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**MISCONCEPTIONS ABOUT COLOUR,
INFRARED RADIATION, AND
ENERGY EXCHANGE BETWEEN
ANIMALS AND THEIR
ENVIRONMENTS**

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“Long-wave IR radiation relationships are of crucial importance to the energy balance of ectothermic animals, but even so, they have either been ignored, or when they have been discussed with regard to reptilian thermal problems, largely misunderstood.” - Kenneth Stafford Norris, 1967

In a recent paper, Willemsen & Hailey (1999) described an intriguing geographic cline in plastron pigmentation in the tortoise *Testudo hermanni*, and suggested that differences in colour along this cline could be the result of a latitudinal cline of natural selective pressure related to thermoregulation in this species. Specifically, they suggested that the cline in plastron pigmentation could afford an adaptive benefit to lighter-pigmented animals in cooler environments by reducing radiant energy emittance from the animals. In other words, they propose that animals with lighter colour will radiate less energy, and thus, should be able to achieve higher body temperatures and/or remain active longer than would darkly-pigmented individuals. However, the physical mechanism of energy exchange proposed by Willemsen & Hailey (1999) is incorrect and leads to erroneous conclusions about natural selection. Their explanation is based upon a common misconception that colour and infrared radiation exchange by living organisms are related (Norris, 1967). This misconception stems from a misapplication of Kirchoff's Law, which states that emissivity equals absorptivity (Appendix 1) at the same temperature and wavelength (Çengel and Boles, 1998). However, animals emit energy at wavelengths different from those at which they absorb radiation in the ultraviolet, visible, and near-infrared wavebands.

The electromagnetic spectrum influencing an ectotherm's body temperature can be pragmatically divided into two wavebands (Tracy, 1982): (1) the waveband 290–2600 nm, which includes the ultraviolet, visible, and short-wave infrared, solar radiation that is transmitted through the Earth's atmosphere, and (2) the waveband 4000–50,000 nm, known as long-wave infrared or “thermal” radiation (Gates, 1980). Animals emit radiation in this latter waveband according to the Stefan-Boltzmann law, where the total energy emitted (E_b) is given by $E_b = A_s \epsilon \sigma T^4$ (Gates, 1980; Tracy, 1982; Mills, 1999). Thus, the radiant heat emitted is a function of the surface area of the object (A_s), the emissivity of the object (ϵ) in the waveband 4000–50,000 nm, the Stefan-Boltzmann constant (σ), and the fourth power of the object's temperature (in Kelvins). Most living organisms have a thermal emissivity (ϵ) of about 0.96–1.0 (Finch, 1972; Porter *et al.*, 1973; Tracy, 1978, 1982) averaged across the long-wave infrared waveband. Colour is a reflective property of organisms associated with the visible wavelengths for humans, in the waveband 400–750 nm, and thus, an animal's colour is not relevant with respect to infrared radiation (Norris, 1967; Tracy, 1982). To illustrate that this is a misunderstanding with a long history, consider the quote from Norris (1967), “It has sometimes been assumed that because a reptile is visibly black it reradiates at a greater rate than a white lizard... [however] visible color is not relevant to a lizard's capacities as a black body emitter, and both the light and dark lizards may emit long-wave radiation at the same rate per unit area.” While Kirchoff's Law specifies the relationship between an object's emissivity and absorptivity to radiation, energy is not emitted at all wavelengths. Instead, the amount and quality of radiation emitted is a function of the temperature of the emitting object according to the Stefan-Boltzmann Law, and the wavelengths in which this energy is emitted are given by Planck's Distribution Law (Gates, 1980). Throughout the range of temperatures achieved by living organisms, Planck's equation shows that no radiation is emitted at wavelengths shorter than about 4000 nm (Gates, 1980; Fig. 5.1, p 79).

Some of the confusion about radiant processes stems from the fact that solar radiation reaching the Earth's surface occurs in wavelengths between 290 nm and 2600 nm (Gates, 1962), including the ultraviolet, visible, and near infrared spectra. The absorption of energy in these wavelengths is not usually well correlated with the colour of the animal (Norris, 1967; Porter, 1967; Gates, 1980) because the energy in the visible spectrum represents less than half of the incident solar radiation (Gates, 1980; Campbell & Norman, 1998). Despite Norris's (1967) recognition that visible colour is a poor predictor of the total absorptivity of solar radiation in living organisms, this important point is not pervasive in the literature. For example, some investigators have attempted to control solar radiant absorptivity of operative temperature models (Tracy,

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1982; Bakken *et al.*, 1985) with paints selected entirely on the basis of their colour (e.g. Vitt & Sartorius, 1999). In such cases, any correlation between absorptivity of solar radiation and the colour of the object is coincidental.

To estimate the total energy absorbed by animals in the solar waveband, one must know the absorptance of ultraviolet, visible, and short-wave infrared components of solar radiation. The percentage of the incident energy that objects absorb in these wavebands can be inferred from measurements with a spectrophotometer. Percentage absorptance must be integrated across the spectrum of the incident radiation (e.g. clear-day solar radiation or radiation filtered by a plant canopy; e.g. Gates, 1980, Fig. 8.17) to calculate an average solar absorptance for the incident radiant waveband (a specific example is given in Appendix 1).

The relationships between colour and absorption of solar radiation are not always predictable. For example, the lizards *Callisaurus draconoides* and *Holbrookia maculata*, as well as the house finch, *Carpodacus mexicanus*, have lower absorptances (Appendix 1) in the visible waveband than they do in the near infrared (e.g. Norris, 1967, Figs. 5 and 6; and Porter, 1967, Fig. 22). On the other hand, the carapace of the desert tortoise (*Gopherus agassizii*) has a higher absorptance in the visible wavelengths than in the near infrared (Fig. 1). Leaves of plants typically have a high absorptance across the ultraviolet and visible bands and extremely low absorptance throughout most of the near infrared (e.g. Gates, 1980; Figs. 8.20 and 8.21). Sometimes, absorptance in the visible waveband may be nearly the same as that in the near infrared. This is true for juvenile collared lizards, *Crotaphytus collaris*, (Norris, 1967; Fig. 16) and bullfrogs, *Rana catesbeiana*, (Porter, 1967; Fig. 21.). Black human skin obviously has higher absorptance than does white human skin in the visible waveband, and absorptivity in the near infrared wavelengths 750–1400 nm correlates with absorptance in the visible waveband; nevertheless, black and white skin have similar absorptance in the waveband 1400–2000 nm (Mount, 1979, Fig. 3.3).

An additional obstacle to predicting patterns among absorptivities for different wavebands for a given organism is the fact that some animals can change their colour and/or absorptance in the visible and near-infrared wavebands. For example, the snake *Crotalus cerastes* can be darkly coloured when it has a low body temperature and lightly coloured when it has a higher body temperature. However, the lighter colour phase absorbs more infrared energy (at wavelengths greater than 900 nm) than does the dark phase (Norris, 1967, Fig. 14). Conversely, dark and light phases of the lizard, *Uma scoparia*, have nearly identical absorptances in the near infrared waveband (e.g. Norris, 1967; Fig. 4).

Even surfaces with the seemingly highly-reflective colour white can have very varied levels of absorptance to solar radiation. For example, the white ventral sur-

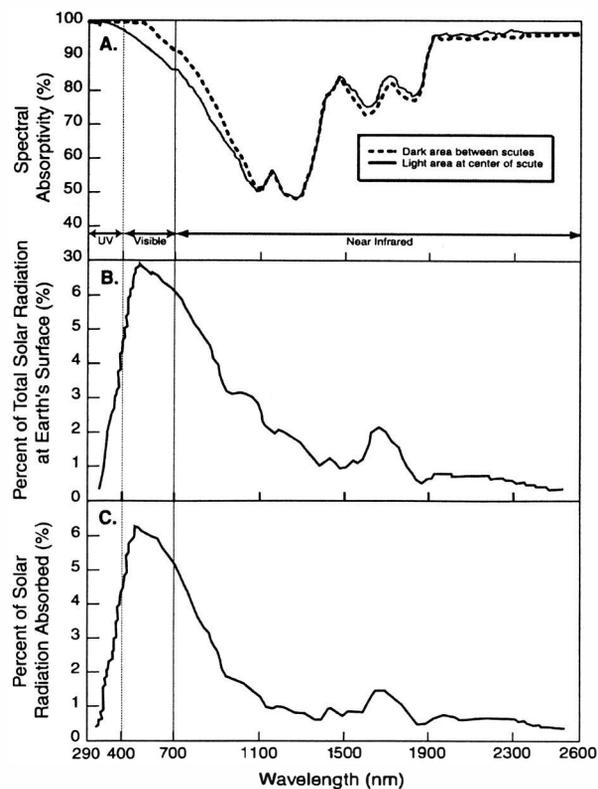


FIG. 1. (a) Absorptance (%) of dark and light portions of scutes on the carapace of an adult desert tortoise (*Gopherus agassizii*) from Clark County, Nevada, USA; (b) Percentage of incident solar radiation at the earth's surface on a clear day; and (c) the percentage of energy absorbed as quantified by the integration of the absorptance of tortoise scutes, with the clear day solar radiation curve.

face of a desert iguana has a mean absorptance in the solar spectrum of 41% (Norris, 1967), a white domestic cat had a measured absorptance of 44.5%, the absorptance of the white stripe of a skunk was 49.3%, the absorptance of a white swan was 36.7%, and the absorptance of white feathers of an Adelie penguin and a kingfisher were 32.4% and 33.9%, respectively (Gates, 1980).

In conclusion, visible colour is not a good predictor of long-wave infrared energy exchange between animals and their environments. Additionally, visible colour is not necessarily related to an animal's absorptivity in other portions of the solar spectrum. These facts indicate that the mechanism proposed by Willemsen & Hailey (1999) to explain the adaptive significance of the cline in plastron coloration in *Testudo hermanni* is not supported by the physical laws governing energy exchange, and therefore the evolutionary mechanisms underpinning the interesting geographic pattern remain to be explained.

APPENDIX 1:

DEFINITIONS AND CLARIFICATION OF TERMS

Definitions of terms from Hunt (1979):

Absorptance: "a ratio of the radiation absorbed by a body of material to the radiation incident upon it."

Absorptivity: "the ratio of the radiant energy number absorbed by a body to that falling upon it. It is equal

to the emissivity for radiation of the same wavelength.”

Emittance: “the ratio of the radiant energy...emitted from a surface at a given temperature to the energy emitted by a perfect black body at the same temperature.”

Emissivity: “the ratio of radiant energy emitted by a body to that emitted by a perfect black body. A perfect black body has an emissivity of 1; a perfect reflector, an emissivity of 0.”

Reflectance: “the ratio of radiation reflected from a surface to the total radiation incident on the surface.”

Reflectivity: “the ratio of radiant energy reflected by a body to that falling upon it.”

Transmittance: “The ratio of the radiation passing through a material to the radiation incident on the upper surface of that material.”

One additional definition comes from Campbell & Norman (1998):

Transmissivity: “the fraction of incident radiant flux at a given wavelength transmitted by a material.”

In general, the words absorbance and absorptivity are often used interchangeably and have no clear distinction in the literature (Holman, 1963; Hunt, 1979; Tabor, 1979; Campbell & Norman, 1998; Mills, 1999). This lack of distinction may cause confusion and thus merits a more careful treatment. More properly absorptivity is a property of the surface that can be expressed as a number that reflects a measured variable. Indeed, words ending in the suffix “-ivity” represent properties (e.g. conductivity, emissivity, diffusivity, etc.), and words ending in the suffix “-ance” represent values (Tabor, 1979). According to Kirchoff’s Law of Radiation, the sum of reflectivity, transmissivity and emissivity (at any particular wavelength) is one; emissivity and absorptivity are equal to one another at any particular wavelength.

Absorptivity (as well as reflectivity and transmissivity) of an organism’s surface is often expressed as a mean value integrated across a broad waveband (e.g. the integrated solar absorbance to clear-day solar radiation). When this integrated solar absorbance is calculated, it is defined by the spectrum of the incident radiation. Thus, an animal can have a mean solar absorbance for clear-day solar radiation, and an entirely different mean solar absorbance for radiation under a leaf canopy (e.g. Gates, 1980, Fig. 8.17) or under a cloudy sky, etc. In other words, integrated, or mean, solar absorbances are integrations of the properties of an organism’s surface with the spectrum of incident radiation. For example, the spectral absorptivity of a desert tortoise is given in Fig. 1a. When the curve (the dashed line in this example) is integrated with incident clear-day solar radiation (Fig. 1b), the result is the curve in Fig. 1c which is the predicted spectral absorption of clear-day solar radiation for that scute surface by a desert tortoise. When the area under

this curve (Fig. 1c) is integrated, the result is the integrated (or mean) absorptivity to clear-day solar radiation by the surface of a desert tortoise – in this case 83.6%.

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EDITOR’S NOTE

The authors of the article that stimulated this contribution, R. E. Willemsen and A. Hailey, provided the following response:

“We agree that although colour can affect absorption of the short-wave IR in sunlight, colour does not matter to emission of long-wave IR by a tortoise (or to absorption of long-wave IR emitted by the ground). Plastral colour can therefore have no effect on thermoregulation, and this explanation of the cline must join the other four already rejected. Of those considered, the only hypothesis remaining is random genetic differentiation; this would explain why pigmentation varied with latitude but not with altitude.”

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