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Source: Journal of Orthoptera Research, 11(1) : 19-24

Published By: Orthopterists' Society

URL: https://doi.org/10.1665/1082-6467(2002)011[0019:IAWTIT]2.0.CO;2

Ion and water transport in the orthopteran alimentary canal: a comparison of Mantidae and Acrididae

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Abstract

We measured hemolymph Na^+ and K^+ concentrations, gut Na^+ and K^+ concentrations, transepithelial electrical potentials (TEPs) and fluxes of Na^+, K^+ and water for the insectivorous praying mantis *Tenodora sinensis* (Orthoptera: Mantidae). In addition, we calculated transepithelial potential differences for Na^+ (E_{Na}) and K^+ (E_K). In the mantid, Na^+ concentrations were higher in the hemolymph than in the crop, caeca, midgut, ileum, and rectum. Potassium ion concentrations were lower in the hemolymph than in the crop and rectum. All mantid TEPs were lumen negative. The crop TEP was less negative than the TEPs for the anterior and posterior caeca, anterior midgut, posterior midgut, and ileum. Mantid E_{Na} values were all negative and E_K values were all positive. Mantid caecal Na^+, K^+ and water fluxes were all relatively small. These data imply that digestion of insect prey occurs largely in the crop, and the caeca and midgut may not play important roles in digestion. To maintain ionic homeostasis, mantids may actively transport Na^+ while passively distributing K^+. We discuss these data for mantids in comparison to previous data on the gut function of desert locusts.

Keywords

Praying mantis, insect gut, entomophagy, ionic gradients, transepithelial potential

Introduction

Research on insect gut function has focused on a few well-studied and economically important insects. These species have been used as models for two of five broad feeder groups, classified by diet: 1) solid-plant, 2) liquid-animal, 3) liquid-plant, 4) solid-animal (Dow 1986) and 5) omnivores. For example, desert locusts have long been used to represent solid-plant feeders (*e.g.*, Dow 1981a), and mosquitoes have been used extensively to represent liquid-animal feeders (*i.e.*, hemolymph feeding insects; Bradley 1987). In contrast, liquid-plant and solid-animal feeders have been largely neglected. Nicolson (1990) examined the gut of a liquid-plant feeder, the carpenter bee, which needs to conserve almost all of the salts in its ion-poor diet. We know of no studies on the alimentary canal of solid-animal feeders. This is unfortunate because entomophagous insects may have an important impact on the distribution and abundance of their prey. When these prey are medical or agricultural pests, entomophagous insects may be potential biocontrol agents. Further study of a solid-animal feeder may provide a good comparison to previously studied solid-plant feeders (*e.g.*, locusts) and omnivores (*e.g.*, cockroaches), especially if they are phylogenetically related. In this study, we examine the gut physiology of a carnivorous orthopteran, the praying mantis *Tenodora sinensis* Saussure (Orthoptera: Mantidae).

Most work on the ionic homeostasis of orthopterans has been on locusts and cockroaches (Zeiske 1992). Locusts, as solid-plant feeders, have a diet high in cellulose and potassium ions (K^+). To maintain ionic balance, K^+ are actively excreted and sodium ions (Na^+) are actively taken up (Dow 1981a), and these transports take place in the anterior caeca (Dow 1981b). On the other hand, cockroaches are solid-feeding omnivores and can be considered as a dietary intermediate between solid-plant and solid-animal feeding orthopterans (Dow 1986). It seems likely that the cockroach midgut is responsible for ion balance, and that specifically a Na^+/K^+ ATPase of the basal midgut actively lowers lumen Na^+ concentration and raises lumen K^+ concentration (O'Riordan 1969, Dow 1986). Hence, the maintenance of ion balance in both of these representative orthopterans may be controlled in the midgut and/or caeca via the action of Na^+/K^+ ATPases.

The praying mantis is predatory throughout its life history. As a solid-animal feeder, the mantid ingests large meals at irregular intervals. These meals are high in Na^+ and protein. The ability to manage this diet efficiently is under selective pressure. Studies have shown that food limitation influences mantid fitness by: 1) decreasing survivorship, 2) delaying maturation and 3) decreasing the body length of adult females and therefore the number of eggs carried (Hurd & Rathet 1986). In light of this selective pressure, we designed our study around predictions based on the notion that the mantis has diverged from its orthopteran ancestors.

The predictions we tested are: 1) concentrations of sodium ions will be higher in the hemolymph, crop, and rectum than other regions of the gut. Ingestion of meals that are high in Na^+ should increase the Na^+ concentration in the foregut, and increased Na^+ concentrations in the rectum would be needed to excrete excess Na^+. 2) Concentrations of potassium ions will be lower in the hemolymph, crop, and rectum than other regions of the gut, because relatively low amounts of K^+ are ingested. 3) Transepithelial potentials will be less negative (relative to the hemocoel) in the crop and more negative in the midgut, than in other regions of the gut. If the crop is relatively impermeable, then its TEP is likely close to zero. Negative TEPs are predicted because ingested cations

must move to the hemocoel, and this seems especially likely to occur at the midgut. 4) For all gut regions other than the crop, E_{Na} will be less than zero, but E_K will be greater than zero. In the crop, neither E_{Na} nor E_K will be different from zero. Ingested Na^+ must move into the hemocoel, creating a negative E_{Na+}, whereas K^+ must move in the opposite direction. The impermeable crop is expected not to have high potentials. 5) Fluxes of Na^+, K^+, and water will not differ from zero for the caeca. Because the mantid's meals are ionically similar to its own tissues, active transports are likely minimal.

Methods

Rearing.— Mantid egg cases were obtained from Carolina Biological Supplies (Burlington, NC, USA) and held at room temperature until hatching. Mantids were held in 40 X 40 X 60 cm wooden cages with plexiglass front panels. Large quantities of sticks and dried grass stalks were provided for cover and excess live food supplied daily. Initial densities of 100 to 120 insects per cage dwindled with increasing insect size, primarily due to cannibalism, so that no more than 30 adults could be maintained in one cage, even when live food was abundant. As they grew through successive instars, mantids were fed progressively larger adult insects: fruit flies, blow flies, cabbage white butterflies and house crickets.

Ion concentrations of hemolymph and body fluids.— All physiological data were collected using methods following Dow (1981a,b), to allow direct comparison of the present data on mantids to Dow's data on locusts. Hemolymph samples from mantids of both sexes were obtained by pricking the coxal membrane with an insect pin and filling duplicate 2-l microcaps. The insects were then decapitated, legs and wings removed, and the body pinned dorsal-side up in a wax-filled dissecting dish. The body was opened with a longitudinal incision and fluid samples taken by micropuncture of the freshly exposed gut. Two-microliter aliquots were diluted in 2 ml of distilled H_2O and analyzed for Na^+ and K^+ by flame emission photometry using a Pye SP90A spectrophotometer, with correction for the interference of Na^+ on the K^+ value.

Microelectrode measurements.— An *in vitro* saline of 330 mosmol (by freezing point depression) and pH 7.0 was used. This saline consisted of (in mmol l^{-1}): Na^+ 100, Cl^- 95, K^+ 12, Ca^{++} 5, Mg^{++} 2, PIPES 10, glucose 20, glutamate 5, citrate 5, sucrose 120. Impalements were made with 10-30 MOhm electrodes (3 mol l^{-1} KCl) on freshly prepared gut. The exposed interior body wall was greased and the cavity flooded with saline as explained in detail by Dow (1981a). Transepithelial potentials were measured at least 2 mm deep, at low resolution, and were insensitive to movement. Values for E_{Na} and E_K were calculated from the ion concentration and TEP data (see Dow 1981a).

Gut perfusion measurements.— Segments of midgut and caeca were isolated as cylinders and double-perfused (1 ml min^1 external, 11 µl min^1 internal) following the method of Dow (1981a). Aliquots of the internal perfusate were collected for ion analysis as described above and the fluxes calculated from the changes in ion concentration of the internal perfusate. Water fluxes were calculated from the changes in concentration of [^{14}C]-inulin, following the method of Dow (1981b).

Statistics.— We tested data for differences in concentrations along the gut for a given cation using one-way ANOVA with Tukey's post-test. We tested TEP difference calculations for difference from zero by determining if the 95% confidence intervals included zero. Confidence intervals were constructed by multiplying standard errors by the percentage points of the *t* distribution appropriate for the given degrees of freedom with $\alpha = 0.05$.

Results

Ion concentrations of hemolymph and body fluids.— Sodium ion concentrations were significantly higher in the hemolymph than in the crop, caeca, midgut, ileum, ($p < 0.001$) and rectum ($p < 0.01$, Fig. 1). Na^+ concentrations were significantly higher in the rectum than in the caeca and the midgut ($p < 0.05$). No other comparisons of Na^+ concentrations were significantly different. In general, the Na^+ concentrations were highest in the hemolymph, intermediate in the rectum, and lowest in the crop, caeca, midgut, and ileum. K^+ concentrations were significantly lower in the hemolymph than in the crop ($p < 0.05$) and rectum ($p < 0.001$, Fig. 2). K^+ concentrations were significantly higher in the rectum than the crop ($p < 0.05$) and the midgut ($p < 0.01$). In general, the K^+ concentrations were lowest in the hemolymph, intermediate in the crop, caeca, midgut, and ileum, and highest in the rectum.

Microelectrode measurements.— All mantid TEPs were lumen negative (Fig. 3). The crop TEP was significantly less negative than the TEPs for the caeca ($p < 0.01$), anterior midgut, posterior midgut, and ileum ($p < 0.05$). No other comparisons of mantid TEPs were significantly different from each other. The crop and rectum had relatively high potentials, whereas the caeca and ileum had lower potentials.

Calculated electrochemical potential differences.— E_{Na} values for mantids were all negative and significantly less than zero (Fig. 4). The crop had significantly less negative E_{Na} values than the caeca, midgut ($p < 0.01$) and ileum ($p < 0.05$). The rectum had significantly less negative E_{Na} values than the caeca and midgut ($p < 0.05$). Conversely, no mantid E_K values were significantly different from zero, except the crop: it was greater than zero (Fig. 4). The rectum had significantly more positive E_K values than the midgut ($p < 0.05$). Mantid E_{Na} and E_K readings were relatively electropositive in the crop and rectum, and relatively electronegative in the caeca, midgut and ileum.

In vitro perfusion.— We measured fluxes of Na^+, K^+, and water in the absence of external gradients for the caeca. Fluxes of K^+ and water differed significantly from zero ($p < 0.05$, Table 1). Fluxes of both cations and water were small relative to the corresponding fluxes for locusts.

Discussion

Our data suggest that mantids, which are challenged with a solid diet high in protein and Na^+, digest much of their food in the crop. The caeca are not an important ion transporter (Table 1), suggesting that the majority of digestion may have already occurred when the food reaches the caeca. It may be that the food is ionically similar to mantid hemolymph, and therefore little active

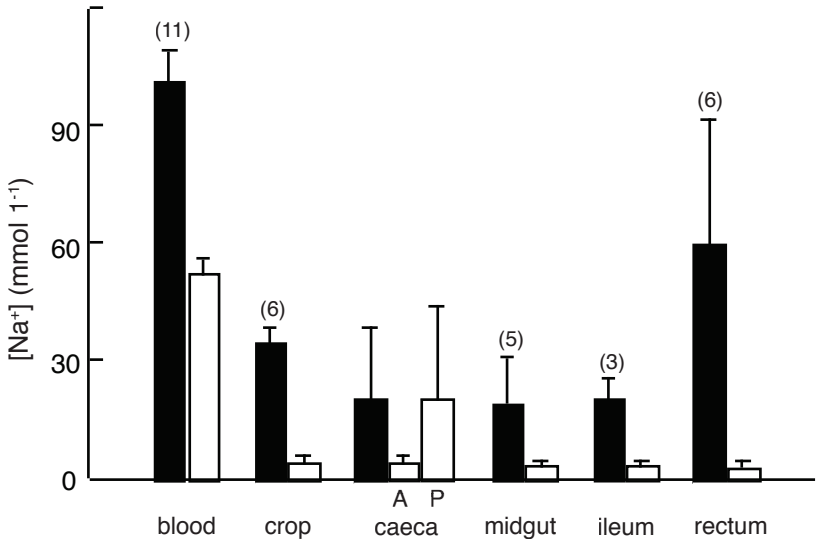

Fig. 1. Na^+ profiles along the gut of the praying mantis (filled bars) and the desert locust (open bars). Locust data are from Dow (1981a). Error bars are 1 $s_{\bar{x}}$. Sample size is four unless shown otherwise in parentheses. A = anterior caeca and P = posterior caeca.

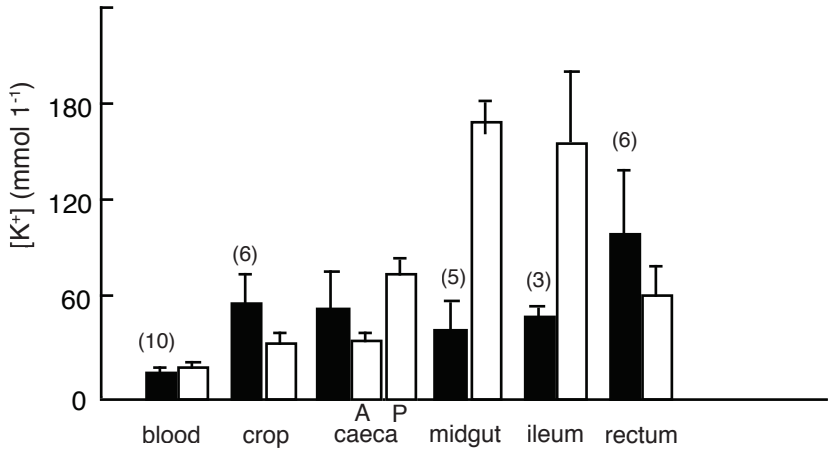

Fig. 2. K^+ profiles along the gut of the praying mantis and the desert locust. See Fig. 1 legend for all other details.

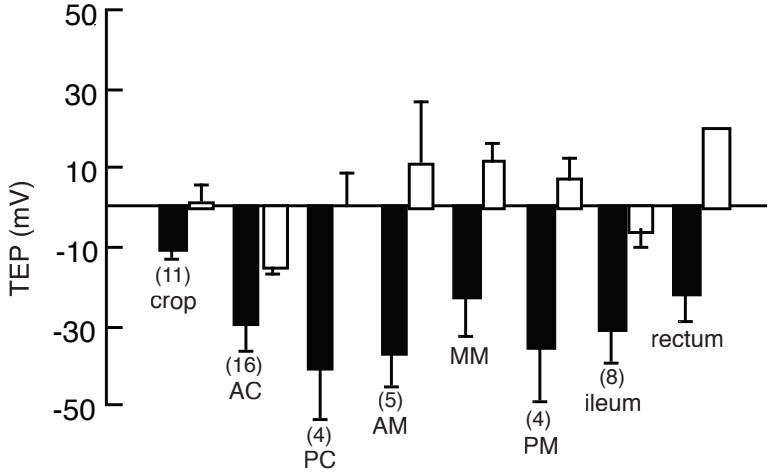

Fig. 3. Transepithelial potential profiles along the gut of the praying mantis (filled bars) and the desert locust (open bars). Sample size is six unless shown otherwise in parentheses. Locust rectum data are from Phillips (1964). Abbreviations are as follows: AC = anterior caeca, PC = posterior caeca, AM = anterior midgut, MM = mid-midgut, PM = posterior midgut. Locust data are taken from Dow (1981a).

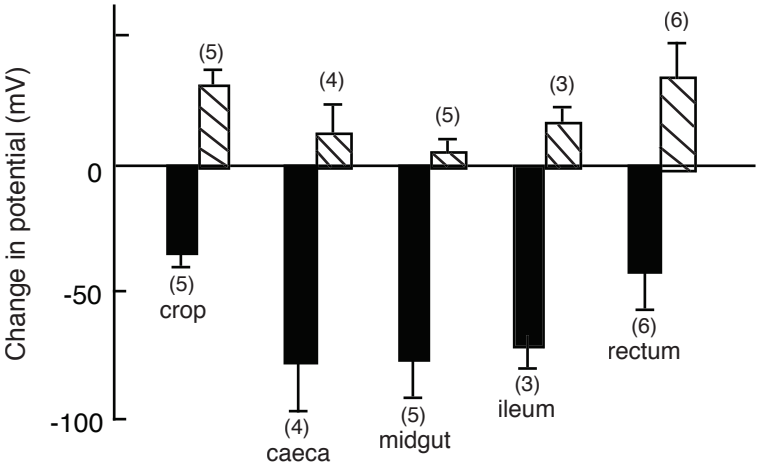

Fig. 4. Electrochemical potential difference profiles showing the relative contributions of Na^+ and K^+ in different regions of the gut of the praying mantis. Black bars are Na^+ values and hatched bars are K^+ values.

Table 1. Na^+, K^+, and water fluxes ($\pm 1\ s_{\bar{x}}$) across mantid and locust caeca in the absence of electrical gradients. Significant comparisons to zero are marked by an *. Locust data are from Dow (1981b).

	n	Na^+ (nmol hr^{-1})	K^+ (nmol hr^{-1})	Water (nl hr^{-1})
Mantid caeca	3	60 ± 25	-14 ± 8 *	70 ± 300 *
Locust caeca	12	234 ± 54	-132 ± 18	1140 ± 158 (n = 4)

transport is needed to maintain ion balance. Our data suggest ionic homeostasis is achieved by active transport of Na^+ throughout the gut and passive distribution of K^+ (Fig. 4).

Gut structure.— The structure of the mantid gut, a huge crop and ileum and a reduced midgut, reflects the mantid's carnivorous diet (see Dow 1986). The large crop is useful for storage of the large infrequent meals characteristic of predators. Perhaps more importantly, the size of the crop suggests its importance in the initial digestion of the prey (Chapman 1985). This is similar to the blood-sucking bug *Rhodnius prolixus*, which uses a very large anterior midgut to concentrate the meal (Farmer *et al.* 1981). In locusts, the ileum plays a major role in the absorption of ions and water (Dow 1981a). The greatly elongated ileum of the mantis reflects two aspects of its predatory lifestyle. First, the largely protein diet will tend to nitrogen-load the insect (Cochran 1985) and the ileum, along with the Malpighian tubules, likely plays an important role in nitrogen balance. Second, ingesting a semi-solid prey means that unlike herbivores, which eat a diet high in water but low in nutrients, mantids must normally conserve water, as evidenced by their dry, compact frass. The elongated ileum would provide a greater surface for water reabsorption (Audsley *et al.* 1992). In addition, the rectum could participate in water resorption.

Ion concentrations.— As predicted, the mantid gut contains higher concentrations of Na^+ than the locust gut (Fig. 1). These concentrations were greatest in the crop and rectum. The high Na^+ concentration in the crop is due to the presence of Na^+-rich prey. Given this Na^+ loading, it is likely that the mantids use Na^+, rather than K^+, as the driving cation for Malpighian tubule secretion. This shift from locusts in cation transport is seen, not only in other protein-feeders such as the blood-sucking bug (Maddrell 1977) and mosquitoes (Petzel *et al.* 1985, 1986), but also in other orthopterans, notably house crickets (Spring & Hazelton 1987, Kim & Spring 1992). One would then predict that the rectum resorbs primarily NaCl, as also seen in house crickets (Spring & Albarwani 1993).

In mantids, K^+ concentrations are relatively constant along the gut, suggesting that the concentration of K^+ is not actively changed during passage (Fig. 2). In locusts, K^+ is particularly high in the midgut and ileum. The relatively low K^+ concentrations in the midgut and ileum of mantids would be consistent with Na^+ being the actively regulated cation with K^+ passively regulated.

Cell and epithelial potentials.— Transepithelial potentials in the mantid gut are more lumen negative than corresponding locust TEPs (Fig. 3). The absolute TEP values indicate higher electrical gradients across the gut of the (predatory) mantid than in the (herbivorous) locust. This may reflect the need to absorb food, which can be limiting (Hurd & Rathet 1986), at a high efficiency. The locust is not typically limited by food quantity (Phillips 1964) and therefore does not require a highly efficient method of nutrient absorption.

Transepithelial potential difference calculations indicate that the mantid gut contains less Na^+ and slightly more K^+ than predicted by the Nernst equation (Fig. 4). The significantly negative values for Na^+ in the caeca, midgut, and ileum suggest that Na^+ is actively regulated at these sites. On the other hand, E_K values are not significantly different from zero for the caeca, midgut, and ileum, implying passive distribution. Locust TEP difference calculations, in contrast, indicate more Na^+, and less K^+, than predicted by the Nernst equation (Dow 1981a). However, the active or passive distribution of ions suggested by TEP difference calculations is not always correct. Dow (1981b) demonstrated, using pharmacological techniques, that Na^+ is actively regulated and K^+ is passively regulated in the locust caeca and midgut. Transepithelial potential difference calculations for locusts therefore, are not consistent in predicting the mode of ion distribution. For mantids, pharmacological data are needed to determine with certainty whether ion distributions are actively or passively controlled.

If we assume that mantids actually do actively distribute Na^+ but passively distribute K^+, an interesting conclusion follows. Kim & Spring (1992) found that house crickets use active transport of Na^+ to drive tubular secretion. In this scenario, both mantids and house crickets use Na^+ to maintain water balance, despite their divergent diets and needs for maintaining homeostasis. This suggests that the control of ion and water balance by the active regulation of K^+, as seen in the desert locust, may be the exception instead of the rule for orthopterans.

Ion and water fluxes.— Finally, as predicted, ion and water fluxes across the mantid caeca were small in comparison to locust fluxes. This reflects the ionic similarity of the mantid diet and mantid hemolymph. This ionic similarity requires little movement of ions or water to maintain homeostasis.

We believe these are the first data on ion and water balance in the gut of a predatory insect. Published research on solid-insect feeders is sparse, in part because they are relatively difficult to rear, despite the fact that they may be potential biocontrol agents. Our data suggest that the gut of this entomophagous insect has evolved, both in structure and function, to handle a diet that has diverged from its phytophagous relatives.

Acknowledgements

JDH was supported by a University of Southwestern Louisiana Doctoral Fellowship. JATD was supported by a Research Fellowship of St. Catharine's College, University of Cambridge. Drs Tom Clark and Paul Leberg critically read an early version of the manuscript. This research was supported in part by USDA-CREEF grant 9501834 to JHS.

Literature Cited

Audsley N., McIntosh C., Phillips J.E. 1992. Isolation of a neuropeptide from locust corpus cardiacum which influences ileal transport. Journal of Experimental Biology 173: 261-274.

Bradley T.J. 1987. Physiology of osmoregulation in mosquitoes. Annual Review of Entomology 32: 439-462.

Chapman R.F. 1985. Coordination of digestion. Pp. 213-240. In: Kerkut G.A., Gilbert L.I. (Eds) Comprehensive Insect Physiology, Biochemistry, and Pharmacology, vol. 4, Regulation: Digestion, Nutrition, Excretion. Pergamon Press Ltd., Oxford.

Cochran D.G. 1985. Nitrogenous excretion. Pp. 467-506. In: Kerkut G.A., Gilbert L.I. (Eds) Comprehensive Insect Physiology, Biochemistry, and Pharmacology, vol. 4, Regulation: Digestion, Nutrition, Excretion. Pergamon Press Ltd., Oxford.

Dow J.A.T. 1981a. Ion and water transport in locust alimentary canal: evidence from in vivo electrochemical gradients. Journal of Experimental Biology 93: 167-179.

Dow J.A.T. 1981b. Localization and characterization of water uptake from the midgut of the locust, *Schistocerca gregaria*. Journal of Experimental Biology 93: 269-281.

Dow J.A.T. 1986. Insect midgut function. Advances in Insect Physiology 19: 187-328.

Farmer J., Maddrell S.H.P., Spring J.H. 1981. Absorption of fluid by the midgut of *Rhodnius*. Journal of Experimental Biology 94: 301-316.

Hurd L.E., Rathet I.H. 1986. Functional response and success in juvenile mantids. Ecology 67: 163-167.

Kim I.S., Spring J.H. 1992. Excretion in the house cricket (*Acheta domesticus*): relative contribution of distal and mid-tubule to diureses. Journal of Insect Physiology 38: 373-381.

Maddrell S.H.P. 1977. Insect Malpighian tubules. Pp. 541-569. In: Gupta B.L., Moreton R.B., Oschman J.L., Wall B.J. (Eds) Transport of Ions and Water in Animals. Academic Press, London.

Nicolson S.W. 1990. Osmoregulation in a nectar-feeding insect, the carpenter bee *Xylocopa capitata*: water excess and ion conservation. Physiological Entomology 15: 433-440.

O'Riordan A.M.1969. Electrolyte movement in the isolated midgut of the cockroach, *Periplaneta americana*. Journal of Experimental Biology 51: 699-714.

Petzel D.H., Hagedorn H.H., Beyenbach K.W. 1985. Preliminary isolation of mosquito natriuretic factor. American Journal of Physiology 249: R379-R386.

Petzel D.H., Hagedorn H.H., Beyenbach K.W. 1986. Peptide nature of two mosquito natriuretic factors. American Journal of Physiology 250: R328-R332.

Phillips J.E. 1964. Rectal absorption in the desert locust *Schistocerca gregaria* Forskål. II. Sodium, potassium and chloride. Journal of Experimental Biology 41: 39-67.

Spring J.H., Albarwani S.A. 1993. Excretion in the house cricket: stimulation of rectal reabsorption by homogenates of the corpus cardiacum. Journal of Experimental Biology 185: 305-323.

Spring J.H., Hazelton S.R. 1987. Excretion in the house cricket (*Acheta domesticus*): stimulation of diuresis by tissue homogenates. Journal of Experimental Biology 129: 63-81.

Zeiske W. 1992. Insect ion homeostasis. Journal of Experimental Biology 172: 323-334.