JOURNAL OF EXPERIMENTAL ZOOLOGY 303A:785–791 (2005)

Effects of Temperature on Maximum Clinging Ability in a Diurnal Gecko: Evidence for a Passive Clinging Mechanism?

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ABSTRACT The thermal dependence of performance of ectotherms, and particularly locomotor performance in lizards, has received much attention. However, only a single study has examined the effects of temperature on adhesive clinging ability in geckos, despite the importance of adhesion for many pad-bearing lizards and invertebrates. We set out to characterize the thermal response of clinging ability in the diurnal gecko, *Phelsuma dubia* in the temperature range of 15–35°C. Our findings indicate that there is no significant trend in clinging ability for *P. dubia* with temperature and that there is high variation about the mean at all temperatures. These findings differ from other whole-organism studies of clinging performance and are suggestive of a passive clinging mechanism that is dominated by intermolecular van der Waals forces. These findings also suggest that clinging ability in this species is not under selective pressures resulting from thermal variation, and that *P. dubia* does not need to regulate body temperature closely to maximize clinging ability. *J. Exp. Zool. 303A:785–791, 2005.* © 2005 Wiley-Liss, Inc.

Temperature is known to profoundly affect many aspects of vertebrate function, including muscle contraction frequency, the maximum speed of locomotion, and digestion rate, among others (e.g., Bennett, '80, '90; Huey, '82; Marsh and Bennett, '86; Huey and Bennett, '87; Huey and Kingsolver, '89; Swoap et al., '93; DeNardo et al., 2002). One well-studied area of research involves the effects of temperature on whole-organism performance capacities, such as maximum speed and endurance (e.g., Marsh and Bennett, '85, '86; Bennett and Huey, '90). Ectotherms have been particularly well studied in this regard because of their tendency to match their internal body temperature in response to the external environment (Huey and Kingsolver, '89; Garland and Losos, '94). A general finding is that the effects of temperature on the physiology of many motor movements are similar in many ectotherms, such that even species with low preferred body temperatures tend to perform better at relatively high temperatures and this performance declines at very high temperatures (e.g., maximum sprint speed, Huey and Bennett, '87; see also Huey et al., '89; Garland et al., '91; Autumn et al., '94, '99; Bauwens et al., '95). Although not completely obvious, the underlying basis of this trend may be that vertebrate muscle responds in a common fashion to variation in temperature.

However, relationships between temperature and other kinds of performance capacity are less well understood. One potential example is the ability of animals to adhere to surfaces via intermolecular van der Waals forces (see Autumn et al., 2000, 2002; Hansen and Autumn, 2005). Adhesive structures have evolved independently in vertebrates and invertebrates multiple times (Ruibal and Ernst, '65; Russell, '79; Williams and Peterson, '82; Irschick et al., '96; Autumn et al., 2000, 2002; Dai et al., 2002), and are used for a variety of purposes, including climbing, holding prey, and holding mates. Within lizards, setae, which are elongated keratinous structures present on the toepads or feet, have evolved independently at least three times (at least once within the lizard genus *Anolis* [Polychrotidae], the Gekkonidae,

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Grant sponsor: NSF Grant; Grant number: IBN-0421917.

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Received 21 March 2005; Accepted 14 June 2005

Published online in Wiley InterScience (www.interscience.wiley.com). DOI: 10.1002/jez.a.210.

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and the Scincidae), and are used exclusively to aid climbing (Ruibal and Ernst, '65; Hiller, '76; Russell, '79; Williams and Peterson, '82; Hansen and Autumn, 2005). Geckos present the most extreme example of specialization for climbing in possessing large toepads and complex behaviors (e.g., the curling and uncurling of their toepads when running) that aid in rapid locomotion. The function of setae in pad-bearing lizards has been examined both at the setal level (Autumn et al., 2000, 2002; Hansen and Autumn, 2005) and the whole-organism level (Irschick et al., '96; Zani, 2000; Elstrott and Irschick, 2004; Bloch and Irschick, 2005).

However, an unresolved issue is how temperature affects adhesion in lizards, either at the setal level, or at the whole-organism level. The only study examining this issue found that clinging performance in the large tokay gecko (*Gekko gecko*) was maximal at 17°C, which is somewhat lower than the preferred temperature of this species (Losos, '90a). This result stands in direct contrast to other studies of whole-organism performance, such as running and jumping, for which performance is typically highest at relatively high temperatures (Huey and Bennett, '87; Losos, '90a; Bauwens et al., '95). Losos' ('90a) study, like previous non-thermal studies on salamanders (Alberch, '81), also examined clinging ability by the angle at which a pane of glass was tilted before the gecko began to slip. This method differs from other studies of clinging ability, which consisted of pulling a lizard on a smooth surface and measuring force using either a pesola scale (Losos, '90b; Zani, 2000), or a force platform (Irschick et al., '96; Elstrott and Irschick, 2004; Bloch and Irschick, 2005). Therefore, more studies are needed to determine if the findings of Losos ('90a) are general for other species and other methods of assessing clinging.

The issue of how temperature affects clinging ability may also shed light on how lizards modulate clinging ability. One possibility is that clinging is entirely a passive process that is dictated purely by van der Waals forces (Autumn et al., 2000, 2002), and not by the recruitment of muscles in the arm. A second possibility is that clinging is an active process that is dictated by both molecular forces and muscular properties. In the first case, one might expect no relationship, or a weak relationship between temperature and clinging. In the second case, depending on the relative roles of the two factors (muscles and van der Waals forces), one would expect a positive relationship between clinging ability and temperature and then rapidly declining, as vertebrate muscle typically performs better at higher temperatures (with the exclusion of extremely high temperatures that are far above the preferred body temperature of the lizard) (Marsh and Bennett, '85, '86; Huey and Bennett, '87; Swoap et al., '93).

We tested these ideas by inducing maximum clinging ability in a group of geckos (*Phelsuma dubia*) across a broad range of body temperatures (15–35°C). We measured clinging ability using a force plate, as in prior studies (Irschick et al., '96; Elstrott and Irschick, 2004; Bloch and Irschick, 2005), and discuss our findings in the context of prior studies of temperature effects on clinging (Losos, '90a), and also the relative possibilities for muscles and van der Waals forces to influence clinging.

METHODS

Specimens examined

Data were obtained from 28 specimens of the diurnal gekkonid *P. dubia*. Specimens included in the analyses were all of adult or sub-adult size, with an SVL between 42 and 64 mm (mean $\pm$ SD: 52 ± 7 mm) and a mass between 2.1 and 6.7 g (3.8 ± 1.2 g). All animals were obtained commercially from Strictly Reptiles (Hollywood, Florida). Animals were housed in pairs in $32 \times 18 \times 22\,\text{cm}^3$ ($L \times W \times H$) plastic terraria with paper towel substrate and Petri dishes of water. They were maintained at the Tulane laboratory in a temperature-controlled room at 28.0 ± 1.0°C on a 12-hr photoperiod supplied by fluorescent visible and UVB spectrum-emitting bulbs. Animals were fed a diet of vitamin-dusted crickets ad libitum on alternate days and misted with water daily. All animals were allowed a 2-week acclimation period prior to performance trials.

We collected body mass and snout-vent length (SVL) measurements prior to clinging performance trials. Subsequent to all trials, animals were euthanized with intraperitoneal nembutal injection, fixed with formalin, and preserved in 70% ethanol. The institutional Animal Care and Use Committee at Tulane University approved all experiments (IACUC approval 0189-2-16-0301).

Performance trials

Clinging ability was measured at different temperatures using a custom-built force plate (see below). Gecko clinging ability was measured at 15°C, 20°C, 25°C, 30°C, and 35°C. At 15°C, the geckos were very sluggish and at 35°C, one individual lost consciousness, so temperatures below and above the chosen range were not attempted out of concern for the well-being of the subjects. We know of no other studies that provide information on field, preferred, or optimal body temperatures, and the closest relatives of *P. dubia* for which this is known, *Rhoptropus*, are desert-dwelling, with very high optima (Peterson, '90). Many diurnal and nocturnal lizards have thermal optima at about 30°C (Autumn, '99). The lizards were placed in a Tritech Research Inc. (Los Angeles, CA) DigiTherm$^{\text{TM}}$ DT2-MP incubator set to the desired temperature 1-hr prior to commencement of trials. Body temperature of each individual was measured immediately prior to each trial using a Cox Technologies DE-305 digital thermometer to ensure that it was within 1.5°C of the desired temperature. The order of the trials was randomized with respect to temperature using the random number generator in Microsoft Excel XP, with the trials being in the following order: 20°C, 30°C, 15°C, 25°C, and 35°C.

Clinging was measured at least twice for each gecko at each temperature, and the highest exerted force at a given temperature was considered the maximal clinging ability at that temperature. No more than two trials were performed on any individual per 1-week period because damage to the superficial epidermal layer of sub-digital lamellae was noted visually after multiple trials in quick succession (also noted by Hansen and Autumn, 2005). Spacing trials in this manner appeared to deal effectively with this problem. A trial was rated as acceptable if the gecko adhered with all toes of both front feet and fully straightened both fore limbs while being pulled back along the acetate (following Irschick et al., '96).

Clinging trials consisted of the removal of the gecko from the incubator, measuring cloacal temperature, and placing the animal's front feet on an acetate sheet affixed with tape to the force plate. The force plate and acetate were oriented horizontally (Elstrott and Irschick, 2004). The lizard was then pulled backwards along the acetate in a smooth and controlled fashion, at a constant rate of approximately 5 cm/sec (i.e., no jerking or high acceleration of the lizard), and only one investigator (P.J.B.) conducted all trials to eliminate interobserver error, following the procedures of Irschick et al. ('96), Elstrott and Irschick (2004), and Bloch and Irschick (2005). The acetate provided a smooth, uniform surface for adhesion, and the effects of claws were not of concern because *P. dubia* lack claws. The custom-designed force plate used in all trials was $30 \times 18 \times 1\,\text{cm}^3$ ($L \times W \times H$), and measured parallel dimensional forces. The output of the plate's strain gauges was sent to a K&N Scientific 12-Bridge, eight-channel amplifier, and subsequently A–D converted at 10 kHz (Instrunet, model 100B). The digital signals were read into a G4 Macintosh computer and smoothed using a low-pass filter in Superscope II v.3.0. The top five clinging readings were recorded for each trial and the highest was retained for analysis.

Statistical analysis

All Superscope II readings were converted from mV to grams and then to Newtons. All statistical analyses were conducted in SYSTAT v.10.2 (Wilkinson, 2002). The assumptions of normality and homoscedasticity of ANOVA were tested using Kolmogorov–Smirnov and $F_{\max}$ tests, respectively (Sokal and Rohlf, '95). We first conducted a single-factor ANOVA (1) that examined differences among treatments in clinging ability. However, we were unable to gain good clinging data for all 28 lizards for all temperatures for this analysis, and hence we conducted a second analysis in which we limited the comparisons to the nine lizards for which we were able to get good clinging trials for all temperatures and used a repeated-measures ANOVA (2), which accounts for the non-independence of the data.

Since clinging ability is dependent on body size (Irschick et al., '96; Elstrott and Irschick, 2004), we evaluated body size differences between temperature treatments for the unbalanced analysis that included all 28 individuals. A single-factor ANOVA on body mass and SVL for each temperature revealed that there were no significant differences in size of individuals among temperatures (mass: $\text{df}_{\text{error}} = 90$, $\text{MS}_{\text{error}} = 1.297$, $F = 0.399$, $P = 0.808$; SVL: $\text{df}_{\text{error}} = 90$, $\text{MS}_{\text{error}} = 37.839$, $F = 0.789$, $P = 0.535$), so further accounting for size was deemed unnecessary. Size considerations were not a concern for the repeated-measures analysis because each treatment included the same sample of individuals.

RESULTS

Variation around the mean clinging force exerted by geckos was universally high at all

TABLE 1. Sample sizes (n), and means ± standard deviations for maximum clinging ability (N)

Temp.	*n*	All data[1]	*n*	Repeated[2]
15	18	1.902 ± 0.427	9	1.891 ± 0.427
20	18	1.670 ± 0.455	9	1.693 ± 0.507
25	24	1.712 ± 0.653	9	1.488 ± 0.565
30	19	1.845 ± 0.748	9	1.655 ± 0.643
35	16	1.725 ± 0.587	9	1.711 ± 0.763

[1] Complete dataset of 28 individuals (note the varying sample sizes for each temperature).

[2] Data including only those nine individuals analyzed with repeated-measures ANOVA.

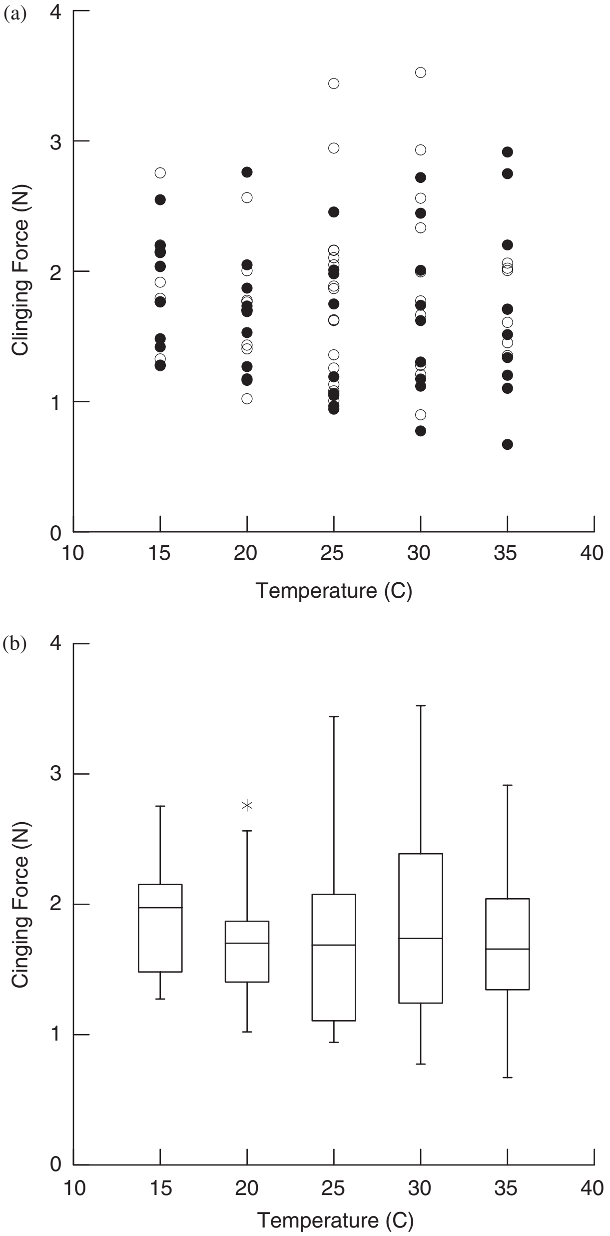

Fig. 1. Clinging force (*N*) as a function of temperature (°C) for *Phelsuma dubia*. (**a**) Data included in repeated-measures ANOVA are represented by (●), all other data are (○). (**b**) Box plots of all clinging data. The line within the box represents the mean; the top and bottom of each box represent the 75th and 25th percentiles, respectively; the top and bottom whiskers represent the 95th and 5th percentiles, respectively; the asterisk represents an outlying datum.

temperatures, with the standard deviation representing approximately a quarter of the mean (Table 1). However, the variance of clinging ability did not differ significantly among temperature treatments when all measurements were considered ($F_{\max}$ test: df = 5, 27, $F_{\max} = 3.061$, $P > 0.05$) and when only those clinging measurements included in the repeated-measures analysis were considered ($F_{\max}$ test: df = 5, 7, $F_{\max} = 3.199$, $P > 0.10$). This high degree of variation was also evident for a plot of the data for all individuals and those for which data at all temperatures were obtained (Fig. 1).

The assumptions of homoscedasticity (see above) and normality were met for both the complete dataset of 28 individuals (KS test: $N = 95$, Max difference = 0.075, $P = 0.196$), and for the repeated-measures dataset (KS test: $N = 45$, Max difference = 0.105, $P = 0.229$). A single-factor ANOVA (1) with temperature as a factor revealed no significant differences in clinging ability among temperature treatments ($\mathrm{df}_{\mathrm{error}} = 90$, $\mathrm{MS}_{\mathrm{error}} = 0.352$, $F = 0.439$, $P = 0.780$). The repeated-measures ANOVA (2) also revealed no significant differences between temperature treatments ($\mathrm{df}_{\mathrm{error}} = 32$, $\mathrm{MS}_{\mathrm{error}} = 0.196$, $F = 0.948$, $P = 0.449$). Therefore, *P. dubia* geckos appear to cling equally well across a variety of temperatures.

DISCUSSION

Most studies relating whole-organism performance capacity and temperature show strong interrelationships (see references cited in introduction), but our findings for clinging ability break from this trend. Our results show no trend in clinging ability in *P. dubia* with changing temperature (Fig. 1), and high amounts of variation in clinging ability at all five temperatures examined (Table 1). There is also no significant trend in the variance associated with clinging ability with changing temperature. A lack of a trend in clinging ability with temperature contrasts with the findings of Losos ('90a) for

G. gecko. In that species, clinging ability showed a non-linear relationship with temperature, with an optimum at ~17°C. However, our finding that there is high variation in clinging ability is consistent with the findings of Losos ('90a: Fig. 2), in which high interday variation in clinging ability was documented.

There are several possible explanations for the differences between our findings and those of Losos ('90a). First, the two studies were conducted on different species. *P. dubia* is a small diurnal gecko that lacks claws, while *G. gecko* is a large nocturnal gecko with claws. Species differences in setal structure or muscular anatomy may lead to these differences, but such an explanation seems unlikely because both of these anatomies are relatively conserved in geckos (Ruibal and Ernst, '65; Russell, '79; Williams and Peterson, '82). Second, it is possible that some of the specimens in our study exhibited differential motivation at different temperatures, leading to misleading levels of performance (Losos et al., 2002). This also seems unlikely because it would require high motivation at low temperature and low motivation at high temperature, and the reverse trend is expected. Furthermore, we were careful to minimize the potentially confounding effects of motivation by evaluating each trial based on quality (see above) and we removed numerous trials where we deemed that the animals were performing sub-maximally. Third, clinging trials on *G. gecko* were performed in a room set at the desired temperature (Losos, '90a,b), while such a room was unavailable for our trials. Although we were careful to ensure that body temperature of the lizards changed minimally during the trial, the variance in body temperature during the trial was undoubtedly higher in our study. However, it is unlikely that this would result in such disproportionate effects on clinging ability because of our measures to control body temperature and because the variance in clinging ability was high even at 20°C, which is approximate room temperature. Fourth, and maybe most importantly, differences in findings may be associated with the methodology used for measuring clinging ability. Losos ('90a) tipped geckos that adhered to plexiglass and recorded the angles at which they fell off, whereas we pulled geckos along an acetate sheet affixed to a force plate. Our force platform approach would seem to measure more active, muscle-intensive clinging performance, whereas the tilting-pane method would seem more suited for measuring passive adhesion (but see below). Another way to view this dichotomy is that we measured maximum clinging ability under forced conditions designed to push the adhesion and muscular system to the maximum (we note that our trials pushed clinging ability to the point of setal failure; see also Hansen and Autumn, 2005), whereas the tilting pane method presumably measures less stressful, and more voluntary aspects of adhesion. Indeed, a priori, one might have predicted the opposite outcome (e.g., a temperature effect for the force platform method, no temperature effect for the tilting pane method) (Losos, '90a). These differences between seemingly subtly different techniques suggest also that behavioral differences in how the environment affects performance may be important (Irschick and Garland, 2001).

Interestingly, the high amounts of variance in clinging ability documented for *P. dubia* and *G. gecko* (Losos, '90a) are not apparent for lizards of the genus *Anolis* (Elstrott and Irschick, 2004), which evolved adhesive setae independently of geckos (Ruibal and Ernst, '65; Irschick et al., '96). High degrees of variance associated with aspects of clinging performance in geckos have also been observed in the recovery of clinging ability after clogging of the setae with microspheres (Hansen and Autumn, 2005). Our findings lend support to the hypothesis that clinging ability is primarily determined by passive processes, specifically van der Waals forces (Autumn et al., 2002), as opposed to being strongly influenced by the active process of muscle recruitment. Since these intermolecular forces are dependent on molecular polarization and the distribution of electrons, one would expect them to be temperature independent over the temperature range examined here (Losos, '90a).

While our findings generally support clinging as a passive mechanism, they do not exclude the role of muscles in adhesion at the whole-organism scale. If these lizards slowly increase clinging force by the sequential recruitment of muscle fibers used to adpress the toe-pad to the substrate (Irschick et al., 2005), then fast muscle contraction associated with higher temperatures would be ineffective at enhancing the clinging ability. Along the same lines, our findings suggest that adhesion is not limited by the ability of the musculoskeletal system to produce power (Irschick et al., 2005), but more likely by the physical strength of the keratin that the setae are composed of (Autumn et al., 2002). This is supported by our observation that the lamellae of *P. dubia* became damaged after multiple clinging trials in quick succession. We do not expect that this damage would bias our results because trials were randomized in order, with respect to temperature. One might expect a greater influence of muscles on non-adhesive clinging ability on substrates in which claws might be used (Zani, 2000; Elstrott and Irschick, 2004; Vanhooydonck et al., 2005). Further studies examining the specific role of muscles in adhesion, perhaps using EMG techniques or paralysis (e.g., Gibb et al., 2004), would be useful.

Finally, our finding for temperature independence in clinging also suggests that a selective regime that optimizes clinging at a specific temperature (Losos, '90a) is unnecessary, implying that geckos need not regulate their body temperature closely in order to maximize their clinging ability (Hertz et al., '93). Thus, our results highlight that geckos may have evolved setal structures as a mechanism to climb effectively across a broad range of temperatures.

ACKNOWLEDGMENTS

This research was supported by an NSF grant to D. Irschick (IBN 0421917).

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