# AN ANALYTICAL MODEL OF THE COUNTER-CURRENT HEAT EXCHANGE PHENOMENA

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ABSTRACT An analytical model for the counter-current heat exchange mechanism in animals has been formulated and a solution has been obtained. The nondimensional parameters that govern the mechanism have been determined in terms of the properties of the animal. The normalized temperatures are functions of normalized distance and, in general, three nondimensional heat transfer conductances. Graphical results are presented for two representative physiological systems. These results allow a delineation of those situations in which counter-current heat transfer is important, and also a quantitative prediction of the heat transfer and temperature distributions. The theory is compared to the available experimental results.

## INTRODUCTION

The thermal energy balance for the extremity of an animal is comprised of three energy flows. These are the thermal energy supplied by the blood flow, the thermal energy generated by metabolic processes, and the energy transfer to the environment by convection, radiation, and evaporation. The mechanism of counter-current heat exchange has often been postulated as an important factor in decreasing the heat transfer to the environment by reducing the amount of thermal energy lost by the blood (i.e. temperature drop of the blood flow) as it flows through the extremity. Its importance derives from the observation that in many species the arteries and veins of the limbs are in close proximity and significant heat transfer may occur between the two vessels.

For an animal in a cold environment, the limb is at a higher temperature than the surroundings and thus heat flows from the limb. The limb is maintained at a steady temperature through thermal energy supplied both by blood flow and metabolism. The temperature of the venous flow is less than that of the arterial flow because of the energy transferred from the blood to the surroundings. With significant heat transfer between the two vessels, the arterial flow is additionally cooled by heat transfer to the venous flow; the venous flow is thus rewarmed through heating from the nearby artery. The final result is that the venous flow returns to the core of the animal at a higher temperature than it would have without the heat transfer between artery and vein. Since the net heat transferred from the blood flow to the surroundings is proportional to the temperature difference of the blood entering and leaving the limb, the counter-current effect reduces the heat loss from the limb and the animal as a whole.

This phenomenon can also be explained in terms of reduced average limb temperature. If heat is transferred from artery to vein, the average arterial temperature and the average limb temperature are less than what they would be in the absence of such heat transfer. The heat transfer to the surroundings, proportional to the average temperature difference between limb and surroundings, is correspondingly reduced. Shunting of the venous flow to superficial veins reduces the counter-current heat transfer, increases the limb temperature, and thus increases the heat transfer to the surroundings. Nervous system control of the shunting provides a mechanism that aids in regulating body temperature.

There have been many previous reports of this mechanism. Scholander (1), Scholander and Krog (2), and Schmidt-Nielsen (3) present excellent qualitative descriptions of this mechanism and its occurrence in nature. Scholander discusses in detail the rete mirabile, a specialized vascular bed consisting of many small arteries and veins in close contact near the base of a limb in such animals as the sloth, anteater, armadillo, whale, seal, manatee, heron, and crane. This structure appears to have evolved in order to provide heat exchange. Scholander and Krog have performed experiments on the rete in a sloth and demonstrated its importance in reducing heat transfer from the limb. Kahl (4) has carried out experiments on the stork in which the surface temperature of the legs was measured. The leg temperature decreased markedly in the vicinity of the rete, and this also indirectly confirms the value of the rete as a counter-current heat exchanger.

The anatomy of the fin of the whale has been studied by Scholander and Schevill (5). In this structure, the arteries are surrounded by multiple veins so that in a cold environment heat can only be transferred from the artery to the veins. Under warm environmental conditions, the venous flow is shunted to superficial veins to facilitate heat transfer from the fin. Here, then, the counter-current mechanism is valuable in regulating body temperature as well as in conserving energy.

It appears that the above specialized structures may have evolved in response to thermal demands. In addition, there are other situations in which it is not clear whether the counter-current mechanism is significant. Bazett et al. (6) has measured the temperature distribution in the arm of man. There is a continuous decrease in arterial and venous temperature in the flow direction. It is not yet certain whether the proximity of the deep veins and arteries significantly reduces the heat loss from the arm. Harrison and Weiner (7) and Dahl and Herrick (8) have demonstrated that the arteries and veins in testes are in intimate contact and that there is a significant decrease in arterial temperature in the flow direction. However, the results are also inconclusive regarding the heat transfer between the vessels.

To date, there have been no satisfactory analytical models developed to describe this mechanism. Scholander and Krog (2) have formulated a very simplified analytical model for the specialized case of heat transfer between only an artery and a vein. Their analysis incorporates the assumption that the temperature difference between the arterial and venous blood is constant with length, which is not true in general. They attempted to verify their model experimentally, but heat transfer considerations of the equipment used seem to invalidate the results. There is a significant axial heat transfer in the copper tube they used to simulate the vessels that is not present in the actual cases. Nevertheless, this represents the first attempt at a quantitative analysis of this problem.

In summary, there have been many qualitative descriptions of this mechanism, but there are available neither adequate models nor sufficient experimental data to quantitatively evaluate the importance of counter-current heat exchange. The objectives of this paper are to (*a*) Determine the heat transfer parameters that govern the counter-current mechanism. (*b*) Formulate an analytical model to aid in evaluating the importance of this mechanism in various situations. (*c*) Present some numerical examples to indicate the significance of this effect in various species.

## ANALYTICAL MODEL

The analytical model chosen to represent the general problem of heat transfer in a limb is depicted in Fig. 1. The significant thermal energy terms are also shown. In general, there will be heat transferred from the arterial to the venous flow, and from both the arterial and venous flows to the environment. The blood temperature will increase or decrease according to the magnitudes of these heat flows.

The mathematical analysis of this model incorporates the following assumptions: (*a*) The temperatures of the arterial and venous flows vary with distance in the flow direction only. The analysis will apply to a multiple vessel system (e.g. a rete) if the heat transfer behavior for all flow passages is similar. (*b*) The thermal conductances between artery and vein, artery and environment, and vein and environment are independent of distance along the limb. (*c*) The mass flow rates of the

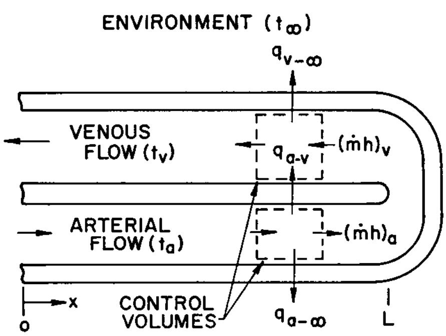


FIGURE 1 Analytical model for counter-current heat exchange.

arterial and venous flows are equal and constant with distance. This will be valid for situations such as a rete, a bird's leg, a man's forearm, etc., where there is not significant recurrent branching of the vessels. (*d*) The thermal energy generated due to metabolism is small relative to the heat transfer terms. This is reasonably valid for a resting, nonshivering animal in which the major portion of the metabolic heat generated does not occur in the skeletal muscles. (*e*) The limb is in a steady state; temperatures and flow rates are not changing with time. (*f*) The thermal properties of the blood and tissue are constant. That is, they are independent of emperature, distance, and time.

The mathematical model is formulated by applying the conservation of energy principle to each of the two control volumes indicated in Fig. 1. In general, for a steady-state system:

$$\text{energy that flows in} = \text{energy that flows out.} \tag{1}$$

The significant energy flows in this model are the energy carried by the fluid and the heat flows. The energy carried by the fluid is the product of the mass flow rate, $\dot{m}$, and the fluid enthalpy, $h$. For negligible pressure changes, the rate of change of enthalpy with respect to distance can be approximated as the product of fluid specific heat, $c$, and the rate of change of fluid temperature with respect to distance, $dt/dx$. Thus the mechanism equation describing the rate of energy change of the blood is given by:

$$\frac{d(\text{energy carried by flow})}{dx} = \dot{m}\frac{dh}{dx} = \dot{m}c\frac{dt}{dx}. \tag{2}$$

The heat flows are described by a mechanism equation that incorporates the thermal conductance, $U$, the heat transfer area per unit length, $A'$, and the temperature difference causing the heat flow ($\Delta t$):

$$q' = UA'\Delta t. \tag{3}$$

Applying the conservation of energy principle to each control volume and using a mechanism equation for each heat flow yields the following two differential equations:

$$\text{Arterial flow: } \dot{m}c\frac{dt_a}{dx} + (UA')_i(t_a - t_v) + (UA')_a(t_a - t_\infty) = 0 \tag{4}$$

$$\text{Venous flow: } \dot{m}c\frac{dt_v}{dx} + (UA')_i(t_a - t_v) - (UA')_v(t_v - t_\infty) = 0 \tag{5}$$

The boundary conditions on the temperature are:

at $\quad x = 0: \quad t_a = t_0$

and at $$x = L: \quad t_a = t_v . \tag{6}$$

Before solving equations 4, 5, and 6, it is convenient to normalize the differential equations. This has the advantage of indicating the nondimensional parameters that govern the problem, and allowing the solution to be presented compactly in terms of these parameters. The following nondimensional parameters are defined:

Nondimensional conductances:

$$\begin{aligned} N_a &= (UA')_a L/\dot{m}c \\ N_v &= (UA')_v L/\dot{m}c \\ N_i &= (UA')_i L/\dot{m}c \end{aligned} \tag{7}$$

Nondimensional temperatures:

$$\begin{aligned} u &= (t_a - t_\infty)/(t_0 - t_\infty) \\ v &= (t_v - t_\infty)/(t_0 - t_\infty) \end{aligned} \tag{8}$$

Nondimensional distance:

$$\xi = x/L. \tag{9}$$

In terms of these quantities, equations 4, 5, and 6 become:

$$\text{Arterial flow: } \frac{du}{d\xi} + N_i(u - v) + N_a u = 0 \tag{10}$$

$$\text{Venous flow: } \frac{dv}{d\xi} + N_i(u - v) - N_v v = 0 \tag{11}$$

Boundary conditions:

$$\begin{aligned} u(0) &= 1 \\ u(1) &= v(1). \end{aligned} \tag{12}$$

Equations 10 and 11 are two coupled, first order, linear, ordinary differential equations. Their solution was obtained by elementary techniques. Equation 10 was solved for $v$ in terms of $u$, and then this expression was substituted into equation 11. The resulting second-order equation was integrated twice to yield a solution for $u$. Having found the solution for $u$, the solution for $v$ was then obtained from equation 10. The constants of integration were evaluated using equation 12. The complete solution is:

$$u = e^{\frac{(N_v - N_a)\xi}{2}} \left[ \frac{B \cosh A(1 - \xi) + \sinh A(1 - \xi)}{B \cosh A + \sinh A} \right] \tag{13}$$

$$v = e^{\frac{(N_v - N_a)\xi}{2}} \left[ \frac{B \cosh A(1 - \xi) - \sinh A(1 - \xi)}{B \cosh A + \sinh A} \right] \tag{14}$$

where:

$$A = \sqrt{(N_a + N_v)(N_a + N_v + 4N_i)}/2$$

$$B = \sqrt{(N_a + N_v + 4N_i)/(N_a + N_v)}$$

The solution to the general problem, equations 13 and 14, is rather unwieldy and it is difficult to present the results graphically due to the presence of three parameters ($N_a$, $N_v$, and $N_i$). In order to gain a better appreciation of the counter-current mechanism, two special cases will be studied. It is felt that the majority of situations found in nature may be closely approximated by one or the other of these two models.

*Model* I, $N_a = N_v$

The schematic flow representations shown in Fig. 2 approximate the situation in the arm of a man, the leg of a bird, and a rete of a sloth leg. For this model, the

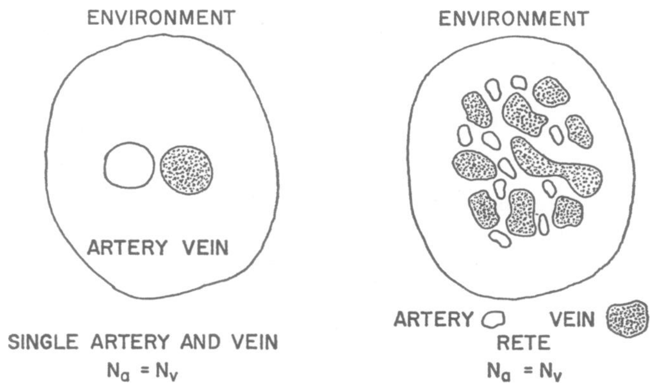


FIGURE 2 Model I configuration for counter-current heat exchange.

conductances for heat transfer from the artery and vein to the environment are taken to be equal because of the symmetry involved. With the specification that $N_a = N_v$, equations 13 and 14 reduce to:

$$u = \frac{B \cosh A(1 - \xi) + \sinh A(1 - \xi)}{B \cosh A + \sinh A} \tag{15}$$

$$v = \frac{B \cosh A(1 - \xi) - \sinh A(1 - \xi)}{B \cosh A + \sinh A} \tag{16}$$

where

$$N_o = N_a = N_v$$

$$A = N_o\sqrt{1 + 2(N_i/N_o)}$$

$$B = \sqrt{1 + 2(N_i/N_o)}.$$

The two parameters that govern the heat transfer and temperature distribution are: $N_o$ = conductance between the arteries or veins and the environment; $N_i/N_o$ = ratio of conductance between arteries and veins to the conductance between the vessels and the environment.

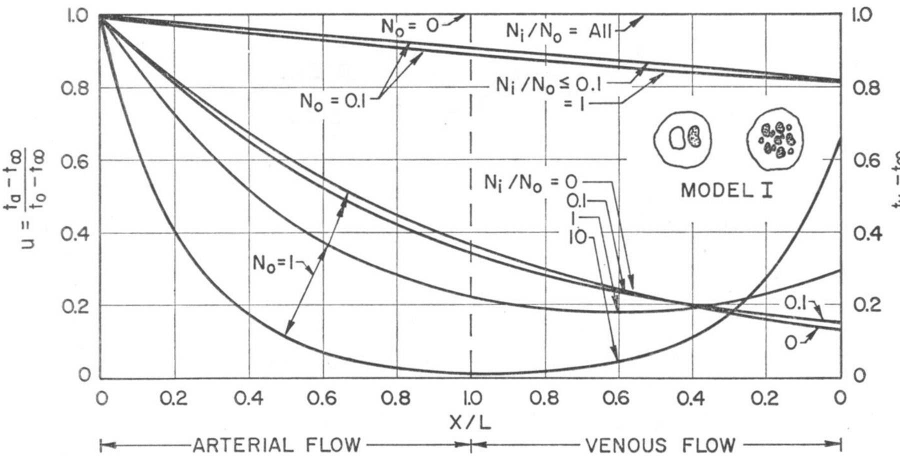


FIGURE 3 Normalized temperature distribution in a limb; Model I.

The solution for this model is presented graphically in Fig. 3 for what are expected to be representative values of $N_o$ and $N_i/N_o$. (The method of estimating the size of the parameters will be discussed later.) Note that the flow direction is from left to right, with the end of the limb in the middle of the graph ($x/L = 1$).

It is seen that for low values of $N_o$, (e.g. $N_o = 0.1$), there is little cooling of either the arterial or venous flow, and the counter-current heat exchange effect is small. For large $N_o$ the temperature drop of the arterial flow is large, and the venous flow at the end of the limb is relatively cold. There is, then, a large temperature difference between the arterial flow and the returning venous flow, and thus a significant potential exists for rewarming the venous flow through counter-current heat exchange. As indicated in Fig. 3, the conductance between the artery and vein must be about the same size or greater than that between the vessels and the surroundings in order to obtain heating of the venous flow. It should also be noted that even for low values of $N_i/N_o$, there will be heat transfer from artery to vein even though the venous temperature continues to decrease. For example, for $N_o = 1$ and $N_i/N_o = 0.1$, the venous return temperature is slightly higher than that for $N_i/N_o = 0$.

*Model* II, $N_a = 0$

The schematic flow model shown in Fig. 4 approximates the situation in the fins of whales and porpoises, and possibly other species. Since the artery is almost completely surrounded by veins in this model, the conductance for heat transfer between the artery and environment is neglected in comparison to the conductance between artery and vein.

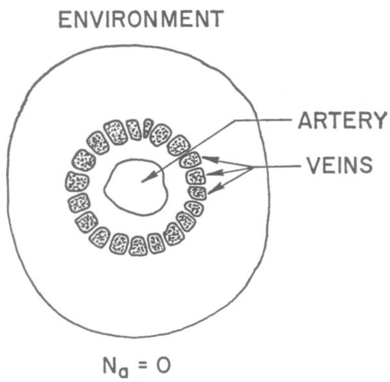


FIGURE 4 Model II configuration for counter-current heat exchange.

With the specification that $N_a = 0$, equations 13 and 14 become:

$$u = e^{N_o\xi/2}\left[\frac{B\cosh A(1-\xi)+\sinh A(1-\xi)}{B\cosh A+\sinh A}\right] \tag{17}$$

$$v = e^{N_o\xi/2}\left[\frac{B\cosh A(1-\xi)-\sinh A(1-\xi)}{B\cosh A+\sinh A}\right] \tag{18}$$

where

$$N_o = N_v$$

$$A = N_o\sqrt{1+4(N_i/N_o)}/2$$

$$B = \sqrt{1+4(N_i/N_o)}.$$

As for Model I, there are the two parameters, $N_o$ and $N_i/N_o$, that govern the heat transfer.

The solution for this model is presented graphically in Fig. 5 for what are expected to be representative values of $N_o$ and $N_i/N_o$. For low values of $N_o$, the

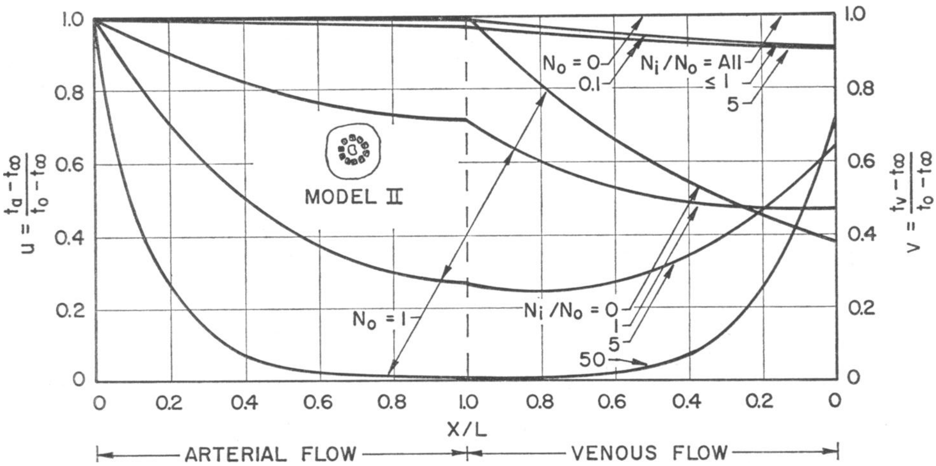


**FIGURE 5** Normalized temperature distribution in a limb; Model II.

results are very similar to those for Model I; the temperature change of either the arterial or the venous flow is small. For large $N_o$ and $N_i$, the counter-current effect is significant, and a considerable rewarming of the venous flow may be obtained. As in Model I, the effect may exist and not necessarily warm the venous flow, but still serve to reduce heat transfer to the environment. For example, for $N_o = 1$ and $N_i/N_o = 1$,the venous temperature continually decreas es in the flow direction, but the exit temperature is 10% higher than if there were no counter-current heat transfer ($N_i/N_o = 0$).

## COUNTER-CURRENT HEAT TRANSFER PERFORMANCE

The heat lost from the limb that is supplied by the blood is obtained from an over-all energy balance on the blood:

$$q = \dot{m}c[t_0 - t_v(0)]$$

or, in nondimensional terms:

$$q/\dot{m}c(t_0 - t_\infty) = 1 - v(0).$$

Thus, $[1 - v(0)]$ is a measure of the heat loss from the limb. The term is also the ratio of the actual energy loss to the energy loss that would occur if the venous flow returned to the body at the environmental temperature.

In Fig. 6, the nondimensional venous return temperature and the nondimensional heat loss from the limb are plotted as functions of $N_o$ and $N_i/N_o$ for both models. For a given configuration, the heat loss from the limb increases as the conductance

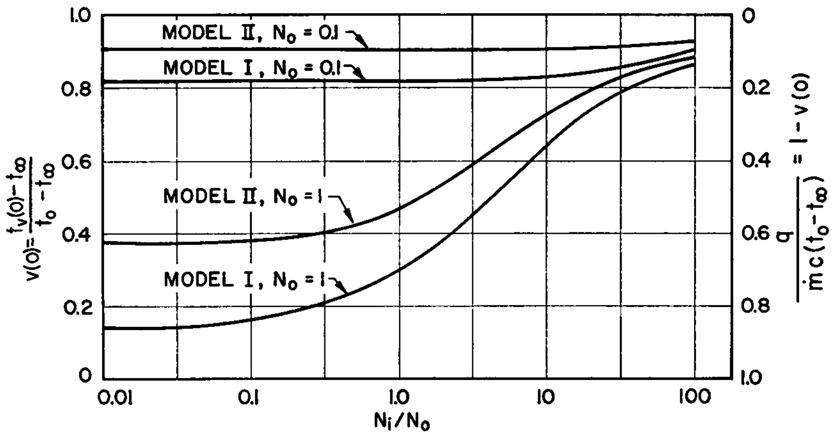


FIGURE 6 Venous return temperature and nondimensional heat transfer as a function of $N_o$ and $N_i/N_o$.

between the vessel and the environment increases. The conductance between the vessels is effective in reducing the heat loss only at relatively high values of $N_i/N_o$. For very large values of $N_i/N_o$, the heat loss is small and not greatly influenced by the size of $N_o$. It should also be observed that the configuration of Model II is more effective in reducing heat loss than that of Model I for equal values of $N_i$ and $N_o$. In Model II, heat transfer to the environment is only from the veins, whereas in Model I, the arteries as well as the veins transfer heat to the surroundings.

## ESTIMATION OF PARAMETERS FOR PHYSIOLOGICAL SYSTEMS

The preceding analysis provides a description of the counter-current heat exchange mechanism in general, nondimensional terms. In order to predict the magnitude of the effect for a given situation, it is necessary to estimate the parameters $N_i$ and $N_o$. In this section, heat transfer theory is employed to estimate these parameters for three representative cases.

### *Human Arm*

This is the situation depicted on the left in Fig. 2. The following properties will be assumed as representative:

Arm diameter: $d_o = 8$ cm,
Arm length: $L = 75$ cm,
Thermal conductivity: $k = 1.6 \times 10^{-3}$ cal/sec-cm-C,
Artery and vein diameters: $d = 0.5$ cm,
Distance between artery and vein: $s = 1$ cm,
Blood flow rate: $\dot{m} = 2$ g/sec,
Blood specific heat: $c = 0.83$ cal/g-C.

The arm will be assumed to be a cylinder with the artery and vein near the center. The resistance to heat transfer will be assumed to be entirely due to conduction through the tissue; the convection resistances inside the vessels and on the skin surface will be neglected as they are small in comparison with the tissue conduction resistance. The conductance for heat transfer between the two vessels is (Krieth [9], p. 90).

$$(UA')_i = 2\pi k/\cosh^{-1}[2(s^2/d^2) - 1] = 3.8 \times 10^{-3} \text{ cal/sec-cm-C}.$$

Therefore:

$$N_i = (UA')_i L/\dot{m}c = 0.17.$$

The conductance for heat transfer between either vessel and the environment can be approximated by (Krieth, p. 27):

$$(UA')_o = 2\pi k/\ln(d_o/d) = 3.6 \times 10^{-3} \text{ cal/sec-cm-C}.$$

Therefore:

$$N_o = (UA')_o L/\dot{m}c = 0.16$$

$$N_i/N_o = 1.05.$$

The accuracy of the values of the parameters depends on the degree to which the various properties are known. The ratio of the two conductances, $N_i/N_o$, is the least uncertain of the two parameters. Its computed value depends only on geometry (anatomy); the mass flow rate, thermal conductivity, and specific heat cancel out of the ratio. The value of $N_i/N_o$ is not too sensitive to the fact that the arm diameter and artery and vein diameters vary with distance along the arm. Additional calculations show that over a wide range of reasonable values of these dimensions, $N_i/N_o$ varies only from 0.5 to 2. The largest uncertainty concerns the blood flow rate; it is probably in the range 0.8–4 g/sec. The tissue thermal conductivity varies up to 50% depending on tissue composition. Therefore, the probable ranges of values for the nondimensional parameters are:

$$N_i = 0.08 \text{ to } 0.4, \quad N_o = 0.08 \text{ to } 0.4, \quad \text{and} \quad N_i/N_o = 1.$$

In Fig. 7, the temperatures experimentally measured by Bazett (6) are plotted and compared to the analytical results. The arterial temperatures are in good agreement with the analysis. The venous temperatures are lower than might be expected, owing, probably, to the heat transfer from the hand which may not be adequately accounted for in the present theory. The effect of metabolic heat generation on the blood temperature distribution is small. Metabolism supplies between 0.2 and 0.5 cal of heat per ml of blood flow, while the heat transfer from the blood for the tests of Bazett is about 8 cal/ml. Thus the metabolic heat production does not significantly alter the temperature distribution.

The results presented in Fig. 6 indicate that for the range of parameters for the

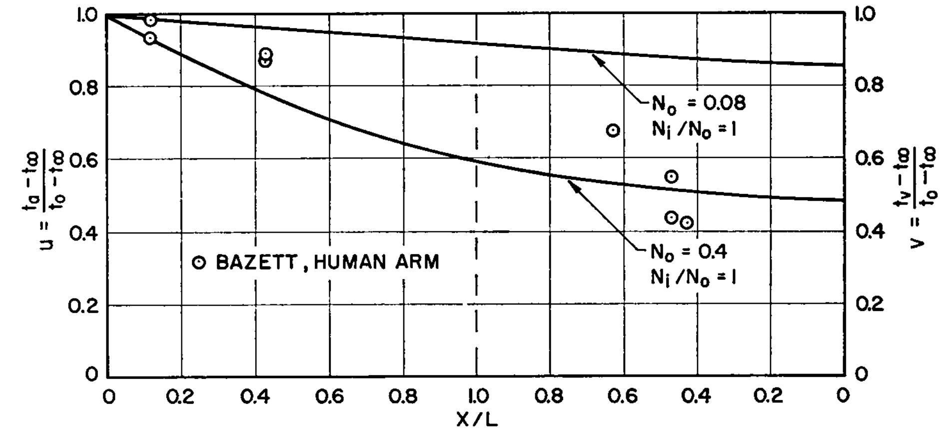


FIGURE 7 Comparison of analytical model with experimentally determined temperatures in a human arm.

human arm, there is probably little, if any, counter-current effect. Additional calculations show that for the largest probable value of $N_o$ (0.4), the venous return temperature for $N_i/N_o = 0$ is only 5% lower than that for the largest probable value of $N_i/N_o$ of 2. Counter-current heat exchange would then reduce the heat loss from the arm by 5% at most.

*Sloth Rete*

This situation is shown schematically on the right in Fig. 2. The estimation of the parameters for a rete is considerably more difficult than for an arm due to the lack of sufficient information concerning the anatomy and blood flow rate. However, considerations of the information and results reported by Scholander and Krog (2) indicate that the following orders of magnitude for the parameters are probably representative:

$$N_i = 60, \quad N_o = 2, \quad \text{and} \quad N_i/N_o = 30.$$

For the above parameter values, the results presented in Figs. 3 and 6 indicate that the rete is very effective in reducing heat loss. This is primarily due to the high value of $N_i/N_o$, which results from the large number of vessels in the rete (on the order of 20–100). Scholander and Krog have measured only the subcutaneous temperatures in the sloth arm. These are probably representative of the artery and vein temperatures (which are nearly equal as $N_i/N_o$ is large), and these are plotted in Fig. 8. The analytical results for $N_o = 0.2$ and 2 are also shown. The agreement with theory is fair considering the large uncertainties involved in estimating the parameters and the lack of direct blood temperature data.

These results also underscore the need for accurate measurement of blood flow rate. The experimental temperature distributions for these tests would be the same when put in nondimensional form if the blood flow rate, and thus $N_o$, had remained the same. The fact that the experimental results are lower at the lower ambient temperatures indicates that the blood flow rate was decreased. This is borne out by results of Scholander and Krog, who detected a decrease in blood flow rate by a factor of two in one test.

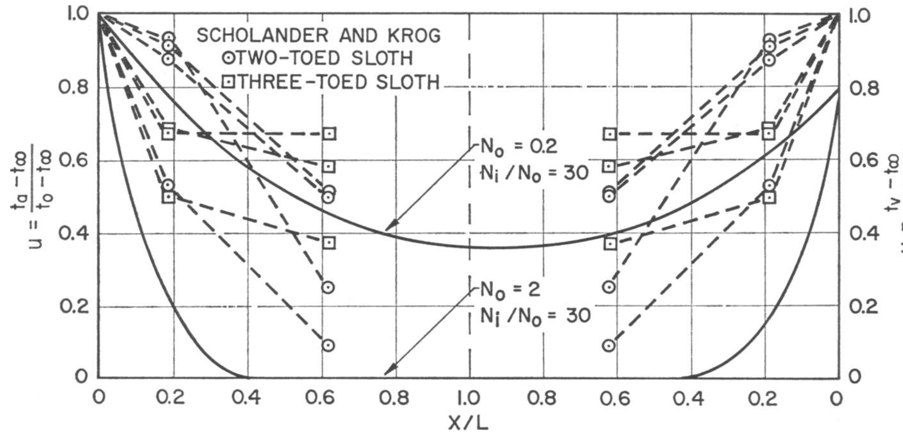


**Figure 8** Comparison of analytical model with experimentally determined subcutaneous temperatures in a sloth limb.

*Porpoise Fluke*

This situation is depicted as Model II, Fig. 4. As with the sloth, there is considerable uncertainty involved in estimating the parameters. Considering the information presented by Scholander and Schevill, it is felt that the following orders of magnitudes for the parameters are probably representative:

$$N_i = 0.2, \qquad N_o = 0.1, \quad \text{and} \quad N_i/N_o = 2.$$

At present, there are no experimental temperature measurements available to compare to the theory. As shown in Figs. 5 and 6, there would not appear to be significant counter-current heat exchange in the fluke for these parameter values. The particular vascular configuration would be valuable, though, in minimizing the heat transfer to the surroundings by insulating the artery from the environment. This is borne out by Fig. 6. The porpoise fluke configuration (Model II) has about one-half the heat loss it would have if the artery were not surrounded by veins (Model I).

It is realized that there is considerable uncertainty involved in the estimation of the parameters presented here. However, it is hoped that these results indicate the size of the parameters encountered in a physiological system and illustrate the method of calculation of the counter-current heat exchange effect.

## RESULTS AND CONCLUSIONS

The following are the results of the analysis presented in this paper and the conclusions that can be drawn:

Nondimensional parameters governing counter-current heat exchange in extremities have been determined. The normalized temperatures are functions of normalized distance and, in general, three nondimensional conductances. These nondimensional conductances are the ratios of the heat transfer conductances between vessels, and between vessels and the environment, to the product of the blood flow rate and specific heat.

An analytical model for counter-current heat exchange has been formulated and solutions obtained. Graphical results are presented for two representative physiological systems. These results are valuable in delineating those situations in which counter-current heat transfer is important, and in quantitatively predicting the heat transfer and the temperature distributions. Performance parameters are also presented to aid in this evaluation.

The conductance between the vessels and the environment controls the heat loss from a limb. Tissue is a poor conductor of heat and the usual anatomical arrangement of vein and artery is not conducive to heat transfer. Significant counter-current heat exchange occurs only if the conductance between veins and arteries is high. In general, specialized anatomical structures (e.g. a rete) are needed in order to reduce heat loss through this mechanism.

Heat transfer calculations are presented for three physiological situations. The method of calculating the heat transfer conductances and the use of the theory are demonstrated.

The data currently available are insufficient for an adequate comparison with the theory developed in this paper. Additional experimentation, in which the quantities incorporated in this theory are measured, is needed in order to gain further insight into the counter-current mechanism.

The counter-current effect becomes more significant as the blood flow rate decreases. In terms of the parameters of this analysis, reduced blood flow increases the nondimensional conductance between the veins or arteries and the environment ($N_o$), the ratio of conductances ($N_i/N_o$) remaining the same. This effect has been noted by Scholander and Krog in their experiments with the sloth. Thus, the vasoconstriction response to cold serves to protect the animal in two ways. The blood flow rate in the limb, and, correspondingly, the total amount of thermal energy carried by the blood, is reduced. In addition, the venous return temperature is raised more than normally through counter-current heat exchange, further reducing the heat loss.

The use of a nondimensional temperature parameter allows generalizing the results for any ambient temperature. However, as previously noted, the effect of ambient temperature on the thermal control system of the animal may produce changes in blood flow rate, blood vessel diameter, and blood flow distribution and must be accounted for.

The results of this analysis indicate that there is not a significant counter-current effect in the arm of a man or the fluke of a porpoise. The effect is shown to be significant in the sloth rete, however. Further experiments in which all of the important parameters are measured are needed to confirm or disprove these conclusions.

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