

Intermittent Locomotion Increases Endurance in a Gecko

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ABSTRACT

Nocturnal geckos can actively forage at low temperatures. A low minimum cost of locomotion allows greater sustainable speeds by partially offsetting the decrease in maximal oxygen consumption ($\dot{V}O_{2max}$) associated with low nocturnal temperatures. The nocturnality hypothesis (Autumn et al. 1997) proposes that the reduced cost of continuous locomotion is a shared, derived characteristic that increases the capacity to sustain locomotion at low temperatures. Yet many lizards move intermittently at speeds exceeding those that elicit $\dot{V}O_{2max}$. We exercised the frog-eyed gecko, *Teratoscincus przewalskii*, continuously and intermittently on a treadmill. At an exercise speed of 0.90 km h⁻¹ (270% maximum aerobic speed), lizards alternating a 15-s exercise period with a 30-s pause period exhibited a 1.7-fold increase in distance capacity (total distance traveled before fatigue) compared with lizards exercised continuously at the same average speed (0.30 km h⁻¹). The average aerobic cost of intermittent exercise was not significantly different from $\dot{V}O_{2max}$. Locomoting intermittently could augment the increase in endurance resulting from the low minimum cost of continuous locomotion in nocturnal geckos. Intermittent behavior could increase the endurance of lizard movement in general.

Introduction

Lizards are ancestrally diurnal (Autumn et al. 1999) and are active generally at temperatures eliciting near-maximal physiological performance (30°–40°C; Avery 1982; Bennett 1982; Huey 1982). By contrast, nocturnal geckos are active at body temperatures as low as 10°C. Yet they actively forage at temperatures that diurnal lizards would be unable to sustain. Au-

tumn et al. (1994) discovered that nocturnal frog-eyed geckos use only one-third the metabolic energy required by diurnal lizards to travel a given distance. The frog-eyed gecko's extraordinarily low minimum cost of locomotion (C_{min}) allows them to aerobically sustain speeds 2.5-fold greater than could be sustained by a diurnal lizard, once the effects of body mass and phylogeny have been taken into account (Autumn et al. 1999).

Based on supportive data from additional nocturnal and diurnal species, Autumn et al. (1997) constructed the "nocturnality hypotheses," which proposed that the reduced cost of locomotion is a shared, derived characteristic that increases the capacity to sustain locomotion at low temperatures. A phylogenetic analysis of lizards including nocturnal, diurnal, and secondarily diurnal lizards has lent further support to the hypothesis (Autumn 1999; Autumn et al. 1999).

Thus far, the nocturnality hypothesis has been tested assuming that lizards move continuously and physiological systems operate in the steady state. Field observations suggest that lizards move intermittently rather than continuously (Bennett and Gorman 1979; Huey and Pianka 1981; Karasov and Anderson 1984; Garland 1985; Pietruszka 1986; van Berkum et al. 1986; McLaughlin 1989). While average rates of locomotion in the field appear to fall below the speed at which the maximal rate of oxygen consumption is attained (i.e., the maximum aerobic speed; MAS), lizards engaged in activities such as territorial defense, foraging behavior, and mate selection move at more rapid speeds (Garland 1985). During intense movement bouts, locomotor speed may be greater than the MAS identified during continuous treadmill tests. However, the duration of high-intensity movements is generally short (i.e., <1–2 min) and is alternated with pause intervals (Bennett and Gorman 1979; Huey and Pianka 1981; Karasov and Anderson 1984; Garland 1985; Pietruszka 1986; van Berkum et al. 1986; McLaughlin 1989).

Previously, we examined the importance of intermittent locomotor behavior in both laboratory and field studies of the ghost crab, *Ocypode quadrata* (Weinstein and Full 1992, 1998; Weinstein 1995). In the field, ghost crabs generally move at average speeds less than the MAS but may make brief movements at speeds that exceed the MAS (Full 1987; Weinstein 1995). In the laboratory, we demonstrated that intermittent movement can alter locomotor performance limits (Weinstein and Full 1992, 1998). When ghost crabs move intermittently, by alternating brief periods of movement with brief pauses, they can travel as much as two to five times farther before they fatigue than if they moved continuously at the same average speed (Weinstein and Full 1992, 1998). Alternatively, using dif-

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ferent exercise and pause intervals, the distance capacity (i.e., total distance traveled before fatigue) during intermittent locomotion can be reduced to one-tenth of that found for continuous locomotion at the same average speed (Weinstein and Full 1992).

The duration of intermittent exercise and pause intervals that increase distance capacity can be temperature sensitive (Weinstein and Full 1998). At low temperature, slower oxygen uptake kinetics result in a shorter duration of exercise that increases intermittent locomotor performance compared with higher temperatures. Using these brief alternating intervals of exercise and rest, ghost crabs at low temperature can increase their distance capacity making it comparable with that of a crab moving continuously at a body temperature 10°C warmer (Weinstein and Full 1998).

Carrier (1987a, 1987b) found that moving intermittently can alter performance in lizards. Lizards can be mechanically constrained from breathing during rapid locomotion since hypaxial muscle activation is required for both running and breathing (Carrier 1989; 1990). Ventilation decreases in iguanids during moderate and high-speed exercise but increases during brief pauses (Wang et al. 1997). While use of a buccal pressure force pump to inflate the lungs improves ventilation for some lizards (Al-Ghamdi et al. 1995; Brainerd and Owerkowicz 1996), breathing is probably still compromised during rapid continuous locomotion (E. L. Brainerd, personal communication).

In this study, we measured the effect of intermittent locomotion in the frog-eyed gecko, *Teratoscincus przewalskii*, for several reasons. First, the performance limits of *T. przewalskii* during continuous locomotion have been characterized (Autumn et al. 1994). Second, frog-eyed geckos move intermittently in the field at speeds exceeding MAS (K. Autumn, personal communication), suggesting that intermittent movement is an ecologically relevant behavior for these animals. Third, intermittent locomotor behavior may challenge the nocturnality hypothesis (Autumn et al. 1999). Since particular exercise and pause durations can significantly decrease distance capacity, moving intermittently could offset the performance advantage conferred by the low minimum cost of locomotion. Conversely, certain regimes of intermittent locomotion could complement the advantage of the low cost of locomotion to increase endurance. And finally, limitations in ventilation have sparked interest in the intermittent locomotion of lizards (Wang et al. 1997). This is the first article to examine the distance capacity and aerobic cost of lizards moving intermittently.

Material and Methods

Animal Collection and Maintenance

Frog-eyed geckos, *Teratoscincus przewalskii* (9.8 g \pm 1.5 SD), were collected in Gansu Province, People's Republic of China, and transported by air to our laboratory in Berkeley, California. Adult specimens were collected (by K. Autumn) under a co-

operative agreement between the Chengdu Institute of Biology, Academia Sinica, the University of California, and the California Academy of Sciences.

Pairs of geckos were housed in 16-L plastic terraria with a moist hide-box and metal screen top. Each cage had direct ultraviolet (UV) lighting from a fluorescent tanning lamp and a heat strip to allow behavioral thermoregulation over a gradient of 25°–40°C. The animals were kept in an environmental room on an 13L : 11D photoperiod at 24°C. The UV light and heat strip were on a 13L : 11D on-off cycle corresponding to the photoperiod. The geckos were fed a diet of mealworms, crickets, and vitamin/mineral supplement and were watered daily. Animals in poor condition or that had recently autotomized their tail were excluded from experiments.

Experimental Protocol

Rest. Geckos rested quietly in a miniature treadmill respirometer placed within a temperature-controlled incubator adjusted to an ambient temperature of 25°C. Geckos rested for 30 min in the treadmill chamber before each trial.

Continuous Exercise. Geckos exercised continuously to fatigue on the treadmill at 0.30, 0.60, and 0.90 km h⁻¹. The speeds selected for this study were based on a previous investigation of *T. przewalskii* (Autumn et al. 1994). A speed of 0.33 km h⁻¹ elicits the maximal rate of oxygen consumption ($\dot{V}O_{2max}$) and is the maximum aerobic speed (MAS; see Autumn et al. 1994) at 25°C. Therefore, a speed of 0.30 km h⁻¹ is submaximal (i.e., <MAS), and 0.60 and 0.90 km h⁻¹ exceed the MAS and are supramaximal (i.e., >MAS).

Intermittent Exercise. Geckos exercised intermittently to fatigue by alternating exercise periods with pause periods. We manipulated four variables in the intermittent exercise trials: exercise duration (*E*), pause duration (*P*), duty cycle ($E/[E + P]$), and absolute speed during the exercise period. Intermittent exercise protocols are outlined in Table 1 and include the corresponding absolute speed and average speed for comparison with continuous exercise.

Oxygen Consumption

Geckos exercised in a miniature treadmill respirometer. The airflow rate was 100 mL min⁻¹. Air leaving the chamber was dried with Drierite, and CO₂ was removed with Ascarite. The oxygen concentration was monitored with an O₂ analyzer (Ametek S3A). The O₂ analyzer was interfaced with a personal computer (Macintosh II) and data acquisition hardware and software (Lab View, National Instruments).

We determined the time to attain 50% of the steady state $\dot{V}O_2$ ($\dot{V}O_{2ss}$; $t_{1/2on}$) and the half-time to return to preexercise values during recovery ($t_{1/2off}$) for geckos exercising continu-

Table 1: Intermittent exercise protocols

Protocol	Exercise Period (s)	Pause Period (s)	Duty Cycle	Absolute Speed (km h ⁻¹)	Average Speed (km h ⁻¹)
1	15	30	.33	.90	.30
2	30	30	.5	.60	.30
3	120	120	.5	.60	.30

Note. Duty cycle is expressed as the exercise period duration (E)/exercise + pause period duration ($E + P$). Absolute speed was the speed during the exercise period. Average speed was calculated for a complete exercise-pause cycle. $n = 5$ for each intermittent exercise protocol. The maximum aerobic speed is 0.33 km h⁻¹ (Autumn et al. 1994).

ously at 0.30 km h⁻¹ (90% MAS). Instantaneous, mass-specific oxygen consumption for these animals was calculated from the O₂ concentration according to Withers (1977) and Herreid (1981). The effective volume of the treadmill chamber was 280 mL.

Distance Capacity

Geckos were considered to be fatigued when they could no longer keep pace with the treadmill belt, even when prodded. Data from trials during which geckos walked erratically were discarded. We used distance capacity (i.e., the total distance traveled continuously or intermittently before fatigue; Weinstein and Full 1992) as an index of endurance instead of time to fatigue because the term “endurance” usually connotes only continuous activity. The distance capacity for each trial was calculated from the treadmill speed and the number and duration of exercise intervals completed. The distance capacity for intermittent exercise was compared with continuous exercise at the same absolute speed (the speed during the exercise period) and with continuous exercise at the same average speed.

Statistics

Values are reported as means \pm 1 SE unless noted. We used a Mann-Whitney U -test to compare values for resting and maximal $\dot{V}O_2$ in this study with previous data. We performed ANOVA to determine the effects of experimental condition on $\dot{V}O_2$ and distance capacity. For comparisons between treatments, we used Scheffé's F -test.

Results

Oxygen Consumption

Resting Rate of Oxygen Consumption. The resting rate of oxygen consumption was 0.11 ± 0.01 mL O₂ g⁻¹ h⁻¹ ($n = 29$ trials) at a body temperature of 25°C. This rate was not significantly different from previous data (Mann-Whitney U -test, $p > 0.05$; Autumn et al. 1994).

Continuous Exercise. After the onset of exercise, $\dot{V}O_2$ increased to attain a steady state $\dot{V}O_2$ (Fig. 1A). The time to attain 50% of the $\dot{V}O_{2ss}$ ($t_{1/2on}$) at 0.30 km h⁻¹ was 83.4 ± 3.6 s ($n = 7$; Table 2). The aerobic cost of steady state submaximal exercise at 0.30 km h⁻¹ and the maximal rate of oxygen consumption (determined at 0.60 km h⁻¹) were not significantly different from values measured previously (Mann-Whitney U -test, $p > 0.05$; Autumn et al. 1994). Four of the five geckos exercising continuously at 0.90 km h⁻¹ fatigued before attaining a steady state.

Following exercise, $\dot{V}O_2$ decreased and returned to preexercise levels. The $t_{1/2off}$ time at 0.30 km h⁻¹ was 223.8 ± 21.4 s (3.7 min; $n = 7$; Table 2).

Intermittent Exercise. For geckos exercising intermittently, $\dot{V}O_2$ increased during the exercise periods and decreased during the pause periods (Fig. 1B–1D). Longer exercise and pause periods resulted in greater oscillations around the average rate of oxygen consumption, and shorter exercise and pause periods resulted in smaller oscillations. The average aerobic cost of intermittent exercise was determined by integrating segments of the intermittent exercise records that contained at least one complete exercise-pause cycle in which the sum of the increase and decrease in $\dot{V}O_2$ were within a constant percentage of the average $\dot{V}O_2$ of the animal. This average $\dot{V}O_2$ (aerobic cost) was expressed per unit time (mL O₂ g⁻¹ h⁻¹).

The average aerobic cost of intermittent locomotion was the same as the aerobic cost of continuous locomotion at the same average speed and at the same absolute speed (Table 3; $p > 0.05$ for all comparisons).

Distance Capacity

Continuous Exercise. Geckos exercising continuously at 0.30 km h⁻¹ (90% MAS) had a distance capacity of 152.0 ± 6.5 m, corresponding to an endurance of 30.4 ± 1.3 min. At a speed of 0.60 km h⁻¹ (180% MAS), the geckos fatigued after 83.7 ± 11.6 m (8.4 ± 1.2 min). At the fastest speed, 0.90 km h⁻¹ (270% MAS), the geckos fatigued after 23.5 ± 2.3 m (1.6 ± 0.2 min). The endurance capacity of these animals is described by the equation $T_{end} = 0.024 v^{-2.63}$ ($n = 15$ trials;

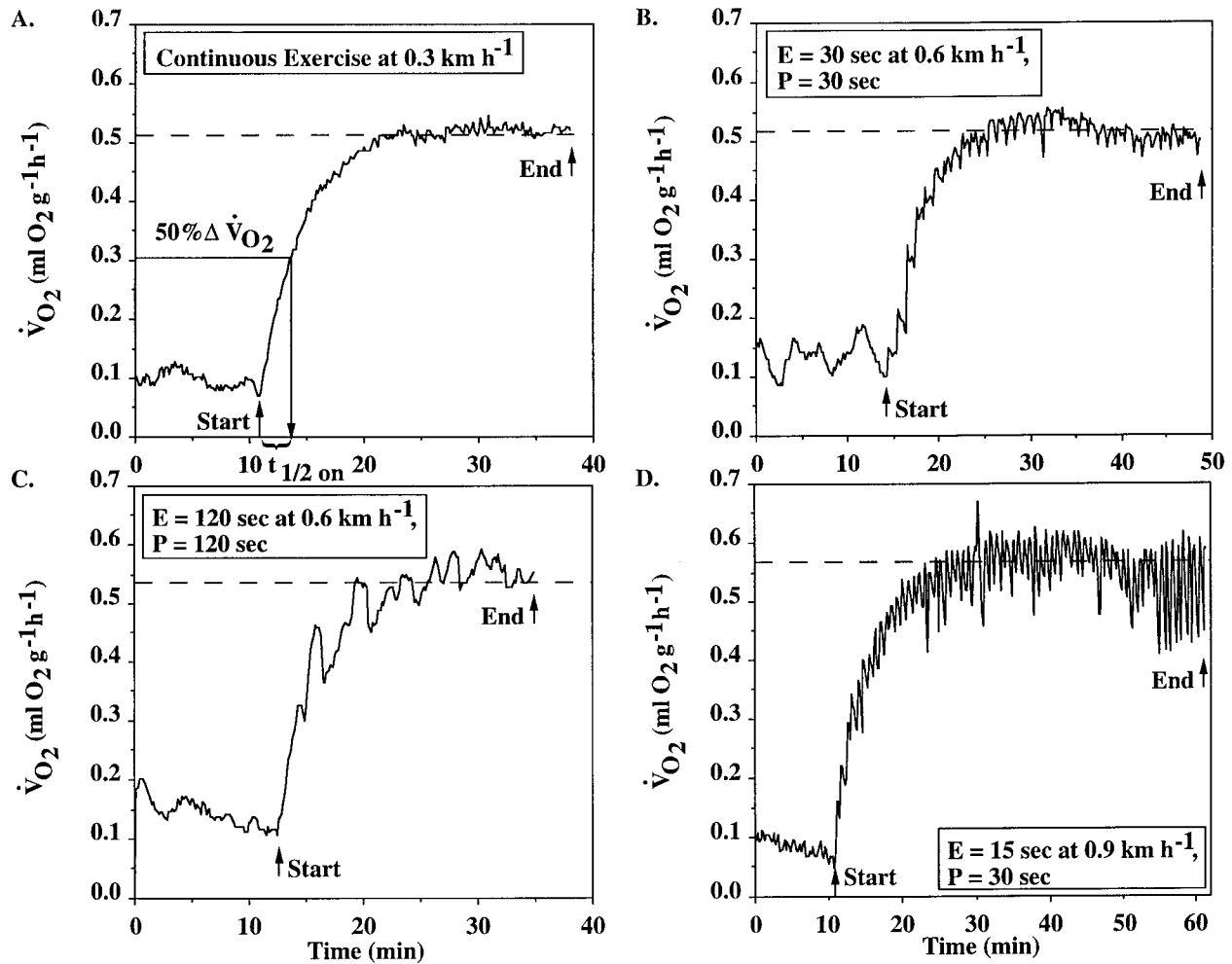


Figure 1. Instantaneous oxygen consumption (\dot{V}_{O_2}) plotted as a function of time for continuous (A) and intermittent (B–D) exercise. We recorded the last 10–15 min of the rest period before the start of the exercise bout. The exercise (E) and pause (P) durations and exercise speed are indicated for the intermittent exercise protocols (B–D). The maximum aerobic speed is 0.33 km h^{-1} (Autumn et al. 1994). The dashed line indicates steady state \dot{V}_{O_2} for continuous exercise or the average aerobic cost of intermittent exercise. The half-time for oxygen uptake at the onset of exercise ($t_{1/2on}$) is illustrated in Figure 1A. Exercise trials ended when the geckos fatigued.

$p < 0.001$), where T_{end} is in hours and v is in km h^{-1} (Fig. 2). This endurance equation was not significantly different from previous data on geckos (homogeneity of slopes test, $F_{1,31} = 4.03$, $p > 0.05$; Autumn et al. 1994). Therefore the two data sets were combined to give the equation $T_{end} = 0.027v^{-2.73}$ ($n = 35$ trials; $p < 0.001$), which was used to construct Figure 2.

Intermittent Exercise. Geckos alternating 15 s of exercise with a 30-s pause period (duty cycle = 0.33) had 10.8-fold greater distance capacity than those exercising continuously at the same absolute speed (0.90 km h^{-1} ; $p < 0.05$; Fig. 2) and a 1.7-fold increase in distance capacity compared with those exercising continuously at the same average speed (0.30 km h^{-1} ; $p < 0.05$; Fig. 2).

For animals exercising intermittently with a duty cycle of 0.5 when E was either 30 s or 120 s, the distance capacity was not significantly different from continuous exercise at the same average speed (0.3 km h^{-1} ; $p > 0.05$ for both comparisons; Fig. 2). However, when E was 30 s, the distance capacity for intermittent locomotion was 2.2-fold greater than for continuous locomotion at the same absolute speed (0.6 km h^{-1} ; $p < 0.05$; Fig. 2).

Discussion

Intermittent Locomotion Can Increase Distance Capacity in Geckos

When lizards move intermittently, locomotor performance limits can be altered. While the distance capacity (i.e., an index

Table 2: Interspecific comparison of distance capacity during intermittent locomotion: increase or decrease (%) relative to continuous exercise at same average speed

	<i>Ocy-pode quadrata</i> (15°C)	<i>Tetratoscinicus przewalskii</i> (24°C)	<i>Ocy-pode quadrata</i> (24°C)
$t_{1/2on}$ (s)	93	83	29
$t_{1/2off}$ (min)	~7–8	3.7	~4
Protocol:			
1	+233%	+67%	...
2	+352%	NS	-70%
3	NS	NS	+119%

Note. Intermittent protocols are listed in Table 1. The same exercise and pause durations and similar relative exercise speeds were used in the ghost crab studies. Values are increases (+) or decreases (-) in distance capacity for intermittent locomotion compared with continuous locomotion at the same average speed. NS = no significant difference between intermittent and continuous exercise. Data for the ghost crab at 15°C are from Weinstein and Full (1998). Data for the ghost crab at 24°C are from Full (1987) and Weinstein and Full (1992). Protocol 1 was not measured for ghost crabs at 24°C.

of endurance) for continuous exercise decreased with an increase in exercise speed in the frog-eyed gecko (Fig. 2), distance capacity could be increased by alternating brief movements with brief pauses. Our most significant finding was that geckos alternating 15 s of exercise with 30-s pauses traveled almost two times farther before fatigue than if they moved continuously at the same average speed, 0.3 km h^{-1} , a speed that is less than the MAS, despite moving at a speed that was 270% of the MAS during the exercise periods (Fig. 2).

Oxygen Uptake Kinetics Correlate with Intermittent Exercise Regimes That Alter Distance Capacity

Previously, we have shown that the exercise-and-pause intervals that increase distance capacity are temperature sensitive in a crab (Weinstein and Full 1998). At low temperatures, slower oxygen uptake kinetics and a lower metabolic rate favor shorter exercise periods, within which metabolic disturbances are minimized. At high temperatures, the kinetics are faster, and longer exercise periods, coupled with proportionately longer recovery periods, are favored.

This article advances our previous findings by showing that the intermittent exercise regimes that increase distance capacity differ among species. As we have seen for the effect of temperature in crabs, we suspect that the differences in performance among species may be related to oxygen uptake kinetics. Similar kinetics for *Tetratoscinicus przewalskii* and the ghost crab (Weinstein and Full 1992, 1998) permit a direct comparison of the intermittent exercise regimes that increase distance capacity for these species (Table 2). The $t_{1/2on}$ time for *T. prze-*

walskii measured in this study, 83 s at 25°C, is similar to that of a 15°C ghost crab (93 s; Weinstein and Full 1998) but slower than a ghost crab exercising at 24°C (29 s; Full 1987). The $t_{1/2off}$ for *T. przewalskii* measured in this study was 224 s (3.7 min; 25°C), which is faster than that of a 15°C ghost crab (~7–8 min; Weinstein and Full 1998) but similar to that of a 24°C ghost crab (~4 min; Full 1987).

The results from this study suggest that the slower oxygen uptake kinetics of *T. przewalskii* compared with 24°C ghost crabs favor shorter exercise periods, just as we found for 15°C ghost crabs (Weinstein and Full 1998). The only intermittent exercise regime that increased distance capacity compared with continuous exercise at the same average speed for *T. przewalskii* was the 15-s exercise/30-s pause protocol (Fig. 2). The same intermittent exercise protocol also increased distance capacity for 15°C ghost crabs (Weinstein and Full 1998). In contrast, a 120-s exercise period alternated with a 120-s pause period significantly increased distance capacity compared with continuous locomotion at the same average speed for a 24°C ghost crab (Weinstein and Full 1992) but not for ghost crabs exercising at 15°C (Weinstein and Full 1998) or *T. przewalskii* (Fig. 2).

While the oxygen uptake kinetics of *T. przewalskii* are slow compared with 24°C ghost crabs, the kinetics are fast compared with other lizards when we take the effects of temperature into consideration. The $t_{1/2on}$ for *T. przewalskii* (83 s at 25°C) is faster than the $t_{1/2on}$ reported for other lizards (<2–5 min at 35°–40°C; Gleeson and Bennett 1982; Gleeson and Dalessio 1989). The $t_{1/2off}$ for *T. przewalskii*, 224 s (3.7 min; 25°C), is also faster than the $t_{1/2off}$ reported for other lizards (~4–12 at 35°–40°C; Gleeson and Bennett 1982; Wagner and Gleeson 1996). We predict that the oxygen uptake kinetics of nocturnal lizards are faster than those of diurnal lizards at comparable body temperatures. Assuming nocturnal geckos possess more rapid oxygen uptake kinetics than diurnal lizards, then perhaps rapid oxygen uptake kinetics is an adaptation that determines the exercise intervals that nocturnal geckos could select to increase distance capacity

Table 3: Average aerobic cost for continuous and intermittent locomotion

Protocol	Intermittent Exercise	Continuous Exercise	
		Same Absolute Speed	Same Average Speed
137 (.06)	.39 (.07)	.50 (.04)
256 (.01)	.51 (.01)	.50 (.04)
351 (.046)	.51 (.01)	.50 (.04)

Note. Values for average aerobic cost (in $\text{mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$) are means \pm 1 SE (in parentheses). The intermittent protocols are listed in Table 1. $n = 5$ for each intermittent and continuous exercise protocol. Animals exercising continuously at 0.9 km h^{-1} (protocol 1) fatigued before reaching a steady state, so the value reported is for the peak $\dot{V}\text{O}_2$. Within each protocol, we did not find any significant differences among exercise groups.

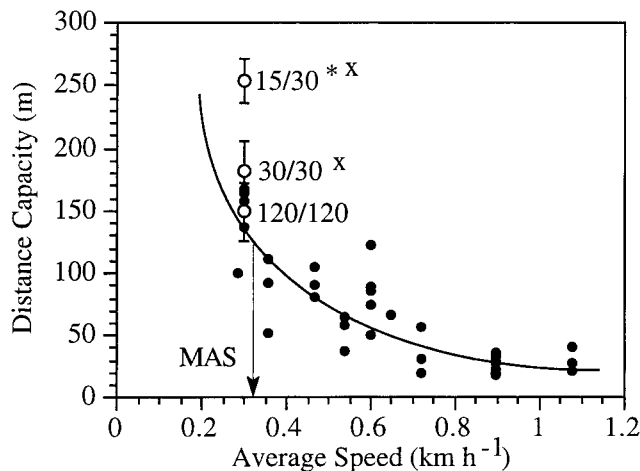


Figure 2. Distance capacity plotted as a function of average speed for continuous and intermittent exercise. The solid curve and filled symbols represent the distance capacity for continuous locomotion. Open symbols represent the distance capacity for intermittent locomotion (mean \pm 1 SE). Numerals next to the open symbols indicate the intermittent exercise protocol (see Table 1). Asterisks indicate significant difference from continuous locomotion at the same average speed. Crosses indicate significant difference from continuous locomotion at the same absolute speed.

during intermittent locomotion. Only future phylogenetic analyses of oxygen uptake kinetics and intermittent locomotor performance will reveal if rapid oxygen uptake kinetics along with a low C_{\min} represent a performance advantage.

Hypothesized Mechanisms of Metabolic Disturbance and Recovery

Oxygen uptake kinetics could be a useful predictor for intermittent exercise performance. Our previous work on the effects of temperature on continuous exercise at the same relative workload (Weinstein and Full 1998) indicates that slower oxygen uptake kinetics (e.g., a longer $t_{1/2\text{on}}$) are correlated with increased reliance on nonoxidative metabolism. Lizards accumulate lactate rapidly during intense activity, but removal is slow (see review by Gleeson 1996). Blood and muscle lactate concentrations may remain elevated long after $\dot{V}O_2$ returns to preexercise levels (Gleeson 1980; Gleeson and Bennett 1982; Wagner and Gleeson 1996; but see Gleeson and Dalessio 1989). Slow rates of lactate removal are likely to have metabolic and performance consequences for lizards moving intermittently. In one experiment that illustrates this point, the iguana, *Amblyrhynchus cristatus*, ran continuously to exhaustion (approximately 9 min) at a single treadmill speed and was allowed a partial (15-min) recovery. Reexhaustion at the same speed elicited the same $\dot{V}O_{2\text{ss}}$ but reduced endurance by about 50% (Gleeson 1980).

We suggest there may be a critical exercise duration related to the muscle's reliance on nonoxidative metabolism at the onset of each intermittent exercise bout. For the gecko, the critical exercise period appears to be ≤ 30 s (Fig. 2), which is approximately one-third the $t_{1/2\text{on}}$. In addition, there may be a critical pause duration necessary to increase the distance capacity for intermittent exercise relative to continuous exercise at the same average speed. The critical pause duration may be related to the rate of lactate removal and the resynthesis of glycogen and high-energy phosphate stores.

Average Aerobic Cost of Intermittent Locomotion Was Not Different from Continuous Locomotion

Aerobic cost measurements can be used to estimate the metabolic cost of intermittent locomotion. The metabolic cost of low-speed continuous locomotion can be determined for lizards by measuring $\dot{V}O_{2\text{ss}}$ since metabolic energy production for continuous locomotion at speeds below the MAS is primarily aerobic even though lactate may accumulate during the initial phase of activity (Gleeson and Bennett 1982). In contrast, there is no $\dot{V}O_{2\text{ss}}$ for intermittent locomotion. When *T. przewalskii* moved for ≤ 120 s, as it did during intermittent locomotion, it did not attain a steady state $\dot{V}O_2$ since $t_{1/2\text{on}}$ was 83 s. Similarly, when it paused for ≤ 120 s, $\dot{V}O_2$ declined but did not return to resting rates since $t_{1/2\text{off}}$ was 224 s. As a result, when *T. przewalskii* moved intermittently, $\dot{V}O_2$ oscillated around an average value. This average $\dot{V}O_2$ was not different from the aerobic cost of continuous exercise at the same average speed (Table 3).

While this study and our earlier studies on ghost crabs indicate that the average aerobic cost of intermittent locomotion is the same or higher than the cost of continuous exercise at the same average speed (Table 3; Weinstein and Full 1992, 1998), none of these studies has measured the total metabolic cost of intermittent locomotion. Since high-intensity exercise results in the accumulation of lactate in lizards and our previous results indicate that ghost crab muscles have elevated lactate and depleted high-energy phosphate stores at the end of a bout of intermittent exercise (Weinstein and Full 1992, 1998), the total metabolic cost of intermittent exercise should include both aerobic and anaerobic energy production. Furthermore, if anaerobic costs are added to aerobic costs, the total metabolic cost of intermittent exercise is likely to be greater than for continuous locomotion.

Intermittent Locomotion Can Augment the Increase in Distance Capacity Resulting from a Low Cost of Locomotion

Animals fatigue rapidly when they move continuously at speeds that elicit their $\dot{V}O_{2\text{max}}$. Endurance or distance capacity can be increased by either increasing $\dot{V}O_{2\text{max}}$ or decreasing the minimum cost of locomotion (C_{\min} ; Full et al. 1988; Gatten et al. 1992). Increasing $\dot{V}O_{2\text{max}}$ without altering C_{\min} increases the

MAS. Decreasing the cost of locomotion without altering $\dot{V}O_{2\max}$ also increases MAS.

Autumn et al. (1997) hypothesized that active-foraging nocturnal lizards have evolved a low C_{\min} , which partially offsets the effect of a $\dot{V}O_{2\max}$ reduced by low temperature. This nocturnality hypothesis is based on at least two assumptions. First, the hypothesis rests on data collected from animals moving continuously for long exercise durations. Second, it requires that geckos in nature move at speeds exceeding the predicted MAS of their hypothetical diurnal ancestors but below the measured MAS of extant nocturnal species (Autumn et al. 1999). Only if these assumptions are true could the additional performance capacity result from the evolution of a low C_{\min} alone.

Results from this study compel us to suggest a second parameter, intermittent locomotion, which could also have evolved to increase locomotor performance at low nocturnal temperatures. We propose this hypothesis for several reasons. First, most lizards, including geckos (K. Autumn, personal communication), move intermittently. Second, because MASs are slow compared with an animal's range of sprinting speeds, animals often move at speeds exceeding MAS. Third, by moving intermittently at speeds exceeding MAS and coupling each exercise bout with a pause, distance capacity can be increased by as much as 4.5-fold (or, alternatively, decreased by as much as 90%) compared with continuous locomotion at the same average speed (Weinstein and Full 1992, 1998).

The consequence of intermittent locomotion can be viewed not as a lowering of C_{\min} but as an effective increase in $\dot{V}O_{2\max}$ and, therefore, MAS (Full and Weinstein 1992; Fig. 3). Intermittent locomotion can decrease the relative workload at a given speed. A speed that requires 93% $\dot{V}O_{2\max}$ during continuous locomotion only demands the equivalent of 72% $\dot{V}O_{2\max}$ if the work is done intermittently with 15-s exercise periods matched with 30-s pauses (Fig. 3). Moving intermittently may increase the "effective MAS" by making the distance capacity of geckos moving intermittently at a low body temperature more similar to lizards moving continuously with a warmer body temperature, thus reducing performance limitations associated with low body temperature. We contend that the intermittent locomotor behavior of the frog-eyed gecko can augment the increase in endurance capacity resulting from a low C_{\min} .

Alternatively, intermittent locomotion at speeds exceeding MAS can decrease distance capacity by as much as 90% compared with continuous locomotion at the same average speed (Weinstein and Full 1992, 1998). Depending on the species and exercise/pause regimes, intermittent locomotion could reduce an animal's "effective MAS" and therefore counteract the performance advantage of a low C_{\min} .

Future research is necessary to test the effect of intermittent locomotion on the nocturnality hypothesis. Additional species must be studied in a phylogenetic framework to establish the generality and evolutionary relationships of intermittent lo-

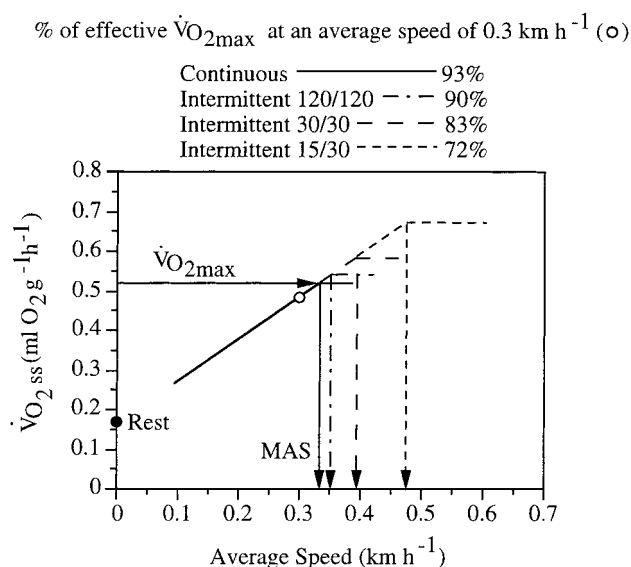


Figure 3. Intermittent locomotion decreases relative workload by increasing effective maximal rate of oxygen consumption ($\dot{V}O_{2\max}$). $\dot{V}O_{2ss}$ increases linearly with speed until geckos attain $\dot{V}O_{2\max}$ at the maximum aerobic speed (MAS). An exercise speed of 0.3 km h^{-1} elicits 93% of $\dot{V}O_{2\max}$. Geckos increase their effective $\dot{V}O_{2\max}$ and MAS by moving intermittently at the same average speed (dashed lines). The submaximal workload becomes a smaller fraction (as low as 72%) of the effective $\dot{V}O_{2\max}$ during intermittent locomotion.

comotor regimes. Mechanistic explanations should be explored, beginning with an examination of oxygen uptake kinetics. Locomotor behavior must be rigorously quantified in the field.

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