

SOLAR RADIATION THROUGH THE LIVING BODY WALLS OF VERTEBRATES WITH EMPHASIS ON DESERT REPTILES¹

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INTRODUCTION

The possible physiological effects of solar radiant energy have been a topic of discussion among biologists for more than 60 years (Ward, 1892; Hertel, 1905; Laurens, 1933). The injurious effects of intense ultraviolet radiation have been well documented (Rusch, 1941; Roe and Stevens, 1965; Hanawalt, 1966) and "it seems to be generally assumed that internal organs could be damaged if the rays reached them" (Waring, 1963).

My interest was aroused because of repeated observations in the literature about the correlation between diurnality and internal pigmentation and its inferred protection from solar radiation. Black peritoneums were noted in colorless fishes, whereas clear peritoneums were found in dark colored forms (Watkins-Pitchford, 1909). Pigments occur around the central nervous system and/or around the gonads of many diurnal vertebrates but not in their related nocturnal forms (Krüger and Kern, 1924; Hill, 1942). Others have discussed internal pigmentation with special reference to the black melanized peritoneum (Klauber,

1939; Cole, 1941; and Collette, 1960). Collette's ecological study of six species of *Anolis* demonstrated that the degree of peritoneal pigmentation was directly related to the amount of time spent in the sun. Others have demonstrated that sunlight kills developing fish embryos (Leitritz, 1960; Perlmutter, 1961) and unpigmented cave animals (Maguire, 1960).

Experiments designed to determine whether harmful solar radiation could penetrate the body wall were first performed by Bodenheimer, Halperin and Swirski (1953). They measured the transmission of light through the excised skin of a specimen of a lizard species, *Chalcides ocellatus*. Although they tried to compensate for scattered light losses by moving the specimen closer to the detector, they found no ultraviolet transmission. Hunsaker and Johnson (1959), after making a detailed survey of amphibians and lizards possessing black peritoneums, attempted to measure ultraviolet light transmission through excised amphibian and reptilian skin. Unfortunately, most of the wavelengths they used (i.e. 187 through 290 mμ) never reach the surface of the earth due to atmospheric absorption. Their work was also hampered because of the low inherent sensitivity of their detector system (a Geiger counter) at the longer ultra-

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violet wavelengths (Porter, 1966). With one exception they were unable to detect transmitted ultraviolet light. Therefore they proposed that the black peritoneum "could serve in the regulation of body temperature of the animals involved."

Even if these authors had been able to demonstrate that the black peritoneum stops ultraviolet light, there still remains the enigma of lizard genera such as the teiid *Cnemidophorus*, which endure strong radiant environments without a black peritoneum. Thus, at first glance the hypothesis of radiation protection by the black peritoneum appears to be rather hopeless, but the alternative of heat regulation seems equally tenuous, especially when so many aquatic amphibians and fish also possess melanized peritoneums. There would seem to be no way in which these species could benefit from heat absorption by the black peritoneum since any heat they gained would be quickly lost to the water.

My study was begun in an attempt to resolve this puzzle of the black peritoneum. In addition, I wanted to measure light transmission through living tissue and determine whether its being alive affected transmission. I also felt that it would be possible to resolve the question of thermoregulatory function by determining the relative amounts of energy absorbed in the skin, in the muscles, and in the black peritoneum. Finally, I have sought to explain my results in terms of the physics of light scattering theory to determine the physical basis for what I observed.

MATERIALS AND METHODS

EXPERIMENTAL ANIMALS

All animals (except those listed from out of state) were captured from one of two areas in southern California; San Geronio Pass, Riverside county, or near the Kelso road north of Amboy, California, San Bernardino county. Usually the animals were used within a week after capture, but in a few instances almost a month elapsed before they were examined. The reptiles were kept indoors in large (up to 2.6 m by 0.6 m) cages illuminated with floodlamps which operated on a regulated light cycle close to the prevailing daylength. A constant supply of *Tenebrio* larvae, lettuce and water was available to the lizards. Snakes were used within 3 days of capture. All other animals were used within 2 days of capture.

Representatives of 18 species of lizards (55 individuals) and 7 species of snakes (9 individuals) were examined with a Beckman DK-2A dual beam, ratio-recording spectrophotometer used as a reflectance and as a transmittance unit. The lizards included *Callisaurus draconoides*, *Cnemidophorus tigris*, *Coleonyx variegatus*, *Crotaphytus collaris*, *Crotaphytus wislizeni*, *Dipsosaurus dorsalis*, *Eumeces gilberti*, *Petrosaurus mearnsi*, *Phrynosoma platyrhinos*, *Sauromalus obesus*, *Sceloporus jarrovi* (from Arizona), *Sceloporus magister*, *Sceloporus occidentalis*, *Sceloporus olivaceus* (from Texas), *Sceloporus orcutti*, *Uma notata inornata*, *Uma scoparia*, and *Uta stansburiana*. The snakes examined included *Arizona ele-*

gans, *Hypsiglena torquata*, *Masticophis flagellum*, *Phyllorhynchus decurtatus*, *Pituophis catenifer*, *Salvadora hexalepis*, and *Trimorphodon vandenburghi*.

SPECTROPHOTOMETER DESCRIPTION

The principle of dual beam operation in the Beckman DK-2A involves a rapid, alternate sampling by the machine of the reference and sample beams (Fig. 1). The detector output is switched from the reference or sample channel to the opposite one every time the mirror oscillates (15 times a second). The movable slit blades automatically maintain a constant beam energy for any wavelength by letting more or less light through when operating in the transmittance mode.

In the energy mode of operation the blades are manually opened and closed. When low levels of light penetrate the body wall of an animal and the detector is near its threshold of sensitivity, widening the slit increases the incident and transmitted energy. By increasing the transmitted energy, the detector can continue to operate. Although energy mode operation reduces resolution somewhat, it is often possible to measure light penetration through the body wall down to about 100 m μ lower than can be detected in the transmittance mode of operation. The penalty paid for using the energy mode is that the energy incident on the animal is no longer constant across the spectrum. The emission spectrum of the source and the spectral sensitivity of the detector must now be determined to obtain the percentage of incident light that is transmitted. The prism dispersion characteristics must also be more carefully appraised. Finally, the absolute sensitivity of the detector in the shorter wavelengths must be established.

A detailed technical analysis and/or description of the calibration procedure, the energy calculations, repeatability of measurement, spectral reflectance of quartz, MgO deterioration, prism dispersion, stray light, light leaks, deviation from the square law, absolute sensitivity, chart resolution, and chemical changes within the body wall may be found in the appendix of the thesis by Porter (1966).

The wavelength range employed in this study was limited to 290 - 2600 m μ , although the capabilities of the spectrophotometer extend beyond these points. This spectral interval includes approximately 97% of the energy from the sun incident on the surface of the earth (Johnson, 1962). The remainder of the sun's energy is in the infrared since wavelengths shorter than 290 m μ do not reach the surface of the earth due to atmospheric absorption. Longer wavelengths were not included because the marked local fluctuations in atmospheric water vapor, which is heavily absorbent at longer wavelengths, make estimates of spectral energy available highly unreliable.

REFLECTANCE MEASUREMENT

The measurement of reflectance (Fig. 1) involves covering the reference port with a white MgO blank and covering the sample port with the specimen to be

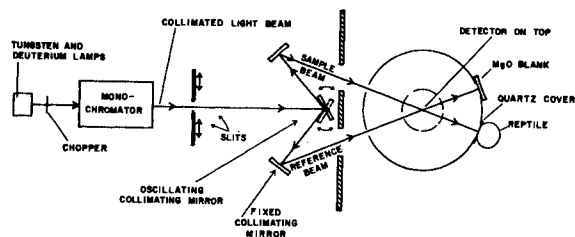


FIG. 1. Schematic top view of the spectroreflectometer. The top half of the integrating sphere has been removed. The MgO blank covers the reference port. The reptile covers the sample port. The light beam is shown entering the wrong side of the monochromator for ease of illustration.

measured. When a translucent specimen is used, it is taped on around the periphery of the sample to permit any transmitted light to escape into the photographic darkroom (Fig. 2B) where the machine is operated. The sample and reference ports are fixed normal to the incident beam so that specular (mirror-like) reflection from the quartz disc covering and flattening an animal is directed back to the monochromator. It was verified experimentally that no specular reflectance reaches the detector.

The detailed preparation of an animal for a reflectance measurement was similar to that described by Norris (1967). A square piece of black plastic electrical tape with a 1 cm² hole in it was placed over the area to be studied. Color control was achieved either by heating the animal nearly to its maximum thermal tolerance (Atsatt, 1939; Cowles and Bogert, 1944; Norris, private communication) to make it blanch and by maintaining the level of heat during the measurement, or by injecting 0.6-0.9 mg ACTH to induce maximal darkening. Maximal darkening in most species occurs approximately one hour after intraperitoneal injection. ACTH continues to affect the color phase for about 24 hours. After flattening the animal against a piece of optical fused quartz (Infrasil I from Englehardt Industries) which was placed over the sample port, a reflectance measurement was made. The quartz was at least 90% transparent to all wavelengths used in this study.

TRANSMISSION MEASUREMENT

The spectroreflectometer was used as a transmittance unit by placing a MgO blank over the sample port and mounting the specimen at the entrance to the sphere in the sample beam (Fig. 2A). The advantage of using a reflectance unit as a transmittance unit for dense, highly scattering materials is that there is no scattered light loss. Figure 2 (top) compares a standard transmittance configuration, which is not designed to measure scattered light, with the hollow MgO-lined integrating sphere of the reflectometer, which is an ideal device for collecting scattered as well as transmitted light. In effect, the latter design greatly increases sensitivity to light which is penetrating dense scattering materials.

Integrating spheres have been used for some time

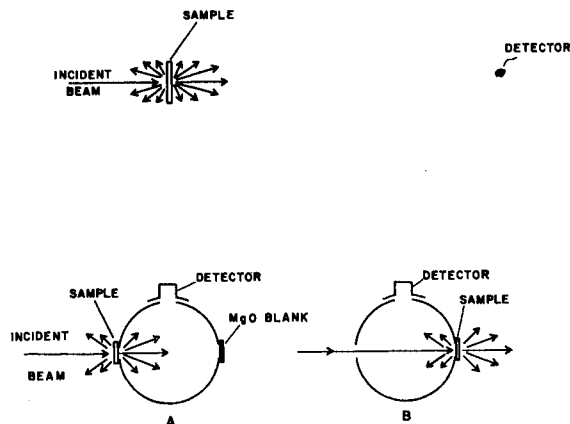


FIG. 2. Comparisons in side view of a standard transmission unit (top) and a reflectance unit (bottom). A, Integrating sphere used as a transmittance unit. B, Integrating sphere used as a reflectance unit. The sample in B is transparent, so its back side is uncovered allowing penetrating light to escape into the darkroom.

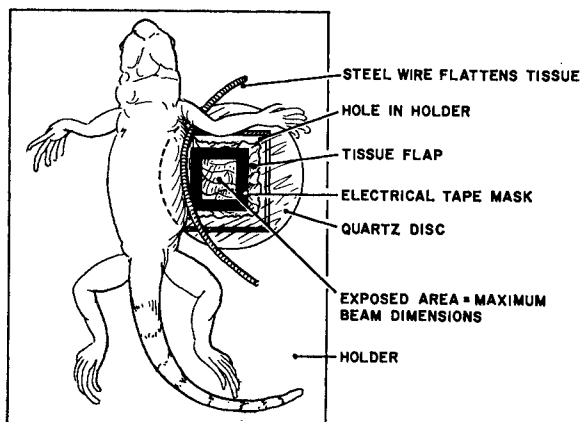


FIG. 3. Anaesthetized animal mounted on holder for transmission measurement through the body wall as seen from outside the sphere looking in. All but the exposed area is fastened and covered with opaque black plastic electrical tape.

for transmission measurements of dense scattering materials, e.g. in the paper industry (Lathrop, 1965), but until very recently (Everett *et al.*, 1966), transmission through biological tissues has not been investigated using integrating spheres.

Preparation for the measurement of light transmission consisted of anaesthetizing the animal (Porter, 1966) and making a ventral U-shaped cut, the precise location of which depended upon whether the dorsal, lateral or ventral body wall was to be tested (Fig. 3). This flap was then flattened on 1.5 mm thick quartz (Infrasil 1). To facilitate handling the animal, the quartz was mounted on a square holder 7.5 cm on a side. The holder was 1.5 mm thick aluminum and was painted black on both sides. An identical assembly, i.e. holder, quartz and mask, was placed over the reference port entrance to eliminate the effects of the

quartz, holder and mask, since the machine compares only the difference between the two beam energies.

LIGHT LEAKS

Any light leaks around the preparation can produce wholly erroneous curves so special pains were taken to be sure that none occurred. After the animal was flattened on the quartz, all exposed areas except the 1 cm² hole in the mask were covered by black plastic electrical tape, which is opaque to any wavelength used in this study. The first of two cheeks for light leaks through the preparation was then performed. The holder with the inside of the body wall toward the observer was interposed between the eye and an incandescent bulb. If there were no light leaks around the flap, the holder with the animal on it was positioned at the entrance to the sphere so that the beam was centered on the 1 cm² hole in the mask. The entire assembly was taped to the sphere and the flap examined from the back through the sphere for light leaks. If no leaks were present, the blank was replaced, all lights were turned off, and the transmission run begun. This procedure was followed for each succeeding run as described below.

SEPARATION OF LAYERS

The process of determining the quantity of energy absorbed by the skin, by the muscles, and by the black peritoneum consisted of measuring transmission through the intact body wall, then peeling each of the above layers from the preparation with a new run at each thickness. After the first transmission run, the animal was removed from the holder, and the black peritoneum was peeled off with forceps. The flap was replaced on the quartz, which had been cleaned and dried, and the animal was taped down for the second run. The removal of the muscle was accomplished by gently separating it from the skin with a sharply pointed probe or fine scissors. The muscle flap was left attached to the body and was folded under the animal while the skin was flattened and taped over the quartz in preparation for the third and last run. By leaving the muscle attached to the body, excessive blood loss was avoided since the major vessels supplying the flap did not have to be severed. Removing the peritoneum and muscles did not alter the reflectance properties of the skin and thus did not change the amount of energy absorbed as the layers were being peeled off. Reflectance measurements of the skin before and after the transmission runs verified that the reflectance was unchanged. The final reflectance run was made with the wet side of the skin backed by quartz which was open to the darkroom as described above for reflectance measurements of translucent materials.

Reflectance measurements of melanin were made on granules obtained from squid (*Loligo opalescens*) ink sacs by squeezing the melanin from them with a probe. The melanin was rinsed several times in distilled water and centrifuged. It was then placed in a desiccator with P₂O₅ and dried for a month. The

granules were packed into a 1 mm deep circular depression in an aluminum blank, and were covered by optical fused quartz. A reflectance measurement was made in the usual way.

GENERAL COMMENTS

If the animal were to be tested for both color phases, the first phase was always light and the second was dark because of the long reversal time to the light phase once the animal had been darkened. Opposite sides of the animal were often used for the two color phases. Since the technique for keeping the animal light under anaesthesia was developed late in this study, all animals illustrated were in the dark phase unless it is stated otherwise.

The living animal preparations proved viable with good blood flow in the flap capillaries for up to 5½ hours, which was the longest time needed to complete both sets of measurements. All heart rates at the end of the experiments were taken by direct observation of the heart contractions.

Thickness measurements of tissues were made with dial calipers. The blades were closed until they indented the tissue slightly. Then they were opened until the calipers could move relatively freely from side to side.

A few transmission measurements of exuvia or shed skin mounted on quartz on the holder were made to estimate the amount of energy absorbed by the keratin overlying the scales, and to compare my results with those of Tereafs (1963). He measured exuvia transmission with a standard transmittance unit and found no transmission at 280 or 270 mμ. My transmission readings, obtained by using the transmittance mode of the spectrophotometer, showed a minimum of 1% transmission at 270 and 280 mμ for 26 specimens representing eight species of lizards and four species of snakes. Thus, if such wavelengths were not absorbed by the atmosphere, they would penetrate the keratinous layer over the epidermis. The difference in results of transmission measurements is undoubtedly due to the use of a standard transmittance unit by Tereafs and the use of an integrating sphere as a transmittance unit by this author. The curves from these measurements were similar in shape to those published by Tereafs. Two of them are incorporated in the results.

The spectral curves in the results have abscissas expanded 10X in the ultraviolet between 350 and 290 mμ. This expansion provides better resolution in these high energy wavelengths (Fig. 5). The curves A, B and C in Fig. 5 drop to just above the zero line at shorter wavelengths and extend horizontally. Actual transmission as determined by the energy mode of operation decreases rapidly from 350 to 290 mμ, but since the transmission is less than 1%, for clarity, the curve is represented by a horizontal line just above the zero line. The actual transmission values are listed in Table 3. Examples of curves obtained by the energy mode occur in figures 19 and 24.

MICROTECHNIQUE

To examine the components of the body wall in detail and to obtain accurate measurements of the thickness of the black peritoneum and of the size of melanin granules, four animals of two species, *Uta stansburiana* and *Cnemidophorus tigris*, were prepared for examination under the light and electron microscope. Their color phases were established according to the procedures outlined above, then they were anaesthetized. Those that were to be used for both the light and electron microscope were opened in the manner described for transmission measurements. The tissue flap was flooded on all sides with isotonic buffered OsO_4 for 15 minutes. The tissue was removed from the animal, immersed in fixative for four hours at 3°C , rinsed four times in frog Ringer's, and dehydrated with ethyl alcohol. The tissues were then embedded in the ethoxyline polymer, EPON, and sectioned. The remainder of the animal was preserved in 10% formalin, decalcified, and embedded in paraffin. After sectioning, alternate slides were stained with Mallory stain with fast green and the rest with hematoxylin and eosin. For those animals examined only under the light microscope, the same procedure was followed except for the opening and flooding with isotonic buffered OsO_4 .

RESULTS

LIZARDS WITH BLACK PERITONEUMS
BODY WALL DESCRIPTION

Under the light microscope a brief examination of a cross section of a whole side-blotched lizard, *Uta stansburiana*, (Fig. 4), a small lizard with a black peritoneum, indicates that the relative thicknesses of the skin, the dorsal musculature, and the black peritoneum are 0.1 mm, 0.3 to 1.2 mm, and 0.01 mm respectively. The melanin concentration in the peritoneum in this species as well as in other lizards possessing black peritoneums varies in different parts of the body cavity. The peritoneum in the pleural cavity is much more lightly pigmented than it is in the peritoneal cavity. In the larger species which possess thick dorsal musculature, pigment concentration is reduced in the peritoneal cavity under the vertebrae and immediately in front of the hind legs on the ventral side of the body.

Melanin may also occur between muscle blocks, around blood vessels at the juncture of these blocks (Fig. 4), and on the dorsal surface of the musculature. These melanin deposits are especially prominent in small species, e.g. *Uta*, and in the young of large species, e.g. *Sauromalus obesus*, the chuckwalla. Melanin, then, is found in all parts of the body wall: in the skin, in the muscles, and in the black peritoneum.

TRANSMISSION MEASUREMENTS

The distribution of melanin in varying concentrations throughout the body wall can have profound effects upon the absorption of energy by different parts of the body wall. Heavy deposition of melanin

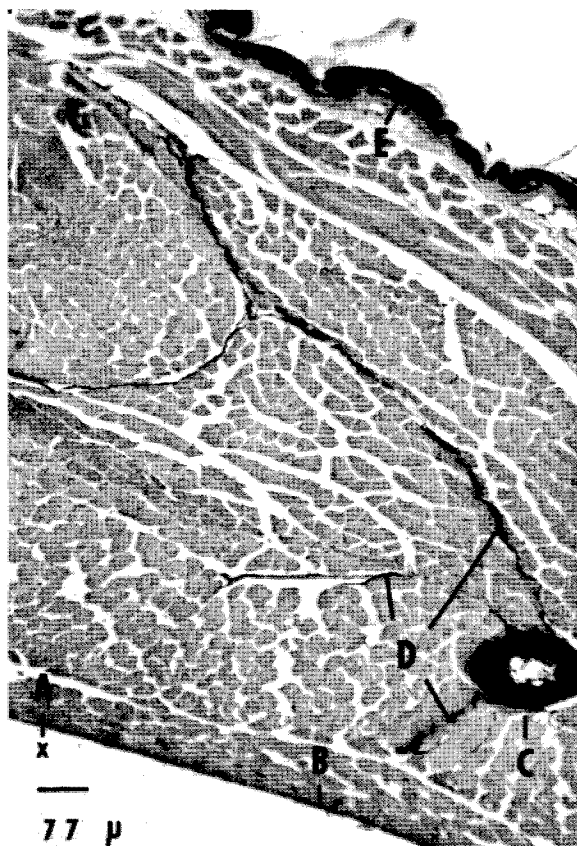


FIG. 4. Cross section through the dorsal body wall of *Uta stansburiana*. A. Pleural cavity B. Lightly pigmented peritoneum C. Blood vessel D. Intermuscular melanin deposits E. Scales.

in the muscles can compensate greatly for a thin body wall in smaller animals although it does not completely exclude shorter wavelengths. More light penetrates the body wall of *Uta stansburiana*, the smallest conspicuous diurnal lizard in southern California, than might have been suspected from earlier work (Bachem and Reed, 1931; Edwards, 1951; Hardy, 1956; Hunsaker and Johnson, 1959).

The lowest curve, A, (Fig. 5) demonstrates that transmission through the entire body wall occurs primarily in the infrared (700 μm to 2600 μm). Much more visible light penetrates the body wall in the red (longer wavelengths) than in the blue. Wavelengths shorter than about 350 μm are not detectable in the body cavity with the spectrophotometer, but even so, almost half of the ultraviolet portion of the spectrum incident on the earth's surface (350 - 400 μm) penetrates the entire body wall of this species. When the black peritoneum is removed, the increased transmission, indicated by curve B, occurs throughout the entire incident solar spectrum. Perhaps most significant is the increase in visible and ultraviolet light transmission when the black peritoneum is removed. Without a black peritoneum, almost all the ultraviolet wavelengths penetrating the atmosphere would also penetrate this reptile's body wall.

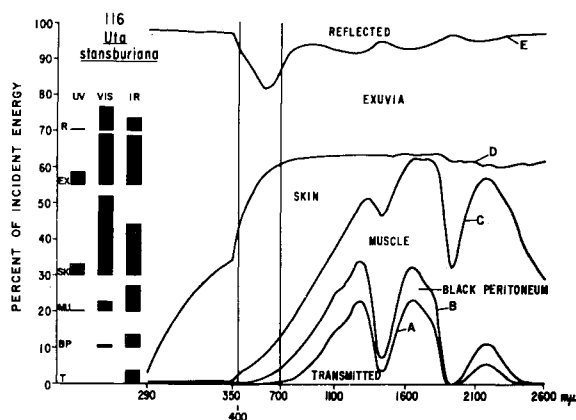


FIG. 5. Spectrophotometric measurements of anaesthetized *Uta stansburiana*. A. Transmission through intact body wall. B. Transmission without black peritoneum. C. Transmission without the body wall musculature (i.e. skin only) D. Transmission of shed skin ("exuvia") E. Reflectance measurement. This curve and all subsequent reflectances where the ordinate is labelled "Percent of incident energy" are upside down and are read from the top down. The words "REFLECTED", "EXUVIA", etc., occupy the areas representing the portions of solar energy reflected, transmitted, or absorbed by the parts of the body wall. The bar graphs represent percentages of solar energy in each category, e.g. reflected energy = "R". The bar values may be read from the ordinate numbers.

The area labelled "Black peritoneum" between the two curves represents the energy absorbed by the black peritoneum. "Muscle," "Skin," and "Exuvia" occupy areas representing the energy absorbed by the respective parts of the body wall. "Transmitted" occupies the area representing light transmitted through the intact body wall and "Reflected" occupies the area representing the reflected energy.

Curve C is the skin transmission and curve E is the reflectance of the animal. The reflectance curve is turned upside down and read from the top down. Plotting this way allows one to instantly assess the percent distribution of solar radiation in the body wall at any wavelength. For example, starting from the top at 700 mμ the percent reflected is 13%, the exuvia absorbs 27%, the skin absorbs 46%, the muscles absorb 10%, the black peritoneum absorbs 3% and 1% is transmitted.

Curve D, a transmission measurement of shed skin or "exuvia," has been superimposed over the area of the chart representing the amount of energy absorbed by the skin (the area between curve E and curve C). Since the thickness and therefore the absorption of the keratin overlying the living epidermis varies with the stage in the sloughing cycle (Maderson, 1965a, 1965b), insertion of a transmission measurement of the keratinous shed skin is an approximation of the energy absorbed by keratin.

The amount of energy in cal cm⁻² min⁻¹ absorbed by the black peritoneum (as well as by the other parts of the body wall) can be calculated since the area be-

tween the lowest curve (A = transmission with the peritoneum intact) and the next highest one (B = transmission with the peritoneum removed) is proportional to the energy absorbed.

The calculation of absorbed energy by each part of the body wall depends upon the basic radiation equation which states that the incident radiation must be equal to the reflected plus transmitted plus absorbed radiation.

$$100\% = \% \text{ reflected} + \% \text{ transmitted} + \% \text{ absorbed} \\ (\text{or})$$

$$1 = R + T + A \quad (\text{Gates, 1962; Birkebak, 1966})$$

If the percent reflected is constant, a change in transmitted energy must result in an equal and opposite change in absorbed energy. Skin reflectance does not change when the black peritoneum or the body wall muscles are removed in part because neither the peritoneum nor the muscles contribute greatly to skin reflectance by their own low reflectances as demonstrated below. Thus as each layer of the body wall is removed, the increase in transmitted light is equivalent to that which was absorbed by the now absent layer.

The percent energy calculations, made for an animal at sea level, were based on the values and assumptions of Norris (1967). The results of such calculations show that the black peritoneum absorbs 4.1% of the total solar energy incident on the animal. If the total energy from the sun and sky incident at sea level at noon on the lizard is 1.635 cal cm⁻² min⁻¹, the energy absorbed by the black peritoneum is 0.0669 cal cm⁻² min⁻¹. Of this 3.6% is infrared, 0.5% is visible, and 0.016% is ultraviolet. Thus, in terms of the total heat available, the energy absorbed by the black peritoneum is small. The muscle absorbs much more, 10% (0.1627 cal cm⁻² min⁻¹) and the skin with its superficial layer of keratin absorbs 71.5% (1.1697 cal cm⁻² min⁻¹) of the total radiation incident on the animal (assuming the tissue is normal to the sun (Norris, 1967)). The values for reflected and transmitted light are 10.5% (0.1716 cal cm⁻² min⁻¹) and 3.8% (0.0625 cal cm⁻² min⁻¹).

Unfortunately, although the energies in the visible and infrared are nearly equal, visual inspection of the curves gives the impression that the infrared contains the greatest amount of energy because of its greater area. This is an artifact due to the use of wavelength rather than frequency or wavenumber units on the abscissa (Gates, 1962, p. 48). To provide a precise visual impression of the distribution of solar energy in the body wall, bar graphs representing energies reflected, transmitted and absorbed by each part of the body wall are present in some illustrations, e.g. Fig. 5. The absorbed energy (read horizontally) is represented by the bars "EX," "SK," "MU," and "BP" and represent the percentage of solar energy absorbed by the exuvia, skin, muscles, and black peritoneum respectively. The "T" bar represents transmitted energy, the "R" bars, reflected energy. The total energy reflected may be determined by adding the three bars in the "R" row. The bars

TABLE 1. Comparisons of diurnal lizards with black peritoneums (percent of incident energy) R = reflected; T = transmitted; Ex, Sk, Mu, BP = energy absorbed by the exuvia (shed skin), the skin, the muscles, and the black peritoneum respectively.

	No. of samples	R	Ex	Sk	Mu	BP	T
<i>Callisaurus draconoides</i> adult=a	2	12.2-13.3	—	63.2-68.9	15.2-15.7	0.7-2.2	3.1-5.7
<i>Callisaurus draconoides</i> hatchling=h	1	10.6	—	67.6	15.9	1.4	4.5
<i>Crotaphytus collaris</i> a	1	10.6	—	68.6	10.7	3.9	6.1
<i>Crotaphytus wislizeni</i> a	2	14.5-25.3	—	49.3-56.0	8.6-9.5	7.0-7.6	9.0-12.0
<i>Dipsosaurus dorsalis</i> a	1	33.6	—	41.2	9.5	11.5	5.0
<i>Dipsosaurus dorsalis</i> juvenile=j	1	16.8	—	56.9	8.5	8.2	9.6
<i>Dipsosaurus dorsalis</i> h	1	20.1	—	54.3	9.1	8.4	8.2
<i>Petrosaurus mearnsi</i> ventral dark a	1	29.5	—	38.9	17.0	5.5	9.3
<i>Phrynosoma platyrhinos</i> a	3	15.0-24.5	—	64.1-67.2	6.0-8.6	1.3-5.3	1.7-7.1
<i>Sauromalus obesus</i> j	1	11.6	—	71.5	7.3	3.0	6.9
<i>Sceloporus magister</i> dorsal dark a	4	7.1-14.2	—	71.1-81.0	2.8-8.1	2.8-4.5	3.1-5.6
<i>Sceloporus magister</i> dorsal light a	3	14.1-22.1	—	64.1-69.0	6.0-8.7	1.3-6.7	1.7-3.4
<i>Sceloporus occidentalis</i> a	2	4.2-9.0	—	75.0-83.2	7.2-7.8	1.5-3.5	4.1-4.6
<i>Sceloporus olivaceus</i> ventral light a	1	17.1	—	66.3	4.9	5.6	5.8
<i>Sceloporus olivaceus</i> dorsal dark a	3	7.3-14.8	—	70.4-76.8	5.9-6.5	2.9-5.6	4.4-5.3
<i>Sceloporus olivaceus</i> dorsal light a	1	13.0	—	62.5	9.8	11.7	2.7
<i>Sceloporus orcutti</i> a	1	12.1	—	64.6	12.7	4.6	5.9
<i>Uma notata inornata</i> h	1	14.8	—	61.3	16.9	2.9	4.1
<i>Uma scoparia</i> a	2	16.1-16.8	—	56.2-57.8	18.6-20.0	2.8-6.1	2.7-3.0
<i>Uma scoparia</i> j	1	17.7	—	54.2	17.3	6.6	4.0
<i>Uta stansburiana</i> dorsal light a	1	10.3	31.3	39.0	9.9	4.1	3.8
<i>Uta stansburiana</i> dorsal light a	1	6.8	—	84.3	3.5	2.4	3.1

(read vertically) under "UV," "VIS," and "IR" represent the respective percentages of ultraviolet, visible

and infrared light which is reflected, absorbed or transmitted. The bar values may be determined by subtracting the ordinate percentage value at the top of each bar from the ordinate value at the bottom of each bar. In the ultraviolet column, most ultraviolet light is absorbed in the exuvia and the skin and little is reflected. The infrared column, on the other hand, shows a much more even distribution of energy reflected, absorbed, and transmitted. The calculated values are in Table 1.

TABLE 1. (continued)

<i>Uta stansburiana</i> dorsal dark a	1	8.9	—	70.3	9.3	4.7	6.7
<i>Uta stansburiana</i> j	1	5.8	—	78.7	7.5	3.3	4.7
Total range		4.2-33.6		38.9-84.3	2.8-20.0	0.7-11.7	1.7-12.0
Transmission changes in the same piece of tissue with color change							
<i>Crotaphytus wislizeni</i> dorsal light skin a	1	25.8		41.5			32.7
dorsal dark skin	1	17.1		61.5			21.5
<i>Sceloporus occidentalis</i> (body wall without peritoneum)							
dorsal light a	1	9.1		83.9			7.0
dorsal dark	1	5.8		83.2			5.9

TABLE 2. Comparisons of lizards without black peritoneums (percent of incident energy) R = reflected; T = transmitted; Ex, Sk, Mu, BP = energy absorbed by the exuvia (shed skin), the skin, the muscles, and the black peritoneum respectively.

Diurnal Lizards	No. of samples	R	Ex	Sk	Mu	T
<i>Cnemidophorus tigris</i> dorsal a	2	15.3-18.9	15.3-19.1	53.1-55.6	6.2-6.7	4.0-5.7
<i>Cnemidophorus tigris</i> skin ripped; absorption value for the total body wall (dorsal) a	1	13.3		84.8		1.9
<i>Cnemidophorus tigris</i> ventral a	1	22.3		63.2	3.9	10.5
<i>Eumeces gilberti</i> dorsal a	2	10.6-17.0		74.0-80.7	5.6-6.0	2.0-3.1
<i>Eumeces gilberti</i> ventral a	1	28.4		60.4	5.3	6.0
Nocturnal Lizards						
<i>Coleonyx variegatus</i> dorsal a	3	15.0-18.2		28.1-39.1	13.9-18.9	25.4-43.0

Dorsal vs ventral transmission

Since the body wall of lizards is thinner ventrally than it is dorsally, it is important to determine whether more light can penetrate ventrally. Transmission measurements comparing the dorsal and ventral transparencies of Gilbert's skink, *Eumeces gilberti*, a lizard without a black peritoneum, showed a dorsal body wall transmission of 2.3% of the total incident energy

(minimum detectable wavelength = 725 $m\mu$), but a ventral transmission of 6% (Table 2) (minimum detectable wavelength = 600 $m\mu$). Ventral transmission measurements on the California rock lizard, *Petrosaurus mearnsi*, a lizard with a black peritoneum, indicated 9.3% of the total incident energy reaches the body cavity (minimum detectable wavelength = 600 $m\mu$). No dorsal transmission measurements were made on this animal. All of these measurements were made by using the less sensitive transmittance mode. Energy mode operation would probably reveal penetration of light to about 100 $m\mu$ lower. The ventral reflectances of all these diurnal lizards which have been measured are higher than dorsal reflectances (Table 2). These results confirm those of Norris (1958), Hutchinson and Larimer (1960) and Norris and Lowe (1964). The higher ventral reflectances reduce the amount of energy left for absorption and transmission, which partly compensates for the thinner body wall. Another condition reducing ventrally transmitted light is that the ventral body wall is normally exposed to lower light intensities than the back because of its frequent proximity to or contact with the substrate.

Intraspecific differences (same age)

To interpret any differences between the transmitted spectra of individuals of dissimilar species, an estimate of the variation within a species was requisite. One such comparison of a species with a black peritoneum, the desert spiny lizard, *Sceloporus magister*, (Fig. 6) shows (Table 1) that the reflectance values

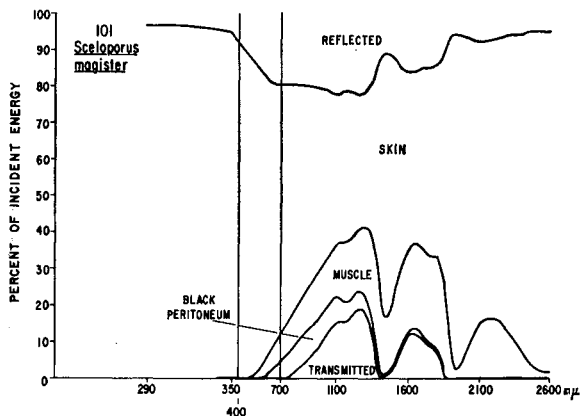
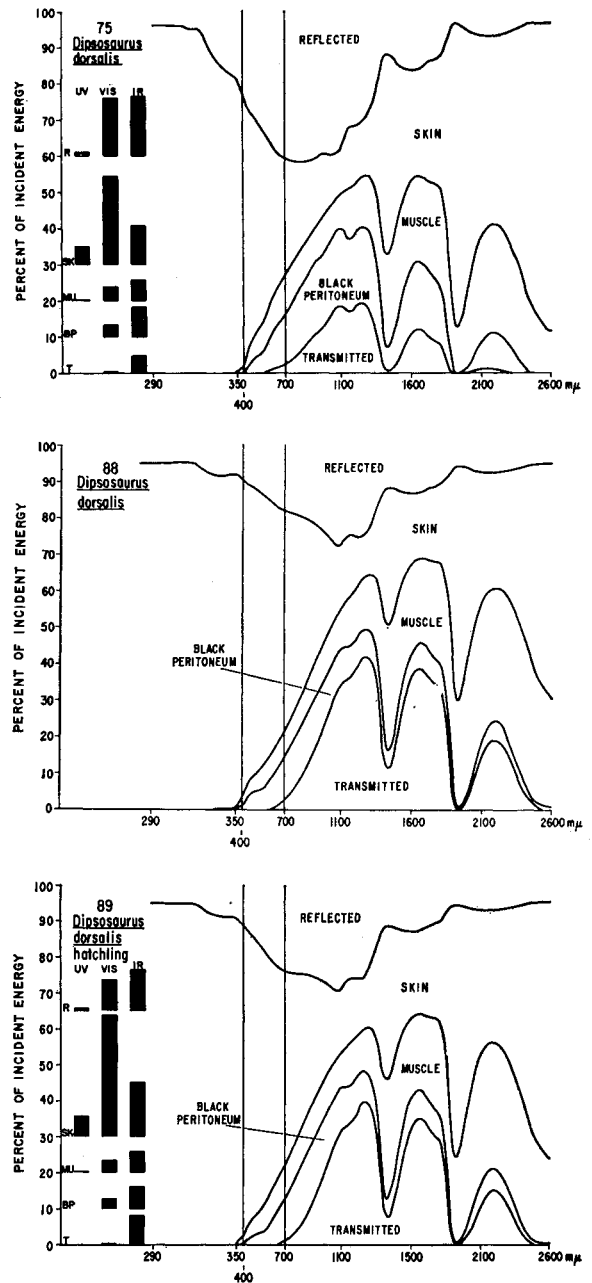


FIG. 6. Spectrophotometric measurements of *Sceloporus magister* in the dark phase.

vary about 7% in each of the two color phases; skin absorption values may vary 10%, muscle values up to 5%, and other values about 2%.

Ontogenetic changes

As mentioned above, a thinner body wall theoretically means less light is absorbed because the absorbing path length, i.e. the body wall thickness, is less. Does the transmission of light to the body cavity change in the transition from a hatchling with a thin



FIGS. 7, 8, 9. Comparisons of an adult (no. 75), juvenile (no. 88), and hatchling (no. 89) crested lizards, *Dipsosaurus dorsalis* showing the marked difference in reflectance and transmission between an adult and immature animals.

body wall to an adult lizard with a thicker body wall? Figures 7, 8, 9 and Table 1 reveal that there are no marked differences between the amounts of ultraviolet and visible light reaching the body cavity in adults and young of the crested lizard, *Dipsosaurus dorsalis*. Infrared penetration, on the other hand, varies considerably, presumably because of the differences in muscle thickness. The young apparently exclude ultraviolet and visible light by heavier deposits of

melanin in the skin and by melanin deposits between the muscle blocks in the dorsal musculature. A young crested lizard (Table 1 and Fig. 9) was considerably darker than adults in the same dark phase. This reflectance difference is apparently due to differences in the amount of melanin in the skin. The spectral characteristics of a young crested lizard are reminiscent of those of a specimen of *Uta stansburiana* or *Sceloporus* sp., especially with respect to the lower skin reflectances and higher skin absorptions. Specimens of the young of two other basking, high temperature species, the zebra-tailed lizard, *Callisaurus draconoides*, and the Mojave sand lizard, *Uma scoparia*, do not seem to follow the ontogenetic pattern of *Dipsosaurus*, but rather have spectral properties quite similar to the adults. Figures 10 and 11 are com-

of *Dipsosaurus* adults and hatchlings respectively. If exclusion of most visible and ultraviolet light from the body cavity is mandatory, a thin muscle thickness must be compensated for by an increase in pigment concentration in the skin and/or elsewhere to maintain similar transmission spectra through the body wall. This seems to be the case in *Dipsosaurus*, whose dorsal body wall thickness increases greatly during development and whose skin absorbs less, but reflects and transmits more. In the other two species, on the other hand, there is less change in body wall thickness and little change in skin reflectance and absorption in ontogeny. The implications of this for thermoregulatory behavior are discussed by Norris (1967).

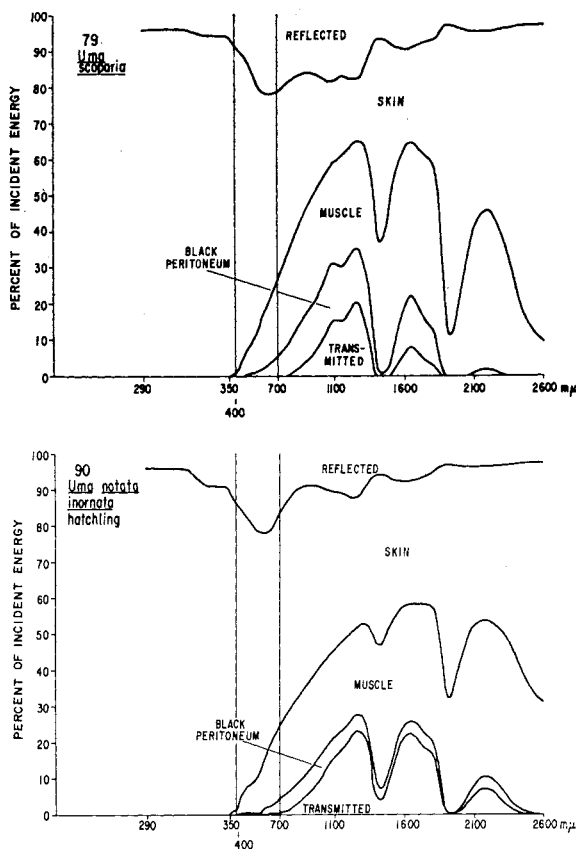
In summary, the crested lizard becomes more highly reflective and loses some of its darkening capability as it matures. In two smaller species preferring high temperatures, there is no marked spectral difference between the adult and young in the dark color phase, although the adult may be capable of brightening more than the young. In all cases the amount of light reaching the body cavity is low in the dark phase. Low light levels are maintained in the light phase in the adult and are probably also maintained in the light phase of the young since its color change capability is less than the adults (Norris, 1967).

Effect of color change

As a lizard becomes more reflective, the melanin granules in the melanophores aggregate. Since only lizards with black peritoneums seem capable of a marked color change, the black peritoneum might be important in absorbing extra light that would penetrate the body wall when the animal blanchd as the radiative heat load increased during the day. To determine whether more light penetrates the skin after blanching, representatives of three species, the western fence lizard, *Sceloporus occidentalis*, the desert crested lizard, *Dipsosaurus dorsalis*, and the leopard lizard, *Crotaphytus wislizeni*, were examined for changes in transmission with change in color.

The first of these experiments involved a leopard lizard, a carnivorous desert animal capable of enduring rather high temperatures and possessing a pronounced color change capability. To test reflectance and transmission measurements were made in the light and dark phases, the same procedure as outlined in Materials and Methods was followed except that in this experiment only the skin was cut on three sides and simultaneously separated from the dorsal musculature, with the side of the skin toward the vertebral column left intact. A 1 cm² mask was used as before and skin reflectance and transmission measurements were made in the light phase. During the color change to the dark phase the skin was laid flat against the musculature in its normal position. Measurements of this same piece of skin indicate marked changes in reflectance and transmission for this species (Table 1).

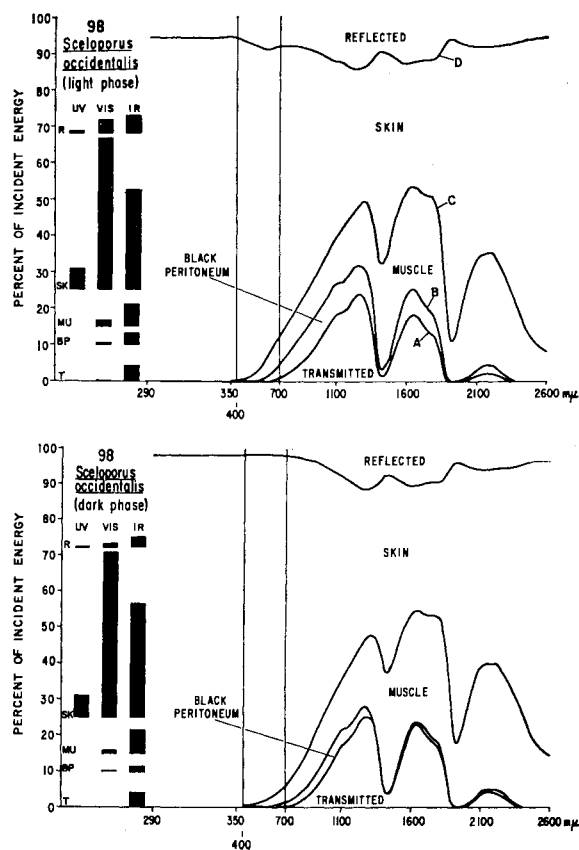
Sceloporus occidentalis was used to test whole body wall transmission changes. Light color phase measurements were made on one side of the vertebral



FIGS. 10 & 11. Comparisons of an adult and hatchling sand lizard from closely related species.

parisons of an adult *Uma scoparia* and a hatchling *Uma notata inornata*. These two species are so very similar in appearance and so closely related (Norris, 1958) that it was felt such a comparison was justified.

The explanation for these contrasting patterns may lie in the notable changes in body wall thickness in the ontogeny of *Dipsosaurus*. On the other hand, the differences in the body wall of adult vs young *Callisaurus* and *Uma* are not nearly as pronounced (1.1 mm vs 0.7 mm and 1.3 mm vs 0.7 mm) as the differences in body wall thicknesses (2.1 mm vs 0.7 mm)



FIGS. 12 & 13. Comparisons of reflectance and transmission in the light and dark color phase (same animal—opposite sides). The depression of the reflectance curve (higher reflectance) in the visible in the light phase is absent in the dark phase. The amount of energy absorbed by the black peritoneum in the dark phase is less than in the light phase.

column and dark phase measurements on the opposite side in the same position. The results of these measurements on *Sceloporus occidentalis* (Figs. 12 & 13 and Table 1) show that more light is reflected and less is absorbed by the skin in the light phase. Also, more light is absorbed in the muscles and by the black peritoneum in the light phase than in the dark phase. While the differences in the amount reflected and absorbed by the skin are significant in this animal, the differences in the amount absorbed by the muscle and the black peritoneum are not very great because of low transmission levels through the skin. Without data on the difference in transmission of the two body halves, no unequivocal conclusions could be drawn. Accordingly, transmission measurements were made through the same location on the body wall in the light and dark color phases of a specimen of *Sceloporus occidentalis*. The results of the experiment (Table 1, part 2) show a 3.3% reflectance change, a 4.3% change in skin absorption and a 1.1% change in transmission with the black peritoneum absent.

These experiments establish that more light penetrates the skin when the animal lightens during the

heat of the day. Most of this light is subsequently absorbed by the muscles and by the black peritoneum. The change in skin transmission and the variation of energy absorbed by the muscles and the black peritoneum are greater in lizards with greater color lability.

Reflectance changes during transmission measurements

To insure that skin reflectance and transmission were not changing during transmission measurements after the black peritoneum and the muscles had been removed, a specimen of the granite spiny lizard (*Sceloporus orcutti*) was subjected to the usual transmission procedure except that repeated reflectance instead of transmission measurements were made after each layer separation. Instead of the back side of the holder facing the inside of the integrating sphere as for a transmission measurement, the back side opened into the darkroom (Fig. 2B). Any transmitted light could thus escape into the room and would not be reflected back through the tissues into the integrating sphere. The results of this experiment showed no reflectance change even with the muscles removed.

Interspecific differences in lizards with black peritoneums

The variation of reflectance and skin absorption within a species is sufficiently broad so that when the results from the 13 species of lizards with black peritoneums are viewed together, they overlap into almost a continuum of reflectance or absorption values. Adult crested lizards (*Dipsosaurus dorsalis*) stand out from the others because of their very high reflectances. Figure 7 illustrates the spectral properties of an adult male crested lizard in the dark phase. The percentage breakdown is in Table 1. Crested lizards remain out in the hot summer days in the desert after almost every other animal has retreated. They have been recorded in the field as having body temperatures of 46.4°C (Norris, 1953), the highest of any vertebrate. The highest reflectance values and the lowest skin absorption values (except for the ventral skin of a California rock lizard) indicate a very low concentration of skin melanin. This is supported by microscopic studies I have made. Otherwise, no clear-cut distinction can be made between the spectral characteristics of one species and those of another.

The total range of values for each of the categories of reflected, transmitted, and absorbed energies and the range for each individual species are in Table 1. The total range of reflectance values tends to be represented in the lower values by *Sceloporus* sp., or similar dark species, and in the highest reflectance values, by *Dipsosaurus* and its high temperature allies. The lower energies absorbed by the skin are represented by *Dipsosaurus*-types and the highest values, by the *Sceloporus*-types. If low amounts of energy are absorbed by the skin, higher amounts of energy are absorbed by the muscles and the black peritoneum. Often more light reaches the body cavity, too. These are only trends and are partially violated

by certain individuals. The young of all the species tend to be similar to the *Sceloporus*-types as mentioned above. The total variation in the amount of energy transmitted to the body cavity (2.7% - 12.0%) may be misleading because most of the variation is due to differences in the amount of infrared transmitted to the body cavity (2.7% - 11.5%). The variation in the amount of visible light entering the body cavity was 0.5% or less. The consistent lack of transmission in the ultraviolet and visible parts of the spectrum by diurnal lizards is remarkable. The greater scope of variation of infrared transmission intra- and interspecifically is apparently due primarily to variations in the thickness of dorsal musculature as will be explained below.

The skin is manifestly the greatest absorber of energy, followed by the muscles and the black peritoneum. This evidence, taken with the presence of black peritoneum in aquatic amphibians and fishes—organisms which seem unlikely to benefit thermally from radiation absorbed by such a structure—argues strongly against a significant role for the black peritoneum in thermo regulation of ectotherms as has been suggested by some authors.

LIZARDS WITHOUT BLACK PERITONEUMS

The black peritoneum has been shown to be a radiation shield, but certain diurnal lizards do not possess a black peritoneum; for example, the whiptail lizard, *Cnemidophorus tigris*. These are among the last animals to retreat during the heat of the day, and are thus exposed to more rigorous conditions than some species with a black peritoneum, such as *Uta*. However, if one examines a whiptail lizard carefully, the animal is found to possess a melanin shield. Instead of occurring in the peritoneum, the heavy melanin deposit is in the skin, not in the lining of the body cavity. Figure 14 is a photograph comparing

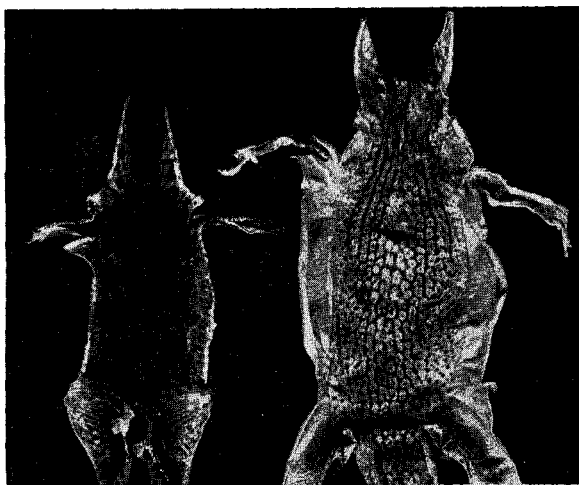


FIG. 14. Ventral surface of the skin from the back of a specimen of the Mojave sand lizard (*Uma scoparia*), a sand dune animal with a black peritoneum (right), and the ventral surface of the skin from the back of a specimen of *Cnemidophorus tigris*, the western whiptail, an animal without a black peritoneum.

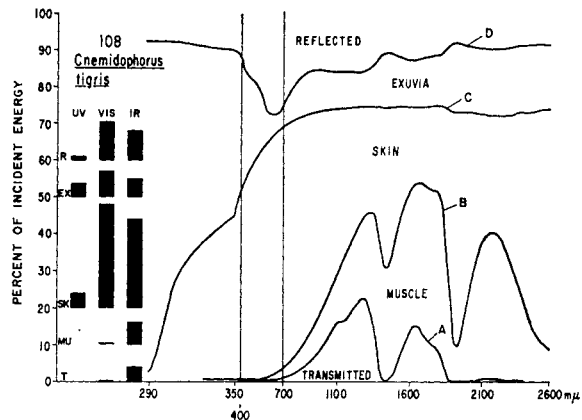


FIG. 15. Spectrophotometric analysis of *Cnemidophorus tigris*. A. Transmission through the whole body wall. B. Skin transmission. C. Transmission through the shed skin. D. Reflectance.

the ventral surface of the skin from the back of a specimen of the Mojave sand lizard (*Uma scoparia*), a sand dune animal with a black peritoneum (right), and a specimen of *Cnemidophorus tigris*, the western whiptail, an animal without a black peritoneum which frequents sandy, gravelly open flats (left). The difference in skin pigmentation is obvious. Figure 15 demonstrates that the total transmission spectrum of *C. tigris* is virtually identical with that of an animal with a black peritoneum. No wavelengths shorter than 400 μ could be measured coming through the body wall. Actually more light came through *Uta*, a species with a black peritoneum but with thinner dorsal musculature (Table 3). Transmission spectra from three other individuals of *C. tigris* and from three specimens of *Eumeces gilberti*, a skink without a black peritoneum but with heavy skin melanization, confirm that a heavy immobile melanin deposit in the skin can be just as effective as a black peritoneum in excluding short wavelengths of visible and ultraviolet light. It should be emphasized that the exclusion of visible and ultraviolet light is the total effect of absorption by all parts of the body wall, not just by the black peritoneum.

Thus, the body wall transmission spectrum for all diurnal lizards tested, with or without black peritoneums, is remarkably constant in the ultraviolet and visible portions of the spectrum. Infrared transmission varied considerably intra- and interspecifically apparently due to variations in muscle thickness. The black peritoneum in diurnal animals is one component of a variable light absorbing system, the body wall, whose total effect on light penetration to the body cavity is the exclusion of measurable ultraviolet light and the virtual exclusion of visible light.

DIURNAL SNAKES

Some diurnal snakes present a unique problem, for they possess black peritoneums only in the posterior half of the body. Three species of desert snakes

TABLE 3. Comparisons of short wavelength ultraviolet transmission.

Operating mode: energy
Slit width: 2.0 mm
Photomultiplier: 20X

Calculation procedure:

$$A \times B = C;$$

$$C/D = E;$$

$$E \times F = G$$

B = A stable reference voltage against which the output voltage from the detector is compared to obtain vertical pen movement in the energy mode; Equivalent to 86×10^{-2} ergs per second at 20X for 1% transmission

C = Source energy (ergs/sec) reaching the body cavity

D = Source energy (ergs/sec) available at operating slit width (for available source energies the machine used in this study, see Porter, 1966)

F = Sun energy available at noon, midsummer (Luckiesh, 1946)

No. 116 *Uta stansburiana* (no peritoneum)
(shortest detectable wavelength with peritoneum = 350 mμ)

Wavelength in mμ	A = percent transmission reading	E = corrected (true) percent transmission	G = sun's energy reaching the body cavity in ergs per cm ² per second
350.....	8.3	8.15×10^{-2}	2.037
340.....	7.5	7.57×10^{-2}	1.764
330.....	6.2	6.44×10^{-2}	1.314
320.....	4.3	4.72×10^{-2}	0.590
310.....	2.2	2.65×10^{-2}	0.126

No. 98 <i>Sceloporus occidentalis</i> (light) (no peritoneum)		No. 117 <i>Dipsosaurus dorsalis</i> (no peritoneum)		No. 108 <i>Cnemidophorus tigris</i> (skin only)	
Wavelength in mμ	G	Wavelength in mμ	G	Wavelength in mμ	G
400	8.010	350	4.909	360	1.223
390	6.943	340	4.233	350	0.172
380	7.334	330	2.331	340	0.118
370	6.933	320	0.686		
360	5.436	310	0.029		
350	0.245				
340	0.071				

(shortest detectable wavelength with peritoneum = 390 mμ)

(shortest detectable wavelength with peritoneum = 350 mμ)

that expose themselves to great amounts of solar radiation are the western patch-nosed snake (*Salvadora hexalepis*), the common whipsnake (the red racer) (*Masticophis flagellum*), and the gopher snake (*Pituophis catenifer*). The peritoneum is lightly flecked with fixed melanophores in the middle of the body of all three species, but the density of pigment increases systematically toward the tail. The thickness of the dorsal musculature, on the other hand, is greater in the middle of the body and much less in the tail. One would predict that the transmission spectra should be almost identical in the middle and in the tail, because one light absorbing system (the muscles) is thinner in the tail and therefore absorbs less, while another light absorbing system (the black peritoneum) is denser, thereby absorbing more light. Figure 16 reveals that transmission curves of the patch-nosed snake for the middle and posterior parts of the body can be almost superimposed. Slightly more infrared penetrates posteriorly, no doubt due to the decreased muscle thickness with its high water mass and resul-

tant high infrared absorbing capability (Fig. 17). Just how precisely the transmission curves match in the visible spectrum for different parts of the body wall of snakes has been determined for the red racer, *Masticophis flagellum*, and the gopher snake, *Pituophis catenifer*. Energy curves disclose a maximum difference of values for the red racer of 0.000145% at 600 mμ. The curves for the gopher snake are similar, the maximum difference in values at the peak being 0.0015% at 550 mμ.

NOCTURNAL LIZARDS

Although light absorption by tissues is not accomplished by pigments alone, pigments, particularly melanin, absorb light very efficiently. The contribution of melanin to the total light absorption by the body wall was assessed by measuring the light transmitted through the relatively unpigmented tissues of the nocturnal Western Banded Gecko, *Coleonyx variegatus*. Such translucent tissue provides an important opportunity for comparison of this nearly unshielded

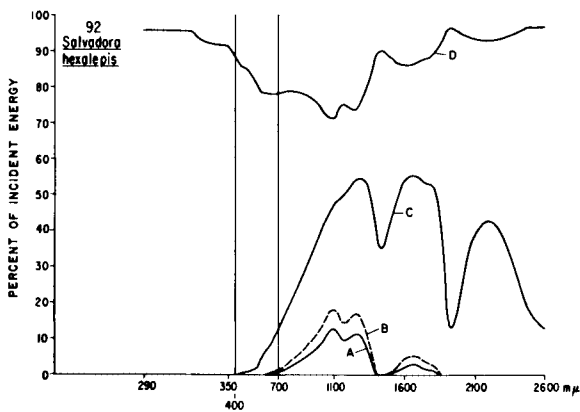


Fig. 16. Spectra of the middle and posterior portion of the body of the diurnal snake, *Salvadora hexalepis*. A. Transmission through the midbody. B. Transmission through the hindbody. C. Skin transmission midbody and hindbody. D. Reflectance midbody and hindbody.

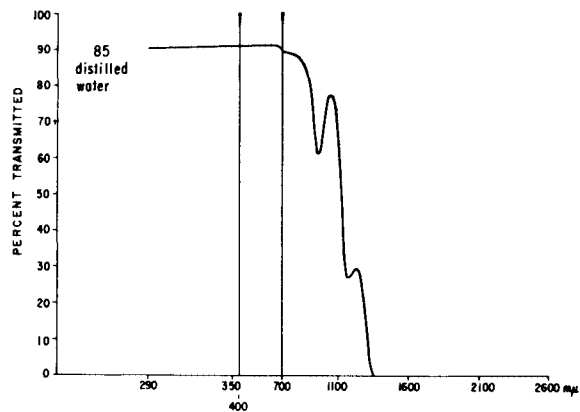


Fig. 17. Transmission through 1 cm of distilled water.

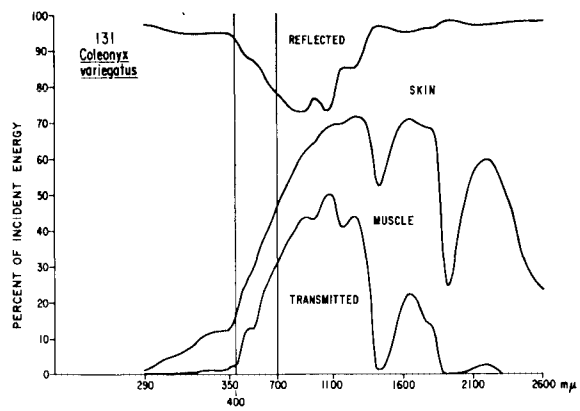


Fig. 18. Spectral measurements of the relatively unpigmented nocturnal gecko, *Coleonyx variegatus*.

form with melanin shielded lizards. Transmission measurements (Fig. 18) reveal that an extraordinarily large quantity of energy penetrates the dorsal body wall of this species. Even though these measurements were made with the less sensitive transmittance set-

ting, penetration of ultraviolet light was detected below 290 mμ. Furthermore, shorter wavelengths of ultraviolet penetrated thicker tissue in *Coleonyx* than in diurnal species (1.2 to 1.9 mm for *Coleonyx* vs 0.3 to 0.9 mm for *Uta* and 1.0 to 1.1 mm for *Cnemidophorus*). The distribution of energy absorbed, transmitted, and reflected is given in Table 2.

COMPARISON OF DIURNAL, CREPUSCULAR, AND NOCTURNAL SNAKES

The greater transmission of light through the tissues of the nocturnal banded gecko, *Coleonyx*, suggested that a similar situation might exist in nocturnal snakes. Moreover, if the body cavity of diurnal reptiles is being shielded from light by pigment deposits including the black peritoneum, the amount of light excluded might be closely related to the habits of the animal, i.e. a diurnal snake should exclude light, especially ultraviolet, from the body cavity, crepuscular animals which are out in the early morning and at twilight might have less effective barriers to light entering the body cavity, and nocturnal snakes might transmit most wavelengths comparatively freely. Indeed, this is precisely what happens (Fig. 19). The

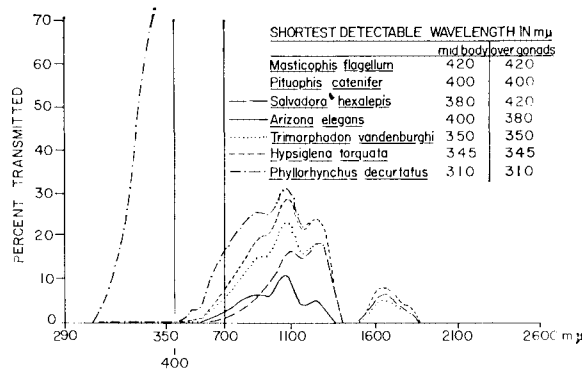


FIG. 19. Comparisons of transmission and shortest detectable wavelength in diurnal, crepuscular and nocturnal snakes. The most thermophilic snake is at the top of the list, the most nocturnal, at the bottom. Transmission curves of the top two animals were not included for clarity. They were between the *Salvadora* and *Arizona* curves in the infrared and lower than all in the visible. A typical energy curve is included above the horizontal *Phyllorhynchus* curve representing the absolute transmission (less than 0.05%) in the ultraviolet.

name list in Fig. 19 is arranged so that the most thermophilic (the red racer) is on top, and the most completely nocturnal (the spotted leaf-nosed snake, *Phyllorhynchus decurtatus*) is on the bottom. The first three snakes are diurnal. The next three are mostly crepuscular in the spring and nocturnal in the summer. The transmission curves of the top two were not included for clarity in the illustration, but they were both between the *Salvadora* and *Arizona* curves in the infrared and below all curves in the visible. The caloric breakdown of energies reflected, transmitted, and absorbed by these animals is given in Table 4. The greater transmission of the tissues of nocturnal

TABLE 4. Comparison of diurnal, crepuscular and nocturnal snakes. R = reflected; T = transmitted; Ex, Sk, Mu, BP = energy absorbed by the exuvia (shed skin), the skin, the muscles, and the black peritoneum respectively.

	No. of samples	R	Sk	Mu	T
<i>Arizona elegans</i>					
midbody.....	1	23.6	49.9	23.9	2.6
over gonads.....	1	23.6	46.6	26.2	3.7
<i>Hypsiglena torquata</i>					
midbody.....	1	18.7	54.5	18.0	8.8
over gonads.....	1	18.7	52.5	18.9	10.0
<i>Phyllorhynchus scurtatus</i>					
midbody.....	2	19.9-20.5	37.8-48.1	23.1-29.6	8.2-12.7
over gonads.....	1	19.9	36.5	25.2	18.4
<i>Pituophis catenifer</i>					
midbody.....	1	13.9	67.5	14.4	3.7
over gonads.....	1	13.9	67.5	14.9	4.2
<i>Salvadora hexalepis</i>					
midbody.....	2	18.2-19.7	56.1-62.6	15.0-19.5	2.7-6.2
over gonads.....	2	18.2-19.7	62.6-64.3	13.6	3.9-4.1
<i>Trimorphodon vandenburghi</i>					
midbody.....	1	24.0	42.8	25.8	7.3
over gonads.....	1	24.0	42.8	24.5	8.6

reptiles and the intermediate characteristics of crepuscular snakes strongly suggest that the body cavity of diurnal reptiles is being shielded from sunlight.

EFFECT OF TISSUE DEATH UPON TRANSMISSION

One of the primary objectives of this study was to compare transmission properties of living and dead tissue. Accordingly, a specimen of *Coleonux variegatus* was anaesthetized, following the established procedure, and measured alive for transmission through the body wall. Then a lethal dose of nembutal (100 times the usual dose) was administered. A repeat of the same transmission run was made immediately. There was no change in transmission. The animal was left on the holder at room temperature for about 24 hours, after which another transmission measurement was performed. Again there was no change.

These results were confirmed using the bullfrog, *Rana catesbeiana*. In this animal there was no change in transmission over 48 hours at room temperature as long as the skin was kept moist. These results are consistent with those of Hardy (1956), who obtained rather fresh human skin, measured its transmission, and by keeping it moist and chilled found no transmission changes even over months.

The lack of transmission changes upon death of tissues can be explained by the fact that, although chemical changes occur and might be detected if the molecules were isolated in dilute solutions, any spectral changes that might occur would be obscured by the extreme scattering and broadening of absorption spectra, phenomena which are characteristic of solid

materials and very concentrated solutions. This is true because adjacent molecules affect electrons in excited states. For example, the spectra of vapors, where the molecules are far apart, usually have more fine detail than the spectra of liquids and solids. The obscuring of hemoglobin spectra in the above transmission measurements is a good example of spectral broadening in a dense medium.

TRANSMISSION MEASUREMENTS OF OTHER ANIMALS

Establishing the fact that there are no detectable changes in total body wall transmission, provided the tissues are kept moist and do not decompose, is important because it makes possible the measurement of tissues of other animals; e.g., birds, fish, and insects which would be very difficult to measure while they are alive.

FISH

A measurement of the transmission of light through the excised lateral body wall of a freshly killed rainbow trout (*Salmo gairdneri*) (Fig. 20) shows pene-

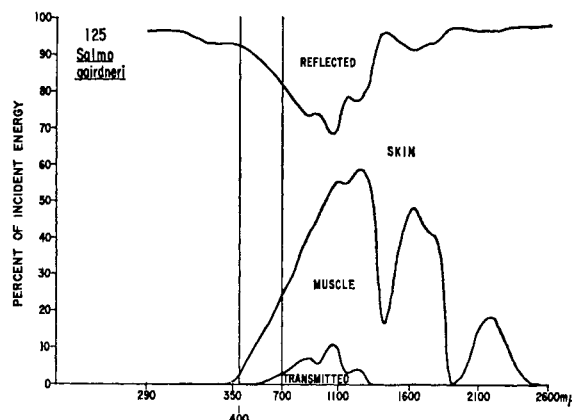


FIG. 20. Analysis of the rainbow trout, *Salmo gairdneri*.

tration to about 550 mμ with the transmittance setting and about 420 mμ using the energy setting. Ultraviolet light as short as 315 mμ penetrates the skin. Such short wavelengths are present in clear streams (Luckiesh, 1944) and would be incident on trout exposing themselves to sunlight. The muscles absorb a great amount of light, 22.7%. The results are similar to those found for some diurnal reptiles. The percents of energy absorbed, transmitted, and reflected are shown in Table 5. The pieces of body wall were manipulated in the same manner as were tissue flaps of reptiles. The holder, mask and quartz were used in all these experiments.

AMPHIBIANS

The bullfrog, *Rana catesbeiana*, has dorsal and ventral transmission spectra very similar to those of diurnal reptiles, with minimum wavelength penetration to about 400 mμ (Fig. 21). The lateral body wall with its thinner musculature permits light down

TABLE 5. Comparisons of non-reptilian vertebrates and a black desert beetle. R = reflected; T = transmitted; Ex, Sk, Mu, BP = energy absorbed by the exuvia (shed skin), the skin, the muscles, and the black peritoneum respectively.

		R	T	Mu	Sk
<i>Salmo gairdneri</i>	UV	0.4	0	0.1	5.6
	Vis	5.6	0.4	5.8	36.0
	IR	10.2	2.6	16.8	16.6
<i>Rana catesbeiana</i>	UV	0.5	0	0	5.5
	Vis	6.2	0.1	2.3	39.3
	IR	8.7	1.9	18.4	17.1
<i>Carpodacus mexicanus</i> (side of rump)	UV	0.5	0	0	5.5
	Vis	5.6	6.2	0	36.0
	IR	13.0	13.6	0	19.6
<i>Carpodacus mexicanus</i> (center of rump)	UV	0.7	0	0	5.4
	Vis	5.3	0.5	0	42.0
	IR	9.9	3.2	0	33.0
<i>Citellus leucurus</i> (no hair)	UV	0.1	0	0	5.9
	Vis	1.6	0.5	0	45.7
	IR	5.5	6.1	0	34.6
<i>Citellus leucurus</i> (with hair)	UV	0.2	0	0	5.8
	Vis	5.2	0	0	42.6
	IR	14.5	1.0	0.1	20.6
<i>Citellus beecheyi</i> (with hair)	UV	0.2	0	0	5.8
	Vis	4.7	0.1	0.2	42.8
	IR	12.0	3.1	1.8	29.3
<i>Perognathus formosus</i> (with hair)	UV	0.5	0	+0	5.5
	Vis	6.7	0	+1.6	39.5
	IR	20.3	1.3	+3.7	20.7
<i>Callosoma semilaeve</i>	UV	0.3	0	0	5.7
	Vis	2.7	0	0	45.1
	IR	5.6	2.4	0	38.2

*The values to the right of the plus sign are those increases in transmission which occurred when the hair was removed.

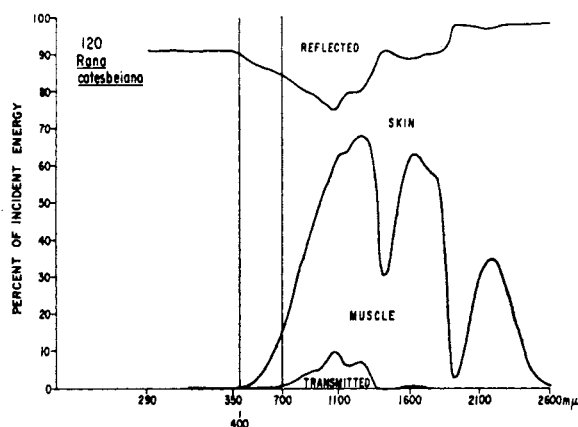


Fig. 21. Spectrophotometry of the bullfrog, *Rana catesbeiana*.

to about 360 mμ to penetrate. The leopard frog, *Rana pipiens*, a species with some pigment in the dorsal peritoneum, shows penetration to 400 mμ dorsally, to 330 mμ ventrally, and to 303 mμ laterally, where the body wall is thinnest. The dorsal transmission was

taken through the tissue above the testis. Transmission measurements taken through the same region in a gravid female *Rana pipiens* showed essentially the same results except that the minimum wavelength detectable in the body cavity was about 430 mμ dorsally.

BIRDS

Transmission spectra of the house finch, *Carpodacus mexicanus*, and the mourning dove, *Zenaidura macroura*, were made with large pieces of excised body wall. Rapid death resulting from a small amount of blood lost precluded taking measurements similar to those of amphibians and reptiles.

In *C. mexicanus* (Fig. 22) no light at any wave-

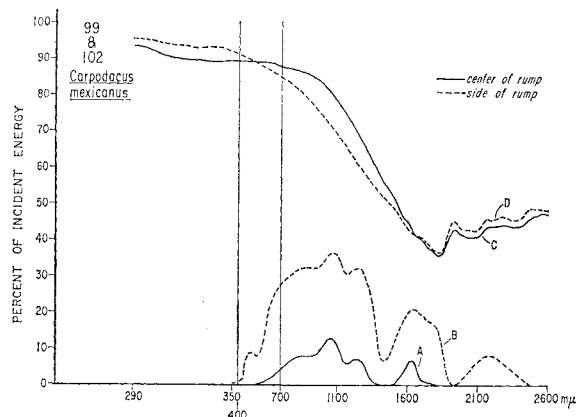


Fig. 22. Reflectance and transmission measurements of the house finch, *Carpodacus mexicanus*. A. Transmission through the dorsal center of the rump without feathers. B. Transmission through the side of the rump without feathers. C & D. Reflectance measurements of feathers on the center and side of the rump respectively.

length penetrates the flattened wing and body feathers overlying the very thin, unpigmented tissue in the lateral, dorsal pelvic region. With the wing feathers removed a small amount (less than 1%) of infrared penetrates between 1650 and 1850 mμ (not shown). When the feathers of the body are removed, wavelengths down to 295 mμ reach the body cavity (curve B). Without feathers, wavelengths down to 360 mμ penetrate the bone and tissues of the central dorsal pelvis (curve A). Similar results were obtained from the mourning dove.

MAMMALS

Three mammals have been examined to date: the antelope ground squirrel, *Citellus leucurus*, the Beechy ground squirrel, *C. beecheyi*, and the long-tail pocket mouse, *Perognathus formosus*. The first two are diurnal and the latter, nocturnal. The antelope ground squirrel is commonly active throughout the day in the desert during the summer.

The first two of the three animals collected were shot, refrigerated immediately and measured the next day. The third animal, the longtail pocket mouse, was captured alive, anaesthetized, and measured in the

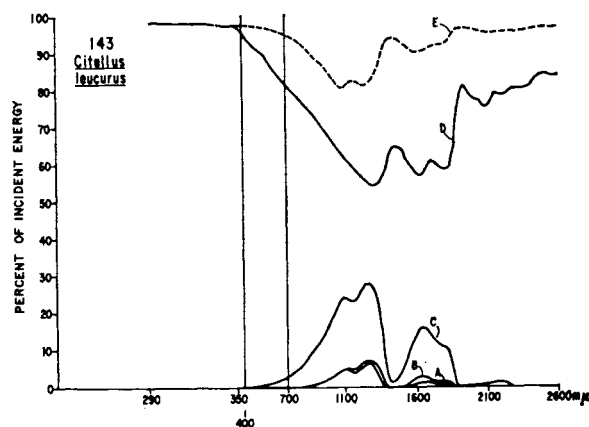


FIG. 23. Spectral properties of the body wall of the antelope ground squirrel, *Citellus leucurus*.

A. Transmission through the intact body wall.
B. Transmission without the thin muscle layer.
C. Transmission without the hair. D. Hair reflectance.
E. Skin reflectance.

same way as a reptile. Measurements of the reflectance and transmission properties of *C. leucurus* (Fig. 23) disclose several interesting facts. Curve A is the transmission through the entire body wall in the dorsal lumbar region. The transmission is more than that of birds which admit no light to the body cavity, but is less than that of many reptiles. Curve B is the change in transmission when the thin muscle layer is removed. Curve C is the increase in transmission when the hair is shaved off. Curve D is the fur reflectance, and Curve E is shaved skin reflectance. One of the most surprising results was the relatively low (5.6%) increase in skin transmission when the hair was removed. This was confirmed in a specimen of *P. formosus*. When the hair was removed, skin transmission increased 5.3%. *C. beecheyi* could not be tested for this, because the skin was accidentally cut during shaving. Another unforeseen result was the significant increase in reflectivity (over bare skin) that hair confers on *C. leucurus*. The skin of this animal is black and lets through considerably less light (minimum detectable wavelength = 350 mμ) than the bare skin of the nocturnal longtail pocket mouse, *P. formosus* (minimum wavelength = 300 mμ). The antelope ground squirrel thus excludes almost all visible light from the body cavity, partly by means of a black skin. The total radiation absorbed by the body wall, however, is reduced by having highly reflective hair over the non-reflective black skin.

The exclusion of ultraviolet light and most or all visible light from the body cavity is accomplished in different ways among the vertebrates, but the total effect has been found to be the same without exception in diurnal forms. The skin, muscles, pigments (especially melanin, which may be found anywhere in the body wall), feathers in birds, and hair in mammals all contribute to light absorption even though each may vary greatly in its absorbing power be-

cause of different thicknesses or density of material in different species.

INSECTS

A black carabid beetle, *Calosoma semilaeva*, was included in this study, because black beetles have been repeatedly observed moving about on the desert during the daytime. Their black color would seem disadvantageous because: (1) black is not concealing coloration for an animal moving across the bright, lightly colored sand and; (2) the color would appear to absorb most of the incident radiation and thereby add to the heat stress on the animal. In view of the consistent exclusion of light from the body cavity of vertebrates, it seemed plausible that the same sort of exclusion of light might be occurring in invertebrates. Measurements of reflectance and transmission through the dorsal body wall and wing covers (Fig. 24) demonstrate that visible light and ultra-

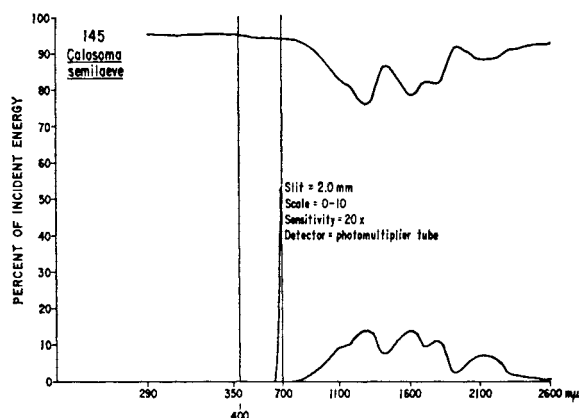


FIG. 24. Reflectance and transmission of a black desert carabid beetle, *Calosoma semilaeva*. The steep vertical line beginning at 700 mμ at 53% is a transmission measurement using the highly sensitive energy mode of operation. Pertinent machine settings are indicated next to the curve.

violet light are excluded from the body cavity by 0.15 mm of tissue (tissue of the nocturnal banded gecko *Coleonyx*, is more than ten times this thick and freely transmits ultraviolet light). Even with maximum sensitivity in the energy mode (slit = 2.0 mm, etc.) the shortest detectable wavelength was about 650 mμ. The beetle reflects only 8.6% of the total incident energy, transmits 2.4%, virtually all in the infrared, and absorbs 89.0% of the incident energy. The beetle's high surface to mass ratio and the inherent strong convective cooling because of this ratio is undoubtedly one of the major reasons it does not overheat and die (Norris, 1967).

The concept of radiation protection for the body cavity of diurnal animals is again suggested by these results because these beetles possess a color which seems disadvantageous in terms of protective coloration and reduction of the radiative heat load, but advantageous in the exclusion of light from the body cavity.

RELATIVE EFFICIENCY OF BODY WALL COMPONENTS FOR
REFLECTING, SCATTERING, AND ABSORBING LIGHT.
MELANIN AND MUSCLE

Several allusions have been made in this paper and elsewhere as to the efficiency of melanin as an absorber of light, but there are no quantitative comparisons in the literature of its efficiency *in situ* compared, for example, to an equal thickness of muscle.

Reflectance: As was noted above, the reflectance of the skin of *Sceloporus orcutti* and others does not change perceptibly when the black peritoneum and the dorsal musculature are separated from the skin. Part of the reason for this is that neither melanin (Fig. 25) nor muscles (Fig. 26) reflect very much

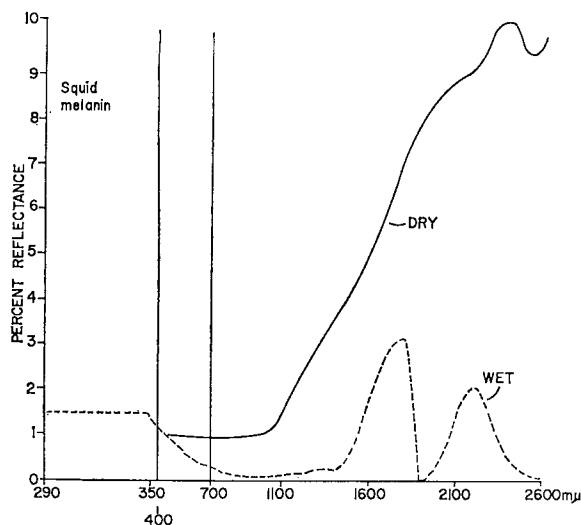


FIG. 25. Reflectance of wet and dry purified squid melanin.

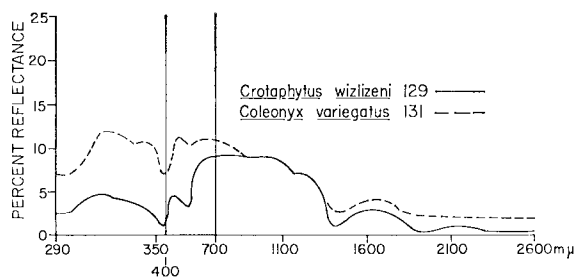


FIG. 26. Reflectances of dorsal musculature with melanin deposits (diurnal *Crotaphytus wizlizeni*) and without melanin deposits (nocturnal *Coleonyx variegatus*).

energy. The curves in these figures present the reflectances of squid melanin granules and the dorsal musculature of two lizards: the nocturnal banded gecko, *Coleonyx variegatus*, and the leopard lizard, *Crotaphytus wizlizeni*, a diurnal moderately high temperature lizard with a black peritoneum. The gecko has no melanin in the musculature whereas *Crotaphytus* does. The side of the muscle opposite the incident light beam was uncovered so that light could pass into the unlit darkroom (Fig. 2B).

The amount of energy reflected by the melanin granules averaged 0.8% in the infrared, 0.5% in the visible and 0.1% in the ultraviolet. Distilled water was added to the melanin to moisten it to simulate the aqueous environment in living tissues. The reflectance dropped in the infrared and visible to 0.12% and 0.36% respectively. There was no change in the ultraviolet. Unpigmented muscle from *Coleonyx* reflected 3.7% infrared, 5.0% visible, and 0.6% ultraviolet. In contrast, the pigmented dorsal musculature of *Crotaphytus* averaged 3.5% infrared, 2.6% visible, and 0.1% ultraviolet.

Absorption: Neither of the above measurements, however, is by itself a quantitative measure of the absorbing power of melanin or muscle per unit thickness. A quantitative measurement can be expressed either as an absorption coefficient, τ , which is an average over the entire thickness, or as a derivative with respect to thickness, $d\tau/dt$. Both involve Beer's (Bouguer's) Law (Koller, 1965) which states that the emergent light intensity at any specified wavelength is equal to the incident intensity times e , a constant, raised to the minus nEa power, i.e.

$$I = I_0 e^{-nEat} \quad (\text{or}) \quad I = I_0 e^{-\tau t}$$

where

I = emergent radiation intensity

I_0 = incident radiation intensity

e = the base of the natural logarithm (approximately 2.718)

n = number concentration of particles

E = mean extinction coefficient (Hodkinson, 1962), efficiency factor (van de Hulst, 1957), (a dimensionless fraction—for a thorough discussion of the various types of E and their implications, see van de Hulst, 1957)

a = mean projected area of a particle, i.e. its geometrical cross section.

t = thickness of the medium

(For a more general development of this equation for the transfer of radiant energy, see Chandrasekhar (1950).)

The product of all exponents, $nEat$, is called the absorbance or the optical density. The product of nEa is the absorption coefficient, τ^3 . Beer's (Bouguer's) law can be solved for τ so that

$$\tau = (\log_e (I_0/I))/t$$

$^3\tau$ is also variously referred to as turbidity, extinction coefficient (e.g. van de Hulst, 1957), or monochromatic extinction optical thickness (e.g. Gates, 1966). Since extinction = scattering + absorption, the designation of τ will depend upon whether scattering is a significant factor in transmission measurements and upon the method of measurement of transmission.

The product Ea is often designated by a single letter, e.g. k , and is variously referred to as the absorptivity, molar absorption coefficient, or specific extinction.

In this manner we derive a number which is independent of thickness. The relative absorption coefficients can now be determined. For dark *Uta stansburiana* the absorption coefficients for the black peritoneum and the muscles at 1000 $m\mu$ are 4055 and 5

TABLE 6. Absorption coefficients in cm^{-1} at 1000 $\text{m}\mu$.

Specimen number	Species	Skin	Muscle	Black peritoneum
82	<i>Callisaurus draconoides</i>	50	10	
83	"	79	9	
75	<i>Dipsosaurus dorsalis</i>	14	4	
88	"	43	4	
89	"	41	6	
109	<i>Eumeces gilberti</i>	100	4	
91	<i>Sceloporus magister</i>	29	5	
94	"	20	3	
100	"	21	1	
101	"	23	3	
98 (light)	<i>Sceloporus occidentalis</i>	50	4	
98 (dark)	"	61	5	
79	<i>Uma scoparia</i>	22	5	
80	"	25	8	
81	"	38	7	
95	<i>Uta stansburiana</i>	83	3	
96	"	108	8	
116	"	94	5	4055

(Table 6). The skin, which has much melanin in the dermal melanophores, has, in comparison, an absorption coefficient of 94. When one considers that these are exponents, it is immediately obvious that the efficiencies are quite different.

A more descriptive and perhaps more readily understood way of describing quantitatively the energy absorbing efficiency of the three parts of the body wall is to plot the percent of transmission with respect to thickness of the medium (Fig. 27).

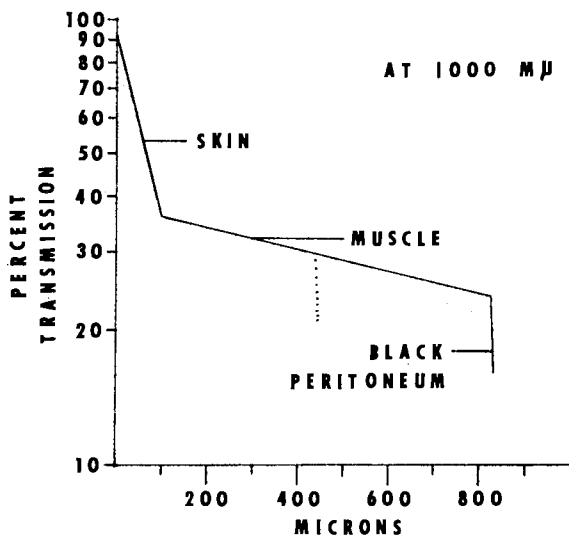


FIG. 27. Light intensity at 1000 $\text{m}\mu$ at any point in the body wall of *Uta stansburiana*. Body wall thickness is in microns. The lines labelled "skin", "muscle", and "black peritoneum" describe the average rate of light absorption for each of the respective body wall layers.

It would be gratifying if these computations were a precise description of the rate of reduction of light intensity, but due to the large values of the absorption coefficients, a small change in t (thickness) in the equation can change the calculated value of τ enough to preclude precision of analysis. The methods

are valuable, however, for providing good approximations of the effect of each layer.

These calculations are important for a theoretical understanding of the energy absorbing interrelationships of the skin, the muscles, and when present, the black peritoneum. For example, the graph of the reduction in light intensity by the parts of the body wall allows one to compare visually the effective change in transmission when the thickness of the muscles decreases, e.g. dorsally to laterally. If the dorsal and lateral reflectance values are the same at the wavelength in question and the lateral muscle thickness is only one half the dorsal value, the line describing the peritoneum's reduction of light intensity would have to move to the left and up to the position of the dotted line (Fig. 27). Since its slope cannot change and if the thickness of the black peritoneum is the same laterally (there is no microscopic evidence that the thickness is different laterally), more light would now penetrate, and the increase would be approximately 5%. (The precise value can be determined using Beer's law). One could determine how much thicker the black peritoneum would have to be for complete exclusion or for the increase in slope of the skin line (i.e. skin darkening) necessary to exclude the same amount of light. Another possibility would be to remove theoretically the peritoneum from an animal, estimate the effect on transmission, and "design" corrective measures; e.g., increase skin pigmentation, increase muscle thickness or muscle pigmentation, or a combination of these. Transmission through an animal without a pigmented peritoneum would require quite a thick body wall if the muscle line had to be extrapolated to zero intensity. This method has potential as a graphic aid in understanding and trying to predict the interrelationships of the light absorbing system, the body wall. The accuracy of the method depends heavily on the accuracy of the thickness measurements.

BLOOD

Since one of the important pigments in the body is hemoglobin, it would be interesting to know how much energy is absorbed by it and whether the energy absorbed constitutes a significant amount of the energy absorbed by the body wall as a whole. To test this, a specimen of *Eumeces gilberti*, a skink without a black peritoneum, and a specimen of *Dipsosaurus dorsalis*, an iguana with a black peritoneum, were anaesthetized with nembutal and measured for reflectance and total body wall transmission. The pleural cavity was then opened, exposing the heart. A syringe with 10% heparin in frog Ringer's solution was inserted into the aorta, and an incision was made in the ventricle. While the heart continued to beat, the blood was gradually replaced by the clear solution.

Transmission measurements of *E. gilberti* made through the same tissue flap afterward indicated that of a very small percentage of the total energy absorbed by the body wall, less than 1% is absorbed by

the blood pigments in the infrared. When the sensitive energy mode of operation was used, the maximum difference in the visible part of the spectrum was $1.4 \times 10^{-4}\%$ at 570 m μ . There was a difference in minimum detectable wavelength of 10 m μ (460 m μ with blood, 450 m μ without it). A crested lizard (having much less skin pigmentation than a Gilbert's skink) showed a difference of less than 1% in the infrared with the peritoneum intact. There was no detectable difference in the visible in the transmittance mode. In the energy mode, however, four times more green light (550 m μ) penetrated without blood. Also, the minimum detectable wavelength dropped from 400 to 350 m μ . To differentiate more precisely how much energy was being absorbed by the blood, a second specimen of *Dipsosaurus*, with the black peritoneum removed, was measured before and after blood replacement. The results were similar to those of the first specimen of *D. dorsalis*; 1.2% difference in the infrared (transmittance mode), four times more green light without blood (energy mode, difference much less than 1%), and minimum detectable wavelength dropped from 420 to 370 m μ .

Thus, the proportion of the energy absorbed by the blood compared to the energy absorbed by the body wall is very small, perhaps in part because so much energy is reflected and absorbed by the skin before it reaches the major blood concentration in the muscles. Although it does not contribute materially to the total heat absorbed, the energy that hemoglobin absorbs contributes to the reduction of light intensity in the body cavity, especially at the higher energy shorter wavelengths.

WATER

Water is the most abundant constituent of living tissues; therefore, its spectral properties are of prime concern, especially because of the often stated idea that ultraviolet light is absorbed in the first 1 mm or so of water. Contrary to this idea, ultraviolet light can and does penetrate water readily. Hulburt (1928) demonstrated more than 80% transmission through 2 cm of sea water at wavelengths as short as 280 m μ . Luckiesh (1944) demonstrated penetration of even shorter wavelengths (253.7 m μ) to depths greater than 34.8 inches. Jerlov (1950) found that in the Mediterranean 310 m μ intensity was reduced only 14% per meter, and off the Swedish coast where the water was quite turbid the ultraviolet absorption at 310 m μ was 90% per meter. To illustrate water's absorption of solar radiation between 290 m μ and 2600 m μ , a quartz container with a 1 cm path length was filled with distilled water and placed at the entrance to the integrating sphere for a transmission measurement. An identical empty container was in the reference beam. The results (Fig. 13) indicate heavy absorption in the infrared but not at visible and ultraviolet wavelengths normally incident on the earth's surface. To be sure, tiny objects and dissolved materials in water scatter and absorb light, especially at shorter wavelengths, but the absorption at normal incident

wavelengths, i.e., greater than 290 m μ , is not as great as is often supposed.

SPINES

Discussion of the absorption of light by the body wall has centered on absorbing pigments, melanin and hemoglobin, and muscle proteins. Absorption is greatly facilitated if the path length through the tissues can be elongated, i.e. if scattering occurs. Scattering is a general term which includes back scattering ("diffuse reflection") and forward scattering (particle diffraction and refraction, transmission through particles, and reflection at glancing angles so that the light ray is still directed forward, no matter how small the angle between the ray and a plane normal to the incident light). All of these phenomena take place at all levels of the tissue. Within the tissues the dominant scattering effects are due to the melanin granules, guanine crystals, and red blood cells because of their large size with respect to the wavelength (Mie scattering). Of particular interest with respect to surface scattering are some tiny

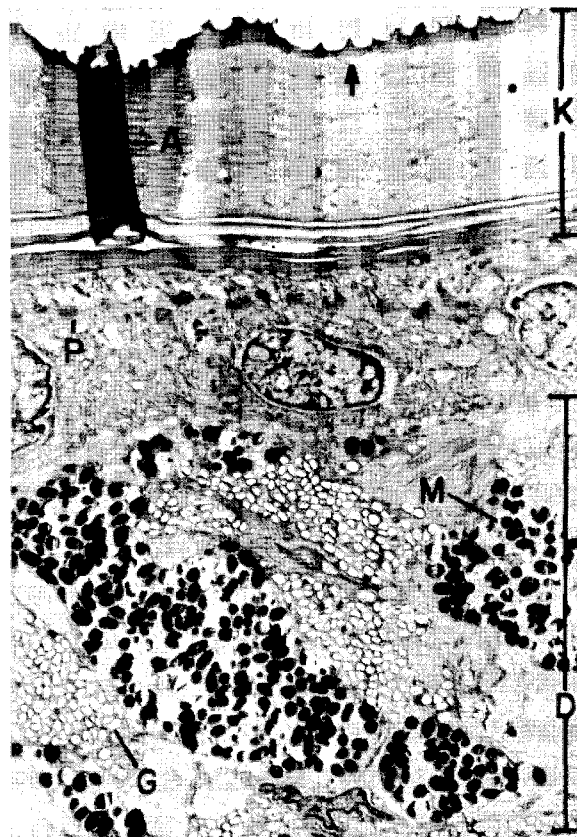


FIG. 28. Cross section through the upper body wall of *Uta stansburiana*. The dark vertical band (A) in the upper left is a fold in the keratin caused by sectioning. Between the keratin (K) with its superficial spines and the dermis (D) with its melanophores filled with melanin granules (M) and its whitish guanine crystals (G) is a layer of living epidermal cells outlined by numerous platelike desmosomes (P). Spine at tip of arrow is 1 μ tall.

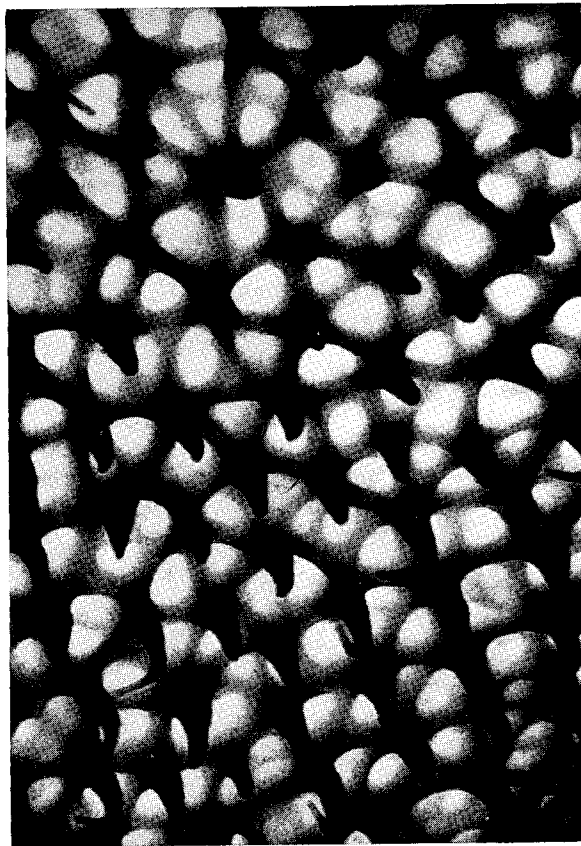


FIG. 29. Top view of spines of gecko, *Gonotodes fuscus* (courtesy of R. Ruibal). Spacing between spines = 0.5μ .

spines which showed up on electron micrographs of tissue from *Uta stansburiana* (Fig. 28). The spines in cross section are about 1μ high, and the distance between peaks varies from 0.7μ at the base to 1.5μ at the tip. Ruibal and Ernst (1965) and Ruibal (1967) have demonstrated that these spines form a regular network over the surface of lizards (Fig. 29). They have found this topography in three different families of reptiles, Iguanidae, Gekkonidae, and Lacertidae. These spines might be acting as a three-dimensional diffraction grating, with the spaces between the peaks acting as the grating slits. The topography is analogous to that of an anechoic room where sound waves are broken up and absorbed by innumerable regularly spaced projections. The diffraction effect would be enhanced by further bending due to refraction. Since the refractive index of keratin is greater than that of air, light would refract into the spines as it penetrates the keratin. The precise angles of dispersion have not yet been determined. These spines also appear to be most closely spaced and most regularly arranged in the small species of lizards, i.e., those which possess thin body walls. It appears, therefore, that these spines might be a morphological adaptation to assist in absorbing light by greatly scattering it before it deeply penetrates the body.

OTHER CONSIDERATIONS

In this analysis of energy reflection, scattering, and absorption by the body wall several matters have not been touched upon. Among them are the reflection, scattering, transmission, and absorption properties of guanine, which is abundant in the skin. Because of the dimensions of its crystals, we can expect guanine to be a good scatterer. It is probably also a good reflector and a poor absorber as judged by its apparent high concentrations in the skins of very reflective lizards such as the crested lizards.

Another important consideration is the possibility of protection of internal organs by other organs. In *Crotaphytus wislizeni*, for example, I have observed part of the liver lying lateral and slightly dorsal to the gonads. In this case the light "microenvironment" of the gonads might differ greatly from the light intensity which would be indicated by a body wall transmission measurement. In this connection *Crotaphytus* lets more light into the body cavity than any other diurnal reptile measured to date.

Finally, the possibility of seasonal changes in body wall transmission have not been investigated. For example, in the field I have observed many sand lizards, *Uma scoparia*, in an emaciated condition in the fall. They are also emaciated after spring emergence (Norris, private communication). More light could enter the body cavity, but the internal organs might be less sensitive to it at this time of year, or the weight loss might be compensated for by increased pigment deposition. These questions remain unanswered.

DISCUSSION

WHY VISIBLE AND ULTRAVIOLET LIGHT ARE "BIOLOGICALLY ACTIVE"

Absorption of radiant energy in the ultraviolet and visible parts of the spectrum occurs primarily through electron transitions, i.e. changes in electron energy levels of atoms and molecules. The difference between the energy levels, or resonance frequencies, of a given atom is fixed, and the minimum value is designated the normal or ground state. When the frequency of the incident radiation coincides with the resonant frequency of the electrons of an atom or molecule, energy is absorbed, and the molecule or atom attains a higher energy level through its excited electrons. In the visible and near ultraviolet only the outer shells of the atom are affected, whereas in the far ultraviolet inner electrons are excited, and in some instances this excitement results in molecular dissociation and ionization. Absorption at infrared frequencies, on the other hand, results in elevated vibrational levels of molecules as a whole; farther into the infrared, absorbed energy, in general, raises the rotational energies. The transition region between electron excitation and vibrational-rotational excitation is the spectral region between approximately $800 m\mu$ and $1900 m\mu$. The lack of strong molecular absorption in this bandwidth accounts for the highest

body wall transmission peaks in this region. The dips in the infrared at 2400, 1950, 1400, and 1150 μ are water absorption bands.

Ultraviolet and visible light are considered "biologically active" because when they are absorbed, the excited or higher energy state is unstable and almost immediately reverts to a lower state, usually the ground state. In the transition from the higher to the lower state the amount of energy previously absorbed is lost. This released energy may be transmitted to other molecules via electron transfer, or it may be emitted as heat or light. Sometimes even though simple resonance transfer between different compounds should not occur, the absorption of energy by one compound may result in the formation of charge-transfer complexes with other species of molecules not absorbing in that part of the spectrum (Yeagers and Augenstein, 1966). For example, photosensitizing furocoumarins absorb energy at about 360 μ and complex with DNA (which has little absorption at this wavelength) with resultant biological damage (Musajo *et al.*, 1966). Alternatively, quanta absorbed may provide sufficient energy to rupture certain chemical bonds, e.g. Dose (1965) has computed that one S-S bond is broken per 50 to 100 quanta of short wavelength ultraviolet. For a thorough discussion of the physical aspects of light absorption see Calvert and Pitts (1966).

FUNCTION OF THE BLACK PERITONEUM

The consistent exclusion from the body cavity of ultraviolet and short wavelength visible light by the intact body walls of every diurnal animal measured, irrespective of body wall components or thickness, suggests very strongly that visible and ultraviolet light, whose quantum energies are sufficient to induce electron transitions, could alter or damage biochemical processes occurring within the body cavity of living organisms. Infrared radiation, on the other hand, whose quantum energy is only sufficient to induce vibrational or rotational molecular changes, penetrates the intact body wall in much greater and more widely varying amounts than ultraviolet or visible light. The greater variability of infrared penetration inter- and intraspecifically suggests that only the higher energy wavelengths capable of inducing electron transitions must consistently be excluded from the body cavity.

Even though the amount of energy in calories $\text{cm}^{-2} \text{min}^{-1}$ absorbed by the black peritoneum is very small when compared with the energy absorbed by the skin and muscles, the number of quanta absorbed is exceedingly large. The quantum energy of a photon at 310 μ , for example is 6.41×10^{-12} ergs. A calorie, in comparison, is 4.184×10^7 ergs. Even a small fraction of a calorie of light at this wavelength reaching the body cavity means that the number of penetrating quanta is high as is the probability of the occurrence of photochemical reactions.

The crucial measurement is one which establishes that, without the black peritoneum, enough damaging

ultraviolet light of available incident wavelengths at naturally available intensities can reach the body cavity where it would be absorbed by the internal organs, e.g. the gonads, and by the intestinal fauna. The calculation of penetrating ultraviolet energy in these wavelengths has been made in detail for a few of the lizards with black peritoneums. The calculations were made possible by a precise calibration of the spectrophotometer source output into the integrating sphere (Porter, 1966).

Results of calculations made from energy mode transmission measurements show that, without the black peritoneum, the energy in the wavelengths shorter than 313 μ penetrating the body cavity of *Uta stansburiana* is about 10.20×10^3 ergs $\text{cm}^{-2} \text{day}^{-1}$ in the first week of June or 5.72×10^3 ergs $\text{cm}^{-2} \text{day}^{-1}$ in April. These figures are based on the measured 2.65×10^{-2} percent transmission at 310 μ for a dark specimen of *Uta stansburiana* and on ultraviolet energies of 3.85×10^7 and 2.16×10^7 ergs $\text{cm}^{-2} \text{day}^{-1}$ for wavelengths shorter than 313 μ as measured by Coblenz and Stair (1944). With a dorsal surface area of about 6 cm^2 (Norris, 1967), the daily dose rates to the body cavity would be approximately 61.2×10^3 ergs day^{-1} and 34.3×10^3 ergs day^{-1} for a day in June and April, respectively. According to Witkin (1966), doses of about 30×10^3 ergs cm^{-2} are sufficient to induce mutations in the intestinal bacteria, *E. coli*. Hanawalt's (1966) LD_{50} values are also 30×10^3 ergs cm^{-2} . Therefore, much more ultraviolet than has been believed previously reaches the body cavity in *Uta*, and, without the black peritoneum, it penetrates at intensities sufficient to induce "biological damage."

Wavelengths as short as 300 μ do not reach the body cavity of all species examined when the black peritoneum is removed. The body wall of *Sceloporus occidentalis*, for example, (Table 3) excludes wavelengths shorter than 330 μ . The possibility that longer wavelengths may also affect internal biochemistry has already been implied in connection with fish embryos and cave animals.

Recently it has been demonstrated that near ultraviolet wavelengths, i.e. 320 to 400 μ , can induce mutation in the bacterium, *Escherichia coli* (Kubitschek, 1967). He suspects that the "photochemical reactions initiated in mutagenesis with near-visible light are quite unlikely to be identical with those initiated in mutagenesis by" short wavelength ultraviolet. Kubitschek found that, for the wavelength interval 320-400 μ , 14×10^6 ergs were required to increase mutations by an order of magnitude. At noon the energy in the above near UV wavelengths reaching the body cavity of a desert iguana without a peritoneum (Table 3, no. 117) would be 85 ergs $\text{cm}^{-2} \text{sec}^{-1}$. The total energy available in the near UV on June 22 at 30 degrees north latitude is roughly equivalent to eight hours of noon time intensity of near ultraviolet. The computation was made using the graphs of Gates (1966) and the atmospheric conditions assumed by Norris (1967). Air mass as a func-

tion of time of day was determined with the Smithsonian Meteorological Tables (1963). If the animal's total daily exposure of near UV is roughly equivalent to four hours of noon intensity and if one third of its torso surface of approximately 70 cm² were exposed to these wavelengths, about 28×10^6 ergs/day would reach the body cavity if the black peritoneum were removed. In other words, at wavelengths between 320 and 400 m μ , twice the minimum energy needed to increase mutations by an order of magnitude in *E. coli* would reach the internal organs of a desert iguana without its black peritoneum.

SUMMARY

A quantitative analysis of the in vivo absorption of solar radiation by vertebrate tissues was made using a Beckman DK-2A spectrophotometer as a transmittance unit. Light and electron microscope studies in conjunction with spectrophotometer measurements have revealed the presence of melanin in very dense concentrations in the skin of animals without black peritoneums, intramuscular deposits of melanin in lizards with thin body walls, and a surface configuration of keratin which could be functioning as a three dimensional diffraction grating.

The correlations in the literature of diurnal habits and the presence of internal pigments in reptiles, and inferred decreased light transmission is confirmed spectrophotometrically. Light transmission in reptiles is a function of body wall thickness and the amount of melanin in the body wall, although the amount of melanin present is by far the most significant factor. For example, the heavily pigmented, though very thin, body wall of a black desert beetle excludes more light from the body cavity than most vertebrates measured. The poor absorption by pure water of ultraviolet light available from the sun is reemphasized. The amount of solar energy absorbed by the blood is determined. A graphic method is used to illustrate the relative absorbing efficiencies of the skin, the muscles and the black peritoneum.

The following information or conclusions are derived from this study:

1. The quantity and quality of light reaching the body cavity of all diurnal animals examined is remarkably consistent irrespective of the presence of a melanized peritoneum. When a black peritoneum occurs, other light absorbing components of the body wall, e.g. skin or intermuscular melanin deposits, are less well developed or absent. The black peritoneum in those species which possess it excludes significant amounts of ultraviolet light over the spectral interval of 290-400 m μ .

2. The pigmented peritoneum seems insignificant in thermoregulation because (a) it absorbs usually about 5% of incident solar energy whereas the skin usually absorbs 60-70% and the muscles 10-20%; (b) it is present in many aquatic amphibians and fishes which would lose any heat gained to the surrounding water; (c) since all diurnal animals are opaque to light passing completely through the body,

they would absorb any penetrating energy anyway. The peritoneum does not seem to be a heat shield for internal organs because there is intimate contact of internal organs with the peritoneum; any energy absorbed by the peritoneum would be conducted very rapidly to the internal organs, thus precluding any significant temperature differential between the peritoneum and the internal organs.

3. Tissue death has no effect on light transmission provided the tissue is kept cool and does not dehydrate.

4. Ultraviolet light of wavelengths as short as 300 m μ and with intensities sufficient to induce mutations could penetrate to the body cavity of reptiles which have had the peritoneum removed.

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