

## Thermal Sensitivity of Sprinting and Clinging Performance in the Tokay Gecko (*Gekko gekko*)

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**Abstract.** -The thermal sensitivity of sprinting and clinging ability was measured in tokay geckos (*Gekko gekko*). Sprinting performance was maximal at high (35-41°C) temperatures, as is the case for other nocturnal lizards, but the optimal temperature for clinging was considerably lower (approximately 17°C). These different optima could be adaptive if maximal sprinting and clinging capabilities are needed at different temperatures. Alternatively, they could result from constraints on adaptive evolution.

**Key Words:** Reptilia, Sauria, Gekkonidae, *Gekko gekko*, thermal sensitivity, optimal performance.

### Introduction

Most physiological processes are temperature-dependent. Ectothermic animals, which do not maintain a constant body temperature, are thus subject to fluctuation in the rate at which they can perform many vital tasks. By regulating body temperature behaviorally, however, many reptiles can maximize performance capability (Huey 1982a). In some cases, maximal performance temperature might differ for different tasks. For example, a wealth of behavioral data indicates that many lizards and snakes increase their body temperature after feeding, which suggests that digestion has a higher optimal temperature than other activities (reviewed in Huey 1982a).

Early work centered on the thermal dependence of sub-organismal traits (e.g., enzyme activity, muscle contractile speed [Huey and Stevenson 1979]). In many cases, however, the effect of temperature on the functional capacities (e.g., sprint speed, critical thermal maximum temperature) cannot be predicted by study at sub-organismal levels (e.g., Licht 1967; Marsh and Bennett 1985, 1986). Consequently, recent studies have focused on whole-organism performance. The thermal dependence of sprinting ability has been studied in great detail. Maximum sprinting speed and/or endurance in many species occurs at the temperature they most

frequently experience in nature (Bennett 1980); however, nocturnal lizards appear exceptional (Huey and Bennett 1987; Huey et al. 1989). The thermal sensitivity of few other whole-organism locomotor performance measures has been determined for lizards. Here I report the thermal sensitivity of tokay geckos (*Gekko gekko*) [Fig. 1] for two ecologically relevant tasks, maximum sprinting and clinging capability. I ask whether maximum performance capability occurs at the relatively low temperatures most commonly experienced by geckos (Huey et al. 1989) and whether the optimal temperature is the same for the two performance measures.

### Methods

Tokays are relatively large geckos found on trees and walls throughout southeastern Asia (Smith 1935). Lizards were captured on Phuket Island, Phuket Province, Thailand, and transported to the University of California, Berkeley in late September 1987. They were maintained in 30 x 17 x 9 cm plastic shoeboxes at ambient temperatures and provided with water and crickets *ad libitum*. An ontogenetic series was used in this study (11 individuals; snout-vent length: 85-180 mm; mass: 10-140 g).

All trials were conducted in a walk-in environmental chamber in the Museum of Vertebrate Zoology, University of

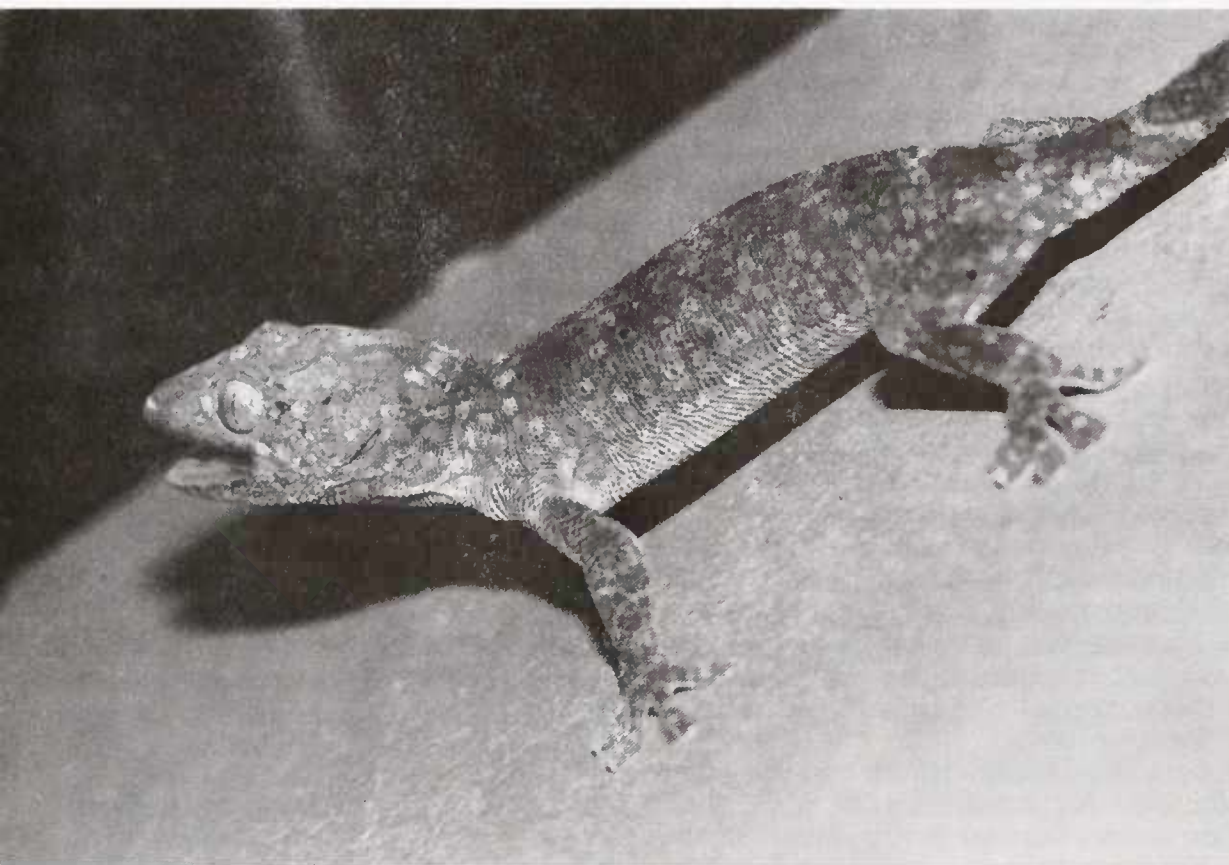


FIG. 1. *Gekko gecko* from Phuket Province, Thailand.

California, Berkeley. within a month of capture. Lizards were placed in the chamber at least one hour prior to performance measurement. Humidity, which could not be regulated, was determined on several occasions using a Bacharach sling psychrometer.

Clinging capability was measured by placing lizards on a plexiglass plate and, at a gradual and steady rate, lifting the end of the plate so that the lizard was clinging with its head directed down. The angle at which the lizard fell from the plate was recorded (protocol modified from Emerson and Diehl 1980; Alberch 1981). Lizards that jumped from the plate were not included in the analysis. As lizards began to slide, they usually attempted to maintain their grip by moving and re-applying their toe pads regardless of temperature. There was no evidence that temperature affected the lizards' efforts to prevent sliding and falling

from the experimental plate.

One trial per lizard was conducted per temperature. Performance at nine temperatures (12, 16, 17, 22, 24, 31 [three times], 34, 35, 41; the order of temperatures is presented in figure 2) was measured over a six-day period. On some days, two trials were conducted.

Sprint capability was measured by placing lizards at the end of a 2.25 m trackway covered with a rough rubber surface and inducing them to run by repeated taps to the tail (protocol following Huey 1982b; Huey et al. 1989; Garland 1985). As the lizard ran, it interrupted light beams stationed every 0.25 m. The time elapsed during each interval was computed by a Compaq personal computer; the fastest single interval during four trials, conducted at hourly intervals, was considered the maximum speed for that lizard at that



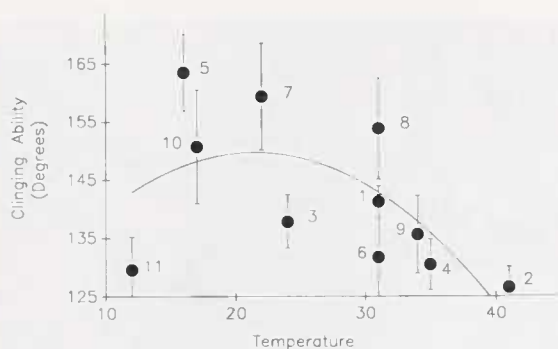


FIG. 2. Clinging ability (mean  $\pm$  1 s.e.) at different temperatures. Clinging ability is measured as the angle of the plate at which a lizard lost its grip and fell. The points are numbered by the order in which the trials were conducted.

temperature. Lizards that did not sprint at maximal capability on any of the trials at a given temperature, as judged by their gait, were not included in the calculations for that temperature. Lizards were tested at five temperatures (30, 36, 19, 26, 41°C, in that order), one temperature per day, over an eight-day period. Trials were never held on three consecutive days. A second trial at 30°C was held at the conclusion of the study to determine whether a performance decline had occurred. Animals whose performance decreased  $> 30\%$  were excluded from the analysis.

## Results

Clinging performance is temperature-dependent, with a peak at 17°C (Fig. 2). A non-linear equation ( $\ln [\text{clinging ability}] = 0.99 + 2.69 * \ln [\text{temp}] - 0.45 * \{\ln [\text{temp}]\}^2$ ;  $F_{2,8} = 5.08$ ,  $P < 0.05$ ) better fits the data than a linear regression ( $F_{1,9} = 2.77$ ,  $P > 0.10$ ).

Although between-day variation exists in clinging ability at a given temperature, no general pattern of increased or decreased performance over the duration of the study exists. For example, three trials were conducted at 31°C. The second trial had the lowest mean, whereas the last trial had the highest mean. Three other sets of trials were conducted at approximately the same temperature (16-17°C, 22-24°C, 34-35°C). In two cases, performance ability decreased

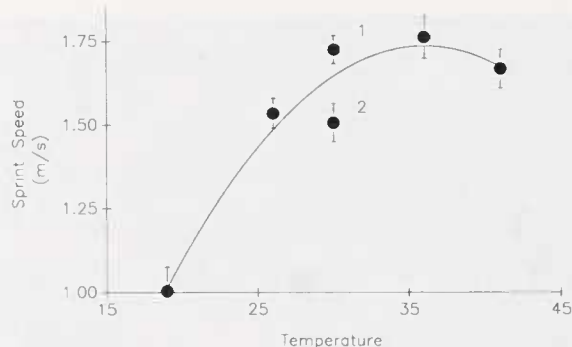


FIG. 3. Sprint speed (mean  $\pm$  1 s.e.) at different temperatures. The numbers indicate which represents the first and the second 30° trials.

in the second trial, but in the third case it increased.

Sprinting capability is also temperature-dependent (Fig. 3). Maximal performance ability occurs at 36-41°C, but interpretation of the results is difficult because performance ability declined over the course of the experiment, as evidenced by the difference in sprinting ability in the two sets of trials at 30°C. Despite this decline, several results are clear from inspection of Fig. 3: 1. performance at 36°C (tested 8 July) is slightly higher than at 30 (7 July); performance at 40°C (tested 13 July, after all trials except the second set at 30) is nearly as high or higher than all other temperatures; 3. performance at 30°C (16 July) is greater than performance at 26°C (11 July), which, in turn, is greater than performance at 19°C (10 July). Consequently, even if performance steadily decreased over time, it is reasonable to conclude that maximal sprint performance occurs around 36-41°C.

## Discussion

Sprinting and clinging are ecologically relevant performance measures for geckos, but their optimal performance temperatures differ greatly for tokays. Sprint performance is greatest at relatively high temperatures, as is the case for a number of other nocturnal gecko species (Huey et al. 1989) and the nocturnal skink

*Eremiascincus fasciolatus* (Huey and Bennett 1987). Clinging capability, the thermal dependence of which has never previously been investigated, is maximal at considerably lower (approx. 17°C) temperatures.

It is difficult to envision how such different optima could evolve adaptively. Most lizards sprint maximally at temperatures close to those they normally experience (Huey 1982a; Huey et al. 1989). The low optimal temperature for clinging matches the field temperatures of many active nocturnal geckos (Huey et al. 1989). However, many nocturnal geckos bask and/or are active to some extent during the day (Bustard 1967, 1968; Werner and Whitaker 1978; Nagy and Knight 1989). Consequently, the high optimal temperature for sprinting seen in many nocturnal lizards might represent adaptation for diurnal capability (Huey and Bennett 1987; Huey et al. 1989). Nonetheless, it seems implausible that one aspect of locomotion, sprint performance, should be selected at high temperatures, whereas another important component of effective movement, clinging, should be favored at considerably lower temperatures.

As an alternative explanation, the differences in thermal optima might result from differences in evolutionary lability of the two performance capabilities and thus represent constraints on adaptive evolution in either sprinting or clinging ability. To understand why these performance abilities are affected differently by temperature, a better understanding is needed of their underlying physical and physiological bases (e.g., Garland 1984, 1985; Marsh and Bennett 1985, 1986). In many species of lizards, sprint performance is maximal at temperatures close to the critical thermal maximum (Huey and Bennett 1987; Huey et al. 1989). The cause for this linkage is unclear. However, if geckos must be able to survive diurnal temperatures (either because they intentionally maintain high temperatures to maximize other processes, or because environmental conditions preclude the maintenance of lower temperatures), then they would have to

evolve high critical thermal maxima. The high sprint performance maximum might be a correlated effect of this physiological adaptation to high temperatures and not be adaptive per se (Huey et al. 1989).

Clinging capability depends upon both physical and physiological processes. Geckos cling to smooth surfaces by dry adhesion. The subdigital lamellar pads of geckos are covered with millions of microscopic setal hairs. When the pads are adpressed to a surface, these hairs form intermolecular bonds with molecules on the surface of the substrate (Hiller 1975). If the surface energy (a measure of the number of free electrons on the surface of the substrate) is relatively high, then enough bonds can form to support the lizard. Because these bonds result from the activity of electrons, the forces theoretically should be temperature-independent over the range of temperatures in this study.

However, geckos have an elaborate muscular and vascular system for the adpression and removal of their toe pads (Russell 1975); the thermal dependence of these muscles has not been investigated. The poor clinging performance of geckos at 10-12°C is clearly the result of physiological incapacitation. At that temperature, geckos were generally inactive, moved slowly and infrequently, and even rarely bit or barked when handled. In contrast to trials at higher temperatures, the lizards did not attempt to adjust their pads or posture when the plate was tilted and quickly lost their hold. More research is required to determine whether the performance decline at temperatures above 17-18°C results from decreased capability of the muscles and enzymes involved in clinging.

One possible confounding effect in the clinging experiments is the variation in absolute humidity. Moisture might decrease the formation of high-energy intermolecular bonds. Absolute humidity in the environmental chamber was measured at several temperatures and increased from 8.5 Barrs at 11.9°C to 25.1 Barrs at 34.3°C (relative humidity,



however, was greatest at intermediate temperatures). Consequently, the greater absolute humidity at higher temperatures in the environmental chamber might have caused a decrease in clinging ability. Further research is needed to investigate to what extent humidity affects clinging.

Although different processes may often be maximized at different temperatures, rarely is the difference as great as is observed between sprinting and clinging in tokay geckos (Huey 1982a). One would not expect these geckos to need maximum ability at these aspects of locomotion at such different temperatures, but neither would one expect the physiological sensitivity of different systems to be so different. Interestingly, the optimal temperature for hearing sensitivity in the tokay gecko is intermediate between the sprinting and clinging optima (Werner 1976). Further research is required to understand the processes shaping and constraining performance evolution.

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