

MATHEMATICAL ANALYSIS OF THE OPERATIVE TEMPERATURE AND ENERGY BUDGET

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Abstract—1. An exact, explicit quartic solution to the energy budget can be used to calculate the operative temperature, the surface temperature of a wet organism, and the metabolic rate.

2. All of the approximations and iteration methods arrive at solutions close to the proper root and do not converge around the other three physically unrealistic roots.

3. A second-order Taylor approximation is satisfactory, but the first-order Taylor approximation is not.

4. A new simple 4th order polynomial is introduced to estimate the saturated vapor pressure function.

5. Partial differential analysis is used to show the errors associated with the use of mounts and mount analogs.

Key Word Index—Energy balance; biometeorology; partial derivatives; sensitivity analysis; numerical methods.

INTRODUCTION

The operative temperature (also called the environmental or effective temperature) and associated energy budget analysis has been extensively used in physiological ecology, biometeorology, and thermal biology in the past decade, although it was first identified more than 40 years ago (Winslow *et al.*, 1937, 1940; Gagge, 1940; Gonzalez *et al.*, 1974; Bakken, 1976). The use of the operative temperature is analogous to the recent use of surface temperatures for both wet and dry energy budgets for plants (Paw U, 1983; Paw U and Daughtry, 1984). When the surface of an animal is wet, the surface temperature can be used in physiological ecology (Campbell, 1977; Tracy *et al.*, 1984); the dry energy budget can be used to show that a mount (basically an organism stuffed with a hollow copper or other metal shell) temperature is ideally the operative temperature.

The energy budget and therefore the operative temperature and surface temperature are usually not analyzed with exact mathematical procedures; it has been stated that such equations are difficult or even impossible to solve explicitly (Gates, 1980; Tracy *et al.*, 1984). The most common technique used for solution is a linearized first-order Taylor approximation of the non-linear terms, the emitted longwave radiation and for wet surfaces, the saturation vapor pressure. Although this linearization allows for simple solution combined with increased understanding of the conceptual relationships between the energy budget variables, its accuracy decreases as the surface or operative temperature departs from the air temperature (Tracy *et al.*, 1984). More accurate solution to the energy budget equation and the operative temperature may be obtained using Newton-Raphson or other iterative procedures (Gates and Papias, 1971; Tracy *et al.*, 1984).

Two problems occur when iterative solutions are

used for the energy budget and operative temperature equations. The first is that the accuracy must be improved by increasing the number of iterations. Thus the computation time is increased, which slows computer runs when the method is used frequently in large programs. The second problem is that the operative temperature equation, when properly solved, should have 4 roots as a result of the longwave radiation being proportional to the fourth power of temperature. At least one of these roots should be realistic in a physical sense. An iterative solution will converge on only one of the four solutions, and the solution might not be the "correct" one. A similar problem exists when the iterative method is used to solve for the wet surface energy budget and surface temperature. In addition to the longwave radiation term, a non-linear saturation vapor pressure term must be included.

In this paper, an exact analytical set of solutions is shown to exist for the operative temperature and estimated metabolic heat production rates. A nearly exact explicit set of solutions is also shown to exist for the surface temperature of wet organisms. The solution for the wet case is nearly exact because the saturation vapor pressure function is described as a fourth-order polynomial instead of the usual transcendental functions previously used. It is also shown that the higher-order Taylor approximations result in more accuracy than the simple linearization of the energy budget. Finally, elementary differential calculus is carried out for sensitivity and error analysis, with applications to the experimental measurement of the operative temperature.

SOLUTION OF THE OPERATIVE TEMPERATURE

The operative temperature T_E is equivalent to the surface and body temperature of a dry, perfect ectotherm, neglecting any thigmothermy. The dry energy

budget is thus greatly simplified:

$$Ri = H + \epsilon \sigma T_E^4 \quad (1)$$

where Ri is the radiation flux density absorbed in both the short- and longwaves, ϵ is the emissivity, σ is the Stefan-Boltzmann constant, T_E is the body and surface temperature of the dry ectotherm and H is the sensible heat flux density (also referred to as the convective heat transfer flux density). If simple gradient-flux relations are assumed, then H is proportional to the difference between the surface temperature T_E and the air temperature T_a . The equation for the operative temperature can be obtained by rearranging the energy budget:

$$Ri = \epsilon \sigma T_E^4 + \rho C_p (T_E - T_a) / r_A \quad (2)$$

where ρ is the air density, C_p is the specific heat of air, and r_A is the aerodynamic resistance to sensible heat transfer (this can be estimated using engineering formulas with the Nusselt or Grashof numbers). The common way to solve for the operative temperature is to linearize equation (2), using a first order Taylor approximation for the longwave term [which appears as the first term on the right-hand side of equation (2)]:

$$T_E = (Ri - \epsilon \sigma T_a^4) / (\rho C_p / r_A + 4 \epsilon \sigma T_a^3) \quad (3)$$

The accuracy of the linear approximation decreases as the difference between air temperature and operative temperature increases.

A simple way to increase the accuracy of the solution is to use a second-order Taylor approximation for the longwave term, which results in a quadratic expression:

$$6 \epsilon \sigma T_a^2 (T_E - T_a)^2 + ((\rho C_p / r_A) + 4 \epsilon \sigma T_a^3) (T_E - T_a) + \epsilon \sigma T_a^4 - Ri = 0 \quad (4)$$

The solution to the quadratic expression is simple, by using the well-known quadratic formula:

$$T_E - T_a = \frac{-b \pm (b^2 - 4ac)^{1/2}}{2a} \quad (5)$$

where a , b and c are the quadratic coefficients for equation (4) in terms of the variable $(T_E - T_a)$.

Iterative solutions are also used to solve the operation temperature equation. The most widely used method is the Newton-Raphson method. In each iteration a new value for the variable is calculated using the previous iteration value, a function of the previous value, and the derivative of the function:

$$T_{i+1} = T_i + f(T_i) / f'(T_i) \quad (6)$$

where T_{i+1} is the latest iteration value of T , T_i is the last iteration value, $f(T)$ is the energy budget residual function, defined as

$$f(T_i) = Ri - \epsilon \sigma T_i^4 - \rho C_p (T_i - T_a) / r_A, \quad (7)$$

and $f'(T_i)$ is the derivative of f ,

$$f'(T_i) = -4 \epsilon \sigma T_i^3 - \rho C_p / r_A. \quad (8)$$

The first iteration value for T_E is usually the linearized solution to T_E (Tracy *et al.*, 1984).

The new solution T_E presented here is an exact

analytical solution for the operative temperature. Equation (2) for the energy budget, used in the definition of the operative temperature, can be treated as a reduced quartic equation (i.e. a 4th-order polynomial) which has an exact solution with 4 roots. Only cube roots and square roots are used in the solution. The solution is facilitated when equation (2) is put in the following reduced quartic form:

$$T_E^4 + T_E (\rho C_p / \epsilon \sigma r_A) - T_a (\rho C_p / \epsilon \sigma r_A) - Ri / \epsilon \sigma = 0 \quad (9)$$

with the quartic coefficients c and d defined such that equations (9) and (9a) are equal:

$$T_E^4 + c T_E + d = 0, \quad (9a)$$

The exact solution to equation (9a) is determined by solving the resolvent cubic equation,

$$y^3 - 4dy - c^2 = 0 \quad (10)$$

which has the real solution,

$$y = (c^2/2 + (c^4/4 - 64d^3/27)^{1/2})^{1/3} + (c^2/2 - (c^4/4 - 64d^3/27)^{1/2})^{1/3}. \quad (11)$$

The 4 exact roots for T_E are then,

$$T_E = -y^{1/2} \pm (-y + 8c/(4y^{1/2}))^{1/2}/2 \quad (12a)$$

$$T_E = -y^{1/2} \pm (-y - 8c/(4y^{1/2}))^{1/2}/2. \quad (12b)$$

SOLUTIONS TO THE SURFACE TEMPERATURE OF WET ORGANISMS

In a similar manner to the solutions presented above for the operative temperature, the wet surface temperature of an organism (also called the wet equivalent blackbody temperature) may be derived. An additional component is the saturation vapor pressure which must be treated. The energy budget from which one may estimate the surface temperature T_s is:

$$Ri = \rho C_p (T_s - T_a) / r_A + \rho C_p (e_s(T_s) - e_a) / (\gamma (r_s + r_A)) + \epsilon \sigma T_s^4 \quad (13)$$

where $e_s(T_s)$ is the saturation vapor pressure of water vapor at the surface temperature, e_a is the ambient water vapor pressure, γ is the psychrometric constant (which is slightly affected by temperature), and r_s is the surface resistance to water vapor flux, with the other terms having been previously defined. The new difficulty which arises from this equation is due to the saturation vapor pressure function, $e_s(T_s)$, which is non-linear. Most approximations of this equation involve transcendental functions of polynomial and/or other sub-functions of temperature, including the well known Goff-Gratch equation and Tetens' equation (Tabata, 1973; Hull, 1974; Ringel, 1974; Wigley, 1974). The saturation vapor pressure function is usually treated as an empirical function, because physical chemistry theory has not reached the level of accuracy obtained by empirical methods, so that any equation which fits the data well may be used, including simplified equations which are used frequently for thermal biology, environmental physiology, and biometeorology (see Campbell, 1977 for one example).

Equation (13) may be solved using linear or qua-

dratic Taylor approximation, with the linear version being common:

$$T_s = T_a + (Ri - \epsilon\sigma T_a^4 - h_e(e_s(T_s) - e_A)/(4\epsilon\sigma T_s^3 + h_i + h_e S)) \quad (14)$$

where S is the slope of the saturation vapor pressure curve $= d(e_s)/dT$, h_e is the transfer coefficient for water vapor defined as,

$$h_e = \rho C_p / (\gamma(r_A + r_s)) \quad (14a)$$

and h_i is the transfer coefficient for heat, defined as,

$$h_i = \rho C_p / r_A \quad (14b)$$

A more accurate approximation may be obtained for equation (13) using a second-order Taylor approximation, leading to a quadratic solution:

$$T_s = T_a + (-b + (b^2 - 4ac)^{1/2})/2a \quad (15a)$$

where

$$a = 6\epsilon\sigma T_a^2 + (d^2 e_s / dT^2) h_e / 2 \quad (15b)$$

$$b = 4\epsilon\sigma T_a^3 + h_i + h_e S \quad (15c)$$

$$c = -Ri + \epsilon\sigma T_a^4 + h_e e_A \quad (15d)$$

with $d^2 e_s / dT^2$ being the derivative of the slope S and the second derivative of the saturation vapor pressure function e_s with respect to temperature.

Previously, iterative solutions have been used to solve for the surface temperature of wet organisms. The residual equation (6) can be again used with the residual functions f and f' now being:

$$f(T_i) = -Ri + \epsilon\sigma T_i^4 + h_i(T_i - T_a) + h_e(e_s(T_i) - e_A) \quad (16a)$$

$$f'(T_i) = 4\epsilon\sigma T_i^3 + h_i + h_e S \quad (16b)$$

A quartic solution method for the wet surface energy budget is plausible except for the non-linearity of the saturation vapor pressure term $e_s(T_i)$. A solution is possible if the saturation vapor pressure function is approximated as a 4th or lower order polynomial. Then the temperature terms arising from the saturation vapor pressure function may be combined with those from the energy budget for a single quartic equation in T_i :

$$e_s(T_i) = \xi + \alpha T_i + \beta T_i^2 + \psi T_i^3 + \mu T_i^4 \quad (17)$$

with the temperatures in either °C or Kelvin. The energy budget requires Kelvin units for the 4th-order longwave radiation term, but it is apparent that a better accuracy of fit will result from the use of °C in the "biological" range of temperatures from freezing to 45°C.

The quartic equation for T_i , with all units in S.I. and temperature in °C, can then be written in the following form:

$$kT_i^4 + a'T_i^3 + b'T_i^2 + c'T_i + d' = 0 \quad (18)$$

with

$$k = \epsilon\sigma + h_e\mu \quad (18a)$$

$$a' = 4\epsilon\sigma K_1 + h_e\psi \quad (18b)$$

$$b' = 6\epsilon\sigma K_1^2 + h_e\beta \quad (18c)$$

$$c' = 4\epsilon\sigma K_1^3 + \alpha h_e + h_i \quad (18d)$$

$$d' = -Ri + \epsilon\sigma K_1^4 + \xi h_e - h_e e_A - h_i T_a \quad (18e)$$

and K_1 being the conversion temperature between the Kelvin scale and the Celsius scale, i.e., 273.15. If equation (18) is divided by k , and the coefficients a , b , c and d are defined as a' , b' , c' and d' respectively divided by k , the quartic equation is now in standard form as before in equation (9a), except that now there are 3rd and 2nd order powers. The solution to such a quartic is slightly more tedious than for equation (9a), and is given in the Appendix. Once again, 4 roots result.

SOLUTIONS TO THE METABOLIC RATE EQUATION

The environmental temperature may be used to estimate metabolic rates; many physiological ecologists have used mount temperatures to estimate the environmental temperature in the field, and then have used this for metabolic rate estimates. The equation for this is:

$$\epsilon\sigma T_E^4 - \epsilon\sigma T_s^4 = h_i(T_s - T_E) - M \quad (19)$$

where M is the metabolic rate. If it is assumed once again that the energy budget is steady state, and that an effective body conductivity h_b can be obtained, then the metabolic rate M may be expressed as:

$$M = (T_b - T_s)h_b \quad (20a)$$

so

$$T_s = T_b - M/h_b \quad (20b)$$

where T_b is the body temperature. Equation (20b) may be substituted into equation (19). In the linear approximation, this is done along with a first order Taylor approximation of the T_s^4 about T_E , leading to the well-known expression,

$$M = h_b h_{ef}(T_b - T_E)/(h_b + h_{ef}) \quad (21a)$$

where h_{ef} is the effective conductivity defined as:

$$h_{ef} = 4\epsilon\sigma T_E^3 + \rho C_p / r_A \quad (21b)$$

A more accurate approximation can be made by using the second-order Taylor approximation, which leads to the following quadratic in M :

$$aM^2 + bM + c = 0 \quad (22a)$$

where

$$a = 6\epsilon\sigma T_E^2 / h_b^2 \quad (22b)$$

$$b = 8\epsilon\sigma T_E^3 / h_b - 12\epsilon\sigma T_E^2 T_b / h_b - h_i / h_b - 1 \quad (22c)$$

$$c = 4\epsilon\sigma T_E^2 (T_b - T_E) + 6\epsilon\sigma T_E^2 (T_b - T_E)^2 + h_i (T_b - T_E) \quad (22d)$$

and the solution to this equation is just the standard quadratic solution equation (5), solved in this case for M .

If the metabolic equation (20a) is substituted directly into equation (19), a quartic results:

$$M^4 + aM^3 + bM^2 + cM + d = 0 \quad (23a)$$

where

$$a = -4h_b T_b \quad (23b)$$

$$b = 6h_b^2 T_b^2 \quad (23c)$$

$$c = -h_i h_b^3 / \epsilon\sigma - h_b^4 / \epsilon\sigma - 4T_b^3 h_b^3 \quad (23d)$$

$$d = (T_b - T_E)h_i h_b / \epsilon\sigma + h_b^4 (T_b^4 - T_E^4) \quad (23e)$$

and the solution to this equation is of the same form as given in the Appendix.

PARTIAL DIFFERENTIAL ANALYSIS

Now that it has been established that explicit analytical expressions may be derived for the operative temperature, the wet equivalent temperature, and the metabolic rate, partial differential analysis may employ the exact solution to determine the sensitivity of the answers to errors in measurements, environmental or behavioral changes, or even thermoregulatory pressures on the evolution of the size and shape of organisms. Previous sensitivity analyses have generally employed iterative solutions and have utilized small changes in a large battery of possible variables to produce changes in the operative temperature. If a mount is used to estimate the operative temperature, frequently only a few meteorological variables are monitored. The differential analysis presented below shows how a change in a variable such as the absorbed radiation will result in a change in the operative temperature, as a function of the operative temperature.

To carry out the analysis, one simply applies the chain rule of partial differentiation to the operative temperature equation (2). It is also instructive at this point to decompose R_i into the shortwave and longwave radiation terms:

$$R_i = (Q(A_p/A) + q)(1 - a) + L_D \quad (24)$$

where Q is the direct shortwave radiative flux density, A_p/A is the area interception factor, defined as the area of an object projected normal to the solar beam (Monteith, 1973) divided by the surface area of the organism, q is the diffuse shortwave radiative flux density, L_D is the absorbed longwave radiation from the atmosphere and environment and a is the albedo (the reflectivity integrated over all shortwave wavelengths). One may now take the partial derivative of the operative temperature T_E [equation (2)] with respect to the absorbed radiation R_i , the albedo a , the area interception factor A_p/A , and the aerodynamic resistance r_A . The resulting equations are:

$$\frac{\partial T_E}{\partial R_i} = (4\epsilon\sigma T_E^3 + h_i)^{-1} \quad (25a)$$

$$\frac{\partial T_E}{\partial (A_p/A)} = Q(1 - a) \frac{\partial T_E}{\partial R_i} \quad (25b)$$

$$\frac{\partial T_E}{\partial a} = -\left(Q \frac{A_p}{A} + q\right) \frac{\partial T_E}{\partial R_i} \quad (25c)$$

$$\frac{\partial T_E}{\partial r_A} = h_i \frac{\partial T_E}{\partial R_i} \quad (25d)$$

$$\frac{\partial T_E}{\partial r_A} = \frac{T_E h_i}{r_A^2} \frac{\partial T_E}{\partial R_i} \quad (25e)$$

The total error in the operative temperature may be estimated from the component errors of each of the energy budget terms. For example, the standard deviation of T_E would be equal to:

$$\sigma_{T_E} = \left\{ \left(\frac{\partial T_E}{\partial R_i} \sigma_{R_i} \right)^2 + \left(\frac{\partial T_E}{\partial r_A} \sigma_{r_A} \right)^2 + \left(\frac{\partial T_E}{\partial T_a} \sigma_{T_a} \right)^2 \right\}^{1/2} \quad (26)$$

assuming the errors of the components are well-behaved statistically.

If mounts or black/gray globes are used to estimate operative temperatures, the associated errors may also be estimated using the above equations. With an error in aerodynamic resistance due to using a globe instead of a mount of δr_A , the error in operative temperature δT_E is:

$$\delta T_E = \frac{\partial T_E}{\partial r_A} \delta r_A \quad (27)$$

The error δT_E due to an error δa in the globe or mount albedo is:

$$\delta T_E = \frac{\partial T_E}{\partial a} \delta a \quad (28)$$

Similar equations can be derived for δT_E due to errors in other variables, but are not presented for the sake of brevity.

RESULTS AND DISCUSSION

A variety of values for absorbed radiation R_i , aerodynamic resistance, and air temperature were used as input for the linear, quadratic, quartic, and iterative operative temperature solutions (Table 1). The errors arising from the linear approximation of the operative temperature are large at high $T_E - T_a$ differences and high r_A (See Fig. 1), as expected for a first-order Taylor approximation (Tracy *et al.*, 1984). For moderate r_A values, the linear approximation errors are 3% or less (see Fig. 2). The second-order Taylor approximation is much more accurate than the linear approximation for both moderate and high r_A , and is almost as accurate as the exact and iterative solutions.

The exact roots to the quartic equation generally involved two complex numbers, one physically nonsensical real number, and the realistic value. The same root was always the realistic value, so that to use the quartic solution operationally, one has to only use the "plus" version of equation (12a). Because the other roots were so different from the realistic value, the iterative solution always converged around the

Table 1. Variables used in calculations

	R_i absorbed radiation (W m^{-2})	T_a air temperature ($^{\circ}\text{C}$)	RH relative humidity (%)	r_s surface resistance (s m^{-1})	r_A aerodynamic resistance (s m^{-1})	r_b body resistance (s m^{-1})	T_E operative temperature ($^{\circ}\text{C}$)
T_E	250-700	0-40	—	—	5-1200	—	—
T_a	250-750	0-40	0-100	0-25	5-50	—	—
M	—	0-30	—	—	5-50	2-1000	0-45

T_E = Operative temperature.

T_a = Surface temperature of wet organism (wet equivalent black body temperature).

M = Metabolic production rate estimated from operative temperature, with body temperatures ranging from 20-40 $^{\circ}\text{C}$.

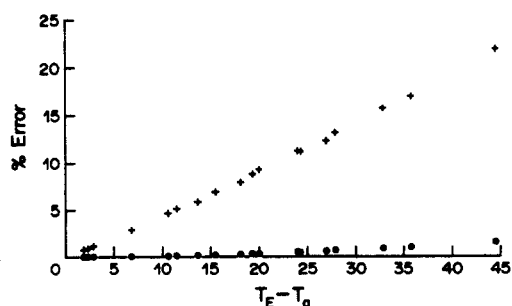


Fig. 1. Percentage error of linear and quadratic approximations of operative temperature, with an aerodynamic resistance of 1200 s m^{-1} . Percent error is defined as the operative temperature error divided by $T_E - T_a$; (+) denotes the linear approximation error and (●) denotes the second-order Taylor, quadratic approximation error.

exact solution root, lending confidence in previous works using the iterative solution method.

For the case of a wet equivalent temperature, it was necessary to fit a 4th-order polynomial to the saturation vapor pressure function. This was successfully accomplished for the temperature range of 0°C – 45°C using polynomial regression (Table 2). The coefficients are similar to Lowe's (1977) 6th-order regression results. The accuracy of the fit was on the same order as the Goff-Gratch equation (0.3% at 0°C being the largest error, reducing to less than 0.1% from 5 to 45°C), within this limited temperature range of biological interest, and was as accurate or more accurate than most of the equations reported in the literature (Osborne and Meyers, 1934; Osborne *et al.*, 1939; Langlois, 1967; Stimson, 1969; Wexler and Greenspan, 1971; Tabata, 1973; Hull, 1974; Riegel, 1974; Wigley, Campbell, 1977). Use of this equation allows a quartic solution and allows simple derivation with respect to temperature, so that the linearized, quadratic, and iterative solutions can be readily solved.

The wet equivalent blackbody temperature analysis was treated in the same manner as that for the operative temperature, except that a range of ambient humidities was added to the variables used (Table 1). As in the case for the operative temperature, the quartic solution yielded only one physically accept-

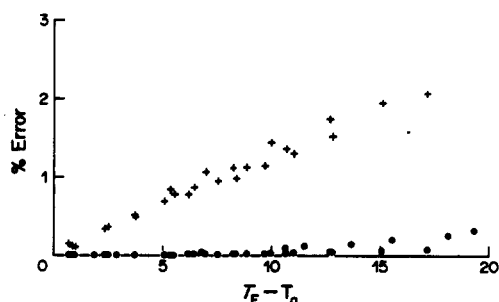


Fig. 2. Percentage error of linear and quadratic approximations of operative temperature, with an aerodynamic resistance of 75 s m^{-1} . Percent error is defined as the error in estimating the operative temperature divided by $T_E - T_a$; (+) denotes the linear approximation error and (●) denotes the second-order Taylor quadratic approximation error.

Table 2. Coefficients used for vapor pressure calculation

$\mu = 5.818 (10^{-4})$	$\text{Pa } ^\circ\text{C}^{-4}$
$\psi = 1.408 (10^{-2})$	$\text{Pa } ^\circ\text{C}^{-3}$
$\beta = 1.675 (10^0)$	$\text{Pa } ^\circ\text{C}^{-2}$
$\alpha = 4.222 (10^1)$	$\text{Pa } ^\circ\text{C}^{-1}$
$\xi = 6.174 (10^2)$	Pa

where

$$e_s = \xi + \alpha T + \beta T^2 + \psi T^3 + \mu T^4$$

with e_s in Pascals and T in $^\circ\text{Celsius}$.

able root, around which the other solutions converged. The iterative solution could be run to an accuracy of 0.001°C within 3–10 iterations, so it was always within this margin of error. The quadratic solution usually gave a solution very close to the exact and iterative solutions, although at high $T_i - T_a$ differences the error increased to almost 15% (Fig. 3). The linear approximation was inaccurate for such conditions (Fig. 3), with errors that could rise beyond 25%.

All methods solved the metabolic equation well. The linear approximation had errors as large as 3% of metabolic rate M when compared to the exact quartic solution. The second-order Taylor approximation was always within 1% of the exact solution.

A partial differential analysis was applied to the issue of using black and gray globes to approximate mounts (Walsberg and Weathers, 1986). The operative temperature error due to using a globe to approximate a bird was considered analogous to the error between using a 6.0 cm diameter globe to model a 6.0 cm cylinder. With the δr_A estimated for convective transfer at the wind speeds reported by Walsberg and Weathers (1986), δT_E from equation (25e) ranges from 3.0 to 3.3°C . If an albedo error of 0.20 occurs, the resulting δT_E error ranges from 0.5 to 2.4°C , based on equation (25c). The shape factor error would occur due to the globe presenting a different shape than a bird to the direct solar beam. A negative error occurs when the bird is oriented with its axis perpendicular to the solar beam; a positive error occurs with the bird axis parallel to the beam.

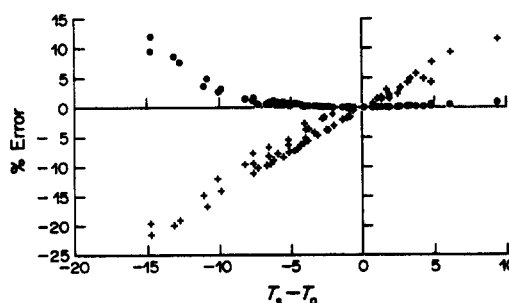


Fig. 3. Percentage error of linear and quadratic approximations of the wet equivalent black body temperature. Percent error is defined as the error in estimating the wet equivalent temperature divided by $T_s - T_a$. The points forming a generally linear pattern from the upper right quadrant to the lower left represent the linear approximation errors (+). The points curving towards the axis in the upper left quadrant and very close to the axis in the upper right quadrant represent the second-order Taylor approximation errors (●).

The error is estimated to be between $+1.8$ and -3.3°C using equation (25b), by assuming the error between the bird shape factor and that of the globe is similar to the error between a bird-sized cylinder and a globe of the same diameter. If all of these errors occurred simultaneously, the operative temperature error δT_e could be as large as 7.5°C , which is slightly larger than the maximum error measured empirically (Walsberg and Weather, 1986). If the bird axis is perpendicular to the solar beam, the error due to the shape factor cancels the error due to the aerodynamic resistance δr_A .

CONCLUSIONS

The results indicate an exact solution to the wet and dry energy budgets is possible using a quartic solution. A second-order Taylor approximation also resulted in reasonable accuracy with the highest error being less than 3% of the surface-air temperature difference in the difference range of -10 – 10°C . The linear approximation had 13 to -13% errors; for surface-air temperature differences of -15°C , the linear approximation error was almost -25% . The quadratic approximation for the metabolic rate equation produced only a 1% error for the worst case, whereas the linear approximation involved a 3% error.

The quartic roots described in this paper prove that for physically realistic meteorological conditions, the iterative and 2nd order Taylor approximations give the correct solutions, and do not converge on false or alternate roots. A new equation presented here accurately describes the saturation vapor pressure function as a simple, easily differentiable 4th-order polynomial.

Partial differential analysis showed that the characteristics of mount models must match the organisms they are intended to simulate. Errors could be more than 7°C if globes are used instead of accurate mount models. The partial differential analysis presented requires only the mount information and a limited amount of other meteorological data. For example, the analysis of effects of the shape or size on aerodynamic resistance only requires the mount or operative temperature and an estimate of the resistance itself; no other data are needed. The partial differential analysis may also be used for other purposes, such as determining the sensitivity of the operative temperature to each component energy budget term.

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REFERENCES

- Bakken G. S. (1976) A heat transfer analysis of animals: unifying concepts and the application to metabolism chamber data to field ecology. *J. theor. Biol.* **60**, 337–384.
- Campbell G. S. (1977) *An Introduction to Environmental Biophysics*, 159pp. Springer, New York.
- Gagge A. P. (1940) Standard operative temperature, a generalized temperature scale, applicable to direct and partitioned calorimetry. *Am. J. Physiol.* **131**, 93–103.
- Gates D. M. (1980) *Biophysical Ecology*, 611pp. Springer, New York.
- Gates D. M. and Papian L. E. (1974) *Atlas of Energy Budgets of Plant Leaves*, 212pp. Academic Press, New York.
- Gonzalez R. R., Nishi Y. and Gagge A. P. (1974) Experimental evaluation of standard effective temperature: A new biometeorological index of man's thermal discomfort. *Int. J. Biometeor.* **18**, 1–15.
- Hull A. N. (1974) Comments on "a simple but accurate formula for the saturation vapor pressure over liquid water". *J. appl. Meteorol.* **13**, 606–607.
- Lowe P. R. (1977) An approximating polynomial for the computation of saturation vapor pressure. *J. appl. Meteorol.* **16**, 100–103.
- Langlois W. E. (1967) A rational approximation for saturation vapor pressure over the temperature range of sea water. *J. appl. Meteorol.* **6**, 451.
- Monteith J. L. (1973) *Principles of Environmental Physics*, 241pp. Edward Arnold, London.
- Osborne N. S., Stimson H. F. and Ginnings D. C. (1939) Thermal properties of saturated water and steam. *J. Res. (NBS)* **23**, 261–270.
- Osborne N. S. and Meyers C. H. (1934) A formula and tables for the pressure of saturated water vapor in the range 0 to 374°C . *J. Res. (NBS)* **13**, 1–20.
- Paw U K. T. (1984) A theoretical basis for the leaf equivalence point temperature. *Agric. Meteorol.* **30**, 247–256.
- Paw U K. T. and Daughtry C. S. T. (1984) A new method for the estimation of diffusive resistance of leaves. *Agric. For. Meteorol.* **33**, 141–155.
- Riegel C. A. (1974) Comments on "A simple but accurate formula for the saturation vapor pressure over liquid water". *J. appl. Meteorol.* **13**, 606–607.
- Stimson H. F. (1969) Some precise measurements of the vapor pressure of water in the range from 25 to 100°C . *J. Res. (NBS)* **73A**, 493–496.
- Tabata S. (1973) A simple but accurate formula for the saturation vapor pressure over liquid water. *J. appl. Meteorol.* **12**, 1410–1411.
- Tracy C. R., van Berkum F. H., Tsuji J. S., Stevenson R. D., Nelson J. A., Barnes B. M. and Huey R. B. (1984) Errors resulting from linear approximations in energy balance equations. *J. therm. Biol.* **9**, 261–264.
- Walsberg G. E. and Weathers W. W. (1986) A simple technique for estimating operative environmental temperature. *J. therm. Biol.* **11**, 67–72.
- Wexler A. and Greenspan L. (1971) Vapor pressure equation for water in the range 0 to 100°C . *J. Res. (NBS)* **75A**, 213–230.
- Wigley T. M. L. (1974) Comments on "A simple but accurate formula for the saturation vapor pressure over liquid water". *J. appl. Meteorol.* **13**, 608.
- Winslow C. E. A., Herrington L. P. and Gagge A. P. (1977) Physiological reactions of the human body to varying environmental temperatures. *Am. J. Physiol.* **120**, 1–22.
- Winslow C. E. A., Gagge A. P. and Herrington L. P. (1940) Heat exchange and regulation in radiant environments above and below air temperature. *Am. J. Physiol.* **131**, 79–92.

APPENDIX

Given the quartic for the surface temperature of a wet organism,

$$T_s^4 + aT_s^3 + bT_s^2 + cT_s + d = 0 \quad (\text{A1})$$

one may derive a solving for y , the resolvent cubic,

$$y^3 - by^2 + (ac - 4d)y - a^2d + 4bd - c^2 = 0. \quad (\text{A2})$$

This yields two complex roots and one real root; only the real root to y is used. The quartic roots are then

$$T_s = -a/4 - R/2 \pm E/2$$

(A3)

and

$$T_s = -a/4 + R/2 \pm D/2$$

(A3a)

where

$$E = (a^2/2 + b - y - 2b - (4ab - 8c - a^3)/4R)^{1/2} \quad (\text{A3b})$$

$$D = (a^2/2 + b - y - 2b + (4ab - 8c - a^3)/4R)^{1/2} \quad (\text{A3c})$$

and

$$R = (a^2/4 - b + y)^{1/2} \quad (\text{A3d})$$