J. Insect Physiol. Vol. 32, No. 10, pp. 891–896, 1986
Printed in Great Britain

0022-1910/86 $3.00 + 0.00
Pergamon Journals Ltd

WATER BALANCE AND OSMOREGULATION IN *STIPS STALI*, A NOCTURNAL TENEBRIONID BEETLE FROM THE NAMIB DESERT

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(*Received* 29 *November* 1985; *revised* 11 *February* 1986)

Abstract—Dehydration (6 days at 26°C) of the Namib tenebrionid beetle, *Stips stali* (Haag), resulted in weight loss (approx 7%), a drop in total body water, and a substantial decline in haemolymph volume (33%). All of these values returned to normal when access to water was permitted (day 6–day 8). Haemolymph osmolality, sodium, potassium and chloride concentrations increased during dehydration and decreased during rehydration, but despite marked changes in the volume of haemolymph, changes in these parameters were subject to osmoregulatory control. However, although the sodium and potassium concentrations had returned to normal at the end of the rehydration period, the level of chloride remained lower than normal. While changes in protein concentrations were as expected from haemolymph-concentration and -dilution, total lipid levels remained constant throughout dehydration. Over the short-term, therefore, *Stips stali* does not or cannot mobilize its lipid, and metabolic water input via this avenue appears to be negligible. Drinking (when fog water is available) probably contributes largely to total water uptake, and together with efficient water conservation, must serve to effectively maintain water balance in these insects.

Key Word Index: Water balance, osmoregulation, *Stips stali*, nocturnal, Tenebrionidae, Namib Desert

INTRODUCTION

Of the numerous and varied studies on desert tenebrionid beetles throughout the world, there is a relative paucity of information pertaining to their capacities for osmoregulation. Riddle *et al.* (1976) compared osmoregulation in three desert arthropods, 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*. Osmotic and ionic regulation have also been studied in larvae of the Namib tenebrionid *Onymacris marginipennis* (Coutchié and Crowe, 1979). More recently, water balance and osmoregulation studies have 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). In the present investigation, the capacity for osmoregulation is examined in a strictly nocturnal, eurychorine tenebrionid beetle from the Namib desert, *Stips stali* (Haag).

METHODS AND MATERIALS

Adult beetles were collected by means of pitfall traps in the Namib Desert, 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; 33 ± 9% r.h.) for 3 weeks prior to investigation. The beetles were fed fresh lettuce and oatmeal.

Both male and female beetles (92.1 ± 3.6 mg, M ± SE), 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 6 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 2 days (drinking permitted). Insects not used in analyses by the end of the experimental period, were apparently healthy.

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 directly from the dorsal vessel (after careful removal of the elytra) into capillary tubes. This was done at a time approximating that when the beetles are active on the surface of the Namib Desert sands (about 2100 h). Haemolymph volume was determined according to the gravimetric method of Richardson *et al.*, (1931). Individual samples were analysed for osmolality (Wescor 5120B 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 BSA as standard. Results were analysed statistically using a one-way analysis of variance and Student's *t*-test.

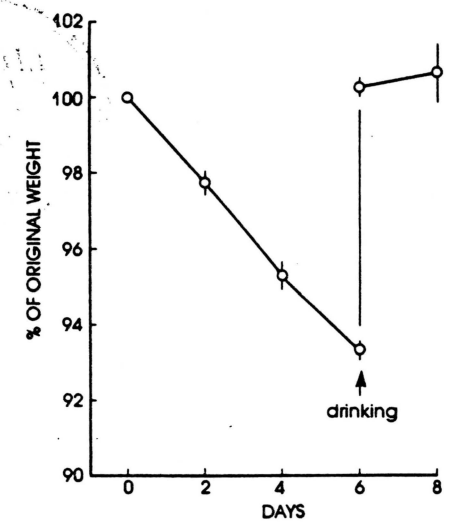

Fig. 1. Effects of dehydration and rehydration on body weight of *Stips stali*. Drinking is shown (arrow) after 6 days of dehydration. Vertical lines represent ± one standard error of the mean. $N = 12$.

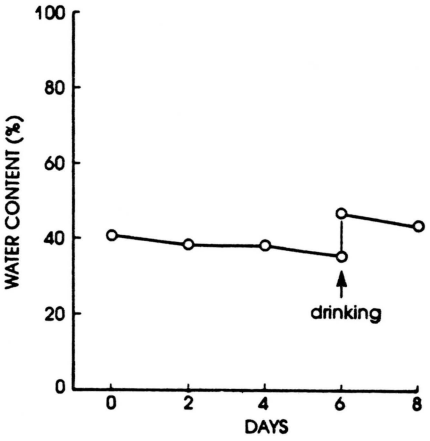

Fig. 2. Water content, expressed as percentage of wet weight, during dehydration and rehydration. Drinking is shown by arrow. Symbols exceed size of SE's. ($N = 10$–12).

RESULTS

Weight changes during dehydration and rehydration

Dehydration resulted in a slow weight loss (Fig. 1). At the end of 6 days, the mean weight of the beetles had decreased by 6.7 ± 0.2% (mean ± SE). Of the total weight loss, approx 7% (0.4 mg) was due to the production of faeces, with much of the faecal material consisting of sand grains.

When allowed access to water on day 6, the dehydrated beetles drank a mean weight of approx 6.4 mg (about 7% of initial body weight); this after 1 hour. This quantity was sufficient to restore body weight to normal.

Water content

In Fig. 2 is shown the water content of *Stips stali* during the period of dehydration and rehydration, expressed as percentage of wet weight. While low values are characteristic of insects possessing relatively heavy exoskeletons, the values obtained for control beetles in this study are lower than those obtained for *Stips stali* in the field (Hattingh *et al.*, 1984).

The initial water content of 40.8 ± 1.1% (day 0) dropped significantly ($P < 0.01$) during dehydration to 35.8 ± 0.5% (day 6). The water content 1 h after rehydration (day 6) was significantly higher than both control values ($P < 0.01$), and those on day 6 before rehydration ($P < 0.001$). On day 8, at the end of the rehydration period however, the water content was not different from the control (day 0).

Lipid content

Diminishing lipid reserves during dehydration have been reported for the cockroach *Periplaneta americana* (Tucker, 1977), and for the tenebrionid beetle *O. plana* (Nicolson, 1980). However, when the lipid content of *Stips stali*, expressed as percentage of dry weight, was plotted against weight loss of individual beetles (Fig. 3), no correlation was found ($P > 0.05$), indicating that the total lipid content remained constant throughout the period of desiccation. A similar situation was found to exist for mature male *Blattela germanica* (Melampy and Maynard, 1937), in which starvation caused little reduction in the amount of lipid.

Haemolymph volume

Haemolymph volume of the average beetle declined substantially during dehydration ($P < 0.01$), from a mean of 16.2–10.8 µl (Fig. 4). When allowed access to water on day 6, the beetles drank to the extent that their immediate post-dehydration haemolymph volume (1 h after drinking) greatly exceeded that of the pre-dehydration period ($P < 0.05$). This volume returned to normal, however, by the end of the rehydration period (day 6).

Estimates of tissue water were obtained by subtracting the weight of haemolymph from the total body water. The value for control beetles (21.3 ± 1.5 mg) was not significantly different from that for beetles dehydrated for 6 days (23.3 ± 0.9 mg).

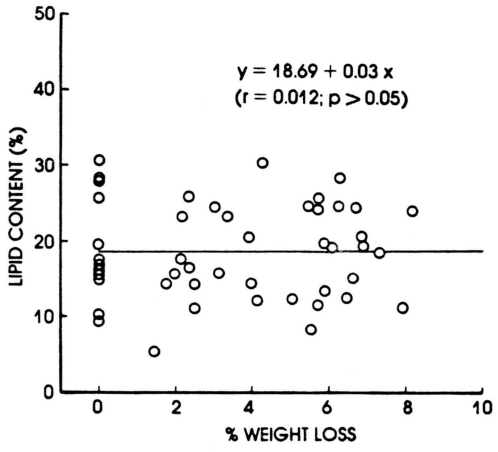

Fig. 3. Relationship between lipid content (as percentage of dry weight) and weight loss during dehydration.

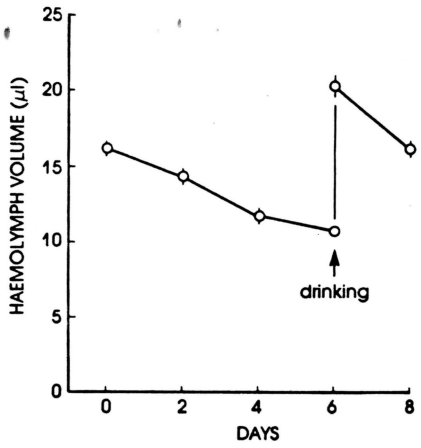

Fig. 4. Changes in the volume of haemolymph (μl) during dehydration and rehydration. The data apply to a standard animal of initial weight 92.1 mg. Drinking shown by arrow. Vertical lines indicate $\pm$ SE ($N = 10$–12).

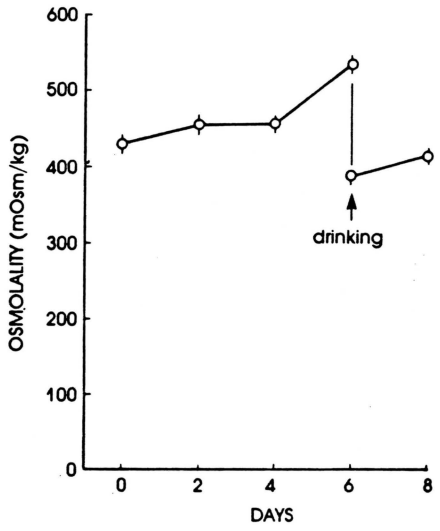

Fig. 5. Effects of dehydration and rehydration on haemolymph osmolality (mOsm/kg). Drinking shown by arrow. $N = 6$.

Haemolymph osmolality

Haemolymph osmolality (Fig. 5) increased during dehydration, differing significantly ($P < 0.01$) between days 0 and 6, the increase being from 428 ± 8 to 533 ± 15 mOsm/kg (24% change). After drinking (1 h), the haemolymph osmolality decreased to 388 ± 7 mOsm/kg, returning to its original level on day 8 (412 ± 11 mOsm/kg).

Sodium and potassium concentrations

The effects of dehydration and rehydration on the sodium and potassium concentrations in the haemolymph of *Stips stali* are shown in Fig. 6. The potassium concentration was fairly well regulated during dehydration and rehydration, although the concentration on day 6 (before being allowed access to water) was significantly higher than on day 0 ($P < 0.05$). Concentrations were also significantly different on day 6, before and after drinking ($P < 0.01$). After a further 48 h, the potassium concentration returned to 27.6 ± 2.0 mEq/l (25.6 ± 1.0 mEq/l—before dehydration).

The sodium concentration (initially 128 ± 3 mEq/l) decreased during the first 2 days of dehydration ($P < 0.05$), and then began to increase, reaching a peak on day 6 when the level was 131 ± 9 mEq/l. When given water on day 6, the sodium concentration dropped to 110 ± 4 mEq/l, returning to an approximation of normality on day 8 (120 ± 4 mEq/l, $P > 0.05$).

Chloride concentration

The chloride concentration in the haemolymph of *Stips stali* increased significantly during dehydration (from 120 ± 4 to 142 ± 6 mEq/l, $P < 0.05$), and dropped sharply when access to water was permitted on day 6 (Fig. 7). The concentration of this ion did not return to normal during the rehydration period, the difference between days 0 and 8 being significant at the 1% level.

Protein concentrations

Dehydration over 6 days produced a gradual increase in the haemolymph protein concentration (Fig. 8), from 5.8 ± 0.3 g/dl on day 0 to 8.2 ± 0.6 g/dl on day 6 ($P < 0.01$). One hour after drinking (day 6) saw a drop in the protein concentration (to 6.9 ± 0.5 g/dl), and this was further extended on day 8 (to 6.6 ± 0.4 g/dl).

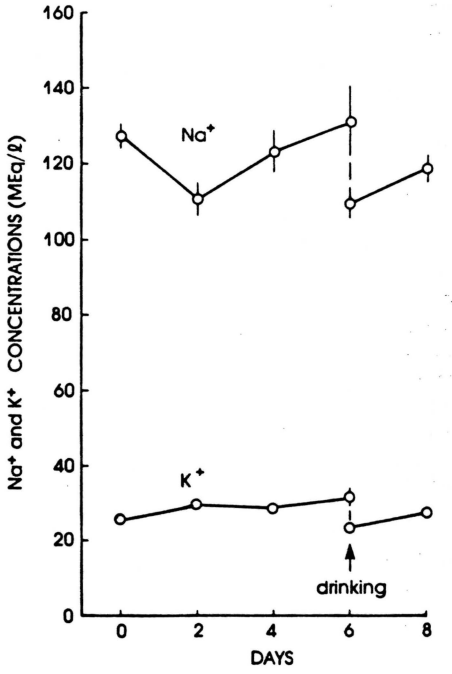

Fig. 6. The effect of dehydration and rehydration on haemolymph Na and K concentrations (mEq/l). $N = 6$.

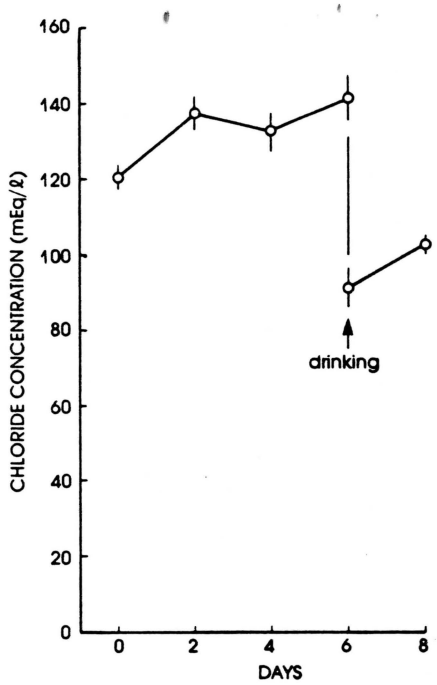

Fig. 7. Haemolymph chloride concentrations during dehydration and rehydration. $N = 6$.

DISCUSSION

Stips stali (Haag) is a nocturnal forager (Koch, 1961) that is slow-moving, short-legged and readily recognised by its flattened body and the pattern of ridges on its pronotum and elytra (Holm and Scholtz, 1980). In the central Namib Desert and Gobabeb (23°34′S, 15°03′E), it is found along the Kuiseb River bed and in the dune field to the south (living on sandy substrates at the base of small bushes and trees—Koch, 1961), but does not occur on the gravel plains to the north (Holm and Scholtz, 1980).

Dehydration of this beetle, over a period of 6 days, produced a weight loss of 6.7%. Similar losses have been recorded for other Namib tenebrionids—for *Onymacris plana*, Edney (1971) demonstrated a weight loss of 5.6% in 5 days at 27°C; for the same species, Nicolson (1980) obtained a loss of approx 6.4% in 6 days at 26°C. In a more recent study, Naidu and Hattingh (1985) showed losses of 10.7, 9.4 and 11.1%, after 6 days at 27°C in *Onymacris unguicularis*, *Onymacris rugatipennis* and *Stenocara gracilipes* respectively.

The weight loss during dehydration was rapidly corrected (about 1 h) when *Stips stali* was allowed access to water. Considering the size of this beetle and the fact that all measurements were made 1 h after drinking, *Stips stali* drank distilled water at an average rate of at least 0.11 mg/min, gaining up to 7% of b. wt. Such 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, unpublished).

While it has generally been assumed (in determinations of evaporative water loss), that weight loss during the experimental period represents water loss only (e.g. Edney, 1971), Nicolson (1980) determined that this was not true for *O. plana*. In her study, she determined that of the total weight loss, 32% constituted dry material (excluding faeces). From estimates from a lipid-weight loss regression line, it was deduced that the loss of dry weight was due to the metabolism of lipid. In *Stips stali*, however, this distinction could not be made. No significant correlation was found to exist between lipid content and weight loss (Fig. 3), indicating that *Stips stali* does not or cannot mobilize its lipid over the short-term; of the total weight lost, the drop in haemolymph represented 88% and faecal production approx 7%. Metabolic water production (by lipid oxidation) is thus negligible, and therefore cannot contribute effectively to the maintenance of water-balance, at least over the short-term. In addition, the total water content was found to remain constant throughout the period of dehydration in *Onymacris plana*, with tissular fluid increasing by 3.5% (Nicholson, 1980). For *Stips stali*, tissular fluid was found to remain constant, and the significant decrease in total water content during dehydration was accounted for by the drop in haemolymph volume and faecal water loss. In this species therefore, weight loss was due almost entirely to the loss of haemolymph and the production of faeces.

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 (total input) is therefore not sufficient to maintain water-balance when *Stips stali* is dehydrated for 6 days. On rehydration (1 h), the water content increased to a value greater than normal, but approached normality at the end of the rehydration period (48 h). In the study by Tucker (1970), on dehydrated and rehydrated *Periplaneta*, the water content (upon rehydration) increases to a value greater than normal, but returns to normal if the animal is allowed food. The cockroach kept on water and no food, however, has a higher water content than normal.

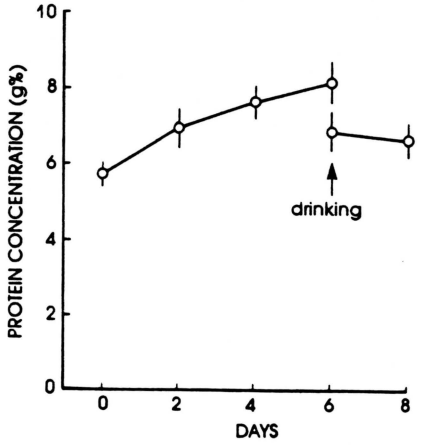

Fig. 8. Protein concentrations in the haemolymph of *Stips stali* during dehydration and rehydration. $N = 6$.

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

	Dehydration		
	Start (Day 0)	End (Day 6)	
Haemolymph volume (μl)	16.2	10.8	
		Observed	Expected*
Osmolality (mOsm/kg)	428	533	642
Sodium (mEq/l)	128	131	191
Potassium (mEq/l)	25.6	31.9	38.5
Chloride (mEq/l)	120	142	180

*Increase expected from simple haemolymph concentration.

The total water content of *Stips stali* acclimated to laboratory conditions, is lower than that of *Stips stali* in the field (Hattingh *et al.*, 1984). This may be due to the fact that in the laboratory, the beetles are not exposed to the multifaceted desiccatory conditions consistent with a desert environment, and the resulting osmotic stress that such an environment must evoke in the physiology of its fauna. Under such circumstances, and coupled with the free availability of water in the laboratory, the need to maintain a high liquid water content appears not to be a prime requisite for survival. The total lipid content of these beetles, however, may be higher (and therein the differential water reserve) than that in the field (not measured by Hattingh *et al.*).

Dehydration over the 6-day period resulted in a loss of 33.5% of the haemolymph volume. Drinking, however, rapidly replenished this volume and in fact increased haemolymph volume by 25% over control values. Haemolymph acts as a water reservoir for the tissues in many insects. Since the lipid content in *Stips stali* remained constant throughout the period of dehydration, it would appear that the haemolymph alone (without metabolic water production, at least from oxidation of lipid), ensured protection of the tissues against the effects of desiccation.

The haemolymph osmolality, cation and anion concentrations found during dehydration and rehydration are not the result of simple haemolymph-concentration and dilution: changes observed in these parameters are disproportionate to changes in the haemolymph volume (Tables 1 and 2). During dehydration the haemolymph volume drops from 16.2 to 10.8 μl. The osmolality during this period, however, increases from 428 to 533 mOsm/kg, and not to the 642 mOsm/kg to be expected if the capacity for osmoregulation were not present. Similarly rehydration (1 h after drinking), when the haemolymph volume increased to 20.3 μl, the measured value for osmolality was 388 mOsm/kg (value estimated from simple haemolymph dilution: 284 mOsm/kg). Larvae (Coutchié and Crowe, 1979), and other adult tenebrionids (Riddle *et al.*, 1976; Broza *et al.*, 1976; Nicolson, 1980; Naidu and Hattingh, 1985), also demonstrate strong regulation of haemolymph osmolality during desiccation and rehydration.

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 was 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 (Edney, 1968; Wall, 1970). Broza *et al.* (1976) demonstrated an increased protein concentration in the tenebrionid *Trachyderma philistina* during dehydration, which dropped when the animals were supplied with water. A simultaneous 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 free amino acid levels were not determined for *Stips stali*, changes in its soluble protein concentration (approximately as expected from concentration and dilution of the haemolymph) showed a similar trend during dehydration and rehydration (Fig. 8) to that in the study by Broza *et al.* (1976). A role for free amino acids in osmotic regulation is also indicated in the apparently paradoxical situation on day 2 of dehydration, when haemolymph osmolality increased significantly ($P < 0.05$) while the sodium levels actually dropped ($P < 0.05$). Similar observations have been made for other tenebrionid beetles (Nicolson, 1980; Hattingh *et al.*, 1984), as well as for the cockroach (Hyatt and Marshall, 1977) and stick insect *Carausius* (Nicolson *et al.*, 1974).

Haemolymph osmolality, sodium and potassium concentrations in *Stips stali* return to normal within 48 h of drinking. In the tenebrionid beetle *Onymacris plana*, however, while sodium is well regulated during dehydration, rehydration (water, no food) produces a sharp drop in its concentration to the extent that it does not return to normal (Nicolson, 1980). When rehydrating *Onymacris plana* were given food, however, their sodium concentrations were found to be significantly higher—even though sodium gains from the food were quite small. In this regard, the possi-

Table 2. Regulation of haemolymph osmolality and ionic concentrations during rehydration

	Rehydration		
	Before (Day 6)	After (Day 6)	
Haemolymph volume (μl)	10.8	20.3	
		Observed	Expected*
Osmolality (mOsm/kg)	533	388	284
Sodium (mEq/l)	131	110	70
Potassium (mEq/l)	31.9	23.9	17.0
Chloride (mEq/l)	142	92	75

*Decrease expected from simple haemolymph dilution.

bility was engendered that feeding may have been necessary for the efficient mobilisation of sodium from storage sites in the tissues. That sodium concentrations in *Stips stali* returned to normal during rehydration in this study could be due to the possibilities that (i) the stress of dehydration was not as severe (6 days), or (ii) feeding is not a necessary stimulus for the re-uptake of sodium from storage sites.

The chloride concentration of *Stips stali* increased during dehydration and decreased with drinking. Haemolymph dilution, upon rehydration, should have caused the concentration of this anion to drop to 75 mEq/l. That the observed concentration after rehydration (1 h) was 92 mEq/l, indicates a degree of ionic regulation. However, even after 48 h the chloride concentrations did not return to control values, indicating an apparent loss of this ion from the haemolymph. Whether all of the chloride (removed from the haemolymph during dehydration), is actually lost by excretion or sequestered in the tissues of *Stips stali* (to be later mobilised by some extraneous stimulus), must yet be determined. Feeding, in the case of the latter, could constitute one such stimulus, as was shown for the sodium ion concentration in rehydrating *O. plana* (Nicholson, 1980).

When confronted with conditions approximating desiccation and a relative abundance of water (in the Namib desert frequent occurrences of coastal fogs provide a valuable water source), *Stips stali* exhibits much the same responses as other tenebrionid beetles examined. The exception is that it does not utilize its lipid when subjected to a short-term dehydration stress. However, this does not appear to place too large a constraint on this beetle, and *Stips stali* seems well suited to its desert abode. Evaporative water loss and water loss due to excretion are 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.

Water balance in *Stips stali*, as in other desert fauna, is dependent on an optimal uptake of water when it is available, and a minimising of its water loss. Dehydrated *Stips stali* take up large volumes of water in the laboratory; in the field, fog-condensate on vegetation or sand may provide a valuable water supply. In addition, osmoregulation (with its inherent sequestration and mobilisation of osmolar effectors), and the fact that it is a nocturnal forager (utilizing conditions which ensure that the desiccatory nature of its environment is not at its most demanding), must lend greater adaptation to the xericity of the region these creatures inhabit.

Acknowledgements—We wish to thank Dr M. K. Seely, Director of the Namib Desert Research Station, without whose help this study would not have been possible. Our thanks are also due to the University of the Witwatersrand and the South African Council for Scientific and Industrial Research for financial assistance.

REFERENCES

Ahearn G. A. (1970) The control of water loss in desert tenebrionid beetles. *J. exp. Biol.* **53,** 573–595.

Broza M., Borut A. and Pener M. P. (1976) Osmoregulation in the desert tenebrionid beetle *Trachyderma philistina* Reiche during dehydration and subsequent rehydration. *Israel J. med. Sci.* **12,** 868–871.

Cooper P. D. (1982) Water balance and osmoregulation in a free-ranging tenebrionid beetle, *Onymacris unguicularis*, of the Namib desert. *J. Insect Physiol.* **28,** 737–742.

Coutchié P. A. and Crowe J. H. (1979) Transport of water vapour by tenebrionid beetles. II. Regulation of the osmolarity and composition of the haemolymph. *Physiol. Zool.* **52,** 88–100.

Edney E. B. (1968) The effect of water loss on the haemolymph of *Arenivaga* sp. and *Periplaneta americana*. *Comp. Biochem. Physiol.* **25,** 149–158.

Edney E. B. (1971) Some aspects of water balance in tenebrionid beetles and a thysanuran from the Namib Desert of southern Africa. *Physiol. Zool.* **44,** 61–76.

Hadley N. F. (1971) Water uptake by drinking in the scorpion, *Centruroides sculpturatus* (Buthidae). *SWest Nat.* **15,** 504–505.

Hattingh J., Ganhao M. and Naidu S. G. (1984) Haemolymph composition in Namib desert tenebrionid beetles. *Comp. Biochem. Physiol.* **78A,** 541–545.

Holm E. and Scholtz C. H. (1980) Structure and pattern of the Namib desert dune ecosystem at Gobabeb. *Madoqua* **12,** 3–39.

Hyatt A. D. and Marshall A. T. (1977) Sequestration of haemolymph sodium and potassium by fat body in the water-stressed cockroach *Periplaneta americana*. *J. Insect Physiol.* **23,** 1437–1441.

Koch C. (1961) Some aspects of abundant life in the vegetationless sand of the Namib Desert dunes. *Jl S.W. Africa Scient. Soc.* **15,** 8–34.

Lowry O. H., Rosenbrough N. J., Farr A. L. and Randall R. J. (1951) Protein measurement with the Folin phenol reagent. *J. biol. Chem.* **193,** 265–275.

Melampy R. M. and Maynard L. A. (1937) Nutrition studies with the cockroach (*Blattella germanica*). *Physiol. Zool.* **10,** 36–44.

Naidu S. G. and Hattingh J. (1985) Osmoregulation in some Namib Desert tenebrionid beetles. *S. Afr. J. Sci.* **81,** 397.

Nicolson S. W. (1980) Water balance and osmoregulation in *Onymacris plana*, a tenebrionid beetle from the Namib desert *J. Insect Physiol.* **26,** 315–320.

Nicolson S., Horsfield P. M., Gardner B. O. C. and Maddrell S. H. P. (1974) Effects of starvation and dehydration on osmotic and ionic balance in *Carausius morosus*. *J. Insect Physiol.* **20,** 2061–2069.

Richardson C. H., Burdette R. C. and Eagleson C. W. (1931) The determination of the blood volume of insect larvae. *Ann. ent. Soc. Am.* **24,** 503–507.

Riddle W. A., Crawford C. S. and Zeitone A. M. (1976) Patterns of haemolymph osmoregulation in three desert arthropods. *J. comp. Physiol.* **112,** 295–305.

Tucker L. E. (1977) Effect of dehydration and rehydration on the water content and Na and K balance in adult male *Periplaneta americana J. exp. Biol.* **71,** 49–56.

Wall B. J. (1970) Effects of dehydration and rehydration on *Periplaneta americana*. *J. Insect Physiol.* **16,** 1027–1042.