

EFFICIENCY OF UPHILL LOCOMOTION IN NOCTURNAL AND DIURNAL LIZARDS

C. T. FARLEY* AND M. EMSWILLER

Department of Integrative Biology, University of California at Berkeley, Berkeley, CA 94720-4480, USA

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Summary

Nocturnal geckos can walk on level ground more economically than diurnal lizards. One hypothesis for why nocturnal geckos have a low cost of locomotion is that they can perform mechanical work during locomotion more efficiently than other lizards. To test this hypothesis, we compared the efficiency of the nocturnal gecko *Coleonyx variegatus* (average body mass 4.2 g) and the diurnal skink *Eumeces skiltonianus* (average body mass 4.8 g) when they performed vertical work during uphill locomotion. We measured the rate of oxygen consumption when each species walked on the level and up a 50° slope over a range of speeds. For *Coleonyx variegatus*, the energetic cost of traveling a unit distance (the minimum cost of transport, C_{\min}) increased from 1.5 to 2.7 ml O₂ kg⁻¹ m⁻¹ between level and uphill locomotion. For *Eumeces skiltonianus*, C_{\min}

increased from 2.5 to 4.7 ml O₂ kg⁻¹ m⁻¹ between level and uphill locomotion. By taking the difference between C_{\min} for level and uphill locomotion, we found that the efficiency of performing vertical work during locomotion was 37% for *Coleonyx variegatus* and 19% for *Eumeces skiltonianus*. The similarity between the 1.9-fold difference in vertical efficiency and the 1.7-fold difference in the cost of transport on level ground is consistent with the hypothesis that nocturnal geckos have a lower cost of locomotion than other lizards because they can perform mechanical work during locomotion more efficiently.

Key words: locomotion, energetics, oxygen consumption, lizards, *Coleonyx variegatus*, *Eumeces skiltonianus*, muscle efficiency, biomechanics.

Introduction

Lizards that are active during the night must walk and run with lower body temperatures than lizards that are active during the day. It is well known that the maximum aerobic capacity of an ectotherm is strongly dependent on body temperature (Bennett, 1982). At lower temperatures such as those encountered by nocturnal lizards, aerobic capacity decreases, generally by a factor of two for each 10°C decrease in temperature (Bennett, 1982). Thus, nocturnal lizards have to walk and run under conditions in which their aerobic capacity is reduced. However, recent research has shown that nocturnal geckos have substantially lower energetic costs of locomotion than diurnal lizards of similar body size, thus offsetting the effect of their reduced aerobic capacity at low temperatures (Autumn *et al.* 1994). For example, when the nocturnal geckos *Teratoscincus przewalskii* and *Coleonyx variegatus* walk 1 m, they only use 33–60% of the metabolic energy that a diurnal lizard of similar body mass uses (Autumn *et al.* 1994; Autumn and Farley, 1992). The energetic cost of traveling 1 m (the ‘minimum cost of transport’) is nearly independent of body temperature (Bennett and John-Alder, 1984; Autumn *et al.* 1994) and, as a result, the cost of transport is lower in nocturnal geckos than in diurnal lizards at all body temperatures. Because these nocturnal geckos have such low

costs of transport, they can sustain a wide range of locomotor speeds in spite of their reduced aerobic capacities at low temperatures.

How do nocturnal geckos move so economically? Legged animals have to perform mechanical work to lift and accelerate the center of mass and limbs during each stride. Some mechanical energy is passively conserved using the inverted pendulum mechanism in walking (Cavagna and Margaria, 1966; Cavagna *et al.* 1963). In addition, some mechanical energy is passively conserved in the form of stored elastic energy in muscles, tendons and ligaments (Alexander, 1988). However, these passive mechanisms do not provide all of the mechanical energy that is required for locomotion. Although it is not known exactly what fraction of the mechanical energy is passively conserved during locomotion, it is certain that some fraction of the mechanical energy is provided by active skeletal muscle. Therefore, it is likely that the energetic cost of transport depends at least partly on the efficiency with which an animal’s skeletal muscles can convert chemical energy to mechanical work during locomotion.

We hypothesize that nocturnal geckos have a low energetic cost of transport compared with that of other lizards because their muscular systems can perform mechanical work more

*Present address: Department of Human Biodynamics, 103 Harmon, University of California, Berkeley, CA 94720-4480, USA.

efficiently during locomotion. The goal of this study is to begin to test this hypothesis by comparing the efficiency of performing vertical work during uphill locomotion for a nocturnal gecko (*Coleonyx variegatus*) and a diurnal skink (*Eumeces skiltonianus*). In addition to providing a test of our hypothesis, these data will provide the first measurement, to our knowledge, of the energetics of uphill locomotion in lizards and may provide insight into the evolution of arboreality in geckos.

Materials and methods

Animals

Live adult specimens of the Western skink *Eumeces skiltonianus* (Baird and Girard) and the Western banded gecko *Coleonyx variegatus* (Baird) were obtained from a commercial collector. Each individual was housed in a separate plastic terrarium. Both species were kept in an environmental room in which the lights were illuminated for 13 h per day. In addition, each cage containing a gecko had direct ultraviolet lighting from a fluorescent tanning lamp and a heat strip to allow behavioral thermoregulation over a temperature range of 25–40 °C. Both species were fed a diet of mealworms, crickets and a vitamin/mineral supplement, and they were given water daily. Animals were fasted for at least 36 h before an experimental trial.

Five individuals of each species were used in the study. The skinks used in the study had an average mass of 4.8 ± 0.7 g (S.D.), and the geckos used in the study had an average mass of 4.2 ± 0.6 g (S.D.). The snout–vent length was approximately 5.2 cm for *E. skiltonianus* and 5.6 cm for *C. variegatus*. The active body temperature in the field is 30 °C for *E. skiltonianus* and approximately 23 °C for *C. variegatus* (Brattstrom, 1965; Cunningham, 1966).

Experimental apparatus

Individuals were exercised in a miniature treadmill-respirometer at an ambient temperature of 25 °C (Herreid *et al.* 1981). The treadmill apparatus was oriented horizontally for level locomotion or tilted to 50° for uphill locomotion. The length of the treadmill-respirometer was adjusted to the body length of the lizards to ensure steady locomotion. The front of the chamber had a dark cover to encourage the animals to stay at the front during locomotion.

The oxygen concentration of the air leaving the treadmill-respirometer was monitored using an O₂ analyzer (Ametek Applied Electrochemistry S-3A/II) interfaced with a personal computer. Before the air reached the oxygen analyzer, it passed through a column of Drierite for water removal and a column of Ascarite for CO₂ removal. The oxygen concentration data were collected using data-acquisition hardware (NB-MIO-16 Board, National Instruments) and software (LabView, National Instruments). Mass-specific, steady-state oxygen consumption (\dot{V}_{O_2}) was calculated from the O₂ concentration after it had remained constant for at least 3 min.

Experimental protocol

The rate of oxygen consumption was measured over a range of speeds on the level and up a 50° incline. For *E. skiltonianus*, treadmill speeds for level locomotion ranged from 0.03 to 0.21 km h⁻¹. For *C. variegatus*, treadmill speeds for level locomotion ranged from 0.03 to 0.24 km h⁻¹. The speeds for uphill locomotion for both *C. variegatus* and *E. skiltonianus* ranged from 0.03 to 0.1 km h⁻¹. The speed range for uphill locomotion was more limited than for level locomotion because the animals reached their maximum rate of oxygen consumption at a lower speed. The rate of oxygen consumption at the highest speed for uphill locomotion was slightly below the maximum rate of oxygen consumption for both species (0.5 ml O₂ g⁻¹ h⁻¹ for *C. variegatus* and 0.7 ml O₂ g⁻¹ h⁻¹ for *E. skiltonianus*).

Each individual performed at least two trials at each speed. An animal was walked at a given speed until the rate of oxygen consumption was nearly constant for 3 min. Trials were discarded if an animal repeatedly bumped against the back of the chamber for more than 10 s. The animals were tapped on the tail or hindleg if they were not keeping pace with the treadmill. The animals were rested for at least 30 min between multiple trials on a given day.

Calculation of vertical efficiency

The vertical efficiency during uphill locomotion was calculated by comparing the metabolic cost of locomotion on level ground with the metabolic cost of locomotion uphill. The slope of the line relating the rate of oxygen consumption to speed of locomotion at speeds up to the maximum aerobic speed is called the minimum cost of transport (C_{\min}). The minimum cost of transport represents the amount of oxygen required to move 1 kg of the animal's body over a distance of 1 m. The metabolic cost of lifting 1 kg vertically by 1 m (C_{vert} , J kg⁻¹ m⁻¹) was calculated from the difference between the minimum cost of transport for level locomotion ($C_{\min, \text{level}}$) and the minimum cost of transport for uphill locomotion ($C_{\min, \text{uphill}}$). A conversion factor of 20.1 J ml⁻¹ O₂ was used, and θ denotes the angle of the hill.

$$C_{\text{vert}} = 20.1(C_{\min, \text{uphill}} - C_{\min, \text{level}})/\sin\theta. \quad (1)$$

The efficiency of lifting the mass of the body up the hill (vertical efficiency) was calculated using a technique outlined in previous studies (Taylor *et al.* 1972; Full and Tullis, 1990). The vertical efficiency (%) was calculated from the mechanical work required to lift the mass of the body vertically during uphill locomotion divided by the change in the rate of metabolic energy consumption between level and uphill locomotion:

$$\text{Vertical efficiency} = \frac{9.8\sin\theta}{20.1(C_{\min, \text{uphill}} - C_{\min, \text{level}})} \times 100. \quad (2)$$

Because the mechanical work performed to lift the center of mass vertically is the primary difference in mechanical work output between level and uphill locomotion, the vertical efficiency can be used as a measure of the efficiency with

which the muscular system performs mechanical work against gravity during uphill locomotion.

Data analysis

For each individual lizard in the study, we obtained a linear regression for the rate of oxygen consumption *versus* speed for level locomotion and for uphill locomotion. For each individual, the slope of the regression for level locomotion was the minimum cost of transport for level locomotion ($C_{\min, \text{level}}$), and the slope of the regression for uphill locomotion was the minimum cost of transport for uphill locomotion ($C_{\min, \text{uphill}}$). The metabolic cost of lifting 1 kg vertically by 1 m (C_{vert} , equation 1) and the vertical efficiency (equation 2) were calculated for each individual. We used analyses of variance to test whether there were significant differences ($P < 0.05$) in C_{\min} between the two species and between level and uphill locomotion. In addition, we tested whether there were significant differences in C_{vert} and vertical efficiency of uphill locomotion between *C. variegatus* and *E. skiltonianus*.

Results

The diurnal skink *Eumeces skiltonianus* required 1.7 times more metabolic energy to travel 1 m than the nocturnal gecko *Coleonyx variegatus* during both level and uphill locomotion (Fig. 1). For both species, the slope of the relationship between the mass-specific rate of oxygen consumption (\dot{V}_{O_2}) and speed was substantially greater for uphill locomotion than for level locomotion. This slope of the \dot{V}_{O_2} *versus* speed relationship is the minimum cost of transport (C_{\min}). The minimum cost of transport for *E. skiltonianus* was $2.54 \text{ ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$ for level locomotion and $4.66 \text{ ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$ for uphill locomotion (Fig. 1; Table 1). For *C. variegatus*, C_{\min} increased from $1.54 \text{ ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$ for level locomotion to $2.65 \text{ ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$ for uphill locomotion. It is interesting to note that *C. variegatus* is so economical that its C_{\min} for locomotion up a 50° hill was similar to the C_{\min} for level locomotion for *E. skiltonianus*.

During locomotion up a 50° slope, the mass-specific metabolic cost of traveling 1 m vertically (C_{vert} , equation 1) was 1.9 times greater for the diurnal skink *E. skiltonianus* than for the nocturnal gecko *C. variegatus* (Table 1). The mass-specific metabolic cost of lifting the body 1 m vertically was $55.7 \text{ J kg}^{-1} \text{ m}^{-1}$ for *E. skiltonianus* and $29.2 \text{ J kg}^{-1} \text{ m}^{-1}$ for *C. variegatus* (Table 1). The vertical efficiency, calculated from the ratio of the mass-specific metabolic cost of lifting the body 1 m vertically to the mass-specific mechanical work of lifting the body 1 m vertically (equation 2), was 1.9 times higher in the nocturnal gecko than in the diurnal skink (Table 1). The nocturnal gecko *C. variegatus* had a vertical efficiency of 37.0% and *E. skiltonianus* had a vertical efficiency of 19.3% (Table 1).

Discussion

Our findings are consistent with the hypothesis that nocturnal geckos have a lower energetic cost of transport than

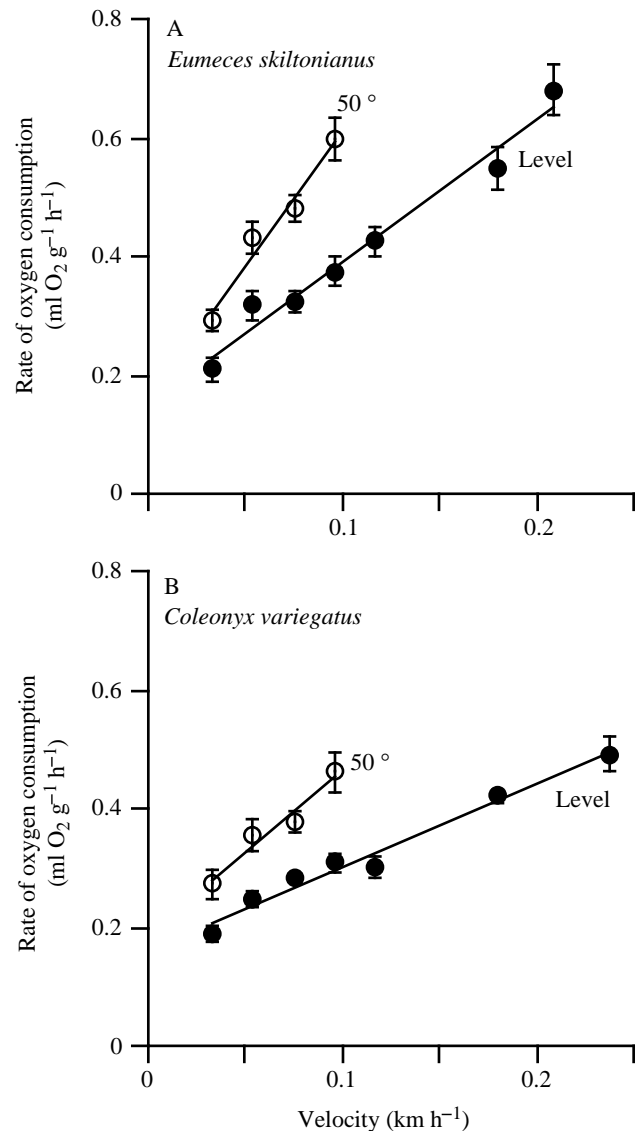


Fig. 1. Rate of oxygen consumption *versus* speed for *Eumeces skiltonianus* (A) and *Coleonyx variegatus* (B). The filled symbols represent the data for level locomotion and the open symbols represent the data for locomotion up a 50° incline. Note that the slope of the relationship between the rate of oxygen consumption and speed is greater for uphill locomotion than for level locomotion for both species. This slope is also greater for *E. skiltonianus* than for *C. variegatus* during both level and uphill locomotion. Each point is the mean for all of the individuals of a species ($N=5$) and the error bars are the standard errors of the means.

that of diurnal species of similar body mass because they are able to perform mechanical work during locomotion more efficiently. The results show that the diurnal skink *E. skiltonianus* requires 1.7 times more metabolic energy to travel 1 m than does the nocturnal gecko *C. variegatus*. Similarly, *E. skiltonianus* requires 1.9 times more metabolic energy to perform a unit of vertical work during uphill locomotion. As a result, the nocturnal gecko *C. variegatus* can perform vertical work during locomotion 1.9 times more efficiently (vertical

Table 1. Results for the energetic cost of locomotion

Species (condition)	Animal	y_0 (ml O ₂ g ⁻¹ h ⁻¹)	C_{\min} (ml O ₂ kg ⁻¹ m ⁻¹)	r^2	C_{vert} (J kg ⁻¹ m ⁻¹)	Vertical efficiency (%)
<i>Coleonyx variegatus</i> (level)	1	0.15	1.43	0.84		
	2	0.13	1.57	0.97		
	3	0.14	1.65	0.84		
	4	0.19	1.48	0.89		
	5	0.16	1.56	0.89		
	Mean	0.15	1.54			
	S.E.M.	0.01	0.04			
<i>Coleonyx variegatus</i> (uphill)	1	0.20	2.34	0.80	23.9	41.0
	2	0.19	2.25	0.80	17.8	54.9
	3	0.17	2.90	0.54	32.8	29.9
	4	0.29	2.48	0.46	26.2	37.3
	5	0.12	3.28	0.90	45.1	21.7
	Mean	0.19	2.65		29.2	37.0
	S.E.M.	0.03	0.19		4.65	5.58
<i>Eumeces skiltonianus</i> (level)	1	0.11	2.69	0.98		
	2	0.10	2.98	0.92		
	3	0.17	2.84	0.80		
	4	0.12	2.00	0.92		
	5	0.20	2.17	0.92		
	Mean	0.14	2.54			
	S.E.M.	0.02	0.19			
<i>Eumeces skiltonianus</i> (uphill)	1	0.04	5.90	0.90	84.2	11.6
	2	0.15	4.21	0.88	32.3	30.4
	3	0.21	4.71	0.50	49.1	20.0
	4	0.15	4.20	0.88	57.7	17.0
	5	0.21	4.37	0.75	55.1	17.8
	Mean	0.15	4.66		55.7	19.3
	S.E.M.	0.03	0.32		8.4	3.08

Data are for each individual used in the study and the mean values for each species. The table includes the y-intercept (y_0), slope (the minimum cost of transport, C_{\min}), and r^2 for the linear regression of the \dot{V}_{O_2} versus speed relationship. For each individual animal ($P < 0.003$ for all regressions). It also includes the metabolic cost of lifting 1 kg of body mass vertically by 1 m (C_{vert} , equation 1) and the vertical efficiency (equation 2).

Note that C_{\min} is lower for *C. variegatus* than for *E. skiltonianus* during both level and uphill locomotion (ANOVA, $P = 0.0002$). In addition, C_{\min} is higher during uphill locomotion than during level locomotion for both species (ANOVA, $P = 0.0001$). C_{vert} is higher (ANOVA, $P = 0.025$) and the vertical efficiency is lower (ANOVA, $P = 0.024$) for *C. variegatus* than for *E. skiltonianus* during uphill locomotion.

efficiency 37%) than *E. skiltonianus* (19%). The similarity between the 1.9-fold difference in vertical efficiency and the 1.7-fold difference in the cost of locomotion on level ground is consistent with the hypothesis. To test the hypothesis further, it is important that future experiments compare more species of nocturnal geckos and diurnal lizards. In addition, future work should focus on the potential mechanisms underlying the increased efficiency of performing mechanical work during locomotion in nocturnal lizards.

The biomechanical and musculoskeletal determinants of the energetic cost of terrestrial locomotion are not entirely understood (Alexander, 1991; Kram and Taylor, 1990). Strong experimental evidence suggests that the metabolic energy consumed by mammals running on level ground is primarily determined by the muscular force needed to support the weight of the body (Kram and Taylor, 1990). However, it appears that

the energy consumed for walking depends to a larger degree on the mechanical work performed (Farley and McMahon, 1992). Force platform measurements indicate that *C. variegatus* and *E. skiltonianus* use an inverted pendulum mechanism for walking at sustainable speeds (Ko and Farley, 1992) that is similar to that used by mammals and birds (Cavagna *et al.* 1977). Thus, the energetic cost of transport for level locomotion in the lizards examined in this study may be closely linked to the efficiency with which the muscular system can perform mechanical work. However, it is possible that two different mechanisms underlie the low cost of level locomotion and the high vertical efficiency of uphill locomotion in the nocturnal gecko. For example, it is possible that the cost of transport for level locomotion is low because the nocturnal gecko's muscular system can generate force to support the weight of the body economically, while the vertical efficiency

of uphill locomotion is high because its muscular system can also perform mechanical work efficiently.

The efficiency with which legged animals can perform vertical work during uphill locomotion varies widely. A survey of the literature revealed that adult mammals can perform vertical work during locomotion with an average efficiency of 43% (Armstrong *et al.* 1983; Cohen *et al.* 1978; Donovan and Brooks, 1977; Margaria, 1976; Raab *et al.* 1976; Taylor *et al.* 1972; Warncke *et al.* 1988; Wunder and Morrison, 1974). However, there is variability among mammalian species with extreme values of 31% vertical efficiency in a squirrel (Wunder and Morrison, 1974) and 66% vertical efficiency in a chimpanzee (Taylor *et al.* 1972). In addition, there does not appear to be a correlation between the economy of level locomotion and the vertical efficiency of uphill locomotion among mammals. Larger mammals have lower costs of transport during level locomotion but do not consistently have higher vertical efficiencies than smaller mammals (Full and Tullis, 1990). The only measurement of vertical efficiency in an insect has shown that the cockroach (*Periplaneta americana*) has a very low vertical efficiency of 3–4% when it walks up hills of 45° or 90° (Full and Tullis, 1990). Our study shows that the vertical efficiency is 37% for a gecko (*C. variegatus*) and 19% for a skink (*E. skiltonianus*). To our knowledge, these are the first measurements of the energetic cost of uphill locomotion in lizards, and the vertical efficiency falls into the range established for legged locomotion in mammals and insects.

How does the nocturnal gecko, *C. variegatus*, perform vertical work during locomotion 1.9 times more efficiently than the diurnal skink, *E. skiltonianus*? There are several possible mechanisms, including differences in the mechanics of uphill locomotion and differences in skeletal muscle efficiency. First, the fluctuations in the horizontal (fore–aft) and lateral components of the velocity of the center of mass may increase substantially when *E. skiltonianus* walks uphill compared with walking on level ground, leading to an underestimate of the difference in mechanical work between level and uphill locomotion and an underestimate of the efficiency of the muscular system in performing the mechanical work of lifting the center of mass vertically (see equation 2). However, a simple calculation demonstrates that it is nearly impossible that this explanation of the lower vertical efficiency in *E. skiltonianus* is correct. We calculate that the mechanical work performed to lift the center of mass vertically per meter traveled on a 50° slope is $7.5 \text{ J kg}^{-1} \text{ m}^{-1}$. If we estimate that the velocity of the center of mass in both the horizontal and lateral directions fluctuates between 0 and 0.2 km h^{-1} during each step of locomotion at an average forward speed of 0.1 km h^{-1} (step frequency 2 Hz), the mechanical work associated with these kinetic energy fluctuations is $0.22 \text{ J kg}^{-1} \text{ m}^{-1}$. This is an overestimate of the velocity fluctuations because it assumes that the forward velocity of the center of mass decelerates to zero during each step and it assumes that the magnitude of the lateral kinetic energy fluctuation is similar to the magnitude of the horizontal

kinetic energy fluctuation. In spite of this obvious overestimate of the velocity fluctuations, the mechanical work associated with lifting the center of mass vertically is about 34 times greater than the mechanical work associated with velocity fluctuations. This example demonstrates that it is nearly impossible for differences in kinetic energy fluctuations during uphill locomotion to explain the differences in vertical efficiency between these two species.

A second possibility is that the locomotor muscles of *E. skiltonianus* have a lower mechanical advantage during uphill locomotion than during level locomotion. This would mean that *E. skiltonianus* would require substantially more metabolic energy to generate muscular force to support the weight of the body during uphill locomotion than during level locomotion (Biewener, 1990; Kram and Taylor, 1990). Thus, the difference in the minimum cost of transport between level and uphill locomotion would reflect both an increase in the muscle force required to support the weight of the body and an increase in the mechanical power output of the center of mass. We do not yet have data to assess whether the mechanical advantage of the locomotor muscles is substantially different for uphill locomotion than for level locomotion.

Third, the high vertical efficiency of *C. variegatus* could occur because its locomotor muscles operate at a higher efficiency than the muscles of *E. skiltonianus*. Skeletal muscle efficiency depends on how the muscles operate and on the intrinsic properties of the muscles. It is possible that the muscles of *C. variegatus* operate closer to the shortening velocity that maximizes efficiency (Hill, 1939) or that the pattern of activation and length change of the muscles of *C. variegatus* allows more pre-stretch, resulting in a higher muscle efficiency (Heglund and Cavagna, 1987; de Haan *et al.* 1989; Josephson and Stevenson, 1991; Curtin and Woledge, 1991, 1993a,b; Barclay *et al.* 1993; Barclay, 1994). It is also possible that the locomotor muscles of *C. variegatus* have a higher peak efficiency than the muscles of *E. skiltonianus*. The peak mechanical efficiency of skeletal muscle varies substantially among species and fiber types and, thus, it is possible that there are large differences in the efficiency of the locomotor muscles from these two species (Woledge, 1968, 1989; Gibbs and Gibson, 1976; Curtin and Woledge, 1993a,b; Barclay, 1994). For example, during isotonic shortening, the rat soleus muscle has an efficiency of 15–18% (Gibbs and Gibson, 1976; Heglund and Cavagna, 1987) and the tortoise iliofibularis has an efficiency of 37% (Woledge, 1968).

We conclude that a nocturnal gecko *C. variegatus* can perform vertical work during uphill locomotion 1.7 times more efficiently than a diurnal skink *E. skiltonianus*. The similarity between the 1.9-fold difference in vertical efficiency and the 1.7-fold difference in the cost of locomotion on level ground is consistent with the hypothesis that nocturnal geckos have a lower cost of locomotion because they can perform mechanical work during locomotion more efficiently. To test this hypothesis further, future research must focus on examining other lizard species, the mechanics of level and uphill

locomotion, and the recruitment, mechanics and energetics of the locomotor muscles. In addition to giving insight into the mechanism underlying the low cost of transport in nocturnal geckos, our findings about the low cost of uphill locomotion in a gecko may provide insight into the ecology and evolution of arboreality in geckos.

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