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Evolution of Temperature-Dependent Sprint Performance

in Nocturnal and Secondarily Diurnal Geckos

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by

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iii

Table of Contents

List of Tables

List of Figures

Abstract

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Temperature has a profound influence on most aspects of an ectotherm's life. Most of the world's 1500+ gecko species are nocturnal and therefore presumably active at body temperatures (T_bs) that are suboptimal for performance. However, several clades and numerous gecko species have independently reverted to diurnality and are therefore active at warmer T_bs allowing for comparisons of temperature-dependent sprint performance between nocturnal and secondarily diurnal species. Following the hotter-is-better hypothesis, which states that warm-adapted species will have better performance than cold-adapted species, we hypothesized that diurnal geckos would have faster maximum speeds than nocturnal species at their thermal optimum. Likewise, the optimality hypothesis predicts co-adaptation between environmental temperatures and optimal T_bs for performance. Thus, we hypothesized that diurnal geckos would sprint faster at warmer T_bs and slower at cooler T_bs relative to nocturnal geckos. We tested these hypotheses by comparing the temperature-dependent sprint performance of 27 gecko species over a range of ecologically relevant T_bs to determine how activity time

(nocturnal/diurnal) affected sprint performance. Conventional statistics and those that accounted for the genetic distances among the species were used to compare the sprint performance of nocturnal and diurnal geckos. Additionally, two clades with closely related nocturnal and secondarily diurnal species were compared using conventional statistics. Nocturnal geckos had slower sprint speeds than diurnal geckos overall, which is consistent with the hotter-is-better hypothesis. In accord with the optimality hypothesis, diurnal species sprinted relatively faster at higher T_bs and slower at cooler T_bs relative to nocturnal species suggesting that there has been an evolutionary shift in the temperature-dependent sprint performance of diurnal species with the higher activity temperatures associated with diurnality. Phylogenetic history did not influence temperature-dependent sprint performance because diurnality has evolved independently several times among the species included in this study and clades with diurnal species are spread throughout the gekkotan tree. Our study provides insight into the ways in which an evolutionary change in activity time can affect the evolution of temperature-dependent sprint performance in geckos and illustrates the likely constraints on performance for other cold-adapted nocturnal species.

Introduction

Background—Many ectotherms use behavioral and physiological adjustments to thermoregulate,

allowing them to maintain body temperatures (T_bs) within a specific range despite varying

environmental temperatures (Cowles and Bogert 1944; Stevenson 1985; Huey et al. 1989;

Espinoza and Tracy 1997; Angilletta et al. 2002). However, factors such as physiology,

evolutionary lability, and thermodynamics can limit the capacity for thermoregulation, which

may have important fitness consequences. For example, critical thermal limits define the

physiological boundaries of an ectotherm's thermoregulatory abilities. The relationship between

T_b and performance can be described by a hump-shaped curve where performance is zero at the

critical thermal minimum and maximum (CT_{min}, CT_{max}) and the thermal optimum (T_o) is the T_b

or range of T_bs over which performance is maximized (Huey and Stevenson 1979; Huey 1982;

Angilletta et al. 2002; Fig. 1). Performance curves are not evolutionarily static; their shapes vary

among and within species. Environmental or behavioral changes that result in a difference in the

thermal conditions experienced by a population can cause evolutionary shifts in the shape of the

curve (e.g., right or left, a widening or narrowing of the breadth, changing the height of the

curve). One hypothesis to explain right or leftward shifts in performance curves is the thermal

optimality hypothesis, which suggests that selection should maximize performance under new

thermal conditions (Kingsolver and Watt 1984). In short, there should be coadaptation of T_o to T_b

experienced during activity. For example, when lower T_bs are experienced because of an

evolutionary switch in a lineage from diurnal to nocturnal activity, there should be corresponding

compensatory changes in physiology, such as a lower T_o for locomotory performance (Huey and

1

Bennett 1987; Autumn et al. 1991). This would lead to an evolutionary shift of the performance curve to the left.

While physiological adaptation can compensate for some thermally induced challenges, performance is subject to the laws of thermodynamics (Hochachka and Somero 2002; Angilletta 2010), which can pose evolutionary constraints. For example, the hotter-is-better hypothesis (Huey et al. 1989) posits that the evolution of performance in cold-adapted species may be constrained and that organisms with a higher T_o will always perform better than organisms with a lower T_o (Huey et al. 1989; Angilletta 2010). Accordingly, nocturnal ectotherms, which generally have lower T_bs than diurnal species living in the same region, should not perform as well as their diurnal counterparts regardless of time of day or temperature. The long evolutionary history of nocturnality and the subsequent re-evolution of diurnality in several lineages of geckos make these organisms particularly well suited for testing for evolutionary constraints on thermal adaptation.

Gecko Evolution—Gekkota is an ancient and diverse lineage of squamate reptiles with more than 1500 extant species (Gamble et al. 2015). Geckos occupy a broad range of climates (tropics, subtropics, temperate regions, hot and cold deserts, etc.) and diversity of habitats nearly worldwide. They also exhibit a range of lifestyles (saxicolous, scansorial, arboreal, and terrestrial) making them a valuable group for testing a diversity of hypotheses in comparative biology (Bauer 2013). The split between the ancestor to Gekkota and other (diurnal) lizards occurred very early (165–180 Ma) in the evolutionary history of squamate reptiles (Gamble et al. 2008). Although 72% of extant gecko species have retained the nocturnal ancestral condition, several lineages have independently evolved diurnality secondarily (Gamble et al. 2015).

Formerly, 15 gecko genera were known to include species that have reverted back to the ancestral squamate condition of diurnality (Röll 2000), but additional origins of secondary diurnality have recently been reported recently (Grismer et al. 2015). Secondarily diurnal geckos may have reverted to diurnality to take advantage of activity temperatures that are closer to their T_o for locomotor performance (Autumn 1999). Unlike most diurnal lizards, which are generally active at T_bs that are higher and near their T_o for performance, nocturnal geckos are active at T_bs well below their T_o (Huey et al. 1989; Angilletta and Werner 1998).

Data from five nocturnal gecko species (Huey et al. 1989) suggested that the optimal temperatures for sprint speed of nocturnal geckos are much higher than would be predicted by the optimality hypothesis, and are similar to those of ancestrally diurnal lizards. Thus, nocturnal geckos operate under suboptimal conditions for performance, posing a thermal handicap (Autumn et al. 1997). This disadvantage suggests that this aspect of the thermal physiology of geckos has been conserved and is a physiological vestige of their diurnal ancestry. However, physiological adaptations, such as a lower minimum cost of locomotion (C_{min}), may have evolved in geckos to partially offset the thermal disadvantage of nocturnality (Autumn et al. 1997, 1999). A lower C_{min} gives nocturnal geckos better fuel efficiency relative to non-gekkotan diurnal lizards. Despite the advantages of a low C_{min}, geckos that have undergone an evolutionary reversal to diurnality have not retained the low C_{min} of their close nocturnal ancestors, but instead have a C_{min} that is similar to typical non-gekkotan diurnal lizards (Autumn 1999). This suggests secondarily diurnal geckos do not need the advantage of a lower C_{min}, presumably because they are active at T_bs that are more favorable for performance. If this is true, the performance of diurnal geckos should be co-adapted to warmer T_bs, and thus diurnal geckos should sprint relatively faster at warmer T_bs compared to nocturnal geckos.

Goals and Hypotheses—Our goal was to understand how activity time (nocturnal versus diurnal) and associated activity temperatures affect sprint performance in geckos. Sprint speed is an ecologically relevant behavior for prey capture and predator evasion and an important component of organismal fitness (Irschick and Losos 1998; Miles 2004; Husak 2006; Husak et al. 2006). Although T_o for sprint performance has been reported for ancestrally diurnal lizards and nocturnal geckos, no study has compared the T_o for sprint performance between nocturnal and secondarily diurnal geckos. We used the most comprehensive and robust phylogeny available for geckos (Gamble et al. 2008, 2011, 2015) to determine the closest nocturnal relatives of a phylogenetically diverse assemblage of diurnal geckos (representing at least 10 independent origins of diurnality) and compared sprint performance between diurnal geckos and their closest nocturnal relatives.

The hotter-is-better hypothesis (Huey et al. 1989) predicts that diurnal geckos will have higher performance than nocturnal geckos as a result of adaption to activity during warmer, and thus more performance-optimal T_bs. This is because performance is not thermodynamically constrained for diurnal species, so they should achieve faster sprint speeds than their nocturnal counterparts. In contrast, the performance of cold-adapted, nocturnal species should be constrained, and consequently lower relative to diurnal species. Thus, we hypothesized that diurnal geckos would achieve faster maximum speeds at their T_o than nocturnal species. Following the optimality hypothesis (Kingsolver and Watt 1984), we hypothesized that secondarily diurnal geckos will perform like typical (non-gekkotan) diurnal lizards rather than their more closely related nocturnal relatives. In other words, we hypothesized that diurnality in geckos would be associated with an increase in sprint performance at warmer T_bs and a decrease in performance at lower T_bs compared to nocturnal geckos. This would result in performance

4

curves for diurnal geckos that were shifted to the right (i.e., higher T_o; Fig. 1) relative to curves for nocturnal geckos.

Materials and Methods

Gecko Species and their Care—A total of 27 species of geckos representing five gekkotan families was included in our sprint analyses (Table 1). Of these, most (24 species; 16 nocturnal and eight diurnal species) were obtained from a professional gecko breeder living near Tulsa, Oklahoma, USA. For these geckos, we sprinted the lizards on site on two occasions: April 2011 and July 2012. Two additional nocturnal species, *Hemidactylus turcicus* (September 2011) and *Ptychozoon kuhli* (April 2011), were sprinted as well. The former species was collected in summer 2011 from a population that had been introduced to a suburban neighborhood in Chatsworth, Los Angeles County, California, USA some 10 years prior (Bernstein and Bernstein 2013). The latter species was represented by wild-caught animals that had been confiscated by the U.S. Fish and Wildlife Service in 2009 and were housed in the California State University, Northridge (CSUN) vivarium. Sprint data were also obtained for *Homonota darwinii* from Santa Cruz Province, Argentina; they were sprinted in Argentina in austral summer 2010 (Weeks and Espinoza, under revision).

Captive geckos were housed in glass or plastic terraria (dimensions varied by taxon, but each was several times the body lengths of each species in all dimensions) with rocks, bark, plastic or live plants, and other cover provided for refugia and sand, soil, or bark as the substratum. Geckos were exposed to a 12:12 photocycle and heat sources provided continuous opportunities to thermoregulate over a range of species-appropriate temperatures. Water was provided *ad libitum*, and the lizards were fed primarily crickets (*Acheta domesticus*) 2–3 times/wk. The enclosures of tropical (but not desert) geckos were sprayed with water twice weekly. Geckos were rarely handled, minimizing human interaction and preserving the natural

fear response. For the duration of sprint experiments (usually a few hours, but up to 1–2 d),

geckos were kept in 3.8-l ventilated plastic bags with a paper towel for cover. Following sprints,

gecko mass was measured with a digital scale (± 0.05 g) and body size (snout-vent length, SVL)

was measured with a transparent plastic ruler (± 0.5 mm). Only adult geckos in good health and

physical condition were included, and we excluded individuals with recently autotomized

(unregenerated) tails and gravid females if eggs were visible or palpable.

Sprint Performance—Geckos were sprinted down a temperature-adjustable racetrack constructed

of a transparent acrylic top and sides (150 × 13 × 13 cm). The track floor consisted of two

aluminum plates (6.0-mm thick), with the top plate (racetrack floor) etched via sandblasting to

achieve a coarseness of 300-grit sandpaper thereby providing traction (Fig. 2). Track temperature

was controlled by adjusting the flow rate of circulating water through loops of copper tubing

(3.0-mm diameter) sandwiched between the plates of the highly conductive floor. The track

temperature was monitored continuously by a thermocouple (type K; 28 AWG) taped to the

middle of the track floor and connected to a thermocouple reader (± 0.1 °C; Omega 871A,

Stamford, CT). The width of the racetrack was adjustable via a transparent acrylic panel that ran

lengthwise down the track. We adjusted the track width to approximately double the width of the

naturally outstretched limbs (at the elbows or knees) for each species to discourage sprinting

lizards from doubling back in the opposite direction during sprint trials. A metric ruler was

affixed to the inside back panel of the track to facilitate the estimation of sprint speed (see *Data

Capture*).

Prior to sprints, each gecko was confined to a small acclimation chamber (starting box:

19.7 × 13 × 13 cm) of the racetrack, which allowed the lizard's T_b to equilibrate to the

temperature of the track via conduction with the floor. Smaller species (< 20 g) were given at least 5 min and larger species (≥ 20 g) were given at least 10 min to equilibrate to the track temperature. Preliminary experiments determined this was sufficient time for the T_bs of geckos within the body-size range studied here to equilibrate to the track temperature (R. E. Espinoza unpubl. data). During this period, geckos were continuously observed to ensure they were in contact with the floor of the track. If they crawled up the walls, they were coaxed back onto track floor with the tip of a fine paintbrush and the temperature equilibration time was restarted.

Geckos were sprinted at five T_bs: 10, 15, 25, 35, and 40 °C (± 0.5 °C), with the order chosen at random for each new set of 1–5 species studied within a given sprint series (1–2-d interval). A few species were not tested at either 10 or 40 °C because these temperatures approached or exceeded their known or expected tolerance limits. Likewise, if the majority of individuals of a species was unable to sprint at 15 °C, the 10-°C sprint trial was not attempted for that species. At 40 °C, geckos were monitored continuously for signs of heat stress (e.g., panting, loss of righting ability), and those that exhibited signs of stress were removed from the racetrack. Most geckos were sprinted twice in succession (typically ~1 min between sprints) at each temperature, but a few very small-bodied species (< 3 g) were sprinted only once at each temperature because they exhibited signs of fatigue after the first sprint. On rare occasions when a gecko did not sprint the first two trials at a given temperature, a third sprint was added. Geckos were not directly handled between sprints to avoid heat transfer. Instead, the lizards were caught in a plastic bag as they exited the track and returned to the starting box for the second sprint. Between sprints at different temperatures, geckos were given at least 1 h to rest at room temperature (22–26 °C). Nocturnal species were sprinted between 1800–0300 h and diurnal species between 0800–1700 h to avoid potential differences in performance associated with

8

activity period. Maximum sprint performance was elicited by chasing the geckos down the track with an artificial "predator," which consisted of black pipe cleaners folded to mimic the form of a large tarantula and attached to the end of a collapsible stainless steel radio antenna. Geckos that autotomized their tails during sprint trials ($n = 5$) were not included in analyses.

Data Capture—Sprints were recorded with a high-definition, wide-angle digital video camera (Nikon Coolpix S9100, Melville, NY) mounted on a tripod at track height. The camera captured gecko sprints at 30 fps. Video files were uploaded onto a Macintosh computer (Apple Corporation, Cupertino, CA) and imported into iMovie v. 9.0 for processing. Sprints were divided into fixed 10- or 20-cm sections (depending on gecko body size, 10 cm for geckos < ~10 g), and sprint rate was determined for each track section. For each temperature, the 10- or 20-cm section over which each individual achieved its fastest time over all sprint trials at a given T_b was used as its maximum performance value for that temperature.

Performance Curves—To objectively describe the shape of the performance curves, we fit statistical models to the sprint data for each species. Five mathematical functions were selected for curve-fitting analyses based upon their general form (Table 2). For all five, parameters for each species were estimated using ZunZun curve fitting and the Akaike information criterion (AIC) (ZunZun.com). For each species, the model with the lowest AIC value was selected as the best-fitting curve because model selection via information theory generally provides less over-fitted models than traditional goodness-of-fit (r^2) values (Angilletta 2006, 2009). The best-fitting model for each species was then graphed in Microsoft Excel.

Data Analyses—Before explaining the details of each statistical procedure, here we provide an overview and corresponding predictions for each analysis. We first used conventional statistics to test for differences in sprint performance between nocturnal and diurnal geckos. Nocturnal geckos were expected to reach T_o at lower T_b than diurnal geckos and to achieve a lower sprint speed overall. Second, in an attempt to be more cognizant of the role of phylogeny in shaping performance curves, we compared closely related nocturnal and diurnal geckos from two clades: the *Rhoptropus* clade (represented by one diurnal and three nocturnal species), and the *Afroedura* clade (represented by three diurnal and one nocturnal species). In a third analysis, data were standardized to remove the overall differences in sprint speeds among the species studied and to remove the general trend of increasing sprint speed at higher T_bs. This permitted an evaluation of our expectation that diurnal geckos would sprint faster at warmer T_bs and slower at cooler T_bs compared to nocturnal geckos independent of general trend effects. Fourth, these standardized data were used to calculate differences in the curviness of the performance curves among species. A partial Mantel test was used to test for correlations between these differences and nocturnality versus diurnality, while controlling for patristic distance. The null expectation was that more closely related species would have similar temperature-dependent performance curves. The details of these analyses are described below.

Temperature-dependent Sprint Performance in Nocturnal and Diurnal Species—Sprint performance data were first analyzed using a general linear mixed effects model in SAS v. 9.3 (SAS Institute, Cary, NC). The maximum sprint speed of an individual at a particular T_b was the dependent variable. The model consisted of four factors: activity period (diurnal vs. nocturnal), species, T_b, and body size (snout–vent length, SVL). Species was considered a random factor and nested within activity, SVL was used as a covariate, and T_b was a repeated measure for

individual lizards. The *R* matrix (the matrix of covariances among blocks of repeated observations) was unstructured, meaning that no specific pattern of covariation among repeated measures was assumed, because the order of different T_bs comprising the repeated measures was randomized and examination of the covariances did not suggest that any pattern existed. A mixed effect model was used because it enables repeated measures testing with missing data. We used AICc (Burnham and Anderson 2002) to select the best-fit model.

Comparisons of Activity Period and Performance within Clades—To determine whether there were differences in temperature-dependent sprint performance of closely related diurnal and nocturnal gecko species, we compared nocturnal and diurnal species within two gecko clades. We started with a tree of species included in our study, which was pruned from a comprehensive (> 100 genera and > 700 species) and robust phylogeny for geckos (Gamble et al. 2012; Fig. 3). From this tree, we identified two clades with nocturnal and diurnal species. The first (*Rhoptropus* clade) included the secondarily diurnal species *Rhoptropus boultoni*, which among our sample of species is the sister taxon to a clade of nocturnal geckos including *Chondrodactylus angulifer*, *Pachydactylus monicae*, and *Colopus wahlbergii*. The second (*Afroedura* clade) included the nocturnal *Afroedura hawequensis*, which among our sample of species is sister to a clade of secondarily diurnal geckos including *Lygodactylus kimhowelli*, *Phelsuma grandis*, and *P. abbotti*. We used a mixed effects model (as described above) to test for differences in temperature-dependent sprint performance between nocturnal and diurnal species within each clade.

Predicting Differences in Sprint Patterns of Nocturnal and Diurnal Species—To better visualize differences in sprint performance between nocturnal and diurnal geckos, we created a detrended graph for which the effects of individual speed and the general trend of increasing

11

speed with higher T_b was removed. For each individual, we plotted a line through the sprint

speeds at two T_bs, 15 and 35 °C, and calculated the deviations in speed from this line for all other

sprint temperatures for the same individual. We used 15 and 35 °C as the anchor points because

sprint data were not available for some species at 10 or 40 °C (see *Sprint Performance* above).

We then calculated the means of the deviations among individuals within a species and then

among species (i.e., grand means) within each activity period. This facilitated a comparison of

sprint speeds by nocturnal and diurnal geckos at 10, 25, and 40 °C without the influence of trend

effects, allowing us to assess the predicted differences in sprint patterns between nocturnal and

diurnal species.

Phylogenetic Analyses of Sprint Performance—To account for the potential influence of

phylogeny on the temperature-dependent sprint performance of nocturnal and diurnal geckos, we

used the deviations from the previous detrended analysis to fit a parabolic curve for each lizard,

which yielded a *c*-coefficient on the T_b^2 term for each individual. The individual *c*-coefficients

were averaged for each species and values for each species were then compared to every other

species as the absolute value of the difference in mean *c*-coefficients. These differences in

curviness were arranged into a half-diagonal matrix comparing every species to every other

species. Matrix correlations were used to relate this *c* matrix to an *activity-period* matrix and a

patristic-distance matrix (a proxy for genetic distances). For the *activity-period* matrix, if the two

species being compared differed in activity period, a 1 was entered, whereas if both were

nocturnal or both were diurnal a 0 was entered. For the *patristic-distance* matrix, RAG1 nuclear

gene sequences (from Gamble et al. 2012) were used to calculate the pairwise, uncorrected p-

distances using PAUP v. 4.0a136 (Swofford 2002). The p-distances are the proportion (p) of

nucleotide sites that are different between two sequences being compared without correcting for

multiple substitutions or variations in evolutionary rates. The RAG1 gene was used rather than one of the mtDNA genes because the latter become saturated above the family level (T. Gamble pers. comm.), which could lead to erroneous results in distance-based comparative analyses for ancient lineages such as geckos (Ho et al. 2005). RAG1 was also chosen because it was the largest nuclear gene fragment (more than twice as large as all other genes used in Gamble et al. 2012), the most variable (allowing for robust genetic-distances estimates), and had been sequenced for most of the species in our study. However, because the RAG1 sequences were incomplete for *Microgecko persicus* and *Stenodactylus sthenodactylus*, we used the distances for *Alsophylax pipiens* and *Mediodactylus russowii*, respectively. The RAG1 distances for these species provided more accurate information than the incomplete sequences for the original two species, but were not expected to otherwise affect the analysis as the proxy species are closely related and, based on other genes, have similar branch lengths to the species they replaced (Gamble et al. 2012). With these three matrices (*c*, *activity period*, and *patristic distance*), we ran a partial Mantel test in PC-ORD v. 6.08 (Gleneden Beach, OR) of *c*-coefficients on activity period, while controlling for patristic distances, which simultaneously tested for the influence of activity period on sprint performance curves.

Results

Variation in Sprint Performance Curves and Speed—For 17 of the 27 gecko species studied

(63%), the temperature-dependent sprints conformed to the shape of a "typical" performance

curve (Fig. 4). In these cases, sprint speeds were relatively slow at low T_bs, increased with

increasing T_b until they reached a peak, and subsequently declined. Eight species (30%) showed

increasing sprint speeds as T_b increased yet no decline in performance over the range of T_bs

tested (Fig. 5). Of those eight species, two (*Rhoptropus boultoni* and *Woodworthia maculatus*)

had rapidly increasing rates of sprint performance with increasing T_bs suggestive of an

exponential function. Two species (7%), *Pachydactlus monicae* and *Phelsuma grandis*, had

performance curves that, when fitted with polynomial functions, had one peak at a lower or

intermediate T_b, and another at a higher T_b, suggesting two T_os (Fig. 6). *Pachydactlus monicae*

showed dramatic declines in performance at 35 °C compared to 25 and 40 °C. *Phelsuma grandis*

had a less dramatic decline at intermediate T_bs, with a smaller peak at 15 °C and a second peak at

40 °C or possibly higher (Fig. 6).

The mean (± SE) maximum sprint speed for all geckos over all T_bs was 1.01 m s^{-1} (±

0.11). The fastest rate among diurnal geckos was 1.28 (± 0.23) m s^{-1} and among nocturnal

geckos was 0.92 (± 0.07) m s^{-1}. The fastest species, *Rhoptropus boultoni* (diurnal), reached 2.73

(± 1.20) m s^{-1} at 40 °C, which was more than twice as fast as the mean maximum speed for the

diurnal geckos sampled. *Cnemaspis africana* was the slowest diurnal species reaching a speed of

0.84 (± 0.15) m s^{-1} at 40 °C. *Stenodactylus sthenodactylus* was the fastest nocturnal gecko, with

a maximum speed of 1.58 (± 0.18) m s^{-1} at 35 °C, or 1.7 times faster than the mean maximum

speed for the nocturnal species sampled. The nocturnal *Eublepharis hardwickii* was the slowest

sprinter, achieving a maximum sprint speed of only 0.30 ($\pm$ 0.04) m s^{-1} at 40 °C, which was three times slower than the mean speed for the nocturnal geckos sampled.

Sprint Performance of Nocturnal versus Diurnal Geckos—For the analysis of all 27 gecko species and the analyses of both the *Rhoptropus* clade and the *Afroedura* clade, the full mixed model without the covariate (body size) best explained the data (Tables 3, 4, 5) indicating that body size (SVL) was not a significant predictor of sprint speed. The interaction between T_b and activity period was significant ($F_{4,131} = 7.25$, $P < 0.001$), meaning the sprint performance of nocturnal and diurnal geckos differed in response to temperature. In particular, nocturnal and diurnal geckos sprinted similarly at lower T_bs, but performance for nocturnal geckos peaked at 25 °C, whereas sprint speed in diurnal geckos continued to increase at higher T_bs (Fig. 7 and 8). The interaction between T_b and species nested within activity period was significant, indicating variation among species within nocturnal and/or diurnal activity periods in their response to T_b ($F_{95,131} = 3.42$, $P < 0.001$). The effects of species nested within activity period on sprint speed were also significant ($F_{25,131} = 6.24$, $P < 0.001$). This analysis detected no difference in sprint performance resulting solely from activity period ($F_{1,131} = 0.96$, $P = 0.330$; Table 6); T_b had a significant overriding effect on sprint speed ($F_{4,131} = 132.89$, $P < 0.001$); warmer geckos naturally run faster.

Comparisons of Activity Period and Performance within Clades—For the *Afroedrua* clade a significant interaction between activity period and T_b was found ($F_{3,17} = 4.05$, $P = 0.024$), indicating that T_b affects the sprint performance of nocturnal and diurnal geckos differently. However, there was no interaction between T_b and activity time ($F_{4,22} = 1.07$, $P = 0.396$) for the

Rhoptropus clade. For both clades there was a significant effect of T_b by species nested within activity period ($F_{8,22} = 4.15$, $P = 0.004$; $F_{8,17} = 10.13$, $P < 0.001$), meaning that species within activity period vary in the effect of T_b on sprint speed. For the *Afroedura* clade, the effect of species nested within activity period was significant ($F_{2,17} = 7.88$, $P = 0.004$), however this was not the case for the *Rhoptropus* clade ($F_{2,22} = 2.13$, $P < 0.143$). For both the *Rhoptropus* clade and the *Afroedura* clade, T_b had a significant effect on sprint speed ($F_{4,22} = 18.26$, $P < 0.001$; $F_{4,17} = 25.13$, $P < 0.001$, respectively), but activity period had either no effect or a marginally significant effect on sprint performance ($F_{1,22} = 3.17$, $P < 0.089$; $F_{1,17} = 3.96$, $P = 0.063$, respectively).

There were differences in the overall patterns of sprint performance between nocturnal and diurnal species within both the *Rhoptropus* and the *Afroedura* clades (Fig. 9 and 10). Within the *Rhoptropus* clade, nocturnal and diurnal species sprinted similarly at lower T_bs, but the nocturnal species in this clade peaked at 25 °C, whereas the sprint speed of the diurnal species increased at higher T_bs (Fig. 9). Likewise, species within the *Afroedura* clade had similar sprint performances among nocturnal and diurnal species at 10 °C, but the diurnal species outperformed the nocturnal species as T_b increased (Fig. 10).

Comparison of Sprint Patterns among Nocturnal and Diurnal Geckos—The standardized (detrended) analysis (Fig. 8) supports the hypothesis that nocturnal species reach their T_o at lower T_bs than diurnal species. Specifically, the curve for nocturnal species arched above zero at 25 °C, indicating that sprints of nocturnal species peaked at 25 °C, which was lower than the performance peak for diurnal species. The data points at 10 °C for both nocturnal and diurnal species were below zero, indicating that both groups sprinted slowly at lower T_bs; however, the

diurnal species were considerably lower than zero, indicating that they sprinted even slower than expected at 10 °C. Consistent with our hypothesis, nocturnal species performed relatively better at 10 °C than diurnal species. The sprint performance of geckos at 40 °C generally supported the hypothesis that diurnal geckos would outperform their nocturnal counterparts at warmer T_bs, in that the mean for diurnal species was above the x-axis, whereas the mean for nocturnal species was below the x-axis. Thus, the diurnal species sprinted faster than expected at 40 °C.

Genetic Effects of Sprint Performance—After accounting for patristic distances among the sampled gecko species, there was no correlation between activity period and the *c*-coefficient ($n = 27$, $r = -0.095$, $P = 0.221$). Activity period and *c*-coefficients also were not correlated (Mantel test; $r = -0.089$), indicating that diurnal or nocturnal activity did not strongly influence the curviness of the quadratic curve. There was no correlation between the *c*-coefficients and patristic distances (Mantel test; $r = 0.090$), indicating that there was not a strong phylogenetic influence on the shape of the quadratic curve. Similarly, activity periods and patristic distances were not correlated (Mantel test; $r = 0.058$). The absence of this correlation is also evident in the phylogenetic tree of sampled taxa (Fig. 3), which shows that diurnality has evolved repeatedly in Gekkota (i.e., diurnal species are not clustered within a single clade; see also Gamble et al. 2015).

Discussion

Variation in Performance Curves—Thermal performance curves are typically bell-shaped and left skewed exhibiting a gradual rise in performance at low T_bs to a peak at mid T_bs, followed by a steeper decline in performance at higher T_bs (Fig. 1; Huey and Kingsolver 1989; Espinoza and Tracy 1997). However, variations of the typical performance curve have been reported. For example, the curve may be broader and flatter at the top indicating a greater performance breadth and lack of a clear peak in T_o. This shape is common in eurythermic ectotherms, which experience more thermal variation. Fluctuating thermal environments may select for greater thermal tolerance, leading to a broader performance breadth, as reported for *Homonota darwinii*, the world's southern-most gecko species (Weeks and Espinoza in revision; Fig. 4). In contrast, for ectotherms that experience little thermal variation, a performance curve with a steeply sided peak is expected (Janzen 1967), such as for tropical lizards (Huey et al. 2009).

Although the sprint performance curves for a majority of the species included in our study was close to "typical," this was not always the case. Eight species had curves that showed no decrease in performance over the range of T_bs tested (Fig. 5). These species would likely exhibit "typical" performance curves had they been sprinted at higher T_bs.

Unexpectedly, two species had sprint performance profiles that had two peaks rather than one (Fig. 6). The double-peaked "curve" for *P. grandis* might be an artifact of over-fitted data: rather than two distinct peaks, this species may have a plateau at intermediate T_bs followed by a rapid increase in performance at higher T_bs. The curve appeared to indicate a rapid increase at 40 °C, despite daytime air temperatures (T_as) range 28–32 °C in their native habitat (Van Heygen 2004). Without measures of sprint performance at additional T_bs, the T_o for *P. grandis* is unclear,

but this species may have T_os well above T_bs typically experienced in nature. Geckos and other lizards have the ability to maintain T_bs higher or lower than operative temperatures via behavioral thermoregulation (Cowles and Bogert 1944). For example, *P. kochi* can achieve T_bs significantly higher than T_as or substratum temperatures (Ikeuchi et al. 2005, Angilletta 2009), so *P. grandis* may achieve higher T_bs than T_as would suggest.

While the sprint curve for *P. grandis* might be an artifact of over fitting, the double-peaked curve of *Pachydactylus monicae* suggests there is a biological basis for the shape of these curves. And although the sinusoidal curve was not selected by AIC, the sinusoidal performance "curve" for *Cyrtopodion elongatum* warrants discussion as well. Both species showed a steep decline in sprint performance at 35 °C and little variation among individuals at each sprint temperature, indicating there may be a common explanation for the two peaks. Notably, both species are nocturnal. While most of the activity of nocturnal species occurs at night, many species of nocturnal geckos bask by day (e.g., Werner and Goldblatt 1978; Arad et al. 1989; Anderson 1999; Baha El Din 2006). The thermal benefits accrued from diurnal thermoregulation may be vital to physiological processes like metabolism and digestion (Kearney and Predavec 2000). Because they may be exposed while thermoregulating by day, diurnally basking nocturnal geckos likely encounter predators, so the ability to sprint quickly at warmer daytime T_bs would be advantageous. Thus, there may be strong selective pressure favoring individuals that could escape predation while basking during the day. Simultaneously, diurnally exposed nocturnal geckos need to maintain reasonable performance during their more typical nocturnal activity when T_bs are cooler. One potential mechanism for the two peaks is duplicate copies of genes, or ecoparalogs, which can be influenced by disparate environmental pressures. Each copy performs the same function, although under different environmental conditions (Sanchez-Perez et al.

2008). Thus, after duplication, selective pressures associated with nocturnality may have influenced the modification of one gene copy involved in locomotory performance to produce a peak at cooler T_bs, while diurnal conditions exerted pressure on another gene copy, leading to a second peak at warmer T_bs. To date, ecoparalogs have only been described from bacteria, so research on gene duplication and ecoparalogs in vertebrates such as geckos could prove illuminating.

Some Geckos are Fast—Rhoptropus boultoni achieved maximum sprint speeds more than twice as fast (2.73 m s^{-1}) as the majority of the other diurnal gecko species tested. From 35 to 40 °C, the sprint performance for *R. boultoni* was still increasing (Fig. 5). As a diurnal species from the Namib Desert where daytime rock surface temperatures can exceed 45 °C, sprint performance may have increased further before achieving T_o. There are clear advantages to producing quick bursts of speed to capture prey and evade predators at high T_bs for this desert species. Interestingly, the congener *R. afer* has the fastest sprint speed recorded for any gecko (>3 m s^{-1}; Higham and Russell 2010). Although specialized morphology, such as longer hind limbs, contribute to the remarkably fast sprint speed of *R. afer* (Higham and Russell 2010), morphological characteristics of *Rhoptropus* in general show evidence of a history of running and saltatory locomotion in open landscapes (Bauer et al. 1996). While a tradeoff between sprinting and climbing abilities might be expected, many morphological characteristics associated with rapid sprint speed may actually increase climbing capabilities (Van Damme and Vanhooydonck 2001). Rapid sprint speed in lizards has been associated with xeric climates, diurnal activity, and a saxicolous lifestyle as is typical for *Rhoptropus*. However, these effects disappeared when phylogeny was taken into consideration in a study of more than 80 lizard

species (Van Damme and Vanhooydonck 2001), which highlights the role of phylogenetic history in the evolution of sprint performance. For *Rhoptropus*, Van Damme and Vanhooydonk did not observe the increased sprint performance in other closely related species, suggesting that specific ecology may have played a stronger role in shaping the sprinting abilities of *Rhoptropus*. Similarly, the evolutionary interplay between physiology, morphology, and environment has likely selected for high locomotory performance in *R. boultoni*, but more research into its exceptional speed is warranted.

Stenodactylus sthenodactylus was the fastest of the nocturnal species, reaching a top speed that was the third fastest of all the gecko species. This species is distributed throughout much of North Africa where it experiences long periods of extremely arid conditions (Baha El Din 2006; Metallinou et al. 2012). *Stenodactylus sthenodactylus* achieved peak sprint performance at 35 °C (Fig. 4), a T_b unlikely to be experienced at night in its native range. One explanation for this is that *S. sthenodactylus* may be occasionally active by day, as are many other predominantly nocturnal species (Werner and Whitaker 1978; Avery et al. 1982). In support of this idea, *S. sthenodactylus* has been observed crawling about in the shade by day (Frankenberg 1978). The need to perform well during bouts of diurnal activity may have selected for high sprint performance at higher T_bs. Although *S. sthenodactylus* has a higher-than-expected T_o, it also has a fairly broad performance breadth and sprinted reasonably well at 20 °C, a T_b it would typically experience during nocturnal activity.

Other Geckos are Slow—Not all gecko species rely on quick escape to avoid predation. *Eublepharis hardwickii*, for example, is a large-bodied gecko that apparently has adopted alternative antipredator strategies. This nocturnal species lives under large rocks and boulders or

21

at the base of trees in the deciduous forests of Bangladesh (Singh 1984). *Eublepharis hardwickii* was the slowest gecko we sprinted, with a maximum speed of only 0.30 m s^{-1} over all T_bs (Fig. 5), suggesting that rapid bursts of speed are not its typical predator-avoidance strategy. Sprint speeds reported for the well-studied congener *E. macularius* were similar to those we recorded for *E. hardwickii* at the same temperature. At 35 °C, McElroy et al. (2008) and Fuller et al. (2011) reported speeds of 0.24 m s^{-1} and 0.18 m s^{-1}, respectively for *E. macularius*, which compares to 0.25 m s^{-1} at 35 °C for *E. hardwickii* in our study. Fuller et al. (2011) attributed the slow sprint speed of *E. macularius* to the availability of cover, suggesting that the energetic costs of rapid sprint speed are more worthwhile for species living in more open habitats. The same may be true for *E. hardwickii*. Alternatively, predators such as our artificial "tarantula" may not be particularly intimidating to robust geckos such as *E. hardwickii*. On occasion we experienced difficulties motivating a few of the geckos, particularly the larger bodied species, to sprint in response to the predator. We found this to be the case most often at lower T_bs. Antipredator behaviors in ectotherms may change as species reach T_bs at the extremes of their performance range. At lower T_bs, lizards may switch from a fleeing strategy to immobile defensive postures (Hertz et al. 1982), attack (Crowley and Pietruszka 1983), or may flee sooner (Rand 1964). While the majority of the geckos in our study relied on rapid sprints to avoid the threat of "predation" at high T_bs, it was not uncommon for some species to stop, turn, and attempt to bite the pursuing "tarantula" when chased at the lower T_bs that impaired locomotory performance. With little chance of outrunning the predator, the change in antipredator behavior from fleeing to fighting is likely adaptive at low T_bs as sprint performance is largely temperature dependent, whereas bite force is not (Herrel et al. 2007).

Morphological Correlates of Performance—The largest species we studied was more than four times the body length of the smallest, yet body size was not a significant predictor of sprint speed. In part, this may because the geckos we studied represented a wide range of body sizes, shapes, and natural history traits that the influence of body size was obscured. While larger lizards generally sprint faster than smaller ones, some of the larger species we studied were slow (e.g., *E. hardwickii*), whereas several smaller species (e.g., *Lygodactylus kimhowelli*) sprinted fairly quickly. Because we tested for the effects of lizard body size (SVL) across a diversity of species rather than intraspecifically, it is less surprising that the effects of body size were negligible. Although other morphometric variables (e.g., hind limb length) are often associated with sprint speed, we focused on SVL because we wanted to ensure that overall body size was not a confounding variable in sprint performance. Variation in morphology likely plays a role in explaining the variation in sprint performance we observed both within and among species; however, it was not our intent to determine which of those traits would predict sprint speed in this study.

Genetic Effects of Sprint Performance— Patristic distance was not correlated with activity period, likely because diurnality has evolved independently several times in Gekkota generally, and among the species included in this study specifically. Although diurnality is generally clustered within particular clades, these clades are spread throughout the gekkotan tree over five of the seven taxonomic families (Gamble et al. 2012, 2015). Therefore, although phylogenetic relationships likely do play a role in the occurrence of diurnality in geckos, they were not influential in our analyses.

Patristic distance was also not strongly correlated with the curviness of the performance curves. These results are supported by the individual ANCOVA analyses of the *Rhoptropus* and *Afroedura* clades. There were significant differences in temperature-dependent sprint performance between species within activity time for both clades, and for the *Afroedura* clade, temperature-dependent sprint performance varied between nocturnal and diurnal species. Similar to the results from our analyses of all sampled species, nocturnal geckos reached T_o at lower T_bs and sprinted slower overall than their diurnal counterparts for both the *Rhoptropus* and *Afroedura* clades. The performance curves for the closely related species within each of these clades indicate that other factors (e.g., morphology and ecology), likely play a stronger role in determining the temperature-dependent sprint performance of these geckos than does their phylogenetic affinities. For example, within the *Afroedura* clade, *P. grandis* sprinted relatively quickly at all T_bs (Fig. 6) and was the second fastest sprinter of all the species tested, whereas its close nocturnal relative *Afroedura hawequensis* sprinted rather slowly at all T_bs (Fig. 5) and was one of the slowest geckos we sprinted. *Afroedura hawequensis* is a nocturnal crevice dweller (Jacobsen 2014) from the southwestern Cape mountains of South Africa, whereas *P. grandis* is a diurnal arboreal species from the forests of Madagascar. The dissimilar climates and ecology may have played a role in the evolution of divergent thermal performance of these species, despite their relatively close relationship. A similar example is evident by comparing sampled *Rhoptropus* to their closely related *Pachydactylus* species. *Rhoptropus* species are saxicolous geckos from open habitats where fast sprint speed and saltatory locomotion may have evolved as a result of environmental pressures (Bauer et al. 1996). By contrast, *Pachydactylus* species are from dense rocky habitats with abundant crevices, which they use as refugia. These species do not possess the remarkable sprinting abilities of their relatives (Bauer et al. 1996). Adaptation to

differing habitats likely played a stronger role in shaping the morphology and physiology of these lineages than did phylogenetic conservatism.

Which Thermal Adaptation Hypothesis Best Explains Gecko Performance?—As we hypothesized, diurnal geckos sprinted relatively faster at lower T_bs and slower at higher T_bs relative to nocturnal species. Both the comparison of sprint speeds between all diurnal and nocturnal species (Fig. 7) and the detrended analysis (Fig. 8) showed that nocturnal geckos reached T_o at a lower T_bs than diurnal species. Although nocturnal geckos had a lower T_o for sprint performance than diurnal geckos, their T_o was not as low as optimality theory would predict given that nocturnal geckos are active at T_bs that are 10–35 °C lower than diurnal lizards (Autumn et al. 1994). According to optimality theory, there should be coadaptation of T_o with T_bs achieved during activity (Huey et al. 1989). For geckos, the lower T_bs achieved by nocturnal species while active and foraging should affect their fitness, leading to corresponding compensatory changes in physiology, such as lower T_o for sprint performance (Huey and Bennett 1987). However, nocturnal geckos often have T_o similar to those of diurnal lizards, and much higher than would be predicted given their nocturnal activity (Huey et al. 1989; Autumn et al. 1994, 1997). Our finding that nocturnal geckos had lower T_o for sprinting than diurnal lizards suggests that there has been some compensatory evolutionary shift in temperature-dependent performance, but not enough to match T_o to the T_bs experienced during activity. In other words, nocturnal geckos are still challenged by being active at times when their T_bs are suboptimal for performance. The reason for this mismatch between T_o and activity temperature is not entirely clear. It may indicate that geckos are evolutionarily conserved with respect to their temperature dependence of sprint performance; however, because at least some secondarily diurnal geckos

have a higher T_o than their nocturnal ancestors, some adaptive change has apparently occurred. One possibility is that temperature-dependent sprint performance is constrained at low T_bs. The hotter-is-better hypothesis suggests there may be an evolutionary constraint on the performance of cold-adapted species resulting from thermodynamics (i.e., the slower rate of biochemical reactions at lower T_bs). Another explanation for this finding is that the T_o of nocturnal geckos may be coadapted to the higher daytime T_bs they experience during inactivity, and which may be required for other vital physiological processes such as digestion and growth, instead of the lower T_bs experienced when active (Huey et al. 1989). Thus, thermal physiology may be conserved for processes such as metabolism, digestion, or assimilation rather than sprint performance. If this were the case, there would be a tradeoff between digestive efficiency and maximal sprint speed, which could impede the evolution of lower T_o for activity (Huey and Hertz 1984). It would be interesting to test for this tradeoff among nocturnal and diurnal geckos.

Secondarily diurnal geckos sprinted relatively faster at warmer T_bs, slower at cooler T_bs, and reached T_o at higher T_bs compared to nocturnal geckos (Figs. 7 and 8). This change in temperature-dependent sprint performance can be visualized as a rightward shift of the performance curve, which we predicted for secondarily diurnal species. The evolutionary shift of the performance curve suggests that the diurnal geckos have at least partially reverted back to the thermal physiology typical of ancestrally diurnal lizards. Unlike the lower T_bs experienced by nocturnal geckos, which pose a thermal disadvantage for sprint performance, higher daytime T_bs would allow diurnal geckos to take advantage of more thermally optimal T_bs for activity (Huey and Kingsolver 1989; Autumn et al. 1994, 1997; Autumn 1999). The rightward shift of the performance curve was associated with both an increased T_o, as would be predicted by the optimality hypothesis, and higher maximum sprint speeds, as predicted by the hotter-is-better

hypothesis. Although this hypothesis is useful in determining the direction of evolutionary change in response to environmental pressures, it neglects the evolutionary constraints imposed by thermodynamics and does not take into account the physiological limitations that may constrain the evolution of T_o, especially for cold-adapted species. Thus, for geckos, the hotter-is-better hypothesis better accounts for the thermodynamic constraints on evolution.

While the overall pattern for sprint performance of diurnal gecko species followed our predictions, there were unexpected results as well. Diurnal geckos outperformed nocturnal species at warmer T_bs, as we hypothesized, but in fact, the analysis removing trend effects of increasing sprint speed at higher T_bs (Fig. 8) showed that diurnal geckos performed even better at warmer T_bs than expected. This is likely because of the remarkably high speeds obtained by several diurnal species when sprinted at high T_bs. The sharp increase in performance at 40 °C of *R. boultoni* especially, but also *P. abbotii* and *P. grandis*, likely contributed to the unexpectedly high sprint speeds of the diurnal geckos as a group.

Similarly, diurnal species sprinted even slower at cooler T_bs than would be predicted once the trend of increasing speed with sprint temperature was removed (Fig. 8). Because most diurnal geckos are from the tropics (Bauer 2013), they would not experience T_bs as low as 10 °C. Unlike nocturnal geckos, diurnal species are not constrained to perform at suboptimal T_bs, and other processes (e.g., digestion) can also occur during periods of inactivity. Evolutionary pressures would not select for high performance at low T_bs, and thus the need for enzymatic activity supporting sprint performance at cool T_bs would be lost. For example, a lower cost of locomotion (C_{min}) has evolved in some nocturnal gecko lineages, which allows for a maximum aerobic speed twice that of typical diurnal lizards at cooler T_bs (Autumn et al. 1997). Interestingly, this physiological adaptation may have been lost in two secondarily diurnal gecko lineages (Autumn

et al. 1999). This lower C_{min} in nocturnal geckos helps partially offset the disadvantages of the cold T_bs associated with nocturnal activity. While these adaptations should be advantageous at warmer T_bs as well, diurnal geckos have not retained this ability (Autumn et al. 1999). Therefore, it is expected that diurnal geckos sprint slowly relative to nocturnal species at cooler T_bs.

Conclusions and Future Directions— Our study was the first to directly compare the T_o of a large assemblage of phylogenetically diverse nocturnal and secondarily diurnal gecko species. It provides insight into the way that a shift in activity time from nocturnality to diurnality and the associated changes in activity temperature affect sprint performance in geckos. Questions remain as to why certain species have evolved faster sprint speeds than others that have presumably experienced similar environmental pressures. No doubt a number of variables influence the evolution of sprint performance in geckos. A more in-depth phylogenetic analysis among clades with a large number of independent origins of secondary diurnality (e.g., Asian *Cnemaspis*) may further elucidate the role of phylogeny in shaping the evolution of sprint performance in geckos that differ in diel activity. The inclusion of additional factors in further analyses, such as habitat, lifestyle, microhabitat use, and morphological characteristics may be illuminating as well.

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Appendix A

Table 1. Biological data for the 27 gecko species included in sprint analyses. Data are means (± SE). SVL = snout–vent length.

Species	Family	*n*	Sex Ratio (M:F)	Activity Cycle	SVL (mm)	Body Mass (g)	Distribution	Habitat	Lifestyle
Rhacodactylus chahoua	Diplodactylidae	6	4:2	Nocturnal	115.2 (2.3)	40.6 (2.2)	New Caledonia	Tropical forests	Arboreal
Woodworthia maculatus	Diplodactylidae	4	2:2	Nocturnal	71.3 (2.1)	15.7 (1.8)	New Zealand	Rocky grasslands	Saxicolous
Eublepharis hardwickii	Eublepharidae	6	2:4	Nocturnal	113.3 (1.1)	49.2 (3.0)	India	Desert/rock	Terrestrial
Afroedura hawequensis	Gekkonidae	5	1:4	Nocturnal	73.0 (0)	12.1 (0)	South Africa	Mediterranean forest, woodlands	Terrestrial
Agamura persica	Gekkonidae	5	2:3	Nocturnal	71.4 (3.0)	11.3 (1.9)	Pakistan, Afghanistan	Desert	Terrestrial
Chondrodactylus angulifer	Gekkonidae	11	5:6	Nocturnal	81.8 (2.5)	23.1 (2.5)	Namibia	Desert/sand	Terrestrial
Cnemaspis africana	Gekkonidae	3	1:2	Diurnal	44.0 (1.0)	2.4 (0.2)	East and West Africa	Montane forest	Terrestrial
Colopus wahlbergii furcifer	Gekkonidae	6	3:3	Nocturnal	49.5 (2.8)	3.6 (0.5)	Namibia, South Africa	Desert	Terrestrial
Crossobamon eversmanni	Gekkonidae	6	2:4	Nocturnal	49.5 (1.5)	2.8 (0.3)	Middle East	Desert	Terrestrial
Cyrtopodion elongatum	Gekkonidae	5	2:3	Nocturnal	47.2 (2.0)	3.4 (0.3)	China, Mongolia, Turkestan	Desert, Mongolian steppe	Terrestrial
Cyrtodactylus pulchellus	Gekkonidae	6	1:5	Nocturnal	97.5 (1.5)	16.1 (1.4)	South East Asia	Forest	Terrestrial
Hemidactylus turcicus	Gekkonidae	8	5:3	Nocturnal	50.2 (0.9)	3.0 (0.2)	Europe, Middle East, North America	Mediterranean/ urban areas	Arboreal

Lepidodactylus lugubris	Gekkonidae	6	0:6	Nocturnal	41.2 (1.2)	2.1 (0.1)	China, India, Vietnam	Forest	Arboreal
Lygodactylus kimhowelli	Gekkonidae	6	3:3	Diurnal	36.7 (1.5)	1.8 (0.4)	East Africa	Coastal forest	Arboreal
Microgecko persicus euphobiacola	Gekkonidae	5	3:2	Nocturnal	30.8 (0.5)	0.6 (0.0)	North Africa	Desert/rock	Terrestrial
Narudasia festiva	Gekkonidae	6	3:3	Diurnal	28.2 (1.8)	0.9 (0.1)	Namibia	Desert/rock	Saxicolous
Pachydactylus monicae	Gekkonidae	5	3:2	Nocturnal	42.2 (0.8)	1.9 (0)	Namibia, South Africa	Desert/rock	Terrestrial
Phelsuma abbotti	Gekkonidae	6	2:4	Diurnal	51.0 (2.8)	5.5 (1.2)	Madagascar	Forest	Arboreal
Phelsuma grandis	Gekkonidae	6	2:4	Diurnal	93.3 (3.5)	34.2 (4.2)	Madagascar	Forest	Arboreal
Ptychozoon kuhli	Gekkonidae	9	3:6	Nocturnal	88.1 (1.0)	11.8 (0.6)	Southeast Asia	Tropical forest	Arboreal
Rhoptropus boultoni	Gekkonidae	4	2:2	Diurnal	48.8 (0.5)	4.8 (0.2)	Namibia, South Africa	Desert/rock	Saxicolous
Stenodactylus sthenodactylus	Gekkonidae	6	2:4	Nocturnal	44.8 (0.7)	2.0 (0.1)	Africa, Southwest Asia	Desert/rock	Terrestrial
Haemodracon riebeckii	Phyllodactylidae	6	1:5	Nocturnal	68.3 (1.3)	11.7 (1.8)	Socotra Island	Tropical desert, rocky areas	Arboreal
Homonota darwinii	Phyllodactylidae	9	3:5	Nocturnal	48.0 (0.6)	2.9 (0.1)	S Argentina, Chile	Rocky Patagonian steppe	Terrestrial
Ptyodactylus ragazzi	Phyllodactylidae	5	2:3	Nocturnal	82.6 (6.5)	14.3 (2.7)	Northern and Central Africa	Boulders/desert	Saxicolous
Pristurus rupestris	Sphaerodactylidae	4	0:4	Diurnal	29.0 (0.7)	1.2 (0.2)	N Somalia, Iran	Desert/rock crevices	Saxicolous
Quedenfeldtia moerens	Sphaerodactylidae	4	1:3	Diurnal	42.0 (2.1)	2.6 (0.2)	Western Morocco	Rocky areas	Saxicolous

37

Table 2. Potential models used to fit curves to the sprint performance data and their mathematical functions. Y values represent the dependent variable, sprint speed, and X values represent the independent variable, temperature.

Model	Function
Gaussian	$Y = ae^{[-0.5(\lvert X-b \rvert /c)^\wedge 2]}$
Modified Gaussian	$Y = ae^{[-0.5(\lvert X-b \rvert /c)^\wedge d]}$
Third-order Polynomial	$Y = a + bX + cX^2 + dX^3$
Fourth-order Polynomial	$Y = a + bX + cX^2 + dX^3 + fX^4$

Table 3. AIC of mixed model analysis for 27 species of geckos. The model selection approach relies on Akaike information criteria (AIC) values among competing models (see Burnham and Anderson 2002). AIC differences, Akaike weights, and evidence ratios are used to evaluate a group of competing models. AIC difference, or Δ_i, is the AIC for the ith model minus the smallest AIC; this is a relative difference measure and models with $\Delta_i < 2$ have substantial support. Akaike weights (w_i) are the relative likelihood that the ith model is the best-supported model given the data and the specified group of competing models. By definition, $\Delta_i = 0$ for the best-supported model and $\Sigma w_i = 1$. Evidence ratio (w_i/w_j) is the comparison of two competing models and gives the relative odds of one model against another (i.e., how much more likely the data would be observed under one model than another). For example, a ratio of six would suggest model i is six times more likely to be the best model than model j. The evidence ratio in the first row of the table compares the best (first row in the table) and the second-best model (second row in the table).

Model[a]	AIC	ΔAIC	Likelihood	wi	wi/wj
Full Model, no covariate	1163.9	0	1	0.982014	54.59815
ANCOVA SVL + full repeated	1171.9	8.0	0.018316	0.017986	
SS SVL (Temp) + full repeated	1196.7	32.8	7.54E-08	7.41E-08	
HS SVL*Temp + full repeated	1196.7	32.8	7.54E-08	7.41E-08	
SS SVL(Species) + full repeated	1245.3	81.4	2.11E-18	2.07E-18	
HS SVL*Species + full repeated	1245.3	81.4	2.11E-18	2.07E-18	

Dropped Temp*Species(Activity)	1352.5	188.6	1.11E-41	1.09E-41
ANCOVA SVL dropped Temp*Species(Activity)	1360.4	196.5	2.14E-43	2.1E-43
Dropped Temp*Species(Activity) & Temp*Activity	1367.6	203.7	5.85E-45	5.74E-45
ANCOVA SVL dropped Temp*Species(Activity) & Temp*Activity	1375.5	211.6	1.13E-46	1.11E-46
Dropped Species	1415.7	251.8	2.1E-55	2.06E-55
ANCOVA SVL dropped Temp*Species(Activity) & Temp + interactions & Species	1426.6	262.7	9.02E-58	8.86E-58
Dropped Repeated (Temp and all interactions)	1779.3	615.4	2.3E-134	2.3E-134
ANCOVA SVL dropped Temp*Species(Activity) & Temp + interactions	1787.5	623.6	3.9E-136	3.8E-136
		1.018316		

[a]HS is heterogeneity of slopes model and SS is separate slopes model.

Table 4. AIC of mixed model analysis for the *Rhoptropus* clade. See Table 3 for definitions of symbols and interpretation of values.

Model*	AIC	ΔAIC	Likelihood	*wi*	*wi/wj*
Full Model, no covariate	257.2	0	1	0.642249	1.822119
ANCOVA SVL + full repeated	258.4	1.2	0.548812	0.352474	
SS SVL(Species) + full repeated	268.2	11.0	0.004087	0.002625	
HS SVL*Species + full repeated	268.2	11.0	0.004087	0.002625	
Dropped Temp*Species(Activity)	279.7	22.5	1.3E-05	8.35E-06	
SS SVL (Temp) + full repeated	280.3	23.1	9.64E-06	6.19E-06	
HS SVL*Temp + full repeated	280.3	23.1	9.64E-06	6.19E-06	
ANCOVA SVL dropped Temp*Species(Activity)	280.9	23.7	7.14E-06	4.58E-06	
Dropped Temp*Species(Activity) & Temp*Activity	282.9	25.7	2.63E-06	1.69E-06	
ANCOVA SVL dropped Temp*Species(Activity) & Temp*Activity	284.1	26.9	1.44E-06	9.26E-07	
Dropped Species	288.1	30.9	1.95E-07	1.25E-07	
Dropped repeated (Temp and all interactions)	336.5	79.3	6.03E-18	3.87E-18	
ANCOVA SVL dropped Temp*Species(Activity) & Temp + interactions	341.4	84.2	5.2E-19	3.34E-19	

ANCOVA SVL dropped Temp*Species(Activity) &	342.5	85.3	3E-19	1.93E-19
Temp + interactions & Species				
				1.557029

* ^aHS is heterogeneity of slopes model and SS is separate slopes model.

Table 5. AIC of mixed model analysis for the *Afroedura* clade. See Table 3 for definitions of symbols and interpretation of values.

Model*	AIC	ΔAIC	Likelihood	*wi*	*wi/wj*
Full Model, no covariate	149.1	0	1	0.868563	7.028688
ANCOVA SVL + full repeated	153.0	3.9	0.142274	0.123574	
SS SVL(Species) + full repeated	159.9	10.8	0.004517	0.003923	
HS SVL*Species + full repeated	159.9	10.8	0.004517	0.003923	
SS SVL (Temp) + full repeated	172.2	23.1	9.64E-06	8.37E-06	
HS SVL*Temp + full repeated	172.2	23.1	9.64E-06	8.37E-06	
Dropped Temp*Species(Activity)	181.7	32.6	8.34E-08	7.24E-08	
ANCOVA SVL dropped Temp*Species(Activity)	185.4	36.3	1.31E-08	1.14E-08	
Dropped Temp*Species(Activity) & Temp*Activity	186.3	37.2	8.36E-09	7.26E-09	
ANCOVA SVL dropped Temp*Species(Activity) & Temp*Activity	190.0	40.9	1.31E-09	1.14E-09	
Dropped repeated (Temp and all interactions)	225.7	76.6	2.33E-17	2.02E-17	
ANCOVA SVL dropped Temp*Species(Activity) & Temp + interactions	229.0	79.9	4.47E-18	3.88E-18	
ANCOVA SVL dropped Temp*Species(Activity) & Temp + interactions & Species	231.0	81.9	1.64E-18	1.43E-18	

Dropped Species	240.1	91.0	1.74E-20	1.51E-20
			1.151327	

* [a] HS is heterogeneity of slopes model and SS is separate slopes model.

Table 6. Mixed model analysis for all 27 gecko species. Species was random a random factor, while activity type and temperature were fixed.

Source	df	F	P
Activity	1, 131	0.96	0.330
Species(Activity)	25, 131	6.24	<0.001
Temperature	4, 131	132.89	< 0.001
Activity*Temperature	4, 131	7.25	<0.001
Temperature*Species(Activity)	95, 131	3.42	<0.001

Appendix B

Figure 1. A hypothetical performance curve representing the relationship between T_b and performance. CT_{min} and CT_{max} are the minimum and maximum temperatures for performance, respectively, and T_o is the temperature at which performance is maximized (Huey and Stevenson 1979; Huey 1982).

Figure 2. The portable, temperature-controlled racetrack (150 × 13 × 13 cm) used for sprinting geckos.

Figure 3. Time-calibrated phylogenetic tree of Gekkota (Gamble et al. 2012) pruned to show the relationships among the 27 species studied here. The tree was generated using five protein-coding nuclear genes and one mtDNA gene, as well as associated tRNAs. Moon symbols represent nocturnal species and sun symbols represent diurnal species. The scale bar represents the uncorrected p-distance.

Figure 4. Temperature-dependent sprint performance curves for 18 species of geckos that exhibit a typically shaped performance curve. Nocturnal species are represented by black squares and diurnal species by white circles. Data are means (m s^{-1} ± SE) and y-axes were scaled to a maximum of 1.4 m s^{-1} except for *Stenodactylus sthenodactylus*, which was scaled to a maximum of 1.8 m s^{-1}.

Figure 5. Temperature-dependent sprint performances of seven species of geckos with "curves" that did not plateau. Nocturnal species are represented by black squares and diurnal species by white circles. Data are means (m s^{-1} ± SE) and y-axes were scaled to a maximum of 1.4 m s^{-1} except for *Rhoptropus boultoni*, which was scaled to a maximum of 3.6 m s^{-1}.

Figure 6. Temperature-dependent sprint performances of two gecko species with atypical "curves" suggestive of two performance peaks. *Pachydactylus monicae* has peaks at 25 °C and second peak at 40 °C or higher, whereas *Phelsuma grandis* has an initial peak at 15 °C. Nocturnal species are denoted by black squares and diurnal species by a white circles. Data are means (m s^{-1} ± SE) and y-axes were scaled to 1.4 m s^{-1} for *P. monicae* and 2.0 m s^{-1} for *P. grandis*.

Figure 7. Temperature-dependent sprint performances of 27 gecko species. Nocturnal species (*n* = 19) are represented by black squares and diurnal species (*n* = 8) by white circles. The performance curves for both the nocturnal (solid) and diurnal (dashed) were fit to a quadratic function. Sprint performance of nocturnal geckos was similar to diurnal geckos at lower temperatures, but peaked at 25 °C and leveled off, whereas the sprint speed of diurnal geckos continued to increase at higher body temperatures. Data are grand means for each species (± SE).

Figure 8. Standardized sprint speeds for nocturnal (black squares, solid lines) and diurnal (white circles, dashed lines) geckos. A line was fit through the sprint speeds at 15 and 35 °C for each individual gecko and deviations from this line were calculated for each sprint temperature. The means of the deviations represent the grand means among species for each activity period (nocturnal or diurnal). Error bars for 10, 25, and 40 °C are ± SE. No error bars were included for 15 and 35 °C because these temperatures were used as the anchor points for the standardization. These data show how performance differs between nocturnal and diurnal species at 10, 25, and 40 °C after removing the effects of the speed of individuals and the general trend of increasing speed with temperature. Deviations from zero on the y-axis show deviations from that trend. The curves were fit to a quadratic function. As hypothesized, nocturnal species peaked at a lower temperature than did diurnal species, as is illustrated by the nocturnal curve, which is highly deviant at 25 °C. The diurnal species were deviant at 10 and 40 °C, meaning they sprinted slower at 10 °C and faster at 40 °C than expected.

Figure 9. Temperature-dependent sprint performances of four species of geckos in the *Rhoptropus* clade. Diurnal species: *Rhoptropus boultoni* (white circles, $n = 4$). Nocturnal species: *Pachydactylus monicae* (black triangles, $n = 5$), *Colopus wahlbergii* (black diamonds, $n = 6$), and *Chondrodactylus angulifer* (black squares, $n = 11$). Nocturnal and diurnal species sprinted similarly at lower body temperatures, but diurnal species sprinted faster at warmer temperatures. Nocturnal species reach T_o at a lower body temperature than diurnal *R. boultoni*. Data are grand means (± SE) for each species.

Figure 10. Temperature-dependent sprint performances of four species of geckos in the *Afroedura* clade. Diurnal species: *Phelsuma grandis* (white diamonds, *n* = 6), *Phelsuma abbotti* (white circles, *n* = 6), and *Pristurus rupestris* (white triangles, *n* = 4). Nocturnal species: *Afroedura hawequensis* (black squares, *n* = 5). Nocturnal and diurnal species sprinted similarly at lower body temperatures, but at warmer temperatures diurnal species sprinted faster than *A. hawequensis*. Data are grand means (± SE) for each species.

Figure 1

Performance

T_{min}

T_o

CT_{max}
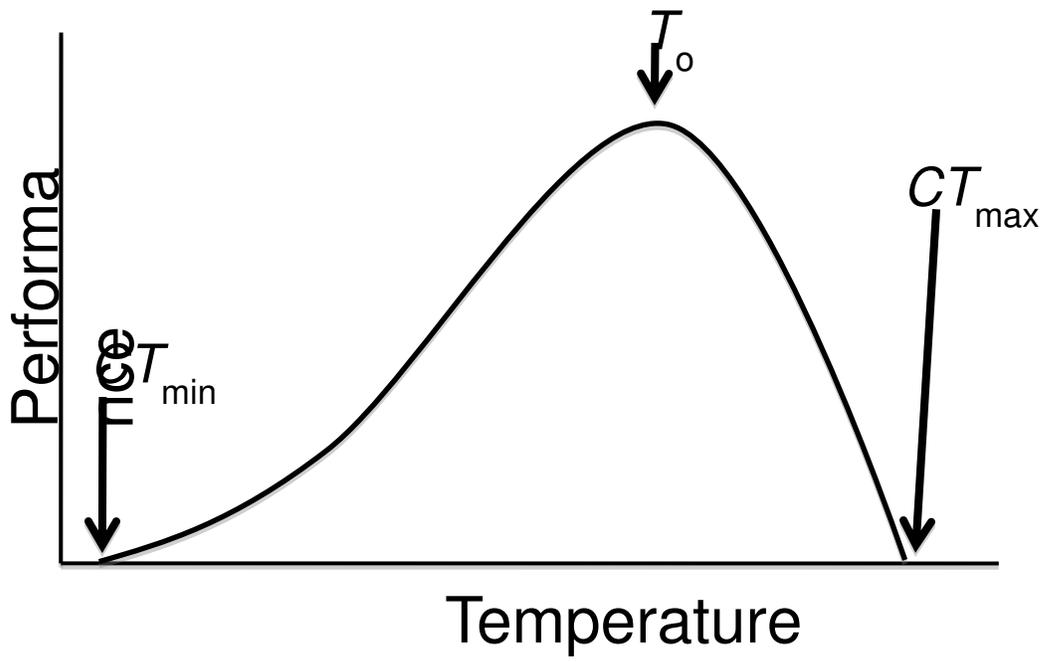
Temperature

Figure 2

Figure 3

Figure 4

Sprint speed (m s^{-1})

Temperature (°C)

Figure 5

Ptychozoon kuhli — n = 10

Cyrtopodion elongatum — n = 5
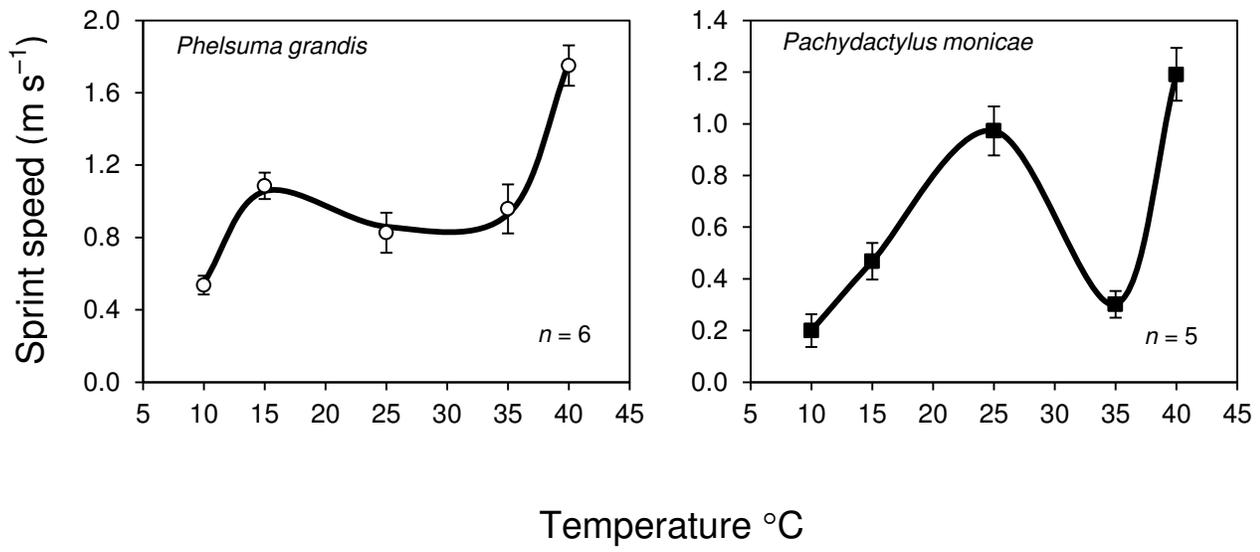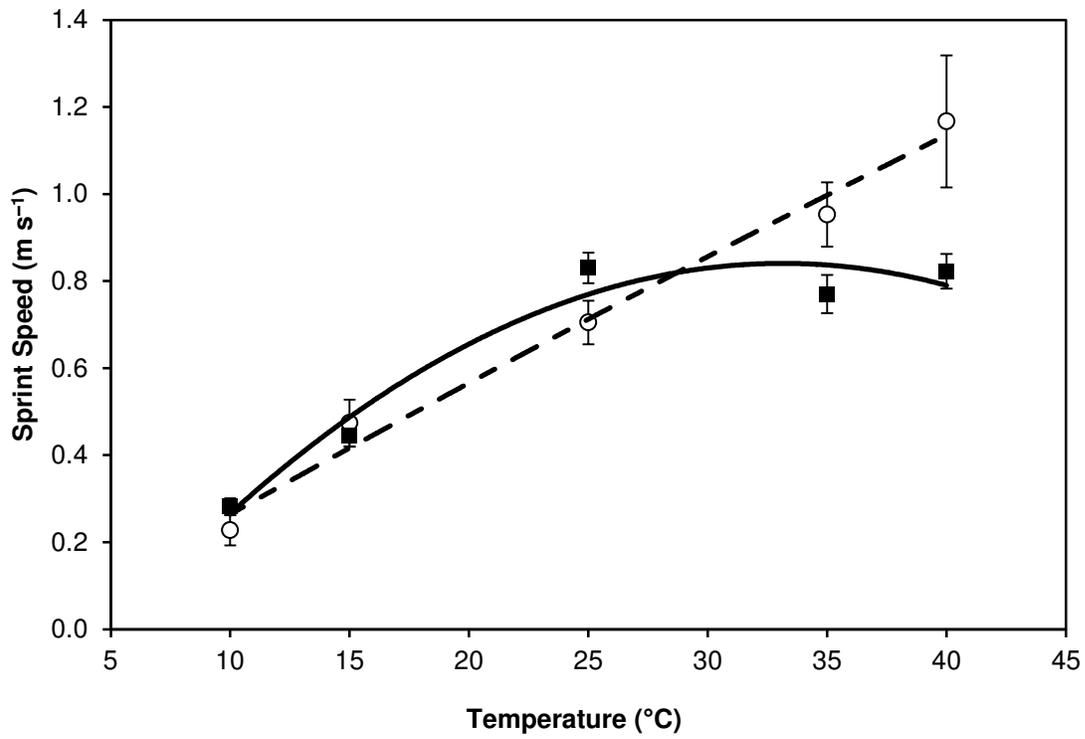
Sprint speed (m s^{-1})
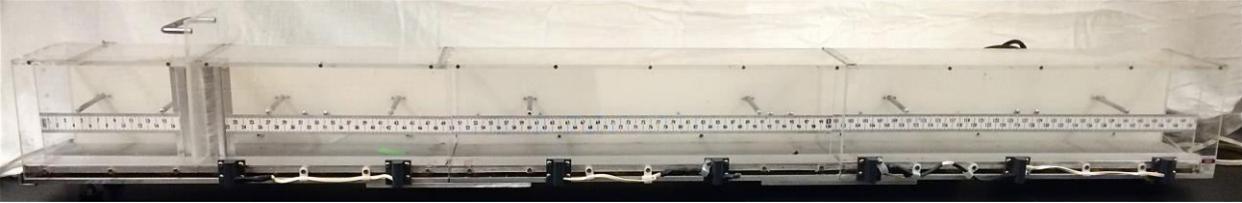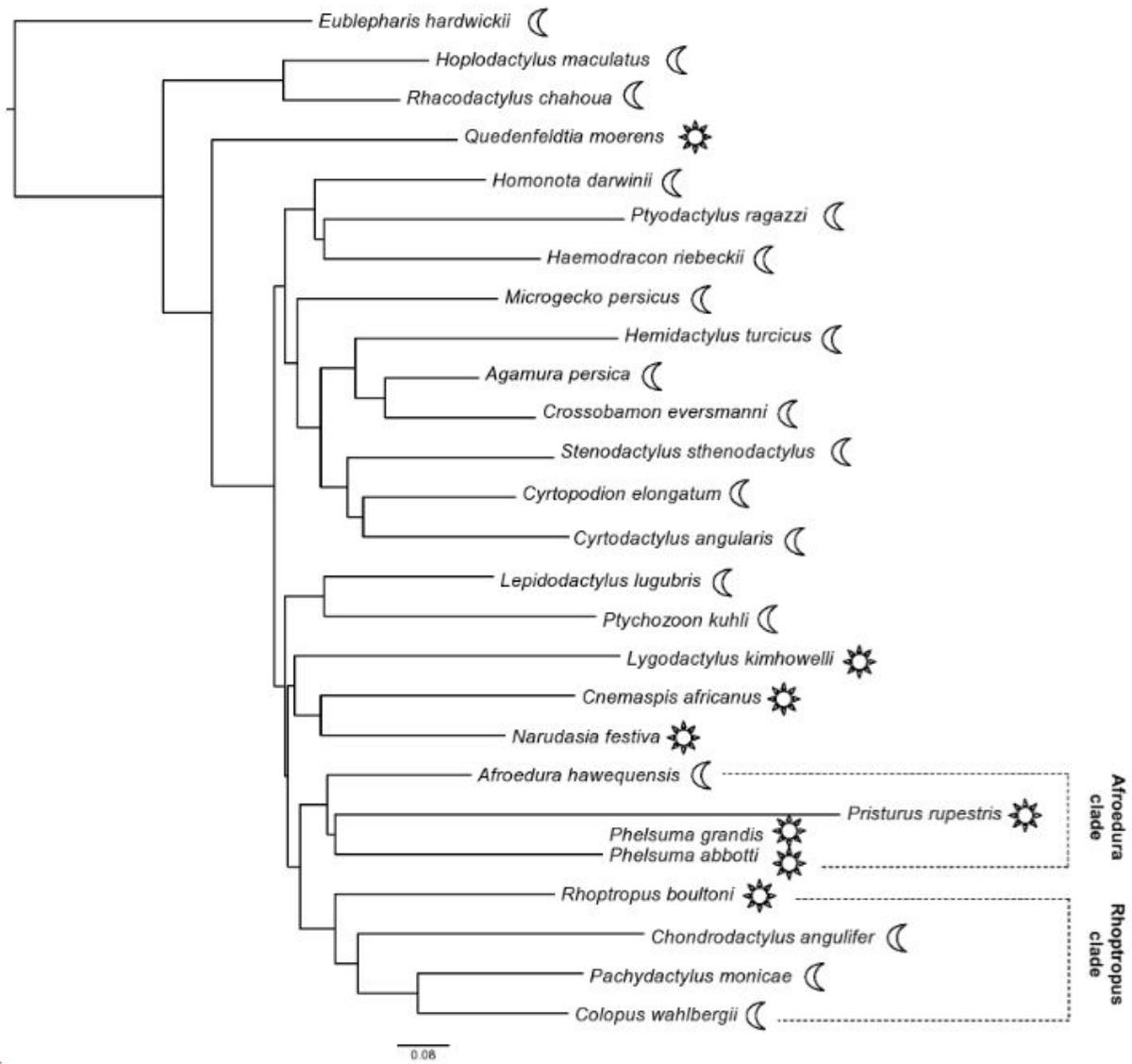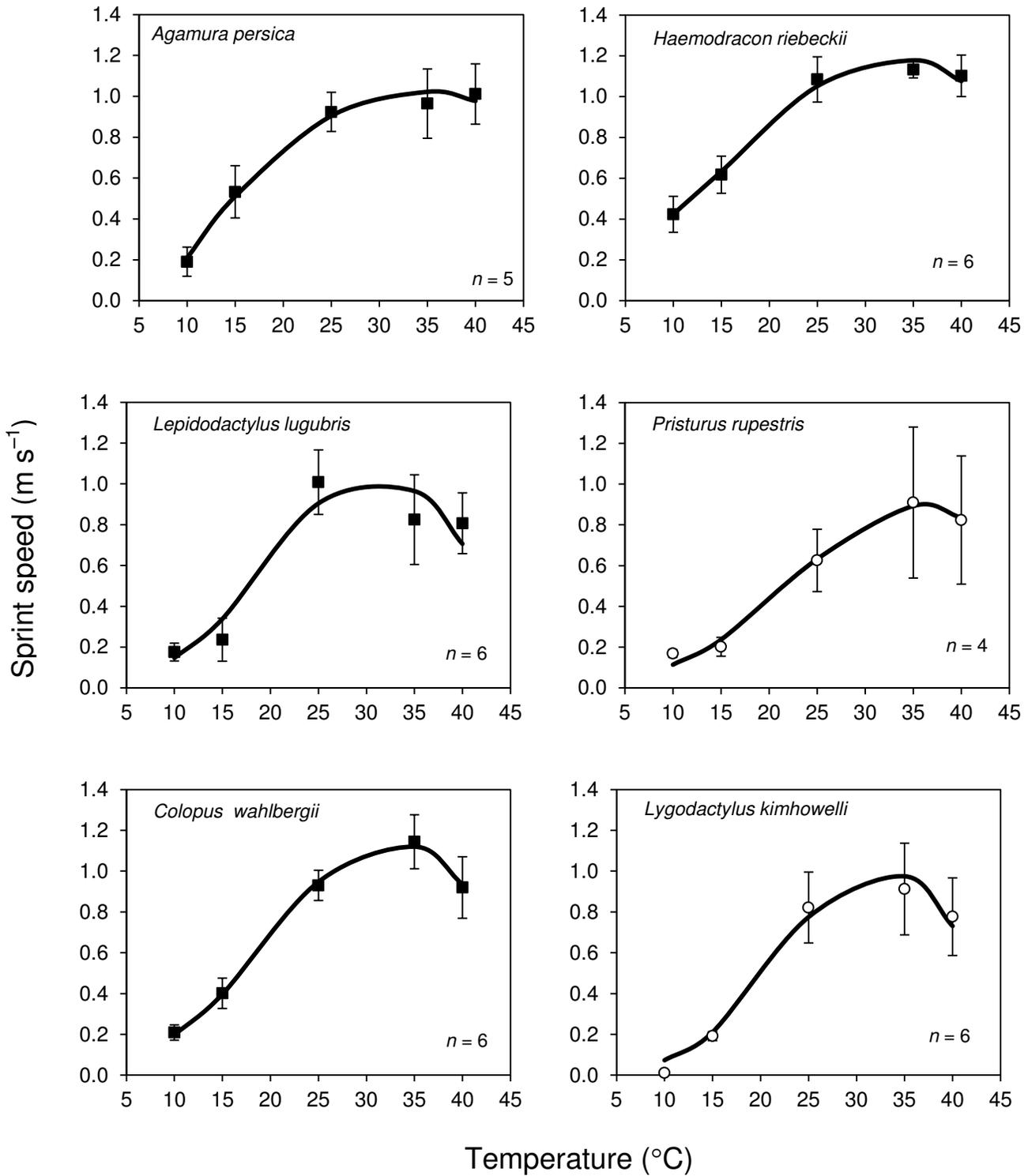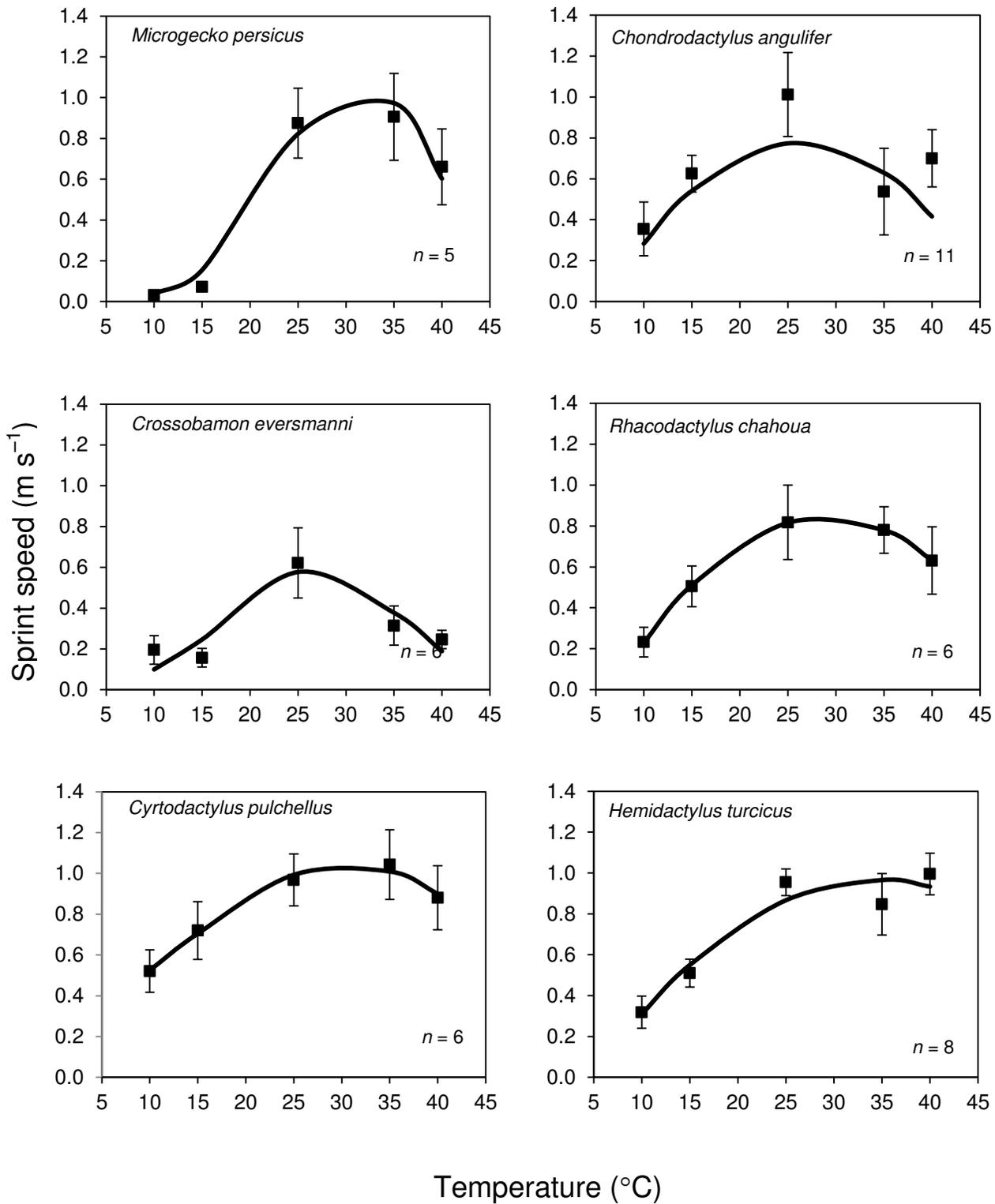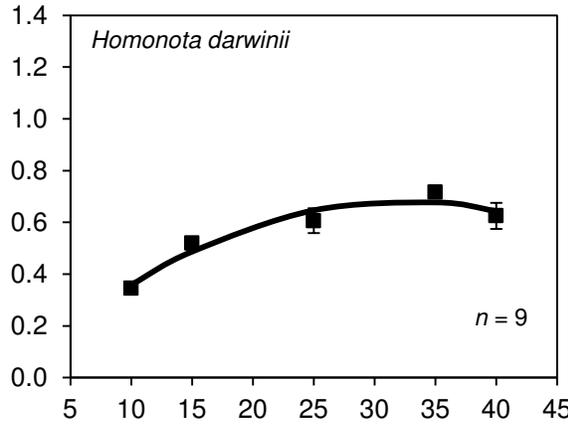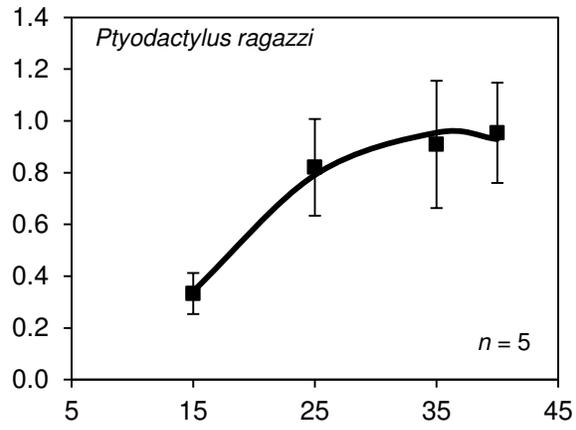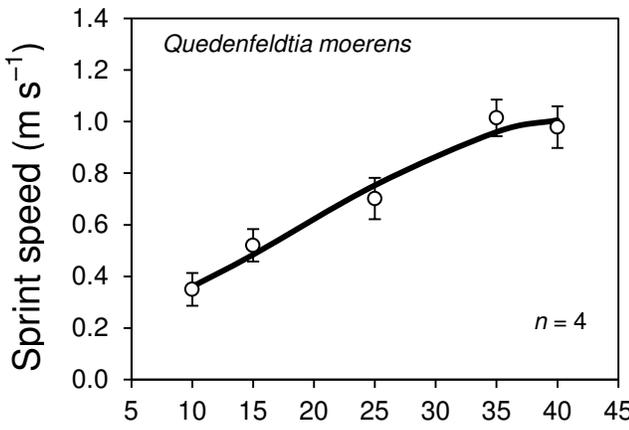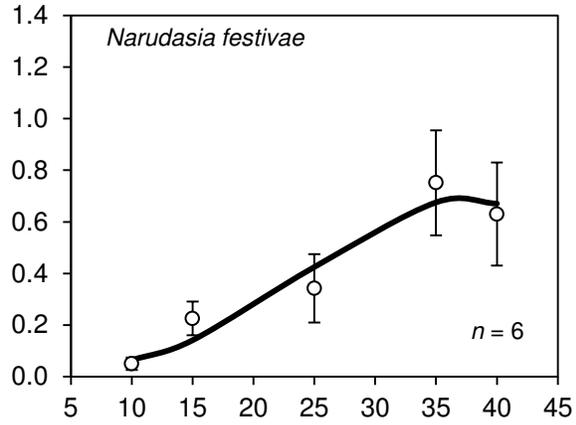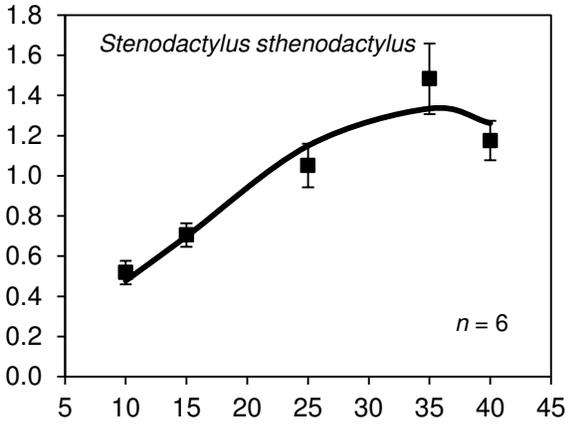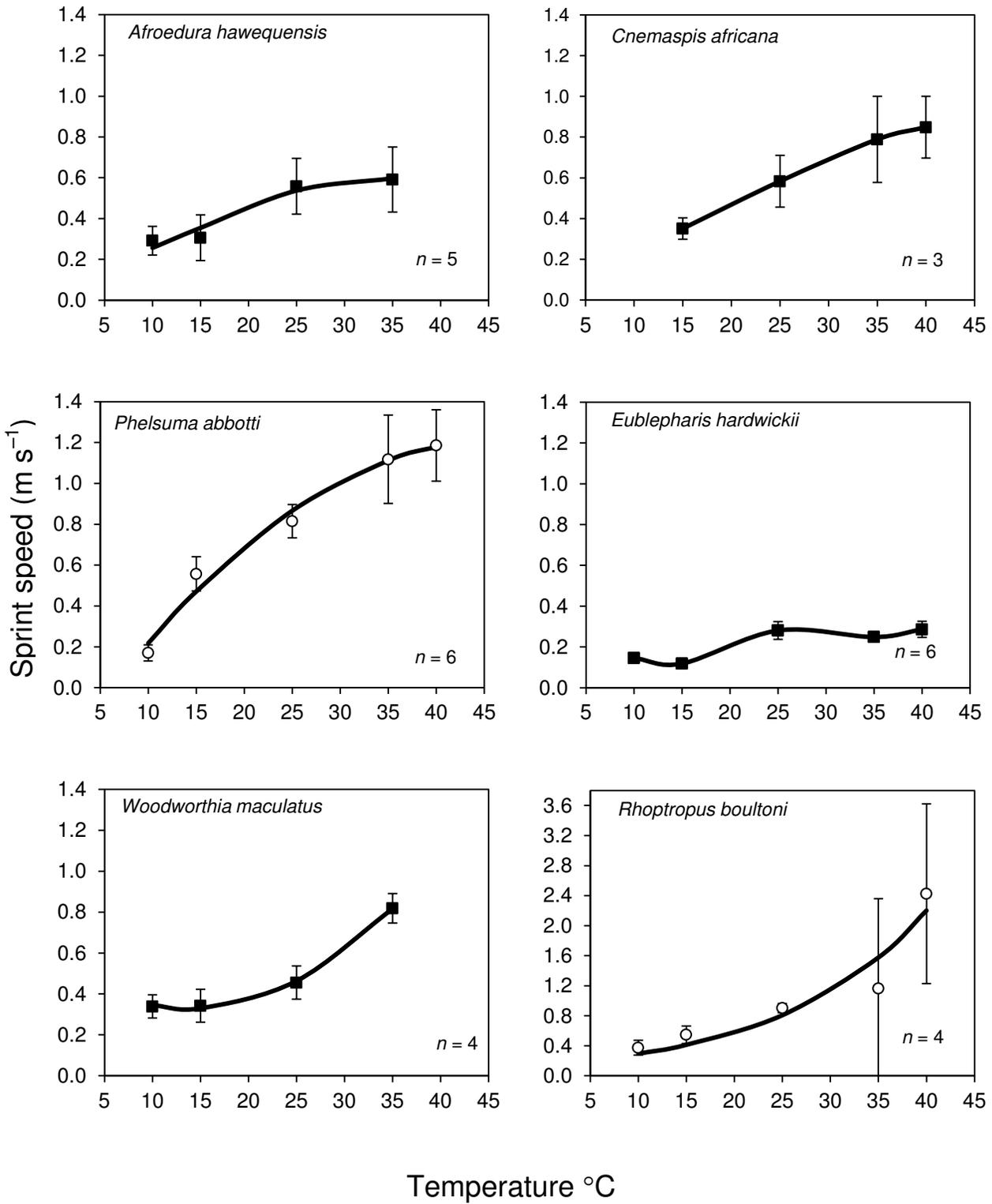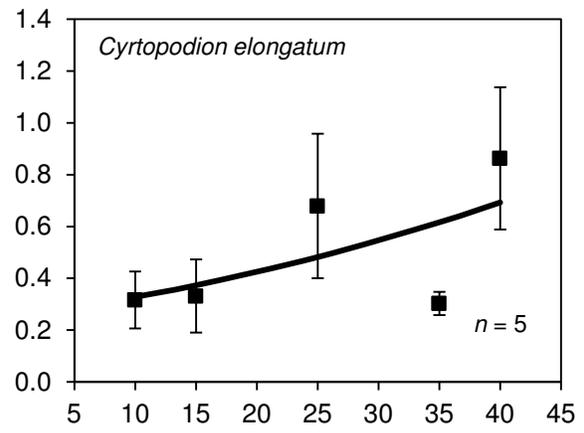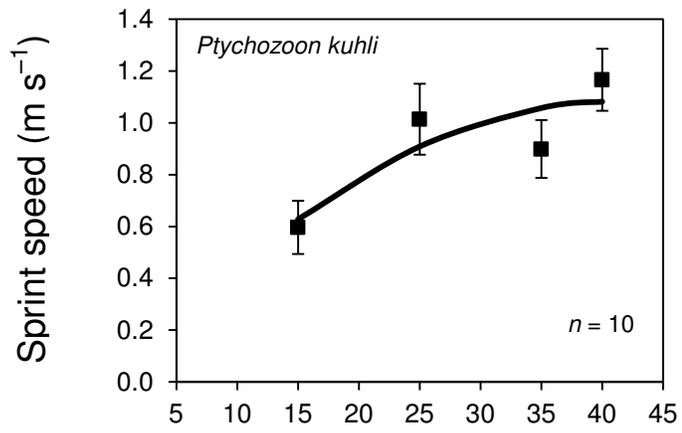
Temperature (°C)

Figure 6

Figure 7.

59

Figure 8.

Figure 9.

Figure 10.