Behavioral Adaptations of Terrestrial Isopods

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SYNOPSIS. In their response to environmental stimuli, terrestrial isopods show various trends that are correlated with their ecology and physiology.

With the transition from sea to the littoral zone (*Ligia*), orientation to light changes from positive to negative. Yet, since these isopods are positively hygrokinetic even at very high humidities, their hygroreaction is of greater significance than their photoreaction.

In isopods from mesic habitats (*Oniscus, Porcellio, Armadillidium*) photoreaction becomes of less significance than in littoral species, until in some species it reverts to positive (*Armadillidium*). Sometimes the positive photoreaction occurs only at high temperatures (*Porcellio*), a pattern of behavior correlated with thermoregulation by evaporative cooling. Similarly, in mesic species the response to humidity becomes less significant than in littoral species, resuming importance mainly when the isopods become dehydrated (*Armadillidium*).

Finally, in isopods from xeric habitats in semi-arid and desert regions (*Armadillo, Venezillo*), photoreaction is strongly negative except in *Hemilepistus* at lower temperatures. All of these isopods are positively hygrokinetic only at low humidities and are strongly negatively thermoactive, indicating a drop in activity at high temperatures. The photonegative response in these isopods is stronger than the hygroreaction.

The terrestrial isopods, suborder Oniscoidea, belong to a group that probably invaded the land much later than did arachnids or insects. It is now believed that there were several invasions of land by isopods (Vandel, 1943, 1964). Edney (1954, 1960) has suggested that the main route of invasion was *via* the littoral zone. Adaptation to terrestrial conditions occurred primarily through modification of the respiratory organs, with the development of pseudotracheae in many species, but there were other changes as well.

Whereas aquatic isopods remained entirely dependent upon free water, some transitional species (*e.g., Ligia*) became less so, gradually developing a capillary water system that transfered moisture to the respiratory organs on the pleopods (Barnes, 1932). Most terrestrial forms can take moisture from the substratum by the uropods and transfer it to the capillary water system. However, forms that are adapted to xeric conditions (*Armadil-*

lo, *Venezillo* and *Hemilepistus*) have lost even the capillary water system.

A morphological adaptation that seems to be correlated with both physiological and behavioral features is the ability to conglobate or curl up and form a ball. This ability is present in all major groups of terrestrial isopods, an indication of its usefulness in life on land. When conglobating, these animals lose considerably smaller amounts of water than do non-conglobating forms (Warburg, 1965b) because most water is lost from the respiratory organs on the ventral side.

Wieser (1963) found in the intertidal isopod, *Campecopea hirsuta*, that its ability to conglobate is at least partly responsible for resistance to desiccation. This isopod clings to the substrate when in moist air, but it curls up in dry air thus reducing evaporation. *Tylos*, which inhabits the littoral zone, behaves similarly.

Among the Porcellionidae, *Cylisticus* is unique in its ability to conglobate, although the ball does not entirely close or enclose the antennae. Similarly, in *Armadillidium* the antennae remain outside. In the Armadillidae, which includes *Armadillo, Venezillo,* and *Buddelundia,*

all can form a complete ball, enclosing the antennae.

Since loss of water is considerably reduced when the animal conglobates, the trait has survival value. In this connection, there is considerable reduction in tegumental glands in the conglobating forms (Gorvett, 1956). Whether these glands have a defense function (Gorvett, 1956) or a physiological function in keeping the pleopods moist, their reduction in size is correlated with the availability of moisture in the habitat (Vandel, 1956). In either case the conglobating forms appear to have been able to survive without these glands.

In the following discussion it is pointed out how the behavioral adaptations to life on land are connected with the physiological and morphological adaptations discussed above.

RESPONSES OF ISOPODS TO EACH OTHER

Edney (1954, 1967) suggested that the principal adaptations of terrestrial isopods are not physiological, but behavioral. Among these are responses to environmental stimuli and to each other, which enable isopods to collect in groups under suitable shelter.

It has been suggested that Oniscus asellus, Porcellio scaber, and Armadillidium vulgare respond to olfactory stimuli that help to guide them into suitable shelter (Abraham and Wolsky, 1930; Brooks, 1942; Fischbach, 1954; Henke, 1960; Kuenen and Nooteboom, 1963; Friedlander, 1965). Each of these species responded to its own smell and, to a certain extent, to that of other species (Kuenen and Nooteboom, 1963).

Other responses that are well developed in terrestrial isopods and bring the animals together are thigmokinesis and thigmotaxis, both of which slow down locomotion as a result of contact. These responses are found also in aquatic isopods, such as Asellus (Banta, 1910). The more terrestrial species (Armadillo, Venezillo) do not show thigmokinetic respon-

ses to such an extent as less terrestrial forms (Oniscus, Porcellio). Furthermore, there is much variability in the responses of individuals, related perhaps to their physiological state.

Another common response of terrestrial isopods is aggregation, or "bunching." Allee (1926) found that temperatures between 20-30°C are optimal for aggregation, and, that isopods in aggregates lose considerably less water than as individuals. Both Oniscus and Porcellio are capable of aggregating in dry environments. In Oniscus the rate of water loss is reduced by more than 50% in aggregates of five animals (Warburg, 1960). Single specimens of Oniscus and Porcellio lose more water when clinging to a substrate than when active (Warburg, 1965b). Attachment to a substrate may serve as protection against predators (Gorvett, 1956; Wieser, 1963), and may also help to keep aggregates intact.

The correlation of aggregation both with temperature and humidity suggests that responses of isopods to each other are closely linked with the responses to environmental stimuli.

RESPONSES TO TEMPERATURE

The effects of temperature on terrestrial isopods were analyzed in a thermogradient by Barlow and Kuenen (1957) and by Warburg (1964; see also Table 1). In all experiments the animals concentrated in the region of lower temperature. They differed only in their pattern of distribution within the gradient.

Barlow and Kuenen studied the behavior of Porcellio, Oniscus, and Armadillidium in a thermogradient of 6 to 30°C. They concluded that the animals preferred the cooler part of the thermogradient. However, their isopods did not respond to the whole temperature gradient because the apparatus was too long.

Warburg (1964) studied the reactions of Oniscus, Armadillidium, and Venezillo arizonicus inside a small thermogradient having accurate control of temperature.

TABLE 1. *Time-distribution in the thermogradient. Percentage of time spent in the thermo-preferendum apparatus at the lowest (L), and highest (H), temperature zones.*

Range of temperature	10–20°C		13–27°C		21–35°C		28–45°C	
	L 10°C	H 20°C	L 13°C	H 27°C	L 21°C	H 35°C	L 28°C	H 45°C
Venezillo	43%	25%	60%	9%	75%	1%	90%	0%
Armadillidium	11%	11%	44%	2%	70%	2%	70%	1%
Oniscus	40%	10%	100%	0%	80%	5%	—	—

The thermoreaction was analyzed by counting position-records of individual animals in each zone every 60 sec, by counting the distribution of five animals every 60 sec, and by measuring the time spent by an individual animal in each zone. The last method proved to be most accurate.

The temperature gradients studied were 10-20°C, 13-27°C, 21-35°C, and 28-45°C. In all these ranges most animals were found more frequently and for longer periods at the lowest temperature available. This reaction was most pronounced in *Oniscus*, less in *Armadillidium*, and least in *Venezillo* (Table 1). However, it was not possible to determine by these methods the real criteria for thermoreaction. Therefore, the number of shifts in direction and the speed of movement were calculated for each experiment. *Oniscus* shifted 44 times at the low temperature range, increasing to 75 shifts, and finally to 399 shifts at the high temperature range. In the highest temperature range the animals ran very rapidly until they collapsed. In *Armadillidium* the number of shifts averaged 70 in the low range, 38 in the second range, and 230 in the high temperature range. Finally, *Venezillo* shifted 140 and 162 times in the lower temperature ranges, dropping to 82 and 38 shifts at the higher temperatures. Thus, *Venezillo* was an exception in shifting less frequently at high temperatures.

The same pattern was apparent with regard to speed. The speed of *Oniscus* was 5 cm/min at the lower temperatures, increasing to 44 cm/min at the higher temperatures. *Armadillidium* moved at a speed of 5-8 cm/min at the lower temper-

atures, increasing to 26-28 cm/min at the higher temperature ranges. Finally, *Venezillo* again responded to rising temperatures by reducing speed from 16-17 cm/min at the lower range, to 13 and 8 cm/min at the higher temperatures.

Thus, in both *Oniscus* and *Armadillidium*, which inhabit mesic habitats, the rise in temperature increased the number of shifts and the speed. No such response was seen in *Venezillo*, which moved less frequently and at a lower speed when temperatures were high. This behavior may be of survival value to an isopod from xeric habitats, where temperatures are rather high in its microhabitat under stones but are certainly much higher on the ground outside (Warburg, 1965a).

Although in all of these experiments the humidity was measured inside the thermogradient, it could not be controlled, and the response to humidity could not be analyzed in this apparatus. However, the response to temperature is clearly linked with moisture in the habitat, with the water economy of the animal, and with the animal's responses to humidity.

RESPONSES TO HUMIDITY

The fact that the response to humidity is correlated with the water balance of the animal, as well as with ambient temperature, led several workers to suggest that isopods respond to saturation-deficit[1] of the air (Miller, 1938, Cloudsley-Thompson,

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[1] Saturation-deficit: amount by which the water vapor present in a sample of air falls short of its saturation-value (Edney, 1954). Equivalent to "vapor-pressure deficit" as used by Edney (this symposium).

1956). We shall see that this problem was not resolved in isopods, and there are several experiments to indicate that some isopods respond to the relative humidity rather than to saturation-deficit (Warburg, 1964).

Among the littoral isopods, *Ligia* was found to prefer very high humidities; in addition, it was able to distinguish between 97% and 100% R.H. (Perttunen, 1961). In so doing, it showed a behavior similar to that of the amphipods, *Orchestia* and *Gammarus*. When tested in a humidity-preference chamber, *Ligia* moved faster and stayed for shorter periods in the dry alternative. The intensity of the humidity-reaction, as measured by the excess percentage of animals in the humid part over those in the dry part, was very high; and the isopods always chose the highest humidity.

A rather similar pattern of behavior was observed in many isopods inhabiting the mesic habitats. *Porcellio* was found to be rather active in the dry side, while about half the animals remained inactive at humidities higher than 60% R.H. (Gunn, 1937). In addition, *Porcellio* proved rather sensitive to humidities between 35-60% R.H. where it could distinguish differences of 6% R.H.; below 35% R.H. the animal could distinguish only differences of 20% R. H. Unlike *Ligia, Porcellio* is unable to distinguish between humidities higher than 65% R.H.

Miller (1938) found that several Californian isopods aggregated at the highest humidity available in a gradient, although this preference was progressively less marked in the range of low humidity. Thus, 81.8% of *Armadillidium vulgare* aggregated at 100% R.H., and there was a similar response from *Porcellio laevis* and *Metoponorthus pruinosus*, but *P. spinicornis* was less hygropositive since only 53.4% of the isopods collected near 100% R.H.

In studying the hygroreaction of *Porcellio, Oniscus*, and *Armadillidium*, Waloff (1941) calculated the speed, number of turnings every 30 sec, number of rests,

and periods of complete inactivity. These measurements were found to be more meaningful than counts of numbers of animals collecting in each alternative. Most commonly, the isopods turned more frequently and traveled greater distances in 0-25% R.H., while the number of rests increased with increasing humidity. At high humidities the isopods rested for long periods. Thus, *Oniscus* rested only at humidities higher than 90% R.H., whereas *Porcellio* rested at humidities of 80% R.H., and *Armadillidium* at 60% R.H. From Waloff's data it appears that speed decreases considerably only at very high humidities, while at lower humidities it remains at about the same level.

Waloff's general conclusion is that the mechanism by which isopods remain in a favorable humid environment is a klinokinesis (an increased frequency of turning in low humidities). However, this does not hold true for *Armadillidium*, in which the frequency of turning did not change appreciably at humidities up to 60% R.H.

From Waloff's findings it is apparent that at all humidities below 50% R.H. the animal's response must have been affected by dehydration. This could occur because the apparatus was very long (about 1.5 m) and because the experiments were carried out in moving air, which increases the loss of water (Warburg, 1965b). The response to humidity is known to increase with desiccation, as was shown by Cloudsley-Thompson (1952, 1956). He discovered this by studying a number of isopods in an alternative chamber, counting the numbers in each alternative during a rather long exposure (75 min). *Philoscia muscorum*, a species inhabiting mesic areas, was found to be more positively hygrokinetic than *Oniscus* or *Porcellio*; least hygropositive was *Armadillidium*. In *Philoscia* and *Oniscus* at both high (30°C) and low (3°C) temperatures, the intensity of the humidity response was reduced as compared with their response at 18°C. In *Porcellio* and *Armadillidium*, however, the activity was

TABLE 2. *Effect of temperature on hygroreaction.*

		I_H	R.H. 30–70% Residence-time	Speed
25°C	A	+25%	40 sec	25 cm/min
	V	+ 3%	45 sec	28 cm/min
35°C	A	+24%	40 sec	30 cm/min
	V	—24%	45 sec	31 cm/min
42°C	A	—20%	40 sec	35 cm/min
	V	—40%	45 sec	35 cm/min

$$I_H = 100\,\frac{H-D}{H+D}\,\%$$

A—Armadillidium; V—Venezillo.
(+) Positive hygroreaction; (—) Negative hygroreaction.

correlated directly with temperature (see Table 2, in Cloudsley-Thompson, 1956).

In some of the earlier experiments it was found that darkness decreased the response to humidity in *Oniscus* (Cloudsley-Thompson, 1952) which may account for the fact that *Oniscus* leaves its microhabitat under stones or logs at night. On the other hand, Den Boer (1961) found that the positive humidity-reaction of *Porcellio* increased in darkness. In view of these conflicting findings, the response to humidity was studied not only at different temperatures and humidity-alternatives but also in light and darkness (Warburg, 1964).

The hygroreaction of both *Armadillidium* and *Venezillo* was tested in a small alternative chamber, 13 cm in diameter, during a 30-min exposure. The results indicate that *Armadillidium* is hygropositive at all humidities between 30-70% R.H. except at very high temperatures (42°C) when it becomes negatively hygrokinetic (Table 2).

On the other hand, the xeric isopod, *Venezillo*, is usually negatively hygrokinetic except at lower temperatures (25°C), when it is indifferent to humidities: $I_H=+3\%$ [intensity index $I_H=$ 100 [(H—D)/ (H+D)] %, indicating the excess time spent by a single animal in the humid zone (H) over that spent in the dry zone (D)].

In both species the residence-time (the time spent in each zone before shifting to the alternative) remained the same and did not change with temperature, whereas

speed increased with temperature as mentioned earlier. In contrast to Waloff, I found that speed did not change significantly even at high humidities. The reason for this may be that Waloff studied *Porcellio* and I used two conglobating species.

The effect of light on the response to humidity was tested at high temperatures (37.5°C) when the low humidity alternative (15% R.H.) was in light and the high humidity (45% R.H.) alternative in darkness (Table 3). Both *Venezillo* and *Armadillidium* showed negative hygroreaction. The same behavior was apparent when the animals were offered 40% R.H. and 70% R.H. They stayed for longer periods at 40% R.H. However, when offered a simultaneous choice of dark and light in 15% and 60% R.H., *Armadillidium* resumed its normal positive reaction to light and humidity (at 60% R.H., $I_H=+15\%$), whereas *Venezillo* preferred darkness and the lower humiditiy (R.H. 15%, $I_H=-21\%$), as is shown in Table 3.

It is clear that *Armadillidium* is positively hygrokinetic except at low humidities (15-45% R.H.), when it can not come to rest, or at high temperatures (37-42°C). On the other hand, *Venezillo* shows a tendency to stay at medium humidities rather

TABLE 3. *Effect of light on hygroreaction (in terms of intensity index (I_H); residence time in parentheses).*

	Light		
25°C	R.H. = 15%	R.H. = 60%	
		A +26 (81 sec)	
		V +23 (15 sec)	
	Light	Dark	
37.5°C	R.H. = 15%	R.H. = 45%	
	A —32 (57 sec)		
	V —18 (50 sec)		
	R.H. = 40%	R.H. = 70%	
	A —32 (39 sec)		
	V —30 (40 sec)		
	Light and dark		
	R.H. = 15%	R.H. = 60%	
	V —21 (31 sec)	A +15 (17 sec)	
	(in dark)	(in light)	

A—Armadillidium; V—Venezillo.
(+) Positive hygroreaction; (—) Negative hygroreaction.

than at low or high ones, and becomes indifferent to humidities only at low temperatures.

As was mentioned earlier, Cloudsley-Thompson (1956) found that *Oniscus, Porcellio,* and *Armadillidium* moved into the dry side at higher temperatures. This response was most pronounced in *Oniscus* and least in *Armadillidium.* In spite of the obvious exception of *Armadillidium,* Cloudsley-Thompson suggested that the response to humidity is correlated with the saturation-deficit rather than with relative humidity and that this response is connected with the rate of water loss. The reason for this conclusion is the finding that the intensity of the humidity-response increased with temperature, although humidities did not change considerably between 3-30°C.

There is good evidence in *Venezillo* and *Armadillidium* to suggest a definite response to the relative humidity, which can not be explained as a response to saturation-deficit (Warburg, 1964). *Venezillo* preferred 45% R.H. (at 27.5°C and 15.1 mm Hg S.D.) to 70% R.H. (at 37.5°C and 14.5 mm Hg S.D.), when the saturation-deficit was similar in both cases. *Armadillidium,* although different from *Venezillo* in its response to humidity, responded to 14.5 mm Hg S.D. (R.H. 70% at 37.5°C), avoiding the same saturation-deficit in other experiments at different temperatures, apparently because light affected this response.

Thus far, no special receptors for humidity have been located. Therefore, it cannot be decided whether hygroreceptors would record evaporation of water and thus respond to saturation-deficit (as suggested by Waloff, 1941) or absorb water vapor, thereby responding to changes in relative humidity (as suggested by Marcus, 1955, for *Porcellio*). The attempts by Gunn (1937), Miller (1938), and Janda and Lang (1939) to locate such receptors failed (none were found on the antennae, thorax, or abdomen). Jans and Ross (1963) suggested that the pit-like terminations on the ventral side of the lateral

plates resemble hygroreceptors as found in other arthropods, but the evidence is histological and needs further experimental support (see also Henke, 1960). Only after verification will it be possible to determine if these structures are indeed hygroreceptors, and then electrophysiological methods can help determine whether they respond to changes in relative humidity or in saturation-deficit.

One main point emerging from this discussion is the fact that the response of isopods to humidity is most pronounced in *Ligia* of the littoral zone and least pronounced in *Venezillo* of the xeric habitat, with the responses of other isopods from mesic habitats (*Philoscia, Oniscus, Porcellio,* and *Armadillidium*) intermediate. The animals respond to humidity mainly by changes in the rate of turning, especially at low humidities (Waloff, 1941), and by changes in the number of shifts and residence-time (Warburg, 1964), but probably not by speed (although both Waloff and Perttunen found that speed dropped at high humidities). The effect of temperature and light on hygroreaction was especially pronounced in *Armadillidium and Venezillo;* in the latter the response to light was of greater significance. This response will be discussed next, taking into account the effects of temperature and humidity.

RESPONSES TO LIGHT

Early studies on photoreaction were mainly descriptive rather than analytical. The main objective was to determine the range of light intensities affecting isopods; another was to determine the exact way in which isopods would react, whether by a directional response (phototaxis) or a random one (photokinesis). Most experiments were carried out at room temperature and no record of humidity was taken. In later experiments records of temperature and humidity were given, and the experiments were designed to determine the effects of these on photoreaction.

Isopods of the littoral zone (*Ligia itali-*

ca) were negatively phototactic at higher humidities (77% R.H.) and at 28°C (Perttunen, 1961). When the temperature was increased to 40°C, this response reversed to a positive photoreaction, which increased with progressive dehydration. Perttunen (1961) further studied the effect of humidity on photoreaction in *Ligia italica* by providing alternatives of 77% R.H. in light and 34% R.H. in darkness. He found that animals normally preferring the dark side would collect instead in the moist side despite the light. This response was more pronounced at lower light intensities of 10 lux, decreasing at 100 lux. At high light intensities (1000 lux), the animals became photonegative; but a shift occurred after 30 min, with the animals reversing to the moist side.

In nature, Barnes (1932) found that *Ligia baudiniana* orients towards shore, regardless of light. When *Ligia* is in sea water, it responds photonegatively. This response is stronger at lower light intensities and at lower temperatures (10°C). Yet when *Porcellio* is immersed in water, it changes from negative to positive photoreaction; in *Oniscus* this reaction is less pronounced (Fischbach, 1954).

Early experiments on the terrestrial isopod, *Oniscus*, indicated a negative response to light at intensities of 1.5-5 meter-candles (Cole, 1907). A similar response was found in *Porcellio* (Torrey and Hays, 1914). This isopod reacted by oriented movements (phototaxis) rather than by random movements (photokinesis). When exposed to light, *Porcellio* became active and moved until it eventually came to rest in darkness.

The extent of water loss also affects photoreaction. In *Oniscus* it was found that the animal became photopositive at humidities below 40% R.H. and at a light intensity of 45 foot-candles. Waloff (1941) correlated this reversal in photoreaction with water loss. When offered a choice between dry and humid, with dry in the dark side, the animals came to rest in the humid side, which was in light. Waloff concluded that the isopods responded initially by negative phototaxis and that this response was stronger than the humidity-response; but that after some activity the animal lost water and shifted to the humid part, thus reverting to positive photoreaction.

Bauers (1953) studied the photoreaction in *Porcellio scaber, Oniscus asellus,* and *Armadillidium vulgare*, keeping records of both temperature and humidity during experiments. He found that *Oniscus* was photonegative at all temperatures, whereas many individuals of *Porcellio*, and especially of *Armadillidium*, became increasingly photonegative with rising temperatures. Between 85-90% R.H. about 50% of the animals of all three species were in darkness, whereas at humidities of 40-45% R.H. the numbers dropped to 36% in *Porcellio* and 31% in *Armadillidium*. The percentage of photonegative *Oniscus* remained the same, regardless of humidities.

In a comparative study of the behavior of some American isopods from mesic and xeric habitats (Warburg, 1960, 1964), the photoreaction at a constant illumination of 10 ft-c was studied under various conditions of temperature and humidity. Single animals were used, to exclude any effect of aggregation. The experimental period was 30 min. During that period the actual time that an animal spent in each alternative was measured. This was preferable to the frequently used but less accurate method of counting the number of animals in each zone.

One criterion used in analyzing the response is the intensity index ($I_P = 100[(L-S)/L+S)]\%$); which measures the average percentage of the total time spent by a single animal in (L) light (+) or in (S) shade (−). In *Armadillidium* at low (10-20°C) and medium (20-30°C) temperatures, the response was $I_P = +14\%$ and $I_P = +23\%$, respectively. At high temperatures (35-40°C) there was an indifference to light, and no photoreaction took place ($I_P = 0\%$).
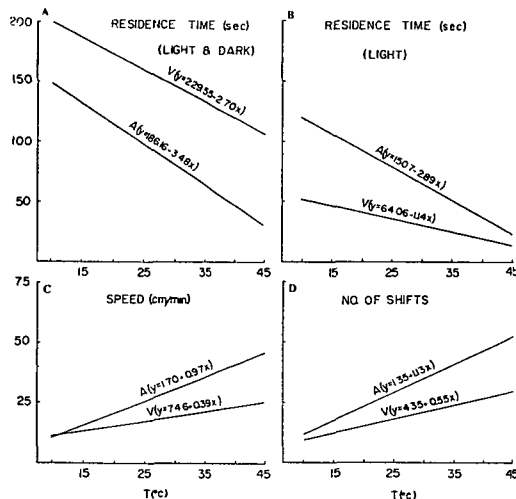
FIG. 1. Analysis of response to photic stimuli.

Venezillo is always photonegative, even at high temperatures ($I_P=-54\%$).

A second criterion for photoreaction is the average residence-time in each zone. In *Armadillidium* the residence-time was longest at low temperatures (160 sec), dropping to 80 sec at medium temperatures and to 47 sec at high temperatures. In *Venezillo* the longest time in each zone was 227 sec at medium temperatures, dropping to 88 sec at high temperatures. In other words, at high temperatures *Venezillo* stayed in each alternative for an average of 40 seconds longer than *Armadillidium*.

The regression of residence-time (y) on temperature (x), was calculated for both *Venezillo* and *Armadillidium* (Table 4, and Fig. 1). In Figure 1A the residence time was calculated for both *Venezillo* and *Armadillidium* for the whole period, whereas in Figure 1B it was calculated only for the period in light. In the first case, the curves for both animals indicate that the time spent in each zone decreased with increasing temperature. Secondly, *Venezillo* appeared to spend more time on the average in each zone than *Armadillidium*. The two curves are similar qualitatively, but differ quantitatively.

The real difference in the response of the two species can be seen in the curves calculated for residence-time in light only (Fig. 1B). The drop in residence-time with increasing temperatures is again apparent. However, it is evident that *Venezillo* stayed for much shorter periods in light than did *Armadillidium*, and the difference in photoreaction of both species, as indicated by residence time, is now shown also to be qualitative.

Next, the speed of locomotion was calculated and regardless of zone, was found to increase in both animals with increasing temperatures (Fig. 1C), but the speed of *Armadillidum* increased much more accordingly.

Finally, the regression of number of shifts on temperature indicates an increase in shifts from one zone to the alternative with rising temperatures (Fig. 1D). At all temperatures *Venezillo* shifted less frequently than did *Armadillidium*.

The effect of humidity on photoreaction was studied by giving the animals a choice between humidities of 15-45% R.H. in one experiment and 40-70% in another, with the lower alternative in light, and the higher humidity in darkness. In these two experiments the photoreactions of both *Venezillo* and *Armadillidium* were positive, and the residence-time was similar in both. If the animals were given a choice of light or shade combined with both high and low humidities, *Venezillo* reversed to its normal photonegative reaction. The residence-time was now much higher, changing to 61 sec compared to the earlier value of 41 sec. Speed was not greatly affected by humidity, and in one *Venezillo* it was 33.5 cm/min (at 40-70% R.H.) and, in a later experiment, 32 cm/min (at 15-45% R.H.). In *Armadillidium*, 55.3 cm/min was the speed at the high range of humidity, and 50 cm/min at the low range.

In Figure 2 the percentage of time spent in light and dark is shown at low and high temperatures. On the whole, *Armadillidium* spent more than 50% of its time in light, whereas *Venezillo* spent less than 25% in light.

TABLE 4. *Analysis of response to photic stimuli.*

x (T°C)	y	N	$\bar{X}$	$\bar{Y}$	Sx^2	Sy^2	Sxy	b	a	Sdy.x.	X_1	Y_1	X_2	Y_2
10–45	No. of shifts Armadillidium (5–110)	42	30.26	35.54	5212	15954	5899	1.13	1.35	15.23	10	12.6	45	52.2
10–45	No. of shifts Venezillo (10–73)	31	29.09	20.35	4071	9131	2269	0.55	4.35	16.46	10	9.8	45	29.1
10–45	Speed Armadillidium (4–74)	42	31.76	32.50	5425	13354	5297	0.97	1.70	14.28	10	11.0	45	45.4
10–45	Speed Venezillo (2–74)	34	30.58	19.38	5288	7648	2082	0.39	7.46	14.62	10	11.4	45	25.0
10–45	Total residence-time Armadillidium (19–448)	42	29.59	83.19	4922	331210	−17164	−3.48	196.16	82.35	10	151.4	45	29.6
10–45	Total residence-time Venezillo (14–450)	31	31.19	145.65	4453	452558	−12011	−2.70	229.55	120.37	10	222.6	45	108.1
10–45	Residence-time in light Armadillidium (18–162)	40	29.90	64.00	5119	73950	−14816	−2.89	150.70	28.59	10	121.8	45	20.7
10–45	Residence-time in light Venezillo (1–82)	36	30.91	28.72	4931	16231	−5624	−1.14	64.06	16.99	10	52.6	45	12.7
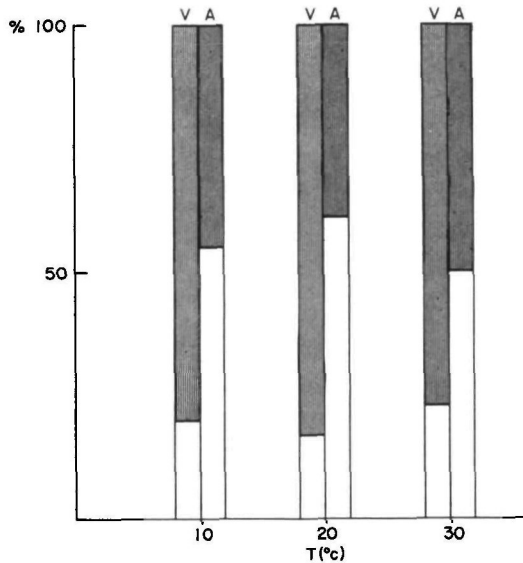
FIG. 2. Percentage of time spent in darkness and light by *Armadillidium* and *Venezillo*. White bar: Positive photoreaction. Dark bar: Negative photoreaction.

In order to determine the exact mechanism of photoreaction in these two species, the response was analyzed for first and last 15-min periods of experimentation (Table 5). It seems that the I_p index, or the response to light in general, did not change considerably with rising temperatures during the first period. However, during the second period, the response of *Armadillidium* became less positive, until at high temperatures it became indifferent to light, as discussed earlier. In *Venezillo* there was no indication of a direct relationship between temperature and the response to light throughout the period. On the other hand, both animals showed a significant increase in the mean number of shifts, both in time and with rising temperatures.

As a result of this analysis, it appears that the number of shifts and the residence-time, but not the speed, effect the response to light and are affected by the length of exposure. Banta (1910) noted a similar increase in activity in *Caecidotea* when it was exposed to light.

Although Abbott (1918) did not find clear evidence that moisture altered pho-

toreaction, he did note an increased activity in dryness, especially in *Porcellio*, but this did not affect photoreaction. Similar observations were noted by both Cloudsley-Thompson (1956) and Den Boer (1961).

During a period of experimentation it sometimes happens that isopods change the pattern of photoreaction from positive to negative and *vice versa* (Warburg, 1960). Thus, when *Venezillo* was offered alternatives of 40% R.H. in light and 70% R.H. in darkness (temperature 38°C), the I_p index was —54% at first, changing into —26% later. The speed remained 39 cm/min throughout the experiment. Residence-time was the only factor that changed, dropping from 88 sec to 61. In this case, both number of shifts and periods of rests were the main mechanism of reaction. There were also other cases where the animals changed both speed and residence-time throughout the experiment. All these phenomena might be explained in part by changes in the internal conditions of the animals due to progressive dehydration. However, in *Venezillo* the rate of water loss is known to be low (Warburg, 1965*b*), and therefore it can

TABLE 5. *Photoreaction as analyzed for the first 15 minutes and subsequent 15 minutes of half-hour experiments.*

	0–15 min		16–30 min	
T°C	Shifts (mean)	I_p-index	Shifts (mean)	I_p-index
Armadillidium vulgare				
10	9	+ 7.3	16	+31.2
25	21	+ 9.3	34	+16.6
30	23	+19.9	38	+34.4
35	27	+ 4.7	43	+ 6.8
40	32	+10.0	57	+ 3.1
Venezillo arizonicus				
10	7	—68.8	15	—58.2
25	12	—10.7	19	—29.2
30	17	—62.5	26	—69.7
35	18	—50.0	28	—67.1
40	30	—47.6	55	—37.0

A—Number of shifts increases in time (and temperature), and the positive photoreaction becomes more definite with time except at 40°C where the high temperature effects a drop in response to light.

V—Number of shifts increases in time, but there is no definite pattern of increased negative photoreaction.

TABLE 6. *Photoreaction in isopods from semi-arid and arid habitats in Israel.*

T°C	22–25				37–40			
R.H. %	0		100		0		100	
	Ipt (av. no. of shifts)	Ipg (X²)	Ipt (av. no. of shifts)	Ipg (X²)	Ipt (Av. no. of shifts)	Ipg (X²)	Ipt (Av. no. of shifts)	Ipg (X²)
A. officinalis	−67.9 (22.5)	−73.7 (93.7)	−85.3 (18.2)	−87.9 (119.7)	−32.1 (31.2)	−65.4 (87.1)	−39.8 (20.5)	−73.3 (92.3)
A. albomarginatus	−54.8 (4.7)	−58.9 (89.4)	−64.2 (5.3)	−70.7 (79.4)	−36.7 (17.2)*	−42.7 (60.1)	−28.7 (8.8)*	−38.0 (45.9)
P. olivieri	−62.4 (51.5)	−74.6 (67.2)*	−87.9 (33.7)	−91.4 (102.1)	−15.4 (68.3)*	−13.6 (34.2)*	+9.5 (54.5)*	+12.2 (60.8)*
H. reaumuri	+22.7 (54.0)	+24.2 (76.6)	+17.8 (32.6)	+12.3 (88.4)	−20.1 (72.3)	−53.5 (62.1)	−35.5 (59.8)	−60.6 (45.5)*

$$Ip = \frac{100\,(L-S)}{L+S}\ \%$$

(+) plus = photopositive; (−) minus = photonegative

p < 0.1% except when asterisk (*) p < 0.5%

Ipt = Intensity of photoreaction as measured by the average time spent by an individual animal in each alternative during 10 experiments using different animals.

Ipg = Intensity of photoreaction as shown by the response of a group of 10 animals counting the numbers in each alternative during 3 experiments using different animals.

TABLE 7. *Summary: Behavioral responses of semi-terrestrial and terrestrial isopods to various environmental factors.*

Species	Family	Habitat	Response to stimulus	Factors affecting response	Author
Ligia italica	Ligiidae	Littoral	Negative photokinesis Positive hygroreaction	40°C reversed to positive Dehydration reversed to positive	Perttunen (1961)
Caecidotea stygia	Asellidae	Aquatic, cave	Negative photokinesis	Activity increased in light	Banta (1910)
Asellus communis	Asellidae	Aquatic	Negative phototaxis & photokinesis	,, ,, ,,	Banta (1910)
Asellus aquaticus	Asellidae	Aquatic	Negative phototaxis & photokinesis		Cole (1907)
Platyarthus hoffmannseggi	Oniscidae	Myrmecophilous	Negative photoklino-kinesis	Dehydration reversed	Brooks (1942) Mathes & Strouhall (1954)
Oniscus asellus	Oniscidae	Mesic	Negative phototaxis ,, ,, ,, ,,		Torrey & Hays (1914) Cole (1907); Hartline (1924) Waloff (1941)
				40% R.H. positive phototaxis Increased with desiccation	Cloudsley-Thompson (1952) Miller (1938); Bauers (1953)
			Positive hygrokinetic ,, ,, ,,	Drops in darkness Increased with desiccation High temperature reversed	Waloff (1941) Cloudsley-Thompson (1952, 1956) Warburg (1964)
Porcelio scaber	Porcellionidae	Mesic	Negative phototaxis & photokinesis Negative photokinesis Negative phototaxis ,,	in light in dark Positive at 25–29°C	Buddenbrook & Schlieper (1926) Torrey & Hays (1914) Bauers (1953) Abbott (1918)
			Positive hygrokinetic ,,	Increased with desiccation	Gunn (1937); Waloff (1941) Cloudsley-Thompson (1956)
Porcellio laevis	Porcellionidae	Mesic	Positive hygrokinetic		Miller (1938)
P. spinicornis occidentalis	Porcellionidae	Mesic	Positive hygrokinetic		Miller (1938)
Metoponorthus pruinosus	,,	Mesic	Positive hygrokinetic		Miller (1938)
Philoscia muscorum	,,	Mesic	Positive hygrokinetic	Increased with desiccation	Cloudsley-Thompson (1956)
Armadillidium vulgare	Armadillidiidae	Mesic	Photopositive Photopositive at day Positive hygrokinetic ,, ,,	Increased with temperature Low temperature reversed Increased with desiccation High temperature reversed	Henke (1930); Bauers (1953) Warburg (1964) Miller (1938); Waloff (1941) Cloudsley-Thompson (1956) Warburg (1964)
Armadillo officinalis	Armadillidae	Mesic	Negative photoreaction	No effect of temperature or humidity	Warburg (present study)
Venezillo arizonicus	Armadillidae	Xeric	Negative photoreaction Positive hygroreaction Negative thermoactive	Indifferent at low temperatures Reversed at high temperature	Warburg (1964) ,, ,,
Porcellio olivieri	Porcellionidae	Xeric	Negative photoreaction	Reversed at high temperature	Warburg (present study)
Armadillo albomarginatus	Armadillidae	Xeric	Negative photoreaction	No effect of temperature or humidity	,,
Hemilepistus reaumuri	Porcellionidae	Xeric	Positive photoreaction	Reversed at high temperature	,,

LITTORAL — FOREST — GRASSLAND — SEMI-ARID — ARID

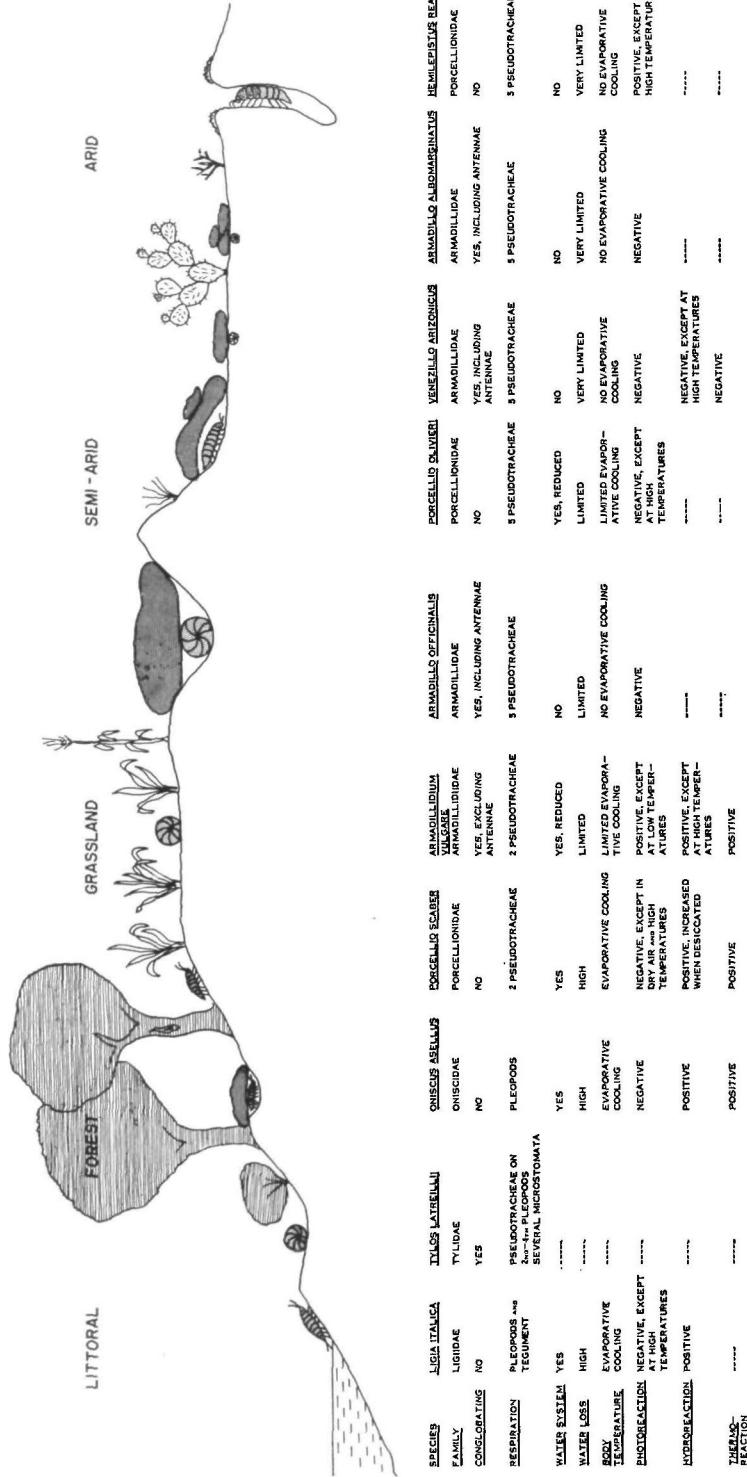| SPECIES	LIGIA ITALICA	TYLOS LATREILLI	ONISCUS ASELLUS	PORCELLIO SCABER	ARMADILLIDIUM VULGARE	ARMADILLO OFFICINALIS	PORCELLIO OLIVIERI	VENEZILLO ARIZONICUS	ARMADILLO ALBOMARGINATUS	HEMILEPISTUS REAUMURI
FAMILY	LIGIIDAE	TYLIDAE	ONISCIDAE	PORCELLIONIDAE	ARMADILLIDIIDAE	ARMADILLIDAE	PORCELLIONIDAE	ARMADILLIDAE	ARMADILLIDAE	PORCELLIONIDAE
CONGLOBATING	NO	YES	NO	NO	YES, EXCLUDING ANTENNAE	YES, INCLUDING ANTENNAE	NO	YES, INCLUDING ANTENNAE	YES, INCLUDING ANTENNAE	NO
RESPIRATION	PLEOPODS and TEGUMENT	PSEUDOTRACHEAE ON 2nd–4th PLEOPODS SEVERAL MICROSTOMATA	PLEOPODS	2 PSEUDOTRACHEAE	2 PSEUDOTRACHEAE	5 PSEUDOTRACHEAE	5 PSEUDOTRACHEAE	5 PSEUDOTRACHEAE	5 PSEUDOTRACHEAE	5 PSEUDOTRACHEAE
WATER SYSTEM	YES	-----	YES	YES	YES, REDUCED	NO	YES, REDUCED	NO	NO	NO
WATER LOSS	HIGH	-----	HIGH	HIGH	LIMITED	LIMITED	LIMITED	VERY LIMITED	VERY LIMITED	VERY LIMITED
BODY TEMPERATURE	EVAPORATIVE COOLING	-----	EVAPORATIVE COOLING	EVAPORATIVE COOLING	LIMITED EVAPORATIVE COOLING	NO EVAPORATIVE COOLING	LIMITED EVAPORATIVE COOLING	NO EVAPORATIVE COOLING	NO EVAPORATIVE COOLING	NO EVAPORATIVE COOLING
PHOTOREACTION	NEGATIVE, EXCEPT AT HIGH TEMPERATURES	-----	NEGATIVE	NEGATIVE, EXCEPT IN DRY AIR and HIGH TEMPERATURES	POSITIVE, EXCEPT AT LOW TEMPERATURES	NEGATIVE	NEGATIVE, EXCEPT AT HIGH TEMPERATURES	NEGATIVE	NEGATIVE	POSITIVE, EXCEPT AT HIGH TEMPERATURES
HYDROREACTION	POSITIVE	-----	POSITIVE	POSITIVE, INCREASED WHEN DESICCATED	POSITIVE, EXCEPT AT HIGH TEMPERATURES	-----	-----	NEGATIVE, EXCEPT AT HIGH TEMPERATURES	-----	-----
THERMO-REACTION	-----	-----	POSITIVE	POSITIVE	POSITIVE	-----	-----	NEGATIVE	-----	-----

FIG. 3. Evolutionary trends of some major types of isopod.

be expected to have less effect on the response of *Venezillo* than of other isopods within the same period of time.

Recently it was possible to study the photoreaction of four species of isopods from xeric habitats in Israel (Table 6). Two of these species are conglobating forms belonging to the Armadillidae. *Armadillo officinalis* var. *syriacus* is abundant in the Mediterranean region. *Armadillo albomarginatus* is found under stones in the Negev Desert. The other two species belong to the Porcellionidae and are commonly found throughout the Negev. *Porcellio olivieri* occurs under stones in creeks, while *Hemilepistus reaumuri* is particularly abundant on loess.

All four species of isopods are mostly photonegative, except *Hemilepistus*, which is photopositive at lower temperatures. When temperatures are high, *P. olivieri* may reverse to positive photoreaction.

On the whole, most land isopods appear to be more photonegative than aquatic ones (Abbott, 1918). Some of the main findings on the responses of isopods towards environmental stimuli are summarized in Table 7 and Figure 3. Light seems to be more important ecologically for some isopods than for others. In isopods from both littoral zone and mesic habitats, the main response to light is photonegative, unless the animals are dehydrated or the temperatures rise, whereupon the response becomes photopositive. Isopods inhabiting grassland or forest (*e.g. Armadillidium*) are more efficient in regulating water and can, therefore, revert to positive photoreaction. In the desert the main pattern is negative photoreaction (*Venezillo arizonicus, Armadillo albomarginatus*), with the exception of *Hemilepistus reaumuri*, which shows a crepuscular pattern of behavior.

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