deck. The modified Q scores and the raw score for number of marker cards exceeded are very similar in information content, having a correlation of .98. Thus, either method could be used; the choice would depend on convenience.

Conclusion and Discussion

We conclude (i) that the marker-card method is as reliable a measure as the ordinary Q-sort method; (ii) that Q and the marker-card score are measuring very nearly the same thing—in this case, presumably conflict; and (iii) that the use of marker cards permits comparison of judgments about a given quantity in the context of different situations and may even permit comparison of results obtained by different research teams if the different teams use the same marker decks.

A fundamental issue involved in scoring the entries on the cards in this study by either Q-sort or marker cards is the "judgability" of the items as indicators of conflict. We noted above that items with the highest variances in scoring, from judge to judge, were concentrated at the low-conflict end of the scale. A possible explanation is that judges are able to make finer distinctions concerning an attribute when it is present than when it is absent. Differences in scoring could also arise from a lack of unidimensionality in the attribute being scaled. If judges find that conflict has several distinct aspects, the task of placing items in a single order becomes more difficult.

Difficulties in making judgments also arose from the fact that the actions were being judged out of context, or in contexts that varied from judge to judge, since no standard context was supplied. But these difficulties lie outside our problem, which was to find an alternative to Q-sorting which would permit intersituational comparisons. Our success in finding an alternative is apparent in our results, but problems of judgability remain with both techniques.

Beyond providing a standard for intersituational comparisons, the marker-card technique has other advantages. It is possible that the use of marker decks will be of help in training judges to score such a variable as conflict. In our study it permitted identification of a judge inadequately trained to do so. Possibly the marker cards will be useful in assigning scale values to batches of data too small for Q-sort, or even to individual items. It further appears that the marker cards should be useful in discriminating among high-conflict items which heretofore would all have tended to appear in the top Q-sort category.

The marker-card technique has given us a reliable alternative to Q-sort for scaling conflict. The method should be capable of extension to dimensions other than conflict.

References and Notes

1. The specimens are to be distributed into the nine "levels of intensity" of the quality being judged in these proportions:

Level	1	2	3	4	5	6	7	8	9
Proportion	5	8	12	16	18	16	12	8	5

Note that the mean and variance are established by the nature of the distribution and would be the same for any such distributions irrespective of the data being scaled.

2. R. North, O. R. Holsti, M. G. Zaninovich, D. A. Zinnes, *Content Analysis* (Northwestern Univ. Press, Evanston, Ill., 1963). For an example of the application of this technique to material from the crisis preceding World War I, see R. North, R. Brody, O. Holsti, *Peace Research Society (International) Papers No. 1* (1964), p. 1.
3. Variance was measured in terms of the arc sine transforms of the ranks, to reduce end effects. In particular, the item ranked r in the set of N marker cards was transformed to:

$$\sin^{-1}\left(\frac{r}{N+1}\right)^{\frac{1}{2}} + \sin^{-1}\left(\frac{r+1}{N+1}\right)^{\frac{1}{2}}$$

4. L. E. Moses and R. V. Oakford, *Tables of Random Permutations* (Stanford Univ. Press, Stanford, Calif., 1963).
5. We take r_{xx} as the average of the inter-judge marker-score correlations. Because Q is the average of two judges' Q values, we must correct for this fact; the Spearman-Brown "prophecy formula" can be shown to be applicable. It yields:

$$r_{QQ} = \frac{2(.733)}{1.733} = .846$$

6. Partial support for the research described was provided by contract NONR 225 (82), Project NR 177 254, Group Psychology Branch, Office of Naval Research. Reproduction of this article in whole or in part is permitted for any purpose of the United States Government. We acknowledge with thanks helpful conversations between one of us (L.E.M.) and Frederick Mosteller of Harvard University. Data analysis for this study was made possible by a grant from the Stanford University Computation Center. We thank Mr. Kuan Lee for his invaluable assistance with the computer programming for this study. Copies of the four marker decks are available upon request from the Stanford Studies in International Conflict and Integration, 550 Salvatierra Street, Stanford, California.

Water Balance in Desert Arthropods

Despite their small size, arthropods may be highly adapted for life in xeric conditions.

E. B. Edney

Deserts are not homogeneous environments. The surface is indeed often very hot and dry and sometimes very cold, but there are plenty of protected niches in which the climate is much less extreme. Adaptations, therefore, are not always concerned with tolerance of, or regulation against, drought and heat, but often take the form of structural and behavioral characters associated with particular modes of life (for example, the flat shape and scoop-like legs of many dune insects), or of phenological mechanisms that permit the animals to take maximum advantage of short climatically favorable seasons. Such adaptations permit the avoidance of desert conditions and are associated only indirectly, if at all, with water stress. Nevertheless, water shortage and high temperatures are encountered by many desert animals, and this article attempts to consider the structural and functional mechanisms of arthropods which are important in relation to these aspects of desert life.

Nothing like a complete picture of such mechanisms is available at present since the physiology of desert insects, let alone other arthropods, has

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received little attention. However, a distinction between desertic and other forms is not always very meaningful, and there is fortunately a good deal of information about xeric insects in general which is relevant to this discussion.

The Matter of Size

The fact that arthropods are relatively small has several important consequences, one of which is that evaporative cooling as a means of long-term temperature regulation is ruled out. Since an animal's total income of heat is roughly proportional to its surface area, maintenance of a temperature below that of the surroundings will be achieved only if the rate of evaporation of water from it is also proportional to the surface. But the smaller an animal is, the greater is the ratio between its surface and its volume, and, as Schmidt-Nielsen has pointed out (*1*), in a particular set of conditions approximating those of a desert on a hot day, the rate of evaporation per unit area which is necessary to produce a tolerable equilibrium temperature may be maintained for a long time by a large animal such as man, but the same rate would quickly exhaust the water reserves of a rat. A tsetse fly, weighing about 20 milligrams would have to lose more than twice its total weight in water each hour to maintain the same temperature. On the other hand, small size permits an animal to occupy climatically equable habitats that are not available to larger ones. In the Egyptian desert, for example, Williams (*2*) found that the ground surface may be at 56°C, while the soil only 10 centimeters below is a mere 34°C; by moving up and down through a distance of 30 centimeters a small animal could live in a constant temperature throughout the daily cycle.

Water Loss through the Integument

Considerations of size not only make long-term evaporative cooling impossible but also underline the importance, particularly for species living in dry conditions, of reducing cutaneous water loss at all times. This need in turn focuses attention on the integument, which is capable of a high degree of adaptive modification both structurally and physiologically [see reviews by Locke (*3*) and Ebeling (*4*)].

Although there is evidence that the thickness and hardness of an arthropod cuticle does affect its permeability to water (*5*), it has been recognized since the early work of Ramsay (*6*), Beament (*7*), Wigglesworth (*8*), and Lees (*9*) that the main barrier to the outward passage of water lies in the epicuticle. More recent work reviewed by Beament (*10*) strongly suggests that impermeability is conferred by one or more layers of closely packed and oriented polar lipid molecules near the surface of the epicuticle. In dry air, the rate of cutaneous transpiration from any arthropod increases as the temperature rises, since dry air has a higher vapor pressure deficit at higher temperatures. However, in many terrestrial arthropods temperature also affects the permeability of the cuticle itself. One such effect is seen as a rather sudden increase in the rate of transpiration at what is known as the transition temperature (*10*), an effect which is more readily observed if transpiration is plotted as a function of the temperature of the evaporating surface (namely, the cuticle) rather than as a function of the ambient air temperature (Fig. 1) (*11*). The transition phenomenon is generally believed to coincide with a physical change, perhaps a disorientation of the lipid molecules, in the epicuticle.

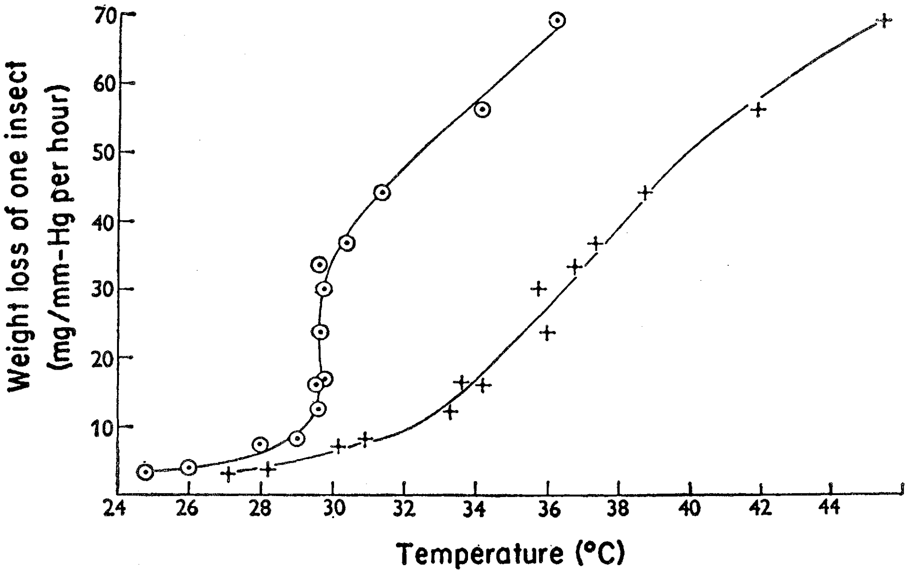

Fig. 1. Transpiration from the cockroach *Blatta* in relation to temperature of the ambient air (crosses) and to the surface temperature of the cuticle (circles). A transition point at about 29°C is evident. Redrawn from Beament (*11*).

The ecological significance of this transition phenomenon is not clear. In many insects and ticks the transition temperature is well above that at which the animal would die—about 50°C in such highly waterproofed insects as *Rhodnius, Pieris* pupae, and *Tenebrio* larvae (*7*), and in argassid ticks (*9*). Yet in others it is lower, and may even be below the animal's optimal temperature; in the firebrat *Thermobia*, for example, which lives well at 30°C, the transition temperature is about 28°C (*12*). On the whole, however, it seems that arthropods with high transition temperatures have low basic rates of transpiration, and it may turn out that the two are in some way related.

There is a clearer picture with regard to the basic rate of transpiration (below the transition temperature, about 20° to 30°C) in different species and the relation of this to their ecology. Table 1 presents data for a number of arthropods from xeric and mesic environments; a general correlation (within taxonomic groups) between dry habitats and low basic transpiration rates can be seen. The relationship does not always hold, however, for within the genus *Glossina* (tsetse flies) Bursell (*13*) found no correlation between resistance to desiccation and habitat in adult flies, although such correlation does exist for the pupal stages of these insects.

It is safe to conclude that the arthropod integument is so organized as to permit a high degree of waterproofing where necessary (this is shown particularly by inactive stages such as eggs and pupae, which cannot replace lost water by feeding) and that by and large this occurs in species living in xeric environments. There is a dearth of information about truly desertic forms, many of which are exposed at least temporarily to very hot, dry conditions (*14, 15*).

Water Loss through the Spiracles

While water loss through the cuticle may be drastically reduced, some loss through the respiratory membranes is inevitable. These moist surfaces occur, in insects and in many other terrestrial arthropods, at the ends of long narrow tracheae, which are invaginations of the integument. Such positioning of the respiratory membranes confers no direct advantage for water conservation; in fact the reverse is probably true. Although outward diffusion of water vapor is reduced, so to a greater extent is the inward diffusion of oxygen, since the latter molecule is larger. An advantage of the tracheal system is that the openings at the animal's surface are readily occlusible by spiracles so that the outward diffusion of water vapor may be prevented except at those times when, owing to intense activity, the spiracles must open widely to permit the maximum uptake of oxygen.

Information concerning the relative loss of water through the spiracles and the general cuticular surface is difficult to obtain since the former is so strongly affected by oxygen demand resulting from activity. Bursell (*16*) found that in tsetse flies, which are certainly subject to water stress, a resting insect loses about 0.12 milligram of water per hour; this amount is reduced to 0.09 milligram if the spiracles are blocked; hence 25 percent of the total loss is spiracular. In partially active flies, however, water loss rose to 0.21 milligram per hour. Similar results have been reported for the desert locust *Schistocerca* (*17*).

The important question of whether increased oxygen uptake necessarily involves a proportionate increase in water loss now arises. On theoretical grounds such a relationship might be expected, but Bursell (*16*) found that while the oxygen uptake of tsetse flies increased by a factor of 22 during flight, water loss was only six times that of a resting fly. Similarly, Weis-Fogh (*18*) found that in desert locusts extra water lost during flight activity was replaced by increased oxidation water, even in dry air.

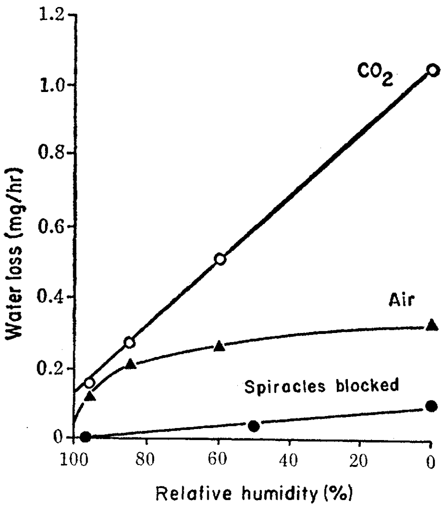

Fig. 2. The rate of water loss from tsetse flies (*Glossina morsitans*) increases linearly with decreasing relative humidity if the spiracles are permanently open (CO_2) or blocked. But the rate falls off in drier air if the spiracles are free (Air), owing to spiracular regulation. After Bursell (*13, 16, 28*).

The physiology involved is by no means clear, and the question deserves much further study. A mechanism which may be relevant is that observed by Buck and others (*19*); in some insects, usually in the pupal or other inactive stage, carbon dioxide is released in widely separated bursts. Between bursts, the spiracles are all but closed, and metabolic CO_2 goes temporarily into solution in the tissues. Reduced pressure resulting from the absorption of oxygen from the tracheal system causes a mass flow of air inwards through the spiracular slits, preventing the outward diffusion of CO_2 and water vapor. Eventually the spiracles open wide for a brief period, and CO_2 is released.

Apart from this possibility, there is good evidence of the extent to which the insect spiracular mechanism helps to regulate the body water content. If the spiracles of tsetse flies are caused to remain open by 10 percent CO_2 in air, then the rate of water loss increases linearly with increasing vapor pressure deficit, and the same is true if the spiracles are blocked (although in this case the absolute rates are much lower). However, if flies with free spiracles are exposed to air, the rate at which water is lost is no longer linearly related to vapor pressure deficit but falls off in drier air as a result of regulation by differential spiracular closure (Fig. 2) (*13, 16*). The rate also decreases as the water reserves decrease, and in the pupa the rate of loss depends upon the amount of desiccation sustained by the previous larval stage. There are, then, several regulatory mechanisms which permit these insects to conserve water when necessary.

Table 1. Transpiration in arthropods from various habitats measured in dry air at temperatures between 20° and 30°C. The values are given as micrograms per square centimeter per hour per millimeter of mercury and may be converted to centimeters per second by multiplying by 2.90×10^{-4}.

Species	Habitat	Transpiration
	Isopod crustaceans	
Porcellio scaber (*25*)	Hygric	110
Venezillio arizonicus (*24*)	Xeric	32
Hemilepistus reaumuri (*21*)	Xeric	23
	Insects	
Calliphora erythrocephala (*51*)	Mesic	51
Blatta orientalis (*51*)	Mesic	48
Glossina palpalis adults (*51*)	Mesic	12
Glossina morsitans pupae (*52*)	Xeric	0.3
Tenebrio molitor larvae (*51*)	Xeric	5
Tenebrio molitor pupae (*53*)	Xeric	1
Thermobia domestica adults (*12*)	Xeric	15
	Myriapods	
Lithobius sp. (*51*)	Hygric	270
Glomeris marginata (*25*)	Hygric	200
	Arachnids	
Pandinus imperator (*55*)	Mesic	82
Androctonus australis (*21*)	Xeric	0.8
Galeodes arabs (*14*)	Xeric	6.6
Ixodes ricinus (*8*)	Mesic	60
Ornithodorus moubata (*8*)	Xeric	4.0

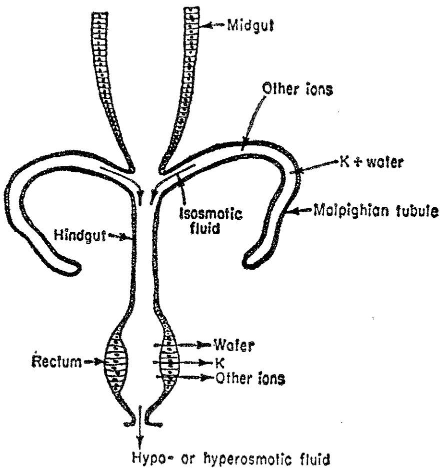

Fig. 3. Diagram of the excretory system of an insect. From Stobbart and Shaw (*54*).

Nontracheate arthropods, such as the crustacean sow bugs, would seem to be most unlikely candidates for successful desert life. Strictly speaking this is true, for, although some species do occur in "deserts," they largely avoid extremes of heat and drought. *Hemilepistus* occurs in north African and middle eastern deserts (*20, 21*); *Venezillio arizonicus* and *Buddelundia* spp. occur in the Arizona desert and in xeric regions of Australia, respectively (*22, 23*), but always in cryptozoic niches. Nevertheless, these animals are exposed from time to time to more xeric conditions than other terrestrial isopods are, and it is significant that the permeability of their integuments to water is relatively low (Table 1). Whether or not impermeability, such as it is, results from an epicuticular lipid layer, as it does in insects, is still debatable owing to conflicting evidence, but recent work by Warburg (*23, 24*) suggests that such a mechanism is present in *Venezillio*, but not in more mesic species. If this is confirmed, the terrestrial isopods will provide good material for a study of the evolution of the lipid waterproofing mechanism.

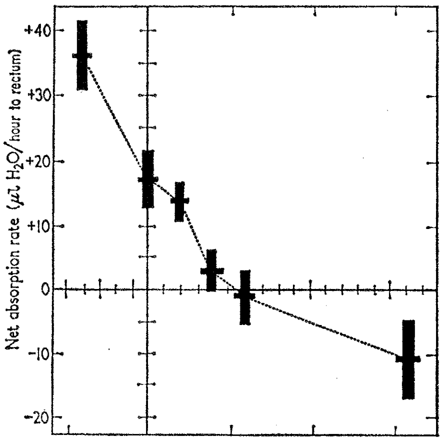

Fig. 4. The relationship between initial osmotic pressure gradient and net rate of water movement across the rectal wall in the desert locust (*Schistocerca*). A positive sign indicates movement from the lumen outwards (ordinate), or that the rectal fluid is more concentrated than the hemolymph (abscissa). From Phillips (*26*).

Sow bugs again are ill-equipped for desert life so far as respiratory water loss is concerned, for they retain the crustacean pleopods (gill-like appendages) as respiratory organs. In the more xeric species, bush-like invaginations of the pleopod surface known as pseudotracheae are present, but their openings do not bear occlusible spiracles, and in *Porcellio*, although the exposed area of the pleopods is only about 3 percent of the total body surface, nearly half of the total water loss occurs there (*25*). Comparable figures for desert species are not available.

Water Regulation by Excretion and Defecation

Insects, like birds and reptiles, excrete waste nitrogen mainly as uric acid so that little or no water need be involved, and, in addition, the fecal pellets may be produced almost dry. This statement oversimplifies the problem, however, for there may be occasions when even a desert arthropod is overloaded with water so that regulation of excretory water loss as well as mere reduction is required. In insects the excretory system consists of a number of blind Malpighian tubules opening proximately into the rectum, the walls of which are glandular. Rectum and tubules function together as an osmotic and ionic regulatory system in a manner analogous to that of the vertebrate nephron (Fig. 3).

The capacity of this system for regulation has been demonstrated by Phillips in a series of papers on the desert locust (*26*). If, in the absence of food, these insects are given a saline solution to drink, the concentrations of Na^+, K^+, and Cl^- in their hemolymph (blood) rise above normal, but not to the full extent of their values in the saline. At the same time, ionic concentrations in the rectal fluid (to be excreted) rise dramatically (Table 2). In locusts given fresh water to drink, changes occur in the reverse direction, and an extremely dilute urine is produced. The function of the rectal wall in regulation involves active transport of water from the lumen into the cells against strong osmotic gradients; the precise mechanism of this movement is obscure. The concentration difference between rectal contents and hemolymph just sufficient to prevent further uptake of water varies, being greater when the insect's reserves of water are low (Fig. 4). In tsetse flies, too, water content of the fecal pellets and the amount of liquid urine produced by a tsetse fly after feeding are both regulated, presumably by a similar process, in accordance with the fly's water reserves (*27*).

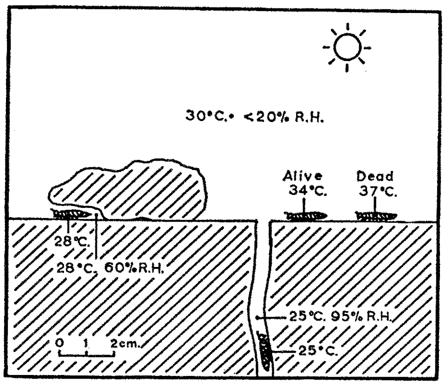

Fig. 5. A set of measurements in the habitat of *Hemilepistus reaumuri* (Isopoda) in the Algerian desert near Biskra. Transpiration reduces the body temperature of a living animal by 3°C compared with a dead, dry, control specimen. The animals dig vertical holes in which conditions are relatively equable. From Edney (*56*).

Tolerance of Water Loss

Camels can put up with a far greater degree of dehydration than man can, and a similar state of affairs might be expected in desert, as compared with mesic, arthropods; but most insects appear to withstand depletion of the body water from a norm of about 75 percent of their fat-free total weight to as low as 60 percent (*28*). I have found that during 1 week a desert cockroach (*Arenivaga* sp.) can withstand a loss of weight in dry air equal to 25 to 30 percent of its original weight. But of course there is a loss of dry weight during this time, and oxidation water is also produced, so that the insect ends up with a water content of about 60 percent. During such dehydration there is evidence of strong osmotic regulation of the hemolymph, for in a less extreme case where the mean absolute amount of water present decreased from 67 to 48 units, the osmotic pressure of the hemolymph rose from 433 only to 452 milliosmoles per liter instead of to 616 milliosmoles which would have been expected in the absence of regulation [Edney (*29*); see Fig. 10].

It seems at present that insects tolerate a greater water loss than most mammals can, but that desert species differ from other species of insects far more with respect to transpiration than with respect to tolerance of low body-water content.

Theoretical considerations suggest, and measurements demonstrate, that in normal circumstances evaporation of water contributes only marginally to the heat balance and thus to the equilibrium body temperature of insects (*30, 31*). Desert locusts flying on a roundabout in dry air have a body temperature only 1°C lower than that which they have in saturated air, where evaporation is negligible (*17*). Nevertheless, not all arthropods have impermeable cuticles; there are routes for water evaporation other than through the cuticle, and circumstances are sometimes abnormal.

Sow bugs (*Hemilepistus reaumuri*) from the Algerian desert dig holes in the ground and stay there during the heat of the day. However, I have observed them to be caught on the surface in strong sunlight when a cloud moves away from the sun, and evaporation then causes a temperature drop of up to 3°C, an effect which is very probably of survival value. Figure 5 shows a set of temperature and humidity measurements made in their habitat (*20*).

A somewhat different process occurs in tsetse flies. The lethal temperature of *Glossina morsitans* is about 40°C for one hour and 45°C for 5 minutes (*32*). Barrass and I (*33*) observed that, at high sublethal temperatures of 39.5° to 40°C, the spiracles of these insects open wide, thus permitting rapid evaporation of water from the respiratory surfaces, which results in a depression of body temperature up to 1.5°C below that of the ambient air (Fig. 6). No such depression occurs if evaporation is prevented by saturated air, or even in dry air if the spiracles are blocked.

Table 2. If desert locusts are given strong saline to drink, ionic concentrations in their hemolymph rise, but not to the level of those in the saline. Ionic concentrations in their rectal fluid become higher than those in the saline. Data from Phillips (*26*).

Liquid for drinking	Ionic concentration (mean values) (meq/liter)		
	Na	K	Cl
	Saline for drinking		
	300	150	450
	Hemolymph		
Water	108	11	115
Saline	158	19	163
	Rectal fluid		
Water	1	22	5
Saline	405	241	569

Whether or not such a small drop in temperature is of survival value seems doubtful. However, measurements made in the field at the hottest time of the year in a tsetse infested area of Rhodesia suggest that it might be. A bait ox was used, and flies observed to feed on it were marked, released, and subsequently found resting on branches in the vicinity. At the hottest time of the day, temperatures where the flies were sitting were nowhere lower than 38°C except in a rot hole which was at 35°C. The relative humidity was about 25 to 35 percent.

Temperatures on the skin of the bait ox where the flies fed were between 36° and 37.5°C in the shade but rose to between 40° to 41.5°C when the skin was exposed to the sun. One reading of 47°C was obtained on the animal's hock. The normal response of an insect to high temperature is to move away, but since tsetse flies are obliged to feed, during which time they imbibe warm blood, they may be unavoidably exposed to dangerously high temperatures for short periods, during which the ability to decrease the body temperature slightly could be of value.

Temperature Tolerance

Statements about upper lethal temperatures are plentiful, but their interpretation is often difficult since experimental conditions have been so various (*34*). Where the ecological significance of high temperatures is in question, we must know the animal's temperature as well as that of its immediate environment, for different parts of the environment (for example, the ground surface and the air immediately above it) may be at quite different temperatures, and both may differ from that of the animal.

Impressively large differences have indeed been observed between the temperatures lethal to arthropods from different environments. For example, the mole-cricket *Gryllotalpa* is normally active between −2.5°C and +11°C and dies at about 20°C, while the firebrat *Thermobia*, which lives in the domestic "deserts" of hot, dry buildings, is active between 12° and 50°C and dies at 51.3°C (*35*).

Lethal temperatures in the neighborhood of 50°C and above have been recorded for several desert arthropods, including various beetles, scorpions, and camel spiders (*36*). So far as I know, the record for tolerance of high temperatures is currently held by the

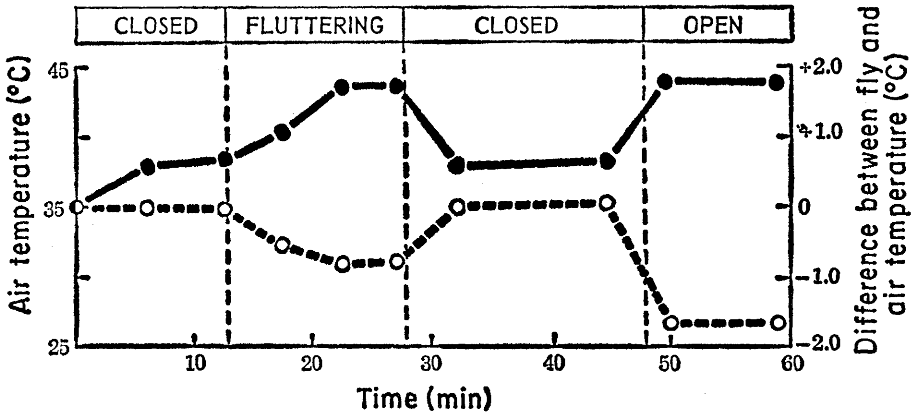

Fig. 6. The effect of spiracular opening on the internal temperature of a tsetse fly. Air temperature, full circles; difference between air and fly temperature, open circles. At about 39°C the spiracles flutter or open, and at the same time the body temperature is depressed. After Edney and Barrass (*33*).

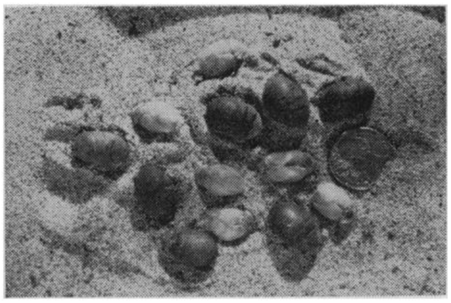

Fig. 7. Adult males (winged) and females of the cockroach *Arenivaga* sp. from sand dunes in Colorado desert near Palm Springs, California.

Fig. 8. At night, adult females and nymphs of *Arenivaga* wander just below the sand surface, leaving ridges. Occasionally they surface and leave the tracks shown in the center of the photograph. The smaller sinusoidal ridge below is made by the larva of a therevid fly.

larva of a midge, *Polypedilum vanderplanki*, which lives in temporary rock pools in West Africa (*37*). If the pools dry before development is completed, the larvae become all but completely desiccated and can then (during cryptobiosis) withstand a temperature of 102°C for a minute or two, after which, upon rehydration, development can proceed.

The surfaces of some insects are known to strongly reflect infrared light [from 69 to 35 percent depending upon the wavelength (*38*)], but visible color differences are probably not of great importance in this respect (*31*). Buxton (*39*) did report a difference of 4.5°C between the temperatures of light and dark colored *Calyptamus* grasshoppers, but Pepper and Hastings were unable to confirm this for another grasshopper *Melanoplus* (*40*). The frequently observed fact that many diurnal desert insects are black, while others (often closely related species) are white, has never been satisfactorily explained.

In general, there is no doubt that resistance to high temperatures is an adaptive feature in desert arthropods, but the interaction of factors which determine their temperatures in the field are not well understood, nor are the responses, both physiological and evolutionary, of the animals to high temperatures. These are important problems which deserve reinvestigation with modern techniques.

Gain of Water

When free water is available, it is utilized, and there is a good deal of evidence that insects regulate their water content by drinking (*41*). Preformed water may also be absorbed with the food, but the significant question of whether water shortage stimulates an insect to eat more simply for the sake of the water that the food contains cannot be answered unequivocally. According to Schultze (*42*), mealworms (larvae of the beetle *Tenebrio molitor*) do just this, although evidence on *Cimex* and *Tineola* (bedbugs and flour moths) is to the contrary (*43*). Many years ago, Buxton (*39*) suggested that desert tenebrionid beetles (*Adesmia* spp.) might gain water by feeding at night on dead plant material whose water content had been enhanced by hydroscopic absorption from air with relative humidities of 80 percent or above. However, he does not report having seen them do this.

Drinking from moist surfaces has been observed in several arthropods. Spiders are able to take up water in this way against a suction pressure of 600 millimeters of mercury (*44*), and even sow bugs can remain in water balance by oral and anal drinking from moist surfaces in air with relative humidities of above 80 percent (*45*). Such means of water uptake may prove to be of considerable significance for desert forms when bulk water is scarce but moist soil is available.

Oxidation Water

Metabolic or oxidation water results inevitably from the oxidation of food materials containing hydrogen, and in many insects, as in some mammals such as kangaroo rats, this is a preponderant source of water. *Tenebrio* larvae, for example, can survive on grain containing only 1 percent of preformed water. However, it is not a question of whether certain insects use oxidation water while others do not, for such water obligatorily enters the total pool, and whether an insect remains in water balance depends also upon the extent of its losses. Once again the question is: do insects under water stress metabolize more food and thus derive more oxidation water than they otherwise would? Complete oxidation of 100 units of a fully saturated fat to CO_2 and water yields 107 units of water, while for carbohydrates the yield is about 50 units. Would a switch to fat metabolism therefore benefit an insect in terms of water?

There are theoretical objections to this hypothesis: for equivalent energy production, fat actually yields less water than carbohydrate does, and, as Mellanby pointed out (*46*), catabolism of fat requires more than twice as much oxygen as catabolism of an equal weight of carbohydrate, and such increased oxygen uptake is likely to involve a proportionately high loss of water from the respiratory surfaces.

We have seen above that the second objection is not necessarily sound. Nevertheless there is no unequivocal evidence that arthropods switch to fat metabolism or even metabolize faster as a result of water shortage. There is indeed evidence that several insects use more oxygen in dry air than in moist, this is true of *Tenebrio* larvae and of tsetse flies (*47*), but they are more active at low humidities, and this could account for their more rapid metabolism.

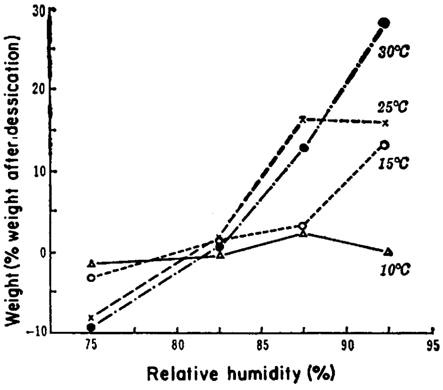

Fig. 9. Above a relative humidity of about 82 percent *Arenivaga* sp. nymphs and adult females gain weight by the absorption of water vapor, at a rate which is affected by temperature. At relative humidities below 82 percent weight is lost. Each point represents the mean weight change of five or more nymphs after 7 days in the conditions shown. From Edney (*29*).

Absorption of Water Vapor

The uptake of water from unsaturated air has been demonstrated in several arachnids, a few insects, and recently in a desert cockroach, *Arenivaga* (*29*). This is a remarkable process involving the movement of water against a potential difference of hundreds of atmospheres. *Arenivaga* sp. (the species has not yet been named) occurs in sand dunes in the Colorado desert of California. The adult females are wingless and larviform; the males are fully winged (Fig. 7). Nymphs and adults wander at night just below the sand surface leaving tell-tale ridges (Fig. 8). They feed on organic debris, and scorpions feed on them.

If these insects are somewhat dehydrated and then placed, without food or water, in air at a relative humidity of 82 percent or above, the nymphs and adult females gain water, while the adult males continue to lose it, as do nymphs of the cockroaches *Periplaneta americana* and *Blatta orientalis*. High temperature accelerates the process, and so does high humidity above the equilibrium point (Fig. 9).

A mere gain in weight is not a very satisfactory indication of uptake of water vapor, but in further experiments I was able to show (Fig. 10) that the absolute water content increases and that oxidation water contributes only marginally to this. The effects of dehydration and of subsequent rehydration upon osmotic pressure of the hemolymph have been referred to above.

The process is very probably adaptive. The insects are obliged to come near the surface to feed; there they are exposed to warm, dry conditions (certainly up to 32°C), and water is inevitably lost. However, by burrowing down through the sand, they reach more humid, cooler areas, and there the insects' reserves may be replenished even in the absence of liquid water.

It is possible to make a rough calculation of the energetics of the process as follows. In one instance, a nymph weighing 100 milligrams absorbed 6 milligrams of water in one day, from air at a relative humidity of 90 percent. The osmotic pressure of the insect's hemolymph is equivalent in terms of water potential to a relative humidity of 99.5 percent, and the energy involved in concentrating water through this range, given by $G = RT \ln P_2/P_1$, where G is the energy, R is the gas constant, T is the temperature in degrees Kelvin, and P_1 and P_2 are the respective water potentials, is 0.026 calories. The mean oxygen consumption of such an insect was 22 microliters per hour, and this is equivalent to the production of 2.6 calories per day; thus, the energy involved in absorption is negligible compared to that produced at the insect's basal metabolic rate.

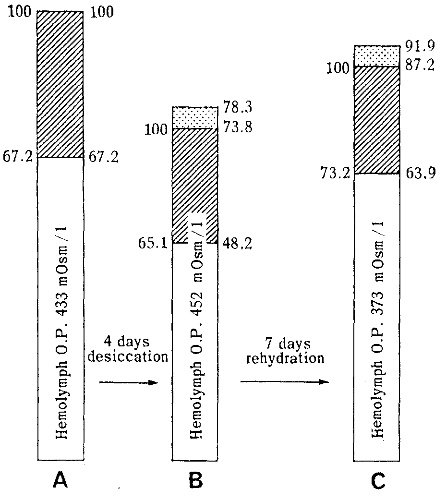

Fig. 10. Water content (blank areas) and hemolymph osmotic pressure in *Arenivaga* nymphs before (A) and after (B) dehydration, and after rehydration (C). Numbers to the right of each column are arbitrary weight units; those to the left are percentages of total wet weight at the time concerned. During rehydration there is a net movement of water from the air into the insects. From Edney (*29*).

The mechanism of absorption, however, is still somewhat mysterious. Beament (*48*) has shown that *Blatta* rapidly absorbs liquid water through the cuticle against strong osmotic gradients, and indeed the mechanism involved may turn out to be the same as that for vapor absorption. Hypotheses based on recent evidence regarding the fine structure of the cuticle have been advanced by Knülle (*49*), Beament (*48*), and Locke (*50*). None of them is entirely satisfactory as yet, and further comment at this stage would be premature.

Conclusion

As judged by the number of species, or of individuals, arthropods are an extremely successful group of desert inhabitants. There is very great structural and physiological diversity within the group, and since adaptations to desert life open to one are not open to all, we should not expect to find the maximum possible development of adaptive features in any arthropod simply because it lives in a desert. Most adult insects fly; their larvae and all other arthropods do not, and their adaptations will differ accordingly. Desert beetles have very impermeable cuticles and tolerate high body temperatures, while desert cockroaches live below the sand, have more permeable cuticles, and absorb water vapor. There is probably no single respect in which all desert arthropods differ from insects of other environments. Perhaps a profitable way of viewing desert animals is to recognize that each is a whole organism with a specific collection of adaptations that must be consistent within themselves and which are associated with a specific mode of life and a specific evolutionary history.

The arthropod organization is capable of producing highly efficient desert species. There is, however, a converse way of looking at the situation, which is often neglected but which may be of general biological interest: does the evolution of adaptations to desert environments necessarily involve loss of viability in more mesic habitats? If so, then what are these disavantages—what, for example, is the disadvantage of a highly impermeable cuticle? In some cases the answer is clear; sandroaches need sand dunes to live in because they are morphologically and behaviorly specialized for this habitat. More often the answer is not obvious.

References and Notes

1. K. Schmidt-Nielsen, *Desert Animals* (Clarendon Press, Oxford, 1964).
2. C. B. Williams, in *Biology of Deserts*, J. L. Cloudsley-Thompson, Ed. (Institute of Biology, London, 1954), pp. 18–27.
3. M. Locke, in *The Physiology of Insecta*, M. Rockstein, Ed. (Academic Press, New York, 1964), vol. 3, pp. 379–470.
4. W. Ebeling, *ibid.*, pp. 507–56.
5. M. Lafon, *Ann. Sci. Nat. Zool.* **5**, 113 (1943); R. Dennell, *Proc. Roy. Soc. London, Ser. B* **133**, 348 (1946).
6. J. A. Ramsay, *J. Exp. Biol.* **12**, 373 (1935).
7. J. W. L. Beament, *ibid.* **21**, 115 (1945).
8. V. B. Wigglesworth. *ibid.*, p. 97.
9. A. D. Lees, *ibid.* **23**, 379 (1947).
10. J. W. L. Beament, *Biol. Rev.* **36**, 281 (1961).
11. ———, *J. Exp. Biol.* **35**, 494 (1958).
12. ———, J. Noble-Nesbitt, J. A. L. Watson, *ibid.* **41**, 323 (1964).
13. E. Bursell, *Trans. Roy. Entomol. Soc. London* **111**, 205 (1959).
14. J. L. Cloudsley-Thompson, *Entomol. Exp. Appl.* **4**, 257 (1961).
15. M. Hafez and A. M. H. Makky, *Bull. Soc. Entomol. Egypt* **43**, 90 (1959); R. F. Lawrence, *S. Afr. J. Sci.* **55**, 233 (1959).
16. E. Bursell, *Proc. Roy. Entomol. Soc. London* **32**, 21 (1957).

17. N. S. Church, *J. Exp. Biol.* **37**, 171 (1960).
18. T. Weis-Fogh, *Phil. Trans. Roy. Soc. London, Ser. B* **239**, 459 (1956).
19. J. Buck, *Annu. Rev. Entomol.* **7**, 27 (1962).
20. E. B. Edney, *Proc. Int. Congr. Entomol. 10th* **2**, 709 (1958).
21. J. L. Cloudsley-Thompson, *Annu. Mag. Nat. Hist.* **9**, 305 (1956).
22. R. Warburg, *Amer. Midland Natur.* **73**, 363 (1965).
23. ———, *Crustaceana* **9**, 302 (1965).
24. ———, *Amer. Midland Natur.* **73**, 363 (1965).
25. E. B. Edney, *J. Exp. Biol.* **28**, 91 (1951).
26. J. E. Phillips, *ibid.* **41**, 15 (1964).
27. E. Bursell, *ibid.* **37**, 689 (1960).
28. ———, in *The Physiology of Insecta*, M. Rockstein, Ed. (Academic Press, New York, 1964), vol. 1, pp. 323–61.
29. E. B. Edney, *Comp. Biochem. Physiol.* **19**, 387 (1966).
30. D. A. Parry, *J. Exp. Biol.* **28**, 445 (1951).
31. P. S. B. Digby, *ibid.* **32**, 279 (1955).
32. R. W. Jack, *Mem. Dep. Agr. S. Rhodesia* **1**, 1 (1939).
33. E. B. Edney and R. Barrass, *J. Insect. Physiol.* **8**, 469 (1962).
34. E. Bursell, in *The Physiology of Insecta*, M. Rockstein, Ed. (Academic Press, New York, 1964), vol. 1, pp. 283–321.
35. G. A. Edwards and W. L. Nutting, *Psyche* **57**, 33 (1950).
36. J. L. Cloudsley-Thompson, *Entomol. Exp. Appl.* **5**, 270 (1962).
37. H. E. Hinton, *Nature* **188**, 336 (1960).
38. F. Rucker, *Z. Vergleich. Physiol.* **21**, 275 (1939).
39. P. A. Buxton, *Proc. Roy. Soc. London, Ser. B* **96**, 123 (1924).
40. J. H. Pepper and E. Hastings, *Ecology* **33**, 96 (1952).
41. G. Altman, *Insectes Sociaux* **3**, 33 (1956); V. G. Dethier and D. R. Evans, *Biol. Bull.* **121**, 108 (1961).
42. F. N. Schultz, *Biochem. Z.* **27**, 112 (1930).
43. K. Mellanby, *Parasitology* **24**, 419 (1932); *Ann. Appl. Biol.* **21**, 476 (1934).
44. D. A. Parry, *J. Exp. Biol.* **31**, 218 (1954).
45. J. O. Spencer and E. B. Edney, *ibid.*, p. 491.
46. K. Mellanby, *Nature* **150**, 21 (1942).
47. P. A. Buxton and D. J. Lewis, *Phil. Trans. Roy. Soc. London, Ser. B.* **226**, 175 (1934).
48. J. W. L. Beament, in *Symp. Soc. Exp. Biol. 19th*, G. E. Fogg, Ed. (Cambridge Univ. Press, Cambridge, 1965), pp. 273–98.
49. W. Knülle, *Z. Vergleich. Physiol.* **49**, 586 (1965).
50. M. Locke, *Science* **147**, 295 (1965).
51. A. R. Mead-Briggs, *J. Exp. Biol.* **33**, 737 (1956).
52. E. Bursell, *Phil. Trans. Roy. Soc. London* **241**, 179 (1958).
53. M. W. Holdgate and M. Seal, *J. Exp. Biol.* **33**, 82 (1956).
54. R. H. Stobbart and J. Shaw, in *The Physiology of Insecta*, M. Rockstein, Ed. (Academic Press, New York, 1964), vol. 1, pp. 189–258.
55. J. L. Cloudsley-Thompson, *Entomol. Exp. Appl.* **2**, 249 (1959).
56. E. B. Edney, *Smithsonian Inst. Annu. Rep.* **1959**, 407 (1960).

NEWS AND COMMENT

Naples Station: Crisis Italian Style at Marine Biology Center

Naples. The Naples Zoological Station, one of the oldest of marine biology stations, is passing through a time of troubles, both financial and administrative. In a general way, the Naples station is a casualty of the conflict between Italian academic traditions and new research modes, as well as of forces gathering momentum within modern biology. The particulars of the crisis, however, depend so greatly on personalities and personal relationships that the tale might better be told in a novel than in a news story.

Last week it became known unofficially that the Italian government would soon announce appointment of a commissioner (commissario straordinario) to take over the functions of the station's governing body for a year and prepare the way for restructuring of the institution. At the same time, it became known that the Ministry of Public Instruction will increase its annual direct support of the station from $112,000 to $144,000. This boost will not solve the station's serious financial problems, but it indicates official feeling that the station needs increased income as well as reform of its statutes.

The Stazione Zoologica di Napoli was established in 1872 by Anton Dohrn, a German research scientist who found the atmosphere of the German universities oppressive. A Darwinian, Dohrn was attracted to the Gulf of Naples by the variety and abundance of marine life which lent itself to the pursuit of one of his main interests, experimental work in support of Darwin's evolutionary theories. Dohrn, who put much of his money in the station, was a practical man as well as a distinguished zoologist. With local help he built his station in what is now a public park that fronts on the bay. An aquarium occupied the ground floor of the original building; receipts from admissions were intended to help defray the costs of research in the laboratories on the two floors above.

Collection of specimens has been the pride and strength of the station. Fishermen permanently employed by the station know most of the creatures in the gulf by their Latin names, as well as when and where they are to be found. A visitor checks in advance on the probable availability of the specimens he wants and then comes to Naples with the reasonable assurance of delivery of a daily order. One visiting scientist contrasted the performance of the station's fishermen with the situation at one well-known American station where, he said, "they hand you a pair of boots and a net and wish you good luck."

"The Aquarium," as it is known to Neapolitans and to the generations of scientists who have worked there, is an international laboratory which, at the same time, is officially an institution which operates under the authority of the Italian government. The staff is predominantly Italian, and, while the foreign governments have contributed generously to the financing of capital improvements, about half of the operating budget comes from Italian sources. At the outbreak of World War I, the laboratory was taken over by the Italian government, because Reinhard Dohrn, Anton Dohrn's son and successor as station director, was a German national. In the early 1920's an agreement was reached under which the station became a nonprofit institution operating under supervision of the Ministry of Public Instruction. The Italian government has consistently provided about half of the station's operating funds, and it is not surprising that Italians are irritated when some foreigners speak as if the station were sustained by funds from abroad.

Direction of the lab has remained, by direct succession, in the Dohrn family. The present director is Reinhard Dohrn's son, Peter Dohrn, 49, who was trained as an M.D. and after World War II studied zoology at the University of Naples. Peter Dohrn is much involved in the present controversy.

Part of Dohrn's and the station's problem is financial. The operating budget has been increasing at the rate of about 5 percent a year, and income, in the familiar pattern of nonprofit institutions, has not. The need for heavy capital investment to rehabilitate and reconstruct a stately but partly decrepit building and to acquire expensive new