TEMPERATURE ADAPTIVE BEHAVIOUR IN THE SCORPION, *OPISTHOPHTHALMUS LATIMANUS* KOCH

By ANNE J. ALEXANDER and D. W. EWER
Department of Zoology, Rhodes University, Grahamstown

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In discussing the possible functions of the pectines of the scorpion, von Ubisch (1922) suggests that they serve 'um den Stigmen frische Luft zuzufuhren' by their fanning movements or, alternatively, they prop up the mesosoma so that fresh air can reach the stigmata. Both of these suggestions imply that under conditions of respiratory stress a scorpion will lift its mesosoma clear of the ground so that the book-lungs have free access to air. Although von Ubisch did not apparently observe such behaviour, the recent report of 'abdominal elevation' in the Australian scorpion, *Urodacus abruptus* Poc. (Southcott, 1955) lends colour to such an hypothesis, although work on the functions of the pectines makes it seem very improbable that they actually serve as 'respiratory fans'. Southcott gives an illustration of a female of *U. abruptus* in the attitude typical of 'abdominal elevating behaviour', and from a comparison of this with some of the stances observed in various South African scorpions it becomes clear that such behaviour occurs also in the latter. *Opisthophthalmus latimanus* Koch, *O. nitidiceps* Poc., *O. austerus* Karsch., *Parabuthus planicauda* Poc. and *Uroplectes triangulifer* Thor. all show the pattern to varying extents, and it was felt that with so many species available for study, it would be profitable to follow up Southcott's observations. Preliminary tests indicated that the biological significance of this phenomenon appeared to be the same in all these species, and the results described below refer particularly to *Opisthophthalmus latimanus* which has been most intensively studied.

In this animal the pattern generally does not consist of a simple elevation of the abdomen, but more usually of a raising up of the entire body of the scorpion by a straightening of all the legs. Fig. 1 illustrates semidiagramatically the differences between (*a*) the normal resting stance of *O. latimanus*, (*b*) the stance in which the whole body is lifted clear of the ground, and (*c*) the more extreme 'abdominal elevation'. There is indeed no sharp distinction between these last two, and other rather rarer variations occur, e.g. that in which the abdomen, lifted clear of the ground, is supported by the tail (Fig. 1 *d*). All of these different stances have in common a straightening of the legs; they will collectively be referred to here as 'stilted poses' and the behaviour itself as 'stilting'. In none of the species studied here, nor in *Androctonus australis* (L.) (Cloudsley-Thompson, 1955), is there any indication that the pectines might be used to prop up the abdomen, as von Ubisch has suggested. As in *Urodacus abruptus*, stilting occurs in both sexes of *Opisthophthalmus latimanus*, and it has been observed in all instars except the first where it might well not be recognizable.

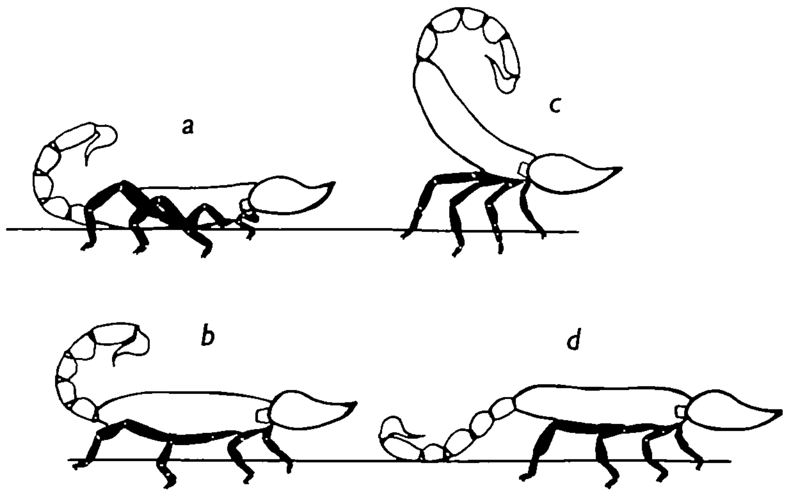


Fig. 1. *Opisthophthalmus latimanus*. Semi-diagrammatic representations of postures adopted. *a*, resting stance, venter to the substratum and legs folded; *b*, stilted pose in which the whole body is lifted away from the substratum by straightening the legs; *c*, stilted pose in which the mesosoma is sharply elevated; *d*, rather rare stilted pose in which the tail appears to help in propping the body away from the substratum.

FUNCTION OF THE STILTING

Working along the same lines as von Ubisch, Southcott (1955) states that stilting occurs in hot and humid conditions, and concludes that 'it would appear most likely that the stance...is an effort to lift the stigmata free from the humid layer of the air and soil, when the scorpion's metabolism is increased by a hot environment'. Cloudsley-Thompson (1955) has pointed out, with reference to the postulate of von Ubisch, that a scorpion has normally a very considerable respiratory margin of safety. For this reason it seems improbable that respiratory adaptive behaviour as such would be of importance in the life of a scorpion.

However, the effect of respiratory stress appeared to be worthy of further experimental investigation. The problem had already been studied in *Androctonus australis* by Cloudsley-Thompson (1955), using streams of gas composed of nitrogen and carbon dioxide. Observation of *Opisthophthalmus latimanus* has, however, shown that if a stilting animal is disturbed by a sudden draught of air, it drops its stilted pose and will often not resume it for some time. It was therefore considered desirable for observations to be made in still air. Furthermore, since extreme respiratory stress, such as that used by Cloudsley-Thompson, might itself inhibit an adaptive response, a series of gas mixtures was used: namely mixtures of air with approximately 20 or 75% carbon dioxide, and air with 60 or 90% nitrogen. In none of these mixtures were there the slightest signs of stilting. This was not due to the inability of the animals to stilt, for, if other suitable stimuli were applied, the scorpions would stilt in these gas mixtures. Moreover, stilting was more easily elicited by these means in those gas mixtures containing the lower concentrations of carbon dioxide or nitrogen, a fact speaking against the importance of stilting in respiratory stress.

As a check, observations were made on scorpions in which the openings of the book-lungs had been blocked. This was done in one of two ways: either the mesosternites were smeared with vaseline, or the openings of the lungs were painted over with Gestetner Correcting Fluid or Samsonite. Observations lasting over 12 hr. showed no stilting by any of the animals, though the fact that two of the animals died shortly after indicates that their respiratory systems had probably been affected by the treatment. Controls with their backs painted all survived.

These experiments, together with the observations of Cloudsley-Thompson (1955) on *Androctonus australis*, make it unlikely that stilting has an adaptive significance in respiratory stress. To comprehend the phenomenon, it is therefore necessary to turn once more to observations of the conditions in which this pattern is shown.

Southcott (personal communication) states that in summer he need only pour a little water into his scorpion culture dishes to elicit stilting behaviour. Unlike *Urodacus abruptus*, *Opisthophthalmus latimanus* shows no such direct relationship between the humidity and stilting; stilting may occur when the scorpion is standing in a pool of water or, conversely, in a desiccator. The character of the substratum, whether it be smooth or rough, whether or not it be covered with chemicals distasteful to the scorpions, does not determine whether the animals will stilt.

However, although the pattern may occur at any time during the day or night, it is most frequently seen during the afternoon. This suggested that temperature might be a factor of importance in determining the onset of stilting. Confirmation of this can be obtained by observing the behaviour of animals in a dish of soil, the dish being warmed or cooled as desired. Below 18° C. stilting is not normally observed and if the soil on which a stilting scorpion is standing be cooled below this temperature, the animal's pose gradually reverts to the normal resting stance. Between 18° and 28° C. animals may or may not be found to be stilting, but at higher temperatures any animal that is standing still will usually be stilting to some degree, or may be reared up against the side of the dish, a condition amounting in effect to a stilted stance.

As mentioned earlier, *O. latimanus* does not stilt in direct response to the presence of water. Unlike the condition in *Urodacus abruptus*, there is no indication here that, with a higher humidity, the stilting behaviour is elicited at a lower temperature. This point was studied by trials on pairs of animals, one animal being kept in a dish at 40–60 % R.H.; the other at 85–90 % R.H. If anything, there was a slight indication that the animals reacted a little more quickly and at a slightly lower temperature when at the lower humidity.

Once it is clear that stilting is not concerned with respiratory adaptation, but is elicited merely by a high temperature, it is reasonable to ask whether the stilted pose may not have some thermoregulatory role. Drawing on the techniques used by

Colbert, Cowles & Bogert (1946) in their experiments on temperature adaptations in alligators, the following arrangement was used. Two live animals were fixed so that one, the experimental animal, could be held in a stilted pose while the other, the control, could be restrained in the normal resting position. In the absence of more complicated apparatus, abdominal temperatures were determined by clinical thermometers whose bulbs were inserted through a small lateral incision. In these experiments the scorpions were placed upon a copper plate lying on the ground. The plate was initially left in the sun to attain a uniform steady temperature. A small shade was then placed so as to screen the area of plate upon which the two animals would be placed, and the scorpions were then quickly put in position and their abdominal temperatures recorded. After 10 min. their temperatures had not changed; the shade was then removed so that the sunlight fell on the animals and the observations on their temperatures were continued. Preliminary experiments showed that the orientation of the animals towards the sun was not critical, and in all those reported below the scorpions were oriented with their longitudinal axes at right angles to the sun's rays.*

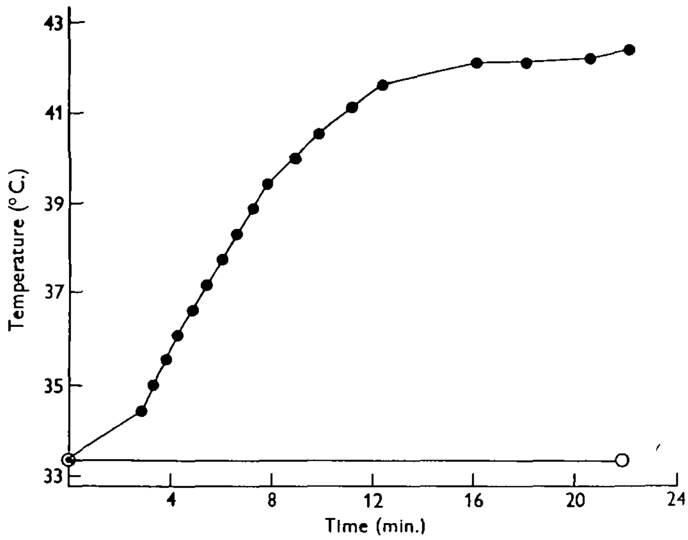


Fig. 2. Effect of the stilted posture on the internal temperature of *Opisthophthalmus latimanus* exposed to direct sunlight. Open circles, experimental animals in stilted posture; closed circles, control in normal resting stance.

A typical result of such an experiment is shown in Fig. 2. Both animals were initially in the shade, their abdominal temperatures were recorded: the screen was then removed and the temperatures of their bodies noted at intervals. As can be seen, the temperature of the control animal rose rapidly, while that of the scorpion held in a stilted position hardly rose above the minimal temperature calibration of the thermometer.

* It must be noted here that the initial temperature of each of the scorpions, 91–93° F. (33–34° C.) reflects, in the main, only the minimal reading on the thermometers used.

The question now arises as to how the stilted pose prevents the large increase in abdominal temperature found in animals held in the resting position. Three possibilities have been considered. The first is that the space provided between the body and substratum by the stilting allows evaporation to occur from the openings of the book-lungs, and that this cools the scorpion's body. The second is that the stilting merely lifts the body away from the substratum so that absorption of heat from this source is curtailed. Thirdly, it is possible that, by raising the abdomen, air currents are permitted to pass beneath and around the scorpion's body, thus cooling it to air temperature. These explanations are not, of course, mutually exclusive.

The first suggestion, namely, that stilting keeps the body temperature low by facilitating evaporation from the book-lungs, has some measure of support in the fact that in insects a high percentage of the cooling which is effected occurs by way of the respiratory openings (Wigglesworth, 1950). The point is, however, easily investigated in the scorpion and Fig. 3*a* shows the result of such an observation on *Opisthophthalmus latimanus*.

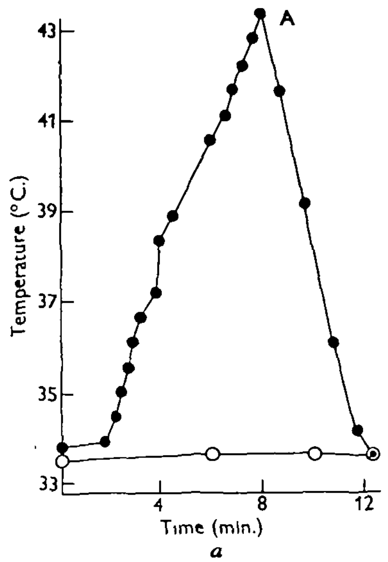
The book-lungs of the experimental animal were painted over with Samsonite to prevent evaporation, initially both experimental and control animals were shaded from direct sunlight and it can be seen that, when the shade was removed, the body temperature of the experimental, stilting animal hardly altered, although that of the control rose rapidly. Certainly any evaporation from the book-lungs contributes only slightly, if at all, to the cooling effect of the stance.

Such a conclusion, though not in keeping with that expected from an insect, is supported by the findings of Parry (1951) with model disks and locusts, namely, that cooling by evaporation is likely to be less important than heat loss by radiation and convection in determining the body temperature of terrestrial arthropods placed in direct sunlight.

The second suggestion, that stilting decreases heat conduction and radiation from the ground surface, is not so easily investigated. Parry (1951) reports that the temperature of a small black disk exposed to direct sunlight will fall by as much as 12° C. if it is moved to a height of 1 in. above the substratum. He considers that at such small distances from the ground the steepness of the 'temperature profile' is probably due to a rapid fall off of radiation effects from the substratum and that convectional losses are likely to be low. To test the importance of convectional loss it is necessary to eliminate as far as possible all 'forced convection' (Digby, 1955), that is, all air currents caused by factors other than the presence of the scorpion itself. This was done by covering the animal, its stand and the thermometer with a bell-jar; both experimental and control scorpions were then exposed to direct sunlight.

As can be seen from Fig. 3*b*, the temperature of the control animal again rose rapidly, but on this occasion, after a short lag, so also did that of the experimental animal. The glass cover was then removed from the latter while the control was shaded from the sun. The body temperature of both animals then fell quickly.

To check that the effect of the glass cover over the scorpion was to decrease the rate of cooling and not to increase the rate of heating by concentrating the sun's rays upon the animal, the simple test of lifting the cover an inch from the substratum was made. Under such conditions the temperature of the stilting scorpion remained nearly constant, as though the cover had been completely removed.



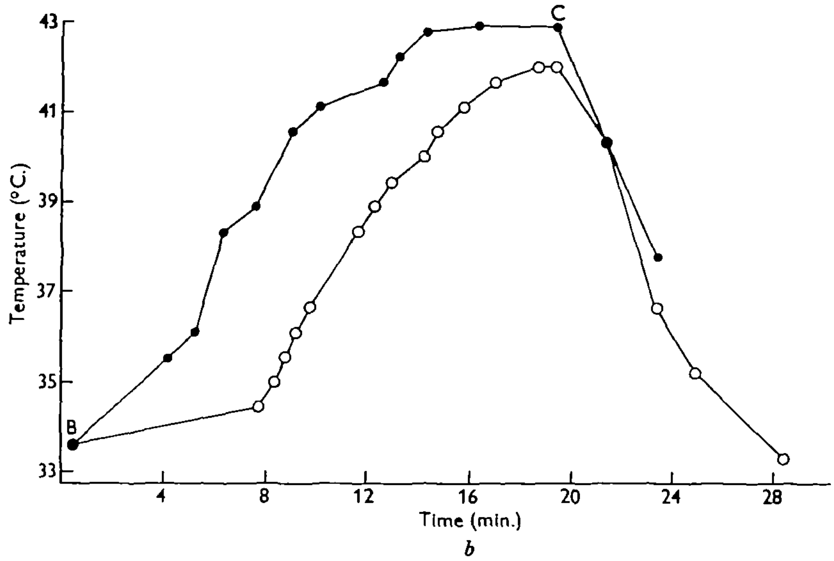


Fig. 3. Effect of stilted posture on the internal temperature of *Opisthophthalmus latimanus*. (*a*) comparison of normal animal in resting stance—closed circles; and experimental animal with book lungs sealed in stilted pose—open circles. Initially both animals shaded but exposed to direct sunlight at time 0. At *A* both animals again shaded. (*b*) a continuation of the experiment slightly later. Both animals initially shaded. At *B* a glass bell jar was placed over the experimental animal and both exposed to sunlight. At *C* the cover was removed from the experimental animal and the control was shaded from direct sunlight.

These results indicate strongly that the temperature-controlling effect of the stilting behaviour is due mainly to an enhanced circulation of air around the scorpion. Since the above effects may all be imitated using recently killed animals held in suitable positions, there is no suggestion that the cooling phenomenon is due to any 'vital' activity of the animal. This incidentally supports Parry's assertion that in dealing with arthropods of a fair size, it is legitimate to work with models of reasonable size and shape.

These results with *Opisthophthalmus latimanus*, while not eliminating the possibility that stilting may lower heat uptake by radiation from the substratum and by natural convection, suggest that the exposure of the whole body surface to local air currents is a more effective mechanism of temperature control. It seems likely that this may be of general importance in the temperature regulation of other arthropods such as ants and certain tenebrionid beetles where patterns akin to stilting are known to occur. The precise importance of local air currents was not directly studied by Parry in his work with models. Digby (1955), who investigated the point with controlled conditions and live animals, reports that, with wind speeds of 20–30 cm./sec., the animal's temperature excess (i.e. the difference between that of the animal and the surrounding air) varies inversely with the square root of the wind speed. Below this wind-speed the natural convection of the animal itself became of more importance. As Digby points out, it is unfortunate that we know so little of wind speed and other microclimatic factors close to the ground.

Once it is clear that the adaptive significance of the stilting behaviour pattern is one of thermo-regulation, two further questions arise: first, where are the thermo-receptors situated and secondly, what are the circumstances in which the pattern is evoked in natural conditions?

THERMO-RECEPTORS

Nothing appears to be known of the location of thermo-receptors in scorpions, nor in fact in other arachnids. It appears desirable to point out initially that stilting is not simply a direct response to the temperature of the substratum, that is, the animal does not lift its belly away from the 'burning' ground. This can be shown by placing the scorpion on a copper plate with running cold water beneath and then directing a heating radiator on to the animal's body from above. Although the substratum on which the animal stands is very much cooler than the air above it, the scorpion will raise its abdomen into the warmer layer of air.

It can readily be shown that the stilting response to high temperature persists after the pectines have been removed; similarly, removal of the pectines does not alter the preferred temperature when the animals are studied in a gradient. Further operative procedures are impossible and the point was therefore examined by observing the response of scorpions to a red-hot cauterizing needle held near different parts of the body. These experiments showed that the poison bulb of the sting is very sensitive to a local heat source; the pedipalps are also sensitive though seemingly less so than the sting; the sensitivity of the legs is still less marked, while no evidence was found for any thermo-receptors upon the back.

It would thus appear that thermal exteroceptors are widely scattered over the scorpion's appendages and, therefore, any attempt to eliminate them experimentally is effectively precluded; thus it cannot be determined whether the stilting response is mediated by way of these thermal receptors. Moreover, it seems possible that a postural thermo-regulatory reaction, such as this, may well be controlled by central thermo-receptors, responding to general body temperature, rather than by thermal exteroceptors.

Some measure of support for this suggestion comes from a consideration of observations on a number of *O. latimanus* which were heated until they adopted extreme stilting poses. Then, with as little disturbance as possible, they were moved to cool dishes in conditions where controls showed no sign of stilting. Here four, of seven animals used, reverted to the stilting pose for at least 3 min. and only later relapsed to the normal resting posture. This indicates that when scorpions have been well heated they may sometimes stilt in a cool dish where exteroceptors would not be receiving stimulation from the environment.

STILTING IN RELATION TO LIFE IN NATURAL CONDITIONS

In attempting to answer the question 'When does *O. latimanus* stilt under natural conditions?' it is desirable to consider first some other aspects of the biology of this scorpion.

The animals live in burrows about 30 cm. deep. In the laboratory they have been allowed to burrow in the soil of glass-sided aquaria and in these burrows their activities may often be watched without disturbing the animals at all. Such observations indicate that scorpions in the laboratory spend many hours of daylight at the entrance of their burrows or 2 or 3 cm. down them. A limited number of observations were made in the field and these confirm the fact that *O. latimanus* is not confined to the depths of its burrow during the day. Excavation of the burrows by the scorpion normally occurs in the late afternoon or at night, both in the field and in the laboratory, while after sundown the scorpions in the laboratory terraria may leave their burrows completely and wander some distance from them. Whether this occurs in the field at night is uncertain owing to the difficulties of observation, but occasionally in the late afternoon an animal has been found away from its burrow.

It seems probable that this 'door-keeping' which occurs during the daylight hours is connected with feeding. Certainly a study of food fragments in and around their burrows shows that *O. latimanus* feeds upon insects such as grasshoppers and a common tenebrionid beetle which are active during the day. Further, a scorpion at the entrance to its burrow will grab viciously at a stick which is moved carefully and 'temptingly' towards it, while a partially immobilized grasshopper placed near the entrance of the burrow will be hastily dragged down by the tenant.

Using a temperature 'orgel' it has been established that the temperature preference of *O. latimanus* lies within the range 32–38° C. The soil temperature at the mouth of the burrows may rise as high as 70° C. So that it would seem that

O. latimanus must be able to tolerate temperatures considerably higher than its preferred one if it is to sit in its burrow mouth and catch prey which comes within grabbing distance. Theoretically the stilting pattern would be of considerable use in such circumstances; in practice it has very frequently been observed to occur in the laboratory terraria where the scorpions are door-keeping during the warm part of the day. Observations in the field are not possible as only the pedipalps of a door-keeping scorpion can be seen clearly.

BEHAVIOUR RESORTED TO WHEN STILTING BECOMES INADEQUATE

It has been found that the lethal temperature of *O. latimanus* lies roughly in the range 40–50° C. It appeared of interest to find out whether, if the temperature of its body approaches the lethal temperature, a scorpion will merely continue to stilt or whether some other pattern is evoked. The answer to this question involves a consideration of responses to directional light.

Many scorpions show a marked photonegative response to directional light. This is true of *Androctonus australis*, *Scorpio maurus* L. and *Buthus occitanus* (Am.) (Sergent, 1947). Of the species studied here it is also true of *Parabuthus planicauda*, but *Opisthophthalmus latimanus* and *O. nitidiceps* show a very striking photopositive reaction. Further, in agreement with the observations of Sergent upon the various European species mentioned above, *O. latimanus* shows well-marked thigmopausic behaviour. A combination of these two elementary behaviour patterns would serve to direct *O. latimanus* to the entrance of its burrow: so long as no other pattern interferes, the scorpion could be expected to remain at the mouth of its burrow, facing the light but not leaving the contact provided by the walls. As has been emphasized above, should a scorpion maintain this position upon a hot day the environmental temperature might well exceed the lethal temperature for several hours and the immediate problem is whether a rising temperature releases an escape reaction.

The problem was studied by placing individuals in long glass troughs whose floors were covered with soil. All the sides of the trough were blackened except one, through which there shone a light. The temperature of the trough could be changed as required. In such a piece of apparatus at room temperature, the scorpions show a marked preference for the end of the trough nearer the light source. As the temperature is raised the scorpions will stilt, but they remain oriented towards the light source. Then with a further increase in temperature there is a sudden reversal of the sign of the light response, the scorpion turns away from the light and moves rapidly to the other end of the trough. If the temperature is then allowed to fall, the scorpion presently reorients towards the light.

Often just before the change of photopositive to photonegative behaviour occurs, there are signs of a general activity: frequently these movements belong to no obvious pattern, sometimes the animal will abruptly, if ineffectively, begin to burrow. The exact interpretation of this latter is not at the moment clear: it might be regarded as an attempt to construct a burrow for protection, a mere effort to get away from an unpleasant stimulus or a displacement activity arising from a conflict between opposing photopositive and photonegative drives.

Interpreted in terms of its normal life, these observations imply that as temperatures rise and general activity of the animal increases, the light reaction will not direct the animal in such a way as to cause it to leave the safety of its burrow, but rather its reversal of sign will result in the scorpion retreating into the deeper parts which, as rough measurements in the field have shown, may be more than 20° C. below the soil temperature outside. It would seem that this reversal of light behaviour is the basis of an escape from a potentially lethal position.

It is interesting to note that the protective behaviour pattern of this scorpion in relation to high temperature has two facets—a static postural behaviour pattern which permits a certain degree of regulation, followed by a dynamic locomotory pattern which allows the animal to evade the difficulty by leaving the potentially lethal environment.

During the course of this investigation one of us (A. J. A.) held a bursary granted by the South African Council for Scientific and Industrial Research, to whom our thanks are due.

SUMMARY

1. Behaviour termed 'stilting' is described for the scorpion, *Opisthophthalmus latimanus*. In this pattern the legs are straightened, lifting the body clear of the substratum.

2. Evidence is submitted that it is not concerned with allowing greater respiratory exchange.

3. Stilting is generally elicited in response to a rise in environmental temperature above 18° C. and is invariably found at temperatures above 28° C.

4. A comparison using scorpions held in the stilted and normal resting stance, shows that, when the environmental temperature rises sharply, the body temperature of the resting animal rises rapidly, while that of the stilting animal is almost unchanged. The mechanism of this effect is shown to be due largely to the increased circulation of air around the animal which is permitted by the stilting.

5. From observations of behaviour in both the laboratory and the field, it appears probable that the stilting pattern is shown by *O. latimanus* during the hot hours of the day when the scorpion waits in the entrance of its burrow to catch prey.

6. Laboratory observations indicate that when the temperature becomes so high that stilting has no longer any protective value, a photopositive reaction, which would keep the scorpion at the entrance of its burrow, changes to a photonegative one and the animal can retreat into the cool depths of its burrow.

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