J. exp. Biol. 158, 439–461 (1991)
Printed in Great Britain © The Company of Biologists Limited 1991

THE FUNCTION OF SPIDER COXAL ORGANS: EFFECTS OF FEEDING AND SALT-LOADING ON *PORRHOTHELE ANTIPODIANA* (MYGALOMORPHA: DIPLURIDAE)

BY A. G. BUTT* AND H. H. TAYLOR†

Department of Zoology, University of Canterbury, Private Bag, Christchurch, New Zealand

Accepted 18 February 1991

Summary

The contributions to ionic regulation of two putative excretory systems, the gut-derived anal system and the coelomoduct-derived coxal organs, were investigated in *Porrhothele antipodiana*. Coxal fluid was produced continuously during feeding. The fluid was transported anteriorly from the openings of the coxal organs on the coxae of walking legs 1 and 3, *via* a cuticular groove on the ventral surface of the cephalothorax, to the pre-oral region. The rate of production ($70\,\mu l\,g^{-1}\,h^{-1}$) and normal composition of the fluid (Na^+ 125, K^+ 36 mmol l^{-1}) could account for the observed loss of Na^+ into the prey remains during feeding and their final enrichment with Na^+ relative to K^+. In normally feeding spiders, coxal fluid was hypo-osmotic to the haemolymph. Salt-loading of the prey induced compensatory changes in both systems. Elevation of the Na^+ or K^+ content of the prey increased anal fluid excretion, the concentration of the corresponding ion in the stercoral fluid and thus the anal output of that ion. Likewise, dietary Na^+-loading increased coxal fluid production and the $[Na^+]$ of the coxal fluid. K^+-loading of the prey did not induce a regulatory response by the coxal organs. Spiders normally released coxal fluid only during feeding. Spiders that had been fed Na^+-loaded prey produced coxal fluid intermittently for several days after the meal. Elevation of haemolymph $[Na^+]$ by injection of Na^+ into the haemocoel also induced coxal excretion in non-feeding spiders, while having little effect on the volume and composition of the anal urine.

Clearance of inulin by the coxal organs was consistent with fluid production by ultrafiltration. It is concluded that in *P. antipodiana* both systems contribute importantly to ion and water balance and both contribute to the regulatory response to ion loading.

It is postulated that the coxal organs of *P. antipodiana* have an additional

* Present address: Department of Physiology, Medical School, University of Otago, PO Box 913, Dunedin, New Zealand.

† To whom reprint requests should be addressed.

Key words: spider, Arachnida, coxal organs, excretory organ, feeding, ionic regulation, noregulation, water balance, *Porrhothele antipodiana*.

(perhaps primary) role in the mechanics of prey ingestion. Delivery of coxal fluid to the pre-oral region may facilitate the supply of predigested prey to the sucking stomach and prevent a rise in viscosity of the food by evaporative concentration. An auxiliary role for the anal urine is as a vehicle for nitrogenous excretion.

Introduction

Spiders have radiated widely in the terrestrial environment, but their physiological adaptations for osmoregulation on land have not been well studied (reviewed by Pulz, 1987). The components of salt and water balance in terrestrial animals are characterised by their variability and intermittent nature. Thus, drinking water is often available sporadically and is generally deficient in ions. Evaporative losses vary with temperature, humidity, air movements and activity. The diet is usually the main source of ions in terrestrial animals. Fluid-feeding predators, like spiders, must deal with irregular influxes of salts whose ionic composition (especially the Na^+/K^+ ratio) are expected to vary with the proportions of intracellular and extracellular fluids ingested. Therefore, an important component of hydromineral homeostasis of terrestrial animals is the capacity of the excretory organs to control the output of ions and water in the final urine.

Control of the volume and composition of the final urine is well documented for other successful terrestrial groups like insects and mammals (Maddrell, 1971; Riegel, 1972; Phillips, 1981). By contrast, knowledge of the excretory physiology of spiders is so limited that it is even uncertain which, of two distinct systems, is their principal excretory apparatus. The first, gut-derived system, consisting of the Malpighian tubules, the stercoral pocket and the midgut diverticula, has been termed the anal excretory system and produces an excretory fluid, the anal urine (Butt and Taylor, 1986). In many respects the anal system resembles the Malpighian tubule/rectal system of insects (Maddrell, 1971). Spiders also possess coxal organs (Buxton, 1913), which structurally resemble the filtration-type excretory organs of other arthropods (Lees, 1946; Woodring, 1973; Riegel and Cook, 1975; Kaufman *et al.* 1982) and are similarly derived from coelomoducts.

In *P. antipodiana*, feeding stimulated an anal diuresis which excreted most of the salts (particularly K^+) and water ingested with the meal (Butt and Taylor, 1986). However, it was also demonstrated that, during feeding, labelled Na^+ from the spider's body pool was released into the prey. The Na^+/K^+ ratio of the remains of the prey at the end of the meal was twice that of the original prey. The site of Na^+ release was not identified but was suggested to be the coxal organs. In this paper we examine further this hypothesis and also consider whether coxal fluid production should be interpreted as part of the excretory mechanism.

Extra-anal excretion of fluid and electrolytes occurs in other arachnid groups. The blood-sucking gamasid mite *Ornothonysus bacoti* (Belozerov, 1958) and the ixodid tick *Dermacentor andersoni* (Tatchell, 1967, 1969; Kaufman and Phillips, 1973) eliminate ingested fluids and electrolytes *via* the salivary glands, while the argasid tick *Ornithodorus moubata* employs coxal organs for excretion of ions an

water both during and following a meal (Lees, 1946; Kaufman *et al.* 1981). If the coxal organs produced the ions that appeared in the prey of *P. antipodiana*, the mechanism of transfer is unclear. The openings of the coxal organs are located on the coxae of the walking legs, at some distance from the mouth, but no labelled Na^+ was lost to the substratum. As spiders partially digest their prey extra-orally (Legendre, 1978; Collatz, 1987), digestive fluids, regurgitated from the midgut, must also be considered as a possible source.

The main objective of this study was to examine whether either the coxal fluid or the regurgitated midgut fluid could quantitatively account for the observed appearance of ions in the prey debris. The coxal organs are indeed shown to be functional and capable of copious emission of a Na^+-rich fluid. We also assessed the excretory function of the coxal organs in relation to that of the anal system. Two questions were of interest in this respect. First, do they make a major contribution to the total output of salts and water in normal spiders? Second, are there compensatory adjustments in the outputs of the anal and coxal systems when salt and water balance are perturbed? In this paper, the responses to dietary and injected salt-loading are reported. A subsequent paper will report the effects of desiccation.

Materials and methods

Adult female *P. antipodiana* (0.7–1.0 g) were collected from Third Bay and Whaler's Bay on the Kiakoura peninsula, New Zealand. Spiders were maintained in the laboratory, with water and cockroach nymphs supplied *ad libitum*. The cockroaches, which were fed a standard diet, were also used as prey in feeding experiments. Experiments were carried out at 20±2°C in individual borosilicate glass dishes lined with Whatman 542 filter paper, changed periodically.

The terminology used for excretory organs and fluids mostly follows that suggested by Butt and Taylor (1986). Fluid voided from the anus is termed *(anal) urine*. When it is mixed with faecal pellets it is referred to as *excreta*. Fluid collected directly from the *stercoral pocket* (analogous to the insect rectum) is called *stercoral fluid*. The stercoral fluid is presumably modified to form the urine. The term *coxal organ* is used in preference to coxal gland, although the latter appears frequently in the literature to describe these coelomoduct-derived structures. The former term is preferred because it does not imply either their mechanism of fluid production (filtration or cellular transport) or their function (excretory or secretory). Furthermore, in ticks there are additional (accessory) coxal glands which appear to have a genuine glandular structure (Kaufman and Sauer, 1982). *Coxal fluid* emerges from the apertures of the coxal organs.

Droplets of excreta which dried on the paper fluoresced and were visible as discrete spots under ultraviolet light. Daily urine production was estimated as described by Butt and Taylor (1986) from the mean diameter of these spots calibrated with known volumes of stercoral fluid. Elution in HNO_3 permitted measurement of the rates of anal Na^+ and K^+ excretion. Droplets of dried coxal

fluid were invisible and did not fluoresce. They were located by first injecting the animals with ^{22}Na and then detecting radioactive regions of the filter paper. Confusion with regurgitated fluid is unlikely since this fluid was viscous and dried to a visible residue. Spots of anal excreta were first visualised and cut out. The paper was then subdivided into small pieces which were placed in a well counter (Ortec). Regions of high ^{22}Na activity were then eluted for the ion determinations.

Haemolymph and stercoral fluid were collected and analyzed as described by Butt and Taylor (1986). Coxal fluid was collected from spiders restrained ventral side uppermost. The cuticular groove linking the coxal openings to the pre-oral region was dammed with a trace of cyanoacrylate cement and built up with dental wax. This prevented contamination of the coxal fluid with food and regurgitated fluid. Coxal fluid was collected in finely tapered siliconed Pyrex capillaries and stored briefly under liquid paraffin. The volume of coxal fluid collected was determined from the length of the column drawn into uniform-bore siliconed capillaries (10 μl Drummond Microcaps). Generally, the groove on one side only was blocked. For measurement of the excretion of [^{3}H]inulin (New England Nuclear), both grooves were occluded to prevent reingestion, and artificial coxal fluid (NaCl 120 mmol l^{-1}, KCl 30 mmol l^{-1}) was applied to the food in the pre-oral region at a rate of 1 μl min^{-1}. After coxal fluid collection, the dam was tested for leakage. Small drops of concentrated amaranth were placed in the coxal groove anteriorly and suction was applied with a capillary pipette placed in the coxal groove just posterior to the blockage. If the fluid collected was stained with amaranth, the coxal fluid sample was rejected.

Samples of regurgitated midgut fluid were collected from spiders with occluded coxal grooves which were enticed to feed on pieces of cleaned cuticle taken from freshly killed cockroaches. It was only possible to collect samples from the initial regurgitation in this manner.

Spiders were salt-loaded by allowing them to feed on salt-enriched prey. Cockroach nymphs (approx. 0.15 g fresh mass) were injected with 2 mol l^{-1} NaCl or KCl, sufficient to raise their Na^+ or K^+ contents to about 40 μmol $animal^{-1}$, an approximately threefold increase in [Na^+] or sixfold increase in [K^+]. Although injection of such large quantities of KCl usually killed the cockroaches, a spider would often feed spontaneously on the freshly dead insects, or could readily be induced to do so by brushing them against the chelicerae. The molar ratios (total Na^+:total K^+) for normal, Na^+-loaded and K^+-loaded cockroaches were approximately 0.5, 3.8 and 0.14, respectively.

Sodium-loading was also achieved by injection of 2 mol l^{-1} NaCl directly into the haemolymph of spiders (30 and 60 μmol g^{-1} animal). Injection of similar quantities of KCl was lethal and manipulation of K^+ content by this means was not pursued further. Salines were injected into the haemocoel *via* walking leg 3, as described by Butt and Taylor (1986).

Osmotic pressure measurements were made by the method of Ramsay and Brown (1955) and chloride was determined potentiometrically by the second method of Ramsay *et al.* (1955). Na^+ and K^+ were estimated by atomic absorption

spectroscopy (Varian Tectron AA1200) using an air–acetylene flame. [^{3}H]inulin activity was measured by liquid scintillation counting (Nuclear Chicago Unilux II, Phillips PW4540), employing standard procedures to correct for quenching and chemiluminescence. ^{22}Na activities were measured in using a sodium iodide well crystal (Bicron) and scaler (Ortec).

Samples for scanning electron microscopy were fixed in 2 % glutaraldehyde in a cacodylate buffer at 4 °C for 6 h, washed overnight in buffer and then post-fixed in 1 % OsO_4 for 6 h to ensure hardening. Fixed tissue was dehydrated through an alcohol series, infiltrated with amyl acetate and freeze dried. Specimens were mounted on stubs with epoxy resin, coated with a 50 nm thick layer of gold (Polaron, E 5000 Coating Unit) and viewed with a Cambridge Stereoscan 600 scanning electron microscope.

Tests of significance of differences between means were performed using either the paired or unpaired Student's *t*-tests. Means in the text and figures are given ±one standard error. Where error bars are not shown they are smaller than the plotting symbols.

Results

General observations

Spiders were lightly anaesthetized with CO_2, restrained ventral side uppermost over a plasticine ridge and observed under low magnification. After allowing 30–60 min for recovery, each was offered the abdominal contents of a freshly killed cockroach nymph. Hydrated spiders usually commenced feeding immediately. In a few cases, stimulation of the chelicerae with forceps was required to initiate feeding. As reported in other spiders (Millot, 1949; Collatz, 1987), *P. antipodiana* regurgitated fluid over its prey during feeding, flooding the pre-oral region. This occurred immediately on prey capture and at intervals during feeding. Brief periods of regurgitation alternated with periods of sustained pumping activity by the sucking stomach, and ingestion of suspended food material.

It was also observed that fluid issued copiously from the coxal apertures during feeding and that this fluid passed anteriorly to mix with the prey. Unfed spiders, restrained for 2 h, produced no coxal fluid and the openings remained closed.

Composition and origin of regurgitated fluid

That the gut was, at least partly, the source of the regurgitated fluid was verified by allowing spiders to drink the red dye amaranth (8 mmol l^{-1} in distilled water) prior to feeding. In these animals, the gut contents and the fluid that was regurgitated over the prey were coloured red. The coxal fluid in these animals was uncoloured. Samples of the regurgitated fluid, uncontaminated with food, were collected from the initial flow onto pieces of cleaned cockroach cuticle. The fluid was opaque, viscous and had Na^+ and K^+ concentrations of 128±12 and 102±10 mmol l^{-1} (N=5), respectively.

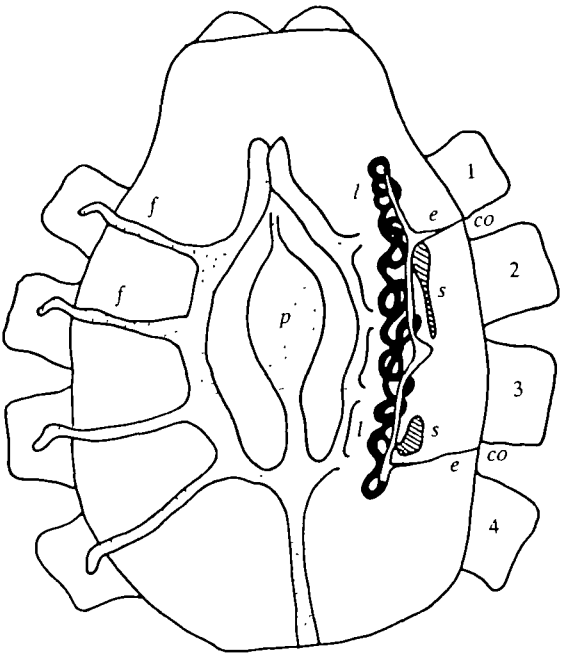
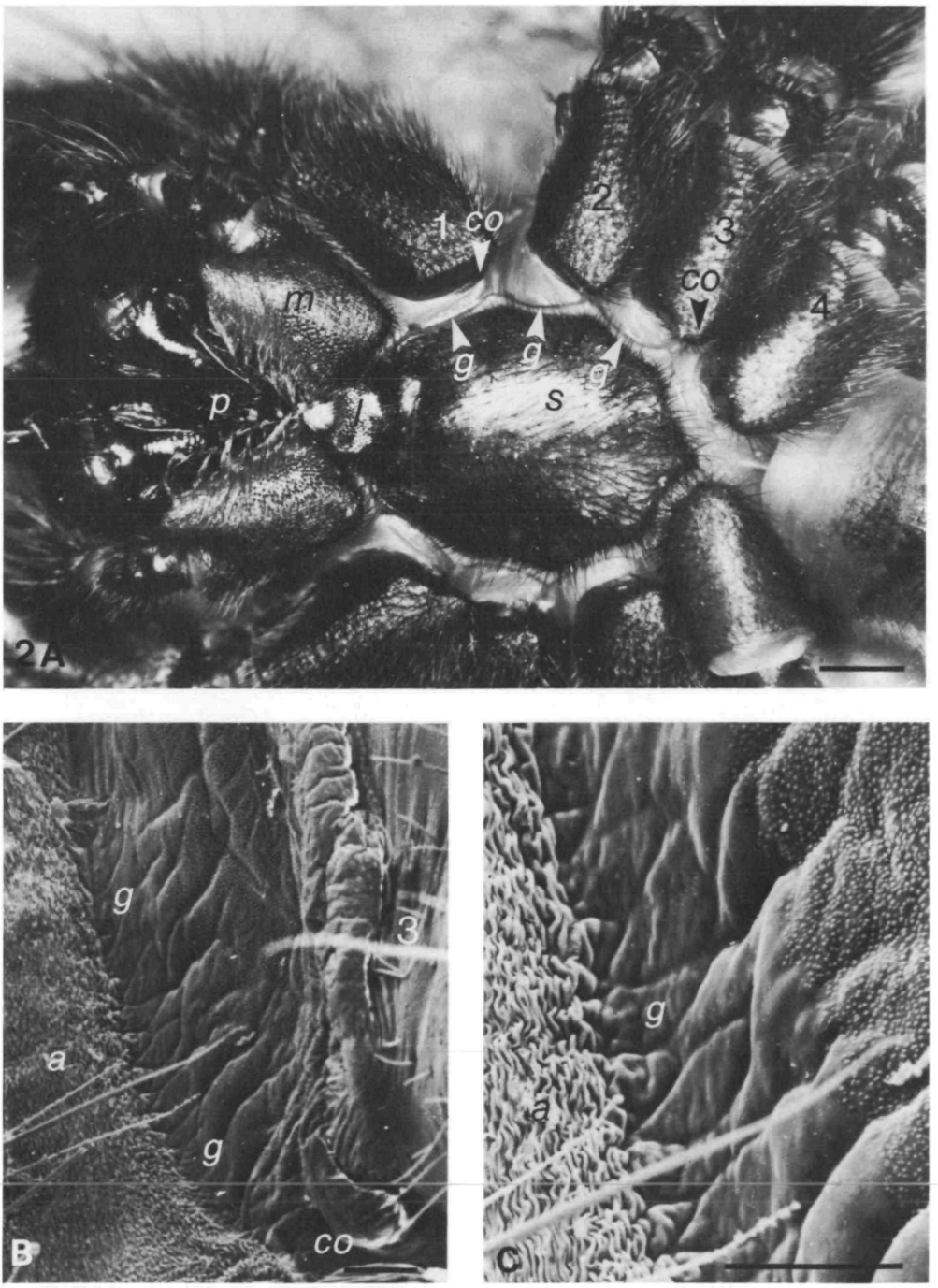


Fig. 1. Schematic diagram of the arrangement of the coxal organs in the cephalothorax of *Porrhothele antipodiana*. *e*, exit tubule; *f*, foregut diverticula; *l*, labyrinth; *co*, openings of coxal organs; *p*, pumping stomach; 1–4, coxae of legs 1–4; *s*, saccule.

Arrangement of the coxal organs

The coxal organs of *P. antipodiana* were laterally located within the cephalothorax (Fig. 1), as described for other mygalomorphs (Buxton, 1913). Their external openings were situated posteriorly on the coxae of walking legs 1 and 3, near the articulation with the sternum (Fig. 1). Coxal fluid did not accumulate near the apertures but was conducted anteriorly to the mouth *via* bilateral ventral cephalothoracic grooves running in the soft arthrodial cuticle that links the coxae to the sternum (Fig. 2A,B,C). The grooves extended from the anterior edge of walking leg 4 to the junction of the maxilla and labium, veering laterally towards

Fig. 2. (A) The ventral surface of the cephalothorax of *Porrhothele antipodiana*. A hydrophilic groove (*g*, arrows) in the soft cuticle between the sternum and coxa runs from opposite the anterior aspect of walking leg 4 to the gap between the maxilla and labium. The positions of the coxal openings on walking legs 1 and 3 are indicated (*co*, arrowheads). Scale bar, 1 mm. (B) Scanning electron micrograph showing the smooth hydrophilic cuticle in the groove in the vicinity of the coxa of walking leg 3. The groove veers towards the coxal opening (at *co*, obscured in this view) on the posterior aspect of walking leg 3. Arthrodial cuticle adjacent to the sternum is highly folded. Scale bar, 100 μm. (C) Higher magnification in the same region showing details of the cuticle in the region of the groove. Scale bar, 100 μm. *a*, arthrodial cuticle; *g*, coxal groove; *l*, labium; *m*, maxilla; *p*, pre-oral region; *s*, sternum; 1–4, coxae of legs 1–4.



the posterior aspect of each walking leg and, in the case of legs 1 and 3, leading to the coxal opening.

In scanning electron micrographs, the cuticle within the groove differed in

texture from the surrounding cuticle. On the sternal side, the arthrodial cuticle was thrown into numerous fine longitudinal folds. On the coxal side the cuticle was formed into a single wider furrow. Within the furrow the cuticle was smooth and lacked the fine stippling of the general surrounding cuticle (Fig. 2C). The base of the groove was unsculptured but the coxal side-wall possessed broad perpendicular ridges. The groove was clearly hydrophilic. Saline placed in the groove quickly spread along it, whereas similar fluid placed on the sternal or coxal cuticle remained as discrete droplets. Consequently, fluid emerging from the coxal openings flowed readily into the ventral grooves, and was transported to the pre-oral region under the combined effect of suction from the mouth and continued secretion from the coxal organs.

Amaranth powder, which was placed on the coxal openings during feeding, stained the emerging coxal fluid. Eventually, the food material in the pre-oral region also became strongly stained with the dye. As feeding and coxal fluid production continued, the intensity of the staining was reduced. On later dissection of the spider, the dye was located in the gut lumen, indicating that coxal fluid was reingested along with the meal.

Composition of the coxal fluid

Coxal fluid was collected from regularly fed spiders which were restrained and provided with a further meal to elicit its production. Restrained spiders would feed continuously for up to 50 min, allowing collection of coxal fluid from one of the four coxal openings. In contrast, consumption of the prey by unrestrained spiders took up to 3 h, during which time the spider frequently left the prey for web construction, grooming or further prey capture.

The coxal fluid was clear, colourless and without obvious suspended material. The mean rate of fluid production, per unit body mass, by single anterior openings of spiders, continuously feeding for 40 min, was $18.2 \pm 1.8\,\mu l\,g^{-1}\,h^{-1}$ (Table 1). Coxal fluid was produced simultaneously from all four coxal apertures. Fluid was collected from a posterior organ in three spiders. The mean rate of production was similar to that of anterior organs ($16.9\,\mu l\,g^{-1}\,h^{-1}$), implying a total output of about $70\,\mu l\,g^{-1}\,h^{-1}$.

Inulin, injected into the haemocoel, appeared in the coxal fluid. The mean ratio, coxal fluid:haemolymph, for [^{3}H]inulin was 1.29 ± 0.05 (Table 1). The value is significantly greater than 1.0 ($P<0.001$). Na^+ and K^+ concentrations of the coxal fluid were markedly different from haemolymph values. Na^+ concentration ($125\,mmol\,l^{-1}$) was about half, whereas K^+ ($35.6\,mmol\,l^{-1}$) was elevated about fivefold. Chloride was measured in three samples of coxal fluid and found to be the major anion (means, $N=3$: Na^+, $139.3\,mmol\,l^{-1}$; K^+ $30.2\,mmol\,l^{-1}$; Cl^-, $127.3\,mmol\,l^{-1}$). Na^+, K^+ and Cl^- accounted for about 90 % of the osmolality. In normal hydrated spiders the coxal fluid was hypo-osmotic to the haemolymph by a factor of two-thirds.

In eight spiders, the rate of formation of coxal fluid was measured at intervals during a 40 min feeding period. Fluid was released at a markedly higher rate in th

Table 1. *The rate of fluid production from single anterior coxal openings, and the osmolality and composition of the coxal fluid (CF) and haemolymph (H) collected from restrained spiders feeding continuously for 40 min on the abdominal contents of freshly killed cockroach nymphs*

		Haemolymph	
	Coxal fluid	Before	After
Rate ($\mu l\,g^{-1}\,h^{-1}$) (N=12)	18.2±1.8	–	–
Osmotic pressure (mosmol kg^{-1}) (N=12)	310±30***	460±15	468±12
Na^+ (mmol l^{-1}) (N=12)	125±13***	233±8	239±7
K^+ (mmol l^{-1}) (N=12)	35.6±2.9***	7.6±0.5	5.46±0.3†
Na^+:K^+ ratio (N=12)	3.8±0.5***	31±2	44±3†
Inulin ratio (CF:H) (N=8)	1.29±0.05	–	–

*** Coxal fluid significantly different (P<0.001) from paired haemolymph value.

† Haemolymph values after feeding significantly different (P<0.01) from value before feeding.

first 5 min (mean 26.5±3.7 $\mu l\,g^{-1}\,h^{-1}$) and declined rapidly to a steady lower rate within 10–15 min (mean during 10–20 min, 18.3±3.5 $\mu l\,g^{-1}\,h^{-1}$). This was also accompanied by a decrease in the [Na^+] of the coxal fluid (0–5 min, 138±18 mmol l^{-1}; 10–20 min, 95±18 mmol l^{-1}).

The composition of the haemolymph was measured in restrained spiders immediately before, and after, feeding (Table 1). Na^+ concentration and osmolality did not change significantly. Mean K^+ concentration decreased significantly from 7.6 to 5.46 mmol l^{-1} during feeding.

Dietary salt-loading

Ionic composition of excretory fluids and haemolymph

The compositions of haemolymph, the coxal fluid and the stercoral fluid were measured in Na^+-loaded and K^+-loaded spiders. Spiders were provided with salt-enriched prey for 12 h. Those that had successfully captured and consumed prey were restrained for collection of coxal fluid (Table 2A, control data are taken from Table 1). Stercoral fluid was collected from a separate group of spiders which were provided with, and observed to have fed upon, salt-loaded nymphs during the previous 24 h (Table 2B). Haemolymph samples were collected from all spiders after the coxal or stercoral fluid sample had been removed. Control spiders were fed normal nymphs from the same culture.

Threefold elevation of the K^+ content of the prey did not change significantly the Na^+ or K^+ concentrations of the haemolymph or coxal fluid, or the Na^+ concentration of the stercoral fluid. However, the K^+ concentration of the stercoral fluid almost doubled (statistically significant, P<0.001) from a mean of

Table 2. *The rate of fluid production by single anterior coxal openings, and the osmolality (OP) and ionic composition of the haemolymph (H), coxal fluid (CF) and stercoral fluid (SF) collected from spiders fed normal and salt-loaded prey*

A. Coxal fluid

		Rate ($\mu l\,g^{-1}\,h^{-1}$)	OP (mosmol kg^{-1})	$[Na^+]$ (mmol l^{-1})	$[K^+]$ (mmol l^{-1})	Inulin ratio, CF:H
Normal	CF	18.2±1.8	310±30	125±13	35.6±2.9	1.29±0.05
(N=12)	H		468±12	239±7	5.5±0.3	
Na^+-loaded	CF	22.6±3.2	592±52*	264±30***	21.4±1.1***	1.23±0.06
(N=6)	H		635±11***	295±9***	8.6±1.2	
K^+-loaded	CF	15.2±1.8	287±28	124±64	33.1±1.3	1.30±0.08
(N=5)	H		443±14	237±10	6.5±0.7	

B. Stercoral fluid

		OP (mosmol kg^{-1})	$[Na^+]$ (mmol l^{-1})	$[K^+]$ (mmol l^{-1})	$[Na^+]/[K^+]$
Normal	SF	504±10	34.6±8.6	125±6	0.28±0.07
(N=9)	H	515±10	226±6	4.5±0.3	
Na^+-loaded	SF		253±22***	74±5***	3.56±0.40***
(N=8)	H		293±16***	6.6±0.3***	
K^+-loaded	SF		23.2±12.5	227±23***	0.10±0.05*
(N=9)	H		216±7	4.2±0.2	

Spiders were provided with prey for 12 h (A) or 24 h (B) prior to sampling.

Significance levels are given for comparisons between spiders fed salt-loaded prey and those fed normal prey (* $P<0.05$; *** $P<0.001$).

125 to 227 mmol l^{-1}. In contrast, dietary Na^+-loading resulted in highly significant ($P<0.001$) increases in the Na^+ concentration of the haemolymph, stercoral fluid and coxal fluid. Haemolymph Na^+ concentration increased by 60–70 mmol l^{-1} in both Na^+-loaded groups (about 230 to 295 mmol l^{-1}), coxal fluid Na^+ concentration doubled (125 to 264 mmol l^{-1}) and the Na^+ concentration of the stercoral fluid increased more than sevenfold (35 mmol l^{-1} to 253 mmol l^{-1}). For both the coxal fluid and the stercoral fluid, the elevation of the $[Na^+]$ in the Na^+-loaded spiders was accompanied by a decrease in $[K^+]$. Mean $[Na^+]$ and $[K^+]$ also changed reciprocally in the stercoral fluid of K^+-loaded spiders, although in this case the decrease in $[Na^+]$ was not significant. Coxal fluid:haemolymph ratios for inulin were similar to the controls in both salt-loaded groups (Table 2A). As in the controls, coxal fluid was hypo-osmotic to the haemolymph in the salt-loaded spiders, but for Na^+-loaded spiders the difference was much less.

The time course and routes of excretion of ingested salt loads

The previous experiment showed that the composition of both stercoral and coxal fluids responded to an increased dietary salt load, suggesting an ionoregulatory role for both the anal and coxal systems. The relative importance of each route

in the excretion of excess ingested ions was further examined by measuring the quantities excreted by the two routes, during and following a meal. The ionic balance of spiders fed Na^+-loaded or K^+-loaded cockroaches was compared with that of control spiders fed prey of normal salt content. Three groups of spiders of approximately equal mean mass were used. All were injected with ^{22}Na for location of extra-anal (presumed to be coxal fluid) deposits. After 48 h of equilibration, the initial rates of anal and coxal excretion were measured and then each spider was provided with three cockroach nymphs for 24 h. The rates of anal urine production and of coxal and anal excretion of Na^+ and K^+ were determined for a further 8 days. Water was available throughout.

Urine production

As noted in a previous study (Butt and Taylor, 1986), feeding was associated with an anal diuresis. In control spiders, urine production increased from the pre-prandial value of about 10 $\mu l\,day^{-1}$ to more than 20 $\mu l\,day^{-1}$ on the day of feeding, and was elevated for 3 days before declining towards the initial value (Fig. 3A). In salt-loaded spiders, the anal urine production was similarly increased on the day of feeding but continued to rise sharply to peaks of 65 $\mu l\,day^{-1}$ (Na^+-loaded) and 79 $\mu l\,day^{-1}$ (K^+-loaded) on the day following feeding. Urine production rate then declined towards control values, but was elevated for longer in the Na^+-loaded group.

Anal Na^+ and K^+ excretion

The anal diuresis greatly increased the excretion of the corresponding salt in the salt-loaded groups. In Na^+-loaded animals, anal Na^+ excretion increased more than 30-fold to a mean of 16.0 $\mu mol\,day^{-1}$ on the day after the meal (Fig. 3B). The rate then declined but did not return to pre-feeding levels for more than 120 h after the meal. A similar pattern of anal K^+ excretion was observed in the K^+-loaded spiders, the maximum rate (18.0 $\mu mol\,day^{-1}$) coinciding with the peak in urine production before declining to prefeeding and control levels (Fig. 3C).

In the control group, the anal excretion of Na^+ and K^+ was increased during the diuresis as reported previously (Butt and Taylor, 1986). In both groups of salt-loaded spiders, there were also increases in the excretion of the cation that was not elevated in the prey (in spite of its lower concentration in the stercoral fluid), presumably reflecting the greater diuretic response in these spiders.

Coxal excretion of Na^+ and K^+

The coxal excretion of Na^+ and K^+, during and following a meal of normal or salt-loaded prey, is shown in Fig. 4. Values after the meal were determined directly by analysis of spots of coxal fluid located by the radioactivity of ^{22}Na injected beforehand. Net loss of Na^+ into the prey during the meal was estimated from the final radioactivity of the prey debris and the specific activity of the coxal fluid. For salt-loaded spiders, coxal fluid specific activity was the mean of an initial sample elicited from the posterior apertures and a sample obtained after the meal

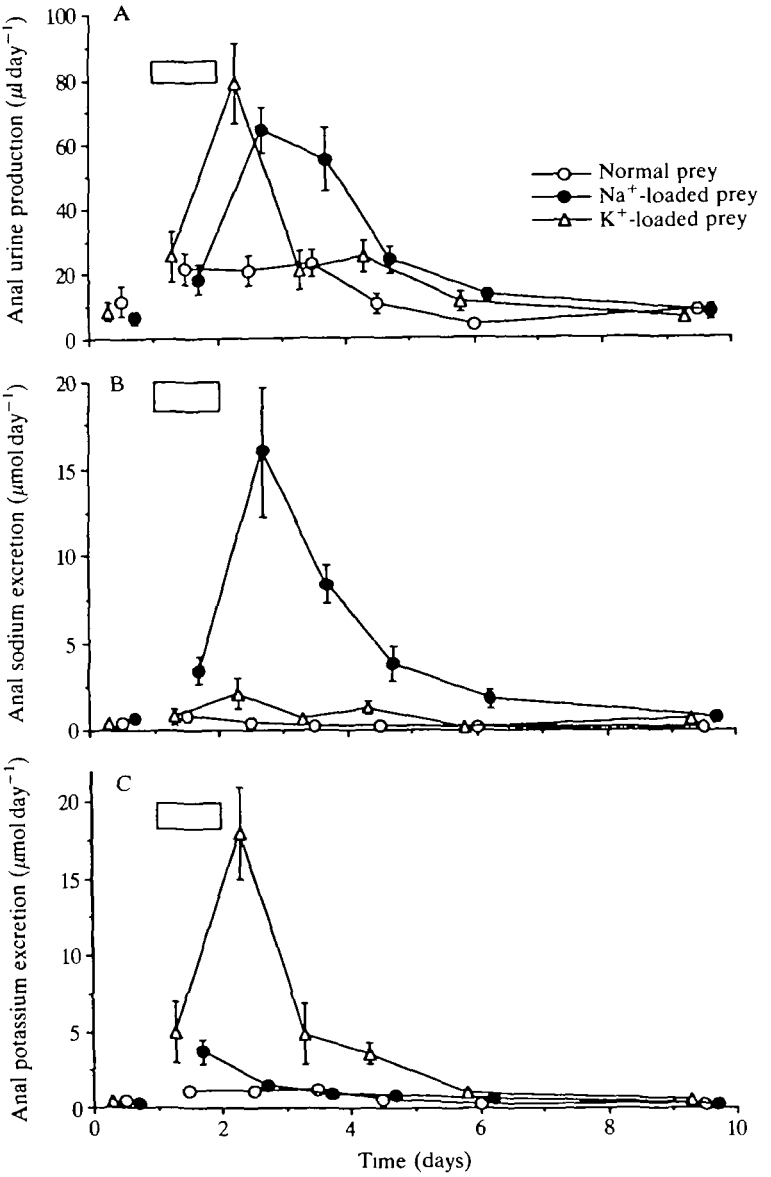


Fig. 3. The effect of a single meal on the anal excretion of urine and electrolytes by *Porrhothele antipodiana*. Spiders were provided with three live cockroach nymphs for 1 day only (indicated by horizontal bar). The nymphs were either non-injected controls or had been injected with 2 mol l^{-1} NaCl or KCl to raise total Na^+ or K^+ content to 40 μmol $nymph^{-1}$. (A) Anal excretion of urine; (B) anal excretion of Na^+; (C) anal excretion of K^+. Means±S.E.M.; N=8, 8 and 10 for normal, Na^+- and K^+-loaded, respectively; coincident points are displaced on x-axis for clarity.

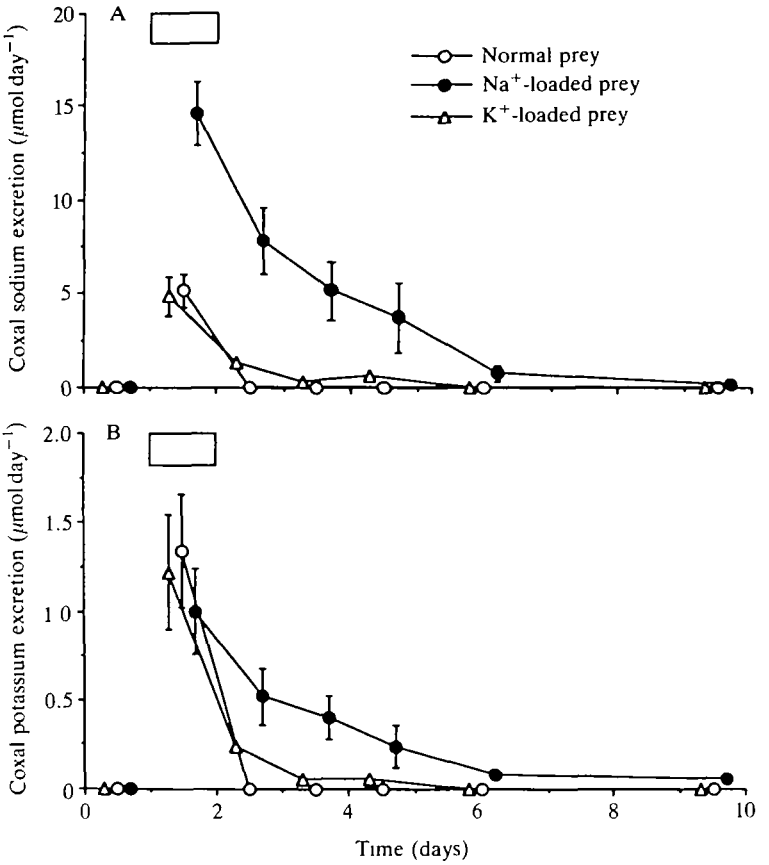


Fig. 4. The effect of a single meal on the extra-anal (interpreted as coxal) excretion of Na^+ and K^+ by *Porrhothele antipodiana*. Ion excretion during the meal (horizontal bar) was calculated from ^{22}Na loss into the prey debris. Other values were obtained by direct measurement of loss to the paper lining of the chamber. (A) Na^+ excretion; (B) K^+ excretion. Other details and *N* values as for Fig. 3.

from the paper lining the chamber. For control spiders, which did not release coxal fluid post-prandially, only the initial sample was used. Net loss of K^+ into the prey was estimated from the values for Na^+ loss and the mean Na^+/K^+ ratio of the coxal fluid samples. Note that the values for net excretion of Na^+ and K^+ into the prey are expected to underestimate total coxal excretion of these ions during the meal because some would have been reingested as feeding proceeded (Butt and Taylor, 1986).

Control spiders deposited 5.2 μmol of Na^+ from the body pool into the prey debris (Fig. 4A). No coxal excretion was detected in the period before or after the meal. Spiders fed Na^+-loaded prey increased the net excretion of Na^+ into the prey to 15 μmol. In addition, coxal fluid release continued for up to 8 days after the meal and a further 20 μmol of Na^+ was excreted *via* this route (Fig. 4A). These spiders were often observed with drops of fluid suspended from the cephalothorax

and pre-oral region after the completion of a meal. This fluid resembled coxal fluid, rather than midgut fluid, being transparent and non-viscous. At times these drops were seen to touch and be absorbed onto the filter paper lining the experimental chambers. Whether coxal fluid is normally lost in this way or reingested is unknown. The web of *P. antipodiana* is hydrophobic, and droplets like these would be less readily lost. Spiders carrying droplets were sometimes observed to ingest the fluid when disturbed. Coxal Na^+ excretion by K^+-loaded spiders was generally similar to that of controls. Small quantities of coxal fluid detected on the chamber lining after the meal accounted for a very small postprandial Na^+ loss (Fig. 4A).

Neither Na^+-loading nor K^+-loading of the prey significantly changed the estimated net K^+ excretion into the prey (Fig. 4B). As shown above (Table 2), dietary K^+-loading did not modify the composition of artificially elicited coxal fluid. However, coxal fluid production after the salt-loaded meals was responsible for an extra-anal excretion of K^+ not observed in the controls. For the K^+-loaded spiders this was very minor (0.32 μmol compared with an anal excretion of 38 μmol during the same period.)

Summary of ion balance

Table 3 summarizes estimates of the mean quantities of Na^+ and K^+ ingested,

Table 3. *A summary of the partitioning of the excretion* via *anal and extra-anal (presumed coxal) routes of Na^+ and K^+ ingested by spiders fed prey of different salt contents*

	Normal (N=8)		Na^+-loaded (N=8)		K^+-loaded (N=10)	
	Na^+	K^+	Na^+	K^+	Na^+	K^+
Total ingested	8.3	17.2	71.8	25.5	8.7	50.2
Extra-anal excretion						
During feeding	5.2	1.4	14.9	1.0	4.9	1.2
After feeding	Trace	Trace	19.6	1.2	2.1	0.3
Total	5.2	1.4	34.5	2.3	7.0	1.5
Anal excretion	2.6	7.9	37.3	10.2	3.6	38.0
Total excretion	7.8	9.3	71.9	12.5	10.6	39.5

1 day feeding plus 9 days post feeding.

All values are given in μmol.

The normal group were fed cockroach nymphs directly from the culture. The Na^+- or K^+-loaded spiders were fed nymphs injected with sufficient NaCl or KCl to raise their total Na^+ or K^+ content to 40 μmol $nymph^{-1}$. All spiders were provided with water.

Details of excretion data and S.E.M. are presented in Figs 3 and 4.

The total ingested was estimated from the measured composition of similarly treated cockroaches and their change in dry mass. The balance is interpreted as net gain or loss by the spider, although this was not measured here (see Butt and Taylor, 1986, for verification of this in normally feeding spiders).

and the quantities of each ion eliminated *via* the anal and coxal excretory systems, for the three experimental groups of spiders illustrated in Fig. 4A,B. Although coxal fluid production by control spiders was limited to the period of feeding itself, it was the major route for Na^+ excretion over the whole 10-day experimental period (67 % of the total). Conversely, the anal system was responsible for most of the K^+ excretion (86 %).

With dietary K^+-loading there was a marked increase in K^+ excretion, but this was due almost entirely to increased anal excretion (controls 7.9 μmol excreted *via* anus; K^+-loaded 38.0 μmol), the coxal organs excreting quantities similar to controls. The coxal organs of these spiders remained the major route for Na^+ excretion, eliminating 7 μmol or 66 % of the total Na^+.

Sodium-loaded spiders increased both coxal and anal excretion of Na^+. The coxal organs excreted 34.5 μmol of Na^+ during and after feeding and, although this represents only 48 % of the total, in absolute terms it was a nearly sevenfold increase over controls. Anal Na^+ excretion also increased greatly, from the control value of 2.6 μmol to 37.3 μmol.

Injected salt load

Spiders were also loaded with Na^+ by direct injection of 2 mol l^{-1} NaCl into the haemolymph (30 μmol g^{-1}, about 21 μmol per spider). Haemolymph [Na^+] was measured over the next 24 h and Na^+ excretion measured for 96 h. Haemolymph [Na^+] increased from 215 to 259 mmol l^{-1} at 1 h post-injection, and returned to pre-injection levels within 24 h (Fig. 5). A rise of about 70 mmol l^{-1} was expected from measurements of the ^{22}Na space of *P. antipodiana* (0.423±0.23 ml g^{-1}, N=5), indicating that much of the injected Na^+ was removed from the haemolymph in the first hour. Little of this Na^+ appeared in the anal excreta. In the day

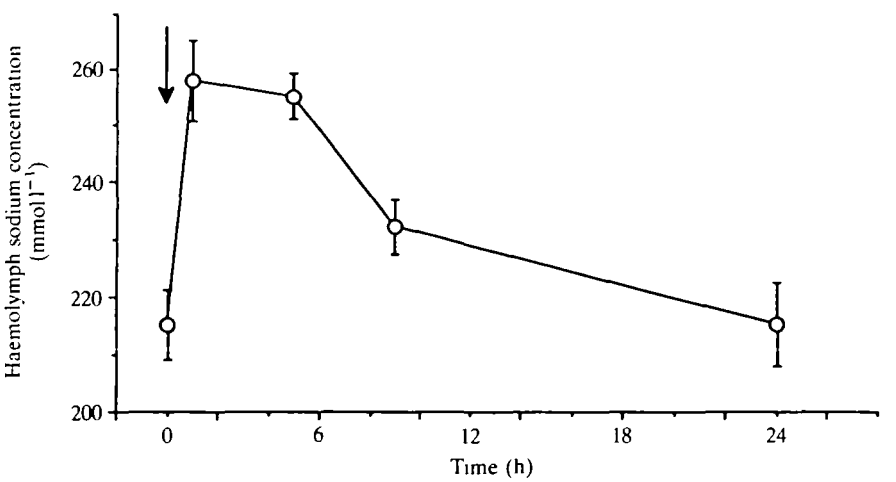


Fig. 5. Changes in the concentration of Na^+ in the haemolymph of *Porrhothele antipodiana* over 24 h following injection (arrow) of NaCl (30 μmol g^{-1}) into the haemocoel. Means±S.E.M., N=5.

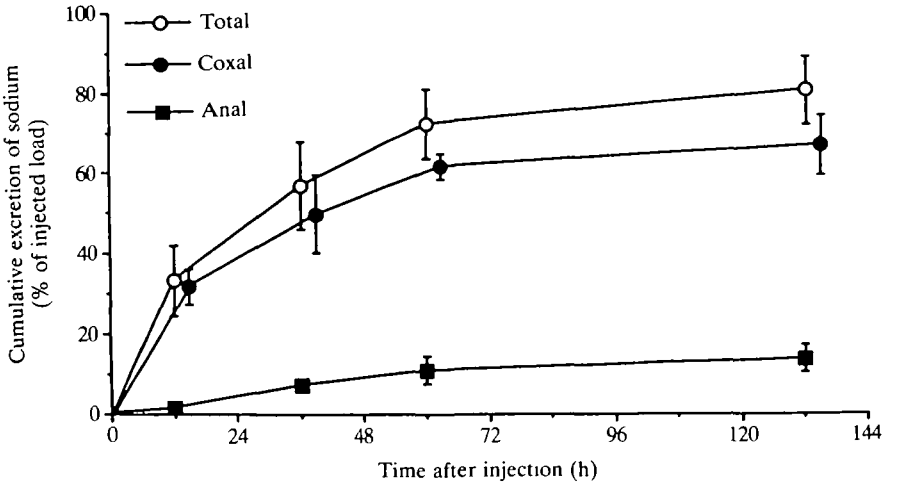


Fig. 6. Cumulative anal, extra-anal (interpreted as coxal) and total excretion of Na^+ following the injection of Na^+ ($60\,\mu mol\,g^{-1}$) into the haemolymph of *Porrhothele antipodiana*. Means±S.E.M., $N=10$.

following injection a mean of only $0.6\,\mu mol$ of Na^+ was excreted by the anal system. On the second, third and fourth days, 1.8, 0.5 and $0.5\,\mu mol$, respectively, were present in the spots of anal excreta. A total of only $3.4\,\mu mol$, about 16% of the injected load, was excreted anally.

A second injection experiment was carried out in which spiders were labelled with ^{22}Na 48 h before injection of $60\,\mu mol\,g^{-1}$ of NaCl. This facilitated location of both extra-anal (presumably coxal) and anal excretion, and allowed measurement of daily total Na^+ loss. In the 132 h following the injection, 80% of the injected Na^+ was excreted (Fig. 6). The anal excreta eliminated 13% of that injected, and the other 67% was excreted by the coxal route. These rates of Na^+ loss were based on chemical analysis of the excretory residues. Quantitatively similar results were calculated from the radioactivity of the spots and also from the loss in radioactivity of the whole spider placed in the well counter (data not shown). The highest rate of coxal excretion of Na^+ occurred in the 12 h following the injection, whereas the highest rate of anal Na^+ excretion occurred during the second day after the injection.

In contrast to an ingested salt load, no significant anal diuresis was detected after injection of Na^+. Na^+ and K^+ concentrations were measured in the stercoral fluid of four unfed spiders 24 h after injection of $60\,\mu mol\,g^{-1}$ Na^+ and in four unfed controls sham-injected with the same volume of isosmotic spider saline (Butt and Taylor, 1986). Values for the controls (Na^+, $42\pm19\,mmol\,l^{-1}$; K^+, $36\pm4\,mmol\,l^{-1}$) were consistent with data reported previously for starved spiders (Butt and Taylor, 1986). The [Na^+] was significantly elevated in the stercoral fluid of the Na^+-loaded spiders (Na^+, $104\pm24\,mmol\,l^{-1}$; K^+, $24\pm8\,mmol\,l^{-1}$), although not to the extent observed in the spiders given Na^+-loaded prey (Table 2B). Coxal fluid was not

collected directly in these experiments, so it is not known whether an increase in coxal fluid [Na^+] had occurred, like that seen after dietary salt loading.

No extra-anal loss could be detected in unfed ^{22}Na-labelled spiders injected with isosmotic saline. The rate of anal Na^+ loss was also very low in these spiders and similar to values reported previously for starved hydrated spiders (about 0.2 μmol day^{-1}; Butt and Taylor, 1986).

Discussion

In an earlier paper (Butt and Taylor, 1986), it was observed that the Na^+/K^+ ratio of the prey of *P. antipodiana* changed from about 0.5 to 1.0 during the course of feeding. Based on the decrease in dry mass of the prey (65 %) during a single meal it was calculated that the spiders (0.8 g mean fresh mass) would have ingested about 7.0 μmol of the prey Na^+ and 14.7 μmol of K^+. As much of the dry matter in the prey remains is probably cuticle, these values are expected to be underestimates. In fact, the decrease in ion content of the prey items was only 2.5 μmol of Na^+ and 14.2 μmol of K^+. Selective extraction of K^+ was discounted and it was hypothesised that a fluid containing a high Na^+/K^+ ratio was conveyed into the prey as feeding progressed. This was supported by the appearance in the prey of radioactively labelled Na^+ from the spider's pool at a rate of 3 μmol g^{-1} h^{-1}.

The data presented here also support this contention. Coxal fluid, collected directly from normally fed spiders, was richer in Na^+ than K^+ (Na^+, 125 mmol l^{-1}; K^+, 36 mmol l^{-1}) and was conducted into the neighbourhood of the prey *via* a specialized cuticular groove. The total rate of coxal fluid production from all four organs was about 70 μl g^{-1} h^{-1}, implying rates of Na^+ excretion of up to 9 μmol g^{-1} h^{-1}. Even allowing that feeding may be discontinuous and that a quantity of the ions entering the prey from the spider might be reingested, it is apparent that coxal fluid production could account for the enrichment of the prey with Na^+. The extent of the recycling of coxal fluid *via* the mouth is difficult to estimate with precision. The present estimates of the potential rates of Na^+ secretion, and the observations of ingestion of the dye amaranth, suggest that it may be the major fraction.

It was also observed that *P. antipodiana* regurgitated digestive fluid during feeding. Clearly this could also contribute to the delivery of ions into the prey. This fluid is probably a combination of the ingested contents of the midgut and foregut, digestive fluid secreted by the midgut diverticula and small quantities of fluid produced by the gnathocoxal acini (Legendre, 1978). Although digestive fluid was excreted over the prey throughout feeding, its initial composition (128 mmol l^{-1} Na^+ and 102 mmol l^{-1} K^+) could not account for the relative enrichment of the prey with Na^+. The secretion of venom is unlikely to influence greatly the ionic composition of the prey. Minute volumes are released (Butt, 1983; Pulz, 1987) and, in *Tegenaria*, the fluid is enriched with K^+ rather than Na^+ (Collatz, 1987).

The midgut fluid of other spiders contains enzymes concerned with the extra-oral digestion of the prey (Comstock, 1940; Legendre, 1978) and it is likely that this too is the case in *P. antipodiana*. However, coxal organ activity has not previously been reported in spiders. Indeed, Millot (1949) proposed that the coxal organs of spiders are obsolete, their excretory function having been taken over by the Malpighian tubules. It is therefore important to establish the circumstances under which coxal fluid is produced in other species. The evidence for the release of coxal fluid over the prey of *P. antipodiana* now appears unequivocal. We also interpret the radioactive spots which appeared on the filter paper lining of the chambers, when the animal was not feeding, as originating from the coxal organs. Direct evidence for this is lacking, as is a plausible alternative. Spiders which produced these invisible salty spots often carried clear droplets ventrally on the cephalothorax. Coxal fluid collected directly and spotted on the paper was similarly invisible, whereas dried midgut fluid and anal fluid both left distinct residues. For *P. antipodiana*, it is unclear whether the function of the coxal organs relates primarily to the mechanics of feeding, or to excretory regulation, or to both. These issues will be elaborated below.

Excretory function has many aspects. The coxal fluid of *P. antipodiana* does not appear to contribute significantly to nitrogen excretion. It was shown elsewhere (Butt, 1983) that its protein content was low ($0.6\,g\,l^{-1}$), and that guanine, although abundant in the stercoral fluid of *P. antipodiana* (Butt and Taylor, 1986), was undetectable in the coxal fluid. Urea, uric acid, hypoxanthine and xanthine, nitrogenous metabolites found in the anal excreta of other spiders (Anderson, 1966), were also undetectable. Thus, nitrogen excretion appears primarily to be a function of the anal excretory system (Butt and Taylor, 1986).

Regulation of water balance is also a function of excretory organs. The production of coxal fluid during the meal is, in effect, a diuresis similar to the anal diuresis that also accompanies the meal (Butt and Taylor, 1986; present study). As discussed elsewhere (Butt and Taylor, 1986), these responses are unlikely to be adaptive to the maintenance of water balance and volume regulation. The small quantity of water gained from the prey, together with evaporative losses, is such that water conservation rather than excretion would normally be necessary. Unlike many insects, *P. antipodiana* was unable to produce a final anal urine hyperosmotic to the haemolymph and it was inferred that the spider needed to drink to support this diuresis. Drinking would also be required to replenish loss of the normally dilute coxal fluid. It was proposed that the main function of the anal diuresis is to provide a vehicle for excretion of ingested ions. The coxal fluid might also function in this way, as discussed below.

The primitive function of coelomoduct-derived excretory organs was considered to be osmotic and ionic regulation (Goodrich, 1945; Barrington, 1967; Clarke, 1979). This function is retained in many present-day arthropods, e.g. the coxal organs of the arachnids *Limulus polyphemus* (Mangum and Mauro, 1980; Towle *et al.* 1980), argasid ticks (Lees, 1946; Frayha *et al.* 1974; Kaufman *et al.* 1981) and orbatid mites (Woodring, 1973) and the antennal and maxillary organs of some

Crustacea (Parry, 1955; Riegel and Cook, 1975). *A priori*, at least one of two criteria must be satisfied by a putative excretory organ concerned with ionic regulation. First, the total output of an ion should be quantitatively important in relation to its turnover. Second, a change in the conditions for ion balance should elicit a regulatory change in output. The coxal organs appear to qualify as ion-excreting organs on both counts.

Clearly in *P. antipodiana* the coxal fluid was an important route for the elimination of ions, particularly Na^+. Although spiders that fed on normal cockroaches produced coxal fluid only during the meal, this was responsible for the excretion of about 63% of the ingested Na^+ and 8% of the ingested K^+ (Table 3). In terms of total ion excretion (coxal and anal) in the 9-day period that included the meal, these values correspond to 67% of the Na^+ and 15% of the K^+. A more detailed analysis of ion balance, which also measured quantities retained by the spider (Butt and Taylor, 1986), was also consistent with this interpretation.

The responses of the coxal organs to dietary salt-loading were consistent with an ion regulatory function, particularly in relation to Na^+. Increased excretion of Na^+ was achieved by elevating the Na^+ concentration in the coxal fluid and by extending its release into the period after the meal (Tables 2, 3; Fig. 4). In fact, the post-prandial release accounted for the major proportion (about 20 μmol) of the increase in coxal Na^+ output (about 30 μmol, Table 3). The effectiveness of the coxal organs in regulation of haemolymph $[Na^+]$ was most apparent after direct injection of Na^+ into the haemocoel. In these spiders, the coxal organs were responsible for elimination of 67% of the injected Na^+ and 84% of the total Na^+ excretion in the 7 days following the injection.

The regulatory response was not restricted to the coxal organs. Anal excretion of Na^+ was increased in the Na^+-loaded spiders. The anal and coxal increases accounted for more or less equal shares of the ninefold rise in Na^+ output. In K^+-loaded spiders, the anal system was entirely responsible for the additional K^+ excretion. The mean total volume of urine produced in 4 days during and following a single meal (Fig. 3A) was 99 μl, close to the value of 93 μl reported previously (Butt and Taylor, 1986). The larger volume of urine produced after consumption of Na^+- and K^+-loaded prey (about 200 μl in both cases) was larger than the quantity of water present in the prey and supports the idea advanced above (and Butt and Taylor, 1986) that the post-prandial diuresis is mainly concerned with salt excretion rather than with volume regulation.

The ionoregulatory responses of the coxal organs appear to be mainly concerned with Na^+. Elevation of $[K^+]$ in the diet had no marked effect on the composition of the coxal fluid or on ion elimination by this route (Tables 2A, 3; Fig. 4A,B). In contrast, the anal system showed clear regulatory responses to both Na^+- and K^+-loading of the prey (Table 2B; Fig. 3A,B). The Na^+/K^+ ratio of the stercoral fluid was capable of being varied by a factor of more than 35, reversing the preponderance of K^+ in the excreta after a normal meal. As with the coxal system, the anal system reacted more strongly to dietary Na^+-loading than to K^+-

loading. In these experiments, the mean $[Na^+]$ of the stercoral fluid varied more than 11-fold (23–253 mmol l^{-1}) whereas $[K^+]$ varied only threefold (74–227 mmol l^{-1}). The adaptive significance of this differential handling of the two cations is unknown. The range of *P. antipodiana* covers the coastal regions including the supralittoral zone. It is reasonable to suppose that Na^+-enriched prey animals and precipitation might be encountered quite frequently. In addition, disturbance of a spider during a meal might lead to its ingestion of a greater proportion of the Na^+-rich extracellular fluids of the prey than the K^+-rich intracelluar fluids. Situations that might lead to ingestion of prey greatly enriched in K^+ seem less likely.

The appearance of the filtration marker inulin in the coxal fluid is consistent with formation based on ultrafiltration. Relatively high haemolymph pressures, which are a prerequisite for ultrafiltration, have been reported in some spiders (Parry and Brown, 1959). The site of ultrafiltration is assumed to be the saccule, which has a structure resembling that of known ultrafiltration sites (Buxton, 1913; Kummel, 1973). Ultrafiltration has also been demonstrated in ticks (Kaufman *et al.* 1982), scorpions (Rasmont, 1958) and orbatid mites (Woodring, 1973). Assuming that inulin was freely filtered, and neither secreted nor reabsorbed by the coxal organs, the observed coxal fluid:haemolymph (CF:H) ratio of 1.29 suggests that about 20–30 % of the filtered water was secondarily reabsorbed. However, these assumptions were not tested in the present study. The antennal organs of the crab *Holthuisana transversa* reabsorb inulin (Greenaway, 1981) and, if this occurred in the coxal organ, water reabsorption would be underestimated. Conversely, Riegel *et al.* (1974) demonstrated that clearance ratios greater than 1.0 could be produced, in the absence of water reabsorption, by lag effects. However, as the coxal organs of *Porrhothele* lack a bladder, such effects are likely to be minor.

In normally feeding spiders, the final coxal fluid was hypo-osmotic to the haemolymph, its ionic composition suggesting secondary reabsorption of Na^+ and secretion of K^+. As the inulin CF:H ratio did not change significantly in Na^+-loaded spiders, it is concluded that the rise in $[Na^+]$ of their coxal fluid resulted from a reduction in the intensity of this reabsorption. Reciprocal changes in $[Na^+]$ and $[K^+]$ in the coxal fluid, and also in the stercoral fluid (Table 2A,B), suggest that the transport of these two ions might be partially linked.

Coxal organ activity clearly made an important contribution to ion homeostasis in all of the situations we examined. It is concluded that these organs should properly be considered as excretory. A strong case may also be made that a major function of coxal fluid release relates to the mechanics of feeding (a secretory, rather than excretory, role), although the evidence is more circumstantial. This hypothesis is supported by its release only during active consumption of the prey in normal spiders which lacked a salt load, and by the cuticular groove that transports the fluid forward to the mouth during feeding. Transport to the mouth and reingestion appear inconsistent with a primarily excretory role. Direct release to the substratum, as in fact occurred in the salt-loaded spiders, would better satisfy

the needs of salt balance. Although *P. antipodiana* is a fluid feeder, it is unable to make an overall gain of water from the prey (Butt and Taylor, 1986). The evaporative losses of recycling the fluid externally from the coxae to the mouth would be expected to exacerbate problems of water conservation. Similarly, the elimination of a dilute fluid in normal spiders, rather than isosmotic initial ultrafiltrate, did not optimise the elimination of ions and the conservation of water.

Extra-anal excretion of fluid and electrolytes occurs in other arachnids, and in the argasid ticks the coxal fluid is released to the exterior, rather than into the host (Kaufman *et al.* 1981, 1982). However, the ixodid tick *Dermacentor andersonii* excretes a Na^+-rich fluid back into the host *via* salivary glands (Kaufman and Phillips, 1973). In this case, the relative sizes of the predator and the vertebrate host ensure that most of the water and electrolytes that are delivered into the host are not reingested and are thus effectively excreted.

The role of coxal fluid secretion in the feeding of *P. antipodiana* must be related to the fact that it is a sucking predator, which partially digests the prey extra-orally. The resulting slurry is ingested by suction generated in the pumping stomach and oesophagus (Legendre, 1978; Collatz, 1987). We propose that the coxal fluid serves as a kind of saliva, which suspends the partially digested food material and maintains its fluidity in the face of a tendency for concentration by evaporation. In the crab spider *Diaea* it was concluded that evaporation from the prey during digestion provided an important constraint on the transfer of food from the prey to the spider, because of a progressive increase in the viscosity of the food (Pollard, 1988, 1989). *Diaea* appeared to reduce the rise in viscosity of the food during digestion by cycling between sucking and relaxation phases of the pumping stomach. The liquefied prey was alternately aspirated into the stomach, to be mixed with more digestive fluid from the midgut, and returned to the intact exoskeleton of the prey.

P. antipodiana, in contrast, macerated its prey to a fine paste, presumably permitting more efficient extraction of nutrients, but also risking greater desiccation of the food. An ultrafiltrate containing low concentrations of proteins and other solutes is better suited than midgut fluid for replenishment of evaporative water loss from the prey. Dehydration of coxal fluid would contribute negligibly to an increase in viscosity, whereas in *P. antipodiana* the enzyme content of the midgut fluid rendered it visibly viscous even as it was secreted.

The role of the coxal fluid in feeding should be examined in other spiders, particularly in those groups that macerate their prey. In primitive mygalomorphs, like *P. antipodiana*, the coxal organ on each side consists of two saccules, an extensive tubular labyrinth and two outlets. In the more advanced spiders there has been a reduction in the complexity of the coxal organs and concentration of the remaining elements in the anterior cephalothorax (Buxton, 1913). In Araneae, only the anterior saccule has been retained and there has been a progressive reduction and simplification of the labyrinth until, in the advanced web-spinning spiders, the labyrinth is reduced to a simple bladder. The possibility that in at least

some of the Araneae the salivary role of the coxal organs has further developed at the expense of the excretory function deserves investigation.

A further interesting possibility is that the coxal organs might sometimes be involved in evaporative thermoregulation. There are several reports that, under conditions of short-term heat load, spiders may extrude and manipulate a droplet of fluid in the region of the mouth (reviewed by Pulz, 1987). The fluid, which may be later reingested, was thought to originate from the gnathocoxal glands or the mouth but, in the light of the present observations, it might also be coxal fluid.

References

ANDERSON, J. F. (1966). The excreta of spiders. *Comp. Biochem. Physiol.* **17**, 973–982.

BARRINGTON, E. J. W. (1967). *Invertebrate Structure and Function*. London: Thomas Nelson & Sons.

BELOZEROV, U. N. (1958). Influence of humidity on *Ornithonyssus bacoti* mites Parasitiformes, Liponyssidae). *Ent. Rev.* **37**, 36–49.

BUTT, A. G. (1983). Salt and water balance of the spider *Porrhothele antipodiana* (Mygalomorpha, Dipluridae). PhD thesis, University of Canterbury, Christchurch, New Zealand, 185pp.

BUTT, A. G. AND TAYLOR, H. H. (1986). Salt and water balance in the spider *Porrhothele antipodiana* (Mygalomorpha: Dipluridae): effects of feeding upon hydrated animals. *J. exp. Biol.* **125**, 85–106.

BUXTON, B. H. (1913). The coxal glands of arachnids. *Zool. Jahrb. (Suppl.)* **14**, 231–282.

CLARKE, K. U. (1979). Visceral anatomy and arthropod phylogeny. In *Arthropod Physiology* (ed. A. P. Gupta), pp. 467–549. New York: Van Nostrand Reinhold Co.

COLLATZ, K.-G. (1987). Structure and function of the digestive tract. In *Ecophysiology of Spiders* (ed. W. Nentwig), pp. 229–238. Berlin, Springer-Verlag.

COMSTOCK, J. H. (1940). *The Spider Book* (revised and edited by W. J. Gersch). New York: Doubleday, Doran & Co. Inc.

FRAYHA, G. J., DAJANI, R. M., ALMAZ, O. AND SWEATMAN, G. K. (1974). Chemical composition of the coxal fluid of the argasid tick, *Ornithodorus savignyi*. *J. med. Ent.* **11**, 168–172.

GOODRICH, F. S. (1945). The study of nephridial and genital ducts since 1895. *Q. Jl microsc. Sci.* **86**, 113–342.

GREENAWAY, P. (1981). The fate of glomerular filtration markers injected into the haemocoel of the amphibious crab *Holthuisana transversa*. *J. exp. Biol.* **91**, 339–347.

KAUFMAN, S. E., KAUFMAN, W. R. AND PHILLIPS, J. E. (1981). Fluid balance in the argasid tick, *Ornithodorus moubata*, fed on modified blood meals. *J. exp. Biol.* **93**, 243–256.

KAUFMAN, S. E., KAUFMAN, W. R. AND PHILLIPS, J. E. (1982). Mechanism and characteristics of coxal fluid excretion in the argasid tick, *Ornithodorus moubata*. *J. exp. Biol.* **98**, 342–352.

KAUFMAN, W. R. AND PHILLIPS, J. E. (1973). Ion and water balance in the ixodid tick, *Dermacentor andersonii*. I. Routes of ion and water excretion. *J. exp. Biol.* **58**, 523–536.

KAUFMAN, W. R. AND SAUER, J. R. (1982). Ion and water balance in feeding ticks: mechanisms of tick excretion. In *Physiology of Ticks* (ed. F. D. Obenchain and R. Galun), pp. 213–244. Oxford: Pergamon Press.

KUMMEL, G. (1973). Filtration structures in excretory systems. A comparison. In *Comparative Physiology: Locomotion, Respiration, Transport and Blood* (eds. L. Bolis, K. Schmidt-Nielsen and S. H. P. Maddrell), pp. 221–240. Amsterdam: North-Holland.

LEES, A. D. (1946). Chloride regulation and the function of the coxal glands in ticks. *J. exp. Biol.* **23**, 379–410.

LEGENDRE, R. (1978). Quelque progrès recént concernant l'anatomie des Araignées (Système nerveux sympathique et appareil digestif). *Symp. zool. Soc., Lond.* **42**, 379–388.

MADDRELL, S. H. P. (1971). The mechanisms of insect excretory systems. *Adv. Insect Physiol.* **6**, 199–331.

MANGUM, C. P. AND MAURO, N. A. (1980). The role of the coxal gland in *Limulus polyphemus*. *Am. Zool.* **20**, 770.

MILLOT, J. (1949). Order des Araneides (Araneae). In *Traité de Zoologie*, vol. 6 (ed. P. P. Grasse), pp. 588–743. Paris: Masson et Cie.

PARRY, D. A. AND BROWN, R. H. J. (1959). The hydraulic mechanism of the spider leg. *J. exp. Biol.* **36**, 423–433.

PARRY, G. (1955). Urine production by the antennal glands of *Palaemonetes varians* (Leach). *J. exp. Biol.* **32**, 408–422.

PHILLIPS, J. E. (1981). Comparative physiology of insect renal function. *Am. J. Physiol.* **241**, R241–R247.

POLLARD, S. D. (1988). Partial consumption of prey: the significance of prey water loss on estimates of biomass intake. *Oecologia* **76**, 475–476.

POLLARD, S. D. (1989). Constraints affecting partial prey consumption by a crab spider, *Diaea* sp. indet. (Araneae: Thomosidae). *Oecologia* **81**, 392–396.

PULZ, R. (1987). Thermal and water relations. In *Ecophysiology of Spiders* (ed. W. Nentwig), pp. 26–55. Berlin: Springer-Verlag.

RAMSAY, J. A., BROWN, J. H. J. AND CROGHAN, P. C. (1955). Electrometric titration of chloride in small volumes. *J. exp. Biol.* **32**, 822–829.

RAMSAY, J. A. AND BROWN, R. H. J. (1955). Simplified apparatus and procedure for freezing point determinations upon small volumes of fluid. *J. sci. Instr.* **32**, 372–375.

RASMONT, R. (1958). Structure et ultrastructure de le glande coxale d'un scorpion. *Soc. R. zool. Belg.* **89**, 241–267.

RIEGEL, J. A. (1972). *Comparative Physiology of Renal Excretion*. Edinburgh: Oliver & Boyd.

RIEGEL, J. A. AND COOK, M. A. (1975). Recent studies of excretion in Crustacea. In *Excretion* (ed. A. Wessing). *Fortschr. Zool.* **23**, 48–75.

RIEGEL, J. A., LOCKWOOD, A. M. P., NORFOLK, J. R. W., BULLEID, N. C. AND TAYLOR, P. A. (1974). Urinary bladder volume and the reabsorption of water from the urine of crabs. *J. exp. Biol.* **60**, 167–181.

TATCHELL, R. J. (1967). Salivary secretion of the cattle tick as means of water elimination. *Nature* **213**, 940–941.

TATCHELL, R. J. (1969). The ionic regulatory role of the salivary secretion of the cattle tick, *Boophilus microplus*. *J. Insect Physiol.* **15**, 1421–1430.

TOWLE, D. W., MANGUM, C. P. AND JOHNSON, B. (1980). Osmoregulation in *Limulus polyphemus*. *Am. Zool.* **20**, 736–000.

WOODRING, J. P. (1973). Comparative morphology, function and homologies of the coxal glands in orbatid mites (Arachnida, Acari). *J. Morph.* **139**, 407–429.