

THERMOREGULATION IN THE HANFORD, WASHINGTON
ELK HERD

by

Stephen E. Petron, Ph.D.

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STEPHEN E. PETRON

A dissertation submitted in partial fulfillment of
the requirements for the degree of

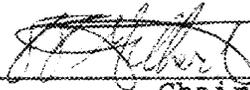
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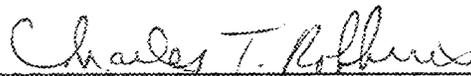
WASHINGTON STATE UNIVERSITY
Department of Zoology

May 1987

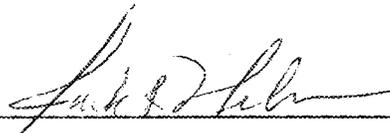
To the Faculty of Washington State University:

The members of the Committee appointed to examine the dissertation of Stephen E. Petron find it satisfactory and recommend that it be accepted.


Chair







ACKNOWLEDGMENTS

I wish to express my gratitude to my committee chairman, Dr. Frederick Gilbert, for his expression of confidence in me, guidance, and assistance in preparing this dissertation. Dr. William Rickard generously apportioned funds for the research, offered valuable comments on the research and preparation of the manuscript, and was a source of sound advice while I was at ALE. Dr. Charles Robbins and Dr. Jack Nelson served on my committee and offered valuable comments on the research and manuscript.

I am indebted to the many staff members of Pacific Northwest Laboratory who generously gave me their time and advice. I owe special thanks to Dr. Les Eberhardt, who willingly shared his knowledge and was always available to lend a hand. Also particularly helpful were Dr. Lee Rogers, Dr. Peter Beedlow, and Mike Thiede. Dr. Bob Busch and Dr. Dick Weller performed the field surgeries. Joan Segna and Susan Thorsten cheerfully provided secretarial support. Gordon Frisbee spent a cold winter collecting data.

The work was performed under U.S. Department of Energy contracts DE-AC06-76RLO 1830 to Pacific Northwest Laboratory and DE-AN06-76-RLO2225 to the Northwest Organization of

Colleges and Universities for Science. Dr. Bryan Valett administered my NORCUS fellowship.

I am most thankful to my wife, Trish, who travelled across the country with me for this endeavor, patiently waited 4 years for the work's completion, and supplied encouragement or prodding whenever needed.

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Abstract

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Washington State University
May 1987

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Body temperature (T_b) rhythms in 5 wild elk (Cervus elaphus nelsoni) were monitored with radio-telemetry in the semi-arid shrub-steppe of south-central Washington. Overall mean T_b equaled 38.4 °C during both summer and winter. Average diurnal T_b variation was 1.1 ± 0.1 (SE) °C during summer and 0.6 ± 0.1 (SE) °C during winter. Mean minimum temperature occurred 6 h after sunrise during both summer (± 2 SE) and winter (± 1 SE). Mean maximum temperature occurred 17 ± 1 (SE) h after sunrise during summer and 15 ± 1 (SE) h after sunrise during winter.

Water content in elk forage decreased from 70% in April to 10% in July. Water dynamics in penned elk were determined using the tritiated water dilution technique. Penned elk used an estimated 4.6 kg H_2O /(100 kg body weight)/day during spring and used an estimated 10.6 kg H_2O /(100 kg body weight)/day during summer.

Thermoregulation was studied in elk using implanted sensors and radio-telemetry. Summer subcutaneous

temperatures increased linearly with operative temperatures up to, but not above 30 °C. Winter subcutaneous temperatures were not correlated to operative temperatures and were maintained 1 °C below body temperature in nonbreeding bulls and cows. Body temperature was independent of operative temperature during both winter and summer. Elk preferred sagebrush (Artemisia tridentata) as bedding habitat during both winter (73%) and summer (69%). Elk positioned themselves in the shade more often during summer (53%) than during winter (27%) suggesting that sagebrush was used for concealment during winter and for thermal cover and concealment during summer.

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DEDICATION

To my mother, Sylvia, who inspired in me a desire for academic achievement, and to my father, Alfred, who through the frequent trips "around the section" to Baker's Lake instilled in me an appreciation for wild things.

SECTION I

TEMPORAL RHYTHMS IN ELK BODY TEMPERATURES

TEMPORAL RHYTHMS IN ELK BODY TEMPERATURES

INTRODUCTION

Thermoregulatory responses of ungulates to their environment have received increasing attention in an attempt to learn more about physiological limits to animal existence and distribution (Moen 1976, Yousef 1976, Parker and Robbins 1984). Nevertheless, little attention has been paid to diurnal body temperature (T_b) rhythms and seasonal changes in such rhythms. Researchers should be aware of the nature and extent of diurnal rhythms in their subjects before attempting to explain variations in animal temperatures as responses to environmental conditions that are correlated to time of day (Enright 1970). The phase of the cycle must be taken into account if data are not continuously recorded, because observations taken at different points in the cycle are not necessarily comparable (Sollberger 1965, Enright 1970).

Data collected to date suggest that T_b 's in ungulates undergo regular diurnal cycles and that the characteristics of these patterns are not seasonally different. Yousef (1976) found that there were no measurable seasonal differences in rectal temperature fluctuations in reindeer (Rangifer tarandus) in Alaska. Bligh and Hawthorn (1965), working on a number of African ungulates, found no difference in T_b

variation between seasons.

Fluctuations in T_b 's can be classed into three ecologically important types: 1) endogenous rhythms that are independent of environmental temperature (Folk 1974, Saunders 1977). For example, Taylor (1970) reported variations in Thomson's gazelle (Gazella thomsonii), zebu steer (Bos indicus), and eland (Taurotragus oryx) of more than 1 °C in a constant 22 °C environment; 2) fluctuations in T_b as an adaptive strategy to cope with high environmental temperatures or conditions of water shortage as shown by Schmidt-Nielsen et al. (1957) in the camel (Camelus dromedarius), Taylor (1970) in a number of African ungulates, and by Zervanos and Hadley (1973) in collared peccary (Tayassu tajacu); and 3) temperature fluctuations that are a passive result of a breakdown or inadequacy in thermoregulatory capabilities where heat dissipation mechanisms cannot keep up with heat gained from the environment and internal thermogenesis (heat exhaustion). The objectives of this study were to determine the extent of diurnal T_b cycling in elk, and to determine if there were seasonal differences in these cycles.

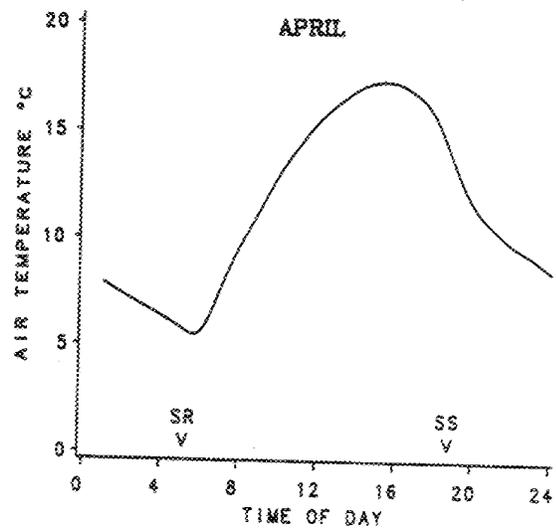
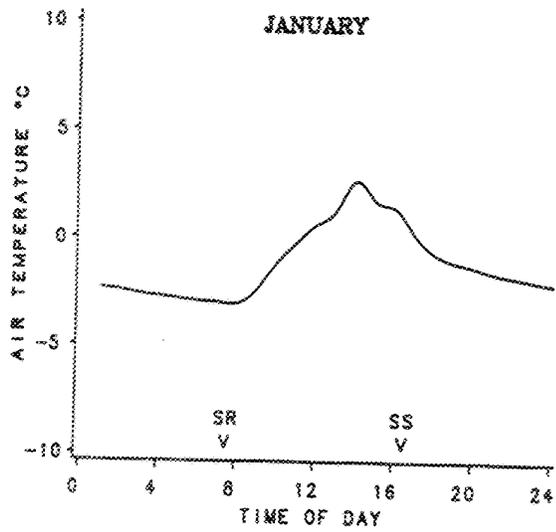
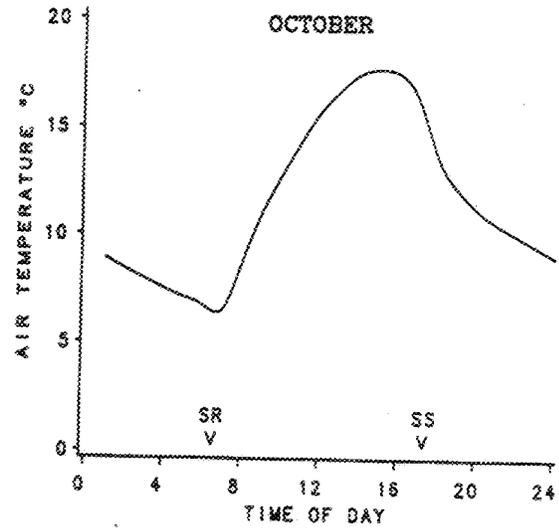
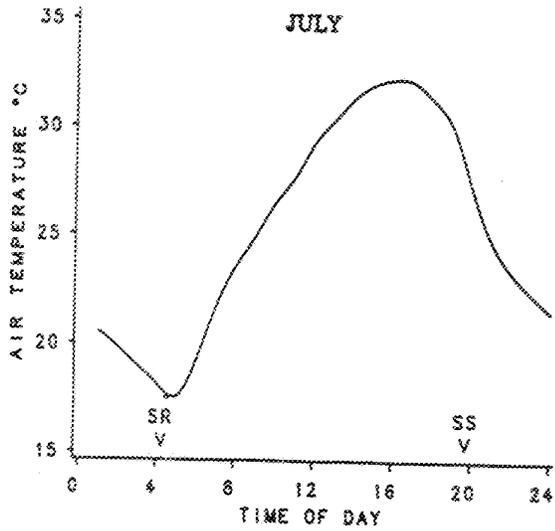
STUDY AREA

This study was conducted on the Arid Lands Ecology (ALE) Reserve, a 330 km² portion of the U.S. Department of Energy's

Hanford Site in the semi-arid shrub-steppe of south-central Washington. The Hanford Site experiences much greater diurnal temperature fluctuations in the summer than in winter (Fig. 1). Summer diurnal air temperature fluctuations can exceed 20 °C, whereas winter temperatures seldom vary more than a few degrees °C (Stone et al. 1983).

METHODS

Five wild elk (2 females, 3 males) were immobilized with rifle-fired darts from a helicopter (Petron et al. 1987). Two males were adults (160, 180) and 1 was a yearling (200). One female was a yearling (825) and the other an adult (765) (with calf). Male 160 was captured in December, 1983, male 180 in June, 1984, and male 200 and females 825 and 765 in June 1985. The animals were immobilized with etorphine for approximately 2.5 hours, during which time each was fitted with a radiotelemetry collar (Cedar Creek Biotelemetry Lab, Bethel, Minn.) and implanted with a cylindrically shaped, temperature-sensitive transmitter (about 3 x 15 cm, Model # IMP/400/EX, Telonics, Mesa, Ariz.). The implant was surgically inserted into the peritoneum through an incision in the paralumbar fossa. It was not sutured in place, and therefore, some movement of the implant could have occurred during the first few postoperative days.



Implants

The temperature implant consisted of a pulsing FM transmitter with a thermistor inserted into the circuitry so that the pulse rate reflected the temperature of the transmitting system. The transmitter, battery, and antenna were encapsulated in a biologically inert coating of physiological embedding wax and resin. The implant was calibrated versus a U.S. National Bureau of Standards certified mercury thermometer by wrapping it in 1 layer of cheesecloth and suspending it in a circulating water bath. Calibration was between 36-41 °C at 0.4 °C intervals. The order of temperature intervals was randomly chosen in order to minimize autocorrelation in the residuals of the calibration curves (Neter et al. 1983). Least squares linear regression was used on data from a minimum of 2 such temperature runs to calculate the final calibration curve for each sensor. Implants were immersed at each temperature setting for a minimum of 30 min. The pulse rate had to be constant for 5 min before it was recorded. Pulse rates were timed using pulse timers accurate to ± 1 msec (models TDPI and TDP2, Telonics). All body transmitters had 99% prediction confidence limits of ± 0.2 °C.

Data collection

Pulse rates were collected using standard telemetry receivers (Cedar Creek Biotelemetry Lab, Bethel, Minn; Telonics) and pulse timers. Data were collected manually for all periods of the year by locating the animals opportunistically and timing the pulse rates of the implants. In addition, manual data were collected every 15, 30, or 60 min during planned 24 h sessions during winter and summer. Pulse rates were also automatically collected for varying periods of time. The system used to automatically record the temperatures has been described by Petron et al. (1987), and consisted of a micrologger (model CR21, Campbell Scientific, Inc., Logan, Utah) that automatically recorded data from the pulse timers and entered them on a cassette recorder. Data were later loaded from the cassette onto a computer through a modem. Pulse rates were recorded every 2 min with this system.

Analysis

Data were processed with a FORTRAN program that converted the pulse rates into temperatures and checked for anomalous data. Data were considered anomalous if they did not fall within physiologically feasible temperature ranges. Data were

standardized against the diurnal light cycle by using the hours after sunrise in place of time for analysis. Hourly temperature means were calculated and used in analysis to avoid unequal weighting, because data collected automatically generated 30 observations per hour as compared to the 1 or 2 observations per hour for manually recorded data.

Data for each animal were summarized for all days during the period when the elk had summer coats (about mid-May through the end of August), and when they had winter coats (September 1 through May 14). Timing of maximum and minimum and magnitude of diurnal variation were calculated from each animal's composite temperature cycle for each pelage. Each elk's cycle was adjusted to the overall elk phase, which was necessary before summary statistics could be performed (Sollberger 1965).

RESULTS AND DISCUSSION

Elk T_b 's varied diurnally during both summer and winter and the cycles were synchronized between seasons and individuals (Table 1). This variation could have been a result of two phenomena. It could have been a strategy for conservation of water and energy by storing heat during the hot times of the day and then releasing it at night through radiative cooling (thermal loading) (Yousef 1976). The

Table 1. Average times of maximum and minimum T_b and amplitude of average diurnal T_b cycles for ALE Reserve elk in winter and summer pelts, 1984-1986.

Elk #	Pelt					
	Summer			Winter		
	Hours		Amplitude	Hours		Amplitude
	<u>after sunrise</u>			<u>after sunrise</u>		
Min	Max		Min	Max		
M160 ^a	5	b	b	8	b	b
M180	3	16	1.1	2	13	0.9
M200	2	16	1.2	8	15	0.6
F765	11	18	1.1	6	16	0.6
F825	10	19	0.9	4	15	0.5
Mean	6	17	1.1	6	15	0.7
SE ^c	2	1	0.1	1	1	0.1

^aM indicates male; F indicates female.

^bInsufficient data for calculation.

^cStandard error of mean of individual average times of maximum and minimum.

rhythm could also have been the expression of an endogenously driven biological rhythm which was independent of the environment (Saunders 1977).

The fact that during both seasons maximum T_b occurred at night and minimum T_b occurred during the day for all the animals is important in determining the which hypothesis is correct.

If the temperature cycle was primarily caused by thermal loading, then the minimum T_b 's should have occurred near sunrise. This timing would have maximized the potential for heat storage during the day (Bligh and Hawthorn 1965, Taylor 1970). This was not observed in this study. Minimum T_b 's occurred during midday (6 h after sunrise) when air temperatures were already high during summer. Persistence of the rhythm during the winter when the animals were not heat-stressed is further evidence that thermal loading was not the primary cause of the rhythm.

The high point in an animal's temperature rhythm should occur during its active period and the low point should occur within the inactive period (Schmidt-Nielsen 1983). ALE Reserve elk fed predominately at night and rested through the day during summer (McCorquodale et al 1986) and winter (S. E. Petron unpublished data). Thus, high nighttime temperatures could have been caused by heat generated from digestion and muscular activity associated with feeding.

The conclusion that could be drawn from the above

evidence is that the temperature cycle observed in elk was not primarily caused by thermal loading; but, rather, was probably endogenously driven and was synchronized with their activity cycle. Before this can be definitively determined though, controlled experiments are needed to evaluate the response of the temperature rhythm in an environment with no time clues or external stimuli. Under these controlled conditions, persistence of the rhythm and a period slightly different than the pretest period would indicate the presence of an endogenously driven rhythm (Aschoff 1964). Definitive proof of the absence of thermal loading would require evaluating the effects that changing environmental conditions have on elk T_b rhythms.

It should be noted though, that the T_b sensor was implanted in the peritoneum, in juxtaposition to the rumen, and therefore was probably more sensitive to heat produced by digestion than if it was placed in other regions of the body. This placement was probably less susceptible to heat generated by local muscular thermogenesis. Bligh and Hawthorn (1965) felt that many of the irregularities that they observed in the T_b 's of the ungulates they were studying were due to the position of the sensor in muscle tissue. Any change in rumen temperature would have been reflected in the rest of the body because the rumen constitutes a significant portion of the animal's heat capacity. Therefore, the T_b 's recorded from the

implant in the peritoneum were representative of T_b .

Although all the animals underwent regular temperature cycles, with generally consistent times of maximum and minimum, the cycles were often interrupted by irregularities (Fig. 2). These irregularities in T_b fluctuations could have been responses to sickness, levels of activity, certain behaviors (bedding in water for instance), or drinking large quantities of water (thereby cooling the region surrounding the rumen, which was where the implant was located). Similar irregularities were observed in T_b cycles of African ungulates (Bligh et al. 1965, Bligh and Hawthorn 1965).

When compared to other large mammals for which diurnal T_b variations have been documented, elk rank among the more thermally stable (Table 2). One of the possible explanations is the excellent thermoregulatory capabilities of the species. Parker and Robbins (1984) showed that elk have well developed insulative winter coats for conservation of body heat in winter and have high evaporative cooling capabilities during summer to dissipate body heat. It is plausible that the ALE Reserve environment did not stress the animals in this study enough to warrant thermal loading. Taylor (1970) suggested this was a possible reason why Bligh and Hawthorn (1965) did not observe greater diurnal variations in their study of some large African mammals.

The magnitude of variation for the average temperature

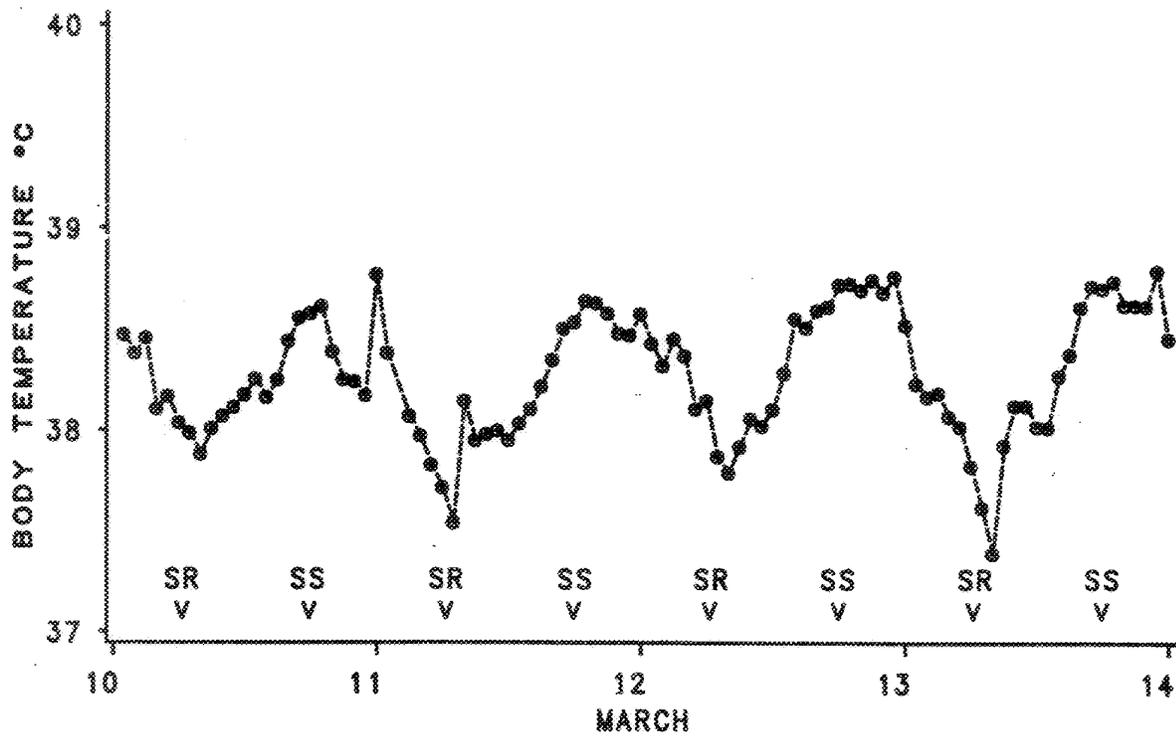


Table 2. Ranking of diurnal temperature variation in ungulates. Data, except for the elk and sheep, taken from Yousef (1976).

Species	Range in T_b °C	Variation in T_b	References
Eland	33.9-41.2	7.3	Taylor 1969
Oryx	35.7-42.1	6.4	Taylor 1969
Buffalo	36.9-40.2	3.3	Bligh and Robinson 1965
Camel	35.2-37.8	2.6	Bligh and Robinson 1965
Burro	36.5-39.0	2.5	Yousef and Dill 1969
Collared Peccary	37.5-39.0	2.5	Zervanos and Hadley 1973
Impala	38.8-40.4	1.6	Maloiy and Hopcraft 1971
Hartebeest	38.8-40.4	1.6	Maloiy and Hopcraft 1971
Giraffe	37.7-39.0	1.3	Bligh and Robinson 1965
Elk (summer) ^a	38.0-39.1	1.1	this study
Red deer	38.5-39.6	1.1	Johnson et al. 1972

^aAverage maximum and minimum of 4 animals

Table 2. cont.

Species	Range in T_b °C	Variation in T_b	References
Grants Gazelle	39.4-40.4	1.0	Taylor 1970
Thomson's Gazelle	39.0-40.0	1.0	Taylor 1970
Welsh Mountain Sheep	-	0.95	Bligh et al. 1965
Elk (winter) ^a	38.2-38.9	0.7	this study

^aAverage maximum and minimum of 4 animals

cycle for the five animals was 57% greater during summer than during winter (Table 1). Thus, environmental temperatures may have had some effect on the T_b 's of elk, by changing one of the characteristics of the rhythm; the amplitude. Summer amplitudes may have been greatest because during this time the animals had a minimal coat, compared to the protective highly insulative winter coat (Parker and Robbins 1984), and, therefore, were more susceptible to environmental changes. Summer air temperatures may have also been closer to a thermal critical limit for elk than winter air temperatures. Rectal temperatures in elk calves remained stable at air temperatures below -20°C (Parker and Robbins 1984). But they did record slight increases in rectal temperatures in elk of all ages during summer at temperatures up to 30°C . Stone et al. (1983) reported that Hanford winter temperatures seldom fall below -10°C , and are often above or very close to 0°C , which is well above the lower critical limit. Summer temperatures near 30°C (common on the ALE Reserve) were probably much closer to the upper thermal limit, especially when compounded by the intense summer solar radiation.

CONCLUSIONS

ALE Reserve elk exhibited diurnal temperature variations year-round. This suggests that physiological researchers

working on elk, and probably other cervids, as warned by Aschoff (1964) and Enright (1970), should be cognizant of the phase and other characteristics of rhythms existing in physiological parameters being monitored. This is important not only in thermoregulatory studies, but also for other physiological studies; including energetics as metabolism and thermoregulation are inextricably linked (Enright 1970). Consequently, comparisons of body temperatures recorded at different times of day versus exogenous independent variables are subject to error because of confounding influences from endogenous temperature rhythms. Three possible scenarios could occur: 1) the rhythm could exactly equal, in the opposite direction, the effect of the independent variable resulting in no apparent trend, 2) the rhythm could override the effect of the independent variable resulting in an apparent response in the opposite direction, and 3) the rhythm could reinforce the effect of the independent variable causing the response to be greater than what is attributable to the independent variable.

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SECTION II
WATER RELATIONSHIPS IN ELK

WATER RELATIONSHIPS IN ELK

INTRODUCTION

Knowledge of the water relations of an animal that lives in a hot-dry environment is required before a thorough understanding of its ecology is possible. Such animals are often faced with increased water demands for thermoregulation in an environment with relatively little water. Increased water requirements accompanied by a scarcity of water have been the bases for many hypotheses concerning the role of water dynamics to many desert animals (Nagy and Costa 1980). Nevertheless, water dynamics of North American ungulates that inhabit arid regions have received only minimal attention. Studies have been conducted on the pronghorn (Antilocapra americana) (Wesley et al. 1970), mule deer (Odocoileus hemionus hemionus) (Knox et al. 1969), and collared peccary (Tayassu tajaca) (Zervanos and Day 1977). There has been only limited research on water use in elk (Skovlin 1982). Parker and Robbins (1984) determined rates of cutaneous and respiratory water loss, but did not determine body water dynamics.

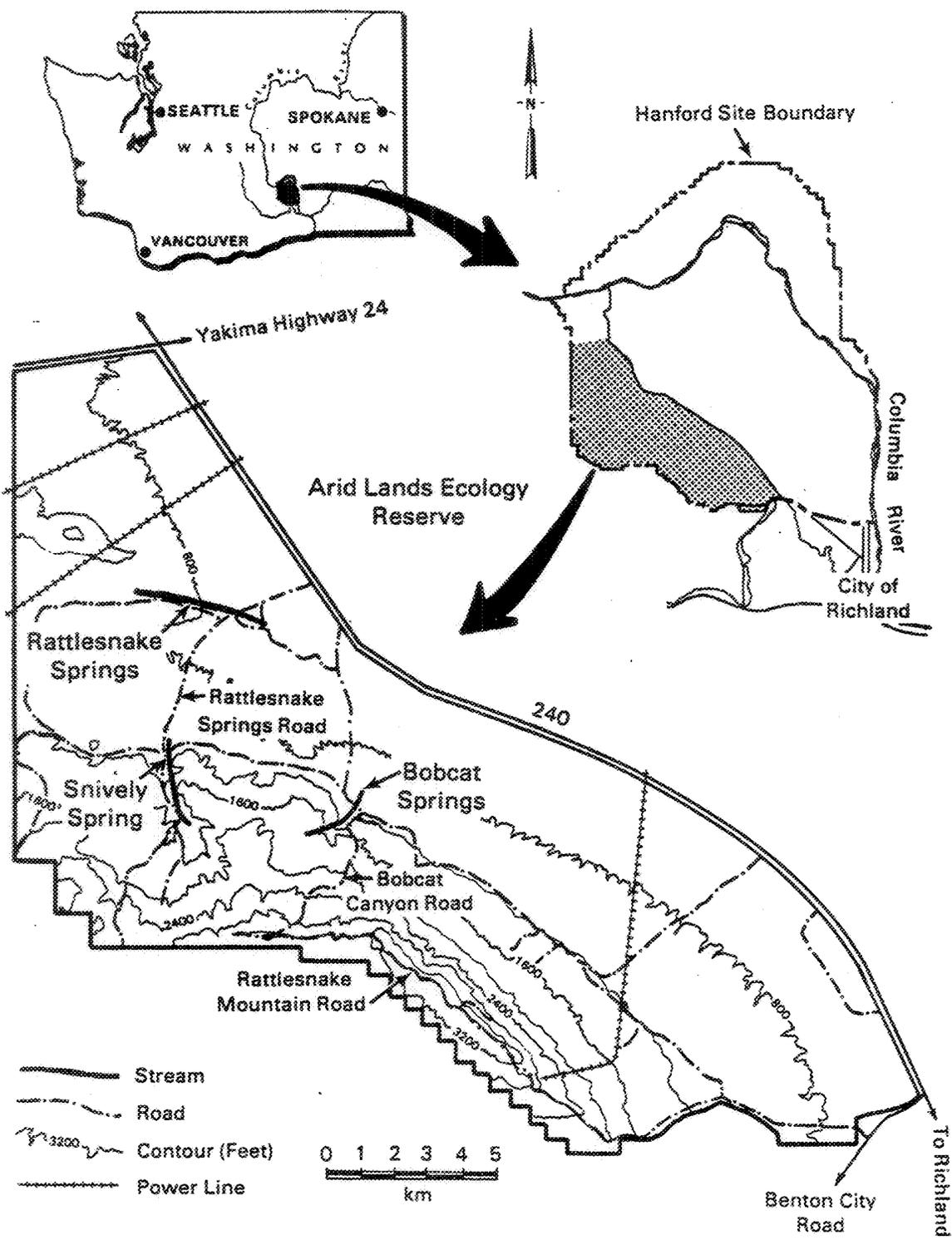
Spatial distribution of sources of drinking water affects temporal and spatial elk distribution (McCorquodale et al. 1986, DelGuidice and Rodiek 1984, Marcum 1975, Simmons 1974,

Lyon 1973, McCullough 1969). McCullough (1969) found that limited available water resulted in herd localization about a single water source in 1 herd of tule elk (C. e. nannodes). McCorquodale et al. (1986) reported that female elk living in an area of limited water sources showed seasonal differences in their use of springs. Nevertheless, these studies did not quantitatively determine actual water use and failed to establish causal links between available drinking water, water use, and animal behavior.

Objectives of this study were: 1) to compare elk water dynamics between spring (low environmental aridity) and summer (high environmental aridity), and 2) to determine availability of forage water to a herd of wild elk.

STUDY AREA

The study area was the Arid Lands Ecology (ALE) Reserve on the U.S. Department of Energy's Hanford Site in south-central Washington, where a herd of Rocky Mountain elk (C. e. nelsoni) have lived since 1972 (Rickard et al. 1977) (Fig. 1). Average annual precipitation amounts to 16.5 cm, most of which falls from November to March, whereas the summer months are hot and dry (Stone et al. 1983). There were 5 sources of drinking water on the study area.



METHODS

Vegetation moisture

Bluebunch wheatgrass (Agropyron spicatum), Sandberg bluegrass (Poa sandbergii), cheatgrass (Bromus tectorum), and sagebrush (Artemisia tridentata) were selected to represent seasonal moisture content of wild elk forage. Sandberg bluegrass and cheatgrass begin growth in autumn, mature in April, and are dry by May (Sauer and Uresk 1976). Plants of this nature, particularly cheatgrass and Sandberg bluegrass themselves, have constituted significant portions of the diet of ALE Reserve elk (McCorquodale 1985). Bluebunch wheatgrass begins growth in early spring and remains green through June. Sagebrush produces new leaves in April, sheds most of them in July or August, retaining some leaves year-round. Bluebunch wheatgrass, sagebrush, and similar plants were used less as elk forage.

Plants were sampled every 15 days from May to August in 1984 and from March to October in 1985 at 8 sites distributed between the lowest, middle and highest elevations of the ALE Reserve. Samples of the current year's growth from 3 separate plants for sagebrush and bluebunch wheatgrass or 3 from separate locations for cheatgrass and Sandberg bluegrass were collected at each site and were placed in separate plastic

bags. The vegetation was weighed, dried for 48 hours at 50 C, and then weighed again. Moisture content was determined as percent water by wet weight. Exposure to the air was kept to a minimum to avoid moisture loss (before drying) or moisture gain (after drying). The samples were averaged for each date for each site over both years.

Penned elk

Two captive adult female elk (WSU 1, WSU 2) were kept in a 1.4 hectare pen at the ALE Reserve. Water and food were supplied ad libitum. Food consisted of air-dry alfalfa and a pelleted mixture of 30% alfalfa, 20% corn, 20% oats, 18% soybean, 3.5% molasses, and 0.5% trace minerals and salts. Shade was provided, enabling the animals to behaviorally thermoregulate.

Water dynamics of penned elk

The tritiated water dilution technique was used to estimate fractional body water turnover and water volume in the penned elk. Water flux was estimated from water turnover and water volume (Knox et al. 1969, Nagy and Costa 1980). Tests were conducted from 12-20 April 1986 and from 8-30 July 1986. Each animal was immobilized with etorphine and a

pretrial blood sample was collected. Immediately following this sample, tritium was injected intramuscularly and the animal was released. A second sample of blood representing an equilibrated concentration of tritium in the body water was collected 24 h later. Subsequent samples were collected periodically until the test was concluded. All samples were collected between 0700 and 1000.

The procedure was changed for the July test for WSU 1 because it aberrantly reacted to etorphine. When a sample was needed, this animal was temporarily placed in a holding pen equipped with a urine collection system. While in the holding pen, WSU 1 was constantly observed and the time of urination recorded. WSU 1 was always released from this pen within 45 min. The collected urine was analyzed for tritium. Rubsamen et al. (1979) working on rabbits and Denny and Dawson (1975) using ruminant-like macropod marsupials found that urine and plasma were equal in tritium activity after equilibration. Thus, it was assumed that equilibrated tritium activity in elk blood and urine were also equivalent. Blood and urine samples were steam distilled and the distillate counted for tritium.

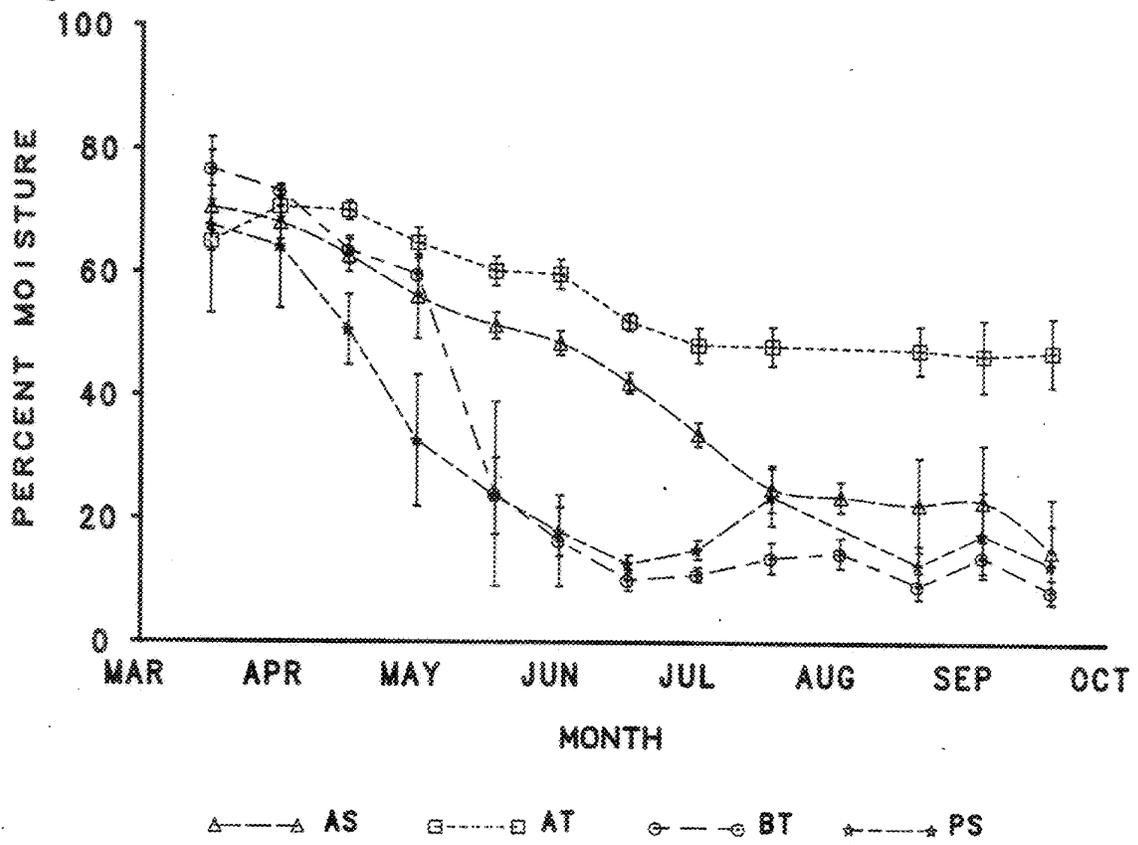
Water turnover, or fraction of the body water replaced over time, was calculated using least squares linear regression of the natural log of the tritium concentration versus the time since injection. Body water pool, was calculated by dividing the amount of tritium injected by the

projected tritium concentration at time 0. Daily water flux was estimated by multiplying the amount of body water by the fractional turnover constant (absolute value of the slope of the regression line) (Knox et al. 1969). Because food and water could not be denied for 24 hours in this study, the elk were allowed to eat and drink during the equilibration period. This may have resulted in an overestimation of the water pool and, consequently, the water flux (Nagy and Costa 1980). However, the fraction of turnover should not have been affected.

RESULTS and DISCUSSION

Vegetation moisture

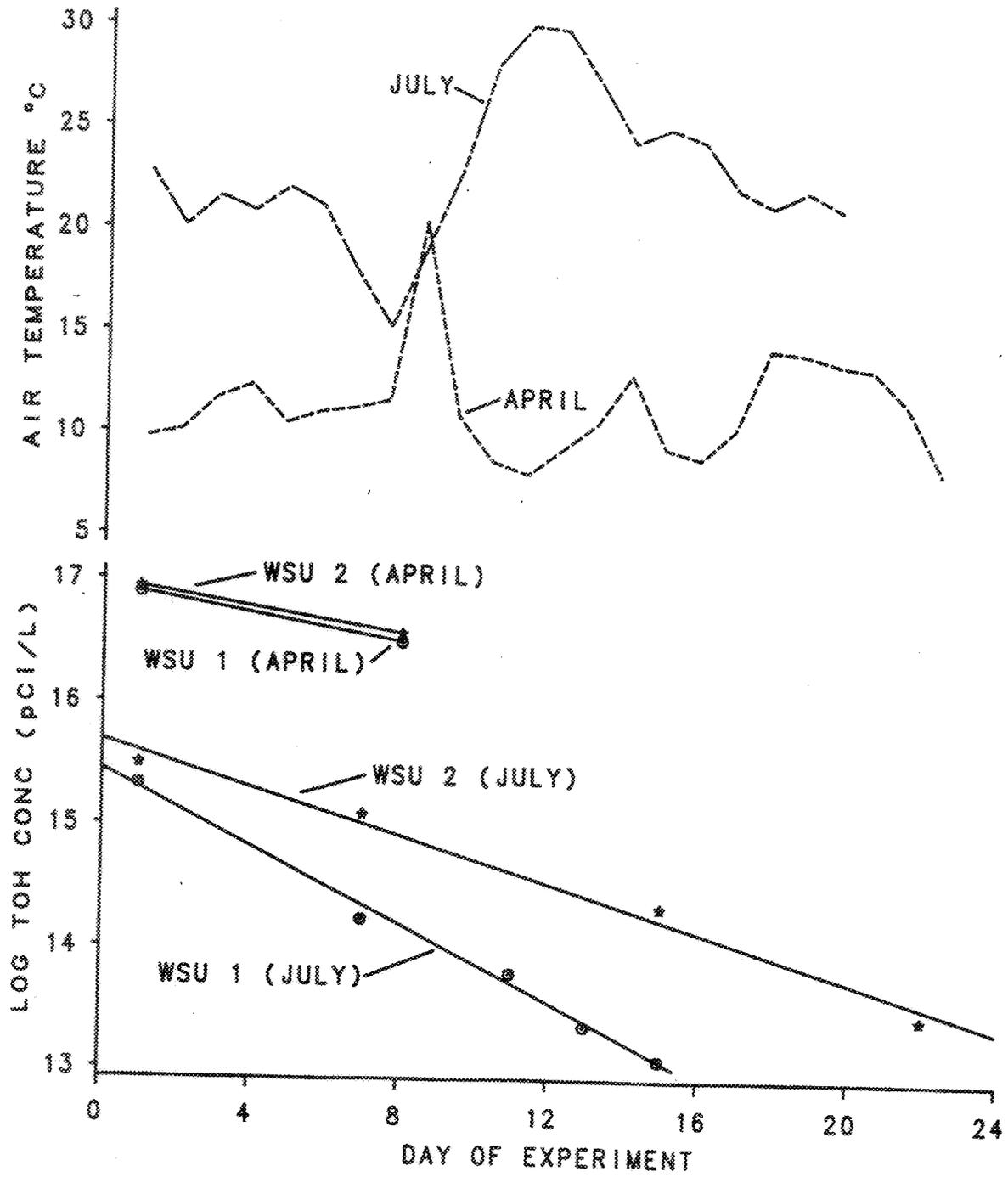
Moisture content of cheatgrass and Sandberg bluegrass decreased from a high of 75% in April to a low of 10% in early July (Fig. 2). Water content of bluebunch wheatgrass declined relatively constantly from 70% in April to 25% in early August. Water content of sagebrush declined from 70% in April to 50% in July. Elk eating forage with 70% moisture must ingest 3.3 kg of forage to obtain 1 kg of dry forage, receiving 2.3 kg of water in the process. Elk eating forage with 15% moisture need to consume only 1.2 kg to ingest 1 kg of dry forage, obtaining only 0.2 kg water in the process.



Consequently, elk could receive 13-times more water from their forage (on a dry weight basis) during spring than during summer.

Water dynamics

Rates of tritium dilution were greater during summer than during spring (Fig.3). The fractional water turnover constant increased from 0.055 (range = 0.053-0.057) in spring to 0.130 (range = 0.099-0.161) during summer. Body water percentage for both penned elk was 84% during spring and 80% during summer, but may be inflated due to possible overestimation of the body water pool. Average water flux in the 2 penned elk increased from 4.6 kg H₂O/(100 kg body weight)/day (range = 4.5-4.7) in spring to 10.6 kg H₂O/(100 kg body weight)/day (range = 8.4-12.8) in summer. The animals were not only exposed to a warmer and drier environment during summer, but they had also undergone seasonal pelage and physiological changes. Parker and Robbins (1984) found that cutaneous water loss was less when elk were in winter coats, probably a result of both a cessation of sweat gland activity and increased resistance to vapor diffusion provided by the thick winter pelage. Siebert and MacFarlane (1971) found fully hydrated camel (Camelus dromedarius) water flux increased 2-times from moderate to hot temperatures. MacFarlane and Howard (1972) reported a 3-fold



increase in water turnover in domestic sheep from winter to summer. Elk in more productive states (growing, lactating, etc) than the penned animals would have a greater flux than indicated in this study (Robbins 1983). Lactation increased water use by 44% in camels and sheep (MacFarlane and Howard 1972) and doubled water turnover in goats (Capra hircus) (Maltz and Shkolnik 1980).

This experiment was originally designed to be conducted on wild elk on ALE Reserve using an animal recapture system to collect body water samples. This approach would have offered the advantage of actually estimating the water flux in the population of wild elk and, therefore, would have allowed a more rigorous examination of the relationships between water fluxes in elk, forage water availability, and drinking water use. Unfortunately, equipment essential to the recapture system became unavailable and, consequently, the experiment had to be conducted on the penned animals. The author believes that data obtained from the penned animals may be used as an general index of the water dynamics of the wild animals, but may not be used in absolute comparisons.

CONCLUSIONS

Water flux increased 2-fold in 2 penned elk from spring to summer. Moisture content of cheatgrass and Sandberg

bluegrass (important forage species) decreased from 70% in April to 10% in July. Therefore water obtained in the forage could decrease from 2.3 kg H₂O/(kg dry forage consumed) in spring to 0.2 kg H₂O/(kg dry forage consumed) in summer.

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SECTION III
ENVIRONMENTAL EFFECTS ON ELK THERMOREGULATION

ENVIRONMENTAL EFFECTS ON ELK THERMOREGULATION

INTRODUCTION

Numerous studies have been conducted on thermoregulation of African ungulates (Yousef 1976, Robertshaw 1976), but there have been few studies that specifically addressed physiological thermoregulation in North American wild ungulates. Parker and Robbins (1984) investigated thermoregulation in elk, Moen and Jacobsen (1975) in white-tailed deer (Odocoileus virginianus), Zervanos and Hadley (1973) in collared peccary (Tayassu tajacu), and Yousef and Dill (1969) in burro (Equus asinus). Most, if not all, studies on wild ungulate thermoregulation have used tethered, corralled, or semi-tame animals. Few studies have been conducted with free-roaming animals in natural surroundings. Zervanos and Hadley's (1973) work on peccary confined in a large enclosure approached a natural situation. They collected data remotely with capsulated temperature-sensitive radio transmitters and allowed their subjects to determine their own means of thermoregulation.

Consideration of freedom of movement and behavioral thermoregulation is important when studying thermoregulation of wild animals. Behavioral thermoregulation can be as important as physiological thermoregulation, and in extreme

environments can be necessary for survival (Taylor and Lyman 1967, Taylor 1969, Finch 1972, Zervanos and Hadley 1973). It is also advantageous for animals to use behavioral thermoregulation in order to conserve energy and water, both of which can be in short supply. In fact, the authors of many of the studies cited concluded that conservation of water was the driving force behind their subjects' thermoregulatory strategies. A final reason for studying thermoregulation in free-ranging animals is that behavioral and physiological thermoregulation could be used together in a compensatory way. Belovsky (1981) modeled behavioral and physiological thermoregulation in moose (Alces alces) and Zahn (1985) modeled thermoregulation in elk. Their thermoregulation models were based only on behavioral observations and environmental conditions, and not on observations of body temperatures.

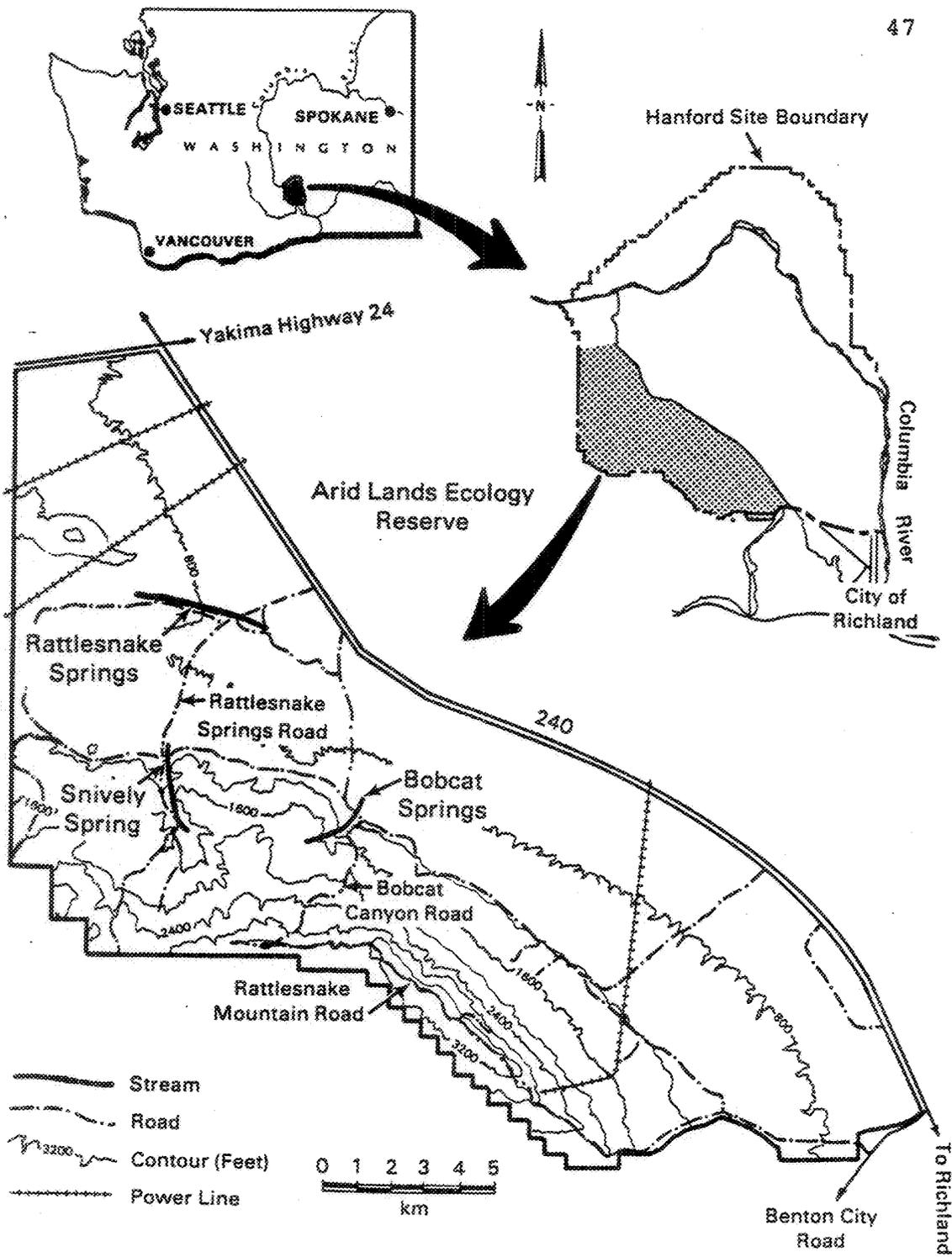
There is a need to monitor both physiological and behavioral thermoregulation in free ranging animals in order to observe interrelationships between these two strategies of thermoregulation. The objectives of this study were to: 1) determine the relationships between ambient, body, and subcutaneous temperatures in wild, free-ranging elk, and 2) evaluate the relative importance of behavioral and physiological thermoregulation.

STUDY AREA

The study was conducted on the Arid Lands Ecology (ALE) Reserve, a 330 km² portion of the U.S. Department of Energy's Hanford Reservation in south-central Washington (Fig. 1). Permanent springs occur at Rattlesnake Springs, Snively Springs, and Bobcat Springs. Sagebrush stands distributed in scattered patches (McCorquodale et al. 1986) offered limited shade. Summer diurnal air temperature fluctuations can exceed 20 °C and temperatures approach 45 °C, whereas winter diurnal temperatures are relatively stable, often vary only a few degrees °C. Winter minimum temperatures seldom fall below -10 °C (Stone et al. 1983).

METHODS

Five wild elk, 3 males, 2 females, were captured (Petron et al. 1987). Two of the males were adults (# 160, # 180) and 1 was a yearling (# 200). One of the females was a yearling (# 825) and the other a lactating adult (# 765). Male 160 was captured in December, 1983, male 180 in June, 1984, and male 200 and females 825 and 765 in June, 1985. The animals were immobilized with etorphine for approximately 2.5 hours, during which time each was fitted with a radiotelemetry collar (Cedar Creek Biotelemetry Lab, Bethel, Minn.; Wyoming Biotelemetry,



Inc., Longmont, Colorado) and implanted with 2 cylindrically shaped temperature-sensitive transmitters (Telonics, Mesa, Ariz.). One temperature transmitter (about 4 x 15 cm, Model # IMP/400/EX) was surgically inserted into the peritoneum through an incision in the paralumbar fossa. The other transmitter (about 2 x 6 cm, Model IMP/300/L) was placed subcutaneously about 3 cm off the midline of the withers by making a small incision in the skin and creating a small pocket in the connective tissue separating the skin and muscle.

Implants

Temperature implants consisted of a pulsing fm transmitter with a thermistor inserted into the circuitry so that the pulse rate reflected the temperature of the transmitting system. Each transmitter, battery, and antenna was encapsulated in a biologically-inert coating of physiological embedding wax and resin. The implants were calibrated versus a U.S. National Bureau of Standards certified mercury thermometer by wrapping them in a layer of cheesecloth and suspending them into a circulating water bath. Peritoneum transmitters were calibrated between 36-41 °C at 0.4 °C intervals and subcutaneous transmitters between 32-42 °C at 0.5 °C intervals. Body implants were immersed at each

temperature setting for a minimum of 30 min and the subcutaneous transmitters for a minimum of 20 min. Regardless of the elapsed time, the pulse rates had to be constant for 5 minutes before they were recorded. Pulse rates were timed using pulse timers accurate to ± 1 millisecond (Telonics, Mesa, Ariz). The order of temperature intervals was randomly determined to minimize autocorrelation in the residuals of the calibration curves (Neter et al. 1983). Least squares linear regression was employed on data from a minimum of 2 such temperature runs to calculate the final calibration curve for each transmitter. All body transmitters had 99% prediction confidence limits of ± 0.2 °C, and all subcutaneous transmitters had 99% prediction confidence limits of ± 0.4 °C.

Data collection

Pulse rates were collected using standard telemetry receivers (Cedar Creek Biotelemetry Lab, Bethel, Minn; Telonics, Mesa, Ariz) and pulse timers. Data were collected manually for all periods of the year by locating the animals when the opportunity existed and timing the pulse rates of the implants. In addition, manual data were collected every 15, 30, or 60 minutes during planned 24 hour sessions during winter and summer. Behaviors recorded were bedding, feeding, walking, running, and standing. Solar exposure and location

were also recorded. General locations were used for determination of movements and specific positions were used to determine micro-habitat selection.

Pulse rates were also collected automatically for periods of variable duration. The automatic collection system has been described by Petron et al. (1987), and consisted of a micrologger (Campbell Scientific, Inc., Logan, Utah, Model CR21) that automatically recorded data from the pulse timers (Telonics, Models TDP1 and TDP2) and entered them on a cassette recorder. Data were later loaded from the cassette into a computer through an interface. Pulse rates were recorded every 2 minutes with this system. Each pulse timer had its own data conversion curve with the micrologger, and these were checked each time the equipment was visited.

Meteorological Monitoring

Meteorological monitoring consisted of short wave solar radiation using a silicon photodiode (Model LI-200s, LI-COR, Lincoln, Nebraska), wind speed using a 3 cup anemometer (Model MET-ONE 014A, Campbell Scientific, Inc.), air temperature and relative humidity using a combination thermistor and polystyrene chip (Model 201, Campbell Scientific, Inc.), and soil temperature using a thermistor (Model 101, Campbell Scientific, Inc.). Soil temperature probes were positioned 1

cm below the surface in solar exposed soil in both 1984 and 1985 and in soil shaded by sagebrush in 1985 only. All other sensors were mounted 0.75 m above the ground. All temperature sensors were calibrated in the laboratory versus a U.S. National Bureau of Standard certified mercury thermometer. Pyranometers and anemometers were calibrated by the manufacturer, and relative humidity sensors were performance checked against a wet-dry bulb sling psychrometer.

In 1984 a set of 3 meteorological stations were moved weekly to 1 of 9 different draws in order to evaluate variability within draws (Fig 1). One of the stations was positioned in the bottom, a second halfway up the side, and a third on the crest in order to evaluate microclimatic differences within a draw. Data were averaged for comparisons to elk temperature after it was determined the differences were minimal. In 1985, 1 station was positioned in a single draw from March to November and was not moved. Meteorological stations were removed before the onset of winter because the recording system would not function at freezing temperatures. Meteorological data for winter 1983-84 were obtained from the Hanford meteorological station located about 10 km away. Meteorological data for the winters of 1984-85 and 1985-86 were taken from another ongoing project that had the same monitoring system (though protected from freezing temperatures). The sensors were mounted 2 meters above the

ground within 200 m of the 1985 summer position.

Operative Temperature

Meteorological data were used as inputs into an environmental index called operative temperature (T_e) (Bakken 1980, 1981). This index incorporates the thermal effect of solar radiation, long wave radiation, ambient temperature, and wind speed, and is defined as $T_e = T_a + R_e/PC_p(RABS-LWLOST)$, where T_e is the operative temperature in °C, T_a is ambient temperature in °C, R_e is a parallel resistance between radiative and sensible resistances in sec/m, PC_p is volumetric heat capacity of air in J/m^3K , RABS is the total of short wave and long wave absorbed radiation fluxes in $watts/m^2$, and LWLOST is the total long wave radiative energy reradiated by the animal in $watts/m^2$. Sensible and radiative resistances were calculated according to Campbell (1977). Radiative resistance was $R_r = PC_p/4A_1QT_k^3$, where A_1 is long wave emissivity of the surface, Q is the Stephan-Boltzman constant, and T_k is the ambient temperature in K. Sensible resistance is a parallel resistance of forced and free convection and is defined by Robinson et al. (1976). Forced convection resistance is $R_{fo} = 217(d/u)^{0.5}$ where d is the characteristic dimension of the elk (Parker 1983) and u is the wind speed in m/sec. Free convection is $R_{fr} = 820(d/(T_s-T_a))^{0.25}$, where T_s

is the surface temperature (Monteith 1973). Forced convection dominates when wind is present and free convection dominates when wind is absent (Robinson et al. 1976). Although incorporating the effects of convection, T_e does not incorporate wind chill, and thus may not allow direct comparisons between environments with significantly different wind speeds (Bakken 1980). But, most of the observations collected in this study were during conditions of relatively low wind speeds, and therefore errors from not incorporating wind chill were probably negligible (Parker and Robbins 1984).

Characteristic dimensions, used in the sensible heat resistance, were calculated as the average of the length and diameter of the animal's trunk (Parker and Robbins 1984). Average shortwave absorptivities (A_s) for summer (0.85) and winter (0.79) pelages were calculated from reflectances measured on hide samples taken from 2 male Hanford elk, one in winter pelage and the other in summer pelage. Albedo of the ground was assumed to be 0.13 (Black and Mack 1986). Animals were assumed to be orientated perpendicular to the sun, because it was not possible to accurately estimate angles of incidence in the field through binoculars. Consequently, this study's values for T_e might be considered to be maximal. Long wave radiation fluxes were calculated using the Stephan-Boltzman equation (Campbell 1977). Animal emissivities and longwave absorptivities were assumed to be

0.98, which was also used by Parker and Robbins (1984). Terrestrial emissivity was assumed to be 0.99 (Campbell 1977). Air emissivities were calculated using the equations given by Campbell (1977).

Analysis

Body temperatures: Temperature data were processed with a FORTRAN program that converted the pulse rates into temperatures and checked for anomalous data. Data were considered anomalous if they did not fall within physiologically feasible temperature ranges. Hourly means of the data were used in analysis to avoid unequal weighting between hours, because data automatically collected generated 30 observations during a hour as compared to the 1 or 2 observations per hour for manually recorded data.

Temperatures for each animal were summarized for all days during the period when the elk had summer coats (May 20 through August 31), and when they had winter coats (September 1 through May 19). Separate analyses were conducted on peritoneal temperatures (T_b) from 0900-1400 and from 1900-0500 to check for possible effects of endogenous cycles in T_b on the results (Section I). These two periods were selected because they represent times of minimal change in T_b attributable to daily rhythms (Section I). Once it was

established that time of day was not a factor in relationships between T_b and environment, data from the complete day were used in analysis.

Relationship between subcutaneous and skin temperatures:

Subcutaneous temperature (T_{su}) is not the temperature of the exchange surface of the animal, so caution is warranted when using it. A discussion concerning T_{su} requires an investigation into the relationship between T_{su} and skin surface temperature (T_{sk}), which is the actual heat exchange surface during summer. According to sensible heat transfer theory, heat flux through the integument is a function of the temperature gradient between the subcutaneous layer and skin surface, the resistance of the system, and the volumetric heat capacity of the integument. This function can be written as:

$$H_{in} = P_{in}C_{in}(T_{su} - T_{sk})/R_{in} \quad (1)$$

where H_{in} is the heat flux across the integument to the skin surface (positive flux indicates flow toward the surface), $P_{in}C_{in}$ is the volumetric specific heat of the integument, and R_{in} is the the average tissue heat transfer resistance (Campbell 1977). R_{in} is not static, but rather, depends on both physical properties of the integument and physiological parameters such as blood flow. This formula can be rewritten in the form:

$$T_{sk} = T_{su} - H_{in}R_{in}/(P_{in}C_{in}) \quad (2)$$

which is a description of a straight line, where the second term equals the difference between T_{sk} and T_{su} . When either H_{in} or R_{in} equals 0, then $T_{sk} = T_{su}$.

Unless both T_{su} and T_{sk} are measured simultaneously, nothing is learned about the relationship between them, because H_{in} and R_{in} are seldom known. It would be of value if this relationship could be expressed in some easily measured comparable parameter. T_e is a logical choice because it allows direct comparisons between different animals and environments, as it incorporates the total thermal consequences of the environment and incorporates animal size into these consequences. T_e is also advantageous because it appears in the equation for heat flux from the skin surface to the environment:

$$H_{sk-e} = (PC_p/R_e)(T_{sk} - T_e) \quad (3)$$

where H_{sk-e} is the heat flux from the skin surface to the environment. By solving equation 3 for T_{sk} :

$$T_{sk} = T_e + H_{sk-e}R_e/PC_p \quad (4)$$

Substituting equation 2 for T_{sk} into equation 4 gives:

$$T_{su} - H_{in}R_{in}/(P_{in}C_{in}) = T_e + H_{sk-e}R_e/PC_p \quad (5)$$

or by solving for T_{su} :

$$T_{su} = T_e + H_{sk-e}R_e/PC_p + H_{in}R_{in}/(P_{in}C_{in}) \quad (6)$$

Equation 6 shows that T_{su} is also a function of T_e and will approach T_e as the two fluxes or two resistances approach

8. Equations 4 and 6 show that T_{su} and T_{sk} are both functions of T_e , and therefore T_e can be used as a common denominator when comparing the two. It should be noted that this relationship involves only sensible heat exchange, and would not be valid at temperatures where there is significant latent heat loss.

Behavior: Only observations of telemetered animals were used to determine habitat preference and behavioral thermoregulation. Observations were required to be separated by a movement of the subject at least temporarily into a different habitat type, which ensured that each observation represented an independent choice. Only bedded elk were used in analysis because it was not possible for standing elk to be in the shade cast by ALE Reserve vegetation. It was important that the opportunity for behavioral thermoregulation was present and thus the animal had to make a choice. Chi square analysis was used for tests of significance.

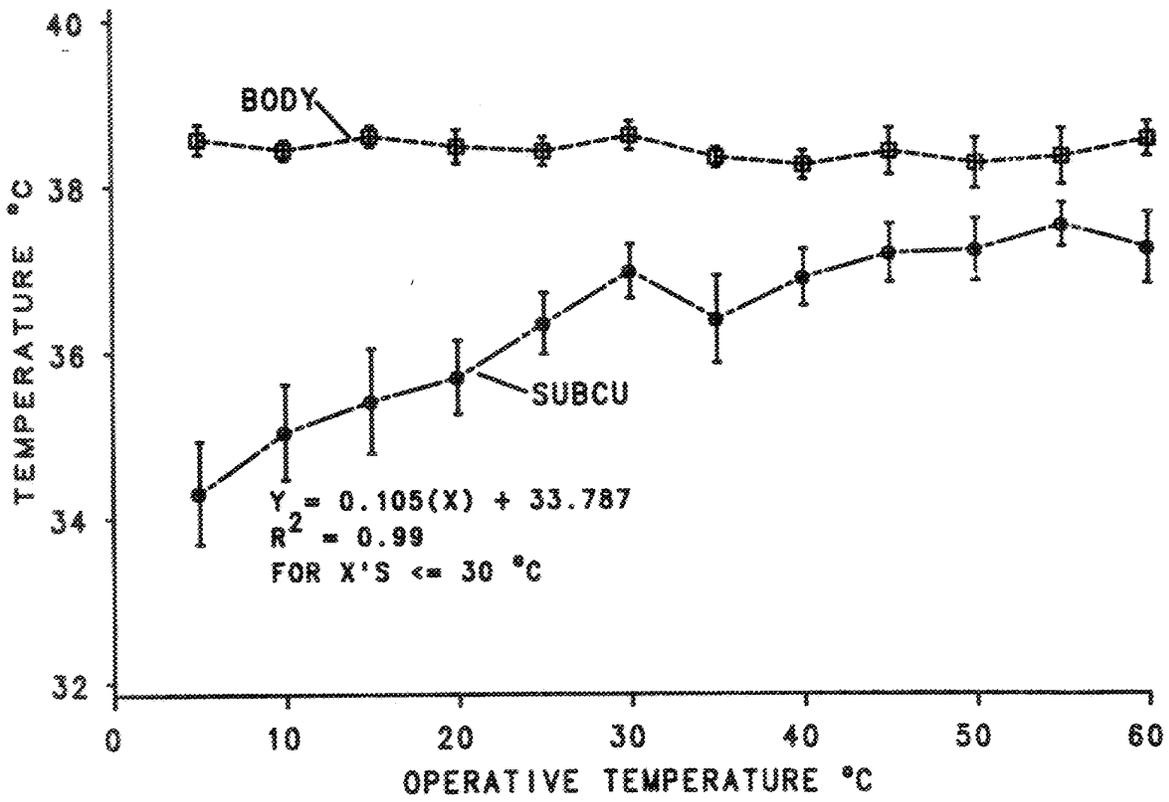
Elk use of a particular habitat for bedding will depend upon the habitat's ability to provide thermal cover, concealment, or a combination of both. To determine which was the case required first a determination of what constituted preferred bedding habitat and second a determination of why the habitats were preferred. Sagebrush use was based upon whether or not a sagebrush shrub was within the subject's

vision and within 100 m of the animal. To test the hypothesis that sagebrush was used for thermoregulation required observing not only whether sagebrush was a preferred habitat, but whether or not the animals positioned themselves in the shade, since they could have been bedded between shrubs and receiving full sun exposure. Shade use was evaluated for those animals bedded in sagebrush, because it was virtually impossible for elk bedded in other habitats to position themselves in the shade.

RESULTS AND DISCUSSION

Subcutaneous Temperature

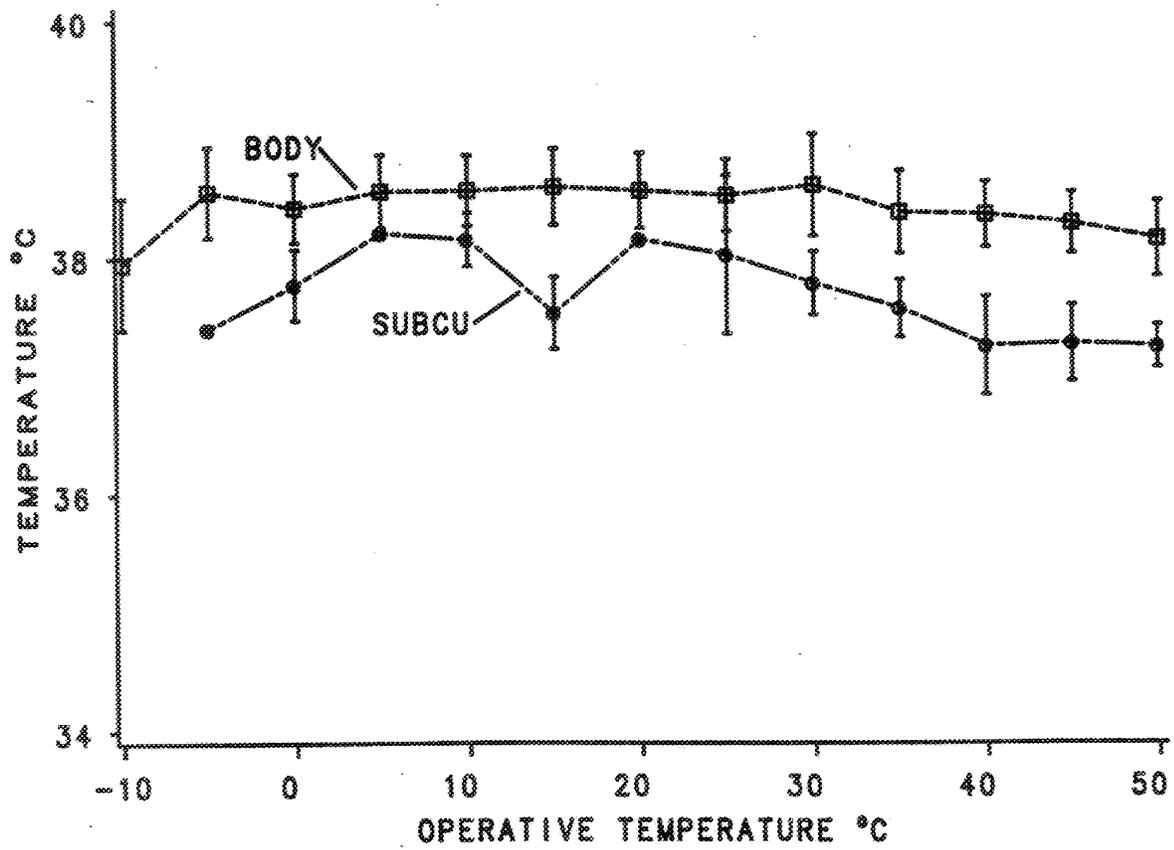
Summer: Summer elk T_{su} rose linearly with T_e up to a T_e of 30 °C, where it flattened out and only increased slightly thereafter (Fig. 2). At 30 °C, different thermoregulatory mechanisms must begin to operate causing a change in the relationship. This was the same temperature at which Parker and Robbins (1984) observed the onset of sweating. Therefore, the animals probably were keeping their skin cool with increased cutaneous evaporation. Parker and Robbins (1984) felt that chilling of skin at high evaporation rates was the cause for the poor correlation they observed between T_{sk} and cutaneous water loss at high temperatures. Note that through



sweating, T_{su} was always maintained below T_b , which indicated the direction of total heat flow was always toward the environment. Up to a T_e of 30°C , thermoregulation must have been mostly passive, with heat lost through reradiation, conduction, convection, and evaporation from the respiratory tract and skin (nonsweating diffusion).

The linear increase in T_{su} (and corresponding increase in T_{sk}) had considerable physiological ramifications. Increased T_{sk} 's reduced conductive and convective heat losses to the environment, but increased heat loss from thermal reradiation. In fact the rise in T_{su} from 34.3 to 37.0 , converted into 28.3 to 35.0°C T_{sk} using equation 7 (below), resulted in a 9% increase in heat lost through reradiation.

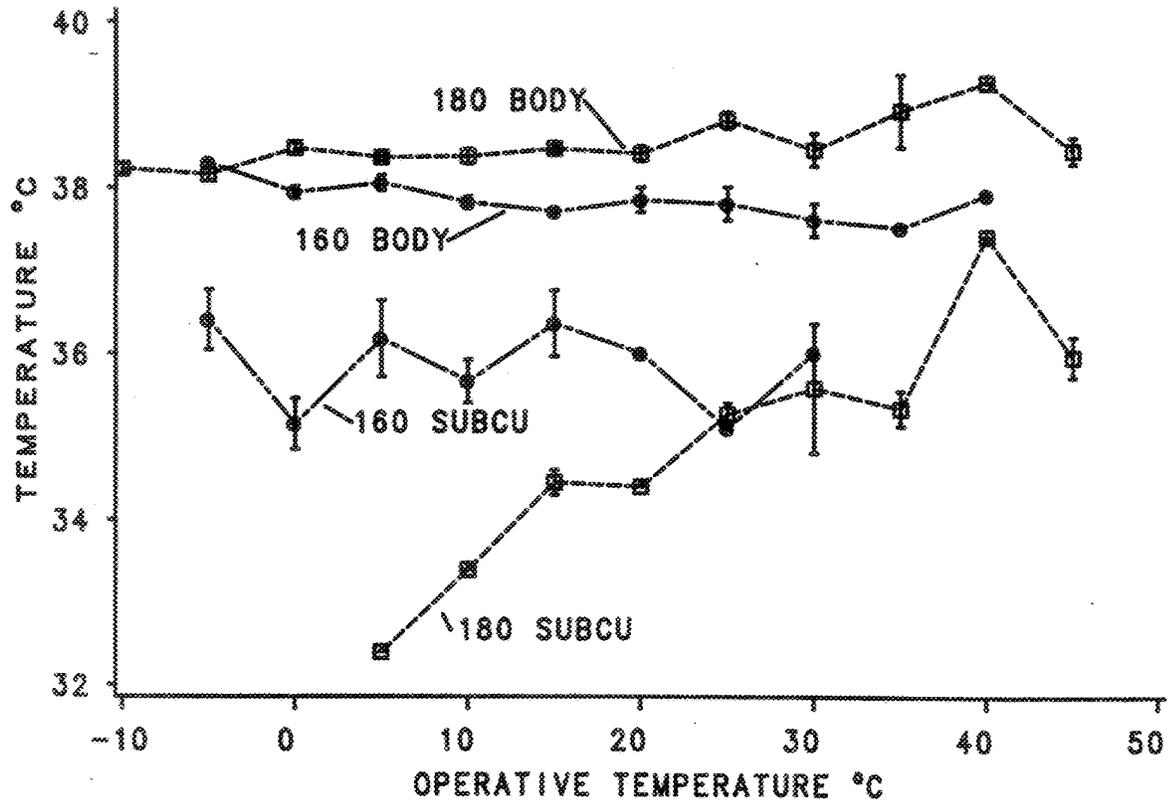
Winter: During winter there was no correlation between T_{su} and T_e in the nonbreeding bull and cows, and T_{su} was maintained about 1°C below T_b (Fig. 3). These two observations can be attributed to the increased insulation of the winter coat and subcutaneous fat layers. Parker and Robbins (1984) felt increased insulation caused the weak relationship they observed between winter environmental temperatures and T_{sk} in elk and mule deer. The added insulatory value of subcutaneous fat between the skin surface and the sensor in this study severed any dependence of T_{su} on the environment. Consequently, T_{su} behaved as a



heterothermic core temperature during winter, differing from the peritoneal temperature, by about 1°C . T_{SU} remained lower than T_{b} because of its proximity to the heat exchange surface of the pelt, with the direction of heat flow toward the surface. The decrease in T_{SU} at higher T_{e} 's resulted because those data were recorded during late April and early May, and at that time of the year the insulative value of the coat was probably diminished.

The two bulls participating in rutting (160, 180) showed a different pattern than the other individuals and also showed differences between each other (Fig. 4). Both animals maintained T_{SU} more than 2°C below T_{b} compared to the 1°C difference for the nonbreeding bull and cows. This could have been a result of individual variation or a result of less insulation which allowed greater heat loss. Maintenance of a higher T_{SU} might have been too energetically costly. Poorer insulation could have been a result of fat reserves depleted by rutting, which is an energy exhausting activity (McCullough 1969, Bubenik 1982). In fact, Bubenik (1982) reported that he used whether or not snow melted on the back of an animal as an index of condition. Melting snow indicated significant heat loss to the environment (poor insulation), and therefore, poor pelage and little subcutaneous fat.

The flat line for 160 (Fig 4) shows that some effective insulation was still present, resulting in an independence



from T_e . In contrast to 160, 180 showed ineffective insulation resulting in a linear relationship between T_{SU} and T_e very similar to the summer relation, but with a steeper slope. This difference could be a result of when the data were collected. T_{SU} data for all the animals except 180 were collected throughout the winter and few observations were collected during the rut. Male 180 winter T_{SU} data were only collected in September, because the implant prematurely failed. Thus, it was possible that the data collected on 180 for winter pelage was not actually representative of winter pelage.

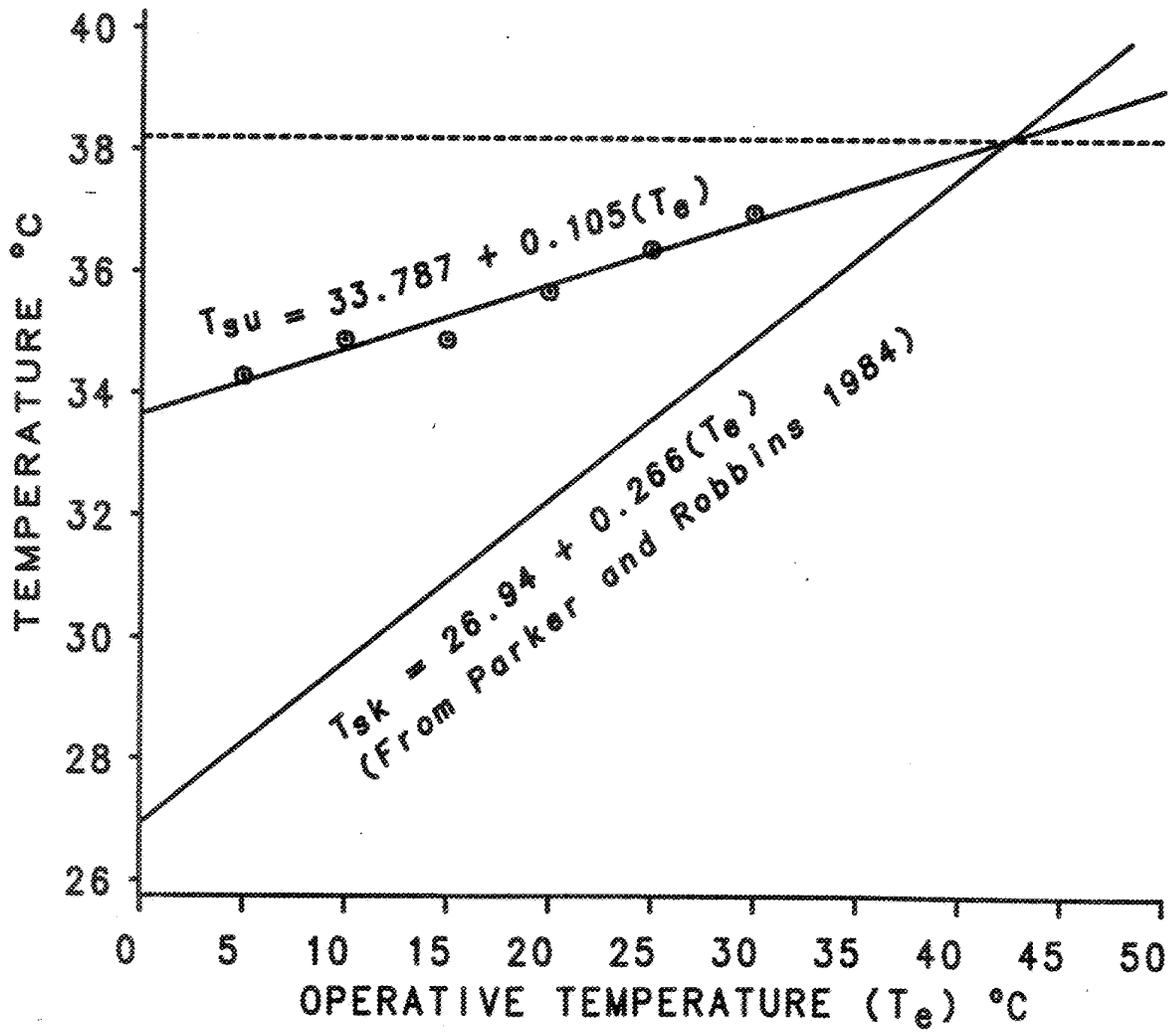
Relationship between subcutaneous and skin temperatures:

Assuming that ALE Reserve elk and Parker and Robbins' (1984) elk responded physiologically the same to environmental conditions, then data obtained in the 2 studies should be comparable. Equation 2 can be empirically evaluated by regressing Parker and Robbins (1984) T_{sk} 's versus T_{SU} for similar T_e 's. The resulting equation was:

$$T_{sk} = 2.52T_{SU} - 58.17 \quad (R^2 = 0.99, n = 6) \quad (7)$$

The significance of this relationship validated comparisons based upon T_e .

Parker and Robbins (1984) found the following relationship between T_{sk} and T_e : $T_{sk} = 26.94 + 0.266T_e$ ($R^2 = 0.81$), which was compared to this study's equation



$T_{SU} = 33.8 + 0.1T_e$ ($R^2 = 0.99$, $n = 6$) in Fig. 5. Data at T_e 's 30°C or lower were only used to ensure that there was minimal latent heat exchange. The intersection of the lines in Fig. 5., the point $T_{sk} = T_{SU}$, indicates the skin and operative temperatures at which the heat flux through the integument (H_{in} in equations 2 and 6) equaled 0. The temperature at this point, $T_{sk} = T_{SU} = 38.2^\circ\text{C}$, was very close to the average T_b 's of 38.6 and 38.4 found by Parker and Robbins (1984) and this study, respectively. Logically, when skin surface temperature equaled core temperature, T_{SU} , which lies between them, also must have equaled core temperature, and $H_{sk} = 0$ in equation 2.

Likewise, the intersection $T_{SU} = T_{sk}$ denotes the T_e at which the heat flux changed direction or the point where $H_{sk-e} = 0$ (equation 6). At T_e 's above about 44°C the heat flux would have been negative and the animal would have been gaining sensible heat from the environment. Consequently at T_e 's above 44°C , elk would have to sweat to lose heat. This T_e was above the isotropic temperature of 38.2 predicted by equation 6 because of behavioral thermoregulation and latent heat loss from evaporation of water which passively diffused through the integument to the skin surface. Also, these T_{SU} 's were for only 1 location on the animal, the back, and admittedly represented the warmest area of the animal. Total heat balance of the animal depended upon heat exchange from

the total surface. Therefore, the fact that the heat flux was toward the animal at this location did not necessarily indicate a heat gain for the entire animal, since considerable regions of the body may have been shaded or in contact with the substrate, and consequently, operating under a different heat exchange regimen.

Body temperature.

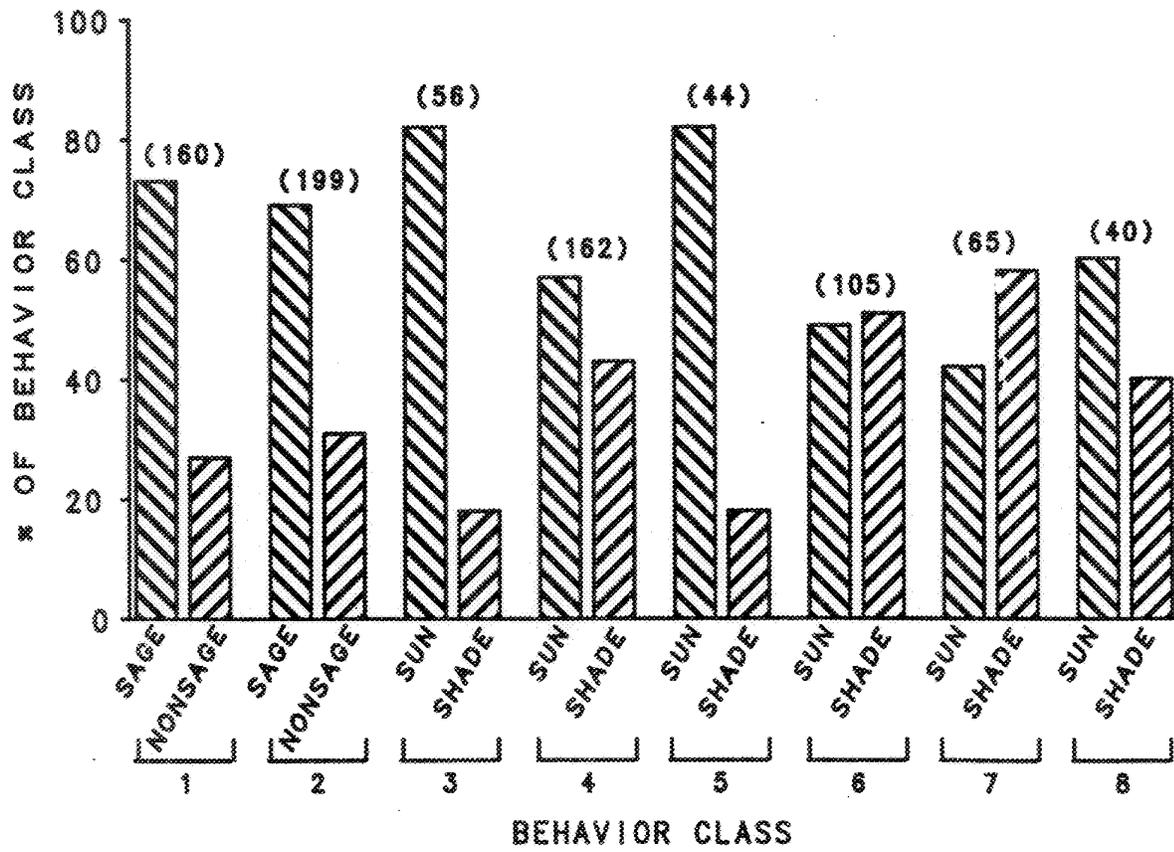
No trend was apparent between T_b and T_e during summer (Fig. 4) or winter (Fig. 5). The time of day when the data were collected also had no effect on the relationship, although T_b was consistently higher at night due to a diurnal physiological rhythm not related to environmental temperature (Section I). Thermal loading, the depression of T_b during cool parts of the day and the elevation of T_b during the warm parts of the day, was not apparent. ALE Reserve elk may have not employed thermal loading because it is often a water conservation strategy (Schmidt-Nielsen et al. 1957, Taylor and Lyman 1967, Taylor 1969, Zervanos and Hadley 1973) and they had no immediate physiological need to conserve water. ALE Reserve elk, although requiring considerable water in the summer (Section II), had an adequate supply of water (Fig. 1).

Elk, in general, also may not employ thermal loading because of their evolutionary history. Elk ancestors evolved

in cold temperate regions of Eurasia where water was plentiful (McCullough 1969, Bryant and Maser 1982, Geist 1982). Elk came to North America across the Bering Land Bridge, spread south in front of the leading edge of the glaciers (Bryant and Maser 1983), and in doing so, always had an abundance of drinking water. They were only exposed to regions of limited water supply relatively late in their evolutionary history. This suggests that elk did not develop water conservation strategies because their habitat over most of their evolutionary history was replete with water.

Behavioral thermoregulation

ALE Reserve elk undoubtedly operated under a multitude of thermoregulatory strategies, one of which could have been behavioral thermoregulation. Summer thermal cover on the ALE Reserve differed from the usual concept of thermal cover for elk because there was little available tree canopy. Sagebrush was the only ALE Reserve plant that was tall enough and far enough from service roads to be used for thermal cover. Elk bedded in sagebrush areas more than areas where grass dominated during both winter (73%, $\chi^2 = 34.2$, $p < 0.05$) and summer (69%, $\chi^2 = 28.3$, $p < 0.05$), but sagebrush use was not different between winter and summer ($\chi^2 = 1.57$, $p > 0.25$) (Fig. 6). This use was higher than the 44% found by



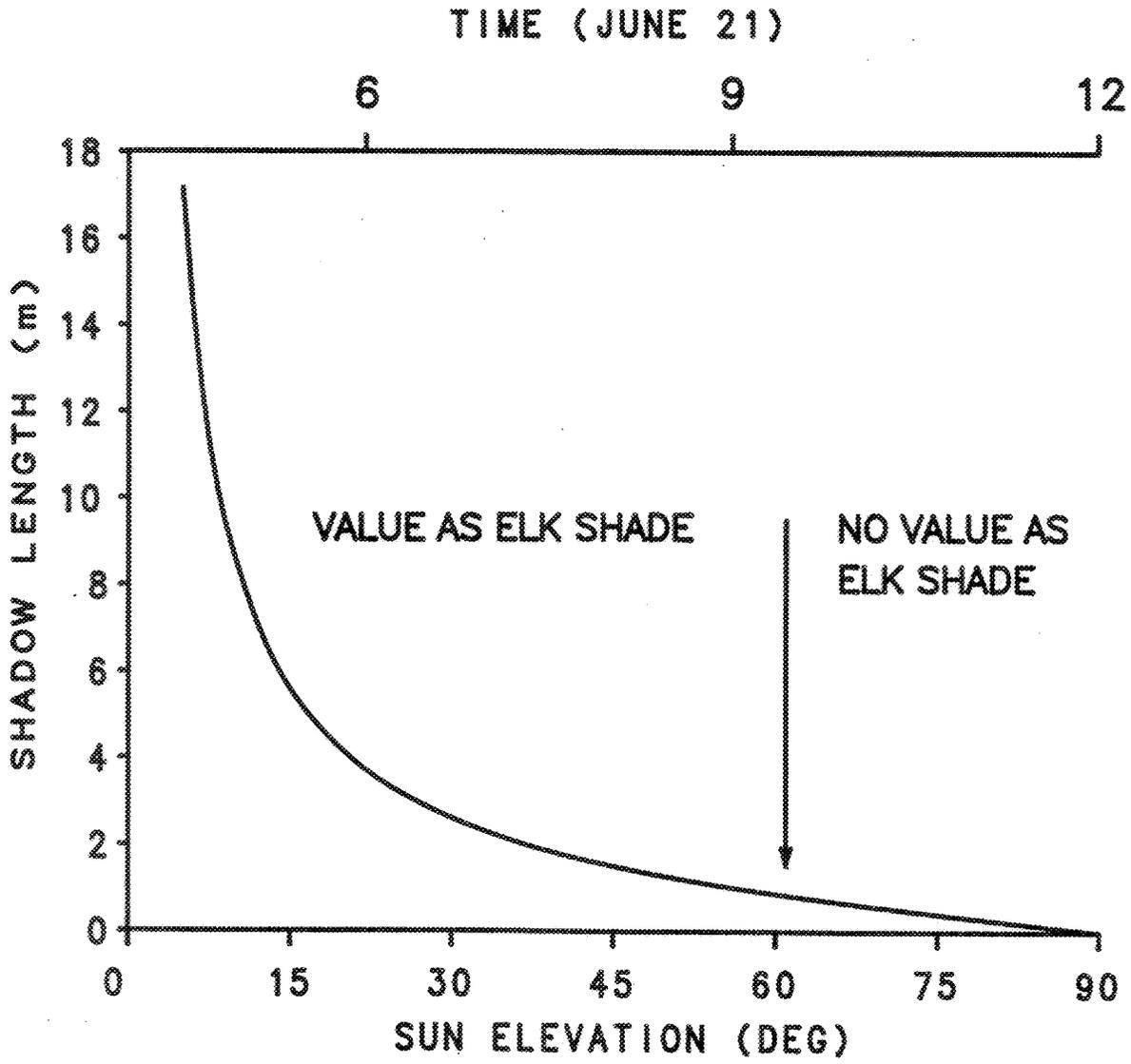
McCorquodale et al. (1986) because they included all elk activities in their estimate. Sagebrush use was significantly greater (winter $\chi^2 = 766$, summer $\chi^2 = 708$, $p < 0.05$) than would be expected from its 10% availability (from McCorquodale 1985), indicating that elk preferred sagebrush areas for bedding habitat.

Elk could have used sagebrush for either concealment, thermal cover, or both. Sagebrush offered concealment year-round. During winter sagebrush provided protection from the wind and during summer it supplied shielding from solar radiation. The hypothesis that elk bedded in sagebrush stands positioned themselves in the shade more frequently during the summer than during the winter was supported by field observations. Bedded elk positioned themselves in the shade of a shrub more frequently during summer than during winter ($\chi^2 = 15.3$, $p < 0.05$). Positioning in the sun in winter allowed thermal gain from solar radiation, whereas in the summer it was avoided.

Yet, why did elk bedded in sagebrush during summer position themselves in shade only about 50% of the time rather than all of the time? One explanation is that elk behavior was the expression of an optimization process which integrated thermal, energetic, water, and social considerations (Geist 1982), and thermal considerations were not always the most important of these. Another possible explanation is the

diminished availability of potentially shaded bed sites. The number of potentially shaded beds was considerably less than the number of potentially sunny beds. Therefore, 50% bedding in the shade suggests attempted behavioral thermoregulation. In addition, available shade was further limited during midday (Fig. 7). When the sun angle was above 60 degrees, shade from a 1.5 m vertical sagebrush shrub was no longer available to the animals because the shadow was underneath the bush. Despite this difficulty, ALE Reserve elk still managed to bed in shade about 50% of the time at midday during summer (Fig. 6). This was significant behavioral selection considering that at that time of day shade was at a premium. To bed this frequently in the shade during midday, elk would have had to search for special places such as taller sagebrush shrubs, leaning shrubs, depressions next to shrubs, indicating the preference for behavioral thermoregulation. Zahn (1985) also found that elk living in areas replete with water behaviorally thermoregulated on clear warm days during summer.

Because ALE Reserve elk frequently did not use thermal cover, other strategies of thermoregulation must have compensated. The facts that body temperatures did not increase in hot weather and that elk used twice the amount of water during summer than during spring (Section II) suggest that the elk compensated for the lack of thermal cover with increased latent heat loss through sweating. It should be



noted that these experiments were conducted on animals with sufficient water supply and that different results might be obtained from animals experiencing depleted water supplies.

CONCLUSIONS

Summer elk T_{SU} rose linearly with T_e up to $T_e = 30$. Above this temperature T_{SU} was constant at about 1°C below T_b , indicating that latent heat exchange became important. Winter T_{SU} differed from summer temperatures and differed between breeding bulls and nonbreeding bulls and cows. Winter T_{SU} was not correlated to T_e indicating the presence of efficient insulation. Winter T_{SU} behaved as a heterothermic core temperature and was maintained about 1°C below T_b for the nonbreeding bull and cows and more than 2°C below T_b in breeding bulls. Summer T_{SU} 's were compared to Parker and Robbins' (1984) T_{SK} 's using T_e 's below 30°C as a basis for comparison. T_{SU} was shown theoretically and empirically to be a function of T_{SK} ($T_{SK} = 2.52T_{SU} - 58.17$). No correlation between T_b and T_e was found, indicating that thermal loading was not used. ALE Reserve elk behaviorally thermoregulated by bedding in the shade of sagebrush. Other thermal regulatory mechanisms apparently adequately compensated for the lack of behavioral thermoregulation because 50% of the total bedded elk located during summer were in the sun, and many were

located in areas devoid of sagebrush. ALE Reserve elk apparently compensate for the inability to behaviorally thermoregulate at times with increased latent heat loss through sweating.

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