than cycloheximide, to inhibit germination and growth of germ tubes might indicate a limited synthesis of proteins and RNA during these earlier stages of development but does not exclude the possibility of such syntheses. Indeed, the occurrence of polyribosomes in urediospores (*4*), the incorporation of radioactive precursors into protein (*5*), and the appearance of isozymes of cytochrome oxidase and acid phosphatase (*6*) indicate that protein synthesis actually does occur in the germinating spore even though there may be no net increase in protein (*5, 7*). Permeability factors could conceivably account for some of the observed differences in sensitivity to inhibitors but do not explain the general effectiveness of inhibitors of RNA synthesis only at early stages and of protein synthesis inhibitors primarily at later stages. More probably, these effects of inhibitors, taken together with cytological evidence that DNA synthesis occurs only during differentiation (*3, 8*), indicate a general onset of protein and nucleic acid synthesis that follows the stimulus to differentiation. They suggest that new RNA must be formed before differentiation, and that new kinds of protein are then synthesized during differentiation of the infection structures.

Reports that actinomycin D inhibits infection of excised wheat leaves and bean leaf discs (*9*), and that it inhibits infection of flax by *Melampsora lini* only if applied earlier than 5 or 6 hours after inoculation (*10*) may be accounted for by the sensitivity of postgermination stages to actinomycin D.

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Lizard Reflectivity Change and Its Effect on Light Transmission through Body Wall

Abstract. *Light transmission through the body wall of living, color-labile desert iguanas* (Dipsosaurus dorsalis) *was measured by spectrophotometry. In the dark phase, the body wall's absorption of ultraviolet light and visible light was approximately twice that of the body wall in the light phase. The shorter wavelengths of ultraviolet could penetrate the body wall in the light phase but not in the dark phase. The intensity and wavelengths of light which could penetrate the body wall without pigments are potentially mutagenic when judged by bacterial standards.*

Damaging physiological effects of solar-radiant energy have been observed for years (*1*). Black peritoneums were noted in colorless fish, whereas clear peritoneums were found in dark-colored forms (*2*). Pigments occur around the central nervous system or around the gonads of many diurnal vertebrates, or in both places, but not in their related nocturnal forms (*3*). An ecological study of six species of *Anolis* (*4*) demonstrated that the degree of peritoneal pigmentation was directly related to the amount of time that the animals spent in the sun. Sunlight kills developing fish embryos (*5*) and unpigmented cave animals (*6*). Quantitative measurements of photobiological effects in specific wavelength bands of near-ultraviolet and visible light are lacking in higher vertebrates. Such photobiological effects of near-ultraviolet and visible light, however, have been measured quantitatively for *Escherichia coli* (*7, 8*). Potential specific mechanisms for the "mutations" observed by Webb and Malina (*8*) in *E. coli* include possible binding of a chromophore or chromophores through intercalation with the DNA of the cell. Riboflavin, vitamin K, or "any of several porphyrins also are possibilities for the chromophore" (*8*).

We now demonstrate that without black peritoneums color-labile desert iguanas would not be able to change color and thereby adapt to the rigors of a hot desert environment without exposing internal biochemical processes to sufficient visible and near-ultraviolet radiation to produce mutations by bacterial standards. Such biochemical reactions might easily affect gonadal maturation.

Color change typically alters reflectivity through the spectral range extending from the near ultraviolet (from about 320 nm) into the near infrared (to at least 1150 nm) (*9*). Change is thus centered within the wavelength band in which more than 80 percent of the incident energy from the sun arrives at the earth's surface. Recent investigations show that such change in the smaller desert lizards can greatly affect the animal's heating and cooling rates (*9, 10*) and suggests a thermoregulatory function (*9, 10*). The smaller reptiles showing labile reflectivity may have melanin deposits in the peritoneum, the membranous sheaths of the testes, the dura, between dorsal muscle blocks, and other tissues. Such black membranes receive their color from aggregations of melanin granules lying within fixed melanophores (*11*).

Some proposed that these black membranes protect internal organs against injurious amounts of ultraviolet light (*11, 12*), while others suggested they absorb significant amounts of heat and thus have a thermal function (*13*). The black peritoneum actually absorbs enough near-ultraviolet light from the sun (*14, 15*) during a day's exposure to prevent "mutations," as judged by bacterial standards (*7*).

Some species of diurnal lizards do not have black peritoneums; instead they have heavy concentrations of fixed melanin in the skin. Measurements of light transmission show that the body walls of such animals exclude as much or more light from the body cavity as the body wall plus the black peritoneum of reflectivity-labile lizards (*14, 15*). The coincidence of mobile dermal melanin and black peritoneums in one group of lizards and the absence of black peritoneums in other lizards with fixed dermal melanin may represent two evolutionary routes toward blockage of damaging radiation.

Reflectance and transmittance of the highly color-labile (*9*) desert iguana were measured with a spectroreflectometer. After the light-color phase had been established by heating the animal into its activity temperature range, and after reflectance had been measured (*9*), the lizard was anesthetized with ether (*14*), and its reflectance was measured again. A ventrolateral U-shaped incision was made in the body wall, the peritoneum was peeled off, and the living animal was mounted over an optical fused quartz disk (*14, 15*). Transmission was measured with the animal mounted so that the body wall flap covered the entrance to the integrating sphere of the spectroreflectometer, with the skin facing the incident light beam (*14, 15*). The hollow integrating sphere with its magnesium oxide lining collects virtually all transmitted light including scattered wavelengths as well as any minute quantity of fluoresced light that may have emerged from the inside of the body wall (*14*).

Immediately after the last measurement in the light phase, adrenocorticotropic hormone (ACTH) was administered to disperse the epidermal melanin, and sodium pentathol was infiltrated. An hour later, after maximum darkening (*9*), reflectance and transmittance were again measured on six adult lizards captured in the Imperial Valley, California (Fig. 1).

Results from two animals were not considered because of excessive blood loss. The variation found in the shortest wavelengths that penetrated the body wall was probably related to differences in body wall thickness and in the fixed dermal and epidermal melanophore pattern components. Transmission was highest at 1100 and 1300 nm, with a sharp water absorption band near 1450 nm and another at 1900 to 2050 nm. Reflectance change was greatest in the visible range, but extended some distance into ultraviolet and near infrared regions. Nearly twice as much visible (400 to 700 nm) and ultraviolet light (290 to 400 nm) penetrates the body wall in the light phase as in the dark phase (Table 1) (*16*). For all individuals with the black peritoneum removed visible and ultraviolet transmission exceeded the minimum levels reported to be mutagenic to *E. coli*, since 4.7 $\times$ 10^7 ergs cm^{-2} of visible light is sufficient to triple the mutations (*8*) and 1.4 $\times$ 10^7 ergs cm^{-2} of near-ultraviolet radiation also induce mutations (*7*).

Two factors probably combine to make the amount of visible light reaching internal organs nondestructive. First, no lizard spends all day in the sun at the beginning of summer, but instead shuttles in and out of direct sunlight during thermoregulation and other activities. Second, the animal's positioning with respect to the sun changes exposure of individual organs within the body cavity to direct sunlight during parts of the day. Taken together [50 percent of the "day" (9 a.m. to 4 p.m.) in the sun and an organ facing direct sunlight 50 percent of the time], a conservative estimate of the amounts of light reaching a given internal organ would be one-fourth of that calculated above, or—for the four animals—an average of 1.4 $\times$ 10^7 ergs cm^{-2} day^{-1} of visible radiation in the light phase with an intact peritoneum. Despite the above-mentioned behavior of lizards, the peritoneum is still essential for protection from visible light; without it, 6.3 $\times$ 10^7 ergs cm^{-2} day^{-1} would penetrate in the light phase; 3.8 $\times$ 10^7 ergs cm^{-2} day^{-1} in the dark phase (if one assumes 4.7 $\times$ 10^7 ergs cm^{-2} will triple the mutations).

Table 1. Body wall transmission, in light- and dark-color phases (from 9 a.m. to 4 p.m.), of total ultraviolet and visible energy reaching the peritoneum.

Specimen number	Total visible energy (ergs cm^{-2})		Total ultraviolet energy (ergs cm^{-2})	
	Light phase	Dark phase	Light phase	Dark phase
1	30.1 $\times$ 10^7	18.9 $\times$ 10^7		
3	20.1 $\times$ 10^7	10.0 $\times$ 10^7	4.9 $\times$ 10^7	1.5 $\times$ 10^7
4	16.3 $\times$ 10^7	10.0 $\times$ 10^7	1.3 $\times$ 10^7*	0.6 $\times$ 10^7*
5	33.9 $\times$ 10^7	22.6 $\times$ 10^7	6.2 $\times$ 10^7	2.8 $\times$ 10^7

*These values are only for 400 to 350 nm. There were no measurements at shorter wavelengths for this animal.

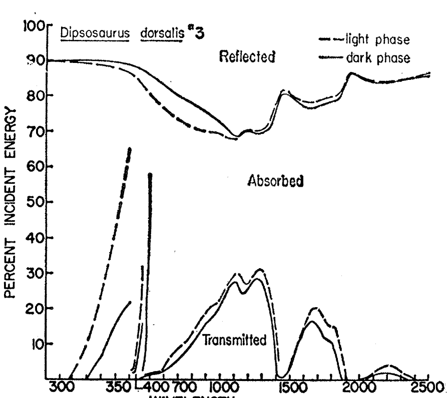

Fig. 1. Reflectance and transmittance in light- and dark-color phases of *Dipsosaurus dorsalis*. The reflectance curves are upside down and read from the top down. The areas in which energies are reflected, transmitted, and absorbed are so labeled. The sum of reflected, transmitted, and absorbed energy at a given wavelength equals 100 percent of energy incident at that wavelength. Measurements of energy mode transmission (*16, 17*) lie between 310 and 400 nm. The abscissa is expanded ten times between 290 and 350 nm.

The peritoneum is also essential for protection from near ultraviolet light, though less obviously so in the dark phase. We calculate (*17*) that, even with shade seeking and posture changes, near-ultraviolet reaching the body cavity if there were no peritoneum would average, for the four animals, 1.9 $\times$ 10 ergs cm^{-2} day^{-1} in the light phase and 0.7 $\times$ 10^7 ergs cm^{-2} day^{-1} in the dark phase. An intact peritoneum provides the body cavity with total (or nearly total) protection from solar ultraviolet irradiation (*14, 15*).

Thus, even given behavioral and postural changes during the day, internal light-shielding membranes are apparently essential for photobiological protection in light-phase animals, and less obviously so in dark-phase animals. Normally, diurnal lizards are in their light phase during most of any warm day. The greatest possible exclusion of visible and ultraviolet light from the body cavity of a reptile probably would be advantageous, since in *Escherichia coli* the number of mutants caused by near-ultraviolet and visible light is directly proportional to the irradiance (*7, 8*). If presumed mutagenic or otherwise damaging effects of ultraviolet and visible light are also proportional to dosage in higher organisms, no threshold intensity may exist.

As the desert iguana warms into its range of temperature for normal activity, and as its skin becomes increasingly pale, a significantly greater proportion of the incident radiation penetrates the body wall to the peritoneum. Even in the moderately thick body wall of the desert iguana (1 to 4 mm), the internal black peritoneum serves as an essential shield against incoming radiation. Without this shield, reflectivity change to the light condition could not be tolerated. In thinner-walled forms, such as the brown shouldered lizard *Uta stansburiana*, additional internal shields (*14, 15*) intercept even more solar radiation. Without these shields, small lizards in their light phase would probably receive damage, immediate or long-term, to internal organs from radiation. Reflectivity change and its associated component of thermoregulation, in small to medium-sized diurnal desert lizards, may be possible only because of the presence of one or more underlying radiation shields.

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21. We thank J. Townsend for the use of his YSI radiometer for initial calibrations of the Beckman DK-2A in St. Louis. Supported in part by USPHS grant ES00139, through the Center for the Biology of Natural Systems, in part by NASA (NSGT 4-62) through the Space Science Center at University of California at Los Angeles and in part by NSF grant GB4566.
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Mole Rat Spalax ehrenbergi: Mating Behavior and Its Evolutionary Significance

Abstract. *Mating behavior of the subterranean mole rat,* Spalax ehrenbergi, *consists of three distinct stages—agonistic, courtship, and copulation.* Spalax *sexual behavior reflects certain cricetid affinities, some features general in rodents, and others presumably related to its subterranean, territorial life. Within four groups of* Spalax ehrenbergi, *each with different numbers of chromosomes, recently found in Israel, mating behavior seems to provide partial reproductive barriers. Selective matings between chromosome forms may complement a cytologic isolating mechanism to prevent widespread natural hybridization.*

The mole rats, genus *Spalax*, are subterranean rodents comprising the monotypic family Spalacidae. Little has been reported on the biology of natural populations of *Spalax* (*1*), nor is its classification satisfactory (*2*). The currently accepted taxonomy (*3*) recognizes three species, *Spalax microphthalmus*, *S. leucodon*, and *S. ehrenbergi*, distributed from southeast Europe through the Middle East to North Africa.

Phenotypic variation in *Spalax* is relatively small, in contrast to its considerable genetic variation. Chromosome variation in *S. leucodon* (*4*) and *S. ehrenbergi* (*5*) is remarkable. Four forms of *S. ehrenbergi* occur in Israel and neighboring areas having diploid numbers ($2n$) 52, 54, 58, and 60, respectively (*5*). These mole rats are distributed clinally and parapatrically from north to south, along biogeographic regions of increasing aridity, probably reflecting adaptive systems. The $2n = 52$ form ranges in the Upper Galilee Mountains; $2n = 54$ form is found in the Golan Heights and Mount Hermon; $2n = 58$ form is found in central Israel; and $2n = 60$ form is found in Samaria, Judea, and northern Negev.

The relative rarity of natural hybrids, karyotypic homozygosity, and the mating trials reported here suggest that the four forms are probably sibling species. If this hypothesis is substantiated, Pleistocene speciation of *Spalax*, masked by convergent morphological adaptations to subterranean life, might have been operating on a larger scale than hitherto assumed. We now report mating behavior of *Spalax* which suggests taxonomic affinities and the operation of ethologic barriers to reproduction between chromosome forms.

Mating experiments were conducted with adult animals of all chromosome forms, collected across Israel from August through November 1967. Each mole rat was kept in a separate cage to prevent casualties. Experiments were conducted in aquaria (70 by 35 cm) with a 5-cm layer of sawdust. For tests, animals were transferred to each other's cage, male to female and vice versa. Observations were recorded on movies, color slides, and tape recorder. When copulation occurred it was usually interrupted before ejaculation to save females for further tests. Description of copulation is based on three matings which were allowed to proceed to termination. Of the three females, one became pregnant but died several days later; the other two were not pregnant.

Seventy-seven mating trials were conducted on 17 females and 13 males, including animals of different chromosome forms. Only nine females were receptive. Receptivity was determined on the basis of behavioral, not vaginal, estrus. Copulation was achieved in 15 trials, involving 8 of 20 homogametic and 7 of 45 heterogametic tests. Homogametic tests involved partners of the same chromosome forms, whereas