CONTINUOUS RADIOTELEMETRIC RECORDS OF THE DEEP BODY TEMPERATURE OF SOME UNRESTRAINED AFRICAN MAMMALS UNDER NEAR-NATURAL CONDITIONS

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The deep body temperatures of a wide range of animals have been recorded in the literature. The majority of these records has depended upon discrete measurements made while the animal was captive and restrained, or immediately after death by shooting. Estimates of the variation in deep body temperature have been achieved by making a series of measurements of rectal temperature of one animal at different times of the day, or by making a series of single measurements on several animals immediately upon captivity or sudden death at different times of the day. Until recently it has been impracticable to make continuous measurements of the deep body temperature of unrestrained mammals in a natural or near-natural environment and virtually no such records existed when this study was undertaken. In consequence, there was no reliable information concerning the temporal pattern of the deep body temperature of a range of mammals under these circumstances, and it was not possible to determine the range of nychthemeral (24 hourly) variations in deep body temperature that occur among the mammalian species generally described as being homoeothermic.

The development of miniature recorder systems and radiotelemetric systems for monitoring physiological parameters of unrestrained animals now makes the collection of such data technically feasible. A battery-operated system of radiotelemetric thermometry designed for this purpose (Bligh & Robinson, 1963; Robinson, 1964) has been used to make a series of continuous 24–48 hr records of the deep body temperatures of several mammalian species in East Africa. These animals were confined in a paddock area, but were otherwise unrestrained at a location where they occur, or have occurred, naturally or where they are customarily husbanded.

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METHODS

The radiotelemetric system employed for recording the deep body temperature of an un-restrained animal has been described by Bligh & Robinson (1963) and Robinson (1964). The prototype employed by Bligh, Ingram, Keynes & Robinson (1964) on a study of the thermoregulation of the sheep was mains-operated. For this investigation the receiver was modified to operate with a 12 V vehicle battery, and was coupled to a Mervyn battery-and-clockwork-operated portable potentiometric recorder. The all-transistor system was of robust construction to withstand rude transport conditions. The construction of the poly-ethylene probe with a thermistor bead embedded in its tip, and the technique employed for its implantation in the animal under local anaesthetic has been described by Bligh et al. (1964).

TABLE 1. Identification and classification of the animals upon which continuous deep body temperature measurements were made

Buffalo		Syncerus caffer			
Giraffe		Giraffa camelopardalis			
Eland		Taurotragus oryx			
Oryx		Oryx beisa		Ruminantia	Artiodactyla
Cattle	East African Zebu	Zebu			
	Ankole	Sanga	Bos indicus		
	Nganda	Zebu/Sanga			
Sheep,	East African	Ovis aries			
Camel		Camelus dromedarius		Tylopoda	
Black rhinoceros		Diceros bicornis		—	Perissodactyla

TABLE 2. The list of individual animals upon which measurements of deep body temperature were made together with the other available details

Animal	Sex	Est. wt. (kg)	Position of probe	Duration of record (hrs)	Location	Comments
Camel 1	M	500	Hump	38	Archer's Post	Dom.
Camel 2	M	450	Hump	46	Archer's Post	Dom.
Camel 3	M	450	Hump	45	Archer's Post	Dom.
Giraffe	F	400	Lower neck	46	Muguga	Untamed
Buffalo 1	M	350	Lower neck	43	Muguga	Semi-tamed
Buffalo 2	M	350	Lower neck	54	Muguga	Semi-tamed
Eland 1	F	200	Lower neck	17	Mbarara	Semi-tamed
Eland 2	F	200	Back	43	Mbarara	Semi-tamed
Oryx	?	150	Lower neck	46	Rumuruti	Untamed
Nganda cow 1	F	300	Lower neck	32	Entebbe	Dom. dehorned
Nganda cow 2	F	300	Lower neck	45	Entebbe	Dom. dehorned
Nganda cow 3	F	300	Lower neck	49	Entebbe	Dom. dehorned
Nganda steer	M	300	Lower neck	48	Entebbe	Dehorned
Ankole steer 1	M	350	Lower neck	46	Mbarara	Dom. dehorned
Ankole steer 2	M	350	Lower neck	46	Mbarara	Dom. dehorned
Boran bull	M	350	Hump	44	Archer's Post	Dom.
E. African sheep 1	F	25	Behind scapula	29	Entebbe	Dom.
E. African sheep 2	F	25	Behind scapula	51	Entebbe	Dom.
E. African sheep 3	F	25	Behind scapula	51	Entebbe	Dom.
Black rhinoceros	M	200	Lower neck	12	Rumuruti	Semi-tamed

The classification of the mammalian species used in this investigation is given in Table 1. Details of the individual animals are given in Table 2. Details of the geographical locations at which the observations were made and the available paddock facilities are given in Table 3.

In all species except the camel and the sheep, the temperature-sensitive probe was

TABLE 3. Location and description of the stations where the animal observations were made

Location	Country	Longitude	Latitude	Altitude (ft.)	Terrain	Animal	Size of paddock (m²)	Availability of shade
Entebbe	Uganda	32° 27'	N 0° 4'	3750	Good grazing	Nganda cattle	4000	Yes
						East African sheep	3800	Yes
Mbarara	Uganda	30° 41'	S 0° 36'	4300	Fair grazing	Ankole cattle	3000	?
						Eland	1750	?
Muguga	Kenya	37° 39'	S 1° 14'	7000	Good grazing	Buffalo	8000	Yes
						Giraffe	1500	Yes
Rumuruti	Kenya	36° 36'	N 0° 16'	6300	Poor grazing	Oryx	750	Yes
						Rhinoceros	600	Yes
Archer's Post	Kenya	37° 49'	N 0° 46'	3200	Semi desert	Camel	200	No
						Boran cattle	200	No

TABLE 4. Summary of deep body temperature, ambient temperature and ambient relative humidity data recorded during the observations on each animal

Animal	Code for Fig. 2	Deep body temperature (°C)			Ambient temperature (°C)			Relative humidity (%)		
		Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean
Camel 1	▲	35·8	39·1	37·5	21	31	26	33	74	52
2		35·7	38·25	37·2	21	32·5	27	28	81	56·5
3		35·1	37·7	36·7	21	35·5	27·5	32	84	55·5
Giraffe	⊙	37·75	39·1	38·5	10·5	21·5	14	48	91	81
Buffalo 1	■	36·9	40·1	38·5	10	24·5	17·5	34	93	67
2		37·6	40·1	38·9	10	24·5	18	42	91	64
Eland 1	●	38·4	39·8	39·1	17	26·5	19	44	91	80
2		38·3	39·85	39·0	14·5	24	20·3	38	93	60
Oryx	○	36·6	40·0	38·5	12	25·5	18	48	92	78
Nganda Cow 1	▷	38·0	39·4	38·7	20·5	27·5	23·5	56	92	73
2		37·6	39·3	38·5	18	26	21·5	43	90	69
3		37·8	40·0	38·6	19	27·5	23	43	90	57
Nganda steer 1	▶	37·8	40·3	39·2	20·5	28	23	52	90	69
Ankole steer 1		36·9	39·0	38·2	14·5	26	20	48	92	75
2		37·6	40·0	38·8	15	26	20·5	48	92	74
Boran bull	◁	37·6	39·3	38·4	20	34·5	26	32	92	59
East African sheep 1	◐	39·8	40·65	40·3	19·5	26	22	50	89	68
2		38·5	40·0	39·2	19	27·5	22	48	92	72
3		38·7	39·9	39·4	18	27·5	22	40	92	71

inserted through a small stab-wound to a depth of 8 cm in the dorsal caudal neck region, the plane of the probe shaft being approximately perpendicular to that of the skin through which it passed. The probe was inserted into the fatty hump of the camel, the skin incision being made close to the mid line at the apex of the hump. The sheep was too small for the probe to be inserted in the usual way, so the probe was directed to lie between the ribs and the shoulder blade (beneath the latter). Procaine hydrochloride 2 % was infiltrated both superficially and deeply at the site selected for insertion of the probe. The insertion of the probe through the small skin incision along a pathway made by the prior insertion of a fine pair of Mayo scissors was then quickly and painlessly achieved. The Perspex hilt of the probe was anchored to the skin with two ligatures. The giraffe and one of the buffaloes remained fractious despite the local anaesthetic, so chlorpromazine 1–2 mg/kg on an estimated body-weight basis was injected intramuscularly to quieten these animals. Chlorpromazine caused a marked fall in deep body temperature during the first night. The first 24 hr of the records were therefore discounted. The thermistor probe was calibrated against a standard mercury thermometer so that the thermistor recorded temperature and temperature changes with an accuracy of $0 \cdot 1° C$. Except when the experiment was terminated by a failure of the thermistor, the thermistor was again calibrated upon its removal. On rare occasions the second calibration revealed an error of $0 \cdot 1$–$0 \cdot 2°$ C over the range of the recorded temperature. The record was then corrected accordingly. Rectal temperature was generally measured just before the animal was released after the attachment of the probe and transmitter, and again immediately before its removal, using a calibrated thermistor thermometer.

The thermistor probe was connected to the transmitter by a thin plastic-covered coaxial cable. The cable was attached to the skin or coat at suitable intervals beneath a small piece of elastic bandage held in position by impact adhesive, leaving the cable loose enough to allow for changes in the distance between the probe and transmitter as the animal moved. The transmitter, which was in a metal casing, had over-all dimensions of $11 \times 6 \times 3$ cm and weighed about 450 g. It was strapped on to a small webbing harness which was placed on the animal's back and held in position by two elastic straps which passed under the belly. The harness tended to slip to one side and needed occasional adjustment until it was found that a small area of contact adhesive (Evostick) beneath the harness prevented slipping. The thin wire aerial extended for 55 cm above the transmitter.

An important feature in the design of the transmitter is that it cannot readily transmit spurious information (Robinson, 1964). Moderate frequency drift was tolerated. A drift beyond this limit, or the overheating of the transmitter components by solar radiation, resulted in the abrupt discontinuation of the signal. Excessive frequency drift, which was rare, could be corrected by an adjustment of the receiver tuning. Solar radiation effects were prevented by fitting a simple radiation shield over the transmitter. This consisted of a block of 1 in. thick expanded polystyrene beneath an aluminium sheet cover. This was held in position by two elastic straps stitched to the harness webbing.

For continuous measurement of body temperature it was necessary to keep the animal within 110 m of the receiver aerial. Ideally an enclosure of 100–150 m square with avail-ability of shade, water and adequate food was required for the experiment. In practice it was necessary to use whatever facilities were available, or could be made available on loca-tion. These varied considerably and details are given in Table 3.

All locations, details of which are given in Table 3, were within 150 km of the equator. Ambient conditions and vegetation differed widely, however, because of the variations in altitude, rainfall and soil structure. There was close to 12 hr between sunrise and sunset at all locations. Sunrise varied between 06.20 hr and 07.00 hr.

Air temperature and relative humidity were recorded continuously with a thermo-hygrograph housed in a portable Stevenson's screen which was erected close to the paddock. Sunshine was observed and recorded at intervals of 15 min. A note was also made of rain-fall although on occasions night rain may have been missed. At Muguga and Entebbe records were checked against independent meteorological data.

For record and presentation purposes, deep-body temperature data were extracted from the continuous records at intervals of 15 min and air temperature and humidity data were extracted from the thermohydrograph charts at intervals of 30 min.

RESULTS

The mean, maximum and minimum body temperature (T_B) during each period of continuous measurement of deep body temperature, together with the mean, maximum and minimum ambient temperature (T_A); and mean, maximum and minimum relative humidity are recorded in Table 4. The same data for deep body and ambient temperatures are
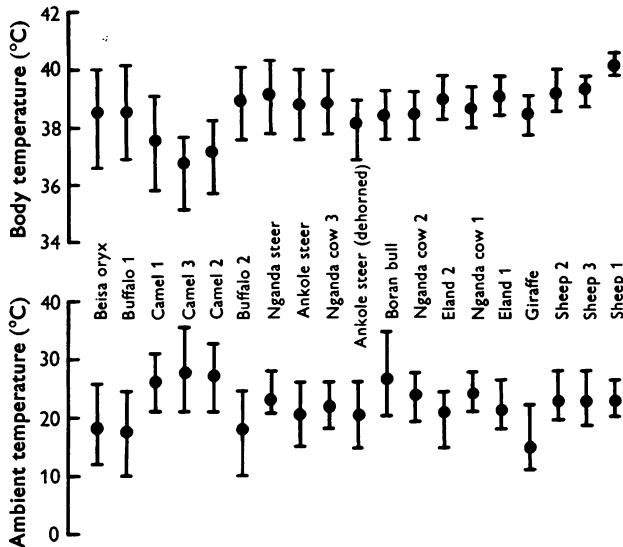
Fig. 1. Diagrammatic representation of the deep body and ambient temperatures during the period of observations on each animal. The solid circles indicate the mean temperatures. The vertical lines through the circles extend from the lowest to the highest temperatures recorded during each period of measurement. The animals have been placed in the order of their thermostability. The data for the animal which showed the largest variation in body temperature are on the left, and that for the animal with the smallest variation in T_B are on the right.

recorded in Fig. 1 in which the animals have been placed in the order of the magnitude of the difference between maximum and minimum deep body temperature. The relation between the range of T_B and the range of T_A during each period of observation is shown in Fig. 2.

Camel. The full experimental data for one camel are given in Fig. 3. The deep body temperature as measured in the hump agreed well with the
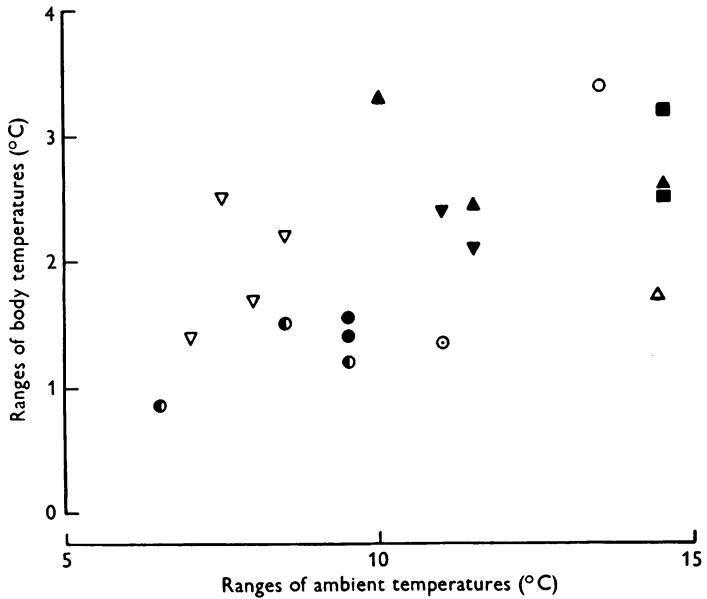
Fig. 2. The relation between the range of body temperature and that of ambient air temperature during each period of continuous measurements. The symbols represent individual animals of different species or breeds (see Table 4 for code).
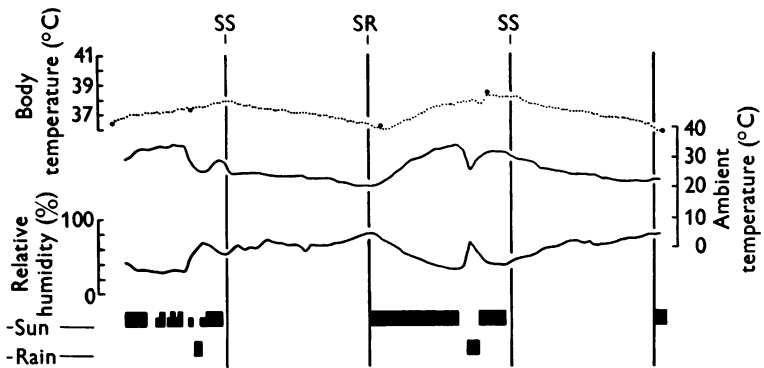

Fig. 3. The experimental data for one camel. The deep body temperature record in this and all subsequent records has been constructed from data extracted from the original recorder chart at intervals of 15 min. Ambient air temperature and relative humidity records were constructed from data extracted from the thermo-hygrograph chart at intervals of 30 min. Sunshine was observed and recorded at intervals of 15 min, and is denoted by the upper series of black blocks. Half-height blocks denote intermittent sunshine. The lower series of blocks denote rainfall. In this and all subsequent figures, the solid circles indicate rectal temperature measurements, and the vertical lines indicate sunrise (SR) and sunset (SS).

rectal temperature measurements. The general temporal pattern of T_B is that of a monophasic nychthemeral variation with the rising phase starting 1–2 hr after sunrise and the falling phase starting about 1 hr after sunset. The variation in T_B is very similar to that of the ambient temperature and could be a passive reflexion of the latter, damped and lagged by the thermal capacity of the body tissues.

The fall in T_B after a rainfall during the second day was possibly associated with the intense sunshine which followed immediately after the
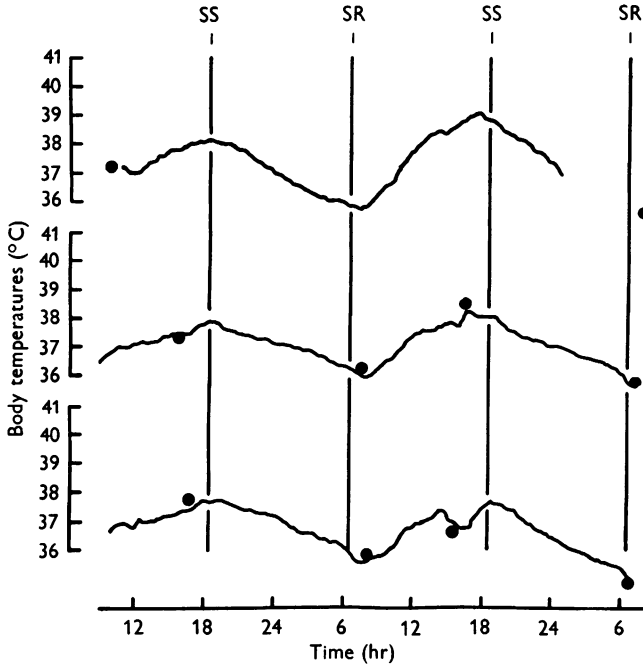
Fig. 4. The deep body temperature records of the three camels.

rain. It was noticed that the coat was saturated with water after the rain, and that this evaporated away in a very few minutes in the sunshine. The temporary fall in T_B is probably the consequence of a high rate of heat loss associated with this evaporation, but whether the fall in T_B was general or localized in the hump tissues is not known.

The deep body temperature records for the three camels are given in Fig. 4. Very similar records of a monophasic nychthemeral variation in T_B between 36 and 39° C were obtained with each animal. In each case there was no rise in T_B before sunrise, and no fall in T_B before sunset. These records do not show the many short-term fluctuations in temperature seen, to varying degrees, in the records of T_B of the other species where

the probe was lying in, or close to, muscular tissue. The hump is composed entirely of fat tissue which does not serve as a variable source of local heat.

Giraffe. This young female adult had been recently captured and transported to Muguga where it appeared to have settled well in the confined area of the paddock. It became excited when enticed into a 'crush' and was given 1 g chlorpromazine I.M. before the thermistor probe could be implanted. Handling problems prevented the measurement of rectal temperature at either the beginning or the end of the experimental period. From the first hour or so of the continuous record of T_B, it would seem that this had been raised considerably as a result of struggling and excitement. Upon release after the implantation of the probe, the giraffe showed no concern about the presence of the probe and transmitter harness.
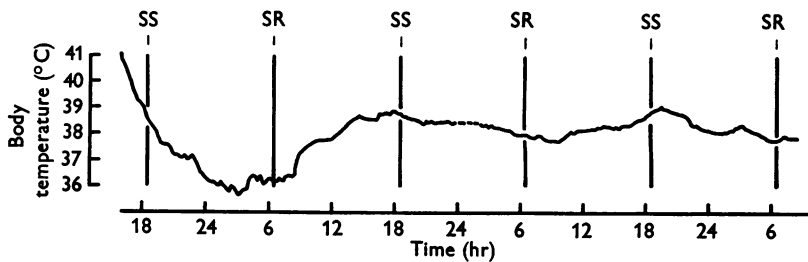
Fig. 5. The deep body temperature record of the giraffe. Where the line is interrupted there was a temporary break in transmission. The animal received 1 g chlorpromazine I.M. 30 min before the commencement of the record.

From the initial value of 41·1° C when radio contact was first established, T_B fell steeply to 35·7° C during the early hours of the next morning. After 24 hr T_B had again risen to 38·6° C. This large movement of T_B during the first day and night was most likely an effect of the chlorpromazine. A similar effect was seen when this drug was used on a buffalo. The record of T_B for the first 24 hr was therefore discarded. However, the first night was the coldest, and this may have had an effect upon T_B. During the subsequent 44 hr T_B remained much steadier, varying only between 37·8 and 39·1° C. The record is given in Fig. 5. From Fig. 1 it is evident that once the drug effect had passed, the giraffe was amongst the most thermostable of the species examined.

Buffalo. The deep-body temperature patterns of two animals were recorded. Both animals had been reared at Muguga and were relatively tame. The records are given in Fig. 6. The first animal was not disturbed by the implantation of the probe and only procaine anaesthesia was necessary. The second animal was much less tolerant of this interference and was given 1 g chlorpromazine I.M. As noted above, the T_B of the
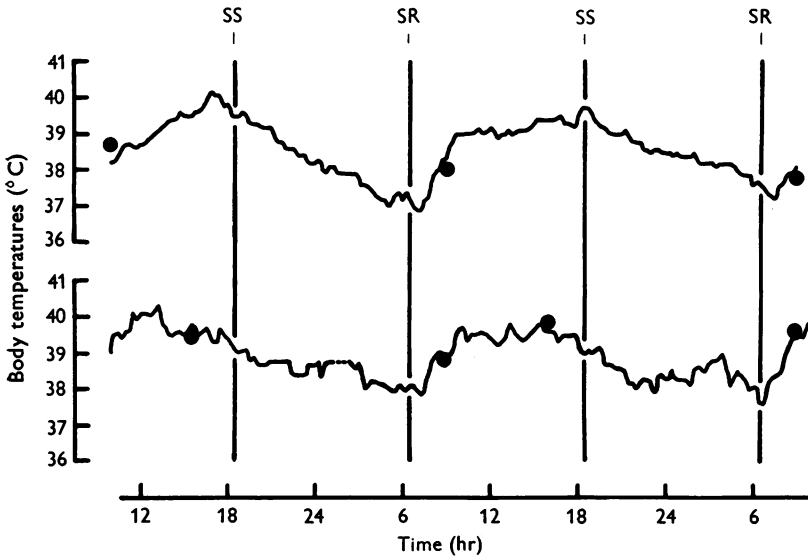
Fig. 6. The deep body temperature records of two buffaloes. The lower record starts 24 hr after the implantation of the thermistor probe when 1 g chlorproma-zine was administered I.M.
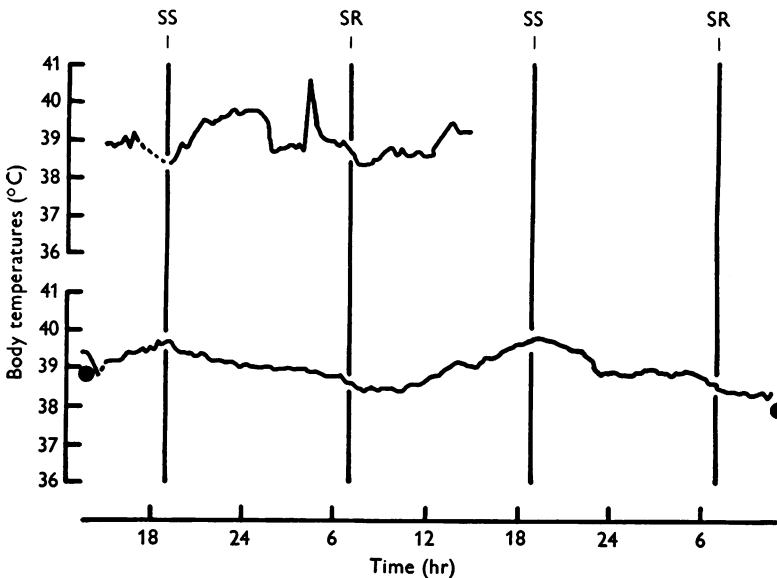

Fig. 7. The deep body temperature records of two elands. The first record ended prematurely when the cable between the thermistor probe and the transmitter was severed.

second animal was more labile during the first 24 hr and this part of the record was excluded. Both records, but particularly that of the second buffalo, show many short-term fluctuations which, it is thought were local thermal effects owing to muscular activity close to the implanted thermistor. However, rectal temperature measurements agreed quite well with simultaneous telemetric values. If the record is smoothed, there is a monophasic nychthemeral variation which would seem to be a fair measure of the thermostability of the buffalo. From Fig. 1 it can be seen that the buffalo has a nychthemeral fluctuation in T_B of a similar order to that found in the camel and was one of the least thermostable of the mammals studied.

Eland. The elands were in temporary captivity and were still nervous and difficult to handle. Although the 'herd' of four females and one male were kept together in the one enclosure, they spent much time during the day walking up and down alongside the perimeter fencing. This fencing was made of rough timbers, and the cable between the probe and the transmitter caught on projections and was severed on several occasions. Each time this happened it was necessary to replace the probe as the probe and cable were integral.

With the first eland the longest period of continuous measurement of T_B was 17 hr and the deep body temperature pattern (Fig. 7) showed fluctuations which cannot be considered as representative. There was a sharp fall in T_B during the night followed by a brief fever-like elevation. After this, the record looks more normal. When the 'fever' portion of the record is taken out, the remainder gives an indication only of the extent of the variation in T_B. In the second eland the probe was placed in the muscle tissue close to the spine behind the shoulder blade, so as to reduce the length of cable and the risk of damage. A good record of body temperature was then obtained (Fig. 7). The recorded temperature varied between 38·3 and 39·8° C. There was good agreement between the recorded temperature and the simultaneous measurement of rectal temperature.

Beisa oryx. The oryx had been captured in Northern Kenya and remained nervous. The record of its body temperature shows many short-term fluctuations including sharp falls in T_B which could not be attributed to the close proximity of active muscles to the thermistor. As with all these observations, there was no opportunity to determine the exact location of the thermistor in relation to tissues and vessels, but it is likely that in this instance the thermistor was thermally influenced by the venous drainage from an area of heat loss as well as by local variations in heat production. It is the least satisfactory of the records and there was no opportunity to record the temperature of a second oryx. However, a smoothed record as shown in Fig. 8 gives an indication of the thermo-

stability of this species. When this is done, the oryx would appear to be less thermo-labile than Fig. 1 suggests. The smoothed record indicates a variation in T_B between about 37·7 and 40·0° C and this adjustment would bring the oryx nearer to the centre of the spectrum of thermostability of the species examined.
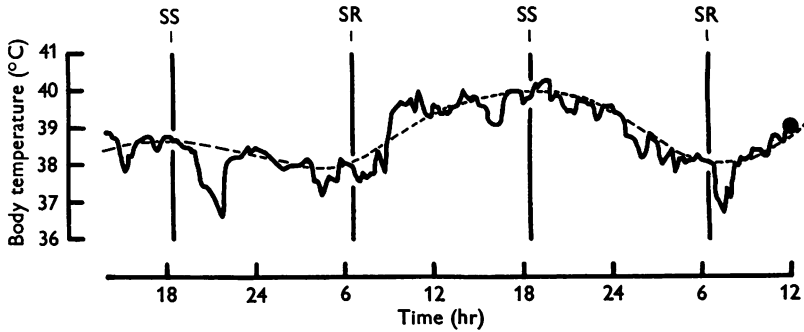

Fig. 8. The deep body temperature record of the beisa oryx. The interrupted line is a free-hand trend line indicating the probable variation in mean T_B.
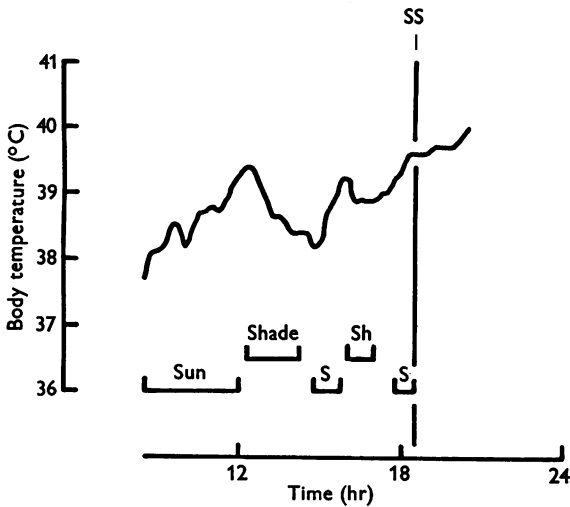

Fig. 9. The 12 hr record of the deep body temperature of a 2-year-old black rhinoceros. The upper brackets indicate that the animal was lying in the shade. The lower brackets indicate that the animal was exposed to the sun.

Black rhinoceros. This 2-year-old male had been reared at Rumuruti and was quite tame. It was normally allowed to roam about the farmstead and it disliked the limitation to its freedom when it was confined to an enclosure. About 2 hr after sunset, when only a 12 hr record of T_B had been

obtained, the rhinoceros decided to quit the enclosure and efforts to restrain it were unsuccessful. The cable between the probe and the transmitter was severed during the escape and factors outside the observers' control precluded a second attempt. The 12 hr record (Fig. 9) suggests that the black rhinoceros has a relatively labile deep body temperature, but this was a small and immature male. An adult may have a quite different pattern.
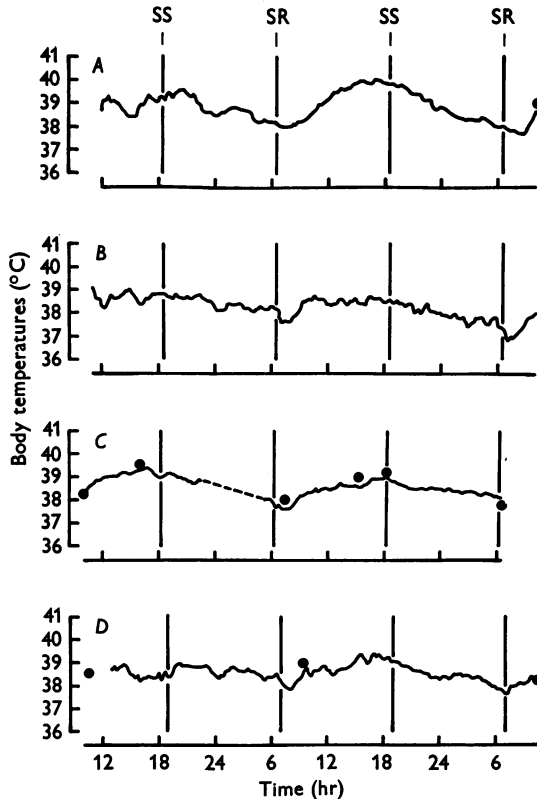

Fig. 10. Records of the deep body temperature of, A and B, Ankole steers at Mbarara; C, A Boran bull at Archer's Post, and D, a Nganda cow at Entebbe.

It was apparent that the choice of environment had an influence upon T_B which fell during the day when the animal was resting in the shade, and rose when the animal emerged into the sunshine to feed.

Cattle. Three breeds of indigenous African cattle were studied. Examples of the records are given in Fig. 10. As can be seen from the mean, maximum and minimum temperatures given in Table 1 and Fig. 1, no obvious breed-specific differences were found in their thermoregulatory capacity.

While one Nganda steer was the least thermostable of the cattle, two Nganda cows were the most thermostable. The boran bull, which was studied in the hot semi-desert conditions of Northern Kenya under the identical conditions under which the camel observations were made, had a nychthemeral variation in T_B within the range of patterns recorded in Nganda cattle under less oppressive circumstances. The two Ankole steers also had ranges of body temperature similar to those for the other two breeds. Although the total range of T_B during the period of measurement was much the same for the two Ankole steers, the nychthemeral variation was smaller in the second one (Fig. 10).
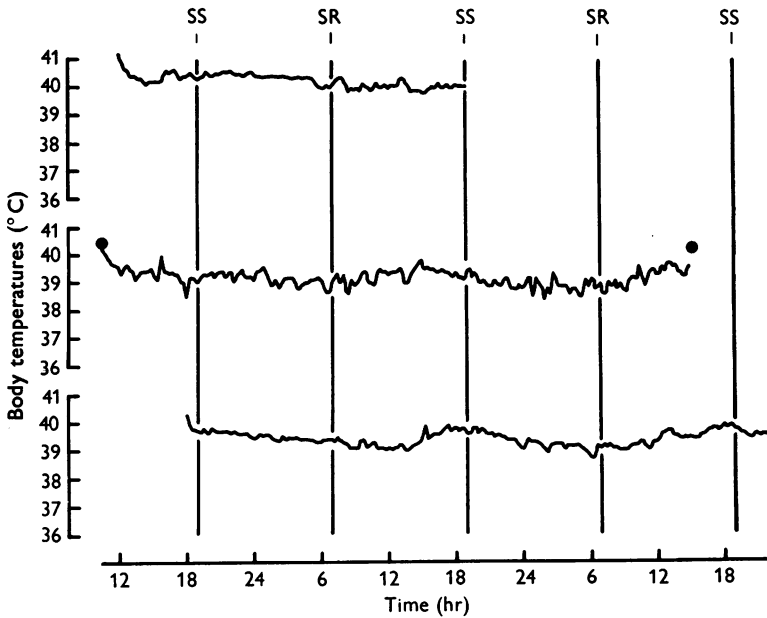

Fig. 11. Deep body temperature records of three 'local' sheep at Entebbe.

Sheep. The three indigenous East African sheep upon which studies were made have not been identified further. The three records are shown in Fig. 11. Although there were many short-term variations in T_B, particularly of the second animal, the nychthemeral variation in body temperature was shallow. From Fig. 1 it can be seen that the sheep was the most thermostable of the species examined.

The observations reported here were made with a threefold purpose:

(1) To assess the feasibility of using a radiotelemetric technique to obtain continuous records of the deep body temperature of unrestrained animals, especially of species which could not be approached frequently for making such measurements. (2) To record the temporal patterns of the deep body temperature of as many mammalian species as possible during the short visit of one of us (J.B.) to East Africa. (3) To consider whether there is a continuous spectrum of thermostability between the thermostable sheep (Bligh *et al.* 1964) and the relatively thermolabile camel (Schmidt-Nielsen, Schmidt-Nielsen, Jarnum & Houpt, 1957), or whether one of these species should be regarded as the more representative mammal in this respect, with the other species representing a specific adaptation to particular environmental circumstances.

Although there is no immediate prospect of extending these observations, it is obvious that the results given here must be regarded as preliminary and that similar studies on a greater number of individuals in each species and on a greater number of species are essential before any firm conclusions can be drawn.

It was originally intended that the animals should be captured by the drug-dart technique and then retained within a compound while recordings of deep body temperature were made. It was soon realized that the cost of experienced assistants, the construction of suitable boundaries and the provision of facilities for implanting the probe, were beyond our financial resources. It was also realized that this technique, without adequate facilities, would involve unwarranted risks, and that the use of drugs of unknown effect and duration of action upon body temperature, would increase the period of captivity and so reduce the number of observations that could be made in the time available. It was, therefore, decided to abandon this approach and to make use, instead, of the goodwill and assistance of organizations and persons who had animals in temporary or permanent captivity and who would permit us to make our measurements upon these animals. This course limited the species, the number of each species and, to some extent, the conditions under which the measurements were made.

The validity of the results presented here depends upon that of the blind-probe technique used for the measurement of T_B. A detailed reason for the choice of this method was given by Bligh *et al.* (1964). It is a compromise technique. The rectum is not a suitable site for the continuous measurement of T_B, especially in animals which cannot be approached for frequent adjustment of the thermometer. Thermometric elements placed in the

lumen of the brachiocephalic trunk (Bligh, 1957), or against the carotid artery (Ingram & Whittow, 1961) permit continuous records of a definable T_B, but require preliminary operation under a general anaesthetic. For these studies it was necessary to employ a technique which permitted the quick but permanent location of the temperature-sensing element, and the replacement of the element should it become defective.

It is obvious that the insertion of a probe into muscle tissue in a location which cannot be exactly determined, either before or after the experiment, involves the possibility and probability that local and non-representative fluctuations in T_B will be recorded. In these observations the short-term fluctuations in T_B were greater and more frequent when the probe was inserted into muscular tissue (e.g. the neck of the buffalo) than when it was in non-muscular tissue (e.g. the fatty hump of the camel). It is considered likely that these fluctuations in T_B were due largely to local variations in muscle activity and heat production in the vicinity of the probe. The oryx showed abrupt falls in T_B which could not be explained by variations in muscle activity or in the blood flow through the muscles. It is possible that the probe lay close to the venous drainage from an area concerned in heat loss. Clearly, no significance can be attached to the short-term variations that have been recorded at least until experimental comparisons have been made between the temperature fluctuations sensed by the probe and the simultaneous record of a representative deep body temperature such as that of the blood leaving the left side of the heart (Bligh, 1957). Experiments to this end are now being made on cattle by one of us (J.B.). However, despite these admitted defects in the technique employed, there was, in general, close agreement between the recorded temperatures and such measurements of rectal temperature as were possible. Where observations were made on more than one member of a species, the extents of nychthemeral variations in T_B were similar, and there was no indication that they depended upon the chance location of the probe. It is our opinion that the variations in body temperature recorded here are valid descriptions of the thermostability of the animals which have been studied.

It is evident from Fig. 2 that when all species are considered the extent of the variation in T_B is significantly and positively correlated with that of T_A. However, if the three breeds of East African cattle alone are considered, the extents of the variations in T_B are independent of those of T_A, while the East African sheep (Fig. 11) have shallow nychthemeral variations in T_B very similar to those reported for a Welsh Mountain sheep in Britain by Bligh et al. (1964). It would seem likely, then, that there is a species-specific variation in thermolability which may be modified by ambient conditions. There is no evidence of inter-breed differences

in the thermostability of sheep and cattle. A comparative study of the temporal patterns of deep body temperature of East African Zebu (tropical) and Hereford (temperate) cattle (Bligh & Lampkin, 1964) also permits this conclusion, while the nychthemeral variations in T_B of camels reported here are similar to those reported for non-dehydrated camels under different ambient conditions in North Africa by Schmidt-Nielsen *et al.* (1957).

Of the non-domestic East African mammals, the buffalo, beisa oryx and the black rhinoceros demonstrated a degree of thermolability almost equal to that of the non-dehydrated camel, while the eland and the giraffe were found to be almost as thermostable as the sheep. Existing records of the body temperatures of African mammals have indicated the possibility of a wide species variation in the degrees of thermostability. Luck & Wright (1959) report that the nychthemeral variation in the T_B of the hippopotamus, which spends much of the day immersed in water, is less than 1° C. By contrast, Allbrook, Harthoorn, Luck & Wright (1958) found a nychthemeral variation of more than 3° C in the T_B of a white rhinoceros, which is an animal of similar body shape and size. Some measurements of the T_B of African elephants immediately after they were shot indicates that the elephant occupies a mid-position in the spectrum of thermolability, with a variation of about 2° C (36·2–38·1° C) (R. V. Short, personal communication).

Whether a similar comparative study on temperate and arctic mammals would yield results which would fall within, or extend, the spectrum of relative thermostability indicated here for tropical mammals, is a matter for future consideration. There is insufficient evidence here to support the suggestion made by Schmidt-Nielsen *et al.* (1957) that tropical mammals, in general, may permit a wide variation in T_B as an adaptation to conditions of heat stress. Equally, the evidence does not support the assertion that practically all mammals except the bats, monotremes and xenarthra regulate their body temperatures within 1° C (Scholander, Hock, Walters, Johnson & Irving, 1950).

The data are insufficient to permit the assessment of the extent to which variations in thermolability are attributable to variations in T_A and to intrinsic species-specific variations in thermostability. Whatever the explanation the data suggest that there is a continuous spectrum of thermostability extending from a nychthemeral variation in T_B of about 1° C in the sheep, to perhaps 3° C in the camel and buffalo. This does not mean that the less thermostable species should not be regarded as homoeothermic. It is a matter of data and definition whether 'homoeo' (= like or similar), in contrast to the more rigid prefix 'homo' (= same), refers in the context of mammalian thermoregulation to a nychthemeral variability

of T_B within 1, 3 or 5° C. The terms 'pleothermy' (Smith, 1958) and 'heterothermy' (Irving, 1962) have been used to indicate much wider variations in tissue temperatures of warm-blooded animals.

The even greater fluctuation in the T_B of the camel when deprived of water (Schmidt-Nielsen *et al.* 1957) does not appear to have been looked for or observed in other species except the donkey, which was studied by these same authors. The indication is that this is a physiological response and not just a physical consequence of dehydration, which Schmidt-Nielsen *et al.* (1957) suggest is a species-specific adaptation to the particularly arid environments in which the camel can survive. Further studies on other species will be necessary to determine whether this is so.

SUMMARY

1. A radiotelemetric system has been used to obtain continuous records of the deep body temperature (T_B) of a selection of unrestrained mammals in environments close to those in which they naturally occur (eland, oryx, buffalo, giraffe and black rhinoceros), or are traditionally husbanded ('local' East African breeds of cattle and sheep).

2. Nychthemeral variations in T_B were found to vary between about 1 and 3° C, the sheep being the most stable and the camel and buffalo the least stable thermoregulators, with a continuous spectrum of relative thermostability between these extremes.

3. The results indicate that differences in thermostability are to some extent species-specific, but that the differences could also be due to the variations in ambient conditions.

4. There is no evidence to suggest that tropical species are, in general, less thermostable than temperate species.

5. It is suggested that the limits to the nychthemeral variation of T_B in a homoeothermic mammal is a matter of data and definition. It is a term which indicates similarity rather than sameness and is adequate to describe the full range of the variations in T_B described here.

REFERENCES

ALLBROOK, D. B., HARTHOORN, A. M., LUCK, C. P. & WRIGHT, P. G. (1958). Temperature regulation in the white rhinoceros. *J. Physiol.* **143**, 51–52 *P.*

BLIGH, J. (1957). The relationship between the temperature in the rectum and of the blood in the bicarotid trunk of the calf during exposure to heat stress. *J. Physiol.* **136**, 393–403.

BLIGH, J., INGRAM, D. L., KEYNES, R. D. & ROBINSON, S. G. (1964). The deep body temperature of an unrestrained Welsh Mountain sheep recorded by a radiotelemetric technique during a 12-month period. *J. Physiol.* **176**, 136–144.

BLIGH, J. & LAMPKIN, G. H. (1964). A comparison of the deep body temperature of Hereford and Zebu cows obtained by radiotelemetry under identical field conditions. *J. agric. Sci.* (In the Press).

BLIGH, J. & ROBINSON, S. G. (1963). Continuous telemetry of the deep body temperature of sheep under field conditions. *J. Physiol.* **165**, 1 *P.*

INGRAM, D. L. & WHITTOW, G. C. (1961). Measurement of changes in the body temperature of the ox (*Bos taurus*). *Brit. vet. J.* **117**, 479–484.

IRVING, L. (1962). The heterothermous condition of the tissues of warm-blooded animals. In: *Comparative Physiology of Temperature Regulation.* Ed. J. P. HANNAN & E. VIERECK. Alaska: Arctic Aeromed. Lab.

LUCK, P. & WRIGHT, P. G. (1959). The body temperature of the hippopotamus. *J. Physiol.* **147**, 53–54 *P.*

ROBINSON, S. G. (1964). A temperature telemetering system with constant accuracy. *Med. Electron. biol. Engng*, **2**, 81–83.

SCHMIDT-NIELSEN, K., SCHMIDT-NIELSEN, B., JARNUM, S. A. & HOUPT, T. R. (1957). Body temperature of the camel and its relation to water economy. *Amer. J. Physiol.* **188**, 103–112.

SCHOLANDER, P. F., HOCK, R., WALTERS, V., JOHNSON, F. & IRVING, L. (1950). Heat regulation of some arctic and tropical mammals and birds. *Biol. Bull., Woods Hole*, **99**, 237–258.

SMITH, A. U. (1958). The resistance of animals to cooling and freezing. *Biol. Rev.* **33**, 197–253.