Winter absconding as a dispersal mechanism of the Cape honeybee

The dispersal characteristics of the African honeybee, *Apis mellifera scutellata*, resulted in a greatly mobile hybrid front in the New World, but in Africa its hybridization zone with the Cape honeybee, *Apis mellifera capensis*, appears very stable.[1] The maintenance of stable hybrid zones is predicated on a balance between dispersal and selection.[2] Knowledge on the extent of gene flow from either race is in its infancy, and the probability of successful dispersal by either race has not yet been considered. Both *capensis* and *scutellata* are notorious for absconding, *capensis* the more so for resource-related seasonal absconding in winter.[3] The two races also differ fundamentally in the ways they conserve heat both behaviourally and physiologically.[4] We investigated the energy consumption and colony survival characteristics of *capensis* in terms of winter absconding in a climate with cycles of warm days interspersed with cold days. These are compared with calculated values for *scutellata* to assess whether *capensis* might have a directional gene flow advantage over *scutellata* in their zone of hybridization.

Materials and methods

Sixteen colonies of the Cape honeybee, *Apis mellifera capensis*, from Port Elizabeth were used in our study. Four colonies (control group) were killed after they were heavily smoked to induce engorgement of honey from their combs. Eight other colonies were collected after smoking and caged in screened hives and placed outside and allowed to succumb (when about 75% of the bees died), four of these during a winter warm spell (warm-starved) and four during a cold period (cold-starved). Hourly temperatures were recorded during these periods. Lastly, four colonies were caught on the move or were very recently settled but without any stores and were killed immediately. The colonies were smoked to induce them to engorge themselves with comb honey because absconding colonies carry food reserves.

All colonies were oven-dried to constant weight at 60°C and average individual bee weights obtained from samples (n = 250) of the whole colonies. Similarly, colony size was calculated from colony mass and the mass of individual bees per sample. The dried bees were powdered in an ultra-high-speed hammer-mill (Retsch, Germany) and samples taken for microcalorimetry (Gallenkamp, UK). In addition, samples of a local honey (*Scutia myrtina*) were lyophilized and measured calorimetrically. Plant 'sugar values' (= mg of sugar per flower per 24 h) from 66 species of plants[5] were used to establish a probable average for any flower, and then converted to energy equivalents, which was 0.87 mg of sugar or 13.4 J per flower per 24 h. Data were analysed with an ANOVA.

Weather conditions during winter for 10 localities were analysed for suitability for possible absconding. Five localities were chosen from the northern side of the *capensis* area and five from the southern side of the *scutellata* area. Temperature data for May–August of 1988–1992 were obtained from the daily weather reports of the Weather Bureau. Since the trend for each locality was so similar for the quinquennium, the data for 1991 were used because they were the most complete (but still contain a few gaps). A temperature of 15°C was chosen as the baseline separating warm and cold days, because temperatures above 15°C are energetically favourable to honeybee flight[4] and a few degrees below which the bees will not fly.

To assess the problems of nest construction at a new site after an absconded colony had settled, we measured the kinds of cells (worker/drone) built under queenright–broodright conditions and then 30 days after the same colonies had been made queenless and broodless. To preclude introgression, colony manipulations were made *in situ* at localities that included pure *capensis*, pure *scutellata* and a range of hybrids (Table 1). Data were analysed using the Kruskal-Wallis test.

Table 1. Comb cells and queen cells constructed by queenright–broodright and queenless–broodless colonies of *capensis*, *scutellata* and their natural hybrids.

	Queenright–broodright		Queenless–broodless		
Locality	Queen cells	Coefficient of variance	Colonies	Worker/drone cell ratio	Queen cells
Port Elizabeth[c+]	4.8 ± 0.2	3.1 ± 0.3	1–9	1:0	9
Addo[c+]	4.8 ± 0.1	2.8 ± 0.4	1	1:0	12
			2	2:1	13
			3	4:1	8
Fort Beaufort[c]	4.8 ± 0.1	4.0 ± 1.7	1	1:1	5
			2	2:1	5
			3	20:1	5
Stutterheim[c]	4.9 ± 0.3	5.2 ± 1.9	1–2	2:1	2 each
			3	1:0	1
Queenstown[s]	4.8 ± 0.2	4.8 ± 2.4	1–2	1:0	10 each
Molteno[s]	5.0 ± 0.2	3.8 ± 1.1	1–2	1:0	1 each
			3	10:1	1
Pretoria[s+]	4.9 ± 0.1	2.6 ± 0.3	1–3	0:1	–

[c+]Pure *capensis*, [c]predominantly *capensis*, [s]predominantly *scutella*, [s+]pure *scutellata* (Hepburn and Crewe[1]).

Results and discussion

The colonies were all small, averaging about 5 000 bees each. The constant dry weights of the bees were: (A) engorged controls from settled colonies averaged 40 ± 4.6 mg/bee; (B) cold-starved, 22.8 ± 1.9 mg/bee; (C) warm-starved, 21.4 ± 0.8 mg/bee, and (D) recently settled colonies, 25.4 ± 3.3 mg/bee. The weights of the group A bees were significantly greater than those of B, C and D, none of the last three differing significantly from one another (Scheffe's test). The colonies caged during the warm winter spell died in about 3 days, those of the cold period in 4 days.

The maximum amount of unripe honey (from uncapped honeycomb cells) that both starved groups could have imbibed just prior to caging would be about 18 mg/bee (the difference between group A and the average of groups B and C). Calorimetric values for a lyophilized local honey yielded a mean of 15.4 J mg^{-1} for the solid sugar product. Correcting this for the water content (~ 15%) of a dilute unripe honey such as the bees would have taken up from their combs when they were smoked gives about 7–8 mg of solid sugar fuel stored in the honey stomach, or roughly about 116 J/bee, with a maximal capacity of 294 J/bee for a bee fully laden with ripe honey.

Using the experimental data of Worswick,[4] who established the different energy consumption rates for the two races at different temperatures, a metabolic budget was prepared from the known metabolic rate values for both *capensis* and *scutellata*. These indices were used to establish fuel consumption for both *capensis* and *scutellata* in relation to differences in temperature for the bees caged during a warm and a cold spell in winter (Table 2). Although the cold-spell bees lived a day longer than the warm-spell bees, comparisons are made for 72 h in each case (Table 2).

In the first instance the unit cost of basal metabolism (J per h per bee) at rest is significantly different between the two races, being 40% cheaper in *capensis* over a wide range of

Table 2. Energy consumption of *capensis* and *scutellata* bees at rest for the warm period (26–29 July 1992) and the cold period (9–12 August 1992) at Grahamstown.

	Warm period					Cold period				
		capensis		*scutellata*			*capensis*		*scutellata*	
Ambient temperature (°C)	Exposed time (h)	Unit cost* (J h^{-1})	Energy used at rest (J/bee)	Unit cost* (J h^{-1})	Energy used at rest (J/bee)	Exposed time (h)	Unit cost* (J h^{-1})	Energy used at rest (J/bee)	Unit cost* (J h^{-1})	Energy used at rest (J/bee)
0–10	32	0.77	24.7	1.3	40.9	65.25	0.77	50.4	1.3	83.4
10.1–12.9	16	0.86	13.7	1.6	25.0	6.75	0.86	5.8	1.6	10.6
13–16.9	16	1.2	18.9	1.9	30.6	–	–	–	–	–
≥ 17	8	1.5	12.4	2.3	18.1	–	–	–	–	–
Total	72	–	69.9	–	114.6	72	–	56.2	–	94.0

*Based on the data of Worswick.[4]

ambient temperatures including both warm and cold winter spells.[4] It is also significant that tight clustering in *capensis*,[4] coupled to a lowered metabolic rate, reduced average survival costs by 20% during cold periods. Nonetheless, the energy values estimated to be contained in the honey stomach of the *capensis* bees (about 116 J per bee prior to their death by starvation) are higher than the calculated values for the 72-h warm period of 69.9 J per bee and 56.2 per bee for the 72-h cold spell. The differences can probably be safely ascribed to variable water content of unripe honey and to the fact that, given higher temperatures, the bees scuttled around the cages and so were not actually resting.

The important differences in the fuel consumption costs for *capensis* and *scutellata* acquire special significance when placed in the context of autumn and winter absconding. Weather data for the winter of 1991 relevant to *capensis* and *scutellata* are shown in Fig. 1. On the *capensis* side of the hybridization zone the average number of cold days per locality is only 21. On the *scutellata* side of the zone the number of cold days averages 37, which are also colder on average than such days on the *capensis* side. More importantly, on the *capensis* side of the zone there is an average of only two spells of cold days lasting 3 or 4 days per locality which are always relieved by warm periods. On the *scutellata* side cold spells increase to an average of three per locality and several of these, particularly at Sutherland, are severe with sustained periods of unrelenting cold.

The combined weather data for the *capensis* and *scutellata* areas clearly show that any absconding colonies of *scutellata* would be exposed to far more unfavourable conditions once they have left the home nest than would similar absconding colonies of *capensis*. In a reciprocal situation *capensis* could swarm more cheaply than *scutellata* in the latter's area. However, while *scutellata* would expend less energy in the *capensis* area than in its own natural domain, the net cost would still exceed the average costs which *capensis* must pay in its own area. In consequence, *capensis* has a decided edge over *scutellata* throughout the hybrid zone. The probability of absconding and successful colony formation clearly lies with *capensis*, just from a consideration of the weather. Added to this risk must be the relative availability of additional flight fuel (dependent upon winter flowering), not losing their queen, finding new nesting sites and constructing suitable comb.

On the *capensis*, largely fynbos, side of the hybridization zone, there is a very high floristic diversity consisting of grassy, dwarf shrub and shrub-woodland[6] with late winter and spring flowering peaks. These peaks vary along an east–west gradient much as does the weather.[3] By contrast, the southernmost parts of the native *scutellata* area, Nama-Karoo and grassland biomes, consist of grassy to dwarf scrubland of moderate species diversity with annual flowering lows in autumn and winter.[1] This simply implies that absconding *capensis* will have an edge over *scutellata* in finding nectar. Indeed, using the plant sugar values from Crane,[5] an average blossom can be expected to provide 13.4 J per blossom per 24 h, or enough to keep a 70-mg worker alive and resting (at 1 J per h per bee) for half a day.

Ability to disperse will ultimately depend also upon flying speeds and costs and the distance a swarm can move in winter. Although there is a 100% variability in the measured and estimated costs of bee flight in the general literature, the most recent data of Balderrama *et al.*[7] are taken for purposes of calculation because they measured metabolic power of bees in free flight both gravimetrically and by respirometry, thereby obtaining a mean value of 12.84 mg sucrose h^{-1} or 10.1 ml O_2, which converts to about 210 J per bee per h for fast flight at 7 m s^{-1} (24 km h^{-1}). Assuming that the average absconding bee leaves the nest with between 116 and 294 J of solid sugar fuel, which provides between 35 and 84 min sustained flying time over a possible distance of 15 to 35 km, we estimate swarm speed at between 10 and 15 km h^{-1} but, because swarms do not fly in bee-line fashion but in a more meandering way like the drifting of rising smoke, this would reduce the effective dispersal potential to between 6 and 8 km h^{-1}. Given a suitably warm winter's day in the fynbos, absconding/migrating should easily cover the 32 km reported by Moore.[8]

There must inevitably be a degree of natural attrition of swarm bees and this inference is readily supported by the common occurrence of *capensis* swarms of tennis-ball size, units uneconomical for heat conservation. This problem is overcome by the coalescence of several-to-many small swarms into larger ones, thereby conferring better heat-saving qualities with the reduction in the total surface area and the increase in volume. A final consideration is that of comb construction at a new nest site once the bees have settled, a problem exacerbated by the possibility of queen loss. And, indeed, queenless swarms of *capensis* are common enough. The sizes of cells that honeybees construct in their combs are readily manipulated by selective breeding.[9] This trait is particularly tantalizing because queenless–broodless *capensis* swarms build only worker cells[10] while similar *scutellata* colonies build only drone-sized cells.[11]

The kinds of comb construction by queenless–broodless colonies of *capensis*, *scutellata* and their natural hybrids are given in Table 1, which show that pure *scutellata* colonies constructed only drone cells whereas pure *capensis* colonies constructed worker cells. In the hybrid zone all of the queenless–broodless colonies produced worker comb and nearly half

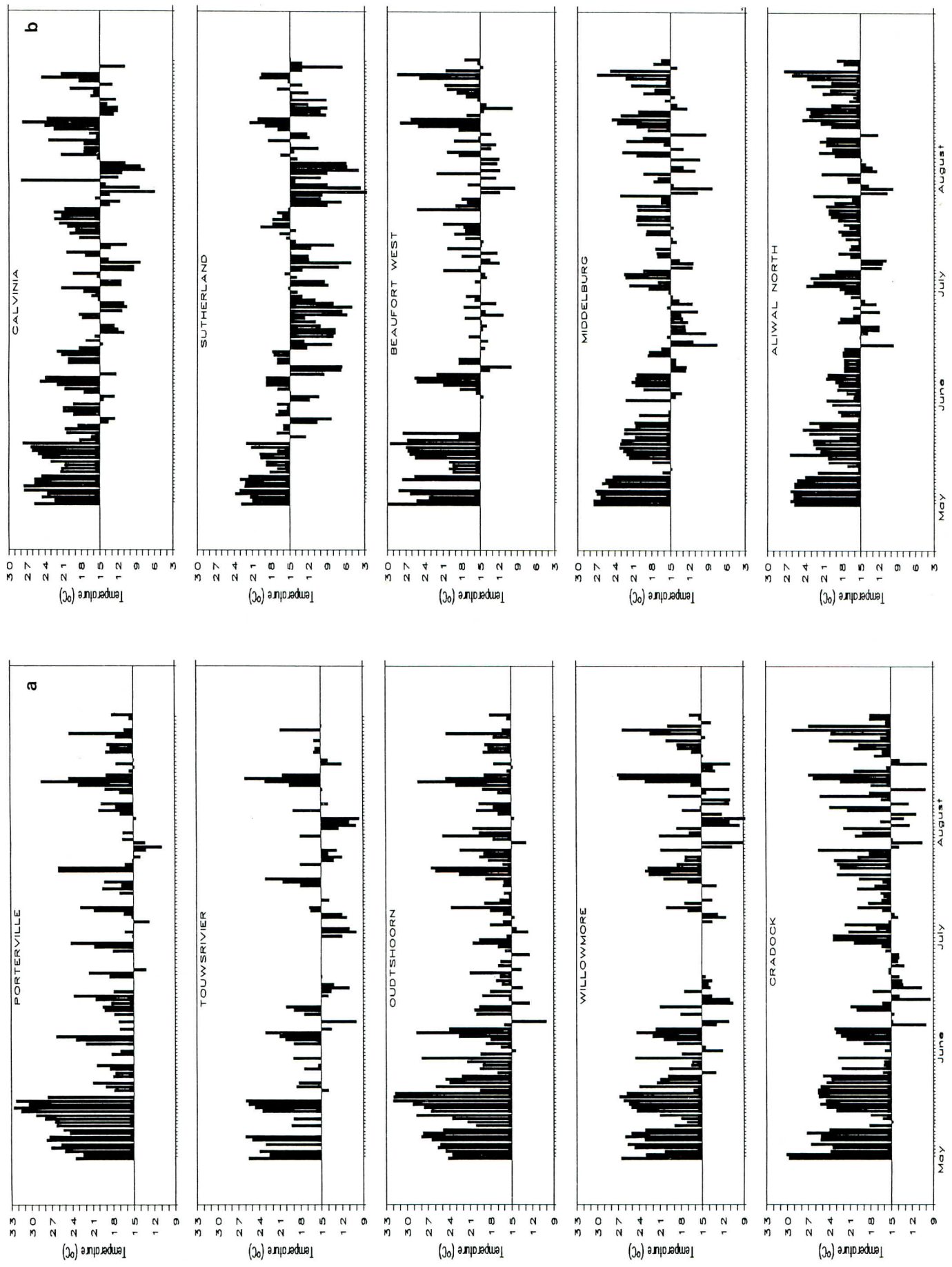

Fig. 1. Daily maximum temperatures (May–August 1991) for localities spanning the width of the *capensis* zone (a) and the *scutellata* zone (b). in a west (top of figure) to east direction (bottom of figure). Values above 15°C represent warm days (suitable for honeybee flight), gaps indicate periods for which no weather data have been collected at a particular locality.

of them also constructed drone cells. There is no clear relationship between the ratio of worker to drone cell areas and the fact that the hybrids were predominantly *capensis* or *scutellata*, but the unmistakeable characteristic of *capensis* to construct worker-sized cells when queenless and broodless penetrates all of the hybridization zone assayed (Table 1). Emergency queen-cell construction by queenless–broodless colonies is, for obvious reasons, a previously unreported aspect of honeybee biology. In such circumstances, *capensis* can construct emergency queen cells and rear queens, whereas *scutellata* cannot. All of the hybrids produced some queen cells containing larvae or pupae after having been queenless and broodless (Table 1). The significance of these data is that, even if they lose their queen, *capensis* swarms have the physiological and genetic capacity to requeen and the behavioural programmes necessary to build comb cells of the required kind; *scutellata* does not.

We conclude that *capensis* enjoys climatic, vegetational, metabolic and reproductive advantages over *scutellata* throughout the hybrid zone. Moreover, risk assessment of absconding in winter shows that *capensis* has the capacity to disperse within the hybrid zone at a time when *scutellata* cannot. Moreover, the export distances of interest of about 100 km is well within the capacity of the *capensis* swarm in winter.

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Effects of indomethacin on furosemide-induced diuresis in the presence and absence of captopril and labetalol in healthy, salt-replete men

This study examines the extent to which antagonism of endogenous noradrenaline and angiotensin II would offset changes in furosemide diuresis resulting from the indomethacin-mediated reduction in prostaglandins in sodium-replete volunteers. Six healthy male volunteers received furosemide (40 mg) intravenously on three occasions; once on its own and twice after oral pretreatment with indomethacin (200 mg) with and without captopril (50 mg) and labetalol (200 mg). Indomethacin was administered 3 hours and captopril and labetalol 1.5 hours before the furosemide injection. The mean cumulative urinary furosemide excretion and excretion rate and sodium excretion rate did not differ significantly on the three regimens, while the percentage fractional sodium excretion was significantly reduced by indomethacin only at 60 min. Indomethacin significantly reduced furosemide-induced diuresis throughout the trial period of 5 hours. The mean total urine volume with furosemide alone was 3 236 ± 709 ml, with furosemide after indomethacin pretreatment 1 650 ± 430 ml and with furosemide after indomethacin plus captopril and labetalol 2 160 ± 354 ml.

The diuretic efficiency of furosemide was significantly decreased by indomethacin during the 30 to 180 min after furosemide administration, but this was not significantly opposed by captopril and labetalol. The results suggest that renal prostaglandins mediate furosemide-induced diuresis, but not natriuresis, and they imply that the local synthesis of vasodilatory prostaglandins is not required to maintain renal perfusion in the sodium-replete state in healthy subjects.

Background

The prostaglandins play an intermediary role in the process of natriuresis induced by furosemide[1] and the latter is associated with increased urinary excretion of prostaglandins.[2] The autacoids probably attenuate the effects of at least two renal vasoconstrictor substances, as the decrease in renal blood flow produced by either angiotensin II or noradrenaline is augmented after pretreatment with indomethacin.[3] Furthermore, they have been shown to inhibit the chloride transport process in the isolated perfused medullary thick ascending limb of Henlé,[4] whereas Ganguli *et al.*[5] demonstrated a sharp rise in medullary sodium chloride content after indomethacin therapy. However, Passmore *et al.*[6] recently suggested a mediatory role for renal prostaglandins in furosemide-induced diuresis, but not natriuresis.

The indomethacin–furosemide interaction is well documented.[7] It not only involves a prostaglandin-related pharmacodynamic interaction and decreased renal clearance of furosemide, but indomethacin abolishes the acute, furosemide-induced rise in renin and thus, by inference, plasma angiotensin II.[1,8] The purpose of this study was to ascertain to what extent antagonism of the endogenously produced noradrenaline and angiotensin II would offset the changes in furosemide diuresis which result from the indomethacin-mediated reduction of prostaglandins in sodium-replete volunteers.

Patients and methods

Six healthy ambulatory male volunteers, mean age 21.7 years and mean weight 76.3 kg, were the subjects. None smoked or had cardiac, hepatic or renal disease. The protocol had been approved by the Ethical Committee of the University of Pretoria and the volunteers gave their written informed consent.

A crossover experimental design was followed allowing at least a 2-week interval between treatments. The volunteers were requested to refrain from adding raw salt to their food but no attempt was made to modify their diet. However, on each day before admission to the Institute at 06:00, three standard meals low in sodium content were provided. Then followed an