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Modeling operative temperature in desert tortoises and other reptiles: Effects imposed by habitats that filter incident radiation

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ABSTRACT

We challenged the common practice of using a single mean absorptance based on unfiltered skylight spectra to model operative temperature for reptiles in filtered light habitats by examining the effects of plant canopies on light transmittance. To assess differences in light filtration over a range of microhabitats, spectra were recorded under canopies of desert plants, tropical plants, and under unfiltered skylight. Spectra were then integrated with absorptivity curves of desert reptiles to determine if differences in light quality among microhabitat types changed integrated mean absorptance. Finally, we used the desert tortoise (*Gopherus agassizii)* as a case study to investigate the effects of filtered microhabitats on paint choice for physical operative temperature models and determined the magnitude of error that could result from discrepancies between paint and animal absorptance. We found that light energy was partitioned similarly among microhabitats with like canopy types and that most variation was explained by differences in transmittance between the visible and near infrared wavelengths. Mean absorptance for reptiles was similar among microhabitats with the greatest differences observed between animals in unfiltered skylight and under tropical canopies. In most microhabitats paint and tortoise absorptances differed, but operative temperatures were nearly identical within microhabitats no matter the absorptance used in the model. The findings of this study support the use of a single mean absorptance in modeling operative temperature for reptiles in a variety of habitats.

1. Introduction

The thermal environment for living organisms can be defined by a suite of heat-transfer processes (e.g., convection, radiation, conduction, evaporation) that ultimately determine the body temperature of ectothermic animals (Gates, 1980). Operative temperature (T_e) is defined as the temperature attained by an inanimate object, of zero heat capacity, with the same size, shape, and properties important to radiative heat exchange as the animal for which the measurement is made (Bakken and Gates, 1975). In other words, T_e integrates the mechanisms of energy transfer to produce a single index that represents the steady-state body temperature of a specific animal experiencing a given set of environmental conditions (Bakken et al., 1985; Tracy, 1982) and can be calculated either mathematically, or using physical models that replicate the properties of animals (Bakken, 1992; Tracy, 1982). There is a vast literature on how to calculate or measure operative temperatures (e.g., Bakken and Gates, 1975; Bakken et al., 1985; Dzialowski, 2005; O'Connor et al., 2000; Tracy et al., 2007), and a similarly rich literature demonstrating the use of operative temperature as a valuable metric in ecological applications (e.g., Bakken, 1992; Christian and Tracy, 1985; Fouts et al., 2017; Grant and Dunham, 1988; Hertz, 1992a, 1992b).

During daylight hours, solar radiation is a major component of the overall energy balance of ectotherms. Solar radiation includes ultraviolet, visible, and short-wave infrared radiation and can be incident on an animal in the form of either direct radiation or scattered skylight (Gates, 1980). The amount of energy gained through solar radiation is not only contingent upon the intensity of radiation, but also on the area and absorptivity (the fraction of incident radiation absorbed) of the surface to incident radiation (Gates, 1980; Tracy, 1982). The absorptivity of an animal varies across the solar spectrum (Norris, 1967; Porter, 1967), and the color of the animal is often not a predictor of its absorptive properties in non-visible regions (Nussear et al., 2000).

Mean absorptance is calculated by integrating the absorptivity of an animal at each wavelength multiplied by the wavelength's intensity across the spectrum (generally from 300 nm to 2500 nm), and dividing

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Table 1
Characteristics of plant species sampled as categorized into microhabitat types. Means are ± one standard deviation.

Species	Microhabitat type	Sample size	Mean diameter (cm)	Mean height (cm)	Mean percent transmittance (%)
Ambrosia dumosa	Desert shrub canopy	6	109.2 ± 19.2	53.3 ± 7.7	13.9 ± 8.5
Ephedra nevadensis	Desert shrub canopy	6	115.0 ± 28.0	76.3 ± 19.1	8.7 ± 5.8
Krameria spp.	Desert shrub canopy	6	93.9 ± 16.6	31.3 ± 1.5	26.1 ± 10.5
Larrea tridentata	Desert shrub canopy	6	181.5 ± 44.0	134.3 ± 28.7	9.9 ± 1.4
Lycium spp.	Desert shrub canopy	6	79.2 ± 27.5	49.0 ± 20.7	23.8 ± 6.3
Psorothamnus fremontii	Desert shrub canopy	6	181.9 ± 54.1	105 ± 14.4	11.5 ± 4.2
Sphaeralcea ambigua	Desert sub-shrub canopy	6	64.7 ± 13.2	57.2 ± 14.8	9.8 ± 2.8
Yucca brevifolia	Desert yucca canopy	6	201.3 ± 57.4	323.2 ± 68.5	6.3 ± 1.5
Yucca schidigera	Desert yucca canopy	6	146.2 ± 42.4	157.7 ± 37.1	4.6 ± 1.5
Caladium bicolor	Tropical canopy	3	39.7 ± 4.1	25.0 ± 6.9	18.4 ± 3.0
Ficus lyrata	Tropical canopy	6	54.2 ± 7.1	46.0 ± 6.9	10.0 ± 3.1
Perilla sp.	Tropical canopy	6	38.3 ± 6.3	29.0 ± 7.0	10.1 ± 2.2
Syngonium podophyllum	Tropical canopy	6	56.2 ± 4.9	36.7 ± 4.7	9.1 ± 2.5
	Unfiltered skylight	75			100

it by the total solar energy (Gates, 1980). Thus, mean absorptance depends on both the absorptivity of the animal and the spectrum of incident light with which absorptivity is integrated (Nussear et al., 2000). Historically, this spectrum has been assumed to be that of a clear day with unfiltered solar radiation (Gates, 1980). The mean absorptance based upon a single integration has been used in mathematical calculations and is mimicked in physical models by using paint that matches the mean absorptance of an animal (Bakken et al., 1985; Bakken, 1992). However, paints composed of carbon pigment have a flat reflective signature across the solar spectrum whereas eumelanin, a pigment found in the integument of many vertebrates, including reptiles, is more reflective in the near infrared region (Harlow et al., 2010). This leads to a mismatch in the shape of the absorptivity curve between paint and the surface of a reptile, even though there is a similar integrated mean absorptance, which could introduce error into operative temperature modeling.

Historical mean absorptance calculations may accurately represent radiant energy gain for animals subject to clear day unfiltered radiation, but do not necessarily predict absorbed radiation by animals in filtered light microhabitats where light is scattered and reflected (O'Connor and Spotila, 1992). Even so, operative temperatures are often calculated using the same mean absorptance values for individuals in microhabitats receiving unfiltered solar radiation as those in other microhabitats receiving radiation filtered through clouds, shrub canopies, forest canopies, and other forms of shade (e.g. Bauwens et al., 1996; Belliure et al., 1996; Christian and Bedford, 1995; Diaz and Diaz, 2004; Grant and Dunham, 1988; Harlow et al., 2010; Shoemaker and Gibbs, 2010). Light transmitted through vegetation is likely to differ in quality (i.e. the distribution of energy across the spectrum), not just quantity, from unfiltered solar radiation, as many studies have found that proportion of understory light in different wavebands (e.g. red:far-red ratios) varies with canopy species (Federer and Tanner, 1966; Muraoka et al., 2001; Sattin et al., 1994), canopy cover (Capers and Chazdon, 2004; Grant, 1997; Lee, 1987; Pecot et al., 2005; Rossi et al., 2001), canopy architecture (Skalova et al., 1999; Volterrani et al., 2017), and leaf water content (Serrano and Penuelas, 2005). These relationships also depend on sky condition (cloudy or sunny) (Capers and Chazdon, 2004; Pecot et al., 2005).

Dzialowski (2005) reviewed the use and accuracy of operative temperature models and stressed, among other factors, the importance of choosing an appropriate paint for physical models that matches the absorptivity of the study animal. However, to our knowledge, the biophysical ecology literature has yet to validate the use of a single mean animal absorptance for deriving operative temperatures for animals in all light environments. Here, we address this issue by investigating the effects of light filtered by plant canopies on absorptance calculations for desert reptiles. The objectives of this paper are to:

1. Determine how light filtered through plant canopies differs in quality among microhabitat types.
2. Determine if differences in light quality among microhabitat types changes integrated mean absorptance for a variety of desert reptiles.
3. Use the desert tortoise (*Gopherus agassizii)* as a case study to:
   i. Investigate whether mean absorptance diverges between real animals and operative temperature models (painted to match the mean absorptance of a tortoise carapace based on clear day unfiltered solar integration) in microhabitats with filtered light.
   ii. Reveal the magnitude of error associated with modeling T_e in microhabitats with filtered light using standard methods for calculating absorptance.

2. Materials and methods

2.1. Spectral measurements

Measurements of solar spectra were taken in the Mojave Desert in southern Nevada on April 17 and 19, 2012 under clear sky conditions within 1.5 h pre- and post-solar noon (11:10 to 14:10) using an ASD FieldSpec 3 portable spectroradiometer with cosine-corrected irradiance receptor. The spectroradiometer recorded irradiance in W/(m^2 • nm) from 350 nm to 2600 nm at a resolution of 1 nm but readings above 1800 nm were inconsistent and thus excluded from analyses. Energy between 1800 nm and 2600 nm typically accounts for only about 5% of the total radiant energy within the detectable range of the spectroradiometer (350 nm–2600 nm). To examine differences in light filtration over a range of microhabitat types, we recorded spectra under canopies of native desert plant species, non-native tropical plant species, and under unfiltered skylight (Table 1). The native species chosen exhibited a range in canopy architecture representative of Mojave Desert vegetation and were grouped into three microhabitat types based on conformation: shrub canopy, sub-shrub canopy, and yucca canopy.

Tropical species had larger leaves and more leaf overlap than any of the desert species sampled and were grouped as a single microhabitat type. We chose these species to represent a contrasting habitat with a more closed canopy. We measured spectra under naturally occurring native and potted non-native species in the same field location. To eliminate any bias due to soil reflectance, soil in the pots of the tropical species was covered with the same substrate found under the native species. Each spectrum was recorded by placing the cosine receptor horizontally level to the ground using a tripod (Fig. 1). To determine the quality of filtered light under plant canopies, we recorded five shaded spectra in different spots under each plant. A paired spectrum was also recorded next to each plant in unfiltered skylight to compare the quality of light in canopy-filtered microhabitats to that of unfiltered skylight. Recording an unfiltered skylight spectrum after each set of readings below a plant canopy accounted for changes in radiation during the

Fig. 1. Example of experimental setup with cosine receptor mounted to tripod under tropical potted plant *Perilla* sp.

sampling period due to sun position or the presence of thin clouds.

2.2. Light quality

Irradiance was measured between 350 nm and 1800 nm. Data between 1350 nm and 1400 nm were omitted from analyses due to instrument noise. For each replicate plant, only the shaded spectrum with the lowest total transmitted energy was selected for analysis to maximize potential effects of canopy light filtration. We calculated total radiant energy for each spectrum by summing energy at all wavelengths. Percent transmittance was calculated for each plant canopy by dividing the total radiant energy transmitted through the canopy by the total radiant energy in the paired unfiltered skylight spectrum (Table 1). Mean percent transmittance at each wavelength was also calculated for each microhabitat type. Radiant energy was then divided into four bands: ultraviolet (UV) 350 nm–400 nm, visible (VIS) 400 nm–700 nm, near infrared (NIR) 700 nm–1400 nm, or short-wave infrared (SWIR) 1400 nm–1800 nm (Metzger, 2012). The proportion of total radiant energy contained in each band was calculated for each spectrum. We used nonmetric multidimensional scaling (NMDS), which is robust to non-normal data, to visualize how light energy was partitioned among bands in different microhabitats using raw proportions. All indices were equally good at separating microhabitats using rank correlation so NMDS was calculated using Bray-Curtis dissimilarity. We conducted a permutational multivariate analysis of variance (PERMANOVA) to test if grouping species into microhabitat types explained differences in how canopy-filtered light energy was partitioned. NMDS and PERMANOVA analyses were conducted using the Vegan package ver 2.0–9 in program R (Oksanen et al., 2012).

2.3. Animal absorptance

Spectral absorptivity data for desert reptiles were obtained from published figures (Norris, 1967; Porter, 1967) using the program GraphClick (Arizona Software, ver 3.0.) and from the primary author of Nussear et al. (2000). A mean absorptance value for each reptile was calculated for each spectrum following Gates (1980) by integrating the published absorptivity curves with the measured irradiance curves for all microhabitats. We used linear models with Dunnett's post hoc comparisons (Package multcomp ver 1.2–21 in R 3.0.2) for each reptile species to determine whether absorptance values for animals in canopy-filtered microhabitats differed significantly from absorptance values for animals in unfiltered skylight.

2.4. Desert tortoise case study

Spectral absorptivity curves of several paint samples were measured from 350 nm to 1800 nm using a spectrophotometer with a reflecting sphere attachment (Model 5420, Beckman Inc., Fullerton, CA). Paint absorptivity curves were integrated with a clear day unfiltered solar radiation spectrum to obtain a mean absorptance for each sample. The process was also repeated using the average absorptivity curve of a desert tortoise carapace (Nussear et al., 2000). For analysis, we chose the paint that most closely matched the mean absorptance of the tortoise carapace to represent the absorptivity of a T_e model (paint 83.2%, tortoise 82.2%). The absorptivity curves of the paint and tortoise carapace were integrated with each microhabitat spectrum yielding a mean absorptance value for a painted T_e model and for a tortoise in each microhabitat. Linear mixed effect models (Package nlme ver 2.1–111 in R 3.0.2) were conducted pairwise, for each microhabitat, to determine whether the absorptance of the T_e model and the tortoise were statistically different. We included plant replicate as a random effect to account for the repeated use of spectra in calculating T_e model and tortoise absorptances.

T_e calculations were made using a mathematical model parameterized with conditions that would maximize differences in absorptance (e.g., intense radiation in the open, minimal convection, large tortoise body size). Weather data were obtained from a HOBO weather station (located in desert tortoise habitat where irradiance was measured) equipped with a solarimeter and thermistors located 100 cm above ground surface and 10 cm below ground surface. We calculated hourly T_e during daylight hours for a 38 cm desert tortoise in southern Nevada using solar radiation, air temperature, and ground temperature measured on the summer solstice (June 21, 2010). Wind speed was artificially adjusted to 1 m/s for all hours to reduce energy exchange via convection. We modeled T_e for three microhabitats: unfiltered skylight (control), tropical *Syngonium podophyllum* (tortoise absorptance lowest and paint absorptance highest), and desert *Yucca brevifolia* (tortoise absorptance highest and paint absorptance lowest). For each microhabitat, T_e was modeled using absorptance values that were calculated by integrating the absorptivity curves of the paint and tortoise carapace with filtered and unfiltered spectra. In filtered microhabitats, all parameters were kept constant, but solar radiation was reduced according to percent transmittance for that species (Table 1). We compared daily minimum, maximum, and mean T_e within each microhabitat using linear models with Tukey's post hoc comparisons (Package multcomp ver 1.2–21 in R 3.0.2).

3. Results

3.1. Light quality

Mean percent of transmitted light varied both among microhabitat types and across the spectrum with clear breaks between the VIS and NIR bands and the NIR and SWIR bands (Fig. 2). Stress was minimal ($S = 0.01$) in a two dimensional NMDS biplot indicating a good

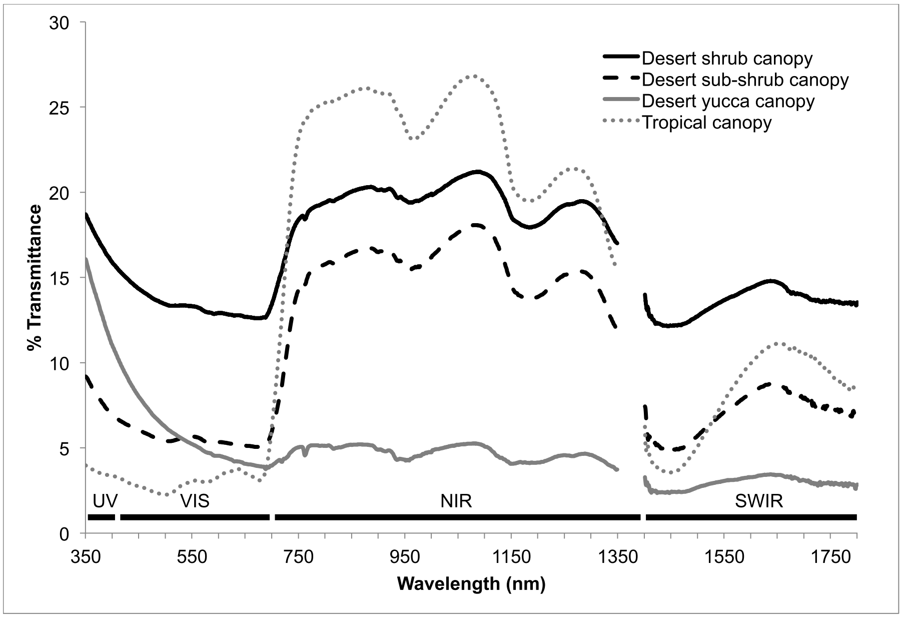


Fig. 2. Mean percent transmittance across the spectrum by microhabitat type (desert shrub canopy solid black, desert sub-shrub canopy dashed black, desert yucca canopy solid gray, and tropical canopy dotted gray). Light band ranges are shown at the bottom (ultraviolet "UV", visible "VIS", near infrared "NIR", and shortwave infrared "SWIR").

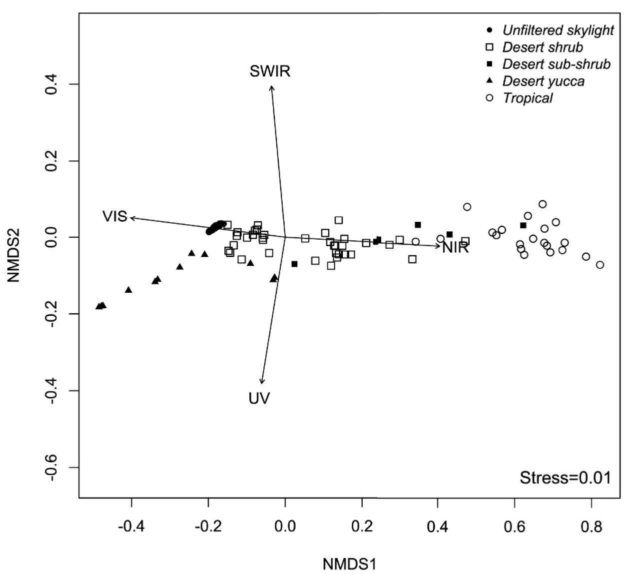


Fig. 3. Nonmetric multi-dimensional scaling biplot illustrating how light energy is partitioned among bands under different microhabitats. Filled circles are unfiltered skylight, open squares are desert shrub species, filled squares are desert sub-shrub species, filled triangles are desert yucca species, and open circles are tropical species. Lines with arrows represent fitted vectors.

representation the data (Fig. 3). The way in which light energy was partitioned into bands varied significantly among microhabitat types (PERMANOVA, $P < 0.01$). Most of the variation occurred across the VIS and NIR gradient associated with axis NMDS1 while little variation occurred across the UV and SWIR gradient associated with axis NMDS2 (Fig. 3). Light filtered through tropical canopies had a higher proportion of energy in the NIR and SWIR bands and a lower proportion of energy in the VIS and UV bands, while light filtered through desert yucca canopies had a lower proportion of energy in the NIR and SWIR bands and a higher proportion of energy in the VIS and UV bands. Light filtered through desert shrub and sub-shrub canopies was partitioned intermediately between the tropical and desert yucca canopies (Fig. 3).

3.2. Animal absorptance

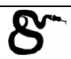
Mean absorptance for reptiles in unfiltered skylight ranged from 52.4% in *Crotalus cerastes* to 96.7% in *Sceloporus occidentalis* (Table 2). Absorptance values, calculated using canopy-filtered spectra, differed from absorptance values calculated using unfiltered skylight spectra by up to 8.3%. The direction and magnitude of absorptance differences depended on both the species of reptile and the species of plant. Calculated absorptance for all of the reptiles was similar to unfiltered skylight under the canopy of only one desert shrub (*Krameria* spp.) ($P > 0.05$, Table 2). The greatest differences in absorptance were observed between unfiltered skylight and tropical canopies. Calculated absorptance differed between all four tropical species and unfiltered skylight for all reptiles ($P < 0.05$, Table 2). However, even these differences were relatively minor (0.6%–8.3% difference in mean absorptance).

3.3. Desert tortoise case study

Mean absorptance of the desert tortoise and T_e model differed significantly in all filtered microhabitats ($P < 0.05$) except under the desert yucca *Y. schidigera* ($F_{1,5} = 1.91$, $P = 0.23$, Fig. 4). The absorptance of the T_e model was higher than the absorptance of the tortoise carapace for all microhabitats except under the desert yucca *Y. brevifolia*. The greatest differences in absorptance were found under tropical plant canopies with a maximum difference of 8.5% under *S. podophyllum*.

Calculated daily measures of T_e for the desert tortoise had no variance so even minor differences were statistically significant (Table 3). Minimum, maximum, and mean T_e were all significantly different between paint and tortoise carapace in the unfiltered skylight microhabitat ($P < 0.05$). All measures of T_e were identical under *Y. brevifolia* while maximum and mean T_e were statistically different under *S. podophyllum*. T_e differences within microhabitats were all 0.2 °C or less (Table 3).

Table 2
Integrated mean absorptance for desert reptiles in unfiltered skylight compared to canopy-filtered microhabitats (abbreviations given across top). For each reptile, significant differences between canopy-filtered microhabitat absorptances and the reference unfiltered skylight absoprtance (first column) are denoted with an asterisk ($P < 0.05$). Positive values indicate that the filtered microhabitat absorptance is higher than the unfiltered skylight absorptance. Absorptance differences greater than 5% are shaded. Plant species abbreviations are: *Ambrosia dumosa* (AMDU); *Ephedra nevadensis* (EPNE); *Krameria* spp. (KRSP); *Larrea tridentata* (LATR); *Lycium* spp. (LYSP); *Psorothamnus fremontii* (PSFR); *Sphaeralcea ambigua* (SPAM); *Yucca brevifolia* (YUBR); *Yucca schidigera* (YUSC), *Caladium bicolor* (CABI), *Ficus lyrata* (FILY), *Perilla* sp. (PESP), and *Syngonium podophyllum* (SYPO).

Animal type	Desert reptile species	Integrated absorptance (%)	Difference in absorptance between canopy-filtered microhabitats listed by species and unfiltered skylight (%)												
		Unfiltered skylight	AMDU	EPNE	KRSP	LATR	LYSP	PSFR	SPAM	YUBR	YUSC	CABI	FILY	PESP	SYPO
	*Aspidoscelis tigris*[b]	80.8	+ 0.8 *	+ 0.9 *	+ 0.3	+ 1.2 *	+ 0.4	+ 0.6 *	+ 1.3 *	+ 0.6 *	+ 0.8 *	+ 1.4 *	+ 1.8 *	+ 1.8 *	+ 2.0 *
	Callisaurus draconoides[a]	66.0	+ 1.5 *	+ 1.8 *	+ 0.6	+ 2.1 *	+ 0.7 *	+ 0.8 *	+ 2.5 *	0.0	+ 0.7	+ 3.4 *	+ 3.9 *	+ 3.7 *	+ 4.1 *
	Crotaphytus collaris[a]	80.6	- 2.3 *	- 2.5 *	- 0.5	- 2.5 *	- 1.2	0.0	- 3.7 *	+ 2.8 *	+ 1.0	- 6.0 *	- 6.2 *	- 5.8 *	- 6.9 *
	Dipsosaurus dorsalis[b]	65.4	- 1.1 *	- 1.2 *	- 0.2	- 1.0 *	- 0.7	+ 0.2	- 1.6 *	+ 1.3 *	+ 0.5	- 2.8 *	- 2.8 *	- 2.7 *	- 3.4 *
	Holbrookia maculata[a]	65.9	+ 2.5 *	+ 2.8 *	+ 0.9	+ 3.4 *	+ 1.1	+1.1	+ 4.0 *	- 0.5	+ 0.7	+ 5.2 *	+ 6.2 *	+ 5.8 *	+ 6.6 *
	Sauromalus varius[a]	67.3	- 2.1 *	- 2.2 *	- 0.4	- 2.1 *	- 1.0	+ 0.4	- 3.3 *	+ 3.1 *	+ 1.5	- 5.7 *	- 5.8 *	- 5.3 *	- 6.6 *
	Sceloporus magister[b]	82.6	- 0.9 *	- 1.0 *	- 0.2	- 0.9 *	- 0.5	+ 0.1	- 1.4 *	+ 1.5 *	+ 0.7	- 2.4 *	- 2.4 *	- 2.2 *	- 2.6 *
	Sceloporus occidentalis[b]	96.7	- 0.4 *	- 0.4 *	- 0.1	- 0.5 *	- 0.1	- 0.1	- 0.7 *	+ 0.5 *	+ 0.2	- 1.0 *	- 1.2 *	- 1.0 *	- 1.1 *
	Uma notata[a]	68.2	- 0.6	- 0.6	0.0	- 0.5	- 0.4	+ 0.4	- 0.9 *	+ 1.3 *	+ 0.7 *	- 1.6 *	- 1.6 *	- 1.4 *	- 2.0 *
	Uma scoparia[b]	83.2	- 0.2	- 0.2	0.0	- 0.1	- 0.1	+ 0.4	- 0.3	+ 1.2 *	+ 0.7 *	- 0.8 *	- 0.7 *	- 0.6 *	- 0.8 *
	Uta stansburiana[b]	88.8	+ 1.1 *	+ 1.3 *	+ 0.4	+1.5 *	+ 0.6 *	+ 0.5	+ 1.7 *	0.0	+ 0.5	+ 2.4 *	+ 2.7 *	+ 2.7 *	+ 3.0 *
	*Crotalus cerastes*[a]	52.4	- 2.8 *	- 3.0 *	- 0.6	- 2.9 *	- 1.5	+ 0.2	- 4.3 *	+ 3.4 *	+ 1.3	- 6.9 *	- 7.2 *	- 6.8 *	- 8.3 *
	Salvadora hexalepis[b]	80.2	- 1.0 *	- 1.1 *	- 0.2	- 1.1 *	- 0.5	+ 0.1	- 1.5 *	+ 1.3 *	+ 0.5	- 2.4 *	- 2.5 *	- 2.3 *	- 2.8 *
	*Gopherus agassizii*[c]	82.2	- 2.2 *	- 2.4 *	- 0.6	- 2.5 *	- 1.1	- 0.2	- 3.3 *	+ 1.9 *	+ 0.5	- 4.9 *	- 5.3 *	- 4.9 *	- 5.8 *

[a]Norris, 1967; [b]Porter, 1967; [c]Nussear et al., 2000

[a]Norris (1967).
[b]Porter (1967).
[c]Nussear et al. (2000).

4. Discussion

4.1. Light quality

The distribution of transmitted light energy across the four light band ranges we considered was similar among species of like canopy type (tropical and desert sub-categories). Under tropical plant canopies, transmitted light quality was indicative of direct filtration through leaves. Less light was transmitted in the UV and VIS bands, while proportionately more light was transmitted in the NIR and SWIR bands. This pattern is consistent with the rapid change in leaf reflectance between red and near infrared regions (Grant, 1997). Leaf pigments absorb much of the photosynthetically active radiation, thus intercepting visible light, while leaves reflect and/or transmit large portions of near infrared radiation to prevent overheating (Gates, 1980).

Desert shrubs tended to have smaller leaves and more non-green branches than tropical species, which produced canopies that were more open and intercepted less light. Light transmitted through desert shrub canopies was more similar to unfiltered skylight, which could be attributed to the larger amount of unscattered direct and diffuse radiation penetrating the canopy through gaps instead of being filtered through plant materials (Endler, 1993). Also, non-green plant parts absorb less light in the visible region and more light in the near infrared region than green plant parts (Serrano et al., 2000). The light quality under desert shrubs was consistent with expectations for transmittance through canopies with higher ratios of branches to leaves. The

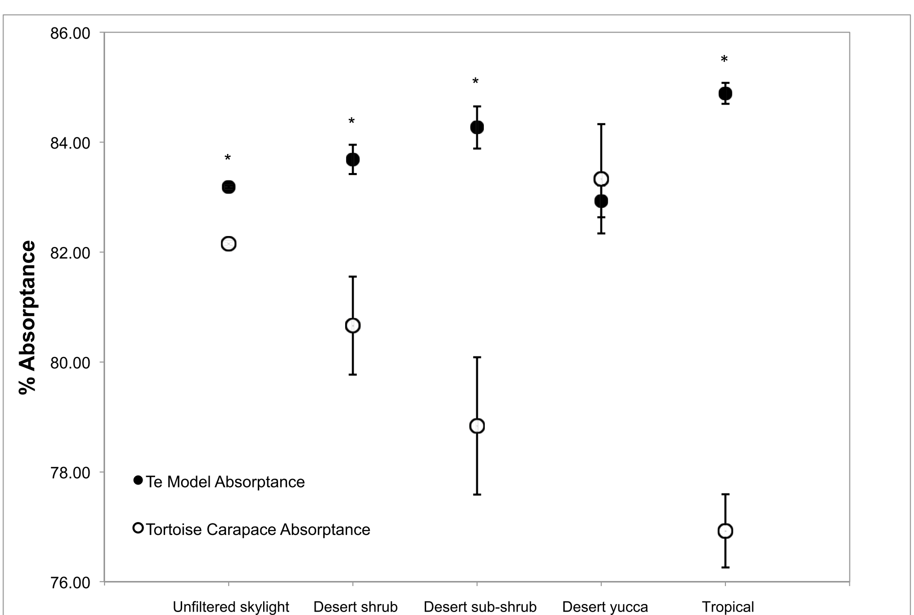


Fig. 4. Mean absorptances for a tortoise (open circles) and a tortoise T_e model (shaded circles) calculated by integrating absorptivity curves of a tortoise carapace and paint with microhabitat spectra. Significant difference in absorptance between tortoise and T_e model within a microhabitat type is indicated with an asterisk ($P < 0.05$). Error bars represent one standard deviation.

Table 3
Minimum, maximum, and mean operative temperatures for a tortoise calculated by integrating unfiltered skylight, tropical *S. podophyllum*, and desert yucca *Y. brevifolia* spectra with tortoise carapace (animal) and paint absorptivity curves. Significant differences within microhabitat are denoted with an asterisk and similar values are grouped by like superscript. Values are ± one standard deviation.

Microhabitat	Absorptance curve	Integrating spectrum	Mean absorptance (%)	Light quantity	Minimum temp (°C)	Maximum temp (°C)	Mean temp (°C)
Unfiltered skylight	Animal	Unfiltered skylight	82.2 ± 0.06	Full	13.3 ± 0.00*[a]	49.3 ± 0.00*[a]	37.4 ± 0.00*[a]
	Paint	Unfiltered skylight	83.2 ± 0.03	Full	13.4 ± 0.00*[b]	49.5 ± 0.00*[b]	37.6 ± 0.00*[a]
S. podophyllum	Animal	*S. podophyllum*	76.4 ± 0.72	Reduced	12.2 ± 0.00	29.3 ± 0.00*[a]	24.7 ± 0.00*[a]
	Animal	Unfiltered skylight	82.2 ± 0.06	Reduced	12.2 ± 0.00	29.4 ± 0.00*[b]	24.7 ± 0.00*[a]
	Paint	*S. podophyllum*	85.0 ± 0.20	Reduced	12.2 ± 0.00	29.5 ± 0.00*[c]	24.5 ± 0.00*[b]
Y. brevifolia	Animal	*Y. brevifolia*	84.0 ± 1.17	Reduced	12.1 ± 0.00	28.8 ± 0.00	24.3 ± 0.00
	Animal	Unfiltered skylight	82.2 ± 0.06	Reduced	12.1 ± 0.00	28.8 ± 0.00	24.3 ± 0.00
	Paint	*Y. brevifolia*	82.7 ± 0.35	Reduced	12.1 ± 0.00	28.8 ± 0.00	24.3 ± 0.00

architecture and leaf size of desert sub-shrubs was intermediate between the desert and tropical canopies as was the quality of transmitted light.

Desert yuccas had dense canopies that restricted virtually all light transmittance, as is the case with other desert succulents (Gates, 1980). Thus, the light detected from the ground below desert yuccas was primarily composed of scattered light reflected from surrounding surfaces, resulting in low and even energy transmittance across the spectrum. The similarities in light filtration observed among species are probably due to a combination of shared characteristics including (1) how leaves absorb, reflect, and transmit radiation for physiological purposes, (2) the ratio of green to non-green plant parts in the canopy, (3) the light scattering properties of canopy structure and architecture, and (4) the degree of canopy closure.

4.2. Animal absorptance

In general, mean absorptance calculations for individual reptile species were similar among all microhabitat types. Calculations for reptile absorptance differed the most between tropical canopies and unfiltered skylight. Gates (1980) calculated a maximum difference in absorptance of 1.9% for reptiles in light of differing quality (low vs. high sun), which is less than the maximum difference found here. Only under dense tropical foliage did calculated absorptances differ from unfiltered skylight by more than 5%.

While statistically significant differences between filtered and unfiltered spectra were detected within species, these differences were often small in magnitude. Measurements in our study were conducted under controlled conditions and yielded very consistent spectra under each microhabitat type. Under more variable field conditions, one would expect more disparity in spectra within microhabitat types, which would likely mask the differences we detected. Additionally, variation in absorptivity within an individual or among individuals of a single reptile species may exceed the differences in mean absorptance that were found between unfiltered and filtered light conditions. For instance, absorptance may range from 65% to 91% at different points on the carapace of *G. agassizii* (Nussear et al., 2000) and dorsal reflectance may change by as much as 27.4% in individual *Pogona vitticeps* due to changes in temperature, circadian patterns, and social interactions (Smith et al., 2016).

It is possible that the differences we observed could be magnified in situations where within-canopy light scattering changes absorptance spectra to a greater degree, such as in forested habitats where canopies are denser and more complexly layered. It is also important to note that only reptile absorptivity curves were considered in this study and the curves used were likely influenced by the reflective properties of the dominant eumelanin pigment found in these animals. Among ectotherms, the skin of amphibian and fish may contain carotenoids and pteridines (Bagnara and Hadley, 1969) and insect exoskeletons are known to have a wide variety of additional pigment types (Shamim et al., 2014), with each pigment displaying different reflective properties. For instance, protoporphyrin and biliverdin pigments found in bird eggs, are more highly reflective in the near infrared region then eumelanin (Bakken et al., 1978) and some frogs exhibit reflective peaks in the near infrared while others do not (Herrerias-Ascue et al., 2016). Therefore, care should be taken when extrapolating these findings to other animal groups. Animals with different pigment types could exhibit a greater disparity in mean absorptance among microhabitat types or between animals and painted models, yielding more substantial errors when modeling operative temperature.

4.3. Desert tortoise case study

Differences in absorptance between a desert tortoise carapace and painted T_e models were greatest under tropical canopies and least under desert yucca canopies. Differences were primarily due to the variability in calculated tortoise carapace absorptance among canopy-filtered microhabitats. This variability did not exist in calculated paint absorptance, as a result of the flatter paint absorptivity curve, and led to the observed discrepancies between tortoise and T_e model absorptance. Operative temperatures were nearly identical when calculated using the tortoise carapace and paint absorptance, even when parameters were set to maximize differences in T_e. This result was especially evident in canopy-filtered microhabitats where there was less radiant energy contributing to T_e. Even if differences in absorptance are great, in microhabitats where little light is transmitted other components of the energy budget become more influential in determining the operative temperature than absorbed radiation. Differences in T_e were smaller than those previously reported for models of dissimilar absorptance in unfiltered skylight, however, the absorptance values compared in this study were also more similar within microhabitats than values compared elsewhere (Bakken and Gates, 1975; Shine and Kearney, 2001).

4.4. Conclusion

Although researchers frequently use operative temperatures to investigate biophysical questions concerning animals in habitats that filter incident light, this is the first study to assess the influence of canopy light filtration on the calculated absorptance of animals or T_e models. We found differences in the quality of light filtered through plant canopies, but these differences had small effects on reptile absorptance and virtually no effect on calculated operative temperatures. Thus, our study supports the common practice of integrating reptile absorptivity curves with unfiltered clear day solar radiation to ascertain a mean reptile absorptance, even when operative temperature is modeled for reptiles in filtered light environments.

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Appendix A. Supplementary data

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