$0.342 \pm 0.052$
(4) Ulna	10	0.979	186.941	3.367	$0.411 \pm 0.069$
(5) Olecranon	10	0.960	94.011	1.041	$0.313 \pm 0.074$
Mechanical advantages of muscles					
(6) Triceps at elbow (5/(3+4))	10	0.685	7.093	0.197	$-0.081 \pm 0.069$
(7) Gastrocnemius at ankle (2/1)	10	0.805	14.728	0.935	$-0.116 \pm 0.069$

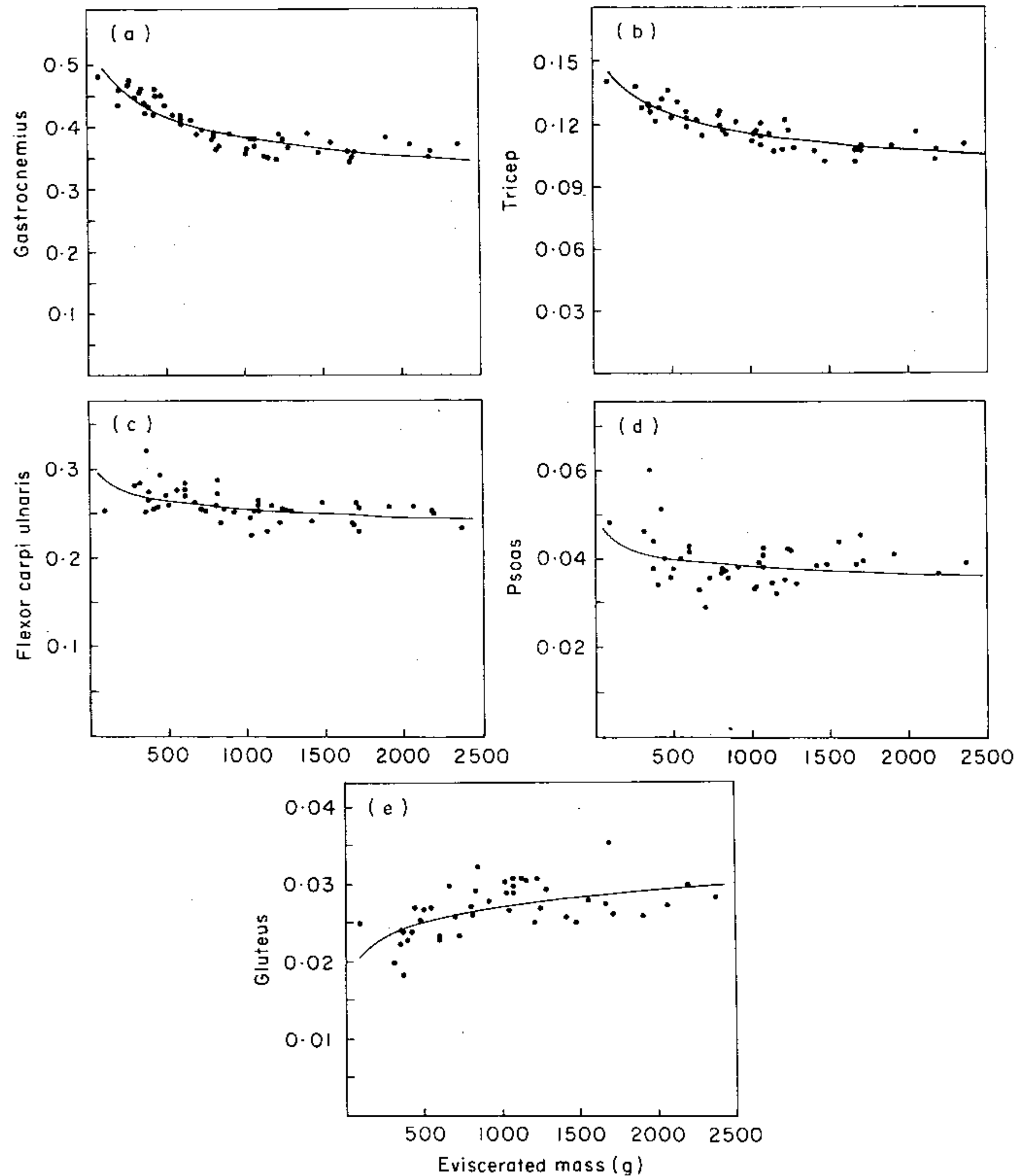


FIG. 2. Graphs of muscle mechanical advantage of *Lepus californicus* plotted against eviscerated body mass. Calculation of mechanical advantage is described in Table I. Equations of plotted lines are listed in Table II.

### Scaling of bone diameter

The mechanical properties of bone (i.e. breaking strength and elastic modulus) are determined by the material of the bone tissue, the organization of this tissue and cross-sectional shape of the bone. Numerous studies have shown that the materials of which bones are made play a large role in determining bone strength and stiffness (Torzilli *et al.*, 1981; Torzilli *et al.*, 1982; Currey, 1979b; Vose & Kubala, 1959). Unfortunately, most studies concerned with the allometry of the strength of bone have ignored this, and have relied on only the thickness of the bone to illustrate its strength (e.g. McMahon, 1975; Alexander *et al.*, 1979). This approach may be necessary when dealing with fossils, but is of dubious value when applied to extant forms.

To facilitate comparison with earlier investigations, measurement of bone diameters have been included here (Table II). Table V lists the allometric equations of bone length vs bone diameter. Exponents greater than one indicate that the bones become thinner relative to their length as the hares grow. Again this pattern is the reverse of what has been observed with increases in size in interspecific comparisons (Alexander *et al.*, 1979; Alexander, 1977; Maloiy *et al.*, 1979; McMahon, 1975) and during the ontogeny of *Alligator* (Dodson, 1975). If the material properties of the bone tissue of *Lepus* were to remain constant during

TABLE IV  
Allometric equations of the form  $Y=aM^b$ , where  $M$  is body mass in grams. A. Hares in the weight range of 90–1100 grams. B. Hares in the weight range of 1100–2700 g. Data were log transformed and equations were fit by least squares regression

Dependent variable $Y$	$N$	$r$	$F$	Factor $a$	Exponent, $b$ and 95% confidence limits
A. Muscle strength (gastrocnemius in N)					
(1) Tetanic force	10	0.986	279.093	0.008	$1.230 \pm 0.059$
(2) Twitch force	10	0.977	171.423	0.004	$1.275 \pm 0.068$
Mechanical advantages of muscles					
(3) Gastrocnemius at ankle	28	0.834	59.272	2.502	$-0.126 \pm 0.050$
(4) Triceps at elbow	23	0.737	24.979	1.229	$-0.081 \pm 0.037$
(5) Flexor carpi ulnaris at wrist	24	0.100	0.226	0.291	$-0.013 \pm 0.042$
(6) Gluteus at hip	21	0.436	4.476	0.012	$0.115 \pm 0.031$
(7) Psoas at hip	20	0.554	8.001	0.122	$-0.180 \pm 0.037$
Lengths of bones (mm)					
(8) Metatarsal	28	0.985	896.581	2.433	$0.419 \pm 0.005$
(9) Calcaneum	29	0.926	163.598	2.241	$0.293 \pm 0.005$
Moments (N mm)					
(10) Breaking (metatarsal)	10	0.965	110.948	0.020	$1.502 \pm 0.049$
(11) Gastrocnemius (around ankle)	9	0.977	147.744	0.016	$1.540 \pm 0.052$
B. Muscle strength (gastrocnemius in N)					
(12) Tetanic force	10	0.933	54.056	0.562	$0.609 \pm 0.009$
(13) Twitch force	10	0.920	44.278	0.284	$0.652 \pm 0.011$
Mechanical advantages of muscles					
(14) Gastrocnemius at ankle	25	0.195	0.924	1.550	$-0.026 \pm 0.017$
(15) Triceps at elbow	25	0.521	8.563	1.247	$-0.095 \pm 0.016$
(16) Flexor carpi ulnaris at wrist	25	0	0	0.249	$0.000 \pm 0.018$
(17) Gluteus at hip	23	0.109	0.274	0.035	$-0.035 \pm 0.017$
(18) Psoas at hip	22	0.322	2.341	0.017	$0.113 \pm 0.012$
Lengths of bones (mm)					
(19) Metatarsal	25	0.767	33.078	16.693	$0.137 \pm 0.005$
(20) Calcaneum tuber	26	0.630	15.684	7.345	$0.112 \pm 0.004$
Moments (N mm)					
(21) Breaking (metatarsal)	9	0.929	44.760	1.332	$0.921 \pm 0.009$
(22) Gastrocnemius (around ankle)	8	0.922	34.328	5.652	$0.676 \pm 0.014$



TABLE V

Allometric equations of the form  $L = aD^b$ , for an ontogenetic series of *Lepus californicus*, where bone ( $L$ ) is expressed as a power of bone diameter ( $D$ ). Both length and diameter are expressed in millimetres. Data were log transformed and equations were fit by least squares regression

Dependent variable $L$	$N$	$r$	$F$	Factor $a$	Exponent, $b$ and 95% confidence limits
Length of bones (mm)					
(1) Humerus	49	0.972	809.288	11.775	$1.110 \pm 0.203$
(2) Femur	49	0.972	805.768	9.421	$1.267 \pm 0.127$
(3) Tibia	51	0.969	775.991	14.527	$1.216 \pm 0.212$
(4) Metatarsal	20	0.962	224.459	9.865	$1.309 \pm 0.184$

ontogeny, then the relative decrease in bone thickness would result in a progressive relative decline in strength as the hares matured.

### Contractile strength of the gastrocnemius

The gastrocnemius forms a critical link in the mammalian locomotor system. It and the plantaris exert propulsive forces through the ankle. However, in an adult hare the plantaris generates only about 65% of the force produced by the gastrocnemius (unpublished data). This makes the gastrocnemius the main propulsive muscle in series between the ankle and the powerful propulsive muscles of the thigh, hip and back. The gastrocnemius is therefore

TABLE VI

Allometric equations of the form  $Y = aM^b$ , for an ontogenetic series of *Lepus californicus*, where  $M$  is full body mass in grams, for the isometric contractile properties of the gastrocnemius muscle. Data were log transformed and equations were fit by least squares regression

Dependent variable $Y$	$N$	$r$	$F$	Factor $a$	Exponent, $b$ and 95% confidence limits
Twitch force (N)	19	0.967	252.173	0.021	$1.006 \pm 0.130$
Tetanic force (N)	19	0.971	282.931	0.044	$0.956 \pm 0.108$
Tetanic out-force (N)	18	0.933	108.318	0.071	$0.755 \pm 0.154$
Time to peak twitch tension (ms)	18	0.000	0.000	55.645	$-0.001 \pm 0.100$
Shortening distance (90% maximum force) (mm)	12	0.920	55.022	0.315	$0.411 \pm 0.123$
* $F = a(L_h)^b$	12	0.940	75.638	0.008	$1.381 \pm 0.354$
Moment around ankle (N) (mm)	17	0.955	158.38	0.217	$1.121 \pm 0.190$
Muscle length (mm)	19	0.975	323.549	2.614	$0.369 \pm 0.043$

\* $F$  = relative functional length of hind limb (shortening distance out-lever/in-lever).

$L_h$  = hind limb length.

a critical link in the locomotor system, and ontogenetic changes in it are likely to reflect general changes which occur during the development of the other hind limb muscles.

The forces that a muscle generates is a product of the amount of contractile tissue pulling in parallel. Consequently, muscular force is proportional to muscle cross-sectional area (Hellam & Podolsky, 1969) and in geometrically similar animals would scale to the 0.667 power of body mass. Allometric equations for the isometric contractile properties of the gastrocnemius are listed in Table VI. Maximum twitch and tetanic force undergo positive allometry being proportional to (body mass)<sup>1.006</sup> and (body mass)<sup>0.956</sup>, respectively. The values of both exponents are not significantly different from the values of one, which would indicate

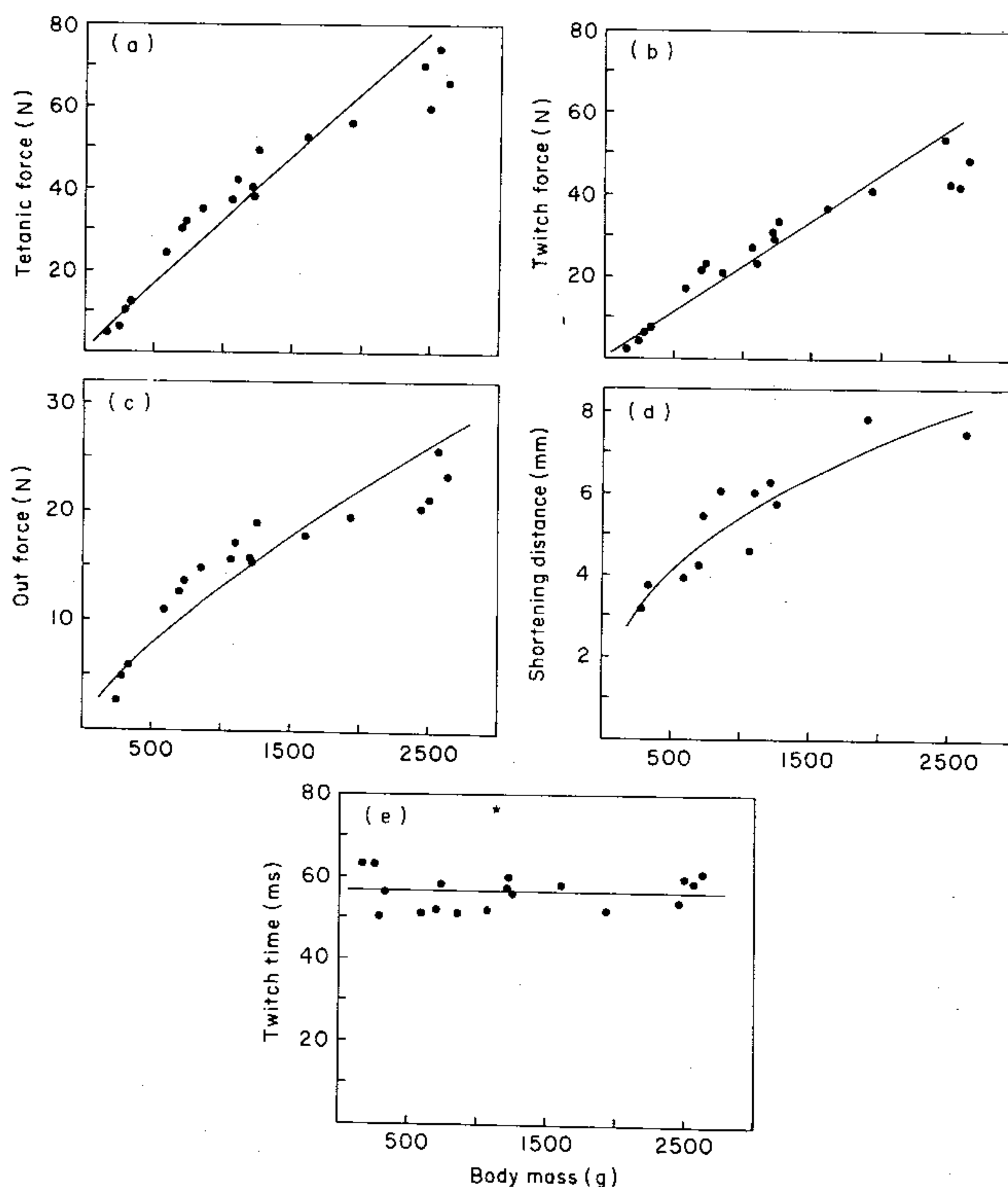


FIG. 3. Graphs of the isometric contractile properties of the gastrocnemius of *Lepus californicus* plotted against body mass. (a) Maximum tetanic force at optimal muscle length. (b) Maximum twitch force at optimal muscle length. (c) Out-force=(maximum tetanic force) (calcaneum tuber length/third metatarsal length). (d) Shortening distance over which muscle can maintain 90% maximum twitch force. (e) Time from initiation of contraction to peak twitch tension. Equations of plotted lines are listed in Table VI.

the maintenance of mechanical similarity. Relative to body mass the gastrocnemius of young hares therefore produces forces as large as those generated by adults. However, a plot of the data (Fig. 3) shows that the relationship is not an ideal power curve. The slope changes throughout postnatal growth, being steeper early in ontogeny. Although this change in the exponent is likely to occur gradually as the animals mature, there does appear to be a decrease in the slope at approximately 1100 g body mass. The data can be more accurately approximated by two regressions, one below and one above this inflection point (Table IV). There is strong positive allometry ( $b=1.23$ ) of contractile force early in postnatal growth, and negative allometry ( $b=0.609$ ) during the second half of postnatal growth. Positive allometry of muscular force during the first half of postnatal growth was predicted from the observation that mechanical advantage decreases as the animal matures. The larger mechanical advantages of the young animals compensate for the relative weakness of their muscles, thereby helping to maintain locomotor function early in ontogeny.

Returning to Fig. 3, it can be seen that the contractile forces of the animals of lowest body mass (infants) and animals of the highest body mass (adults) lie on or below the line (designating mechanical similarity), while the contractile forces of animals in the mid-range (juveniles) fall above the line. From this it is apparent that relative to body mass, juveniles are stronger, i.e. the gastrocnemius of juveniles generate larger forces than those of infants or adults. This becomes even more apparent when the out-force (tetanic force  $\times$  calcaneum length/metatarsal length) at the ball of the foot is plotted against body mass (Fig. 3). Here also, juveniles fall well above the line while the infants and adults fall below the line. Juveniles can produce the largest relative out-forces. In this case, however, the exponent of the line is 0.75, indicating that infants can produce relatively greater out-forces than adults. This production of relatively larger out-forces by infants results from the greater mechanical advantage around their ankle joint.

These differences in relative out-force should have a marked effect on locomotor ability during growth. The modelling which follows is an attempt to calculate relative, not absolute, locomotor ability and is based upon the assumption that ontogenetic changes in the strength and lever system of the gastrocnemius will mirror similar changes in the rest of the hind limb. This assumption is likely to be roughly correct due to the critical link that the gastrocnemius maintains between the ankle and the muscles of the thigh. From Newton's second law of motion we know that the acceleration of an object equals the force applied to the object divided by its mass. Accordingly, the hares capable of producing the largest out-forces relative to their body mass should be capable of the greatest accelerations. Infants should accelerate more rapidly than adults, and juveniles should have the greatest accelerations. This relationship is dramatically illustrated by plotting the relative acceleration (out-force/body mass) against body mass (Fig. 4). This plot makes it clear that the juveniles have the highest rates of acceleration. In fact, juveniles in the range of 600–750 g have estimated rates of acceleration more than two times greater than those calculated for adults. Consequently, juveniles should be able to start up, slow down and change the direction of travel more rapidly than adults.

Although acceleration is of critical importance to a hare, its ability to escape predation will, in most cases, also depend upon absolute running speed. How will the ontogenetic changes in acceleration affect running speed? The data collected in this study do not provide a measure of the absolute running speed of a hare. However, the data make it possible to estimate the terminal velocity of a leap starting from zero velocity. If we make the simplifying



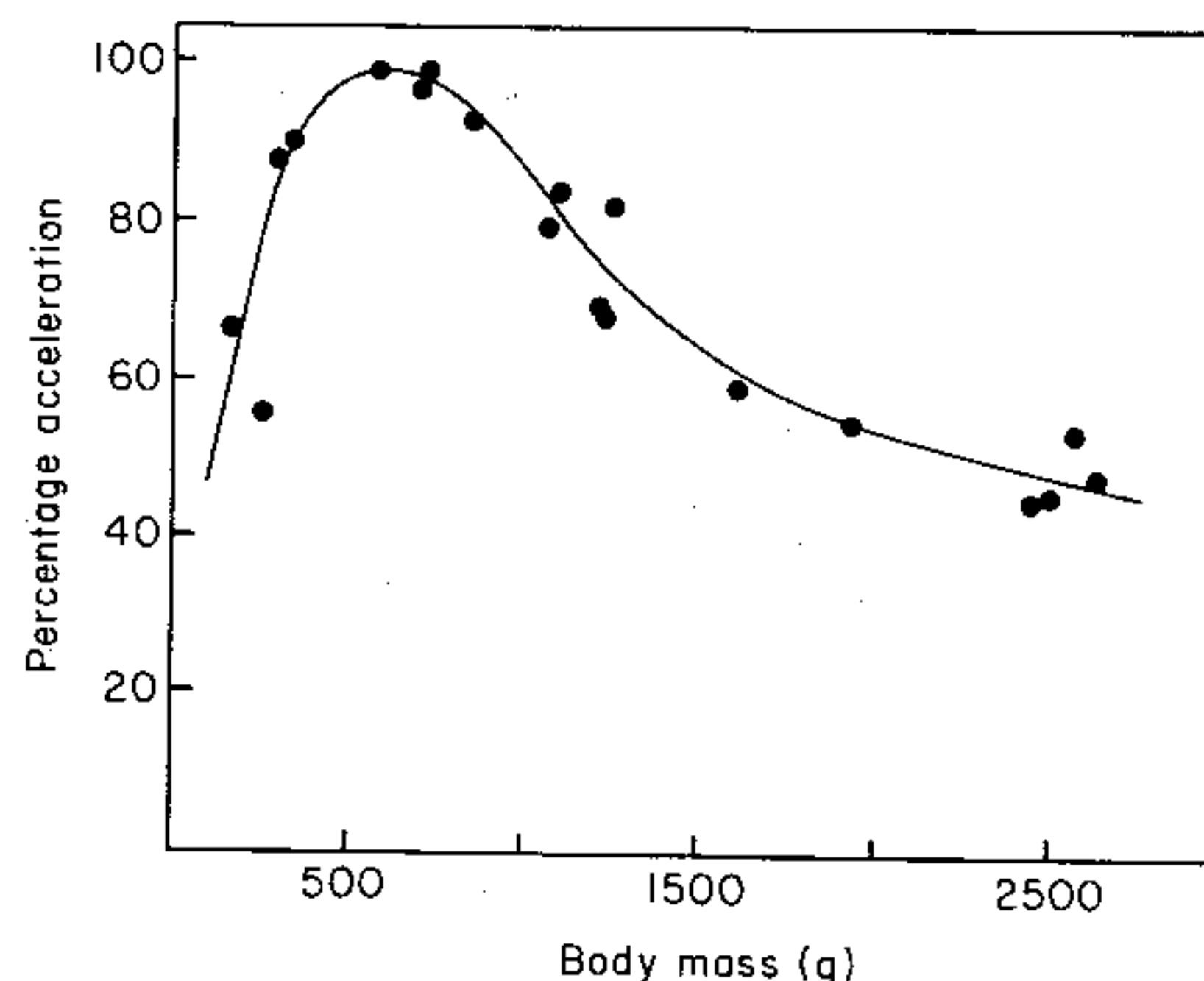


FIG. 4. Graph of estimated acceleration (out-force of gastrocnemius/body mass) of *Lepus californicus* plotted against body mass. Data are plotted relative to maximum estimated acceleration. The line was fit by eye.

assumption that the acceleration remains constant throughout the propulsive phase of the locomotor cycle, then the terminal velocity of a start-up stride can be approximated by the acceleration multiplied by the distance over which the hind limb is extended. This approximation is possible because velocity equals acceleration multiplied by the time over which the acceleration occurs, and time is a function of the distance over which the limb is extended.

The distance over which the limb is extended depends on more than just the length of the limb. Ontogenetic changes in lever relationships (Table II) and in the shortening distance over which the muscle can maintain a given force (Table VI) result in an increase in the functional length of the limb as the hare matures. This must be taken into account before an estimate of terminal velocity can be made. As the animal grows the muscle in-lever becomes relatively short compared to the out-lever (Table II). Consequently, a unit shortening of the muscle of an adult will result in a greater excursion at the distal end of the out-lever than the same unit shortening in a younger animal. At the same time the shortening distance over which the muscle can maintain a given force (in this case 90% maximum) scales as  $(\text{body mass})^{0.411}$ . Hence, the gastrocnemius of adults can maintain a greater percentage of maximum force as the foot is plantar extended. This phenomenon has also been reported for the tibialis anterior muscle during growth in the domestic rabbit (Alder *et al.*, 1958). Thus, the functional length of the limb may be estimated by the shortening distance over which the muscle maintains 90% maximum force, multiplied by the out-lever and divided by the in-lever (Table VI). This parameter is proportional to  $(\text{limb length})^{1.38}$ , so adults not only have relatively longer limbs but also can move their limbs through relatively greater distances, while maintaining a given level of force.

It is now possible to estimate terminal velocity,  $V_t$  as;

$$V_t = aL^{1.38},$$

where,  $a$  is acceleration, and  $L$  is the length of the hind limb.

In this way, terminal velocity was estimated for each animal and plotted against body mass (Fig. 5). The analysis shows that infants have estimated terminal velocities which are much

lower than adult values. However, there is a rapid increase in velocity during growth so that by the time a hare has reached 600 g body mass it has achieved a level that is maintained throughout the rest of ontogeny. This non-intuitive prediction should be viewed with skepticism due to the limited data and simplifying assumptions on which the model is based. However, the model does illustrate that the positive allometry of muscular out-force compensates, at least in part, for the short limbs of the young hare. Juvenile hares appear to have greater terminal velocities at the end of an initial leap and will be able to jump farther than would be the case if out-force scaled isometrically with body mass.

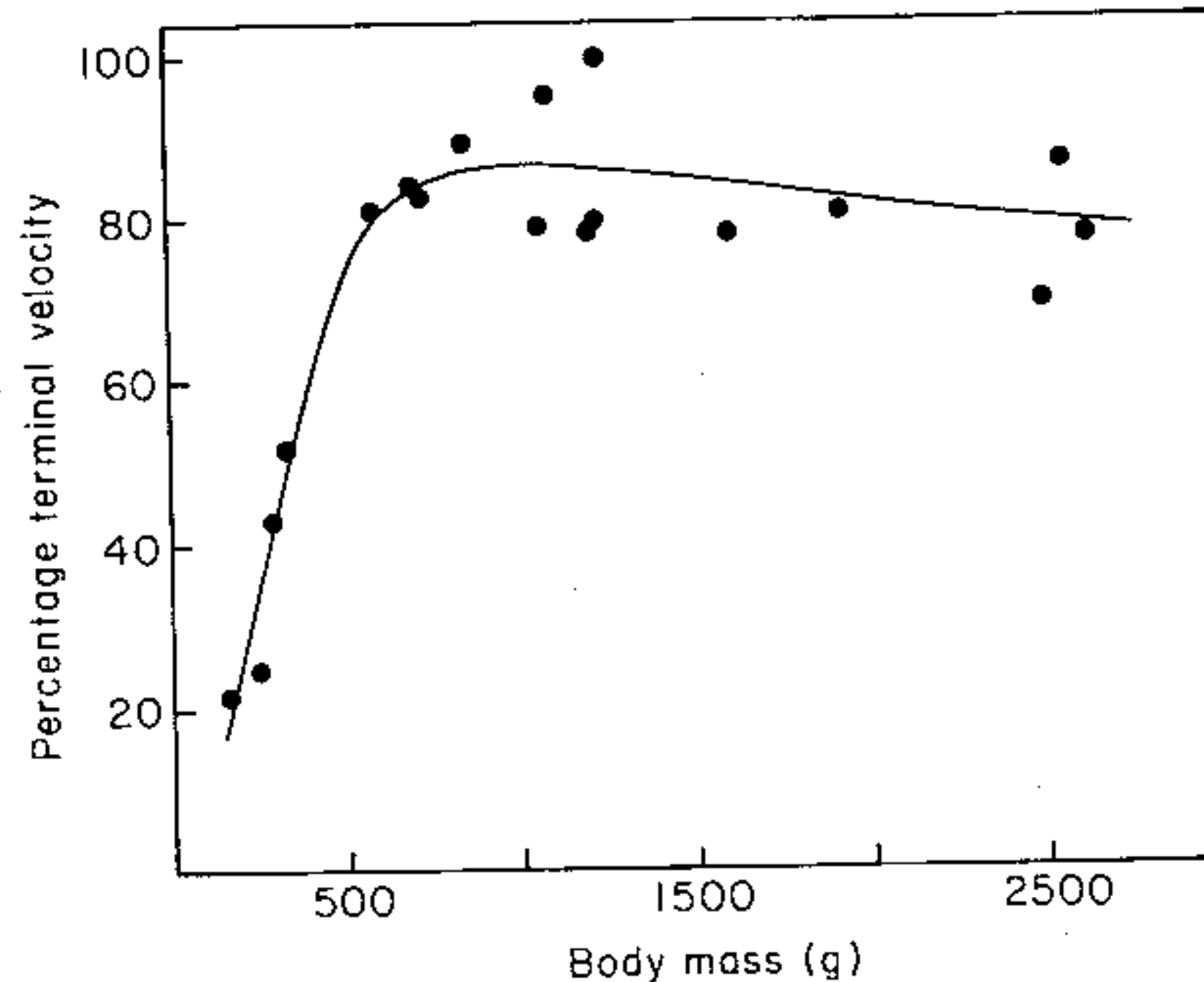


FIG. 5. Graph of estimated terminal velocity out of a leap initiated from zero velocity of *Lepus californicus* plotted against body mass. Data are plotted relative to maximum estimated terminal velocity. Calculation of terminal velocity is described in the text. The line was fit by eye.

The prediction that maximum terminal velocity will be the same for both juveniles and adults is likely to be incorrect because the model ignores the speed of shortening of the muscles. The speed of shortening of a muscle fibre is the product of the intrinsic speed of shortening of the individual sarcomeres multiplied by the number of sarcomeres in the muscle fibre (Goldspink, G., 1977). The intrinsic speed of sarcomere shortening is inversely proportional to the isometric-twitch contraction time (Close, 1965b). In *Lepus californicus*, the isometric-twitch contraction time of the gastrocnemius does not change during postnatal growth (Table VI, Fig. 3), suggesting that the intrinsic speed of the sarcomeres will also remain constant. Consequently, any change in the contractile speed during growth is likely to result solely from changes in the number of sarcomeres in series. During growth, mammalian muscle increases in length by the addition of more sarcomeres to existing muscle fibres (Elliott & Crawford, 1965; Griffin *et al.*, 1971; Goldspink, G., 1968). Because the gastrocnemius of *Lepus* increases in length (scaling to the 0.369 power of body mass) and probably maintains the same intrinsic speed of shortening during growth, the gastrocnemius of adults will have greater contractile velocities than those of juveniles. This difference will allow the acceleration to act through a greater proportion of the stride in adults and could result in adults having greater terminal velocities than juveniles. The greater contractile velocities of adult muscles will also permit adults to move their limbs more rapidly, so that adults can attain and run at greater velocities than juveniles.

### Bone strength

To understand the effects that skeletal ontogeny has on locomotor ability and behaviour, the process must be viewed in relation to the magnitude of the forces imposed on the skeleton by muscles. The strength of bone in bending is of interest because it is a closer approximation to the type of loading that causes bone to fail in life (Currey, 1970). It is also similar to the kind of loading imposed on bones by the muscles. Table VII lists the allometric equations for the mechanical properties of the third metatarsal and femur under three point bending.

Ideally the load required to break a bone should scale to body mass in the same way as do the forces imposed on the bone by the muscles. Bones should be structured to withstand the loads that muscles impose upon them. As size increases in geometrically similar animals, muscular force scales as an area, so the breaking load would scale as (body mass)<sup>0.667</sup>. Alternatively, if animals were to maintain locomotor function, with increases in body size, muscular force would scale isometrically with body mass, causing breaking load to be proportional to (body mass)<sup>1.0</sup>. During the ontogeny of *Lepus* the breaking strength of the third metatarsal and the femur scale as (body mass)<sup>0.986</sup> and (body mass)<sup>0.749</sup>, respectively (Figs 6, 7). It is not clear why the strength of these two bones scale differently. Nevertheless, most important to this investigation is the fact that both the strength of the metatarsal and the strength of the main muscle that loads the metatarsals (gastrocnemius; Table VI) scale roughly to the first power of body weight. This suggests that locomotor function will be maintained throughout postnatal growth.

TABLE VII  
Allometric equations of the form  $Y = aM^b$ , for an ontogenetic series of *Lepus californicus*, where  $M$  is full body mass in grams, for the mechanical and structural properties of the third metatarsal and femur. Data were log transformed and equations were fit by least squares regression

Dependent variable $Y$	$N$	$r$	$F$	Factor $a$	Exponent, $b$ and 95% confidence limits
Breaking load (N)					
Metatarsal	19	0.981	448.286	0.042	0.986 ± 0.098
Femur	12	0.986	370.735	0.633	0.759 ± 0.088
Maximum stress (Mn/m <sup>2</sup> )					
Metatarsal	19	0.920	94.313	1.817	0.631 ± 0.060
Femur	12	0.925	59.577	11.100	0.364 ± 0.058
Yield stress (MN/m <sup>2</sup> )					
Metatarsal	19	0.906	78.097	1.108	0.690 ± 0.069
Femur	12	0.918	53.992	8.045	0.402 ± 0.053
Second moment of area (10 <sup>-12</sup> m <sup>4</sup> )					
Metatarsal	19	0.969	270.907	0.004	0.949 ± 0.065
Femur	12	0.995	1075.045	0.002	1.082 ± 0.073
Elastic modulus (GN/m <sup>2</sup> )					
Metatarsal	19	0.894	67.928	0.016	0.927 ± 0.152
Femur	12	0.913	50.584	0.090	0.716 ± 0.225
Breaking moment of Metatarsal (N mm)	19	0.982	298.508	0.050	1.356 ± 0.134



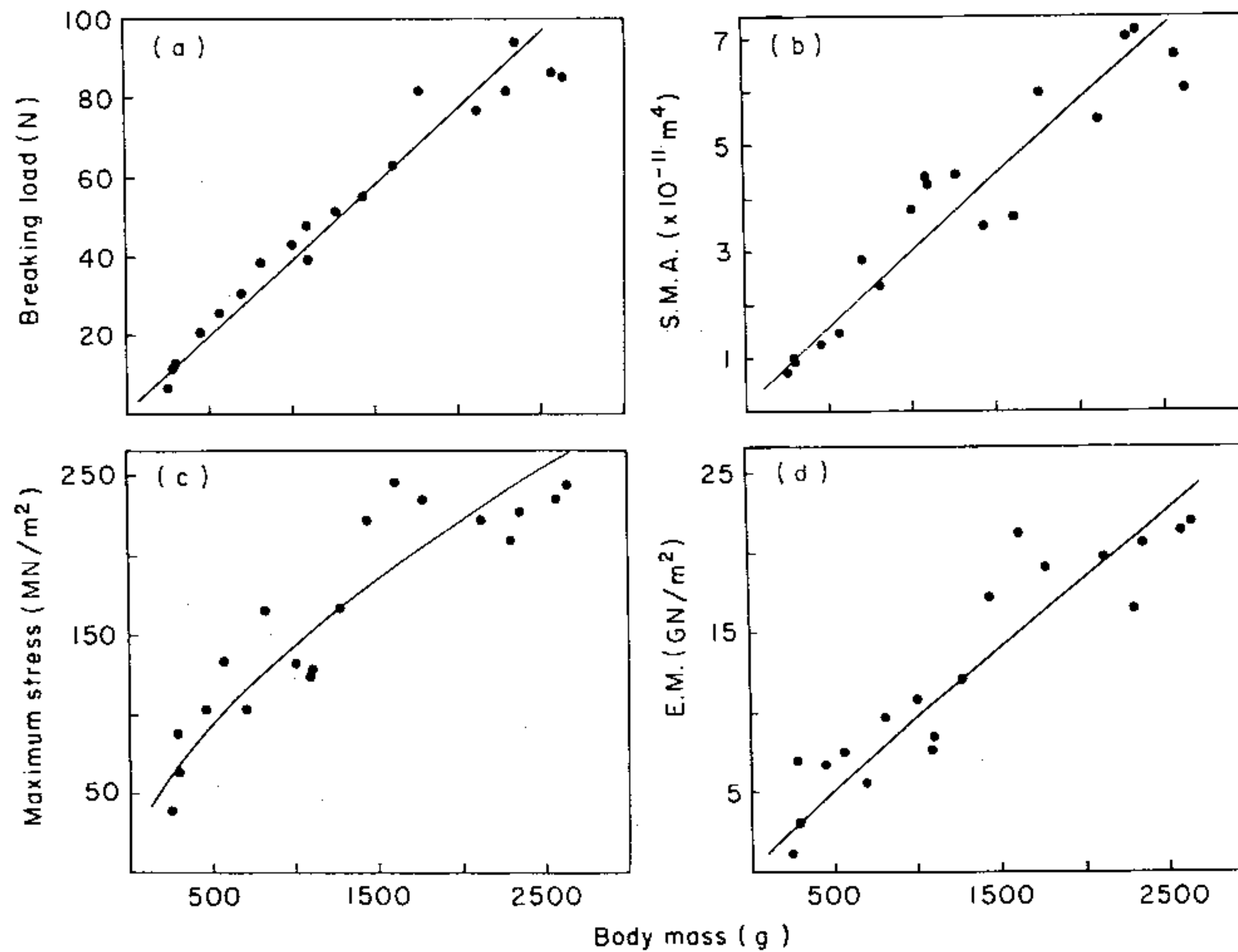


FIG. 6. Graphs of mechanical and structural properties of the third metatarsal of *Lepus californicus* plotted against body mass. (a) Maximum load the bone can support under three point static bending. (b) Second moment of area of cross-section at point of loading. (c) Maximum stress bone can withstand under three point static bending. (d) Elastic modulus of bone under three point static bending. Equations of plotted lines are listed in Table VII.

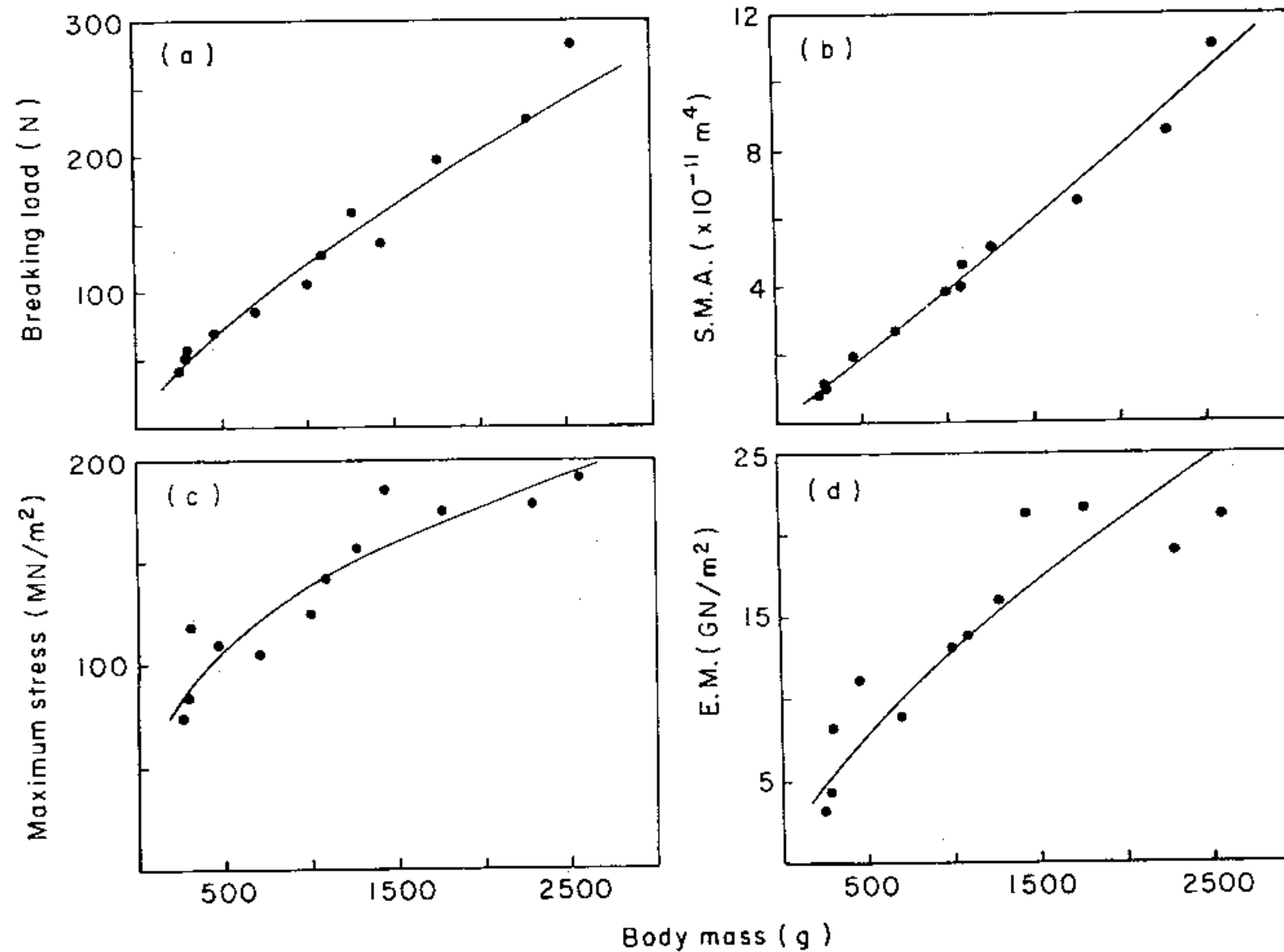


FIG. 7. Graphs of mechanical and structural properties of femur of *Lepus californicus* plotted against body mass. Parameters are the same as those described in Fig. 6. Equations of plotted lines are listed in Table VII.

A more realistic comparison is that between the breaking moment of the metatarsal and the moment applied around the ankle by the gastrocnemius. The breaking moment is the product of the breaking load multiplied by the distance between the support and the point of loading, and is proportional to (body mass)<sup>1.36</sup> (Table VII). The moment applied around the ankle by the gastrocnemius is the product of the isometric-tetanic force of the muscle multiplied by the length of its moment arm, the calcaneum, and is proportional to (body mass)<sup>1.12</sup> (Table VI). Although these two moments scale differently, Fig. 8 clearly shows the allometry of the two moments to be almost identical below 1100 g body mass. If regressions are run only on the individuals below 1100 g, the breaking moment and the moment of the gastrocnemius are proportional to the 1.50 and 1.54 powers of body mass, respectively (Table IV). The exponents of the power equations describing these two sets of data are not significantly different ( $P < 0.001$ ). During roughly the first half of postnatal growth, mechanical similarity is therefore maintained between bone and muscular strength. Above 1100 g mechanical similarity is not maintained, and the breaking moment increases more rapidly than the moment of the gastrocnemius (Fig. 8).

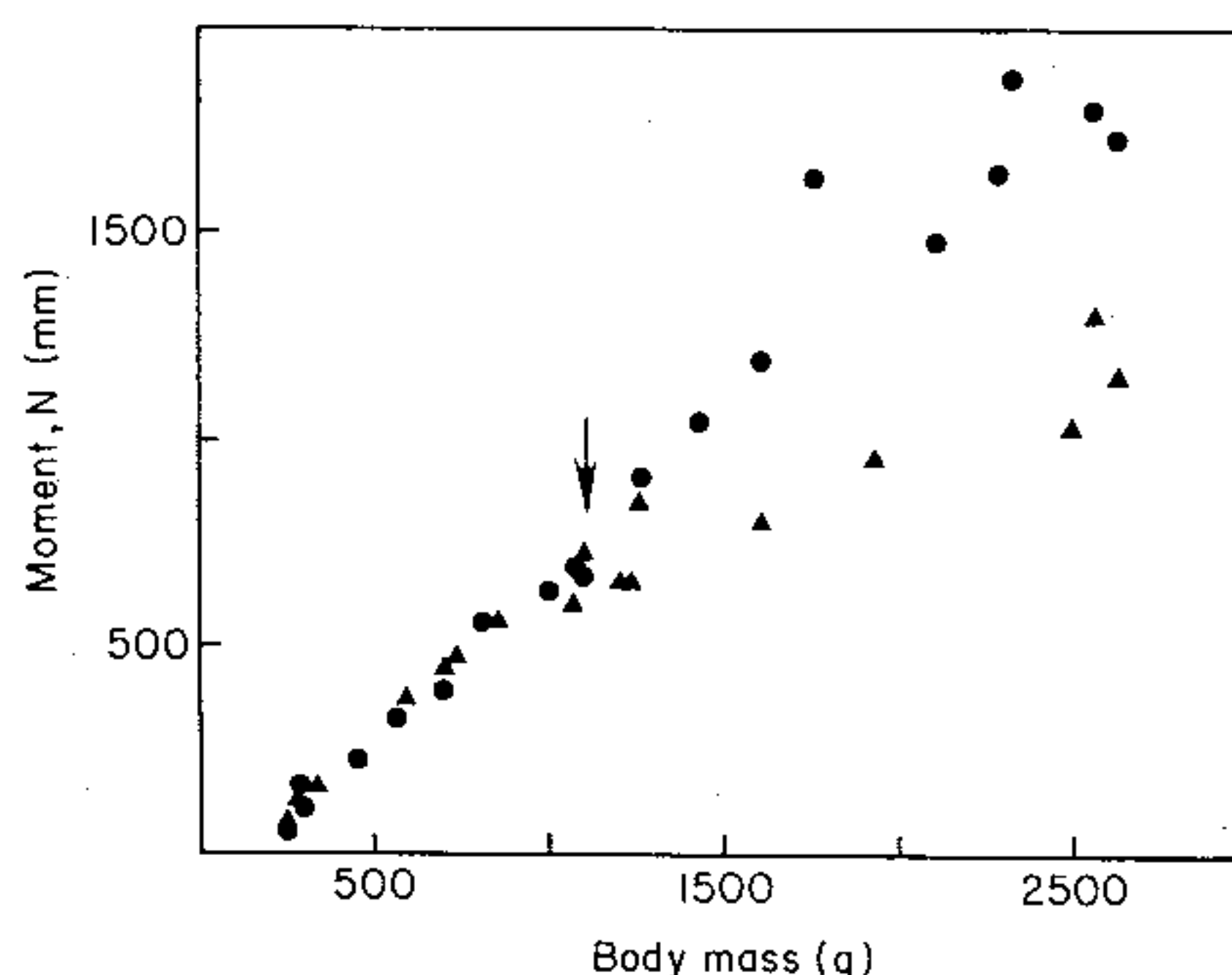


FIG. 8. Graph of moments of *Lepus californicus* plotted against body mass, comparing the breaking moment of the third metatarsal (dots) to the moment imposed on the bone by gastrocnemius (triangles). Calculation of moments is described in the text. Arrow indicates (1100 g) point at which the two moments begin to diverge.

The similarity between the two intercepts (Fig. 8) is largely fortuitous. The portion of the ankle between the centre of rotation and the metatarsals (not measured in this study) will decrease the moment supplied by the gastrocnemius to the metatarsal. Consequently, the data artificially overestimate the  $Y$  intercept of the moment supplied by the gastrocnemius. In the addition, under normal conditions the force delivered by the gastrocnemius is divided among four metatarsals. Thus, the actual moment imposed on the metatarsals by the gastrocnemius will be below the breaking moment of the bone.

To understand the maintenance of mechanical similarity between bone strength and muscle strength, it is necessary to look at the mechanical and structural properties of the bones. It is convenient to compare stresses at the point where the material being tested stops behaving elastically (elastic limit) or at the maximum stress the material can withstand before breaking (Currey & Butler, 1975). In geometrically similar animals these values of stress

should not change with increases in size. This is so because stress is force per area. The forces imposed on the bones should be directly proportional to the strength of the muscles, which will scale as the cross-sectional area of the muscles (Hellam & Podolsky, 1969). Thus, in geometrically similar animals bone stress would be proportional to  $(\text{body mass})^{0.667}$  divided by  $(\text{body mass})^{0.667}$ , or  $(\text{body mass})^{0.00}$ . As can be seen in Table VII, the values of the exponent  $b$  for stress are all well above the isometric value of zero. Hence, the ability of the bones to withstand stress is relatively greater in adults than in younger animals (Figs 6, 7). An ontogenetic increase in the ability of bone to withstand stress has also been reported for humans (Currey & Butler, 1975), domestic rabbits (Bonfield & Clark, 1973) and dogs (Torzilli *et al.*, 1981).

The modulus of elasticity ( $E$ ; stress divided by the strain) is a measure of the stiffness of a material (Wainwright *et al.*, 1976). In the ontogeny of *Lepus*,  $E$  is proportional to  $(\text{body mass})^{0.716}$  for the metatarsal and  $(\text{body mass})^{0.927}$  for the femur. Consequently, the bones of adults are stiffer than the bones of younger animals. Progressive increase in  $E$  also occurs in bone during postnatal growth in humans (Currey & Butler, 1975) and dogs (Torzilli *et al.*, 1981).

Maximum and yield stress, and modulus of elasticity of bone have been shown to increase dramatically with increases in mineralization of only a few percent (Currey, 1975; Vose & Kubala, 1959). During the postnatal growth of *Lepus* the ash content (e.g. mineralization) of femur cortical bone increases from approximately 55–75% (Fig. 9). The most pronounced rise in mineralization occurs below 600 g body mass.

The second moment of area ( $I$ ) is a measure of the way in which the material is distributed about the neutral plane of bending. During bending the maximum stresses occur at the upper (compressional) and lower (tensional) surfaces of the bone. For this reason the material should be concentrated at the outside edges of the bone rather than near the neutral plane where the stresses are lower (Wainwright *et al.*, 1976). Placing the material as far as possible from the neutral plane maximizes  $I$  and hence minimizes stress. The second moment of area has units of length to the fourth power, and so in geometrically similar animals would be proportional to  $(\text{body mass})^{4/3}$ . In the ontogeny of *Lepus*,  $I$  scales as  $(\text{body mass})^{0.928}$  for the

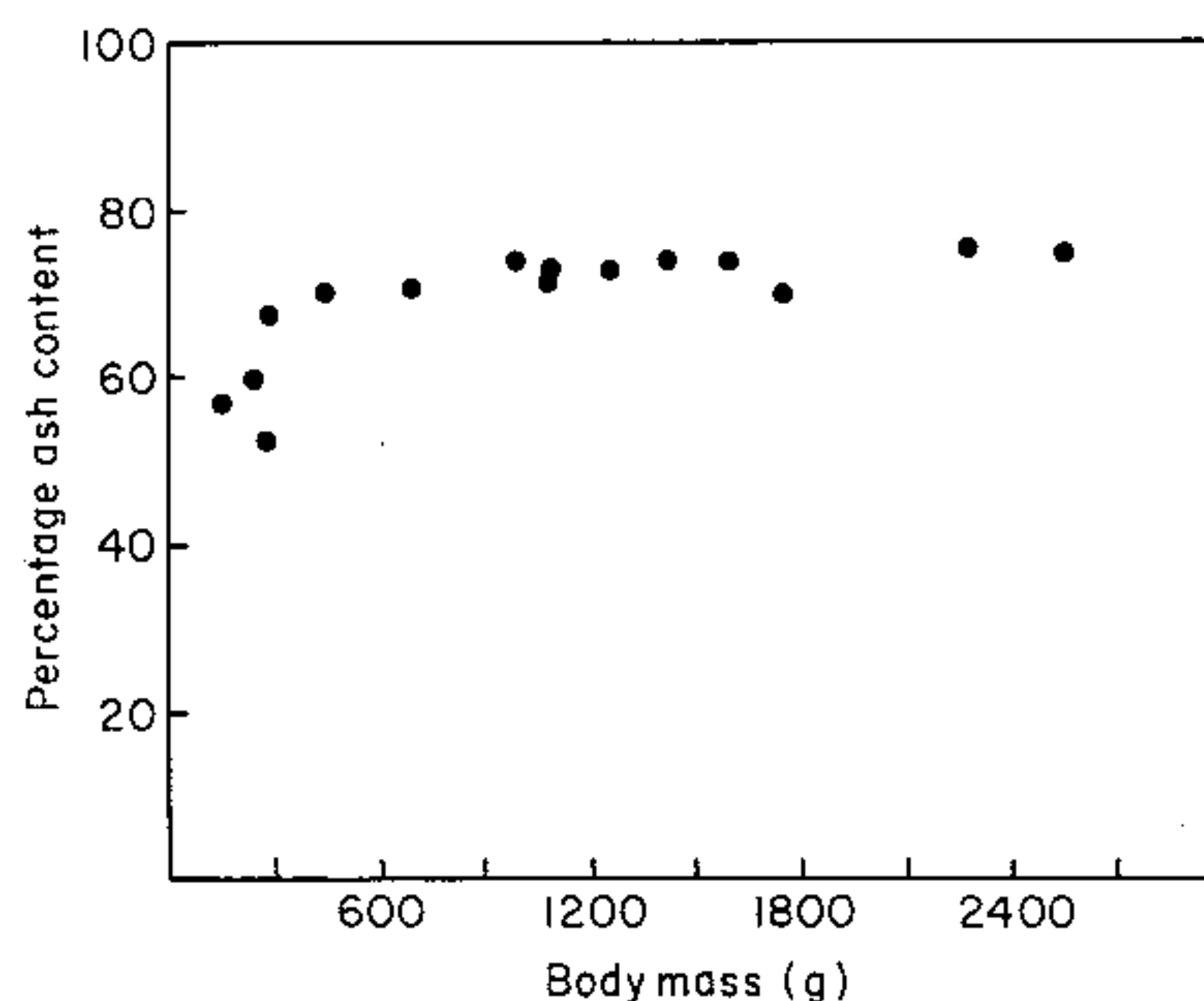


FIG. 9. Graph of per cent ash content of femur of *Lepus californicus* plotted against body mass.



metatarsal and as (body mass)<sup>1.044</sup> for the femur (Figs 6, 7). Therefore, the second moment of area is relatively larger in young animals than it is in adults. The large second moment of area in young hares will reduce the stress that the bone tissue experiences, and thus act to compensate for the low mineralization and intolerance to stress observed in juvenile bone tissue. Moreover, the negative allometry of  $I$ , acting contrary to the changes in the bone tissue, permits the relative strength of the whole bone to remain constant during early postnatal growth.

## Discussion

### *Development of locomotor function*

Initial postnatal changes in the strength and lever system of the gastrocnemius (Figs 2, 3), are such that infants, which have the same relative contractile strength as adults, would appear to be capable of greater absolute rates of acceleration than are the adults. As growth progresses the out-force of the gastrocnemius continues to increase relative to body mass, reaching a maximum in animals of 600–800 g body mass (approximately 20% adult size). Young hares of this size have estimated rates of acceleration that are more than twice those of adults (Fig. 4). Higher rates of acceleration make it possible (in theory) for juveniles to reach roughly the same terminal velocity as adults in leaps initiated from zero velocity (Fig. 5). In effect, the higher accelerational potential of juveniles would appear to compensate for the short length of their limbs and limb muscles and the smaller distance through which their muscles can shorten while delivering a high fraction of their maximum tetanic force.

Maintenance of locomotor function also appears to play a guiding role in the ontogeny of bone strength. During the first half of postnatal growth (below 1100 g body mass) the breaking moment of the third metatarsal scales isometrically to the moment imposed on the bone by the gastrocnemius. Consequently, the relative strength of the bone remains constant during this initial portion of postnatal growth (Fig. 8). However, above 1100 g the breaking moment of the metatarsal increases more rapidly than the moment of the gastrocnemius. Relative to the strength of the gastrocnemius, the metatarsal of adults is therefore stronger than that of juveniles.

The observation that bone undergoes adaptive remodelling in response to changing levels of strain (Wolff, 1870) is now strongly supported by experimental evidence (Hert *et al.*, 1972; Bouvier & Hylander, 1981; Lanyon *et al.*, 1982). Bones appear to change in shape, cross-sectional area and undergo Haversian substitution in a way that maintains the normal level of imposed strain below a critical level. Consequently, it should not come as a complete surprise that the relative strength of the metatarsal remains constant during the initial portion of postnatal growth. However, it should not be forgotten that this isometry of bone and muscle strength occurs during the period of most pronounced growth and allometry. During this period, *Lepus* experiences its highest rates of growth (Haskell & Reynolds, 1947). The mechanical advantage of the gastrocnemius decreases while the muscle experiences a relative increase in strength (Table IV). The absolute strength of the bone tissue of the metatarsal increases while the second moment of area undergoes a relative decrease. Hence, dramatic alterations appear to be requisite for the maintenance of isometry between bone and muscle strength during growth. Moreover, unlike remodelling in mature bone, where an increase

in the level of strain results in an increase in the second moment of area, mechanical adaptation in growing hares is associated with a relative decrease in the second moment of area.

The functional consequence of these early ontogenetic changes (i.e. positive allometry of muscle and bone strength, positive allometry of limb length, negative allometry of muscular mechanical advantage and negative allometry of bone second moment of area) is a rapid enhancement of running ability. The remarkable degree of cursorial ability (Hildebrand, 1974; Vorhies & Taylor, 1933; Howell, 1965) and specialization (Gambaryan, 1974; Bramble & Carrier, 1979; Carrier & Bramble, 1980) of adult hares suggests that there is very strong selective pressure on running ability. This selective pressure probably results largely from predation, and because of developmental constraints (e.g. short limbs and weak muscles) would be most severe early in ontogeny. Modifications of the ontogenetic program which circumvent these developmental constraints in such a way that locomotor ability is improved will be of selective value. The relatively large second moment of area, by lowering the stress that the weak bone tissue experiences, and the relatively large muscle mechanical advantages, by increasing the force that the weak muscles impart to the ground, compensate for restrictions that growth and development place on the locomotor system.

#### *Bone-muscle development and locomotor behaviour*

This study measured morphological, physiological and mechanical properties of a few isolated parts of a very complex muscular-skeletal system. It is assumed that the observed ontogenetic changes reflect changes that occur simultaneously in the rest of the system. The apparent high accelerational potential of juveniles and the apparent equality between juveniles and adults in parameters such as terminal velocity and breaking strength of bone, do not imply that juveniles are as competent at running as are adults. They are not. Nevertheless, the author's experience of chasing (on foot) over 300 wild jackrabbits, has convinced him that juveniles may be almost as effective at escape as are the adults.

No attempt has been made to quantify the escape behaviour of *Lepus californicus*, but certain trends were discernible in the field. The youngest animals (newborns to roughly 300 g body mass) rely heavily upon crypsis to avoid predation. Although animals only an hour old will run away if approached closely, their hops are unsteady. Hares up to 300 g can be captured by hand. Once the mass of the young hare has reached 600 g, the situation has changed and its capture can be quite difficult. Hares between approximately 600–1200 g never venture far from the ubiquitous stands of big sagebrush (*Artemisia tridentata*), that constitute the dominant herbaceous cover. Moreover, when these hares are pursued they run with an erratic, swiftly turning and darting style, attempting to disappear behind the cover of the sagebrush. In contrast, adults (animals above 1500 g) are often found foraging far from the sagebrush in open fields of grass. Once adults are flushed they run in a straight line, away from the danger, to the nearest stand of sagebrush. The straight running of adult hares differs from the erratic escape paths of juveniles and may be a consequence of adults being more able to maintain a large enough distance between themselves and their pursuers so that sharp turns are not advantageous (see Howland, 1974). Whatever the reason for this difference, when pursued by a running human or a speeding automobile, juveniles depend more heavily on abrupt changes of direction than do adults.

The cryptic behaviour of hares less than 300 g is not surprising in light of their short limbs

and muscles, weak muscles and low estimated terminal velocity. These animals do not forage for themselves, being entirely dependent on their mother's milk (Haskell & Reynolds, 1947). Also, because they are small and cryptically coloured, the tendency to remain stationary is an appropriate strategy. Above 300 g the young hares begin to supplement the milk diet with solid food, and at roughly 500 g they forage independently (Haskell & Reynolds, 1947). Animals of this size and above will be more exposed to predation. It is significant that hares of roughly this size possess the greatest calculated rates of acceleration, develop calculated terminal velocities of the same magnitude as adults, and become difficult to capture in the field. Figure 10 plots the timing of weaning and the first independent foraging against the estimated percent acceleration and terminal velocity. The ontogeny of the muscular-skeletal system seems to be programmed so that the age of independent foraging corresponds to the attainment of effective running ability.

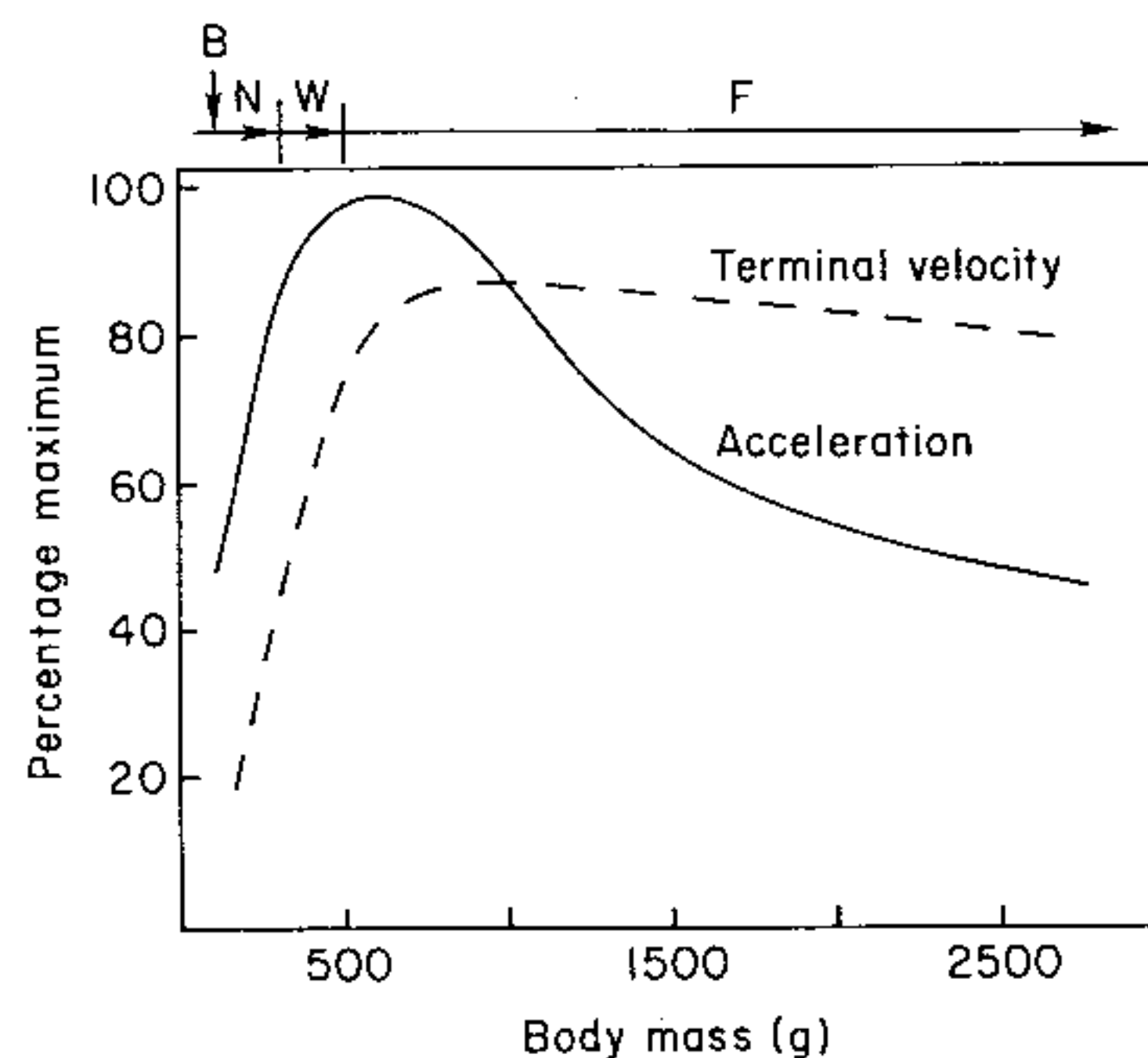


FIG. 10. Graph comparing the estimated locomotor ability of developing hares with the timing of parental care. The time line above indicates body mass at: birth (B), during the period of nursing (N), during the period of weaning (W), and the subsequent independent foraging (F), (data from Haskell & Reynolds, 1947). The plotted lines represent the estimated acceleration (Fig. 4) and the estimated terminal velocity (Fig. 5).

The erratic behaviour of the juvenile hares is consistent with the relatively high out-forces that their gastrocnemius is capable of generating. However, the reluctance of juveniles to venture far from protective cover, suggests that they may lack the endurance and the absolute running speed of the adults. Although juveniles may have greater rates of acceleration than adults and terminal velocities out of an initial leap which approximate those of adults, absolute running speed is likely to be lower in juveniles. The limb muscles of adults are longer and so will have more sarcomeres in series (Goldspink, 1968; Elliott & Crawford, 1965). Speed of muscular shortening is the product of the intrinsic speed of shortening of individual sarcomeres multiplied by the number of sarcomeres in series (Goldspink, 1977). Since in these hares, the intrinsic speed of sarcomere shortening is not likely to vary during growth (see section on contractile properties of gastrocnemius), the contractile velocities of the limb muscles of adult hares should be greater than those of juveniles. An increase in



contractile velocity during postnatal growth has been observed in mice (Close 1965*a*), rats (Close, 1964), and cats (Close & Hoh, 1967). Greater velocity of contraction will allow adults to attain and run at higher speeds than juveniles.

*Ontogenetic vs. interspecific and phylogenetic allometry*

As in the ontogeny of *Lepus californicus*, much of the size related change of shape that occurs in interspecific comparisons results from the need to maintain locomotor function. Because muscular force is dependent on the cross-sectional area of the contractile tissue (Hellam & Podolsky, 1969), an increase in size will result in a loss of strength unless there is a disproportionate increase in the muscular cross-sectional area relative to body mass. Alexander *et al.* (1981) have found that as size increases in adult mammals, the cross-sectional area of the limb muscles scales as (body mass)<sup>0.80</sup>. This is positive allometry and provides larger mammals with greater strength than would be available if geometric similarity was maintained. But for mammals to maintain mechanical similarity, even greater positive allometry would be required, with cross-sectional area of the limb muscles scaling as (body mass)<sup>1.0</sup>. Thus, larger mammals are relatively weaker. To compensate, the muscles of larger mammals act through greater mechanical advantages than the muscles of small mammals (Alexander *et al.*, 1979; Alexander, 1977; Goldstein, 1972). The calculations of Alexander *et al.* (1981) indicate that with this added mechanical advantage, the forces applied to the ground are proportional to (body mass)<sup>0.90</sup>. This is close to (although below) the exponent value of 1.0, which would be necessary to maintain mechanical similarity.

Interspecific maintenance of mechanical similarity also seems to occur with regards to the strength of bones. McMahon's (1973, 1975) model of elastic similarity, which has been successful in predicting bone proportions in Bovidae (see Alexander, *et al.*, 1979), is based on the premise that mechanical function is maintained with increase in size. Alexander's (1977) analysis of limbs of bovids has shown that the maximum stresses in bones, muscles and tendons are probably independent of body mass. Also, the breaking strength of the femur of adult gulls, as estimated by Dinnendahl & Kramer (1957), appears to maintain mechanical similarity, scaling to (body mass)<sup>1.0</sup>. In all cases studied, this isometry of bone strength relative to body mass is brought about, at least in part, by a differential thickening of the bone diameter.

Mechanical similarity seems to be maintained both ontogenetically and interspecifically, although by different means in each case. Interspecific increases in size are associated with a relative loss of whole muscle strength, and positive allometry of muscle mechanical advantage and bone diameter (above references). Ontogenetic trends are the reverse. The strength of muscle increases with positive allometry, while the mechanical advantages of muscles and the diameter of bones show negative allometry. This reversal of trends is likely to result from the differences that exist between adults and juveniles in the mechanical and physiological properties of bone and muscle tissue. The mechanical and physiological properties of adult bone and muscle tissue are relatively constant. Roughly speaking, the strength of the muscle tissue of an adult mouse is the same, on a per gram basis, as the strength of the muscle tissue of an elephant (Hill, 1950; Schmidt-Nielsen, 1977). In addition, the strength of bone tissue is independent of body size (Biewener, 1982; Alexander, 1977; Currey, 1970). Consequently, as size is increased interspecifically, mammals must alter their shape to avoid substantial decreases in parameters which are controlled by area to volume relationships. On the other



hand, the rapid growth of mammals requires mechanical and physiological changes in bone muscle. The bones and muscles of a newborn mammal are not at all like those of an adult. As a result, the changes in shape, muscle physiology and bone mechanical properties that maintain locomotor function in mammalian ontogeny are very different from those that maintain locomotor function in interspecific increases in size.

This difference could have significant bearing on mammalian phylogeny. Since the ontogeny of certain musculo-skeletal parameters have a "trajectory" (Alberch *et al.*, 1979) that is very different from the interspecific trajectory, then it is unlikely that mammalian phylogenetic change in these parameters could be produced by simple displacement along the ontogenetic trajectory, as in progenesis or hypermorphosis (terminology of Alberch *et al.*, 1979). Shea (1981) has found different scaling of body proportions between ontogeny and interspecific increases in size in the great apes, and has come to a similar conclusion.

It is more reasonable to suppose that, in mammals, phylogenetic changes in the muscular-skeletal system result from adjustments in the rate of change of one parameter relative to another (i.e. neoteny or acceleration; Alberch *et al.*, 1979), or of adjustments of the period in ontogeny during which the change occurs (i.e. displacement; Alberch *et al.*, 1979). In this context it is interesting that mammalian growth is characterized by allometric rates that change during ontogeny. This is clearly indicated by the inability of the power equation to describe mammalian growth (Gould, 1966). In *Lepus* ontogenetic changes in the rate of change occur for bone lengths, muscle force, muscle mechanical advantage, and bone stress and modulus of elasticity. This is due to a cessation of change in these parameters while muscle mass and body mass continue to increase. Variation in the rate of change of one parameter relative to another has now been observed during the growth of lagomorphs (this study), primates (Shea, 1981; Lumer & Schultz, 1941, 1947) and rodents (Green & Fekete, 1933). Changes in the allometric exponent have also been observed in the growth of the House wren (Huggins, 1941). Therefore, it is reasonable to propose that much of the change in the musculo-skeletal system that mammals have undergone during phylogeny has been brought about by adjustments in the rate of change of one parameter relative to another (neoteny or acceleration).

This is in marked contrast to the probable mode of phylogenetic change in the muscular skeletal system of reptiles and amphibians. Dodson (1975) stresses that during the growth of *Alligator* ontogenetic changes of shape are not different from phylogenetic changes of shape. He states "no changes have been recognized in ontogeny by which it may be unequivocally identified. There is nothing about a 150 mm skull of *Alligator* that marks it as a small individual of a large species rather than a large individual of a small species". Such a similarity between ontogenetic and interspecific comparisons has also been suggested for certain body proportions in anurans (Emerson, 1978) and land tortoises (D. M. Bramble, pers. comm.). Also contrasting with the ontogeny of *Lepus* are the changes in muscle lever systems and bone diameters. As *Alligator* matures the mechanical advantage of the caudifemoralis and the posteroventral pectoralis muscles increases (Dodson, 1975). In addition, the limb bones become relatively thicker as the reptile matures. These trends of increasing mechanical advantage and bone thickness during ontogeny appear to parallel the phylogeny of both reptiles and mammals, but do not parallel mammalian ontogeny.

It is unclear why the ontogeny of the muscular skeletal system of *Aligator* should differ from that observed in mammals. However, one factor that probably plays a role is the effect that the difference in the rate of growth of mammals and reptiles has on bone and muscle

development. Mammals have determinate growth. They grow rapidly, reaching the adult size and proportions relatively early in life. Reptiles, on the other other hand, grow continuously throughout their lives, at rates that are roughly an order of magnitude below those of mammals (Case, 1978). This difference will limit the options available to the two groups during ontogeny. For instance, the speed of growth controls not only the quantity of bone deposited per unit of time but also the type of bone deposited (Enlow, 1969; Ricqlès, 1976). The bone tissue of mammals, beginning early in life, typically changes from woven to lamellar to haversian architecture (Currey, 1977; Torzilli *et al.*, 1982), undergoing extensive secondary substitution and cancellous remodelling (Ricqlès, 1976). In contrast, the bone tissue of reptiles undergoes very little secondary substitution or cancellous remodelling, remaining relatively constant throughout life (Enlow, 1969; Ricqlès, 1976). This relative lack of ontogenetic change in the material properties of reptilian bone tissue is similar to the uniformity of skeletal tissue observed among adult mammals and may restrict ontogenetic patterns of skeletal allometry to those observed in interspecific comparisons. The rapid growth of mammals may necessitate a greater plasticity in the ontogeny of bone.

### Summary

During the postnatal growth of *Lepus californicus*, hind limb length and gastrocnemius contractile distance undergo positive allometry, scaling as (body mass)<sup>0.39</sup> and (body mass)<sup>0.41</sup>, respectively. The mechanical advantage of important locomotor muscles decrease during growth, being absolutely less in adults than in younger hares. In particular, the mechanical advantage of the gastrocnemius scales as (body mass)<sup>-0.12</sup>. This, in combination with positive allometry of gastrocnemius contractile force (proportional to (body mass)<sup>1.23</sup>) gives juveniles (500–1200 g) higher estimated rates of acceleration than adults, and estimated terminal velocities (out of leaps initiated from zero velocity) of the same magnitude as adults. In addition, during the first half of postnatal growth mechanical similarity is maintained between the breaking moment of the metatarsal (proportional to (body mass)<sup>1.50</sup>) and the moment imposed on the metatarsal by the gastrocnemius (proportional to (body mass)<sup>1.54</sup>). Consequently, the relative strength of the bone remains constant during this initial portion of postnatal growth. The observed ontogenetic changes contribute to the rapid enhancement of locomotor ability, such that young hares of only 20% adult body size are effective at predator escape. Moreover, the ontogeny of the muscular-skeletal system seems to be programmed so that the age at which the young hare must forage independently corresponds to the attainment of running ability.

Changes of shape and physiology associated with increasing size in the ontogeny of *Lepus* differ from analogous changes in mammalian phylogeny and reptilian ontogeny. It is suggested that these differences result from a basic dissimilarity between the bone and muscle of growing mammals as compared to adult mammals and growing reptiles. The bone and muscle of a growing mammal changes in mechanical and physiological character as the animal matures. In contrast the bone and muscle of adult mammals and growing reptiles is relatively uniform in physiological and mechanical properties.

I wish to express my gratitude to Dennis M. Bramble without whose continual support, assistance and open-mindedness this project could not have been completed. This work also benefited from the comments of Sharon Emerson, Joe Fetcho, Carl Gans, William Gray, James Lords, Paul Maderson, Leonard Radinsky and one anonymous reviewer. James Lords, Kenneth Devries and Peter Fordyce

rendered much appreciated technical assistance in the measurement of muscle and bone strength. Joyce Nikolai's knowledge of computers greatly simplified the data analysis. Joel Russell and John Shaw generously assisted in the collection of some of the data. For helping in the collection of hares, I thank Charles Stoddart, Frederick Knowlton, Susan Beck, Walter Mulbry and Joel Russell.

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