

Behavioral thermoregulation in terrestrial arthropods

Daniel Kipervaser
dkiper@lamar.colostate.edu

Colorado State University
Department of Biology

Abstract:

Thermoregulation can be found in endotherms and ectotherms alike; however, it is particularly important to ectothermic organisms as their internal temperature often parallels ambient temperatures in the absence of mitigating conditions. Ambient temperatures can frequently exceed an organism's physiological tolerance levels or reach levels at which the organism is prevented from functioning normally. When temperatures rise above tolerance levels, ectothermic organisms enter into a state described as heat stupor or cold torpor, in which they cannot move or respond to stimulus. Under less extreme temperatures, response to stimulus may be less frequent or simply slower.

Studies indicate that temperature can affect an organism's ability to forage or to hunt, to evade predators or to defend against them. Furthermore, temperature can also affect mating success and development. While endothermic organisms can alter their metabolic rates to adjust their internal temperatures, ectothermic organisms have only limited options. One option is to adjust temperature through physiological thermoregulation. This is frequently how such organisms tolerate extreme cold or raise their internal temperature. However, if ambient temperatures rise above the level of heat tolerance, ectothermic organisms will often thermoregulate behaviorally.

With arthropods as model organisms, I will highlight methods of behavioral thermoregulation. Behavioral thermoregulation is found in both solitary and social insects. It often involves locational changes seeking to optimize microhabitats, but can also be achieved by changing body position and performing certain activities. Improved survivorship and reproductive success is strongly linked to remaining active as long as possible. Behavioral thermoregulation allows the arthropods to maintain favorable body temperatures during several key developmental stages, affecting size, developmental rate and distribution.

Introduction:

The ability to thermoregulate is essential to all organisms. There are certain ranges within which any given organism can perform biological functions. As the body temperature approaches either the upper or lower extreme, its ability to perform those functions diminishes (Schmalhofer 1999). As a result all organisms have a series of physiological or behavioral methods of maintaining body temperature at a tolerable level and most can also employ these same methods to optimize their body temperatures.

Endothermic organisms alter their metabolic rate to change body temperature in response to sub-optimal environmental temperatures. While an endotherm has a largely physiological response to cold or heat stress, there are also several important non-physiological responses to these ambient conditions. Ectothermic organisms generally do not have a physiological response to thermal stress. The body temperature of an ectothermic organism closely follows ambient temperatures in the absence of any thermoregulatory response (Bryant et al 2000). However, ectothermic organisms have at their disposal a variety of behavioral thermoregulatory mechanisms that allow them to compensate for sub-optimal ambient temperatures. In many

cases these behavioral methods of thermoregulation allow the organism to maintain a body temperature that is several degrees above or below the ambient temperature (Lubin and Henschel 1990, Ruf and Fiedler 2002 and Rehnberg 2002).

Thermoregulation in ectotherms has been linked to several critical components of life history. Body temperature has a direct influence on early stage physiological development, activity patterns, foraging, mating success and predator evasion. Ectothermic behavioral thermoregulation will be reviewed with terrestrial arthropods as model organisms.

Factors influencing body temperature

Several factors affect the body temperature of an organism in its environment. Many attempts have been made to model the internal temperature of organisms in the field (Riechert and Tracy 1975, Tracy and Christian 1986 and Bryant et al. 1998). However, the number of variables involved in modeling field body temperature can make it very cumbersome to calculate. Furthermore, the assumptions about the system needed for the model typically yield only coarse predictions (Ward and Seely 1996). As a result, simple models are generally more desirable and experiments investigating thermoregulation and body temperature consider only a few of the most influential thermal components at a time or take body temperature measurement directly. Some of the main factors influencing body temperature are air temperature, solar radiation, radiation from nearby surfaces, absorptivity of the organism, wind speed and convection (Tracy and Porter 1969 and Stevenson 1985). The relatively small body size of most terrestrial arthropods results in low thermal inertia; small variations in energy flow can translate into significant changes in body temperature (Casey 1981 and Stevenson 1985). Coloration and

behavior can also have vast implications during most stages of an arthropod's life history. It is these characteristics that will be explored in the sections to follow.

Thermoregulation through modified posture, orientation and movement patterns

The simplest form of thermoregulation involves modifying activity patterns such that the organism is only active when energy expenditure would not be excessively high. When body temperatures are too high or low, the organism is not able to move efficiently. In these cases, it is most thermally efficient to simply sit and wait until thermal conditions have become milder and additional thermoregulatory methods can be employed to bring the body temperature into an operative range (Stevenson 1985). Nevertheless, some terrestrial arthropods will choose to remain active despite dangerously high ambient temperatures. They will move across open areas where they are exposed to extreme conditions (high radiation and ambient temperatures) as quickly as possible (Lubin and Henschel 1990, Turner et al 1993 and Cloudsley-Thompson 2001). While this exposure is certainly more deleterious to the organism than remaining hidden, the act of moving quickly may have mitigating effects on body temperature elevation. Moving quickly can increase convective forces and therefore increase heat loss. The energy costs of running are negligible when balanced against the benefits (Bartholomew et al 1985).

Behavioral thermoregulation is essentially achieved by modifying the exposure to radiation and convection. Radiation from the sun and from the substrate surface contributes heat to the body while convective forces result in heat loss. During the early part of the day when ambient temperatures, and consequently body temperature, are low, some arthropods will bask in the morning sun (Heinrich 1996, Forsman et al 2002). The insect will raise its body temperature

by taking on a posture that maximizes exposure to solar radiation and minimizes convective cooling.

Recently, Forsman and associates (2002) determined that thermoregulation through basking behaviors coevolved with color patterns in the pygmy grasshopper *tetrix undulata*. This species of grasshopper has variable color ranging from dark to pale and these color patterns are linked to particular genetic codes. Theory suggests that the darker morphological varieties will heat up faster than the lighter morphs and have an advantage in colder climates. Conversely, the lighter morphs will be at a disadvantage under the same conditions because it would take longer to become active. An alternative possibility is that there may be a preference for different optimum body temperatures. In this case, we would not necessarily expect either variety to be at a disadvantage but darker morphs would have a higher preferred temperature.

The researchers observed the basking behavior of four groups of grasshoppers. Two groups had their natural colors and were divided as dark morphs and pale morphs. The other two groups were painted the opposite of their natural color. In other words, there was a group that is naturally dark, but painted pale and a group that is naturally pale, but painted dark. All groups were reared at the same temperature. Forsman and associates hypothesized that if the thermoregulatory behavior (in this case basking) were a flexible behavior changing in response to ambient conditions, then a pale grasshopper painted dark would behave more like a naturally dark grasshopper. The reverse would occur with the dark grasshopper painted light. However, if the behavior is genetically linked to coloration, then we would expect no difference in behavior between a natural pale grasshopper and a pale grasshopper which has been painted dark (the latter of which would be experiencing an elevated body temperature).

In fact, their results seem to support the latter hypothesis. The dark individuals that were painted light showed little difference in thermoregulatory behavior from those who were left unpainted. These conclusions were also consistent with thermoregulatory behaviors associated with heat avoidance.

When temperatures are too high and the organism risks overheating, arthropods such as dragonflies will choose alternate body positions. Some species of dragonfly will assume the “obelisk” position; with the abdomen pointing upwards. In this position the dragonfly can reduce the surface area available to radiation and maximize the surface area exposed to convective forces (Stevenson 1985 and Heinrich 1996). Another commonly observed behavior that reduces the risk of overheating in terrestrial arthropods is “stilting.” When stilting, an organism can reduce the effects of radiation from the substrate surface by raising its body out of the boundary layer of hot air above the ground (Heinrich 1996 and Schultz 1998). While stilting is not the most effective method of reducing body temperature, raising the body can theoretically reduce temperatures by 4°C or more (Stevenson 1985 and Ward and Seely 1996). Given the choice, individuals may select a more effective thermoregulatory behavior. Ward and Seely (1996) found that despite extreme temperatures, desert tenebrionids were rarely observed stilting; rather, they were more frequently observed searching for cooler locations.

A less common method of cooling body temperatures is through regurgitation. Some species of wasp and bee will deposit a small amount of regurgitant on their heads to increase evaporative heat loss. This can be a very effective method of cooling and can reduce local body temperature by as much as 4°C but the insect does incur the cost of a significant loss of body moisture (Coelho and Ross 1996). It is unlikely that this method of thermoregulation would be common in non-pollinators. Insects that pollinate have more access to temporary stores of

excess water. Ground-dwelling arthropods are unlikely to maintain significant water reserves and would likely choose other less costly methods of thermoregulation.

The role of microhabitat choice in thermoregulation

Although ectotherms may be able to thermoregulate in a variety of physiological and behavioral ways, these methods are generally secondary to microclimate choice. Actively foraging insects can thermoregulate by taking advantage of cooler microclimates as they move through the thermally heterogeneous landscape. Creating a thermal refuge can also be one of the most effective methods of avoiding overheating.

Burrowing decreases exposure to solar radiation and within a burrow, temperatures may not only be up to 45°C cooler than surface temperatures but also exhibit a much narrower range of temperatures (Lubin and Henschel 1990). Burrows can be placed so as to maximize convection as well. If the burrow is placed such that wind can enter, body temperature can be controlled very effectively despite extremely high ambient temperatures. A strategically located nest may serve a similar function as a burrow. Not only can an organism retreat and remain inactive appropriately designed web, but it can also perform several tasks through brief excursions and then return before overheating (Lubin and Henschel 1990). In this way, an ectotherm can still forage even during the hottest times of the day yet still remain close to its preferred body temperature.

Microhabitat choice is the most important component in thermoregulation for stationary or sit-and-wait predators such as spiders. Web site location represents a balance between prey availability and thermal considerations. A habitat with a satisfactory prey base is selected, and then within this area, the location of the web is chosen so as to minimize the effects of the daily

temperature extremes. Specifically, the web is oriented such that the spider can remain active as long as possible, thereby remaining able to respond to prey stimuli (Reichert and Tracy 1975, Lubin et al 1993 and Barghusen et al 1997).

Some tenebrionid beetles will move up into the shrub canopy to avoid thermal extremes that might result in inactivity (Ward and Seely 1996). Schultz (1998) found that tiger beetles in forests would actively seek out patches of light on the forest floor produced by temporary gaps in the canopy. The beetles would aggregate there in large numbers to bask and forage. In this study, Schultz found that thermal considerations were of primary concern despite pressure from increased predation risk.

Microhabitat selection not only affects foraging time but can also potentially affect mating and reproductive success (Reichert and Tracy 1975, Porter and Tschinkel 1993 and O'Donnell and Foster 2001). Hedrick and associates (2002) studied the effect of temperature in the mating calls of *gryllus integer*. They found that these crickets were actively seeking warmer microhabitats. Hedrick et al propose that it is more energetically efficient for a male to call loudly from these warmer microclimates than from cooler zones. As a result, choosing the correct microclimate may directly affect mating success.

Thermoregulation in social and gregarious arthropods through behaviors and temperature moderating structures

Social and gregarious arthropods have more methods of behavioral thermoregulation at their disposal than their solitary counterparts. Bryant and associates (2000) studied the thermal ecology of two species of gregarious nettle-feeding nymphalid butterfly larvae and two solitary species. They found that the gregarious species had a substantial advantage over the solitary

because they were able to thermoregulate much more effectively. The gregarious larvae cluster together in response to cooler temperatures effectively increasing their collective mass and adjusting their surface to volume ratio. In doing so, they were able to retain more metabolic heat and reduce convective heat. These gregarious larvae were able to begin foraging for the best quality nettles in the early spring when temperatures are rather restrictive. They were also able to maintain an optimal temperature for development with very little deviation. They report that deviations of even 2°C can have a substantially negative effect. Over the course of the summer, those species that were able to tightly regulate their body temperature had higher body weights, which directly related to overwintering survival. Developmental rates may also have implications for dispersal and range extension.

In 2001, O'Donnell and Foster studied the thermoregulatory behavior of worker bumble bees. They reported that worker bumble bees alter their rate of task performance for fanning and incubating depending on environmental cues. Successful brood development and maturation depend on the hive staying within a certain temperature range (Seely and Heinrich 1981). To maintain these temperatures, worker bees will behaviorally thermoregulate in four ways. To raise temperatures, a bee will incubate the cells by coiling her body around brood cells and creating heat by contracting flight muscles. As a group, the bees will also cluster so as to reduce heat loss. When temperatures are too high, a worker bee will fan the hive by beating her wings creating an air current inside the hive and cooling the local temperature. At the same time, the bees will also spread out, reducing the heat retained by clustering. The researchers found that individual worker bees respond differently to thermal cues and also observed bees simultaneously performing contradictory tasks. However, over the entire colony, thermoregulatory responses were predictable.

Joos and associates (1988) studied the role of the communal silken “tent” built by the eastern tent caterpillar. The researchers created several models of the tent and predicted both the thermal properties of the tent and the interaction of the tent and several thermoregulatory behaviors observed in the caterpillars. The tent is a multi-layered structure with a thermally heterogeneous interior that nevertheless maintains a consistently higher temperature than the ambient temperature. Solar radiation heats up the surface of the tent which acts as a sort of greenhouse. Their models indicate that a caterpillar using a tent will be able to thermoregulate more effectively than one that does not and that aggregated caterpillars using the tent are able to maintain higher temperatures than solitary caterpillars using the tent.

In 2002, Ruf and Fiedler corroborated these earlier predictions by measuring the temperature of caterpillars in the various locations within and outside of the tent. They also observed the thermoregulatory behavior of these caterpillars and correlated their behaviors with body temperature and ambient temperature. They found that the caterpillars changed position inside and on the outside of the tent to stabilize their body temperature within a narrow range despite broadly varying ambient temperatures. When temperatures were low, the caterpillars would aggregate on the irradiated side of the tent allowing them to maintain a higher body temperature by reducing surface to volume ratios and seeking a warmer microclimate. During the early afternoon, when temperatures in the tent would increase, aggregations would loosen and individuals would seek the cooler areas in the tent. During the hottest time of the day, temperatures inside the tent would become dangerously high. At this point, the caterpillars would leave the tent and climb onto the surface seeking a shaded location. Towards the end of the day as ambient temperatures drop, they would migrate back into the tent.

Other arthropods such as the fall webworm (*Hyphantria cunea*) also benefit from temperature moderating structures. While they build a web that is far less dense than the structures created by tent caterpillars, they are still very effective at decreasing convective heat loss by slowing air movement and by absorbing radiant energy.

Other social caterpillars use temperature moderating structures for heat avoidance. *Eucheira socialis* is a winter foraging caterpillar. These nocturnal social caterpillars construct a sack-like nest called a bolsa. Within the bolsa, the caterpillars actively avoid solar radiation. Fitzgerald and Underwood (2002) suggest that these caterpillars experience voluntary hypothermia so that they can remain active at night. Increasing body temperature during the day would require acclimatization for nocturnal activity, thereby hampering their ability to move and forage.

Conclusions:

Stevenson (1985) observes, “ectotherms use behavioral mechanisms to seek appropriate thermal conditions within their environments, because their metabolic rates and other physiological mechanisms are usually insufficient to control body temperature under a single set of environmental conditions.” The inability to properly thermoregulate can have a deleterious effect on an organism at nearly every stage of its life history. Impaired development, compromised mobility, ineffective foraging, poor predator evasion and unsuccessful mating attempts are some of the many consequences of inadequate thermoregulation.

Behavioral thermoregulation is a highly effective method of maintaining preferred body temperatures. Some arthropods such as the gregarious nymphalid butterfly larvae are able to

maximize developmental rate by maintaining their body temperature within an extremely narrow range despite highly variable ambient temperatures.

The most effective method of behaviorally thermoregulating is simply avoiding extreme environmental conditions that result in suboptimal body temperatures. For this reason, modifying daily activity patterns and selecting favorable microclimates can affect the greatest changes in body temperature. The other behavioral methods of thermoregulation can cause a smaller but still significant change.

The creation of habitats with heterogeneous microclimates such as burrows and other temperature modifying structures provides a great deal of flexibility for thermoregulation. Gregariousness also provides additional means of body temperature maintenance that are unavailable to solitary organisms. Behavioral thermoregulation has been a topic of research for decades and remains a field of active research. In recent years, emphasis has been placed on the thermoregulatory behaviors of social and gregarious insects. I suggest that future research not only continue to investigate these behaviors but also attempt to discover the genetic roots of these behaviors.

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