

## THE SUBELYTRAL CAVITY OF DESERT TENEBRIONIDS

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## ABSTRACT

Tenebrionid beetles are a conspicuous component of the world's hot deserts. Different species exhibit considerable variability in physiology, morphology, behavior, and life history; most aspects of their biology are influenced by the interrelated problems of excess heat and insufficient moisture which all desert organisms face. This paper is a review of research and thought concerning an adaptation characteristic of desert tenebrionids, an air space between fused elytra and the dorsum of the abdomen called the subelytral cavity.

The subelytral cavity may be seen as a hermetic seal which reduces transpiration regardless of its size, and as a protected space within the beetle which, whether airtight or not, allows the abdomen to expand to store food, water, or eggs. I hypothesize that the cavity itself is probably an architectural constraint resulting from the need for abdominal expansion within the heavily sclerotized, fused elytra that evolved primarily as a water conservation adaptation.

## RESUMEN

Los escarabajos son un componente conspicuo de los desiertos calientes del mundo. Las diferentes especies muestran variabilidad considerable en la fisiología, la morfología, el comportamiento y el ciclo biológico. La mayoría de los aspectos de su biología están bajo influencia de los problemas vinculados de calor excesivo y de humedad no suficiente, como es el caso con todos organismos del desierto. Este trabajo es una revista de las investigaciones y los pensamientos sobre una adaptación característica de tenebrionidos del desierto, eso es, un espacio de aire entre los elitros fusionados y el dorso del abdomen, lo cual se llama la cavidad subelital.

La cavidad subelital se puede considerar como un sello hermético lo cual reduce la transpiración a pesar del tamaño, y como un espacio protegido adentro del escarabajo lo cual, aunque hermético o no, permite el abdomen estirarse para guardar comida, agua, o huevos. Yo presento el hipótesis que la cavidad misma probablemente es un constreñimiento arquitectural resultando de la necesidad de expansión abdominal dentro de los elitros fusionados y fuertemente esclerotizados los cuales evolvieron primariamente como una adaptación para la conservación de agua.

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Tenebrionid or darkling beetles form a significant portion of the fauna of hot deserts throughout the world. Under some conditions, the biomass of tenebrionids living in a desert area may exceed the combined biomass of the entire vertebrate community (Thomas 1979). In such numbers, these beetles must exert a considerable ecological influence in the desert ecosystem. Coleoptera seem to be one of the insect orders best adapted to desert life (Cloudsley-Thompson & Chadwick 1964), and the Tenebrionidae are probably the best-represented beetle family in deserts (Crawford 1981). Of the more than 15,000 described species of tenebrionids, more are xerophilous than mesophilous or hydrophilous. The family is at its most diverse in the Namib Desert in southwestern Africa, where several hundred species are found representing over 90 genera (Koch 1962).

Desert tenebrionids are not a phylogenetically distinct lineage within the family Tenebrionidae. There are xerophilous forms from three tenebrionid subfamilies, and

desert beetles belonging to dozens of different tribes occur in different parts of the world. However, most desert tenebrionids are distinguished from most other tenebrionids in that they are flightless, with fused elytra enclosing an air space called the subelytral cavity. Although different species of tenebrionids display a diversity of physiological, morphological, and behavioral adaptations to deal with various problems of desert life, presence of a subelytral cavity is widespread.

The subelytral cavity, then, is a characteristic desert tenebrionid adaptation, a feature common (with exceptions, especially among smaller species) to an otherwise diverse group of coleopterans. For at least seventy years, there has been much speculation (and some research) concerning the ecological function of this structure, i.e., what is its importance to the beetle? This review provides a brief overview of the biology of desert tenebrionids, and summarizes some interesting aspects of work done on a particularly fascinating desert tenebrionid adaptation, the subelytral cavity.

I must mention at this point that generalizations are inevitable when reviewing the biology of such a large and diverse group of organisms as desert tenebrionids. The information has been culled from observations on a large number of species, and no one species is "typical" of the group. Generic and specific names will not be given except where necessary, since these names will not be meaningful to the non-specialist. Interested readers will find the names in the literature referenced.

#### BIOLOGY OF DESERT TENEBRIONIDS

Although they display considerable behavioral and morphological variation, desert tenebrionids may generally be described as rather slow moving, black, flightless beetles. Adults and larvae are considered detritivorous (Wallwork 1982), although adults have also been observed feeding upon carrion (McKinnerney 1978) and dung (Buxton 1924), and some larvae are root-feeders (Rafes 1960). Tenebrionids may play an important role in detritus cycling in ecosystems where few microbial decomposers are active outside the tenebrionid gut. This is most important on the vegetationless dunes of the Namib Desert, where allochthonous detritus serves as the trophic base for the dune community (Seely & Louw 1980).

All known desert tenebrionids are subterranean as larvae and may spend several months developing in the soil. The number of instars is variable, often exceeding ten. One, two, and three year life cycles have been identified. Adults or larvae overwinter in the annual cycles, and both stages of a single species overwinter in the longer cycles (Allsopp 1980). Adult longevity in different species varies from a few weeks up to five years (Crawford 1981, 1990). Reproduction is iteroparous. Fecundity varies widely, with females usually depositing a few eggs at a time (Wallwork 1982).

Central to the tenebrionid life strategy is the avoidance of extreme environmental conditions by retreating to refuges during periods of inactivity. The egg, larval, and pupal stages are always completed underground, and some dune-dwelling forms are even "ultrapsammophilous," developing entirely in loose, shifting sand. Adults alternate between active foraging on the ground surface (exceptionally, in vegetation (Crawford 1990)) and inactivity within a refuge. Type of refuge utilized varies with the edaphic and vegetational characteristics of the beetle's habitat. Dune species may simply burrow into the sand, while species on ordinary soil substrates may occupy abandoned rodent burrows, ant nests, etc, or dwell beneath stones, wood, or debris (Crawford 1981).

Diel activity patterns are species, genus, and even tribe specific (Koch 1961). Tenebrionids may be diurnal, nocturnal, or crepuscular. Also, the adults of most species are active only during certain seasons of the year. Many long-lived species spend the remainder of the year in a state of dormancy within their refuges. In the southwestern United States, tenebrionid activity reaches a peak during the rainy season (Tanner &

Packham 1965). Different species, though, reach their peak of activity in different seasons. This temporal separation of the detritivore niche, on both daily and annual scales, may allow more species of tenebrionids to co-exist in a single habitat, although interspecific competition has not been demonstrated in these beetles (Wise 1981). In any case, limiting activity to certain parts of the day or year probably helps the animals to minimize water loss and avoid extreme temperatures, and enables them to deal with the variability and unpredictability of climatic factors inherent in desert ecosystems (Ahearn 1971, Kramm & Kramm 1972, Wallwork 1982).

An important feature which distinguishes the two major desert tenebrionid subfamilies is the possession of abdominal defensive glands. These are present in the subfamily Tenebrioninae and always lacking in the Tentyriinae (Doyen & Tschinkel 1982). When disturbed, these glands emit a dark reddish secretion with a disagreeable odor. The secretions differ chemically from species to species, but practically all contain various quinones, and 1-alkenes and other hydrocarbons are common components as well (Tschinkel 1975). Defensive secretions appear to make tenebrionids relatively unpalatable to many vertebrates (Eisner & Meinwald 1966) and invertebrates (Slobodchikoff 1979), although beetles possessing them still serve as food for a large set of vertebrate and invertebrate predators (Allsopp 1980).

A few desert tenebrionids are so aberrant in morphology and habits that much of this discussion probably does not apply to them. An example is the Old World genus *Cossyphus*. These are exceedingly flat beetles which apparently mimic winged seeds found in the vegetable debris they live in (Cloudsley-Thompson 1977).

More detailed information about the biology of desert tenebrionids can be found in the comprehensive works of Crawford (1981, 1990) and Wallwork (1982).

#### THE DESERT ENVIRONMENT: THERMAL AND WATER BALANCE

Desert climates present organisms with the basic problems of avoidance of excessive heat and dehydration (Hadley 1972). Extreme diurnal temperatures and intense solar radiation may challenge an organism's thermal tolerance. Rainfall is low in absolute amount, and may be seasonally distributed. High year-to-year and spatial variation of rainfall is also typical in deserts, leaving some local areas much drier than others (W. G. Whitford pers. comm.). Also, the heat, low relative humidity, and drying winds combine to accelerate evaporation of what little water is available.

In extreme environments, such as deserts, organisms may be more limited by the abiotic environment than by interactions with other organisms. Wise (1981) was unable to demonstrate competition among several species of tenebrionids for a detritus resource. It seems likely that tenebrionids are limited less by the amount of available detritus than by the harsh abiotic conditions of the desert environment. The high diurnal temperatures limit the amount of time that the beetles can forage actively on the ground surface, and lack of water may frequently reduce the beetles' metabolic and reproductive rates. In severe years, drought may also contribute directly to mortality. Probably all aspects of tenebrionid life are directly or indirectly affected by the interrelated problems of maintaining a favorable temperature and getting and keeping sufficient water.

Like other poikilotherms, tenebrionids can be active only when their body is warm enough for efficient metabolism to proceed, yet below some lethal temperature. Desert organisms may be selected for increased tolerance of high temperatures, which may result in an ability to withstand high temperatures for relatively long periods without perishing (higher "lethal temperature"), and/or a preference for relatively high temperatures.

Lethal temperatures of various species of tenebrionids have been measured in several studies (e.g., Cloudsley-Thompson 1964, Edney 1971a, Zachariassen 1977, Seely et al. 1988). Maximum lethal temperatures of tenebrionids in general vary between about 43° and 53° C. (Seely et al. 1988). Beetles from mesic habitats fall towards the low end of this range (about 43-45° C.). Cloudsley-Thompson (1964) measured similar upper lethal temperatures for diurnal desert beetles, but other investigators documented higher tolerances for desert beetles, especially for summer-active diurnal species (Edney 1971a, Zachariassen 1977).

Measurements of temperatures that beetles experience in the field, or of temperatures preferred by beetles in the laboratory, may be more ecologically meaningful than upper lethal temperatures. Studies of temperature preference and field temperature have been reviewed by Seely et al. (1988), who found trends similar to those seen with lethal temperatures. Beetles from mesic and montane areas (Zachariassen 1977, Doyen & Slobodchikoff 1984) often prefer temperatures below 20° C. Temperature preferences of desert species vary from about 20° C. for some nocturnal species up to about 43° C. in some Namib species which utilize a strategy called maxithermy: Maintenance of body temperatures near the upper lethal temperature limit for as long as possible (Hamilton 1975, Henwood 1975, Seely et al. 1988). Although desert beetles often have higher temperature preferences than mesic beetles, there is much interspecific variation in preference within desert species (El Rayah 1970, Henwood 1975, Slobodchikoff 1983). Much of this variation may be due to specific adaptations which different beetles use to optimize their thermal regime in an often inhospitable thermal environment.

The long legs of surface-active tenebrionids are a morphological feature that aids in thermoregulation. Beetles modify their behavior by "squatting" or "stilting" to take advantage of, or to avoid, the soil substrate which is usually warmer than the air temperature (Henwood 1975). Minimal hemolymph circulation to the tarsi limits heat conduction to the body.

It appears that the most important thermal adaptations in tenebrionids are behavioral. Many species avoid high diurnal temperatures by limiting periods of activity to cooler seasons (Ahearn 1971) and/or cooler times of the day (Cloudsley-Thompson 1964). Day-active beetles may retreat to refuges during the hottest part of the day (Hadley 1970, Edney 1971b), or may take temporary refuge in the shade of vegetation (Edney 1971a) or dunes (Koch 1961), or even atop quartz pebbles (Hamilton 1975).

It is uncertain what accounts for increased thermal tolerance in desert versus mesic tenebrionids. Evaporative cooling is insignificant in desert tenebrionids. They are so effective at conserving water that what little is transpired has a negligible cooling effect (Edney 1971b). Higher thermal tolerance may be due in part to the presence of more stable enzyme systems which denature at higher temperatures (Hadley 1972).

In general, water is the most important limiting factor of desert ecosystems, because free water is not commonly available. An organism must be able to obtain sufficient water where and when it does exist, and it also must be able to minimize water loss so that its water requirement does not exceed its supply.

Desert tenebrionids' water requirements are not great. Both larvae and adults feed on detritus which is often low in moisture content. Oxidation water may satisfy most of their water needs (Hadley 1972). Cloudsley-Thompson & Chadwick (1964) state that "these insects are able to live on dry food and exist without water." The authors imply that the beetles can complete their entire life cycle without access to free water, a notion which to my knowledge has been neither demonstrated nor refuted.

Regardless of their ability to do without, it is clear that tenebrionids will drink water when it is available, often consuming large quantities after a rainfall (Slobodchikoff & Wisman 1981). Between rain events, dew is an important source of water for species in some deserts (Hamilton & Seely 1976, Broza 1979).

Although desert tenebrionids are efficient at obtaining water and may have some resistance to desiccation, their ability to avoid water loss may be the most important factor involved in maintaining a favorable water balance. They exhibit some of the lowest rates of water loss of all arthropods (Edney 1971b). Water is lost to insects by two routes: Excretion, which includes feces, defensive secretions, and eggs; and transpiration via the tracheal system or directly through the cuticle.

Feces are an insignificant source of water loss in desert tenebrionids, since efficient resorption of water by the hindgut produces fecal pellets low in moisture (Ahearn 1970). Release of repugnant abdominal (and occasionally oral) secretions results in a relatively large loss of water (Ahearn 1970). Production of eggs certainly involves a loss of water for female beetles, but the implications (in terms of survivorship and life-history tactics) remain uninvestigated.

Water loss via transpiration is limited in desert beetles both by passive morphological features and active physiological control. The dominant morphological features are the thick fused sclerites which limit cuticular transpiration, and the fused elytra making up the subelytral cavity, which will be discussed in greater detail below. Active physiological control of cuticular and/or spiracular transpiration is evidenced by the fact that freshly killed beetles lose water much more quickly than identical living specimens (Ahearn 1970).

In addition to thick, fused sclerites, the low rates of cuticular transpiration of desert tenebrionids result from epicuticular lipids which are water impermeable at higher temperatures than the lipids of mesic species (Ahearn 1970).

Transpiratory water loss in insects occurs through the spiracles. Tenebrionids possess two large spiracles laterally on the thorax (in the membrane between the prothorax and the mesothorax) and several metathoracic and abdominal spiracles which open into the subelytral cavity. As discussed below, the subelytral cavity plays a large role in limiting spiracular water loss.

The rate of transpiratory water loss, as well as the relative importance of cuticular versus spiracular transpiration, is largely determined by temperature. Thus, heat and water loss are interrelated problems which desert organisms must deal with in tandem. Transpiration increases as temperatures increase (Ahearn & Hadley 1969, Ahearn 1970, Zachariassen et al. 1987). This may be partly due to epicuticular breakdown above a species-specific transition temperature. There is also a general increase in spiracular transpiration due to increased metabolic rate (and hence, oxygen demand) as temperatures increase. Zachariassen et al. (1987) found that the metabolic rate of carabids and tenebrionids is "the single determinant" of transpiratory water loss, between species and at different temperatures.

Ahearn (1970) reports that at relatively low temperatures some desert tenebrionids exhibit very low loss rates, and these losses are dominated by cuticular transpiration. As temperatures approach the beetle's transition temperature (about 40° C.), increased metabolic rates cause a breakdown of spiracular control, and spiracular transpiration becomes the dominant component of water loss.

#### THE SUBELYTRAL CAVITY

Koch (1962) states that 98% of tenebrionids in the Namib Desert are flightless, the few winged species being restricted to pockets of mesic habitat, such as river-beds or pans. Buxton (1923) hypothesized that winglessness is solely an adaptation to excessive windiness in deserts, pointing out that wingless beetles are also found on mountain tops and windy islands. Schmoller (1970) gave credence to this hypothesis fairly recently in his review of desert arthropods. However, evidence will be reviewed below which

indicates that winglessness is an indirect result of the formation of a hermetically sealed air space beneath the elytra. Consequently, the elytra must be fused together, precluding the use of wings. The vestigial wings beneath the sealed elytra display varying degrees of atrophy. In different genera they may be reduced to small, slender tubes, tiny scales, or they may be completely absent (Fiori 1977).

Fiori (1977) describes the morphology of the tenebrionid subelytral cavity in some detail. The elytra are usually fused permanently at the elytral suture with a "dovetail" or "double-dovetail" joint. The elytra are fused with the mesonotum towards the front and with the meso- and metaepimera and metaepisternum at the sides. The elytra may simply abut these parts, or they may lie in furrows or grooves, or there may be a permanent dovetail joint. The joints may be permanent at all points, or the permanent joints may alternate with temporary (non-fused) connections. Fringes of hairs on the elytra or urosterna may assist in making an effective seal in places where the joint is not fused. The overall effect is a hermetically sealed air space underneath the elytra. A small area at the posterior end can be voluntarily opened by the beetle in order to ventilate the abdominal spiracles, which open into the subelytral cavity. The floor of the subelytral cavity consists of the meso- and metanotum and the first seven abdominal uroterga. The uroterga are reduced to soft membranes in beetles with subelytral cavities. A small proportion of the cavity may contain any wing remnants the species may possess; the remainder of the cavity is simply an air space.

The subelytral cavity is not unique to the Tenebrionidae, though it probably serves different functions in different groups. Dytiscids (Coleoptera) possess a clearly defined subelytral cavity, as do some cave-dwelling beetles belonging to the families Carabidae and Anisotomidae (Fiori 1977). Desert-dwelling carabids also generally possess subelytral cavities (Zachariassen et al. 1987), which probably serve the same general function as the tenebrionid cavities.

The subelytral cavity is so widespread among desert tenebrionids and is such a prominent anatomical feature that it probably performs an important function or functions for the beetle. Biologists have suggested at various times that the cavity helps the beetle deal with many problems it encounters, from handling excessive heat or wind to obtaining or conserving food and water. It may even enhance reproductive success. Testing any given hypothesis has proven difficult for several reasons. First, the cavity may serve several functions, yet it may not serve any unique function. For example, the beetles obviously have many different adaptations for managing the heat and water problems of their desert environment. Second, cavity size and shape varies continuously from beetles with massive subelytral cavities to winged forms with no cavity at all, and there is no clear-cut line between xerophilous and mesophilous species. Many species occupy intermediate habitats. Lastly, the subelytral cavity can be visualized as a volume of air surrounded by a beetle. The cavity and the structures that form it are such an integral part of tenebrionid anatomy that it may be difficult to imagine and impossible to test what the beetle would be like without it.

An early and still persistent hypothesis about the function of the subelytral cavity is that it protects the beetle from excess heat. The basic idea is that the elytra absorb radiation by acting as a cover over the beetle. The subelytral cavity acts as an insulating dead-air space, retarding inward conduction of heat to the beetle. Hadley (1970) found that in direct sunlight, the temperature of the air in the subelytral cavity was 2-8° C. warmer than body temperature or outside air temperature. It should be noted that beetles were unable to maintain an equilibrium temperature, and would eventually die if kept in direct sunlight. However, the buffering capacity of the cavity may delay heat build-up, allowing the beetles to make short foraging trips in the sun.

Hadley (1970) also suggested the more subtle hypothesis that the subelytral cavity increases convective cooling. He cited Bolwig's (1957) laboratory study of thermal toler-

ance in tenebrionids. Bolwig found that at about 40° C., one beetle species would attempt to cool itself by exposing its genitalia and ventilating its subelytral cavity. The latter behavior resulted in fluctuations in subelytral cavity temperature. However, it must be noted that this behavior may be an artifact of the laboratory conditions, which included the use of an electric heater as a heat source.

Other experimental evidence provides little support for the hypothesis of a thermal function for the cavity. Cloudsley-Thompson (1964) found no difference in temperature between the subelytral cavity and the outside air. Also, the lethal temperature of another species did not change after a piece of elytra had been removed, although elytral removal causes increased transpiration, which may cool the animal. Fiori (1977) points out that several studies have found lower cavity temperature in white-elytra than in black-elytra beetles (Bolwig 1957, Edney 1971a). This suggests that any thermal effect the subelytral cavity may exert is too small to mask the effect of elytral color.

The early desert ecologist P. A. Buxton (1923) formed his "winglessness as an adaptation to excessive wind" hypothesis after rejecting the hypothesis of the subelytral cavity as a heat insulator. He may have been the first to note that not only diurnal, but also many nocturnal tenebrionids have large subelytral cavities (Buxton 1923, 1924). Koch (1961) states that increases and reductions in subelytral cavity volume are to be found in both nocturnal and diurnal forms. It might also be mentioned that although arid-mountainous and a few mesic species have well developed subelytral cavities, they exhibit no more heat tolerance than winged mesic species without subelytral spaces.

The small size of arthropods may ultimately preclude any effective adaptations (other than behavioral adaptations) for regulating temperature. Although desert tenebrionids are generally fairly large beetles (often exceeding 1 cm), they are still too small to possess much thermal inertia. Tenebrionids' internal body temperatures generally parallel black bulb temperatures (Seely et al. 1988). Thus, the beetles act as physical bodies in terms of heat gain; they quickly equilibrate with external temperatures (Edney 1971b, Henwood 1975). Without active (physical or physiological) cooling mechanisms, beetles must avoid prolonged exposure to temperatures above their tolerance limit.

It is now generally believed that one of the major functions of the subelytral cavity is to conserve water by reducing transpiration. Although Buxton (1923) did not propose a water-conserving function for the cavity, a statement he wrote was prophetic of research and thought to come:

"The extremely close fit between the margins of the elytra and the sternite is remarkable: it would appear to hinder the ventilation of the subelytral space into which the spiracles open."

The importance of this airtight cavity has since been demonstrated by modifying it, so that it is no longer airtight (Dizer 1955). Pieces of elytra were removed from various species of beetles, some from the Turkmenistan Desert with well developed subelytral cavities, and some lightly sclerotized and winged forms from the Russian steppe. After elytral removal, the beetles with (formerly) hermetic subelytral cavities showed a great increase in rate of water loss, while the water loss of winged species increased only a little. Similar results were obtained independently some nine years later by Cloudsley-Thompson (1964), who found Dizer's work after his experiments were completed. In three short pages, Cloudsley-Thompson simultaneously rejected the idea of a heat function for the cavity (discussed above) and demonstrated via elytral removal experiments the efficacy of the cavity in reducing transpiration. These findings were reconfirmed by Ahearn & Hadley (1969). These authors hypothesized that transpiration is decreased because the abdominal spiracles open into the relatively humid subelytral cavity rather than the outside air. The spiracles are protected from the drying effects of wind, and

the high humidity within the cavity reduces the vapor pressure gradient between the tracheae and their exterior environment, reducing evaporation via the spiracles.

Ahearn (1970) presented evidence that the airflow with the beetle's tracheal system is unidirectional, with the thoracic spiracles serving only to take in air. Although the thoracic spiracles are not protected by the subelytral cavity, little water should be lost from them since air does not flow outward through them. All moist exhalent air empties into the subelytral cavity, increasing its humidity and slowing evaporation even more.

Fiori (1977) argued that the subelytral cavity reduces transpiration mainly by slowing evaporation from the membranous abdominal uroterga and their lateral and intersegmental membranes, which constitute the floor of the cavity. He noted that the abdominal spiracles are imbedded in atria and can be closed, indicating that they may already be adequately protected. Probably, the cavity prevents potential loss from both sources. In any case, water that would otherwise be lost is conserved, enabling the beetle to survive longer dry periods.

For the subelytral cavity to effectively reduce transpiration, it must be airtight. Provided a hermetic seal is achieved, the size of the cavity should not affect its water conserving efficiency. However, great interspecific variation exists in the size (volume) of the cavity in relation to the size of the beetle. There is no clear correlation between cavity size and size of beetle, habitat, or activity times.

Cloudsley-Thompson (1971) maintained that cavity size has no direct effect on individual beetle fitness, and cited variability in cavity size as an example of non-adaptive variation.

In his morphological study of the subelytral cavity, Fiori (1977) observed that the size of the cavity functions to allow abdominal expansion in these heavily sclerotized beetles. The abdomens of these beetles can only expand via extension of intersegmental membranes between the uroterga which make up the floor of the cavity. The subelytral cavity thus provides room for the uroterga to raise up with increase in abdominal volume. Fiori noted that the ability to expand the abdomen may be important to beetles which must feed on large quantities of their detrital food, which generally is of low nutritional value. He observed that after feeding, the uroterga may expand to occupy almost the entire subelytral space.

Slobodchikoff & Wisman (1981) elaborated on the abdominal expansion hypothesis, although Fiori (1977) was not cited. They hypothesized that the abdominal expansion into the subelytral cavity allows tenebrionids to drink and store large quantities of water. This may be important in enabling the beetles to take advantage of ephemeral water sources, such as rain puddles, which are present only for a short time following the occasional rain event. Slobodchikoff & Wisman's (1981) observations on changes of cavity depth as the beetle's water status changed supports their hypothesis.

Fiori (1977) also invokes his abdominal expansion hypothesis to explain the sexual dimorphism in subelytral cavity size seen in many species. Females generally possess cavities which are proportionally larger than those of males. Fiori suggested that females need a larger subelytral cavity to accommodate additional abdominal expansion caused by the growth of eggs in the ovarioles and egg-calyces prior to oviposition.

The subelytral cavity may be seen as a hermetic seal which reduces transpiration regardless of its size, and as a protected space within the beetle which, whether airtight or not, allows the abdomen to expand to store food, water, or eggs. Its effect as a heat absorber has not been clearly demonstrated, and may not be significant.

I hypothesize that the cavity itself is probably an architectural constraint resulting from the need for abdominal expansion within the heavily sclerotized, fused elytra that evolved primarily as a water conservation adaptation. The cavity may represent the same type of architectural constraint as the triangular spandrels which support the domes of cathedral ceilings (Gould & Lewontin 1979). The spandrels are beautiful in



their own right, containing artwork seemingly perfectly suited to presentation on a triangular space. However, the spandrels were not designed to bear artwork—they are simply necessary architectural by-products of mounting a dome on rounded arches. So too may the actual cavity of desert tenebrionids be an architectural by-product of having a well sclerotized and hermetically sealed abdomen. The real adaptation here is the set of elytral joints described by Fiori (1977) which serves to create an airtight abdominal exoskeleton. The cavity is present simply to give the beetle needed "wiggle room" within its exoskeleton. Any other use the beetle has for the cavity (such as the possible insulating effects of the air space) may be seen as secondary uses in the same way that the cathedral spandrels were put to use bearing artwork.

Although the subelytral cavity is an intriguing "place," little recent work has been done on it (C. S. Crawford pers. comm.). It appears that research on the subelytral cavity follows close behind new suggestions concerning its function. Most of the investigations into the subelytral cavity seem to have been sparked by ideas in the seminal papers of Cloudsley-Thompson (1964) and Fiori (1977). Our understanding of the subelytral cavity is far from complete. Research will continue when someone forwards a new hypothesis, a reason to question our current notions.

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#### REFERENCES CITED

- AHEARN, G. A. 1970. The control of water loss in desert tenebrionid beetles. *J. Exp. Biol.* 53: 573-595.
- AHEARN, G. A. 1971. Ecological factors affecting population sampling of desert tenebrionid beetles. *Am. Midl. Nat.* 86: 385-406.
- AHEARN, G. A., AND N. F. HADLEY. 1969. The effects of temperature and humidity on water loss in two desert tenebrionid beetles, *Eleodes armata* and *Cryptoglossa verrucosa*. *Comp. Biochem. Physiol.* 30: 739-749.
- ALLSOPP, P. G. 1980. The biology of false wireworms and their adults (soil-inhabiting Tenebrionidae) (Coleoptera): A review. *Bull. Entomol. Res.* 70: 343-379.
- BOLWIG, N. 1957. Experiments on the regulation of the temperature of certain tenebrionid beetles. *J. Entomol. Soc. S. Afr.* 20: 454-458.
- BROZA, M. 1979. Dew, fog, and hygroscopic food as a source of water for desert arthropods. *J. Arid Env.* 2: 43-49.
- BUXTON, P. A. 1923. *Animal life in deserts—a study of fauna in relation to environment*. Edward Arnold & Co., Ltd. 176 pp.
- BUXTON, P. A. 1924. Habits of some tenebrionid beetles. *Entomol. Mon. Mag.* 60: 3-7.
- CLOUDSLEY-THOMPSON, J. L. 1964. On the function of the sub-elytral cavity in desert Tenebrionidae (Col.). *Entomol. Mon. Mag.* 100: 148-151.
- CLOUDSLEY-THOMPSON, J. L. 1971. Non-adaptive variation and group selection. *Sci. Prog., Oxf.* 59: 243-254.
- CLOUDSLEY-THOMPSON, J. L. 1977. The genus *Cossyphus* (Col., Tenebrionidae): A striking instance of protective resemblance. *Entomol. Mon. Mag.* 113: 151-152.
- CLOUDSLEY-THOMPSON, J. L., AND M. J. CHADWICK. 1964. *Life in Deserts*. Dufour, Philadelphia, PA. 218 pp.

- CRAWFORD, C. S. 1990. Scorpiones, Solifugae, and associated desert taxa, pp. 421-476 in D. L. Dindal, [ed.] *Soil Biology Guide*. John Wiley & Sons, NY, NY. 1349 pp.
- CRAWFORD, C. S. 1981. *Biology of Desert Invertebrates*. Springer-Verlag, NY, NY. 314 pp.
- DIZER, Y. B. 1955. On the physiological role of the elytra and sub-elytral cavity of steppe and desert Tenebrionidae [in Russian]. *Zool. Zh. S. S. R.* 34: 319-322.
- DOYEN, J. T., AND W. R. TSCHINKEL. 1982. Phenetic and cladistic relationships among tenebrionid beetles (Coleoptera). *Systematic Entomol.* 7: 127-183.
- EDNEY, E. B. 1971a. The body temperature of tenebrionid beetles in the Namib Desert of southern Africa. *J. Exp. Biol.* 55: 253-272.
- EDNEY, E. B. 1971b. Some aspects of water balance in tenebrionid beetles and a thysanuran from the Namib Desert of southern Africa. *Physiol. Zool.* 44: 61-76.
- EISNER, T., AND J. MEINWALD. 1966. Defensive secretions of arthropods. *Science* 153: 1341-1350.
- EL RAYAH, E. A. 1970. Some reactions of two desert beetles *Adesmia antiqua* and *Pimelia grandis* (Tenebrionidae) to temperature. *Entomol. Exp. Appl.* 13: 286-292.
- FIORI, G. 1977. La cavita sottoelitrare dei tenebrionidi apomorfi. *Redia* 60: 1-112.
- GOULD, S. J., AND R. C. LEWONTIN. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc. R. Soc. Lond.* 205: 581-598.
- HADLEY, N. F. 1970. Micrometeorology and energy exchange in two desert arthropods. *Ecology* 51: 434-444.
- HADLEY, N. F. 1972. Desert species and adaptation. *American Scientist.* 60: 338-347.
- HAMILTON, W. J. III. 1975. Coloration and its thermal consequences for diurnal desert insects, pp. 67-89 in N. F. Hadley, [ed.] *Environmental physiology of desert organisms*. Dowden, Hutchinson, and Ross, Stroudsburg, PA.
- HAMILTON, W. J. III, AND M. K. SEELY. 1976. Fog basking by the Namib Desert beetle, *Onymacris unguicularis*. *Nature (London)* 262: 284-285.
- HENWOOD, K. 1975. A field-tested thermoregulation model for two diurnal Namib Desert tenebrionid beetles. *Ecology* 56: 1329-1342.
- KOCH, C. 1961. Some aspects of abundant life in the vegetationless sand of the Namib Desert dunes-positive psammotropism in tenebrionid beetles. *J. SW. Afr. Sci. Soc.* 15: 9-33.
- KOCH, C. 1962. The Tenebrionidae of southern Africa XXXI. Comprehensive notes on the tenebrionid fauna of the Namib Desert. *Ann. Transvaal. Mus.* 24: 61-103.
- KRAMM, R. A., AND K. R. KRAMM. 1972. Activities of certain species of *Eleodes* in relation to season, temperature, and time of day at Joshua Tree National Monument (Coleoptera: Tenebrionidae). *Southwest. Nat.* 16: 341-355.
- MCKINNERNEY, M. 1978. Carrion communities in the northern Chihuahuan Desert. *Southwest. Nat.* 23: 563-576.
- RAFES, P. M. 1960. The life forms of insects inhabiting the Naryn sands of the semidesert Transvolga region. *Entomol. Rev.* 38: 19-31.
- SCHMOLLER, R. R. 1970. Terrestrial desert arthropods: Fauna and ecology. *The Biologist* 52: 77-98.
- SEELY, M. K., AND G. N. LOUW. 1980. First approximation of the effects of rainfall on the ecology and energetics of a Namib Desert dune ecosystem. *J. Arid Env.* 3: 25-54.
- SEELY, M. K., C. S. ROBERTS, AND D. MITCHELL. 1988. High body temperature of Namib dune tenebrionids-why? *J. Arid Env.* 14: 135-143.
- SLOBODCHIKOFF, C. N. 1979. Utilization of harvester ant debris by tenebrionid beetles. *Environ. Entomol.* 8: 770-772.
- SLOBODCHIKOFF, C. N. 1983. Water balance and temperature preferences, and their role in regulating activity times of tenebrionid beetles. *Oikos* 40: 113-119.
- SLOBODCHIKOFF, C. N., AND K. WISMAN. 1981. A function of the subelytral chamber of tenebrionid beetles. *J. Exp. Biol.* 90: 109-114.
- TANNER, V. M., AND W. A. PACKHAM. 1965. Tenebrionidae beetles of the Nevada test site. *Brigham Young Univ. Sci. Bull., Biol. Ser.* 6: 1-44.

- THOMAS, D. B. JR. 1979. Patterns in the abundance of some tenebrionid beetles in the Mojave Desert. *Environ. Entomol.* 8: 568-574.
- TSCHINKEL, W. R. 1975. A comparative study of the chemical defensive system of tenebrionid beetles. *Chemistry of the secretions. J. Insect Physiol.* 21: 753-783.
- WALLWORK, J. A. 1982. Desert soil fauna. Praeger Pub. NY, NY. 296 pp.
- WISE, D. H. 1981. A removal experiment with darkling beetles: Lack of evidence for interspecific competition. *Ecology* 62: 727-738.
- ZACHARIASSEN, K. A. 1977. Ecophysiological studies on beetles from arid regions in east Africa. *Norw. J. Entomol.* 24: 167-170.
- ZACHARIASSEN, K. A., J. ANDERSON, G. M. O. MALOY, AND J. M. Z. KAMAU. 1987. Transpiratory water loss and metabolism of beetles from arid areas in east Africa. *Comp. Biochem. Physiol.* 86A: 403-408.

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## THE RELATIONSHIP BETWEEN FALL ARMYWORM (LEPIDOPTERA: NOCTUIDAE) INSTAR AND SUSCEPTIBILITY TO INSECTICIDES APPLIED TO SWEET CORN

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### ABSTRACT

Toxicities of 2 concentrations of fenvalerate and methomyl to second, fourth and sixth instar fall armyworms, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), were determined in laboratory and field tests. In laboratory tests, the LC<sub>50</sub> for both methomyl and fenvalerate increased as larval age increased from second to fourth to sixth instar. Fenvalerate was more toxic than methomyl to second instars but less toxic than methomyl to sixth instars. In the 1986 field tests with whorl stage sweet corn, all treatments effectively reduced whorl damage caused by second, fourth and sixth instars compared with the untreated. Both rates of methomyl were significantly more effective than either rate of fenvalerate in reducing whorl damage caused by fourth or sixth instar fall armyworm. In 1987, both rates of methomyl and the 0.224 kg AI/ha rate of fenvalerate significantly reduced second and fourth instar fall armyworm whorl damage compared with the untreated, but only the 1.0 kg AI/ha rate of methomyl significantly reduced sixth instar whorl damage. All insecticide treatments resulted in significantly fewer second instars recovered from the whorls, but only the methomyl treatments resulted in significantly fewer fourth instars compared with the untreated. Greater whorl damage was caused by fourth and sixth instars compared with second instars. Results indicate that timing of application is as important as selection of pesticide for management of fall armyworm on whorl stage sweet corn.

Key Words: *Spodoptera frugiperda*, corn, whorl damage, fenvalerate, methomyl.

### RESUMEN

Se determinaron en pruebas de laboratorio y de campo la toxicidad de dos concentraciones de fenvalerato y metomilo a los segundos, cuartos y sextos instares del qusano