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WATER BALANCE AND OSMOREGULATION IN *PHYSADESMIA GLOBOSA*, A DIURNAL TENEBRIONID BEETLE FROM THE NAMIB DESERT

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Abstract—Dehydration (10 days at 26°C) of the Namib tenebrionid beetle *Physadesmia globosa* resulted in rapid weight loss (approx. 19%), and a substantial decline in haemolymph volume (61%). Although the lipid content decreased significantly during this period, metabolic water production was insufficient to maintain total body water. Rehydration (no food) resulted in increases in body weight and haemolymph volume (sub-normal), and total body water to normality. Haemolymph osmolality, sodium, potassium and chloride concentrations increased during dehydration, but despite a marked decrease in the volume of haemolymph, changes in these parameters were subject to osmoregulatory control. Protein concentrations increased during dehydration and decreased during rehydration. Rapid rehydration (1 h) is well-controlled: while haemolymph volume increased dramatically, haemolymph osmolality, sodium, potassium and chloride were strongly regulated. However, extended rehydration (over 4 days) appears not to be as well managed by *Physadesmia*, with haemolymph osmolality and sodium concentrations decreasing despite no significant change in haemolymph volume from immediate post-rehydration (1 h) values. The potassium and chloride concentrations, however, appeared to be under stricter control during this period. Drinking (when fog water is available) probably contributes largely to the total water input of Physadesmia, and this together with efficient water conservation must serve to maintain effectively long-term water balance in these insects.

Key Word Index: Water balance, osmoregulation, *Physadesmia globosa*, Tenebrionidae, Namib desert

INTRODUCTION

Arthropods of the Namib desert experience potentially severe temperature and desiccation stresses (Koch, 1960; Louw, 1972; Seely, 1978, 1983). Osmotic stress, a consequence of prolonged desiccation, may be dealt with in a number of ways. Potentially important in this regard, is the capacity for osmoregulation.

Among adult tenebrionids, capacities for osmoregulation have been examined in only a small proportion of the total number of these beetle species inhabiting xeric regions of the Old and New World (Cloudsley-Thompson and Chadwick, 1964; Jaeger, 1965). Osmoregulation was compared in three desert arthropods (Riddle *et al.*, 1976), one of which was the tenebrionid beetle *Eleodes hispilabris*. The effects of dehydration and rehydration on the haemolymph of the tenebrionid beetle *Trachyderma philistina*, have been examined by Broza *et al.* (1976), and in a similar study, Nicolson (1980) demonstrated the capacity for osmoregulation in the Namib desert beetle, *Onymacris plana*.

Water balance and osmoregulation studies have also been reported for the free-ranging Namib tenebrionid beetle, *Onymacris unguicularis* (Cooper, 1982); and, in a comparative study, for *Onymacris unguicularis*, *Onymacris rugatipennis*, and *Stenocara gracilipes* (Naidu and Hattingh, 1985). More recently, the capacity for osmoregulation was demonstrated in the strictly nocturnal, eurychorine Namib tenebrionid, *Stips stali* (Naidu and Hattingh, 1986). In the present investigation, we examine the capacity for osmoregulation in *Physadesmia globosa* (Haag), a diurnal adesmiine tenebrionid beetle from the Namib desert.

MATERIALS AND METHODS

Adult beetles were collected from a dry river bed (edge of dune field) at Gobabeb, Namibia/South West Africa. They were flown to Johannesburg, where they were kept in glass terraria partly filled with sand, in a controlled laboratory environment (28 ± 2°C; 12 h/12 h; 36 ± 7% r.h.) for 3 weeks prior to investigation. The beetles were fed fresh lettuce and oatmeal.

Both male and female beetles (weight range: 400–1400 mg; M ± SE: 641.4 ± 25.5 mg), were used for study. For dehydration, the beetles were weighed and placed in a desiccator over silica gel (10–15% r.h.), for a period of 10 days at 26°C. After this they were allowed to drink distilled water to repletion, and maintained at 50–60% r.h. for a further 4 days (drinking permitted). Insects not used in analyses by the end of the experimental period (after rehydration), were not all healthy: some were unable to right themselves when turned on their backs (Juliano, 1986).

Beetles were weighed every second day to the nearest 0.1 mg. Water content was determined by freeze-drying. Lipid content was estimated by extraction with three changes (24 h each) of a 2:1, methanol–chloroform mixture (v/v) at room temperature, with a final freeze-drying providing fat-free dry weights.

Haemolymph samples were collected from the coxa or directly from the dorsal vessel (after careful removal of the elytra) into capillary tubes. Haemolymph volume was determined according to the gravimetric method of Richardson *et al.* (1931). Individual samples were analysed for osmolality (Wescor 5120 B vapour pressure osmometer), chloride, sodium and potassium concentrations (Radiometer CMT 10 chloride titrator for chloride and FLM 3 flame photometer for sodium and potassium), and for total protein according to the method of Lowry *et al.* (1951) using bovine serum albumen as standard (Naidu and Hattingh, 1986).

Results were analysed statistically using a one-way analysis of variance and Student's *t*-test.

RESULTS

Weight changes during dehydration and rehydration

Dehydration resulted in a relatively rapid weight loss (Fig. 1). At the end of 10 days, the mean weight of the beetles had decreased by 19.4 ± 2.2% (M ± SE). Of the total weight loss, approx. 6% was due to the production of faecal material.

When allowed access to water on day 10, the dehydrated beetles drank a mean weight of approx 67 mg (about 12% of initial body weight); this, after an hour. This quantity was insufficient to restore body weight to normal ($P < 0.05$), and further rehydration (days 12 and 14) caused no significant change in this parameter—the difference in percentage body weights between day 0 and day 14 being significant at the 1% level.

Water content

In Fig. 2 is shown the water content of *Physadesmia globosa*, during the period of dehydration and rehydration, expressed as percentage of fat-free weight.

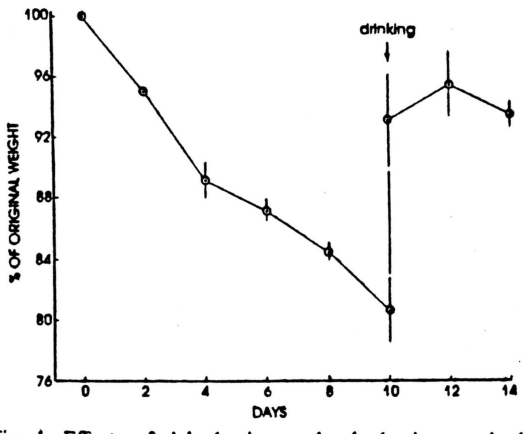

Fig. 1. Effects of dehydration and rehydration on body weight of *Physadesmia globosa*. Drinking is shown (arrow) after 10 days of dehydration. Vertical lines represent ± one standard error of the mean. $N = 5$–12.

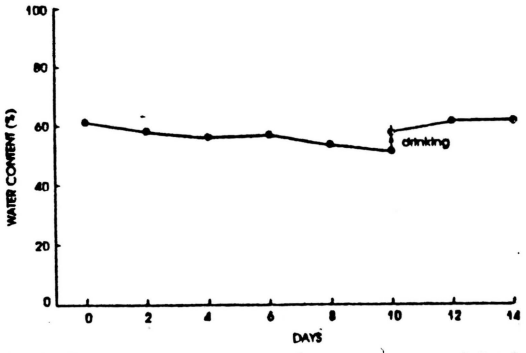

Fig. 2. Water content, expressed as percentage of fat-free weight, during dehydration and rehydration. Drinking is shown by arrow. Symbols exceed size of SEs. $N = 5$–12.

The initial water content of 61.0 ± 1.2% (day 0) dropped significantly ($P < 0.01$) during dehydration to 51.8 ± 1.2% (day 10). On rehydration, the total body water increased to the extent that values obtained on day 10 (1 h after drinking—58.0 ± 2.2%), day 12 (61.6 ± 1.1%), and day 14 (61.9 ± 1.1%), were not significantly different from the Control ($P > 0.05$).

The decrease in water content from 61.0 to 51.8% during dehydration, means that of the total weight loss of 124.4 mg (19.4% in a beetle weighing initially 641.4 mg), 19.5 mg represents a loss of dry material (of which 7.5 mg was faecal loss).

Lipid content

When the lipid content of *Physadesmia globosa*, expressed as percentage of fat-free dry weight was plotted against weight loss of individual beetles (Fig. 3), a significant negative correlation was found ($P < 0.01$), indicating that the total lipid content decreased during the period of desiccation.

Haemolymph volume

Haemolymph volume of the average beetle declined substantially during dehydration ($P < 0.01$), from 131.1 µl on day 0 to 50.8 µl on day 10 (Fig. 4).

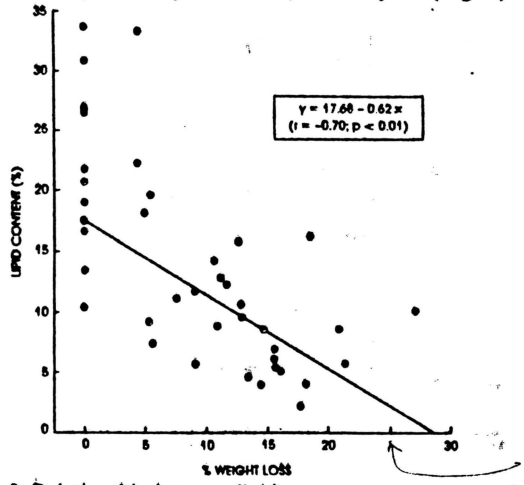

Fig. 3. Relationship between lipid content (as percentage of fat-free dry weight) and weight loss during dehydration.

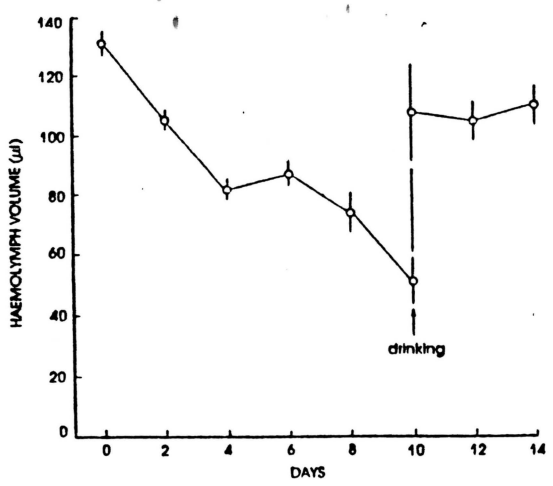

Fig. 4. Changes in the volume of haemolymph (μl) during dehydration and rehydration. The data apply to a standard animal of initial weight 641.4 mg. Drinking shown by arrow. Vertical lines indicate ± SE. $N = 5$–12.

Maximal decreases in this parameter occurred between days 0–4 and 8–10 ($P < 0.05$), with haemolymph volume remaining constant between days 4–8 ($P > 0.05$). When allowed access to water, the immediate post-dehydration haemolymph volume (day 10, 1 h after drinking) greatly exceeded that of day 10 of dehydration ($P < 0.01$), with variability between individuals also increasing. One-way analysis of variance showed that while the haemolymph volume on day 10 (1 h after drinking) was not significantly different from the Control ($P > 0.05$), volumes in the ensuing period (days 12 and 14) were significantly lower than control values ($P < 0.05$).

Estimates of tissue water were obtained by subtracting the weight of haemolymph from the total body water. Hydration of non-fatty tissues

$$\left(\frac{\text{Tissue water}}{\text{Tissue water + fat-free dry weight}}\right)$$

in beetles dehydrated for 10 days (46.4 ± 0.6%) was significantly lower ($P < 0.05$) than that for control beetles (50.0 ± 1.2%).

Haemolymph osmolality

Haemolymph osmolality (Fig. 5) increased significantly ($P < 0.01$) during dehydration, from 425.1 ± 10.3 mOsm/kg on day 0 to 641.7 ± 11.7 mOsm/kg on day 10 (51% change). Maximal increases in this parameter occurred between days 0 and 2 ($P < 0.01$) and days 8 and 10 ($P < 0.01$), with osmolality remaining fairly constant ($P > 0.05$) between days 2 and 8. After drinking (1 h), the haemolymph osmolality decreased to 446.8 ± 55.0 mOsm/kg (not significantly different from Control values), but dropped even further on day 12 (367.4 ± 17.6 mOsm/kg), and remained at this level after 4 days of rehydration (372.4 ± 10.3 mOsm/kg). The values on days 12 and 14 were significantly lower than that of the Control ($P < 0.05$).

Sodium and potassium concentrations

The effects of dehydration and rehydration on the sodium and potassium concentrations in the

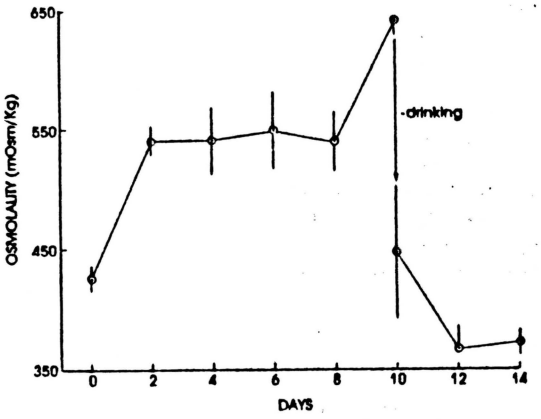

Fig. 5. Effects of dehydration and rehydration on haemolymph osmolality (mOsm/kg). Drinking shown by arrow. $N = 5$–18.

haemolymph of *P. globosa* are shown in Fig. 6. The potassium concentration appeared to be fairly well regulated during dehydration and rehydration, although values obtained during the dehydration period were significantly higher ($P < 0.05$) than the control (15.56 ± 0.85 mEq/l). Concentrations were also significantly different on day 10 ($P < 0.01$), before (29.35 ± 1.24 mEq/l) and 1 h after (20.18 ± 0.90 mEq/l) drinking. At the end of the rehydration period (day 14), the potassium concentration returned to normal (15.36 ± 0.79 mEq/l, $P > 0.05$). The sodium concentration (initially 116.33 ± 1.71 mEq/l) decreased during the first 2 days of dehydration ($P < 0.05$), and then began to increase, reaching a peak on day 10 when the level was 161.00 ± 7.24 mEq/l. When given water on day 10, the sodium concentration dropped to an approximation of normality (119.60 ± 3.80 mEq/l, $P > 0.05$), but in the ensuing period of rehydration this parameter was depressed even further (day 12—83.60 ± 3.83 mEq/l;

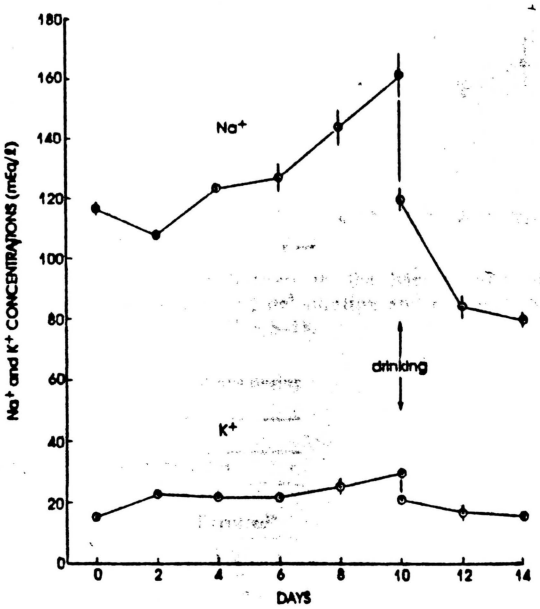

Fig. 6. The effect of dehydration and rehydration on haemolymph Na and K concentrations (mEq/l). $N = 5$–18.

day 14—79.20 ± 2.22 mEq/l). Values on these days (12 and 14) were significantly lower than Control values ($P < 0.01$).

Chloride concentration

The chloride concentration in the haemolymph of *P. globosa* (Fig. 7) increased significantly during dehydration (from 99.06 ± 1.35 mEq/l on day 0 to 160.33 ± 5.17 mEq/l on day 10, $P < 0.01$), and dropped sharply 1 h after access to water was permitted (114.60 ± 4.38 mEq/l—day 10), although still significantly higher than Control values ($P < 0.05$). While further rehydration (day 12) saw the concentration of this anion drop even lower (83.20 ± 6.78 mEq/l), this parameter was not significantly different from the Control on day 14 of rehydration (96.60 ± 3.36 mEq/l).

Protein concentration

Dehydration produced an overall increase in the haemolymph protein concentration (Fig. 8), from 3.58 ± 0.34 g/dl on day 0 to 5.18 ± 0.46 g/dl on day 10 ($P < 0.05$). The increase was neither progressive nor constant, however, with values fluctuating considerably. A tendency to increase was apparent 2 days into the dehydration period (not significant), but the concentration dropped to normal on day 4 (3.65 ± 0.55 g/dl), and remained at this level until day 8 (3.63 ± 0.22 g/dl) of the dehydration period. On day 10, the haemolymph protein concentration was significantly increased ($P < 0.05$) relative to both day 8 and day 0 values. One hour after drinking (day 10) saw a drop in the protein concentration to 3.90–0.70 g/dl ($P > 0.05$, relative to normal), but this decrease was further extended on day 12 to 2.01 ± 0.22 g/dl ($P < 0.05$, relative to control values). On day 14 of rehydration, however, the protein concentration increased to the extent that it was not significantly different from the Control (2.50 ± 0.43 g/dl, $P > 0.05$).

Haemolymph osmoregulation

The haemolymph osmolality, cation and anion concentrations found during dehydration and rehydration are not the result of simple haemolymph-concentration and -dilution: assuming that the absolute amount of solute remains constant in the haemolymph, the changes observed in these parameters are disproportionate to changes in the haemolymph volume (Tables 1 and 2). During dehydration the haemolymph volume drops from 131.1 to 50.8 µl. The osmolality during this period, however, increases from 425 to 642 mOsm/kg, and not to the 1097 mOsm/kg to be expected if the capacity for osmoregulation were not present. Similarly during rehydration (1 h after drinking), when the haemolymph volume increased to 107.0 µl, the measured value for osmolality was 447 mOsm/kg (value estimated from simple haemolymph dilution: 305 mOsm/kg).

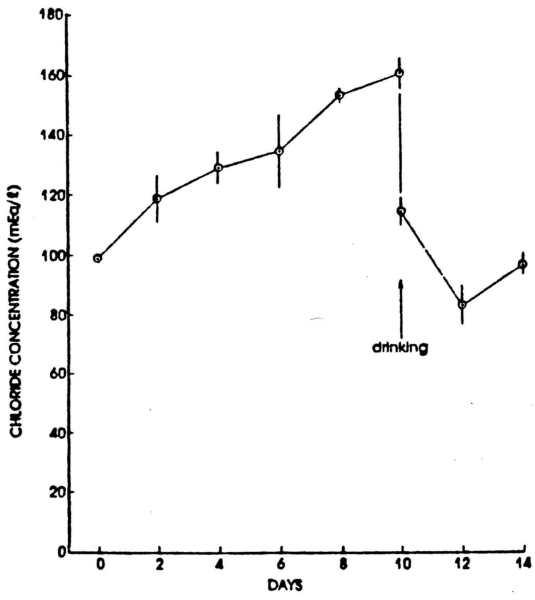

Fig. 7. Haemolymph chloride concentrations during dehydration and rehydration. $N = 5$–18.

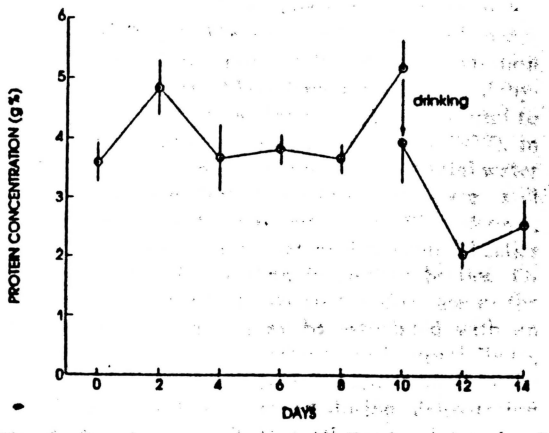

Fig. 8. Protein concentrations in the haemolymph of *Physadesmia globosa* during dehydration and rehydration. $N = 5$–18.

Table 1. Regulation of haemolymph osmolality and ionic concentrations during dehydration

	Dehydration		
	Start (Day 0)	End (Day 10)	
Haemolymph volume (µl)	131.1	Observed 50.8	Expected*
Osmolality (mOsm/kg)	425	642	1097
Sodium (mE/l)	116	161	299
Potassium (mEq/l)	15.6	29.4	40.3
Chloride (mEq/l)	99	160	255

*Increase expected from simple haemolymph concentration.

Table 2. Regulation of haemolymph osmolality and ionic concentrations during rehydration (1 h)

	Rehydration		
	Before (Day 10)	After (Day 10)	
Haemolymph volume (μl)	50.8	Observed 107.0	Expected*
Osmolality (mosm/kg)	642	447	305
Sodium (mEq/l)	161	120	76.4
Potassium (mEq/l)	29.4	20.2	14.0
Chloride (mEq/l)	160	115	76

*Decrease expected from simple haemolymph dilution.

DISCUSSION

Dehydration of *Physadesmia globosa*, over a period of 10 days at 28°C, produced a weight loss of 19.4% (weight loss on day 6—12.9%). Although not directly comparable, the weight loss of *P. globosa* appears to be higher than that recorded for most other diurnal Namib tenebrionids (Table 3). A weight loss of 22.9% has been recorded in *Trachyderma philistina*, a tenebrionid beetle of the northern Negev desert (Broza *et al.*, 1976). In this study, however, *T. philistina* were exposed to a temperature of 40°C for 5 days (0–10% r.h.). In contrast to some Namib tenebrionids examined (Edney, 1971), no significant correlation between original weight and weight loss (as a percentage of original weight) could be demonstrated for *Physadesmia globosa*.

When allowed access to water, *P. globosa* drank at an average rate of 1.1 mg/min, gaining a mean of 12% of initial body weight (measurement 1 h after drinking). However, no further increase in body weight was found with further rehydration. Rapid weight gain by drinking has also been measured in scorpions (Hadley, 1971), cockroaches (Wall, 1970; Tucker, 1977), and other desert tenebrionid beetles (Broza *et al.*, 1976; Nicolson, 1980; Naidu and Hattingh, 1986). The weight gain after drinking in *Physadesmia* shows a similar pattern to that observed by Tucker (1977) in *Periplaneta*. She found that if water alone was given, the cockroaches never regain their original weight.

The weight loss in *Physadesmia* during dehydration is not solely the result of water loss. During 10 days of dehydration the mean loss of dry weight was 12 mg (excluding faeces). At the same time the total lipid extractable with methanol–chloroform decreased from 17.5 to 5.6% fat-free dry weight (estimates from regression line, Fig. 3). This represents a decline of 27 mg (from 41 to 14 mg). Allowing for cuticular lipids, this is more than enough to account for the loss of dry weight. Thus it may tentatively be assumed that 12 mg of lipid is metabolised during dehydration, producing approx. 13 mg of oxidation water. Other insects which draw on reserve lipids during periods of desiccation are the cockroach *Periplaneta americana* (Tucker, 1977) and the tenebrionid beetle *Onymacris plana* (Nicolson, 1980). Tucker (1977) measured the lipid content of the cockroach by extraction in acetone and found a decrease from 24 to 5% dry weight in larvae dehydrated for 13 days. Nicolson (1980) obtained a decrease of from 34 to 25% in the total lipid extracted with methanol–chloroform in beetles dehydrated for 12 days. However, relatively unchanging lipid reserves during dehydration have been observed in the mature male cockroach *Blattela germanica* (Melampy and Maynard, 1937), and nocturnal tenebrionid beetle *Stips stali* (Naidu and Hattingh, 1986).

Water obtained from the oxidation of reserve foodstuffs, is an important source of water for a variety of animals with no access to water. However, as determined in this study, the percentage total water content in dehydrated animals is lower than in hydrated ones (Fig. 2). Metabolic water (by lipid oxidation) is therefore not sufficient to maintain water-balance when *Physadesmia globosa* is dehydrated for 10 days. A similar situation was found to exist for dehydrating *Periplaneta* (Tucker, 1977), in which lipid reserves decreased by 19% but total water contents of dehydrated cockroaches were still significantly lower than Controls. In *Physadesmia*, hydration of non-fatty tissues in dehydrated beetles was significantly lower than in control beetles. Of import in this regard, is that such a decrease in the tissue fluid component may be associated with an increase in tissue osmotic pressure; and, especially so, if sodium and potassium ions are sequestered in the animals general body tissues during dehydration (Wall, 1970; Tucker, 1977). In the study by Tucker (1977), uncoordinated and "spastic" movements in *Periplaneta* (particularly noticeable in one individual)

Table 3. Weight losses of diurnal Namib tenebrionids subjected to dehydration

Species	Dehydration period (days)	Temperature (°C)	Relative humidity (%)	Weight loss (% of orig. wt)	Source
O. plana	5	27	0 (nominal)	5.6	Edney (1971)
O. plana	6	26	10–15	6.4	Nicolson (1980)
O. rugatipennis	5	27	0 (nominal)	7.2	Edney (1971)
O. rugatipennis	6	27	10–15	9.4	Naidu and Hattingh (1985)
O. unguicularis	6	27	10–15	10.7	
S. gracilipes	6	27	10–15	11.1	
C. amabilis	5	27	0 (nominal)	8.8	Edney (1971)
G. moralesi	5	27	0 (nominal)	12.8	
P. globosa	6	28	10–15	12.9	This study

were attributed to such an increase in tissue osmotic pressure.

Expressed as percentage of total wet weight, the water content of *Physadesmia globosa* acclimated to laboratory conditions, is lower than that of *Physadesmia globosa* in the field (Hattingh *et al.*, 1984). Other laboratory-acclimated Namib tenebrionids show a similar trend: *O. plana* in the laboratory has a lower normal water content (Nicolson, 1980) relative to its freshly field-caught counterpart (Hattingh *et al.*, 1984). In the nocturnal tenebrionid *Stips stali* acclimated to laboratory conditions (Naidu and Hattingh, 1986), water contents are lower than in the field (Hattingh *et al.*, 1984). That water contents appear lower in the laboratory acclimated animals, may be due to these beetles being better fed and hence fattier. A greater fat content would result in a lower overall water content (percentage wet weight), because of the lower relative hydration of adipose tissue (approx. 10%).

The capacity for osmoregulation during dehydration and short-term rehydration is demonstrable in *Physadesmia globosa*. Larvae (Coutchié and Crowe, 1979), and other adult tenebrionids (Riddle *et al.*, 1976; Broza *et al.*, 1976; Nicolson, 1980; Naidu and Hattingh, 1985, 1986), also demonstrate strong regulation of haemolymph osmolality. Extended rehydration of *Physadesmia* (days 10–14), however, produced large decreases in the haemolymph osmolality, sodium, potassium and chloride concentrations, indicating that osmoregulation during prolonged exposure to an abundance of water is not strongly controlled. Haemolymph osmolality, cation and anion concentrations have also been found to be more strongly regulated during dehydration than rehydration in other tenebrionids. Stronger regulation of cations in dehydrated *O. marginipennis* larvae than in hydrated ones was noted by Coutchié and Crowe (1979); Nicolson (1980) obtained similar results with sodium concentrations in *O. plana*; and, inadequate regulation of chloride was observed in rehydrating *S. stali* (Naidu and Hattingh, 1986).

For the maintenance of haemolymph osmolality (within limits conducive to survival) during drastic changes in haemolymph volume, it would appear that osmotically active substances must be removed from the haemolymph during dehydration, and returned to it when water is taken up. Excess sodium ions have been suggested to be sequestered in the tissues of dehydrated *Periplaneta*, and these are later mobilised when the insect is able to drink (Wall, 1970). The hypothesis that the fat body is the major storage site for sodium in the cockroach has gained support from the work of Tucker (1977), and Hyatt and Marshall (1977). Free amino acids may also play a role in osmotic regulation (Djajakusumah and Miles, 1966; Broza *et al.*, 1976). Increased protein concentrations during dehydration and decreased protein concentrations during rehydration have been reported for the tenebrionid beetle *T. philistina* (Broza *et al.*, 1976) and *S. stali* (Naidu and Hattingh, 1986). In the study by Broza *et al.* (1976), a concomitant decrease in the free amino acid level was observed during dehydration, in spite of the substantial decrease in haemolymph volume. The converse was also true in that despite the increased haemolymph volume upon rehydration, the free amino acid concentration also increased. An active removal of free amino acids from the haemolymph during dehydration and quick replacement after drinking was suggested. While amino acid levels were not determined for *Physadesmia globosa*, changes in its soluble protein concentration showed a similar trend to that in the study by Broza *et al.* (1976). A role for free amino acids is also indicated in the apparently paradoxical situation on day 2 of dehydration: the haemolymph osmolality increased significantly from the control to approximately that expected from heamolymph concentration, but the sodium levels actually dropped despite the substantial decrease in haemolymph volume. Similar sodium decreases in early dehydration have been shown for other tenebrionid beetles (Nicolson, 1980; Hattingh *et al.*, 1984; Naidu and Hattingh, 1986), as well as for the cockroach (Hyatt and Marshall, 1977) and stick insect *Carausius morosus* (Nicolson *et al.*, 1974).

While haemolymph sodium concentrations in *Physadesmia globosa* return to normal and are subject to osmoregulatory control early in rehydration (1 h), this parameter was significantly lower on days 12 and 14 even though the haemolymph volume did not change significantly during this period. In the tenebrionid beetle *Onymacris plana*, sodium is well regulated during dehydration, but rehydration (water, no food) produces a sharp drop in its concentration to the extent that it does not return to normal (Nicolson, 1980). In this, and other studies on the cockroach (Wall, 1970; Tucker, 1977; Hyatt and Marshall, 1977), however, only a small proportion of the sodium removed from the haemolymph during dehydration was shown to be excreted. When rehydrating *O. plana* were given food, their sodium concentrations were found to be significantly higher—even though sodium gains from the food were quite small. Rehydrating *Periplaneta* were also shown to require food if their haemolymph sodium concentration was to return to normal (Tucker, 1977). In this regard, feeding may have been a necessary stimulus for the efficient mobilisation of sodium from storage sites in the tissues (Nicolson, 1980). The sodium concentrations in rehydrating *Physadesmia* are not easily explained. After returning to approximately normal during initial rehydration (1 h), the sodium concentration dropped substantially with extended rehydration, indicating removal of this cation from the haemolymph; this, even though haemolymph volume remained constant during this period. One possibility could be that rapid mobilisation of these ions (sequestered in body tissue) during early rehydration (haemolymph osmoregulation) results in intracellular dilution. In the ensuing period there is slow movement of sodium back into tissues producing a sodium sink in the haemolymph. In this regard, the potassium levels show a similar non-significant downward trend with prolonged rehydration. The chloride concentration also decreases substantially during extended rehydration (day 12), but returns to normal on day 14.

When confronted with desiccatory conditions, *Physadesmia globosa* exhibits much the same responses as other tenebrionid beetles: it has a powerful capacity to osmoregulate. When exposed to a relative

abundance of free water, however, *Physadesmia* displays an osmoregulatory capability which may be described as biphasic: rapid rehydration is well controlled; longer exposures to free water (4 days in this study) are not. In the Namib desert, *Physadesmia globosa* obtains water from droplets condensed on vegetation during infrequent fogs (Seely, 1979; Hattingh *et al.*, 1984). Namib fogs last for a mean duration of 3.1 ± 2.5 h, occurring between 21h00 and 12h30; after this time, all remaining free water is rapidly evaporated by the sun; Seely *et al.*, 1983). Access to continuous free water (at least over 4 days) is a phenomenon not common to fauna of the Namib desert. The inability of these beetles to handle exposure to 4 days of water (as in this study) therefore places these animals at no great disadvantage and certainly does not preclude a stable existence in the desert. On the contrary, osmoregulation in response to a sudden abundance of water, e.g. during a fog (in which a similar free fluid environment is created) would be well controlled. In *P. globosa*, water-uptake mechanisms are probably geared for indiscriminate water imbibition, i.e. regardless of state of hydration—a feature which would confer considerable advantage to an animal, in which the threat of desiccation is much more real than the threat of water intoxication.

In *Physadesmia globosa*, as in other desert animals, water balance is dependent on an optimal uptake of water, and keeping water loss to a minimum. In the laboratory, *Physadesmia* take up large volumes of water; in the field, precipitating fogs (when they occur) provide a valuable source of free water. Between fogs, water input probably occurs largely by consumption of wind-blown detritus, and metabolic water production may assume greater importance. Water loss due to excretion is low; and, since the abdominal spiracles of desert tenebrionid beetles open into the subelytral cavity and not directly to the exterior (Ahearn, 1970), respiratory water loss must be subject to some degree of control. In addition, osmoregulation (with its inherent sequestration of osmolar effectors) provides a temporal buffer for survival and longevity during periods in which these animals are in negative water balance.

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