THERMAL BALANCE MODEL FOR CATTLE GRAZING WINTER RANGE

by

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ABSTRACT

Beef cattle grazing semi-arid foothill range of the Northern Rockies during winter may be exposed to cold temperatures and high winds while grazing pastures with low nutritional value. Cattle can physiologically and behaviorally respond to the changing environment to lower metabolic requirements and reduce the effects of cold exposure. Requirements of grazing cattle may be overpredicted with models developed in controlled settings that do not account for energy conserving behaviors. We refined a simple thermal balance equation to model heat exchange of free-ranging cattle. We accounted for the complex interactions between animal behavior and the changing natural environment by applying the insulation characteristics of cattle's tissue and coat to, first, a simple geometric shape of an asymmetric ellipsoid, and second, to a three-dimensional computer model of a cow at different orientations to the sun and wind. A group of mature cows grazing native range were observed from dawn to dusk from 28 November 2003 to 21 January 2004. These observations were used to evaluate our model and as reference for analyzing cattle behavior in response to environmental variables. Correlation (r) between predicted and measured surface temperatures was 0.82, indicating the model successfully quantifies heat exchanges of cattle exposed to cold conditions in the field. We compared our model predictions with heat production measured in three studies, and with predictions based on the National Research Council beef cattle model. In all cases our model predictions were similar to those reported. Model simulations indicate behavior such as lying and orientation to the sun helped mitigate the effects of extreme weather, and that for many combinations of winter weather variables there is only a small increase in metabolic requirements due to cold exposure in mature beef cattle in a maintenance state. Our results indicate solar radiation contributes strongly to a cow's thermal balance. Thus, previous estimates that did not account for the irradiative environment may have overestimated metabolic requirements of acclimated cattle grazing winter range.

INTRODUCTION

As an alternative to the costly practice of feeding hay, beef cattle may graze semi-arid foothill range during winter (Olson 1991). Low nutritional value of dormant forage and chronic exposure to cold may strain cattle's energy reserves and reduce rebreeding potential. Episodes of severe winter weather may expose cattle to periodic cold stress (Blaxter, 1967).

Nutritional recommendations for beef cattle are often based on results of studies conducted in controlled environments, or accompanied by feeding large amounts of forage and supplements (Christopherson et al., 1979). Heat production, at least in feedlot cattle, is closely related to metabolic energy consumed (Birkelo et al., 1991), and such recommendations may overestimate maintenance requirements of a mature cow grazing in winter.

Thermal balance of cattle in winter can be described with a simple equation that incorporates metabolic heat production, and pathways of heat gains and losses (Campbell and Norman, 1998):

$$(R - L) + M - (\lambda E + H + G) + q = 0 \qquad (1.1)$$

where R is short- and long-wave radiation absorbed, L is long-wave radiation emitted from the body, M is metabolic heat production, λE is latent heat loss, H is sensible heat loss, G is heat conducted to the surface, and q is heat stored in the body. By re-arranging this biophysical equation, metabolic heat production required to counter the thermal energy demands of heat loss pathways (metabolic requirement; M_r) can be predicted.

We hypothesized that free ranging cattle responding physiologically and behaviorally to the environment may effectively conserve energy during winter and mitigate environmental stressors. Similar to wildlife in northern climates, acclimated cattle may reduce metabolic rate (Cuyler and Oritsland, 1993), seek shelter (Redbo et al., 2001), change activity patterns (Schaefer and Messier, 1996) and alter their behavior in many ways to adjust to a changing environment. For a grazing animal, these complex relationships between and among environmental variables, and animal characteristics and behavior make it difficult to quantify changes in net energy requirements for maintenance in response to environmental stressors .

Our objective was to refine the simple thermal balance equation to predict metabolic requirements of cattle in the field during winter. To meet our objective we developed a procedure to extrapolate heat exchange processes and insulation characteristics determined in controlled studies to a natural winter environment.

In a step by step process, we applied each component of the thermal balance equation to a three-layer ellipsoid of dissimilar axes that represents a grazing cow (Chapter 2). In our model, metabolic requirements in Watts are determined on a surface area basis that can be readily related to metabolic body mass. The surface area involved in each heat transfer process, described by variables in Equation 1.1, is determined according to the orientation of the ellipsoid's primary axis relative to the sun and wind. In this way we account for the interactions between free-ranging cattle and the changing environment.

We developed and evaluated our model in part based on 19 days of observing grazing cattle in an exposed pasture in southwest Montana. Activity, orientation and surface temperatures of a small group of cows were recorded from dawn to dusk over a two month period. In Chapter 3 we highlight a series of concepts on relationships among gregarious animals ("herd effect"), environmental variables ("agreement"), and their interactions ("multicollinearity"), which need to be addressed to account for different animal responses to changing weather conditions.

Together, the mechanistic procedure and behavior analysis comprise a model that predicts energetic costs of different winter weather conditions and animal behavior scenarios (Chapter 4). Our model, like many in the biological and ecological fields, simplifies complex relationships of the natural environment in an attempt to quantify and increase our understanding of the underlying processes. Assumptions and constraints associated with developing the model do not negate the logic behind the model, but impose limitations on it’s use. We address and resolve some of these limitations by adopting a three dimensional computer model, developed for inanimate objects, to simulate thermal balance in cattle grazing winter range (Chapter 5).

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MODEL DEVELOPMENT

Introduction

High winter-feed costs for beef cattle in Montana are partly due to the practice of feeding hay. Many producers may be feeding more hay than needed to meet perceived energetic demands elevated by cold weather (Birkelo et al., 1991; Jensen et al., 1999). Models derived from controlled environments may not accurately predict metabolic demands of cattle grazing winter range (Bergen et al., 2001; Block et al., 2001). Such models do not account for the behavioral and physiological responses of free ranging cows (Malechek and Smith, 1976; Yousef, 1989), or complex interactions between environmental factors and animal behavior to reduce the impact of the environment (Lefcourt and Schmidtmann, 1989).

Standard operative temperature, which includes body and boundary layer resistances to heat loss, ambient temperature, radiation, and wind (Bakken, 1981) can provide an accurate measure of the natural thermal environment (Parker and Gillingham, 1990; Beaver and Olson, 1996). However, most studies of an animal's thermal environment do not account for changes in resistance values that depend on animal location, position and orientation (Gonyou and Stricklin, 1981; de Lamo et al., 1998).

As the sun angle changes daily and seasonally, or wind changes velocity and direction, an animal's exposed surface area and insulation are affected differentially. A cow standing perpendicular to the sun's ray will absorb more short-wave radiation than a cow standing parallel to the sun (Clapperton et al., 1975). The flow field around an animal and consequently the boundary layer's resistance to heat loss will differ depending on animal shape and orientation to the wind (Wu and Gebremedhin, 2001). A wind blowing at 6 m s^{-1} parallel to the coat surface may disturb insulation 5-7% less then the same winds blowing at right angles which ruffles the fur (Cena and Monteith, 1975).

Our objective was to develop a comprehensive model for grazing cattle in a natural winter environment that accounts for behavioral responses to various conditions, and to determine the influence of environmental factors on the thermal exchange of the animal at different degrees of orientation to the sun and wind.

Materials and Methods

To develop the model we collected data on 12 pregnant, Angus X Hereford cows age three- to eight-years-old. Cows grazed native range on a year-round basis at the Montana Agricultural Experiment Stations' Red Bluff Research Ranch near Norris, Montana (45º35'N; 111º39'W; elevation 1600m). The gently sloping (4 %) west-facing bench is exposed to prevailing south winds that generally keep the pasture snow-free.

An 18 ha rectangular (600 x 300 m) north-south oriented area was enclosed with a 3-wire electric fence powered by a battery and solar panel. Two V-shaped, east-west oriented windbreaks were located in the middle of the pasture perpendicular to the prevailing strong south winds, and were the only shelter from the wind except for a few small depressions.

Cattle were observed hourly from 8:00-17:00 three days a week from 28 November 2003 to 21 January 2004. A single observer recorded each animal's activity (standing, lying, walking, grazing, or other), exposure (exposed, huddled, or behind wind break), orientation before and after they were approached (10 degrees increments clockwise, 0 = North), and mid-body surface temperatures in ^{o}C with surface emissivity (ε_s) = 0.97 (Campbell an Norman, 1998) on the left and right sides using a hand-held infrared thermometer (Cole Parmer; Model 08407-20). Readings for all 12 head were centered on the hour between 8:00-17:00, and took 15-20 minutes depending on the location and dispersion of cattle in the field. If a cow appeared to be disturbed by the presence of the observer, i.e. changed orientation by more than 30 degrees, the initial orientation was used to analyze behavior, otherwise orientations before and after approach was averaged. Surface temperatures were measured immediately after the initial orientation reading or before the final orientation reading. Each side's surface temperature was then related to its respective orientation reading.

A weather station (Campbell Scientific Inc., Logan, Utah) was located near the pasture's south end at the height of a cow's backbone (1.3 m). The station recorded climate variables every 10 minutes during the trial. Variables recorded include total sun plus sky radiation (average flux density in W m^{-2}) with a pyranometer (CS, Model LI200X), net radiation (algebraic sum of incoming and outgoing all-wave radiation) with a net radiometer (Model Q-7.1, Radiation Energy Balance Systems, Inc., Seattle, Wash.), ambient temperature and relative humidity (CS Probe, Model CS500), and wind direction and velocity (Wind Monitor 05103, R.M. Young, Traverse City, Mich.).

Model Development

The model was written and analyzed in R 1.7.1 (Ihaka and Gentleman, 1996). Empirical animal and weather data were applied to an ellipsoid constructed in Rhino 3.0 (Robert McNeel and Associates., Seattle, Wash.) that represents our cows. Ellipsoid dimensions were 1.5 m, 1 m, and 0.6 m for the primary, secondary, and tertiary axes, respectively. Surface area and volume were 3.27 m^2 and 0.47 m^3. The ellipsoid was assigned three layers of heat conductance (tissue, coat, boundary layer). We modeled changes in radiation absorbed and heat conductance according to the surface area of the ellipsoid exposed to environmental variables at different orientations.

Animal observations and weather station data were combined and missing values were removed, leaving 2,185 individual cow observations on 19 days over the two-month period (186 hours). Sun zenith and azimuth angles were calculated according to Campbell and Norman (1998), and transformed to the same compass coordinate system as orientation. We were only interested in cattle orientation as it relates to the direction of the sun's rays or wind, so the absolute difference between orientation and relevant angles to the direction of the sun or wind were reduced to a 0^o - 90^o scale ($180^o = 0^o$, $270^o = 90^o$ etc.). The wind direction monitor was not correctly calibrated. Wind direction at the site is predominantly from the south, so wind direction was set at 180^o.

This model was used to analyze current year's data, and predict metabolic requirements for cattle exposed to similar weather conditions (Chapter 4). The model depends on surface temperatures measured in the field, therefore its predictive ability was limited to our particular data, and could not be applied to hypothetical sets of weather conditions without concomitant measures of surface temperature. To expand the model's predictive ability beyond the original set of conditions, a computational model was developed based on coefficients of the first model.

Radiation Absorbed

Radiation absorbed consists of short- and long-wave energy fluxes in hemispherical and directional environments absorbed by the body. The amount of radiation depends on sky conditions, ground cover, and the shape and orientation of the body relative to the sun. Therefore radiation absorbed was described by its components: absorptance (α), view factor (F), and flux density of short-wave radiation, including direct beam (I_{Dn}), diffuse (I_{dh}), reflected (I_r), and long-wave radiation from the atmosphere (L_a) and the ground (L_g):

$$R = \alpha_I (F_{IDn} \bullet I_{Dn} + F_{Idh} \bullet I_{dh} + F_{Ir} \bullet I_r) + \alpha_L (F_{La} \bullet L_a + F_{Lg} \bullet L_g) \qquad (2.1)$$

Absorptance was a constant and equaled 0.95 for short-wave radiation, and 0.97 for long-wave radiation (Campbell and Norman, 1998). Cattle orientation to the solar beam influences the view factor for the direct component of short-wave radiation (F_{IDn}). Direct short-wave beam (I_{Dn}) and diffuse radiation on a horizontal surface (I_{dh}) were derived from pyranometer readings (I_{Th}) and sky transmittance (Liu and Jordan 1960). Long-wave radiation was not measured directly, but was derived from net-radiometer, pyranometer and temperature readings. The hand-held infrared thermometer was held to the soil surface as the observer walked approximately 50 paces in a random direction every two hours. The average ground temperature, with emissivity set at 0.95, was used to estimate long-wave emitted from the soil surface.

View factor (F) is the projected two-dimensional surface area (A_p) of an ellipsoid of surface area "*A*". The angle between the primary axis of the body (orientation) and the sun's direct beam on the horizontal (azimuth) and the vertical (zenith) planes changes as the sun moves across the sky during the day (Fig. 2.1).

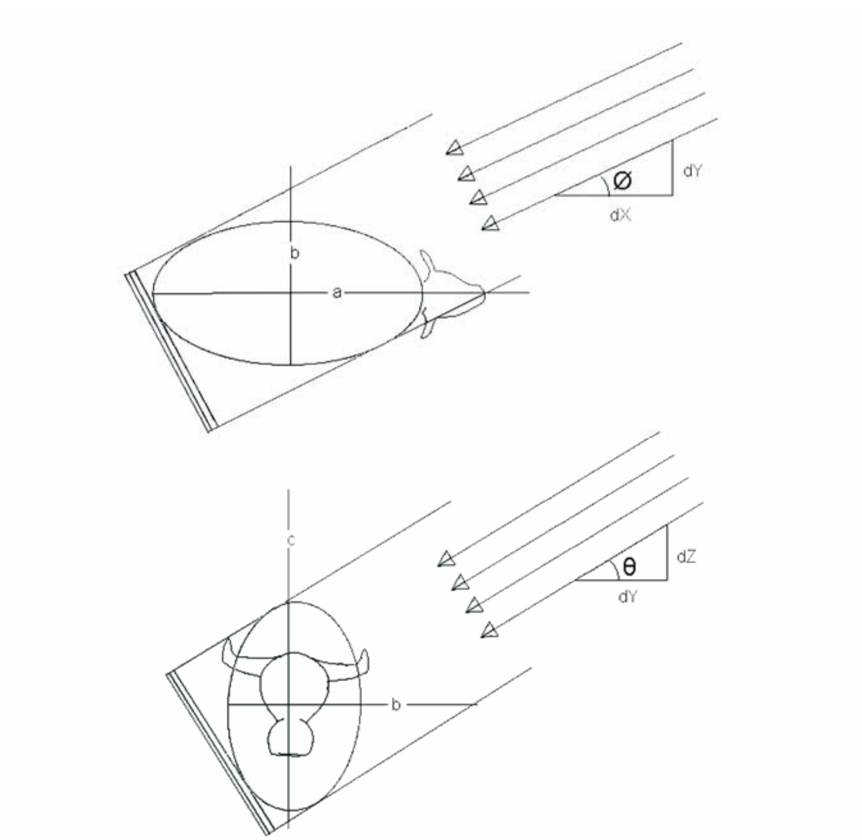

Fig. 2.1. View factors on horizontal x-y axis (top) and vertical y-z axis (bottom) used to estimate view factor of an ellipsoid (a ≠ b ≠ c).

View factor was calculated for an ellipsoid whose axes ratios are similar to cows used in the study (T. Aviram, personal communication):

$$F = A_p A^{-1} = \pi \cdot [(a^2k^2 + b^2) / (1 + k^2)]^{-0.5} \cdot [(j^2 \cdot (a^2 + k^n b^2) / (1 + k^n) + c^2) / (1 + j^2)]^{-0.5} \cdot A^{-1} \qquad (2.2)$$

where:

A = total surface area = 3.27 m^2,

A_p = the projected area

a = primary axis (head – tail) = 1.5 m,

b = secondary axis (right – left) = 0.6 m,

c = secondary axis (dorsal – ventral) = 1 m,

k = dY/dX = tan Ø (azimuth),

j = dZ/dY = tan θ (90^o - zenith), and

n equals: 2 – (4/3)*tan(2θ).

The *n* coefficient was formulated in the following manner:

I) We formulated an expression $(j^2 \cdot (a^2 + k^n b^2) / (1 + k^n))$. If $\theta = 0^+$, the expression equals $(a^2 + k^2b^2) / (1 + k^2)$, and $n = 2 + f_{(\theta)}$ when $f_{(0)} = 0$.

II) For the case where k < 1, and the sun gains elevation (j > 0), k^n must increase. Therefore, *n* was made to decrease from *n* = 2 at a rate that depends on θ.

III) We assumed that the "b" and "c" axes are equal (a prolate spheroid), and computed the projected area of this prolate spheroid (Campbell and Norman, 1998).

IV) Coefficients for tan θ were derived after running multiple iterations of Eq. 2.2 to lower the error term between view factors of an ellipsoid (results of Eq 2.2) and of a prolate spheroid (result of step III), at $\theta = 0^o$ and $\theta = 25^o$, which is the approximate zenith of the sun in winter at 45^o N.

Equation 2.2 is an approximation of F for an asymmetric ellipsoid at most orientations. At $Ø = 0^o$ or 90^o, or at $\theta = 0^o$, Eq. 2.2 takes on the form: $\pi \cdot a \cdot \sqrt{[(i^2 \cdot b^2 + c^2) / (1 + i^2)]}$, where i represents either k or j. For these three special cases, there are no approximations, and Eq. 2.2 is accurate with no error term.

View factor for direct short-wave radiation as a fraction of total surface area (F_{Dn}) ranged from 0.15 for cows orienting parallel to the sun's azimuth (Ø = 0^o) to 0.35 for cows orienting perpendicular (Ø = 90^o). Axis "c" is 67% longer than axis "b", therefore F_{Dn} was 4.5% higher in the morning and afternoon than during mid-day (Fig. 2.2). In the winter months at our latitude (45^{o}35'N), the sun's minimum zenith was approximately 65^o, which had little impact on the view factor of an ellipsoid of these dimensions. For cattle at different latitudes or times of year, differences in elevation angles within a day may be more important in the model. This could be accomplished by repeating Step IV above with the appropriate zenith for that latitude or season.

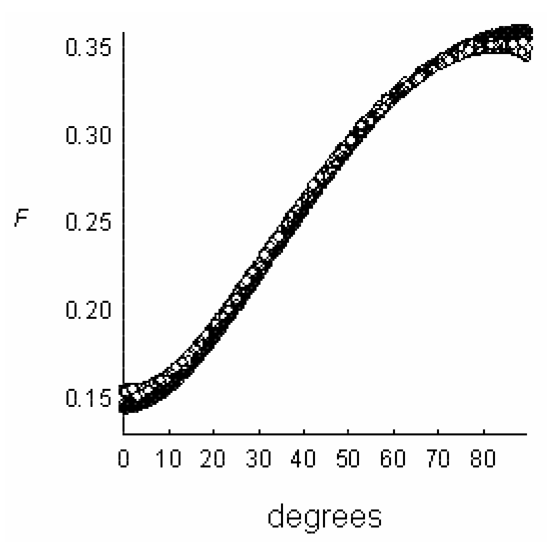

Fig. 2.2. View factor (F) of an ellipsoid at different orientations to the azimuth (Ø): ○ mid-day observations (θ > 14.65^o), ● morning and afternoon observations (θ <14.65^o).

Heat Transfer

Heat is conducted between the core and the environment in our model through three layers: tissue, coat, and the boundary layer. Conductivities of the three layers, modeled after equations from the literature described below, were applied to our representative ellipsoid. Thus our model accounted for changes in surface boundary conditions and wind disturbance to the coat due to varying body shapes, orientation to the direction of airflow, and activity. Physical characteristics of cattle coats vary between breeds and husbandry practices (Webster et al. 1970). Varying coat characteristics were beyond the scope of this model because our cows were all from the same herd, and been subject to the same husbandry practices since the previous winter.

Tissue Conductance. Constricted peripheral blood vessels can reduce conductance of heat to one third that of dilated blood vessels (Monteith and Unsworth, 1990). Tissue conductance is assumed to be a linear function between the value of complete vasodilation at upper critical temperature (UCT), and the value of complete vasoconstriction at a lower critical temperature (LCT; Parker and Gillingham, 1990). These upper and lower limits were set at ambient temperatures of -7 ^{o}C and -30 ^{o}C. Upper and lower critical temperatures are not constant, but vary with insulation, season, acclimation, etc.. We selected -7 ^{o}C and -30 ^{o}C by maximizing the correlation between model output and field measurements. Our data set had only a few observations less than –30 ^{o}C; temperatures were mostly 0 to –10 ^{o}C, on cloudy and windy days. Thus, our LCT and UCT values are appropriate for conditions described above, and may not represent values for other cattle in winter or even other winters. We tried to identify appropriate UCT and LCT values in the range of –35 to 5 ^{o}C, but the slope of the linear model seemed to influence variation in output much more than the end points. Beyond

-7 °C and -30 °C, conductance values remained constant and were 24.4 W m^2 °C^{-1} (resistance = 0.041 m^2 °C W^{-1}) and 7.04 W m^2 °C^{-1} (resistance = 0.142 m^2 °C W^{-1}), respectively (Monteith and Unsworth, 1990).

Coat Convection and Conductance. Coat conductance (h_c) was determined in three consecutive steps. First, free convection (h_{cfree}) was estimated based on the temperature gradient between the skin and the surface. Second, forced convection where wind penetrates the coat (h_{cw}) was derived from the h_{cfree} value. Third, we calculated the surface area exposed to wind ($A_w A^{-1}$).

Conductivity within the thick winter coats dominated by free convection was derived from the Nusselt number (Nu), the thermal conductivity of still air (*k*), and a characteristic dimension (*d*):

$$h_{cfree} = Nu * k / d \qquad (2.3)$$

where the Nusselt number (Nu) is derived from a relationship to the Grasshoff number of a vertical plate (Cena and Monteith, 1975):

$$Nu = 0.58\ Gr^{0.25} \qquad (2.4)$$

Grasshoff number of air at T_c and υ is:

$$Gr = 9.8\ d^3\ \Delta T / T_c\ \upsilon^2 \qquad (2.5)$$

where T_c is the temperature at the mid-point between the skin and the outer surface of the coat:

$$T_c = T_{skin} - 0.5 \bullet (T_{skin} - T_{surface}) \qquad (2.6)$$

We assumed T_{skin} is regulated by vasoconstriction and under the thick winter coat remains constant at 29.8 ^oC), and υ is viscosity of air at T_c (Campbell and Norman, 1998):

$$\upsilon = (13.3 + T_c \cdot 0.09) \cdot 10^{-6} \quad (2.7)$$

Initially, we varied T_{skin} by temperature or by vasoconstriction/dilation, but these simulations yielded smaller correlations and greater slope and intercept values. Therefore, we concluded that even if skin temperature decreases somewhat with air temperature, the variation is small enough that a constant value best represents this stage.

To determine h_{cfree} (Eq. 2.3), thermal conductivity of still air (k) at T_c, and a characteristic dimension were needed. In our model we estimated k as (Worcester Polytechnic Institute, 2004):

$$k = 1.52 \cdot 10^{-11}\, T_c^3 - 4.86 \cdot 10^{-8}\, T_c^2 + 1.02 \cdot 10^{-4}\, T_c - 3.93 \cdot 10^{-4} \quad (2.8)$$

A standing cow is vertically oriented therefore we used the "vertical plate" relationship, replacing the plate diameter factor in Cena and Monteith's (1975) original equation with a characteristic dimension (d) which is twice the cube root of the ellipsoid volume.

Values for still air conductance calculated from Eq. 2.3 for Winter 2003-2004 ranged from 1 $Wm^{-2}\,^oC^{-1}$ to 4 $Wm^{-2}\,^oC^{-1}$, with a mean of 2.88 $Wm^{-2}\,^oC^{-1}$. The mean value corresponds to 98 $mW\,m^{-1}\,K^{-1}$ for cattle hair 3.4 cm in length. These values are similar to values for cattle and sheep with 4 cm thick fleece (Cena and Monteith, 1975).

Second, forced convection under windy conditions (h_{cw}) was derived from correcting h_{cfree} for wind velocity (Campbell, 1980):

$$h_{cw} = h_{cfree} (1 + c \cdot \mu) \tag{2.9}$$

where μ is wind speed in m s^{-1}, and *c* is a constant defined by Campbell et al. (1980) as between 0.03 – 0.23 m s^{-1} with typical values of 0.1 for coats 3-4 cm deep. For our model, again by maximizing the correlation between model output and field measurements, *c* equaled 0.04 m s^{-1}, which is near the bottom of the range.

Insulation of cattle coats changes little at wind speeds of up to 5 m s^{-1} (Bennett and Hutchinson, 1964), and our cows may have been indirectly selected for heavy winter coats through culling. Under-coat averaged 1.8 cm in length, and guard hairs averaged 5 cm in length. But, since guard hair is mostly laying flat on top of the under-coat, to compare the effective depth in a live animal to the literature the average of the undercoat and guard hair (3.4 cm) is a good approximation, and essentially represents cross-sectional "depth". Despite winds reaching 16 m s^{-1}, cattle hair never seemed to be disturbed, except for a narrow strip on their back when cows were facing away from the wind (personal observation). Therefore, a low value for *c* is relatively consistent with Campbell et al.'s (1980) results from pelts of sheep, caribou, and wolves.

Third, we determined coat convection for the whole animal (h_c) as a percent of coat surface area exposed to direct wind (A_w / A) at different orientations:

$$h_c = h_{cw} \cdot A_w / A + h_{cfree} \cdot (1- A_w / A) \tag{2.10}$$

where A_w is the projected area resulting from an ellipsoid of surface area *A* orienting to the wind ($Ø_w$) at angles on the horizontal plane from 0^o to 90^o:

$$A_w = 0.5\pi \sqrt{} [(0.75^2 \cdot k_w^2 + 0.3^2) / (1 + k_w^2)] \tag{2.11}$$

where k_w is equal to $\tan(Ø_w)$.

If $Ø_w = 90$, then $\tan Ø_w \rightarrow \infty$, and $A_w = 0.375\pi$

Using A_w improved our estimate because heat transfer due to free convection decreases with increasing $Ø_w$ angles, while simultaneously increasing surface area exposed to direct wind.

Equations 2.4 through 2.10 were adopted from procedures describing conduction and convection of a flat plate. Using a two dimensional view factor (Eq. 2.11) does not accurately represent the irregular three-dimensional shape (Wu and Gebremedhin, 2001) of a live animal, or account for turbulence on the ventral side and laminar flow towards the dorsal side (Budaraju et al., 1994). A more representative estimate would be obtained if values could be related to the ellipsoid's curvature in relation to wind direction, rather than a simple surface area ratio.

Boundary Layer Heat Loss. The environmental heat transfer coefficient (h_e) for sensible heat loss from the surface of the cow to the environment ($T_s - T_a$) was:

$$h_e = h_r + h_a \tag{2.12}$$

where h_r is the coefficient for irradiative conductance of the surrounding air, and h_a is the boundary layer convection coefficient (Campbell and Norman, 1998):

$$h_r = 5.67^{-8} \bullet 4 \bullet (T_a + 273)^3 \ \ Wm^{-2}\,{}^oC^{-1} \tag{2.13}$$

where T_a is ambient temperature, and boundary layer convection coefficient was derived following Mitchell (1976) for a spheroid:

$$h_a = Nu\ k / d \tag{2.14}$$

where Nu is related to Reynolds number:

$$Nu = 0.6\ Re^{0.53} \tag{2.15}$$

Reynolds number is computed from wind velocity, dimension, and air viscosity:

$$Re = \mu\ d / \upsilon \tag{2.16}$$

The radius (cube root of the volume in case of a sphere) can be applied as a boundary layer characteristic dimension (*d*) to animal shapes ranging from spiders to cattle (Mitchell, 1976). Because of the asymmetric shape of an ellipsoid compared with a sphere, we derived the radius from the surface area exposed to wind (A_w). Thus, our model accounts for the ellipsoid's orientation to the wind:

$$d = \sqrt{A_w / \pi} \tag{2.17}$$

The *k* and υ values in Eq. 2.14 and Eq. 2.16 were determined the same as in Eq. 2.7 and 2.8, except T_a replaced coat temperature (T_c).

Evaluation

Standard operative temperature (T_{es}) is defined as the temperature of an enclosure with free-convection conditions in which the animal with the same body temperature T_b would have the same net heat loss as it does in its actual environment (Bakken, 1992). Standard operative temperature is calculated using the conductivities of tissue, coat and boundary layer (Bakken, 1981):

$$T_{es} = T_b - [(T_b - T_e) \cdot (r_{bs} + r_{es}) / (r_b + r_e)] \tag{2.18}$$

where r_b and r_e are body and environmental resistances respectively, r_{bs} and r_{es} are r_b and r_e in the standard environment of $\mu < 1$ m s^{-1}, and T_e is the operative temperature (Campbell and Norman, 1998):

$T_e = T_a + (R - \varepsilon_s \sigma T_a^4) / h_e$ (2.19)

where T_a is ambient temperature, R is radiation absorbed, ε_s is the emissivity of the animal's surface, σ is the Stephen-Boltzman constant ($5.67 \cdot 10^{-8}$), and h_e is the environmental heat transfer coefficient from Eq. 2.12. By replacing measured surface temperatures with T_{es}, we were able to simulate hypothetical weather conditions, and evaluate the model by comparing T_{es} (predicted from modeled conductance and convection values) to surface temperatures (measured).

Surface temperature was used in our original model to calculate free convection through the coat (Eq. 2.6). In our expanded model, we replaced the value for free convection from Eq. 2.3 with a polynomial model ($R^2 = 0.9997$) based on data collected during the 2003-2004 winter:

$h_{cfree} = 0.0312\ \Delta T^2 + 2.601\Delta T - 2.55$ (2.20)

where ΔT is the difference between T_{skin} and T_a.

The correlation (r) between T_{es} and T_s was 0.82, but T_{es} was more then 15 degrees lower than measured T_s (Fig. 2.3a).

The x-axis of Fig. 2.3a represents measured temperatures (T_s), but the y-axis is the result of Eq. 2.18 to predict surface conditions (T_{es}) with variables supplied by our model. Resistances to heat flow in the standard environment r_{es} and r_{bs} in Eq. 2.18 are only estimates, causing an inherent inaccuracy when computing T_{es}.

Resistance to heat loss coefficients in our model were derived from cattle acclimated to an extreme environment; extrapolating these values to standard environment values may not be appropriate. Similarity between calculated T_{es} and T_{es} predicted from a linear regression to temperature and wind was dramatically reduced when wind velocity was zero (Beaver et al., 1996), indicating r_e and r_b estimates may not be accurate in the transition to lower wind speeds.

To determine standard environment values, we predicted r_e and r_b values by temperature, wind and orientation with polynomial regression models ($R^2 = 0.99$ and 0.87, respectively). Any change to the model that affected r_e and r_b values reduced the correlation between measured and predicted values. Changing only r_{es} and r_{bs} values altered the slope and intercept of Fig. 2.3a, but did not affect the correlation (Fig. 2.3b,c,d).

The fit of the model, described by the correlation coefficient of 0.82, was maximized in the process of model development, and supports our values selected for the constants *c*, *d*, T_{skin}, and tissue conductance. The lack of fit described by the changing slope and intercept indicates that a "standard environment" may need to be redefined, and that refining it according to season and animal species may increase the accuracy of T_{es}.

Our correlation coefficient reflects the variable conditions of our data from the 2003-2004 winter. Our model does not account for physiological and morphological differences between individual cows such as weight, dimension, back-fat thickness, and hair length. Applying the model to the herds' average surface temperatures increases the correlation to 0.88. The model could not be further refined to account for variation among cows because of the low number of individuals used in this study, and their homogeneity.

Implications

Cattle grazing winter range in Montana may adjust their behavior in response to changing environmental conditions, thus reducing energy demands during the winter

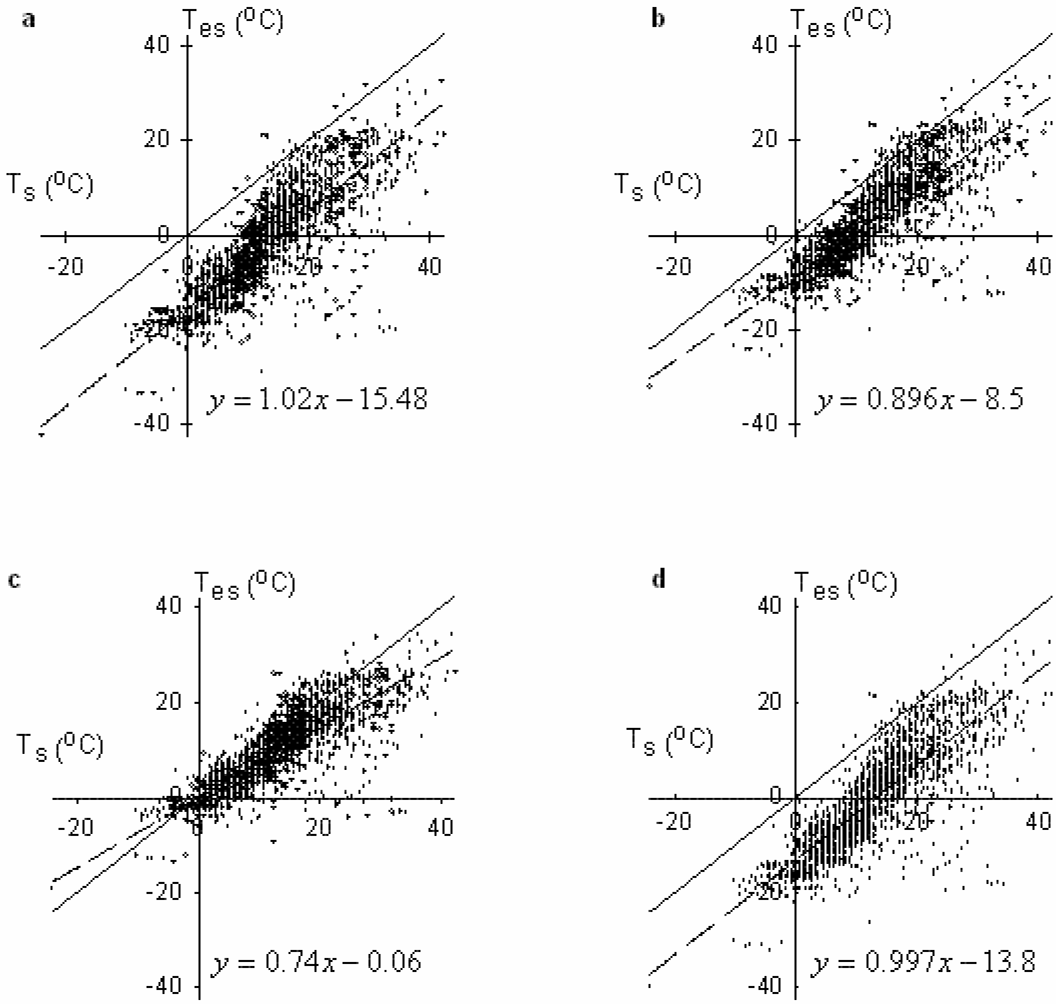

Fig. 2.3. Predicted standard operative temperature (T_{es}) and surface temperatures (T_s) measured with an Infra-red thermometer. a) r_{es} and r_{bs} estimated with a subset of Winter 2003-2004 data for wind velocities lower then 1 m s^{-1}. b) r_{es} and r_{bs} estimated with a subset of Winter 2003-2004 data for wind velocities lower then 2 m s^{-1}. c) r_{es} and r_{bs} estimated for ambient temperature of 0 °C, wind velocity of 1 m s^{-1} and an orientation of 45° to the wind. d) r_{es} and r_{bs} estimated for ambient temperature of –25 °C and wind velocities of 5 m s^{-1}.

months. A comprehensive thermal balance model can be a useful tool to quantify metabolic requirements resulting from behavioral adjustments. For free-ranging animals, complex interactions between animal and constantly changing conditions lower the predictability of models derived from controlled environments. We combined the physical laws of heat and mass transfer with the geometry of cattle orientation and degree of exposure in a step-by-step mechanistic model that accounts for many of these interactions. Heat exchanges between cows and a winter environment were computed based on the scientific literature, and evaluated with empirical data collected from a winter study.

The purpose of this paper was to describe the development of the model and its underlying concepts. Although it was developed for cattle grazing winter range, it may apply whenever results from controlled environments are extrapolated to a natural environment setting. Further variations and refinements of this model that incorporate more complex animal shapes, and results of various simulations and possible applications are described in Chapter 5.

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A NOTE ON ANALYZING BEHAVIOR

Introduction

Studies on the metabolic requirements of cattle and wildlife during winter often fail to account for interactions between animal behavior and their environment. Cattle and wildlife may conserve energy and reduce cold stress associated with ambient weather conditions by altering activity patterns (Olson and Wallander, 2002; Schaefer and Messier, 1996; Redbo et al., 1996), seeking shelter (Beaver and Olson, 1997; Houseal and Olson, 1996; Redbo et al., 2001), and lowering metabolic rate (Arnold et al., 2004; Cuyler and Oritsland, 1993; Mesteig et al., 2000).

An animal's degree of thermal discomfort is determined by interactions of internal (physiological) and external (environmental) factors. To maintain thermal balance in a constantly changing winter environment, cattle must acclimate to short-term deviations from the running average of environmental conditions (Senft and Rittenhouse, 1985). Forage intake and time that cattle spend grazing remain relatively constant during winter, and are unresponsive to short-term deviations from mean ambient temperatures (Beverlin et al., 1989; Prescott et al., 1994). Other behavioral responses, unrelated to foraging behavior, mitigate a cow's ability to tolerate a wide range of weather conditions during winter. Orienting to the sun to maximize irradiative heat gain on cold, sunny days may contribute significant energy to an animal's thermal balance (Walsberg, 1992). Cattle that cannot seek moderate microclimates may rely on behaviors such as changing orientation to reduce cold stress.

We developed, evaluated, and applied a model of the thermal exchanges of cattle grazing winter range in Montana. Thermal exchanges between the animal and its immediate outdoors' environment during the day were considered a series of independent heat-transfer states that depend on animal exposure (e.g. exposed or protected by natural or manmade cover), and orientation to the sun's direct beam and to the wind. To determine the appropriate state for every hourly observation, we analyzed how temperature, radiation and wind affect animal behaviors such as orientation to the wind and sun. In this paper we propose three concepts: agreement factor, herd effect, and multicollinearity, to improve the analysis of animal behavior in response to microclimatic variables.

Methods

Twelve Angus x Hereford cows were observed three times a week from 28 November 2003 to 21 January 2004 at the Montana Agricultural Experiment Stations' Red Bluff Research Ranch near Norris, Montana (45º35'N; 111º39'W). One observer (I. Keren) recorded each animal's activity (standing, lying, walking, grazing, or other), exposure (exposed, huddled, or behind wind break), and orientation (10 degrees increments clockwise, 0 = North). Animal temperature data were collected at the same time, and required the observer to walk among the cows in the pasture. To avoid bias in analyzing behavior, orientation was recorded from a distance before approach, and a second time after an individual was observed. If a cow was disturbed by the presence of the observer, i.e. changed orientation by more than 30 degrees, the initial orientation was used to analyze behavior, otherwise orientations before and after approach were averaged. Readings for all 12 head were centered on the hour between 8:00-17:00, and took 15-20 minutes depending on the location and dispersion of cattle in the field.

Analysis

Data were analyzed using circular statistics (Lund and Agostinelli, 2003) in R (Ihaka and Gentleman, 1996). Sun zenith and azimuth angles were calculated according to Julian date and time (Campbell and Norman, 1998), and transformed to the same compass coordinate system as cow orientation. A calibration error occurred when mounting the wind direction monitor. Since wind direction at the site is predominantly from the south, wind direction was set at 180^o. Absolute difference between orientation and the azimuth or wind direction was reduced to a 0^o-90^o scale ($180^o = 0^o$, $270^o = 90^o$ etc.), so cattle orientation relative to the sun and wind can be treated as a linear function between 0^o and 90^o.

Herd Effect

Distances between grazing cows are affected by the troop length (distribution of the herd in a one-dimensional field) and distance to nearest neighbors (Shiyomi and Tsuiki, 1999; Shiyomi, 2004). Orientation of individual cows may also partially result from social interactions with other animals and overall movement pattern of the entire group. If social interactions are not accounted for when analyzing environmental effects on individual animals, the contribution of external factors may be overestimated, and how individuals respond to environmental factors *despite* opposing social pressure may not be represented fully.

In some cases, herd effect issues that might hinder the use of individual animals as replicates may be avoided by scaling down the analysis, using the mean of small groups as the experimental unit instead of the individual (Phillips, 2002). With cattle orientation, the mean is not always an appropriate parameter, because it can result in a misleading orientation. For example, if two cows orient at 10^{o} and 170^{o} (clockwise, with 0^{o} being North), the mean orientation would be 90^{o} (due east).

Multilevel analysis extends ordinary regression analysis to hierarchical data, eliminating the need to cluster data to a reduced form. This technique is often used to analyze individual human behavior in a social context (Leyland and Groenewegen, 2003), but it has not been applied in the context of animal behavior (Knowles and Green, 2002). Using multilevel analysis where inter-level (herd to individual) interactions exist allows environmental predictors, acting at the population level, to influence individual response directly or indirectly through group predictors (Blakely et al., 2000).

To account for herd effect, we used two circular properties (Lund and Agostinelli, 2003): mean vector (or herd orientation - V_h) and the mean resultant length of the vector (or density - ρ). Herd orientation is the circular mean of individual orientation vectors (V_{ind}) grouped by hourly readings. Density is the sum of vectors in a group divided by sample size, and ranges from 0 whereby individuals are oriented in opposite directions, to 1 whereby all individuals are oriented in the same direction.

Herd effect can be defined as the unwillingness of an individual to act differently from its companions (Sibbald and Hooper, 2003). This definition implies a positive relationship between sociability and group activity, whereby it is harder for an individual to differ from a group that is acting in uniform rather than a group of individuals acting at random. Therefore, the expression $(V_{ind} - V_h) \cdot \rho$ is a quantitive measure of herd effect.

The intercept (β_0) and slope (β_1) of an ordinary linear regression $y_i = \beta_o + \beta_1 x_i + \varepsilon_i$, in themselves, depend on predictor variables at a higher level (e.g. herd), and therefore differ for every group of lower level (e.g. cow) observations. The general rearranged notation is (Hox, 1995):

$$Y_{ij} = \gamma_{00} + \gamma_{p0} X_{pij} + \gamma_{0q} Z_{qj} + \gamma_{pq} Z_{qj} X_{pij} + \mu_{pj} X_{pij} + \mu_{0j} + \varepsilon_{ij} \tag{3.1}$$

where X is the predictor at the individual level, Z is the predictor at the herd level, μ is the herd level error term, ε is the individual level error term, p and q are the number of explanatory variables of X and Z, respectively, and γ are herd level slope and intercept of the individual level β_{oj} and $\beta_{1j,}$ where:

$$Y_{ij} = \beta_{oj} + \beta_{1j} X_{ij} + \varepsilon_{ij} \tag{3.2}$$

$$\beta_{oj} = \gamma_{00} + \gamma_{01} Z_j + \mu_{0j} \tag{3.3}$$

$$\beta_{1j} = \gamma_{10} + \gamma_{11} Z_j + \mu_{1j} \tag{3.4}$$

First, we propose to use this approach to analyze cattle orientation where the low-level (cow) predictor is herd effect and the high-level (herd) predictors are environmental factors. This may be the most appropriate way to analyze behavior of small herds, such as in our example on orientation to the sun. The same approach can be applied to multiple larger herds, adding sub-groups within a herd as a mid-level, if appropriate (Moerbeek, 2004).

Second, we propose to use this concept to describe the activity of members in a herd who use windbreaks. By describing the activity in mathematical form, this increases our understanding of the dynamics behind individual "decisions" concerning the windbreak.

Daily use (percent of the time) of a windbreak by a group of cows is correlated with wind velocity and standard operative temperature (Olson and Wallander, 2002). An individual's "decision" to use a windbreak can be predicted by one of several available analysis methods, reviewed and compared by Allcroft (2001).

We propose that the intercept of any statistical model describing animal behavior is not a constant value, but depends on other individuals in the group, following the basic poynomial:

$$f_{(x)} = -a\ x^2 + b\ x \qquad (3.5)$$

where x is the number of cows already exhibiting the predicted activity. In our example of use of a windbreak, x denotes the number of cows already behind the windbreak at the time of the ij'th observation. Equation 3.5 was formulated so at low x values the herd effect increases an individuals tendency to join the others, whereas at high x values, the windbreak gets crowded and the tendency is reduced. The coefficients "a" and "b" denotes "herd effect", much like ρ in the previous example.

Multicollinearity

Correlation and redundancy in weather data may exist between temperature and wind, different wavelengths of radiation, and indices of daily, monthly, or yearly averages. Attempts to fit regression models with redundant weather predictors often lead to problems associated with multicollinearity in research of animal-habitat relationships (Morrison et al., 1992).

Multicollinearity in a statistical model can cause low R^2s, low significance (high p-value), and unreliable parameter estimates (Leamer, 1973). Of greater concern, data cannot be interpreted in the classic parameter-by-parameter fashion, and peculiarities in the maximum likelihood surface make least squares estimates irrelevant (Leamer, 1973). Although fixed parameters in multilevel modeling are relatively insensitive to severe multicollinearity, they cause bias in the variance-covariance matrix and estimates of standard error (Bonate, 1999; Shieh and Fouladi, 2003).

Agreement

With their influence on surface temperature, radiation intensity and wind velocity can be used to predict cattle orientation in winter. Wind lowers surface temperature and radiation increases surface temperature, but whether there is a counteracting or additive effect on cattle orientation depends on the relationship between wind direction (W_D) and the sun's azimuth (AZMT). Cattle maximize irradiative heat gain at perpendicular orientations to the sun's azimuth ($Ø_{azmt} = 90^o$), and minimize convective heat loss at parallel orientations to wind direction ($Ø_{WD} = 0^o$) (Fig. 3.1).

Agreement is defined as the relative angle (0^o - 90^o) between wind direction and the sun's azimuth. An optimum orientation in which cattle can minimize convective heat loss and maximize convective heat gain simultaneously exists only if $diff_{(WD,\ AZMT)}$ is 90^o. Conversely, when $diff_{(WD,\ AZMT)}$ is 0^o, any orientation will result in lower irradiative gains or greater losses from wind convection (Fig. 3.2).

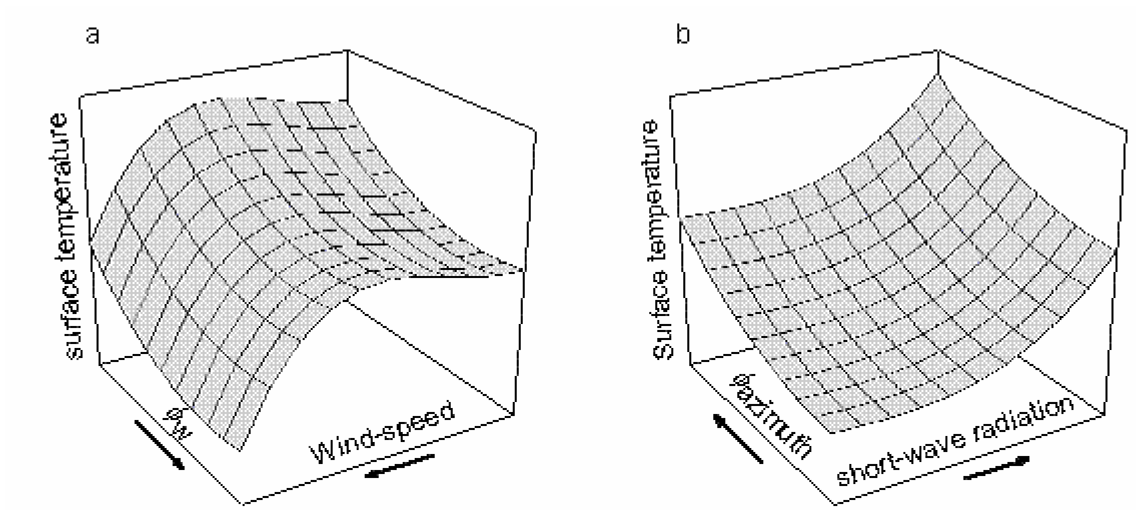

Fig. 3.1. Cattle's surface temperatures by a) wind and orientation, and b) short-wave irradiance on a horizontal surface and orientation. Graphs based ($R_a^2 = 0.06$, $R_b^2 = 0.56$) on data collected in winter 2003-2004.

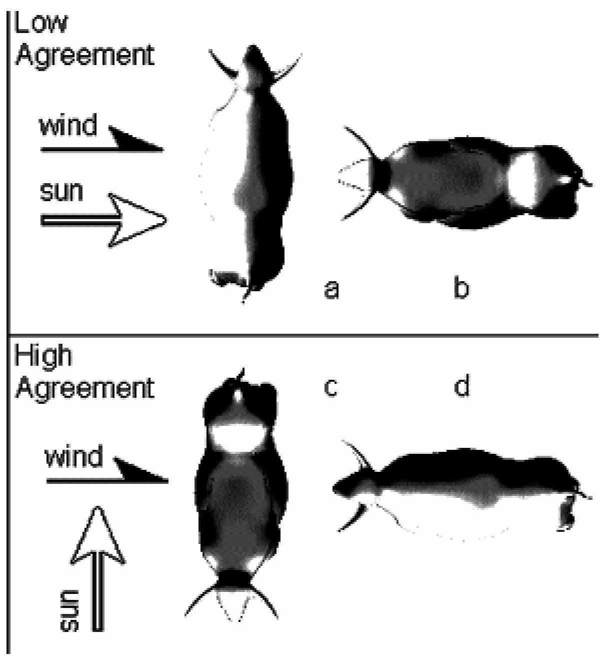

Fig. 3.2. The angle between wind direction and the sun's azimuth as it relates to potential cattle orientations. In the top panel, the angle between wind direction and sun azimuth is 0°. In the bottom panel, the angle is 90°. a) orientation maximizes irradiative heat gain but also convective heat loss. b) orientation minimizes convective heat loss and irradiative heat gain. c) orientation minimizes irradiative heat gain and maximizes convective heat loss. d) only orientation and agreement that maximizes irradiative heat gain and minimizes convective heat loss.

The relationship between wind and radiation is positive or negative for cows experiencing high agreement or low agreement respectively, i.e. in high agreement, the environmental demands to orient in a certain direction are divided among positively related forces, whereas in low agreement each may result in an opposite behavior. Adding an agreement factor allows us to simplify the interaction term between radiation and wind.

We termed the 90^o angle "high agreement" (Robinson-Cox, personal communication) based on previous observations of cattle facing away from the wind, and the assumption that a parallel orientation to the wind has thermal advantages. The latter may not always be a viable assumption. Heat loss from the flow field around a simulated cow model is lower when cows are oriented 90^o to the air-stream (Wu and Gebremedhin, 2002). Direction of the airflow had little effect on total sheep insulation, in contrast to insulation at specific spots on the fleece (Curtis, 1983). Low R^2s in Fig. 3.1a indicate wind speed and direction do not influence a live animal's surface temperature in dry conditions, even at the low ambient temperatures of a Montana winter. Predictions from our model indicate layers of insulation are affected differently by winds of varying speeds, and due to this complex relationship, no one orientation has a thermal advantage across all wind-speeds.

A decisive conclusion as to which orientation is more thermally advantageous depends on a region's prevailing climate, and is beyond the scope of this paper. However, this does not detract from the validity of using agreement angle in modeling animal orientation, or of the concept of complex secondary interactions between environmental predictors that influence animal behavior.

Conclusion

Complex relationships between animal behavior and changing natural environments may reduce our ability to extrapolate results obtained in a controlled setting to the field. We accounted for different animal behaviors (namely orientation and use of windbreaks) in a mechanistic model developed to predict metabolic requirements of cattle in the field. Our model was developed based on empirical observations of grazing cattle, but to attain a complete and independent model, it must be complemented with an accurate analysis of how cattle might respond to different environments.

This paper is the result of our search for an appropriate and accurate method to analyze cattle behavior in response to environmental predictors. The complexity of the natural environment, coupled with the various levels on which a gregarious animal might base its "behavioral decisions" renders most traditional analysis methods inappropriate. However, a more complete conceptual accounting of the interactions among animals, and among environmental predictors may allow us to quantify, and ultimately simplify the interaction terms enough to reach an unbiased interpretation of animal behavior and their response to a winter environment.

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MODEL APPLICATION

Introduction

To meet the metabolic requirements of cattle, producers in the Northern Rockies may feed 2 - 2.5 tons of hay per cow during winter, a practice that may constitute 60 % of production costs in a cow-calf operation (Olson, 1991). To reduce feed costs, beef cattle may graze semi-arid foothill range of the Northern Rockies, although this might expose them to cold temperatures and high winds while grazing pastures with low nutritional value, in some cases resulting in lower weights and body condition-scores, that may lower calf performance and rebreeding potential (Webster, 1971).

Cattle energetic requirements and metabolism under cold conditions are often studied in controlled environments such as environmental and metabolic chambers, or by using heat sources covered with a pelt. Field studies are often accompanied by feeding high amounts of forage and supplements (Blaxter, 1967; Christopherson et al., 1979). Cattle may respond differently when exposed to winter conditions while grazing (Yousef, 1989).

Extrapolating energetic requirement values from a controlled to a natural environment may lead producers to feed more hay or grain than may be needed. Resting heat production increases only by a third of the predicted NRC (1981) maintenance energy requirements for environments of –6° C and –15° C (Bergen et al., 2001). From the most recent NRC model (1996), net energy for maintenance (NE_{main}) of feedlot steers was overestimated in cold weather, under-predicting average daily gains at –18° C (Block et al., 2001).

Acclimated cattle may behave similarly to wildlife in northern climates when not constrained by artificial research conditions, and respond physiologically or behaviorally to environmental conditions in the field. To maintain thermal balance and lower energetic requirements during winter, cattle and wildlife may conserve energy by lowering metabolic rate (Cuyler and Oritsland, 1993; Mesteig et al., 2000), seeking shelter (Olson and Wallander, 2002; Redbo et al., 2001), altering activity patterns (Olson and Wallander, 2002; Schaefer and Messier, 1996), and orienting to the sun and wind in ways that minimize convective heat loss or maximize surface area exposed to irradiative heat gain (Gonyou and Stricklin, 1981).

Thermal balance of cattle can be determined using a simple equation that incorporates metabolic heat production, and all pathways of heat gains and losses (Campbell and Norman, 1998):

$$(R - L) + M + q - (\lambda E + H + G) = 0 \qquad (4.1)$$

where R is short- and long-wave radiation absorbed, L is long-wave radiation emitted by a body, M is metabolic heat production, λE is latent heat loss, H is sensible heat loss, G is heat conducted to the surface, and q is heat stored in the body. Metabolic heat production levels have been predicted by balancing this biophysical equation in a hot environment (Brosh et al., 1998; da Silva, 2000, Berman, 2004). It has not been used to predict metabolic requirements of beef cattle exposed to winter conditions until recently (Chapter 2).

We modeled the thermal exchanges between cows and their immediate outdoors environment. Heat production required to maintain thermal balance was calculated for a series of independent scenarios that include various activities (e.g. grazing, standing, lying), degree of exposure (e.g. exposed, or protected by natural or manmade cover), and orientations that cows exhibit in the field. Our objective was to apply a model that accurately predicts thermal energy gains and losses in free-ranging cattle exposed to winter conditions. A comprehensive dynamic model which accounts for weather conditions and animal behavioral responses may help to more accurately predict metabolic requirements of grazing cattle and help producers improve cattle wintering practices in Montana.

Methods

Animals and Study Site

The mechanistic model we evaluate and apply was developed (Chapter 2) based on data from 12 pregnant Angus X Hereford cows, age three and eight years old (six in each group) grazing native range, and experienced with winter at the Montana Agricultural Experiment Stations' Red Bluff Research Ranch near Norris, Montana (45º35'N; 111º39'W; elevation 1600m). The site is sandy and silty range common to the foothills of the Northern Rockies. The dominant plant species are bluebunch wheatgrass (*Agropyron spicatum*) and Idaho fescue (*Festuca idahoensis*). The gently sloping west-facing bench is exposed to prevailing south winds that keep the pasture snow-free most of the time.

The two age groups grazed together as one group, were supplemented three times each week (1.8 Kg head^{-1}, 21% C.P. cake), and had free access to mineral salt and water in two 570 liter troughs on the east side of the pasture, which were kept ice-free with propane stock tank heaters. Supplements were provided on alternate days when behavior was not observed.

Cattle were observed three times a week from 28 November 2003 to 21 January 2004 every hour between 8:00-17:00. Cows were weighed, body condition was scored on a scale of 1-9 (Vizcarra, 1996), and their back-fat was measured with an Ultrasound (Aloka Model 200E) at the beginning and end of the field observation period. We measured body dimensions (shoulder to tail length, shoulder height, and chest girth) and sampled hair length (undercoat and guard hair) on all cows at the start of the trial to help create realistic dimensions for the computer model. Guidelines for animal care (Montana State University Animal Care and Use Committee) were followed at all times.

A weather station (Campbell Scientific Inc., Logan, Utah) was located near the pasture's south end at the height of a cow's backbone (1.3 m). The station recorded net radiation, short-wave radiation, ambient temperature, humidity, and wind velocity and direction every 10 minutes during the trial (Chapter 2).

Model Development

From the thermal balance equation, latent heat loss, conductance, and storage were assumed to be negligible for cattle exposed to our winter conditions. Cattle do not sweat during winter and heat loss via respired water vapor is negligible (Diesel et al., 1990, Giesbrecht, 1995). Conductance of heat of cattle standing or walking on hard ground is only through the hoofs, and was also assumed to be near zero. We assumed fat stores in the body are a long-term energy reservoir and are not involved in short-term responses to cold in mature animals. Components of Eq. 4.1 can now be described in detail as (Campbell and Norman, 1998):

$$R + h_b(T_b-T_s) - \varepsilon_s \sigma T_a^4 - h_e(T_s-T_a) = 0 \qquad (4.2)$$

where R is all forms of short- and long-wave radiation absorbed by a body, h_b is the coefficient for heat transfer through tissue, skin, and coat, T_b is body core temperature assumed to be constant at 39 ^oC, T_s is surface temperature, $\varepsilon_s \sigma T_a^4$ represents long-wave radiation emitted by a body that consists of surface emissivity (ε_s), the Stephen-Boltzman constant (σ), and ambient temperature (T_a), and h_e is the environmental heat transfer coefficient of the surrounding boundary layer.

Equation 4.2 describes the gradient between a constant body core temperature and the environment, which drives heat flow through a series of layers of insulation, and produces:

$$M_r = (T_b - T_{es}) \cdot h_b h_e / (h_b + h_e) \qquad (4.3)$$

where M_r (in W m^{-2}) is the added heat required to maintain the balance described by Eqs. 4.1 and 4.2, and T_{es} is the standard operative temperature defined as the temperature of an enclosure with irradiative and free-convection conditions in which heat loss for an animal of T_b is the same as in it's natural environment (Bakken 1992).

Campbell and Norman (1998) refer to M_r as "the rate of metabolic heat production". The actual value of metabolic rate may be influenced by levels of activity and plane of nutrition, but is not predicted by our mechanistic model in which a cow is treated as a 3-layer shell with no internal heat source. At high T_{es}, predicted values of M_r may be lower than the minimum basal rate physiologically possible, i.e. cattle are above LCT (lower critical temperature). Predicted metabolic requirements should not exceed a metabolic rate of 500 W m^{-2} (Campbell and Norman, 1998). Since no adverse effects of cold exposure were observed in cattle during Winter 2003-2004, and our model predictions were never more then 180 W m^{-2}, this value could not be validated and a limit on predicting metabolic requirements at the low end (point of hypothermia) could not be set in our model.

Analysis

The model was created and evaluated in R (Ihaka and Gentleman, 1996). We evaluated results from two model simulations. First, we predicted metabolic requirements based on our specific winter 2003-2004 data-set, and compared subsets of this simulation's predictions to independent data sets of empirical findings. Second, we simulated all possible permutations of five model variables: short-wave irradiance on a horizontal surface (I_h), ambient temperature (T_a), wind velocity (μ), orientation of the body's primary axis to the sun's azimuth ($Ø_{pa}$), and "agreement", or wind direction relative to the sun's azimuth ($Ø_{ws}$).

Simulation 1

To help develop the model, we selected twelve cows from the larger Red Bluff herd to record activities, orientations, use of windbreaks and surface temperatures of grazing cattle in winter. Cows were selected with no criteria except age (three- and eight years old). All twelve cows grazed together in one pasture; behavior did not differ between the two age groups, so age was not a variable in the model or analysis.

Therefore, we analyzed model predictions using a mixed effects model (Pinheiro et al., 2004) on the entire group, with cow identification as the random variable.

During winter 2003-2004, we measured surface temperatures of cattle in the field using a hand-held Infra-Red thermometer (Cole Parmer; Model 08407-20). These measures integrate a cow's thermal environment into one variable (T_s) in degrees C, analogous to the calculated standard operative temperature (Chapter 2). Replacing T_{es} in Eq. 4.3 with T_s removed a potential source of error from the T_{es} equation, and increased the accuracy of model predictions.

We selected subsets of data from our Winter 2003-2004 data-set to match environmental conditions reported in three empirical studies (Rutley and Hudson, 2000; Han et al., 2003; Young, 1975). We selected studies which, based on the research subjects, environment, and level of feeding, etc., compare with conditions from our data.

Our model was designed to predict metabolic requirements based on complex scenarios of free-ranging cattle, and therefore uses variables such as time of day, long-wave radiation emitted from the ground, cloud cover, wind direction, and cattle activity and orientation. These variables are rarely described by others in enough detail to predict metabolic requirements for large herbivores during winter.

Environmental variables are often highly correlated, and cattle respond differently to different combinations of them (Chapter 3). Predicting metabolic requirements, holding many of the model variables constant at a mean level, would have been unrealistic because of inherent variation. By using subsets of the Winter 2003-2004 data to compare with empirical studies, we accounted for the correlation between variables and the potential responses of cattle under conditions of their studies. Thus, we more accurately simulated their environments despite their limited weather and animal behavior information.

Simulation 2

In our study, cattle were exposed to different combinations of environmental variables that can be thought of as treatment cells (warm/windy/cloudy, or cold/calm/clear skies, etc.). However, we had several missing cells of weather combinations and varying sample sizes because weather variables are correlated, and do not adhere to a complete multifactorial design.

On overcast days, emitted long-wave radiation was reradiated from the atmosphere back towards the ground, inducing warmer ambient temperatures than on clear days. In our area, strong winds are associated with an atmospheric pressure gradient formed between warm air in the Intermountain area and arctic airflow from Canada. Cold days reduce the gradient and therefore are associated (from our data-set, $r = 0.47$) with light north winds compared with strong south winds on warm (>-10 ^{o}C) days.

The large variation in the number of observations in different weather cells partly reflects our systematic sample design; cows were supplemented three times each week, and responded to human activity by the water troughs, so natural behavior in response to environmental conditions could not be observed on those days. Therefore, we observed animal behavior and measured surface temperature data on the other days regardless of weather conditions that day. Winter 2003-2004 was relatively warm (Weatherbase,

2004) and daily average conditions were normally distributed, so most cells in our data are of mild, average, weather conditions, and only a few reflect extreme cold conditions.

We constructed a matrix of sky and ground conditions on a clear day at 12:38 PM, and simulated all possible permutations of five model variables at five levels. Generating a balanced matrix of weather variables for the second simulation was a two-step process. First, we ran multiple simulations with different combinations of extreme weather variables. Second, we generated environmental variables in equal increments within the limits established from the first step.

Ground surface temperatures and net-radiometer readings are incorporated in our model, but are not independent of ambient temperature and solar radiation. Regression models describing the relationship of ground temperature and net-radiation to short-wave radiation and ambient temperature on clear days were constructed (R^2 = 0.88 and 0.92, respectively). Realistic values for net-radiometer and ground temperature data were predicted using these regression models for every permutation of temperature and short-wave radiation.

This simulation clearly defines interactions among model variables, tests the boundaries of our model, and accounts for some of the missing cells in the first simulation. It allowed us to transform the complex model to a simplified polynomial regression form (Venables and Ripley, 2002) of only five variables. A good polynomial model achieves high predictability and low error terms with relatively few terms. The best model was selected based on results of the first simulation, Akaike's information criterion (AIC, lower is better), and by removing biologically irrelevant interactions among variables after reviewing plotted data.

Results and Discussion

Simulation 1 - Model Variables

Temperatures during our study period ranged from -40 ^{o}C to 5 ^{o}C, averaged –4 ^{o}C, and were below 0 ^{o}C 75% of the time. Cows in our study weighed between 485 Kg to 757 Kg (average 654 Kg) at the beginning of the trial period, and 480 Kg to 773 Kg (average 653 Kg) at the end. Heat lost under all daytime weather conditions predicted by our model ranged from 56.6 W m^{-2} (first quartile) to 91.6 W m^{-2} (third quartile), with a maximum of 161 W m^{-2} and a mean of 73 W m^{-2}. Metabolic requirements can be readily transformed from units of W m^{-2} (heat flux) to units of Kcal (energy) required to maintain the heat flux. Thus, dawn to dusk metabolic requirements of a 654 Kg cow from 28 November 2003 to 21 January 2004 were 1.6 Kcal h^{-1} $Kg^{-0.75}$.

Behavioral and environmental factors had varying effects on predicted metabolic requirements of our cattle (Table 4.1). We predicted metabolic requirements for the different activities: lying, walking, grazing, or other, relative to standing (the intercept). Lying reduced metabolic requirements by 10%, and by 26% on average for all existing environmental conditions (51 W m^{-2} relative to 69 W m^{-2}). Standing increases metabolic requirements from lying 8 to 25% (Susenbeth et al., 2004). We did not model heat conducted to the ground. Because the ellipsoid shape represents a cow lying down relatively well, we did not change our calculations for surface area exposed to wind or sun. Grazing behavior is not reported in Table 4.1 because it did not differ ($\alpha > 0.1$) from standing.

Table 4.1. Regression coefficients, standard errors and P-values of a linear mixed effect model[a] describing the influence of activity, climate variables, and orientation on metabolic requirements (W m^{-2}).

Predictor variables		Estimate	SE	P-value[b]
Intercept[c]		82.3	2.37	<0.001
Behavior	Lying	-9.09	0.93	<0.001
	Walking	4.16	2.19	0.058
	Other	4.66	1.25	<0.001
Climate	Short-wave radiation (W m^{-2})	-0.11	0.008	<0.001
	Wind speed (m s^{-1})	1.25	0.18	<0.001
	Temperature (^oC)	-1.11	0.34	0.001
	Agreement (^{o})	-0.12	0.03	<0.001
Interactions[d]	W x T	-0.48	0.02	<0.001
	A x T	$1.3x10^{-2}$	$6.0x10^{-3}$	0.033
	S x O	$-5.5x10^{-4}$	$6.4x10^{-5}$	<0.001
	S x W	$7.6x10^{-3}$	$7.9x10^{-4}$	<0.001
	S x A	$1.2x10^{-3}$	$2.8x10^{-4}$	<0.001
	S x T	$5.1x10^{-3}$	$8.5x10^{-4}$	<0.001
	S x W x A	$1.1x10^{-4}$	$3.7x10^{-5}$	0.002
	S x T x A	$-6.0x10^{-5}$	$2.6x10^{-5}$	0.016
	S x W x T x A	$3.0x10^{-5}$	$5.9x10^{-6}$	<0.001

[a] All predictor variables are fixed, with cattle ID added as a random variable.
[b] Only significant (<0.1) factors are reported
[c] Intercept is for a standing cow, where all quantitative variables are equal zero.
[d] Interactions of climate variables and angles, W is wind speed; S is short-wave radiation; T is temperature, O is orientation of primary axis to the sun (0^o- 90^o); A is agreement**.**

Short-wave radiation was a significant factor, reducing metabolic requirements by 25-36% during the day (average short wave radiation measured by the pyranometer was 184.2 W m^{-2} from 8:00 - 17:00, and 265 W m^{-2} between 10:00 and 15:00 when the pasture was exposed to sun's direct beam). The positive coefficient for temperature x short-wave interaction may reflect warm, sunny days, when cattle were near or above their upper critical temperature (Renecker and Hudson, 1986).

Metabolic requirements were not directly effected by orientation to the sun (main effect), but depended on short wave radiation (evident from the interaction term). Orienting perpendicular to the sun increases a cow's surface area exposed to the direct beam component of short-wave radiation. The thermal advantage of a perpendicular orientation will therefore be most pronounced on clear days, when the direct beam component makes up a larger percent of the total incoming solar radiation, and depending on the dimensions of the animal, and time of day (Chapter 2). In this simulation, the relatively small effect orientation appeared to have on metabolic requirements may reflect too few clear days when cows could experience high levels of direct short-wave radiation.

Orientation to the sun must be evaluated also in the context of potential tradeoff in orientation to the wind. Wind velocity and radiation increase and decrease metabolic requirements respectively, depending on the surface area exposed. A cow orienting relative to the sun or wind will inevitably be oriented relative to the other variable. The angle between wind direction and the azimuth can be used as a reference to evaluate a potential tradeoff between these two opposing factors (Chapter 3). Wind blowing from the same direction as the sun's azimuth is considered in "low agreement", because at any orientation, a cow must trade off either minimizing convective heat loss or maximizing heat gain. A 90^{o} angle between the two variables is considered "high agreement", because cows can orient in a way that is advantageous relative to both variables.

Statistical significance of orientation may have been reduced because of low agreement. Agreement in our data-set ranged only from 0^{o} to 60^{o} because wind direction was set at 180^{o}. This also means agreement angles were mostly low (less then 45^{o}) during mid-day when the effect of radiation is most pronounced.

Wind velocity influenced our cows less than short-wave radiation. Average wind velocity at the study site was 6 m s^{-1}, reaching a maximum of 16 m s^{-1}. Relative humidity between the first and third quartiles ranged from 43% to 66%. The lesser impact of wind may have been the result of the dry winter air. The contribution of wind velocity to heat loss might be higher under more humid conditions due to evaporative cooling. The presence of two windbreaks on our site meant that wind velocity was the only environmental factor that cattle were able to mitigate in any other way besides changing orientation. Cattle used the windbreaks during the day only on two occasions, but were observed lying or standing behind the windbreak almost every morning as the observer arrived (personal observation).

Cattle face away from strong winds during cold winter days. Resistance to heat transfer of fur pelts mounted on a flat heated plate parallel to the direction of low-velocity air-flow was 5% higher than those mounted perpendicular to the air-flow (Cena and Monteith, 1975; Campbell, 1980). However, Curtis (1983) did not find any thermal advantage for sheep orienting away from the wind. In a three-dimensional simulation, heat loss was greater for a cow orienting parallel to 1 to 4 m s^{-1} wind than when orienting perpendicular (Wu and Gebremhedin, 2002). During our 2003-2004 winter observation period, wind did not seem to be an important factor influencing orientation of our cattle, except on days when loose snow on the ground was lifted by strong gusts of wind (personal observation).

Our model seems to settle this apparent disagreement. At low wind speeds, a perpendicular orientation reduces overall coat conductance because the leeward side is completely protected. With strong perpendicular winds, coat insulation is disturbed (Ames and Insley, 1975), and whole body conductivity is lower with a parallel orientation. The inflexion point in our case was at approximately 5.2 m s^{-1} wind (Fig. 4.1), but this value may vary greatly because it depends on hair characteristics, animal shape, ambient temperature, and the irradiative environment.

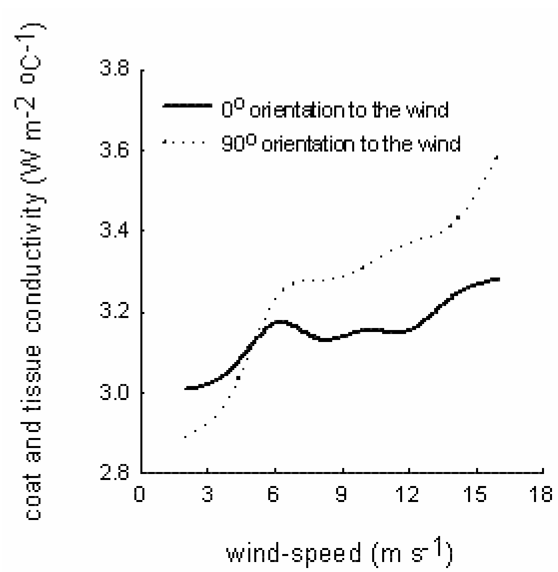

Fig. 4.1. Whole body conductivity as a function of wind speed at the extremities of orientation to wind direction. Solid line represents average conductivities of cows orienting perpendicular to the wind, and dotted line is cows orienting parallel to the wind.

Simulation 1 - Empirical Studies

We compared predictions from our model to three independent empirical studies that represent a variety of cold environmental conditions and research methods. Values obtained from our model were relatively close to those reported, but our model slightly under-predicted requirements for two of the three studies, and over-predicted in one.

Beef Cattle - Heifers. Resting metabolic rates of beef heifers (*Bos taurus*) housed outdoors and exposed to acute cold stress (-30 ^{o}C) for 4-5 hours were determined in a metabolic chamber (Young, 1975). Resting metabolic rates of these 422 – 491 Kg heifers were 4 Kcal h^{-1} $Kg^{-0.75}$ at mild temperatures (-1 to 3 ^{o}C), and 6 Kcal h^{-1} $Kg^{-0.75}$ at cold temperatures (-24 to –33 ^{o}C). Adjusted to their average body mass (456 Kg), our model predicted metabolic requirements of 3.3 Kcal h^{-1} $Kg^{-0.75}$ under mild conditions, and 4.6 Kcal h^{-1} $Kg^{-0.75}$ under cold conditions.

Metabolic requirements on a body weight basis predicted by our model for our lightest cow (480 Kg) were consistently 20% higher than the average metabolic requirements predicted for all twelve cows. Predicted requirements were 10% lower for our heaviest cow (757 Kg). Adjusting our model predictions to account for Young's (1975) lower body weights, predicted requirements are 4.8 and 5.7 Kcal h^{-1} $Kg^{-0.75}$, somewhat higher and slightly lower, respectively, than their measures.

Cattle in Young's (1975) study were acclimated in an open pen, exposed to solar radiation and ambient temperatures of -24 to -30 ^{o}C, but then brought into the metabolic chamber of -30 ^{o}C for measurements. The reported monthly ambient temperatures do not account for solar radiation and various ways that cows could conserve heat in the yard (e.g. orientation, huddling with other animals, etc.). Even for an individual acclimated to cold, when brought into a chamber, measured values may have represented a response to an acute cold incident, not basal metabolic rate, which might explain his slightly higher values.

Bison. Estimates of the metabolic requirements of free-ranging plains bison (*Bison bison*) were determined over a two year period with two methods (Rutley and Hudson, 2000). Dry matter intake estimates were 4.5 to 5 times higher based on bite counts rather than based on a chromium marker. This difference caused large variation in estimates of metabolic requirements for maintenance (ME_{main}). Requirements determined by the marker method were 270 ± 68 kJ $Kg^{-0.75}$ d^{-1} in December 1994, and 260 ± 22 kJ $Kg^{-0.75}$ d^{-1} in December 1995. Requirements based on bite counts were 818 ± 57 kJ $Kg^{-0.75}$ d^{-1} in December 1994.

Rutly and Hudson (2000) concluded they underestimated ME_{main} when using the chromium marker, and that the true value lies somewhere between the two methods. Differences between methods were consistent across seasons. Estimates based on the marker were higher than apparent ME_{main} in pen trials as well.

Using their reported body mass, our model predicted 265 kJ $Kg^{0.75}$ d^{-1} for their 1994 trial, and 297 kJ $Kg^{0.75}$ d^{-1} for their 1995 trial, similar to their marker estimates. Our predictions indicate that the chromium marker method did not underestimate requirements during winter, and that the true value is close to the chromium marker value.

Yellow Cattle. Yellow cattle (*Bos taurus*) grazing on the Tibetan Plateau (ambient temperature in January ranges from 0 to –30 ^{o}C), supplemented with a maintenance ration, were fasted for 4 to 7 days and then fasting heat production (FHP) was measured with a respiratory mask (Han et al., 2003). Fasting heat production at an ambient temperature of –5 ^{o}C and wind velocity of 2.5 m s^{-1} was 255 kJ d^{-1} $Kg^{-0.75}$.

Fasting heat production at ambient temperature of –15 ^{o}C and wind velocity of 5.2 m s^{-1} was 303 Kj d^{-1} $Kg^{-0.75}$.

Under these conditions, our model predicted similar values for cows weighing 300 Kg (the average weight of their mature cattle). Predicted heat production was 260 kJ d^{-1} $Kg^{-0.75}$ at mean ambient temperature of -5 ^{o}C and mean wind velocity of 2.46 m s^{-1}, and 301 kJ d^{-1} $Kg^{-0.75}$ at mean ambient temperature of -15 ^{o}C and wind velocity of 3.3 m s^{-1}.

Our model predictions of the metabolic requirements for fasted Yellow cattle matched their reported values better than our predictions for the two Canadian studies. This may be attributed to their more detailed description of weather conditions that allowed us to match a relatively accurate subset of weather conditions.

Our model predicts heat production of 333 kJ d^{-1} $Kg^{-0.75}$ at wind velocity of 5 m s^{-1} and ambient temperature of –13.6 ^{o}C. At wind velocity of 5.5 m s^{-1} this value increased to 362 kJ d^{-1} $Kg^{-0.75}$. Our estimates are higher than their measured rates; our model was developed at 1600 m, whereas they measured the Yellow cattle at more than 2250 m. Values reported by Han et al. (2003) include 2.5 year-old cows, which are most likely lighter than the mature 300 Kg cows that we based our predictions on.

Our cows seem to be affected by wind more than Yellow cattle described by Han et al. (2003), which have heavier fleeces than other breeds of cattle. Therefore, Yellow cattle may be better insulated than our cows and not as affected by wind velocity.

On cold clear days, their cattle may have absorbed more solar radiation (Han et. al, 2002) because the ratio of direct to diffuse components of short-wave radiation is higher at lower latitudes (36^o N at their site compared with 45^o N at our site), and the higher elevation of their study sites may have contributed to clearer skies.

Simulation 2

The first run of this simulation was used to detect possible limitations of our model. As a reference point for the three environmental variables, we used one standard deviation lower than the mean, the mean, and three standard deviations higher than the mean weather variables from our Winter 2003-2004 data. All permutations of temperature, wind, radiation, and orientation were repeated with wind direction at 0^o and 90^o relative to the sun, which correspond to disagreement and agreement of wind and radiation, respectively.

Our model evaluates the amount of radiation absorbed by the surface of a cow according to it's orientation relative to the sun's elevation and azimuth (Chapter 2). If $\sin^{-1}$ of the total short-wave irradiance on a horizontal surface (I_h) exceeds the solar constant at the zenith, the model returns a negative surface area value. At the date and time (21 January, 12:38 PM) chosen for this simulation, 569 W m^{-2} was the maximum value possible for I_h.

In our model, metabolic requirements increased linearly as ambient temperatures decreased up to T_a = -60 ^oC, which is the lower temperature limit of our model. At this extremely cold temperature and below, average metabolic requirements exceeded 400 W m^{-2}, reaching values of 1200 W m^{-2}. More importantly, the relationship between ambient temperature, wind velocity, and radiation did not make sense at these extremes; requirements increased due to higher radiation loads, and lower wind velocities. The effects of wind velocity on metabolic requirements, and the way it interacted with other variables was constant at velocities up to 50 m s^{-1}. There did not seem to be a limit on extreme wind velocities that the model could handle.

Once these limits were established, a four (variables) by five (levels) matrix of equal increments was expanded to include all possible permutations of environmental factors and orientation. Levels of the different variables were: short-wave radiation (0, 142, 285, 427, 570) W m^{-2}, ambient temperature (-5,-10,-15,-20,-25) ^{o}C, wind (0, 4, 8, 12, 16) m s^{-1}, and orientation relative to the sun (0^{o}, 22.5^{o}, 45^{o}, 67.5^{o}, 90^{o}). Metabolic requirements were best described as a function of all five variables, where the predictors short-wave radiation, temperature, and wind are polynomials of the third degree (Table 4.2). The effect that environmental variables had on metabolic requirements in this simulation was rather intuitive (Fig. 4.2, 4.3), and similar to those discussed in Simulation 1, except for orientation and agreement.

Orientation significantly reduced ($\alpha < 0.1$) metabolic requirements under all conditions, and interacted with other variables besides radiation to reduce metabolicrequirements. In the completely balanced design of these data, agreement reduced metabolic requirements somewhat (P-value = 0.104). However, agreement is important biologically because it represents surface area exposed to the wind in the context of tradeoffs with radiation (Fig. 4.4). Orientation to the wind is not an independent variable in our model, but is reflected in the relationship between orientation relative to the azimuth, wind velocity, and agreement.

Table 4.2. Estimates, standard errors, and P-values of polynomial regression coefficients (adj.R^2 = 0.8976).

	Estimate	Standard Error	Pr(>|t|)
Intercept	6.5E+01	6.4E+00	<0.001
I_h	1.5E-01	2.2E-02	<0.001
I_h^2	-8.8E-04	7.8E-05	<0.001
I_h^3	8.9E-07	9.0E-08	<0.001
T_a	2.2E+00	1.3E+00	0.089
T_a^2	3.3E-01	9.4E-02	<0.001
T_a^3	8.3E-03	2.1E-03	<0.001
μ	1.4E+01	7.7E-01	<0.001
μ^2	-1.1E+00	1.0E-01	<0.001
μ^3	3.0E-02	4.1E-03	<0.001
$Ø_{pa}$	-1.5E-01	5.9E-02	0.013
$Ø_{ws}$	-8.3E-02	5.1E-02	0.104
I_h x $Ø_{pa}$	3.8E-04	1.9E-04	0.045
I_h x Ta	1.3E-03	5.9E-04	0.030
I_h x μ	1.1E-04	1.3E-03	0.928
I_h x $Ø_{ws}$	3.6E-05	1.5E-04	0.807
$Ø_{pa}$ x μ	3.9E-02	6.0E-03	<0.001
$Ø_{pa}$ x $Ø_{ws}$	1.8E-03	9.3E-04	0.049
T_a x μ	-9.0E-02	1.9E-02	<0.001
M x $Ø_{ws}$	2.7E-02	5.2E-03	<0.001
I_h x $Ø_{pa}$ x T_a	-1.4E-08	5.6E-06	0.998
I_h x $Ø_{pa}$ x μ	-1.2E-04	1.7E-05	<0.001
I_h x $Ø_{pa}$ x $Ø_{ws}$	-9.8E-07	2.7E-06	0.712
I_h x T_a x μ	-1.5E-04	5.5E-05	0.006
I_h x μ x $Ø_{ws}$	-2.7E-05	1.5E-05	0.067
$Ø_{pa}$ x μ x $Ø_{ws}$	-6.1E-04	9.4E-05	<0.001
I_h x $Ø_{pa}$ x μ x $Ø_{ws}$	7.2E-07	2.7E-07	0.008

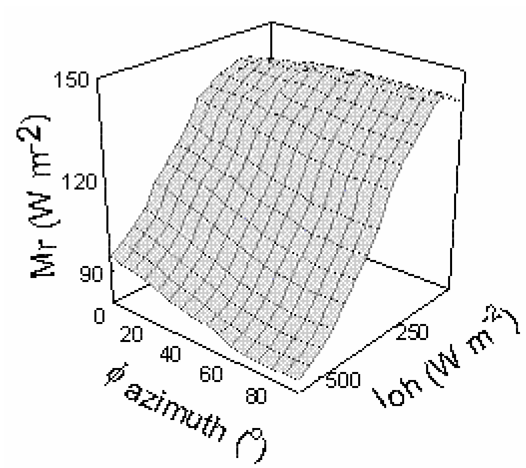

Fig. 4.2. Predicted metabolic requirements of cattle as a function of short-wave irradiance on a horizontal surface (I_{oh}) and orientation of the primary axis relative to the sun's azimuth. Ambient temperatures range from -5 to -25 ^{o}C, wind velocities range from 0 to 16 m s^{-1}.

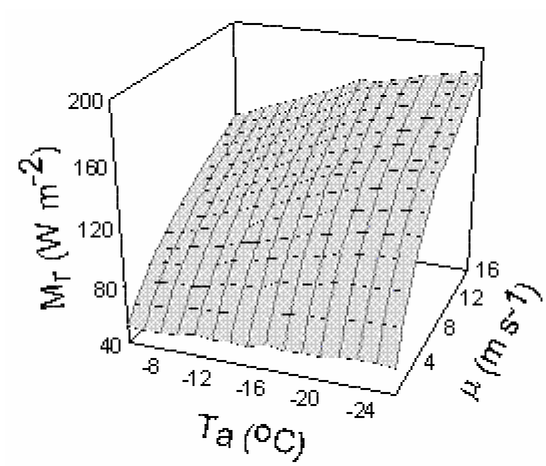

Fig. 4.3. Predicted metabolic requirements of cattle as a function of ambient temperature and wind velocity across all orientations and agreement angles. Maximum short-wave radiation equals 570 W m^{-2}.

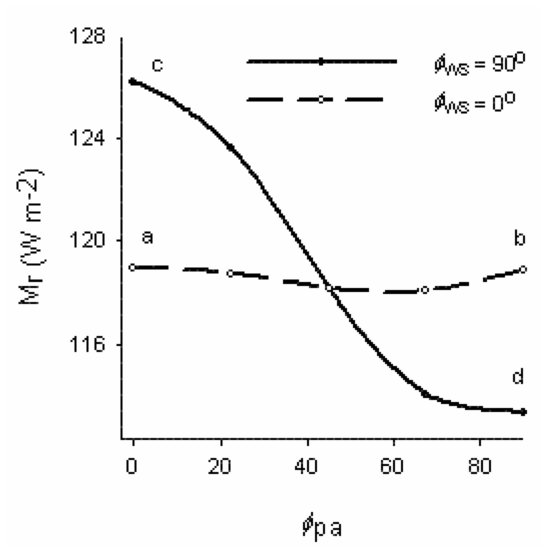

Fig. 4.4. Predicted metabolic requirements as a function of orientation to the wind. Solid line; fitted curve through observations when the wind and the azimuth are in complete agreement. Dashed line; when the wind and azimuth are in complete disagreement. Letters correspond to cows in Fig. 3.2; a) convective heat loss is minimized, but so is radiation absorbed, b) radiation absorbed is maximized, but so is convective heat loss, c) radiation absorbed is minimized and convective heat loss is maximized, d) radiation absorbed is maximized and convective heat loss is minimized.

At wind velocities less than 2 m s^{-1}, and an irradiative environment of I_h = 570 W m^{-2}, our model predicted that the metabolic requirements for beef cattle are constant between –10 to –30 ^{o}C (Fig. 4.5). This range of values may be somewhat lower than conservative estimates of thermal neutral zone (Webster, 1974), but may reflect that culling cows that fail to rebreed following winter selects for cattle matched to conditions typical of our area.

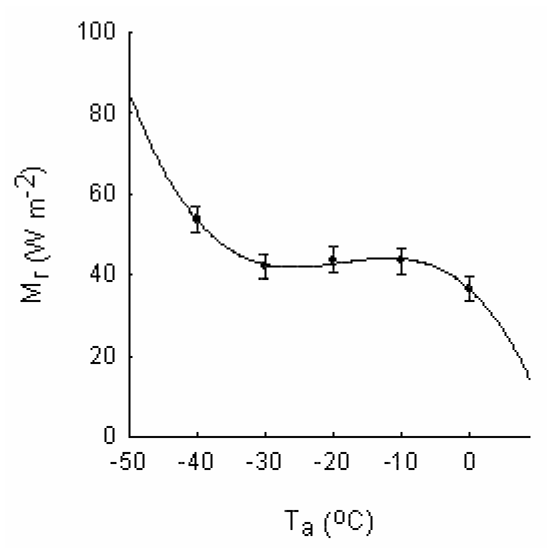

Fig. 4.5. Predicted metabolic requirements, averaged for all orientations and agreement angles, as a function of ambient temperature. Short-wave radiation is 570 W m^{-2}, wind velocity is less than 2 m s^{-1}.

Results of this simulation illustrate the importance of the irradiative environment in countering the cooling effect of wind. Metabolic requirements of cattle vary with wind velocity and orientation to the wind (Fig. 4.6). The difference between Fig. 4.6a and 4.6b in the effect orientation has on metabolic requirements at high wind speeds (c vs. d) represents the complexity of the relationship between radiation and wind. When radiation and wind are in agreement (Fig 4.6a), a proper orientation results in an additive effect of these two variables. Contrary, when agreement angles are low, then there is a contrasting effect at any orientation.

Fig. 4.6b compares the advantage of an orientation which minimizes convective heat loss relative to one that maximizes heat gain. At –15 °C, an orientation of 0° to the wind direction does not have a thermal advantage over orientations that increase surface area exposed to 285 W m^{-2} of short-wave radiation. The inflection point (e) is at wind velocities higher than 11 m s^{-1}, where an orientation which reduces convective heat losses becomes thermally advantageous.

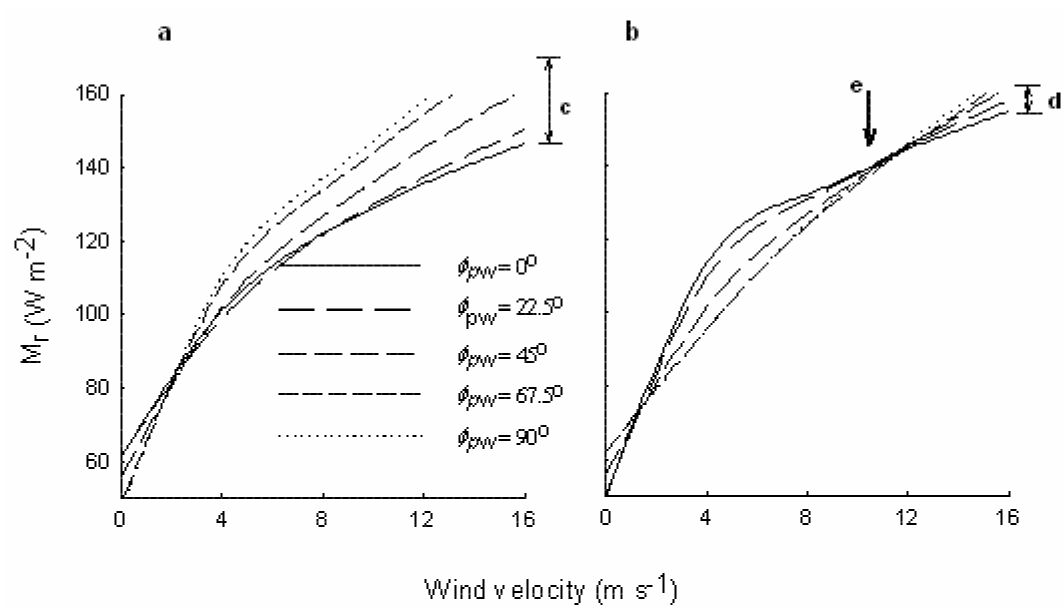

Fig. 4.6. Predicted metabolic requirements as a function of wind velocity when agreement is highest (a) and lowest (b) at incrementing orientations relative to the wind. Data is averaged across all levels of short-wave radiation (285 W m^{-2}) and ambient temperatures (-15 °C).

Implications

Our model was a useful and seemingly accurate tool to quantify metabolic requirements of free-ranging cattle under naturally occurring cold weather conditions in southwestern Montana. Our model predicted values of metabolic requirements in winter similar to results reported by empirical studies with three different methods and different animals.

Results from two model simulations indicate there is only a small increase in metabolic requirements due to cold exposure in mature beef cattle in a maintenance state. For many combinations of winter weather variables, metabolic requirements predicted by our model were close or lower than basal metabolic rate. Thus, requirements may have been previously overestimated for acclimated cattle grazing winter range. Behavioral responses to environmental variables such as lying and orientation helped mitigate the effects of extreme weather conditions, allowing cattle to maintain a relatively constant metabolic rate.

In our area, where high winds are associated with moderate temperatures, cattle did not seem to be as negatively affected by wind as reported by others, or make direct use of windbreaks during the day, perhaps because this reduces their grazing time. Cattle may obtain thermal benefits from windbreaks at night and in early morning when solar radiation does not counter the negative effect of wind.

Solar radiation contributed to lower metabolic requirements especially on cold, clear days, and because of our representative ellipsoid's dimensions, in early morning when the sun is at lower elevation angles. Our model emphasizes the contribution of the irradiative environment to cattle's ability to conserve energy in winter, and illustrates the potential benefits of considering daily exposure to direct solar radiation when, for example, choosing winter pastures or deciding on winter husbandry practices.

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THERMAL IMAGING SOFTWARE

Introduction

Studies on the metabolic requirements of cattle and wildlife during winter often fail to account for interactions between animal behavior and their environment. Cattle and wildlife may conserve energy and reduce cold stress associated with ambient weather conditions by altering activity patterns (Olson and Wallander, 2002; Schaefer and Messier, 1996; Redbo et al., 1996), seeking shelter (Beaver and Olson, 1997; Houseal and Olson, 1995; Redbo et al., 2001), and lowering metabolic rate (Arnold et al., 2004; Cuyler and Oritsland, 1993; Mesteig et al., 2000).

Cattle that cannot seek moderate microclimates may rely on short-term responses to a changing environment to mitigate cold stress. Orienting to the sun to maximize irradiative heat gain on cold, sunny days may contribute significant energy to an animal's thermal balance (Walsberg, 1992), and thereby allow an exposed cow to tolerate a wide range of weather conditions during winter. As the sun angle changes daily and seasonally, or wind changes velocity and direction, an animal's exposed surface area and insulation are affected differentially. A cow standing perpendicular to the sun's ray will absorb more short-wave radiation than a cow standing parallel to the sun (Clapperton et al., 1965). The flow field around an animal and consequently the boundary layer's resistance to heat loss will differ depending on animal shape and orientation to the wind (Wu and Gebremedhin, 2001).

Models derived from controlled environments may not accurately predict metabolic demands of cattle grazing winter range (Bergen et al., 2001; Block et al., 2001). Such models do not account for the behavioral and physiological responses of free ranging cows (Malechek and Smith, 1976; Yousef, 1989), or complex interactions between environmental factors and animal behavior to reduce the impact of the environment (Lefcourt and Schmidtmann, 1989).

In previous work (Chapters 2-4), we modeled heat exchange of cattle grazing winter range. An ellipsoid representing a cow was allowed to rotate to simulate different orientations of cattle with respect to wind direction and the sun's direct beam. All forms of heat losses or gains through three layers of insulation (tissue, coat and boundary layer) were computed in series for every degree of exposure to the sun and wind. We then solved the thermal balance equation (Campbell and Norman, 1998) for cattle observed at one hour increments during the winter of 2003-2004.

Our model predicted that cattle can tolerate a wide range of winter conditions in Montana, and that similar to wildlife, cattle may be able to lower metabolic rates to conserve energy during winter, despite episodes of extreme cold conditions. Cattle mitigated the effects of microclimate and reduced energetic demands through short-term behavioral responses to the changing environment, mainly orientation to the sun’s direct beam and seeking shelter from strong winds.

By outlining a procedure to estimate heat loss from a dynamic, three-dimensional shape exposed to changing environmental conditions, we developed a model that accounts for animal behavior in the natural environment, and accurately predicts metabolic requirements of free-ranging cattle. However, in developing our model, we had to concede the complexity of some biological processes for the sake of calculations, which somewhat limits our model's predictions, for the following reasons.

Animals are not simple geometrical shapes as our representative ellipsoid, and the model may imprecisely estimate irradiative gains or boundary layer turbulence. A cow is treated as a 3-layer shell with no internal heat source. Each layer's heat transfer values are calculated independently based on external environmental conditions, and not in series. i.e. blood vessels constrict or dilate to change tissue resistance based on ambient temperature, and not skin temperature. Heat can only be lost to, not gained from, the environment, and mechanisms of thermal regulation that require energy input such as shivering or panting were not modeled. Thus, our model predicts the energy demands of a set of environmental conditions, and applies them to cattle's insulation characteristics to predict metabolic heat production required (M_r) to counter the demand and maintain a thermal balance. The pathway in which M_r is gained and thermal balance achieved, whether through the heat increment associated with feed or other mechanisms is beyond the scope of our model. During warm spells, predicted values of M_r in winter may be lower than the minimum basal metabolic rate physiologically possible, i.e., if cattle are above LCT (lower critical temperature), the actual metabolic rate, which may be influenced by levels of activity and plane of nutrition, is not predicted.

In part, our model was developed based on empirical data. Cattle grazing a relatively flat, exposed pasture in southwestern Montana were observed from dawn to dusk at one-hour intervals. Our model predictions for complex scenarios and different environments, or on a 24 hour basis, are limited. We used the model to predict metabolic requirements of cattle and bison under a wide range of winter weather conditions from independent empirical studies (Han, 2003; Rutley and Hudson, 2000; Young, 1975). These studies estimated fasting heat production, resting metabolic rate, and net energy requirement for maintenance using a respirometer, environmental chamber, and a chromium marker, respectively. Our model predicted requirements that matched the reported values. Our model was developed based on a small group of Hereford x Angus beef cattle that were relatively homogeneous in their physical characteristics such as size and weight, back-fat thickness and body condition score, coat color and hair lengths. Using the model to predict requirements of other animal species or even breeds of cattle may be limited.

Exposure of cattle to a certain set of environmental conditions is continuous in nature, but the continuity could not be accounted for in our model; we sampled animal behavior at one hour increments. Much of the unexplained variation among individuals cows within a given observation might reflect the relatively long sample increment, i.e., a cow standing perpendicular to the sun’s rays for the better part of an hour will have a different value than one turning to the same direction just before it was observed, yet in the model both are "assigned" the same "ranking" of environmental conditions and orientation.

We developed a three-dimensional computer model of a cow to improve on our previous assumptions in calculations, refine our geometric shape, expand our model beyond the limitations of our empirical data, and account for the continuous nature of the environmental influence on free ranging cattle. We applied RadTherm Pro 7.1., a thermal solution software developed for inanimate objects, to a living organism. This platform enabled us to simulate complex scenarios of the interactions between animal activity and weather conditions.

<u>Model Development</u>

A three-dimensional computer model of a cow built in Rhino 3.0 (Robert McNeel and Associates. Seattle, Wash.) was integrated with thermal analysis software RadTherm Pro 7.1. (Thermoanalytics Inc., Calumet, Mich.). Our model consists of a three-layer geometric shape of a standing cow (Fig. 5.1).

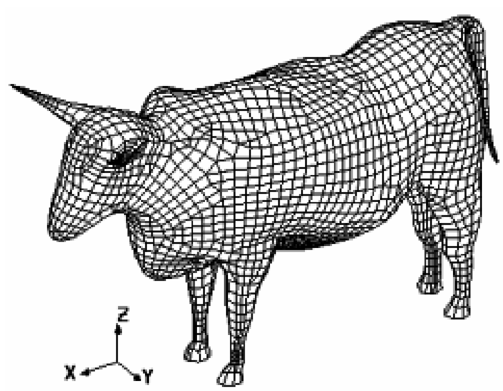

Fig. 5.1. Wire frame image of a three-dimensional computer model of a cow.

To help develop the model, we used available data from our previous work on behavior (activity and orientation) and surface temperatures of twelve mature Angus x Hereford cows (654 Kg) observed from 23 November 2003 to 21 January 2004 at the Red Bluff Research Ranch near Norris, Montana (for a complete description of materials and methods of model development, see Chapters 2 and 4). At the start of the observation period, cows were weighed, body condition was scored, back-fat was ultra-sounded, and dimensions and hair length of the cows were measured. These values were used to determine the model cow's dimensions and thickness of various layers. Conductance coefficients for the three layers, and material properties were derived from our measured data and results of our previous model based on the scientific literature (Chapter 2). We validated the model by comparing RadTherm output for the outermost layer with our measured surface temperature data.

Input

The model consists of three homogeneous physical layers (Table 5.1) applied to a surface geometry. The surface geometry was exposed to multiple runs of simulated natural environments based on our weather station data.

Table 5.1. Properties of two[a] layers in our model.

Layer	thickness (mm)	density ($Kg\ m^{-3}$)	conductivity ($W\ m^{-1}\ K^{-1}$)	specific heat ($J\ Kg^{-1}\ K^{-1}$)
Back-fat[b]	36.458	850	0.211	7.15
Coat[c]	34	56.67	0.128	1200

[a] as material for the middle layer we used 0.05 mm thick Leather in RadTherm's library.
[b] From (Price and Schweigert, 1987)
[c] Coat density adapted from Gilbert and Bailey (1991)

RadTherm does not allow changing conductivity values of a material during a run. To account for increased convective heat losses in cattle coats exposed to high wind velocities (Ames and Insly, 1975), we wrote a routine that incorporates the value for free convection of the coat into McAdam's laminar flow model used in RadTherm to estimate boundary layer conditions. We used the moving vehicle scenario available in RadTherm to account for changes in cattle orientation during the day through the "heading" curve option.

Validation

The model can be readily validated using an Infra-red thermometer to compare predicted surface temperature in the outermost layer of the computer model with measured surface temperature (Fig 5.2). However, we did not observe our cows with the purpose of validating the software in mind. Thus, because of our sampling routine, our field data does not convert well to a RadTherm scenario, for the following reasons.

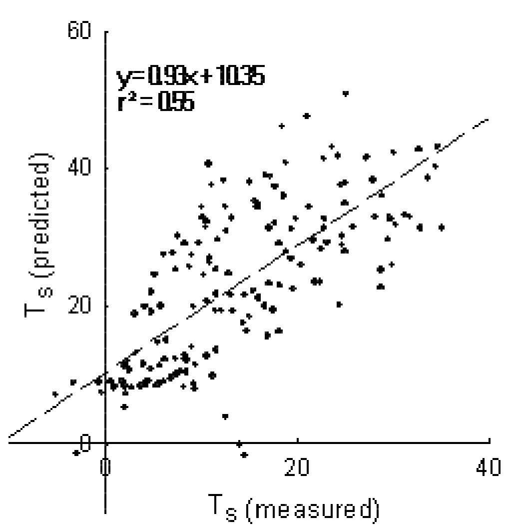

Fig. 5.2. Measured (Infra-red thermometer) and predicted (RadTherm) surface temperatures for January 2004.

RadTherms assumes a linear relationship between samples in it's heading curves, i.e., if a cow was oriented 20° at 10:00 AM and 200° at 11:00 AM, a linear curve with a slope of 3° min^{-1} is assumed for that hour. Since we sampled orientation every hour, cows may have been at a constant orientation for the better part of the hour, changing only at the end, or had ample opportunity to change orientations many times in between samples. Thus, large differences may exist between the scenario and the true orientation. A more appropriate validation would require a continuous data set, i.e. a cow would have to be followed continuously and changes in orientation, rather than an absolute number recorded at fixed increments.

We set the time step in RadTherm to 60 minutes because of hardware limitations, while in the field twelve cows were observed over a 10 to 20 minute period every hour, depending on the group's dispersion and location in the field. For our validation, we compared the RadTherm solution to the average surface temperature and orientation of all twelve cows. This may have contributed to the low fit in some cases, and predictions may be better if we had observed an individual cow and compared only those measures with RadTherm predictions.

We did not directly record some of the input required as material properties for the different layers such as coat density and thickness. Values had to be assumed based on the literature and our data on individual hair length. More complete information of our cow's insulation characteristics would allow us to create more realistic layers of insulation.

Despite the limitations described above, RadTherm predictions matched our empirical data quite well. Correlation coefficients (r) for all 19 days in the winter of 2003-2004 on which cattle were observed were 0.8 and 0.7 for the left and right sides, respectively. Focusing on the month of January, which had a wide range of weather conditions, the correlation was similar; 0.85 and 0.68 for the left and right sides, respectively. Surface temperatures of the entire RadTherm cow object relative to averages of the left and right sides varied among days; R^2s in January ranged from 0.5 to 0.9 (Fig. 5.3). Variation of the fit between days may be attributed to different environmental conditions, although there was not a consistent pattern for higher or lower R^2s, or the values of slope and intercept between measured and predicted values.

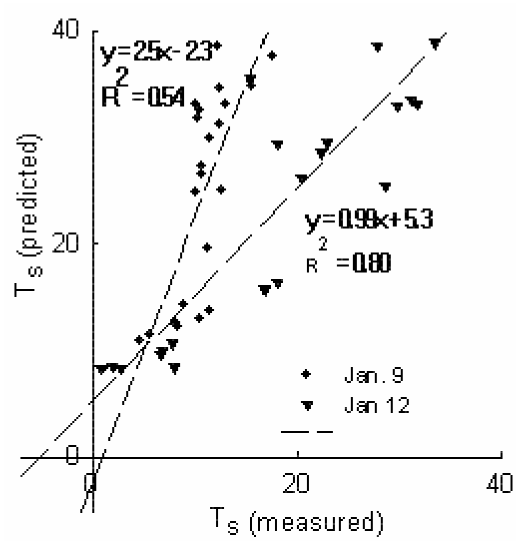

Fig 5.3. Measured (Infra-red thermometer) and predicted (RadTherm) surface temperatures for two days on January 2004.

Simulation

We predicted the energy (W m^{-2}) needed to maintain the innermost node (body core) at a temperature of 39 ^oC on two days; January 5, 2004 and January 12, 2004. The simulation was run three times: with orientation measured in the field, for cattle oriented parallel to the sun's azimuth, and for cattle oriented perpendicular to the sun's azimuth. Wind direction was set at 180^o (south), the prevailing wind direction at our site. We chose these two days because of their similar wind velocity and irradiative environment at different temperatures; January 5 was a cold clear day, whereas January 12 was a warm day. Wind velocity relative to typical days at our site was low, and similar between the two days (Table 5.2). We selected these particular days because they differed only in ambient temperature so there was no interaction with other weather variables, and more importantly, because of their good fit between measured (T_{sm}) and predicted (T_{sp}) surface temperatures;

January 5: $T_{sp} = 0.89\ T_{sm} + 1.8\ ^{o}C$, $R^2 = 0.77$

January 12: $T_{sp} = 0.99\ T_{sm} + 5.3\ ^{o}C$, $R^2 = 0.80$

Table 5.2. Day-time (07:40 - 17:30) average weather conditions on two days in January.

Variable recorded	5-Jan	12-Jan
Temperature (^{o}C)	-28.5	-3.5
Wind velocity (m s^{-1})	2.76	2.40
Short-wave irradiance on a horizontal surface (W m^{-2})	195	204
Net-radiation (W m^{-2})	11	81

Metabolic requirements predicted by RadTherm were 15 Mcal d^{-1} for the 24 hours starting at 8:20 AM on Jan. 5, and 11 Mcal d^{-1} for the same time frame on Jan. 12. Predicted energetic requirements of beef cattle on native range in Nebraska using the NRC (1996) model, were 14.5 and 10.5 for the months of December and January, respectively (Lardy et al., 2004).

Our predicted values are for two days only, whereas they used the long term temperature average. Based on a 30 year average, monthly temperatures in Nebraska are -3.8 and -5.4 ^{o}C for December and January respectively (NSCO, 2004). January 5th, the coldest day in our data set, was part of a cold spell that lasted only a few days; although January 12 was warmer than the monthly average (-8 ^{o}C), it was not the warmest day in our data set.

The values obtained with the NRC model are for summer calving cows on native range during winter, but were not adjusted for the "on pasture" feature of the NRC model, which would have returned unreasonably high values (Lardy et al., 2004). They also recommend setting wind velocity in the NRC model to less than 8 km hr^{-1} (2.2 m s^{-1}) to avoid overpredicting requirements. Although in this comparison our wind velocity values were only slightly higher than the value above, based on other simulations of windier days, our model predictions remain stable even at higher wind velocities, partly because we can account for cattle behavior (unpublished data).

Daily requirements of a cow in this simulation varied greatly between days (Table 5.3). On January 12, cows were above their LCT during the day time, and metabolic requirements were only higher than the basal metabolic rate (approximately 50 W m^{-2}) when night was included. The night of January 4-5 was a cold night (average -35 ^{o}C from 17:30 on Jan. 4 to 7:40 on Jan. 5). Measured surface temperatures at 9:00 AM (the start of the simulation) averaged -24 ^{o}C. Still, the predicted average requirement for that day was relatively low (59 W m^{-2}), and similar to the value obtained from a 90^{o} orientation.

Results of this simulation highlight how cattle behavior such as orientation to the sun reduces environmental stress. In the first half of January, view factor (F), the predicted surface area exposed to direct solar radiation (solar apparent area) as a fraction of total surface area, for a cow at an orientation of 90^{o} was 0.29. On January 5, F was 0.28, which is an efficiency (the ratio between the actual F and the maximized potential at an orientation of 90^{o}) of 96.5%, compared with January 12 when F equaled 0.21

(efficiency = 72.4%). For reference, an orientation of 0^o to the azimuth on January 5 would have resulted in a 28% increase in requirements (76 W m^{-2} versus 59 W m^{-2}).

Table 5.3. Day time (09:20 - 17:20) averages of predicted metabolic requirements (W m^{-2}) at simulated and observed orientations, and for a 24 hour period, on two days in January.

Orientations to the azimuth	5-Jan	12-Jan
observed	59	36
90^o	59	32
0^o	76	48
24 hour[a]	94	68

[a] Average for a 24 hour period starting at 08:20 AM and ending the following morning. The "observed" day time orientation was used, and cattle were assumed to be behind the windbreak at night.

Implications

In this study we successfully applied RadTherm Pro-7.1 to a biological system. A three-dimensional computer model of a cow exposed to natural weather conditions was a useful tool in the study of heat exchanges between cattle and their winter environment.

The model was created within the confines of our data and the software, which as yet, is not completely appropriate for modeling of a biological system because of the inability to redefine material properties during a simulation. In our model, properties of the different layers are affected by environmental variables and the passage of time, e.g. coat hair ruffled by wind, back-fat layer is thicker at the start of the season, etc. However, custom algorithms can address some of these problems, and the model predicted metabolic requirements for grazing cattle in winter well within the known and expected range of values.

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CONCLUSION

Cattle grazing winter range in Montana may adjust their behavior in response to changing environmental conditions, thus reducing energy demands during the winter months. A comprehensive thermal balance model can be a useful and accurate tool to quantify metabolic requirements resulting from behavioral adjustments.

Until recently, complex relationships between animal behavior and ever changing microclimates reduced our ability to extrapolate results obtained in a controlled setting to the field. Simulation models of complex systems and scenarios can be developed with relative ease, yet few studies have attempted to account for the dynamic relationships between animals and environmental variables.

We developed a model to predict metabolic requirements of cattle in the field based on the scientific literature and empirical data. The physical laws of heat and mass transfer through the insulation layers of mature beef cattle were applied to a rotating three-dimensional shape representing a cow in different activities and orientations relative to environmental variables.

Results from our model simulations indicate there is only a small increase in metabolic requirements due to cold exposure in mature beef cattle in a maintenance state. Thus, requirements may have been previously overestimated for acclimated cattle grazing winter range in the Intermountain west. Behavioral responses to environmental variables such as lying down and orientation to the sun and wind helped mitigate the energetic demands of extreme weather conditions, allowing cattle to maintain a relatively constant metabolic rate.