ERRORS RESULTING FROM LINEAR APPROXIMATIONS IN ENERGY BALANCE EQUATIONS

C. Richard Tracy*

Department of Zoology, Colorado State University, Fort Collins, CO 80523, U.S.A.

Fredrica H. van Berkum, Joyce S. Tsuji, R. D. Stevenson, Jay A. Nelson,†
Brian M. Barnes and Raymond B. Huey

Department of Zoology NJ-15, University of Washington, Seattle, WA 98195, U.S.A.

Abstract—1. Linearization techniques commonly used to solve energy budget equations of animals and plants can result in inaccurate estimates of body temperature (T_b).
2. Errors can be large when actual T_bs differ from the temperature used in linearization techniques; this is especially true for wet-skinned animals.
3. Iterative solutions of linearized equations can give accurate calculations of T_b.

Key Word Index—Energy balance; biophysical ecology; iterative numerical methods.

INTRODUCTION

Biophysical analysis of the exchanges of energy and mass between organisms and their environments play an increasingly important role in ecological, physiological and evolutionary studies of animals and plants (see Gates and Schmerl, 1975; Monteith, 1973; Campbell, 1977; Gates, 1980; Tracy, 1982). These analyses use mechanistic equations to predict body temperature (T_b) (Machle and Hatch, 1947; Tracy, 1976; Porter *et al.*, 1975; Bakken and Gates, 1975; Spotila *et al.*, 1973), environmental heat loads (Buettner, 1951; Kleiber, 1972; Strunk and Tracy, 1973; Bakken and Gates, 1974; Gonzalez *et al.*, 1974; Robinson *et al.*, 1976; Mahoney and King, 1977; Bakken *et al.*, 1978; Belovsky, 1981), metabolic rates (Strunk and Tracy, 1973, 1980; Bakken, 1980; Spotila and Gates, 1975; Robinson *et al.*, 1976; Mahoney and King, 1977) and evaporative water loss (Penman, 1948; Kerslake and Waddell, 1958; Tracy, 1976; Campbell, 1977; Welch and Tracy, 1977; Tracy *et al.*, 1980). These equations often cannot be solved explicitly for T_b because they contain higher-order unknown terms as described below. Nevertheless, numerical solutions can be obtained by using iterative computer routines (Tracy, 1976; Bakken, 1981), or by approximating or linearizing the higher-order unknown terms (Bakken, 1981; Campbell, 1977). Here, we describe linearization techniques and demonstrate that two commonly used linearization techniques can generate substantial computational errors under biologically realistic conditions. We also illustrate biological situations that are prone to error, and demonstrate a simple iterative method that circumvents the errors.

LINEARIZED ENERGY BALANCE EQUATIONS

Linearization techniques are often employed in energy balance equations used to calculate the T_bs of plants and animals. In these simple energy budgets, absorbed radiation is balanced by convection [a function of the temperature difference between the air (T_a) and the body (T_b)] and long-wave reradiation (related to the fourth power of T_b):

$$0 = Q - h_c(T_b - T_a) - \epsilon\sigma T_b^4, \quad (1)$$

where h_c is the convection coefficient, ϵ is the emissivity of the body surface and σ is the Stefan–Boltzmann constant. It is difficult to solve this equation for T_b because of the fourth-order unknown term. However, this term can be replaced with a linear approximation using a Taylor series expansion with T_a as the "linearization temperature" (Campbell, 1977). When T_b is not greatly different from T_a, the fourth-order term can be taken to be

$$T_b^4 \cong T_a^4 + 4T_a^3(T_b - T_a). \quad (2)$$

Substitution of equation (2) into equation (1) allows an explicit solution for T_b:

$$T_b = T_a + (Q - \epsilon\sigma T_a^4)/(h_c + \epsilon\sigma 4T_a^3). \quad (3)$$

When evaporative heat loss is an important mode of heat transfer from the organism (e.g. from a wet-skinned animal), the energy balance equation must be expanded to include a term for evaporation (Campbell, 1977):

$$0 = Q - h_c(T_b - T_a) - \epsilon\sigma T_b^4 - \lambda h_d(\rho_{s,sat} - \rho_a), \quad (4)$$

where λ is the latent heat of vaporization, h_d is the conductance to the loss of water vapour and $(\rho_{s,sat} - \rho_a)$ is the vapour density difference between saturated air at the surface of the animal and the ambient air. If the organism has a significant resistance to water loss due to an impermeability of the skin, the vapour density of the air at the surface of the animal will not be saturated and another formu-

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*To whom all correspondence should be addressed.
†Present address: Department of Zoology, University of Wisconsin, Madison, WI 53706, U.S.A.

lation will have to be employed (Tracy, 1982). When the organism has a wet surface, h_d is the conductance due to the boundary layer (Tracy, 1976, 1982), but when the organism has a relatively impermeable "skin", h_d can be the conductance of the skin alone (Tracy, 1982). Under some circumstances, h_d is a complex function of the permeability of the skin and of the resistance to water transport due to the boundary layer (Tracy, 1982).

$\rho_{s,sat}$ is a complicated function of body temperature (Tracy et al., 1980) making equation (4) impossible to solve analytically. However, Penman (1948) simplified such equations by developing a linear approximation of the term $(\rho_{s,sat} - \rho_a)$:

$$(\rho_{s,sat} - \rho_a) \cong (\rho_{a,sat} - \rho_a) + s(T_b - T_a), \qquad (5)$$

where $\rho_{a,sat}$ (g m^{-3} K^{-1}) is the vapour density of saturated air at T_a, and s is the slope of the non-linear relationship between saturation vapour density and temperature (Penman, 1948),

$$s = -0.0953 + 0.0732436\ T$$
$$- 0.001516388\ T^2 + 0.000033869548\ T^3. \qquad (6)$$

Theoretically, s should be evaluated at $(T_a + T_b)/2$, but usually s is evaluated at T_a because T_b is unknown (Penman, 1948; Campbell, 1977). In this paper, we also use T_a as the linearization temperature for evaluating s. The complete linearized energy balance equation used to calculate the T_b of an evaporating organism (with wet skin) uses both Taylor and Penman approximations:

$$T_b = T_a + [Q - \lambda h_d(\rho_{s,sat} - \rho_a)$$
$$- \epsilon\sigma T_a^4]/(h_c + \lambda h_d s + \epsilon\sigma 4T_a^3). \qquad (7)$$

Because these linearized heat balance equations [equations (3) and (7)] can be solved explicitly for T_b, they have two major advantages over equations (1) and (4): (1) the relationships between T_b and the other variables are simple enough to allow analytical interpretation of the physical interactions between an organism and its environment, and therefore (2) T_b can be easily calculated by hand or with a pocket calculator. Nevertheless, use of linear approximations may compromise accuracy for convenience. In some cases, the reduction in accuracy may be negligible. Simplifying the Taylor series expansion [equation (2)] by excluding higher-order terms results in an underestimate of T_b, and the underestimate is proportional to $T_b - T_a$. Similarly, the Penman approximation is accurate only when T_a and T_b are very similar. Disparity between T_a and T_b results in an underestimation of T_b, if $T_b \gg T_a$, and an overestimation, if $T_b \ll T_a$.

ERROR ANALYSIS

The accuracy of these linear approximations has not been thoroughly investigated, although Bakken (1981) and Roughgarden et al. (1981) compared the linearization of T_b^4 in energy balances of dry-skinned animals to a numerical solution and came to conclusions similar to ours for our equation (4). To determine whether the Taylor and Penman approximations actually induce serious errors in the computation of T_b, we compared linearized estimates of T_b using equations (3) and (6) with computer-
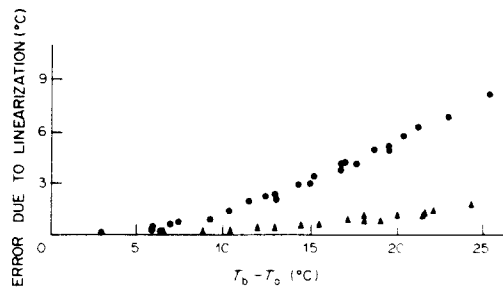

Fig. 1. Difference (or errors) between calculations of T_b from numerical computer algorithms and explicit solutions of linearized equations for sample, realistic combinations of variables of the environment and animal. Errors are plotted as a function of the difference between T_b and the linearization temperature, T_a. Calculations for dry-skinned animals ($\blacktriangle$) used a Taylor series approximation, whereas those for wet-skinned animals ($\bullet$) employed a Taylor and a Penman linearization.

generated numerical values [we used the half-interval search method, Poole and Borchers (1979)] of T_b using equations (1) and (4), and a variety of realistic combinations of the environmental variables ($Q = 300, 600$ and 900 W m^{-2}; r.h. $= 20, 50$ and 95%; wind speed $= 0.1, 1.0$ and 3.0 m s^{-1}; and T_a taken at many points between 273–323 K). Equations (6) and (8) were solved for both wet- (e.g. frogs) and dry-skinned animals (e.g. lizards).

Our analyses show that use of linearizations can result in substantial errors in estimates of T_b for dry- and wet-skinned animals. Estimates from equations containing only the Taylor series approximation were usually very similar to the numerical solutions (less than 0.5°C error, see Fig. 1). Nevertheless, differences between the linearized and numerical solutions were as great as 1.6°C for many realistic combinations of environmental variables. In unusual, but realistic environments, errors can be as high as 5.5°C. For example, a 100 g, dry-skinned animal exposed to high radiation (900 W m^{-2}) at low wind speeds (0.1 m s^{-1}) at a low T_a (10°C) gave an error of 5.5°C. Similar conditions might be found in sheltered spots at high elevations. Estimates from equations containing both the Taylor and Penman linearizations were often unacceptably inaccurate (Fig. 1). Errors as large as 5–8°C were commonly produced under a variety of realistic conditions. As expected, the magnitude of the error in both tests was large when combinations of variables (i.e. conditions of the animal and environment) forced the surface temperature of the organism away from T_a (Fig. 1).

Errors caused by linearization can be minimized with some mathematical and biological insight. The linearization temperature need not be restricted to T_a (Bakken, 1981). An experienced investigator often can estimate T_b knowing the environmental conditions and substitute this "guess" as the linearization temperature. If this guess is an accurate estimate of the actual T_b, then the error generated due to linearization can be very small.

ITERATIVE METHOD

We suggest an alternative, and less subjective, method of calculating complex equations: one that

combines the convenience of using the linearized equations with the accuracy of computerized numerical solutions (Strunk and Tracy, 1973; Bakken, 1981; Roughgarden et al., 1981). This method uses equations with linearizations, such as equation (3) and (6), but solves them iteratively. Specifically, these equations are initially solved using T_a as the linearization temperature. Then the calculated T_b is used as the linearization temperature for the next iteration. Subsequent iterations yield increasingly accurate estimates of T_b. For example, suppose one were to solve for the T_b of a wet-skinned animal using equation (6). If T_a was used as the linearization temperature and T_a was 20°C different from the actual T_b of the animal, then the calculated T_b would be in error by approx. 6°C (see Fig. 1). If this calculated T_b was then used as the linearization temperature in a second iteration [i.e. recalculation of T_b using equation (6)], then the resulting error in the newly calculated T_b would be only approx. 0.3°C (see Fig. 1). A third iteration would reduce the calculational error to less than 0.05°C. Thus, two iterations of this method eliminates nearly all error, particularly for equation (3), and three iterations always reduces errors to less than 0.05°C.

CONCLUSIONS

Linearizations of high-ordered terms in energy balance equations can result in unacceptable errors compared to implicit solutions using a computer and numerical algorithms. These errors can be avoided by three means:

(1) by using linearizations only when environmental conditions are unlikely to result in large differences between T_b and the linearization temperature;

(2) by using an educated guess for the linearization temperature; and

(3) by solving the linearized equations iteratively by the method proposed in this paper.
The accuracy of the first two methods depends upon the investigator's mathematical and biological insight, and the magnitude of the error cannot be known for certain without further evaluation. In contrast, the third method does not require any special understanding of biophysical interactions, it permits an investigator to calculate T_b to any desired degree of accuracy, and frees the investigator from the possible inconvenience and expense of using a computer.

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