Sodium and potassium concentrations in floral nectars in relation to foraging by honey bees

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Sodium and potassium concentrations have been measured in nectar from a variety of flowering plants visited by honey bees (*Apis mellifera capensis*). In 18 plant species the mean sodium concentration was 9,8 ± 1,4 mmol (± *S.E.*), and the mean potassium concentration was 18,7 ± 4,3 mmol. These results are compared with nectar ion concentrations in carpenter bee and hummingbird flowers. Analysis of honey bee body fluids showed that, although haemolymph ion concentrations were closely regulated, the levels of sodium and potassium in the urine did not necessarily reflect those in the nectar being gathered.

Natrium- en kaliumkonsentrasies in nektar van verskeie spesies blomplante, wat deur heuningbye (*Apis mellifera capensis*) opgesoek word, is bepaal. In 18 plantspesies was die gemiddelde natriumkonsentrasie 9,8 ± 1,4 mmol (± S.F.), en die gemiddelde kaliumkonsentrasie 18,7 ± 4,3 mmol. Hierdie resultate word vergelyk met die nektarioonkonsentrasies in blomme wat deur houtkapperbye en kolibries besoek word. 'n Analise van heuningbyliggaamsvloeistowwe het getoon dat, alhoewel hemolimfkonsentrasies streng gereguleer word, die natrium- en kaliumvlakke in die uriene nie noodwendig dié van versamelde nektar weerspieël het nie.

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An important aspect of pollination biology concerns the energetics of the relationship between flower and pollinator (reviewed by Heinrich 1975, 1983). This is because nectar is predominantly a sugar solution and most pollinators have very high energy demands. However, Baker & Baker (1975) emphasized that the nectar of flowering plants contains a complex array of chemicals in addition to sugars: amino acids, lipids, proteins, organic acids, vitamins and inorganic minerals. These other constituents of nectar, as well as its water content, may be important in filling the nutritional and homeostatic needs of flower visitors. However, the only systematic look at ion concentrations in floral nectars is the work of Hiebert & Calder (1983), who examined a variety of hummingbird flowers and found sodium concentrations to be much lower than those of potassium. The ionic balance of nectivorous insects has also received little attention, but there have been indications that sodium may be in short supply in their diet (Arms, Feeny & Lederhouse 1974; Barrows 1974; Nicolson & Louw 1982).

The aim of the present study was, firstly, to sample a selection of the flowering plants upon which honey bees forage, to see whether low nectar sodium concentrations are a general phenomenon. Secondly, haemolymph and urine were examined in bees foraging on different nectars, to see whether nectar composition is reflected in the chemistry of the body fluids.

Methods

Nectar was collected during spring (September–October) from a variety of flowering plants upon which bees (*Apis mellifera capensis* Escholtz) were observed to be foraging. All the species examined were indigenous to South Africa, except for *Echium fastuosum*, *Grevillea robusta* and four species of Myrtaceae. Flowers were sampled in the early morning (8h00–10h00), at various sites including the campus of the University of Cape Town and Kirstenbosch Botanic Gardens. Micropipettes (Drummond Scientific Co., 2 or 10 μl) were used for withdrawing nectar from the corolla: usually the viscosity of the nectar was low enough for the micropipette to fill by capillarity. The volume of nectar in each flower was determined from the column length in the micropipettes. Where the flower consisted of an inflorescence (e.g. *Leucospermum*), the quantity of nectar was expressed as μl per inflorescence.

The sugar concentration of the nectar was measured using a portable refractometer (Bellingham and Stanley Ltd), and appropriate dilutions were made when either the volume of nectar was too small or the sugar concentration exceeded the scale of the refractometer. The refractometer readings were converted to grams solute per 100 ml solution.

Sodium and potassium concentrations of the nectar were measured by means of standard flame photometric techniques (Instrumentation Laboratory Model IL 243).

In order to examine the ionic balance of honey bees foraging on nectars of varying ion concentrations, we made the asssumption that the bees foraging on a particular plant were flower-constant for that species. Flower constancy in honey bees has been well documented (Heinrich 1975; Seeley 1985). Bees foraging on three different species were collected and killed with ethyl acetate, then stored on ice and immediately transported (10–15 min) back to the laboratory. The haemolymph and urine were then sampled using 1 or 2 μl micropipettes, the haemolymph being withdrawn through an incision in the third abdominal segment and the urine being obtained by gentle squeezing of the abdomen. Sodium and potassium concentrations of the body fluids were determined as for nectar. All results are presented as mean ± S.E.

Results and Discussion

Ionic composition of nectars

The results of the nectar survey of selected flowering plants are presented in Table 1. Sodium concentrations of the nectar varied from 1,5 mmol in *Callistemon viminalis* (Myrtaceae) to 21,0 mmol in two species of *Leucospermum* (Proteaceae), with a mean value of 9,8 ± 1,4 mmol for the 18 species examined. Potassium concentrations also showed considerable variation, ranging from 4,3 mmol in *Wachendorfia thyrsiflora* (Haemodoraceae) to 68,4 mmol in *Callistemon citrinus*. The mean potassium concentration in these nectars was 18,7 ± 4,3 mmol. Potassium and sugar concentrations were very poorly correlated ($r = 0,13$), while the correlation between sodium and sugar concentrations was somewhat better ($r = 0,58$).

Sodium and potassium ions together (without associated anions) accounted for 4,6 ± 0,8% of the apparent sucrose equivalent, with the highest cation contributions being 14% in *Callistemon viminalis* and 10% in *Grevillea robusta*. This would result in considerable errors in determining the energy content of these nectars directly from refractive index (Inouye, Favre, Lanum, Levine, Meyers, Roberts, Tsao & Wang 1980). In contrast, the very rich nectar utilized by *Xylocopa capitata* is so low in cations that the error in calculating its energy content would be only 0,3% (Nicolson 1990).

It is apparent from these results that honey bees have a much wider choice of ion concentrations in nectar than do carpenter bees. In the Cape Town area, *Xylocopa capitata* forages almost exclusively on *Podalyria calyptrata* and two species of *Virgilia*, with occasional visits to other members of the Fabaceae: nectar ion concentrations for four species of *Xylocopa* flowers are only 1,9 ± 0,8 mmol for sodium and 4,0 ± 1,0 mmol for potassium (Nicolson 1990).

In an earlier survey of ion concentrations in nectar, Hiebert & Calder (1983) examined 19 species of flowers known to be visited by hummingbirds. These flowers belonged to nine families, all different from the plant families examined in the present work, with one exception: *Aloe* (Liliaceae). Potassium concentrations in these hummingbird flowers (Hiebert & Calder 1983: Table 1) averaged 24,7 ± 5,4 mmol and were not significantly different from the values for bee flowers in Table 1. However, sodium concentrations in the hummingbird flowers, averaging 3,4 ± 1,0 mmol, were significantly lower than in the bee flowers sampled in the present study (t test, $p < 0,001$).

Table 1 Nectar volume and composition of selected forage plants of honeybees

Species	Volume (µl)	Sugar (g/100 ml)	Na (mmol)	K (mmol)
Boraginaceae				
Echium fastuosum	2,0 ± 0,2	21,0 ± 0,4	5,0 ± 0,3	11,5 ± 0,3
Fabaceae				
Indigofera langebergensis	0,7 ± 0,1	41,6 ± 0,4	8,1 ± 0,2	7,7 ± 0,2
Myrtaceae				
Eucalyptus melliodora	5,0 ± 0,2	13,0 ± 0,3	12,0 ± 0,3	16,2 ± 0,3
E. ficifolia	12,3 ± 0,2	14,2 ± 0,4	2,5 ± 0,3	7,0 ± 0,3
Callistemon citrinus	14,3 ± 0,8	37,3 ± 3,7	15,9 ± 2,1	68,4 ± 10,5
C. viminalis	–	9,9 ± 0,2	1,5 ± 0,1	39,2 ± 1,3
Liliaceae				
Aloe ferox	12,4 ± 0,3	57,4 ± 1,5	13,5 ± 0,1	27,5 ± 0,4
Iridaceae				
Watsonia meriana	11,6 ± 0,4	12,0 ± 0,4	5,0 ± 0,2	7,4 ± 0,2
Chasmanthe floribunda	41,9 ± 7,4	16,6 ± 1,5	1,6 ± 1,1	14,2 ± 0,8
Haemodoraceae				
Wachendorfia thyrsiflora	6,5 ± 0,3	12,0 ± 0,1	4,3 ± 0,3	4,3 ± 0,2
Proteaceae				
Leucospermum oleifolium	63,5 ± 2,3	59,0 ± 1,5	21,0 ± 0,4	8,8 ± 0,4
L. erubescens	76,6 ± 3,5	20,3 ± 0,3	21,0 ± 0,2	5,5 ± 0,3
L. cordifolium	–	30,6 ± 0,5	10,2 ± 0,2	7,5 ± 0,3
L. cuneiforme	94,7 ± 2,8	21,0 ± 1,3	13,2 ± 0,3	14,2 ± 0,4
L. catherinae	–	19,0 ± 0,2	11,7 ± 0,2	12,7 ± 0,2
Protea eximia	–	22,5 ± 0,2	7,0 ± 0,2	24,5 ± 0,2
Mimetes cucullatus	–	22,2 ± 0,3	13,0 ± 0,2	5,5 ± 0,2
Grevillea robusta	–	21,7 ± 0,4	9,0 ± 0,3	55,0 ± 2,8

$n = 6$ for volume, Na and K concentrations

$n = 10$ for sugar concentrations.

The only other information on nectar ions comes from an earlier study by Waller, Carpenter & Ziehl (1972), who analysed the honeystomach contents of honey bees foraging on a variety of crop and other plants. Combining all the available data on nectar ion concentrations (Waller *et al.* 1972; Hiebert & Calder 1983; Nicolson 1990; and the present study) gives mean values of 5,6 ± 0,8 mmol for sodium and 19,2 ± 2,7 mmol for potassium (n = 51 species: the anomalous data obtained by Waller *et al.* for onion flowers have been omitted). There is great variation between species, however, and regression analysis shows that the concentrations of these two ions in floral nectars are in fact slightly negatively correlated (r = 0,0076).

Nectar is generally derived from phloem sap (Durkee 1983). Levels of sodium in phloem sap are two orders of magnitude lower than those of potassium (Ziegler 1962, cited by Dadd 1968), so the predominance of potassium over sodium in floral nectars is not unexpected. However, Table 1 shows that sodium concentrations in some floral nectars are surprisingly high.

The tables on the mineral composition of honey presented by White (1975) show great variability among samples, but it is clear that potassium concentrations are far higher than those of sodium. These data cannot, however, be compared directly with measurements made on floral nectars because honey production involves processing and concentrating of the nectar by house bees.

Bee and bird pollination

Although there are differences in sugar concentration between bee- and bird-pollinated flowers (e.g. Pyke & Waser 1981), it is difficult to say, with the limited data available, whether honey bee and hummingbird flowers differ in ionic characteristics. Firstly, both the present study and that of Hiebert & Calder (1983) include flowers which are visited by both bees and birds. *Leucospermum,* of which five species are included in Table 1, is a bird-pollinated genus which is utilized extensively by honey bees when the latter are present at high densities (Rebelo 1987). Secondly, mean values have been influenced by the plant families chosen for analysis (e.g. high potassium concentrations in the Ranunculaceae; Hiebert & Calder 1983). Thirdly, nectar sugar (and presumably ion) concentrations are greatly affected by environmental conditions, as described for another species of *Echium* by Corbet (1978). Hiebert & Calder (1983) found differences in composition when they compared nectars of some species in two successive years, and in different seasons. Similarly, values for nectar volume and sugar, sodium and potassium concentrations differing greatly from those in Table 1 have been measured at different times for *Grevillea robusta* and *Leucospermum oleifolium* (Proteaceae) (Nicolson and W.-Worswick, unpublished data). Ambient temperatures and relative humidities were not measured either in the present study or in that of Hiebert & Calder (1983), because in both cases the aim was to demonstrate the sodium and potassium concentrations available to pollinators, not to provide a definitive analysis of the nectars.

The genus *Erica* would be excellent material for a direct comparison of ionic or other constituents in the nectar of bee- and bird-pollinated flowers. Rebelo, Siegfried & Oliver (1985) have classified the 426 species in the south-western Cape according to their pollination syndromes: 80% are pollinated by insects, and 15% by sunbirds.

Table 2 Ionic composition of body fluids of honey bees foraging on three different nectars

Species	Ion	Nectar	Haemolymph	Urine
Echium	Na	5,0 ± 0,3	35,7 ± 0,6	5,5 ± 1,5
fastuosum	K	11,5 ± 0,3	26,5 ± 0,3	18,8 ± 0,6
Eucalyptus	Na	12,0 ± 0,3	39,8 ± 0,7	43,7 ± 0,5
melliodora	K	16,2 ± 0,3	24,7 ± 0,4	47,0 ± 0,5
Leucospermum	Na	21,0 ± 0,4	37,4 ± 6,4	14,4 ± 2,9
oleifolium	K	8,8 ± 0,4	24,4 ± 5,5	11,7 ± 4,4

Na and K concentrations in mmol

n = 6 for nectar, 10 for haemolymph and urine.

Body fluid composition in relation to nectar ions

In honey bees foraging on three different plants with nectars varying widely in ionic content, haemolymph sodium and potassium concentrations were closely regulated (Table 2). The values shown are slightly lower than the 47 mmol sodium and 27 mmol potassium given by Florkin & Jeuniaux (1974) for the haemolymph of *Apis mellifica* adults (subspecies not named).

In the case of bees foraging on *Echium fastuosum* and *Leucospermum oleifolium,* there was reasonable agreement between the levels of sodium and potassium in the nectar and the urine (Table 2). However, bees foraging on *Eucalyptus melliodora* produced urine with sodium and potassium concentrations approximately three times as high as those in the nectar. This contrasts with the carpenter bee *X. capitata,* which when foraging on *Virgilia divaricata* forms a urine with the same low sodium concentration (3–4 mmol; Nicolson 1990). Carpenter bees are solitary and forage only to satisfy their own needs and those of their offspring, whereas honey bee foragers gather nectar for the colony as a whole. We might expect nectar and urine concentrations of individual bees to be less closely related in social species.

There is little evidence in the literature that honey bees may show preferences for different ion concentrations in nectar, with one interesting exception. Unusually high levels of potassium (up to 300 mmol) were measured in the nectar of onion flowers by Waller *et al.* (1972), who suggested that this reduced the attractiveness of onion flowers to bees. They found that potassium content had a marked effect on the acceptability of sugar solutions to honey bees foraging at a feeder. Artificial food sources have been used extensively in research on the feeding preferences of honey bees: one such experiment has shown that a colony need for water can affect choice of sugar concentration (Ohguchi & Aoki 1983). Carefully designed experiments of this type would be ideal to determine the ionic preferences of honey bees.

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