THE BEHAVIOUR OF THE RESTING ROCK HYRAX IN RELATION TO ITS ENVIRONMENT

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INTRODUCTION

GENERAL

This paper concerns the relationship between the behaviour, physiology and environment of the two genera of hyrax which commonly occupy rocky outcrops, using the holes and crevices under the rocks as shelter and feeding on any trees, shrubs or herbs which may be growing near the rocks. The larger animal of the two is the genus *Procavia* which has a remarkably wide distribution throughout Africa and the Middle East and is thus subject to an extremely wide range of climatic conditions, ranging from the hot waterless Sahara to the snowline of Mount Kenya. The smaller genus, *Heterohyrax*, is not so widely distributed but occupies an almost identical niche to *Procavia* and is in fact sometimes found sharing a rock outcrop with its larger cousin (Turner and Watson 1965). Both *Procavia* and *Heterohyrax* are diurnal and have similar social behaviour so that in the following account most statements can be taken as applying to both genera. Only *Procavia* has been studied closely in captivity, however.

ACTIVITY

The rock hyrax is a very inactive mammal and apart from two brief but intense feeding periods which total less than one hour per day (Sale 1965c and 1966) spends most of its time resting. Out of the mating season, which involves the adults in a certain amount of "extra-normal" activity, records from constant observation periods in the field show that adult animals spend approximately 95% of the day in inactivity. This estimate partially depends on the assumption that very little activity takes place in the holes where it is, of course, impossible to observe directly. Apart from feeding, (which can be easily observed) most hyrax activities are accompanied by some degree of distinctive vocalisation, such as a growling noise when fighting, and can thus be detected by listening carefully at the entrances of holes. Suckling has frequently been detected in this way inside holes in the wild. Confirmation that there is little activity inside the holes has been obtained by watching captive animals inside an artifical "warren" under red illumination. Watching undetected through one-way lenses, one has been able to observe the group in as near natural conditions as possible. Much of the time the animals in the hole (warren) are huddled or heaped together in one corner. Occasionally an animal will leave the group to wander in the hole or go outside to urinate. Fig. 1 shows the basic activity pattern for two colonies of *Procavia*, and of the time spent outside the greater part is occupied in resting. As pointed out elsewhere (Sale 1965c) casual feeding never occupies more than a few minutes at a time, adult fighting is mainly confined to males in the mating season and play is an activity confined to young animals, who are more active

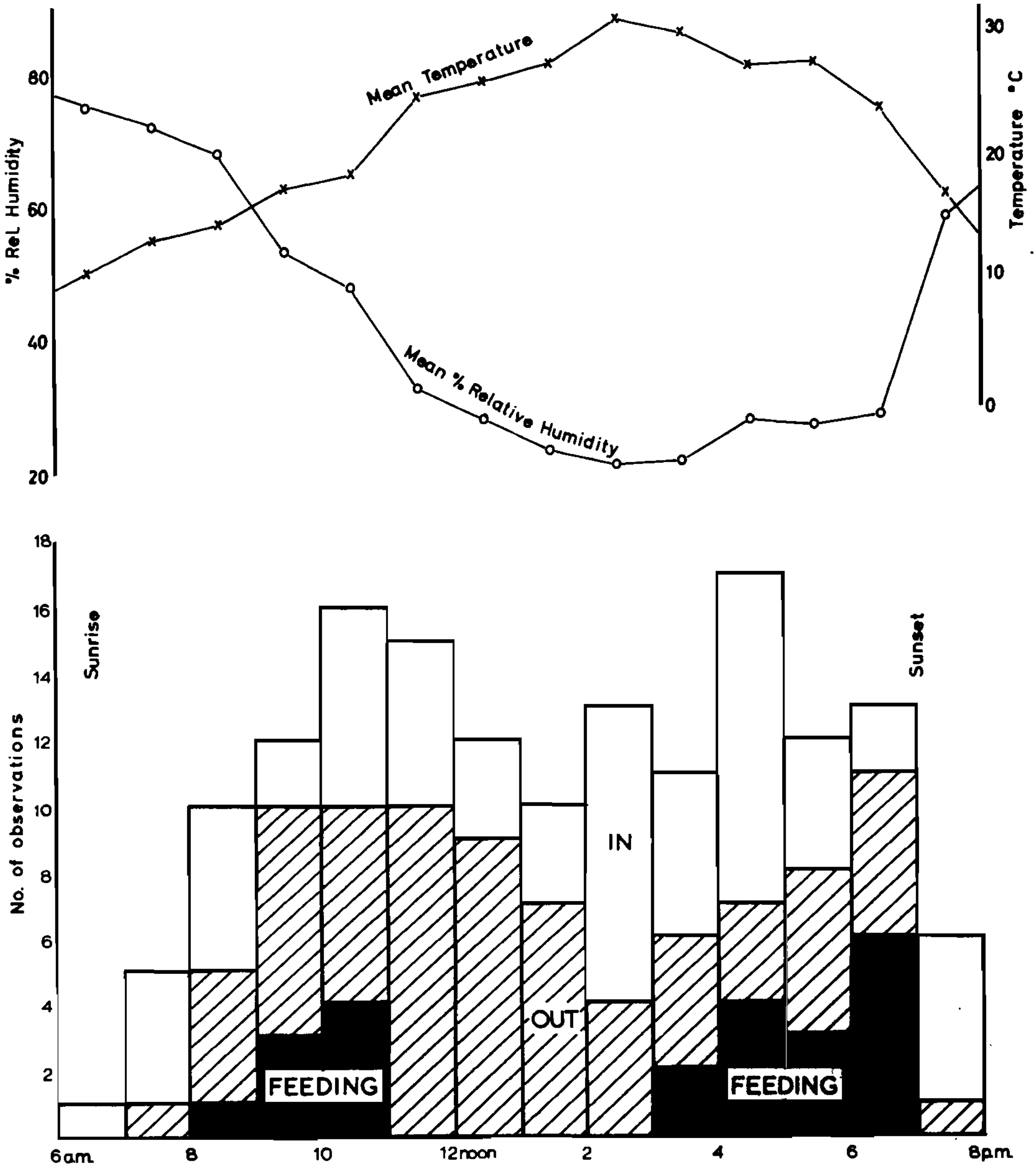

Figure 1: The basic daytime activity pattern of two adjacent colonies of *P. habessinica*, showing the relationship of activities to mean air temperature and relative humidity outside the holes. Compiled from data collected during casual visits over a year. Each "feeding" observation represents one feeding period of approximately 20 minutes duration. "In" indicates that no animals were observed and were therefore assumed to be inside the holes. "Out" indicates that at least some of the colony were outside either resting, grooming, casually feeding (taking an occasional bite from a nearby plant, as opposed to the serious continual feeding period mentioned above) or playing (juveniles only). For full discussion see text.

Figure 2: Typical heaping inside the artificial warren, with the younger animals forming the upper tier.

than the adults. Animals of all ages spend a little time grooming themselves but this is negligible over 24 hours.

RESTING PATTERNS

HEAPING

The resting animal may be involved in one of three basic social groupings. The first of these may be described as "heaping" which is really an intensified form of huddling, the second pattern to be described. Heaping normally involves three or more animals that have packed themselves very tightly together, some of the group being raised up on the backs of the others which are crouching on the ground (Fig. 2). The animals on the top of the "heap " are often the younger members of the group but not invariably so. Generally the heap is so arranged that all heads are towards the outside, i.e. a radiating pattern is adopted ensuring that two animals are never face-to-face. Heaping is a common formation of animals inside the hole and is also occasionally seen outside on the rocks in the cold of the early morning (Fig. 3). The latter fact provides a clue as to the significance of heaping which is undoubtedly connected

Figure 3: Intermediate stage between heaping and huddling in *Heterohyrax*, shortly after emerging from their holes in the morning. The radiating formation of the animals serves to avoid intra-specific aggression and to keep a wide look-out for predators.

with the poor thermo-regulation of hyrax (see below). Heaping is also observed outside when it is unusually cold in the middle of the day and occurred much less frequently inside the artificial warren of a captive colony during the hot season. The simplest "heap" is formed when the newborn animal climbs onto its mother's back and the significance of this innate behaviour pattern has already been discussed in the context of post-partum behaviour (Sale 1965a).

HUDDLING

Huddling is similar to heaping but does not involve animals being raised up on the backs of others i.e. there is a single tier, all crouching on the ground but in close lateral contact with one another. The degree of contact between the members of the group is thus less in a huddle than a heap. The huddling animals may adopt a radiating formation with all heads on the outside (Fig. 3) or may arrange themselves in a linear fashion. In the latter case, as many as ten animals crouch side-by-side in a row, all facing the same direction. In both the radiating and linear formations (and heaping) an animal wishing to join the group goes to the front and pushes himself backwards in between two of the huddling (or heaping) animals. This back-presentation to other animals in any situation where antagonism is likely to be aroused is very characteristic of hyrax behaviour and will be discussed fully later.

Huddling occurs both inside and outside the hole and, like heaping, its occurence bears a relationship to temperature conditions. When animals first emerge from their hole in the morning (7.30-8.30 a.m.) they generally form into a huddle on top of a rock where they catch the first rays of the rising sun. In a colony site there is often one rock which is always illuminated by the sun before the others and all the animals will crowd onto it as soon as a small area is being illuminated. As neighbouring rocks receive the sun, groups of animals will break away from the main huddle and form smaller huddles on these rocks. On particularly cold mornings some heaping may also be observed and this gradually changes to huddling, often passing through an intermediate stage where most of the animals are huddling but one individual remains on top of the others (Fig. 3). The animals move about very slowly with a sluggish crawl, tending to drag their bellies on the ground, when they first emerge in the morning, and only assume their normal gait and speed after one or two hours. This behaviour, reminiscent of a reptile, suggests that the body temperature is very low in the morning and that the animals need to warm up before any sort of activity, such as feeding, can be undertaken. Hyrax will huddle in the middle of the day if the weather is cold and have occasionally been observed huddling before retiring to the holes at sunset. Generally in Kenya, however, huddling is not observed in the evening, presumably because the animals are rarely cold enough to induce the behaviour. The evening feed is an active period and generally insufficient time elapses between the end of it and nightfall to allow body temperature to decrease appreciably. With the very brief twilight in the tropics, there is often little drop in air temperature before actual nightfall. In March 1965 I observed pronounced evening huddling in *Procavia* in Upper Galilee, Israel, and was informed that this was common. March is still quite cold in Israel, especially in the higher regions and no doubt the rapid lowering of the air temperature in the late afternoon was responsible for this regular occurrence of evening huddling.

SOLITARY RESTING

The third pattern of resting behaviour is quite distinct from the two patterns so far described, both in the relation of animals to one another and in the posture of the individual animal. Whereas in heaping and huddling the hyrax clump together in a tight formation, in this type, which I shall refer to as "solitary resting", the animals tend to be scattered and although sometimes lying in twos or threes, they are never in physical contact with other members of the group. Frequently adjacent animals adopt a head-to-tail orientation (Fig. 4) but where two animals are facing in the same general direction they always arrange themselves in a radiating fashion, with their heads pointing slightly away. Typically the animal is lying in the prone position, with the whole body relaxed and the entire ventral surface in contact with the flat rock. The forefeet are extended in front with their soles on the rock and in the

Figure 4: Solitary resting *Procavia*, showing two degrees of relaxation: the animal on the right has its entire ventral surface in contact with the ground and the soles of his sprawled hind feet upturned. The animal on the left shows a less relaxed posture but the soles of the feet are more or less exposed. Hyrax always avoid the head-on position as it promotes aggression and this "head-to-tail" formation is commonly found in resting animals.

completely relaxed position the chin rests on the rock between the forefeet. The position of the hind feet in the fully relaxed animal is of particular interest; they are sprawled out backwards at an angle to the lateral margin of the body and with the soles facing upwards (Fig. 4). Since sweat glands are only present in the soles of the feet, this posture is of great importance in promoting heat loss from the body.

Solitary resting is most commonly seen in animals that are basking in the sun on an exposed rock surface. Such basking regularly follows the morning huddling described above and occupies much of the resting time outside the hole (see Fig. 1). The basking pattern develops as huddling animals separate from their mates and stretch out in the rapidly rising sun to receive a "solar charge" that dispels sluggishness and warms them up ready for the morning feeding period around 10.0 a.m. After having exposed one side of their bodies to the sun, animals can often be seen to deliberately get up and turn round, lying down again in the opposite direction so as to subject their other flank to the warming rays. After feeding, further basking takes place periodically throughout the day until the evening feeding period, beginning between 4.0 and 6.0 p.m. This basking is alternated with periods of resting in the shade or retreat to the hole. The resting may be in a crouching or prone position depending on the ambient temperature: if it is very hot the latter posture will be adopted. Hyrax generally seek shade on a rock, whether it be provided by vegetation such as a spreading bush or an overhanging rock. Shaded rock is cooler to lie on than soil and a resting animal is less likely to be crept up on unawares if he avoids the deep shade beneath bushes some distance away from other members of the colony. A major period of retreat to the hole, lasting up to three hours, is usual in the middle of the day when temperatures are highest. As seen from Fig. 1, hyrax are rarely seen on the rocks between 2.0 and 3.0 p.m. and infrequently up to 4.0 p.m. The normal daily cycle of activity that has been outlined is adjusted with varying weather conditions; when there is heavy cloud cover animals will probably appear late in the morning and may remain out longer in the middle of the day (Turner & Watson 1965).

TEMPERATURE PATTERNS

It appears that the behaviour pattern shown by resting hyrax is greatly influenced by prevailing temperature conditions. As the ambient temperature increases a typical transition from heaping, through huddling, to solitary resting takes place. This transition involves a decreasing degree of bodily contact between members of a group and an increasingly relaxed posture on the part of the individual animal. One indication of the latter is the presence of general pilo-erection in heaping and huddling animals and its complete absence in basking individuals. The slowness of movement as the animals emerge from the holes after sunrise and the prolonged periods of basking remind one forcibly of the behaviour of poikilothermic reptiles such as the agama lizard which frequently occupies the same rocks as a colony of hyrax. This comparison has led me to investigate the relationship between ambient temperature and the body temperature of the hyrax. Although these investigations are not yet complete, preliminary results show some interesting correlations.

DIURNAL FLUCTUATIONS

Simultaneous field measurements of air temperature and the rectal temperatures of animals that had been trapped or had just been shot showed that hyrax body temperatures have a wide range and apparently bear an approximate relationship to ambient temperature (Fig. 5). Measurements of rectal temperatures in captive animals, over a long period, show a range from 34·4 to 38·9° C (i.e. 4·5° C) in individual animals, who sometimes show diurnal changes of as much as 2·3°C. While some changes can be shown to be related to solar radiation (see below), internal mechanisms appear to be primarily responsible for daily body temperature variations in hyrax. Strong evidence in support of this is the fact that an animal kept in a constant temperature of 21°C, a fairly constant humidity and 12 hr. of artificial light daily, for over three months, showed a similar diurnal range to other animals. (At the higher environmental temperature of 29°C, however, the same animals' body temperature became constant at 37·8°C and varied only if air temperature was altered.)

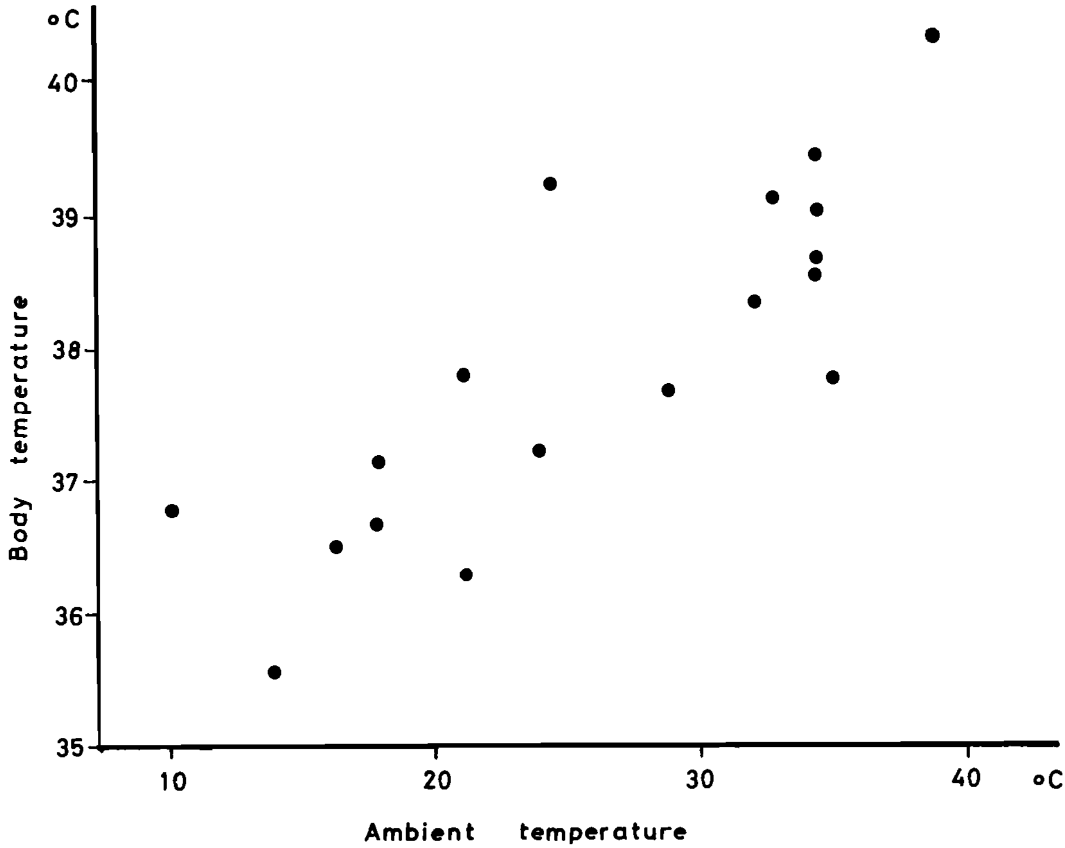

Figure 5: Graph showing relationship between hyrax body temperature and ambient temperature in the field.

LONG-TERM FLUCTUATIONS

Not only are diurnal changes apparent but there are long-term body temperature fluctuations which are common to all the animals from the same wild colony. Fig. 6 shows the weekly averages of mid-morning body temperatures of three animals captured in the same colony. Two of the animals (a male and a female) were housed in a hutch outside, and were thus subject to ambient temperature fluctuations, while the third (a male) was in a metabolism cage at a constant room temperature of 21 °C. The three animals showed cycles of fluctuations which are roughly in phase and have a periodicity of approximately four weeks. The fact that external conditions of one of the animals (who was not subject to sunlight or solar radiation) were constant demonstrates that the control of this cycle must also be internal and has a common time base in all three animals.

THE EFFECT OF SOLAR RADIATION

As well as internally-controlled cycles of fluctuation, it has been possible to demonstrate a rapid rise in hyrax body temperature as a result of basking in the direct rays of the sun. A young newly-captured *Heterohyrax* of under 3 months old was kept under observation and its behaviour related to changes in rectal temperature, heart rate and respiratory rate. A summary of a typical morning's performance is presented below.

Time	*Behaviour*	*Temperature*	*Heart rate*	*Respiratory rate*
6.30 a.m.	Moving around sluggishly	33·2°C	180	32
8.15	Moves into sun	33·9	—	—
9.00	Lying in sun	39·1	248	28
9.10	Moves into shade	39·2	248	28
1.00 p.m.	Still in shade	33.9	180	24

In an animal so young it is unlikely that the adult temperature control mechanism will be fully operating and so the great fluctuations of temperature shown in the table cannot be taken as indicative of the magnitude of adult fluctuations. Nevertheless the observations on this juvenile animal show the rapid effect that solar radiation has on hyrax body temperature, in this case causing a rise of 5·2°C in 45 min. Heart rate is accelerated with rise in body temperature but there is no significant rise of respiratory rate (hyrax show a negligible amount of panting). It has not yet been possible to carry out detailed measurements of this kind on an adult animal and these results from a juvenile represent only a preliminary observation. They may, however, prove to be of value in showing that hyrax body temperature is greatly influenced by solar radiation. While basking (and thus solar radiation) must clearly have an influence on diurnal temperature changes, the fact that significant changes continue in the absence of sunlight shows that an internal mechanism is primarily responsible.

THE SIGNIFICANCE OF THESE FLUCTUATIONS

Two types of temperature fluctuation cycle are suggested in hyrax. The diurnal one, which has yet to be fully investigated, probably bears a relation to the daily activity cycle of the animal. Such evidence as has been obtained shows that body temperature is highest around 9 a.m. (basking period) and, after a decline around midday, rises steadily again throughout the afternoon, before dropping gradually to a minimum around 4 a.m. Body heat would thus be stored when the animal was subject to greatest external heat (when basking) and any excess dissipated when the animal is in the cool of the hole (midday and night). The effect of this is to reduce the body temperature gradient with ambient and thus minimise the loss of water from the body by evaporative cooling (Kirmiz 1962). The function of basking is not entirely clear but may involve restoring the heat which the body has lost overnight. The morning rise in body temperature due to an endogenous mechanism would thus merely be increased by basking, the total effect being to mobilise the otherwise torpid animal in preparation for the morning feeding excursion. It would seem that basically the hyrax has poor temperature regulation and has developed a built-in diurnal temperature cycle to compensate for this. In the absence of high solar radiation, e.g. on a dull morning in the rainy season, the cycle produces a sufficient temperature rise to mobilise the animal, although the rate and degree of mobilisation may be reduced. Observations of behaviour confirm that activity is delayed and reduced on cold "sunless" mornings and Coe (1962) states that Mount Kenya hyrax remain in their holes during cloudy periods. He recounts an occasion when a whole colony remained continuously underground for three days during a period of particularly bad weather. The fact that diurnal fluctuation disappeared with a high ambient temperature of 29°C (see above) suggests that, because of the smaller temperature gradient between the air and the body, the latter was able to maintain sufficient heat for activity throughout the day and the cycle was no longer necessary. In other words, at high ambient temperatures, with reduced heat loss, the animal is able to maintain a constant body temperature and has no need of the diurnal cycle.

The diurnal temperature cycle of the hyrax must be largely responsible for the apparent approximate relationship between body temperature and ambient temperature demonstrated in Fig. 5. This cycle and the accompanying independence from moderately low ambient temperatures and drinking water, contributes to the ability of hyrax to live in a wide range of climatic conditions. The results discussed above have mainly been from an alpine hyrax, adapted to low ambient temperatures, and it would be interesting to ascertain the temperature patterns for animals from a hot area, such as the *Procavia* around Lake Magadi in Kenya.

The second fluctuation cycle demonstrated (Fig. 6) also requires further investigation. If it is clearly shown to be of monthly frequency, it may be connected with the alleged high incidence of male sexual calling in *Procavia* during a full moon (Coe 1962). Certainly such a relationship between calling and the lunar cycle exists in *Dendrohyrax* and the study of temperature cycles in this genus ought to be rewarding.

THE RELATIONSHIP BETWEEN RESTING BEHAVIOUR AND TEMPERATURE

It appears that diurnal fluctuations of ambient temperature have had a long-term influence on the hyrax's physiology, producing a built-in cycle of body temperature which approximately follows mean ambient temperature fluctuations. This, together with very efficient water reabsorption by the kidney and hind gut (Sale 1965b), enables hyrax to live in areas where drinking water is rarely available and is undoubtedly a major physiological factor in the wide distribution of *Procavia*. It also has a profound effect on the animal's resting behaviour.

THE FUNCTION OF HEAPING, HUDDLING AND BASKING

The fact that body temperature drops considerably during the night explains the marked heaping and huddling behaviour and general torpidity of the animal in the early morning,

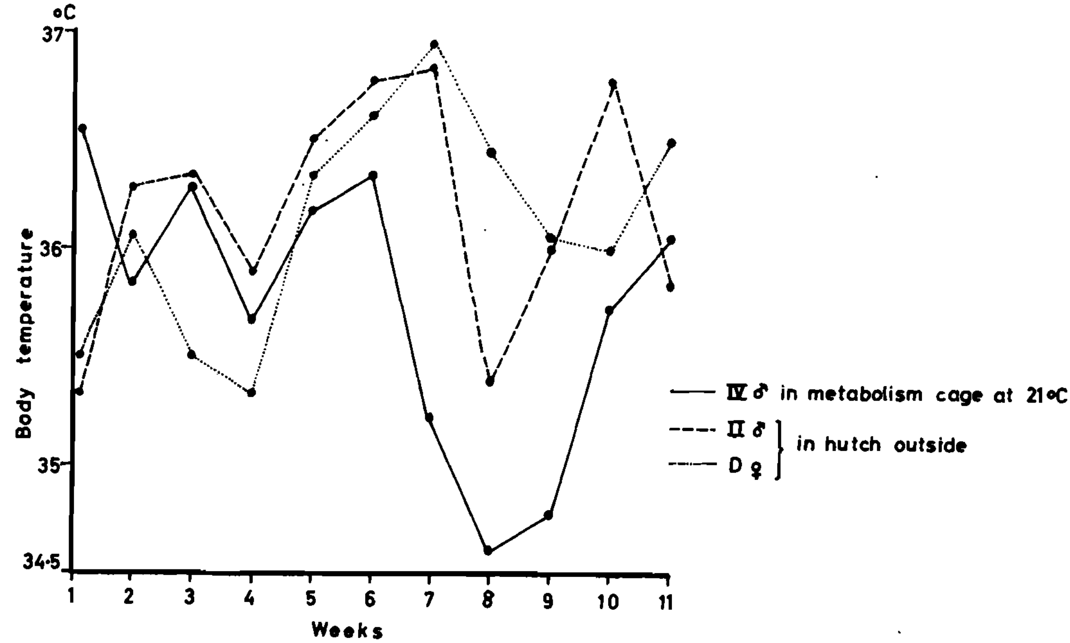

Figure 6: Temperature fluctuation cycle of three *Procavia*, one of which was under constant environmental conditions.

followed by basking. Unlike many ungulates which feed in the hours immediately following sunrise, the hyrax spends this time in raising its body temperature to a level that permits unimpeded activity. Were hyrax to crawl slowly around their feeding area on emerging from their holes, they would render themselves very vulnerable to predators as they often feed some distance from their holes and not infrequently have to interrupt feeding and dash for shelter as a predator appears (Sale 1965c). As seen from Fig. 1, hyrax often do not feed until 10.0 a.m. Obviously both heaping and huddling provide reciprocal insulation to the animals involved and greatly assist in preventing further heat loss from their bodies. Once the sun has reached the rocks, it is clearly of advantage to separate from the group and expose their bodies fully to its warming rays; hence the basking behaviour.

It is important to note that the animals only remain in a tightly packed group as long as demanded by temperature considerations. For the major part of the time, whether solitarily resting, feeding or indulging in minor activities, they remain out of physical contact with one another. A fairly strong social drive is manifested during the two brief periods of group feeding but again a social grouping is virtually enforced by the environment. In this case the vulnerability of animals feeding alone is so great that individual survival demands that feeding be a group exercise (Sale 1965c). Evidence that the hyrax is not basically an intensely social animal is manifold. The absence of a strong mother-young bond (Sale 1965a) and a complete lack of social grooming are examples. The fact that one genus, viz. *Dendrohyrax*, lives a solitary existence and shows no necessity for companionship is also strong evidence. Furthermore, intra-specific aggression has a low threshold in adult hyrax of both sexes, especially in *Procavia* (see below). Heaping and huddling are thus seen as a physically close social grouping forced on an otherwise not highly sociable animal by its heat and water physiology, acting under the influence of the environment.

AGGRESSION AND APPEASEMENT BEHAVIOUR

The imposed close contact with other members of the group during heaping and huddling has apparently been an important factor in the development of a well defined pattern of appeasement behaviour in rock hyrax. As mentioned elsewhere (Sale 1970) the highly aggressive hyrax has an unmistakable threat behaviour pattern. The distinct threat pattern will be seen in a highly motivated animal but the mere fact of two hyrax meeting face-to-face (head-on) often induces incipient threat, indicated by the raising of the dorsal gland hairs and a slight retraction of the upper lip. If both animals persist in this orientation serious threat is likely to occur and develop into a fight. In practice, however, this rarely happens. Firstly, head-on encounters between adults are generally carefully avoided. As mentioned above, an animal joining another animal or a group from the front generally does so by reversing into position. Within the group individuals invariably orientate themselves so that they are facing slightly away from their neighbours (Fig. 3). This leads to the characteristic radiating or "fan" pattern of a huddling group. While the prime function of this pattern is to avoid aggression, it often serves a secondary defensive function, particularly when the animals are outside on a rock, liable to be approached from any direction by a predator such as a leopard. Basking animals, which are normally not in physical contact with one another, often lie head-to-tail (Fig. 4) and avoid facing each other in this way. If two animals do meet head-on or an animal is approached directly by another one, unless an aggressive encounter is being sought, one animal will turn its head deliberately away and follow this by presenting its hindquarters or flank to the other animal. This deliberate back-presenting is a very marked behaviour pattern in the hyrax and functions as an appeasement gesture, averting continued threat or the development of a fight. The positioning of the dorsal gland hairs in the centre of the back is appropriate to this backing behaviour (Sale 1970). A threatening animal has its gland hairs erected, forming a conspicuous flash which will be absent in an animal indicating peaceful intentions. A further factor contributing to the evolution of such unusually well defined appeasement may be the poor near vision of hyrax which could result in mistaken interpretation of the behaviour were its components not as distinct as they are.

CONCLUSION AND SUMMARY

The aim of this paper has been to demonstrate, using the hyrax as an example, the interdependence of an animal's behaviour, physiology and environment. The common practice of studying the three as separate divisions of biological science often obscures the essential relationship between them. I am convinced that we often miss fascinating and important aspects of an animal's biology by allowing our interest in it to be limited by a particular technique.

In this case we have noted a markedly stereotyped sequence of behaviour patterns in the resting rock hyrax which appeared to bear a relationship to mean ambient temperature conditions. An investigation of hyrax body temperature in relation to ambient temperature showed a general relationship between them which could be attributed to an endogenous diurnal cycle of temperature fluctuation in the animal. Such a fluctuation cycle can be correlated with the varying degrees of physical contact noted between resting animals. The close physical contact when ambient and body temperature is minimal has been partially responsible for the development of marked appeasement behaviour in the hyrax. This study of a single environmental factor, viz. ambient temperature, and its interrelationship with body temperature and social behaviour, thus serves as an illustration of the dynamic interdependence that exists between a living organism and its habitat.

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