

The relationship between maximum jumping performance and hind limb morphology/physiology in domestic cats (*Felis silvestris catus*)

Michelle A. Harris^{1,*} and Karen Steudel²

¹Biology Core Curriculum, University of Wisconsin-Madison, 307 Noland Hall, 250 N. Mills Street, Madison, WI 53706, USA and ²Department of Zoology, University of Wisconsin-Madison, Birge Hall, 430 Lincoln Drive, Madison, WI 53706, USA

*Author for correspondence (e-mail: maharris@facstaff.wisc.edu)

Accepted 23 September 2002

Summary

A critical role of functional morphology is to demonstrate form–function relationships that can then be used by evolutionary biologists to infer the evolutionary history of the structure in question. Tests of theoretical expectations about the effects of many aspects of morphology/physiology on locomotor performance have had very mixed results. If systems such as jumping can be shown to reliably predict performance from morphology, this would provide a foundation upon which hypotheses for the evolutionary origin of certain morphologies can be generated. The present study examined whether a relationship exists between maximum takeoff velocity (TOV) and several carefully chosen morphological and physiological traits in domestic cats (*Felis silvestris catus*). Based on the contributions of extensor muscle work to increasing the kinetic and potential energy of the center of mass (CM) during takeoff, we predicted that maximum

TOV would be dependent upon relative limb length, relative extensor muscle mass, body mass and the percentage of fast-twitch muscle fibers. Both maximum TOV and this series of traits were measured in 18 cats. We found that variation in cat maximum TOV is significantly explained by both hind limb length and fat mass relative to lean body mass, but not by extensor muscle mass relative to lean mass or fast-twitch fiber content. The effect of body fat mass is pervasive because it reduces the proportion of muscle mass/body mass and thus increases the muscle work invested in increasing the CM potential energy as compared with kinetic energy during takeoff.

Key words: takeoff velocity, muscle, morphology, physiology, form–function, locomotion, jumping, cat, *Felis silvestris catus*.

Introduction

Functional morphological studies increase our overall understanding of organismal design by explaining the functional capacities of structural features (i.e. the ‘how does it work?’ questions regarding morphological features; Bock, 1988). Some workers (Cummins, 1975, 1983; Amundson and Lauder, 1994) consider this non-purposive concept of function to be functional morphology’s main contribution. A more widely held view is that empirically established structure–function relationships provide a foundation for evolutionary investigations of the existence of certain structural features (the ‘why is it designed this way?’ inquiries; Bock and von Walther, 1965; Bock, 1988; Galis, 1996; Streelman, 1997). This etiological conceptual value of functional morphology is based on the premise that morphology determines performance and that natural selection will occur based on performance (Bock and von Walther, 1965; Arnold, 1983; Webster and Webster, 1988; Emerson and Arnold, 1989; Garland and Carter, 1994; Garland and Losos, 1994).

Relationships between morphology and locomotor performance

Although theoretical expectations about the relationship between limb design and locomotor performance have been available for many years (e.g. Hall-Craggs, 1965; Alexander, 1968, 1977; Gambaryan, 1974; Bennet-Clark, 1977; Alexander and Jayes, 1983; Gabriel, 1984; Hildebrand, 1985), only recently have these expectations been subjected to rigorous empirical study. Much of the impetus for this work resulted from Arnold’s (1983) conceptual model of natural selection gradients, which proposed that performance is an intermediate step between morphology and fitness.

The empirical demonstration of relationships between morphological characters and their predicted functions can be problematic. Recent tests of theoretical expectations about the effects of many aspects of morphology/physiology on locomotor performance have had very mixed results. If a system is found that reliably predicts locomotor performance from limb morphology, it will allow us to produce hypotheses

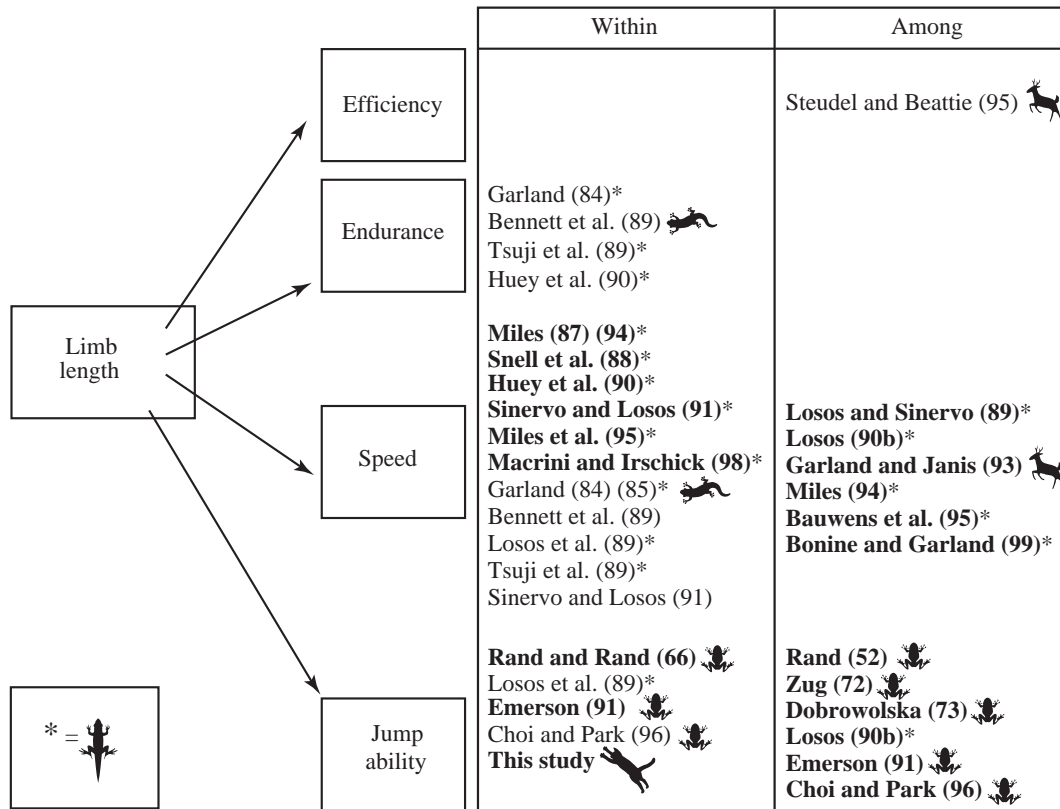


Fig. 1. Summary of studies of the relationship between limb length and various locomotor performance categories in terrestrial vertebrates. The year of each study is shown in parentheses. Studies shown in bold represent reports of significant relationships between limb length and designated locomotor performance; those shown in regular font did not find significant relationships. Studies designated with an asterisk used lizards as the model species. The animals used in the remaining studies (salamanders, large ungulates, frogs and cats) are indicated by silhouettes. Note that the majority of the investigations of the limb-length–jump performance relationship have used frogs as subjects, and that the current study is the only one to use an endothermic system.

about evolutionary selective pressures that have affected limb design.

Increasing limb length is thought to positively affect locomotor efficiency, endurance and speed and to increase jumping ability. To date, however, all studies involving limb skeletal morphology and endurance or efficiency have reported no statistically significant correlations (e.g. Garland, 1984; Garland and Else, 1987; Bennett et al., 1989; Tsuji et al., 1989; Huey et al., 1990; Steudel and Beattie, 1995). Many, although not all, studies of the relationship between limb morphology and maximum speed have demonstrated positive correlations. All interspecific studies of maximum speed (Losos and Sinervo, 1989; Losos, 1990b; Garland and Janis, 1993; Miles, 1994; Bauwens et al., 1995; Bonine and Garland, 1999) and some intraspecific studies of the limb-length–speed relationship (Miles, 1987, 1994; Snell et al., 1988; Huey et al., 1990; Sinervo and Losos, 1991; Miles et al., 1995; Macrini and Irschick, 1998) have produced positive results, while other intraspecific studies of this relationship have not (Garland, 1984, 1985; Bennett et al., 1989; Losos et al., 1989; Tsuji et al., 1989; Sinervo and Losos, 1991; see Fig. 1).

Searches for a correlation between morphology and jump

distance have generally fared better in both interspecific (Rand, 1952; Zug, 1972; Dobrowolska, 1973; Losos, 1990b; Emerson, 1991; Choi and Park, 1996) and intraspecific (Rand and Rand, 1966; Emerson, 1991; see Fig. 1) examinations; however, see Losos et al. (1989) and Choi and Park (1996). These leaping studies have used frogs or lizards as subjects, but the present study uses a novel mammalian experimental system, the domestic cat, to further elucidate the relationship between jump performance and morphology.

Jump performance depends on takeoff velocity

Previous studies on jumping have invoked ballistics formulae to predict that the velocity with which an animal's center of mass (CM) leaves the ground determines the distance or height that it will travel after leaving the ground (Hill, 1950; Hall-Craggs, 1965; Alexander, 1968; Bennet-Clark, 1977; Emerson, 1978, 1985, 1991; Gabriel, 1984). The direction of this movement is determined by the angle of takeoff. Marsh (1994) concluded that jump performance can indeed be accurately predicted using ballistics equations if horizontal and vertical distances traveled by the CM before takeoff are also included. Because jump distance and height are largely dependent on takeoff velocity (TOV), morphologies predicted

to optimize TOV are the focus of the current study. TOV should also be important for cats, which are proficient predators that often hunt by pouncing on an unsuspecting prey item after springing from a stationary crouch (Turner and Meister, 1988). The faster the takeoff, the more quickly the cat reaches its prey.

Mechanical energy and takeoff velocity

TOV is determined by the mechanical work generated from hind limb extensor muscles during the time from the deepest crouch to the point of last contact with the ground (Alexander, 1968; Marsh, 1994). This extensor muscle work is used to increase both the kinetic and potential energy of the CM as it is lifted from its original position to its height at takeoff (h_t) (Marsh, 1994; Peplowski and Marsh, 1997). Extensor muscle work can be thought of as the product of the extensor muscle mass (m') and the work done per unit extensor muscle mass (k):

$$\text{muscle work} = km' . \tag{1}$$

Because the total amount of work done by extensor muscles during takeoff involves changes in both kinetic and potential energy, it can be represented as:

$$km' = 1/2mv^2 + mgh_t , \tag{2}$$

where m is body mass, v is TOV and g is gravitational acceleration. In a vertical jump where the optimal takeoff angle is 90° , h_t can be approximated by the length of the outstretched hind limb (l) at takeoff. The work per unit mass (k) should be proportional to the abundance of fast-twitch fibers in a muscle, as these large-diameter fibers contract more quickly and forcefully than do slow fibers (Murphy, 2000). Myosin heavy chain (MHC) Type IIx composition of a fiber (%MHC IIx) will be considered an estimate of work done per unit muscle mass because its relationship with maximum contraction velocity is well established (Burke et al., 1973; Talmadge and Roy, 1993; Kelly and Rubinstein, 1994; Fauteck and Kandarian, 1995). Studies of humans also provide good empirical evidence that increasing amounts of fast-twitch muscle fiber increase skeletal muscle power and individual jump performance (Viitasalo et al., 1981; Tihanyi et al., 1982; Bosco et al., 1983; Melichna, 1990; Matolin et al., 1994; Hakkinen et al., 1984).

After substituting %MHC IIx for k and substituting hind limb length (l) for h_t , equation 2 can be solved for TOV:

$$v^2 = 2(\%MHC IIx)(m'/m) - 2gl . \tag{3}$$

Based on equation 3, TOV should be increased by increasing MHC IIx fiber content and higher extensor muscle mass but should be decreased by greater body mass and longer hind limbs. Under this model, hind limb length is predicted to negatively affect TOV, because longer legs increase the work done to raise the CM as potential energy is increased before takeoff.

Ballistics and takeoff velocity

Most previous studies have expected increasing hind limb length to have a positive influence on leaping distance

(Alexander, 1968; Bennet-Clark, 1977; Emerson, 1978, 1985), which is the opposite of the prediction in equation 3. This expectation is based on the ballistics formula:

$$v^2 = 2al , \tag{4}$$

where a is the acceleration generated while the animal is in contact with the ground. In an animal where the jump force is produced solely by the hind limbs, l is assumed to estimate the distance through which acceleration is generated. The longer the hind limb, the greater the distance through which the CM is accelerated, and thus the greater the velocity at takeoff. Equation 4 assumes that acceleration remains constant during the takeoff period, although empirical evidence indicates that this assumption is incorrect. For example, Marsh and John-Alder (1994) used simultaneous film and force plate measurements of a jumping frog to show that the velocity of the CM increases slowly for approximately the first 50 ms of a 120 ms takeoff period and then increases more rapidly until the time of takeoff. Nonetheless, the general relationship between TOV and the ability of muscles to produce acceleration, however variable, seem clear.

There is considerable empirical evidence that lizards and frogs with longer hind limbs do indeed jump further than those with shorter hind limbs (Rand, 1952; Rand and Rand, 1966; Zug, 1972; Dobrowolska, 1973; Emerson, 1991; Choi and Park, 1996; Losos, 1990a,b; however, see Losos et al., 1989). These results suggest that increasing limb length does positively affect TOV despite changing acceleration rates during the takeoff period and the increasing investment made by extensor muscles in raising potential energy. The effect of hind limb length on TOV can be seen more clearly if we combine equations 2 and 4:

$$\text{muscle work} = mla + mlg . \tag{5}$$

Longer hind limbs should increase both the kinetic energy and potential energy of the CM during the takeoff period. Perhaps the effect of hind limb length on kinetic energy outpaces its effect on potential energy, particularly during the latter portion of the takeoff period.

Takeoff velocity and body fat

The positive effect of longer limb length on TOV will be decreased, however, in animals with high body fat contents. The hind limb extensor muscles in an animal with high body fat levels will expend more work in increasing the body's potential energy during takeoff than would the muscles of a leaner animal of equal body mass and hind limb length. Although previous jump performance studies report significant positive correlations between jump distance and body size in both frogs (Zug, 1978; Emerson, 1978, 1991; Marsh, 1994) and lizards (Pounds, 1988; Losos et al., 1989; Losos, 1990b; Bels et al., 1992, although see Choi and Park, 1996), none of these studies present data on body fat levels in their subjects. It is likely that body fat levels were uniformly low in the animals used such that 'body size' largely represented lean mass. Little is known about the extent of body fat in wild carnivores

(Pond, 1978). Studies on other species suggest considerable variability. Sherry (1981) reports a 17% seasonal weight change in red deer stags *Cervus elaphus*, and Scollay (1980) reports a 14% weight change for male squirrel monkeys *Saimiri sciureus* during the breeding season. Prestrud and Nilssen (1992) present data on wild trapped arctic foxes *Alopex lagopus* showing fat content as percent skinned carcass mass, averaging around 10% during the summer but over 20% during winter months. Winter data include many values between 20% and 30% fat, with one value over 40%. Furthermore, we would expect that the increased weight of female cats during pregnancy would affect jumping performance in a manner similar to that of body fat. Thus, the percentage of mass in most of our laboratory specimens that is not due to lean mass is not seriously incompatible with that seen in the wild.

The present study

In the present study, we investigate the morphological/physiological determinates of among-individual variation in domestic cat jump performance, measured by maximum TOV. We looked for correlates between TOV and body mass, hind limb length, extensor muscle mass, body fat content and the percentage of fast-twitch muscle fibers in the lateral gastrocnemius muscle in 18 individuals. It was hypothesized that individual cats would show significant variation in their TOVs, and that this variation would be explained by differences in the morphological/physiological variables listed above. Specifically, we predicted that increasing %MHC IIx fibers and increasing hind limb length and extensor muscle mass relative to lean mass would be positively related to maximum TOV, while increasing body fat mass relative to lean mass would negatively affect TOV. We also estimated the jump motivation level for each cat and tested whether this had a significant effect on TOV (M. A. Harris, K. Steudel and J. Bachim, in preparation).

Materials and methods

Considerable effort was made to use valuable research animals in the most efficient and responsible manner possible. Eighteen adult cats *Felis silvestris catus* were donated to the study by the UW-Madison Psychology Department. These cats were otherwise scheduled for euthanasia. The skeletons and their respective morphological measurement records were donated to the UW Zoological Museum, where they are documented as voucher specimens and are available for examination by museum guests.

Five (two males and three females) of the 18 cats donated by the Psychology Department were part of a study in which lesions of the visual cortex were made to one side of the brain (a unilateral lesion). The purpose of that research was to study the method of physiological compensation by remaining brain areas after early visual cortex damage. Four of these cats received this lesion when they were eight weeks old, and the remaining cat received the lesion when she was only one day old. Because the jump performance of these lesioned cats was

not significantly different from non-lesioned animals, and because there was no difference in the amount or intensity of training required to induce maximal jumps between the two groups, no distinction was made between them in the analyses presented here.

Test subjects

A total of 18 domestic cats (13 intact females and five neutered males), ranging in body mass from 2.66 kg to 7.93 kg, was used in this study. All cats were at least two years old and not more than 10 years old, were in excellent physical health and were accustomed to frequent human contact. Cats were housed in metal wire mesh kennels (1.9 m high × 1.6 m long × 1.1 m wide) with concrete flooring and had access to resting boxes and wooden shelves within these cages. They were provided with Science Diet cat food (Hill's company, Topeka, KS, USA) and water *ad libitum* until 18–24 h before a jump training or video-taping session (see below).

Jump training

Between three and six sessions were devoted to acclimating each cat to lab surroundings before jump training was initiated. During these 20–45 min acclimation sessions, cats were allowed to roam freely in the lab and had access to canned, moist cat food. Cats were not allowed inside the jump enclosure during these sessions.

Each cat was subjected to a schedule of jump training sessions before maximum jumps were recorded on video tape. Between two and seven jump training sessions, each 20–60 min long, were required to train each cat to jump maximally. Cats participated in one jump training session per day. Food was withheld from the cats 18–24 h before each of these sessions. After each jump training session, animals were allowed access to their food for at least 60 min before it was again removed in anticipation of the following day's lab session, if one was scheduled.

Cats were trained to jump inside a rectangular enclosure (2.4 m high × 0.9 m long × 0.4 m wide; see Fig. 2) made of Plexiglas and masonite. This enclosure limited the direction and height of each jump. Cats were introduced to the enclosure through a trap door and were then placed on an adjustable takeoff platform inside the enclosure. Cats jumped from this takeoff platform to a stationary landing box (0.30 m × 0.45 m × 0.40 m) mounted on the upper left edge of the enclosure. The position of this platform, and thus the jump height, was adjustable.

A training protocol was designed such that placement inside the jump enclosure stimulated jump behavior. In an effort to obtain maximal jumping performances, rewards were offered as soon as each cat successfully jumped to the landing box. Rewards were canned cat food accompanied by affection (petting) from an observer and, ultimately, removal from the enclosure. If jumps were not spontaneous, the takeoff platform was shaken and/or the cat was squirted with water until it jumped to the landing box. In this way, the takeoff platform was presented as an unpredictable, unstable environment,

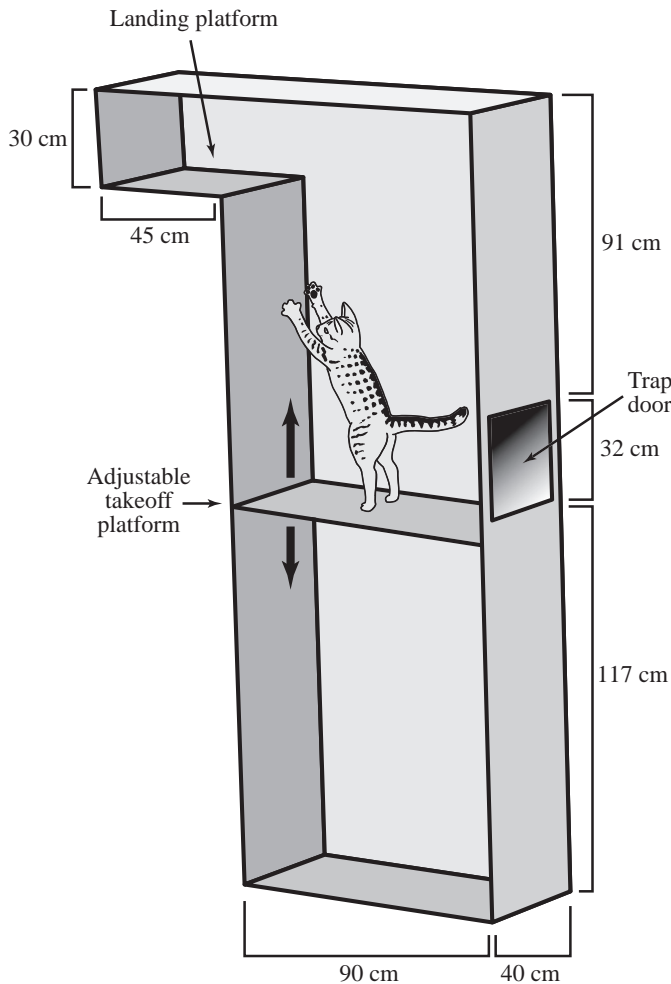


Fig. 2. Diagram of jump enclosure. Cats took off from an adjustable platform and jumped upwards to the stationary landing box.

while the landing box represented a safe haven for each cat where rewards were available. Perhaps most importantly, each cat learned that jumping to the landing box was the only means of exit from the enclosure.

After each jump, cats were allowed to eat food and/or receive affection for approximately one minute before being removed from the landing box. Cats that ignored the food and affection attempts, and instead tried to jump out of the landing box, were removed immediately. The takeoff platform was then lowered by 5–10 cm, and the cat was returned to the takeoff platform through the trap door. This procedure continued until the cat had made between five and 10 total jumps or until the cat struggled in an obvious way to reach the landing box. No more than 10 jumps per session were allowed in order to minimize fatigue effects. Cats made approximately 10 jumps before becoming visibly fatigued. During subsequent sessions, the takeoff platform was lowered to within 5 cm of each cat's previous maximum jump, and the process continued until an approximate maximum height was achieved (i.e. the last height at which the cat successfully made it to the landing box, but only after an obvious struggle).

Measurement of takeoff velocity

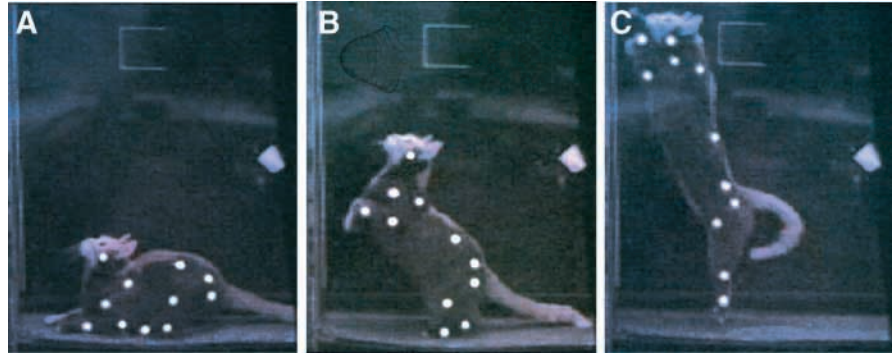
At least 24 h after an approximate maximal height was determined for each individual during training, each cat was video-taped jumping to this height. Approximate maximal heights were either matched or exceeded on video-taping days. Maximum vertical jump height for each cat was defined as the last successful jump to the landing platform before consistent misses at the next greater height (i.e. just 5 cm higher). TOV was measured from high-speed videos of the takeoff portion of each cat's maximum jump. The maximum TOV for each cat was measured on two different days in order to determine the repeatability of each individual's performance. The highest TOV of these two days was considered to be the maximum performance. Cats performed no more than 10 jumps on video-taping days and were weighed within 24 h of their maximal jumps.

The movement of reflective markers placed on the cat's body was used to measure the maximum velocity of overall body center of mass (CM) position during the takeoff period. These movements were recorded by a high-speed (200 frames s^{-1}) video camera. Each cat was labeled with reflective dots to indicate the location of the following anatomical landmarks: mid zygomatic arch (head), spinous process of scapula at anterior border, humerus greater tuberosity (shoulder), lateral epicondyle (elbow), styloid process of ulna (wrist), thoracic–lumbar vertebral junction (T13), iliac crest, greater trochanter (hip), lateral epicondyle of the femur (knee), lateral malleolus (ankle) and metatarso–phalangeal joint (5th MT) (see Fig. 3).

At least one day prior to video-taping, the 11 anatomical landmarks were shaved, external measurements of body segments between anatomical landmarks were made, and the left side of the cat's body was dyed black. Body segment measurements were used to calculate the CM for each segment (see below). Cats were anesthetized with halothane gas during this process. The reflective dots were attached to the marked anatomical points using rubber cement paste on the day of video-taping. A black 'calibration' backdrop inside the jump enclosure was used to convert video digitization units into real distance measures. The takeoff platform was narrowed so that cats jumped perpendicular to the camera.

Spotlights illuminated the reflective dots on the cat's body as it jumped. Videos were taken using a Nac MOS-TV 200/60 high-speed video camera. The x - y coordinates of each dot were manually digitized by projecting the video image onto a piece of graph paper using a stop-action VCR and liquid-crystal display (LCD) projector. Videos were digitized at a rate of 100 frames s^{-1} . A customized computer software program was written to compute the overall body CM position from the mass of individual body segments, the CM location for each of these segments, and the position of segment CMs over time. Regression equations reported by Hoy and Zernicke (1985) to predict segment masses from body mass and segment length in domestic cats were used in this algorithm. The location of this overall CM was located at three key positions during the jump: the last

Fig. 3. Digital video frames showing typical stages of the takeoff period preceding cat jumps: (A) deep crouch, (B) mid-takeoff and (C) full extension of torso and hind limb at takeoff. Note the three calibration lines (joined, forming two right angles) in the background and the reflective dots designating the 11 anatomical landmarks whose movement was used to calculate maximum takeoff velocity (TOV).



frame showing hind paw contact with the ground ('takeoff'), and one frame before and one frame after takeoff. TOV was defined as the change in CM position over the three frames surrounding and including takeoff (a 0.02 s time span).

Hind limb dissections and body fat measurement

A standard euthanasia procedure was used in which each cat was first anesthetized with halothane gas. An injection of sodium pentobarbital was then administered intravenously in the femoral vein until all respiratory and cardiac activity had ceased. Hind limb muscles were dissected and measured within 2 h of euthanasia.

The three hind limb muscles analyzed in this study were the semimembranosus (hip extensor), the vastus lateralis (knee extensor) and the lateral gastrocnemius (ankle extensor) (Fig. 4). All of these muscles have been shown to be electrically active during cat jumps (Zomlefer, 1976; Smith et al., 1977; Zomlefer et al., 1977; Walmsley et al., 1978; Zajac et al., 1981, 1983; Zajac, 1985; Abraham and Loeb, 1985). These muscles were removed from the right leg. They were separated and cut at the termination of muscle fibers at the origin and insertion, and the mass of each muscle was recorded. Dissected muscles were placed on ice in a standard freezer until all dissections were completed and were then transferred to a -80°C freezer and stored until fiber type analysis. The individual masses of these three muscles were summed to give total muscle mass. We chose to use these three muscles rather than all of the extensor muscles because each of the three chosen muscles is a major extender of its respective joint and each is easily dissected.

The entire left limb was removed by cutting through the ilio-sacral and pubic articulations. After removal of all muscles and tissues from the leg, the lengths of the femur, tibia, tarsals and third metatarsal were recorded and summed to give a total hind limb length value. After removal of the left leg and the three extensor muscles from the right leg, the percent fat content of the carcasses was measured using a DPX-L X-ray bone densitometer (version 1.5g, copyright 1988–95, Lunar Corp., Madison, USA). Fat mass was calculated for each cat as the product of % body fat and whole body mass. Lean body mass was computed by subtracting fat mass from whole body mass.

Myosin heavy chain analysis

The MHC Type IIB isoform fibers are fast-twitch and develop the largest tetanic tension in comparison with the Type I slow-twitch and Type IIa fast-twitch, moderate-tension fibers (Burke, 1994; Kelly and Rubinstein, 1994). Talmadge et al. (1996) found that the IIx isoform, rather than the IIB isoform, is present in cat limb muscles. In cats, therefore, the percentage of MHC Type IIx isoform in extensor muscles should be correlated with jump performance.

The lateral gastrocnemius muscle was chosen for fiber type analysis because it is known to be activated during the cat jump takeoff period (Smith et al., 1977; Abraham and Loeb, 1985)

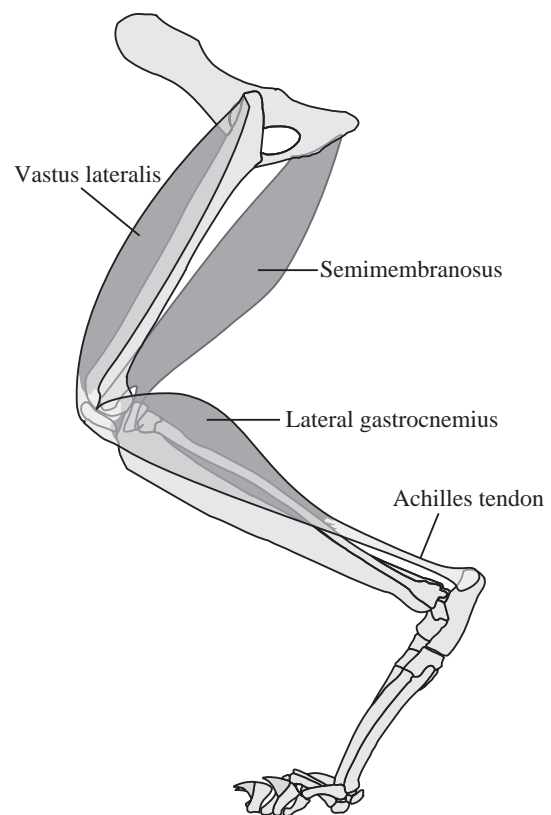


Fig. 4. Diagram of the left hind limb bones of a cat showing the three extensor muscles measured in this study: semimembranosus (hip extensor), vastus lateralis (knee extensor) and lateral gastrocnemius (ankle extensor).

and is known to contain all three MHC types. The most predominant is the Type IIX isoform; mean fiber type percentages reported for cats are between 66% and 72% (Braund et al., 1995; Talmadge et al., 1996). In this study, the lateral gastrocnemius muscles from each cat were prepared for electrophoretic separation in the following manner: the middle one-third, cross-sectional portion of each muscle was dissected, quick-frozen in liquid nitrogen, and smashed into smaller pieces with a hammer. These pieces were then immersed in more liquid nitrogen and ground into a fine powder with mortar and pestle. Muscle powder was added to chilled rigor buffer solution (5 mmol l⁻¹ KCl, 2 mmol l⁻¹ EGTA, 2 mmol l⁻¹ MgCl₂, 2 mmol l⁻¹ NaN₃, pH 7.2) to produce a final concentration of approximately 0.3 mg myofibrillar protein ml⁻¹. This protein solution was added to urea-thiourea sample buffer (8 mol l⁻¹ urea, 2 mol l⁻¹ thiourea, 0.05 mol l⁻¹ Tris, pH 6.8), 75 mmol l⁻¹ DTT (dithiothreitol), 3% SDS (sodium dodecyl sulfate) and 0.05% bromophenol blue to produce a final concentration of approximately 0.15 µg myofibrillar protein µl⁻¹. Samples were boiled at 100°C for 3 min and stored at -70°C.

The three MHC isoforms present in cat skeletal muscle were separated by pulse electrophoresis in SDS-polyacrylamide (SDS-PAGE) gels using a protocol modified from Talmadge and Roy (1993). All gels were run in vertical slab gel units (Hoefer SE 600, Pharmacia Westshore Technologies, Muskegon, MI, USA) using ECPS 3000/150 power supplies (Pharmacia). Gels were 18 cm × 16 cm and were 0.75 mm thick. The stacking gel was composed of 4% (w/v) acrylamide, with an acrylamide:*N,N'*-methylene-bisacrylamide (bis) ratio of 50:1, deionized water, 70 mmol l⁻¹ Tris (pH 6.8), 0.4% (w/v) SDS, 30% (v/v) glycerol, 4.0 mmol l⁻¹ EDTA, 0.04% (w/v) ammonium persulphate (APS) and 0.36% (v/v) TEMED (*N,N,N',N'*-tetramethylethylenediamine). The separating gel consisted of 9% (w/v) acrylamide, with bis cross-linking of 1.5% (ratio 67:1), deionized water, 200 mmol l⁻¹ Tris (pH 8.8), 0.4% (w/v) SDS, 30% (v/v) glycerol, 100 mmol l⁻¹ glycine, 0.03% APS and 0.15% TEMED. Polymerization of these gels was initiated with the TEMED and APS. The electrode buffer was the same for both upper and lower reservoirs and consisted of 0.38 mol l⁻¹ glycine, 0.05 mol l⁻¹ (w/v) Tris, 0.01% (w/v) SDS and deionized water (pH 8.9; Talmadge and Roy, 1993). The upper buffer was supplemented with 0.2 mmol l⁻¹ DTT immediately before the start of electrophoresis. Gels were run at constant current (13 mA) for 32 h using a pulse unit connected to a Hoefer model SE600. Pulse cycles of 20 s on/off were used, resulting in an overall variation of voltage between 18 mV and 510 mV. Temperature remained constant at 10°C for the duration of the electrophoresis. Gels were stained with silver and scanned with a BioRad Imaging Densitometer (Model GS-670; Pharmacia Westshore Technologies).

MHC isoforms were quantified using Molecular Analyst (version 1.4) software (Pharmacia Westshore Technologies). Relative proportions of each isoform were calculated by dividing the optical density of each individual isoform band by the summed optical density of all three bands within each

column (i.e. by the total MHC isoform content within each individual cat). The proportion of each MHC isoform is thus expressed as the percentage that it contributes to the total area of MHC bands (Fauteck and Kandarian, 1995).

Statistical analysis

Linear correlation analyses and paired *t*-tests were used to compare maximum velocities on days 1 and 2 to assess performance repeatability. Fat mass was calculated as % body fat multiplied by body mass, and lean body mass was calculated as body mass minus fat mass. Significant correlations were found between lean body mass and hind limb length ($r=0.709$, two-tailed $P=0.001$), muscle mass ($r=0.917$, $P<0.001$) and fat mass ($r=0.739$, $P<0.001$). To examine the effects of these three variables independent of body size, 'lean' mass residuals were calculated from a linear regression of each variable vs. lean body mass.

Multiple regression analyses were performed to develop a model containing variables that together explain the most variation in TOV. Lean mass residuals for hind limb length, muscle mass and fat mass were entered, together with lean mass and %MHC IIX content, as independent variables. A backwards elimination criterion was then used to eliminate variables that did not explain a significant amount of variation. Kinetic energy was calculated using whole body mass and maximum TOVs measured from each individual. Potential energy was calculated using whole body mass and hind limb length. The ratio of potential to kinetic energy was compared with fat mass. All analyses were performed using SPSS versions 8.0 and 11.0.

Results

Multiple regression results

Only two of the morphological variables showed significant correlation with maximum TOV. Maximum TOV was negatively correlated with fat mass relative to lean body mass but was positively correlated with hind limb length relative to lean body mass. A correlation matrix of all possible bivariate relationships between variables entered into the multiple regression analysis is shown in Table 1.

MHC IIX was the first variable to be eliminated in the multiple regression, followed by lean mass and residual muscle mass. Backwards elimination of these insignificant predictors yielded a multiple regression model containing only two significant independent variables: residual hind limb length and residual fat mass. This two-variable model explained over 62% of the variation in maximum TOV ($r=0.790$, $F=12.5$, $P=0.001$, $N=18$). Models containing lean mass and residual muscle mass in addition to residual hind limb length and residual fat mass modestly improved the predictability of the model, to approximately 72% ($r=0.847$, $F=8.26$, $P=0.002$, $N=18$).

The ratio of potential to kinetic energy

The importance of fat mass in determining TOV may result

Table 1. Correlation matrix of variables analyzed in the multiple regression analysis

| | TOV (cm s ⁻¹) | Lean body mass (g) | Residual fat mass | Residual HLL | Residual muscle mass | Type IIx isoform content [†] |
|----------------------|------------------------------|--------------------------|----------------------|-----------------|-------------------------|---|
| TOV | – | –0.218 | –0.674 | 0.503 | 0.220 | –0.227 |
| | | 0.385 | 0.002* | 0.033* | 0.380 | 0.381 |
| Lean body mass | | – | 0 | 0 | 0 | –0.420 |
| | | | 1.0 | 1.0 | 1.0 | 0.093 |
| Residual fat mass | | | – | –0.140 | 0.008 | 0.119 |
| | | | | 0.580 | 0.975 | 0.650 |
| Residual HLL | | | | – | 0.028 | –0.142 |
| | | | | | 0.912 | 0.586 |
| Residual muscle mass | | | | | – | –0.421 |
| | | | | | | 0.092 |

Residuals of hind limb length (HLL), fat mass and extensor muscle mass were calculated from linear regression analyses of each of these variables vs. lean body mass. Lean mass = body mass – (body fat content × body mass). $N=18$ cats unless otherwise specified. [†] $N=17$ cats for which the quantity of myosin heavy chain (MHC) isoform IIx was measured. Two-tailed P values are listed beneath correlation coefficients. P values designated with an asterisk indicate significant correlations at $\alpha=0.033$ [based on the Bonferroni method of controlling multiple comparison error rates; $\alpha=0.05$ is divided by 15 (the number of comparisons made)]. TOV, maximum takeoff velocity.

from its disproportionate effect on the work that muscles must do to increase potential energy relative to kinetic energy. A plot of the ratio of potential energy to kinetic energy as a function of lean residual fat mass shows a significant positive relationship between these two variables (Fig. 5). In other words, the investment in potential energy relative to kinetic energy increases as the amount of body fat relative to lean body mass increases ($r=0.678$, $P=0.002$, $N=18$).

Variation between individuals

Considerable morphological and jump performance variation among individual cats was observed (see Table 2). The mass of these cats ranged nearly threefold, from 2.66 kg to 7.93 kg, while maximum TOV ranged from 286.3 cm s⁻¹ to 410.8 cm s⁻¹. Body fat content also varied widely, from 11% to 48% of total body mass. This body fat content was probably slightly, but consistently, overestimated, however, because the carcasses scanned for fat measurement were missing one (mostly lean) leg and the three dissected muscles from the remaining leg. There was no difference between mean female (343.5 cm s⁻¹) and mean male (342.8 cm s⁻¹) maximum TOVs ($t=0.03$, two-tailed $P=0.98$, $N=18$).

Because measurement of the proportion of MHC IIx was possible for only 17 of the 18 cats, analyses were constrained to this subset of cats where appropriate. MHC content among these 17 cats ranged almost twofold, from 44.7% to 81.4% of all the MHC isoforms present in the lateral gastrocnemius muscle. MHC Type I isoform content ranged from 0.7% to 30.5% (see Table 2). For all cats, the IIx band was the most predominant isoform present (Fig. 6). For the nine cats for which MHC content was measured on two separate gels, one-way analysis of variance (ANOVA) indicated highly significant variation between cats as compared with the variation between MHC content readings from two different

gels ($F_{8,9}=9.8$, $P=0.001$ for MHC IIx; $F_{8,9}=9.2$, $P=0.002$ for MHC I).

Jump technique

Jump technique had become very stereotypical by the time each cat had reached its maximum performance level. It consisted of a very deep crouch, lift-off of the forelimbs and, finally, an explosive extension of the hind limbs and back before takeoff (Fig. 3A–C). Each successful jump ended when the cat pulled its entire body up to the landing box with its

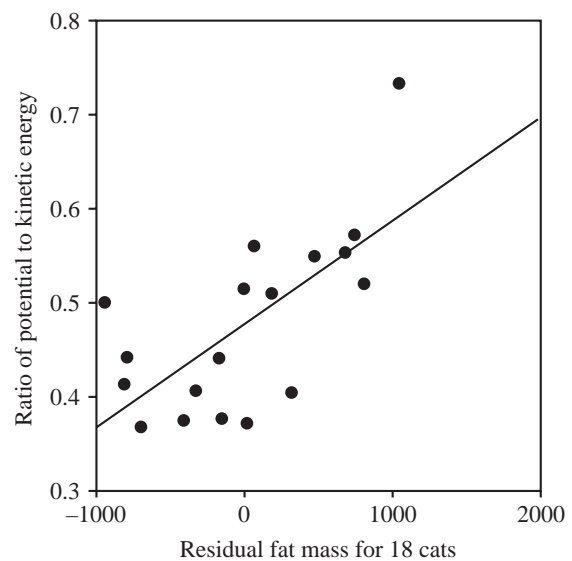


Fig. 5. Ratio of potential to kinetic energy generated during takeoff vs. residual fat mass (calculated from a regression of fat mass on lean body mass) (Pearson product-moment correlation coefficient: $r=0.678$, $P=0.002$, $y=0.479x+0.00011$).

Table 2. Summary of morphological and jump performance data for the 18 cats used in this study

| Cat | Sex | Body mass (g) | Hind limb length (cm) | Muscle mass (g) | % MHC | | % Body fat | TOV (cm s ⁻¹) | Number of attempts |
|------|-----|---------------|-----------------------|-----------------|-----------|---------|------------|---------------------------|--------------------|
| | | | | | type IIx* | type I* | | | |
| A | F | 3640 | 29.10 | 51.15 | 72.6 | 10.3 | 29 | 334.5 | NM |
| B | F | 2670 | 28.55 | 46.05 | 80.5 | 0.7 | 17 | 387.3 | NM |
| C | M | 5600 | 31.74 | 95.90 | 44.7 | 30.5 | 31 | 410.8 | NM |
| D | F | 4130 | 26.90 | 55.65 | 75.7 | 8.2 | 39 | 318.6 | NM |
| E | F | 3020 | 26.11 | 57.20 | 69.4 | 11.2 | 15 | 368.7 | 1 |
| F | F | 2660 | 26.69 | 48.67 | 64.0 | 14.2 | 11 | 358.8 | 3 |
| G | F | 3240 | 26.74 | 64.55 | 75.9 | 6.9 | 21 | 344.6 | 3 |
| H | M | 5140 | 27.71 | 78.80 | 69.1 | 8.2 | 35 | 324.6 | 5 |
| I | F | 3690 | 25.47 | 54.60 | 76.1 | 3.3 | 33 | 301.4 | 3 |
| J | F | 3620 | 28.18 | 55.50 | 75.2 | 10.1 | 15 | 331.8 | 5 |
| K | F | 5310 | 28.45 | 68.80 | 55.3 | 13.0 | 42 | 312.6 | 3 |
| L | M | 5560 | 28.65 | 79.80 | 76.5 | 3.8 | 37 | 316.8 | 4 |
| M | M | 3970 | 29.82 | 69.40 | 81.4 | 2.9 | 20 | 375.6 | 5 |
| N | F | 3770 | 26.66 | 60.25 | NM | NM | 26 | 372.4 | 1 |
| O | F | 5100 | 27.84 | 60.70 | 75.9 | 3.0 | 41 | 314.3 | 3 |
| P | F | 2950 | 27.89 | 55.65 | 70.1 | 6.7 | 25 | 367.5 | 4 |
| Q | M | 7930 | 30.58 | 98.95 | 65.2 | 12.7 | 48 | 286.3 | 2 |
| R | F | 3550 | 28.06 | 79.25 | 56.8 | 12.7 | 16 | 352.5 | 1 |
| Mean | – | 4197 | 28.06 | 65.60 | 69.7 | 9.3 | 28 | 343.3 | 3.1 |
| S.D. | – | 1346 | 1.58 | 15.42 | 9.83 | 6.85 | 11 | 33.1 | 1.4 |

Hind limb length includes the lengths of the femur, tibia, tarsals and metatarsals. Muscle mass is the combined mass of lateral gastrocnemius, vastus lateralis and semimembranosus muscles. The % myosin heavy chain (MHC) type IIx and type I are the amount of these isoforms in the lateral gastrocnemius muscle (*measured on 17 rather than 18 cats). % Body fat is the % fat composition of the carcass after the left hind limb and three extensor muscles of the right leg (semimembranosus, vastus lateralis and lateral gastrocnemius) were removed. The number of unsuccessful jumps made at a supramaximal height was considered to be an indirect measure of motivation level (measured on the last 14 cats only). TOV, maximum takeoff velocity; NM, not measured.

forearms. The time interval for all jumps from deep crouch to takeoff was 150–270 ms, which is comparable to the 150 ms ‘launching phase’ reported by Zomlefer (1976) for a maximal vertical jump made by a cat to a suspended cotton ball 1.3 m above the ground. Zomlefer also calculated the TOV for one maximal jump from a force-time curve and estimated it to be 343 cm s⁻¹. This is comparable with the maximal TOVs measured here. At takeoff, the CM was found to be located between the 13th thoracic vertebra and the iliac crest, approximately midway between the dorsal and ventral surfaces.

Performance repeatability

A general linear model repeated-measures ANOVA indicated highly significant variance in the mean TOVs between cats as compared with the variance in TOV within the two days it was measured for each cat ($F_{17,18}=11.4$; $P<0.001$, $N=18$). TOV was a repeatable performance for the 18 cats on the two days it was measured, as shown in Fig. 7 (Pearson product-moment correlation coefficient $r=0.841$, $P<0.0001$). A paired t -test indicated no difference in mean TOV on day 1 vs. day 2 ($t=-1.072$, $P=0.299$, $N=18$). In other words, TOV on day 1 was not consistently higher or lower than day 2 TOV. There was no significant relationship between (day 1 – day 2) TOV and mean TOV ($r=-0.103$, $P=0.685$), which indicates that better jumpers

did not tend to jump with maximal velocity on day 1 only or on day 2 only. Ten cats achieved their highest TOV on day 1, and eight cats achieved their highest TOV on day 2.

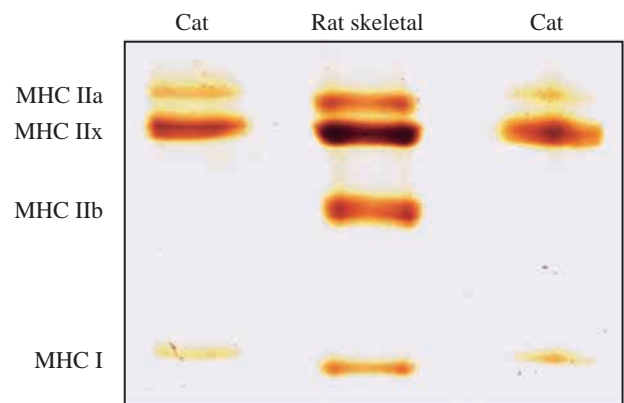


Fig. 6. Scan of SDS-PAGE gel showing myosin heavy chain (MHC) isoforms isolated from the cat lateral gastrocnemius muscle and from a rat skeletal muscle standard. Note that rat skeletal muscle contains a fourth isoform, Type IIb, which is not found in cat skeletal muscle. In the cat samples, the MHC Type I isoform migrates the furthest, followed by the Type IIx and Type IIa isoforms, respectively.

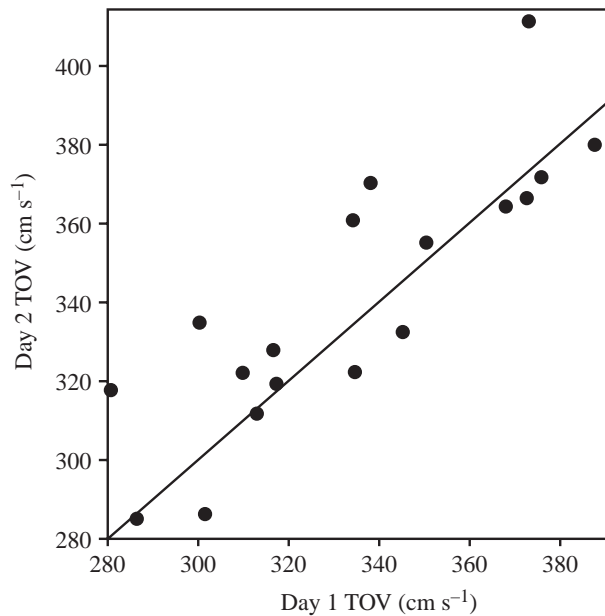


Fig. 7. Maximum takeoff velocity (TOV) on day 2 vs. day 1, demonstrating the repeatability of jump performance over the two days on which it was measured for each cat (Pearson product-moment correlation coefficient: $r=0.841$, $P<0.0001$, $y=0.889x+41.88$). There was no difference in mean TOV on day 1 vs. day 2 (paired t -test: $t=-1.072$, $P=0.299$). The reference line shown has a slope of 1.0.

Discussion

The present study demonstrates that maximum TOV in domestic cats is significantly and positively related to hind limb length relative to fat-free body mass and negatively related to the amount of fat present relative to lean body mass. Surprisingly, however, lean body mass, %MHC IIx fibers in the lateral gastrocnemius, and extensor muscle mass relative to lean body mass did not explain significant amounts of TOV variation. There were no detectable gender differences in maximum TOV.

Body fat content, hind limb length and muscle mass

The variation in body fat content among individual cats in this study was considerable. As stated previously, the absolute measurements for body fat were probably overestimated, but were done so in a consistent way (in other words, the tissues removed from each carcass before body fat measurement were dissected in a consistent manner). In either case, it is accurate to conclude that body fat content varied nearly fourfold from the leanest to the fattest cat (mean=28%, S.D.=11.0%, S.E.M.=2.6%). One other study that analyzed the chemical composition of 20 domestic cat carcasses (14 males and six non-pregnant females; Hendriks et al., 1997) also reported a nearly fourfold range, 6.2–23.6%, in lipid content per unit wet tissue (mean=11.2%, S.D.=5.3%, S.E.M.=1.2%).

Fat mass relative to lean body mass explained the most variation in maximum TOV. The large explanatory power of relative fat mass (standardized β coefficient=-0.62) reveals the

considerable influence of body fat levels on an explosive performance such as jumping. This result appears to be driven by significantly larger portions of extensor muscle work invested in raising potential energy relative to kinetic energy levels during takeoff in fatter animals (see Fig. 5). While this effect may be more important in these laboratory animals than would be the case in the wild, there is considerable variation in % fat in the wild, as documented above, and female cats must still jump even while carrying the extra weight of pregnancy. We believe, therefore, that these results can be generalized.

Hind limb length relative to lean body mass was the second best predictor of TOV (standardized β coefficient=0.41) in the four-variable regression model. These results suggest that the negative effect of increasing limb length on the amount of extensor muscle work invested in raising potential energy is surpassed by the positive influence of longer hind limbs on kinetic energy production. When accelerations during takeoff increasingly exceed g (9.8 m s^{-2}), the effect that longer limbs have on increasing CM kinetic energy levels outpaces their contribution to increasing CM potential energy. In our cats, we calculated average CM accelerations ranging from 11.9 m s^{-2} to 24.6 m s^{-2} [where average acceleration = $(\text{TOV} - \text{initial velocity})/(\text{takeoff duration})$]. If cats perform like the frogs in the Marsh and John-Alder (1994) jumping study, the average accelerations that we measured kinematically underestimate the accelerations produced during the last half of the takeoff period.

Extensor muscle mass relative to lean body mass was not found to explain a significant portion of the variation in cat TOV. The lack of a relationship between residual extensor muscle mass and TOV in the present study may be explained by the influence of body fat mass on the muscle mass/body mass ratio (m'/m in equation 3). As fat mass increases, m'/m decreases, and so TOV should be decreased. Linear regression analyses of our cat data confirm these relationships: m'/m decreases as fat mass increases ($r=-0.720$, $F=17.24$, $P=0.001$, $N=18$; see Fig. 8a), and m'/m is significantly and positively related to TOV ($r=0.647$, $F=11.51$, $P=0.004$, $N=18$; see Fig. 8b). Two interspecific frog studies did find positive correlations between hind limb muscle mass and maximum jump distance (Emerson, 1978) and between hind limb muscle mass and TOV (Choi and Park, 1996). Miller et al. (1993) report that large leopard frogs (*Rana pipiens*) jump further than smaller leopard frogs, and also found that large frogs have relatively larger gastrocnemius muscles. Although they did not directly examine the relationship between jump distance and relative gastrocnemius size among their individual frog subjects, they hypothesize that larger frogs jump further because of their relatively larger hind limb extensor muscles.

Myosin heavy chain isoform content

Variability in the MHC IIx isoform content of the lateral gastrocnemius muscle among the 17 cats was considerable (mean=69.7%, S.D.=9.83%, S.E.M.=2.38%). Talmadge et al. (1996) report a similar mean \pm S.E.M. ($72 \pm 2\%$) for the lateral

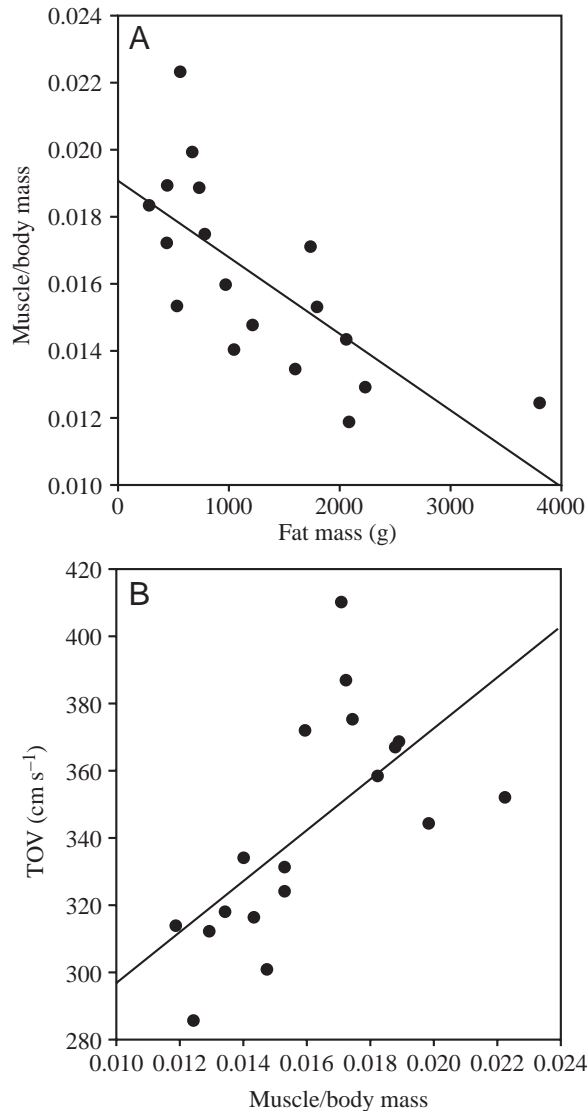


Fig. 8. (A) Significant negative relationship between the ratio of extensor muscle mass/body mass and body fat mass ($r=-0.720$, $P=0.001$, $y=-2.3\times 10^{-6}x+0.019$). (B) Significant positive relationship between maximum takeoff velocity (TOV) and the ratio of extensor muscle mass/body mass ($r=0.647$, $P=0.004$, $y=7571x+220.9$).

gastrocnemius muscle in their sample of three domestic cats. Similarly, the MHC I isoform content measured in the present study (mean=9.3%, S.D.=6.85%, S.E.M.=1.66%) demonstrated a similar central tendency to that reported by Talmadge et al. (1996) for the Type I isoform in the same muscle (mean=13%, S.D.=1.73%, S.E.M.=1%).

Unexpectedly, the amount of fast-twitch fiber present in the lateral gastrocnemius muscle (an important ankle extensor; Zomlefer et al., 1977; Zajac et al., 1981; Abraham and Loeb, 1985) was not found to be related to TOV. This result is counterintuitive because the proportion of fast-twitch fibers is known to be correlated with maximum shortening velocity, and thus should be a good estimate of the work done per unit muscle during the takeoff period.

The lack of a relationship between fast-twitch fiber content and TOV may be explained by the biarticular action of the lateral gastrocnemius; this muscle spans both the knee and the ankle joints. Although the main effect of lateral gastrocnemius contraction is to extend the ankle joint, the degree and rate of fiber shortening is limited by knee joint extension during takeoff. It has been hypothesized that this decrease in lateral gastrocnemius shortening velocity has two advantages for humans during jumping: (1) it allows larger forces to be produced at the rapidly extending ankle joint and (2) it allows knee extensor muscles to be fully activated until takeoff without damaging the knee joint by the high joint angular velocities produced (Bobbert and van Ingen Schenau, 1988; van Soest et al., 1993).

The degree and rate of lateral gastrocnemius fiber shortening is further complicated by this muscle's insertion into the Achilles tendon, a series elastic element (SEE). Stretching (or compliance) of the SEE in the lateral gastrocnemius and other triceps surae muscles results in storage of energy before fibers contract. Release of this energy enables fibers to shorten at lower velocities and produce more force during takeoff, resulting in high power output at the ankle joint during the latter part of takeoff (Bobbert, 2001). Our expectation of a linear positive relationship between lateral gastrocnemius fiber-shortening velocity and TOV may therefore be too simplistic for this complicated muscle-tendon system. Possibly, examination of the relationship between fast-twitch fiber content and TOV in the monoarticular vastus lateralis muscle or other hind limb muscles would produce a different result.

Conclusions

We found that cats with longer hind limbs and lower fat mass relative to their lean body mass achieved higher TOVs. These two variables explained significant variation in maximum TOV in a manner consistent with predictions based on the work done by extensor muscles to increase both kinetic and potential energy during takeoff. This study is the first to confirm the limb length-jump performance relationship in an endothermic vertebrate. Contrary to predictions, however, extensor muscle mass relative to lean body mass and percentage composition of MHC Iix were not found to significantly predict TOV.

The results of the present study as well as of other examinations of the limb morphology-leaping performance relationship suggest that jumping may be more highly and consistently correlated with morphology/physiology than are other performance variables. This implies that the evolution of limb design can most readily be studied on an ecologically relevant performance variable whose relationship to morphology is relatively simple biomechanically and on which data can be collected under carefully controlled lab conditions. Furthermore, the use of a large, easily trained subject will limit additional sources of experimental error. If these criteria are met, significant correlations between morphology and performance are more likely to be revealed.

The work presented here could not have been accomplished without the generous help of people representing several academic departments within the University of Wisconsin-Madison system. They are: Muscle Biology – Marion Greaser, Paul Mozdziaik, Chad Warren; Physiology Department – Jim Ervasti, Samantha Harris, Jose' Sant'Ana Pereira, Tim Piazza, Kevin Strang; Psychology Department – Pat Cofta, Kurt Illig, Peter Spear; RARC – Lisa Krugner-Higby; Zoology – Jeff Baylis, John Dallman, Bill Feeny, Dick Ganje, Ted Garland, Frank Iwen, Bob Jeanne; Undergraduate assistants – Jodi Bachim, Julie Bock, Julia Disterhaft, Andrea Finn, Megan O'Leary, Agnes Rogalski, Jennifer Stephani and Lisa Van Pay.

References

- Abraham, L. D. and Loeb, G. E.** (1985). The distal hindlimb musculature of the cat: patterns of normal use. *Exp. Brain Res.* **58**, 580-593.
- Alexander, R. McN.** (1968). *Animal Mechanics*. Seattle: University of Washington Press.
- Alexander, R. McN.** (1977). Terrestrial locomotion. In *Mechanics and Energetics of Animal Locomotion* (ed. R. McN. Alexander and G. Goldspink), pp. 168-202. New York: John Wiley & Sons.
- Alexander, R. McN. and Jayes, A.** (1983). A dynamic similarity hypothesis for the gaits of quadrupedal mammals. *J. Zool.* **201**, 135-152.
- Amundson, R. and Lauder, G. V.** (1994). Function without purpose: the uses of causal role function in evolutionary biology. *Biol. Philos.* **9**, 443-469.
- Arnold, S. J.** (1983). Morphology, performance and fitness. *Am. Zool.* **23**, 347-361.
- Bauwens, D., Garland, T., Jr, Castilla, A. M. and Van Damme, R.** (1995). Evolution of sprint speed in lacertid lizards: morphological, physiological, and behavioral correlations. *Evolution* **49**, 848-863.
- Bels, V. L., Theys, J., Bennett, M. R. and Legrand, L.** (1992). Biomechanical analysis of jumping in *Anolis carolinensis* (reptilia: iguanidae). *Copeia* **2**, 492-504.
- Bennett, A. F., Garland, T., Jr and Else, P. L.** (1989). Individual correlation of morphology, muscle mechanics, and locomotion in a salamander. *Am. J. Physiol.* **256**, R1200-R1208.
- Bennet-Clark, H.** (1977). Scale effects in jumping animals. In *Scale Effects in Animal Locomotion* (ed. T. Pedley), pp. 58-72. New York: Academic Press.
- Bobbert, M. F.** (2001). Dependence of human squat jump performance on the series elastic compliance of the triceps surae: a simulation study. *J. Exp. Biol.* **204**, 533-542.
- Bobbert, M. F. and van Ingen Schenau, G. J.** (1988). Coordination in vertical jumping. *J. Biomech.* **21**, 249-262.
- Bock, W. J.** (1988). The nature of explanations in morphology. *Am. Zool.* **28**, 205-215.
- Bock, W. J. and von Wahlert, G.** (1965). Adaptation and the form-function complex. *Evolution* **19**, 269-299.
- Bonine, K. E. and Garland, T., Jr** (1999). Sprint performance of phrynosomatid lizards, measured on a high-speed treadmill, correlates with hindlimb length. *J. Zool.* **248**, 255-265.
- Bosco, C., Komi, P., Tihanyi, V. J., Fekete, G. and Apor, P.** (1983). Mechanical power test and fiber composition of human leg extensor muscles. *Eur. J. Appl. Physiol.* **51**, 129-135.
- Braund, K. G., Amling, K. A., Mehta, J. R., Steiss, J. E. and Scholz, C.** (1995). Histochemical and morphometric study of fiber types in ten skeletal muscles of healthy young adult cats. *Am. J. Vet. Res.* **56**, 349-357.
- Burke, R. E.** (1994). Physiology of motor units. In *Myology*, 2nd edn (ed. A. G. Engel and C. Franzini-Armstrong), pp. 464-483. New York: McGraw-Hill, Inc.
- Burke, R. E., Levine, D. N., Tsairis, P. and Zajac, F. E.** (1973). Physiological types and histochemical profiles in motor units of the cat gastrocnemius. *J. Physiol.* **234**, 723-748.
- Choi, I. and Park, K.** (1996). Variations in takeoff velocity of anuran amphibians: relation to morphology, muscle contractile function and enzyme activity. *Comp. Biochem. Phys.* **A 113**, 393-400.
- Cummins, R.** (1975). Functional analysis. *J. Philos.* **72**, 741-765.
- Cummins, R.** (1983). *The Nature of Psychological Explanation*. Cambridge, MA, USA: MIT Press.
- Dobrowolska, H.** (1973). Body-part proportions in relation to the mode of locomotion in anurans. *Zool. Pol.* **23**, 59-108.
- Emerson, S.** (1978). Allometry and jumping in frogs: helping the twain to meet. *Evolution* **32**, 551-564.
- Emerson, S.** (1985). Jumping and leaping. In *Functional Vertebrate Morphology* (ed. M. Hildebrand, D. M. Bramble, K. R. Liem and D. B. Wake), pp. 58-72. Cambridge: Belknap Press.
- Emerson, S.** (1991). The ecomorphology of Bornean tree frogs (family Rhacophoridae). *Zool. J. Linn. Soc.* **101**, 337-357.
- Emerson, S. B. and Arnold, S. J.** (1989). Intra- and interspecific relationships between morphology, performance and fitness. In *Complex Organismal Functions: Integration and Evolution in Vertebrates* (ed. D. B. Wake and G. Roth), pp. 295-314. New York: John Wiley & Sons.
- Fauteck, S. P. and Kandarian, S. C.** (1995). Sensitive detection of myosin heavy chain composition in skeletal muscle under different loading conditions. *Am. J. Physiol.* **268**, C419-C424.
- Gabriel, J. M.** (1984). The effect of animal design on jumping performance. *J. Zool.* **204**, 533-539.
- Galis, F.** (1996). The application of functional morphology to evolutionary studies. *Trends Ecol. Evol.* **11**, 124-129.
- Gambaryan, P. P.** (1974). *How Mammals Run*. New York: John Wiley & Sons.
- Garland, T., Jr** (1984). Physiological correlates of locomotor performance in a lizard: an allometric approach. *Am. J. Physiol.* **247**, R806-R815.
- Garland, T., Jr** (1985). Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard *Amphibolurus nuchalis*. *J. Zool.* **207**, 425-439.
- Garland, T., Jr and Else, P. L.** (1987). Seasonal, sexual, and individual variation in endurance and activity metabolism in lizards. *Am. J. Physiol.* **252**, R439-R449.
- Garland, T., Jr and Janis, C. M.** (1993). Does metatarsal/femur ratio predict maximal running speed in cursorial mammals? *J. Zool.* **229**, 133-151.
- Garland, T., Jr and Carter, P. A.** (1994). Evolutionary physiology. *Annu. Rev. Physiol.* **56**, 579-621.
- Garland, T., Jr and Losos, J. B.** (1994). Ecological morphology of locomotor performance in squamate reptiles. In *Ecological Morphology: Integrative Organismal Biology* (ed. P. C. Wainwright and S. M. Reilly), pp. 240-302. Chicago: University of Chicago Press.
- Hakkinen, K., Alen, M. and Komi, P. V.** (1984). Neuromuscular, anaerobic, and aerobic performance characteristics of elite power athletes. *Eur. J. Appl. Physiol.* **53**, 97-105.
- Hall-Craggs, E. C. B.** (1965). An analysis of the jump of the Lesser Galago (*Galago senegalensis*). *J. Zool.* **147**, 20-29.
- Hendriks, W. H., Moughan, P. J. and Tarttelin, M. F.** (1997). Body composition of the adult domestic cat (*Felis catus*). *J. Anim. Physiol. An. N.* **77**, 16-23.
- Hildebrand, M.** (1985). Walking and running. In *Functional Vertebrate Morphology* (ed. M. Hildebrand, D. M. Bramble, K. R. Liem and D. B. Wake), pp. 38-57. Cambridge: Belknap Press.
- Hill, A. V.** (1950). The dimensions of animals and their muscular dynamics. *Science Progress.* **38**, 209-230.
- Hoy, M. and Zernicke, R. F.** (1985). Modulation of limb dynamics in the swing phase of locomotion. *J. Biomech.* **18**, 49-60.
- Huey, R. B., Dunham, A. E., Overall, K. L. and Newman, R. A.** (1990). Variation in locomotor performance in demographically known populations of the lizard *Sceloporus merriami*. *Physiol. Zool.* **63**, 845-872.
- Kelly, A. M. and Rubinstein, N. A.** (1994). The diversity of muscle fiber types and its origin during development. In *Myology*, 2nd edn (ed. A. G. Engel and C. Franzini-Armstrong), pp. 119-132. New York: McGraw-Hill, Inc.
- Losos, J. B.** (1990a). The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution* **44**, 1189-1203.
- Losos, J. B.** (1990b). Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. *Ecol. Monogr.* **60**, 369-388.
- Losos, J. G. and Sinervo, B.** (1989). The effects of morphology and perch diameter on sprint performance of *Anolis* lizards. *J. Exp. Biol.* **145**, 23-30.
- Losos, J. B., Papenfuss, T. J. and Macey, J. R.** (1989). Correlates of sprinting, jumping, and parachuting performance in the butterfly lizard, *Leiolepis bellii*. *J. Zool.* **217**, 559-568.
- Macrini, T. E. and Irschick, D. J.** (1998). An intraspecific analysis of trade-

- offs in sprinting performance in a West Indian lizard species (*Anolis lineatopus*). *Biol. J. Linn. Soc.* **63**, 579-591.
- Marsh, R. L.** (1994). Jumping ability of Anuran amphibians. *Adv. Vet. Sci. Comp. Med.* **38B**, 51-111.
- Marsh, R. L. and John-Alder, H. A.** (1994). Jumping performance of hylid frogs measured with high-speed cine film. *J. Exp. Biol.* **188**, 131-141.
- Matolin, S., Vaverka, F., Lunak, J., Novak, J., Horak, V. and Krejci, P.** (1994). Histochemical and functional parameters in Nordic combination athletes. *Physiol. Res.* **43**, 243-251.
- Melichna, J.** (1990). *Movement and Morphological Adaptability of Skeletal Muscle*. Prague: Charles University.
- Miles, D. B.** (1987). Habitat related differences in locomotion and morphology in two populations of *Urosaurus ornatus*. *Am. Zool.* **27**, A44.
- Miles, D. B.** (1994). Covariation between morphology and locomotory performance in sceloporine lizards. In *Lizard Ecology: Historical and Experimental Perspectives* (ed. L. J. Vitt and E. R. Pianka), pp. 207-259. Princeton: Princeton University Press.
- Miles, D. B., Fitzgerald, L. A. and Snell, H. L.** (1995). Morphological correlates of locomotor performance in hatchling *Amblyrhynchus cristatus*. *Oecologia* **103**, 261-264.
- Miller, K., Monteforte, P. B. and Landis, L. F.** (1993). Scaling of locomotor performance and enzyme activity in the leopard frog, *Rana pipiens*. *Herpetologica* **49**, 383-392.
- Murphy, R. A.** (2000). Muscles acting on the skeleton. In *Principles of Physiology* (ed. R. M. Berne and M. N. Levy), pp. 154-163. St Louis: Mosby.
- Peplowski, M. M. and Marsh, R. L.** (1997). Work and power output in the hindlimb muscles of Cuban tree frogs *Osteopilus septentrionalis* during jumping. *J. Exp. Biol.* **200**, 2861-2870.
- Pond, C. M.** (1978). Morphological aspects and the ecological and mechanical consequences of fat deposition in wild vertebrates. *Ann. Rev. Ecol. Syst.* **9**, 519-570.
- Pounds, J. A.** (1988). Ecomorphology, locomotion, and microhabitat structure: patterns in a tropical mainland *Anolis* community. *Ecol. Monogr.* **58**, 299-320.
- Prestrud, P. and Nilssen, K.** (1992). Fat deposition and seasonal variation in body composition of arctic foxes in Svalbard. *J. Wildlife Man.* **56**, 221-233.
- Rand, A. S.** (1952). Jumping ability of certain anurans, with notes on endurance. *Copeia* **1**, 15-20.
- Rand, A. S. and Rand, P. J.** (1966). The relation of size and distance jumped in *Bufo marinus*. *Herpetologica* **22**, 206-213.
- Scollay, P.** (1980). Cross-sectional morphometric data on a population of semi-free ranging squirrel monkeys, *Saimiri sciureus* (Iquitos). *Am. J. Phys. Anthropol.* **53**, 309-316.
- Sherry, D.** (1981). Adaptive changes in body weight. In *Body Weight Regulatory System: Normal and Disturbed Mechanisms* (ed. L. A. Cloth), pp. 161-168. New York: Raven press.
- Sinervo, B. and Losos, J. B.** (1991). Walking the tight rope: a comparison of arboreal sprint performance among populations of *Sceloporus occidentalis* lizards. *Ecology* **72**, 1225-1233.
- Smith, J. L., Edgerton, V. R., Betts, B. and Collatos, T. C.** (1977). EMG of slow and fast ankle extensors of cat during posture, locomotion and jumping. *J. Neurophysiol.* **40**, 503-513.
- Snell, H. L., Jennings, R. D., Snell, H. M. and Harcourt, S.** (1988). Intrapopulation variation in predator-avoidance performance of Galapagos lava lizards: the interaction of sexual and natural selection. *Evol. Ecol.* **2**, 353-369.
- Studel, K. and Beattie, J.** (1995). Does limb length predict the relative energetic cost of locomotion in mammals? *J. Zool.* **235**, 501-514.
- Streelman, J. T.** (1997). Why morphologists need etiological function. *Zool. Jena* **100**, 58-62.
- Talmadge, R. J. and Roy, R. R.** (1993). Electrophoretic separation of rat skeletal muscle myosin heavy-chain isoforms. *J. Appl. Physiol.* **75**, 2337-2340.
- Talmadge, R. J., Grossman, E. J. and Roy, R. R.** (1996). Myosin heavy chain composition of adult feline (*Felis catus*) limb and diaphragm muscles. *J. Exp. Zool.* **275**, 413-420.
- Tihanyi, J., Apor, P. and Fekete, G.** (1982). Force-velocity-power characteristics and fiber composition in human knee extensor muscles. *Eur. J. Appl. Physiol.* **48**, 331-343.
- Tsuji, J. S., Huey, R. B., Van Berkum, F. H., Garland, T., Jr and Shaw, R. G.** (1989). Locomotor performance of hatchling fence lizards (*Sceloporus occidentalis*): quantitative genetics and morphometric correlates. *Evol. Ecol.* **3**, 240-252.
- Turner, D. C. and Meister, O.** (1988). Hunting behaviour of the domestic cat. In *The Domestic Cat: the Biology of its Behaviour* (ed. D. C. Turner and P. Bateson), pp. 111-121. New York: Cambridge University Press.
- van Soest, A. J., Schwab, A. L., Bobbert, M. F. and van Ingen Schenau, G. J.** (1993). The influence of the biarticularity of the gastrocnemius muscle on vertical-jumping achievement. *J. Biomech.* **26**, 1-8.
- Viitasalo, J. T., Hakkinen, K. and Komi, P. V.** (1981). Isometric and dynamic force production and muscle fiber composition in man. *J. Hum. Movement Stud.* **7**, 199-209.
- Walmsley, B., Hodgson, J. A. and Burke, R. E.** (1978). Forces produced by medial gastrocnemius and soleus muscles during locomotion in freely moving cats. *J. Neurophysiol.* **41**, 1203-1216.
- Webster, D. B. and Webster, M.** (1988). Hypotheses derived from morphological data: when and how they are useful. *Am. Zool.* **28**, 231-236.
- Zajac, F. E.** (1985). Thigh muscle activity during maximum-height jumps by cats. *J. Neurophysiol.* **53**, 979-994.
- Zajac, F. E., Zomlefer, M. R. and Levine, W. S.** (1981). Hindlimb muscular activity, kinetics and kinematics of cats jumping to their maximum achievable heights. *J. Exp. Biol.* **91**, 73-86.
- Zajac, F. E., Levine, W. S. and Dungan, D.** (1983). Partitioning of cat posterior thigh muscles into two groups based on EMG activity during jumping. *Soc. Neurosci.* **9**, 62.
- Zomlefer, M. R.** (1976). Biomechanics of the jumping cat. *PhD dissertation*. University of Maryland, College Park.
- Zomlefer, M. R., Zajac, F. E. and Levine, W. S.** (1977). Kinematics and muscular activity of cats during maximum height jumps. *Brain Res.* **126**, 563-566.
- Zug, G. R.** (1972). Anuran locomotion: structure and function. I. Preliminary observations on relation between jumping and osteometrics of appendicular and postaxial skeleton. *Copeia* **4**, 613-624.
- Zug, G. R.** (1978). Anuran locomotion-structure and function, II: Jumping performance of semiaquatic, terrestrial, and arboreal frogs. *Smith. Contr. Zool.* **276**, 1-31.