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Thermal benefits of melanism in cordylid lizards: a theoretical and field test

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Abstract. The hypothesis that low skin reflectance (melanism) provides an advantage for thermoregulation under cold conditions has received mixed support in ectothermic vertebrates. We selected a model system, three allopatric closely related species of cordylid lizards that differ in skin reflectance, to test this hypothesis. *Cordylus niger* and *Cordylus oelofseni* are melanistic and inhabit peninsular and montane areas, respectively, whereas *Cordylus cordylus* is more widespread and inhabits low inland areas. By combining theoretical, experimental, and field data on these species, we demonstrate that the difference in body temperature (T_b) between melanistic and non-melanistic lizards under ecologically relevant climate variation ranged from 0° to 2°C. Despite its small magnitude, however, the faster heating rate and higher T_b of melanistic species relative to non-melanistic species conferred an advantage under cold conditions. Comparison of habitat thermal quality (d_c) and thermal accuracy (d_b) across species indicated that, in winter, melanism conferred the greatest advantage during small windows of thermal opportunity. This finding was most pronounced for *C. oelofseni*, which is most constrained by cold temperatures in its habitat. By contrast, due to their rock-dwelling habits, melanistic and non-melanistic species benefited from rock refugia in summer, giving similar levels of thermoregulatory effectiveness across species, regardless of skin reflectance. This study therefore demonstrates that skin reflectance variation across cordylids has significant effects on their thermal balance. Furthermore, studies investigating the role of varying skin reflectance in field populations and species should incorporate fine and broad temporal scales (daily, monthly, and seasonal), environmental variability, and cost–benefit trade-offs of thermoregulation.

Key words: adaptive coloration; Cape Floristic region; Cordylidae; cost-benefit thermoregulation; ectotherm; environmental variability; fynbos; radiotelemetry; temperature preference.

INTRODUCTION

Body temperature (T_b) has direct effects on many fundamental physiology functions and life history traits of ectotherms (e.g., digestion, muscle performance, development time; Huey 1982, Angilletta 2001, Ragland and Kingsolver 2008). A significant deviation from the optimum T_b may compromise organism fitness and a deviation from the tolerable temperature range may have detrimental effects on survival (Huey and Stevenson 1979, Angilletta et al. 2002). Therefore, it is essential to understand the intrinsic factors that affect thermal energy budgets (i.e., energy gain and loss) of ectotherms and how these mechanisms vary across species, climate regimes, and habitat types. Such factors include morphological (e.g., body size, skin reflectance), physiological (e.g., cardiovascular control, evaporative cool-

ing), and behavioral traits (e.g., body posture and orientation).

Skin reflectance (r) has a direct effect on the quantity of solar radiation absorbed by an organism. An individual with low r will heat faster and reach a higher equilibrium T_b than an individual with a high r given similar body size, posture, and environmental conditions (Norris 1967, Watt 1968, Kettlewell 1973, Gates 1980). Therefore, at a broader scale, the lower r of a melanistic species should provide a thermal advantage in cold regions compared to the higher r of a non-melanistic species, whereas the opposite should be expected in warm regions. Although these thermal relationships have been modeled theoretically (Porter and Gates 1969, Kingsolver 1983, Walton and Bennett 1993) and tested under controlled conditions (e.g., Kingsolver 1987, De Jong et al. 1996), only a few studies have explored the functional consequences of skin reflectance variation across field populations or closely related species (e.g., Ellers and Boggs 2004). Most field studies have been undertaken using insects and have generally found strong support for the benefits of low r in thermoregulation under cold conditions (e.g., Willmer and Unwin

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1981, Turner and Lombard 1990, Ellers and Boggs 2004), while the few studies using ectothermic vertebrates have provided mixed support (e.g., Bittner et al. 2002, Tanaka 2007, see Clusella-Trullas et al. 2007b for a review). Confounding effects such as across species variation in behavioral and physiology adaptations (e.g., sun–shade shuttling, peripheral blood flow) may explain the lack of data supporting the patterns expected. In addition, when relationships between T_b and r have been found in the direction predicted, several authors have argued that the magnitude of the T_b difference between melanistic and non-melanistic individuals is too small to be ecologically relevant (e.g., Crisp et al. 1979, Stevenson 1985, Luke 1989). However, recent data from a macrophysiological study (Clusella-Trullas et al. 2008) supports the adaptive role of skin reflectance for thermoregulation across lizard species, and highlights the need to further investigate r variation and its thermal role among populations and species in the wild.

The occurrence of closely related species of cordylid lizards that mainly differ in skin coloration in the Western Cape Province of South Africa (Mouton and van Wyk 1990, Daniels et al. 2004) offers a unique opportunity to test the thermal consequences of varying r in field populations. Melanistic species occur in cooler mountain and coastal areas compared to lighter-colored species, which are mostly distributed in low inland areas, and suggests that melanism is a phenotypic trait necessary to optimize these species' thermal energy budgets in cooler climates (Mouton and Oelofsen 1988, Badenhorst et al. 1992, Mouton and van Wyk 1995). Several studies have speculated on the thermoregulatory function and evolutionary adaptation of melanism in cordylids and suggest that melanism may be thermally beneficial to species inhabiting areas with high incidence of fog and cloud cover (Mouton and Oelofsen 1988, Badenhorst et al. 1992, Brody et al. 1993). However, these hypotheses have not been explicitly tested despite their value for understanding these species' thermal responses to changing climate regimes predicted for this region (Tyson et al. 2002, Hannah et al. 2005). Indeed, if melanistic species are highly restricted in land fragments (e.g., mountain tops) and are adapted to cold conditions, future warming may severely impact their geographic distribution and survival (Pounds et al. 1999, Thomas et al. 2004).

In this paper we first quantify the magnitude of the difference in body temperature (ΔT_b) between melanistic and non-melanistic cordylid species. The determination of ΔT_b is made both theoretically by predicting T_b under several climate scenarios using a steady-state energy model (Porter and Gates 1969) and empirically, by measuring T_b of melanistic and non-melanistic individuals under controlled and natural conditions. Second, we test if ΔT_b confers a thermal advantage for each species in its respective environment. We chose two melanistic species (*Cordylus niger* and *C. oelofseni* from a coastal and montane site, respectively) and one non-

melanistic species (*Cordylus cordylus* from a low-elevation, inland site) (see Plate 1). We determined the thermal quality (the availability of operative temperatures [T_e] relative to preferred body temperature [T_p]; Hertz et al. 1993) of each species' habitat considering that both melanistic and non-melanistic species could occur in each site and identify periods of potential thermal constraint (daily and seasonal). In addition, we calculated the thermoregulatory accuracy of each species (deviation of T_b from T_p ; Hertz et al. 1993) in their respective natural habitats to identify which species is most likely constrained by environmental temperature. By comparing both thermal quality and accuracy, we identify which species is likely to experience the highest costs to maintain preferred temperatures. Specifically, we predict that despite the potentially small magnitude of ΔT_b , melanism should be particularly advantageous in cold conditions, especially for montane species in which thermal opportunities likely frequently fall below optimal and critical physiological levels (e.g., lower temperature limits to activity and growth).

METHODS

Skin reflectance and steady-state energy model

We determined skin reflectance (r) from the mean of five readings taken across the dorsal area of live melanistic and non-melanistic lizards using a Beckman DK-2A spectroradiometer (operational range: 290–2600 nm; Beckman, Fullerton, California, USA) in the laboratory of Warren Porter at the University of Wisconsin, Madison, Wisconsin, USA. Lizards were originally collected from field populations in the Western Cape Province of South Africa. We used a steady-state (time-independent) energy budget model (Porter and Gates 1969) to predict T_b of a melanistic and a non-melanistic individual under varying incident radiation flux, air temperature, and wind speed relevant to field conditions (for details of model and its assumptions see Appendix A).

Thermal responses

Heating experiments took place in a walk-in environmental chamber ($16^\circ \pm 0.5^\circ\text{C}$; Stellenbosch University, Stellenbosch, South Africa) by positioning a halogen bulb (R7s, 500 W, peak wavelength ~ 1000 nm; Haloline, Osram, Germany) 60 cm above a glass plate with a matt base to avoid additional light reflection. A copper-constantan thermocouple (Type T, 24 standard wire gauge [SWG]) measured shaded air temperature (T_a) 2 cm above the glass plate. The experimental set-up was isolated by styrofoam walls to avoid air turbulence from the chamber's air vents. We measured operative temperature (T_e) of a melanistic and a non-melanistic hollow copper model (methods of Bakken and Gates 1975, see Appendix B for calibrations) that had the same size, shape, and r as *C. niger* (paint number 1318 gray primer, Krylon, Cleveland, Ohio, USA; $r = 7.1\%$) and *C. cordylus* (fresh green, Dulux Duco, Slough, UK; $r =$



PLATE 1. (Top) *Cordylus niger* (melanistic) and (bottom) *Cordylus cordylus* (non-melanistic) basking in their respective field sites. Photo credits: S. Clusella-Trullas.

13.1%). These two species were chosen for their similarity in body size and mass (Table 1 and Appendix A). We placed paired models directly under the light source and switched on the bulb for 20 min after their T_e had equilibrated to room temperature. We followed a similar protocol for live lizards, but lizards were tested individually under the lamp to avoid potential group stress. Each lizard was placed under the bulb after being cooled to 16°C in a climate chamber (Labcon, Labotec, Midrand, South Africa). A thermocouple (Type T, 36 SWG) placed 1.5 cm into the cloaca measured T_b . When T_b reached 35°C, we switched the lamp off and removed the lizard unharmed. All thermocouples were calibrated to $\pm 0.05^\circ\text{C}$ prior to trials.

Because halogen bulbs emit a “redder” wavelength than natural light, these experiments were repeated on models and live lizards under natural sunlight. Four pairs of melanistic and non-melanistic models and a single *C. niger* and *C. cordylus* of similar size (snout-vent length [SVL] = 76.5 mm, mass = 15.29 g, and SVL = 73.3 mm, mass = 15.11 g, respectively) were placed in an open-sky area for 4 h while measuring shaded T_a , wind speed (03101-5 cup anemometer, R. M. Young Wind

Sentry, Traverse City, Michigan, USA), and incident solar radiation (LI-200SA pyranometer, LI-COR, Lincoln, Nebraska, USA). A summer day with intermittent cloud cover was used to avoid overheating live lizards.

Following methods used by Bittner et al. (2002), data from copper models (at 10-sec intervals) were fitted to the equation $T_e = b_1(1 - \exp[-b_2(t - t_0)])$ (von Bertalanffy growth model; Lovich et al. 1990), where b_1 is the equilibrium temperature, and b_2 is the instantaneous heating rate (in minutes). To analyze live lizard heating curves, we plotted T_b (from 16°C to 35°C) against time for each individual lizard and used the slope as the individual heating rate ($^\circ\text{C}/\text{min}$). We compared mean heating rates of melanistic and non-melanistic models using t tests for dependent samples, and t tests for independent samples for live lizards after verifying assumptions of these analyses.

Field study: species and sites

We studied *C. cordylus* (non-melanistic) at Joostenberg (33°46' S, 18°47' E; 290 m elevation), an inland hill with abundant shale rock formations. We studied *C. niger* (melanistic) at Mauritzbaai (32°59' S, 17°52' E; 5 m elevation), a coastal site with granite rock formations and *C. oelofseni* (melanistic) at Landdroskop (34°02' S, 19°00' E; 1080 m elevation), a small plateau with sandstone boulders in the Hottentots Holland mountain range. These species have allopatric distributions with limited dispersal ability, but share many morphological and life history traits. All species are diurnal, heliothermic, sit-and-wait predators, live on rock outcrops and shelter in crevices (Wirringhaus 1990, Cooper et al. 1997, Branch 1998). They have contrasting skin coloration against the rock they inhabit (at least within the visible range), and thus melanism is unlikely a result of background matching for protection against predators (mostly birds). They are viviparous with similar reproductive seasons, have generalist diets feeding primarily on invertebrates (Clusella-Trullas and Botes 2008), and have no sexual dimorphism in body size (Cordes et al. 1995). Field data collection was undertaken in summer 2005 and winter 2006.

TABLE 1. Skin reflectance (mean \pm SD) of *Cordylus niger* (melanistic, $n = 3$), *Cordylus oelofseni* (melanistic, $n = 3$), and *Cordylus cordylus* (non-melanistic, $n = 2$).

Wavelength	Reflectance (%)		
	<i>C. niger</i>	<i>C. oelofseni</i>	<i>C. cordylus</i>
Ultraviolet (290–400 nm)	2.4 \pm 0.5	2.9 \pm 0.4	1.8 \pm 0.1
Visible 2 (400–500 nm)	2.3 \pm 0.5	2.9 \pm 0.4	4.0 \pm 0.4
Visible 1 (500–700 nm)	3.2 \pm 0.0	3.3 \pm 0.4	15.5 \pm 2.4
Infrared 2 (700–1450 nm)	7.7 \pm 0.9	8.5 \pm 1.3	22.1 \pm 2.2
Infrared 1 (1450–2600 nm)	5.7 \pm 0.6	7.3 \pm 1.7	6.8 \pm 0.5
Mean	5.3 \pm 0.4	6.9 \pm 1.2	15.2 \pm 1.6

Note: Mean body masses (calculated from ~60 lizards per species) are 14.0 \pm 1.6 g for *C. niger*, 8.1 \pm 1.2 g for *C. oelofseni*, and 13.7 \pm 3.1 g for *C. cordylus*.

Physiology, activity patterns, and climate

Adult lizards were collected from their respective sites in January 2006, and preferred set-point temperatures (T_p) were determined from T_b selected in a laboratory thermal gradient (see Clusella-Trullas et al. 2007a for detailed methods and data). Lizards were not gravid during these experiments, and there was no effect of sex on T_p in both field-fresh and acclimated states (Clusella-Trullas et al. 2007a). To determine species' thermal indices, we used the bounds of the central 50% of the observed T_b 's (Hertz et al. 1993). Critical thermal maximum (CT_{max}) and minimum (CT_{min}) were estimated according to standard protocols (e.g., Kour and Hutchison 1970, Lutterschmidt and Hutchison 1997). In brief, lizards were acclimated for three weeks at $27^\circ \pm 2^\circ\text{C}$ (14:10 h L:D), given water ad lib., fed twice a week, and deprived of food two days before trials. Each lizard was first equilibrated to a start T_b of 30°C (or 15°C for CT_{min}) and heated (or cooled) at $1^\circ\text{C}/\text{min}$ for CT_{max} (onset of heat-induced spasms) and CT_{min} (loss of righting response) trials, respectively. All lizards recovered from thermal limit trials unharmed.

We established climate stations in each site in summer (December to February) and winter (June to August). We monitored T_a , wind speed, and incident solar radiation (1 m above ground; with instruments as for *Thermal responses* section) while simultaneously recording activity patterns, T_b and T_e . A Campbell CR10 and calibrated AM32 multiplexer (Campbell Scientific, Logan, Utah, USA) recorded data every 15 min 24 h/day for 5–7 consecutive days. We counted the number of active lizards and recorded respective behaviors between 0700 and 1800 h by walking 30-m transects in a random direction across each study site every 2 h. All lizards located within ~ 6 m in either side of the transect line were included.

Body (T_b) and operative (T_e) temperatures

Lightweight radio-transmitters equipped with a temperature-sensitive pulse device (BD-2T, 0.93 g, representing $<10\%$ of body mass for all species; Holohil Systems, Carp, Ontario, Canada) provided T_b of 6–10 lizards per population in summer and winter (respective sample sizes and sex ratios are given in Table 4). We monitored transmitter pulse rates using a stopwatch and hand-held receiver (IC-R10, Icom America, Bellevue, Washington, USA). Calibrated transmitters were glued flat on the abdomen area of lizards allowing easy movement of the animal in crevices while avoiding direct solar radiation (see Appendix B for T_b calibration). The scaled skin of these species provided a solid attachment surface while enabling harmless removal at the end of the study. Typically, we monitored T_b hourly from 0700 to 1800 h for at least five consecutive days in summer and in winter. Daily visual observations further confirmed that lizards behaved normally with transmitters attached.

We measured T_e with copper models built as described in the *Thermal responses* section. Calibrations confirmed that models were good estimators of T_e for all species (Appendix B; Dzialowski 2005). We distributed 25 pairs of models, each representing a melanistic and a non-melanistic individual, within habitats used by lizards (i.e., rock surfaces and crevices) excluding ground surfaces since brief excursions to the ground only occurred at high speed when catching insects. Individuals rarely left crevices or rock surfaces where they typically basked, used a sit-and-wait strategy for prey, or interacted with other individuals. Models were distributed along eight transects that radiated at 45° angles from the central climate station. We divided each transect into three equal portions and positioned a pair of models within each portion at a random distance within the interval (on rock or crevice) and random height and orientation by using a random numbers table. The combinations of locations, orientations, and postures sampled a complete array of thermal options available to the lizards at different times of the day (i.e., from complete sun to complete shade) at each site. We assigned each pair a category describing the slope, substrate, aspect, and sun–shade status at midday for all sites to enable comparisons between sites. Additionally, we placed four thermocouples inside crevices with entrances orientated towards the four cardinal compass points. Data were logged at 15-min intervals for 24 h/d for at least five consecutive days per season per site.

Statistics and thermal indices

To compare T_b , T_e , and thermal indices (d_c , d_b) across species while accounting for the non-independence of multiple measurements per individual, repeated measures ANOVAs were performed in SAS version 8.0 (SAS Institute 1999). A compound-symmetry covariance structure was used in proc-mixed with a reduced maximum-likelihood estimation method (Littell et al. 1996). Species and individuals were entered as categorical variables and time as continuous variable in the models. Data are reported as mean \pm standard deviation (SD).

Following Hertz et al. (1993), we calculated the habitat thermal quality as the mean of the absolute value of the deviations of T_e from T_p ($=d_c$). A high d_c value indicates that the habitat has few optimal T_e 's (i.e., low thermal quality), whereas a low value of d_c indicates that thermoregulation may be unnecessary to maintain T_p . We calculated the accuracy of T_b by averaging the deviations of field active T_b from T_p ($=d_b$). If T_b is beyond the set-point range, d_b is the difference between T_b and the nearest boundary of T_p . If T_b is within T_p , d_b equals zero. A high value of d_b indicates that optimal temperatures are rarely maintained. We combined d_c , d_b , and field behavioral observations of lizards to assess the effectiveness of thermoregulation (Blouin-Demers and Weatherhead 2001). We calculated mean d_c and d_b of each species using data from three days that were

representative of the range of typical conditions found in summer and winter in each study site, allowing a comparison of seasons within a species and across species. Days with atypical conditions (e.g., an exceptionally warm winter day) were analyzed separately as these reflected climatic conditions unrepresentative of the season.

RESULTS

Skin reflectances

Mean r values of melanistic (*C. niger*, *C. oelofseni*) and non-melanistic (*C. cordylus*) lizards were 6.1% and 15.2%, respectively, with most differences occurring in the visible and near infrared portions of the spectrum (Table 1).

Steady-state energy model

When modeling the effects of total incident radiation (Q_s), air temperature (T_a), and wind speed (V) on T_b (Fig. 1), we found that given constant T_a and low V , the difference in T_b between a melanistic and a non-melanistic lizard (ΔT_b) of similar size was greater at higher values of radiation. For example, at $Q_s = 800$ W/m² ($T_a = 25^\circ\text{C}$, $V = 0.5$ m/s), ΔT_b of a melanistic ($r = 5.3\%$) and a non-melanistic ($r = 15.2\%$) lizard was $\sim 2.5^\circ\text{C}$; whereas at 200 W/m², ΔT_b was $\sim 1^\circ\text{C}$ (Fig. 1A). Increasing V rapidly reduced ΔT_b (Fig. 1B). At constant Q_s and low V , a change in T_a barely affected ΔT_b (Fig. 1C).

Thermal responses: heating experiments

Under halogen lights, mean equilibrium temperature of melanistic models ($49.3^\circ \pm 3.1^\circ\text{C}$) was significantly higher than non-melanistic models ($48.3^\circ \pm 3.2^\circ\text{C}$) ($t = 4.292$, $df = 24$, $P < 0.001$; Fig. 2A). Mean instantaneous heating rate of melanistic models (0.134 ± 0.021 min⁻¹) was also significantly higher than non-melanistic models (0.126 ± 0.018 min⁻¹) ($t = 3.46$, $df = 24$, $P < 0.005$; Fig. 2A). However, the mean heating rate of *C. cordylus* ($0.97 \pm 0.05^\circ\text{C}/\text{min}$) was lower than that of *C. niger* ($1.01^\circ \pm 0.08^\circ\text{C}/\text{min}$) measured under controlled conditions, but was not significantly different ($t = 0.996$, $df = 8$, $P = 0.35$; Fig. 2B).

When exposed to sunlight (natural outdoors experiment), T_b of *C. niger* was either equal to, or greater than, T_b of *C. cordylus* (mean $\Delta T_b = 0.7^\circ \pm 0.5^\circ\text{C}$; range = 0° to 2.4°C ; Fig. 3). For instance, ΔT_b equaled 0.5°C for 66% of the experimental time (Fig. 3). Melanistic models also had higher T_e than non-melanistic models ($\Delta T_e = 1.2^\circ \pm 0.6^\circ\text{C}$, range = 0.3° to 2.9°C) and a minimum ΔT_e of 0.5°C was maintained 90% of the time (Fig. 3). In the absence of clouds, ΔT_e equaled $1.5^\circ \pm 0.4^\circ\text{C}$ at midday.

Physiology and climate

While CT_{\max} did not differ between species, CT_{\min} of *C. oelofseni* was significantly lower than that of *C. cordylus* and *C. niger* when acclimated for three weeks under common temperature conditions (Table 2). Climate

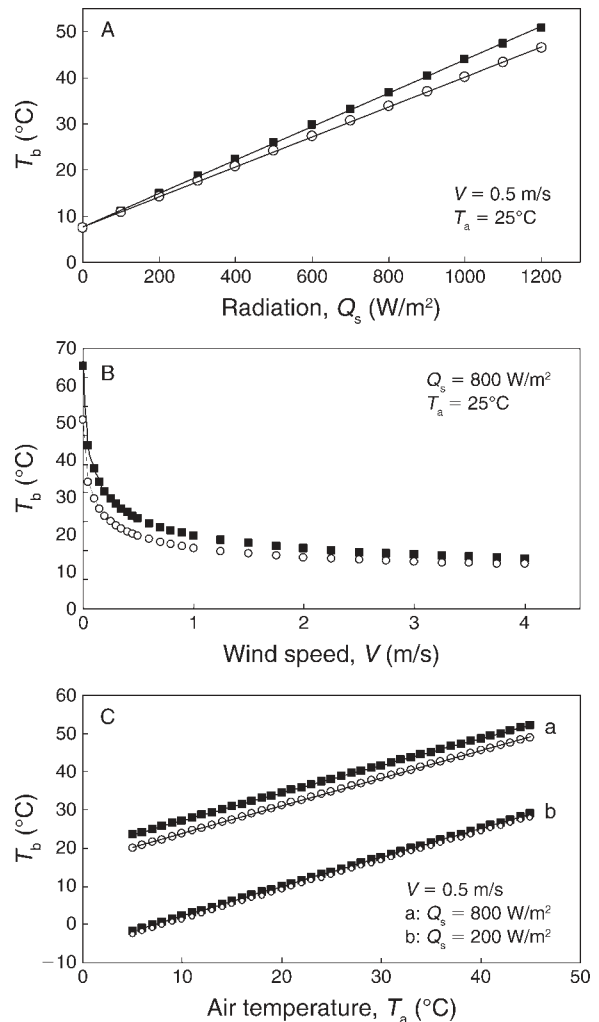


FIG. 1. Predictions of the steady-state energy flux model showing the effects of (A) total incident radiation Q_s , (B) wind speed V , and (C) air temperature T_a on body temperature T_b . Constant environmental parameters are indicated within the figures. Solid squares and open circles are the T_b predictions for lizards with skin reflectance of 5.3% and 15.2%, respectively.

conditions (from stations placed in each site) were relatively similar across sites in summer, although the inland site (Joostenberg) had the highest level of Q_s , V , and T_a (Table 3). By contrast, conditions differed more in winter across sites: Joostenberg (inland) and Landdrooskop (mountain) were the coldest sites, while Mauritzbaai (coastal) and Landdrooskop were the windiest (Table 3).

Field data: intraspecific analyses

Cordylus cordylus (non-melanistic), inland site.—The thermal habitat quality (d_e) of *C. cordylus* was more suitable in summer than winter (Fig. 4A, Table 4). In summer, a non-thermoregulating lizard could maintain T_b near T_p most of the day. However, it could also reach high thermal thresholds at midday. From 0700 to 1800

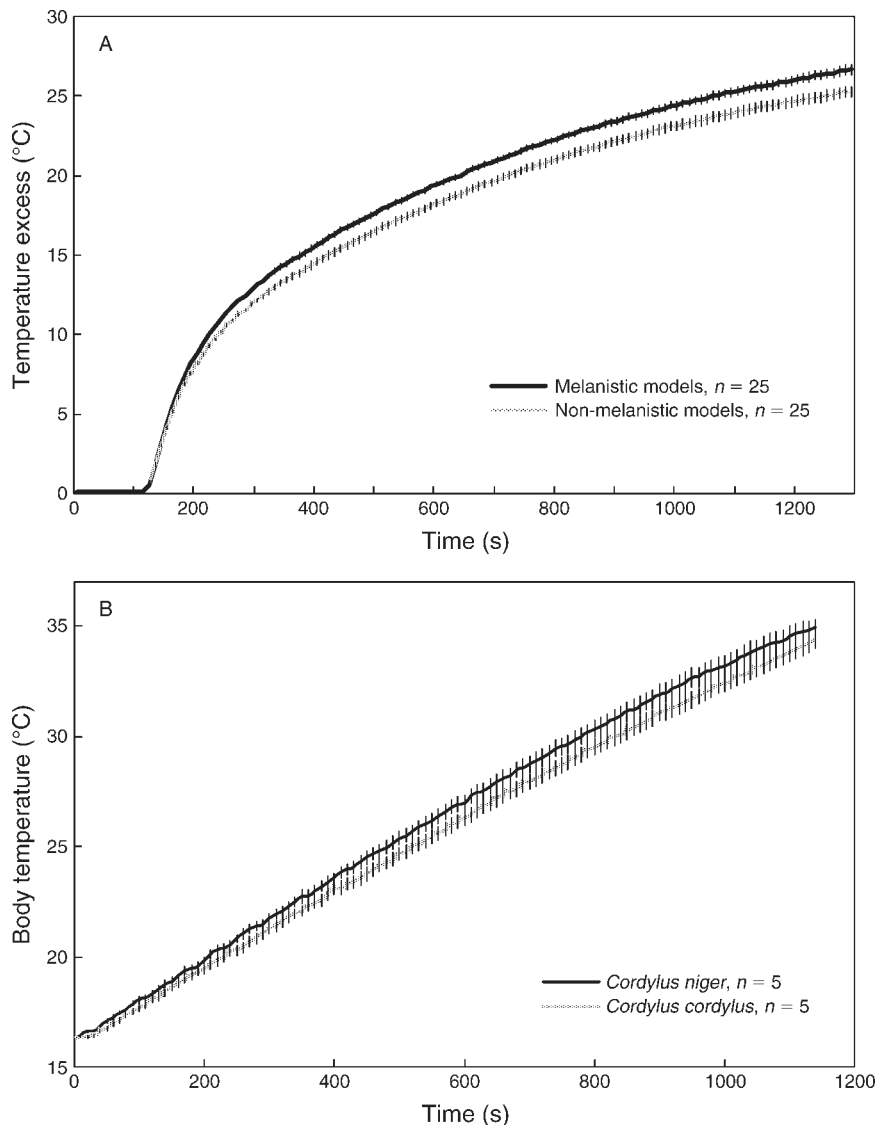


FIG. 2. Heating curves for (A) melanistic and non-melanistic copper models and (B) *Cordylus niger* and *Cordylus cordylus* measured under a 500-W halogen bulb. In (A), temperature excess equals T_e (model temperature) minus T_a (shaded air temperature). At 120 s, the bulb was switched on. In (B), lizards were cooled to 16°C before trials started. Values are means \pm SE.

hours, 34% and 9% of all T_e 's were higher than T_p and CT_{max} , respectively, with 74% of T_e 's above T_p occurring between 1100 and 1500 h (Appendix C). The daily pattern of d_e in summer (Fig. 4A) indicated that the thermal habitat quality improved quickly from 0700 to 1000 h, then declined slightly from 1200 to 1400 h, and improved further for the rest of the day, averaging $\sim 2^\circ\text{C}$ variation in d_e at 1800 h. Under these same conditions, the d_e of a melanistic individual (calculated from melanistic models) increased by $0.2^\circ \pm 0.1^\circ\text{C}$ from 1200 to 1400 h, resulting in lower overall thermal quality of the habitat. However, crevices with favorable temperatures would be equally available for melanistic and non-melanistic individuals during these periods. By

contrast, in winter, *C. cordylus* was constrained by the thermal environment (98% of all T_e 's $< T_p$). The d_e in winter improved throughout the day (Fig. 4A), with the most suitable period at 1500 h, when d_e averaged $\sim 10^\circ\text{C}$. Relative to a non-melanistic lizard, the d_e of a melanistic lizard (calculated from melanistic models) improved by $0.3^\circ \pm 0.2^\circ\text{C}$ throughout the day in winter.

As expected, the deviation of T_b from T_p (i.e., d_b) was smaller in summer than winter (Fig. 4B, Table 4), 18% of T_b 's fell within T_p in summer, while only 7% did so in winter. During both seasons, d_b was generally lower than d_e (Table 4, Fig. 4A, B), reflecting active thermoregulation. In summer, lizards basked early in the morning (from 0700 to 0900 h), then they remained in

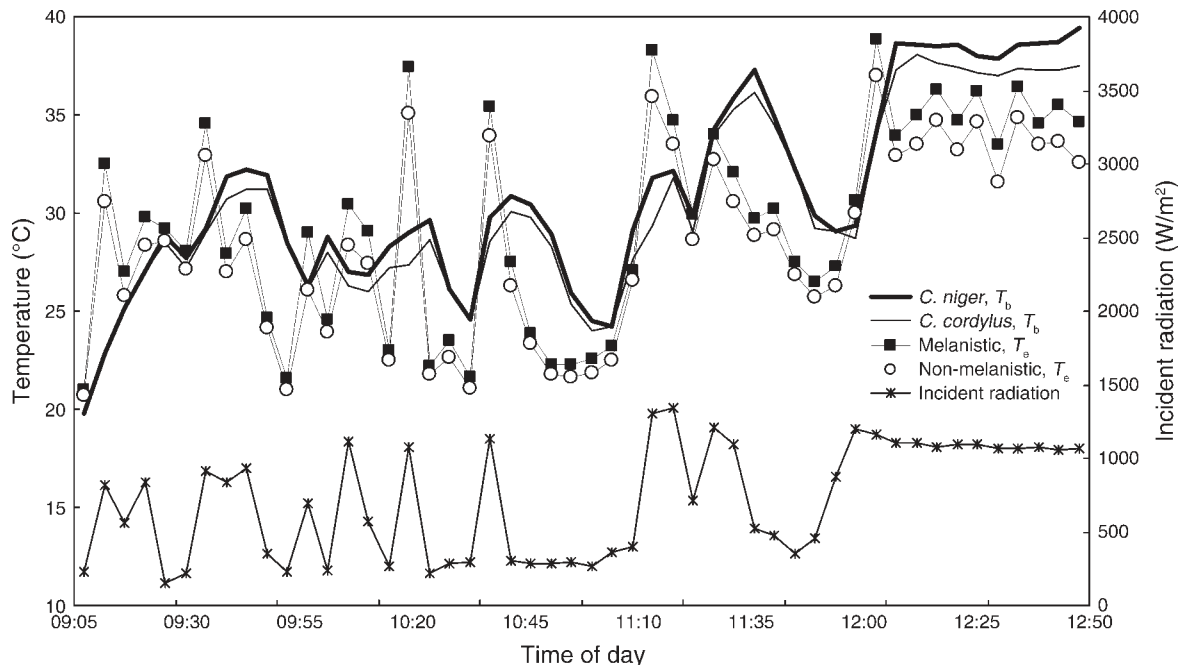


FIG. 3. Body temperature (T_b) of a melanistic (*Cordylus niger*) and a non-melanistic (*Cordylus cordylus*) lizard, as well as the mean operative temperature (T_e) of melanistic and non-melanistic copper models exposed to natural conditions. Incident solar radiation measured at lizard level is also plotted (right-hand y-axis). Shaded air temperature and wind speed at 1 m height averaged $17.3 \pm 1.4^\circ\text{C}$ and 2.0 ± 0.6 m/s, respectively. Note that T_e lines are means of five models, while lizard T_b data are for single individuals. Therefore, these data do not fully reflect the variation across microsites, lizards, and models (for model calibrations, see Appendix B).

crevices to avoid the midday heat and basked again before sunset (Fig. 5A). In winter, lizards maintained T_b close to T_p during clear days (Fig. 5B) and were active from ~ 1100 to 1700 h, corresponding to the period with lowest d_e (Fig. 4A). On a foggy day, lizards remained mostly inactive, although T_b was slightly higher than available T_e (Fig. 5C).

Cordylus niger (melanistic), coastal site.—The thermal habitat quality of *C. niger* was moderately suitable in summer (Table 4), 17.2% of all T_e 's were above T_p , and only 1% of T_e 's were above CT_{\max} (Appendix C). Therefore, this species did not face much risk of reaching high lethal thresholds unless confronting atypical hot conditions. Summer d_e was at its best between 1200 and 1600 h (3.4 ± 0.3 ; Fig. 4A) and differed significantly from winter d_e (Fig. 4A, Table 4). Lizards were constrained by the thermal environment in winter (99.7% of T_e 's $< T_p$), and d_e typically improved at most 8°C throughout the day (Fig. 4A). The thermal habitat available to a non-melanistic lizard (calculated from non-melanistic models) under these winter conditions was reduced by $0.2^\circ \pm 0.2^\circ\text{C}$ throughout the day. On a completely overcast day, the difference between melanistic and non-melanistic models was negligible and averaged $0.04^\circ \pm 0.05^\circ\text{C}$.

The deviations in d_b were significantly lower (greater thermal accuracy) in summer than in winter (Fig. 4B, Table 4). In summer, d_b was similar to d_e (Table 4, Fig.

4A, B), suggesting that *C. niger* did not thermoregulate to a great extent except to avoid high T_e 's. Observations in the field indicated that *C. niger* was active throughout the day (Fig. 6A). By contrast, in winter, d_b was lower than d_e , indicating increased behavioral thermoregulation compared to summer (Table 4, Fig. 6B). During cold days with clear skies, lizards basked during the warmest periods of the day (from 1100 to 1500 h; Fig. 6B) and reached T_b close to T_p . During overcast winter days, little activity occurred, although T_b was slightly higher than crevice T_e (Fig. 6C).

Cordylus oelofseni (melanistic), mountain site.—The thermal quality of *C. oelofseni*'s habitat in summer was moderately suitable and was significantly higher than winter (Fig. 4A, Table 4). In summer, most T_e 's were

TABLE 2. Mean (\pm SD) critical thermal maximum (CT_{\max}) and minimum (CT_{\min}) of the study species determined after three weeks of acclimation at $27.0^\circ \pm 2.0^\circ\text{C}$.

Species	CT_{\max} ($^\circ\text{C}$)† (n)	CT_{\min} ($^\circ\text{C}$)‡ (n)
<i>Cordylus cordylus</i>	41.6 ± 1.0 (10)	7.5 ± 0.7 (10) ^a
<i>Cordylus niger</i>	41.0 ± 0.6 (8)	7.4 ± 0.5 (7) ^a
<i>Cordylus oelofseni</i>	40.8 ± 0.5 (10)	6.3 ± 0.8 (9) ^b

Notes: For CT_{\min} , statistically homogeneous groups are indicated by similar superscript letters (post hoc unequal sample honest significant difference test). Sample sizes are given in parentheses.

† ANOVA, $F_{2,25} = 2.73$, $P > 0.08$.

‡ ANOVA, $F_{2,23} = 7.21$, $P < 0.005$.

TABLE 3. Air temperature and wind speed (1 m above ground) and incident solar radiation (at ground level; mean \pm SD) obtained from study climate stations in summer and winter.

Site and season	Air temperature (°C)	Wind speed (m/s)	Solar radiation (W/m ²)
Joostenberg site (inland; <i>Cordylus cordylus</i> : non-melanistic)			
Summer			
Mean	22.7 \pm 1.9	4.2 \pm 0.7	342.1 \pm 47.9
Maximum	29.9 \pm 3.2	6.9 \pm 0.9	1123.0 \pm 54.4
Minimum	16.8 \pm 1.3	1.4 \pm 0.9	0
Winter			
Mean	11.4 \pm 1.1	2.0 \pm 0.7	111.3 \pm 43.9
Maximum	17.2 \pm 3.1	5.5 \pm 1.9	631.1 \pm 218.9
Minimum	7.9 \pm 1.6	0.5 \pm 0.4	0
Mauritzbaai site (coastal; <i>Cordylus niger</i> : melanistic)			
Summer			
Mean	20.7 \pm 1.9	2.8 \pm 1.1	309.9 \pm 83.7
Maximum	29.7 \pm 3.6	4.7 \pm 1.0	1086.7 \pm 144.6
Minimum	14.2 \pm 1.0	0.8 \pm 1.2	0
Winter			
Mean	13.6 \pm 1.4	3.0 \pm 0.7	107.1 \pm 70.0
Maximum	17.9 \pm 2.4	5.7 \pm 1.2	569.6 \pm 290.1
Minimum	9.3 \pm 3.5	0.7 \pm 0.5	0
Landdroskop site (mountain; <i>Cordylus oelofseni</i> : melanistic)			
Summer			
Mean	21.0 \pm 3.0	1.9 \pm 0.4	254.3 \pm 35.5
Maximum	28.8 \pm 3.5	4.9 \pm 1.6	997.6 \pm 118.9
Minimum	15.0 \pm 2.5	0.1 \pm 0.2	0
Winter			
Mean	10.7 \pm 6.5	2.9 \pm 2.0	171.9 \pm 66.0
Maximum	16.9 \pm 8.5	5.9 \pm 3.5	733.8 \pm 127.6
Minimum	5.6 \pm 5.2	0.3 \pm 0.3	0

Note: Data are presented as the grand mean of daily (24 h) means, maxima, and minima for periods of 5–7 days, \pm SD.

lower than T_p (72.3%), although warm temperatures were also available (20.8% of all T_e 's $>$ T_p and 4.7% $>$ CT_{max} ; Appendix C). In summer, d_e was lowest from 1400 to 1600 h (4°C; Fig. 4A). By contrast, the thermal quality in winter was very low throughout the day (\sim 24°C; Fig. 4A). Indeed, 100% and 11.3% of all T_e 's were below T_p and CT_{min} , respectively. Under these conditions, the mean d_e and maximum T_e available to a non-melanistic lizard (calculated from non-melanistic models) was reduced by $0.3^\circ \pm 0.1^\circ\text{C}$ and $0.6^\circ \pm 0.3^\circ\text{C}$, respectively. During an entirely overcast day, the difference in d_e between melanistic and non-melanistic models was $0.05^\circ \pm 0.07^\circ\text{C}$. By contrast, during an atypical warm day (Fig. 5C), this difference was comparable to that found during cold days (i.e., $0.3^\circ \pm 0.3^\circ\text{C}$), whereas the difference between maximum T_e of melanistic vs. non-melanistic models was more pronounced ($1.3^\circ \pm 0.1^\circ\text{C}$).

The thermal accuracy (d_b) was significantly greater in summer than winter (Fig. 4B, Table 4). In addition, d_b was lower than d_e in summer (Table 4), suggesting that lizards were effectively thermoregulating for at least part of the day. Daily patterns of d_b and d_e in summer (Fig. 4A, B) showed that between 0900 and 1200 h d_b was at its lowest (\sim 1°–2°C from T_p), although mean T_e deviated up to 5°C from T_p . Therefore, lizards were actively thermoregulating in the morning as shown by the number

of lizards basking \sim 0900 h (Fig. 7A). By contrast, they seemed to be less effective thermoregulators in winter. Despite a closer value of T_b than T_e to T_p throughout the day in winter (Fig. 4A, B), d_b remained very high (Table 4). Although active lizards were not observed during censuses made during overcast winter days (Fig. 7C), T_b of *C. oelofseni* was slightly greater than crevice T_e . On an exceptionally warm winter day, lizards basked frequently and maintained T_b close to T_p (Fig. 7B).

Field data: interspecific analyses

In summer, there were no significant differences in T_b across species ($F_{2,15} = 0.42$, $P = 0.667$; Table 4). Mean summer T_e (determined from the copper models which matched lizard reflectance from the respective sites) was significantly different across species ($F_{2,104} = 5.11$, $P < 0.01$; Table 4). However, the mean deviation of T_b and T_e from T_p (i.e., mean d_b and d_e) were not significantly different among species (T_b , $F_{2,104} = 1.57$, $P = 0.21$; T_e , $F_{2,104} = 2.66$, $P = 0.08$).

In winter, the T_b of *C. oelofseni* was significantly lower than that of *C. cordylus* and *C. niger* ($F_{2,22} = 23.96$, $P < 0.001$; Table 4), but *C. cordylus* and *C. niger* were statistically homogeneous. Mean T_e in *C. oelofseni*'s site was significantly lower than that in *C. niger* and *C. cordylus* sites ($F_{2,89} = 15.01$, $P < 0.001$; Table 4). In addition, mean d_b and d_e were significantly greater for *C.*

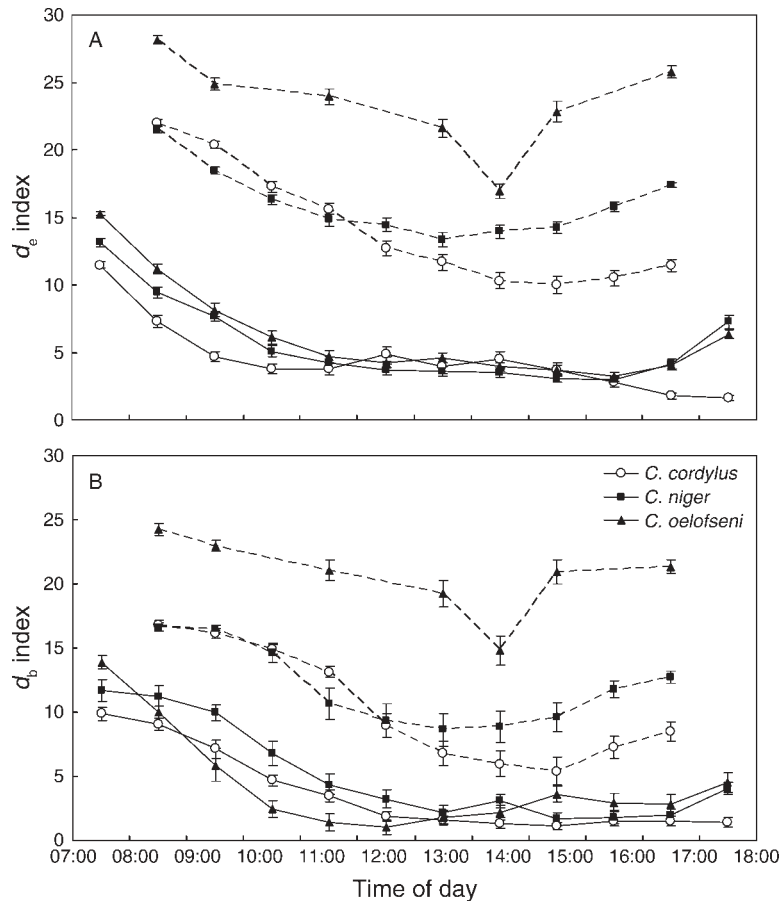


FIG. 4. Daily patterns of (A) habitat thermal quality, d_e ($^{\circ}\text{C}$), and (B) lizard thermal accuracy, d_b ($^{\circ}\text{C}$), in winter (broken line) and summer (continuous line) for three cordylid species in their respective habitats. Values shown are mean hourly d_e and d_b calculated for three days \pm SE.

oelofseni than for *C. cordylus* and *C. niger*, but d_b and d_e of *C. cordylus* did not differ from *C. niger* (d_b , $F_{2,76} = 27.34$, $P < 0.001$; d_e , $F_{2,76} = 27.34$, $P < 0.001$).

DISCUSSION

This study demonstrates that the variation in coloration among cordylid lizards in the Western Cape does indeed reflect a variation in skin reflectance and has significant effects on the thermal balance of these organisms. Moreover, differences between T_b of melanistic and non-melanistic individuals (ΔT_b) predicted from theoretical relationships were in accordance with experimental trials using both live lizards and T_e models under controlled and natural conditions. Overall, ΔT_b and ΔT_e ranged from $\sim 0^{\circ}$ to 2°C (Figs. 1–3) under varying, ecologically relevant climatic conditions. Although these differences are typically small, the faster heating rate and higher T_b of melanistic relative to non-melanistic lizards distinctly conferred an advantage under cold conditions. Indeed, these differences are likely to be more substantial when translated in terms of time spent above a critical threshold such as the minimum T_b for food assimilation, reproduction or

growth. For example, periods during which melanistic and non-melanistic T_e are above (or below) CT_{\min} in winter can be readily calculated from data gathered in the field (following, e.g., Sinclair 2001; see Appendix D). In Landdrooskop (mountain site), a non-melanistic lizard would spend, on average, 17 additional minutes per day below CT_{\min} compared to a melanistic lizard. This difference mostly results from models exposed to full sun (additional 27 min/d below CT_{\min}) and to partial shade (18 min/d; Appendix D). Given the thermal sensitivity of physiological rate functions in ectotherms (Beyer and Spotila 1994, Bauwens et al. 1995, Angilletta 2001), the additional time period per day during which T_b remains below or above a critical threshold or is maintained within the preferred range should confer a selective advantage, especially if summed across an entire winter season or an individual lizard's lifetime. A detailed understanding of traits such as the optimal temperature for digestion, growth and embryonic development, and longer time-series of T_b could provide further insight into the relative costs and benefits of melanism in these species.

TABLE 4. Summary of mean body (T_b) and operative (T_e) temperatures, habitat thermal quality (d_e), and accuracy of thermoregulation (d_b) of three *Cordylus* species.

Species and season	T_b (°C)	T_e (°C)	d_e (°C)	d_b (°C)
<i>Cordylus cordylus</i> ($T_p = 30.7$ – 33.6)				
Summer	27.8 ± 4.3 (3F:3M)	31.2 ± 7.4	4.5 ± 0.9	3.7 ± 0.7
Winter	20.5 ± 6.0 (4F:4M)	16.5 ± 6.1	14.4 ± 2.0	10.5 ± 2.3
<i>Cordylus niger</i> ($T_p = 32.0$ – 33.4)				
Summer	27.1 ± 4.9 (4F:2M)	27.6 ± 5.7	5.7 ± 0.6	5.2 ± 1.0
Winter	20.1 ± 5.5 (5F:3M)	16.0 ± 4.3	16.0 ± 2.0	11.9 ± 3.5
<i>Cordylus oelofseni</i> ($T_p = 32.8$ – 34.6)				
Summer	28.7 ± 4.9 (3F:4M)	28.6 ± 6.9	6.3 ± 0.2	4.4 ± 0.3
Winter	12.5 ± 4.5 (6F:4M)	9.3 ± 5.7	24.0 ± 4.9	20.6 ± 3.7

Notes: Sample sizes and sex ratios (females : males) of radio-telemetered lizards are given in parentheses next to T_b data. Grand means (\pm SD) were calculated from three days data in each species' site (from 07:00 to 18:00 hours and 08:00 to 17:00 hours in summer and winter, respectively). Set-point boundaries of preferred T_b 's (central 50%) are indicated next to species names.

In winter, cordylid lizards followed patterns observed for species in other temperate regions where thermal conditions often force lizards to maintain T_b well below preferred levels (e.g., Van Damme et al. 1987, Sievert and Hutchison 1989, Grbac and Bauwens 2001) despite efforts to thermoregulate (Table 4, Fig. 4). The finding that d_b was consistently lower than d_e (i.e., effective thermoregulation) in all species in winter suggests a similarity to the model proposed by Blouin-Demers and Weatherhead (2001; and see Blouin-Demers and Nadeau 2005). This model predicts that species living in suboptimal conditions can depart from perfect thermoconformity if the opportunity for thermoregulation is available despite high costs associated with challenging environments (e.g., predation risks). However, an integrative model of thermoregulation is potentially more complex (Huey and Slatkin 1976, Martin and Huey 2008) and possibly species-dependent and spatially and temporally scale-dependent. For example, during overcast days, individuals of *Cordylus oelofseni* were rarely observed in the open where the thermal benefits of melanism were mostly negligible ($<0.05^\circ\text{C}$), and may not have outweighed the potential costs (Huey and Slatkin 1976). Instead, their T_b closely matched crevice T_e and supported thermal conformity.

Overall, *C. oelofseni* was the most constrained species given the recurrent cold temperatures in the mountain site in winter (Table 3). Differences in thermal habitat quality (d_e) between non-melanistic vs. melanistic models in this site indicated that melanism could confer a great advantage during small windows of thermal opportunity. For example, when clear skies occurred in winter (e.g., Fig. 7B), lizards were readily seen basking. In this case, the benefits of thermoregulation largely outweighed the costs, and melanism conferred temperatures closer to preferred levels (and prolonged activity periods) in an environment that was typically suboptimal. Therefore, it is not surprising that melanism, which is thought to have evolved in cordylids as a result of past cold climate regimes (Mouton and Oelofsen 1988,

Daniels et al. 2004), has been maintained across multiple generations in these mountain populations.

By contrast, comparison of d_b , d_e , and behavioral patterns of *Cordylus cordylus* and *C. niger* did not seem to indicate a stronger advantage of melanism on the coastal (Mauritzbaai) compared to the inland (Joostenberg) site. Although fog conditions reduce the amount of incident solar radiation reaching the ground surface (Bonan 2002), coastal fog in the Western Cape mainly occurs in summer (as a result of warm moist air over the cold water of the Benguela-upwelling zone; Tyson and Preston-Whyte 2000) when the range of available T_e is broad (Fig. 4A). In addition, the incidence of high winds in the region (Tyson and Preston-Whyte 2000) should enable melanistic lizards (such as *C. niger*; Fig. 6A) to thrive in relatively hot environments and avoid high-temperature thresholds via convective cooling. Despite the calculated reduction of the thermal habitat quality ($\sim 0.2^\circ\text{C}$) for a melanistic lizard at Joostenberg (inland site), favorable T_e in crevices should be equally available to melanistic and non-melanistic lizards and provide similar thermal refugia to both during the warmest periods of the day. By contrast, we found that melanism at Joostenberg (inland) would also give lizards a T_b advantage in winter.

Two results from this study merit further detailed attention. First, T_b was often maintained slightly above mean or maximum crevice T_e even when the latter was the most favorable T_e available (Figs. 5–7), which suggests that lizards may have used additional microsites hidden from our direct observations (e.g., within crevices or between boulders). Many variables such as crevice depth, orientation and position within a boulder, and the size and properties of the latter, contribute to the complexity of the thermal environment in rock retreats (e.g., Huey et al. 1989). Despite the small deviation of T_b from T_e in all species, this study suggests that thermal investigations of rock-dwelling species should thoroughly explore crevice networks to reflect

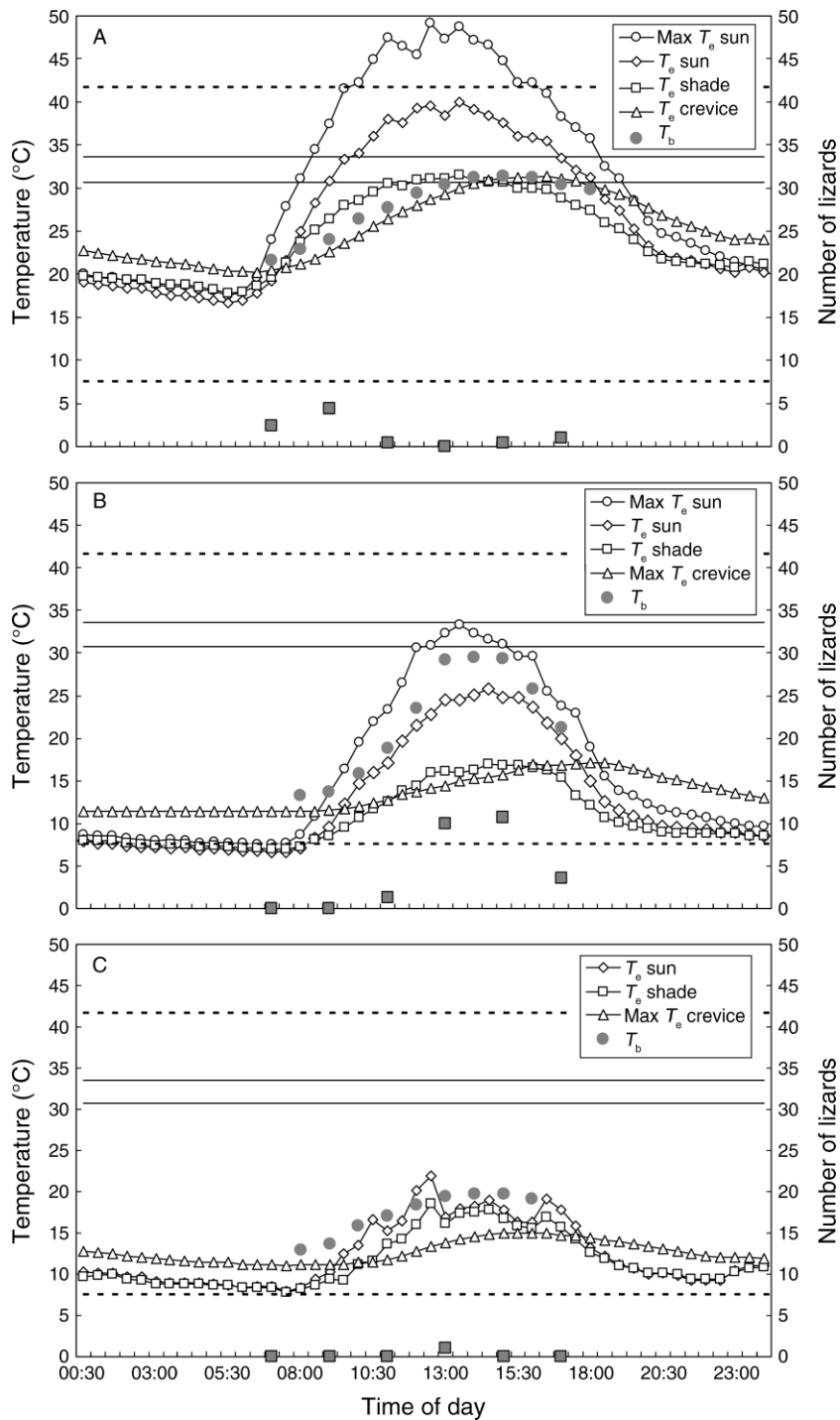


FIG. 5. Grand means of hourly body temperature (T_b), operative temperature (T_e), and number of individuals observed in the open (outside crevices) as a function of time of day for *Cordylus cordylus* at Joostenberg, South Africa. Operative temperatures are means of (1) T_e 's (or maximum T_e 's) in full sun, (2) T_e 's in shade, T_e 's (or maximum T_e 's) in crevices in (A) summer (five days), (B) winter (five days), and (C) a foggy day in winter. The set-point boundaries of T_p and thermal limits (CT_{max} and CT_{min}) are indicated by continuous and broken horizontal lines, respectively. Squares represent the mean number of active lizards (right-hand axes) observed (mostly basking) along 50-m transects every two hours.

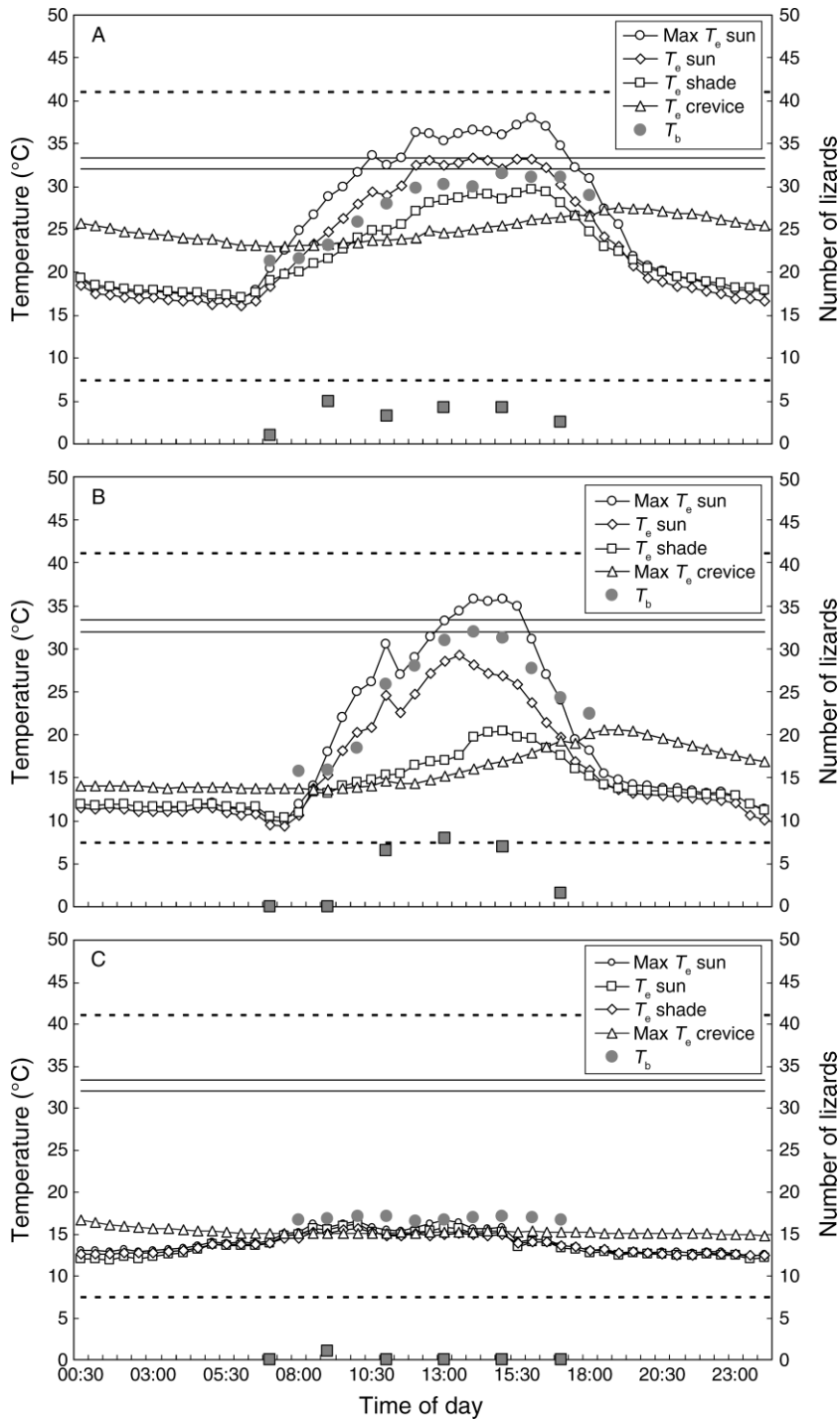


FIG. 6. Grand means of hourly body temperature (T_b), operative temperature (T_e) and number of individuals observed in the open (outside crevices) as a function of time of day of *Cordylus niger* at Mauritzbaai, South Africa. Operative temperatures are means of (1) T_e 's (or maximum T_e 's) in full sun, (2) T_e 's in shade and (3) T_e 's (or maximum T_e 's) in crevices in (A) summer (five days), (B) winter, clear skies (two days), and (C) winter, overcast (two days). T_p , CT_{max} , and CT_{min} are indicated by continuous and broken horizontal lines, respectively. Squares represent the mean number of active lizards (right-hand axes) observed along 50-m transects every two hours.

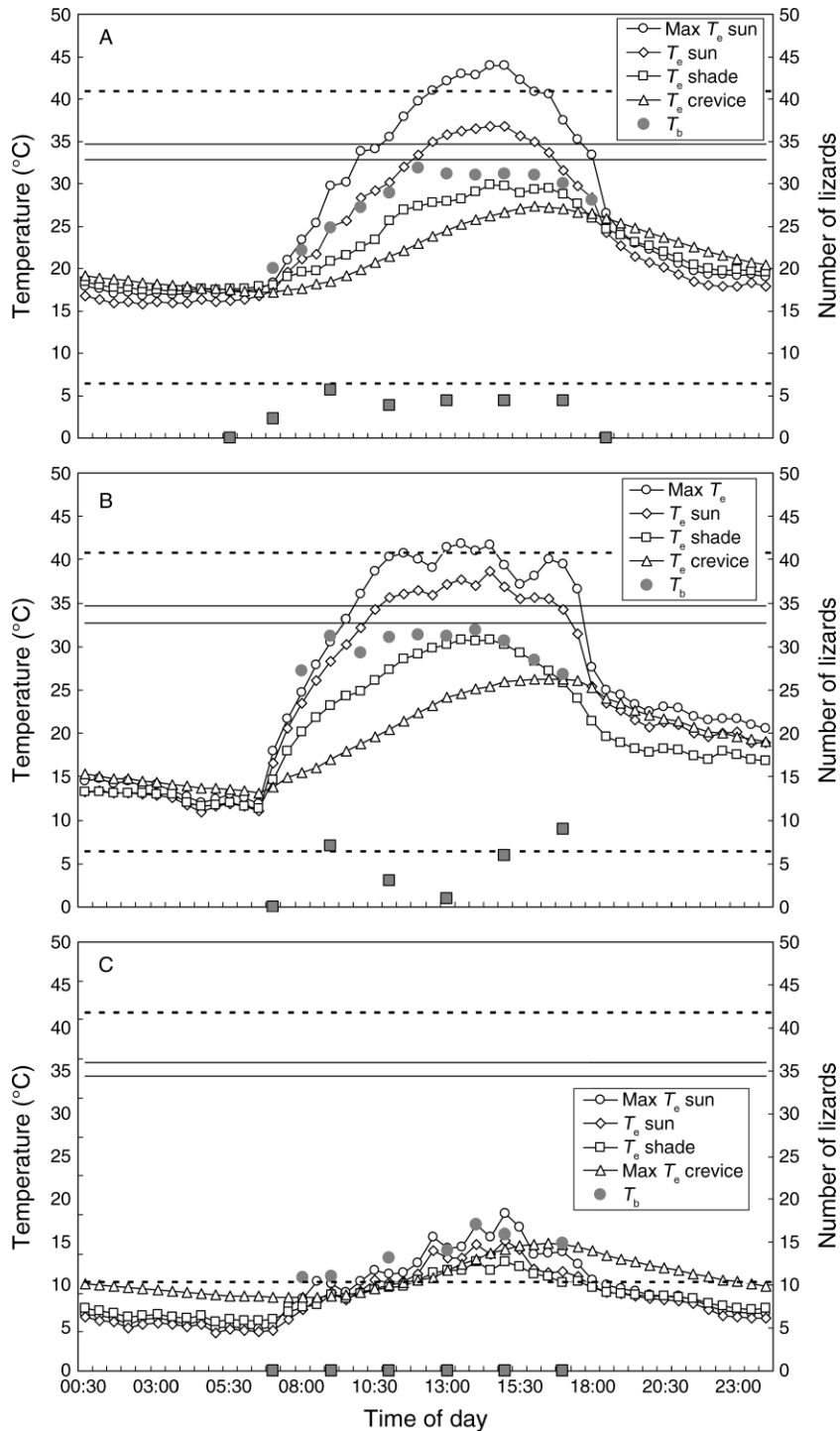


FIG. 7. Grand means of hourly body temperature (T_b), operative temperature (T_e), and number of individuals observed in the open (outside crevices) as a function of time of day of *Cordylus oelofseni* at Landdroskop, South Africa. Operative temperatures are means of (1) T_e 's (or maximum T_e 's) in full sun, (2) T_e 's in shade, and (3) T_e 's (or maximum T_e 's) in crevices in (A) summer (five days), (B) a winter, warm day, and (C) winter, overcast (two days). T_p , CT_{max} , and CT_{min} are indicated by continuous and broken horizontal lines, respectively. Squares represent the mean number of active lizards (right-hand axes) observed along 50-m transects every two hours.

the spatial and temporal variation of thermal opportunities offered by rock retreats.

Second, when the habitat provided a large range of thermal opportunities, T_b was often below the lower boundary of T_p (e.g., Figs. 6A and 7A) suggesting that lizards actively maintained T_b below preferred levels. Several hypotheses may explain this finding. The maintenance of T_b below T_p may be a means to reduce the risk of overheating under warm conditions. Indeed, the narrow range of T_p and the proximity of CT_{max} to T_p (e.g., Fig. 6A, in accordance with the asymmetry of thermal performance curves; Van Berkum 1988, Huey and Kingsolver 1989, Martin and Huey 2008) indicate that any further increase in T_b during the warmest periods of the day may be hazardous, especially when the availability of T_e below T_p is low. However, even when a broad range of thermal options was available (e.g., Fig. 7A, B), T_b was also maintained below T_p , making this hypothesis, at least sometimes, unlikely. Alternatively, phenotypic plasticity (e.g., seasonal acclimatization) and differences in sex ratios among populations may have affected T_p boundaries across seasons (e.g., Patterson and Davies 1978, Christian and Bedford 1995). However, since no significant acclimation or sex effects on T_p have been found for several cordylid species held in the laboratory (Wheeler 1986, Clusella-Trullas et al. 2007a), this possibility seems unlikely. Lastly, behaviors such as feeding, mating, and maintaining territories may impose significant deviations from optimal T_b despite high habitat thermal quality (e.g., Shine 1980). In fact, the overlap of T_b and T_p is highly variable across species and is influenced by diet, season, climate, habitat type, and geographic location (e.g., Grbac and Bauwens 2001, Gvoždík 2002, Diaz and Cabezas-Diaz 2004, Vitt et al. 2005). Therefore, the present data do not allow us to fully ascertain the cause of this consistent effect, but trade-offs between thermoregulatory costs and benefits (time and energy; Huey and Slatkin 1976, and see Blouin-Demers and Weatherhead 2001) seem like the strongest candidate in dictating natural T_b variation in these field populations.

In conclusion, using a multifaceted study that incorporates theoretical, experimental, and field data gathered at wide spatial and temporal scales, we have demonstrated the beneficial role of melanism in cordylids. Furthermore, by using spatially complex rock outcrops typical of cordylid habitat, these species were less thermally constrained under warm temperatures than under cold temperatures. Therefore, as predicted, melanism conferred an advantage in winter rather than a disadvantage in summer for all species. Indeed, the greatest thermal advantage was found in the species located in the mountain site where T_e frequently fell below physiological thresholds in winter. Future tests of the adaptive thermal advantage of skin reflectance (or the thermal melanism hypothesis) should consider cost/benefit tradeoffs of thermoregulation to understand fully the impacts of climate and its variation on lizard ecology.

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APPENDIX A

The steady-state energy model and its assumptions (*Ecological Archives* E090-160-A1).

APPENDIX B

Calibrations: copper models, live lizards, and radio transmitters (*Ecological Archives* E090-160-A2).

APPENDIX C

Frequency distributions of operative (T_e) and body (T_b) temperatures in three species of *Cordylus* (*Ecological Archives* E090-160-A3).

APPENDIX D

Table presenting d_c , d_b , time spent above and below critical thresholds for a melanistic and a non-melanistic lizard on a typical summer and winter day (*Ecological Archives* E090-160-A4).