THERMOLABILITY, HEAT TOLERANCE AND RENAL FUNCTION IN THE DASSIE OR HYRAX, *PROCAVIA CAPENSIS**

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ABSTRACT

In a series of experiments, designed to examine renal function and thermoregulation in the dassie, the following observations were made: The dassie is unable to exist indefinitely on a dry diet without water. After 8 days without water, feed intake ceases. Water consumption is relatively low, amounting to 45,7 ml/kg, which suggests efficient renal function. Faecal water loss is minimal when the animals are dehydrated. A faecal moisture value as low as 35 per cent was obtained after nine days of dehydration. The capacity of the dassie kidney to concentrate electrolytes and urea is very high. The maximum recorded osmolality of the urine was 3 088 mOsm/kg, which is comparable to that of the camel. The most unusual feature of renal function in the dassie is the excretion of large amounts of undissolved calcium carbonate in the urine. The body temperature at comfortable ambient temperatures (20C) was lower than expected for a mammal of this size and may be implicated in spermatogenesis in the intra-abdominally situated testes of these animals. The dassie appears to be very thermolabile and has surprisingly low heat tolerance. Above 35C (ambient) the animals develop hyperthermia and exhibit fairly profuse nasal sweating. The upper incipient lethal temperature appears to be above 35C but less than 40C.

INTRODUCTION

Although a considerable amount of significant data has been recorded in regard to the behaviour and general ecology of *Procavia* (Sale 1965, 1966a, 1966b, 1970), the water economy of these animals has been neglected. The various factors which could influence the water economy are well known and in the case of mammals in general have been adequately reviewed by Chew (1965). Moreover, if the dassie is as resistant to desiccation as is popularly believed, then renal function in these animals should play an extremely important role in this regard. Apart from passing reference to the fact that these animals produce a "concentrated" urine no evidence is available on renal efficiency under either normal or stress situations. For this reason, then, the present investigation was undertaken to measure renal function under both normal conditions as well as under the stress of dehydration. In addition, an attempt was made to verify the limited data of Sale (1970) in regard to the thermolability and heat tolerance of the dassie. The purpose in examining these physiological parameters was to evaluate the ability of this species to survive in hot arid regions.

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PROCEDURE — RENAL FUNCTION STUDY

All the experiments were carried out in a temperature controlled room in which humidity, day and night temperatures and daylight length were automatically controlled.

Experiment 1

The purpose of this experiment was to investigate the effect of dehydration upon renal function. A total of five female animals was employed and these were housed individually in specially designed metabolism cages. The metabolism cages were constructed from metal wire mesh, coated with a synthetic plastic material. Faeces were retained on a fine gauge stainless steel wire-mesh tray and urine collected by means of a polyethylene funnel leading into a glass container. This container rested in crushed ice, surrounded by an insulated container of expanded polystyrene, maintaining the urine at a temperature of ±2C over a 24-hour period.

Prior to the experiment the animals were familiarised with their surroundings and tamed as far as possible over a four week period. The actual experiment was carried out over a period of 17 days. For the first six days the animals were allowed water and feed *ad lib.* From the seventh day to the sixteenth day water was withheld, while feed was still provided *ad lib.* On the seventeenth day the animals were once again allowed free access to water. Daylight temperature was maintained at 23C and night temperature at 19C throughout the experiment. In addition, a constant lighting regime of 14 hr. light and 10 hr. of darkness was maintained.

The animals were fed the same ration throughout the experimental period on an *ad lib.* basis. This ration consisted of 80 per cent lucerne hay and 20 per cent coarsely ground maize meal. The ration was provided in the form of large compressed pellets which ensured that minimum wastage and spilling occurred. An analysis of this ration showed it to contain 12,2 per cent crude protein, 30 per cent crude fibre, 3,6 per cent ether extract and 6,6 per cent ash on a moisture-free basis.

Each morning at the same time (0830 h) the cages and funnels were washed in detergent and rinsed with deionised water. The total weight of faeces and volume of urine was recorded daily. An aliquot of both urine and faecal matter was obtained, sealed in air-tight containers and frozen for later chemical analyses. Whenever possible aliquots of freshly voided faecal matter were collected and treated in the same way as the above. The daily aliquots were analysed for moisture content in order to determine the total dry matter in the faeces and the fresh samples were analysed for moisture content in order to assess the effect of dehydration upon the moisture content of the faeces.

The urine samples were centrifigued at 3 000 rpm for 20 minutes in a clinical centrifuge in order to remove a white precipitate which was present in most samples. The supernatant was then analysed to establish the sodium, potassium, urea and chloride concentration of the urine. In addition, representative samples from one individual were analysed for total nitrogen and uric acid content and the osmolality of all samples was determined. The following methods were employed: sodium and potassium were determined using standard flame photometric techniques (Instrumentation Laboratory). Chloride determinations were carried out using an automatic chloride meter working with electrolytically generated silver ions (Buchler Cotlove).

Urea content was analysed on the basis of the diacetyl monoxime reaction (Technicon autoanalyzer method). Total nitrogen was determined by the micro-Kjeldahl method, uric acid by incubating the sample with uricase (Storey 1964), and osmolality on a direct reading osmometer (Advanced Instruments 31 LAS). All moisture determinations were done by drying to a constant weight at a temperature of 95C. Daily water and feed intake were recorded and the animals were weighed at the beginning and at the end of the experimental period.

On completion of the experiment it was discovered that one of the animals had exhibited haematuria throughout the experiment. All data for this animal were discarded and the mean values reported under results were obtained from four animals.

Field Studies

In order to substantiate certain laboratory observations six wild dassies were shot under field conditions. Blood and urine samples were collected immediately after killing the animals and preserved for chemical analysis. Samples were also collected of dry urine which had collected and dried on rock surfaces in characteristic white accretions. This material was also analysed chemically.

RESULTS AND DISCUSSION – RENAL FUNCTION STUDY

Experiment I

Water Consumption

Theoretically, the amount of water consumed per unit of body weight should give some indication of the organism's degree of adaptation to an arid environment. This implies that the well adapted organism will make more efficient use of water and will therefore require less free water. Nevertheless, this parameter is open to misinterpretation in view of the many factors such as ambient temperature and nature of the diet which can influence it greatly. For example, Gauthier-Pilters (1961) found that daily water consumption by dromedaries in the Sahara varied from 23 liters during July to zero during the cooler months of October and November. Also, Macfarlane (1964) has found that the water intake of Merino sheep doubles when they are shifted from a diet of oat chaff to lucerne hay.

Chew (1965), in reviewing the free water intake of mammals in captivity, concludes that although the amount of water drunk by normally hydrated animals is correlated with body weight, there is perhaps a closer correlation with energy intake and body surface area. Examples of daily free water intake cited by him are as follows:

Rattus norvegicus albina	—146 ml/kg
Peromyscus leucopus noveboracensis	—116 ml/kg
Pigs growing	—186 ml/kg
Camelus dromedarius	—61 ml/kg*
Shorthorn cattle	—51 ml/kg
Sheep, Corriedale	—39 ml/kg
Elephas maximus	—38 ml/kg

* This figure obtained from Macfarlane (1964).

The above data relate to animals kept at comfortable temperatures (20–25C) and fed on a dry diet with the exception of the camel, which was foraging freely at a mean maximum of 35C, and the elephant which was exposed to an average temperature of 10C. In all probability the figure obtained for the camel would be lower at a temperature of 20C and that for the elephant, somewhat higher.

In the present investigation at a similar ambient temperature the mean daily water intake of the dassie on a dry diet was 140,4 ml for the first six days of the experiment. The mean weight of the animals was 3,07 kg which meant the relative water intake was 45,7 ml/kg. When this figure is compared with the data given above for other species it appears that the dassie, although not exhibiting as low an intake as some, is nevertheless among the lowest and suggests that the animal makes efficient use of ingested free water. After a period of 10 days dehydration, mean water consumption rose to 245 ml, which apparently was sufficient for rehydration of the tissues as on the following day (day 18) the mean consumption fell to 45 ml.

Hanse (1962) found that the mean water consumption of dassies on a dry diet was 36 ml per day. However, he has not described the weights of the animals nor the conditions under which they were fed and it is therefore not possible to make a direct comparison with his data.

Feed intake

An important consideration when evaluating the adaptation of mammals to an arid environment is to study the effect of withholding water on daily food consumption. For example, when water is suddenly withheld from *Peromyscus* feed intake drops from 37–50 per cent on the first day (Chew 1951). In the case of albino rats there is a decrease of 60 per cent on the first day (Adolph 1943). In domestic rabbits feed intake declines rapidly until it is less than 2 per cent of normal after 3 days (Cizek 1961). Merino sheep cease eating after 2 days without water (Macfarlane *et al.* 1961).

In contrast to these species the feed intake of the camel remains normal until it has lost 20–25 per cent of its body weight (Schmidt-Nielsen *et al.* 1956). Moreover, the kangaroo rat (*Dipodomys spectabilis*) requires no water when fed a diet high in carbohydrate (Schmidt-Nielsen *et al.* 1953). The results from the present investigation show that on the first day after water had been withheld the mean feed intake in the dassie fell approximately 20 per cent. On the third day of dehydration the animals still maintained ±43 per cent of their original intake, while on the seventh day the intake had declined to a negligible amount (Fig. 1). It should also be noted that on the seventh day the animals had lost only 13 per cent of their original body weight. Therefore, when judged on the basis of feed intake during dehydration, it appears as if the dassie occupies an intermediate position between those species which are extremely well adapted to a desert environment and those which are not. Nevertheless, it is clear from these data that the dassie is unable to exist indefinitely without free water on a dry diet. On day 15 and 16 the feed intake for all animals was zero. This result would at first appear to be a direct contradiction of the popularly held belief that dassies are able to exist without access to free water. This, however, may not be so, as under natural field conditions, preformed water could be obtained by feeding on succulent vegetation and from water absorbed by plants when the relative humidity of the atmosphere is high. The latter source of water is considered of great importance to desert antelope by Taylor (1969) and may play an important role in the water economy of the dassie. The late feeding time of the dassie, midmorning as opposed to first light and at night in the case of antelope, may however preclude this item as an important source of moisture for these animals. The problem can only be resolved by further careful field investigations.

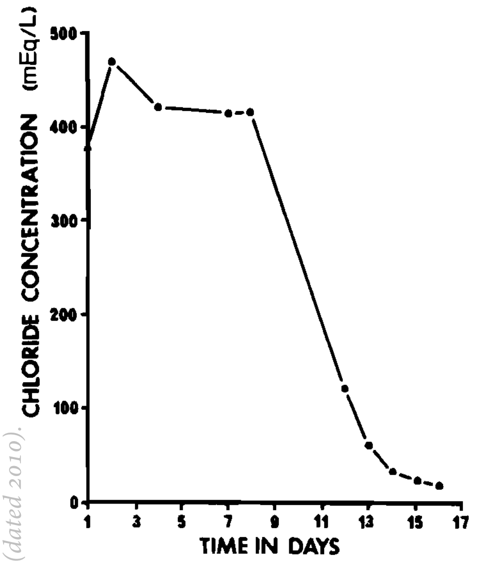

FIGURE 1
Mean feed intake during the experimental period. Water was withheld from day 7 to day 16.

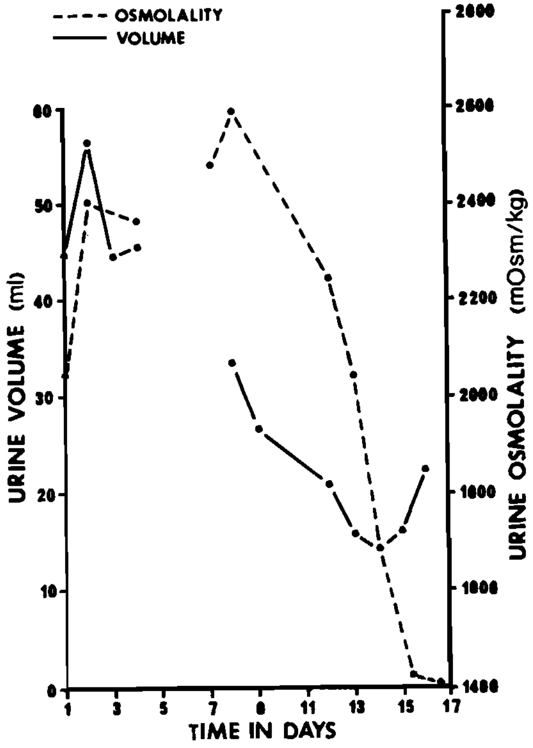

FIGURE 2
Mean urine volumes and osmolality during the experimental period. Water was withheld from day 7 to day 16.

Urine volume

The data pertaining to the effect of dehydration upon urine volume in the dassie is graphically illustrated in Fig. 2. When water was provided *ad lib.* the mean urine volume varied between 42,0 and 56,5 ml per day. During dehydration this volume declined gradually to reach a minimum of 14,3 ml on day 14, the eighth day of dehydration, the minimum volume during dehydration being less than one third of the original volume. It should, however, be noted that after the eighth day of dehydration urine volumes rose slightly and, on the first day after water provision following the dehydration period, urine volumes declined very sharply reaching zero in two of the four animals. This sharp decline in urine volume following the consumption of as much as 240 ml after 10 days of dehydration can possibly be explained as follows. During the last five days of dehydration (days 12–16) the urine volumes stabilised between 14,3 and 22,5 ml while the feed intake during this period was negligible. This meant that the animals were relying upon tissue catabolism to furnish essential nutrients and metabolic water for vital functions. On day 17, at the end of the dehydration period, the animals consumed sufficient water to rehydrate their tissues and the need for the production of metabolic water was obviated. Moreover, the need for excreting metabolic end products arising from tissue catabolism for the purpose of producing metabolic water was also obviated, hence the extremely low urine volumes which were recorded.

Comparing the above results with those obtained in other species it is evident that the dassie does not reduce its urine volume markedly in response to dehydration. For example, during dehydration merino sheep show a reduction in urine volume from 1 600 ml per day to 300 ml after three days, and after the sixth day volumes reached a minimum of 100 ml (Macfarlane *et al.* 1961). In the white rat a 24-hour fast without water causes a reduction of 84 per cent in urine volume (Heller 1949). It seems that in the case of the dassie, renal function is geared to a low water intake and functions at near maximum efficiency when the animals are on a dry diet, even when provided with water *ad lib.* Apparently the animals drink just sufficient water to maintain their water balance and are not able to respond to dehydration by a dramatic reduction in urine volume. If, however, the animals had been fed on fresh green material with a high water content the reduction may have been more marked.

Finally, although the reduction in urine volume illustrated in Fig. 2 may appear to be considerable, it is not a true reflection of the water reabsorbing capacity of the kidney when it is compared with the concomitant decline in osmotic concentration of the urine illustrated in the same figure.

Faecal excretion

Faecal water loss represents an important water loss in most animals. In all true desert species this is minimised by reabsorption in the terminal portion of the digestive tract and the faeces are usually excreted in the form of dry pellets. Chew (1965) has summarised the limited data available on this subject. He concludes that diet, particularly cellulose, has an important effect on the moisture content of the faeces. Furthermore, faecal water loss is not apparently related to either size or the taxonomic position of the animal and most species respond to dehydration by reducing faecal water loss. Schmidt-Nielsen *et al.* (1956) found that the faecal water content in camels amounted to 52 per cent when the animals were fully hydrated and declined to 43 per cent during dehydration. These are among the lower values quoted by Chew (1965) as compared to the highest, 82 per cent in Shorthorn cattle.

The results obtained for the dassie in this investigation are shown in Fig. 3. These data show that faecal excretion, as measured by the actual weight, declined sharply during dehydration. This decline is in part due to the marked reduction in feed intake as well as a reduction in water content. The former effect can be visualised more easily from the curve pertaining to dry matter excretion and the latter by comparison between the two curves.

These curves, however, do not show the exact percentage of moisture contained in the faecal matter which has been freshly voided. For this purpose freshly voided samples were

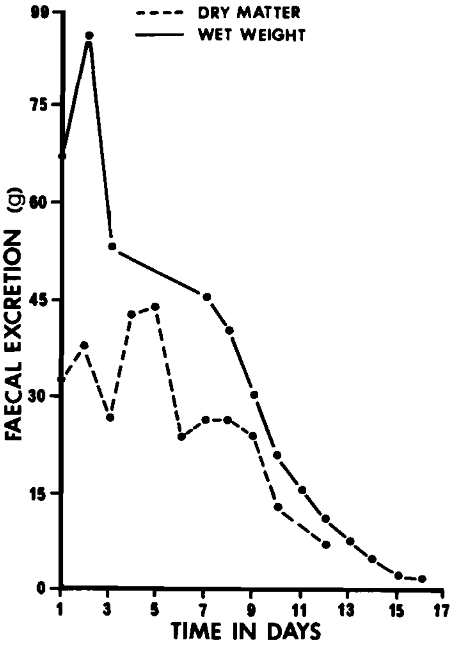

FIGURE 3
Mean faecal excretion during the experimental period. Water was withheld from day 7 to day 16.

collected and analysed for moisture. These results showed that the percentage of faecal moisture varied between 58–70 per cent during the period of water administration, while one sample, on the tenth day of dehydration, had as little as 35 per cent moisture. Owing to the minimal faecal excretion rate at the end of the dehydration period it was not possible to collect a sufficient number of fresh samples for accurate analyses and the above data do not allow any definite quantitative conclusions. Nevertheless, from the limited data and careful observations it was clear that the dassie minimises water loss via this pathway when under the stress of dehydration, and that the digestive tract is well adapted to water reabsorption.

Urinary electrolytes

The concentrating ability of the kidney can be assessed in part by measuring the concentration of urinary electrolytes. The results obtained in respect of the concentration of urinary electrolytes in the dassie are presented in Figs. 4 and 5.

These data show that in the case of all three electrolytes, sodium, potassium and chloride, maximum concentrations were reached within the first 2 days of the dehydration period. Moreover, these values were not appreciably greater, with the possible exception of sodium, than during the *ad lib.* period of water intake. Furthermore, all these electrolytes showed a marked reduction in concentration during the latter part of the dehydration period which corresponds to the decline in feed intake and urine volume discussed previously.

It would appear then that, even on *ad lib.* water intake, renal function was near maximum efficiency and continued while feed intake was still appreciably high during the first two days of dehydration. Thereafter, however, feed intake and therefore electrolyte load decreased sharply and, apparently, electrolyte concentration as a result declined simultaneously. The simultaneous and marked decline of volume and concentration can be interpreted as a decline in net excretion rate as well.

With regard to the maximum values obtained for electrolyte concentration, it can be concluded that the concentrating ability of the dassie's kidney is high. For example, the maximum mean value obtained for sodium was 177 mEq/L which is not particularly high when compared with say, the normal value for humans of 130 mEq/L. The maximum mean value obtained for chloride, 470 mEq/L, and potassium 494 mEq/L, are, however, very high when compared to normal values for humans of 140 mEq/L and 45 mEq/L respectively (Wootton 1964).

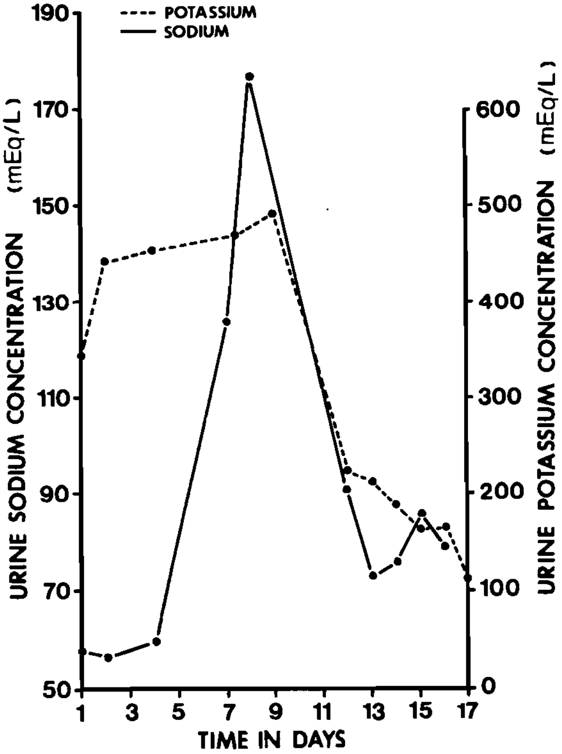

FIGURE 4
Mean sodium and potassium concentration of the urine during the experimental period. Water was withheld from day 7 to day 16.

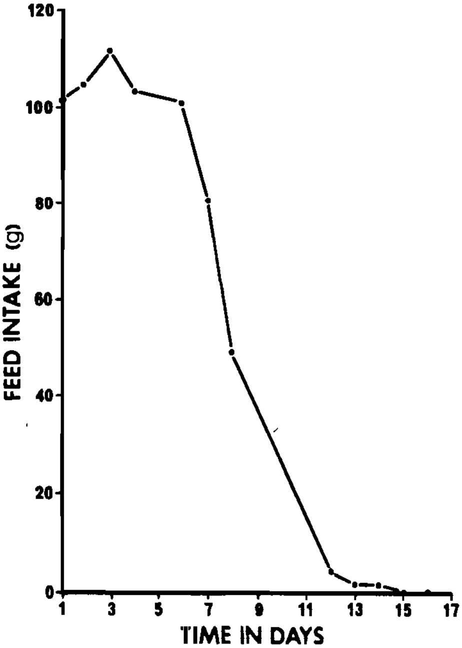

FIGURE 5
Mean chloride concentration of the urine during the experimental period. Water was withheld from day 7 to day 16.

The comparatively low concentration of sodium and the very high concentration of potassium suggest that aldosterone secretion rate was near maximum prior to dehydration. This probably resulted in selective reabsorption of sodium at the expense of increased potassium excretion. The high potassium concentration must, however, also be attributed to the fact that the dassie is an herbivorous animal and as such is exposed to a high potassium load by the nature of its diet. Finally, if the electrolyte concentration curves are compared with the osmolality curve in Fig. 2 they are very similar. It would appear then as if the electrolyte content of the urine was the major influence on the osmolality of the urine.

Calcium carbonate

During the period of *ad lib.* water consumption, and while feed intake was still moderately high during the initial part of the dehydration period, a white precipitate always appeared in the urine. This precipitate was centrifuged down before aliquots were removed for sampling and it was found to be almost insoluble in water. When feed intake declined to a negligible amount the precipitate disappeared and only reappeared after the animals had resumed their normal feed intake after the dehydration period. The precipitate was, therefore, in all probability of dietary origin and at first it was thought to be a nitrogenous salt which precipitated out after the urine had become exposed to air. Qualitative analysis, however, proved that the salt consisted mostly of calcium carbonate.

The excretion of large amounts of undissolved calcium carbonate via the renal pathway is a remarkable feature of renal function in the dassie. Even allowing for the high calcium load in the diet of the animals, it is difficult to speculate on any possible physiological advantage of this excretory pattern. In mammals that have been studied up to now, excess calcium is mostly excreted via the gastro-intestinal tract into the faeces. The above excretory pattern certainly deserves further careful investigation, particularly in view of the possible medical implications of the problem.

Osmolality

The osmoconcentration, or more correctly in this case, the osmolality of the urine is a reflection of total solutes in the urine and as such is an excellent criterion for measuring the concentrating ability of the kidney. The osmolality of dassie urine before and during dehydration is graphically illustrated in Fig. 2.

The osmolality curve as discussed previously follows a similar trend to the electrolyte curves during dehydration. Moreover, it again appears as if renal efficiency was near maximum prior to dehydration. With declining feed intake electrolyte load declined and osmolality declined simultaneously. This decline in osmolality was accompanied by a decline in urine volume which means that the net excretion of solutes declined during dehydration. Urea is an exception to the latter generalisation and will be discussed later. The mean maximum osmolality achieved by the dassie was 2 800 mOsm/kg while the value for an individual animal was as high as 3 088 mOsm/kg. These values are indicative of a superior concentrating ability of the dassie kidney when compared with other mammals as follows:

Species	*Maximum urine conc. mOsm/kg*	*Reference*
Beaver	520	Schmidt-Nielsen *et al.*, 1961.
Man	1 160	West *et al.*, 1955.
Rabbit	1 390	Dolph *et al.*, 1962.
P. capensis	3 088	Present investigation.
Camelus dromedarius ..	3 178	Schmidt-Nielsen *et al.*, 1956.
Merino sheep	3 190	Mc Donald *et al.*, 1958.
Dipodomys spectabilis ..	6 000	Schmidt-Nielsen *et al.*, 1961.
Jerboa	6 500	Schmidt-Nielsen *et al.*, 1961.

The above data then show that, although the dassie exhibits a highly efficient renal concentrating ability, approximately equal to that of the camel, it is not as spectacular as that of the jerboa or kangaroo rat.

Nitrogen excretion

Total nitrogen excretion was only measured in one individual and these results are contained in Table 1.

TABLE 1

THE EFFECT OF DEHYDRATION UPON TOTAL URINARY NITROGEN IN AN INDIVIDUAL DASSIE. DEHYDRATION BEGAN ON DAY 7

Day	*Total nitrogen mg N/100 ml*
1	2 269
2	2 099
3	2 142
4	2 184
5	2 092
6	1 901
7	1 244
8	2 135
9	2 686
10	2 813
11	3 542
12	3 711
13	4 341
14	3 294
15	3 040
16	2 856

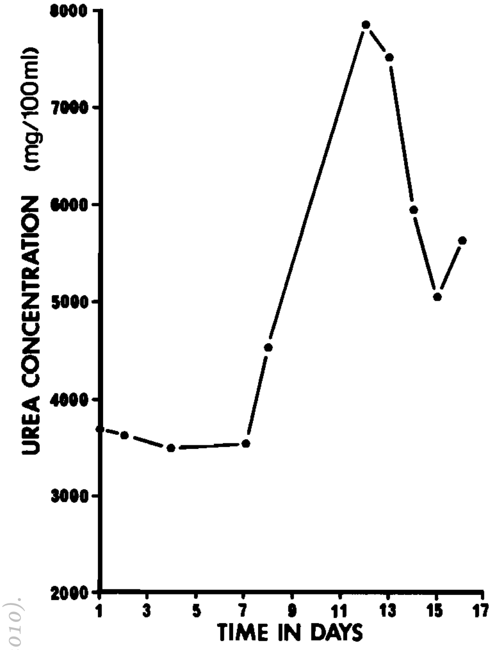

FIGURE 6
Mean urea concentration of the urine during the experimental period. Water was withheld from day 7 to day 16.

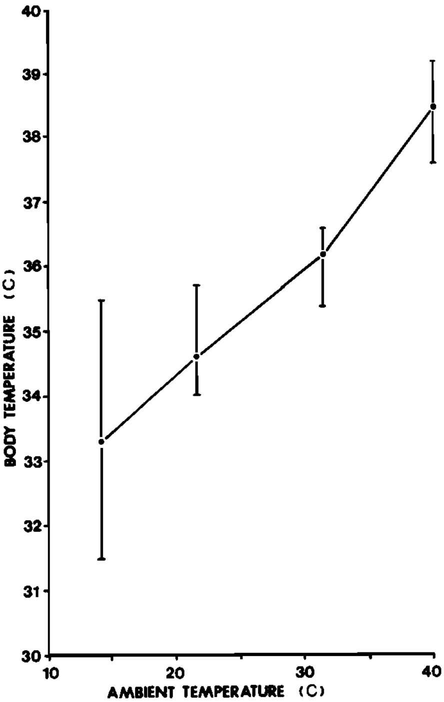

FIGURE 7
The effect of ambient temperature upon body temperature. The rise in ambient temperature took place over an 8-hour period. Circles represent mean values and T-bars the range.

The total nitrogen data contained in Table I indicate that this parameter, unlike the electrolyte concentration, did respond to dehydration by exhibiting a marked increase in concentration. The highest values were obtained between day 11 and 13 but eventually, as feed intake became negligible, these values also declined slightly. When the data in Table I are compared with the mean urea concentration illustrated in Fig. 6 it is evident that the trends exhibited by both solutes are very similar. It would seem then as if urea is the most important compound in the total nitrogen excreted by these animals. This fact is further borne out by a comparison of the absolute values for urea and total nitrogen excretion. The values obtained for uric acid concentration varied between 20,4 and 35,6 mg per 100 ml. It would appear, then, that this solute did not represent an important fraction of the total nitrogen excreted.

With regard to the maximum mean values obtained for urea and total nitrogen excretion, it is evident that the capacity of the dassie kidney to concentrate urea is very high. The maximum mean of 7 880 mg per 100 ml is more than five times the normal value for humans, 1 500 mg per 100 ml. It is, however, only slightly higher than the mean maximum obtained for sheep on restricted water intake, 7 340 mg per 100 ml (Erasmus 1967). Moreover, it is far less than the values obtained for *Dipodomys merriami* by Schmidt-Nielsen *et al.* (1948) namely 23 040 mg per 100 ml.

A comparison of the osmolality curve in Fig. 2 with the urea concentration curve in Fig. 6 shows that urea did not exert a major influence on osmolality as the curves exhibit opposite trends during most of the dehydration period. This confirms the previous deduction that osmolality of dassie urine is largely governed by its electrolyte content which is not unexpected. It is also not unexpected that, in spite of declining osmolality, volume and electrolyte content, the urea concentration increased during dehydration. The former declined as a result of declining feed intake, while obligatory nitrogen excretion continued as tissue catabolism increased with declining feed intake. The reduction in volume of the urine therefore was accompanied by an increase in urea concentration.

PROCEDURE – THERMOREGULATION STUDIES

Experiment 2

In this experiment an attempt was made to evaluate the heat tolerance of the dassie. Four animals were used and acclimated to a moderate temperature cycle namely 25C during the day and 19C at night, for four weeks prior to the experiment. After the acclimation period they were exposed for five days to a cycling temperature pattern consisting of 30C from 1000 h to 1500 h and 19C from 2000 h to 0930 h the following morning. During the period 1500 h to 2000 h the temperature gradually declined from 30C to 19C. This phase was followed by a similar period of five days with one difference namely, that the maximum temperature between 1000 h and 1500 h was increased to 35C. After 5 days the maximum temperature was increased to 40C and the experiment was terminated after one day's exposure to this temperature cycle. During the experiment feed and water intakes were recorded daily, both being provided *ad lib.* and the behaviour of the animals was observed.

Experiment 3

The purpose of this investigation was to measure the effect of both high and low ambient temperatures upon the body temperature of the dassie. Six animals, which had previously been acclimated to daylight temperatures of 25C and night temperatures of 19C, were employed. Each animal was confined in a cylinder of wire mesh in which it could lie comfortably but in which it was unable to turn around. Eight hours prior to the start of the experiment a thermistor probe was surgically implanted into the abdominal cavity of each animal through a small incision immediately posterior to the last rib. The thermistor probes were connected by means of extension leads to a tele-thermometer placed outside the temperature-controlled chamber. In this way it was possible to measure ambient and body temperature electronically from a remote position out of sight and hearing of the animals.

Five hours after the animals had recovered from the anaesthetic (pentobarbitone sodium and ether) their body temperatures and heart rates became stable. During the recovery period the chamber was kept at 21C and after the five-hour recovery period gradually reduced to 14C over a period of 4 hours. The temperature was kept at this level for 8 hr and then gradually increased to 40C over a period of 8 hr. In view of previous experience of the sensitivity of the animals to high ambient temperatures the period of exposure to temperatures above 35C was limited to 30 minutes. During the experimental period body temperature and ambient temperature were recorded at regular intervals. The experiment was conducted under conditions of constant light to avoid any possible effect of darkness upon metabolic rate and/or body temperatures.

RESULTS AND DISCUSSION – THERMOREGULATION STUDIES

Experiment 2

In this experiment an attempt was made to assess the heat tolerance of the dassie. As described previously, the animals were exposed to cycling temperatures allowing cooling at night at 19C, but every five days the ambient temperature during the day was increased by 5C from 25C to 40C. Feed and water were provided *ad lib.*

A study of the animals' behaviour during this period showed that, although the animals assumed an extended prostrate posture at 30C, they seemed to tolerate this temperature fairly well. At 35C, however, the animals appeared to be under considerable stress and a salt-like encrustation appeared on the dorsal surface of the nostrils or rhinarium. Also of great interest was the fact that, even though provided with water throughout the experimental period, the animals never used the available water during the day for cooling purposes. They only drank in the late afternoon at the customary time while ambient temperature was declining toward 19C. This behaviour pattern is in agreement with the field studies by Sale (1965) who established a bimodal feeding pattern, consisting of a morning feeding period about three hours after sunrise and an evening period about two hours before sunset. For this to persist in captivity under stress of high ambient temperature is remarkable.

The poor heat tolerance of the animals exhibited at 35C was confirmed on the first day they were exposed to 40C. Within 90 minutes of exposure to 40C and a relative humidity of 25 per cent, two of the animals died unexpectedly and the experiment was immediately terminated. It was concluded that the dassie has a very poor heat tolerance which was unexpected when one considers that its distribution includes hot, arid regions. The upper incipient lethal temperature for the dassie cannot be pinpointed from the above experiment but it would appear to be above 35C but less than 40C.

The salt-like encrustation which appeared on the dorsal surface of the rhinarium was removed and dissolved in distilled water. The colour of this precipitate was white while the margin of the precipitate was a light yellow suggesting the presence of sebum. Flame photometric analyses of the dissolved sample showed the presence of small amounts of sodium and potassium but no definite quantitative or qualitative conclusions could be drawn on the chemical nature of the precipitate.

At post mortem a portion of the rhinarium was removed and examined histologically. The sections were not prepared in series and therefore no definite conclusions in respect to the histology of this area can be made. Nevertheless, the sections revealed that the dorsal surface of the rhinarium is strongly keratinized, and contains numerous hair follicles. Sebaceous glands are also plentiful in this region. Beneath the sebaceous glands, superior to the nasal cartilage, there is a large glandular structure. This structure has the appearance of a convoluted – tubular gland, suggesting a sudoriferous function and is the probable source of the salt-like precipitate appearing on the exterior of the rhinarium.

FIGURE 8
Illustrating the large and engorged stomach of the dassie after a relatively brief feeding period.
Photo: P. C. Belonje.

Experiment 3

In this experiment thermoregulation at various ambient temperatures was examined. Great difficulty was encountered in restraining the animals during the experiment without causing discomfort. Their life in rock crevices demands deft manoeuvres within a confined space. It was therefore not surprising that, although the animals were confined in a narrow cylinder in which they could not turn around, they were able to rotate their bodies within the cylinder. Temperature data have been graphically illustrated in Fig. 7. These data clearly show how thermolabile the dassie is and how body temperature is influenced by ambient temperature. The poor ability of the animals to thermoregulate at and above 35C is also shown by the data and confirms the observations made in Experiment 3. In the case of one individual the body temperature fluctuated by as much as 6,7C. Moreover, at comfortable ambient temperatures (20C) the mean body temperature of the animals was much lower (34,6C) than would be expected in a mammal of this size. These comparatively low body temperatures may also be important in allowing spermatogenesis to take place in the intra-abdominally situated testes of the dassie. At this stage, however, the argument remains speculative. The above data confirm the limited data of Sale (1970).

Field studies

During limited field observations the feeding pattern established by Sale (1965) was confirmed. The animals fed for brief periods in the early morning and late afternoon although on cool days they will feed intermittently throughout the day. During the heat of the day they retreated to the less severe micro-climate of rock crevices. Even though feeding periods were brief, the animals were able to consume surprisingly large amounts of plant material in this period. In Fig. 8 the large distended stomach of a dassie is shown which had been shot at 1100 h after the morning feeding period. This illustration clearly shows how large the stomach is in relation to other viscera and the gross engorgement after feeding. The ability to feed swiftly by using the large cutting surface of the molars has been cited by Sale (1965) as a distinct advantage for predator evasion and escape from high diurnal temperatures. It would now seem as if the digestive tract is also well adapted to this feeding pattern.

In those dassies which could be reached immediately after being shot body temperatures were taken. The figures obtained were 34,8C at an ambient temperature of 20,2C; 35,8C at an ambient temperature of 20,2C and 36,6C at an ambient temperature of 24C. One juvenile was captured but died shortly afterwards due to unavoidable exposure to the sun for less than one hour, its body temperature being 45,6C at death. Although these data are too limited for definite conclusions, they nevertheless confirm the comparatively low body temperature of the dassie and its poor thermoregulating ability which was apparent in the laboratory studies.

The six blood samples which were collected in the field were analysed for sodium, potassium, chloride and urea content. The values obtained were within the range expected in mammalian plasma with the exception of urea which was high, namely 45,2 mg per 100 ml (range 23–100). Finally, when urine samples were collected by means of a syringe directly from the bladder, the urine was again found to contain the same fine precipitate of undissolved calcium carbonate. This confirmed the laboratory observation described previously.

As a result of this observation the communal urinating sites of the dassies among the

FIGURE 9
Typical habitat of the Cape dassie showing streaks of calcium carbonate on rock surfaces which originate from the urine of this species.

cliffs and rocky screes (Fig. 9) were examined. It was found that, when these were beneath an overhang and therefore protected from the rain, the urine dried into a brown tar-like accretion. When the urinating site was on a steep rock face, however, the urine dried to form a white accretion. The former situation provides an accretion containing a complex of urinary compounds and faecal matter and is in all likelihood the well-known "klipsweet" which was used by farmers in South Africa and Arabs in North Africa as a home remedy for various complaints. In the latter situation on the steep rock face, all soluble salts are removed by the leaching effect of rain water and only a white precipitate remains. This white precipitate, in some cases forming actual stalagmites (Fig. 10), was collected for chemical analysis and was found to consist mostly of calcium carbonate, the same compound found as a precipitate in the urine during laboratory studies.

FIGURE 10
A stalagmite, consisting mostly of calcium carbonate, which was formed at the communal urinating site of a colony of Cape dassies.

CONCLUSION

It was tentatively concluded from this preliminary investigation that the success of the dassie in hot arid environments can largely be attributed to its well-defined behaviour pattern, particularly feeding behaviour. By means of this behaviour cycle animals avoid the stress of high ambient temperature and low humidity by retreating to the protective micro-climate of rock crevices. As a result, selection pressure for superior thermoregulation at high atmospheric temperatures has been largely absent and the animals are poor thermoregulators from the physiological viewpoint.

The renal efficiency of the animals is high but not as spectacular as in some desert mammals such as the jerboa or the kangaroo rat. Nevertheless, although the animals require either free water when on a dry diet, or access to some succulent feed or dew, there can be no doubt that their efficient kidney function allows them to exist on minimal moisture intakes. The behaviour pattern of the dassie, supported by efficient renal function, are therefore thought to be the main contributing factors to its success.

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