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Effects of Solar Radiation on Animal Thermoregulation

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1. Introduction

Solar radiation affects all aspects of the Earth's environment both directly and indirectly. Radiation from the sun produces a wide range of wavelengths that reach Earth and are absorbed or reflected from animate and inanimate surfaces. Visual, ultraviolet and infrared wavelengths, and solar intensity are the primary variables measured to evaluate their effects on the behavioral, thermoregulatory, and cellular responses of organisms. This review will focus on the effects of solar radiation on animal thermoregulation and the various methods used by scientists to assess the effects of infrared radiation on skin temperatures.

1.1 Ectotherms vs. endotherms

All organisms regulate their internal body temperature (T_B) to maintain a relatively constant temperature within a small range; in effect the rate of heat gained or produced must be balanced with heat lost to the environment. Animals are generally divided into ectotherms or endotherms based on how they maintain internal T_B . Ectotherms, previously referred to as “cold-blooded”, are animals such as invertebrates, amphibians, reptiles, and fish who regulate their T_B externally primarily through behavioral mechanisms that alter heat exchange between their bodies and the environment. Endotherms such as birds and mammals, once described as “warm-blooded”, are able to generate heat internally. Comparatively, leaky cell membranes, a greater amount of enzymes, and insulation (hair, feathers, and subcutaneous fat) contribute to endotherms having a higher basal metabolic rate than ectotherms, allowing them to maintain a relatively constant T_B separate from their ambient surroundings—known as homeothermy or euthermy (Nagy, 2004). Notwithstanding, some larger invertebrates and fish employ muscle activity to perform some degree of homeothermy for short periods and some small mammals and birds relax their thermogenic abilities to enter states of torpor or may even hibernate at certain times of year—a thermoregulatory strategy known as daily or seasonal heterothermy.

1.2 Heat transfer and thermoregulation

Each species has an optimal temperature where cellular processes are ideally maintained to optimize energy expenditure. Heat transfer across the body surface must be balanced lest an individual succumb to extreme heat gain or loss, a possibility especially in extreme environments such as polar or desert regions. Most organisms attempt to remain within a favorable range of temperatures. For homeotherms, this is known as the thermal neutral zone (TNZ). This optimal range of ambient temperatures typically lies between 30-42°C for

homeothermic or euthermic organisms (Speakman, 2004). Within this range, metabolic rate is minimal. Outside the TNZ, metabolic energy is required to maintain T_B within the optimal range. Metabolic activity involving temperature-dependent enzyme activity will not function properly if the animal becomes hypo- or hyperthermic. Thus, thermoregulation is an integral part of an organism’s energy balance.

Visual and ultraviolet wavelengths of solar radiation may be reflected or absorbed by animal surfaces, producing distinctive coloration and/or synthesis of vitamin D in terrestrial vertebrates, but infrared radiation is absorbed directly. Infrared radiation can increase T_B near to or exceeding the upper critical temperature (UCT). The UCT is the greater temperature limit where behavioral modifications are not enough to inhibit heat absorption and therefore energy must be expended in the attempt to dump excess heat. The temperature range from the UCT to the upper lethal temperature (ULT), the T_B where an organism can no longer thermoregulate and dies of overheating, is known as the zone of evaporatory cooling where evaporation of metabolic water is the most efficient, and sometimes only, method available for transferring excess heat. On the other hand, the lower critical temperature (LCT) is the turning point at which more heat is lost to the environment than is normally metabolically produced. The lower lethal temperature (LLT) is the extreme cold temperature where an animal can no longer produce enough heat and dies of hypothermia. The range of temperatures between the LCT and LLT is known as the zone of metabolic regulation, where heat production through metabolic processes such as shivering or non-shivering thermogenesis is necessary to increase T_B . Figure 1 depicts a general TNZ graph, LCT, UCT, and zones of energy use (Randall, 2002).

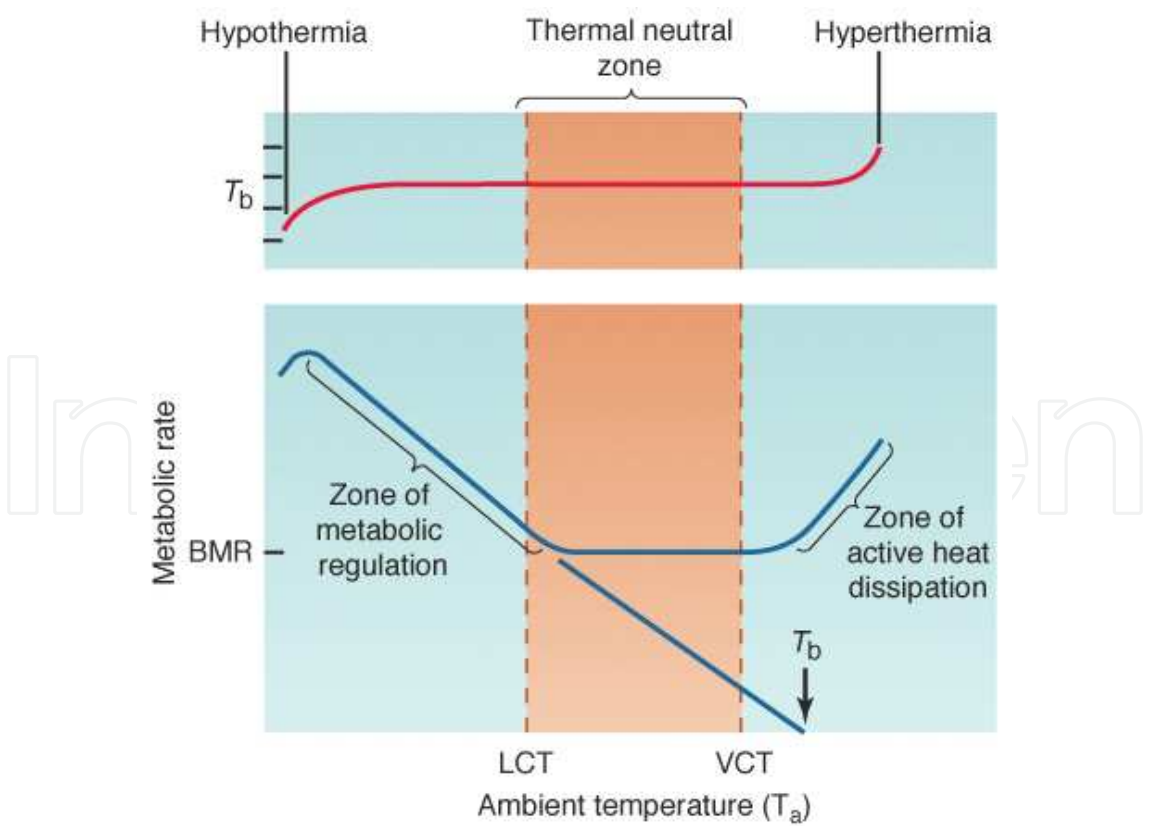


Fig. 1. Thermal neutral zone graph showing lower and upper critical temperature, zones of metabolic regulation and evaporation. Source: Randall/Eckert Animal Physiology 5ed.

Heat is transferred by four mechanisms: radiation, conduction, convection, and evaporation. Many species combine methods to absorb or transfer heat as efficiently as possible. Solar radiation plays a large part in determining not only ambient and body temperatures but animal behavior as well. A wide variety of species have developed methods to reduce the cost of thermoregulation by behaving certain ways: seeking shade, burrowing, panting, gular fluttering, wing flapping when exposed to temperatures above the UCT, entering short bouts of torpor or longer bouts of hibernation, increasing insulation, or migrating.

1.2.1 Radiation

The sun is Earth's principal source of radiative energy. With a surface temperature of approximately 6000K, the sun's electromagnetic radiation transmits some of this heat in the form of infrared radiation to our atmosphere and to varied surfaces on Earth (Speakman, 2004). Infrared radiation, undetectable to the human eye, is the peak wavelength emitted by objects with a surface temperature of -20° to 40°C . Special cameras sensitive to infrared wavelengths allow humans to record thermal images and videos of infrared radiation emitted by both inanimate objects and organisms, making it possible to effectively measure the surface temperature of whatever is within the camera's field of view (McCafferty, 2007). The amount of radiated heat detected depends upon factors such as the emissivity and absorptivity of an inanimate object or organism. Emissivity is defined relative to what is known as a black body, a perfect emitter with an emissivity of 1.0. Most animals have an emissivity value within 0.90-0.98, often dependent on surface properties such as fur or skin color. Surfaces either reflect or absorb light to varying degrees contingent on pigment levels and texture that in turn affect emissivity. Dark colors absorb energy within the infrared spectrum, increasing the absorptivity of inanimate objects or organisms compared to light colors which reflect visual wavelengths of solar energy. Water content, often high in living organisms, additionally contributes to an animal's elevated emissivity, since water is itself an excellent emitter.

1.2.2 Conduction

Heat transfer between two solid objects in contact with one another is known as conduction. Heat energy travels down a thermal gradient and thus is conducted from a warmer object to a cooler one. This attribute also allows for conduction within a single body, if the core of an object or organism is warmer than the surface layer for example, heat will be conducted along the gradient. The rate at which this transmission occurs depends on several factors such as the material properties of both items, distance heat must travel, and the actual surface area that is physically in contact. Like radiation, thermal conductivity relies on certain properties of the materials in question. Insulation is the opposite of conductivity, meaning objects or organisms having little to no insulation may have a high thermal conductivity. This increases the rate and likelihood of heat transfer through conduction. Ectotherms such as insects, amphibians, reptiles, and fish have little insulation, making them more likely to gain or lose heat to their surroundings. In a given environment, a sun warmed rock in an otherwise cool environment can be critical to an ectothermic animal trying to remain active. In fact, insulation would be

detrimental to ectotherms relying on external heat sources, because any such barrier would slow the rate of heat transfer into the body (Speakman, 2004). Endotherms such as birds and mammals have varying degrees of insulation made from feathers, fur, and/or fat deposits allowing them to retain their internal heat and thus rely less upon external heat sources.

The ratio of surface area to the volume of an organism is also an important component of heat transfer through conduction. Animals not only gain or lose heat via conduction with surfaces and objects in the environment they come in contact with, but also from the core of the body outwards toward the skin surface. Larger animals create thermal inertia, requiring less energy to balance heat loss and so have a low thermal conductance. Smaller animals lose heat rapidly and need more energy per gram of tissue to maintain heat balance with their higher thermal conductivity. Behavioral adjustments that change the amount of exposed surface area as well as physiological responses can increase or decrease an animals' thermal conductivity in either short periods of time or for seasonal modifications.

1.2.3 Convection

Rather than two solid objects adjacent with one another, convection requires one fluid coming in contact with another fluid (water or air) of a different temperature. Rather than heat transferring at the molecular level or through electromagnetic waves, heat is dispersed via the bulk motion of fluids (Cengel, 2003). Once again the temperature gradient between the two surfaces influences the rate of heat transfer. Conduction and convection along the human body is illustrated in Figure 2. Water conducts heat 23-25 times greater than air, making water an efficient medium for heat loss exhibited by both animals and humans moving towards sources of water during periods of intense solar radiation and high ambient temperatures (T_A). Wind is also an efficient mode of convection. When cool air flows over the warmer skin surface of an animal, this may allow that organism to remain active longer on warm, sunny days. Convection even occurs within the body. Blood transfers heat throughout the body, bringing warmth from the core to the extremities, or bringing cooled blood from the surface back to overheated organs or muscle tissue.

1.2.4 Evaporation

Evaporation uses the energy required to convert liquid water to gas, allowing organisms to transfer heat even if the T_A is greater than T_B . This is often the only mechanism available to organisms during prolonged exposure to solar radiation that efficiently dumps excess heat in an effort to maintain a safe T_B . Both environmental as well as metabolic water (Figure 2) can be used to transfer heat from an organism's body to the surrounding air (Gupta, 2011). Though highly effective, if the air is saturated with moisture already, such as during periods of high relative humidity or in constantly humid environments, evaporation as a thermoregulatory mechanism is rendered almost useless because net evaporation ceases when the air can no longer absorb additional moisture (Speakman, 2004).

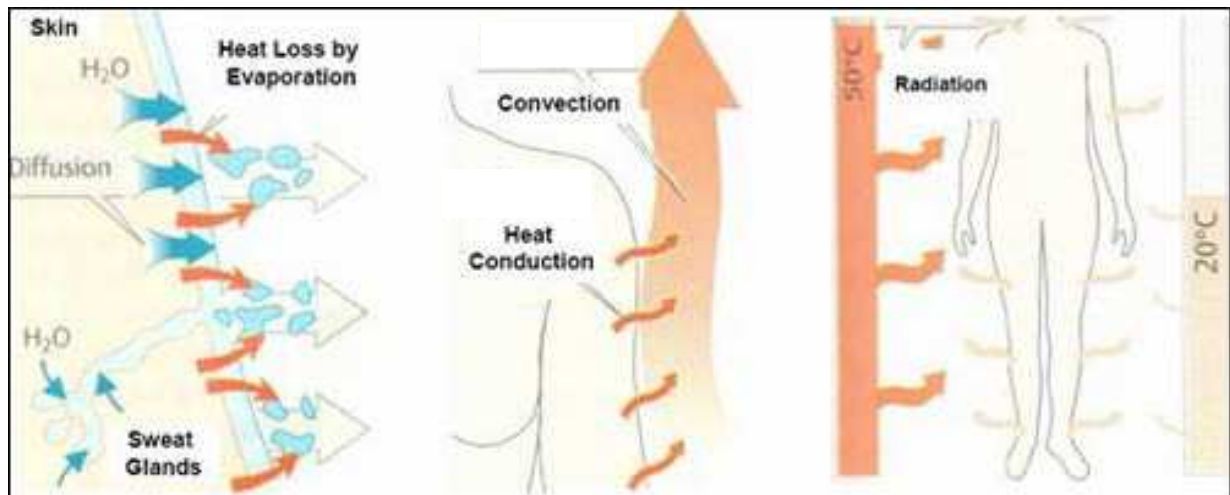


Fig. 2. Heat loss via evaporation, convection, conduction, and radiation using the human body as an example. Source: Gupta, 2011.

1.3 Ultraviolet radiation

The emitted solar spectrum contains ultraviolet (UV) radiation that is separated into different wavelength bands: UVA (315-400 nm), UVB (280-315 nm), and UVC (200-280 nm). UVC and 70-90% of UVB wavelengths are typically blocked by the ozone layer (Rafanelli et al., 2010; Schaumburg et al., 2010). However, due to ozone deterioration there is an increase in UVB levels, especially over Antarctica. Certain environments, such as polar areas, are more susceptible to varying levels of UV radiation (Rafanelli et al., 2010). Organisms across all taxa are directly or indirectly affected by UV radiation. Such responses are discussed in more detail later in this chapter.

1.4 Infrared technology

Not too long ago, infrared technology was out of reach of the scientific community. Cameras with infrared (IR) imaging were large, poorly maneuverable as field equipment, and expensive. However, it is currently possible to obtain hand held thermal cameras for under \$2,000. The introduction of smaller, manageable, and relatively inexpensive equipment has opened the gates for biologists to begin using infrared imaging in their research. Already a number of experiments have validated their use and lauded their capability to be invaluable to research. Thermal images can be obtained to document the variation on an organism's body surface owing to different types and properties of insulation, or other thermal or physiological properties of an organism's body. This provides researchers with added insight on both the physiological and behavioral effects that solar radiative heat gain may have on thermoregulatory responses of animals.

2. Ectotherms

2.1 Invertebrates

Insects and other invertebrates live within their own microclimates and just a small change in position can affect their T_B . Some species of ants, for example, move between nest areas

during seasonal changes or use objects such as leaves or rocks to alter their insulative properties. Fire ants are able to raise their nest temperature by modifying their nest shape relative to the sun's angle, while wood ants use solar radiation in combination with behavioral modifications to maintain ideal nest temperatures (Vogt et al., 2008; Galle, 1973). Non-communal insects such as grasshoppers bask to increase their T_B (O'Neill & Rolston, 2007). Butterflies in general often bask or use ground contact to gain heat by conduction and convection then seek shade or minimize their exposed wing surface area to either facilitate heat loss or decrease heat absorption (Clench, 1966). Basking monarch butterflies take to the air during periodic cloud cover before returning to their clusters (Calvert et al. 1992). The lack of direct sunlight is enough for them to expend energy, creating heat through movement of their body. The difference in temperature from direct solar radiation to cloud cover likely stimulates this adaptive response in butterflies, causing them to return to the safety of the colony in the chance that any sustained cloud cover could lead to lower thoracic temperatures during migrational flight (Calvert et al., 1992). Several species of Arctic butterflies select specific basking substrates and orient their wings perpendicular the sun, allowing them to absorb heat in order to continue locomotion even at very low T_A (Kevan & Shorthouse, 1970). Without the ability to maintain their threshold temperature during flight, stranded butterflies could be subjected to increased predation and risk exposure to cold stress.

Honeybees use solar radiation at T_{AS} under 30°C , the minimum thermal threshold, as an alternative to generating energy to raise thoracic temperatures. Relying on solar radiation to increase T_B enhances muscle efficiency during flight and allows the bees' suction pump to function at low T_A . If overheating occurs, bees actively seek water to ingest, using the liquid to cool thoracic temperatures (Kovac et al., 2010). Other insects such as wasps also use solar radiation to increase thoracic temperature so their own active production of heat is reduced (Kovac et al., 2009).

Insects are not the only invertebrates to be affected by solar radiation; those living within the intertidal zone of oceanic coastlines are subjected to solar rays as well. Although many organisms can avoid direct solar radiation by moving to safe hiding places between rocks, in tide pools, or in the sand via burrowing, others are limited in their ability to use locomotion to do so. For example, marine snails will flee from areas exposed to direct solar radiation and move to cooler areas close by often in shade or under the waterline (Chappon & Seuront, 2001). Periwinkles are unable to flee the declining water level and are thus equipped to withstand relatively short periods of desiccation and thermal stress. In fact, they often orient themselves frontally or dorsally facing the sun to limit the amount of sunlight hitting their lateral surfaces. By reducing the surface area perpendicular to the radiation, periwinkles can maintain a lower T_B when subjected to the desiccating heat and solar intensity during low tides (Muñoz et al., 2005).

2.2 Amphibians and reptiles

Small amphibians and reptiles must be careful to maintain a certain T_B and are often affected by microclimate changes. It is well known that ectotherms use basking to supplement heat gain, making solar radiation an important thermoregulatory tool (Nagy,

2004). Turtles will often choose habitats with access to direct solar radiation and bask on sunny days (Dubols et al., 2009). Ectotherms will frequently expose a maximum amount of surface area toward the sun, regulating the interception of solar radiation through body orientation. Some reptiles have dark patches to aid in heat absorption. Certain species of lizards orient their bodies either parallel or perpendicular to the sun's rays based on T_A . Lizards living in high altitudes increase basking frequency, are more likely to orient perpendicular to the sun, and restrict durations of activity to minimize the range of temperatures to which they are exposed (Adolph, 1990; Hertz & Huey, 1981). However, this can raise their chances of being captured by a predator. Kestrels in Norway return to their nests with an increasing amount of lizards, which typically peaks in midday. Solar intensity, as well as T_A , often influences the abundance of lizards available to kestrels due to possible patterns in lizard behavior (Steen et al., 2011). The giant tortoise from South Africa is another species known to orient itself based on solar radiation. When facing away from the sun, the carapace casts a shadow on the head and neck area allowing the tortoise to inhibit the rate at which its T_B increases. This maintenance of a larger thermal gradient between the skin surface and T_A allows the tortoise to forage for longer periods under direct solar radiation (Coe, 2004). Some species of toads living at high altitudes are more active on sunny days, raising their T_B by 20° or more in some cases (Lambrinos & Kleier, 2003). Heat gain using solar radiation also aids in digestion and increases growth rates of toads and other anurans at both extreme and moderate elevations. When food is withheld, toads end basking and allow their T_B to decline (Lillywhite et al., 1973). Dependence on solar radiation makes it possible for most species of reptiles and amphibians to live at high elevations in tropical regions.

3. Endotherms

Evaporative cooling, relying on environmental or body water, is an important mechanism used by many endotherms to avoid overheating. Numerous species have evolved behaviors that facilitate heat loss or minimize heat gain from solar radiation. Evaporation can occur passively through the skin of mammals and birds. Animals lacking sweat glands rely on saliva spread onto the surface of their body or may pant. By changing their posture or orientation to the sun, some animals expose a larger percentage of their surface area to cooler substrates allowing heat to be conducted away from their bodies. Solar radiation correlates with changing postures or orientations to reveal more of their surface area and is employed by some species such as sea lions to increase or decrease exposure to solar radiation. Anteaters, whose prey is not very energy rich, often use solar radiation to offset metabolic costs of thermoregulation by avoiding sunlit areas on hot days. They also switch their foraging behavior to nocturnal periods when days are exceptionally hot (de Sampaio et al., 2006).

3.1 Ratio of surface area to volume

Organisms with a large ratio of surface area to volume such as small passerines and mammals must be careful to maintain heat balance, as they are prone to rapid heat exchange. They require a large amount of energy intake to aid in heat balance; birds and bats even more so due to the high metabolic cost of flight. Treecreepers, a type of bird found

in forests of Spain, selectively forage on certain areas of trees depending on the T_A . In warm temperatures the birds tend to forage on shaded areas whereas they prefer areas exposed to sunlight in cooler temperatures (Carrascal et al., 2001). By maintaining T_B using behavioral thermoregulation the birds are able to save energy that can be allotted to other expenses such as predator avoidance, especially since foraging in sunlit patches increases their predation risk. In fact, the overall abundance and species richness of birds in a montane forest was calculated to be mainly a function of solar radiation (Huertas & Diaz, 2001). By choosing areas higher in available sunlight, small birds can lower their metabolic cost of thermoregulation and improve survival in cold temperatures. In warm environments small birds are able to balance thermoregulation by avoiding sunlit areas. Verdins are able to reduce their metabolic rates by shifting to wind and solar-shielded microsites, allowing for a highly reduced rate of evaporative water loss. In order to maintain efficient use of energy and water, verdins must actively select thermoregulatory beneficial areas within their habitat (Wolf & Walsburg, 1996).

3.1.1 Torpor

Small mammals often use torpor as a thermoregulatory strategy. By decreasing T_B and metabolic rate, small animals can substantially reduce energy expenditure. Though it requires energy to arouse from torpor, some mammals can choose sites exposed to solar radiation during the day and are able to bask in sunlight, using the passive absorption of radiant heat to rewarm their body and profit from the energy saved while torpid (Warnecke et al., 2008).

3.2 Birds

Birds lack sweat glands so they must rely on other mechanisms of heat reduction. Even something as simple as changing orientation in relation to the sun can have a large effect in reducing heat gain. Flying is an energetically expensive mode of locomotion that can generate high heat loads. Herring gulls, for example, are able to lessen heat gained by reducing exposed surface area and orienting their bodies in a way that presents only the white-feathered surface, allowing for a greater degree of reflection rather than absorption of solar energy (Lustwick et al., 1978). The Great Knot, a shorebird from Australia, raises its back feathers to initiate a possible increase in convective or cutaneous cooling (Battley et al., 2003). Cormorants often spread their wings on land; most likely a wing-drying strategy but also a mechanism used to dissipate heat. During periods of low wind these cormorants rely on the sun to dry their plumage. This behavior saves cormorants the large energetic cost it would take to dry their feathers using metabolic heat to evaporate the water (Sellers, 1995).

Depending on the environment, many incubating birds that are restricted to their nest site must tolerate direct solar radiation. For example, the Heermann gull resorts to ptilomotor responses, posture changes, and increased respiration through a gaping mouth, employing several mechanisms of heat dissipation to offset heat gain from direct radiation as well as conduction from the nest substrate (Figure 3) (Bartholomew & Dawson, 1979).

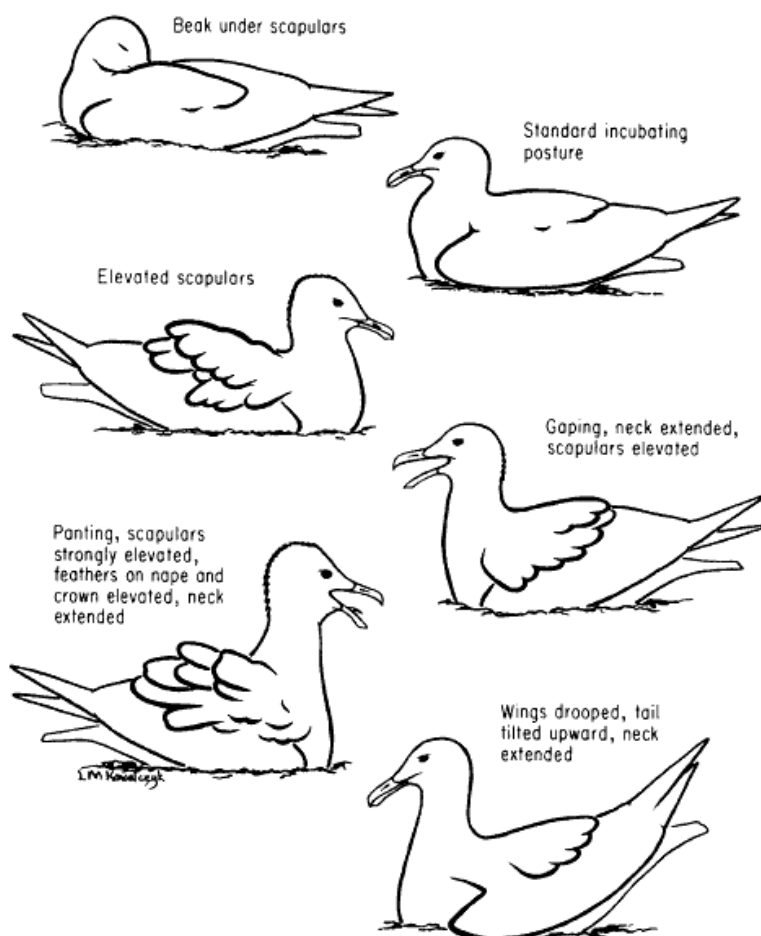


Fig. 3. Thermoregulatory posture changes in the Heerman gull. Source: Bartholomew & Dawson, 1979.

Kentish plovers abandon their nests when exposed to high T_A and solar intensity. This species rushes to a nearby water source to soak their ventral surface, quickly reducing their T_B by convection. Although this raises the possibility that egg temperature will increase to dangerous levels in the absence of the individuals that are incubating the egg, overall this behavior allows the plovers to stay at their nests for longer periods (Amat & Masero, 2009). Adult birds and their chicks nesting in extreme environments such as the arctic tundra are exposed to long periods of sunlight along with low T_A , low sun angles and unobstructed wind. By exposing more surface area (i.e. facing away from the sun), Greater Snow goose chicks, which have yellow down in comparison to the grey down and white feathers of older chicks and adults, are able to increase the amount of radiative heat gain. The plumage of younger goslings may even absorb solar radiation at a higher rate than adult plumage (Fortin et al., 2000). Grackle chicks exhibit shade seeking behavior, moving around the edges of the nest in attempts to keep their highly vascularized heads shaded. These chicks also orient their bodies toward the sun to diminish absorptive surface area which is a behavior also seen in chicks of Ferruginous hawks, gulls, and adult titmice and chickadees (Glassey & Amos, 2009; Tomback & Murphy, 1981 Bartholomew & Dawson, 1954 Wood & Lustick, 1989 in Glassey & Amos 2009). Moderating heat load is extremely important, especially by

nestlings and small passerines, for without such behavior or access to shade in high T_{AS} small birds can succumb to heat stress within 20 min (Glassey & Amos, 2009).

3.3 Mammals

Most species of mammals, particularly larger ones, are well insulated with fur, fat, or a combination of both. Often this creates conflicting thermoregulatory demands depending on the gradient between body and ambient temperature as well as environmental variables such as solar radiation, wind speed, humidity etc. A variety of behavioral responses to solar radiation exposure have evolved in mammals.

3.3.1 Behavioral

Many mammals use simple methods such as body orientation or posture changes to balance radiant heat gain from solar radiation. The black wildebeest, which inhabits the savannah, a habitat that has little natural shade, orients itself either parallel or perpendicular to the sun depending largely upon skin temperature. As the intensity of solar radiation increases, wildebeests are more likely to change their position when standing so their bodies are parallel to the sun's rays. By minimizing the surface area exposed to solar radiation in a parallel orientation, wildebeests absorb 30% less radiant heat than if they stood in a perpendicular stance (Maloney et al., 2005). The angle of the sun, both daily and seasonal, also affects wildebeest body orientation. During the cooler season, when solar angle and intensity is reduced, the preference of body orientation decreases. By reducing heat gain these large mammals are able to lessen the energy needed for evaporative cooling. However, this orientation behavior decreases when there is a reliable source of water available (Maloney et al., 2005). Other African species, such as the eland, blue wildebeest, and impala also use preferential body orientations, positioning their bodies parallel to the sun in summer and perpendicular in winter (Figure 4) (Hetem et al., 2011). Once again, energetic demands drive these behaviors relative to the amount of direct solar radiation.

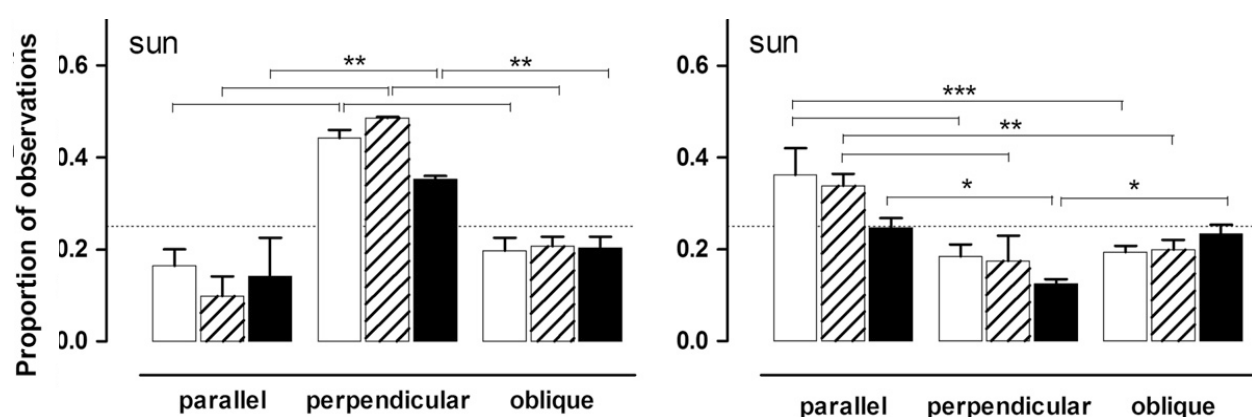


Fig. 4 Proportion of observations (mean \pm SD) in which eland (open bars), blue wildebeest (hatched bars) and impala (black bars) orientated parallel, perpendicular and oblique to incident solar radiation in winter (left panels) and summer (right panels). The dotted line represents the proportion expected if orientation was random (0.25); significant differences between orientations indicated by * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Source: Hetem et al., 2011

Marine mammals that haul out on land, such as the pinnipeds, face a thermoregulatory challenge when it comes to reproductive or molting periods. Developed for efficient locomotion and thermoregulation in an aquatic environment they often have thick fur, blubber, or a combination of both to protect them from frigid temperatures beneath the ocean surface. On land, however, these insulative properties, along with a low ratio of surface area to volume, become a hindrance to heat transfer across the body surface. The flippers of sea lions are long, hairless, and often thought to have a thermoregulatory function. South Australian fur seals, New Zealand and California sea lions respond to solar radiation by regulating the amount of flipper surface area that is exposed to solar radiation (Beentjes, 2006; Gentry, 1973). As temperature and solar intensity increases, sea lions unfold from a prone position with flippers tucked beneath their body to a dorsal up position with all four flippers laid out on the sand and exposed to the air for conductive and convective heat transfer (Figure 5) (Beentjes, 2006; Gentry, 1973).

Of course, the best method to inhibit solar radiation is to block or avoid it. Cape ground squirrels use their own tails to shade their bodies as well as orient themselves so that their backs are oriented toward the sun when the T_A exceeds 40°C . T_B is actually reduced over 5°C , allowing these squirrels to continue foraging for longer periods when exposed to direct solar radiation (Bennett et al., 1984). Male South Australian fur seals exhibit shade seeking behavior, not only blocking solar radiation but also transferring heat via conduction to a cool rocky substrate (Gentry, 1973). Marine mammals as large as the northern elephant seal, which periodically haul out on land, are able to use sand to block some of the solar radiation they would otherwise be subjected to during breeding or molting periods. This behavior known as sand-flipping, observed in some species of pinnipeds that use their fore-flippers to scoop sand up onto their backs, increases in New Zealand sea lions as solar radiation increases (Beentjes, 2006). The layer of moist and/or cooler sand facilitates heat transfer through conduction as well as creates a barrier against direct solar radiation. Southern sea lions have been observed to dig their foreflippers into the cool substrate to shield themselves from the sun's rays (Campagna & Le Boeuf, 1998). Flipper waving is another behavior often seen in several species of pinnipeds, exhibited by seals lying on their side, raising a flipper and sometimes moving it back and forth, using convection to diffuse heat from the body before letting it rest again. As solar radiation warms the substrate, heat gain increases through conduction and reflection, making behaviors such as posture changes, sand-flipping, and flipper waving by hauled-out pinnipeds increasingly beneficial to their overall energy balance. For some pinnipeds, solar radiation is often an indirect or combined stressor when associated with T_A and/or wind speed. Intense solar radiation, such as the levels recorded near the equator and other tropical regions, may only be tolerated if evaporative cooling is used, which may partially explain why tropical pinnipeds are often found near upwellings of cold water rather than in warm ocean currents.

Daily and seasonal migrations are often a result, at least in part, of solar radiation intensity. The marked ibex, which lives in arctic environments, has a low tolerance for heat gain. During the summer, males change their behavior, feeding mainly in the early morning rather than midday or evening. As solar radiation increases throughout the day, the marked ibex migrate to higher elevations, thus using the cooler air to reduce heat gain. Throughout the afternoon and evening, this species feeds in the cooler hours of the day before moving to higher altitude as T_A increases (Aublet et al, 2009).

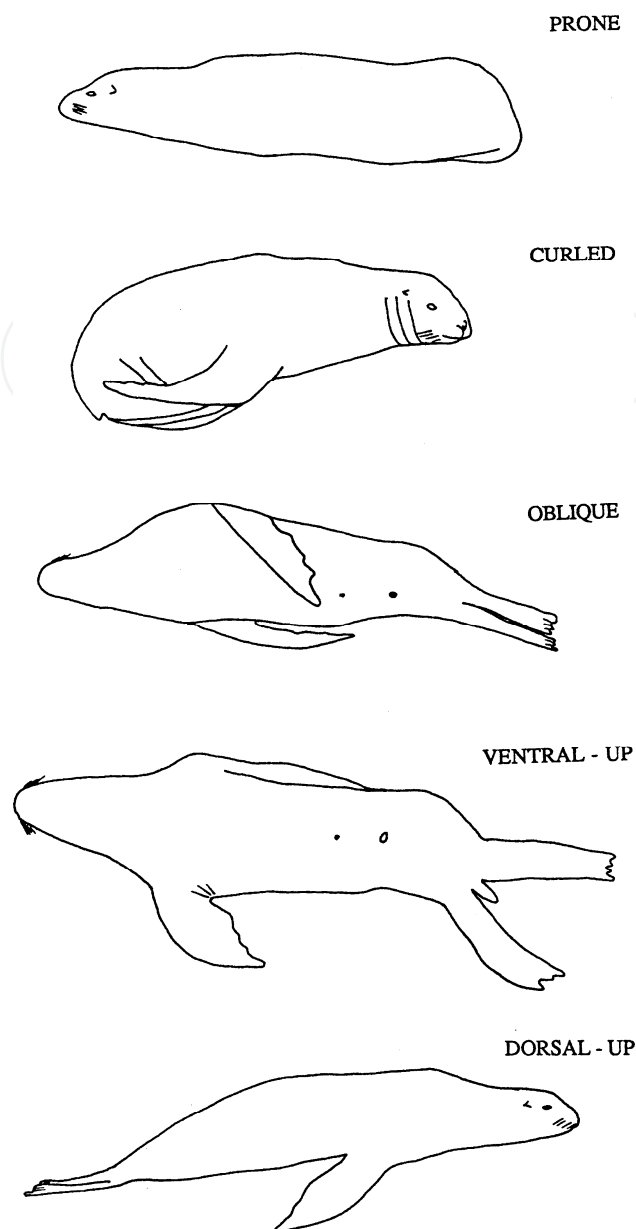


Fig. 5. Postures (prone, curled, oblique, ventral-up, and dorsal-up) used by New Zealand sea lions as solar radiation and ambient temperature increase. Source: Beentjes, 2006.

Seasonal migration can also be affected by solar radiation. Models using data collected over long periods or seasons are created to calculate the range of intensities of solar radiation over a large area such as a nature reserve or park. Collared pandas within Foping Nature Reserve, China have been radio tracked and their distributions in the park were overlaid with a map of 12 months of solar radiation data. During the warm months pandas moved to areas with lower solar radiation, whereas during the colder months they were recorded in areas of higher radiation. The model suggested that solar radiation does affect the distribution of giant pandas (Liu et al., 2011).

Smaller mammals are prone to losing heat rapidly due to their high ratio of surface area to volume but they are also susceptible to losing water through evaporation at a rapid rate. Degus, a species of rodent found in arid and semiarid environments, minimize the distances

they travel out in the open, away from the shelter of scrub brush. One hypothesis for this behavior is predator avoidance, but another possibility is to avoid heat gain in areas subjected to direct solar radiation. Degus also exhibit seasonal changes in behavior, reducing activity near midday in summer while remaining steadily active during winter. Temperatures $\geq 30^{\circ}\text{C}$ have not been measured in the microhabitat beneath the shrubs, preventing degus from reaching hyperthermic body temperatures while they remain sheltered from solar radiation. In order to both avoid predation and maintain efficient heat balance degus use the microhabitats underneath shrubs, especially during periods of high ambient temperature (Lagos et al., 1995).

Various species of bats roost in trees, exposed to sunlight and other environmental variables during day, unlike cave dwelling bats who are contained in a relatively stable microclimate and shielded from solar radiation. The wing membranes of bats, like sea lion flippers, are naked and incorporate a large amount of overall body surface area. This makes bat wings a likely tool for thermoregulation. Flying foxes, found mainly in the tropics, likely lack sweat glands and are exposed to the high temperatures and humidity of the forests they inhabit. These bats exhibit wing fanning and body licking, incorporating evaporation and convection to facilitate heat loss (Ochoa-Acuña & Kunz, 1999). Through exposure of greater amounts of wing surface, flying foxes can increase the area available for heat transfer as required during periods of increasing body and ambient temperature. Other species have special adaptations to aid them in releasing excess heat. The Brazilian free-tailed bat is known to fly during periods of daylight in the warmer environments it inhabits as well as taking part in long migrations. These bats have a unique vascular radiator lacking any insulative fur along their flanks (Reichard et al., 2010a). By flushing the area with warmed blood Brazilian free-tailed bats are able to efficiently dump heat when necessary while conserving body heat in the high altitudes they forage in by shunting blood away from the radiators (Reichard et al., 2010; Reichard et al., 2010b).

3.3.2 Physiological

Solar radiation is not only important when researching wild mammals but domesticated animals as well, especially livestock left out in large pastures with little to no shade. When cattle, goats, and sheep are exposed to the sun, they experience greater heat loads than those present in enclosed shelters or in shaded areas (Al-Tamimi, 2007; Brosh et al., 1998; Sevi et al., 2001). For some species of cattle, a high heat load during the summer results in reduced growth and reproductive rates, causing a decrease in overall productivity (Brosh et al., 1998). Dairy cows experience a decrease in fertility when under severe heat stress, more so in the summer than the winter (De Rensis & Scaramuzzi, 2003; Schütz et al., 2009). In addition to behaviors like shade-seeking, physiological responses such as increased respiration rate, heart rate, skin temperature, and of course high T_B are often the first signs of heat stress resulting from direct solar radiation. Above the UCT, evaporation through respiratory and cutaneous water loss can aid in reducing T_B . Blood vessels dilate near the skin surface allowing increased blood flow to areas that facilitate heat loss through multiple modes of heat transfer. This response is only efficient as long as blood temperature is less than T_A ; because it is the thermal gradient that drives heat loss across the skin barrier. Heat loss can be supplemented by behavioral changes such as feeding in the late afternoon or even at night so that the heat increment of feeding is produced during cooler periods, allowing heat loss through both conduction and radiation. Increased rates and total intake of

water is often observed in livestock, compensating for the water lost through evaporation. Some species of goats and cattle are able to reduce their T_{Bs} in the early morning as a preparatory strategy for the increased amount of solar radiation they will be exposed to during the warmer parts of the day (Al-Tamimi, 2007; Brosh et al., 1998).

3.3.2.1 Evaporation

Many animals are able to use their own body parts, fluids, or environment to reduce heat absorption or expedite heat loss. Since water transfers heat 25X faster than air, metabolic as well as environmental water is used in evaporative cooling. It is beneficial to have an external water source nearby as the rate of body water turnover increases with solar radiation in most species, though at different levels depending on body mass and other characteristics (Figure 6) (King et al., 1975). Environmental water is an excellent source if available and many animals, including humans, use rivers, lakes, ponds, and the ocean to transfer excess heat. South Australian, Northern fur seals and Stellar sea lion females are able to tolerate solar radiation by keeping themselves wet, via mass movements to the shoreline while New Zealand sea lions immerse their hind flippers in tide pools or stay within the splash zone (Beentjes, 2006). Humans and other organisms that have sweat glands secrete the plasma portion of their blood onto the surface of their skin where it evaporates, the heat energy being used to transform liquid to gas. Organisms lacking sweat glands must devise other means of cooling their T_{B} effectively. Dogs, cats, even sea lions, pant when they become overheated, using the evaporation of their saliva and moist tissue to dump heat. Kangaroos lick their own wrists where the skin is thinner and blood vessels are closer to the surface, aiding heat balance in the high solar and arid regions of Australia (Dawson et al., 2000). South Australian fur seal males unable to gain access to water due to territorial defense use their own urine for evaporatory cooling. After urinating on the rocks, males wet their ventral side and rear flippers, then lie on their side and raise a hindflipper into the air to enable convective heat loss. Female Stellar sea lions are often seen to huddle around small tidepools with increasing temperatures (Gentry, 1973).

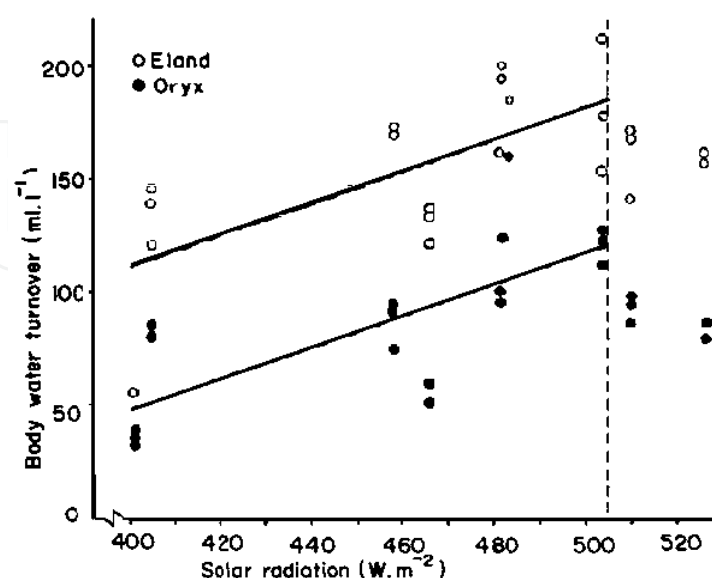


Fig. 6. Relation between daily total body water turnover and solar radiation in domestic Eland and oryx under African ranching conditions. Source: King et al., 1975.

4. Reproduction

Breeding demands a large amount of energy intake by both sexes, even more so when males must physically compete with one another to gain access to one or several females. Pinnipeds all have blubber layers of varying thickness to insulate them against cold water. Elephant seals are no exception, with males weighing over 2 tons. Male northern elephant seals must compete for reproductive access to females and physical combat among competing males can last upwards to 45 minutes (Norris et al., 2010). Blubber acts as insulation both in and out of water but is much heavier on land. Combative males produce a great amount of extra heat that must be expelled during and immediately after physical interactions with other males. Weaker males may retreat to the ocean for multiple cooling avenues that aid in thermoregulation but alpha males, if they wish to maintain their access to females and increase mating success, cannot leave their harem and thus are subjected to environmental variables such as T_A , solar radiation, wind, and humidity. The only heat loss mechanisms readily available to alpha males on land are conduction and radiation to a cooler substrate and convection from prevailing winds (Norris et al., 2010).

Solar radiation has a significant effect on the circulatory physiology of male northern elephant seals. Infrared thermal images show that certain areas of skin function as thermal windows, vasodilating the blood vessels and shunting warm blood directly to the skin surface, facilitating heat transfer to the air by convection or substrate by conduction. By increasing skin temperature in specific areas, males are able to increase the temperature gradient more so than if blood was perfused along the entire body surface. On warm days, conduction and radiation work against the males, thus on days with high solar radiation and low wind the males are inactive, allowing skin temperature to rise 42°C (Figure 7) (Norris et al., 2010). In this manner they can lower their metabolic rate and conserve energy. Even pups of the California sea lion have been observed to sleep and stay still during periods of intense solar radiation for the same reason. On days when wind speed is high and/or clouds block direct solar radiation, male elephant seals are more likely to be active or engage in combat behavior, enabling them to rely on convection or even evaporation via precipitation to increase the rate of heat transfer (Norris et al., 2010).

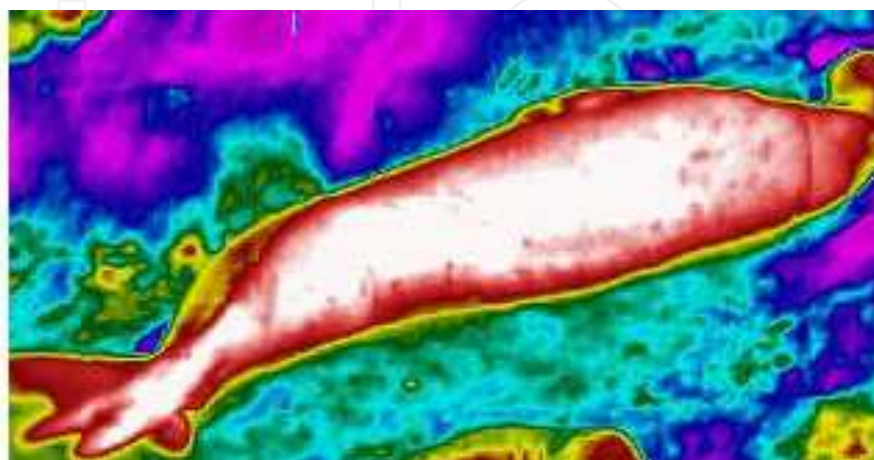


Fig. 7. False color thermal image of a male northern elephant seal; max skin temperature of 42°C. Source: Norris unpublished data

Males of some pinniped species claim a territory rather than a harem and must rely on the habitat within their territory to entice or gain access to reproductive females. For example, South Australian fur seals exhibit several behavioral mechanisms to dissipate excess heat before finally abandoning their territory for access to water as T_B approaches a certain thermal threshold often correlated with substrate (rock) temperature. Reproductive success of male New Zealand fur seals may depend on how much water is present within their territory. Males with areas including tide pools or along the shoreline have more access to females than males with no water in their territory. Male Northern fur seals that abandon their territories suffer a 50% reduction in mating success, whereas males of Southern Australian fur seal with no access to water average only 1.7 copulations per male compared to 3.6 copulations per male near a water source (Gentry, 1973). Southern sea lion males with territories lacking water access experience half the copulation frequencies of males with available water. During their forays to the water line, female Southern Australian fur seals expose themselves more frequently to males versus females that remain stationary and thus may contribute to an increased pregnancy rate (Campagna & Le Boeuf, 1998).

5. Ultraviolet radiation

Ultraviolet light has a wavelength shorter than visible light and is named as such due to the emitted electromagnetic waves with frequencies above that of visible violet light. UVA and UVB wavelengths emitted by the sun affect animal behavior and physiology. UVA radiation is exploited by some pollinating insects to facilitate the detection of flower condition for nectar production in pollination. UVB radiation may affect reproduction and development as well as synthesis of vitamin D (Schaumburg et al., 2010). Overexposure to UVB is known to increase mutation rates in individual cells of whole organisms. The targets of UVB damage within living cells include nucleic acids, proteins, and lipids. Damage to these can inhibit DNA and cellular processes as well as impair cell membranes.

5.1 Aquatic organisms

Wavelength and intensity of solar radiation are modified as they travel through water but at shallow depths UV radiation is only able to penetrate a certain distance. Organisms found in epipelagic and littoral zones include phyto- and zooplankton, invertebrates, fish eggs and larvae, as well as entire ecosystems such as coral reefs. Some species of zooplankton change their vertical migration patterns within aquatic habitats to avoid exposure to UV radiation. Others respond by increasing pigmentation, an energetically costly process that can increase the organism's visibility to predators (Häder et al., 2007). The photochemical efficiency of some algae, such as those responsible for red tide, decreases when subjected to high solar radiation for short periods of time. However, if the algae are exposed to UV radiation for prolonged periods, they may be able to acclimate to this extended time by increasing protein repair and synthesizing UV-absorbing compounds (Guan et al., 2011). UV radiation induces decreased production of biomass such as phytoplankton, which can lead to a reduced capacity to sequester carbon dioxide, a gas that causes increased insolation of the Earth's atmosphere and is postulated as a major contributor to climate change (Hoffert & Caldeira, 2004).

Although many ectotherms are able to use solar radiation as a heat source, ultraviolet radiation can have detrimental effects, especially on certain early development stages. In larval stages of some fish, UV radiation can affect development, increase mutation rates, or cause skin and ocular damage. When exposed to full solar UV radiation, yellow perch eggs actually perish before they hatch (Häder et al., 2007). Invertebrates such as sea urchins are also inhibited by UVB radiation at different life stages. In some species apoptosis or abnormal development occurs in the embryos, while adults of other species exhibit a covering behavior, using pieces of debris to block direct contact with solar rays penetrating through shallow water (Häder et al., 2007; Nahon et al., 2009). UVB radiation is known to decrease survivability of amphibian embryos or larvae depending on species (Häkkinen et al., 2001).

The mortality of coral reefs throughout the world has been well documented and is partly attributed to rising ocean temperatures, pollution, and UV radiation. Bleaching occurs at a thermal threshold and the coral dies soon after the photosynthetic energy producing zooxanthellae are expelled. Corals exposed to high levels of UV radiation receive damage to both the symbiotic zooxanthellae and the coral tissue (Lesser & Farrell, 2004). Pathways involving carbon fixation and photochemistry in the zooxanthellae along with DNA damage and necrosis of the host coral tissues are the results of thermal stress due to the high irradiance of solar radiation. The presence of high UV radiation can lower the bleaching threshold, decreasing the time it takes to bleach in an environment that may otherwise not be as stressed. However, some coral reef species are able to sequester substances acquired through their diet into UV-absorbing elements (Dunne & Brown, 2001).

5.2 Terrestrial organisms

UVB radiation is known to both negatively and positively affect species. While growth of leaves and stems are inhibited by UVB along with reduced daytime seedling emergence and biomass in early stages of growth, some species of plants exposed to the radiation are less likely to be attacked by leaf beetles (Ballere' et al., 1996). Other plants such as soybeans also receive reduced herbivorous damage when exposed to UVB (Zavala et al., 2000). Thrips, insects that feed on plant leaves, actually avoid exposure to UVB solar radiation, suggesting that insects can behaviorally respond to that particular wavelength presence (Mazza et al., 1999). UVB can also have an indirect effect upon some species of insect larvae, as those who eat UVB radiated plant material are found to have decreased growth rates and suffer more mortalities versus larvae that feed on non-radiated plant matter (McCloud & Berenbaum, 1994).

Humans are sensitive to solar radiation and may experience sunburn, heat strokes, eye diseases, and skin cancer when overexposed. Low doses of UV radiation are required for vitamin D synthesis and can be used to treat some illnesses. By regulating dosages of UVB radiation to humans with allergic chronic dermatitis, nickel sensitivity, and psoriasis, physicians are able to successfully treat and suppress hypersensitivity. Photoimmunology is a relatively new field and human experiments are often rare due to ethical guidelines and research protocols. Immune system responses by humans to prolonged exposure to UV radiation are usually detrimental. UV damage often includes changes in intracellular signaling, T-cell numbers in exposed skin and inhibition of natural killer cell activity

(Duthie et al., 1999). Even humans with varying levels of pigmentation in their skin, such as those of diverse racial descent, are affected differently when exposed to UVB (Coelho et al., 2009; Duthie et al., 1999). Langerhans cells, antigen-presenting cells within the epidermis, die due to membrane disruption and organelle damage in Celtic descendants while cells in the darker skin of Aboriginal or Asian Australians are depleted by apoptosis (Duthie et al., 1999). The melanin produced in the skin when humans are exposed to UV radiation is actually able to absorb UV, shielding nuclear DNA (Coelho et al., 2009). Long term exposure can lead to degeneration of skin cells, underlying fibrous tissue and/or blood vessels leading to premature skin aging and skin cancer. Other possible effects include ocular inflammation and cataracts that can cause blindness. Most tissue damage is due to high levels of UVB wavelengths while more indirect damage via reactive oxygen intermediates affecting DNA, proteins, and lipids is caused by UVA radiation (Figure 8) (Rafanelli et al., 2010).

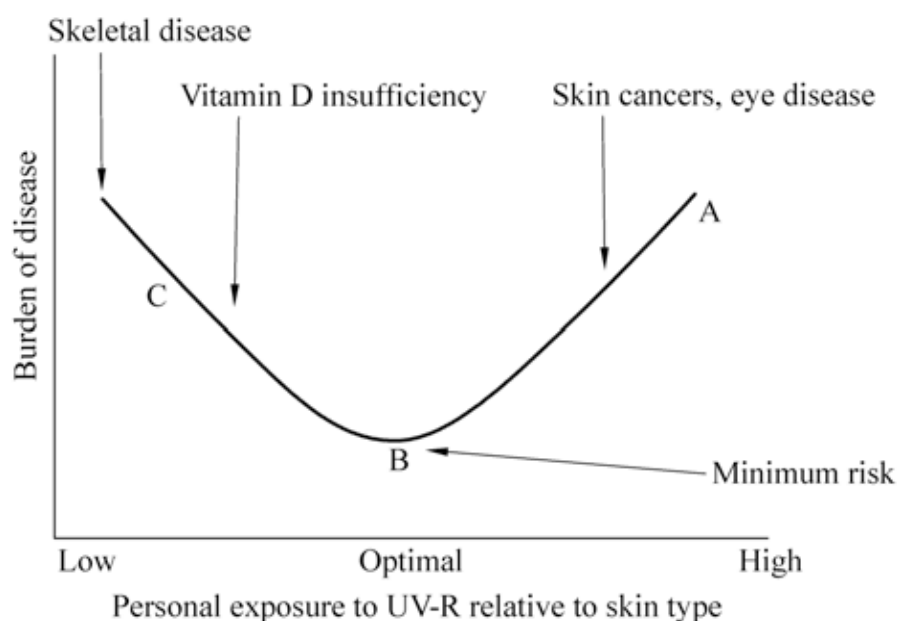


Fig. 8. Relationship of exposure to UV-R and burden of disease. Source: WHO, Ultraviolet radiation and the INTERSUN Programme in Rafanelli et al., 2010

Vitamin D is necessary for healthy growth and function of most terrestrial vertebrates. Exposure to direct sunlight allows UVB photons to enter the skin and begin a chain reaction resulting in the formation of vitamin D. This nutrient is essential for efficient intestinal absorption of calcium, especially in humans (Holick, 2008). However, an organism's diet is often a supplemental source of vitamin D in addition to providing the building blocks of vitamin D synthesis. In bats, diet strongly affects the levels of circulating vitamin D metabolite. Certain cave dwelling species, receiving little to no direct sunlight, actually have the highest recorded concentrations in vertebrate taxa. Unlike the plant visiting bats, which have levels not even sufficient for humans, sanguivorous and piscivorous species have access to dietary vitamin D, increasing their serum concentrations of the vitamin D metabolite (Southworth et al., 2009). Ectotherms, who often bask in sunlight, are able to use this behavior to regulate their own vitamin D levels when dietary intake is insufficient

(Karsten et al., 2009). Deficiency of vitamin D in humans can lead to increased risks of bone fractures from osteoporosis, common cancers, cardiovascular disease, autoimmune and infectious diseases (Holick, 2008).

6. Infrared thermal cameras

A specialized sensor in units of Watts/m² normally measures solar radiation while a UV meter is needed to determine UV radiation either by wavelength or a UV index. The effects of solar and UV radiation on organisms are harder to quantify. Observed behaviors can be statistically associated with monitored solar intensity and/or UV radiation to calculate whether there is a significant effect. Physiological responses however, must be measured with other equipment or using procedures involving immobilization, radioactive tracers etc. Such methods can cause stress to the animal in question or establish a bias in some way as is often the case with attaching equipment to wild animals or bringing them into a laboratory setting. Often the variable being monitored is some form of temperature, be it core/body, skin, or intramuscular. Temperature is often the first physical measurement affected by solar radiation. Infrared radiation (IR), simply put, is the thermal emission of an object or organism. Thermal infrared cameras are able to detect various wavelengths in the infrared spectrum that can be accurately measured based on the temperature of a surface using the physical laws of radiative transfer.

The use of thermal cameras is relatively new to scientific field research. In the past, thermal cameras were expensive, large, bulky, and hindered by the need for a large external power source. As the technology has progressed, the IR detector itself has become smaller and thermal cameras have been used for military applications, on airplanes, helicopters, and today the individual soldier. Currently a handheld IR camera can be purchased for under \$2,000 and is often used by electricians, engineers, and construction companies to detect problem areas in work zones and other facilities. Scientists too, are now able to purchase high definition IR cameras that can be easily carried into the field and wirelessly linked with data loggers and tablets.

Thermal cameras allow for a non-invasive scrutiny of an organism's skin surface temperature, giving the ability to see temperature variability across the body rather than just one to a few individual areas recorded by a thermocouple or other device (Figure 9) (McCafferty, 2007; Norris et al., 2010). Clear links between heat loss and areas of the body such as the head and appendages have been established due to thermal imaging (McCafferty, 2007; McCafferty et al., 2011). Behavioral responses to solar radiation and other environmental variables can be paired with changes in skin surface blood circulation. The surrounding environment is imaged at the same moment as the organism being studied, allowing for temperature measurements of the substrate to be collected for future analysis. Thermograms of insects such as bees make measuring individual or hive temperatures quick and simple without having to use smoke or gaseous chemicals that take time and may affect the bees' thermoregulatory properties (Kovac et al., 2010). Thermal video of emerging bats can be recorded and their flight trajectories tracked using specialized computer analysis programs (Hristov et al., 2008). Thermal imaging can even be used for plant and crop research, measuring temperature in relation to solar radiation absorption and water treatment (Jones et al., 2009).

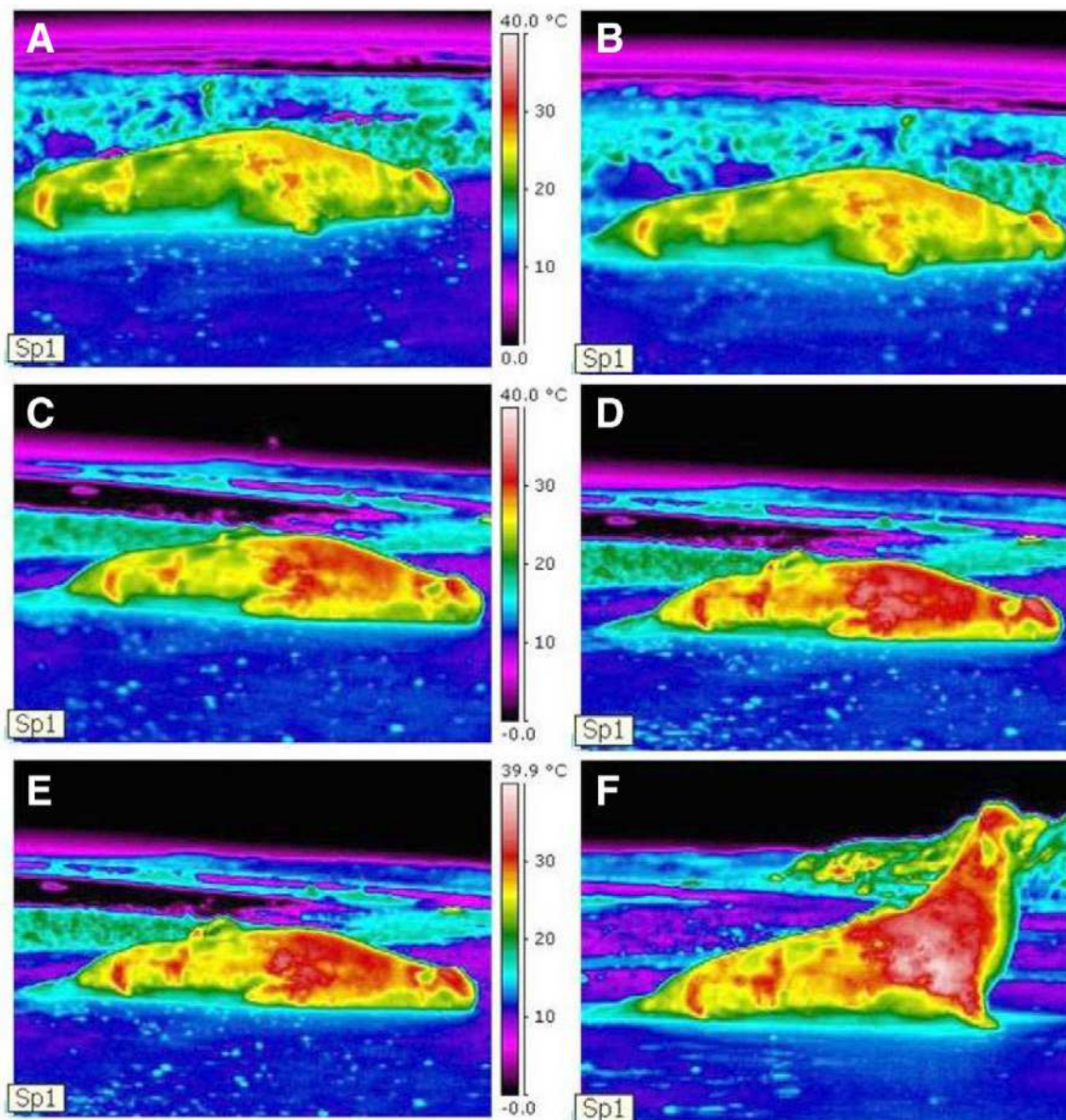


Fig. 9. Post combat thermal images sequence (A-F) of an alpha male northern elephant seal taken at intervals of ~1min immediately following a combat lasting 11 min. Skin temperature variability is clearly displayed over time. Source: Norris et al., 2010.

The use of thermal cameras for biological study has been well validated in the past for both individual studies and those involving groups of animals (McCaffery, 2007). Using either the IR camera or computer software paired with it, maximum, minimum, and mean temperatures can be measured and calculated rapidly and efficiently. However, distance from the organism, emissivity, relative humidity, and T_A must be known to reduce errors in the camera's detection of surface temperature. Solar and UV radiation measurements can now be statistically paired with the temperature data, skin variability in temperature, thermal gradient between skin temperature and ambient/substrate temperature, and other environmental or physiological measurements. Use of IR cameras eliminates the need to capture or handle animals in physiological, behavioral, and ecological studies involving thermoregulation.

7. Conclusions

Solar radiation is essential for life, transferring energy to plants that form the basis of food webs. Assorted wavelengths emitted by the sun initiate a variety of responses across most species. Organisms have evolved thermoregulatory behaviors and responses to concentrated or extended periods of solar radiation as well as to changes in ambient temperature, which is also affected by solar intensity. Ultraviolet radiation can have both beneficial and detrimental effects on organisms depending on dosage and wavelength. Infrared radiation can be used as a measure of surface temperature using thermal infrared cameras, now relatively affordable, and have been validated for scientific research.

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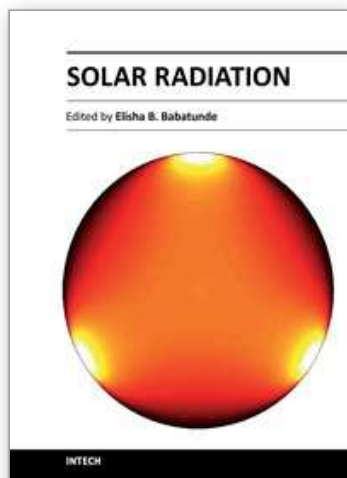
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The book contains fundamentals of solar radiation, its ecological impacts, applications, especially in agriculture, architecture, thermal and electric energy. Chapters are written by numerous experienced scientists in the field from various parts of the world. Apart from chapter one which is the introductory chapter of the book, that gives a general topic insight of the book, there are 24 more chapters that cover various fields of solar radiation. These fields include: Measurements and Analysis of Solar Radiation, Agricultural Application / Bio-effect, Architectural Application, Electricity Generation Application and Thermal Energy Application. This book aims to provide a clear scientific insight on Solar Radiation to scientist and students.

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