

EXCRETION IN INSECTS: ENERGETICS AND FUNCTIONAL PRINCIPLES

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(Received 26 February 1982 - Accepted 1 March 1982)

SUMMARY

The contention of Maddrell (1981) that the rate of fluid secretion by insect Malpighian tubules is much slower than the rate of primary urine production (glomerular filtration rate) of vertebrates is valid only when the comparison is made with mammals and birds. Fishes and reptiles have filtration rates similar to or even slower than the rates observed in insects.

Calculations of the concentration or dilution work involved in primary urine production show that the (weight-specific) energy requirement of the insect excretory system is similar to or surpasses that reported for reptilian, and even mammalian, kidneys.

Because the energy demand of any excretory system is small when compared to the resting metabolism of the entire organism, it is likely that selection pressures acted less on a reduction of energy expenditure for excretion and ionic regulation than on the adaptations to the demands of specific environments and life styles, leading to diversified specializations of excretory (and regulatory) mechanisms.

INTRODUCTION

The functional design of the 'insect excretory system' has been the topic of a recent paper by Maddrell (1981). The author has raised a number of interesting questions to which he supplied answers from his important published work. His challenging arguments cannot fail to elicit a response from physiologists who see the topic in a somewhat different light. In the following critique I wish to suggest alternative perspectives.

The main argument presented by Maddrell is that insect Malpighian tubules have an exceptionally low solute permeability and that the fluid movement is slow when compared with that seen in nephridia of vertebrates: 'most vertebrates filter their extracellular fluid 10 to 20 times more rapidly than do most insects'. As a consequence, reabsorption of useful substances 'need only occur at about 1-2% of the rate required in many vertebrates'. In Maddrell's view, this slow rate of fluid movement represents a considerable saving of energy.

Flow rate

Maddrell (1981) compares flow rates through Malpighian tubules with the glomerular filtration rates (GFR) measured in some vertebrate species. The average GFR of the vertebrates listed in his table 3 is 1.54 ml/kg.min, equivalent to 162 min for a volume equal to total extracellular fluid. The average rate of fluid movement through insect Malpighian tubules (computed from values given in the same table) requires 2656 min for a volume equal to total extracellular fluid.

This difference is deceptive, however. High GFR values occur only in mammals and birds, and in amphibians while they are in water. During their terrestrial phase, amphibians have very low glomerular filtration rates. The filtration rates of fishes and of reptiles, especially those of marine fishes and of terrestrial reptiles, are not higher than those reported for insects. Indeed, the only reptile ('snake') listed by Maddrell has a filtration rate only 16% higher than the fluid flow through the Malpighian tubules of the insect *Calliphora*.

If Malpighian tubules are compared with glomerular nephridia of fishes and reptiles, as is done here in Table 1, the difference in flow rate disappears. Indeed, the nephridial function of land-living reptiles shows many similarities with that of insects: in both types of animals the urine is voided into the hindgut (rectum, cloaca) where reabsorption of water (and of certain ions) occurs. Reptiles as well as insects excrete uric acid (urates) through their nephridia as nitrogenous end-product. Both have, to use Maddrell's words, 'a slowly operating excretory system'.

Maddrell (1981) is aware that the GFR of 'frog' and 'snake' is low, and he relates this to the fact that these animals are ectothermic and hence have a low metabolic rate. He then argues that insects because of their much smaller size have a much higher weight-specific metabolic rate which 'would suggest that they should filter the hemolymph faster than do larger ectotherms' while the available data 'indicate that, if anything, the opposite is the case'.

The correlation between metabolic rate and filtration rate is indeed dubious. It is true (see Table 2) that larger mammals, generally, have a lower GFR than smaller ones. The GFR, however, is subject to considerable variation in accordance with salt and water load. As shown in Table 2 for the example of the chicken, the filtration rates of water-loaded animals can be five times greater than that of dehydrated specimens. Such changes of GFR are not accompanied by a corresponding change in overall metabolic rate. Indeed, all available information points to a causal relationship between habitat, nutritional state and salt and/or water intake on the one hand, and the rate of fluid secretion on the other.

Energetics

Under certain circumstances, as after a blood meal in bloodsucking insects like *Rhodnius*, the Malpighian tubules become formidable excretion devices which surpass the excretion power of the most active diuretic human kidney (see Maddrell & Gardiner, 1976). In this condition the Malpighian tubules produce a luminal fluid with an amino acid concentration less than 1% of that of the haemolymph (Maddrell & Gardiner, 1974). The concentration difference thus achieved represents an energy

Table 1. *Glomerular filtration rates of fishes and reptiles compared with rates of fluid secretion ('filtration') by Malpighian tubules of insects (insect data from Maddrell, 1981)*

Species	Habitat*	Filtration rate (ml/kg.min)	Time to filter total volume of extracellular fluid (min)†	Reference
Fishes				
<i>Ephatretes stouti</i>	M	0.005	48860	Munz & McFarland, 1964
Pacific hagfish				
<i>Opsanus tau</i>	M	0.003	83333	Lahlou <i>et al.</i> 1969
Toad fish				
<i>Squalus acanthias</i>	M	0.058	4286	Shannon, 1940
Spiny dogfish				
<i>Anguilla anguilla</i>	M	0.007	34883	Chester Jones <i>et al.</i> 1969
European eel				
<i>Myoxocephalus scorpius</i>	M	0.002	115385	Forster, 1953
Daddy sculpin				
<i>Lampetra fluviatilis</i>	F	0.19	1339	Hickman & Trump, 1969
River lamprey				
<i>Salmo gairdneri</i>	F	0.13	1974	Holmes & Stainer, 1966
Rainbow trout				
<i>Carassius auratus</i>	F	0.34	735	Maetz, 1963
Goldfish				
<i>Esox lucius</i>	F	0.04	6122	Hickman, 1965
Pike				
<i>Cyprinus carpio</i>	F	0.03	7500	Pora & Prekup, 1960
Carp				
<i>Opsanus tau</i>	F	0.015	17241	Lahlou <i>et al.</i> 1969
Toad fish				
Reptiles				
<i>Gopherus agassizii</i>	T	0.08	3165	Dantzler & Schmidt-Nielsen, 1966
Desert tortoise				
<i>Phrynosoma cornutum</i>	T	0.06	4237	Roberts & Schmidt Nielsen, 1966
Horned lizard				
<i>Tropidurus</i> sp.	M/T	0.06	4143	Roberts & Schmidt-Nielsen, 1966
Galapagos lizard				
<i>Varamus gouldii</i>	T	0.11	2209	Green, 1972
Sand goanna				
<i>Crocodylus porosus</i>	M/T	0.03	10000	Schmidt-Nielsen & Davis, 1968
Marine crocodile				
<i>Chelonia mydas</i>	M	0.24	1048	Schmidt-Nielsen & Davis, 1968
Marine turtle				
<i>Laticauda colubrina</i>	M	0.01	30000	Schmidt-Nielsen & Davis, 1968
Banded sea snake				
<i>Crocodylus johnsoni</i>	F	0.10	2500	Schmidt-Nielsen & Davis, 1968
Freshwater crocodile				
<i>Pseudemis scripta</i>	F	0.08	3164	Dantzler & Schmidt-Nielsen, 1966
Freshwater turtle				
Insects				
<i>Calliphora erythrocephala</i>	T		625	
<i>Dysdercus fasciatus</i>	T		1500	
<i>Schistocerca gregaria</i>	T		1700	
<i>Carausius morosus</i>	T		2750	
<i>Rhodnius prolixus</i>	T		10000	
		15 (!)	20 (during diuresis)	
<i>Aedes taeniorhynchus</i>	T		2000	

* T = terrestrial, M = marine, F = freshwater.

† The extracellular fluid of the vertebrates is assumed to be 25 % of the body weight (see Maddrell 1981).

Table 2. *Glomerular filtration rates of mammals and birds*

Species	Filtration rate (ml/kg.min)	Time to filter total extracellular fluid volume (min)*	Reference
Mammals			
<i>Tursiops gilli</i> Dolphin	1.75	143	Malvin & Rayner, 1968
<i>Steno bredinensis</i> Dolphin	2.42	103	Malvin & Rayner, 1968
Dog	3.2	78	Kurtzman <i>et al.</i> 1972
<i>Macaca speciosa</i> Macaque monkey	3.82	65	Tisher <i>et al.</i> 1970
<i>Tachyglossus aculeatus</i> Echidna	1.17	213	Bentley & Schmidt-Nielsen, 1967
Rabbit	3.12	80	Smith, 1951
<i>Trichosurus vulpecula</i> Brush possum	3.32	75	Reid & McDonald, 1968
<i>Dipodomys spectabilis</i> Kangaroo rat	6.8	37	Schmidt-Nielsen, 1952
<i>Chinchilla laniger</i> Chinchilla	7.0	35	Weisser <i>et al.</i> 1970
Birds			
<i>Gallus domesticus</i> Chicken			
Normally hydrated	1.23	203	Korr, 1939; Dantzler, 1966
Hydrated (100 ml H ₂ O)	2.47	101	Korr, 1939
After infusion of 50 mM NaCl/kg	0.49	510	Dantzler, 1966

* Extracellular fluid volume assumed to be 25 % of body weight (see Maddrell, 1981).

difference; it is thermodynamically irrelevant whether this is accomplished by active transport or by a process of filtration through a selective filter. At the enormous secretion rate which easily amounts to 15 $\mu\text{l/g}\cdot\text{min}$, the energy required to accomplish a concentration gradient of 1:100 is considerable, far greater than the energy requirement of the mammalian kidney. The following calculation makes this clear.

Assuming transport of neutral solutes, the energy consumption of a concentration or dilution process is given by $W = nRT \ln(U/P)$, where W is the free enthalpy (concentration work), R the universal gas constant ($8.314 \text{ j}\cdot\text{mol}^{-1}\cdot\text{K}^{-1}$), T the absolute temperature (e.g. 296 K), U is the molar concentration of the tubular fluid (urine), P is the molar concentration of the plasma, and n is the number of moles transported to achieve the concentration or dilution of a unit volume. The energy consumption per unit time is thus given by $\dot{W} = nfRT \ln(U/P)$, where f is the volume of fluid processed per unit time.

In fed *Rhodnius*, the plasma concentration of amino acids (Maddrell & Gardiner, 1974) amounts to about 35 mM/l ($3.5 \times 10^{-5} \text{ mol/ml}$) and that of the tubular fluid is equal to about 0.34 mM/l ($3.4 \times 10^{-7} \text{ mol/ml}$). The amount of amino acid reabsorbed or excluded, therefore, amounts to $3.4 \times 10^{-5} \text{ mol/ml}$. The energy required for the production of 1 ml of tubular fluid is thus equal to 0.39 J. At a rate of fluid secretion of 15 $\mu\text{l/g}\cdot\text{min}$ (0.015 ml/g.min) the rate of energy consumption is $5.9 \times 10^{-3} \text{ J/g}\cdot\text{min}$.

The concentration work of the human kidney has been calculated to amount to 3.77 J/ml of urine produced (Lifson & Visscher, 1944). The antidiuretic human kidney produces about 1 ml of final urine per min, or 1.5×10^{-5} ml/g.min. At this low excretion rate energy consumption is thus 5.65×10^{-5} J/g.min. During diuresis, energy consumption is not very different, however: although the rate of production of final urine may be ten times higher, the concentration work (per unit volume) is lower.

It appears now that the production of a dilute urine (with regard to amino acids) by the Malpighian tubules in a diuretic *Rhodnius* costs about 100 times more energy per unit time and unit weight than does the urine production in a typical mammalian kidney. The computation, of course, is incomplete since it does not take into account the secretion or filtration work. According to the generally accepted view, fluid secretion (filtration) in Malpighian tubules is the consequence of active K^+ (and/or Na^+) transport. In the vertebrates it is the work of the heart which produces the necessary filtration pressure. If 25% of the cardiac output goes to the kidneys, the energy needed for glomerular filtration cannot be greater than 25% of the work of the heart, or 2.1×10^{-4} J/g.min, and most likely amounts to not more than about half this value, i.e. 1×10^{-4} J/g.min.

In *Rhodnius*, the K^+ -concentration in the lumen of Malpighian tubules is much greater than that of the haemolymph (Ramsay, 1953; Maddrell, 1969). In the unfed animal, the ratio U/P was found to average 17.7:1 (Ramsay, 1953); in fed animals in the condition of diuresis, a ratio of 10:1 can be assumed from the data in Maddrell (1969), and may be greater. According to Ramsay (1952, 1953) the K^+ -concentration in the haemolymph is about 5 mM/l. Production of 1 ml of tubular fluid would thus minimally involve transport of about 0.05 mmol (5×10^{-5} mol) of K^+ . The energy requirement of this cation transport can be calculated according to the equation $W = nRT \ln(U/P) + n(F \cdot E_m)$, where W , R , T , U , P and n have the meaning already stated above, F is the Faraday (96500) and E_m is the transepithelial potential (in V). For a concentration gradient of 10:1 and an n value of 5×10^{-5} mol, W equals 0.12 J/ml of tubular fluid formed. At a secretion rate of 0.015 ml/min this is equal to 1.8×10^{-3} J/min.

Adding the 'driving energy' to the concentration work, the energy demand of the diuretic *Rhodnius* Malpighian tubules amounts to 7.7×10^{-3} J/g.min; that of the antidiuretic mammalian (human) kidney would be 1.56×10^{-4} J/g.min. The energy demand of the diuretic Malpighian tubules of the insect would thus be about 50 times greater than that of an antidiuretic (and diuretic) mammalian kidney.

Diuretic *Rhodnius* represents an extreme case. In other insects secretion rates are generally much lower, and in unfed *Rhodnius* secretion occurs at a rate of only about 0.015 μ l/min. At this low rate, however, the U/P ratio for K^+ can be as high as 64:1 (Ramsay, 1952). For the sake of argument we may assume that a similarly high ratio, say 50:1, occurs also in the Malpighian tubules of other insect species. Ramsay (1953) had found that, generally, the transepithelial electric potential of Malpighian tubules is inside positive (not negative as in *Rhodnius*). The potentials are always large (up to +58 mV). Assuming a transepithelial potential of 50 mV, the energy requirement of the K^+ -transport into the tubules would thus be 3.6 J/ml of tubular

fluid. At a secretion rate of $0.015 \mu\text{l}$ ($1.5 \times 10^{-5} \text{ ml}$) per g.min, the energy consumption of the K^+ -transport would be $5.4 \times 10^{-5} \text{ J/g.min}$. This value is only slightly less than the concentration work of the (anti)diuretic human kidneys ($5.6 \times 10^{-5} \text{ J/g.min}$). Thus, even if only the K^+ -transport is considered, the 'insect excretory system' requires about as much energy as does the mammalian kidney.

It should be noted that the computation of the energy requirement of human (and mammalian) kidneys includes the demands of urea excretion which accounts for about 90% of the total energy expenditure. In the calculation of the energetics of Malpighian tubule function, the cost of nitrogen excretion was neglected, mainly on account of insufficient data on which to base such a conclusion. This nitrogen excretion certainly increases the energy requirement of the insect excretory system.

Any comparison of insects with another animal group, such as terrestrial reptiles, ought to take into account the problem of scaling. This is difficult, however, since extrapolation beyond the normal weight range is rather uncertain. It is reported (Edwards, 1975) that the GFR values of mammals and reptiles are proportional to $M^{0.75}$ (where M represents body mass) down to a body weight of 5 g. If we take a GFR of $100 \mu\text{l/min}$ ($= 0.1 \mu\text{l/g.min}$) as representative of a 1 kg reptile (see Table 1), the GFR of a fictional reptile of the size of *Rhodnius* or *Calliphora* (50 mg) would be $1.2 \mu\text{l/g.min}$ or 12.5 times less than the secretion rate observed in diuretic *Rhodnius*, and about 5 times greater than that of the Malpighian tubules of adult *Calliphora* (see data of Berridge, 1968). The scaling factor in the case of insects, however, is proportional to $M^{1.0}$ rather than to $M^{0.75}$. The weight-specific excretion rate of a fictional 1 kg *Calliphora* would thus be the same as that found in a 50 mg specimen and would, therefore, be about 12 times faster than that of a 1 kg reptile.

Even if it is unrealistic to extend scaling beyond the natural weight range of an animal group, the arguments presented here illustrate that excretory rates of insects are not much slower, and may even be faster than those of lower vertebrates.

Energy budget

According to the investigations of Borsook & Winegarden (1931), the human kidney has an energy requirement for urine production (involving all manners of active transport) amounting to less than 5% of the overall energy consumption of that organ, and less than 1% of the energy consumption of the entire organism. Potts (1954) has reached similar conclusions from his computation of osmotic work of a number of invertebrate species: the work of the nephridia is never more than 1 or 2% of the resting metabolic rate of the whole animal. It thus appears that within the overall energy budget of an insect, any saving of energy due to greater efficiency of the secretion/reabsorption processes of the Malpighian tubules would be of minor importance unless the energetic efficiency of the system is unusually low.

If evolutionary pressures have determined the design of the mechanisms involved in Malpighian tubule function, they must have predominantly acted on the detailed adaptations to the specific life styles of each species so that optimal control over volume and composition of body fluids are achieved. The overall saving of energy due to a slowing of the secretion rate seems, by comparison, of minor importance.

Conclusion

Comparative physiology is at its most intriguing when it attends to the diversity of functions, but it is at its best when it can discover similarities of function in species of quite different systematic position. In this regard, the comparison of terrestrial-ectothermic vertebrates like reptiles with likewise terrestrial and ectothermic insects appears promising.

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