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LANGMAN, VAUGHAN ARTHUR
THERMOREGULATION AND BEHAVIOR IN GIRAFFE
(GIRAFFA CAMELOPARDALIS).

UNIVERSITY OF ALASKA, PH.D., 1978

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THERMOREGULATION AND BEHAVIOR IN GIRAFFE
(*Giraffa camelopardalis*)

A

THESIS

Presented to the Faculty of the
University of Alaska in partial fulfillment
of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

By

Vaughan Arthur Langman, B.S., M.Sc.
Fairbanks, Alaska
May 1978

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THERMOREGULATION AND BEHAVIOR IN GIRAFFE

(*Giraffa camelopardalis*)

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THERMOREGULATION AND BEHAVIOR IN GIRAFFE

(*Giraffa camelopardalis*)

Vaughan Arthur Langman, Ph.D.
University of Alaska, 1978
Supervisor: Robert A. Dieterich

ABSTRACT

The duration and intensity of the cow-calf bond during lying out, and while in calving pools and nursery herds, have been analyzed in a wild population of giraffe (*Giraffa camelopardalis giraffa*). Field observations were made on naturally marked and radio-collared giraffe. Radio tracking was used to follow and observe giraffe of a known age for up to one and a half years. The giraffe calf participates in various calf subgroups while the cow travels to browse and water, but a strong maternal bond persists between the giraffe cow and the calf until the cow's next calving.

Biotelemetry was used to measure rectal temperature from captive giraffe. Giraffe of three ages and sizes were all thermally labile irrespective of the state of hydration; the average nychthemeral variation in rectal temperature was 3.8° C. Longwave radiation was the major source of heat gain (50%). The major avenue of heat loss was by radiation at the coat

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surface (65%). Heat storage substituted for evaporative cooling at all ages. Reciprocal heat exchange between the structures of the nasal turbinates and the air moving to and fro in the nasal passages saves 70% of the heat and water loss which would otherwise occur if the expired air were not cooled and dehumidified before leaving the body during respiration.

Infant and juvenile giraffe store heat during the day-time instead of losing heat by evaporation. Body temperature therefore rises diurnally. This rise is limited by behavioral means. It has been suggested, therefore, that the extended lying out period with restricted movement is a behavioral means by which infant and juvenile giraffe avoid the accumulation of heat.

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ACKNOWLEDGEMENTS

For the opportunity to do field behavior observations, I would like to thank H. C. Hohesion, D. Ruecassel, and D. Jackson for their cooperation and help. Also, Dr. S. K. Bearder and E. Swileana who aided me greatly in the field. Drs. R. A. Dieterich, P. C. Lent, and H. P. Croze are thanked for their comments. Ethnor Laboratories donated the sentanyl biocitrate and azaperone used as capture drugs in this study. This research was supported in part by bursaries from the C.S.I.R. and the University of Pretoria.

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LIST OF SYMBOLS

T_{ex}	Exhaled air temperature	(°C)
$T_{ex\ sat}$	Exhaled air at T_{ex} and 100% saturated with water vapor	(mg H_2O/l air)
T_{re}	Rectal temperature	(°C)
$T_{re\ sat}$	Air 100% saturated with water vapor at T_{re}	(mg H_2O/l air)
T_a	Ambient temperature	(°C)
I_a	Air partially saturated with water vapor at T_q	(mg H_2O/l air)
T_r	Temperature of the radiating surface	(°C)
T_g	Temperature of the ground	(°C)
rh	Relative humidity	(%)
Rg	Incident longwave radiation from the ground	(cal/cm^{2}min)
Ra	Incident longwave radiation from the sky	(cal/cm^{2}min)
S	Direct solar radiation on a horizontal surface	(cal/cm^{2}min)
s	Incident diffuse solar radiation on a horizontal surface	(cal/cm^{2}min)
a	Absorptance of shortwave radiation by the coat	
rg	Shortwave radiation reflected from ground	(cal/cm^{2}min)
ε	Emissivity	
σ	Stefan-Boltzmann constant	

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Habs	Total radiant heat absorbed by a cylinder	(cal/cm^{2}min)
V	Wind speed	(cm/sec)
D	Diameter	(cm)
W	Body weight	kg
M	Metabolic rate	(cal/cm^{2}min)
H_{sw}	Cutaneous evaporative heat loss	(cal/cm^{2}min)
H_{ex}	Respiratory evaporative heat loss	(cal/cm^{2}min)
HS	Heat storage	(cal/cm^{2}min)
V_t	Tidal volume	l/breath
V_e	Respiratory minute volume	l/min
W_h	Humidity ratio	g H_2O/g dry air
P_w	Vapor pressure at saturation	mm Hg
P	Barometric pressure	mm Hg
D_o	Density of dry air	g dry air/ ml air

0.83 kcal/°C/°kg	Heat capacity of animal tissue
0.24 cal/°C/g	Heat capacity of air
580 cal/g	Latent heat of vaporization

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GENERAL INTRODUCTION

Very little direct experimentation on the thermoregulatory physiology of the largest terrestrial mammals has been reported in the literature. Mammals weighing over 1,400 kg are too large for conventional laboratory holding facilities and must be studied either in their natural habitat or in large open holding pens. A study of temperature regulations in large mammals penned in near natural conditions presents problems not only of handling but also of the measurement of ambient conditions contributing to heat gain and heat loss. Combined with physiological measurements on captive animals, information should also be obtained on behavior and particularly thermoregulatory behavior of free ranging animals. Studies on large mammals are, however, necessary for a more complete understanding of the relationships between body size and thermoregulation.

This study will deal with the thermoregulation and behavior of giraffe under free ranging and near natural conditions. The evolution of giraffe during the Miocene in Eurasia through their present distribution in Africa has taken place in warm semi-arid habitats (Arambourg 1963). The family Giraffidae has only two members: okapi (*Okapia*

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johnstoni) and giraffe (*Giraffa camelopardalis*). Ansell's (1968) classification recognizing one species and nine subspecies has been used throughout this text. Giraffe are wide spread over Africa, but are limited to semi-arid bush and tree habitat. They are not found in deserts, rain forests, or mountain ranges. Giraffe are exclusive browsers at levels above 2.5 m exploiting a food source unavailable to other ruminants. Adult giraffe may feed throughout the day exposed to long and shortwave radiation and ambient temperatures ranging from night time lows of 5°C and to daytime highs of 37°C. Giraffe are the largest living ruminants with adult body weights ranging between 1,000 to 1,600 kg (Hall-Martin 1977). Their past evolutionary history as well as their large body size make giraffe an ideal experimental animal for the investigation of size related thermoregulatory adaptations for survival in hot, semi-arid environments.

A summary of all publications on giraffe taxonomy, behavior, ecology, and physiology has been prepared by Dagg (1971). Two long term studies of giraffe behavior and ecology have shown a lack of territoriality in the males and an absence of maternal care in cows with calves (Foster 1966, Foster and Dagg 1972). Little or no information is available in the literature on any aspect of giraffe

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physiology with the exception of research into the cardiovascular physiology (Goetz and Budtz-Olsen 1955, Goetz and Keen 1957, Goetz et al. 1960, Franklin and Haynes 1927). Two short term studies involving the measurement or physiological parameters from captive or newly captured giraffe have been attempted. The first involved monitoring the body temperature via biotelemetry of a captive juvenile giraffe (Bligh and Harthoorn 1965). The results of this study indicated giraffe may have a narrow range of daily body temperature fluctuations. The second study involved the capture and instrumentation of wild giraffe for the measurement of blood pressure (Van Citters et al. 1966, Van Citters 1968).

The overall objective of this study was to relate the thermoregulatory physiology of a large mammal, the giraffe, to its behavior under natural conditions. The approach to the completion of these objectives has been taken in two phases, a field study of the behavior of free ranging giraffe and a study of the thermoregulatory physiology of giraffe kept in pens under near natural conditions. The two phases of this study have been further divided into three chapters.

The objective of phase 1 (Chapter 1) was the investigation of the cow-calf relationships in giraffe. Past research on giraffe behavior indicated that the cow and

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calf remained together for a relatively short period and that a low level of maternal care was evident (Innis 1958, Dagg and Foster 1976, Foster and Dagg 1972). The young of large mammals are of particular interest when considering size related thermoregulatory adaptations. Therefore, the question was asked, if young giraffe are separated from their mothers at an usually early age, what survival advantages are gained from a short weaning period and lack of maternal care.

The main objective of Chapter 2 was to measure the thermoregulatory response of giraffe to naturally occurring heat gain and heat loss factors and to calculate the heat flow between the giraffe and the environment. There is a high degree of complexity involved in the measurement and calculation of heat balance between an animal and the environment and although several investigators have begun to work on problems of biophysical measurements (Porter and Gates 1969, Gates and Schmeral 1975, Finch 1971, 1973), the techniques remain in the early stages of development.

Heat balance measurements made with giraffe showed very low levels of respiratory water loss. The objective

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of Chapter 3 was to determine how giraffe were able to reduce respiratory water and heat loss. The ability of other wild and domestic animals to reduce respiratory water loss was also measured to obtain an interspecies comparison.

The work included in these three chapters is an attempt to bring together in a research context two disciplines which have always existed together in nature--physiology and behavior. By working in both fields, it is hoped that this volume will present the unique thermoregulatory and behavioral adaptations of giraffe for survival in semi-arid habitats. This work is also intended as a contribution to the very limited information available on thermoregulation in large mammals.

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CHAPTER 1

COW-CALF RELATIONSHIPS IN GIRAFFE

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INTRODUCTION

The maternal behavior of giraffe has been a topic of controversy in both scientific and popular literature. The first behavior study of giraffe, which indicated a weak cow-calf bond, was published by Innis in 1958. Her conclusions were confirmed in three subsequent papers by Foster (1966), Dagg (1971), and Foster and Dagg (1972). The latter described the weaning period for giraffe as one month. Foster and Dagg (1972) found no correlation between the cow-calf bond and the survival of the calves. Their results showed that the cow and calf remained together for the first six weeks postpartum after which the calf might wander off from the cow on its own. Contradictory information on nurseries and giraffe cows actively protecting their calves has been published by Guggisberg (1969). Spinage (1968) also notes that the maternal behavior in giraffe may be more intense and lasting than previously described.

Hiders and followers are the two basic divisions of ungulate cow-calf relationships which occur in the first 30 days postpartum. The hiders such as Grant's gazelle (*Gazella granti*, Walther 1965) characteristically remain hidden and separated from the mother (lying out) except

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during nursing periods. The followers (e.g., wildebeest *Connochaetes taurinus*, Talbot and Talbot 1963) follow the cow within a few hours and thereafter accompany her while she travels and feeds. A complete summary of these two types of behavior has been presented by Lent (1974). He defined the differences between the two categories on the basis of spacing between the mother and infant in the first weeks postpartum. Walther (1961, 1964, 1965) originally defined and described the two groups calling them the "Ablieger Typ" (lying out type) and "Nachfolger Typ" (following type). Ewer (1973) argues that the two behaviors cannot be easily used as rigid classifications. She has pointed out that the short periods of isolation found in animals such as the wildebeest and domestic sheep may represent vestigial lying out. Ewer notes, however, that lying out seems to be a very successful adaptation for the reduction of infant mortalities.

The relationships between the cow and calf after they join the herd, either within 30 days postpartum (hiders) or within a few hours postpartum (followers), also varies between species and can be used to divide cow-calf behavior into three general groups. The eland, elk, mountain sheep, and pronghorn (Table 6, Group 1) are hiders (Lent 1974). When the cow and infant rejoin the herd, close contact with

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Table 1. Weaning periods and duration of the mother-infant relationships in several mammalian species.

Species	Weaning Period	Duration of Mother-Infant Bond	Author
Group 1			
Pronghorn *Antilocapra americana*	3.5-4 months	3.5-4 months	Kitchen 1974
Elk *Cervus canadensis nelsoni*	3-5 months	1 year	Altmann 1956
Mountain Sheep *Ovis canadensis stonei*	4-6 months	1 year	Geist 1971
Eland *Taurotragus oryx*	3-5 months	3-5 months	J. C. Hillman pers. comm.
Group 2			
Bison *Bison bison bison*	7-8 months	8-12 months	McHugh 1958
Buffalo *Syncerus caffer*	10.5 months	18 months plus	Sinclair 1970 Grimsdell 1969
Group 3			
Shiras Moose *Alces alces shirasi*	4-6 months	1.5 years	Altmann 1958, 1963
Black Rhinoceros *Diceros bicornis*	17.5 (max. lactation--no weaning data)	18 months	Goddard 1967
Elephant *Loxodonta africana*	4-8 years	12-15 years	Douglas-Hamilton 1972 H. Croze pers. comm.

the mother breaks down and the socialization of the infant takes place in calf sub-groups. Bison, buffalo, and wildebeest (Table 1, Group 2) are followers. The cow and calf rejoin the herd when the calf is able to follow the cow. Although in both Groups 1 and 2 the calves join calf subgroups, in Group 2 a close contact between the cow and calf is maintained and the weaning periods are longer than those reported in Group 1.

Moose, rhino, and elephant (Table 1, Group 3) maintain close mother-infant contact throughout the weaning period and usually up to the next parturition. There are no secondary social groups in Group 3, such as calf sub-groups and nursery herds. The transition for mother-infant relationships was from low mother-infant contact and strong calf subgroups (Group 1), to a combination of close mother-infant contact and calf subgroups (Group 2), and finally very close mother-infant ties and an absence of calf subgroups and nursery herds (Group 3).

The weaning periods and temporal lengths of the cow-calf bonds reported in the literature for these wild ungulates are much longer than those described for giraffe. The data presented for the length of the weaning period and duration of cow-calf relationships in giraffe would indicate that this species doesn't fit into any of the previously

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described patterns. If giraffe calves were partially ruminate at one month and were capable of surviving on their own at six weeks, it would represent one of the shortest weaning periods and mother-infant relationships reported for any artiodactyls. Therefore, when this study of the behavior of giraffe (*Giraffa camelopardalis giraffa*) was undertaken, it was decided to investigate the cow-calf relationships closely to determine if the cow-calf bond was of a short duration, and, if so, what were the adaptive advantages of a weak maternal instinct and short weaning period.

The study area was the southernmost section of the Timbavati Private Nature Reserve, bordering the Kruger National Park in the Eastern Transvaal lowveld, Republic of South Africa. The study area was 183 km^2 and supported an estimated population of 600 giraffe. The primary vegetation types of the study area were *Combretum apiculatum*, *Sclerocarya caffra*, and *Acacia nigrescens*, savanna woodland and riparian forests (Porter 1970). The fauna and flora of Timbavati has been described by Hirst (1965).

METHODS AND MATERIALS

Field observations were made from a Land Rover with Nikon 7×50 binoculars and recorded in a field notebook. A

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stopwatch was used to measure the duration of various behaviors. Directional information was taken from a transect compass. All photographs were taken with a Mamiya Sekor camera fitted with a 200 mm lens. Long-term observations were made on giraffe which had either been captured and radio-collared or on naturally marked giraffe. The capture and immobilization techniques used in this study have been published separately (Langman 1973). The telemetry system and methods used to collar and radio-track giraffe have also been reported by Langman (1974).

The radio-tracking system was used to locate and observe the same individuals and their respective groups for long periods of time. A member of an age category, in this case infant or juvenile, was located, captured, and a radio collar placed around the base of the neck. The giraffe was then relocated each morning, followed, and observed all day. Observations were continued until 250 observation hours had been logged for each individual. After this period of intense observation, the collared individuals were located and observed for short periods three to four times a week until the collars stopped transmitting.

Naturally marked giraffe have also been used in this study. A naturally marked giraffe exhibited a combination of two distinct and easily recognizable scars or other

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morphological traits (i.e., horn missing and Y-shaped scar on the left side). Naturally marked giraffe were given a name and code letter and recorded as to location, group association, and behavior at the time of sighting. All sightings were followed and observed until a definite record could be made of the above. When radio-telemetry was not being used, naturally marked giraffe, when resighted, were followed until they could no longer be located. Observations of cows and calves which were not marked in either of the two ways mentioned above were recorded as to location, general behavior, herd association, and age composition of the herd.

The data presented were analyzed statistically using fourfold tables (Bliss 1967). Yate's correction for continuity has been applied in all instances where the expected frequencies (ϕ) were less than 100. P values at 1 DF where $P \leq 0.05$ were considered significantly different. P values at 1 DF where $P \leq 0.01$ were considered as highly significant differences. Values for P were taken from an abridged table of the percentage points of the χ^2 distribution (Bliss 1967).

Various giraffe social groups and behaviors were named and used as working definitions during field observations. The definitions of these terms have been included below and will be referred to repeatedly throughout the paper.

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Lying Out

Lying out as defined by Lent (1974) and Walther (1961, 1964, 1965) was divided into two basic types: single lying out and group lying out. Both behaviors involved infant or juvenile giraffe lying or standing in an area without any adult giraffe within 0.5 km. Single lying out involved only one infant or juvenile while group lying out involved two or more. As is typical of hiders, neither infant or juvenile giraffe left the lying out area unless grossly disturbed. Calves lying out would not approach their cow when she returned until they received tactile stimulation in the form of nudging or licking.

Approach-Investigation

When an adult or sub-adult giraffe approached a novel or potentially dangerous stimulus in the environment and issued a nasal hissing, the behavior was listed as approach-investigation. Investigation behavior was initiated by new objects in an old setting or old objects in a new setting, much the same as that described by Hafez (1962) for cattle. There were also elements of calf shielding (Altmann 1956) in the approach of adult females which were moving with a nursery herd. The range of the total number of approaches and vocalizations was wide; therefore, the basic requirements for classification were a single approach and nasal hissing.

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Nursery Herds

Nursery herds were defined in this study as two or more infants and/or juveniles and their cows moving or browsing together. This definition of a nursery herd is similar to that used by many authors (Altmann 1956; Grimsdell 1969) to describe several cows with their calves or a herd which exhibits temporarily longer relationships than those found between individuals in feeding groups.

Calving Pools

Calving pools were formed when the cows of the nursery herd left all of their calves with one female while they traveled to other areas for browse or water. Calving pools have been described by Altmann (1956) in Cervids and by Hersher, Richmond, and Moore (1963) in domestic sheep and goats. Calving pools in this paper have been strictly separated from group lying out by the requirement that a calving pool must have at least one adult female present with the calves. The adult female "in charge" of a calving pool serves an important protective function in that the calves in the calving pool will follow her when she moves away from an alarming stimulus. Observation of groups with more calves than cows were included in the data as calving pools.

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The investigations of the behavior of giraffe in the Republic of South Africa involved over 2,000 giraffe observation hours during a two-year period. The cow-calf relationships reported in this paper are a portion of the above study and include 291 observations involving 1,070 individuals.

RESULTS

The following sections discuss the relationships between adult females, infants, and juveniles. The age categories used as working definitions during field observations were as follows: adults, immatures, juveniles, and infants (the last three were referred to collectively as sub-adults). These age categories represent a gradually changing system in which both the behavior and general physiology of the giraffe are maturing. The age categories used have been defined by a combination of morphology and behavior (Table 2). The data used to classify the three groups were derived from the combined sightings of naturally marked and radio-collared giraffe. Those animals which matured to a transition state were difficult to classify and have been generally included in the next older age group.

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Table 2. Classification and definitions of the three sub-adult age categories.

Classification	Approximate Age	Characteristics
Infant	0-60 days	1. Umbilicus present, horns undeveloped 2. 80% diurnal activity resting or lying out; suckles 3-4 times per day 3. Daily range 0.1-0.2 km 4. Regularly part of calving pools, group lying out, and single lying out 5. Accompanied female parent
Juvenile	60 days- 1.5 years	1. Horn tuffs present and horns definite 2. 80% diurnal activity browsing; suckles 1-2 times per day for 9 months 3. Daily range 0.1-0.5 km 4. Regularly part of calving pools, group lying out, and single lying out 5. Accompanied female parent
Immature	1.5-3 years female 1.5-4 years male	1. Horn tuff present but short; no suckling 2. No urine testing or flehmen by the male; no urination and lack of response to male stimulation by the female. Smaller general body size when compared with adults. 3. Daily range 2-6 km 4. Does not participate in calving pools, group lying out, or single lying out 5. Does not accompany female parent.

Although gradual, the transition from infant to juvenile involved a change in size, horn structure, and time spent browsing. There is a marked difference in daily activity between the two classifications (Fig. 1). This difference can be partially attributed to the developing ability of the juveniles to digest browse. Figures 2, 3, and 4 are photographs of infant, juvenile, and immature giraffe, respectively.

Cow-calf relationships have been divided into five main types (Table 3). Cow-calf sightings and single lying out behavior were similar statistically and situated at the same stage during the development sequence of the calf from birth to the time of separation from the cow. Nursery herds, calving pools, and group lying out behavior were all statistically similar with a high number of juvenile versus infant sightings (Table 3). These group configurations occurred after the isolation period and up to the time that the cow next gave birth.

Cow-Calf

All observations of females and calves which involved one or more cows and only one calf have been analyzed in this section. During the first one to three weeks postpartum, the calf was isolated from other calves and adults by the cow. A giraffe cow would frequently leave her calf

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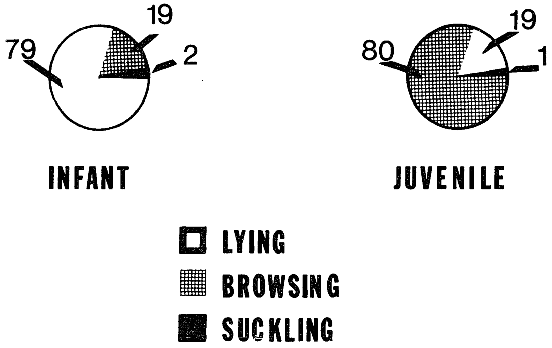

Figure 1. A comparison of the percentage of diurnal time spent by juvenile and infant giraffe in the activities of lying, browsing, and suckling.

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Figure 2. An infant (note unbilicus) left by cow in a single lying out situation. The photographs included as figures 2, 3, and 4 were giraffe observed for long periods of time and are good examples of the age category definitions presented in Table 2.

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Figure 3. Radio-collared female juvenile (HI) 14 days after capture. The naturally marked cow FG was browsing in the background.

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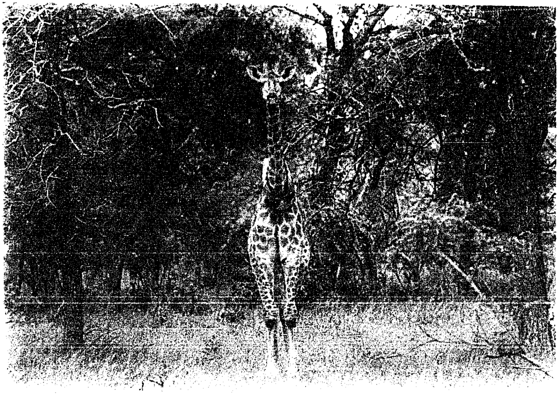

Figure 3. Radio-collared female juvenile (HI) 14 days after capture. The naturally marked cow FG was browsing in the background.

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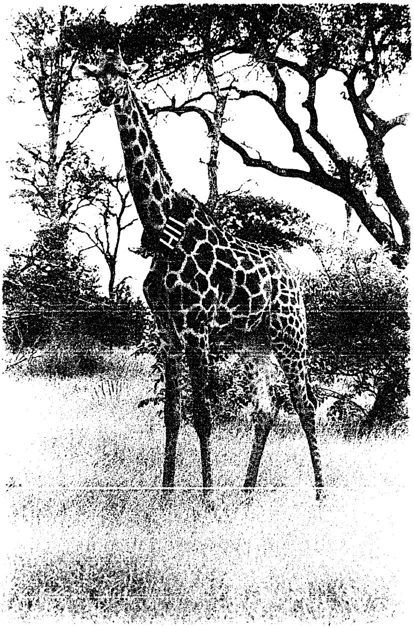

Figure 4. The radio-collared female immature HII which, although captured in a female herd, associated primarily with other male and female sub-adults.

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Table 3. A comparison of the numbers of juveniles and infants present in five discrete social groups.

	Average No. of Juveniles and Infants	Average No. of Juveniles	Average No. of Infants	Infant-Juvenile Ratio
Cow-calf	1.00	0.305	0.695	1:0.420
Single lying out	1.00	0.462	0.539	1:0.857
Nursery herd	2.36	1.53	0.73	L:2.08
Calving pool	2.68	1.90	1.07	1:1.775
Group lying out	2.29	1.47	0.83	1:1.785

in a thicket or high grass area during the day while she traveled to find browse or water. The cow returned two to four times a day at varying intervals to allow the calf to suckle. She might remain in the area browsing after nursing the calf, or leave again immediately after standing a short period surveying the surroundings.

Single infants and juveniles were in the company of one adult female in 72.6% of the total number of sightings. If this category was expanded to one or two adult females, it included 90.5% of the total number of observations. There was no statistically significant difference between sighting of single juveniles or infants with one adult female as opposed to two or more adult females (Table 4).

Suckling periods ranged between 45 seconds and 4 minutes. When the cow was not disturbed, she spread her hind legs, raised her tail, and micturated while the infant or juvenile suckled (Fig. 5). If the cow was disturbed, the suckling period was shorter and she assumed an alert position and turned her head towards the disturbance. As in many other species, the calf bumped the udder while nursing to stimulate milk let down. The infant or juvenile approached the female with the head and neck slightly lowered and directed toward the udder. Giraffe cows did not allow any other calves except their own to suckle. The

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Table 4. A comparison of the presence of single juvenile or infants with one or more adult female giraffe.

Adults	Infants	Juveniles	N	$P = y/N$	Expectations ϕ	
					Infants	Juveniles
one adult female	50	19	69	0.73	47.96	21.05
two or more adult females	16	10	26	0.62	18.07	7.93
	66	29	95	0.695	66.03	28.98

$\chi^2 = 0.61012$; $P = 0.44387$

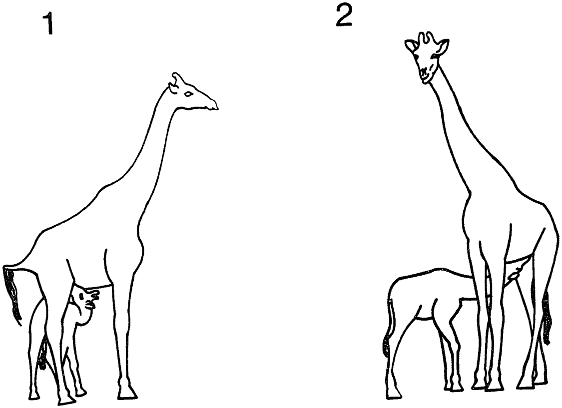

Figure 5. (1) The nursing position assumed by an undisturbed cow and calf. The suckling initiates micturation which is accompanied by the lifting and partial curling of the tail. (2) The nursing stance assumed by a cow observing some disturbance in the environment.

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interval between nursing periods increased as the age of the giraffe calves increased.

Giraffe calves were observed with their cows for as long as 14 months (Table 5). Giraffe calves of six months were observed both suckling and browsing. Suckling attempts have been recorded from several calves which were over nine months old; however, no known age calves past the age of six months were observed successfully nursing. Many observations of a cow nursing a calf with an estimated age of a year or more have been made. From these it would seem that the tolerance of the cow towards the calf determines how long the calf will be allowed to suckle. Complete rumination in giraffe calves occurred between six to eight months; however, the cow-calf relationship extended for 14 to 16 months. Again, this period is based on known age animals. The relationship between the cow and calf may be extended for much longer periods and is primarily dependent on the cow's calving frequency.

"Stepping behavior" was observed from both juveniles and infants when the cow was not ready for suckling or had allowed suckling and was moving away. The calves which were persistent in their nursing attempts would push on the female's hindquarters with their chest or push and hit the female's rump with their head and neck. The three primary motions of stepping behavior in giraffe are

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Table 5. The behavior and temporal association of the adult female FG, a naturally marked giraffe, and her calf HI, a radio-collared juvenile female.

22- 6-73	1-3 weeks	HI lying out and FG returned at intervals for nursing. No browsing observed from HI.
25- 9-73	3 months	HI lying out alone. FG traveling several km for browse. HI did not browse during lying out period. FG returned at intervals for nursing.
9-11-73	5 months	HI radio-collared; captured in a nursery herd; HI browsed during lying out periods; observed in calving pools, group lying out, and nursery herds.
29-12-73	6 months	HI was suckling and browsing.
6- 2-74	8 months	FG "in charge" of a calving pool of two juveniles and HI.
2- 3-74	9 months	HI observed trying to suckle but FG did not allow her to do so.
24- 4-74	10 months	HI and FG together browsing.
8- 8-74	14 months	HI sighted browsing with young female HII; FG browsing nearby.
1-10-74	16 months	FG sighted with three other adult females; HI not sighted.
15- 2-75	20 months	HI sighted moving and browsing with a group of 11 giraffe; FG not sighted; radio-collar still intact and marked.

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illustrated in Figure 6. All three were observed in various sequences, as well as singly. Although this behavior was interpreted as an attempt by the calves to stimulate nursing, suckling rarely followed the stepping behavior pattern.

Rubbing on the hind leg with head and neck was exhibited by infants and juveniles walking alongside a moving cow (Fig. 6, No. 3). The approach of the calf from the rear of a standing cow was more common. The calf laid its head on the female's rump and pushed forward with the chest in a jumping motion (Fig. 6, No. 2). This behavior was often accompanied by a downward stamping of the calf's foreleg. A variation of this behavior has been illustrated (Fig. 6, No. 1). In this case, the calf pushed with its shoulder and neck with a pronounced stamping of the foreleg.

Single Lying Out

Giraffe cows with infants and juveniles left them in an open area or thicket while they traveled to food and water. The same area was sometimes used by several cows at different times. Such areas usually afforded good visibility for 50-100 meters. Single lying out was primarily practised by cows with newly born calves.

Calves would normally follow the female by "heeling" which involved following and walking at her side (Altmann

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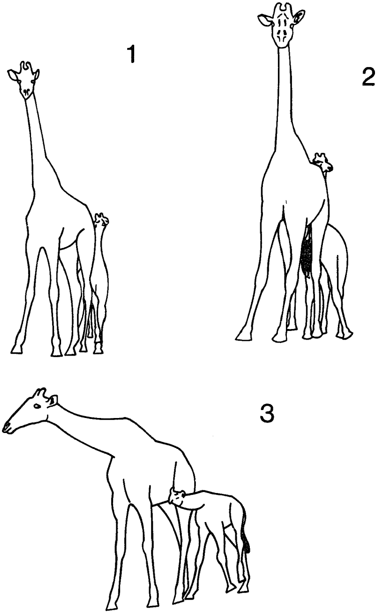

Figure 6. (1) The stepping behavior depicted in this diagram involved stamping with the calf's foreleg and rubbing the female's hindquarters with his head and neck. (2) This type of stepping behavior was very much the same form as the Sprungintention elicited by adult males during precopulatory behavior. (3) One of the motions of stepping behavior associated with a cow moving away after nursing. The calf moves alongside the cow rubbing its head and neck on the rear flank.

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1963). However, when the time came for the female to travel to areas of browse or water, they came together and a short time later the female walked away and the calf remained either lying or standing in a thicket or open grass plain. It was difficult to determine whether the cow or the calf selected the lying out location. The calf would select its own site if the cow left without the calf realizing it. This selection of a lying out area was carried out much the same as reported for Grant's gazelle (Walther 1965) and waterbuck (*Kobus defassa ugandae*, Spinage 1969). When the cow and calf were standing together and the cow left, the calf would lie down in the same location without exhibiting any type of search behavior.

If the calf was left lying in a thicket, it lay down with its head resting on its rump or with the head and neck up. When the calves were sleeping, the coat pattern and reduction in size made them difficult to locate visually. In most of the observations of an infant left by a cow, the infant rose only when frightened and performed comfort movements. If the calf was disturbed, it circled while running and headed back toward the same general area.

An adult female with distinctive markings on both sides of her neck and a long scar on her right flank was code marked FG when she was near full term pregnancy. FG

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occupied a seasonally stable home range of 41 km^2 (Fig. 7), which was situated around many of the most commonly traveled roads in the study area. FG and later her calf coded HI were sighted and observed for 20 months (Table 5). FG was observed many times leaving HI in a thicket or in open grasslands. The pattern was the same as that described above.

The instance of lying out used as an example below involved FG and HI when the latter was less than three weeks of age. The approximate age of HI was determined from previous sightings of FG prior to calving, development of the horn size, and absence of browsing. FG and HI were observed from about 150 m. When the Land Rover was sighted, FG made a semi-circular approach towards the Land Rover and stopped approximately 90 m away with HI close behind. After four approaches, FG and HI went into a dense thicket. FG emerged about 50 m away after clearing the edge of the brush, but HI was not with her. The thicket was examined and HI was found lying in the brush.

HI was lying on her sternum with her head up looking towards the Land Rover. HI rested first with the head up and occasionally looking around; eight minutes later, she laid her head down on her rump and went to sleep. The periods of sleeping increased, but were broken at intervals when HI raised her head.

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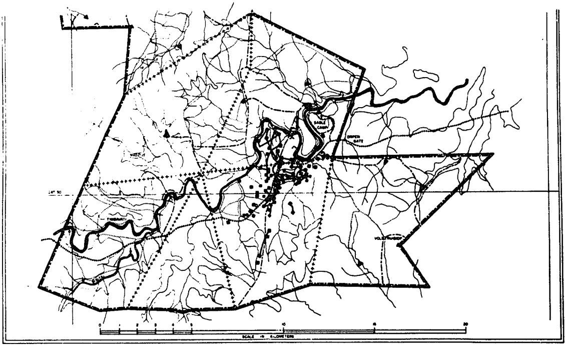

Figure 7. The 41.025 km^2 home range for the adult female FG and the radio-collared juvenile female HI during a 20-month period. Each square marks an individual sighting. The squares connected by lines represent long-term observations where the location of the giraffe was marked every 4 hours.

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Two hours later, FG returned within 400 m, stopped, and looked towards the Land Rover. HI stood up and performed the comfort movements of stretching and grooming, but did not move towards FG. FG moved closer with her head turned towards the Land Rover at all times. HI stood watching FG approach but did not move, even when FG was within 10 m. After watching the Land Rover for 10 minutes, FG went up to HI and nudged her neck and mane with her nose. Immediately afterwards, HI went to FG and suckled for 4 minutes. When the suckling terminated, they moved off together.

Home Range

The home range for FG and HI for 20 months has been presented in Figure 7. By using the minimum home range method (Mohr and Stumpf 1966) and connecting the outermost sightings, the minimum home range was determined to be 41.025 km^2. During the wet season, this range included several natural waterholes; however, during the dry season there was no area of standing water available.

Adult female giraffe drank regularly during the dry season when water was within a distance of a few kilometers. However, the excursions of FG to one of the dams marked on the map have not been observed or recorded. HI was radio-collared and could be located in 30 minutes within the home range. However, throughout the observation period,

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HI was not sighted closer than 1.5 km to permanent water. No giraffe calves--infant or juvenile--were observed traveling with their cow to a dam to drink and only on two occasions were juveniles observed drinking water. FG's home range was similar in size to the home ranges of eight other radio-collared and naturally marked female giraffe utilized in this study.

Approach-Investigation

The investigation pattern when giraffe encountered novel additions in their environment has been included here because of the high proportion (63%) of cow-calf groups in which this behavior was recorded. The investigation behavior described had three basic components: the approach, approach stance, and nasal hissing vocalization. The types of stimuli which were investigated in the manner described were lion kills, new structures such as bomas and tents, and, most commonly, the vehicle and observer. The approach-investigation patterns usually involved the multiple approach of the stimulus, a characteristic stance, and a nasal hissing vocalization emitted while facing the stimulus at the termination of each approach. Although single adult male and female giraffe were observed investigating different stimuli, this behavior was more frequently recorded in situations involving females and infants or juveniles.

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The first three social groups listed in Table 6 contained 63.7% of the total number of observations. By adding the sightings from the female-herds, which may represent herds temporarily formed by adult females who have left their calves either lying out or in calving pools, the percentage increased to 76.7%.

Figure 8 illustrates an average approach investigation pattern with the vehicle and observer serving as the stimulus. The approach usually involved the giraffe moving up to 100 m towards the stimulus, stopping in the stance illustrated in Figure 8, and issuing a long audible hissing caused by exhaling air through the nose. The vocalization was followed by the giraffe remaining stationary observing the stimulus from one to five minutes and then moving with its back and then side towards the stimulus in gradual arch to a second position. The whole sequence might have been repeated up to 15 times with 12 total vocalizations or completed with the first approach and a single vocalization. The approach pattern commonly involved the giraffe completing an arc of approximately 180°; however, it was not unusual to have a total arc of 360°.

The highest percentage of approach-investigation behavior involved females, and particularly females with calves (Fig. 9). Juveniles and infants were present in 66%

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Table 6. The number of observations of investigation behavior in eight giraffe social groups. Sightings of investigation were recorded throughout the study during routine field observations.

Social Group	No. of Sightings	% of Total
Cow-calf	11	37.0
Nursery Herd	2	6.7
Calving Pool	6	20.0
Female Herds	4	13.0
Single Female	2	6.7
Reproductive Pair	1	3.3
Male Herd	2	6.7
Single Male	2	6.7

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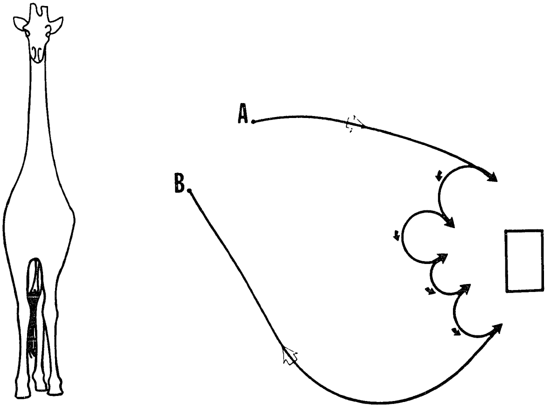

Figure 8. The characteristic approach-investigation pattern and stance elicited by adult males and females. The giraffe in the diagram approached from point A stopping at each large arrow facing the vehicle. The stance was assumed at the termination of each approach during approach-investigation behavior. This posture was held during the nasal hissing vocalization accompanying the termination of the approach.

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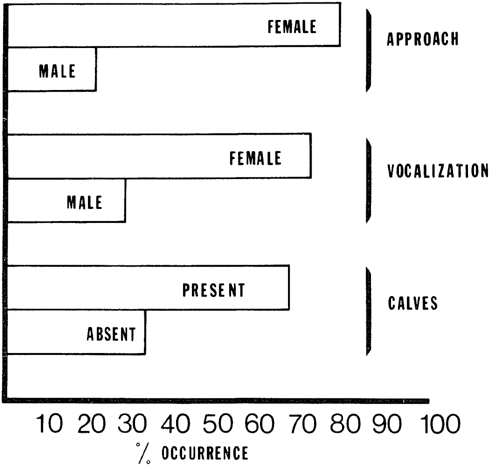

Figure 9. A comparison of the occurrence of approach and vocalization behavior in adult females and males in the presence or absence of calves.

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of the observations. There was no significant difference between approach and vocalization behavior when compared with the presence or absence of juveniles and infants (Table 7).

The analysis of the components of investigation behavior showed that the highest number of observations for approach combined with vocalization were recorded for adult females and the lowest for adult males. The ratios of vocalizations and approaches showed a slightly higher frequency of vocalizations for adult females with a ratio of 1.19:1 and a higher frequency of approaches for adult males with a ratio of 1:1.27.

There was a wide range of variation in the approach-investigation behavior pattern described. All of the observations were characterized by the approach of the novel stimulus and the approach stance. After this initial sequence, the entire pattern might have been terminated or repeated. The most approaches recorded was 15 and the maximum number of vocalizations recorded was 14.

The behavior pattern could be experimentally released by carefully moving the Land Rover across the path of an adult female and infant. Also, during the observation of calving pools, the continued gradual following of the calving pool or close observation of several of its members induced approach-investigation behavior from the

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Table 7. Presence or absence of infants and juveniles during approach-investigation.

	Infants & Juveniles				Expectations ϕ	
	Present	Absent	N	$P = y/N$	Present	Absent
Approach	73	19	92	0.794	74.6	17.2
Vocalization	61	12	73	0.835	59.3	13.65
	134	31	165	0.813	133.9	30.85

$\chi^2 = 0.23668$; $P = 0.6299$

resident female. After the completion of an approach-investigation pattern by the female "in charge," a decreased observation distance was usually permitted.

Nursery Herds

Nursery herds were defined in this study as two or more infants and/or juveniles and their cows moving together. Using this definition, sightings which involved two or more calves and an equal or greater number of cows (i.e., three cows and two calves) were recorded as nursery herds. Calving pools and group lying out were the two primary social groups formed from nursery herds.

The nursery herds observed in this study ranged in size from four to 13 members with 6.8 as the average number of giraffe per herd. The mean number of adult females per herd was 4.44, and the mean number of calves was 2.36. The ratio of cows to calves for the nursery herds observed was 1.88:1. The statistical comparison of the number of infants and juveniles in herds with an equal number of females and herds with an unequal number of females has been presented in Table 8. There was a significant difference between the presence of infants and juveniles in herds in which the number of females equaled the number of calves. The percentage of infants sighted in nursery herds with an unequal number of cows to calves made up only 2.6% of the total sightings.

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Table 8. A comparison of nursery herds with the number of adult females equal to the number of sub-adults and with the number of adult females unequal to the number of sub-adults.

					Expectations	
	No. of Infants	No. of Juveniles	N	P = y/N	No. of Infants	No. of Juveniles
No. Adult Females = No. Sub-adults	45	67	112	0.40	34.6	77.5
No. Adult Females ≠ No. Sub-adults	4	35	39	0.103	12.05	26.9
	49	102	151	0.309	46.65	104.4

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A further analysis of the composition of the nursery herds had been presented in Table 9. Both juveniles and infants were sighted in a high percentage of the total observations in homogeneous groups. There were only 19 giraffe (12.5%) sighted in nursery herds which were heterogeneous in composition.

The nursery herds observed were fluid and the associations were of short duration. A cow with an infant might travel with another cow with a calf of the same age for one to seven days. During their association, the cows formed calving pools or left both calves lying out. The same females and infants or juveniles were seen together repeatedly in nursery bands over a period of four to five months. This was a non-migratory population which tended toward repeated encounters between individuals and thereby repeated herd association. However, the only lasting bond between individuals was the cow-calf relationship.

In order to clarify the various functions of nursery bands, it was important to gain an understanding of the day-to-day behavior patterns of cows and calves. A relatively typical pattern of behavior for ten days of observations on a radio-collared juvenile and her mother has been described below. The formation and break-up of nursery herds, calving pools, and group lying out has been presented as it was observed.

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Table 9. Analysis of the age composition of the sub-adult members of nursery herds.

	No. of Infants and Juveniles				Expectations ϕ	
Age Category	Homogeneous Groups	Heterogeneous Groups	N	$P = y/N$	Homo.	Hetero.
Infants	40	9	49	0.816	42.83	6.17
Juveniles	92	10	102	0.902	89.148	12.85
	132	19	151	0.874	131.98	19.02

$\chi^2 = 1.496$; $P = 0.2257$

M was the code used for the radio-collared juvenile female, and F-I was the naturally marked cow. Beginning on 11/11/73, M was observed with a juvenile male in a group lying out situation. Approximately 2.5 hr later, an adult female came to the area and both M and the other juvenile moved away with her; F-1 was not sighted and observations were terminated due to darkness. On the next day (12/11/73) M was radio-located in a calving pool at 0800 with F-1 "in charge." M and the juvenile male of 11/11/73 were browsing near two infants lying side by side in a small open area. F-1 left the calves at 0930 hr after nursing M. During the next 4 hr, the cows of all of the calves except the juvenile male returned to the area for short periods to allow their calves to suckle. The interim period between visits was an example of group lying out as no adults were present. The group of calves did not leave this area during the entire observation period. At 1300 hr, M and the juvenile male stopped browsing and were standing in the open ruminating. Both infants were still lying down rising at short periods to stretch and lie down again. The cow of one of the infants, a naturally marked female coded K, was browsing nearby, and by her presence had created a calving pool. At 1800 hr, the nursery herd had completely reformed with all of the cows and calves reunited.

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This herd configuration was constant until 17/11/73 when the group was sighted at 1300 hr in a calving pool formation with female K "in charge"; however, neither the juvenile male nor his cow could be located. At 1830 hr the entire nursery herd reformed with the juvenile male and his cow approaching from a densely wooded area. This was the last time this nursery herd was sighted together. On 18/11/73 at 0800 hr, a calving pool consisting of M and the same male and female infants with an unmarked cow "in charge" was observed. This smaller nursery herd was constant for three more days until M and F-1 moved off together.

Calving Pools

Calving pools were formed when the cows of a nursery herd left all of their calves with one or two females while they traveled to other areas for browse or water. All observations involving more calves than cows were included in the data as calving pools. The most common form of calving pool involved only one cow and her calf and the calves of several other cows. The average size of the calving pools recorded in this study was 4.25 giraffe. There was an average of 1.27 adult females and 2.96 infants and/or juveniles per calving pool. This gave a ratio of 1:2.33 cows to calves.

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The age composition of the calving pools has been analyzed in Table 10. There was a highly significant difference between the homogeneity and heterogeneity of infants and juveniles in calving pools. Calving pools containing juveniles were homogeneous in 74.6% of the observations. However, infants were observed nearly equally in both all-infant and mixed calving pools with both infant and juvenile age groups.

There was a significant difference between calving pools with more than two females in attendance and those with one or two females. Infants were present almost exclusively (97.3%) in calving pools with one to two cows (Table 11). Juveniles were also found most commonly (87.9%) in calving pools with one or two females. However, they were observed in calving pools with more than two cows several times more than the infants. The ratios of infants to juveniles recorded in nursery herds and calving pools are 1:2.08 and 1:1.77, respectively. These data are what might be expected if calving pools formed from nursery herds.

Calving pools were formed in relatively open areas and tended to be reformed in the same location repeatedly. As was the case with single and group lying out behavior, the calving pools were formed along routes of travel for giraffe.

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Table 10. The statistical analysis of the age composition of calving pools.

	No. of Infants and Juveniles				Expectations ϕ	
Age Category	Homogeneous Groups	Heterogeneous Groups	N	$P = y/N$	Homo.	Hetero.
Infant	35	42	77	0.455	49.1	27.8
Juvenile	97	33	130	0.746	83.0	47.0
	132	75	207	0.638	132.1	74.8

$\chi^2 = 16.53$; $P < 0.001$

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Table 11. The analysis of the adult female composition of calving pools.

	No. of Infants and Juveniles				Expectations ϕ	
Age Category	Groups with 1-2 females	Groups with 3 or more females	N	$P = y/N$	Groups with 1-2 females	Groups with 3 or more females
Infant	73	2	75	0.973	68.48	6.53
Juvenile	116	16	132	0.879	120.52	11.48
	189	18	207	0.973	189.00	18.01

$\chi^2 = 4.259$; $P = 0.027$

calf and nudged its mane with her nose or nudged and licked the mane. Immediately after contact, the calf nursed. After suckling, the cow either left without the calf, or if it was late in the afternoon, they moved off together. This sequence occurred many times with two or three females simultaneously.

The calving pool only lasted a single day and the calves were collected by their respective females by nightfall. This was the expected pattern as the sub-adults involved in the calving pools were still dependent on the cows for a large part of their energy. The adult females and calves, in the case of a group of eight or more, represented two nursery herds, or a nursery herd and one or more unattached cow and calf pairs. Large calving pools of 10 to 14 adult and sub-adult giraffe broke into smaller units and eventually dissolved by nightfall.

On three occasions, a single calf was left after all of the cows had returned and collected their calves. Two observations were infants and one was a radio-collared juvenile (M). All were last seen following an adult female and her calf. It was not possible to relocate one of the infants. The other was a distinctly marked female and was observed two days later with her cow. M was radio located the next day in a calving pool.

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These areas tended to be located on high ground and not in dense riverine bush. The formation and break-up of calving pools were observed many times. Cows and calves were observed in the mornings browsing in and around a relatively open area. The juveniles were browsing or ruminating and the infants were lying down. Suckling was frequently observed during this period.

Gradually, several adult females would leave the area moving and browsing. Their calves, who normally followed them within a few meters, remained with the other calves in the area. This process continued until there was only one or two females and their calves and the calves of all the other females. When the other cows were out of sight, the calves, if disturbed, the cow "in charge" approached her calf and nudged it with her nose until it began to move; the other calves seemed to be stimulated by the cow's behavior and followed her away from the area. The attending cow or cows did not allow any other calf except their own to suckle.

The other cows returned periodically during the day for nursing. When a cow returned to a calving pool, the infant or juvenile stood and watched her approach, but did not leave the area to go to her. When the cow was within 2 or 3 m of the calf she stopped and then proceeded to the

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There were many different variations of the basic pattern described, but there were two which were most common and noteworthy. During the course of the day, the cow originally "in charge" of the calving pool might be relieved by a returning cow. Secondly, the attending cow might gradually wander off from the calving pool and create a group lying out situation.

Group Lying Out

When two or more young giraffe were observed lying down or browsing within a restricted area together and were not in the company of an adult female, it was recorded as group lying out behavior. The average number of infants and juveniles and the infant-juvenile ratios were comparable for nursery herds, calving pools, and group lying out. Comparisons of observations of single individuals lying out gave much lower figures throughout and tended to be generally atypical of the other three categories. Because of these and other data, group lying out behavior was considered a function of nursery herds, while individual lying out was included in the results of single cow and calf relationships.

The group composition associated with lying out behavior (Table 12) shows no significant difference between infants and juveniles and the homogeneity or heterogeneity

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Table 12. Analysis of group composition during lying out behavior.

Age Category	No. of Infants and Juveniles		N	$P = y/N$	Expectations ϕ	
	Homogeneous Groups	Heterogeneous Groups			Homo.	Hetero.
Infant	13	8	21	0.62	14.5	5.89
Juvenile	23	8	31	0.74	21.4	8.69
	36	16	52	0.69	35.9	14.58

$\chi^2 = 0.404$; $P = 0.5283$

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of their groups. Both age categories tended to be found in homogeneous groups of a single age structure. The trend throughout all of the groupings has been a homogenous age structure for the sub-adults. In all instances, the juveniles have shown a greater tendency towards homogeneous groups than the infants.

The difference in diurnal activity between the partially ruminate juveniles and non-ruminate infants probably accounted for the significant difference between them in Table 13. The infants were observed almost equally standing as lying during lying out. However, the juveniles were more frequently observed standing, which included walking and browsing.

There was no significant difference between the two age groups when the overall density of the trees in the lying out areas was compared. The two age groups were both more frequently observed in relatively open areas as compared with bush thickets. These data, however, may have been biased by the observer's ability to see the giraffe in open areas versus the closed dense thickets.

Group lying out behavior was initiated and maintained in very much the same way as calving pools. The females began browsing in the morning with the calves moving together in an open area. Instead of one cow remaining

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Table 13. Analysis of the body positions assumed during lying out behavior.

	Body Positions				Expectations ϕ	
Age Category	Standing	Lying	N	P = y/N	Standing	Lying
Infant	8	11	19	0.42	13.11	5.89
Juvenile	23	3	26	0.95	17.94	8.06
	31	14	45	0.69	31.05	13.95

$\chi^2 = 8.950$; $P = 0.00355$

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behind while the others went to find water or browse, all of the cows in the nursery herd left their calves. The calves remained in the general area even when frightened or forced to move away by a disturbance. As with the calving pools, the cows returned during the day to allow the calves to suckle. The range of behavior for group lying out was from calves being left on their own during most of the day with the cows returning only for short periods for suckling, to situations where a cow or all of the cows returned after one to two hours and remained with their calves.

Calving pools and group lying out had two primary traits in common. The infants and juveniles, unless grossly disturbed, would not leave the area. This meant that when either of the behaviors were maintained for extended periods, the daily movement for those calves was less than 0.5 km. Secondly, juveniles spent their time browsing while the infants remained lying down during their participation in either calving pools or group lying out. Calving pools and group lying out are closely connected fluid formations which changed from one to the other throughout the day.

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DISCUSSION

The mother-infant relationship in giraffe as reported in this paper would place this species in the "Ablieger Typ" or hider category. The giraffe cow separates herself from the herd prior to parturition as reported for both hiders (Bubenik 1965; Altmann 1958; Rudge 1970) and followers (Hafez 1962; Scholeth 1961). Postpartum the calf was isolated and engaged in single lying out for one to three weeks while the cow traveled to water, browse, and social interactions with other giraffe. The isolation of the calf postpartum was of a similar duration to the waterbuck (Spinage 1969) and red deer (*Cervus elaphus* L.).

It was difficult to determine whether the cow or the calf selected the hiding or lying out location. The cow was responsible for the general location of the area by controlling the movements of the calf in and out of new areas. However, the exact hiding location seemed to be chosen alternatively by the calf and by the cow. The distance traveled by the cow from the lying out area was from 20 m to 3 km which is similar to the postpartum movements of the Defassa waterbuck cow.

The giraffe varies from the typical hider species in that the cow will approach the calf's hiding place and lick

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and smell the calf prior to nursing. This tactile stimulation and direct approach of the calf has also been reported in captive sitatunga (*Tragelaphus spekei*) (Walther 1964).

The giraffe again contrasts with the other hider species in the duration of the hiding period. Lent (1974) illustrated the typical hider species as having a set hiding period which diminished with age until the cow and calf had a follower type of relationship. Individual and group lying out would greatly extend the hiding period of giraffe calves beyond the longest periods now recognized for Reedbuck (*Redunca arundinum*) (Jungius 1970) and Uganda kob (*Kobus ellipsiprymnus thomasi*) (Leuthold 1967).

The breakdown of the giraffe cow-calf bond at the time of the next parturition was similar to a large number of ungulate species. The separation of the giraffe cow and calf initiated the immature stage of the giraffe calf's development.

The weaning period of six to eight months and cow-calf relationship of 14 months reported here for giraffe are not unusal for large African mammals. The first seven to 21 days postpartum the calf was left lying up while the cow traveled to browse or water. This phase in the development of the calf was similar to the postpartum period reported for elk (Altmann 1963), waterbuck (Kiley-Worthington 1965), and pronghorn (Kitchen 1974).

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It would be of very little adaptive advantage for giraffe calves to become independent at an early age. Giraffe calves up to one to two years do not benefit from the height and general body size which serves adults as anti-predator mechanisms. The short weaning period and cow-calf bond described by Innis (1958) and Foster and Dagg (1972) would not allow time for the calf to learn the characteristics of the home range or develop other responses which might be gained from a longer relationship with the cow.

The isolation of the giraffe cow and calf postpartum probably allowed for the imprinting of the calf on the cow. Hersher et al. (1963) and Rudge (1970) have shown this period of separation from the group to be important for the continuation of normal maternal behavior from the ewes in goats and sheep. Although there must exist a mutual feedback between the giraffe cow and calf, the actual importance of the isolation period for imprinting and continued normal maternal behavior has not been determined in this study.

The progression of lying out behavior presented included single lying out primarily involving infants and group lying out which involved calves who were members of a nursery herd. There were many species where lying out

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behavior was present only within the first 30 days postpartum. These instances of lying out had three functions; the development of the calf to a stage where it was capable of following the cow and the herd, the development of the cow-calf bond and learning anti-predator responses (Geist 1971). The single lying out behavior recorded in newly born giraffe was probably much the same as the above in its derivation and function. Group lying out behavior was associated with nursery herds although many of the advantages were the same as with single lying out.

A lone infant lying in a thicket in the sleeping position (lying on the sternum with the head resting on the rump) provided very little visual stimulus to the observer. The cryptic marking on the coat and greatly reduced size which resulted from the sleeping position provided a high degree of camouflage protection. The coat pattern may provide camouflage protection for the giraffe calf for the first year postpartum or longer which would seem to be enough for its continued evolutionary selection.

There were several adaptive advantages gained from the lying out behavior pattern of a newly born calf. A lactating cow which may be under physiological stress postpartum is free to concentrate on feeding and not on the protection of the calf. A giraffe calf which hides

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most of the day and moves very little conserves energy and body water which would be lost following the mother. Giraffe calves have a surface to volume ratio several times greater than adult giraffe which, combined with a smaller mass, necessitates a higher expenditure of metabolic water for thermoregulation. The infant giraffe discussed were dependent on suckling for their energy and fluid intake and long trips with an adult cow would increase energy and fluid requirements. Because of the vast size difference between herself and her calf, the cow negotiated natural barriers and difficult terrain traveling to areas of browse and water which might be difficult, if not impossible, with the calf.

Group lying out and single lying out of giraffe calves has probably led to erroneous reports on cow-calf relationships. The popular belief that giraffe cows have twins or care for orphaned calves usually come from field observations of a cow with two calves of a similar size and age. These observations would represent the first nursery herds formed after the isolation period where one of the cows has left her calf with the other female.

Foster and Dagg (1972) reported no relationship between the mother-young bond and survival of the young. These observations were based on a comparison of survival of

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calves which were regularly seen without their mothers, and calves which were seen with their mothers. Although habitat and subspecies differences must be considered, these observations of calves without their cows would have no bearing on their chance of survival.

Stepping behavior was similar to "Sprungintention" which has been observed during precopulatory behavior in giraffe (Backhaus 1961). Sprungintention involved a bull giraffe approaching a female from the rear and stepping down with his foreleg between her hind legs. Ewbank (1967) also described pawing and nuzzling of the inguinal region of ewes by their lambs when the ewe refused to nurse them. However, this latter behavior was similar to "Milchtritt" reported by Schenkel (1947) in wolves. The Milchtritt, or milk step, was elicited by wolf pups pushing on the female's mammary glands with their release of oxytocin and thereby milk; however, stepping behavior seemed to be directed towards gaining the attention of the cow and did not necessarily lead to nursing. The suckling and nursing behavior observed here was similar to that reported in other large mammalian species.

The approach and investigation patterns found in giraffes were similar to those in elk (Altmann 1952), bison (McHugh 1958), and cattle (Hafez 1962). Calf-shielding in elk occurred when a nursery herd was disturbed

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by an observer, and one adult female approached the observer while the others moved away. Investigation behavior may function to help ascertain whether certain stimuli in the environment, such as vehicles or resting lion prides, are an immediate danger or are potentially dangerous and should be avoided but not at the expense of leaving the area prior to feeding or drinking.

Giraffe were particularly well suited for investigation by utilizing their height and well developed vision. An adult giraffe remained at a distance which permitted escape while at the same time investigating whatever stimulus might be present.

Giraffe nursery herds and calving pools were similar to many of the wild species previously discussed such as the elk, bison, pronghorn, as well as domesticated Masai cattle (Reinholt, pers. comm.). Although there were juvenile sub-groups formed in the giraffe nursery herds and calving pools, they were comprised of weak young to young bonds, and the members of the sub-groups changed frequently when compared to such species as the mountain sheep (Geist 1971). Unlike species where the cow-calf bond was secondary to calf-calf bonds, the bond between the giraffe cow and calf is maintained.

When disturbed, the female "in charge" of a calving pool went to her calf and collected it by nudging it away

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from the source of the disturbance. This behavior excited the other members of the calving pool who followed the female "in charge" and her calf. There were no cows observed "in charge" of calving pools who did not have a calf in the calving pool.

The data presented in this paper for cow-calf relationships in giraffe disagree with data available on giraffe in the literature. The study areas and subspecies were different from those utilized by Foster (1966) and Foster and Dagg (1972). However, the study area was within 16 km of the study area used by Innis (1958) and involved the same subspecies. Behavior observations in the current study, as well as the lack of any discernable adaptive advantages for a weak maternal instinct in giraffe, leads me to hypothesize that similar weaning periods, cow-calf relationships, and a strong maternal instinct exist in the various East African giraffe subspecies.

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CHAPTER 2

THERMOREGULATION AND HEAT BALANCE IN GIRAFFE

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INTRODUCTION

The variation in body size among mammals has been the subject of numerous physiological investigations concerned with metabolic rate, temperature regulation, and locomotion. Kleiber (1932, 1961) scaled basal metabolic rate to body weight and obtained a relationship of 70 kcal $W(kg)^{0.75}$ for a wide range of body sizes. The energetics of locomotion has been measured in a number of species and the energy cost of locomotion scaled to body size (Taylor and Rowntree 1973a, 1973b; Taylor et al. 1970; Taylor et al. 1972). The relationship of body size to temperature regulation has been described by Gates (1962), Bakker (1975), and Schmidt-Nielsen (1964).

The data available for the largest terrestrial mammals has largely been obtained from the extrapolation of curves derived from data on animals in the small and medium size ranges. In homeotherms the indications are that the larger the animal, the lower the metabolic rate per kilogram of body mass. Concurrently, the possibility that the largest terrestrial mammals do not use evaporative cooling in hot climates has been proposed by Spotilia and Gates (1975). They hypothesized that large animals can use the thermal inertia inherent in their body mass to buffer environmental

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heat loads and thereby isolate themselves from the need for evaporative cooling.

Obtaining data on metabolic rate, temperature regulation, and the relationship between large mammals and their thermal environment has become increasingly important for the full understanding of the scaling relationships proposed. However, experimental designs involving the adults of any of the largest terrestrial mammals present certain difficulties in data collection. Logistic problems associated with feeding, handling, and instrumenting also seem to increase in direct proportion to body size.

The experimental animal chosen for this research was the giraffe (*Giraffa camelopardalis*) the largest living ruminant and the tallest terrestrial mammal.

Physiological studies of giraffe have primarily taken the form of extensive research into blood pressure problems associated with bending to the ground while drinking (Goetz and Budtz-Olsen 1955; Goetz and Keen 1957; Goetz et al. 1960; Van Citters et al. 1966; Van Citters 1968). These studies followed anatomical investigations of the carotids and retia mirabile by earlier investigators (Lawrence and Rewel 1948; Franklin and Haynes 1927). The only investigation of thermoregulation in giraffe was taken from deep muscle temperatures measured via radio-biotelemetry from a

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a single juvenile in Nairobi, Kenya (Bligh and Harthoorn 1965). The results of these data indicated giraffe were thermally stable.

The objective of this research was to determine how giraffe thermoregulate and therefore how giraffe maintain a balance between heat gain and heat loss. This was done by measuring the nychthemeral patterns of rectal temperature, normal ranges of standing metabolic rate, and the major heat gain and heat loss factors effecting giraffe.

METHODS

A field station was constructed by the author near Athi River, Kenya, approximately 32 km southeast of Nairobi (lat. 1.27S; long. 36.58E; alt. 1,410 m). The holding compound for the giraffe was sectioned into two large open pens, two smaller pens with partial roofing, and a crush area. With the exception of the two large pens, a 1 m thick rock floor was laid over all of the other holding sections to promote drainage and allow the areas to be swept daily. A blind-ended crush was constructed which was 1.5 m wide and 3 m long with closed sides up 2.5 m and heavy siding continuing up to 5 m with a platform for equipment and personnel at the top. The crush was designed to be closed with the

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the giraffe inside and unable to turn around thus allowing the animals to be handled for routine treatment and experimentation.

Six giraffe were captured by the Seago and Parkinson Zoological Collectors capture team. All of the animals were captured by vehicle chases lasting less than two minutes and all were Masai giraffe (*Giraffa camelopardalis tippelskirchi*). Heights, weights, and approximate ages for the captured giraffe are presented in Table 14. Due to the expense and danger to the animals, only three of the giraffe were weighed on a weighbridge and the remainder of the weights were calculated using relationships provided by Hall-Martin (1977).

During the initial two month period of captivity, the giraffe were fed a combination of naturally-occurring browse and commercialy available lucerne hay. The animals were never driven or exposed to loud noises or painful crushing techniques. They were gradually trained to enter and stand in the blind ended crush lured by preferred foods. Eventually the crush was closed and the animals handled for successively longer periods. This technique kept the giraffe in good physical condition during the entire experimental period and yielded tractable animals.

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Table 14. The measured and calculated physical dimensions of the giraffe used in heat balance measurements.

Name	Body Weight (kg) Actual	Body Weight (kg) Calc.*	Surface Area (m^2)**	Diameter (cm)	Sex	Age (yr.)	Horn-Hoof (m)
Tommy	--	237	3.21	50.9	Male	0.5	2.7
Lady Gay	--	285	3.55	55.4	Female	0.75	2.8
Makia	575	597	5.27	108.4	Female	4.0	3.6
Sirwe	580	584	5.29	70.0	Male	5.0	3.5
Malaya	640	663	5.59	110.0	Female	7.0	4.1
Big Boss	--	1,061	7.42	89.0	Male	7.0	4.7

* $W = 25.092\ LG^2 + 45.758$ ($r^2 = 0.990$) (Hall-Martin 1977)

** $SA(m^2) = 0.15\ W^{0.56}$ (Brody 1945)

G (Girth), L (Total body length)

RECTAL TEMPERATURE

Rectal temperature measurements were made by suturing a 17 cm temperature probe into the rectum and along the skin at the back. The probe was connected by heavy duty coaxial cable to a biotelemetry transmitter contained in a case on a collar around the base of the neck. The transmitting antenna was attached underneath the machine belting (Fig. 10). The receiver was placed in a small hut and connected to a large FM receiving antenna. All recordings were demodulated in the receiver and recorded as a DC output on a single pen chart recorder. The temperature probe contained one calibrated YSI thermistor. Using the factory calibration for the thermistor, the transmitter and probe could be calibrated using a decade box to match the entire range of resistances. This calibration was compared with recorded temperatures from a gradually cooling water bath. The two calibration curves were identical over the range of temperatures used. The entire system was designed and built by Mr. G. Hill, C.S.I.R. Pretoria, South Africa.

The periods of continuous rectal temperature recording ranged from two to seven days. The first 24 hr and last 24 hr of each recording period were used as normals during which the animals were allowed water and food ad lib. After the initial 24 hr period, water was withdrawn from the experimental animals. At the completion of the dehydration period

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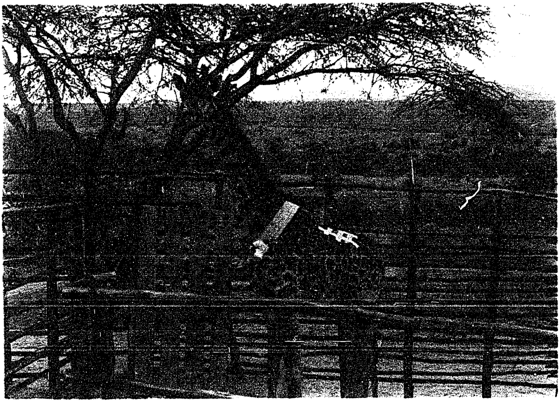

Figure 10. The giraffe female "Makia" illustrating the instrumentation used to measure rectal temperature continuously. Included in the photograph are the biotelemetry collar with transmitter and the rectal probe lead running down the back to the rectum.

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the giraffe were given water and the amount consumed within the first 0.5 hr was recorded.

SWEAT RATES

Sweat rates were measured at different times of the day and at different ambient and rectal temperatures. Sweat capsules were non-ventilated and were applied to the side, neck, back, leg, and face of the giraffe, for periods of 0.5 hr. Each capsule was filled with indicating Drierite and weighed to the nearest 0.1 g before and after each run. The technique and type of sweat capsules used were the same as those described by Maloiy and Taylor (1971) and Finch (1972, 1973). All measurements were recorded as g $hr^{-2}m^{-2}$.

METABOLIC RATE

A closed system oxygen collection method was used to measure oxygen consumption. The methods are described in Chapter 3. Measurements were obtained for tidal volume (V_t), minute volume (V_E), respiratory rate (resp/min), oxygen consumption ($l\ min^{-1}$), and respiratory water loss (mg H_2O/l air). All oxygen consumption measurements have been reduced to STP. Two methods were used to determine respiratory water loss. Both methods have been described in Chapter 3. Air samples were collected in the Douglas bags and the percentage of O_2 and CO_2 determined with a

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Taylor-Seromex Oxygen analyzer and a Beckman 864 infrared CO_2 analyzer.

CLIMATIC FACTORS

The measurement of local climatic variables was extremely important in the determination of heat gain and loss by the giraffe. Relative humidity (rh) and ambient temperature (Ta) were recorded continuously inside a Stevenson's Screen using a thermohydrograph. Wet and dry bulb thermometers were also kept inside the Stevenson's Screen and read manually at hourly intervals during all experimental runs. Ground temperatures were recorded automatically on a multi-pen recorder using a YSI telethermometer probe buried 2 cm below the surface of the ground in an area which received constant shortwave radiation from 0600 hr until 1800 hr daily. Windspeed was recorded manually each hour from a four cup anemometer set at 2.1 m above the ground level.

Diffuse solar radiation was recorded continuously on a multi-pen recorder using a solarimeter (Kipp and Zonan, Albedometer). The albedometer was mounted in an open area 2 m above the ground surface on a tripod designed to minimize shadow. The 2 m placement was considered the right height to measure reflected radiation reaching the abdomen of a giraffe.

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SURFACE TEMPERATURE

Surface temperatures were recorded from the back, side, neck, and leg of two of the experimental animals. A finger-like thermistor probe was sutured to one of the areas listed and continuous recordings obtained for 48 hr periods using the telemetry transmitter. Continuous climatic information was collected during all test runs. The test runs included in the data were all taken during the hot season (December-February) and on days which were 90% cloudless.

COAT ABSORPTION

Percentage absorption and reflectance of the giraffe coat to shortwave solar radiation was measured on skin samples approximately 60 cm wide cut around the entire girth of the trunk of three adult giraffe necropsied in the field. A micro albedometer (Swissteco, 26 Miami Street, Hawthorn, Vic. 3123, Australia) was used throughout the reflectance measurements. The technique and instrument have been described in detail by Hutchinson, Allen, and Spence (1975).

HEAT BALANCE

The assumption was made that heat gain equalled heat loss. The relationship used to describe this situation was developed by Gates (1962) and Porter and Gates (1969).

$$M + Habs = \varepsilon\sigma Tr^4 + Hconv + Hsw + Hex \pm HS \qquad (1)$$

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M is the standing metabolic rate; Habs is the heat gained from the combined effect of long and shortwave radiation; in $\varepsilon\sigma Tr^4$, ε is the specific emissivity of the giraffe coat; σ is the Stefan-Boltzmann constant (0.82×10^{-10} cal cm^{-2}min^{-1}), and TR is the temperature (°K) of the outermost radiating surface. The heat loss by forced convection (Hconv), heat loss by sweating (Hsw), and heat loss during respiration (Hex) will all be described individually. The heat gain or loss by heat storage (HS) can be positive or negative in the heat balance equation. All of the calculations for heat balance will be presented in the units cal cm^{-2}min^{-1}. The surface areas (Table 14) used in the heat balance equation were calculated using Brody's (1945) equation [$SA(M^2) = 0.15\ W^{0.56}$].

HEAT GAIN

Environmental Radiation

The heat gain calculations involved the determination of individual metabolic rates, as previously described. Metabolic rates were calculated using the relationship of 85 kcal$\cdot W^{0.75}$ for the giraffe where actual measurements were not available. The radiation component of heat gain was determined in two parts; shortwave solar radiation and longwave infrared radiation emitted from the ground and

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atmosphere. The following equation (Gates 1962, Porter and Gates 1969) was used to calculate heat gain from both long and shortwave radiation:

$$\mathrm{Habs}(\mathrm{cal\ cm^{-2}min^{-1}}) = \frac{aS(2/\pi)+as+arg(S+s)+Ra+Rg}{2} \qquad (2)$$

The entire equation has been divided by 2 because only half of the animal could be exposed to any single factor at one point in time. The term (a) represents the mean absorptivity (%) of the coat to shortwave radiation. The absorption of animal fur to longwave radiation was considered to be a 100% in this study (Spotila and Gates 1975, Finch 1973). The direct solar radiation (S) was produced from a single point source and radiated only two quadrants of the giraffe's trunk at any time (2/π). The diffuse solar radiation (s) was composed of shortwave radiation scattered by dust and water in the atmosphere. The reflected solar radiation [rg(S+s)] consisted of both the diffuse and direct solar radiation reflected from the ground and surroundings. The rg indicates the percentage of reflected direct and diffuse shortwave radiation striking an inverted horizontal surface.

Longwave radiation (>0.8) consists of radiation impinging from the atmosphere (Ra) and radiation emitted from the ground (Rg). The calculation of Ra during the period when shortwave radiation was present (0600 hr to

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2000 hr) involved the calculation of the vapor pressure in the air (e, mmHg).

$$Ra(\mathrm{cal\ cm^{-2}min^{-1}}) = \varepsilon\sigma Ta^4(0.44 + 0.08\sqrt{\varepsilon}) \tag{3}$$

At night time (2000 hr to 0600 hr), the atmosphere radiates as a "grey body" and the absorption concurrently drops from 100% to 40%.

The longwave radiation emitted from the ground (Rg) remains 100% absorbed day and night because the earth continually radiates as a "black body." Therefore, the Rg can be derived from ground surface temperatures.

$$Rg(\mathrm{cal\ cm^{-2}min^{-1}}) = \varepsilon\sigma T_g^4 \tag{4}$$

The term ε is the emissivity of the longwave radiator which is 1.00 for objects which radiate as a "black body."

HEAT LOSS

Radiation

The heat loss by radiation and reradiation from an animal is dependent on the surface temperature (T_r). The outermost surface temperature can either be calculated using Newton's law of cooling (Porter and Gates 1969, Tracy 1972) or taken from actual measurements of surface temperature (Finch 1972, 1973). Surface temperature measurements were

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made on the giraffe in this experiment and were related to ambient temperatures in order to routinely calculate T_r given a known ambient temperature. The equation used to calculate the longwave radiative heat loss from the giraffe was the basic Stefan-Boltzmann equation.

$$\text{Heat Loss by Radiation (cal cm}^{-2}\text{min}^{-1}) = \varepsilon\sigma T_r^{4} \quad (5)$$

The emissivity (ε) for animal coats is approximately 0.95-1.00 (Hammel 1956).

Convection

The convective heat loss was calculated from the following equation.

$$\text{Hconv(cal cm}^{-2}\text{min}^{-1}) = h_r(T_r - T_a) \quad (6)$$

The convection coefficient (h_r) times the difference between the temperature of the outermost radiating surface (T_r) and the ambient temperature (T_a) equals convective heat loss. The convection coefficient (h_r) was calculated using the wind speed and trunk diameter of the animal.

$$h_r(\text{cal cm}^{-2}\text{min}^{-1}{}^{\circ}\text{C}^{-1}) = 1.95 \times 10^{-3}(V^{0.6}/D^{0.4}) \quad (7)$$

The diameter (D) is measured in cm, the wind speed (V) is measured in cm sec^{-1}, and $1.95 \times 10^{-3}(\text{cal cm}^{-2}\text{min}^{-1}{}^{\circ}\text{C}^{-1})$ is a constant.

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Heat Storage

Heat storage (HS) was calculated using the equation developed by Hardy and Dubois (1938) for man.

$$\mathrm{HS(cal\ cm^{-2}min^{-1})} \quad = \quad 0.83W(4\Delta T_{re} + \Delta T_{s})/5\mathrm{(kcal/hr)} \qquad (8)$$

The equation can be broken down into its individual components; 0.83, represents the specific heat capacity for live tissue ($\mathrm{kcal\,°C^{-1}kg^{-1}}$); W, the weight in kg; ΔT_{re}, the change in rectal temperature and ΔT_{r}, the change in surface temperature.

RESULTS

RECTAL TEMPERATURE

Over 2,000 hr of rectal temperature and climatic data were collected over a two year period. The total number of hours of rectal temperature recordings taken via radiobiotelemetry were divided between hydrated and dehydrated giraffe approximately 60% and 40%. The environmental and temperature measurements were divided into hydrated and dehydrated data sets and averages were calculated for all experimental runs. The results have been presented graphically in Figure 11; no significant differences were noted between hydrated and dehydrated giraffe.

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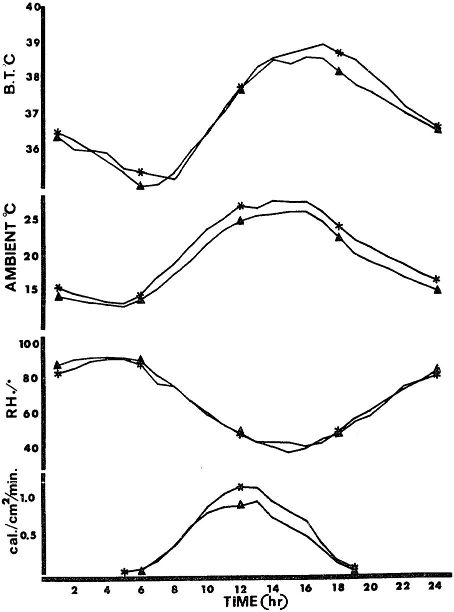

Figure 11. Daily mean total long and shortwave solar radiation (cal cm^{-2}min^{-1}), relative humidity (rh), ambient temperature (°C), and body temperature (B.T. °C) of hydrated (*) and dehydrated (▲) giraffe incompassing a total of 2,000 hr of observations.

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During dehydration the giraffe lost an average of 10% of their body weight (Table 14). Although this percentage of dehydration was not as severe as that reported for camels, it was equivalent to the dehydration experiments on eland and oryx (Taylor 1970, Schmidt-Nielsen et al. 1967). The giraffe, like the camel, rehydrated within five minutes after water was presented and only consumed small amounts over the next 0.5 hr. The degree of dehydration in giraffe was measured by recording the amount of water consumed within 0.5 hr after the dehydration period was terminated.

The average change in rectal temperature for the hydrated giraffe was 3.7°C and for the dehydrated giraffe was 3.8°C (Fig. 11). The dehydrated giraffe experienced lowest rectal temperatures at 0800 hr while rectal temperatures in hydrated giraffe were lowest at 0600 hr. Both hydrated and dehydrated animals showed the same period of depressed rectal temperatures at 0500 hr to 0800 hr. The maximum rectal temperatures were recorded at 1600 hr for the hydrated giraffe and 1700 hr for the dehydrated giraffe although once again the period of maximum rectal temperatures (1400 hr to 1700 hr) was the same for both groups.

Changes in T_{re} have been graphed against T_a for both hydrated and dehydrated giraffe in Figures 12 and 13. Due to the cyclic nychthemeral rectal temperature changes, both

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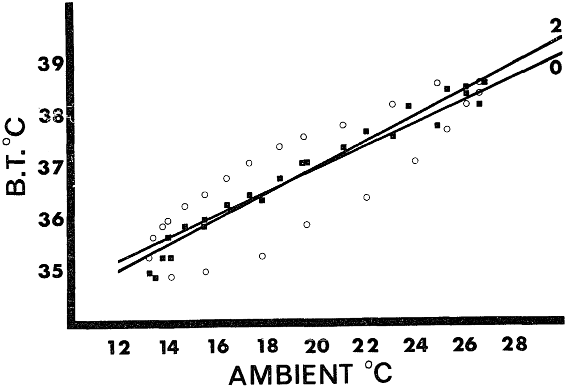

Figure 12. Comparison of rectal temperature (B.T. °C) and ambient temperature for dehydrated giraffe. Circles are points in real time (lag time = 0) and the squares are points lagged by 2 hr. The line 0 represents the regression line drawn for real time data and line 2 is the regression line for the 2 hr lagged data.

Line 0 $y = 33.02 + 0.199T_a$, $r^2 = 0.6447$ ($P < 0.001$)

Line 2 $y = 32.03 + 0.246T_a$, $r^2 = 0.983$ ($P < 0.001$)

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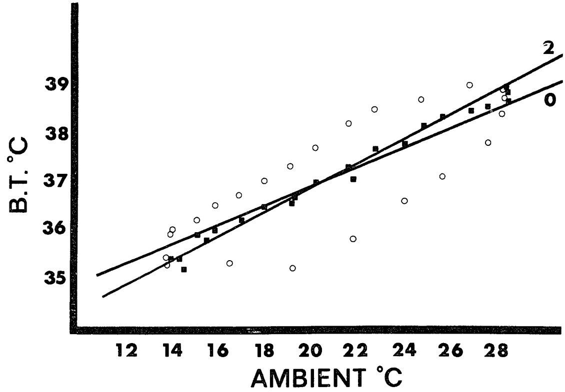

Figure 13. Comparison of rectal temperature (B.T. °C) and ambient temperature for hydrated giraffe. Circles are points in real time (lag time = 0) and the squares are points lagged by 2 hr. The line 0 represents the regression line drawn for real time data and the line 2 is the regression line for the 2 hr lagged data.

Line 0 $T_{r\varepsilon} = 32.7 + 0.216T_a$ $r^2 = 0.7213$ ($P < 0.001$)

Line 2 $T_{r\varepsilon} = 32.1 + 0.25T_a$ $r^2 = 0.9635$ ($P < 0.001$)

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graphs resemble limit cycles when plotted in real time. However, by progressively lagging the rectal temperatures back first one hour and then two hours, the regression coefficient improves (Table 15). The two hour lag has the highest correlation coefficient explaining 96 to 98% of the variance in the relationship.

These data are hourly averages taken from the temperature regulation versus the state of hydration test runs involving all of the adult giraffe. The average body weight of the adult giraffe used in this experiment was 715 kg. A computer run co-spectral analysis was performed on 120 hr of continuous rectal temperature versus ambient temperature data collected from the giraffe B.B. weighing 1,061 kg. Using co-spectral analysis, a lag time of 2.01 hr was calculated for this test run. A co-spectral analysis of 100 hr rectal temperature versus ambient temperature data collected from giraffe L.G. (285 kg) gave a lag time of 1.62 hr. The small giraffe had minimum rectal temperatures at 0630 hr and maximum at 1500 hr.

The lag time between T_{re} and T_a for the adult giraffe reflects their large thermal inertia. When the ambient temperature began to drop approximately 1600 hr, the heat accumulation in the body tissues of the giraffe caused a delay in the onset of body cooling. The difference in lag

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Table 15. Variation accounted for (r^2) in the correlation of rectal temperature versus ambient temperature for the hydrated and dehydrated giraffe in real time (lag = 0) and with the rectal temperature lagged 1 hr and 2 hr back.

	Lag Time (hr)	r^2
Dehydrated	0	0.6447
	1	0.8669
	2	0.9830
Hydrated	0	0.7213
	1	0.9105
	2	0.9635

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time between the large and small giraffe was directly proportional to the difference in their body mass.

The fluctuations in T_a and T_{re} for two experimental runs have been graphed together in Figure 14. Both runs represent giraffe which have been given food and water ad lib. The hot season run represented by the triangles is the total collection of data points for T_{re} and T_a taken from giraffe Sirwi (580 kg). The 110 hr cold season run represented by the asterisk (*) was recorded using giraffe Big Boss (1,061 kg). These data indicated that when the mean ambient temperature is reduced, the T_{re} cycles retain their amplitude over a lower range of T_{re}. The reverse was true in the hot season where the amplitude was the same but the range of T_{re} was much higher than the cold season values.

HEAT BALANCE

Heat Loss

Although exhaled air was 100% saturated, the heat loss during exhalation in giraffe was very small. This was achieved by lowering the temperature of expired air below that of body temperature. This process, the reciprocal heat sink mechanism, functions in the nasal passages of giraffe and is described in detail in Chapter 3. Heat loss values obtained during exhalation and used in the heat balance

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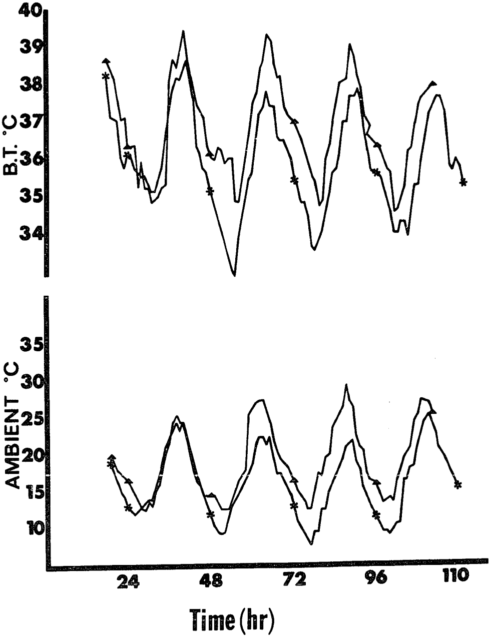

Figure 14. Effect of season on nychthemeral body temperature in hydrated giraffe. Actual rectal temperature (B.T. °C) and ambient temperature (°C) data points measured during the hot season (▲) and during the cold season (*) graphed in real time (lag time = 0).

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equation are presented in Table 16. The heat loss by exhalation was included in all of the following calculations although for giraffe the values were very small.

Sweating

No active sweating was recorded from any of the giraffe tested. There was no relationship between the amount of moisture collected using the sweat capsules and either the T_a or T_{re}. Giraffe have large epitrichial sweat glands over most of the body surface (Dimond and Montagna 1976). However, the possession of sweat glands does not indicate function and there are a number of animals such as Coke's Hartebeest (*Alcelaphus buselaphus cokii*) which have nonfunctional sweat glands (Finch 1972, 1973). The average cutaneous moisture loss was 95 g $hr^{-1}m^{-2}$, a value below the suggested level of insensible cutaneous water loss of 100 g $hr^{-1}m^{-2}$ (Finch 1973) and well below active sweating values measured from eland, buffalo, and camels (Robertshaw and Taylor 1969, Schmidt-Nielsen et al. 1957). Although two of the giraffe had individually measured cutaneous water losses slightly higher than the suggested insensible water loss minimum (Table 17), the lack of correlation between T_{re} or T_a and cutaneous moisture loss lead to the conclusion that there was no active sweating for heat loss.

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Table 16. Total heat exchange 0700 hr to 1600 hr (cal cm^{-2}9 hr^{-1}). The error % represents the percentage of difference between total heat gain and total heat loss assuming heat gain should be equal to heat loss. The hourly calculations of all heat gain and heat loss values have been presented in Appendix A.

	Gain		Loss							
Name	M	Habs	$E_r T_r^4$	Hconv	H_{sw}	H_{ex}	HS	Gain	Loss	% Error
Lady Gay	63	503	381	54	35	4	+35	566	509	10
% Contribution	11	89	75	11	7	1	7			
Malaya	82	536	385	47	51	4	+91	618	578	7
% Contribution	13	87	67	8	9	1	16			
Big Boss	81	564	395	77	50	6	+93	645	621	4
% Contribution	13	87	64	12	8	1	15			
Total Heat Exchange 2100 hr to 0500 hr (cal cm^{-2}8 hr^{-1})										
Malaya	62	181	288	10	--	3	-56	299	301	1
% Contribution	21	61	96	3	--	1	19			
Lady Gay	60	200	304	12	--	4	-26	286	321	11
% Contribution	21	70	95	4	--	1	9			

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Table 17. Measured and calculated physiological parameters used for the determination of heat gain and loss.

Name	Metabolic Rate (M) (kcal/min)		T_{re} (°C)	Sweating Rates (g $hr^{-1}m^{-2}$)	Expiratory Heat Content (cal l^{-1})	Minute Volume (l min^{-1})	
	Actual	Calc.		H_{sw}	H_{ex}	Actual	Calc.
Tommy	--	3.57[1]	37.7	67.5	8.09[2]	--	30.1[3]
Lady Gay	--	4.09[1]	37.5	67.5[2]	8.09[2]	--	34.9[3]
Makia	6.70	6.93[1]	37.4	107.8	8.77	50.5	61.6[3]
Sirwi	6.95	6.97[1]	37.4	108.5	8.78	54.5	61.6[3]
Malaya	7.96	7.51[1]	37.4	97.5	6.53	58.0	66.6[3]
Big Boss	--	10.97[1]	37.8	97.5[2]	8.09[2]	--	99.8[3]

[1] 85 kcal $kg^{0.75}$.

[2] Not measured.

[3] Stahl 1967.

The cutaneous moisture loss measured in this experiment and labeled insensible moisture loss was more probably either a continuous low level sweat discharge or sweat discharged in small bursts. The first type of sweating has been described for water buck that primarily pant to cool and the second for oryx; in both cases the level of sweating was 100 g $hr^{-1}m^{-2}$ (Robertshaw and Taylor 1969). This level sweat discharge was comparable to the values measured from giraffe (Table 17). If giraffe do have this type of low level sweating, it would be similar to the isolated discharge of the epitrichial glands of the Welsh Mountain Sheep (Bligh 1967). Therefore, the level of insensible water loss or water loss by simple diffusion across the skin should be considered to be below 50 g $hr^{-1}m^{-2}$ (Allen and Bligh 1969; Bligh and Allen 1970) rather than 100 g $hr^{-1}m^{-2}$ (Finch 1973) in order to include low level sweat gland discharge.

Convection

Convective heat loss was influenced by the relatively stable pattern of wind in the study area. The highest wind speeds were recorded between 0700 hr and 1800 hr coinciding with the highest ambient temperatures. The diurnal range of wind speeds was 7.3 m sec^{-1} to 0.94 m sec^{-1} with an average of 3.5 m sec^{-1}. The nocturnal wind speeds were

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much lower with a range of 4.4 m $\sec^{-1}$ to 0.54 m $\sec^{-1}$ with an average of 2.3 m $\sec^{-1}$. The relatively low wind speeds and large body diameters of the giraffe (Table 14) reduced the heat loss by forced convection.

Radiation

The heat loss by radiation was calculated using an emissivity value of 0.97 (Hammel 1956, Gates 1962). The temperature of the radiating surface (T_r, °C) was calculated using the equation derived from the linear regression analysis of all nychthemeral surface temperature measurements taken from the neck, side, back, and legs.

$$T_r = 6.67 + 1.22\,T_a \qquad r^2 = 0.6604 \qquad (P < 0.001) \qquad (9)$$

The heat loss by radiation was the major avenue for heat loss in the giraffe. Longwave radiation heat loss was responsible for 96% of the nocturnal heat loss and 60-66% of the diurnal heat loss (Fig. 15 and 16).

Heat Storage

Heat storage was positive during the day as reflected by the increase in rectal temperature. The importance of heat storage in the diurnal heat balance was dependent on the size of the giraffe (Fig. 15). The diagram in Figure 15 represents the percentage contribution of each of the

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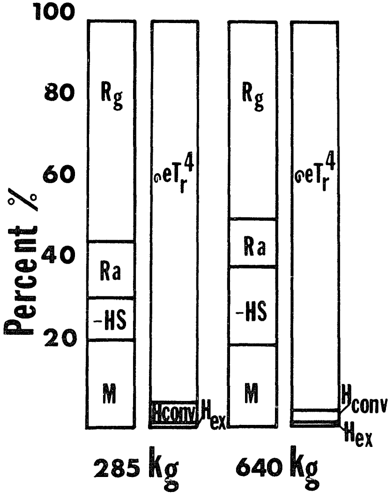

Figure 15. Percentage contribution of each heat gain factor and heat loss factor to the total heat balance for three different 9 hr days (0700 hr to 1600 hr) and for three different giraffe.

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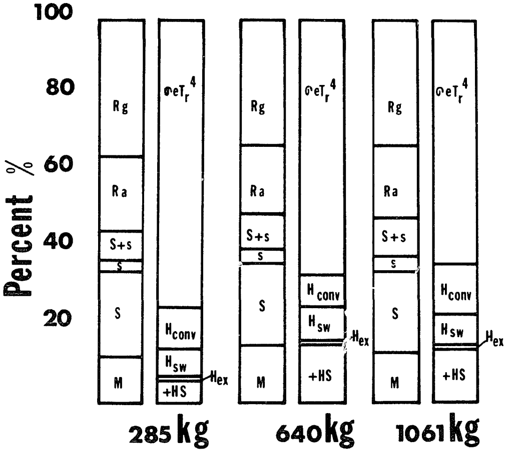

Figure 16. Percentage contribution of each heat gain and heat loss factor to the total nocturnal heat balance for two different giraffe. These nocturnal measurements are a continuation of the days for the giraffe Lady Gay and Malaya presented in Figure 15.

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factors described in the heat balance equation to the diurnal heat gain or loss in three giraffe with different body weights. Heat storage in the 285 kg giraffe contributed 7% to heat loss. Convection and the evaporation of cutaneous moisture contributed 23%; the remaining 77% was lost by radiation. Heat storage in the two larger giraffe contributed 14% and 16% to the total diurnal heat loss. Heat storage in the larger giraffe contributed more to the heat loss than either heat loss by convection or heat loss from cutaneous evaporation. Heat loss by radiation was lower (67% and 64%) in the larger giraffe (Fig. 15).

The heat storage factor was negative during the nocturnal decrease in rectal temperature. Figure 16 represents the heat gain and heat loss factors by their percentage contribution to nocturnal heat balance. The heat stored during the day was gradually lost during the night. The difference in heat storage capacity between the larger 640 kg giraffe and the 285 kg giraffe can be seen in Figure 16. The percentage contribution of heat storage to the overall heat balance was 19% for the 640 kg animal and 10% for the 285 kg animal.

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HEAT GAIN

Metabolic Rate

The metabolic rate measured for the three giraffe listed in Tables 14 and 17 was approximately 85 kcal·$W^{0.75}$. Klieber's (1961) linear relationship for body weight verus metabolic rate stated that basal metabolic rate would approximate 70 kcal·$W^{0.75}$ for animals over a wide range of body weights. The giraffe were not in a post-absorbitive state or lying down during the collection of respired air for metabolic rate measurements. Therefore, the metabolic rates in Table 17 are higher than the basal metabolic rate. In the giraffe, a significant relationship between metabolic rate and T_{re} was also noted (Fig. 17). Metabolic rate increased 1.8 fold for the 580 kg giraffe and a 1.6 fold for the 640 kg giraffe over a 3°C temperature range (36°C to 39°C).

Sirwi (580 kg)

$$M(O_2 l/min) = 0.27T_{re} - 8.7 \quad r^2 = 0.5257 \quad (P < 0.01) \quad (10)$$

Malaya (640 kg)

$$M(O_2 l/min) = 0.29T_{re} - 9.03 \quad r^2 = 0.4999 \quad (P < 0.01) \quad (11)$$

The calculated Q_{10} was 2.1 over the range 36°C to 39°C.

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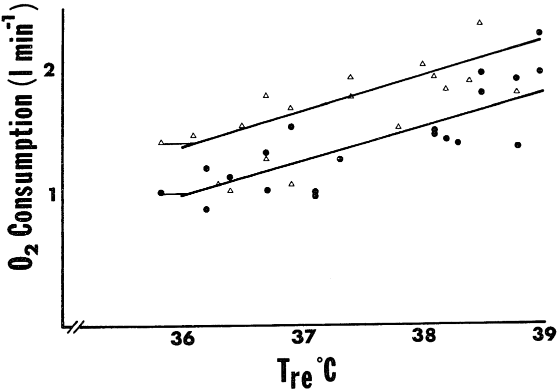

Figure 17. The metabolic rate (O , l min⁻) for two giraffe at various rectal temperatures (T_{re} °C) △, the giraffe Malaya weighing 640 kg; ●, the giraffe Sirwi weighing 580 kg. The regression line for the 640 kg giraffe was calculated using equation 11 and the regression line for the 580 kg giraffe was calculated using equation 10.

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Using this relationship, changes in rectal temperature which were greater than the average values presented but within the range of T_{re} measured (35°C to 41°C) would increase the metabolic rate 2.6 fold in the 640 kg giraffe and 3.6 fold in the 580 kg giraffe. Also, the equations show that a T_{re} of 36.6°C for the 580 kg giraffe and 35.6°C for the 640 kg giraffe would give metabolic rates of 70 $\text{kcal}\cdot W^{0.75}$ (Kleiber 1961). The average calculated RQ was 0.86. Applying equations 10 and 11 (Fig. 15) to the average nychthemeral T_{re} values calculated for the hydrated and dehydrated giraffe gives the nychthemeral patterns shown in Figure 18.

The contribution of the metabolism to heat gain (Fig. 15 and Fig. 16) was relatively constant during the diurnal and nocturnal heat exchanges reported. Metabolic heat production, although depressed with the lower T_{re} occurring at night, contributed approximately 7% more to the overall heat balance at night than during the day.

Long and Shortwave Radiation

Average long and shortwave radiation impinging on the giraffe during a 24 hr period has been graphed in Figure 19. Data were taken from both hydrated and dehydrated data sets and therefore represents averages calculated over the entire period of climatic data collection. The longwave radiation

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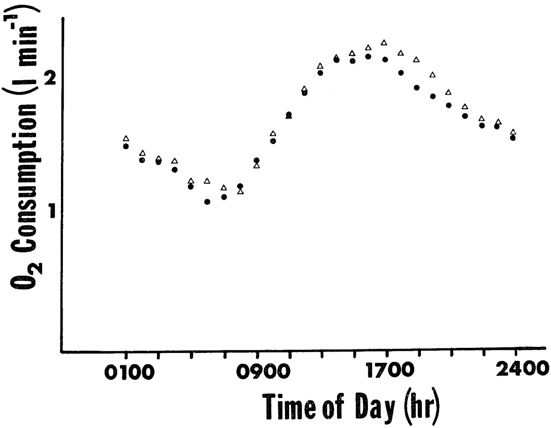

Figure 18. Nychthemeral pattern of oxygen consumption over two 24 hr periods calculated in hydrated (Δ) and dehydrated (●) giraffe; all points were calculated using equation 10.

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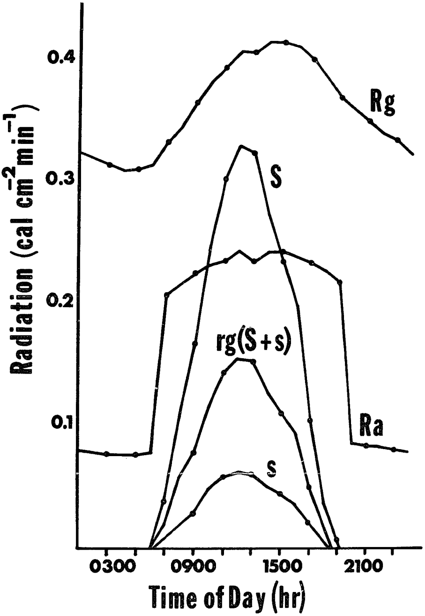

Figure 19. Average long and shortwave radiation (cal cm^{-2}) for the dehydrated and hydrated giraffe (2,000 hr) graphed over a 24 hr period. The curves all represent the radiation actually falling on the giraffe, therefore the total radiation is the sum of all individual short and longwave components.

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from the atmosphere (Ra) was calculated using the relationship presented in the methods section. The longwave radiation emitted from the ground was calculated from either measured ground temperature or from the below equation derived from the linear regression analysis of ground temperature (T_g, °K) and ambient temperature (T_a, °C).

$$T_g = 0.93 + 1.56T_a \quad r^2 = 0.806 \quad (P < 0.001) \; n = 400 \quad (12)$$

During the diurnal period (0600 hr to 1900 hr), levels of short and longwave radiation were summed to derive the values Habs presented in Table 16 and Appendices. Diurnal levels of longwave radiation contributed approximately 56% of the heat gained during the day and approximately 60% of the nocturnal heat gain (1900 hr to 0600 hr). In contast, the combined shortwave or solar radiation heat load contributed only 33-35% of the total diurnal heat gained and contributed nothing to the nocturnal values. The very sharp increase in longwave radiation emitted from the atmosphere at 0600 hr was attributed to the change in emissivity of the earth's atmosphere at night time versus daytime (Gates 1962). Gates' theory of "grey body" emittance calculated as a 40% decrease in absorptivity was used to calculate the atmospheric longwave radiation during the noctural period. Therefore diurnal atmospheric longwave radiation was

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considered to be emitted from a "black body" emitter which increased the absorptivity to 100%.

Table 16 contains the total heat exchange calculations from three diurnal test runs and two nocturnal test runs. The percentage contribution of each of the heat gain and heat loss mechanisms have been graphically presented in Figure 15 and Figure 16. The percentage error estimates are equal to the percentage of the difference between the total heat gained and the total lost for each giraffe.

DISCUSSION

The change in metabolic rate accompanying the change in rectal temperature was similar to the flucuating metabolic rate reported in other thermally labile animals (Schmidt-Nielsen et al. 1957, Taylor 1970). The lower metabolic rate brought a reduction in the energy consumption during the night time. Those animals which became thermally labile when dehydrated, camel and oryx, conserve metabolic heat and energy during the night time by decreasing the rectal temperature and concurrently the metabolic rate.

Heat storage was one of the most important factors for the conservation of water and for heat balance in the giraffe. Several investigators have shown instances of heat storage in other animals (Schmidt-Nielsen et al. 1957,

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Taylor 1970). The roll of heat storage versus evaporative cooling has been one of the key questions concerning thermoregulation in large mammals (Spotilia and Gates 1975). Dependence on body size and the roll of heat storage in comparison with evaporative or behavioral thermoregulation have been questions which required data from thermally labile animals of different weights and information on the heat exchange between the animal and the environment.

Adult giraffe used heat storage for up to 19% of their thermoregulatory strategy. This degree of dependence on heat storage was similar to the dependence of eland on sweating (27%) and of the hartebeest on panting (12%) (Finch 1972, 1973). Although both of these species relied on radiation for a majority of their heat loss (62% and 76%), the eland was considered a sweater and the hartebeest a panter. Therefore, adult giraffe should be considered heat storers as this thermoregulatory strategy has been utilized in place of evaporative cooling.

Evaporative cooling has an advantage over the heat storage strategy when the young of the species are considered. Young eland and hartebeest can either sweat or pant. However, heat storage relies on a large body size and therefore a large thermal inertia for gradual heating and cooling. This means that young and therefore small giraffe are unable to use heat storage as effectively as the adults.

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The young giraffe measured in this experiment did however use heat storage instead of evaporative cooling for thermoregulation.

The question of how it was possible for a young giraffe to use heat storage and thermal lability and at the same time have a much smaller body weight relative to the adults can be examined using Figure 20. The curve in Figure 20 was drawn assuming a 9 hr heat accumulation of 70 cal cm^{-2} for body weights over the range of body weights measured from giraffe (Hall-Martin 1977, Dagg 1971). Heat storage (HS, kcal/hr) as represented as a change in rectal temperature, was calculated from a simplification of the relationship developed by Hardy and Dubois (1938).

$$\Delta T_{re} = \frac{HS\ kcal/hr}{0.83\ W} \qquad \text{(Taylor 1970)} \qquad (13)$$

The maximum change in rectal temperature observed during the measurements reported was 9.1°C. If this value was taken as the maximum allowable prior to thermal stress, giraffe with body weights less than 400 kg would be unable to tolerate environments which would impose this degree of heat stress. The 70 cal cm^{-2} heat storage factor used to calculate the points in Figure 20 was not an extreme value and up to 100 cal cm^{-2} may be accumulated in adult giraffe continually exposed to solar radiation while feeding. Therefore, the young giraffe with lower body weights must avoid the accumulation of heat or somehow control it.

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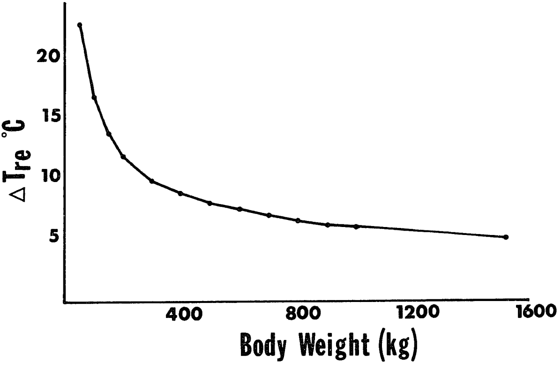

Figure 20. Change in rectal temperature (T_{re}) for giraffe over the range of naturally occurring body weights of giraffe assuming a 9 hr heat storage of 70 cal cm^{-2}.

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One of the possibilities for decreasing heat gain would be to keep the metabolic contribution small by avoiding an exercise heat load. Shade seeking would reduce the heat gain from direct shortwave solar radiation and longwave radiation from the atmosphere; factors contributing 39% of the radiative heat load (Table 16 and Appendix A). Lying down in shaded or non-shaded areas would reduce the radiant profile and decrease the surface area available for radiant heat gain.

The behavior of young giraffe described in Chapter 1 reflects the required behavioral modifications necessary for small thermally labile giraffe to avoid thermal stress. Giraffe of less than one year of age were not sighted near standing water and were not observed drinking during the two year study of behavior reported in Chapter 1. Giraffe less than one year of age did not accompany their cows to dams or other areas to drink. Therefore, it is suggested here that the use of thermal lability or heat storage combined with a behavior which minimizes environmental heat gain has created a situation where young giraffe are not dependent on standing water. Young giraffe survive and grow in their first year by gaining water from nursing and from preformed water in the browse.

The thermoregulatory strategy which has evolved in giraffe has one main factor separating giraffe from the

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other thermally labile animals reported in the literature. Giraffe are thermally labile independent of their state of hydration in contrast to the camel and eland which adopt thermally lability during water deprivation. The reason that giraffe have become dependent on heat storage in the hydrated and dehydrated state and camels and eland have not may be the difference in adult size and body weight. Giraffe have a greater adult body weight than either eland or camels and therefore a greater heat storage capacity. Also sweating may be a less efficient method of thermoregulation for very large mammals that would be forced to expend a high percentage of their body water for the maintenance of a constant body temperature.

The labile rectal temperature and corresponding cyclic metabolic rate have an implication for water metabolism of giraffe. By using their large body mass to store heat during the periods of intense long and shortwave radiation and dumping the heat stored at night by passive non-evaporative means the giraffe (Table 16, Appendix A) all saved approximately 1.0% to 1.5% of the body weight in water. The water savings for the 9 hr days listed in Table 16 were 2.2 l (285 kg giraffe), 8.8 l (640 kg giraffe), and 12 l (1,061 kg giraffe). These calculations were made by determining the amount of water required to dissipate the heat stored by evaporation.

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The amount of water loss through evaporation was also decreased by the reduction of the temperature of the exhaled air. The water saving due to the reciprocal heat sink mechanism operating in the nasal cavity of the giraffe saved approximately 2 l of water per giraffe over a 24 hr period (Chapter 3). The combined water recovery and a lack of active sweating would mean the saving of an average of 12 l of water per day or 2% of the body weight of the adult giraffe. Taylor (1970) has demonstrated that eland and oryx with free access to water dissipate an amount of water equal to 2% of their body weight for evaporative cooling during exposure to an ambient temperature of 22°C and in the absence of radiation. The absence of a solar heat load may have reduced the amount of water required for evaporative cooling in these two species.

The giraffe drank 3% of their total body weight per day in water when fed on dry foods. The supplementation of the dry foods by naturally-occurring browse reduced the daily water intake by 43%, 1.7% of the total body weight. This data indicates that giraffe may be able to obtain a large part of their daily water requirements from preformed water in the browse (Taylor 1968). The adaptations discussed previously combined with the ability to obtain preformed water may make giraffe independent of standing

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water for long periods of time. The ability to travel long distances from permanent standing water would aid giraffe in exploiting semi-arid habitats where suitable browse may be widely separated from the sources of water.

The possibility exists that giraffe are only thermally labile when heat acclimated, a factor not tested in this experiment. The transition between homeothermia and heterothermia is made by camels using water deprivation as a stimulus. The possibility of changing from a sweater to a heat storer has been documented for camels and eland, therefore the ability of giraffe to respond to other environmental clues such as a change in ambient temperature ranges remains a viable possibility. The test of this hypothesis could be carried out experimentally on giraffe which are maintained in a Northern Hemisphere zoo using an experimental design similar to the one presented in this chapter.

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CHAPTER 3

NASAL HEAT EXCHANGERS IN GIRAFFE

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In the previous chapter it was concluded that temperature regulation in the giraffe involved passive acceptance of a heat load and that the main advantage of this phenomenon was to minimize water loss. If this hypothesis is correct, mechanisms which conserve water should be well developed in the giraffe. Loss of water during expiration is one such mechanism.

INTRODUCTION

In mammals and most probably in reptiles and birds also, inspired air is heated to body temperature and humidified to 100% saturation before reaching the respiratory exchange surfaces, the normal functioning of which depends on this preconditioning (Walker, Wells, and Merrill 1961). If on exhalation the air travels through the oral cavity, a majority of the heat and water added during preconditioning is lost. This type of heat loss can be easily demonstrated in panting animals (Schmidt-Nielsen, Bretz, and Taylor 1970). However, if on exhalation the air is passed through the nasal cavity, varying amounts of water and heat may be recovered provided that certain conditions exist (Collins, Pilking and Schmidt-Nielsen 1971).

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Efficient heat and water recovery from exhaled air requires that an animal inhales and exhales nasally over nasal turbinates which have both a large surface area and a configuration which forces the air to pass over the nasal mucosa in very thin layers. The blood supply to the nasal mucosa must be limited in order to allow the turbinates to cool during inspiration by losing heat and water to the inspired air. The nasal mucosa must remain cool and act as a reciprocal heat sink for the exhaled air which when coming in contact with the turbinates loses both heat and water by condensation and exits 100% saturated but at a temperature lower than body temperature. The absolute humidity and temperature of the ambient air may alter the efficiency of the system described by their combined effect on the temperature of the nasal mucosa during inspiration.

Heat and water recovery by nasal turbinates acting as reciprocal heat sinks has been described extensively in small animals as a necessary adaptation for life in hot arid environments (Jackson and Schmidt-Nielsen 1964, Schmidt-Nielsen, Hamsworth, and Murrish 1970, Schmidt 1976). A variable function for the nasal turbinates in penguins involves heat and water recovery in the cold and nasal heat dumping at ambient temperatures of 0°C to 10°C (Murrish 1973). The heat dumping by nasal breathing is accomplished by the sympathetically effected vasodilation of blood vessels

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in the nasal mucosa heating the mucosal surface and stopping the reciprocal heat sink phenomena necessary for heat and water recovery.

The present research was initiated to determine if a large mammal like the giraffe could meet the physical requirements for nasal heat exchange and, if so, were the benefits the same as those for small animals.

METHODS

The giraffe were captured and held at a field station near Athi River, Kenya (see Chapter 1). The other species such as wildebeest (*Connochaetes taurinus*), waterbuck (*Kobus ellipsiprymnus*), sheep, donkey, goats, and cows were all held at the Muguga Veterinary Research Station near Limuru, Kenya. All the animals appeared to be in good physical condition and had been in captivity for at least two months before use.

Expired air temperatures were measured at the opening of the nares by placing a plastic T-piece 12.5 mm in diameter into the right or left nostril. The T-piece was inverted and wedged against the dorsal opening of the nares. A 35 gauge thermocouple was inserted into the T-piece and fixed in place with the tip extending into the air stream.

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Expired air temperatures were measured with a Westcor TH 50, DC thermocouple recorder and traced on a strip chart recorder. The input scale on the recorder was adjusted to compensate for different respiratory rates. The recorder was calibrated using a reference temperature from the Westcor TH 50 and water warmed to approximately body temperature and measured with a calibrated mercury thermometer. Wet and dry bulb temperatures were measured with a sling psychrometer. Rectal temperatures were measured with a clinical thermometer.

All animals tested were restrained either standing or sitting. Measurements were not begun until the animal appeared to be calm and a steady respiratory pattern had appeared. The giraffe were harnessed and an airtight mask placed over the nose and mouth. A three way modified Otis-McKerrow valve was used as an inlet and a one way Collins "J" valve as the outlet. The "J" valve was connected to the dessicant cannister containing Drierite to absorb water vapor and the expired air was collected in Douglas bags. The volume of air expired was measured on a 50 l Parkinson and Cowan volumeter. As the air left the volumeter, it was passed through a second canister of Drierite to collect and measure any water remaining in the air after passing through the first cannister.

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A head taken from a young female giraffe during necropsy was sectioned sagitally. The left section with intact turbinates was removed and cut in serial cross sections approximately 25 mm in width cranially from the entrance of the nares. More than 40 additional necropsies were performed during the course of the study. Each head was cut sagitally and measurements were taken of the nasal turbinates and the neurocranial and splanchocranial lengths.

Data were collected at two barometric pressures (580 mm Hg, 2,246 m above sea level, and 638 mm Hg, 1,410 m above sea level) and over a wide range of ambient temperatures and humidities. Water content of the air was calculated as the humidity ratio, W (g H_2O/g dry air) from the following equation assuming 100% saturation for exhaled air (Chambers 1970).

$$W = 0.662 \times P_w/P - P_w \tag{14}$$

W is the humidity ratio; 0.622 constant derived by dividing the gas content for air (joule/°K mol) by the gas constant for water (joule/°K mol); P_2, water vapor pressure (mm Hg); and P, the barometric pressure in mm Hg. W_{in} for the air at T_a was calculated using a psychrometric chart for 760 mm Hg. A reading was taken of P_w at the T_a and rh (relative humidity) of the inspired air and converted using eq. (14) to the W for the correct P.

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Comparisons of the water content of the expired air actually collected and that calculated from nasal expired air temperatures (T_{ex}) required all readings be standardized to g H_2O/liter air. This was accomplished by multiplying W above by the density of dry air (D_o) at the appropriate T_a and P.

$$D_o = (0.001293/1 + 0.00367\ T_a) \times (P/760) \tag{15}$$

The final conversion unit can be derived from eq. (16).

$$\begin{aligned} &W(\text{g } H_2O/\text{g dry air}) \times D_o(\text{g dry air/ml air}) \times 10^3 \\ &\quad = 10^3 \text{ g } H_2O/\text{liter air} \end{aligned} \tag{16}$$

The calculated respiratory water loss (g H_2O/l air) was determined by subtracting the water content of the inspired air at T_{in} from the water loss at T_{ex} and 100% saturation ($T_{ex\ sat}$). The respiratory water added during inspiration was equal to $T_{re\ sat}$ (100% saturation at T_{re}) minus the water content of the inspired air at I_a. The percentage recovery for respiratory water was calculated by dividing the water recovered on expiration by the water added during inspiration ($T_{re\ sat} - T_{ex\ sat}/T_{re\ sat} - I_a$).

Net heat loss on expiration at $T_{ex\ sat}$ had two basic components, that due to the heat capacity of the air and that due to the heat of vaporization of water. Calculation

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of the percentage of heat recovery involves the comparison of convective and evaporative heat added on inspiration to bring the inspired air to $T_{re\ sat}$ with the heat loss on expiration at $T_{ex\ sat}$. Heat gain and loss by air was determined using the heat capacity for air (0.24 cal $°C^{-1}g^{-1}$). Heat recovered during expiration at $T_{ex\ sat}$ was derived using eq. (17).

$$D_{T_{ex}} \times 0.24 \times (T_{re}-T_{ex}) + (T_{re\ sat}-T_{ex\ sat}) \times 580 \text{ cal/g} \quad (17)$$

The heat recovered on expiration in eq. (17) was divided by the heat added to the inspired air calculated in eq. (18).

$$D_{T_a} \times 0.24 \times (T_{re}-T_a) + (T_{re\ sat}-I_a) \times 580 \text{ cal/g} \quad (18)$$

In both equations (17) and (18), the value for latent heat of vaporization (580 cal/g) should be substituted by the appropriate heat of vaporization at T_{ex} (eq. 17) and T_z (eq. 18).

RESULTS

In all animals, expired air temperature measured at the opening of the nares was lower than body temperature (Table 18). The giraffe was the best able to lower the

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Table 18. Calculation of water and heat recovering during expiration in the giraffe compared with other ungulate species. Values are presented as averages; or values calculated from the averages. All water loss and heat loss data were calculated from nasal temperatures except for the giraffe (collected) which are averages derived from actual collections of respiratory water loss. The % recovery of water and heat has been calculated in all instances by dividing the amount recovered on expiration by the amount added on inspiration.

Animal	T_a °C	T_{re} °C	T_{ex} °C	$(T_{re\ sat}-I_a)$ mg H_2O/l air	$(T_{ex\ sat}-I_a)$ mg H_2O/l air	Water % Recovery	Heat % Recovery
Giraffe							
Collected	22.4	37.2	--	35.7	11.6	67	--
Nasal (calculated)	21.1	37.3	28.0	34.9	15.3	56	58
Sheep	24.1	39.0	35.3	38.8	29.1	25	26
Donkey	23.6	37.6	32.3	35.4	22.6	36	38
Waterbuck	22.4	38.4	28.6	36.1	13.9	61	63
Goats	23.4	29.4	29.5	41.5	18.0	57	59
Cow	21.1	38.8	30.5	38.3	18.5	52	52
Wildebeest	23.6	39.1	34.2	40.0	27.1	32	33

T_a (ambient temperature), T_{re} (rectal temperature), T_{ex} (expired air temperature), $T_{re\ sat}$ (100% saturation at T_{re}), $T_{ex\ sat}$ (100% saturation at T_{ex}). I_a (absolute humidity of inspired air).

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water content of expired air, although the goat and waterbuck measurements were almost as good. The calculation of percentage recovery of water and heat by the body has been presented for comparison between species (Table 18). The total amount of heat and water lost during a respiratory cycle depends on the respiratory rate and tidal volume. While the data in Table 18 can be used as an indication of the efficiency of the nasal temporal heat exchangers in the animals tested, it cannot be used to calculate daily heat and water loss unless the respiratory rate and minute volume are known.

The giraffe was the most extensively studied species. Its nasal T_{ex} ranged from 23.7°C to 30.9°C, the lowest recorded for any of the species. Water contained in each liter of expired air at T_{ex} ranged from 3.6 to 19.3 mg/l air. Relationships between water contained in expired air and T_a or rh are shown in Figures 21 and 22. Water content of expired air was estimated directly or was calculated from rectal and expired air temperatures. Although the calculated water content data were represented by a smaller sample size, all of the data points for T_{re}, $T_{re\ sat}$, and $T_{ex\ sat}$ fit within the range of water content measured directly.

On an average, a 9°C separation was noted between the recorded T_{ex} and T_{re} for the nasal calculated water loss

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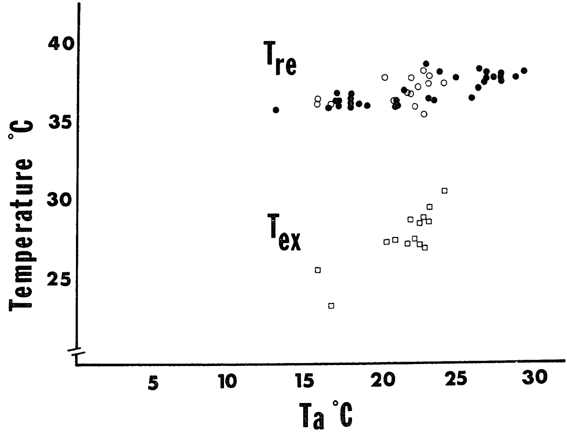

Figure 21. Relationships between exhaled air temperature (□; T_{ex}), rectal temperatures (o; T_{re}), and ambient temperature (T_a). The temperature data presented were measured during the collection of respiratory water loss (closed symbols) and the measurement of expired air temperatures (open symbols).

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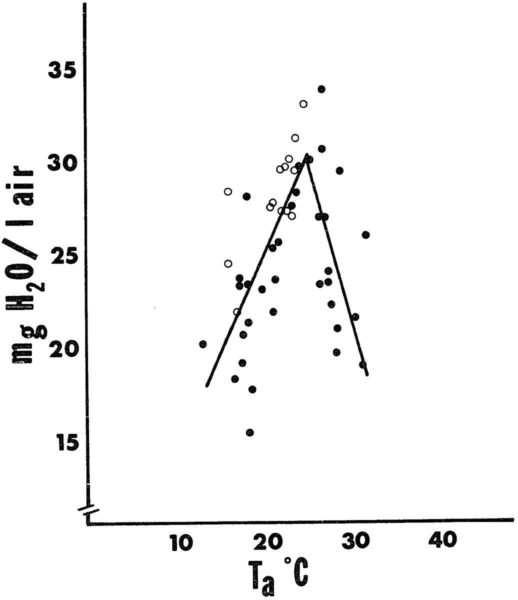

Figure 22. Relationship between water content of respired air ($T_{ex\ sat}$, mg H_2O/l air) and ambient temperature (T_a). Unfilled circles represent water loss calculated from nasal expired air temperatures. Filled circles represent collected respiratory water.

$T_a > 25°C$ $T_{ex\ sat} = 71.8-1.68\ T_a$ $r^2 = 0.272$ ($P<0.1$)

$T_a < 25°C$ $T_{ex\ sat} = 3.28-1.12\ T_a$ $r^2 = 0.685$ ($P<0.001$)

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data (Fig. 21). As the T_a increased, the T_{ex} also increased. The T_{re} for the two sets of data increased with T_a above 20°C. Possibly a plateau T_{re} (37.5°C) was noted at and above T_a of 25°C.

The graph of water content (mg H_2O/l air) during expiration ($T_{ex\ sat}$) at different ambient temperatures showed a peak water content value at a T_a of approximately 25°C (Fig. 23). At T_a higher than 25°C, the respiratory water loss per liter declined. Two regression lines were fitted to the data; one using all data points measured at T_a less than 25°C ($P < 0.001$) and a second using all data points greater than 25°C ($P < 0.10$). Relative humidity was the other major external factor effecting respiratory heat loss. Respiratory water loss increased with increasing rh until approximately 55%. At relative humidity values greater than 55% there was a marked decrease in respiratory water loss (Fig. 23). Regression lines were fitted to relative humidity (rh) data points less than 55% ($P < 0.01$) and greater than 55% ($P < 0.001$).

Relative humidity and temperature of ambient air were inversely related throughout the experimental period (Chapter 2, Fig. 11). When the T_a was lower than 25°C, the rh was greater than 55%. Ambient temperatures greater than 25°C occurred simultaneously with maximum solar heat load

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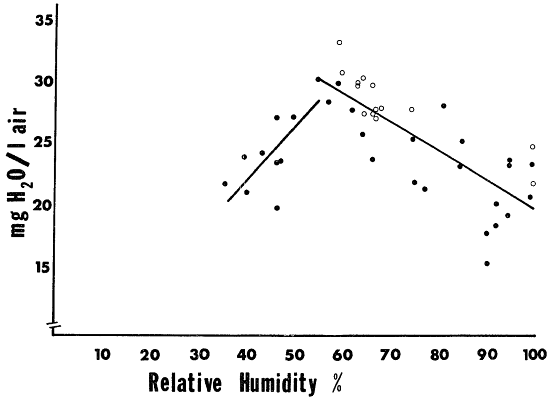

Figure 23. Relationship between water content of respired air ($T_{ex\ sat}$, mg H_2O/l air) and relative humidity (rh). Unfilled circles represent water loss calculated from nasal expired air temperatures. Filled circles represent collected respiratory water loss.

rh < 55%

$T_{ex\ sat} = 5.8 + 0.418$ rh $r^2 = 0.542$ ($P<0.01$)

rh > 55%

$T_{ex\ sat} = 43.14 - 0.227$ rh $r^2 = 0.602$ ($P<0.001$)

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and minimum relative humidity. The changes in T_{re} with increasing T_a (Fig. 21) follow the same pattern as the nychthemeral changes in T_{re} recorded during a long term study of thermoregulation in giraffe (Chapter 2).

Respiratory water loss, in g min^{-1} (Fig. 24), increased steadily with ambient temperature. The regression line fitted to the data showed a strong correlation ($P<0.001$) between ambient temperature and total respiratory water loss ($T_{ex\ sat}$). The regression fitted to the data for ambient temperature and net respiratory water loss ($T_{ex\ sat} - I_a$) also showed a strong correlation ($P < 0.001$). As the ambient temperature increased the rectal temperature of the giraffe also increased and with it the respiratory rate and minute volume. Although the amount of water contained in each liter of air decreases at temperatures higher than 25°C, the number of liters of air respired per minutes increased causing a steady increase in respiratory water loss. Therefore, the respiratory water loss values calculated as mg H_2O/l air (Fig. 22 and 23) represent the efficiency of the turbinates in the recovery of respiratory water. The regression lines for respiratory water loss presented in Figure 24, represent total and net water loss and reflect changes in minute volume.

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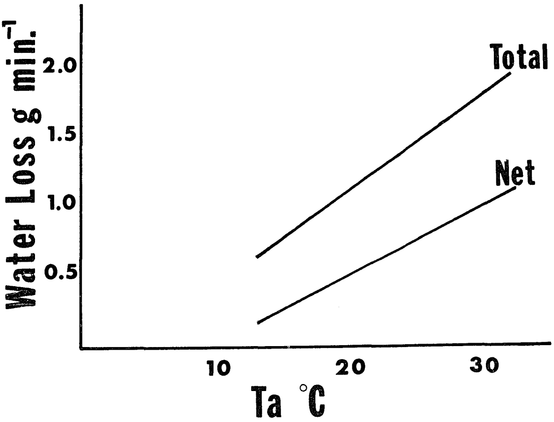

Figure 24. Regression lines for the relationship between total collected respiratory water loss ($T_{ex\ sat}$) and net respiratory water loss ($T_{ex\ sat} - I_a$) and ambient temperature.

Net H_2O loss ($T_{ex\ sat} - I_a$)

($T_{ex\ sat} - I_a$) = $0.049\ T_a - 0.465$ $r^2 = 0.579$ ($P<0.001$)

Total H_2O loss ($T_{ex\ sat}$)

$T_{ex\ sat} = 0.069\ T_a - 0.25$ $r^2 = 0.687$ ($P<0.001$)

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The giraffe nasal mucosa which includes the nasal turbinates and nasal septum, fulfill the physical requirements for a reciprocal heat exchanger. The nasal turbinates have a large surface area and are anatomically placed together in close proximity to the intra-nasal septum (Fig. 25 and 26). An increased surface area and exposure time for heat exchange are provided by the elongated nasal cavity. An average neurocranial-splanchocranial ratio of 1:2.20 was derived from a sample of over 40 giraffe skulls giving a range of 1:1.54 to 1:2.89. The airstream seems to be able to go either up and through the turbinates (Fig. 25b) or down between the turbinates and nasal septum (Fig. 25a and 25c). Figure 26 illustrates the much larger surface area exposed to air flow achieved by anatomically connecting the turbinates to a single point on the wall of the nasal cavity.

DISCUSSION

Evidence has been obtained of the ability of the giraffe to regain and conserve body water during expiration and the structure of the nasal passages is consistent with this evidence. The distance between the center of the airstream traveling through the turbinates and turbinate

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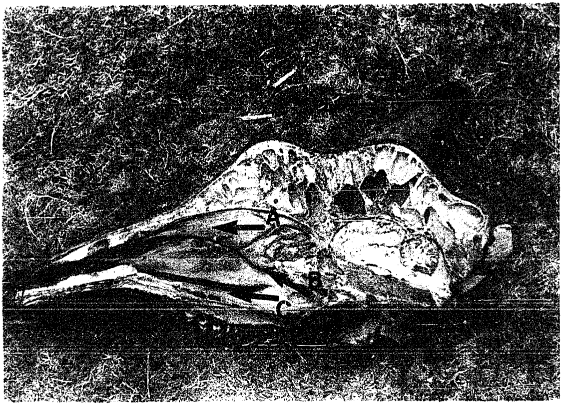

Figure 25. A sagittal section of the skull of an adult male giraffe (*Giraffa camelopardalis tippeleskirchi*) illustrating the extensive nasal surface area and large splanchocranial length. (A) Air traveling above the palate would have the greatest distance between the center of the airstream and nasal mucosa. (B) Air inhaled or exhaled through the turbinates would have the center of the airstream within 0.5 mm to 2 mm of the turbinate wall. (C) This path through the nose brings the airstream in close proximity to the turbinates and highly vascular nasal septum.

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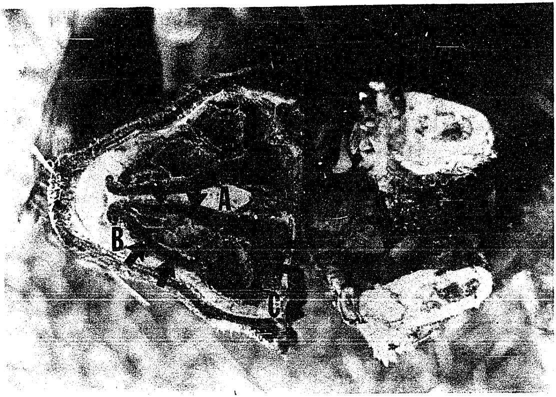

Figure 26. A cross section cut at the third molar of an adult male giraffe showing the position of the nasal turbinates and air pathways. Pathways A, B, and C correspond to the pathways shown on the sagittal section in Fig. 25.

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walls was found to be approximately 0.5 mm to 2 mm (Fig. 25b). This distance was considered small enough to allow maximal heat exchange and water evaporation and condensation in the nasal cavity of the smallest mammals yet studied (Schmidt-Nielsen et al. 1970). The elongated nasal cavity combined with a low rate of respiration (6 resp/min) and a high relative minute volume of 64.8 l/min extended the exposure time for heat exchange. The neurocranial-splanchocranial ratio for giraffe that do not pant to cool was greater than the same ratio measured for wildebeest that are efficient thermal panters (Taylor, Robertshaw, and Hofmann 1969).

The above anatomical data combined with the high percentage of heat and water recovery on expiration (Table 18) both indicate the existence of a highly efficient nasal heat exchanger functioning in the giraffe. In the other animals, the levels of efficiency in the recovery of water and heat on expiration varied. Measurements in the goat and waterbuck showed high levels of temporal heat exchange which probably reflect anatomical nasal passages that meet the requirements for efficient transfer of heat between the airstram and nasal mucosa.

Thermal cooling abilities of wildebeest and zebu were functionally and anatomically compared by Taylor et al.

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(1969). The zebu which was nearly twice as efficient as the wildebeest in our experiments, had a low neurocranial-splanchocranial ratio, and a narrow nasal cavity which contrasted with the much wider nasal cavity of the wildebeest. This data combined with the low efficiency of respiratory water recovery reported in this paper indicated that the wildebeest has evolved an upper respiratory system designed for respiratory heat loss. The cow, which both pants and sweats to cool, has the ability to recover both heat and water on expiration reflecting the cooling of nasal mucosa on inspiration.

Extensive work has been done (Baker and Hayward 1968, Baker 1972, Taylor and Lyman 1972) on the cool venous blood returning from the nasal mucosa cooling the warmer arterial blood in the carotid retia. This type of counter-current heat exchanger has been described for sheep and goats (Baker and Hayward 1968, Taylor 1966). Giraffe and cattle have carotid retia, however equines do not (Lawrence and Rewel 1948, Sisson and Grossman 1953). One of the major limitations of the counter-current heat exchanger in the cavernous sinus is the nasal heat exchanger. Either the nasal mucosa can vasoconstrict and act as a heat sink for heat and water recovery, or vasodilate and cool the blood in the capillaries of the mucosa and lose heat and water during expiration.

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The vasoconstricted state can be used for the conservation of water in hot climates and water and heat in cold climates. In the vasodilated state, blood is cooled for use in the counter-current heat exchanger in the cavernous sinus.

The mechanism controlling the water loss per liter of expired air was not clearly explained by the data presented in Figures 22 and 23. Several factors could have altered the efficiency of the nasal turbinates as reciprocal heat sinks at ambient temperatures greater than 25°C and rh values less than 55%. The most probable cause was the increase in evaporative heat loss to the inspired air at lower relative humidities decreasing the temperature of the turbinates.

However, the function of the turbinates as heat exchangers was well defined by the data presented. The turbinates functioned as efficient reciprocal heat sinks and were capable of a high degree of heat and respiratory water recovery.

The nasal heat exchanger functioning in giraffe can save from 1.51 l to 3.0 l of water per day, a savings of 7% to 15% of the total daily water loss. The heat recovery on expiration would be an average of 8% of the daily metabolic heat production. Giraffe would greatly benefit from the water savings by storing the heat recovered. Therefore, it is postulated here that the recovery of respiratory water was the major function of the nasal heat exchanger in giraffe.

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A wide spectrum of form and function exists for nasal heat exchangers found in mammals as well as some birds and reptiles (Murrish and Schmidt-Nielson 1970, Murrish 1973). The dog, when thermally stressed, pants by inhaling nasally and exhaling orally. Therefore, it could be hypothesized that the dog can keep the brain cool by inspiring through the nasal heat exchanger and lose body heat by exhaling orally; a hypothesis supported by the work of Chatonnet, Cabanac, and Satta (1964). A large number of species have been reported which store either environmental heat or heat generated by exercise. Most of these species have both nasal and carotid counter-current heat exchangers.

Eland, gazelle, goats, cats, and dogs, all have functioning counter-current heat exchangers associated with the carotid retia. These same animals must also have nasal heat exchangers controlling the temperature of venous blood going to the cavernous sinus. There is also a high probability that there exists a control system similar to those reported for the cat, sheep, and dog for the control of the temperature of the nasal mucosa. The anatomical structure and efficiency of the nasal heat exchangers varies between species. This variation may account for the ability of the gazelle to keep running and cool the brain while the cheetah must stop (Taylor and Rowntree 1973, Taylor and Lyman 1972).

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It is apparent from the data presented in this paper and from past work that nasal heat exchangers are functioning in a wide range of species and represent an important adaptation for heat and water exchange. Future research efforts should involve the investigation of the function of nasal heat exchangers in animals exposed to the severe cold where in many instances inspired air may have to be raised through 80°C before it reaches the lungs.

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GENERAL DISCUSSION

The short weaning period and apparent lack of maternal care reported for giraffe by Foster and Dagg (1972) created several questions concerning the adaptive advantage of a short weaning period to an animal with a long life span. The long and intense period of maternal care reported for giraffe in Chapter 1 was typical of the type of cow-calf relationships found in many long-lived large mammal species (Douglas-Hamilton 1972, Grimsdell 1969). The sightings of abandoned calves in previous studies (Foster and Dagg 1972, Innis 1959) were probably the result of disconnected observations, a problem which has been overcome using radio-telemetry (Chapter 1). However, the results of the behavior observations in Chapter 1 created a new problem concerning the function of lying out behavior. The question of why giraffe have evolved a system to continue the lying out period of calves past the 5-30 day postpartum period typical of other hider species (Lent 1974) remained unanswered by the data presented in Chapter 1.

Three ages and therefore body sizes of giraffe were used for the study of thermoregulation and heat balance (Chapter 2). The initial assumption was that although adult giraffe may have the body size required to use heat

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storage, the juvenile giraffe did not. Juvenile giraffe should not therefore be able to allow heat to accumulate in the body tissues without experiencing large changes in rectal temperature. It was also reasoned that juvenile giraffe might use evaporative cooling during exposure to high ambient temperatures.

The juvenile giraffe and adult giraffe showed similar nychthemeral flucuations in rectal temperature and an absence of evaporative cooling in response to increasing ambient temperature (Chapter 2). Juvenile and adult giraffe remained thermally labile whether deprived of water or given water ad lib, with fluctuations in rectal temperature similar to camels or eland (Schmidt-Nielsen et al. 1957, Taylor 1970). Heat storage contributed less to the overall heat balance of the juveniles when compared to the adults.

The question which arises if giraffe are using heat storage instead of evaporative cooling is that the larger body mass the more efficient heat storage becomes, if efficiency is measured by the magnitude of daily fluctuations in rectal temperature. Therefore, young giraffe which have a relatively small body mass would be at a disadvantage and should be forced to either use evaporative cooling in the form of sweating or exhibit daily fluctuations in rectal temperature which are much greater than those

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measured in the adults. However, the juvenile giraffe used in this study neither increased their evaporative heat loss by sweating nor exhibited larger daily flucuations in rectal temperature than the adults.

The only remaining solution to this problem would be behavioral thermoregulation. By limiting the degree of exposure to long and shortwave radiation and not building up an exercise heat load, the young giraffe would be able to maintain the same daily rectal temperature fluctuation seen in the adult and avoid using evaporative cooling mechanisms.

The behavior of young giraffe described in this thesis resolved the problem presented by a species which used heat storage in place of evaporative cooling. Infant and juvenile giraffe do not follow the much larger cow to water to browsing areas, but remain either lying or browsing within a very limited area during the day and move with the cow to new areas in the late afternoon. Neither infants nor juveniles were observed drinking from areas of standing water during the behavior study reported in Chapter 1, and it is suggested they exist entirely during the first year to two years of life on the water gained from the milk and later from preformed water in the browse.

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Thermal lability has been described in camels, eland, and oryx in response to water deprivation (Schmidt-Nielson et al. 1957, Taylor 1970). Allowing rectal temperature to increase during the day and passively losing the stored heat at night was a response stimulated by a 10% or more loss of body water. All of the above animals, when given free access to water, responded to an increase in environmental heat load by actively sweating. Therefore, heat storage was used when heat loss by evaporative means was too costly in body water for the dehydrated animals.

Giraffe have been shown to be thermally labile when they have free access to water. The nychthemeral rectal temperature fluctuations recorded for giraffe in this study were comparable to the variations reported for camels (Schmidt-Nielsen et al. 1957). However, giraffe do not respond to the stimulus of water deprivation as do camels, but use heat storage in the same way the hydrated camel uses sweating.

The giraffe respond to environmental heat loads by using their body mass as a heat sink to passively store the heat during the day. The giraffe measured in this study showed low levels of evaporative heat loss from sweating and respiration. The nasal turbinates were used as reciprocal heat sinks for the condensation of water and latent

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heat of vaporization on expiration. Although there was an increase in heat gain from the use of the turbinates for water conservation (Chapter 3), this excess heat was also stored and lost passively during the night.

The water conserving mechanisms described for the giraffe saved approximately 12 l of water per day. If Adolf's (1949) equation for daily water intake (water intake ml/hr = $0.01W^{0.88}$) was applied to giraffe with the average body weight of 715 kg, the estimated intake would be 34 l/day. The measured average water consumption per day for the giraffe was 21 l, 38% less than the predicted value. However, if the water savings calculated from reduced cutaneous and respiratory evaporation losses are added to the observed daily water consumption, the values closely approximate the water consumption values derived from Adolf's equation.

The heat gain and loss during ingestion and excretion were calculated using equations derived by R. White (pers. comm.). The contribution by these pathways to the overall heat balance during a diurnal 9 hr period was less than 1% of the total and therefore ignored in the calculations of heat balance.

The data presented in this thesis indicated that giraffe, when heat acclimatized, do not respond to environmental heat

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loads by evaporative cooling either in the form of sweating or panting. Giraffe allowed the excess environmental heat to accumulate in their body tissue and subsequently allowed their rectal temperature to increase an average of 3.8°C between 0800 hr and 1800 hr. A well developed nasal heat exchanger was utilized by giraffe to further add to the amount of water conserved by using heat storage instead of evaporative cooling. Young giraffe because of their smaller body mass were not able to store as much heat as the adult without allowing a very large increase in rectal temperature or resorting to evaporative cooling. The infant and juvenile giraffe studied in the wild limited their activities during the day, and it is suggested here that they used behavioral thermoregulation to avoid a large diurnal heat accumulation.

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APPENDIX

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APPENDIX A. An hourly calculation of heat gained and lost by giraffe Big Boss weighing 1061 kg. All values presented are in cal/cm^2. The percentage error represents the percentage difference between the total heat gained and the total heat.

Hour	M	Habs	$\varepsilon\sigma T_r^4$	H_{conv}	H_{sw}	H_{ex}	HS	Gain	Loss	Error %
0800	0.150	0.673	0.648	0.041	0.092	0.011	+.253	0.823	1.045	21
0900	0.150	0.841	0.679	0.041	0.092	0.011	+.285	0.991	1.108	11
1000	0.150	1.033	0.713	0.094	0.092	0.011	+.384	1.183	1.294	9
1100	0.150	1.169	0.736	0.139	0.092	0.011	+.162	1.319	1.140	14
1200	0.150	1.199	0.748	0.230	0.092	0.011	+.189	1.349	1.270	6
1300	0.150	1.197	0.748	0.168	0.092	0.011	+.111	1.349	1.168	18
1400	0.150	1.199	0.772	0.182	0.092	0.011	+.111	1.349	1.168	13
1500	0.150	1.105	0.772	0.209	0.029	0.011	+.015	1.255	1.099	12
1600	0.150	0.991	0.772	0.185	0.092	0.011	+.079	1.141	1.139	0.2
Total for 9 hr	1.350	9.407	6.588	1.289	0.828	0.099	1.557	10.757	10.361	4
% Contribution	13	87	64	12	8	0.9	15			

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APPENDIX B. An hourly calculation of the heat gained from long and shortwave radiation by the giraffe Big Boss weighing 1061 kg. All values presented are in cal/cm^2 unless otherwise marked. The totals for each radiation component were used in the H_{abs} in Appendix A. The T_r and V values presented were used for the hourly calculations of heat loss by radiation (T_r^4) and by convection (H_{conv}). Values for T_r and T_g were derived using the regression equations presented below.

$$Y_{Tg} = 0.93 + 1.56\ T_a \qquad r^2 = 0.8056$$

$$Y_{Tr} = 6.67 + 1.22\ T_a \qquad r^2 = 0.6604$$

Hour	S	s	S+s	rg	$\frac{aS(2/\pi)}{2}$	$\frac{as}{2}$	$\frac{arg(S+s)}{2}$	$\frac{Ra}{2}$	$\frac{Rg}{2}$	Tg (°C)	Tr (°C)	V cm/sec
0800	0.329	0.041	0.370	0.27	0.081	0.016	0.038	0.204	0.334	27.5	27.4	64.4
0900	0.660	0.081	0.741	0.27	0.162	0.031	0.077	0.216	0.355	32.1	31.0	64.4
1000	1.044	0.129	1.173	0.27	0.256	0.049	0.122	01228	0.378	36.8	34.7	210.0
1100	1.318	0.163	1.481	0.27	0.323	0.063	0.154	0.236	0.393	39.9	37.2	378.6
1200	1.374	0.169	1.543	0.27	0.337	0.065	0.160	0.236	0.401	41.5	38.4	853.8
1300	1.374	0.169	1.543	0.27	0.337	0.065	0.160	0.234	0.401	41.5	38.4	502.4
1400	1.318	0.163	1.481	0.27	0.323	0.063	0.154	0.242	0.417	44.6	40.8	546.7
1500	1.099	0.136	1.235	0.27	0.269	0.052	0.128	0.239	0.417	44.6	40.8	691.5
1600	0.824	0.102	0.926	0.27	0.202	0.039	0.096	0.237	0.417	44.6	40.8	559.2
Total for 9 hr					2.290	0.443	1.089	2.072	3.513			
% Contribution					24	5	12	22	37			

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APPENDIX C. An hourly calculation of heat gained and lost by giraffe Malaya weighing 640 kg. All values presented are in cal/cm^2. The percentage error represents the percentage difference between the total heat gained and the total heat.

Hour	M	Habs	$\varepsilon\sigma T_r^4$	H_{conv}	H_{sw}	H_{ex}	HS	Gain	Loss	Error %
0800	0.069	0.766	0.623	0.008	0.094	0.007	+.117	0.835	0.841	0.7
0900	0.097	0.854	0.612	0.053	0.094	0.007	+.181	0.951	0.947	0.4
1000	0.109	1.003	0.696	0.042	0.094	0.007	+.374	1.112	1.213	8
1100	0.127	1.029	0.725	0.105	0.094	0.007	+.184	1.156	1.115	4
1200	0.139	1.132	0.736	0.146	0.094	0.007	+.105	1.271	1.088	14
1300	0.164	1.111	0.748	0.131	0.094	0.007	+.165	1.275	1.145	10
1400	0.199	1.092	0.766	0.142	0.094	0.007	+.234	1.291	1.243	4
1500	0.217	1.018	0.760	0.040	0.094	0.007	+.108	1.235	1.009	18
1600	0.247	0.924	0.754	0.121	0.094	0.007	+.044	1.171	1.020	13
Total for 9 hr	1.368	8.929	6.420	0.788	0.846	0.072	1.512	10.297	9.621	7
% Contribution	13	87	67	8	9	0.7	16			

APPENDIX D. An hourly calculation of the heat gained from long and shortwave radiation by the giraffe Malaya weighing 640 kg. All values presented are in cal/cm^2 unless otherwise marked. The totals for each radiation component were used in the H_{abs} in Appendix A. The T_r and V values presented were used for the hourly calculations of heat loss by radiation (T_r^4) and by convection (H_{conv}). Values for T_r and T_g were derived using the regression equations presented below.

$$Y_{Tg} = 0.93 + 1.56\ T_a \qquad r^2 = 0.8056$$

$$Y_{Tr} = 6.67 + 1.22\ T_a \qquad r^2 = 0.6604$$

Hour	S	s	S+s	rg	$\frac{aS(2/\pi)}{2}$	$\frac{as}{2}$	$\frac{arg(S+s)}{2}$	$\frac{Ra}{2}$	$\frac{Rg}{2}$	Tg (C)	Tr (C)	V cm/sec
0800	0.604	0.075	0.679	0.27	0.148	0.029	0.071	0.201	0.317	23.6	24.4	--
0900	0.847	0.104	0.951	0.27	0.208	0.040	0.099	0.197	0.310	21.9	23.1	--
1000	1.044	0.129	1.173	0.27	0.256	0.049	0.122	0.210	0.366	34.5	32.9	65.3
1100	1.143	0.141	1.284	0.27	0.245	0.054	0.133	0.212	0.385	38.4	35.9	285.2
1200	1.274	0.158	1.432	0.27	0.312	0.061	0.149	0.217	0.393	39.9	37.2	469.4
1300	1.209	0.149	1.358	0.27	0.296	0.057	0.141	0.216	0.401	41.5	38.4	383.9
1400	1.120	0.139	1.259	0.27	0.275	0.053	0.131	0.219	0.413	43.8	40.2	313.3
1500	0.956	0.118	1.074	0.27	0.234	0.045	0.112	0.218	0.409	43.1	39.6	51.9
1600	0.748	0.092	0.840	0.27	0.183	0.035	0.087	0.214	0.405	42.3	30.0	33.3
Total for 9 hr					2.157	0.423	1.045	1.904	3.399			
% Contribution					21	4	10	18	33			

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APPENDIX E. An hourly calculation of heat gained and lost by giraffe Lady Gay weighing 285 kg. All values presented are in cal/cm^2. The percentage error represents the percentage difference between the total heat gained and the total heat.

Hour	M	Habs	$\varepsilon\sigma T_r^4$	H_{conv}	H_{sw}	H_{ex}	HS	Gain	Loss	Error %
0800	0.117	0.599	0.649	0.049	0.065	0.008	+.054	0.716	0.825	13
0900	0.117	0.678	0.669	0.062	0.065	0.008	+.094	0.795	0.898	11
1000	0.117	0.772	0.689	0.046	0.065	0.008	+.087	0.889	0.895	0.7
1100	0.117	0.894	0.703	0.107	0.065	0.008	+.103	1.011	0.986	2
1200	0.117	1.112	0.716	0.125	0.065	0.008	+.074	1.229	0.988	20
1300	0.117	1.150	0.726	0.107	0.065	0.008	+.089	1.267	0.995	21
1400	0.117	1.126	0.732	0.128	0.065	0.008	+.058	1.243	0.991	20
1500	0.117	1.087	0.737	0.121	0.065	0.008	+.022	1.204	0.953	21
1600	0.117	0.967	0.737	0.154	0.065	0.008	+.009	1.084	0.973	10
Total for 9 hr	1.055	8.385	6.358	0.899	0.585	0.072	0.590	9.438	8.504	10
% Contribution	11	89	75	11	7	1	7			

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APPENDIX F. An hourly calculation of the heat gained from long and shortwave radiation by the giraffe Lady Gay weighing 285 kg. All values presented are in cal/cm^2 unless otherwise marked. The totals for each radiation component were used in the H_{abs} in Appendix A. The T_r and V values presented were used for the hourly calculations of heat loss by radiation (T_r^4) and by convection (H_{conv}). Values for T_r and T_g were derived using the regression equations presented below.

$$Y_{Tg} = 0.93 + 1.56\ T_a \quad r^2 = 0.8056$$

$$Y_{Tr} = 6.67 + 1.22\ T_a \quad r^2 = 0.6604$$

Hour	S	s	S+s	rg	$\frac{aS(2/\pi)}{2}$	$\frac{as}{2}$	$\frac{arg(S+s)}{2}$	$\frac{Ra}{2}$	$\frac{Rg}{2}$	Tg (°C)	Tr (°C)	V cm/sec
0800	0.133	0.025	0.158	0.17	0.033	0.009	0.010	0.212	0.335	27.8	27.7	63.0
0900	0.250	0.066	0.316	0.21	0.061	0.025	0.026	0.218	0.348	30.6	29.9	85.8
1000	0.415	0.099	0.514	0.23	0.102	0.038	0.046	0.224	0.362	33.5	32.2	50.1
1100	0.612	0.126	0.738	0.34	0.150	0.049	0.097	0.227	0.371	35.4	33.6	194.8
1200	1.277	0.146	1.423	0.25	0.313	0.056	0.137	0.232	0.379	37.1	34.9	215.0
1300	1.515	0.119	1.634	0.18	0.371	0.046	0.113	0.234	0.386	38.5	36.1	183.7
1400	1.422	0.093	1.515	0.20	0.349	0.036	0.117	0.234	0.390	39.3	36.7	242.7
1500	1.251	0.106	1.357	0.21	0.307	0.041	0.109	0.236	0.394	40.0	37.3	219.9
1600	0.893	0.069	0.962	0.25	0.219	0.027	0.093	0.234	0.394	40.0	37.3	326.3
Total for 9 hr					1.905	0.327	0.748	1.817	3.359			
% Contribution					23	4	9	22	41			

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APPENDIX G. An hourly calculation of heat gained and lost by giraffe Malaya weighing 640 kg. All values presented are in cal/cm^2. The percentage error represents the percentage difference between the total heat gained and the total heat.

	Gain		Loss							
Hour	M	Habs	$\varepsilon\sigma T_r^4$	H_{conv}	H_{ex}	H_{sw}	HS	Gain	Loss	Error %
2200	0.147	0.420	0.638	0.064	0.007	--	-0.076	0.643	0.709	9
2300	0.134	0.397	0.621	0.032	0.007	--	-0.199	0.730	0.660	10
2400	0.132	0.381	0.605	0.012	0.007	--	-0.076	0.589	0.624	6
0100	0.147	0.374	0.597	0.011	0.007	--	-0.108	0.629	0.615	2
0200	0.132	0.371	0.593	0.015	0.007	--	-0.092	0.595	0.615	3
0300	0.134	0.366	0.589	0.015	0.007	--	-0.029	0.529	0.611	13
0400	0.117	0.355	0.577	--	0.007	--	-0.177	0.649	0.584	10
0500	0.087	0.351	0.573	0.017	0.007	--	-0.168	0.606	0.597	1
Total for 8 hr	1.030	3.015	4.793	0.166	0.056	--	-0.925	4.970	5.015	1

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APPENDIX H. An hourly calculation of heat gained and lost by giraffe Lady Gay weighing 285 kg. All values presented are in cal/cm^2. The percentage error represents the percentage difference between the total heat gained and the total heat.

	Gain		Loss							
Hour	M	Habs	$\varepsilon\sigma T_r^4$	H_{conv}	H_{ex}	H_{sw}	HS	Gain	Loss	Error %
2200	0.124	0.436	0.650	--	0.008	--	-0.044	0.604	0.658	8
2300	0.124	0.431	0.648	--	0.008	--	-0.036	0.591	0.656	10
2400	0.124	0.417	0.633	0.064	0.008	--	-0.036	0.577	0.705	18
0100	0.124	0.417	0.634	0.040	0.008	--	-0.083	0.624	0.682	9
0200	0.124	0.412	0.629	0.029	0.008	--	-0.040	0.576	0.666	14
0300	0.124	0.403	0.623	0.016	0.008	--	-0.089	0.616	0.647	5
0400	0.124	0.408	0.627	0.031	0.008	--	-0.056	0.588	0.666	12
0500	0.124	0.410	0.628	0.028	0.008	--	-0.049	0.583	0.664	12
Total for 8 hr	0.992	3.334	5.072	0.208	0.064	--	-0.433	4.759	5.344	11
% Contribution	21	70	95	4	1		9			

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