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WINE husbandmen generally recognize that piglets require a warm, dry environment for survival, especially during the first few days after birth. But only recently have we begun to learn why this is so, corroborating what Samuel Brody observed: animal scientists often attempt to explain scientifically what husbandmen have recognized for many years (Campbell and Lasley, 1969).

An attempt will be made here to integrate environmental and thermoregulatory aspects of the neonatal piglet's energy budget with a view toward the relation between thermoregulatory development and survival. Emphasis will be placed on the physical interaction between the piglet and its external environment and on the nature of piglets' thermoregulatory responses to cold.

Birth: An Abrupt and Profound Environmental Change. The neonatal animal exists in two environments. The external environment surrounds the whole body, while the individual cells exist in the internal environment. The neonate must respond to its new and fluctuating external environment to sustain internal homeokinesis. Many die neonatally; some presumably are unable to adjust to independent extrauterine life.

Wild animals are usually born during seasons favoring survival, whereas many domestic species have become continuous breeders. Domestic neonates are often reared in external environments to which they are un-adapted. Moreover, animals have little opportunity to choose or alter their external macroenvironments in modern livestock production systems. Provision of an optimal environment is therefore imperative. However, precise requirements are not yet known, and animal-shelter recommendations remain tenuous.

Piglet Survival. Roughly a quarter of the live piglets farrowed in this country die before weaning (A.R.S., 1965). Most losses come during the first 3 postnatal days (Bauman, Kadlec and Powlen, 1966). Neonatal mortality is therefore a significant problem in swine production.

The piglet must adjust to a new energy budget at birth. It is susceptible to cold, and as a direct effect, chilling may irreversibly lower body temperatures of neonatal piglets. In litters farrowed during cold weather, chilling reportedly caused about a quarter of the piglet deaths during the first postnatal day, but less than 5% of those on the second and third days; after 5 days of age, no deaths were attributed (directly) to chilling (Bauman et al., 1966). Indirectly, chilling may weaken defensive responses to critical challenges: chilling impairs subsequent cold-resistant ability (Curtis, Heidenreich and Harrington, 1967); chilled piglets are less able to avoid being overlaid by sows (Pomeroy, 1960); and chilling is empirically recognized as a predisposing factor for diseases fatal to many piglets (Vickers, 1960a, b). Unfortunately, evidence for chilling as a cause of neonatal morbidity or mortality is difficult to obtain and is largely empirical. However, the thermal environment is probably at least as important to neonatal stability of piglets as has been thought.

Energy Flow. The piglet is the intermediate unit in a tripartite energy-flow system. The other parts are the energy source and the heat sink. Life requires a continuous flow of energy from the source through the piglet to the sink (Morowitz, 1968). This energy flow maintains the piglet's functional integrity by establishing order and material cycles at all levels of functional organization. The secondary use of heat to maintain the body's warmth is also essential.

The piglet's energy source is generally food, although natal energy reserves are catabolized, especially during the first postnatal day, and heat may be gained from the external environment. Metabolizable food en-
nergy comprises the heat increment plus net energy for maintenance and growth. Net energy not contributing directly to a net gain in tissue energy is also converted to heat, which joins the heat increment to yield metabolic heat. Metabolic heat is used, in part, to keep the body warm and is finally dissipated to the external environment as useless heat. Thus, while the piglet can gain heat from the external environment, there must be a net loss to that environment for life to continue; the external environment is a net heat sink.

**Piglet—Environmental Heat Exchange: Fundamentals**

The internal body temperature reflects the amount of heat stored; it is the product of the body's heat content and heat capacity. A relatively stable internal temperature—homeothermity—results from a dynamic equilibrium between the rate at which metabolic heat is produced and the rate at which heat is exchanged with the external environment. These terms are related to the change with time in the amount of heat stored by the piglet's body as:

\[ M + G = L + \Delta S \]  

(Equation 1)

where \( M \) = metabolic heat production; \( G \) = heat gained from the external environment; \( L \) = heat lost to the external environment; and \( \Delta S \) = the change in the amount of heat stored in the body. These terms all have the units, (kcal hr.\(^{-1}\)). Although "flux" and "flux density" are often used ambiguously, "flux" is the total energy passing through a given surface per unit time; "flux density" is the energy passing through a unit area of a given surface per unit time (Sarbacher, 1959; Kleiber, 1961). The terms in Equation 1, and similar terms in other equations in this paper, represent true fluxes. When the change in heat storage is zero, the piglet is in heat balance and body temperature remains constant.

The piglet exchanges heat with its external environment in four ways. Radiation, conduction and convection are sensible heat transfers and evaporation is an insensible heat transfer. When a temperature gradient exists, there is a net sensible flux of heat in the direction of lower temperature. Hence, the piglet can either gain or lose heat by sensible means, depending on the direction of the piglet-environmental temperature gradient. Heat can be lost but it cannot be gained by evaporation, which depends on a vapor-pressure gradient.

If \( R, K, H \) and \( LE \) represent heat fluxes due to radiation, conduction, convection and evaporation, respectively, and if the subscripts \( g \) and \( L \) represent heat gain and loss, respectively, they can be substituted appropriately into the first heat-balance equation to give the second:

\[ M + R_G + K_G + H_G = R_L + K_L + H_L + L E_L + \Delta S \]  

(Equation 2)

Finally, respective sensible heat gains and losses can be combined to give net heat fluxes, signed by the subscript \( N \). When net heat exchange is determined as gain flux minus loss flux, then a negative net heat flux represents a net loss of heat by the piglet and a positive net flux indicates a net gain. The net fluxes can be substituted for sensible gains and losses of heat in the second equation, giving, after rearrangement of terms, the third equation, representing the net heat balance:

\[ M + R_N + K_N + H_N - L E_L = \Delta S \]  

(Equation 3)

**General Relationship for Heat Exchange.**

The rate of heat exchange or heat flux, \( Q \) (kcal hr.\(^{-1}\)), between the piglet's surface and its physical environment depends generally on: the gradient between the appropriate piglet-surface parameter, \( P_s \), and the corresponding microenvironmental parameter, \( P_e \); the strength with which these two parameters are joined by the appropriate physical coupling factor, \( z \) (Gates, 1968); and the effective piglet-surface area, \( A_s \), over which the particular energy exchange occurs. The general heat-flux equation shows how these terms are related:

\[ Q = A_s z (P_e - P_s) \]  

(Equation 4)

Since the piglet-surface parameter is generally greater than the corresponding microenvironmental parameter, the gradient, and therefore the net heat flux, is usually negative for the piglet. The piglet usually loses heat to its external environment.

The piglet's external microenvironment or effective external environment comprises five integral parameters: air temperature; air velocity; ambient vapor pressure; environmental
radiative-surface temperature, or simply wall temperature; and contact medium temperature. Each of the parameters, except air velocity, affects the piglet’s heat balance according to its gradient with a corresponding piglet-surface parameter (see Equation 4). Air velocity, on the other hand, affects the coupling factors for convective and evaporative fluxes.

To understand the piglet’s energetic interaction with its external environment, one must know the terms in the heat-flux equation for each of the four modes of heat exchange. In general, the microenvironmental parameter and physical coupling factor in Equation 4 are determined mainly by the character of the microenvironment and/or by physical constants; the piglet-surface parameter, effective piglet-surface area, and physical coupling factor are influenced by the piglet’s physical and behavioral thermoregulatory responses to the environment.

Although accurate quantitation of all the terms for each of the heat-transfer modes is not presently possible, the ways in which the terms influence heat exchange need nonetheless to be recognized because they effect the environmental thermal demand (Smith, 1964) or thermostatic heat requirement (Kleiber, 1961). That is, these terms in the respective heat-flux equations determine the net amount of heat the piglet loses to its environment per unit time, and therefore the amount which must be replaced metabolically to ensure homeothermity.

A semiquantitative understanding of these influences can be achieved through a brief consideration of the physical bases for heat exchange. The reader is referred to texts by Jakob and Hawkins (1957) and by Munn (1966) for more detailed considerations.

Evaporative Heat Loss. Evaporation occurs as water molecules gain enough kinetic energy to cause a net escape of molecules from a wet surface. Continuous evaporation requires that the water vapor be removed from just above the evaporative surface; otherwise that space becomes saturated and evaporation ceases.

Evaporative moisture flux, $E$ (kg hr.$^{-1}$), is determined by an equation which has specific terms corresponding to each general term in the general flux equation:

$$E = A_{se} V (e_a - e_{sa})$$

(Equation 5)

where $A_{se}$=piglet’s evaporative surface area (m$^2$); $V$=vapor-diffusion coefficient (kg hr.$^{-1}$ m$^{-2}$ mb$^{-1}$); $e_a$=ambient vapor pressure (mb); and $e_{sa}$=saturation vapor pressure at piglet’s surface (mb). Hence, evaporative moisture flux is determined by the strength with which saturation vapor pressure at the piglet’s surface is coupled with ambient vapor pressure by the vapor-diffusion coefficient, as well as by the vapor-pressure gradient and the evaporative surface area. The assumption is made that the surface is completely wet. The vapor-diffusion coefficient is usually determined empirically and is influenced by air velocity; air movement helps to maintain the obligatory vapor-pressure gradient in the space immediately surrounding the piglet (McLean, 1963).

Equation 5 gives the rate at which water is evaporated from a surface. The amount of heat lost during the evaporative process is symbolized $LEL$ (kcal hr.$^{-1}$). It is the product of evaporative moisture flux, $E$, from Equation 5, and water’s latent heat of evaporation, $L$ (kcal kg.$^{-1}$) (Kleiber, 1961).

Radiative Heat Exchange. If it is assumed that the piglet is within a shelter (where, according to Wien’s displacement law, essentially all radiant flux occurs in the thermal wavelengths), it is necessary to consider only the net thermal-radiative flux. The piglet emits thermal radiation to all objects in its environment. All these objects simultaneously radiate to the piglet. The direction and magnitude of net radiant flux, $R_R$ (kcal hr.$^{-1}$), equals the absorbed minus the emitted radiant flux, which can be calculated approximately by the net radiation equation:

$$R_R = A_{sr} \sigma (T_{er}^4 - T_{sr}^4)$$

(Equation 6)

where $A_{sr}$=piglet’s radiative surface area (m$^2$); $\sigma$=Stefan-Boltzmann radiation constant=4.93x10$^{-8}$ (kcal hr.$^{-1}$ m$^{-2}$ °K$^{-4}$); $T_{er}$=average environmental-surface temperature (°K); and $T_{sr}$=piglet’s radiative-surface temperature (°K).

Two other physical factors influence radiant exchange. The radiant emissivity of a surface is the ratio of its emissive flux to that of a black-body surface under identical conditions; absorptivity is the fractional part of the incident radiation that is absorbed by the surface in question. These factors, together with the Stefan-Boltzmann constant, couple the piglet’s radiative-surface temperature with wall temperature to determine net radiant flux. In thermal wavelengths, emissivities and absorptivities of animals’ surfaces are near unity.
Therefore, emissivity and absorptivity were omitted from the net radiation equation, although high values for these indicate that the piglet's surface is strongly coupled to its radiant environment.

Conductive Heat Exchange. Piglets exchange heat by conduction with media which contact their bodies. Heat conduction occurs when energy is transmitted from one molecule to another. Heat is conducted through the thin, stagnant film of air—the boundary layer—which surrounds the piglet, and conductive exchange also occurs between the piglet and the floor on which it lies or objects against which it leans. Conducted heat, unlike radiated heat, is transferred only in one general direction for a given situation. The piglet either gains or loses heat by this pathway, depending on the direction of the temperature gradient.

Unidirectional, steady-state conductive flux, \( K_{X_s} \) (kcal hr.\(^{-1}\)), is determined by the following equation:

\[
K_{X_s} = A_{sk}\kappa (T_{x_1} - T_{sk}) (\Delta x)^{-1}
\]  

(Equation 7)

where \( A_{sk} \) = conductive-surface contact area (m\(^2\)); \( \kappa \) = medium's heat conductivity (kcal hr.\(^{-1}\) m\(^{-1}\) \(^\circ\)C\(^{-1}\) m); \( T_{sk} \) = piglet's conductive surface temperature (\(^\circ\)C), which is assumed to be the same as the conducting medium's surface temperature, \( T_x \); \( \Delta x \) = distance from contact surface (\( x_0 \)) to some point, \( x_1 \), in the conducting medium (m); and \( T_{x_1} \) = medium temperature at \( x_1 \) (\(^\circ\)C). Hence, steady-state, unidirectional (perpendicular to contact surface) heat transfer at the piglet-medium contact surface is a function of contact area and of temperature gradient in the medium, as coupled by the medium's heat conductivity.

In practice, conduction usually occurs in the unsteady state, since the medium's temperature gradient, and therefore conductive flux, decreases with time because the medium warms. Conduction in the unsteady state has been described by Jakob and Hawkins (1957).

Convective Heat Exchange. Convection is the transport of heat and water vapor by air movement. There are two kinds of convection: natural and forced. Natural convection occurs in still air and results primarily from a temperature gradient between the edge of the boundary layer and surrounding air. Convective eddies of warmed and humidified air are spontaneously bouyed away from the boundary layer of stagnant air surrounding the piglet by the cooler and denser ambient air beyond the boundary layer. As the warmer air is displaced, it removes heat and water vapor. During forced convection, an airstream is directed over the piglet's surface by a draft or by body movements, as during shivering (Kleiber, 1961). This airstream also removes warmed and humidified air from around the body, thus maintaining essential temperature and vapor-pressure gradients between the body and the external environment.

Before heat or water vapor can be convected away from the piglet, they must first cross the boundary layer. Heat is conducted through the boundary layer; water vapor diffuses through it. Then warmed, humidified air at the outer edge of the boundary layer is convected away.

Convective heat flux, \( H_N \) (kcal hr.\(^{-1}\)), is determined by the convection equation:

\[
H_N = A_{sh}h(T_a - T_{sh})
\]  

(Equation 8)

where \( A_{sh} \) = piglet's convective surface area (m\(^2\)); \( h \) = convection coefficient (kcal hr.\(^{-1}\) m\(^{-2}\) \(^\circ\)C\(^{-1}\)); \( T_a \) = air temperature beyond the boundary layer (\(^\circ\)C); and \( T_{sh} \) = piglet's convective surface temperature (\(^\circ\)C). Net convective heat flux is hence determined by the strength with which the piglet's convective surface temperature is coupled to air temperature by the convection coefficient. The convection coefficient, in turn, is dependent on that same temperature gradient, as well as on air velocity, ambient vapor pressure, roughness of the piglet's surface, and also the piglet's dimensions, position and orientation with regard to airflow.

The convection coefficient is usually determined by empirical fitting. It accounts for both conduction through the boundary layer and subsequent convection away from the piglet, since the two processes are inexorably related and difficult to quantitate separately. The greater the convective flux across the boundary layer, the more heat is available for convection away from the piglet. The means of effecting forced convection not only enhance warm eddies leaving the body, they also disturb and effectively reduce the thickness of the boundary layer, resulting in a simultaneous reduction in its insulative value (see Equation 7).

With regard to size, the smaller the animal, the larger the convection coefficient (Gates, 1968); hence, surface area affects net convective flux via both the area term in the convection equation per se and the convection
coefficient. Because the convection coefficient for the relatively small piglet is relatively large, the piglet’s convective surface temperature is coupled quite vigorously to air temperature. Convective heat exchange would therefore be expected to influence the piglet’s energy budget significantly.

When forced convection is appreciable, natural convection is negligible. Under practical conditions, appreciable air movement, and therefore forced convection, usually occurs. Natural convective flux is significantly influenced by the piglet-air temperature gradient, but air velocity is a more important determinant of forced convective flux. In general, forced-convective heat loss is proportional to the square root of air velocity, \( v \) (Hardy, 1949):

\[
H \propto \sqrt{v} \quad \text{(Equation 9)}
\]

**Piglet—Environmental Heat Exchange: Experiments**

In general, respective piglet-surface temperatures are more similar than are the corresponding environmental temperatures in the various flux equations. Hence, values for microenvironmental parameters influence the partition of heat exchange to a greater extent than do those for the piglet-surface parameters. That is, the partition of heat loss into its components is determined in practice largely by the physical environment. Partitional data have been collected both from piglets held in a nylon sling (Butchbaker and Shanklin, 1964) and from unrestrained piglets (Mount, 1962; 1964b; 1966; 1967). Conduction to the floor was not considered in the partition of heat loss from suspended piglets, which are therefore similar to standing piglets. The data for unrestrained piglets have been adjusted in most cases for heat loss from a piglet lying in a relaxed posture on an experimental floor of bare concrete (Mount, 1967).

**Effects of Air and Wall Temperatures.** When air and wall temperatures were lowered from 30 to 20 C, the piglet’s total heat loss rate increased by 65% (Mount, 1962; 1964b) to 100% (Butchbaker and Shanklin, 1964). An increase was predictable from sensible or temperature-dependent heat-exchange relationships: as environmental temperatures drop, respective piglet-environmental temperature gradients widen and consequently sensible heat fluxes increase.

When air and wall temperatures were both 30 C, 87% of the heat lost by the neonatal piglet lying on concrete was via sensible means (i.e., radiation, conduction and convection), whereas about 93% was lost sensibly at 20 C (Mount, 1967). The data for the suspended piglet were about 75% at 30 and 87% at 20 C (Butchbaker and Shanklin, 1964).

After amniotic fluid has been evaporated or otherwise removed from the surface, insensible or evaporative heat loss in piglets occurs almost entirely from the respiratory tract. The piglet evaporates very little moisture from its skin surface since it sweats little, if at all, and so its surface is ordinarily not moist. The absolute rates of evaporative heat loss were similar at both 20 and 30 C air and wall temperature (Mount, 1962). However, with increases in these temperatures, evaporative heat-loss rate expressed as a portion of total heat loss increases; total and sensible heat losses decrease when environmental temperatures increase. Insensible heat loss accounted for about twice as large a portion of total heat loss at 30 as at 20 C (13 vs. 7%) (Mount, 1962; 1967).

It is apparent that piglets lose heat mostly via sensible fluxes. Sensible heat-loss has been further partitioned into radiant, conductive and convective components. At air and wall temperatures of 20 C, about 42% of the sensible heat lost by piglets lying on concrete was via radiation, 42% was via convection and 16% was via conduction to an experimental floor (Mount, 1962). At 30 C, respective portions were about 49% radiative, 34% convective and 17% conductive. Data from suspended piglets (Butchbaker and Shanklin, 1964) had similar trends, except that conductive flux was not a factor. Under these experimental conditions, about 2 of the sensible heat loss was via radiation and about 2 via convection when environmental temperatures were 20 C, whereas at 30 C the partition was roughly 2 radiative and 2 convective.

It should be noted that air velocity was low in the apparatuses in which both sets of data were collected; natural convection was probably predominant. The close relationship between the microenvironment and radiant and convective heat fluxes observed in these data was predicted when respective coupling factors for radiant and convective heat losses were discussed earlier.

When wall temperature is lower than air temperature, radiative heat loss becomes even more important. When both are 30 C, the radiative-convective partition of sensible heat loss is about 60:40, whereas when air temperatures is 30 but wall temperature is 20 C, the
partitions is about 75:25; similarly, when both temperatures are 20°C, the partition is about 50:50, but when wall temperature drops to 10°C, the partition is about 60:40: radiant:convective (Mount, 1964b).

These data suggest that radiant and convective heat losses are most important to the energy budget of the neonatal piglet. However, under practical conditions conductive heat loss may be more important than is generally recognized.

*Effect of Air Velocity.* The data just reviewed indicate that in practically still air, radiant exchange accounts for at least half of the sensible heat loss. In appreciable air movement, the convective component would be expected to be relatively more important. Indirect evidence corroborates the predicted effect. It was assumed that changes in oxygen-consumption rate directly reflect changes in rate of metabolic heat production and total heat loss. Increasing air velocity from 5 to around 160 (cm sec⁻¹) resulted in about a 20% increase in oxygen-consumption rate at air and wall temperatures of 20°C and in a 25% increase at 30°C (Mount, 1966). At 5 (cm sec⁻¹), natural convection obtains, whereas 160 (cm sec⁻¹) is an appreciable draft. Most of the increase in oxygen consumption rate was presumably due to increased convective heat loss and the need to replace this in restoring thermal balance.

The observed increases in heat-production rate were not, however, as great as predicted from an inert model. Behavioral and physical thermoregulatory responses to the draft probably accounted partly for this. Although convective heat loss is enhanced by air movement, radiant flux apparently still predominates. Increased air velocity also increases evaporative rate at the skin, but this is almost negligible in dry neonatal piglets.

*Effect of Ambient Vapor Pressure.* The greater the ambient vapor pressure, the greater the convective heat loss (Butchbaker and Shanklin, 1964). It might be suspected that moister air has better conductive properties and thus transfer of heat across the boundary layer would be facilitated by increasing air’s vapor pressure. However, conductive capacity or thermal admittance (i.e., the square root of the product of heat conductivity and heat capacity) of moist air is similar to that of dry air; water vapor’s heat conductivity is less than dry air’s (Handbook of Chemistry and Physics, 1965), but air’s heat capacity increases slightly with increasing water-vapor content (C. B. Tanner, personal communication). Perhaps ambient vapor pressure affects convective flux because it influences the density, viscosity and/or specific heat of air—all among the determinants of the convection coefficient (Munn, 1966).

Ironically, ambient vapor pressure is a more important determinant of convective heat-loss rate than of evaporative heat flux for the neonatal piglet (Butchbaker and Shanklin, 1964), probably because evaporative rate is low.

*Effect of the Floor’s Thermal Properties.* Insulation is the reciprocal of conduction. In particular, piglets lying on foamed plastic (2.5 cm thick) lose about 1/6 as much heat to the floor as when on concrete (2.5 cm) and about 1/3 as much as on wood (1.27 cm) (Mount, 1967). Bedding materials also influence heat loss to floors in a predictable manner. Straw (2.5 cm) reduces heat loss to the floor to about 40% of that on concrete alone; wood shavings (2.5 cm) reduce the loss to 66% of that on bare concrete (Mount, 1967).

The lying posture affects the rate of heat loss to the floor significantly by influencing the piglet-floor contact area (see Equation 7). Warmer ambient conditions and/or bedding cause a relaxation of the lying posture, and thus an increase in the contact area. However, it has been observed that the effect of increased contact area is offset by other factors, including the thermal insulation of the bedding, so that heat loss to the floor as a portion of total heat loss remains about the same regardless of ambient temperature (Mount, 1967). Of course, as the conductive surface area of the piglet changes in one direction, the effective areas for radiative and convective exchanges generally change in the other.

Not all the heat lost by the piglet to the floor is via conduction. Conduction occurs only across piglet-floor contact surfaces, while the piglet undergoes radiant exchange with the floor from any other part of its body surface which is exposed to the floor.

Physical and Behavioral Thermoregulatory Responses to Cold by Neonatal Piglets: Determinants of Total Heat-Loss Rate

Heat flux is determined generally by exchange area, coupling factor, microenvironmental parameter and piglet-surface parameter. The microenvironmental parameters largely determine the partition of heat loss into the various modes of heat exchange. The piglet affects total heat-loss rate, and thereby en-
vironmental thermal demand, by changing the
effective temperature and other physical char-
acteristics of its surface (physical thermo-
regulation) and by altering, via postural
changes mainly, its effective surface area for
heat exchange (behavioral thermoregulation).
Of course, total heat-loss rate is also a func-
tion of the microenvironmental parameters.

**Physical-Thermoregulatory Responses to Cold**

**Thermal Insulation.** The homeotherm's
body attempts to conserve metabolic heat in
cold environments. Total thermal insulation
comprises tissue, pelage and air components
(Bianca, 1968).

Tissue insulation resists heat flow from the
body core to the surface. It consists prin-
cipally of subcutaneous fat, especially when
peripheral vasoconstriction occurs (Miller and
Blyth, 1958). Vasoconstriction reduces periph-
eral blood flow and, hence, the circulatory
transfer of heat from core to surface. Conse-
quently, surface temperature drops, reducing
surface-environmental temperature gradients
and, therefore, the rate of sensible heat loss.

The piglet is at a disadvantage with respect to
tissue insulation because it has little subcu-
taneous fat at birth (Dawkins and Hull,
1964).

Pelage insulation is the most important
component of total thermal insulation in most
animals (Bianca, 1968). It resists transfer of
heat between the skin and the outer edge of
the haircoat. Pelage insulation results mostly
from still air amongst hairs through which heat
must be conducted. Stagnant air is a poor
conductor of heat. Hence, pelage insulation
can be considered as an extension of the
boundary layer. Piloerection roughens the sur-
face and increases the thickness of the layer
of stagnant air through which heat must be
conducted, i.e., air amongst airs plus boundary
layer. Both effects impede heat loss by re-
ducing the convection coefficient. Unfortu-
nately, the neonatal domestic piglet has a
sparse, fine haircoat and so its pelage, whether
piloerected or not, is not very insulative. In-
deed, piloerection in piglets conceivably ex-
poses more skin surface for radiant heat loss
(Tregear, 1965). Insulative value of the pelage
increases with increasing hair density; both
convective and radiative heat losses are re-
duced by increasing pelage. Thus, the neonatal
piglet, with its sparse, fine haircoat, is also at
a disadvantage with regard to pelage insula-
tion, although hair density, as (mg cm$^{-2}$),
doubles during the first 2 weeks after birth
(Mount, 1964a). It is interesting that neonatal
wild piglets have considerably more pelage
than neonatal domestic piglets, which ap-
parently is responsible in part for the wild
piglets’ being markedly more thermostable in
the cold (Foley et al., 1970).

Air insulation represents the true boundary
layer—the thin, stagnant film of air surround-
ing the outer edge of the pelage (Bianca,
1968). The boundary layer has been referred
to previously. It is an excellent thermal insu-
lator, but can be disturbed and thus have
its effectiveness impaired.

**Thermal-Insulative Responses.** At birth,
piglets are already able to respond to cold
by both peripheral vasoconstriction and pilo-
erction (Mount, 1963b; 1964a). However,
their absolute thermal insulation is limited by
the paucity of subcutaneous fat and haircoat.
Nonetheless, when air and wall temperatures
were both lowered from 30 to 20 C, skin tem-
perature dropped from 37 to 33 C, the new
equilibrium temperature resulting from vaso-
constriction and lower air temperature
(Mount, 1964b). Thus, at 20 C the piglet-
environmental temperature gradient is 13 C
(33–20 C) rather than 17 (37–20 C), so the
rate of sensible heat loss would be depressed
(see Equations 6, 7 and 8).

At air and wall temperatures of 30 C, and
in almost still air, a 2-kg piglet had a total
heat-loss rate of 9.5 (kcal hr.$^{-1}$), 8.3 sensibly
and 1.2 insensibly, whereas at 20 C the total
rate was 15.7 (kcal hr.$^{-1}$), 14.6 by sensible
means and 1.1 by insensible (Mount, 1967).
Hence, when environmental temperatures
dropped from 30 to 20 C, there was, as pre-
dicted, a significant increase in sensible heat-
loss rate. However, total thermolytic rate at
20 C was only about $\frac{2}{3}$ that predicted from
an inanimate model (Mount, 1964b): the dis-
crepancy was probably due to reduction in
piglet-surface temperature and behavioral al-
terations in effective body surface area in the
live animal.

**Behavioral-Thermoregulatory Responses to
Cold**

The neonatal piglet responds to cold by
altering the amount of its surface area which
is effective in piglet-environmental heat ex-
change. It reduces effective surface area with
decreasing environmental temperatures: at
20 C the surface area effective for radiant ex-
change is about 15% less than at 30 C
(Mount, 1964b). Postural changes are also
important with regard to heat loss to the floor;
the chilled piglet supports itself in order to decrease contact area with a relatively cold floor and to gain advantage for shivering. Changes in air temperature result in postural changes which in turn result in as much as a halving of heat loss to the floor, due largely to a reduction in contact area (Mount, 1967). Changes in both surface area and posture also affect convective flux; area is an important term in the convection equation and posture influences the convection coefficient.

**Huddling.** A litter of piglets in a cold environment characteristically huddle, a socio-behavioral means of heat conservation. Each piglet's microenvironment is influenced by its littermates. For example, no heat exchange occurs across surfaces in contact with other piglets and net radiant exchange between surfaces with the same temperature is zero (see Equation 6). Huddling reduces the environmental thermal demand by as much as 40% (Mount, 1960). Consequently, a piglet which becomes separated from its littermates experiences a much different microenvironment than one which huddles.

**Age-Independence of Thermal-Insulative Responses**

In spite of increases in pelage density (Mount, 1964a) and subcutaneous fat depots (Brooks et al., 1964; Manners and McCrea, 1963), there is no improvement in effective thermal-insulative responses of piglets to cold during the first postnatal week (Mount, 1963b).

**Metabolic Thermoregulatory Response to Cold by Neonatal Piglets**

According to Kleiber's Law (Kleiber, 1961), an animal existing in its thermoneutral zone of effective environmental temperature must produce about 70 kcal of heat per unit of metabolic body size per day to meet the environmental thermal demand and thus to maintain homeothermic balance. Metabolic body size is defined as the \( \frac{3}{4} \) power of body weight in kilograms. Therefore, \( M \) (kcal day\(^{-1}\))\(=70 \ W^{\frac{3}{4}}, \) where \( W=\)body weight (kg).

The reader is referred to Bianca’s (1968) scheme of environmental thermal zones and their critical limits of environmental temperature. The zone of thermoneutrality lies between the maximal and minimal critical limits of effective environmental temperature. Within the thermoneutral zone, heat-production rate is minimal; the piglet maintains homeothermicity by altering heat-loss rate via physical and behavioral thermoregulation, not by altering heat-production rate.

The minimal critical temperature is a function of heat loss, and therefore of heat conservation. When environmental temperature becomes so low that the piglet can no longer maintain homeothermicity simply by increasing effective thermal insulation, it must increase metabolic rate above the standard (Kleiber, 1961), thermoneutral level. The effective environmental temperature below which the piglet must increase metabolic rate above the minimal level is called the minimal critical temperature. Hereinafter, “environmental temperature” means “effective environmental temperature”\(;\) drafts, moisture and radiant sinks, for example, make for an effectively colder environment than indicated simply by air temperature.

As the piglet becomes better able to conserve heat, it simultaneously becomes better able to withstand lower environmental temperatures without needing to augment heat-production rate above the standard, thermoneutral level to maintain homeothermic balance; thus its minimal critical temperature drops. The neonatal piglet’s minimal critical temperature is 33–35 C (Bianca and Blaxter, 1961; Mount, 1959; 1963a), where effective thermal insulation is maximal and below which the rate of metabolic heat production increases as the piglet attempts to effect heat balance. The piglet is peculiarly susceptible to its thermal environment; it has a relatively high minimal critical temperature. At birth the lamb’s critical temperature is around 29 C (Alexander, 1961) and the calf’s is about 13 C (Gonzalez-Jiminez and Blaxter, 1962). By the time the piglet reaches a body weight of 10 kg, however, its minimal critical temperature has fallen to 19 C (Bianca and Blaxter, 1961).

The piglet continues increasing heat-production rate with decreasing environmental temperature until the absolute minimal critical temperature or homeothermic cold limit is reached. At this point—around 5 C—metabolic rate is maximal: summit metabolism obtains. Further reduction in environmental temperature results in a decrease in body temperature. Hypothermia may be irreversible if it is not corrected. Death occurs when body temperature becomes so low that metabolic processes cease or when some secondary factor leads indirectly to death. For some individual neonatal piglets an environmental temperature of 10 C leads to lowered body
temperature; 5°C is certainly below the homeothermic cold limit of most piglets (Mount, 1963a; Curtis et al., 1967).

The piglet is cold-stressed at environmental temperatures higher than those which directly threaten survival. It is cold-stressed even within the thermoneutral zone, namely, at the point where physical and behavioral thermoregulatory mechanisms are invoked to resist cold exposure (Bianca, 1968). On the basis of energy budget alone, survival is threatened only outside the homeothermic zone, i.e., above the maximal critical temperature or below the homeothermic cold limit. Mortality occurs as a direct effect of chilling when hypothermia becomes irreversible. But morbidity ensues at environmental temperatures above the homeothermic cold limit, as well. Death may occur as an indirect effect of cold stress if this morbidity predisposes the piglet to some secondary, adverse factor.

From Kleiber's Law it follows that the smaller the animal, the larger the necessary heat-production rate per unit body weight. Also, smaller animals generally have higher minimal critical temperatures and require relatively greater increases in metabolic rate during cold exposure to effect heat balance. These phenomena are all generally associated with the relation between body mass and body surface area; the smaller the animal, the more surface area per unit body weight, and therefore the more heat-exchange area per unit body weight.

The oxygen-consumption rate of the fetal lamb is similar to the ewe's on a unit body weight basis. However, at birth the lamb rapidly increases heat-production rate in adjusting to the postnatal environment (Dawes and Mott, 1959). The neonate must suddenly begin to produce heat at the rate predicted more-or-less by Kleiber's Law; that rate is proportional to metabolic body size, not body weight.

By analogy, we might assume that a 150-kg pregnant sow has a metabolic rate of 80 kcal per unit of metabolic body size per day. The sow's metabolic body size would be 42.8 kg
\(^{0.75}\), so her metabolic rate would be 3424 (kcal day
\(^{-1}\)). On a per unit body weight basis, the sow's metabolic rate would be 3424/150, or 22.8 (kcal kg
\(^{-1}\) day
\(^{-1}\)). If, as the lamb, the 1.5-kg fetal piglet has a metabolic rate comparable to its dam's per unit body weight, its metabolic rate would be 34.2 (kcal day
\(^{-1}\)).

Immediately after birth, this 1.5-kg piglet would theoretically need to produce heat according to its metabolic body size. Its metabolic body size is 1.355 kg
\(^{0.75}\), so it would need to produce heat at the theoretical rate of 70 x 1.355, or 95 (kcal day
\(^{-1}\)) at thermoneutrality. Hence, even at environmental temperatures above 34°C, the piglet must increase heat-production rate at birth from about 35 to about 95 (kcal day
\(^{-1}\)), theoretically, to maintain heat balance. Indirect calorimetric measurements on neonatal piglets at 35°C indicated that their heat-production rate is around 100 (kcal day
\(^{-1}\)) (Curtis, Christison and Robertson, 1970), approximately that predicted. The neonatal piglet thus has a tremendous environmental thermal demand, due to its age, size and paucity of pelage and subcutaneous fat. Although it does respond to cold by increasing thermal insulation already at birth, the magnitude of this response, while not negligible, is nonetheless insufficient to prevent the piglet's having an extraordinarily high minimal critical temperature.

In summary, the piglet is extremely sensitive to its thermal environment at birth, and an environment optimal for the piglet is too warm for the sow.

Age-Dependent Change in Cold Resistance. The piglet improves markedly in thermostability during the first postnatal day or so (Newland, McMillen and Reineke, 1952; Curtis et al., 1967). At 6 hr., the piglet's rectal temperature fell about 4°C during a 90-min. exposure to an environmental temperature of 5°C; the 30-hr.-old piglet's rectal temperature dropped less than 1°C during similar cold exposure (Curtis et al., 1967). This change was associated with age per se rather than with concomitant body weight changes.

The piglet's thermostability during severe cold stress, e.g., when the individual piglet's environmental temperature is 5°C, is a function of mechanisms which either conserve or produce heat. The early postnatal improvement in thermostability cannot be attributed to an age-dependent improvement in heat-conserving ability since indeed the effectiveness of thermal-insulative mechanisms does not improve during the first postnatal week (Mount, 1963b).

On the other hand, the metabolic rates of piglets, both at thermoneutrality and during cold exposure, are higher after the first postnatal day or so (Mount, 1959; Curtis et al., 1970). Hence, the first one or two postnatal days seem to be important to the ontogeny of thermoregulation in piglets. During this period the thermoneutral metabolic rate and body
temperature both increase and the ability to augment thermogenesis in response to cold exposure improves (Mount, 1959), while at the same time thermostability is ameliorated (Curtis et al., 1967). Also, survival rate improves in piglets during the same period (Bauman et al., 1966) and piglets less than one day old preferred an effective environmental temperature of 32°C when huddled, whereas those over one day of age preferred 30°C (Mount, 1963c).

**Nature of the Metabolic Response to Cold by Neonatal Piglets**

The apparent reason for improved thermostability during cold exposure in 2-day-old piglets is an increased efficiency of heat production. The functional ontogeny responsible for the more effective metabolic response to cold is not well understood at this time.

Carbohydrate is the neonatal piglet's primary energy substrate (Goodwin, 1957; McCance and Widdowson, 1959). Natal carbohydrate reserves are high in piglets relative to those present in other neonates (Shelley, 1961). It has even been inferred that piglets can increase the rate of carbohydrate oxidation, but not the rate of lipid metabolism, in response to cold exposure (LeBlanc and Mount, 1968). Nevertheless, in spite of high depot and circulating carbohydrate levels, piglets aged 8 hr. are unable to maintain homeothermia at environmental temperatures between 0 and 10°C (Curtis, Heidenreich and Foley, 1966), whereas those aged 30 hr. are practically able to do so (Curtis et al., 1967). It has been suggested that piglets are unable to utilize available carbohydrate efficiently (Curtis et al., 1966; Swiatek et al., 1968). Carbohydrate is available and piglets are able to mobilize it in response to cold; utilization is apparently the limiting factor in very young piglets. Piglets do increase metabolic rate upon cold exposure from birth on, but the rate of oxygen consumption is greater at all environmental temperatures during the second than during the first postnatal day (Mount, 1959; Curtis et al., 1970).

Plasma levels of free fatty acids were observed to increase in response to either injected norepinephrine or cold exposure in neonatal piglets (Curtis and Rogler, 1970). Furthermore, piglets aged two days had higher levels of plasma free fatty acids than did piglets less than a day old after either of these treatments under conditions of these experiments. We suggested such a change in the lipolytic and fat-catabolic response to cold to be partly responsible for the neonatal improvement of thermostability in piglets.

Insulin secretion in pigs is antagonized by catecholamines (Hertelendy et al., 1966). Therefore, if the piglet responds sympathetically to cold, as indicated by evidence for vasoconstriction (Mount, 1963b), glycogenolysis (Curtis et al., 1966) and adipokinesis (Curtis and Rogler, 1970), its rate of insulin secretion might be reduced during cold exposure. This in turn could impair carbohydrate utilization. Indeed, impaired glucose tolerance (Curtis et al., 1966) and low plasma insulin levels (Swiatek et al., 1968) observed in neonatal piglets held below thermoneutrality suggest impaired carbohydrate-utilizing capability during cold stress.

Hence, since at birth the piglet apparently relies primarily on carbohydrate oxidation for heat production, sympathetic response to cold might, ironically, be detrimental to the thermogenic response, insofar as the important contribution by glucose utilization is concerned. Then, if and when hypothermisity did ensue, insulin secretion might be further antagonized by that lower body temperature (Blackard, Nelson and Labat, 1967).

We have therefore suggested that in older, more thermostable piglets, sympathetically-induced lipid catabolism adequately supplants glucose oxidation during acute cold exposure, thereby permitting the older piglet to meet its environmental thermal demand. The younger piglet, on the other hand, would be critically dependent on the poorly regulated carbohydrate oxidation for heat production.

Data on plasma levels of free fatty acids during cold exposure and following norepinephrine injection support this hypothesis (Curtis and Rogler, 1970). Respiratory-quotient (RQ) data have lent more support; when piglets aged either 12 or 84 hr. were studied both at 35°C (thermoreutral) and 5°C (cold stress), age and cold stress both significantly depressed RQ (Curtis et al., 1970). Another report (Mount, 1969a) indicated an age-dependent depression of RQ, but RQ was not significantly different at 32 and 16°C. Of course, even those measurements made at 32°C were made in the zone of cold stress (Bianca, 1968) for the piglet less than a day old since its minimal critical temperature is higher than 32°C (Bianca and Blaxter, 1961; Mount, 1959; 1963a). Further studies are required before the hypothesis has been thoroughly tested.
While the rapid postnatal improvement in thermostability among piglets is remarkable, even more remarkable is the capability of the 2-day-old piglet to meet the enormous environmental thermal demand present in an environmental temperature of 5°C. Once the piglet has attained the age of 2 days, its chances for survival are good, provided the sow supplies enough milk.

Summary of Practical Considerations: Environment and Survival

Fundamentally, the neonatal piglet is susceptible to cold. It possesses so little thermal insulation that it must increase heat-production rate to maintain homeothermicity whenever effective environmental temperature drops below 34°C or so. Deaths among piglets are prevalent during or shortly after that period, namely, the first postnatal day, when piglets are most susceptible to cold (Bauman et al., 1966). Cold resistance improves markedly during the first two postnatal days in piglets, largely because the metabolic response to cold improves. The 2-day-old piglet is relatively thermostable in most practical situations. In contrast to the piglet at birth, the 2-day-old piglet can usually meet its environmental thermal demand for some time even when held individually at an environmental temperature of 5°C.

The thermostability of the piglet during the first postnatal day is not particularly dependent on whether it has suckled (Mount, 1969b). Husbandmen intend for each piglet to nurse shortly after birth. But indifference of the piglet to nursing is probably more a symptom than a cause of subsequent morbidity. The piglet possesses a considerable energy reserve at birth (Shelley, 1961; Swiatek et al., 1968; Curtis et al., 1966). The problem seems to be less one of substrate availability than of utilization capability during the first day postnatum; during this period even the well-fed piglet derives much energy from tissue carbohydrate depots which are present at birth.

Sows do not instinctively remove amniotic fluid from piglets’ surfaces. This fluid is removed either by contact with other surfaces or by evaporation. While present it negates what little pelage insulation would exist if dry and it also impairs piloerection. While the fluid is being evaporated the latent heat represents a large energy expenditure for the piglet. On one hand, the piglet must expend a considerable amount of heat. Piglets should be dried by the herdsman immediately after birth.

Chilling occurs at environmental temperatures considerably higher than the homeothermic cold limit (around 5°C for the individual piglet), the temperature at which maximal insulative and metabolic responses are insufficient to maintain homeothermic balance. Therefore, cold stress is better measured in terms of metabolic rate than in terms of body temperature. For example, it might arbitrarily be considered that a piglet existing in a microenvironment which demands a doubling of metabolic rate over the standard, thermoneutral level is “chilled”. With regard to environmental thermal demand, the 2-day-old piglet and the piglet at birth are chilled by practically the same environmental conditions; their environmental thermal demands are practically the same. However, the older piglet has a higher metabolic rate at all environmental temperatures and so it is better able to meet the thermal demand and, thus, to maintain homeothermic balance.

Under most practical conditions, from a strictly energy-budget point of view, the vigorous piglet, especially when huddled with littermates, theoretically does not require supplemental heat after about the second or third postnatal day. Some heat is usually supplied to facilitate removal of moisture from the shelter, which also requires ventilation. Atmospheric moisture must be removed from farrowing houses to help suppress disease, but ventilation systems should be designed so they do not induce drafts around the piglets (Sainsbury, 1967).

Finally, it is important to recognize that the piglet’s physical microenvironment comprises more than simply air temperature, especially when that parameter is not monitored in the microenvironment of the piglet. Air temperature alone is a poor index of a piglet’s microenvironment. The radiation environment, for example, is a particularly important microenvironmental parameter, but it is usually ignored.

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