Temperature-dependent Color Change in Kenyan Chameleons

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Abstract

Skin reflectance at different body temperatures was measured in three species of Kenyan chameleons (Chamaeleo dilepis, Chamaeleo jacksonii, and Chamaeleo ellioti). Total reflectance, calculated by averaging reflectances measured at 290 through 2,600 nm, was significantly greater at 35° C than at 20° C in C. dilepis (31% at 20° C to 46% at 35° C) and in C. jacksonii (7% at 20° C to 11% at 35° C). Reflectance changes with temperature were not the same at all wavelengths. Significant change was largely confined to visible and near-infrared spectral regions (600–1,000 nm). Chamaeleo ellioti did not show a significant change in total reflectance with temperature. Energy balance equations and climatic data representing long-term averages for each month of the year were used to assess the potential for alteration of equilibrium body temperature and rate of radiant heat gain by temperature-dependent color change in C. dilepis and C. jacksonii. The observed changes in reflectance produced changes in estimated equilibrium body temperature of 0.7° C in C. dilepis and 0.2° C in C. jacksonii, as averaged over the entire year. Dark chameleons are predicted to heat more rapidly than light chameleons. The dark coloration observed frequently during morning basking in chameleons may serve to reduce the basking period and, hence, reduce time spent at suboptimal performance temperatures.

Introduction

Color and the ability to change color have long been recognized as potentially important features of reptile thermoregulation (Parker 1934; Atsatt 1939; Cole 1943; Cowles and Bogert 1944; Hutchison and Larimer 1960; Bartlett and Gates 1967; Norris 1967). Because color represents the reflec-

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tance and absorptance of an animal's surface to visible wavelengths of solar radiation, variation in color (as well as variation in the absorption of non-visible wavelengths) alters the rate of radiant heat gain (Bartlett and Gates 1967; Norris 1967; Gibson and Falls 1979). The thermoregulatory significance of color, however, may be confounded with the competing and perhaps antagonistic functional requirements of crypsis (Norris 1967; Crisp, Cook, and Hereward 1979).

Chameleons are noted for their ability to change color, which provides excellent camouflage (Gans 1967; Hebrard and Madsen 1984). Thermoregulation, however, may be an additional, perhaps primary (Burrage 1973), function of color lability in chameleons. For example, chameleons in nature are often dark (and presumptively absorptive to incident solar radiation) while basking at cool air temperatures in the morning but become lighter (and presumptively more reflective) later in the day as air temperature and body temperature rise (Burrage 1973; Hebrard, Reilly, and Guppy 1982; Reilly 1982; B. M. Walton and A. F. Bennett, personal observation). In addition, chameleons are slow moving, so that color lability may help to compensate for the inability to move rapidly into favorable or away from unfavorable thermal microhabitats. However, the temperature dependence of reflectance and absorptance and the influence of color change on the rate of heat gain have not been quantified previously in chameleons. To assess the potential thermoregulatory role of color lability in chameleons, we conducted a study of color change in response to temperature in three species of Kenyan chameleons: *Chamaeleo dilepis*, *Chamaeleo jacksonii*, and *Chamaeleo ellioti*. These species occur in habitats that differ in elevation and vegetation, representing differential functional requirements for camouflage and thermoregulation. We sought to address the following questions: (1) Do reflectance and absorptance change with temperature? (2) Do changes in reflectance and absorptance extend to all aspects of the light spectrum (ultraviolet, visible, infrared)? (3) What effect does color change have on the rate of radiant heat gain and equilibrium body temperature in typical microclimatic conditions? This study is part of a larger project investigating the thermal ecology and the thermal dependence of organismal performance in chameleons.

Material and Methods

Study Animals

Chamaeleo dilepis occupies the hot shrubby coastal savanna of East Africa. This species is semiarboreal, spending approximately one-third to one-half of its activity period on the ground (Hebrard and Madsen 1984; B. M. Walton

and A. F. Bennett, personal observation). The individuals used here were collected in February 1990 in Kibwezi, Kenya (2°41'S, 37°96'E; elevation 900 m). *Chamaeleo jacksonii* occur at mid-elevation in forested areas, but also in dense shrubbery in and about urban areas. Those used in the current study were collected in March 1990 in Nairobi, Kenya (1°15'S, 36°46'E; elevation 1,700 m). *Chamaeleo elliotii* are found in midelevation forests in the western highlands of Kenya. Those used here were collected in March 1990 in the Nandi Forest region in Kapsabet, Kenya (0°19'N, 35°13'E; elevation 1,800–2,100 m).

Reflectance and Absorptance Measurements

Reflectance was measured with a Beckman DK-2A spectroreflectometer in the laboratory of Dr. Warren Porter of the University of Wisconsin—Madison. Five males of each species were measured at two body temperatures, 20° and 35°C, which are within the typical daily range of field body temperatures for these species (A. F. Bennett, B. M. Walton, and J. Losos, unpublished data). All animals were recently arrived from Kenya, in good health, and well hydrated. Chameleons were placed on their side and strapped securely onto an aluminum block, through which water flowed to cool or heat the animal to experimental temperature. After the animal had equilibrated at the experimental temperature, the animal and block were placed over the sample port of the spectroreflectometer, exposing a 1-cm² midlateral region of the animal's skin to the light beam. Measurements were restricted to broadest midlateral region of the body to reduce the potential for light leakage. Some variation in reflectance may occur among regions of the body because of mottling. However, mottling was minimal and usually not apparent in animals that were darkened or blanched at the experimental temperatures. Reflectance (%) was measured from 290 through 2,600 nm in comparison to a highly reflective reference surface of barium sulfate (reflectance = ca. 100%). A reflectance scan over all wavelengths was completed on an individual at one temperature within 5 min. Cloacal temperature was verified with a Miller and Weber quick-reading thermometer at the beginning and end of each measurement. Only trials in which body temperature varied less than 1°C from the beginning to the end were used for subsequent analyses. Average reflectance within several spectral regions (ultraviolet, visible, and infrared) and across the entire spectrum (total reflectance) was calculated using the computer program of McCullough and Porter (1971) and was based on the spectral distribution of solar radiation under clear skies at latitudes and elevations of the collection localities. Absorptance (%) was calculated as 100% − reflectance. Although handling may influence

the color of chameleons, the degree of blanching and darkening observed during the experiments appeared qualitatively similar to that observed in natural, field conditions at similar temperatures.

Calculation of Radiant Heat Gain and Predicted Body Temperature

The effects of color change (i.e., change in reflectance and absorptance) on the rate of radiant heat gain and equilibrium body temperature were estimated using a steady-state energy balance model based on the equation of Porter and Gates (1969):

$$Q_a + M - \lambda E_b = \epsilon \delta (T_b - [M - \lambda E_b]/K + 273)^4$$
$$+ b_c(T_b - T_a - [M - \lambda E_b]/K),$$

where Q_a is the amount of energy gained from radiant sources, M is the rate of energy metabolism, λ is the latent heat of vaporization of water, E_b is the rate of evaporative water loss, ϵ is the emissivity of chameleon skin, δ is the Stefan-Boltzmann constant, K is the thermal conductance of lizard skin, b_c is the coefficient of convection, T_a is air temperature, and T_b is core body temperature. Rates of energy exchange are estimated in terms of W/m². We estimated Q_a according to Porter and Gates (1969) using the following equation:

$$A Q_a = a_s A_s S + a_s A_s s + a_s r(S + s) + a_t A_a R_a + a_t A_g R_g,$$

where A is the total surface area of the lizard, A_s is the surface area exposed to direct sunlight, A_s is the surface area exposed to scattered sunlight, A_t is the surface area exposed to long-wave thermal radiation from the sky or substrate, a_s is absorptivity of chameleon skin to solar radiation, a_t is absorptivity of lizard skin to long-wave thermal radiation, S is the intensity of solar radiation striking the lizard, s is the intensity of scattered solar radiation, R_a is the intensity of long-wave thermal radiation from the sky, R_g is the intensity of long-wave thermal radiation from the environment, and r is the reflectance of the environment surrounding the lizard to solar radiation. Basking chameleons flatten laterally and orient one lateral surface approximately normal to the sun's rays (Burrage 1973; Hebrard et al. 1982; B. M. Walton and A. F. Bennett, personal observation); hence, we assume that $A_s = A_s = A_a = A_g = 0.5A$. The lizard was assumed to be perched at a height of 2 m, basking, and fully exposed to incident solar radiation. To obtain surface area of one flattened side of an animal, we used the following procedure: (1) the animal was immobilized by brief

cooling in a refrigerator; (2) the animal was placed on its side onto a sheet of paper and its outline was traced; (3) the paper silhouette was then cut out and weighed; (4) surface area of the silhouette was calculated using the following relationship: (area of silhouette)/(mass of silhouette) = (area of entire paper sheet)/(mass of entire paper sheet). Surface areas determined by this method were similar to those calculated using the empirically derived regression equation of Norris (1967). Equilibrium body temperature and the rate of heat gain from radiant energy at that temperature were estimated for a hypothetical basking chameleon by iteratively varying body temperature (T_b) until both sides of the energy balance equation were equal. Values of model parameters or equations used to estimate model parameters are given in Appendixes A and B. Only those chameleon species that showed significant changes in reflectance with temperature were modeled with these equations (i.e., *C. dilepis* and *C. jacksonii*).

Results

Overall Pattern of Reflectance and Absorptance

Chamaeleo dilepis was more reflective and less absorptive than either *Chamaeleo jacksonii* or *Chamaeleo ellioti* (table 1; fig. 1A–C). *Chamaeleo dilepis* showed particularly high reflectance and low absorptance at visible (400–700 nm) and near infrared (700–1,450 nm) wavelengths in comparison with the other two species. All three species showed local reflectance minima at 1,450 and 1,900 nm, corresponding to the reflectance bands for water.

Effect of Temperature on Reflectance and Absorptance

Reflectance was higher and absorptance was lower at 35°C than at 20°C in *C. dilepis* and *C. jacksonii*. The magnitude of the temperature effect differed between species and among wavelengths. *Chamaeleo dilepis* had the greatest change with an increase of 15.1% in total reflectance between 20° and 35°C (table 1). However, temperature did not produce color change at all wavelengths. Significant change in reflectance was confined to 600 through 1,100 nm (visible through near infrared wavelengths). Reflectances in the ultraviolet, visible wavelengths less than 600 nm and in the infrared beyond 1,100 nm were not significantly different (fig. 1A–C). *Chamaeleo jacksonii* showed a 4.2% increase in total reflectance between 20° and 35°C, and
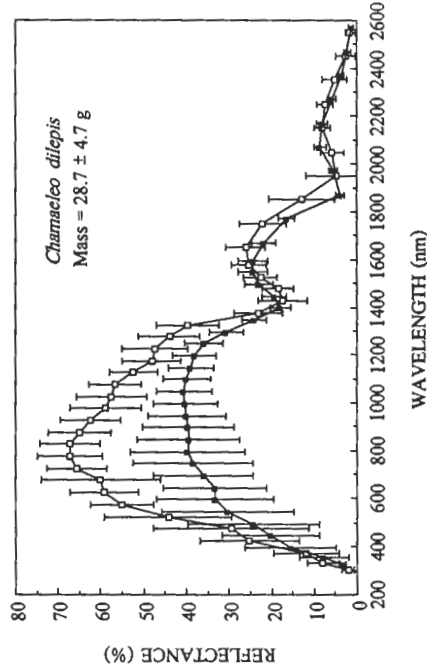
TABLE 1
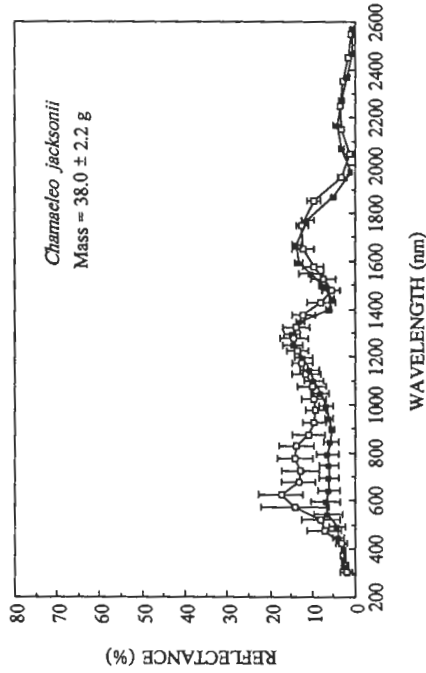Mean reflectance (±95% confidence limits) within spectral regions ranging from 290 to 2,600 nm

Spectral Region (nm)	Reflectance (%)					
	Chamaeleo dilepis		Chamaeleo jacksonii		Chamaeleo ellioti	
	20°C	35°C	20°C	35°C	20°C	35°C
Ultraviolet:						
290–400	10.8 ± 7.9	9.2 ± 5.7	2.0 ± .01	2.6 ± 1.1	4.6 ± 2.6	4.8 ± 3.1
Visible:						
405–500	22.0 ± 13.7	26.8 ± 10.8	3.6 ± 1.7	7.0 ± 4.5	12.4 ± 6.1	16.6 ± 10.1
505–700	32.4 ± 13.6	54.0 ± 7.0	5.6 ± 2.6	14.0 ± 4.2	21.2 ± 5.5	29.0 ± 16.1
Infrared:						
705–1,450	37.8 ± 8.2	58.0 ± 7.2	7.4 ± 1.1	11.2 ± 3.0	26.4 ± 7.2	27.2 ± 7.5
1,455–2,600	15.4 ± 1.9	16.2 ± 3.2	7.6 ± 1.1	7.0 ± .9	11.1 ± 1.0	9.4 ± 1.9
Total:						
290–2,600	30.7 ± 9.0	45.8 ± 5.2	6.7 ± .9	10.9 ± 1.9	20.8 ± 4.4	23.4 ± 8.1
Critical value of t^a	4.12		10.15		1.08	
Two-tailed P	.015		.0001		.34	

[a] Paired t-test (df = 4) comparing total reflectance at 20° and 35°C; reflectances (%) were arcsin transformed.

A.

Chamaeleo dilepis
Mass = 28.7 ± 4.7 g

B.

Chamaeleo jacksonii
Mass = 38.0 ± 2.2 g

again this change was confined largely to visible and near-infrared wavelengths (650–950 nm). *Chamaeleo elliotti* had a 2.6% increase in total reflectance between 20° and 35°C, but this increment was not statistically significant.
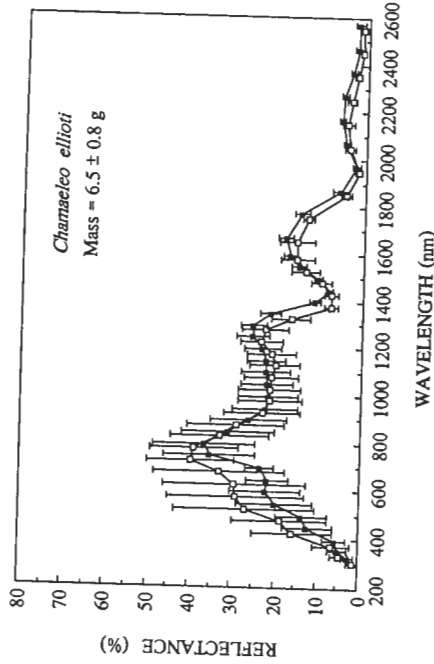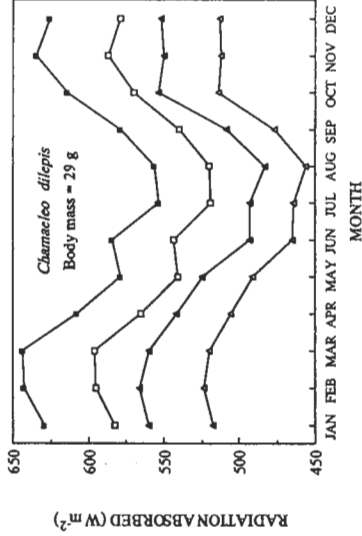
C.

Fig. 1. Reflectance (%) profiles for three chameleon species at two temperatures (darkened squares, 20°C; open squares, 35°C). Data are presented as means ± 95% confidence limits of the mean.

Effect of Color Change on Rate of Radiant Heat Gain and Body Temperature

Energy balance modeling provided an estimate of the effect of color change on rate of radiant heat gain and equilibrium body temperature for the two species, C. dilepis and C. jacksonii, that exhibited significant changes in reflectance and absorptance. For C. dilepis, a 15% increase in total absorptance yielded yearly mean increases in the estimated rate of radiant heat gain of 35 W m^{-2} at 0900 hours Kenyan Standard Time (KST) and 43 W m^{-2} at 1500 hours KST (fig. 2A). This change in radiant heat gain translates into an average increase in estimated body temperature of 0.7°C under both 0900 and 1500 conditions (fig. 3A). The 4% increase in absorptance shown by C. jacksonii resulted in a yearly mean increase in the estimated rate of radiant heat gain of 9 or 12 W m^{-2} at 0900 and 1500 hours KST, respectively (fig. 2B). This change in radiant heat gain translated into a mean increase in body temperature of 0.2°C (fig. 3B). In both species, rate of radiant heat gain changed 2–3 W m^{-2} and the predicted equilibrium body temperature changed approximately 0.05°C with a 1% change in absorptance. To calculate the rate of temperature change associated with a given heat flux, we assumed that the animal will heat or cool homogeneously, that 4.18 J of heat causes
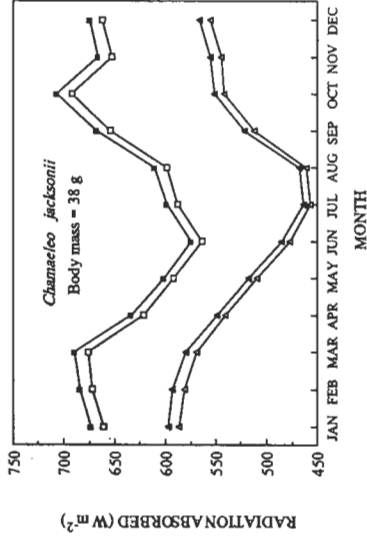
Fig. 2. Predicted radiation (direct solar, diffuse solar, reflected solar, and thermal radiation) absorbed (W m⁻²) by two chameleon species experiencing climatic conditions typical for each month of the year at 0900 and 1500 hours. Open symbols indicate values calculated for an animal with high total reflectance (Chamaeleo dilepis, 46%; C. jacksonii, 11%). Darkened symbols indicate values calculated for an animal with low total reflectance (C. dilepis, 31%; C. jacksonii, 7%). Triangles indicate values estimated for typical morning climatic conditions at 0900 hours. Squares indicate values estimated for typical afternoon climatic conditions at 1500 hours.
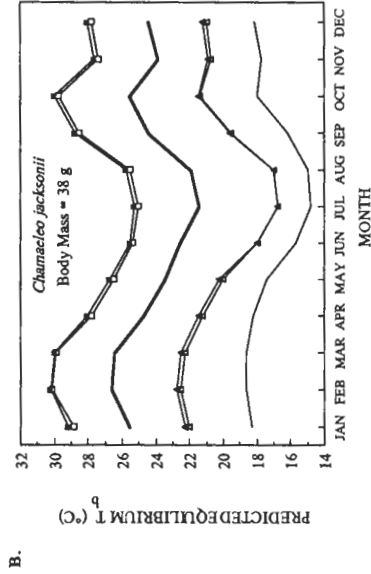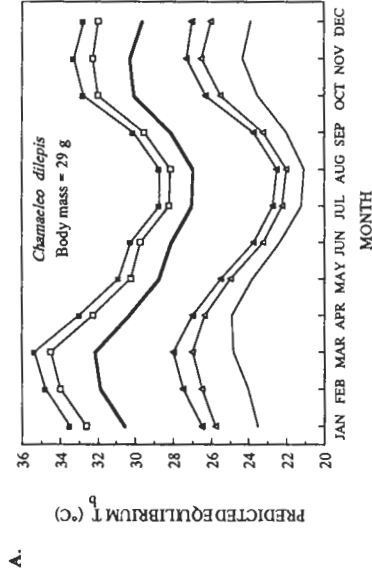
Fig. 3. Predicted equilibrium body temperature (T_b) of two chameleon species experiencing climatic conditions typical for each month of the year at 0900 and 1500 hours. Thin solid line indicates mean monthly air temperature at 0900 hours. Thick solid line indicates mean monthly air temperature at 1500 hours. Other symbols are the same as in fig. 2.

a 1°C temperature change in 1 g of water, and that reptile tissue warms 1.22-fold faster than an equivalent volume of water (Bartholomew and Tucker 1963). For *C. dilepis*, dark-colored animals are predicted to increase in temperature 0.17°C min^{-1} and 0.21°C min^{-1} faster than light-colored animals, under average morning (0900 hours) and afternoon (1500 hours) conditions, respectively. Dark *C. jacksonii* are predicted to increase in temperature 0.04°C min^{-1} and 0.06°C min^{-1} faster than light *C. jacksonii* at 0900 hours and 1500 hours, respectively.

Discussion

Several authors have noted that chameleons change color in response to temperature (see, e.g., Burrage 1973; Durve and Sharma 1975), but the magnitude of this change in regard to spectral properties of the skin has not been quantified previously (but see Cleworth, cited in Burrage 1973). Despite their reputation for color lability, the magnitude of color change as a function of temperature observed in chameleon species examined here was not exceptional in comparison with that of other lizards. *Chamaeleo elliotti* failed to show significant color change in response to temperature. Further, the 15% change in reflectance observed in *Chamaeleo dilepis* was similar to maximum changes observed by Norris (1967) in *Dipsosaurus dorsalis* and *Holbrookia maculatum*. Previous studies, however, used electric shock and pharmaceutical treatments in addition to temperature to elicit maximum blanching and maximum darkening (see, e.g., Norris 1967; Porter 1967; Gibbons and Lillywhite 1981). We used only temperature to elicit color change (and only two temperatures within the total range experienced by these species). Thus, chameleons may be able to undergo a greater magnitude of change than reported here. For instance, if reflectance is assumed to be a linear function of temperature among chameleons, then total reflectance may change by as much as 37% (55% − 18%) between the critical thermal maximum (43.6°C) and critical thermal minimum (7.6°C) of *C. dilepis* (A. F. Bennett, B. M. Walton, and J. Losos, unpublished data). The predicted changes in total reflectance within the critical thermal ranges for *Chamaeleo jacksonii* (critical thermal range: 5°–41°C) and *C. elliotti* (critical thermal range: 3.5°–42°C) are 10% (13% − 3%) and 6% (24% − 18%), respectively. Temperature-induced color lability was greatest in long visible (>600 nm) and near-infrared wavelengths, as has been reported in other lizards (Norris 1967; Porter 1967; Pearson 1977; Rice and Bradshaw 1980; Gibbons and Lillywhite 1981; Bowker 1985), although some desert iguanids apparently have greater lability in the near ultraviolet than do chameleons (Norris 1967).

Our field observations of several chameleon species suggest that color change may be an important component of thermoregulatory behavior. In the morning when the animals begin activity, many individuals will move to the end of a branch or top of a bush, orient themselves with one lateral aspect approximately normal to the sun, laterally flatten the body, and bask while dark brown to black. Often, only one side of the animal exposed directly to solar radiation is darkened. At this time, the animals may be clearly exposed and have apparently abandoned crypsis. As the air temperature rises and the body temperature approaches the preferred temperature

(A. F. Bennett, B. M. Walton, and J. Losos, unpublished data), the animal will move out of the sun and often changes to a lighter color. Similar observations have been reported previously for several chameleon (Burrage 1973; Hebrard et al. 1982) and other lizard species (Bartholomew 1982). Despite these observations, energy balance modeling suggests that color lability produces only modest differences in the equilibrium body temperature achieved (fig. 3). Maintenance of the equilibrium temperature, however, may not be as important as the rate at which the animal achieves that equilibrium. In at least $C.$ $dilepis$, color change appeared to provide a substantial increase in the rate of radiant heat gain. Dark animals warmed 7% faster than light animals (fig. 2A). Our calculations probably underestimate the thermal consequences of color change in chameleons, inasmuch as chameleons may be capable of greater color lability than measured here and environmental conditions are certainly more variable than the averages used in the current calculations.

Potentially, color modulation of heat flux could have several benefits. For example, low reflectance and increased rate of radiant heat gain may decrease the time spent by cool animals heating to preferred or optimal body temperature, thus freeing time for other behavioral demands and lessening exposure to predation. Basking lizards at body temperatures below that allowing optimal locomotory performance may be at a greater risk of predation (Huey and Slatkin 1976; Christian and Tracy 1981). Although we have no observations of predation on chameleons at cool body temperatures, locomotory performance is temperature-dependent. For example, sprint speed at 20°C may be 40% lower than that at preferred temperatures of $C.$ $dilepis$ and $C.$ $jacksonii$ (A. F. Bennett, B. M. Walton, and J. Losos, unpublished data). Rapid heating could be particularly important to high-elevation chameleons that begin morning activity at temperatures that severely limit activity and to those that may have only short periods of insolation sufficient to raise body temperatures to preferred or optimal levels (Hebrard et al. 1982; Reilly 1982). Conversely, increased reflectance may allow prolonged activity during exposure to high levels of solar radiation by slowing the increase of body temperature toward upper critical limits (Norris 1967; Pearson 1977). We have observed $C.$ $dilepis$ crossing open terrain and roads at midday when the intensity of solar radiation is clearly substantial. In these instances, the animals were invariably pale yellow or bright green and apparently highly reflective. In fact, we found no evidence that individuals in such circumstances were heat stressed. Ten $C.$ $dilepis$ that were found crossing roads on clear, hot days between 1100 and 1400 hours in February 1990 had a mean T_b of 34.37°C (range = 32.2°–35.8°C), which is only slightly higher than the average preferred body temperature selected by this species

in a laboratory thermal gradient (33°C; A. F. Bennett, B. M. Walton, and J. Losos, unpublished data). High reflectance is also characteristic of desert reptiles that are active or bask during periods of intense insolation (Klauber 1939; Norris 1967; Burrage 1973).

Previous authors have speculated on the selective importance of crypsis versus thermoregulation in determining a reptile's color lability, often suggesting that these functions need not be antagonistic (Atsatt 1939; Cowles 1958; Hutchison and Larimer 1960; Norris 1967). We suggest that the data for chameleons reinforce this view. *Chamaeleo jacksonii* and *C. elliotti*, which show limited or no changes in reflectance with temperature, are found in lush midelevation forests that remain green even during the dry season. In this instance, the requirements of camouflage are probably met with a relatively narrow range of greens and browns. In addition, these animals can easily escape hot conditions by moving into the ample shade found in forest habitats, rather than becoming highly reflective. Moreover, these forests can be quite cool, especially in the morning. Thus, the lower reflectances of *C. jacksonii* and *C. elliotti* may aid warming. On the other hand, the East African savanna presents a broader palette of colors to be matched by *C. dilepis*. The savanna may be lush and green in the wet season, but during the dry season the vegetation is a patchwork of greens, browns, tans, and pale yellows. Accordingly, *C. dilepis* are generally green in the wet season but vary in color during the dry season (Hebrard and Madsen 1984). In the dry season, males, which tend to perch in dry, defoliated shrubs, are most often yellow or tan, while females, which remain in green shrubs, are most often green in color. Males are also more active than females and are more likely to move through open terrain characterized by tawny-colored grasses. Such seasonal variation in cryptic coloration may coincide with seasonal thermoregulatory demands. During the dry season, the potential for damaging radiative heat loads is greatest. Females, which remain in leaved bushes, may avoid overheating without changing color by moving into the shady interior of the bush. The apparently reflective pale yellow color of many male *C. dilepis* may slow the rate of radiant heat gain, while preserving crypsis on a tan or yellow background.

In summary, reflectance increases with temperature in some, but not all, chameleon species. While color change is clearly important for crypsis, it also has a potential role in thermoregulation. In the current study, the species with the greatest color lability (*C. dilepis*) occurs in savanna habitat characterized by intense solar radiation and seasonal variation in vegetation color. Species from more moderate forested habitats show less color lability. In these cases, the thermoregulatory and crypsis functions of color change are complementary.

Acknowledgments

Appendix A

TABLE A1

Parameters of the chameleon heat balance model

Model Parameters (and Symbol)	Value or Formula	Reference
Stefan-Boltzman constant (δ)	5.6697×10^{-8} W m^{-2} k^{-4}	Gates 1980
Properties of the animal:		
Mass (g):		
Chamaeleo dilepis	29	Current study
Chamaeleo jacksonii	38	Current study
Body "diameter" (d), width of a laterally compressed chameleon (cm)	1.5	Current study
Thermal conductance of lizard skin (W m^{-2} °C^{-1})	502	Porter and Gates 1969
Absorptance of skin at experimental temperatures:		
20°C:		
C. dilepis	.69	Current study
C. jacksonii	.93	Current study
35°C:		
C. dilepis	.54	Current study
C. jacksonii	.89	Current study
Absorptance (a_s) and emissivity (ϵ_s) of lizard skin to long-wave thermal radiation	.96	Bartlett and Gates 1967

TABLE A1 (*Continued*)

Model Parameters (and Symbol)	Value or Formula	Reference
Amount of long-wave thermal radiation lost by lizard	$\varepsilon_l \delta (T_b + 273)^4$, where T_b is the measured body temperature	Bartlett and Gates 1967
Coefficient of convection (h_c)	$3.49(v/d)^{0.5}$, where v is wind velocity and d is lizard diameter	Gates 1980
Amount of heat energy exchanged by evaporation (E_b)	$.08 e^{0.005867 T_b}$, where e is the base of natural logarithms and 20°C $< T_b < 36$°C	Porter et al. 1973
Amount of heat energy due to metabolism (M)	$.0056 \times 10^{0.0387 T_b - 1.771} m^{0.82}$, where m is mass	Bennett and Dawson 1976
Properties of the environment: Substrate reflectance to solar radiation	.2	Morhardt and Gates 1974
Amount of scattered solar radiation reaching substrate (%)	15 (of direct solar radiation)	Gates 1980
Emissivity of substrate (ε_s)	.9	Sellers 1965
Amount of long-wave radiation from sky	$1.22 \delta (T_a + 273)^4 - 171$, where T_a is the local air temperature as measured by the Kenya Meteorological Department	Swinbank 1963
Amount of long-wave radiation emitted from substrate	$\varepsilon_s \delta (T_s + 273)^4$, where T_s is the substrate temperature (assumed here to equal T_a)	Gates 1980

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Appendix B

TABLE B1

Climatic data used in chameleon heat balance equations

Month	Air Temperature (°C) 0900 Hours	Air Temperature (°C) 1500 Hours	Wind Speed (m s⁻¹) 0900 Hours	Wind Speed (m s⁻¹) 1500 Hours	Intensity of Solar Radiation (W m⁻²) 0900 Hours	Intensity of Solar Radiation (W m⁻²) 1500 Hours
A. *Chamaeleo dilepis:*[a]						
January	23.5	30.5	2.6	4.1	395.2	446.0
February	24.0	31.8	2.1	4.6	402.0	457.8
March	24.8	32.1	2.1	3.6	378.4	456.1
April	24.9	30.3	3.6	4.1	339.5	404.8
May	23.8	28.7	4.6	4.6	317.6	366.6
June	22.4	28.1	4.6	5.1	268.6	384.3
July	21.2	27	4.6	5.1	284.6	337
August	21.1	26.9	4.1	5.7	265.2	342.1
September	22.0	28.1	4.1	5.7	307.4	374.2
October	23.5	30.0	3.1	4.6	382.6	423.2
November	24.3	30.2	2.1	4.1	364.0	462.9
December	23.9	29.6	2.1	3.6	374.2	451.9
B. *Chamaeleo jacksonii:*[b]						
January	18.3	25.5	3.6	6.2	400.3	451.0
February	18.6	26.6	3.1	6.2	390.2	456.9
March	18.6	26.4	3.1	6.7	369.9	466.2
April	18.2	24.7	3.1	5.7	326.0	397.0
May	17.4	23.4	2.6	4.1	282.9	360.7
June	15.7	22.5	2.6	3.6	248.3	324.3
July	14.8	21.4	2.6	3.1	223	373.3
August	15.0	21.9	2.6	3.6	228.0	387.7
September	16.2	24.4	2.1	4.1	299.8	451.0
October	18.0	25.5	2.6	5.1	331.1	502.5
November	17.7	23.8	3.6	5.7	339.5	456.1
December	18.1	24.4	4.1	6.7	353.1	464.5

Source: Kenya Meteorological Department 1984.

Note: All values are monthly means for data available from 1938 through 1980.

[a] Voi Meteorological Station: 3°42′S, 28°34′E; elevation 560 m.

[b] Jomo Kenyatta Airport, Nairobi: 1°19′S, 36°55′E; elevation 1,624 m.

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