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ANALYSIS OF CONTACT-REHYDRATION IN TERRESTRIAL GASTROPODS: OSMOTIC CONTROL OF DRINKING BEHAVIOUR

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SUMMARY

1. Contact-rehydration in slugs is mediated by a specific behavioural pattern in which dehydrated slugs move onto a moist surface, assume a flattened posture while water is absorbed through the surface of the foot and move off once they are rehydrated.

2. 'Drinking behaviour' is initiated when slugs have been dehydrated to the threshold level of 60–70% of initial body weight (IBW).

3. Drinking behaviour is terminated once slugs have rehydrated to their individual rehydration set-points. The mean 'rehydration set-point' for *Limax* is 93·6 ± 12·2% IBW (±S.D.). Slugs can achieve their individual set-point regardless of the extent of initial dehydration.

4. Drinking behaviour can be initiated by injections of hyperosmotic mannitol solution and terminated by injections of dilute saline. This indicates that variation in the osmolality of the haemolymph is involved in the control of the behavioural sequence.

INTRODUCTION

Due to the dessicating effects of their environment, many terrestrial organisms experience periods of dehydration. Among the more susceptible are gastropods and amphibians which can experience substantial dehydration due to evaporative water loss from their moist integuments (Dainton, 1954; Machin, 1964; Prior, Hume, Varga & Hess, 1983; see Bentley, 1971, for a review of amphibians). Maintenance of water balance in these organisms involves several behavioural responses that minimize evaporative water loss. Among these are preferences for regions of high humidity (Johnson, 1969; Cook, 1981) and manoeuvres such as burrowing in frogs (e.g. Packer, 1963; McClanahan, 1967; Heatwole, Cameron & Webb, 1971) and huddling in slugs (Cook, 1981; Prior, 1981, 1983). Nevertheless, these animals do experience periods of dehydration. They can, however, rapidly recover by absorption of water through their integuments (Stille, 1958; Dainton, 1954; McClanahan & Baldwin, 1969; Bentley, 1971; Prior, 1982).

It has been demonstrated that oral ingestion of water does not contribute significantly to rehydration in amphibians (e.g. Bentley & Yorio, 1979). Although the

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question of oral ingestion in slugs had remained unresolved (e.g. Kunkel, 19[redacted] Machin, 1975), the present observations, together with those of Dainton (1954), establish that rehydration of slugs occurs *via* water absorption through the surface of the foot. Thus, in both amphibians and terrestrial slugs the process of contact-rehydration is crucial for the maintenance of water balance.

Specific behavioural responses are known to be associated with contact-rehydration. For example, certain toads and frogs rehydrate by positioning themselves with their ventral pelvic regions in contact with moist substrates (e.g. Stille, 1958; McClanahan & Baldwin, 1969; Bundy & Tracy, 1977). Slugs and snails have been 'allowed to rehydrate' on moist soil or paper towels, but their behaviour during rehydration has not been analysed (e.g. Riddle, 1981; Blinn, 1964). The reason for this is that most of these studies have been designed to analyse rates of water uptake rather than the behavioural control of the rehydration process (e.g. Dainton, 1954; Packer, 1963; Spight, 1967; Warburg & Degani, 1979; Bentley & Yorio, 1979; Canziani & Canata, 1980).

The present results demonstrate that contact-rehydration in slugs is accomplished by a well regulated behavioural sequence in which dehydrated animals move onto a moist surface, remain there while water is absorbed through the surface of the foot, and leave once they are rehydrated. It is also shown that this response can be initiated and terminated by changes in the osmolality of the haemolymph. In that drinking behaviour in vertebrates can likewise be mediated by changes in body fluid osmolality (Fitzsimons, 1979), contact-rehydration can be appropriately referred to as 'drinking'. A preliminary report of these observations has appeared in abstract form (Prior, 1982).

MATERIALS AND METHODS

The terrestrial slugs, *Limax maximus* Linnaeus, 1758 and *Lehmannia valentiana* (Férussac, 1823), were collected locally in Lexington, KY. Both freshly collected slugs and slugs reared from eggs in the laboratory were used with no observable difference in results. The animals were kept in the laboratory in well vented plastic refrigerator boxes (32 × 10 × 25 cm) which were lined with paper towels saturated with tap water. The slugs were fed laboratory rodent chow (Purina) and maintained on a 14: 10 light: dark cycle at 18 °C during the light period and 12 °C during the dark.

In order to stabilize the relationship between body weight and hydration, slugs were fasted for 5–7 days in small containers lined with wet paper towels. This procedure resulted in stable body hydration (86·2 ± 1·2 % of the wet weight) and haemolymph osmolality (140·5 ± 4·0 mosmol kg^{-1} H_2O), and minimal daily variation in body weight (1–2 %; Prior *et al.* 1983). This procedure allowed the use of 'percent of initial body weight' (% IBW ± S.D.) as a measure of relative body hydration. Fully hydrated slugs (100 % IBW) were used in all experiments, and changes in body hydration were related to their fully hydrated weights.

Slugs were air-dehydrated as previously described (Prior *et al.* 1983; Prior, 1983) by placing them in drying chambers (155 mm diameter plastic plate) fitted with screen mesh tops. At room temperature (18–22 °C) and 10–40 % relative humidity, the slugs dehydrated to 60–70 % IBW in about 2 h.

Drinking responsiveness was tested by placing a slug into a test chamber (dry plastic plate, 15 cm diameter) containing a 4 cm×4 cm pad of tissue paper (Kimwipe) saturated with distilled water. The slugs were placed 2·0 cm from the wet pad in this chamber and allowed to move about. The slugs were weighed when they were fully hydrated (100 % IBW), after dehydration to 60–70 % IBW, and when they voluntarily moved off the moist pads at the end of rehydration. The degree of rehydration achieved by the slugs is reported as % IBW and is referred to as the rehydration set-point. If a slug did not position itself upon the wet surface it was returned to the drying chamber and tested again after it had been further dehydrated. All drinking experiments were conducted between 7.00 a.m. and 1.00 p.m.

Foot surface area was measured by tracing the outline of the foot while it was viewed through the bottom of a Petri plate. These outlines were traced on paper and the areas determined with an electronic digitizer (Houston Hipad/IBM-PC).

Various solutions (0·05–1·5 ml) were injected into the haemocoel through the posterior body wall with 23 guage hypodermic needles: 1·0× saline (140–145 mosmol kg^{-1} H_2O), described by Prior & Grega (1982); 1·0 molal mannitol made up in 1·0× saline; 200 mosmol kg^{-1} H_2O mannitol made up in 1·0× saline; 0·1× saline made by diluting 1·0× saline with distilled water. It has been previously shown that such injections can rapidly adjust the osmolality of the haemolymph to predicted levels (Prior, 1983). Haemolymph samples were obtained by cutting a superior tentacle and allowing the haemolymph to drain into a small centrifuge tube. Haemolymph osmolality was determined by freezing point depression (Advanced Instruments Osmette A) or with a vapour pressure osmometer (Wescor 5120). Blue Dextran (Sigma; average $M_r = 2 \times 10^6$) solutions were dialysed against distilled water ($3000 M_r$ cut-off) for 24 h before use.

RESULTS

Drinking behaviour

When slugs that had been dehydrated to 60–70 % IBW were placed in test chambers (Fig. 1A) they moved directly onto the wet pads, came to rest and assumed a characteristic posture in which they were dorsoventrally compressed with the edges of the foot (i.e. foot fringe) expanded and the superior tentacles half extended (Fig. 1C). In moderately dehydrated slugs (60–70 % IBW) the process of contact-rehydration required 10–20 min. After rehydration, the slugs extended their superior tentacles and moved off the moist pads onto the dry surface of the chambers where, within 5 min, they came to rest with their tentacles fully withdrawn. Fully hydrated slugs, in contrast to dehydrated ones, neither stopped on the wet pads nor assumed the drinking posture. Instead, they moved about for several minutes with their superior tentacles fully extended. If they did contact the moist pad they continued directly across it before coming to rest on the dry area of the chamber (Fig. 1B).

Integumental absorption of water

To test the hypothesis that contact-rehydration involves oral ingestion of water, hydrated slugs were placed in the test chambers as usual, but the pads were

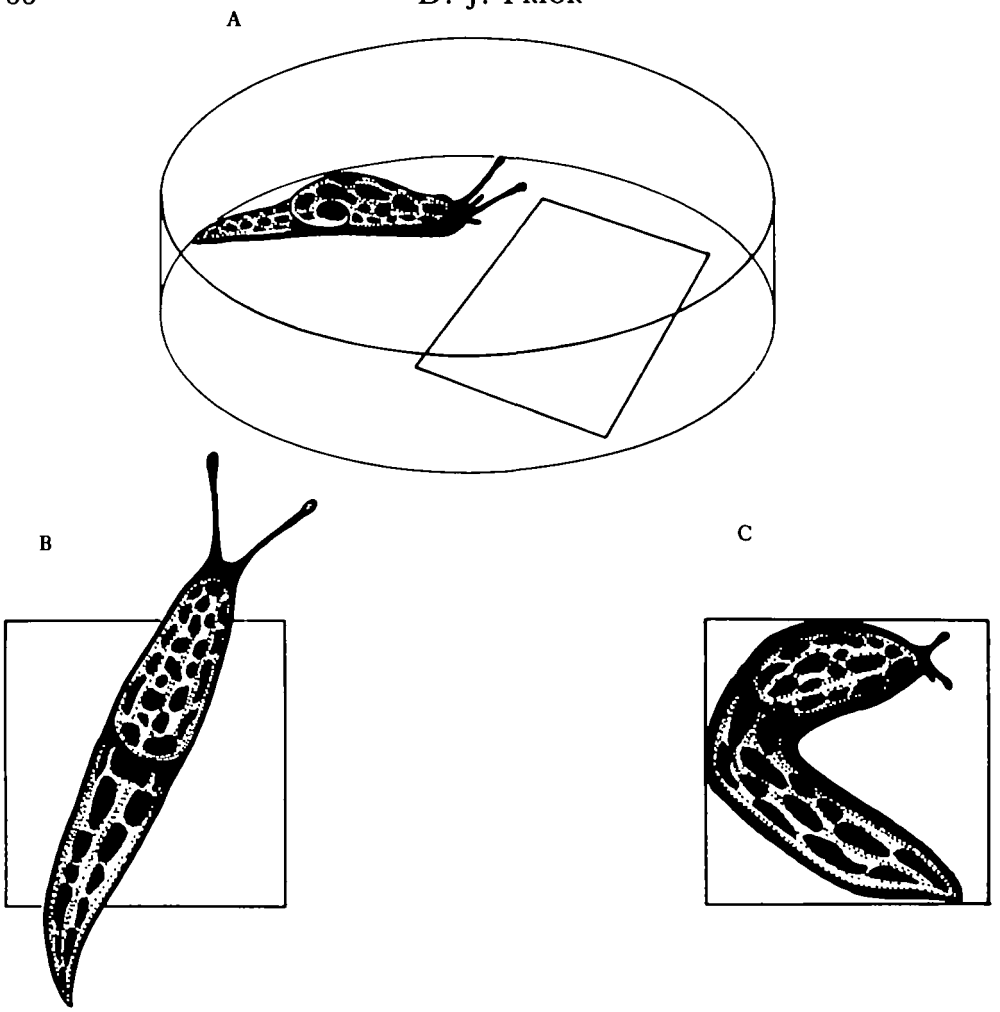

Fig. 1. The drinking test chamber, illustrated in A with a specimen of *Limax maximus*, consisted of a large (15 cm diameter) dry plastic Petri plate with a moist pad of tissue paper (Kimwipe) near the centre. A drinking trial was initiated by placing a slug in the chamber about 2 cm from the pad. (B) illustrates the appearance of a fully hydrated slug moving across the pad without stopping. Note that the superior tentacles are fully extended. (C) illustrates a dehydrated slug in the drinking posture on the pad, with it's superior tentacles half extended and it's body somewhat flattened with the foot fringe expanded.

saturated with a 1% solution of Blue Dextran. The slugs moved onto the pads, assumed the characteristic posture and remained until they were rehydrated. Once they had moved off the pads at the termination of the behaviour, they were weighed to determine the amount of water absorbed. The 16 slugs that were tested gained from 0·14 to 1·5 g in weight during contact-rehydration ($\bar{X} = 0{\cdot}38 \pm 0{\cdot}33$ g; $\bar{X}$ initial weight = $1{\cdot}44 \pm 0{\cdot}28$ g). If this increase in weight had been due to oral ingestion of solution from the pads, the digestive tracts of the slugs should have been filled with dark Blue Dextran. The slugs were dissected and the buccal mass, oesophagus, crop and intestines examined. In 14 of the slugs there was no trace of blue marker. In two of the slugs, there were a few flecks (3–5) of mucus-entrapped marker in the ante[illegible]

[redacted]ccal mass. These observations demonstrate that rehydration was completed without oral ingestion of water, thus indicating that contact-rehydration occurred *via* integumental absorption of water.

Dehydration threshold

Drinking behaviour was not observed in slugs that had been dehydrated to between 90 and 75 % IBW. However, when these slugs were further dehydrated to 60–70 % IBW and retested, they displayed the complete drinking behaviour. The threshold dehydration for the initiation of drinking was determined by sequentially testing individual slugs as they were progressively dehydrated. In order to do this, it was necessary to dehydrate slugs in small increments between trials. The threshold dehydration was estimated by taking the mean of the dehydration levels at the last negative trial and the trial during which drinking occurred. In those cases in which the difference in dehydration between the two trials was less than or equal to 5 % IBW ($N = 26$), the mean threshold dehydration was $67{\cdot}6 \pm 4{\cdot}8$ % IBW (±S.D.).

Rehydration set-point

In order to determine whether drinking was terminated at a specific level of rehydration (i.e. rehydration set-point) slugs were weighed before and after their contact with the wet pads. The mean rehydration set-point from 345 trials with 83 *Limax* was $93{\cdot}6 \pm 12{\cdot}2$ % IBW (±S.D.). Slugs were repeatedly tested in order to assess the precision of the rehydration process in individuals. As seen in Table 1, there

Table 1. *Rehydration set-points of individual* Limax maximus *and* Lehmannia valentiana

(A) The rehydration set-point for each slug is the mean of three (*Limax*) or six (*Lehmannia*) trials and is expressed as the mean % initial body weight (% IBW ± S.D.)

Limax set-points (x̄ % IBW ± S.D.)		*Lehmannia* set-points (x̄ % IBW ± S.D.)
1. 86·8 ± 3·6	11. 94·0 ± 7·2	1. 71·8 ± 7·1
2. 88·4 ± 9·6	12. 92·9 ± 11·4	2. 77·4 ± 2·7
3. 77·6 ± 4·8	13. 94·0 ± 5·3	3. 64·4 ± 2·8
4. 86·8 ± 9·3	14. 84·9 ± 0·5	4. 82·9 ± 3·5
5. 87·6 ± 0·4	15. 101·9 ± 5·6	5. 82·3 ± 5·1
6. 91·9 ± 5·9	16. 79·5 ± 3·2	6. 78·8 ± 4·5
7. 96·6 ± 10·3	17. 89·0 ± 3·7	7. 87·3 ± 3·6
8. 85·8 ± 2·3	18. 102·8 ± 6·0	8. 81·2 ± 3·7
9. 82·5 ± 7·2	19. 79·0 ± 4·8	9. 90·1 ± 5·4
10. 88·5 ± 9·8	20. 92·6 ± 8·5	10. 69·8 ± 1·1

(B) The measurements in (A) are from experiments in which slugs were dehydrated to various extents ranging from 48·1 to 77·3 % IBW. Listed in (B) are the dehydration levels (% IBW) for each of the trials of 12 of the slugs from (A). The slug numbers correspond to those in (A).

Limax dehydrations (% IBW)		*Lehmannia* dehydrations (% IBW)
1. 50·5, 67·8, 64·9	11. 69·0, 71·9, 68·2	1. 70·1, 66·8, 60·8, 58·1, 65·0, 64·0
5. 54·8, 73·3, 53·8	12. 73·9, 66·0, 66·6	3. 63·5, 65·6, 60·5, 42·1, 60·3, 75·8
8. 53·5, 69·8, 64·9	18. 76·8, 70·4, 73·8	8. 56·5, 58·0, 48·1, 71·0, 57·6, 67·0
13. 74·6, 72·0, 57·5	19. 60·2, 64·6, 65·3	10. 65·0, 70·0, 67·6, 65·0, 56·2, 69·5

was considerable variation in the individual set-points and their standard deviation. The set-points in this group of trials ranged from 64·4 to 102·8 % IBW and the standard deviations were from ±0·4 to ±11·4 % IBW.

The set-point of a slug was unaffected by the extent of dehydration that preceded drinking (Table 1B). For example, even though *Limax* 5 was dehydrated to 54·8, 73·3 and 53·8 % IBW in three trials, the mean rehydration set-point was 87·6 ± 0·4 % IBW. In addition, dehydration to similar levels did not necessarily result in precise rehydration. *Limax* 11 was dehydrated to 69·0, 71·9 and 68·2 % IBW in three trials yet had a mean rehydration set-point of 94·0 ± 7·2 % IBW (see Table 1B for additional examples). There was no correlation between the extent of dehydration and the rehydration set-point (analysis of variance $N = 209$ trials; F value = 108; $P < 0{\cdot}30$). Thus, regardless of the extent of dehydration, the slugs remained on the pads only until their rehydration set-points had been reached. This was accomplished by varying the length of time spent on the wet pads.

Osmotic control of drinking behaviour

Dehydration of slugs to the threshold for drinking (67·6 % IBW) results in an increase of haemolymph osmolality from 140 to 200–210 mosmol kg^{-1} H_2O (Prior

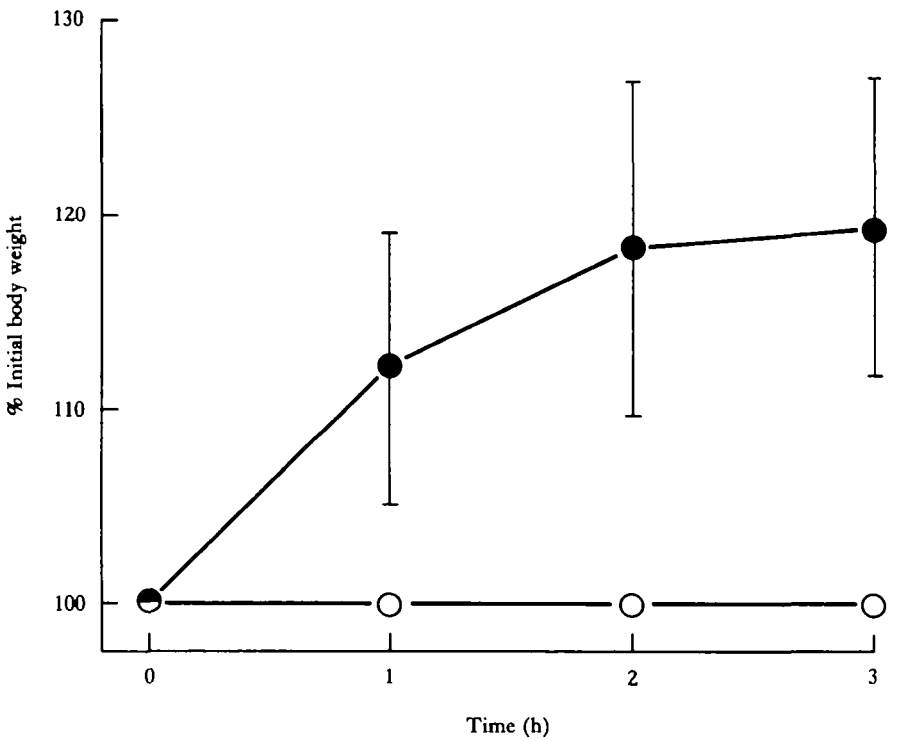

Fig. 2. The drinking responsiveness of fully hydrated *Limax maximus* was tested after they had been injected with either 1·0 molal mannitol solution (haemolymph increased to 200–220 mosmol kg^{-1} H_2O) or equal volumes of isosmotic slug saline (keeping the haemolymph osmolality constant at 140 mosmol kg^{-1} H_2O). The mannitol-injected slugs ($N = 14$; ● – ●) assumed the drinking posture and absorbed water. The saline-injected slugs ($N = 10$; ○ – ○) neither assumed the drinking posture nor gained weight. Each point is the mean % of initial body weight (% IBW ± S.D.) of the indicated number of slugs.

al. 1983). In order to determine if the increase in haemolymph osmolality could initiate the drinking response, fully hydrated slugs were injected with sufficient hyperosmotic mannitol solution to raise haemolymph osmolality to 200–210 mosmol kg^{-1} H_2O. All the injected slugs ($N = 14$) moved onto the wet pads and remained in the drinking posture until they were removed to be weighed (Fig. 2). When returned to the test chambers after each weighing, they reassumed their drinking posture on the wet pads. In contrast, drinking behaviour was not observed in control slugs that had received equal volume injections of isosmotic saline ($N = 10$, Fig. 2).

The mean osmolality of the haemolymph of slugs immediately after termination of drinking was 117·3 ± 32·0 mosmol kg^{-1} H_2O (±S.D., $N = 11$) which is well below that of dehydrated slugs prior to contact-rehydration (200–210 mosmol kg^{-1} H_2O). To determine if dilution of the haemolymph was sufficient to terminate drinking, dehydrated slugs (60–68 % IBW) that had just assumed the drinking posture (60 s) were injected with diluted saline (0·1×). Control slugs which had been dehydrated to the same extent were injected with equal volumes of isosmotic mannitol solution (200 mosmol kg^{-1} H_2O) in order to simulate the volume increase without changing haemolymph osmolality. After the slugs had been injected they were placed in separate dry Petri plates for 10 min before being tested. None of the 0·1× saline-injected slugs

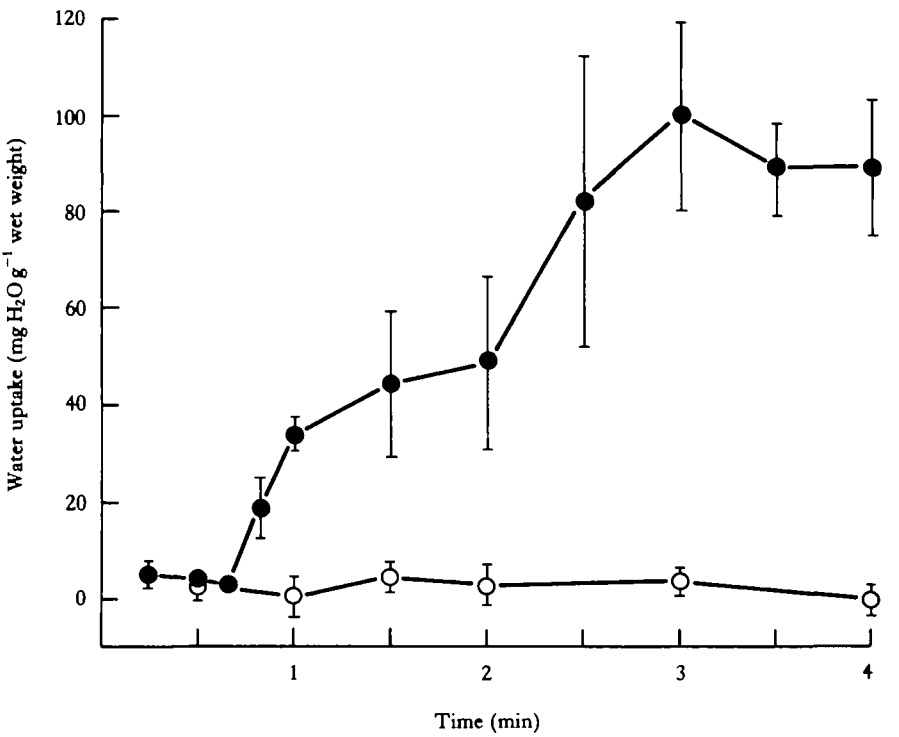

Fig. 3. Water uptake by *Limax maximus* as measured by increase in body weight, is plotted as a function of time. All the slugs in this experiment weighed between 1·0–1·5 g and were used for only one measurement. The drinking response was initiated by dehydrating slugs to between 60–70 % IBW (● – ●) and placing them on a wet pad for from 20 s to 4 min after which they were weighed (to 0·1 mg) to determine water uptake. The fully hydrated control slugs (○ – ○) were likewise placed on the wet pads for varying lengths of time. Each point is the mean ± S.D. of from five to nine measurements. All experiments were done between 7.00 a.m. and 1.00 p.m.

($N = 8$) displayed drinking behaviour. In contrast, six of the seven mannitol-injected slugs reassumed the normal drinking posture on the wet pads.

Water uptake during contact-rehydration

The rate of water uptake by dehydrated slugs during contact-rehydration was compared with that of fully hydrated slugs on a moist surface. Dehydrated slugs (60–70 % IBW) were placed directly upon a moist pad and left for varying time intervals, after which they were weighed to determine water uptake (Fig. 3). After a delay of 40–50 s, water uptake in the dehydrated slugs rapidly increased. For example, during the 2–3 min period, water uptake in the drinking slugs (weighing 0·5–1·2 g) was 51·0 mg H_2O min^{-1}, but was negligible in the fully hydrated slugs (Fig. 3).

It was possible that expansion of the foot could account for the difference in water uptake between dehydrated and hydrated slugs. This alternative was examined by comparing the foot areas of individual slugs ($N = 16$) when they were fully hydrated, dehydrated and when they were in the drinking posture. During dehydration, foot area decreased in proportion to the extent of dehydration ($r = 0{\cdot}76$). The mean foot area of slugs dehydrated to 45–65 % IBW was 55·5 ± 6·7 % (S.D.) of the area of fully hydrated slugs. Expansion of the foot margin at the onset of drinking resulted in an increase in foot surface area (see Fig. 1C). However, the mean foot area of the slugs during drinking was 97·1 ± 13·7 % (S.D.) of their foot area when fully hydrated. Thus the increase of the foot surface that occurs during drinking cannot alone account for the dramatic increase in water uptake by dehydrated slugs.

Water absorption during contact-rehydration is necessarily dependent upon the surface area of the foot. A power function analysis of 28 drinking trials revealed, as expected, that the foot surface area varied as the 2/3 power of body weight ($Y = 2{\cdot}23X^{0{\cdot}65}$; $r = 0{\cdot}98$, where Y = area in cm^2, X = body weight in g). This relationship was used to calculate the mean rate of water uptake per unit surface area of the foot over the full course of a drink. The mean rate of water uptake in slugs weighing between 0·5 and 2·0 g was 7·8 ± 2·8 $\mu l\,cm^{-2}\,min^{-1}$ (±S.D., $N = 119$).

DISCUSSION

During drinking behaviour, slugs move onto a moist surface, remain there while water is absorbed through the surface of the foot, and leave once they reach their rehydration set-point. A crucial aspect of this sequence is that by moving off the pads, the slugs actively terminated the behaviour. This demonstrated that the behavioural sequence is regulated, rather than simply being an orientation to a moist area where slugs might remain indefinitely.

The present results demonstrate that contact-rehydration is due to integumental absorption of water. Large amounts of water were absorbed during rehydration, yet Blue Dextran was not found in the digestive system. Some of the earlier reports of buccal movements during rehydration (e.g. Kunkel, 1916) may be explained by the existence of a separate feeding system which could be initiated when a food stimulus is present in the substrate solution. Nevertheless, in the present experiments no such

sponse was observed, thus contact-rehydration was analysed in terms of integumental absorption of water.

Osmotic control of drinking behaviour

The present observations demonstrate that increasing the haemolymph osmotic pressure of slugs to about 200 mosmol kg^{-1} H_2O by either dehydration or injection of a hyperosmotic mannitol solution results in the initiation of drinking behaviour (Table 1, Fig. 2). Correspondingly, dilution of the haemolymph of dehydrated slugs by either contact-rehydration or by injection of 0·1× saline terminates the drinking response. These observations suggest that haemolymph osmotic pressure is involved in the control of drinking. Furthermore, these results indicate that drinking is not controlled by the volume changes that accompany dehydration and rehydration. For example, dehydration resulted in a reduction in haemolymph volume, while mannitol injections resulted in an increased in haemolymph volume, yet both treatments initiated drinking.

It has recently been shown that the feeding responsiveness of slugs also can be modulated by variations in haemolymph osmotic pressure (Prior, 1983). Likewise, body fluid osmotic pressure is known to be involved in the control of drinking and hydration-induced variations in feeding in other invertebrates (e.g. Dethier, 1976) and many vertebrates (e.g. Fitzsimons, 1979; Hsiao & Langenes, 1971; Kakolewski & Deaux, 1972). In all of these cases, injections of hyperosmotic and hypo-osmotic solutions mimicked the effects of dehydration and rehydration respectively. The present observations support the view that the initiation and termination of regulatory drinking behaviour in slugs is controlled by specific changes in haemolymph osmotic pressure.

Water uptake during contact-rehydration

Water uptake by dehydrated slugs far exceeded that of fully hydrated control slugs (Fig. 3). The difference between the haemolymph osmotic pressures of dehydrated slugs (200 mosmol kg^{-1} H_2O) and hydrated slugs (140 mosmol kg^{-1} H_2O) could have accounted for the observed difference in water uptake. This possibility was examined by calculating the net fluxes of water that would be expected due to the two osmotic gradients. The permeability of salamander skin (11 $\mu l\,cm^{-2}\,h^{-1}$ at 200–220 mosmol l^{-1}; Bentley & Heller, 1965) and the osmotic gradients between haemolymph and distilled water (140 mosmol kg^{-1} H_2O = 3·36 atm = 340 kPa; 200 mosmol kg^{-1} H_2O = 4·81 atm = 487 kPa) were used to calculate the rates of water uptake in hydrated and dehydrated slugs. Making these assumptions, the predicted rate of water uptake in hydrated slugs was 0·12 $\mu l\,cm^{-2}\,min^{-1}$ while in dehydrated slugs it was 0·18 $\mu l\,cm^{-2}\,min^{-1}$. This 33 % difference cannot account for the large difference in water uptake during drinking (Fig. 3). Because the mean foot areas of fully hydrated and drinking slugs do not differ, one must conclude that there is an increase in the permeability of the foot epithelium during contact-rehydration. As will be shown in the following paper, inulin is absorbed through the foot during drinking, thus suggesting that water uptake may occur by bulk flow *via* an epithelial paracellular pathway.

Dual threshold control of drinking behaviour

The drinking response in *Limax* is initiated when slugs have been dehydrated to 67·6 ± 4·8 % IBW (±S.D.) and is terminated when they are rehydrated to 93·6 ± 12·2 % IBW (±S.D.). In contrast most vertebrate species drink exactly enough water to replace a deficit (e.g. Adolph, 1950; ±1·0 % IBW in rat and dog). The lack of precision in the mean rehydration set-points of many slugs may well be related to their greater tolerance to dehydration.

The existence in slugs of a threshold for drinking and a rehydration set-point suggests that drinking behaviour is regulated by a dual threshold control system which initiates the response at a lower hydration limit and terminates it at an upper hydration limit. Although the drinking threshold is rather specific (S.D. = ±4·8 % IBW), the rehydration set-point has a standard deviation of ±12·2 % IBW and a range of 69·6 to 113·9 % IBW ($N = 345$).

The refractory zone between the upper and lower limits reflects the voluntary hydration range of the slugs. Drinking was initiated only when slugs were dehydrated to about 67 % IBW, which is approaching the lethal limit (40–50 % IBW). In contrast, termination of drinking is less crucial for survival and, correspondingly, the upper limit has a broad range. In that slugs need only rehydrate to within the tolerable hydration range, the termination of drinking would require a less precise threshold than would initiation.

A more precise threshold near the 'lethal' limit is also typical of the dual threshold control of thermoregulatory shuttling behaviour in lizards (see Crawford, 1982 for a review). The range of body temperatures at which lizards left the hot side of a chamber was 42–47 °C, which is close to the upper lethal temperature (50–60 °C for *Dipsosaurus dorsalis*; Berk & Heath, 1975). In contrast, they left the cold side at 28–40 °C. Thus there was a more precise response threshold near the lethal limit than at the tolerable limit. In each case the systems respond to a near lethal stress by initiation of a regulatory response that returns the animal to within the preferred range.

In conclusion, the present observations demonstrate that drinking behaviour in slugs is a water regulatory response that is under the control of a dual threshold system. Thus the process of contact-rehydration in slugs, and perhaps other moist-skinned organisms as well, may now be viewed as a discrete and well regulated response to dehydration stress.

I wish to acknowledge Dr James Fitzsimons of the Physiological Laboratory, University of Cambridge, who taught me about the physiology of drinking during Michaelmas Term, 1980, and Dr John Treherne in whose laboratory I was a visitor when I first discovered drinking in slugs. The Blue Dextran experiment was prompted by a personal communication from Dr Ingrith Deyrup-Olsen. Fig. 1 was drawn by Ilyse Atema. I am pleased to acknowledge the facilities made available by Alan Stein and his associates at 803 South. This work was supported by the Whitehall Foundation, and an NIH-RCDA grant.

This is contribution no. 201 from the Tallahassee, Sopchoppy and Gulf Coast Marine Biological Association.

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