

LOCOMOTOR PERFORMANCE AT LOW TEMPERATURE AND THE EVOLUTION OF NOCTURNALITY IN GECKOS

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Abstract.—Nocturnal geckos are active at body temperatures 10–35°C below the thermal optima for maximum rate of aerobic metabolism ($\dot{V}_{O_{2max}}$) of diurnal lizards. Therefore, given ancestral (diurnal) lizard physiology, nocturnality causes a substantial thermal handicap in locomotor performance. In prior studies, we hypothesized that a low minimum cost of locomotion (C_{min}) in geckos was an adaptation that increased locomotor endurance capacity at low, nocturnal temperatures. However, C_{min} is only part of an integrated system that, in conjunction with the maximum rate of oxygen consumption, sets the maximum speed that can be sustained aerobically (termed the maximum aerobic speed or MAS). We conducted the first phylogenetic analysis of MAS and $\dot{V}_{O_{2max}}$ in lizards and found that the greatest changes in MAS, C_{min} and $\dot{V}_{O_{2max}}$ (at activity temperatures) in the evolutionary history of lizards all coincided with the evolution of nocturnality in geckos. Geckos active at 15–25°C did not become optimized for nocturnal temperatures, or fully offset the thermal effects of nocturnality by evolving maximal rates of oxygen consumption comparable to diurnal lizards active at 35°C. Geckos did evolve MAS twice that of diurnal lizards running at low temperatures by evolving a remarkably low C_{min} . Allometric analysis and phylogenetically independent contrasts of $\dot{V}_{O_{2max}}$, C_{min} , and MAS indicate a 72% evolutionary decrease in $\dot{V}_{O_{2max}}$ (at activity temperatures) and a 50% evolutionary decrease in C_{min} concordant with the evolution of nocturnality in geckos. Experimental measurements show that decreased C_{min} in six species of gecko increased MAS by 50–120% compared to diurnal lizards at low temperatures. Thus, geckos sufficiently overcame the near paralyzing effects of nocturnal temperatures, but only offset about 50% of the decrease in MAS resulting from the low maximum rate of oxygen consumption. Although the nocturnal environment remains severely suboptimal, the evolution of a low cost of locomotion in the ancestor of geckos was highly adaptive for nocturnality. We also present a generalized approach to ecophysiological evolution that integrates phylogeny with the causal relationships among environment, physiology, and performance capacity. With respect to a clade, two hypotheses are central to our integrative approach: (1) a change of an environmental variable (e.g., temperature) causes a performance handicap; and (2) evolution of a physiological variable (e.g., minimum cost of locomotion [C_{min}]) increases performance in the derived environment. To test the hypothesis that evolution of a physiological variable is adaptive in nature, we suggest determining if individuals in nature perform at levels exceeding the performance capacity of their hypothetical ancestors and if this additional performance capacity is due to the evolution of the physiological variable in question.

Key words.—Energetics, exercise, integrative biology, lizard, locomotion, optimality, physiology.

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Lizards are ancestrally diurnal, and most major lizard clades have remained exclusively (e.g., Iguania, Teiidae, Lacertidae, Varanidae) or predominantly (e.g., Scincidae) diurnal. Nocturnality has evolved in lizards only several times during the past 200 million years, and most nocturnal lizards are geckos (clade Gekkonoidea; Kluge 1987). This study focuses on physiological and performance consequences of the evolution of nocturnality in this large and diverse group. Because of reduced environmental temperatures in the absence of solar radiation, nocturnal geckos are usually active with body temperatures 10–35°C lower than those of typical heliothermic, diurnal lizards (Cowles and Bogert 1944; Huey et al. 1989; Autumn et al. 1994, 1997).

Until recently, geckos have been classified as “reclusive” or “sit-and-wait” predators (Andrews and Pough 1985; Pianka 1986). There is an emerging view of geckos as active, olfactory predators that sustain locomotion for long distances (Werner et al. 1997a,b). Geckos are unique among squamates in their degree of olfactory development (Schwenk 1995). Active foraging using olfactory cues may even be the ancestral state for the gecko clade (Cooper 1995). Surprisingly,

although geckos are well suited to nocturnality, gecko physiology is not optimized to perform best at the low body temperatures they experience in nature. (We define the thermal optimum as the temperature at which a given performance variable is maximized, not necessarily the temperature that maximizes fitness currently or in the past.) Thermal optima for a variety of performance variables are high (approximately 35°C or greater) in both nocturnal and diurnal lizards (Huey et al. 1989; Autumn and Full 1994; Autumn and DeNardo 1995; Autumn et al. 1994, 1997; but for hearing see Werner 1983). Given a Q_{10} of 2.5 (Bennett 1982) and a thermal optimum of 35°C, activity at 20°C results in a 75% decrease in performance. This raises the question of how geckos manage to sustain locomotion at the low, nocturnal temperatures they experience in nature.

Sustained Locomotion at Low Temperature

Endurance capacity (time to fatigue at aerobically submaximal speeds) and the greatest speed that can be sustained by aerobic metabolism (maximum aerobic speed, MAS) are strongly affected by temperature in both diurnal (for review see Bennett 1982) and nocturnal lizards (Autumn et al. 1994, 1997). Huey and Pianka (1981) found that foraging diurnal lizards (with body mass of approximately 6 g) move at speeds of 0.39–0.56 km h⁻¹. This speed range is far greater than the

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maximum sustainable speed of small diurnal lizards at typical nocturnal temperatures. Diurnal lizards become sluggish at temperatures below 20°C, and must resort to supplemental anaerobic metabolism to move at even very slow speeds (e.g., 0.1 km h⁻¹; Bennett 1982). In contrast, nocturnal geckos can sustain speeds up to three times that of comparable diurnal lizards at low temperature (0.24–0.33 km h⁻¹; Autumn et al. 1994, 1997). Thus, at low, suboptimal temperatures, nocturnal geckos have performance approaching that of diurnal lizards at high, optimal temperatures.

The evolution of nocturnality in geckos now seems puzzling because it is not clear how to reconcile the adaptive evolution (greatly increased sustained locomotor performance) on one hand and the maladaptive evolution (thermal suboptimality) on the other (see Endnote). A traditional character-mapping approach to testing hypotheses of adaptation (for review see Losos and Miles 1994) cannot solve this puzzle. Without integrating the mechanistic, physiological interactions among the reconstructed characters on the phylogenetic tree (Mangum and Hochachka 1998), we cannot causally separate the performance consequences of change at the environmental level from adaptive changes at the physiological level.

In prior studies, we hypothesized that excellent fuel economy (low minimum cost of locomotion, C_{\min}) is a shared, derived character in geckos that increases locomotor endurance capacity at low, nocturnal temperatures (the nocturnality hypothesis; Autumn et al. 1994, 1997; Fig. 1). However, C_{\min} is only part of a complex integrated system that, in conjunction with the maximum rate of oxygen consumption ($\dot{V}_{O_{2\max}}$), sets the maximum speed that can be sustained aerobically (MAS). Locomotion at speeds below the MAS is fueled primarily by aerobic metabolism and is sustainable for long periods of time. At speeds above the MAS, fatigue occurs rapidly because locomotion is fueled primarily by accelerated glycolysis (John-Alder and Bennett 1981; Gatten et al. 1992). The MAS is a function of both $\dot{V}_{O_{2\max}}$ and fuel economy (minimum cost of locomotion, C_{\min}). C_{\min} determines the speed at which $\dot{V}_{O_{2\max}}$ is attained. Both C_{\min} and $\dot{V}_{O_{2\max}}$ are strongly affected by body mass, and $\dot{V}_{O_{2\max}}$ is highly sensitive to temperature. Because C_{\min} is independent of temperature (John-Alder and Bennett 1981; Rome 1982; Bennett 1983; John-Alder et al. 1983; Bennett and John-Alder 1984; Autumn et al. 1994; but see Weinstein and Full 1994), the thermal sensitivity of MAS and endurance is due primarily to the thermal sensitivity of $\dot{V}_{O_{2\max}}$ (Bennett 1982; Gatten et al. 1992; Autumn et al. 1994; Fig. 2).

Therefore, to test the nocturnality hypothesis that an evolutionary decrease in C_{\min} increased sustained locomotor performance capacity at low temperature in geckos, it is necessary to reconstruct the evolution of each variable and tease apart the separate mechanistic effects of evolutionary change in each of the variables involved in determining MAS: body mass, temperature, $\dot{V}_{O_{2\max}}$ and C_{\min} . To do this, we use an approach that integrates historical and mechanistic biology. We will show how applying this integrative approach solves the evolutionary puzzle of why geckos have increased locomotor performance and are still thermally suboptimal at night. We formalized our methodology so that it can be used to solve similar problems in the evolution of integrated systems.

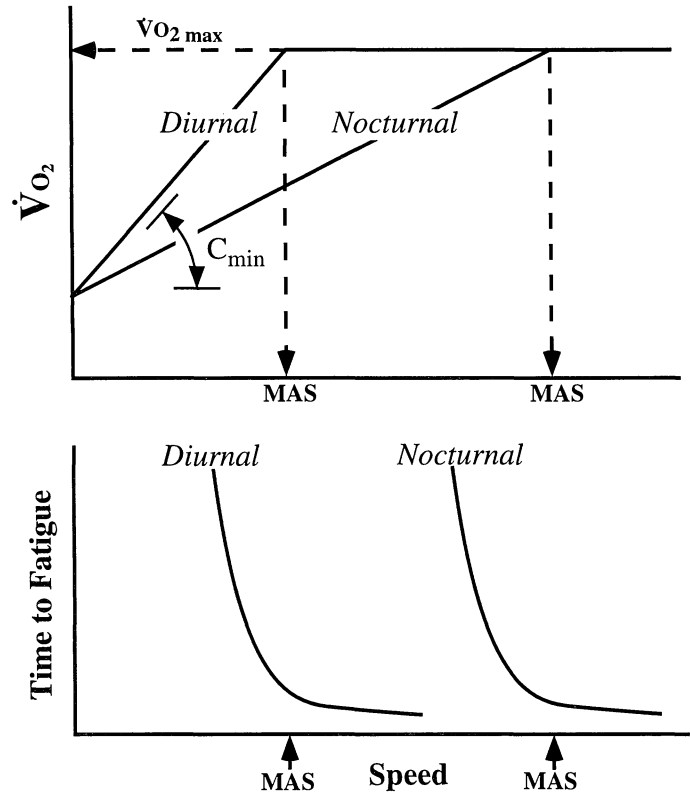


FIG. 1. Theoretical effect of low cost of locomotion (C_{\min}) in nocturnal lizards on endurance capacity. If nocturnal lizards have a lower C_{\min} (they can move further per unit energy) than comparable diurnal lizards, $\dot{V}_{O_{2\max}}$ will be reached at a higher speed. This increased maximum aerobic speed (MAS) increases endurance capacity at sustainable speeds in nocturnal lizards and could offset the thermal handicap of activity at low temperatures.

An Integrative Approach: Mechanism and History

How the relationship between environment, physiology, and performance has evolved is one of the main questions of the emerging field of evolutionary physiology (Garland and Carter 1994; Hochachka 1998; Mangum and Hochachka 1998), and it involves reconstructing the phylogenetic history of environmental, physiological, and performance variables. Mechanistic and evolutionary issues have generally been treated separately (Huey and Bennett 1986; but see Bradley 1994); a remaining challenge is the integration of mechanism and history (Losos 1996; Hochachka 1998; Mangum and Hochachka 1998) to generate quantitatively testable hypotheses of physiological adaptation. Figure 3 is a diagrammatic overview of how we have approached this problem. Mechanism and history form two dimensions that we integrate into our scheme.

Mechanism represents repeatable, controlled experiments that causally link the variables of interest. History forms the second dimension of our integrative approach. This historical dimension is a hypothetical chronicle of past events (O'Hara 1988). The events in this case are evolutionary changes at the environmental and physiological levels (see Huey and Bennett 1986; Huey and Kingsolver 1989). Because it is dif-

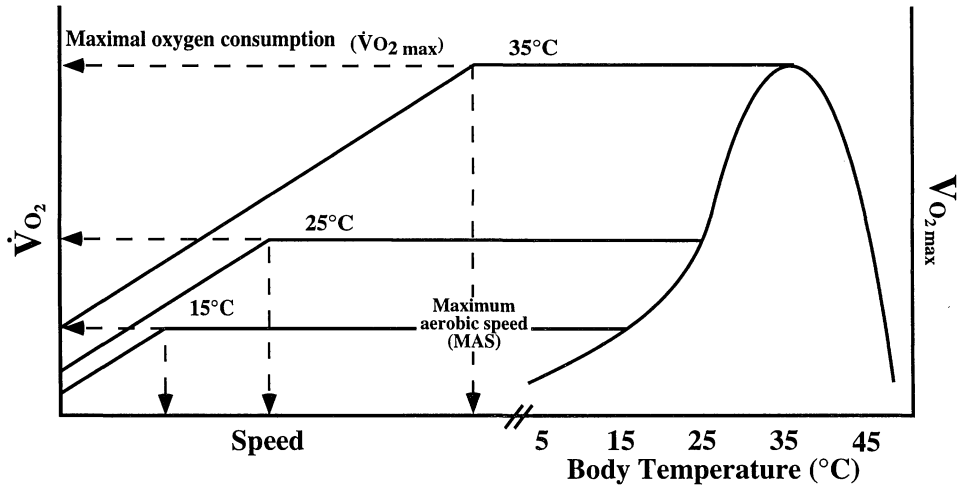


FIG. 2. Theoretical relationship between the rate of oxygen consumption (\dot{V}_{O_2}) and running speed (on the left) and the thermal sensitivity of maximal oxygen consumption (on the right) in ectotherms. For terrestrial locomotion, the aerobic cost, or steady-state \dot{V}_{O_2} increases linearly with running speed. The slope of the \dot{V}_{O_2} -versus-speed line is the minimum cost of locomotion (C_{min} , amount of energy required to move 1 g over 1 km). The maximum aerobic speed (MAS) is the speed at which the maximal rate of oxygen consumption ($\dot{V}_{O_{2max}}$) is reached. Only speeds below the MAS can be sustained for long periods of time. The thermal sensitivity of $\dot{V}_{O_{2max}}$ is the primary component in the thermal sensitivity of the MAS because C_{min} is not thermally sensitive. The range of sustainable speeds is lower at low temperatures (15°C and 25°C) because $\dot{V}_{O_{2max}}$ (and therefore MAS) is reduced.

difficult to reconstruct the past action of natural selection (Lauder 1982; Greene 1986; Huey and Bennett 1986; Huey 1987; Lauder et al. 1993; Lauder 1996), we do not assume that selection for and only for increased performance in a new environment caused evolution at the physiological level.

Our integrative approach centers on two hypotheses that address the effects of evolutionary events on performance.

Hypothesis 1: Given an Ancestral Physiology (f_a), a Derived

Environment (E_d) Imposes a Handicap on Performance (P).—

This hypothesis focuses on the effects of change at the environmental level on performance (Fig. 3). Because physiology is a partial function of the environment ($f_a[E]$), an evolutionary shift to a new environment (E_d) may cause a chronic change in physiological function that in turn causes a decrease (handicap, H) in performance capacity (Fig. 3). The new (derived) performance capacity (P_d) equals ancestral

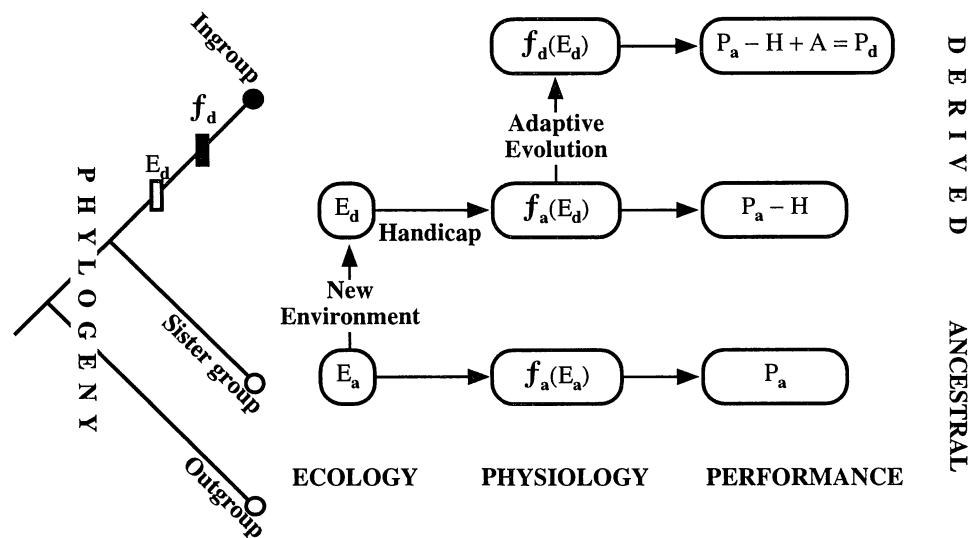


FIG. 3. Diagrammatic overview of the integrative approach used in this study. The horizontal axis represents the causal (experimentally supported) relationships between an environmental variable (E), physiological capacity, and performance capacity. Physiological capacity is a partial function of the environment, $f(E)$. The vertical axis represents phylogeny, and ancestral performance capacity is represented by P_a . If performance capacity is maximal in the ancestral environment (E_a), then E_a is said to be optimal. A shift to a new environment (E_d) causes a change at the physiological level that in turn causes a decrease (handicap, H) in performance capacity. The new (derived) performance capacity (P_d) equals $P_a - H$. Because performance capacity is submaximal, E_d is suboptimal. Evolution of a new physiological state (f_d) changes performance in E_d by A. If A is positive (performance in E_d increases due to f_d), the evolutionary change from f_a to f_d is adaptive. If $A = H$, then $P_d = P_a$, and the evolution of f_d fully offsets the handicap of E_d .

performance capacity (P_a) minus H. Because performance capacity is submaximal, E_d is by definition suboptimal for f_a . E_a may be optimal (in that case P_a would be maximal), but not necessarily. The hypothesis is that the ancestral environment provides greater absolute performance than the derived environment, given ancestral physiology.

Hypothesis 2: The Derived Physiology (f_d) Increases Performance in the Derived Environment (E_d).—This hypothesis focuses on the effects of evolutionary change at the physiological level on performance (see Huey and Bennett 1987). Evolution of a new physiological state (f_d) changes performance in E_d by amount A. If A is positive (performance in E_d increases due to f_d), the evolutionary change from f_a to f_d is adaptive (Greene 1986; Losos and Miles 1994) and may be termed an aptation (Baum and Larson 1991; Larson and Losos 1996). If A equals H, then P_d equals P_a , and the evolution of f_d fully offsets the handicap of E_d . However, even if f_d fully offsets the handicap of E_d , E_d may not be optimal for performance (see below). This is because the adaptive change in performance may not be dependent on the presence of the handicap (f_d allows increased performance in E_a as well as in E_d). The hypothesis is that the derived physiology provides greater absolute performance than the ancestral physiology, in the derived environment. Note that we are separating the model into two steps for logical, not biological reasons. The changes in environment and physiology could be sequential in either order: a taxon could enter a new environment and subsequently evolve a better physiology (for unspecified selective reasons) or the new physiology could predate the new environment and might have even made colonization of the new environment possible. The changes in environment and physiology could also be simultaneous, but because we are not concerned with reconstructing the past action of selection, the order of events does not affect our conclusions.

Optimality

Current and past approaches to studying the evolutionary effects of environmental variation on performance have focused on critical minima and maxima (Cowles and Bogert 1944; Gilchrist, et al. 1995) or on performance breadth and optima (e.g., Hertz et al. 1983; for an overview see Huey and Stevenson 1979). In particular, the performance breadth and optima approach has been the most popular and productive lately (e.g., Huey and Kingsolver 1993; Bauwens et al. 1995; Gilchrist et al. 1997). However, natural selection is likely to focus on absolute not relative performance (Huey and Bennett 1987), and adaptive evolution may occur without maximizing relative performance (optimality). For example, during the evolution of nocturnality in geckos, adaptive evolution has occurred (absolute performance has increased), but optimality has not (Huey et al. 1989; Autumn and Full 1994; Autumn et al. 1994, 1997). Because of this, we extended the models of evolution of performance curves presented by Huey and Kingsolver (1989): our new terms describe both absolute and relative performance (see Fig. 4) in the context of an evolutionary response to environmental change.

Huey and Bennett (1987) described a hypothesis of “perfect coadaptation” where lizard body temperatures match

physiological optima. They also described a case of “partial coadaptation,” where evolution of the relative performance optimum only partially matched a change in environment. With partial coadaptation, the derived species experiences a performance decrease in the derived environment, but not as great a decrease as the ancestral species would experience in the derived environment. Here, we expand Huey and Bennett’s (1987) classification of coadaptation of performance optima and environment into two independent criteria, optimality and adaptive evolution (Fig. 4). This has the advantage of separating hypotheses of adaptive evolution that focus on absolute performance from hypotheses of optimality that focus on relative performance (for a discussion of why this is important see Hailman 1988). The hypothesis of adaptive evolution is that part or all of the handicap has been offset, whereas the hypothesis of optimality is that the derived environment is optimal for the derived physiology.

Consider two steps in an adaptive process: (1) ancestral physiology enters new environment, causing a handicap; and (2) evolution of a new physiology increases performance in the new environment. There are several ways that adaptation and optimization can occur. For example, assume that the ancestral environment, E_a , is optimal for the performance of P, given the ancestral physiology, f_a . By definition, P is maximized by $f_a(E_a)$. Also assume that hypotheses 1 and 2 (above) are true, and the derived environment, E_d , is suboptimal for f_a , and the derived physiology, f_d , increases performance in E_d . By our definition, the change from f_a to f_d is adaptive. If the change from f_a to f_d fully offsets the handicap of E_d then derived performance in E_d equals ancestral performance in E_a . E_d is optimal if performance is maximized by f_d in E_d (Fig. 4A). This is not the only way to fully offset the handicap: even if f_d fully offsets the handicap of E_d , performance may be still greater in another environment (Fig. 4B), making E_d suboptimal. If the change from f_a to f_d does not fully offset the handicap of E_d , then derived performance in E_d is less than ancestral performance in E_a . In this case, E_d may (Fig. 4C) or may not (Fig. 4D) be optimal given the derived physiology.

The hypothetical examples in Figure 4A–D represent a range of possibilities, but are by no means exhaustive. The main point is that adaptive physiological evolution can be optimizing and fully offset (compensate for) the handicap (Fig. 4A), not be optimizing and fully offset the handicap (Fig. 4B), be optimizing and not fully offset the handicap (Fig. 4C), and not be optimizing and not fully offset the handicap (Fig. 4D). In the examples above (and in Fig. 4), we represent the ancestral condition as optimal, but this need not be the case. We only assume that given the ancestral physiology, performance is greater in the ancestral environment than in the derived environment: adaptive physiological evolution increases performance in the derived environment relative to the ancestral physiology.

An Application of the Integrative Approach: Performance at Low Temperature and the Evolution of Nocturnality in Geckos

Homology of Nocturnality in Geckos

The homology of nocturnality is well supported in geckos by both functional (Walls 1942) and phylogenetic evidence.

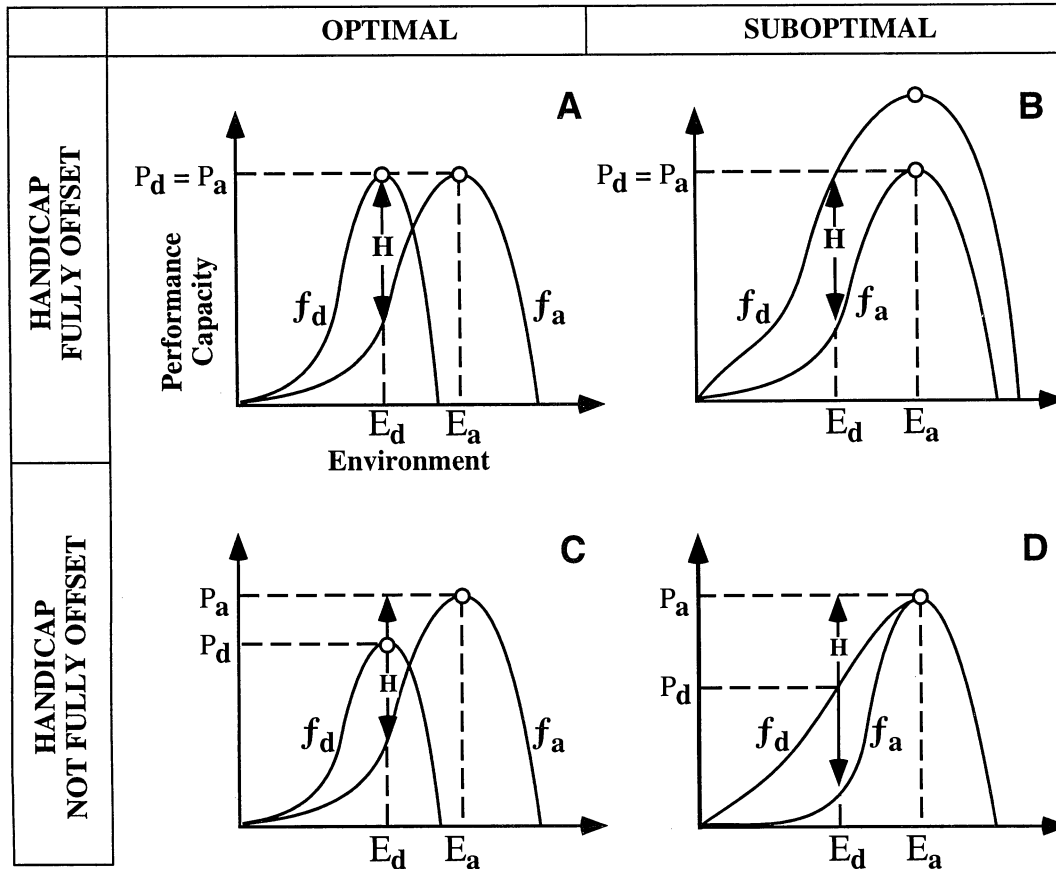


FIG. 4. Hypotheses of the evolution of an environmental variable, physiological capacity, and their combined effect on performance capacity (parts A, C, D based on Huey and Bennett 1987; Huey and Kingsolver 1989). This figure shows the independence between hypotheses of adaptive evolution and hypotheses of optimality. In all cases, ancestral performance capacity (P_a) is maximal in the ancestral environment (E_a), and the derived environment (E_d) represents a handicap (H ; decrease in performance capacity), given the ancestral physiology (f_a). In all cases, adaptive evolution has taken place: the derived physiology (f_d) increases derived performance capacity (P_d), relative to f_a in E_d . (A) $P_d = P_a$, therefore the evolution of f_d fully offsets the handicap of E_d . Also, because P_d is maximized in E_d , E_d is optimal for f_d . (B) f_d fully offsets the handicap of E_d , but E_d is not optimal. This is because the adaptive change in physiology allows increased performance in E_a as well as in E_d . (C) The evolution of f_d does not fully offset the handicap of E_d , but E_d is optimal. (D) The evolution of f_d does not fully offset the handicap of E_d , and E_d is not optimal.

The Eublepharidae, the sister clade to all other geckos (Kluge 1987), contains only nocturnal species. Secondarily diurnal geckos such as species of *Lygodactylus*, *Phelsuma*, *Rhoptropus*, and *Sphaerodactylus* are deeply nested within the gecko tree, and cladistic revisions of gecko systematics are unlikely to affect the parsimony of nocturnal homology for the Gekonoidea. A preliminary phylogenetic analysis of 145 living taxa also supports the hypothesis that the most recent ancestor of geckos was nocturnal (Autumn and Full 1994). Thus, the most parsimonious model is that the direction of evolution was from diurnality to nocturnality and that nocturnality is a homologous character state in geckos.

The Nocturnality Hypothesis

We conducted laboratory measurements of the physiological variables underlying sustained locomotor performance in six formerly unstudied species of geckos. Our goal was to test the hypothesis that an evolutionary decrease in minimum cost of locomotion caused an increase in sustained

locomotor performance capacity at low temperature in geckos. This hypothesis is equivalent to hypothesis 2 (above) in our approach, and has been referred to as the "nocturnality hypothesis" (Autumn et al. 1997). There is substantial support for hypothesis 1 (above) in lizards (for review see Bennett 1982), and we did not test it directly in this study. Data presented in two prior studies (Autumn et al. 1994, 1997) support the nocturnality hypothesis. Frog-eyed geckos (*Teratoscincus przewalskii*; Autumn et al. 1994) and banded geckos (*Coleonyx variegatus*; Autumn et al. 1997) have one-half to one-third the C_{min} of comparable diurnal lizards, which may indicate an evolutionary decrease in C_{min} in geckos. Three key questions remain that make this an ideal system in which to apply our integrative approach. (1) Is a low C_{min} a general pattern derived at the level of geckos or a unique character of the two species studied thus far? (2) Did the decrease in C_{min} increase performance capacity (MAS) in the most recent common ancestor of living geckos? (3) How can geckos have increased performance at low temperatures and

yet low temperatures remain suboptimal? To answer these questions, we measured C_{\min} in six species of nocturnal gecko (*Eublepharis macularius*, *Pachydactylus bibroni*, *Diplodactylus galeatus*, *D. intermedius*, *Nephrurus asper*, and *N. levis*) and used the method of phylogenetically independent contrasts (Felsenstein 1985) to evaluate the evolution of the integrated system formed by the combined effects of temperature, body mass, $\dot{V}_{O_{2\max}}$ and C_{\min} , on MAS.

METHODS

Animals and Husbandry

All lizards measured were adult specimens. We conducted our measurements on the "thermoregulatory treatment group" of *Eublepharis macularius* from the study by Autumn and DeNardo (1995) after they reached maturity. (The animals were originally acquired as captive-born neonates from the Institute for Reptile Reproduction, Hayward, CA). *Pachydactylus bibroni* were collected and imported from Namibia (near Spitzkoppe) in October 1996 under permits from the Namibia Ministry of Environment and Tourism (no. 19913, no. 22941). All other species (*Diplodactylus galeatus*, *D. intermedius*, *Nephrurus asper*, *N. levis*) were collected and imported from the Northern Territory, Australia (near Alice Springs), in December 1994 under permits from the Northern Territory (no. DASC94020) and Australian Wildlife Protection Authority (no. PWS P941937).

Lizards were housed individually or in pairs in clear plastic terraria. Cages contained utility-grade sand (*Diplodactylus*, *Nephrurus*) or paper towels (*Eublepharis*, *Pachydactylus*) as a substrate and shelters (deli cups, PVC pipe segments) for refuge. Lizards were provided a thermal gradient by placing a 7.5 cm wide Flexwatt heating strip (Flexwatt Corp., West Wareham, MA) under one end of each cage. Ambient temperature of the animal housing room was $24 \pm 1.5^\circ\text{C}$, while the cage space immediately above the heat strip was 35°C . Light and heat were synchronized on a 13:11 L:D cycle. Lizards were fed three- to six-week-old crickets to satiation three times per week. Crickets were dusted with calcium carbonate powder prior to feeding. Cages were sprayed with water twice per week.

Oxygen Consumption Measurements

We exercised the lizards in a miniature treadmill-respirometer at body temperatures of 25°C (*E. macularius* and *P. bibroni*) or 20°C (*Nephrurus* and *Diplodactylus* sp.). Air leaving the chamber passed through a filter composed of Drierite, Ascarite, and Drierite layers (in that order) to remove water and CO_2 . The oxygen concentration was monitored by an O_2 analyzer (Ametek S3A) interfaced with a personal computer (Macintosh II) and data acquisition hardware (NBMIO-16 Board, National Instruments) and software (LabVIEW vers. 2.2.1, National Instruments). The precision of the O_2 analyzer is $\pm 0.001\%$, whereas the deflections used for measurements were greater than 0.01% . Each oxygen concentration measurement was based on a mean of 100 samples taken at 1 KHz. We sampled oxygen concentration every 10 sec, over the entire run. Response time of a flow-through system depends on the effective volume of the system and on the flow

rate, so we chose a flow rate (50 ml min^{-1}) that minimized response time ($< 10 \text{ sec}$ to full deflection) while yielding a deflection greater than 0.01% at steady state. We calculated mass-specific, steady-state rate of oxygen consumption (\dot{V}_{O_2}) from the O_2 concentration.

Lizards fasted before trials, and we placed them in the treadmill chamber for a 30-min equilibration period, which was sufficient for body temperature to reach equilibrium. We adjusted the length of the chamber to slightly greater than body length to ensure steady locomotion rather than intermittent sprinting. A plastic bristled brush provided aversive stimulus at the rear of the chamber. We used a dark screen in the front to simulate a refuge, which seemed to be a positive stimulus. The brush and screen, combined with bright fiber-optic lighting from the sides of the chamber, seemed to contribute greatly in obtaining steady runs. We also used a lightweight metal prod to tap on the tail or hind leg if the brush was not sufficient. Prior to measurement, we had each lizard do numerous practice trials of walking on the treadmill. The lizards' treadmill locomotion improved over the course of these practice trials as they learned to walk steadily at the front of the treadmill. After data collection began, we terminated a trial if an animal repeatedly bumped against the brush, struggled, or refused to walk for more than 10 sec.

We measured resting metabolic rate ($\dot{V}_{O_{2\text{rest}}}$) in inactive, fasted animals during laboratory photophase (the normal dormant period for the geckos). The calculation of aerobically submaximal \dot{V}_{O_2} for an individual at a single speed was from the mean of steady-state \dot{V}_{O_2} during the last 3 min of at least 10 min of continuous locomotion. We defined a steady-state as a window of 3 min of \dot{V}_{O_2} data through which a regression on time had a slope of less than $0.05\% \text{ O}_2/\text{min}$ and did not include an obvious peak in \dot{V}_{O_2} . Most trials included more than 20 min of continuous locomotion at a single speed. At speeds above MAS, some individuals were not able to sustain locomotion for more than 6 min; however, these speeds were not included in the calculation of C_{\min} . Each trial included a single speed, and individuals were allowed to rest for at least 30 min between trials. Speeds at or near MAS, where the animal could not sustain locomotion for more than 10 min, were conducted on animals that had rested for at least 24 h since their last trial. The speeds individuals of each species ran were as follows: *D. intermedius* and *D. galeatus*: 0.13, 0.17, 0.21, 0.26, 0.30 km h^{-1} ; *E. macularius*: 0.07, 0.12, 0.16, 0.20, 0.24, 0.28 km h^{-1} ; *N. asper*: 0.13, 0.17, 0.21, 0.26, 0.30, 0.34, 0.39 km h^{-1} ; *N. levis*: 0.08, 0.13, 0.17, 0.21, 0.26 km h^{-1} ; *P. bibroni*: 0.08, 0.12, 0.16, 0.20, 0.28 km h^{-1} .

In most cases, we used at least three measurements for each individual at each speed, which represents 130 trials over six speeds in six individuals of *E. macularius*, 90 trials over six speeds in six individuals of *P. bibroni*, 48 trials over seven speeds in three individuals of *N. asper*, 52 trials over five speeds in three individuals of *N. levis*, 45 trials over five speeds in five individuals of *D. galeatus*, and 50 trials over five speeds in three individuals of *D. intermedius*.

The typical relationship between aerobically submaximal \dot{V}_{O_2} and running speed is a linear equation (Autumn et al. 1994; for review see Gatten et al. 1992), $\dot{V}_{O_2} = y_0 + C_{\min} \times \text{speed}$, where y_0 is the y-intercept of the \dot{V}_{O_2} -versus-speed curve, or idling cost, and C_{\min} is the slope. We defined the

maximum rate of oxygen consumption ($\dot{V}_{O_{2max}}$) for each individual of each species as the mean \dot{V}_{O_2} attained when an increase in speed resulted in no significant increase in \dot{V}_{O_2} . The maximum aerobic speed (MAS) is the speed at which $\dot{V}_{O_{2max}}$ is attained.

Statistical Analysis

To identify the MAS for each individual, we first calculated linear regressions of \dot{V}_{O_2} on speed for the three lowest speeds; then, by sequentially including higher speeds, we compared the fit of the data to the regressions. We selected MAS as the speed above which the r^2 of the regression decreased. This method agreed closely with a visual analysis of the data. We used the programs StatView version 4.5 and SuperANOVA 1.11 on PowerBook 5300 (Apple) and PowerCenter 150 (Power Computing) computers.

For comparison with the six nocturnal gecko species in this study, we reviewed prior studies that measured $\dot{V}_{O_{2max}}$, C_{min} , and MAS in lizards during controlled treadmill locomotion (Table 1). We used standard allometric analysis (least squares regression on log-transformed values) to visualize the effect of differences in $\dot{V}_{O_{2max}}$ and C_{min} on MAS in nocturnal and diurnal species. First, we considered the effect of nocturnality on $\dot{V}_{O_{2max}}$ by asking what would Q_{10} have to be for temperature to fully explain the difference in $\dot{V}_{O_{2max}}$ between nocturnal and diurnal lizards. Bennett's (1982) data on Q_{10} as a function of body mass predicts Q_{10} of 2.5 for lizards 10 g and under and Q_{10} of 2.25 for lizards between 10 g and 100 g. If by using these values of Q_{10} , $\dot{V}_{O_{2max}}$ for nocturnal lizards at 35°C are similar to those of diurnal lizards of similar size, we conclude that a decrease in temperature accounts for the differences in $\dot{V}_{O_{2max}}$.

We then compared C_{min} in diurnal and nocturnal species to test the hypothesis that C_{min} is lower in nocturnal lizards. Next, we considered the combined effects of differences in $\dot{V}_{O_{2max}}$ and C_{min} on MAS by comparing MAS in diurnal lizards at 35°C and nocturnal lizards at 20°C or 25°C to predicted values in nocturnal species at 35°C (using a Q_{10} of 2.5 for lizards 10 g and under and Q_{10} of 2.25 for lizards between 10 g and 100 g; Bennett 1982, 1983). Two of the diurnal species, *Phrynosoma douglassi* (Autumn et al. 1997) and *Eumeces skiltonianus* (Farley and Emshwiller 1996) were measured at lower temperatures than they experience during activity. Therefore, we adjusted $\dot{V}_{O_{2max}}$ and y_0 using a Q_{10} of 2.5 (Bennett 1982, 1983) to reflect a temperature of 35°C, which yielded $\dot{V}_{O_{2max}}$ and MAS values consistent with the other diurnal species in the analysis (see Results).

Phylogenetic Analysis

Regressions using standardized, phylogenetically independent contrasts of C_{min} on body mass followed the protocol of Felsenstein (1985) and Garland et al. (1992). We used the computer program CAIC version 2.0.0 (Purvis and Rambaut 1995) to calculate independent contrasts. Phylogenetic relationships for independent contrasts follow Kluge (1987), Estes et al. (1988), Garland (1994), Pianka (1995), and the generic taxonomy of *Nephrurus* and *Diplodactylus*. We used a phylogenetic model of equal branch lengths and regression

through the origin (Garland et al. 1992) to calculate allometries of standardized independent contrasts (IC) of log $\dot{V}_{O_{2max}}$, log C_{min} , and log MAS versus log body mass. To compare values of $\dot{V}_{O_{2max}}$, C_{min} , and MAS in diurnal and nocturnal lizards we first plotted the IC allometry using only diurnal taxa. We then recalculated the IC allometry by including data from the nocturnal geckos *Teratoscincus przewalskii* (Autumn et al. 1994) and *Coleonyx variegatus* (Autumn et al. 1997), and the six species in this study. We then plotted the contrasts within the geckos and between Gekkonoidea and Autarchoglossa on the IC allometry for diurnal lizards. A main goal of this study was to reconstruct MAS at low temperature given ancestral and derived values of C_{min} in the ancestor of geckos. To accomplish this, we first plotted contrasts among diurnal taxa. Second, we recalculated the contrasts, including gecko taxa and plotted the contrasts within the geckos and between Gekkonoidea and Autarchoglossa. Third, we recalculated the contrasts, including gecko taxa with predicted values of MAS given ancestral values of C_{min} (calculated from standard allometric analysis), and plotted the contrast between Gekkonoidea and Autarchoglossa. The difference between the Gekkonoidea–Autarchoglossa contrasts given ancestral and derived values of C_{min} represents the potentially adaptive evolution in MAS in the ancestor of geckos.

To check the statistical assumptions of independent contrasts and linear regression, we searched for correlations and patterns in plots of residuals versus IC in body mass, and IC in log $\dot{V}_{O_{2max}}$, log C_{min} , and log MAS. In support of the assumptions, there was no significant correlation ($P \gg 0.05$) or pattern evident in these plots.

RESULTS

Maximum Aerobic Speed and Minimum Cost of Locomotion

MAS for *E. macularius* fell between 0.20 and 0.24 km h⁻¹ (Fig. 5). Regression analysis showed a strong correlation between $\dot{V}_{O_{2max}}$ and speed for each individual ($r^2 > 0.94$; Table 2). For all but two individuals, a MAS of 0.20 km h⁻¹ yielded a higher r^2 for $\dot{V}_{O_{2max}}$ versus speed than did a MAS of 0.24 km h⁻¹. MAS for *P. bibroni* fell between 0.20 and 0.24 km h⁻¹ (Fig. 5). Regression analysis showed a strong correlation between $\dot{V}_{O_{2max}}$ and speed for each individual ($0.99 > r^2 > 0.65$; Table 2). For most individuals a MAS of 0.24 km h⁻¹ yielded a higher r^2 for $\dot{V}_{O_{2max}}$ versus speed than did a MAS of 0.20 km h⁻¹; r^2 for MAS = 0.20 km h⁻¹ did not differ from r^2 for MAS = 0.24 km h⁻¹ by more than 0.06, therefore MAS for *P. bibroni* probably lies much closer to 0.24 than to 0.20 km h⁻¹. MAS for *N. asper* was 0.21 km h⁻¹ for two individuals and 0.30 km h⁻¹ for one individual (Fig. 5). MAS for *N. levis* was 0.17 km h⁻¹ in two individuals and 0.21 km h⁻¹ in one individual. The MAS values for the two species of *Nephrurus* were extremely well supported by r^2 values for $\dot{V}_{O_{2max}}$ versus speed of at least 0.97 (Table 2). In *D. galeatus*, MAS was 0.21 km h⁻¹ in all but one individual (that had a greater $\dot{V}_{O_{2max}}$ than the other individuals of this species), yielding a MAS of 0.26 km h⁻¹ (Fig. 5). In *D. intermedius*, a MAS of 0.26 km h⁻¹ yielded r^2 -values greater than or equal to the r^2 for a MAS of 0.21 km h⁻¹.

For all individuals of all species except *D. galeatus* and

TABLE 1. Energetic cost of controlled treadmill locomotion at aerobically submaximal speeds in lizards. Activity denotes diurnality (D) or nocturnality (N). T_b is the body temperature during the experiment. C_{\min} is the minimum cost of locomotion, measured by calculating the slope of the regression of the rate of oxygen consumption on speed. MAS is the maximum aerobic speed, calculated statistically as the speed above which there is no significant increase in the rate of oxygen consumption. Values of body mass in parentheses refer to measurements of $V_{O_{2\text{rest}}}$ in parentheses.

Species	Activity	Mass (g)	T_b (°C)	$\dot{V}_{O_{2\text{rest}}}$ (ml $O_2 g^{-1} h^{-1}$)	$\dot{V}_{O_{2\text{max}}}$ (ml $O_2 g^{-1} h^{-1}$)	$\dot{V}_{O_{2\text{max}}}$ (ml $O_2 g^{-1} h^{-1}$)	V_{O_2} (ml $O_2 g^{-1} h^{-1}$)	C_{\min} (ml $O_2 g^{-1} km^{-1}$)	MAS (km h^{-1})	Reference
<i>Amblyrynchus cristatus</i>	D	2885	35	0.1	0.665	1918	0.292	0.373	1	Gleeson 1979
<i>Coleonyx variegatus</i>	N	4.2	25	—	0.5	2.1	0.16	1.49	0.23	Autumn et al. 1997
<i>Conolophus subcristatus</i>	D	3885.3	35	0.1	0.623	2420	0.31	0.361	0.867	Gleeson 1979
<i>Cyclura nubila</i>	D	1136	35	—	0.893	1014	—	—	—	Christian and Conley 1994
<i>Diplodactylus galeatus</i>	N	4.3	20	0.112	0.377	1.62	0.001	1.689	0.22	This study
<i>Diplodactylus intermedius</i>	N	4.9	20	0.107	0.466	2.28	0.093	1.434	0.26	This study
<i>Dipsosaurus dorsalis</i>	D	51.3	40	0.319	2.002	102.7	0.62	1.442	0.8	John-Alder and Bennett 1981
<i>Eublepharis macularius</i>	N	32.8	25	0.14	0.505	16.6	0.273	1.09	0.213	This study
<i>Eumeces skiltonianus</i> ¹	D	4.8	35	—	1.65	7.92	0.35	2.55	0.51	Farley and Emswiler 1996
<i>Heloderma horridum</i>	D	803	31	—	1.01	811	—	—	—	Beck et al. 1995
<i>Heloderma suspectum</i>	D	396	31	—	1.13	447	—	—	—	Beck et al. 1995
<i>Heloderma suspectum</i>	D	463.9	35	—	0.896	416	0.258	0.617	1.03	John-Alder et al. 1983
<i>Iguana iguana</i>	D	850	35	0.183	0.832	707	—	—	0.5	Gleeson et al. 1980
<i>Nephurus asper</i>	N	25.1	20	0.069	0.312	7.82	0.124	0.762	0.24	This study
<i>Nephurus levis</i>	N	12.7	20	0.05	0.268	3.41	0.091	0.97	0.183	This study
<i>Pachydactylus bibroni</i>	N	14.8	25	0.13	0.532	7.88	0.225	1.194	0.24	This study
<i>Phrynosoma douglassi</i> ¹	D	4.5	35	—	1.1	5.0	0.425	2.55	0.265	Autumn et al. 1997
<i>Teratoscincus przewalskii</i>	N	11.2	25	0.1	0.518	5.80	0.165	1.06	0.33	Autumn et al. 1994
<i>Tiliqua rugosa</i>	D	548	35	0.144	0.6	329	—	—	—	Christian and Conley 1994
<i>Tiliqua rugosa</i>	D	474	35	0.073	0.722	342	0.107	0.921	0.67	John-Alder et al. 1986
<i>Tupinambis nigropunctatus</i>	D	865	35	0.136	0.672	581	0.348	0.521	0.84	Bennett and John-Alder 1984
<i>Varanus acanthurus</i>	D	73.6	35	—	2.31	170	—	—	—	Thompson and Withers 1997
<i>Varanus breviceauda</i>	D	(53.4)	—	(0.117)	—	—	—	—	—	—
<i>Varanus caudolineatus</i>	D	17.5	35	0.156	3.23	56.4	—	—	—	Thompson and Withers 1997
<i>Varanus caudolineatus</i>	D	14.9	35	—	6.29	94	—	—	—	Thompson and Withers 1997
<i>Varanus eremius</i>	D	(13.1)	—	(0.173)	—	—	—	—	—	Thompson and Withers 1997
<i>Varanus exanthematicus</i>	D	(35.9)	—	(0.172)	—	—	—	—	—	—
<i>Varanus gilleni</i>	D	1025	35	0.189	1.260	1292	—	0.62	1.2	Gleeson et al. 1980
<i>Varanus gilleni</i>	D	8.4	35	—	5.179	43.5	—	—	—	Thompson and Withers 1997
<i>Varanus gilleni</i>	D	(20.0)	—	(0.179)	—	—	—	—	—	—
<i>Varanus gouldii</i>	D	1086	35	0.09	1.354	1470	—	—	—	Christian and Conley 1994
<i>Varanus mertensi</i>	D	904	35	0.078	0.909	822	—	—	—	Christian and Conley 1994
<i>Varanus panoptes</i>	D	931	35	0.132	1.340	1248	—	—	—	Christian and Conley 1994
<i>Varanus rosenbergi</i>	D	1287	35	0.132	1.133	1458	—	—	—	Christian and Conley 1994
<i>Varanus tristis</i>	D	103.2	35	—	3.00	310	—	—	—	Thompson and Withers 1997
		(99)	—	(0.159)	—	—	—	—	—	—

¹ Measured at 25°C and adjusted to 35°C assuming a Q_{10} of 2.5 (Bennett 1982).

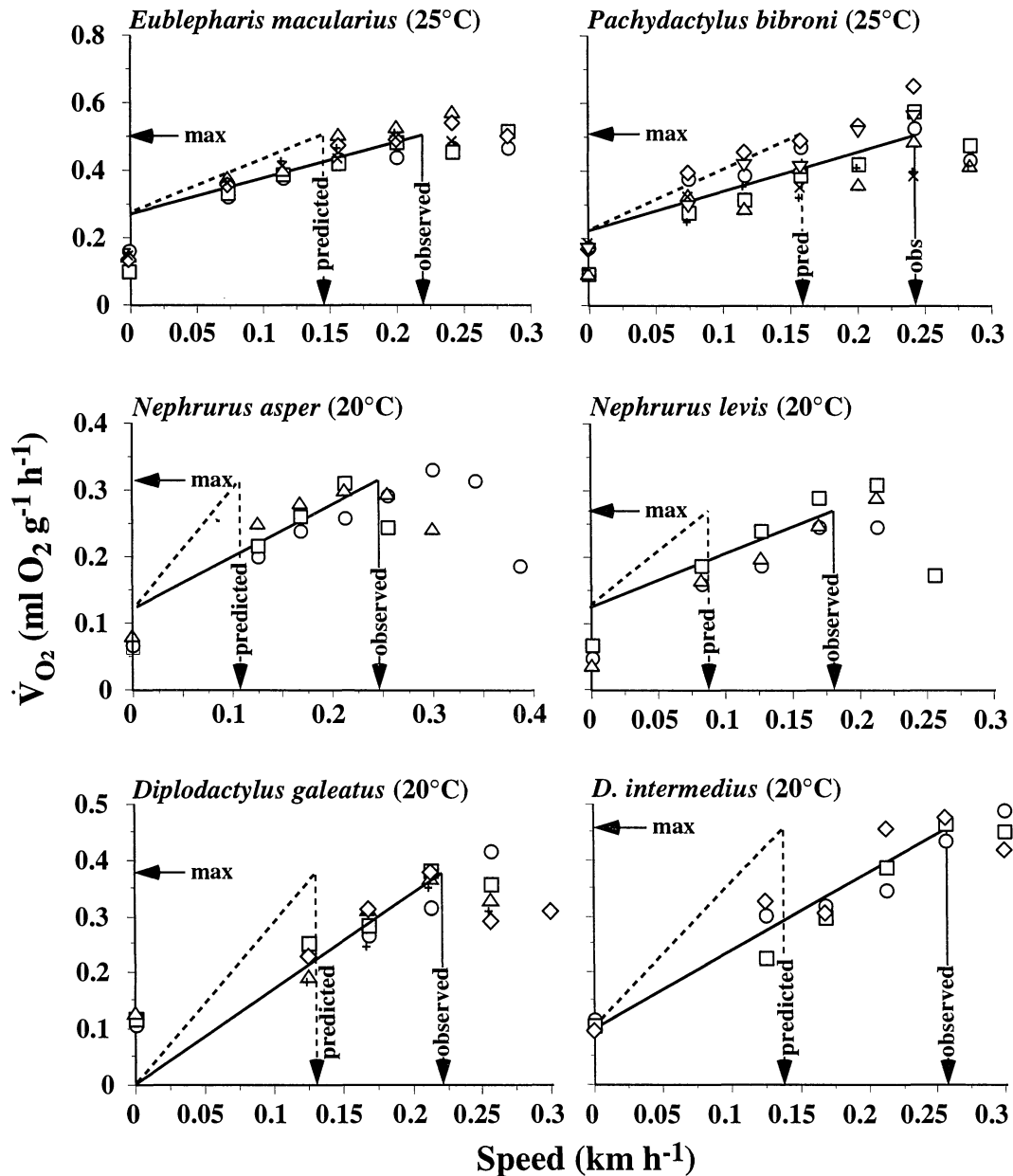


FIG. 5. Mass-specific steady-state rate of oxygen consumption (\dot{V}_{O_2}) during treadmill exercise in six species of nocturnal gecko (*Eublepharis macularius* and *Pachydactylus bibroni* measured at 25°C; *Diplodactylus galeatus*, *D. intermedius*, *Nephurus asper*, and *N. levis* measured at 20°C). Geometric shapes represent different individuals. The slopes of the solid lines relating aerobically submaximal \dot{V}_{O_2} and speed represent the mean minimum cost of locomotion (C_{min}) calculated from individual animals (see Table 2). The slopes of the dashed lines represent C_{min} predicted for a diurnal lizard of similar mass (see Fig. 6A). The low C_{min} in nocturnal species increased the maximum aerobic speed (MAS; solid vertical arrows) over predicted values (dashed vertical arrows) by 45% in *E. macularius*, 54% in *P. bibroni*, 117% in *N. asper*, 112% in *N. levis*, 63% in *D. galeatus*, and 87% in *D. intermedius*. Predicted values of MAS are based on observed mean values of y_0 and \dot{V}_{O_2max} (horizontal arrows), and allometrically predicted C_{min} for each species. Because we calculated C_{min} first for each individual and then calculated mean C_{min} , the observed MAS does not always coincide with any one treadmill speed used in the experiments.

D. intermedius, the ratio of y_0 to \dot{V}_{O_2rest} (Table 2) was within the range found in other vertebrates (Paladino and King 1979; John-Alder and Bennett 1981; Bennett 1983; Autumn et al. 1994) and invertebrates (Full 1987). In *D. galeatus*, y_0 was near zero, while \dot{V}_{O_2rest} was 40% greater than predicted by allometry (Andrews and Pough 1985). In *D. intermedius*, y_0

was low (-0.013 ml O₂ g⁻¹ h⁻¹) in one individual, while \dot{V}_{O_2rest} was 37% greater than predicted by allometry (Andrews and Pough 1985). Unlike individuals of the other species that were quiescent during measurements of \dot{V}_{O_2rest} , the *Diplodactylus* remained active in the chamber, which may account for the elevated \dot{V}_{O_2rest} .

TABLE 2. Energetic cost of treadmill locomotion at aerobically submaximal speeds in six species of nocturnal gecko.

Animal #	Mass (g)	$\dot{V}_{O_{2rest}}$ (ml O ₂ g ⁻¹ h ⁻¹)	y_0 (ml O ₂ g ⁻¹ h ⁻¹)	C_{min} (ml O ₂ g ⁻¹ km ⁻¹)	r^2	$\frac{y_0}{\dot{V}_{O_{2rest}}}$	$\dot{V}_{O_{2max}}$ (ml O ₂ g ⁻¹ h ⁻¹)	$\frac{\dot{V}_{O_{2max}}}{\dot{V}_{O_{2rest}}}$	$\frac{\dot{V}_{O_{2max}}}{\dot{V}_{O_{2rest}}} - \frac{\dot{V}_{O_{2max}}}{\dot{V}_{O_{2rest}}}$ (ml O ₂ g ⁻¹ h ⁻¹)	MAS (km h ⁻¹)
<i>Eublepharis macularius</i>										
1	29.9	0.159	0.256	0.993	0.92	1.6	0.441	2.8	0.282	0.20
2	34.2	0.100	0.248	1.145	0.99	2.5	0.481	4.8	0.381	0.20
3	28.0	1.141	0.278	1.229	0.94	2.0	0.568	4.0	0.427	0.20
4	31.6	0.135	0.287	1.050	0.97	2.1	0.538	4.0	0.403	0.24
5	36.8	0.162	0.282	1.124	0.99	1.7	0.506	3.1	0.344	0.24
6	36.0	0.145	0.288	1.000	0.98	2.0	0.495	3.4	0.350	0.20
Mean	32.8	0.140	0.273	1.090	—	2.0	0.505	3.7	0.364	0.21
<i>Pachydactylus bibroni</i>										
1	18.2	0.170	0.312	0.800	0.72	1.8	0.529	3.1	0.359	0.24
2	16.2	0.096	0.133	1.664	0.90	1.4	0.579	6.0	0.483	0.24
3	12.6	0.087	0.221	0.936	0.65	2.5	0.484	5.6	0.397	0.24
4	10.8	0.166	0.280	1.410	0.95	1.7	0.649	3.9	0.483	0.24
5	18.8	0.100	0.206	0.855	0.73	2.1	0.394	3.9	0.294	0.24
6	12.3	0.159	0.196	1.500	0.93	1.2	0.557	3.5	0.398	0.24
Mean	14.8	0.130	0.225	1.194	—	1.8	0.532	4.3	0.402	0.24
<i>Nephrurus asper</i>										
1	22.5	0.066	0.111	0.654	0.99	1.7	0.330	5.0	0.264	0.30
2	22.6	0.065	0.081	1.069	1.00	1.3	0.310	4.8	0.245	0.21
3	30.1	0.077	0.179	0.563	0.99	2.3	0.297	3.9	0.220	0.21
Mean	25.1	0.069	0.124	0.762	—	1.8	0.31	4.5	0.243	0.24
<i>N. levis</i>										
1	17.2	0.070	0.073	1.000	0.97	1.0	0.247	3.5	0.177	0.17
2	11.3	0.045	0.120	0.940	0.96	2.7	0.310	6.9	0.265	0.17
3	9.7	0.035	0.081	0.970	0.99	2.3	0.247	7.1	0.212	0.21
Mean	12.7	0.050	0.091	0.970	—	2.0	0.268	5.8	0.218	0.18
<i>Diplodactylus galeatus</i>										
1	3.7	0.105	0.050	1.350	0.93	0.5	0.415	4.0	0.310	0.26
2	4.6	0.115	0.057	1.474	0.93	0.5	0.381	3.3	0.266	0.21
3	3.8	0.123	-0.048	1.986	0.96	-0.4	0.365	3.0	0.242	0.21
4	5.5	0.108	0.011	1.746	1.00	0.1	0.380	3.5	0.272	0.21
5	3.9	0.108	-0.063	1.887	0.98	-0.6	0.346	3.2	0.238	0.21
Mean	4.3	0.112	0.00	1.69	—	0.0	0.38	3.4	0.266	0.22
<i>D. intermedius</i>										
1	4.1	0.118	0.165	0.995	0.85	1.4	0.442	3.8	0.324	0.26
2	4.7	0.108	-0.013	1.897	1.00	-0.1	0.473	4.4	0.365	0.26
3	5.9	0.096	0.126	1.411	0.79	1.3	0.482	5.0	0.386	0.26
Mean	4.9	0.107	0.10	1.44	—	0.9	0.46	4.4	0.358	0.26

Standard Allometric Analysis

Maximum Rate of Oxygen Consumption

The allometric slopes (Fig. 6) relating mass and maximum rate of oxygen consumption $\dot{V}_{O_{2max}}$ are similar in diurnal lizards and geckos (ANCOVA, $F = 0.33$; $df = 1, 23$; $P = 0.57$), and similar to those in mammals (slope = 0.79–0.86; Taylor et al. 1970). However, the intercepts differ significantly between diurnal and nocturnal lizards (ANCOVA, $F = 8.6$; $df = 1, 23$; $P = 0.01$), reflecting the 15–20°C difference in body temperature. Relative to diurnal lizards, geckos have only 24% the maximum rate of oxygen consumption during typical activity temperatures. A Q_{10} of 2.5 for lizards 10 g and under and Q_{10} of 2.25 for lizards between 10 g and 100 g accounts for most of the difference in $\dot{V}_{O_{2max}}$ between nocturnal and diurnal lizards. Using these values of Q_{10} , predicted $\dot{V}_{O_{2max}}$ for nocturnal lizards at 35°C are well within the 95% confidence limits of the standard $\dot{V}_{O_{2max}}$ allometry for diurnal lizards at 35°C (Fig. 6A). Using Q_{10} values of 2 and 3 to predict $\dot{V}_{O_{2max}}$ at 35°C in nocturnal lizards also

produced predicted values for nocturnal lizards at 35°C well within the 95% confidence limits of the standard $\dot{V}_{O_{2max}}$ allometry for diurnal lizards at 35°C.

Minimum Cost of Locomotion

Mass-specific minimum cost of locomotion (C_{min} ; Table 2) in the six nocturnal species measured in this study was 40–60% lower than predicted by standard allometry for diurnal lizards of similar body mass (Fig. 5). The allometric slopes relating mass and C_{min} (Fig. 6) are similar in diurnal lizards and geckos (ANCOVA, $F = 0.2$; $df = 1, 23$; $P = 0.9$) and are similar to the slope for mammals, birds, amphibians, and invertebrates (slope = -0.30; Full 1989). However, the intercepts differ significantly between nocturnal and diurnal lizards (ANCOVA, $F = 4.12$; $df = 1, 23$; $P = 0.05$), indicating that the typical allometric relationship between C_{min} and body mass found in lizards and other terrestrial organisms is conserved in geckos and geckos have a lower C_{min} than diurnal lizards at a given body mass.

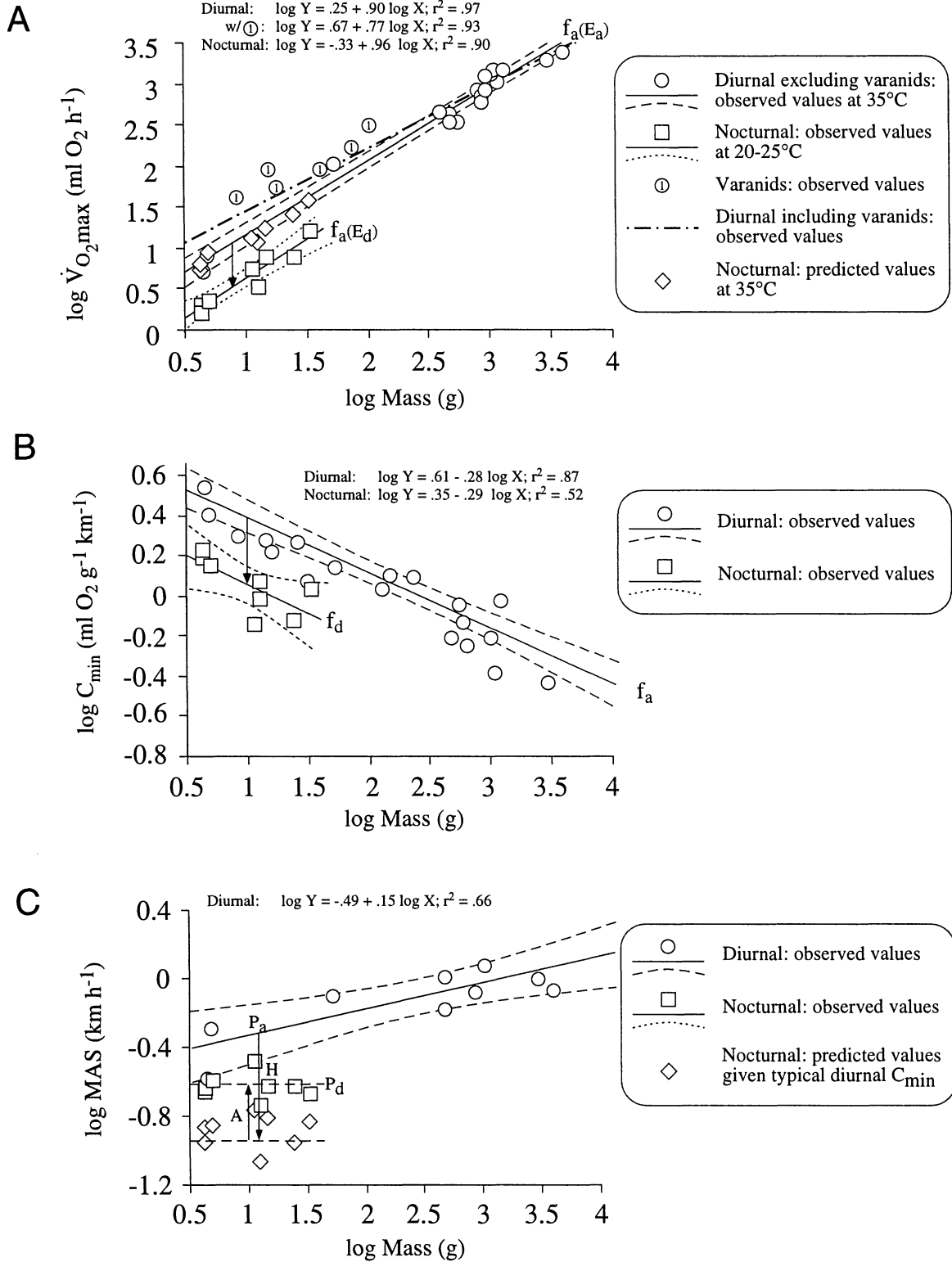


FIG. 6. Standard allometric analysis of maximum rate of aerobic metabolism ($\dot{V}_{O_2\max}$), minimum cost of locomotion (C_{\min}), and maximum aerobic speed (MAS) as a function of body mass in diurnal lizards (circles) and nocturnal geckos (squares). Diamond symbols represent predicted values for nocturnal geckos (see below). Solid lines represent least squares regressions with 95% confidence limits (CL) for diurnal lizards (dashed lines) and nocturnal geckos (dotted lines). In the context of our integrative approach (Fig. 2), the environmental variable, E, represents the thermal environment; the physiological variable, f, represents $\dot{V}_{O_2\max}$ or C_{\min} ; the performance variable, P, represents MAS. The subscripts, a and d, represent ancestral and derived character states, respectively. (A) $\dot{V}_{O_2\max}$ versus body mass in lizards at or near their activity temperatures. Diurnal lizards (circles) are active at high body temperatures (approximately 35°C) that result in high $\dot{V}_{O_2\max}$, whereas nocturnal geckos are active at low body temperatures (20–25°C) that represent a handicap on $\dot{V}_{O_2\max}$. The

Maximum Aerobic Speed

Due to the effect of a decreased $\dot{V}_{O_{2max}}$ (Fig. 6A) combined with the effect of low C_{min} (Fig. 6B), the geckos averaged maximum aerobic speeds 200% of the values predicted for lizards of the same size with typical C_{min} (Fig. 6). However, the low C_{min} was not sufficient to fully offset the effects of low temperature, and average MAS in the geckos (0.239 km h^{-1}) was 50% of the allometrically predicted value for a diurnal lizard with body mass of 13.75 g (the average body mass of the six gecko species in our sample, and the two species measured by Autumn et al. 1994, 1997).

Phylogenetic Analysis

Maximum Rate of Oxygen Consumption

The slopes of the phylogenetically independent contrast (IC) allometry relating mass and maximum rate of oxygen consumption $\dot{V}_{O_{2max}}$ are similar for contrasts within diurnal lizards (clades Iguania and Autarchoglossa; Fig. 7) and within geckos (clade Gekkonoidea; Fig. 7, Fig. 8A). The slopes of the $\dot{V}_{O_{2max}}$ allometries were also similar to the slopes of the $\dot{V}_{O_{2max}}$ standard allometry (Fig. 6A), indicating that the effect of body mass on $\dot{V}_{O_{2max}}$ in diurnal and nocturnal taxa largely transcends phylogeny. In support of hypothesis 1 (see introduction), the contrast between Gekkonoidea and Autarchoglossa fell far below the 95% confidence limits of the IC allometry, reflecting the decrease in $\dot{V}_{O_{2max}}$ caused by the change from diurnal to nocturnal activity in the hypothetical ancestor of geckos. The fit of the diurnal ($r^2 = 0.98$) and nocturnal ($r^2 = 0.95$) contrasts was high and only one contrast differed substantially from the overall pattern: the contrast between Anguimorpha and Scincomorpha (Fig. 7).

Minimum Cost of Locomotion

The slope of the C_{min} IC allometry (Fig. 8B) within diurnal taxa was similar to the slope of the standard allometry (Fig. 6B), indicating that the effect of body mass on C_{min} in diurnal lizards largely transcends phylogeny. In support of hypothesis 2 (see introduction), the contrast between Gekkonoidea and Autarchoglossa fell far below the 95% confidence limits of the IC allometry, showing a significant decrease in C_{min}

in the most recent common ancestor of living geckos. There was no significant correlation between IC in mass and IC in C_{min} within gecko taxa. Three diurnal lizard contrasts fell substantially outside the 95% confidence limits of the IC allometry: (1) *Dipsosaurus* versus the clade containing *Iguana*, *Conolophus*, and *Amblyrynchus*; (2) *Iguana* versus the clade containing *Conolophus* and *Amblyrynchus*; (3) *Iguania* versus *Scleroglossa*. One contrast within the geckos fell outside the 95% confidence limits of the diurnal lizard IC allometry: *E. macularius* versus *C. variegatus*. This difference may be due in part to the fact that *Eublepharis macularius* had the greatest and *C. variegatus* had the least body mass of the gecko species in our dataset.

Maximum Aerobic Speed

The slope of the MAS IC allometry (Fig. 8C) within diurnal taxa was significant (ANCOVA, $F = 7.122$; $df = 1, 8$; $P = 0.003$), and was similar to the slope of the standard allometry (Fig. 6B). This suggests that, like $\dot{V}_{O_{2max}}$ and C_{min} , the effect of body mass on MAS in diurnal lizards largely transcends phylogeny. The contrast between Gekkonoidea and Autarchoglossa fell far outside the 95% confidence limits of the IC allometry, indicating an evolutionary decrease in locomotor performance capacity at low temperature in nocturnal lizards as a result of the decrease in $\dot{V}_{O_{2max}}$ (Fig. 8A). The amount of the decrease was only 50% of that predicted for geckos with typical values of C_{min} . This difference was due to the decrease in C_{min} (Fig. 8B), which supports hypothesis 2 (see Introduction): a decrease in C_{min} increased MAS in the most recent common ancestor of living geckos. However, the decrease in C_{min} was not sufficient to fully offset the effects of activity at low temperature.

DISCUSSION

The immediate goal of our study was to answer three questions. (1) Is a low minimum cost of locomotion (C_{min}) a shared, derived character of geckos? (2) Did the decrease in C_{min} increase performance capacity (MAS) in the most recent common ancestor of living geckos? (3) How can geckos have increased performance at low temperatures and yet low temperatures remain suboptimal? Because this study was an ap-

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allometric slopes (solid lines) relating mass and $\dot{V}_{O_{2max}}$ are similar in diurnal lizards and geckos (ANCOVA, $F = 0.15$; $df = 1, 22$; $P = 0.7$), although the intercepts differ significantly (ANCOVA, $F = 10.3$; $df = 1, 22$; $P = 0.004$). Dot-dashed line includes the diurnal species plus six additional varanid species from Thompson and Withers (1997) (circles with numeral 1), and has a reduced slope due to phylogenetic pseudoreplication of varanids. Dashed and dotted lines represent 95% CL for mean y-values in diurnal and nocturnal lizards, respectively. Diamonds represent the $\dot{V}_{O_{2max}}$ predicted for the nocturnal geckos using a Q_{10} of 2.5 for lizards 10 g and under and Q_{10} of 2.25 for lizards between 10 g and 100 g (Bennett 1982, 1983). The arrow represents the effect (thermal handicap) of nocturnal activity on $\dot{V}_{O_{2max}}$ in lizards. (B) C_{min} versus body mass in lizards. Nocturnal geckos (squares) have a C_{min} one-half to one-third that of diurnal lizards (circles) of similar body mass. The allometric slopes (solid lines) relating mass and C_{min} is similar in diurnal lizards and geckos (ANCOVA, $F = 0.02$; $df = 1, 23$; $P = 0.9$), whereas the intercepts differ significantly (ANCOVA, $F = 4.12$; $df = 1, 23$; $P = 0.05$). Dashed and dotted lines represent 95% CL for mean y-values in diurnal and nocturnal lizards, respectively. Because C_{min} is thermally insensitive (Rome 1982), the difference between geckos and other lizards cannot be explained by a difference in temperature. A decrease in C_{min} (arrow; superior fuel economy) partially offsets the handicap of nocturnality by increasing MAS in geckos. (C) Maximum aerobic speed versus body mass in lizards at or near their activity temperatures. The slope ($t = 2.99$, $n = 9$, $P = 0.02$) and intercept ($t = -4.03$, $n = 9$, $P = 0.004$) of the allometry within diurnal lizards were significantly different from zero, and the slope was similar to the allometric slope relating MAS and body mass in mammals (0.12; Taylor et al. 1970). Some nocturnal geckos at low temperature (20–25°C) have nearly the MAS of diurnal lizards at high temperature (35°C). The diamond symbols represent the predicted MAS of geckos at low temperature given a typical C_{min} . The downward arrow represents the effect of the thermal handicap (H, see Fig. 2, Fig. 6A) on MAS. The upward arrow represents the adaptive effect (A, see Fig. 3) of low C_{min} (Fig. 6B) on MAS.

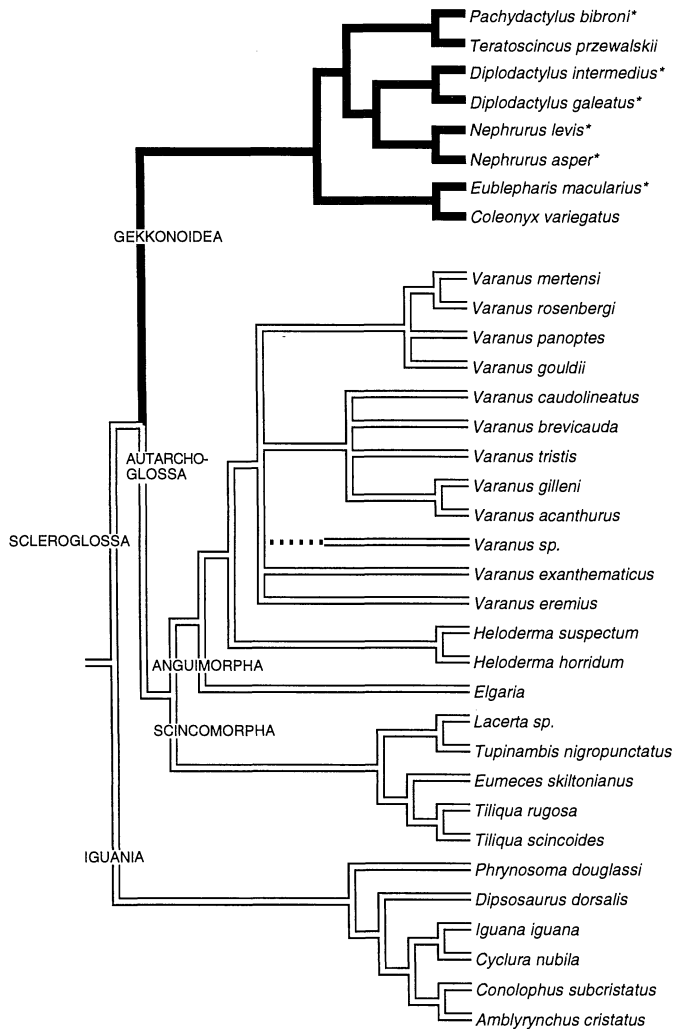


FIG. 7. Phylogenetic hypothesis of the taxa used in this study. Complete $\dot{V}_{O_{2max}}$, C_{min} , and MAS data were available from only a subset of these taxa (see Table 2). The topology follows Kluge (1987), Estes, et al. (1988), Etheridge and de Queiroz (1988), Garland (1994), and Pianka (1995). Varanid taxa identified only to genus (Bakker 1972), represented on a dotted branch, were included only in the analysis of C_{min} , and do not duplicate the other varanid taxa because they are the only varanids for which C_{min} has been measured. Polytomies should be interpreted as soft (i.e., there is not enough information to resolve relationships among taxa, but we do not assume that the taxa split simultaneously). Branch lengths represent order of branching, not absolute time. Asterisks denote species from this study.

plication of our integrative approach to the study of eco-physiological evolution (Fig. 3), it is also important to ask if the answers to our questions could have been found *without* integrating history and mechanism.

The mechanistic dimension of our study addressed the effect of the nocturnal environment on locomotor physiology (maximum rate of oxygen consumption), and the effects of maximum rate of oxygen consumption ($\dot{V}_{O_{2max}}$) and minimum cost of locomotion (C_{min}) on locomotor performance (MAS). The historical dimension addressed the evolution of the relationships between nocturnality, body mass, $\dot{V}_{O_{2max}}$, C_{min} , and locomotor performance.

Nocturnality Decreases Maximum Rate of Oxygen Consumption

In our integrative approach (Fig. 9), the physiological variable, f , represents $\dot{V}_{O_{2max}}$ or C_{min} . Hypothesis 1 (see introduction), that the transition from the diurnal to nocturnal environment decreases performance given ancestral lizard physiology, is well supported. In lizards, the effect of body mass and temperature on $\dot{V}_{O_{2max}}$ does not differ between nocturnal and diurnal lizards (Fig. 6A; Bennett 1982; Autumn and Full 1994). Therefore, the nocturnal and diurnal $\dot{V}_{O_{2max}}$ allometries represent the same underlying physiological character, f_a , under different environmental conditions: high, diurnal temperatures (E_d) and low, nocturnal temperatures (E_n). Nocturnal environments decrease $\dot{V}_{O_{2max}}$ because they are cold. The diurnal IC allometry for $\dot{V}_{O_{2max}}$ was a remarkably good fit to the data (Fig. 8), which suggests that there have been few major evolutionary changes in $\dot{V}_{O_{2max}}$ independent of mass and temperature. Our analysis suggests that the greatest evolutionary change in $\dot{V}_{O_{2max}}$ (at activity temperatures) in the evolutionary history of lizards occurred in the ancestor of geckos. This seemingly maladaptive evolutionary change is explained by the 10–15°C difference in body temperature between the diurnal and nocturnal species in our dataset. The effective difference in $\dot{V}_{O_{2max}}$ of field-active individuals of nocturnal and diurnal species of similar body mass is likely to be greater than calculated here because the temperatures we used for the nocturnal species (20°C and 25°C) are relatively moderate in comparison to the temperatures that many temperate geckos experience during activity (10–15°C; Autumn et al. 1994).

The next greatest evolutionary change in $\dot{V}_{O_{2max}}$ was between clades Anguimorpha and Scincomorpha (Fig. 7), which fell outside the 95% confidence limits of the allometry. $\dot{V}_{O_{2max}}$ probably increased in the ancestor of Anguimorpha, the clade containing Anguinae, Helodermatidae, Lanthanotidae, Varanidae, and Xenosauridae (Estes et al. 1988). Unlike the case of the geckos, the increased $\dot{V}_{O_{2max}}$ in Anguimorpha is probably due to physiological differences rather than temperature effects (Gleeson et al. 1980). This implies that a high $\dot{V}_{O_{2max}}$ is not a derived character of Varanidae and supports the findings of Beck et al. (1995) and Christian and Conley (1994). Instead, the ancestor of Varanidae may have inherited a high $\dot{V}_{O_{2max}}$ that was derived at the level of Anguimorpha and subsequently lost in some species (e.g., *Varanus mertensi*). The addition of six new varanid species by Thompson and Withers (1997) to the $\dot{V}_{O_{2max}}$ dataset affected the allometric relationship (see Fig. 6A) by lowering the slope and raising the intercept. Phylogenetic analysis (Fig. 8A) eliminated the pseudoreplication caused by this comprehensive study of varanid taxa, which reinforces the importance of integrating historical information in determining the relationship between nocturnality, body mass, and $\dot{V}_{O_{2max}}$.

Fuel Economy Increased in the Ancestor of Geckos

The results of this study suggest that low C_{min} is a major difference between geckos and other lizards that increases endurance capacity at low temperatures (Fig. 2), not just a unique characteristic of *Teratoscincus przewalskii* (Autumn et al. 1994) and *Coleonyx variegatus* (Autumn et al. 1997).

C_{\min} in the six gecko species measured was 40–60% lower than predicted by standard allometry for diurnal lizards of similar mass (Fig. 5). For a low C_{\min} to translate into increased MAS, it must truly reflect a low energetic cost of locomotion. Another possibility is that a low C_{\min} is a statistical artifact caused by an elevated y_0 (increased energetic cost at low speeds). This possibility is not supported by our data; ratios of y_0 to $\dot{V}_{O_2\text{rest}}$ were below two in all six species (Table 2), which is typical for terrestrial animals (Bennett 1983; Full 1987). In the two *Diplodactylus* species, $\dot{V}_{O_2\text{rest}}$ was elevated above predicted values (Andrews and Pough 1985). However, y_0 was lower than predicted in *D. intermedius* and *D. galeatus*, which has the effect of increasing C_{\min} . Despite the low y_0 , C_{\min} in *Diplodactylus* was approximately 40–47% lower than predicted by standard allometry. As a result of their low C_{\min} , MAS in the six gecko species was 150–220% of predicted values (Fig. 5). The similarity in allometric slopes between the diurnal and nocturnal C_{\min} allometries (Fig. 6) suggests that all lizards share a common functional relationship of C_{\min} to body mass and that the significant difference in intercepts is caused by the evolution of mass-independent characters that are common to geckos and lacking in diurnal lizards.

How would variation in Q_{10} affect our conclusions? A change in Q_{10} for $\dot{V}_{O_2\text{max}}$ in geckos would affect our comparison of $\dot{V}_{O_2\text{max}}$ and MAS in Figure 6 by shifting the diamond symbols up or down in Figures 6A and 6C. If Q_{10} is lower than 2.25–2.5, less of the difference in $\dot{V}_{O_2\text{max}}$ would be explained by temperature. Geckos would have a lower thermal sensitivity, but also absolutely lower values of $\dot{V}_{O_2\text{max}}$. If Q_{10} is greater than 2.25–2.5, geckos would have greater $\dot{V}_{O_2\text{max}}$ at 35°C than diurnal lizards do. A change in Q_{10} for $\dot{V}_{O_2\text{max}}$ in geckos would not affect the independent contrasts of $\dot{V}_{O_2\text{max}}$ because the IC values are not Q_{10} -adjusted (with the exception of the diurnal species, *P. douglassi* and *E. skiltonianus*). A change in Q_{10} for $\dot{V}_{O_2\text{max}}$ would affect the predicted Gecko–Autarchoglossa contrast in MAS without low C_{\min} in Figure 8C (diamond symbol), but not the actual measured value (triangle symbol) for Gecko–Autarchoglossa. For this study, we have chosen the values of Q_{10} that have the most support from the literature (Bennett 1982; Musatov 1993). There are no published data on Q_{10} for $\dot{V}_{O_2\text{max}}$ in geckos in the 25°C and 35°C temperature range. Measurements of Q_{10} for $\dot{V}_{O_2\text{rest}}$ in geckos between 25°C and 35°C varies from 1.4 to 5.3 (Al-Sadoon and Abdo 1989; Zari 1997). More data are clearly needed on $\dot{V}_{O_2\text{max}}$ in nocturnal lizards at high temperature. However, the nocturnal geckos and diurnal lizards measured so far are similar in their thermal sensitivity of aerobic metabolism (Autumn and Full 1994), yet many nocturnal lizards are active foragers (Cooper 1995; Werner et al. 1997a,b) in spite of aerobic limitations at low body temperatures.

Increased Fuel Economy Partially Offsets the Thermal Handicap of Nocturnal Activity

Did the decrease in C_{\min} increase performance capacity (MAS) in the most recent common ancestor of living geckos? The answer is complicated by the (maladaptive) decrease in MAS caused by the thermal handicap on $\dot{V}_{O_2\text{max}}$. To answer

this question, we must separate the effects of change in $\dot{V}_{O_2\text{max}}$ from the effects of change in C_{\min} . The effects of $\dot{V}_{O_2\text{max}}$ and C_{\min} on MAS can be represented algebraically by the relationship,

$$\text{MAS} = \frac{\dot{V}_{O_2\text{max}} - y_0}{C_{\min}} \quad (1)$$

In lizards, the idling cost (y_0) has the same thermal sensitivity as does $\dot{V}_{O_2\text{max}}$, and C_{\min} is not thermally sensitive (John-Alder and Bennett 1981; Rome 1982; Bennett 1983; John-Alder et al. 1983; Bennett and John-Alder 1984; Autumn et al. 1994; but see Weinstein and Full 1994). The combined effects of the maladaptive thermal handicap and the adaptive decrease in C_{\min} can be approximated by

$$\Delta\text{MAS} = \frac{\Delta_1(\dot{V}_{O_2\text{max}} - y_0)}{\Delta_2 C_{\min}} \quad (2)$$

For the handicap to be fully offset, Δ_2 must equal Δ_1 . This is not the case in our study. In a comparison of geckos to typical diurnal values, Δ_1 is approximately equal to 24%, whereas Δ_2 is between 40% and 60%.

Ancestral performance capacity (MAS), P_a (Fig. 8C), is equal to 0.479 km h⁻¹, the allometrically predicted MAS for a diurnal lizard of 13.75 g (the average body mass of the geckos). The performance handicap, H , is the difference between P_a and 0.132 km h⁻¹, the allometrically predicted MAS at nocturnal temperatures, given ancestral C_{\min} . This amounts to a handicap of 0.337 km h⁻¹, or 72%. The performance advantage, A , is the difference between P_a and the derived performance capacity (P_d) yielded by derived values of C_{\min} . The geckos averaged MAS of 0.239 km h⁻¹, a performance advantage of 0.107 km h⁻¹ due to decreased C_{\min} . Thus, we accept the hypothesis that there was an evolutionary decrease in minimum cost of locomotion that caused an increase in sustained locomotor performance capacity at low temperature in geckos (hypothesis 2; see introduction). However, despite a near doubling of MAS, the adaptive decrease in C_{\min} only offsets about 50% of the thermal handicap. Due to their excellent fuel economy, at low temperature geckos have 38–69% of the range of sustainable speeds of diurnal lizards at high temperature.

The Nocturnal Environment is Suboptimal for Sustained Locomotion in Nocturnal Lizards

All else being equal, optimality theory predicts the coadaptation of physiological thermal optima and activity temperatures in ectotherms (Huey and Bennett 1987; Hailey and Davies 1988; Huey and Kingsolver 1989, 1993; Huey et al. 1989). Coadaptation is evolution in one character (e.g., activity temperature) that causes selection for evolution in another character (e.g., thermal optimum). In other words, ectotherms should perform best at the temperatures they experience during activity. This hypothesis is supported by a pattern of evolutionary correlation between optimal temperature (T_o) for sprinting and T_b in iguanians and Australian skinks (Huey and Bennett 1987; Garland et al. 1991; Huey and Kingsolver 1993). The pattern of evolution in T_b accompanied by evolution in T_o is statistically well supported in iguanians (Huey and Kingsolver 1993). The pattern in skinks

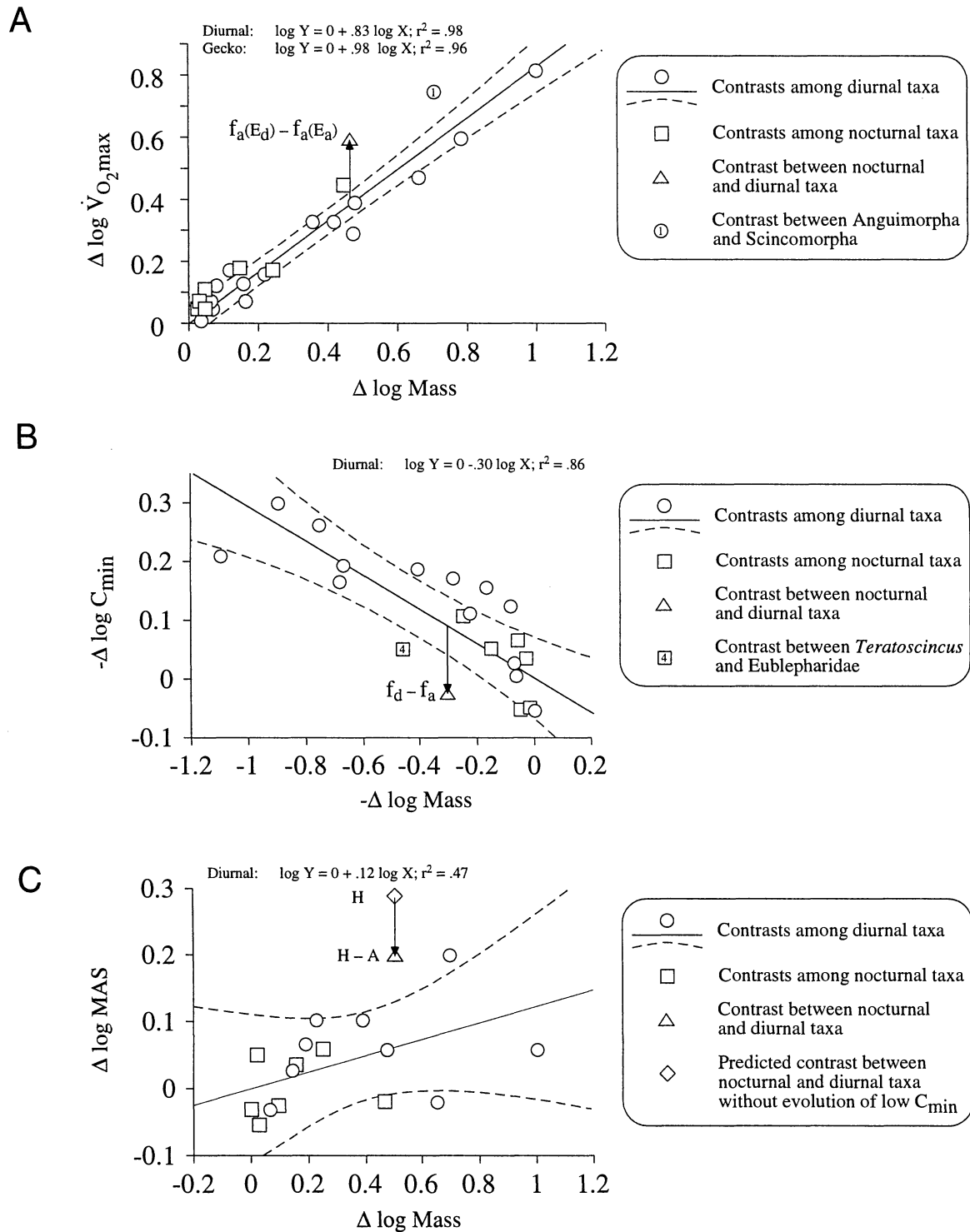


FIG. 8. Phylogenetically independent contrasts of maximum rate of aerobic metabolism ($\dot{V}_{O_2 \max}$), minimum cost of locomotion (C_{\min}), and maximum aerobic speed (MAS) as a function of body mass within diurnal lizard sister taxa (circles), gecko sister taxa (squares), and between geckos and their sister taxon, Autarchoglossa (triangles). Solid lines represent least squares regressions through the origin, with 95% confidence limits (CL) (dashed lines) for diurnal lizard contrasts calculated with the exclusion of geckos. Contrasts falling near the regression lines represent sister taxa for which evolutionary change in body mass was accompanied by a typical change in the dependent variable ($\dot{V}_{O_2 \max}$, C_{\min} , or MAS). In the context of our integrative approach (Fig. 2), the environmental variable, E, represents the thermal environment; the physiological variable, f , represents $\dot{V}_{O_2 \max}$ or C_{\min} ; the performance variable, P, represents MAS. The subscripts, a and d, represent ancestral and derived character states, respectively. (A) Contrasts in $\dot{V}_{O_2 \max}$ versus body mass in lizards. Contrasts within diurnal lizards (circles) and within nocturnal geckos (squares) fall within or very near the 95% CL (except for the contrast between Anguimorpha and Scincomorpha; numeral 1), whereas the contrast between nocturnal geckos and their diurnal sister taxon (triangle) falls well below the 95% CL. The difference between y-value of this contrast and the y-value predicted by the regression

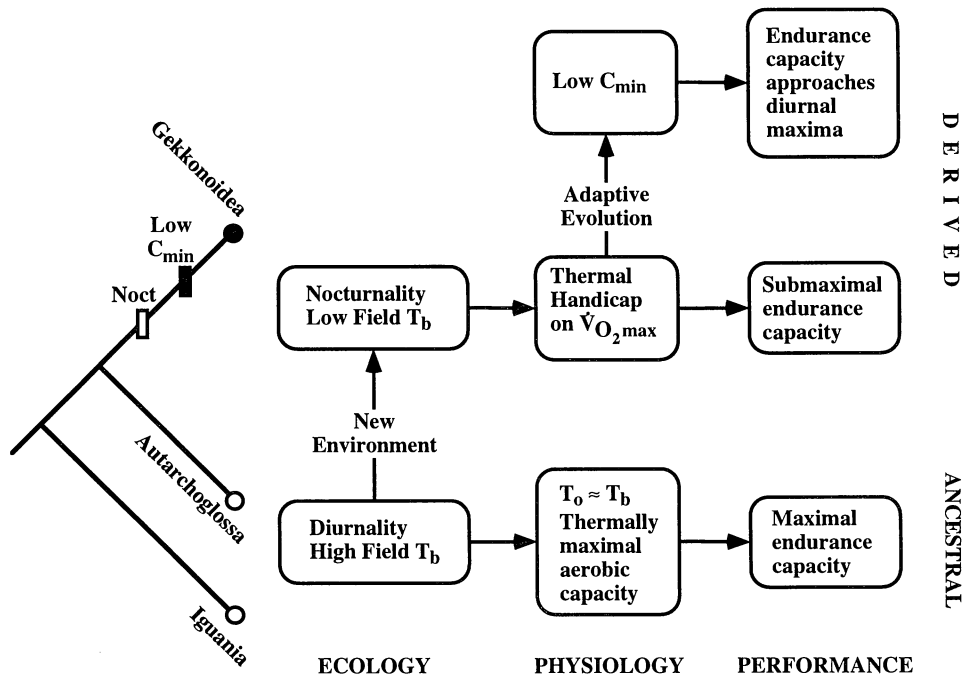


FIG. 9. Diagrammatic overview of the findings of this study. Lizards are ancestrally diurnal and are able to achieve physiologically optimal body temperatures over a wide range of environmental temperatures. Diurnal lizards are capable of performance at maximal levels. The evolution of nocturnality presents a potential problem. There is a restricted opportunity for thermoregulation at night and nocturnal lizards are active at much lower body temperatures than are diurnal lizards. Because the rate of physiological processes decreases exponentially with temperature, nocturnal lizards have to overcome a thermal handicap that decreases performance capacity. The ancestor of living geckos (by far the most successful and diverse group of nocturnal lizards) probably had excellent fuel economy (low C_{min}) that expanded endurance capacity and helped to offset the thermal handicap. If so, this lizard would have had increased but submaximal endurance capacity at low temperatures.

is more ambiguous (Garland et al. 1991). In contrast, nocturnal geckos do not show close coadaptation. Despite being active at T_b of 10–35°C below those of diurnal lizards, geckos have maintained T_o for sustained locomotion (Autumn and Full 1994; Autumn et al. 1994), sprinting (Huey et al. 1989), and growth (Autumn and DeNardo 1995) that are surprisingly comparable to those of diurnal lizards. This represents a substantial evolutionary mismatch in nighttime T_b and T_o , and may be a pattern of constraint that may reflect the historical

legacy of diurnality in lizards (Autumn et al. 1994, 1997; but see Huey et al. 1989). Because C_{min} is not thermally sensitive (John-Alder and Bennett 1981; Rome 1982; John-Alder et al. 1983; Bennett and John-Alder 1984; Autumn et al. 1994; but see Weinstein and Full 1994), adaptive evolution of low C_{min} increases sustained locomotor performance capacity at all temperatures (see Fig. 4B). Even if evolution of C_{min} fully offset the thermal handicap of nocturnality, nocturnal temperatures would remain suboptimal for sustained locomotion

(arrow) represents the thermal handicap of nocturnality (H; see Fig. 2). This indicates that the greatest change in maximum rate of oxygen consumption (at activity temperatures) occurred in the ancestor of geckos as a result of nocturnal activity. The next greatest change occurred at the level of Anguimorpha (numeral 1), the clade containing Anguinae, Xenosauridae, Helodermatidae, *Lanthanotus*, and *Varanus* (Estes et al. 1988). Unlike the case of the geckos, the increased $\dot{V}O_{2max}$ in Anguimorpha is probably due to physiological rather than behavioral differences. (B) Contrasts in C_{min} versus body mass in lizards. The contrast between geckos and their diurnal sister taxon (triangle) falls well below the 95% CL of the diurnal lizard IC allometry (dashed lines), indicating that C_{min} decreased significantly in the ancestor of geckos. The difference between y-value of this contrast and the y-value predicted by the regression (arrow) represents the evolution of superior fuel economy in geckos. Contrasts within diurnal lizards (circles) and within nocturnal geckos (squares) fall within or very near the 95% CL of the phylogenetically independent allometry except for the contrasts *Dipsosaurus* versus the clade containing *Iguana*, *Conolophus*, and *Amblyrynchus*; *Iguana* versus the clade containing *Conolophus* and *Amblyrynchus*; *Iguana* versus *Scleroglossa*; and *Eublepharis macularius* versus *Coleonyx variegatus*. (C) Contrasts in MAS versus body mass in lizards. The slope of the phylogenetically independent allometry within diurnal lizards was significantly different from zero (ANCOVA, $F = 10.98$; $df = 1, 8$; $P = 0.01$), and was similar to the allometric slope relating MAS and body mass in mammals (0.12; Taylor et al. 1970). Most contrasts between diurnal taxa (circles) and between nocturnal taxa (squares) fall within or very near the 95% CL, whereas the gecko-Autarchoglossa contrast (triangle) falls well outside the 95% CL. The difference (arrow) between y-value of the gecko-Autarchoglossa contrast and the predicted y-value of the gecko-Autarchoglossa contrast using ancestral values of C_{min} (diamond) represents the adaptive effect (A; see Fig. 3) of the decrease in C_{min} on MAS at nocturnal temperatures. Note that in this analysis, a value of the gecko-Autarchoglossa contrast (triangle) closer to the regression line represents an increase in MAS in geckos relative to their hypothetical ancestor.

(Fig. 4B, 6A). This explains the question of how geckos could perform better at low temperature than diurnal lizards, but are still suboptimal. Without an integration of mechanism and history, we could not have revealed that the adaptive evolution is due to one character (C_{\min}) that is not thermally sensitive, whereas the suboptimality is due to another character ($\dot{V}_{O_{2\max}}$) that is thermally sensitive.

Does Evolution of Increased Performance Capacity Confer an Advantage in Nature? Only if Performance Load in the Derived Environment Exceeds Ancestral Capacity

The ecological relevance of a change in performance capacity depends on the actual performance loads experienced by animals in nature. Increases in performance capacity should not be considered advantageous if animals do not use the additional capacity. The adaptive consequences of physiological evolution that offsets a handicap will depend on whether individuals in nature perform at levels exceeding the performance capacity of their hypothetical ancestors and whether this additional performance capacity is due to the evolution of the physiological variable in question.

Previous studies have generated correlations between laboratory measurements of locomotor performance capacity, underlying physiological variables, and indices of locomotor performance load in nature (Bennett and Gleeson 1979; Gleeson 1979; Huey et al. 1984; Walton 1988). However, some studies failed to show a correlation between performance capacity and certain indices of performance load (e.g., Bennett et al. 1984; Huey et al. 1984; Huey and Bennett 1986; Walton 1988). This may be due in part to the fact that many indices of locomotor performance load are only indirectly related to physiological capacity. A common shortcoming is the lack of a direct quantitative correspondence between the measure of capacity and load. For instance, a frequently used index of locomotor load, the proportion of time spent moving, does not provide sufficient information to indicate the portion of endurance capacity used in nature. To determine what portion of endurance capacity is used in nature, frequency, speed, and duration of locomotion must be measured in the field (Gatten et al. 1992; Weinstein and Full 1992). The solid theoretical understanding of the physiology underlying sustained locomotion (for reviews see Bennett 1982; Gatten et al. 1992) establishes a tight linkage between endurance capacity and performance load (frequency, speed, and duration). Without this linkage, one cannot directly test the hypothesis that performance capacity reflects performance in nature.

Testing the Nocturnality Hypothesis in Nature

A low C_{\min} confers an advantage to nocturnal lizards in theory. This advantage will be realized only if these lizards move at speeds above the predicted MAS given an ancestral value of C_{\min} and move at speeds below their own MAS. In other words, to quantitatively test the hypothesis that a character that increases performance capacity is an advantage in nature, *derived performance load should exceed ancestral capacity*, or in our notation, the difference in performance between $f_d(E_d)$ and $f_a(E_d)$ is actually used in nature. For example, MAS in *N. asper* is 0.24 km h⁻¹ at 20°C and the

predicted MAS given an ancestral value of C_{\min} is 0.11 km h⁻¹ (Fig. 5). Therefore, if locomotor speed in nature is consistently below 0.11 km h⁻¹ (at 25°C), this would imply that a low C_{\min} is not adaptive for sustained locomotion at night. Also, if geckos move at speeds significantly greater than their own MAS, and therefore do not utilize sustained locomotion, aerobic metabolism would not play a major role in determining performance capacity. If this were the case, a low C_{\min} would not be an advantage for sustained locomotion at night (although it would still be an advantage in lowering the energy budget for locomotion [Bennett 1986] or possibly in reducing recovery time after locomotion at nonsustainable speeds [Wagner and Gleeson 1997]). However, if geckos in nature move at speeds between their predicted and observed MAS (Fig. 5), they would perform at levels exceeding the performance capacity of their hypothetical diurnal ancestors, and this additional performance capacity would be due to the evolution of a low C_{\min} .

Although there is a growing body of data revealing geckos as mobile, foraging predators (Cooper 1995; Werner et al. 1997a,b), they are likely to be moving at speeds much lower than those observed in diurnal active foraging "marathon-runners" such as *Cnemidophorus* or *Varanus*. This is because the speeds sustained during active foraging are relative to the MAS, instead of an absolute measure (Bennett 1983). Because $\dot{V}_{O_{2\max}}$ is reduced at low temperature, MAS will be much lower, making active foraging nocturnal lizards more like high-altitude climbers for whom every step is an aerobic challenge, rather than marathon-runners who perform at high power output. For example, a typical diurnal lizard speed of 1 km h⁻¹ (Garland 1994) may be a physiologically slow speed for a large, warm lizard, a moderate speed for a small, warm lizard, and a nonsustainable speed for cold lizards of any size (Garland 1994). The sustainable speeds we measured in the geckos are at least 66% lower than 1 km h⁻¹. Geckos can sustain locomotion at 50% of their MAS for 30 min or more (Autumn et al. 1994), and can therefore cover quite a bit of ground, but to the field observer the animal would seem very slow. For example, the greatest MAS of any gecko measured so far (*T. przewalskii*) is 0.33 km h⁻¹ at 25°C. At 50% MAS at 25°C (0.165 km h⁻¹) a *T. przewalskii* can sustain locomotion for over 60 min (Autumn et al. 1994). At this speed it takes the lizard 1 min to move only 2.75 m, but it can cover 165 m in 1 h, and it takes it 6.06 h to walk 1 km. However, 50% the MAS of *T. przewalskii* at 25°C (0.165 km h⁻¹) is approximately equal to 100% of the MAS of a diurnal lizard of similar size at 25° (the predicted MAS for *T. przewalskii* with a C_{\min} typical of a diurnal lizard is 0.17 km h⁻¹). Thus, without its excellent fuel economy, *T. przewalskii* would have a difficult time moving at all, let alone the hundreds of meters they have been observed moving in a single night (K. Autumn, pers. obs.).

Intermittent locomotion can alter endurance capacity (Weinstein and Full 1992). A 15-sec exercise, 30-sec pause exercise protocol at speeds above MAS doubled endurance capacity in frog-eyed geckos (R. B. Weinstein, unpubl. data). Most other combinations of exercise and pause intervals did not increase endurance capacity. Because recovery time after supermaximal exercise is greatly increased at low temperatures (Wagner and Gleeson 1997), a low C_{\min} could further

enhance endurance capacity during intermittent locomotion by decreasing recovery time. By taking frequency, speed, and duration of movement into account in the data analysis, it is possible to correct for intermittent locomotion: combinations of exercise and pause intervals observed in nature can be used in a laboratory experiment to test the hypothesis that intermittent exercise alters endurance capacity (Weinstein and Full 1992). This will yield an adjusted range of predicted speeds, based on locomotor behavior in nature and laboratory measurements of treadmill endurance capacity. The intermittent locomotion experiments must be carried out following the field study, because only field observation will determine if animals move intermittently and, if so, identify which exercise/pause durations they use in nature.

Some of the next steps in studying locomotor performance at low temperature and the evolution of nocturnality in lizards are quantitative measurements of locomotor performance loads in nature (see above), measurements of fuel economy in secondarily diurnal geckos, and measurements of fuel economy in other nocturnal taxa, such as skinks and snakes. The latter two will address the generality of the evolutionary pattern we found in nocturnal geckos. Excellent fuel economy should be an advantage at high, diurnal temperatures as well as at night. An obvious question then is why geckos do not take advantage of their increased performance and be active at high temperatures. If they did, they could be "superlizards." In fact, some geckos have become secondarily diurnal and are active at high temperatures (e.g., *Lygodactylus*, *Phelsuma*, *Rhoptropus*, *Sphaerodactylus*). The next logical question (addressed by Autumn 1999) is whether diurnal geckos retain the excellent fuel economy of their nocturnal ancestors. If secondarily diurnal geckos have reverted to a high C_{\min} similar to ancestrally diurnal lizards, this will suggest that low C_{\min} has disadvantages (Autumn 1999). Nocturnality is probably independently derived in geckos, snakes, and skinks. The only study on the locomotor energetics of a nocturnal snake (*Crotalus cerastes*; Secor et al. 1992) showed that, like geckos, it has a low C_{\min} . If independent instances of nocturnality are concordant with independent instances of low C_{\min} , there may be a general evolutionary association between activity time and fuel economy.

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ENDNOTE. We follow Greene (1986) and Baum and Larson (1991) in using a phylogenetic, performance-based definition of an adaptive phenotypic change. We define a character-state transformation as adaptive if it increases performance in the derived environment (Greene 1986). Because the survival and reproduction of organisms depend on the integration of many of performance variables and because it is difficult to reconstruct the

past action of natural selection (Lauder et al. 1993; Lauder 1996), an increase in performance is not necessarily indicative of an increase in fitness. Our study focuses on macroevolutionary patterns; because microevolutionary forces maintaining current character states may be different from the causes of their evolution, the current performance-fitness relationships within populations are a complementary, but separate issue.

APPENDIX
Definition of terms.

Term	Definition
A	Performance advantage
C_{\min}	Minimum cost of locomotion ($\text{ml O}_2\text{g}^{-1}\text{km}^{-1}$; $\text{Jg}^{-1}\text{km}^{-1}$; inverse of fuel economy)
E_a	Ancestral environment
E_d	Derived environment
f_a	Ancestral physiology
f_d	Derived physiology
H	Performance handicap
IC	Phylogenetically independent contrast
M	Body mass (g)
MAS	Maximum aerobic speed (km h^{-1})
P_a	Ancestral performance capacity
P_d	Derived performance capacity
T_b	Body temperature ($^{\circ}\text{C}$)
T_o	Optimal temperature ($^{\circ}\text{C}$)
T_p	Preferred body temperature ($^{\circ}\text{C}$)
\dot{V}_{O_2}	Rate of oxygen consumption ($\text{ml O}_2\text{g}^{-1}\text{h}^{-1}$)
$\dot{V}_{\text{O}_2\text{max}}$	Maximum rate of oxygen consumption during exercise ($\text{ml O}_2\text{g}^{-1}\text{h}^{-1}$); aerobic capacity
$\dot{V}_{\text{O}_2\text{rest}}$	Resting rate of oxygen consumption ($\text{ml O}_2\text{g}^{-1}\text{h}^{-1}$)
Y_0	Y-intercept of \dot{V}_{O_2} versus speed function ($\text{ml O}_2\text{g}^{-1}\text{h}^{-1}$); idling cost