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thesis entitled
The Development of Pelage Insulation
and its Relationship to Homeothermic
Ability in an Altricial Rodent,
Peromyscus leucopus.

presented by

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has been accepted towards fulfillment
of the requirements for

Master of Sci. degree in Zoology

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Date 23 June 1986

THE DEVELOPMENT OF PELAGE INSULATION AND ITS RELATION TO HOMEOTHERMIC ABILITY IN AN ALTRICIAL RODENT, PEROMYSCUS LEUCOPUS

By

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A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Zoology
and The Museum

1986

ABSTRACT

THE DEVELOPMENT OF PELAGE INSULATION AND ITS RELATION TO HOMEOTHERMIC ABILITY IN AN ALTRICIAL RODENT, *PEROMYSCUS LEUCOPUS*

By

Frank M. Knight

Dry heat transfer through the piloerected fur of dorsal pelt samples from neonatal *Peromyscus leucopus* was examined using a heated flat plate apparatus equipped with a microfoil heat flux meter. The effective thermal conductivity (k_e', W cm^{-1} $^{o}C^{-1}$) changes significantly only between 4 and 6 days of age, corresponding to the appearance of a noticeable layer of fur. From 6 days to weaning (about 20 days of age) k_e' does not change significantly. Insulation (I) is highly correlated with pelt thickness; however, insulation does not change as the pelt thickness increases from 0.85 cm to its thickest value, 1.10 cm. The minimum insulation, 290 ^{o}C cm^2 W^{-1}, accounts for 30% of the surface-specific whole-body insulation at the youngest age examined (4 days). The maximum pelt insulation, 1400 ^{o}C cm^2 W^{-1}, is achieved at 18 days of age. By 16 days of age, the fur development is 95 to 100% completed and provides 66% of the surface-specific whole-body insulation. The increase in surface-specific whole-body insulation (as determined from metabolic data) during ontogeny is entirely explained by the development of the fur. Furthermore, the development of the pelt insulation is more effective than that of thermogenic capacity in permitting maintenance of high T_Bs at low T_As.

DEDICATION

This thesis is dedicated to my family: my father, Glen; my mother, Madelyn; my brother, Mark; and my sister, Kelly; and to the friends I made in Michigan.

ACKNOWLEDGMENTS

I thank Dr. Richard W. Hill for his patience, support and advice throughout this work. I thank Dr. Thomas Adams for his invaluable technical advice and Dr. John A. King for his support and encouragement. Brian Mavis provided computer consultation for which I am indebted to him. Craig Stewart, Dr. D. R. Webb, Dr. P. A. McClure and Pam Emily read and recommended revisions in earlier manuscripts--thank you. The Department of Zoology and The Museum at Michigan State University provided financial support and facilities for this research.

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The energetic expense for an endotherm to maintain a high, stable body temperature (T_b) is largely dependent on its thermal insulation. Modulation of insulation broadens the range of ambient temperatures (T_a) over which the animal can maintain T_b without an elevation in its basal metabolic rate. At T_as below the lower critical temperature of the thermal neutral zone, a well-insulated animal can maintain its T_b at a lower energetic cost than a poorly insulated one. Furthermore, the well-insulated animal needs to increase its metabolic heat production less per degree decrease in T_a. Although insulation can be important at $T_a > T_b$, this thesis is primarily concerned with the role of insulation as resistance to heat loss from mammals at $T_a < T_b$.

Although fur is not a mammal's only source of insulation, it is perhaps the most obvious source. However, the ancestral interscalar hairs of mammal-like reptiles probably served only as tactile structures (Spearman,1964). Among extant mammals hair may serve multiple functions, but thermal insulation is the most important for most species and especially for those which must endure cold.

The potential of fur as an inexpensive form of energy

GENERAL INTRODUCTION

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The potential of fur as an inexpensive form of energy conservation has important implications for the abundance and distribution of mammals, their life history strategies and their daily and seasonal behavior patterns. Consequently, pelage insulation has been the focus of many ecological studies (especially since Scholander, 1950). However, only a few have given attention to the pelage of neonatal mammals. Among the earliest workers to consider the development of fur insulation are Hahn (1956), Mount (1964) and Hissa (1968). They report the effect on metabolic rate of removing the hair from rats (Hahn), pigs (Mount), lemmings and hamsters (Hissa) at several preweaning ages. The only published research to my knowledge which specifically examines the changing thermal properties of fur during the postnatal development of a mammal is by McClure and Porter (1983). McClure and Porter applied a model based on engineering theory (Kowalski and Mitchel, 1979) which was adapted for computer analysis, EZFUR (Conley, 1983), to study the fur of precocious _Sigmodon hispidus_ neonates. With this computer program it is possible to resolve the mechanisms of heat transfer through the fur layer and from the outer fur surface for a given set of boundary conditions. Furthermore, sensitivity analysis used in conjunction with EZFUR can resolve which changing fur characteristics (e.g., density of hair, hair diameter) are most responsible for changes in the pelage thermal properties.

There is still much to be known about how fur insulation works and how it varies -- among species, among environments, along gradients, and through time. The next chapter reviews some of the progress which has been made in these areas. The third chapter is a research report which is intended to make a contribution to our understanding of the relation between the post-natal development of fur and the ontogeny of homeothermy. The final chapter describes some problems of fur and its development which have yet to be elucidated.

LITERATURE REVIEW

Cena and Clark (1978) reviewed some of the literature on animal coats and human clothing. They perceived two major areas of emphasis since World War II: 1) farm and animal production and 2) thermal-physiological limitations to the distribution of wild animals. In this thesis I take an ecological perspective. Readers who are particularly interested in research applied to agriculture may appreciate the following references: Mount (1960, 1964), Cena and Clark (1978), Wathes and Clark (1981), Gatenby et al. (1983), Gebremedhin et al. (1983).

Prior to 1945 studies on mammalian pelage focused on the description of seasonal molts and factors affecting molts in species of particular interest to the furrier industry (see review by Johnson, 1977). Relatively little research quantified mammalian insulation before 1950 [Giaja (1931) and Babenyscheff (1938) as cited by Scholander (1950)]. The comparative work by P. F. Scholander, Vladimir Walters, Raymond Hock and Lawrence Irving in 1950 is the classical study on pelage insulation. Perhaps every publication on pelage insulation since has cited this landmark.

The current trend is a reductionist approach which emphasizes the mechanisms of heat transfer through fur (Chappell, 1980; Conley, 1983; Gebremedhin et al., 1983; Gatenby et al., 1983; McClure and Porter, 1983). An accurate understanding of the mechanisms of heat flow through fur permits the development of models with which biologists can manipulate fur characteristics, geometry and environmental conditions to predict energetic consequences. Furthermore, partitioning heat flow into conduction, convection, radiation and evaporation enhances our resolution of insulative differences among species, among environments and through time.

Mechanisms

H. T. Hammel (1955) was one of the first to investigate the mechanisms by which heat moves through fur. He examined flat samples of pelts on a guarded hot plate apparatus and measured the temperature gradient through the fur with a ladder of thermocouples. Hammel tested pelts of 15 species, fresh and dried, with fur erected and down. To explore the contribution of free convection in the fur layer to the total heat transferred, Hammel replaced the air with freon which has four times the density and half the conductivity of air (k_a). He assumed, a *priori*, that the greater conductivity of a fur sample (k_f) relative to still air was entirely due to movement of air in the fur sample. Then (k_{freon}/k_a) X $(k_a/k_{f\ in\ air})$ = $(k_{f\ in\ freon}/k_{f\ in\ air})$

should equal the reduction in convection predicted on the basis of the relative density of air to freon, 1:4. Because the measured values "agreed" with predicted ones for a lynx and skunk, Hammel concluded that free convection in the fur layer contributes 25 - 50% of the total heat transferred through the fur.

Hammel's a priori assumption is not correct. 1) The conductivity of an entire pelt sample would be effectively elevated by conduction through the tissue layer and hair shafts above that which is measured for still air. 2) The value for still air against which Hammel compares the overall conductivity of fur is for pure conduction through air. Therefore, radiation within the fur layer and from its surface also contributes to a higher conductivity value for fur. The agreement Hammel found between his prediction and data is difficult to analyze because free convection in a porous medium, like fur, is not a simple function of the density of the fluid (Kowalski and Mitchell, 1980). Furthermore, the design and operation of his apparatus could have induced a forced or turbulent convective environment which would further complicate the situation (Hammel makes no mention of wind-speed measurements).

Although his convective analysis has some shortcomings, Hammel's application to animal insulation of an approach previously applied only to textiles is a major contribution.

In a series of three papers, Cena and Montieth (1975a,b,c) applied an engineering approach to develop a model that relates fur structure and environmental boundary conditions to heat transfer through fur. Such a modeling approach may be the only way to estimate the radiation among hairs effecting heat transfer. Cena and Montieth's radiation model hinged on predicting the "fraction of radiation intercepted by a ray in unit depth of coat" from the mean diameter of hairs, density of hairs (hairs/cm^2) and the angle between the hairs and the normal to the skin. Therefore, they verified this prediction with values calculated from measurements of fur transmissivity and reflectivity.

In the second paper Cena and Montieth measured the overall conductivity (as had been done by Hammel) and used their radiation model to develop a "radiative conductivity." Next, they estimated on the basis of cross-sectional area the coat conductivity attributable to conduction along hair shafts to be "unlikely to exceed 10% or 3 mW m^{-1} K^{-1}." Because the overall conductivities of furs were 50 to 200% greater than that of still air, convection and radiation must be important. According to the predictions of the Cena and Montieth radiation model, radiant transfer could account for the enhanced conductivity of most furs. However, they stated that "free convection is likely to be implicated when the apparent conductivity exceeds 50 mW m^{-1} K^{-1}." Wind tunnel tests performed by the authors supported the model predictions in that overall conductivity was independent of wind speed up to 3 m/s. In order to pursue the exceptional cases where the overall conductivity exceeds 50, Cena and Montieth attempted to apply dimensionless-group correlations. Unfortunately, the relations they chose were for fluids in the absence of a porous medium, like fur. Consequently, the authors grossly overestimated the magnitude (and likelihood) of free convection in the fur.

Skuldt et al. (1975) simply avoided the problem of free convection. They examined radiant and conductive mechanisms in artificial fur by performing their experiments with the hot plate above the heat sink and the hairs of the pelt hanging downward. By thus inverting the temperature gradiant, buoyancy effects were minimized. To varify this, a clear plastic film was stretched over the tips of the fur. The plastic reduced the heat flux less than 10 %, suggesting that free mixing of the air within the fur with the surrounding air was not an important means of heat transfer in their system.

The experiments by Skuldt and colleagues were performed on artificial fur for which the fiber lengths, proportion of under- and guard-fur, fiber diameters, density of fibers (fibers/area) and fiber conductivity were all known. Therefore, it was rather straight forward to apply the Cena and Montieth radiation model. The experimental result that the overall conductivity decreased with increasing fiber density supported the model's predictions: if heat transfer was by pure conduction, the overall conductivity would increase with increasing fiber density because the fibers have a higher conductivity than still air. Farther from the skin, fur density decreases and the overall conductivity increases. To resolve the relative contribution of radiation and conduction, Skuldt et al. placed a metal foil with a transmissivity of 0.1 across the fur tips. This reflected most of the heat radiating from the fur, but did not significantly impede conduction. They concluded that radiation accounts for nearly half of the total heat transfered through the fur [in the absence of convection]. Consequently, one should be cautious in using conductance values to describe furs or animals, as such are not properties because conductances are dependent upon the environment in which they are tested.

The experimental design of Skuldt and colleagues would have been ideal for testing Cena and Montieth's prediction that free convection is likely to be implicated when the overall conductivity exceeds 50 mW m^{-1} K^{-1}. By manipulating fur characteristics such as densities to exceed this conductivity, and testing the furs in the downward and upward orientation with and without the plastic film; their report could have resolved the importance of free convection in the fur much better.

The papers discussed so far dealt with flat samples of fur. These experiments and models are informative, but cannot be ideally applied to whole animals. Recently, a model for flat samples (Kowalski and Mitchell, 1979) was adapted to incorporate the effects of size and shape

(Conley, 1983). Although in 1980 Kowalski and Mitchell experimented with fur-covered cylinders in a wind tunnel and modeled convection, Conley did not include convection in his version. The Kowalski and Mitchell model (ca. 1979) used Roseland diffusion approximations to predict simultaneous conduction and radiation in porous media. This was an advancement over Cena and Montieth's model which offered only a prediction of the radiation component. However, the nested integrations and numerical approximations made Kowalski and Mitchell's model very complex and cumbersome to use. Therefore, they provided an algebraic version derived by regression analysis that produced the same results.

In Conley's dissertation he adapted this algebraic model for whole animals and tested the accuracy against measurements he made on *Peromyscus* and a domestic rabbit. Conley concluded that his version is accurate to within +/- 10%. Although Conley's model is as or more accurate than most direct methods, his model is actually a regression analysis, and cannot be confidently extrapolated to mammals whose body size or fur characteristics are much different from those of the deer mouse and rabbit. Furthermore, this model only applies to mammals in a wind-free environment and assumes that free convection does not occur within the fur layer.

Because Conley made his model available as a FORTRAN program, it has been utilized by several biologists and provided interesting insights (e.g., McClure and Porter, 1983; Gebremedhin et al., 1983; Webb and McClure, in review). Our understanding of free convection in fur, however, has not been much advanced since Hammel (1955). A paper in preparation by Somerton and Knight applies the principles of hydraulic diameter to estimate the permiability and then the Darcy-modified Raleigh number to predict when, if ever, free convection will occur in the fur. Our understanding of radiation is also still imperfect: experiments by Skuldt et al. (1975) suggested that it could account for nearly 50% in no wind conditions, but Kowalski and Mitchell (1980) say that "at low free steam air velocities" radiation effects at most 15% and less as wind speed increases. There is apparently much interaction among the mechanisms of heat transfer within a porous material which makes their description with respect to fur characteristics more challenging and interesting.

Variation in Space

Surprisingly little research has been done on variation in fur insulation along thermal gradients such as those which occur with latitude and altitude. Perhaps Scholander et al. (1950) provided an adequetly intuitive answer that seemed sufficiently comprehensive that further extensive investigation was not provoked. Scholander and colleagues examined 16 species from 9° N latitude (Panama Canal Zone) and 18 species from 71° N latitude (Point Barrow, AK). Their results were clear that arctic species have better pelage insulation than tropical ones. The insulation of small arctic mammals (shrews and weasels) overlapped with the values found for some tropical mammals. This study also revealed a nearly linear relation between the depth of the fur and its insulation across all species.

The work by Scholander et al. was an entirely interspecific comparison-- not even one genus was examined from both a northern and southern site (the sites were so extreme that there may not be a single genus represented at both). Intraspecific data for latitudinal variation are still unavailable. A few such reports do exist for altitudinal gradients. Seele (1968) found the density of hairs (especially underfur) to increase with altitude in chinchillas in the Andes. Wasserman and Nash (1979) found that the fur length of *Peromyscus maniculatus* increased from 1524 to 2438 m altitude, but not from 2438 to 3353 m in the Colorado Rocky Mnts. Their "limited" data suggested that fur density is greater at 3353 m than at 1524 m. It is disappointing that 93 mice did not provide more information in Wasserman and Nash's study.

Shump and Shump (1980) provided an interesting story on the relation between insulation and spacial distribution. They studied 5 species from 3 genera of bats in western N.Y. Shump and Shump found that insulation correlated with the exposure of roosting site. The best insulated species (2 *Lasiurus* species) roost singly in trees while the other three species use shelters and sometimes cohabit the same cave. *Eptesicus fuscus*, the best insulated of the three, roost singly near the shelter's entrance. The least well insulated bat is gregarious and roosts in the most remote chambers where the environment is the most stable.

Variation in Time

Seasonal Changes

The most studied temporal aspect of fur insulation is seasonal changes. In this review I will only discuss a few papers which examined seasonal changes in the fur of the genus of paricular interest in this thesis, *Peromyscus*. For a more comprehensive review, one should see Johnson (1977).

Huestis' (1931) objective was to quantify a qualitative observation: "color differences in geographical races of mice," *Peromyscus maniculatus rubidus*. He also made comparisons between seasons. Huestis recognized three types of hairs: black overhairs, large banded hairs and fur hairs. For mice from all localities the total density nearly doubled from summer to winter. The summer coat (n=81) was composed of 15.8% black overhairs, 7.2% large banded hairs and 76.9% fur hairs; the winter coat, 16.3, 8.9 and 74.8% respectively (the area sampled was not reported, so number of hairs could not be converted to density.) Therefore, underfur density did not increase proportionally more than guard fur (overhairs and large banded hairs). In fact, the winter coat was composed of a larger proportion of guard hairs than was the summer coat. Unfortunately, as previously discussed, the relation between hair density and insulation is poorly understood.

Sealander (1951) also observed seasonal differences in fur density in _P. leucopus_, but the differences for _P. maniculatus bardii_ were not significant. Surprisingly, he found no difference in fur lengths between winter and summer animals (although he admited to "difficulties involved in obtaining accurate measurements of hair lengths" and as a consequence "only a few measurements were made"). Perhaps for small body sizes, reducing convection by increasing the fur density is more beneficial than reducing the overall conductance by increasing thickness which may also reduce mobility. Furthermore, radiant heat transfer, which may be an especially important avenue of heat loss for a mouse out under the night sky, is decreased by increasing fur density (Skuldt et al., 1975). Sealander's results were for animals caught in the winter or summer and, therefore, acclimatized. He compared these to animals caught in the summer and acclimated for 30 days to cold temperatures and winter animals acclimated to warm temperatures. Within only 30 days there was a significant reduction in fur density of the winter animals kept warm, but no significant change in the other group.

Hart and Heroux (1953) used a heated flat plate apparatus to measure seasonal changes in pelt insulation of _P. m. gracilis_ directly, rather than infering insulation from hair densities and lengths. The pelage insulation of winter acclimatized mice (0.228, units below) was greater than that of summer mice (0.180). "However, summer mice had a higher oxygen consumption rate [at 1-2^{o}C] than winter mice for equivilent insulation." Therefore, winter acclimatized mice were tolerating lower T_Bs or were reducing heat loss more efficiently by physiological means in addition to piloerection (T_B was not reported). Hart and Heroux found a linear relation between pelt insulation and oxygen consumption rate: for winter mice, M= 202.8-153.7I; and for summer, M= 214.2-153.7I, where M is ccO_2 hr^{-1} $mouse^{-1}$ and I is $^{o}C/cal/hr/m^2$ (which I presume was meant to be equivalent to ^{o}C m^2 hr cal^{-1}).

In 1955 Hart extended the earlier work to compare nine species. From this study Hart concluded that 1) the seasonal change in fur insulation is primarily effected by changes in fur depth (the regression of insulation with depth was not different between seasons); 2) animals with longer fur have greater absolute seasonal changes in insulation (0.049 for deermice, 0.627 for black bears); but, 3) the relative changes are not so different among species (21% for deermice, 33% for red foxes, 51% for black bears). Hart's results contradicted Sealander's (1951) shakey conclusion that fur length does not change between seasons in deermice.

Ontogenetic Changes

During the ontogeny of a mammal, at least two physical chracteristics change which affect insulation: body size and fur. At least since Bergman wrote in 1847 "From the relation of surface area and volume, it follows that larger animals can keep themselves at the same body temperature with a relatively smaller [rate of] heat production than smaller animals do" (quoted from Kleiber, 1975, p.222), the importance of body size to heat loss has been a controversial topic. Scholander (1955) argued that the effect of larger body size on reducing heat loss is inconsequential in comparision to the effect of thicker pelage. The importance of body size, then, is that larger animals can carry more pelage insulation than a small animal without being encumbered. On the other hand, Brown and Lee (1967) found a significant relation between body size and thermal environment in the wood rat. They argued that any energetic savings, even if very small, were advantageous. Brown and Lee did not, however, compare the relative fur insulation of the rats from the different populations to test Scholander's claim more quantitativley.

Pearson (1948) claimed that there exists a minimum body size for endothermic homeothermy. Near this body size (about 2 grams) basal metabolism increases dramatically, so that at smaller sizes metabolism approaches infinity. According to Tracy (1977) the metabolic rates Pearson used for shrews (the smallest mammals) were not measured in the thermal neutral zone. Basal values of metabolic rate for these animals do not suggest a rapid increase in metabolism as size approaches some hypothetical minimum. Tracy says that there is no theoretical minimum size for a homeotherm, but that "the range of thermal environments in which an animal can maintain a minimum metabolic rate and a constant body temperature becomes smaller for smaller animals." The smallest mammals are the newborn of altricial species which are not only small but hairless. The implications of Tracy's ideas for these neonates are that increasing effective body size by huddling and utilizing the stable microclimate of a nest are important if a stable body temperature is desirable.

Two engineers, Balmer and Strobusch (1977), attempted to explain the absence of pelage on altricial newborn in terms of body size. For inanimate internally heated objects, there exists a critical radius below which the addition of insulation actually increases heat loss. Balmer and Strobusch claim that newborn rats and mice are smaller than their theoretical critical radius; therefore, it is "adaptive" for them to be hairless. Porter et al. (in press) claim that the application of the critical radius principle to living animals is inapproprate because living animals violate several of the basic assumptions of the theory. The nakedness of an altricial newborn is no more (or no less) enigmatic than the underdeveloped condition of other physical and physiological systems of these neonates.

Especially among these altricial species, the fur changes dramatically during ontogeny. These changes accompany physiological changes which together effect a more adult-like ability to maintain a high, stable body temperature. There is an abundant literature on the development of thermoregulatory ability [see Hill (1983) for review of Peromyscus]. Although it is doubtful that any of these researchers did not notice the growth of fur during ontogeny, only a few have tried to quantify these changes and their effects.

Hahn (1956), Mount (1963) and Hissa (1968) examined the effect of removing the hair from neonatal mammals. Hahn found that shaving 14-day-old rats had little effect on either the rate at which they cooled to 15°C when exposed to T_A of 10°C, or their O_2 consumption at 29°C. Shaved 40-day-old rats did cool faster, but used no more O_2 than unshaved ones. On the other hand, shaving 18-day-olds affected both cooling rate and O_2 consumption. Hahn concluded that the thin fur of the 14-day-old is not an effective source of insulation. Near weaning, the fur plays a major role in thermoregulation. However, by 40 days of age, other heat loss retarding mechanisms (e.g., body size and vasomotor control) are sufficient to permit the adult to maintain high T_B at 29°C without an elevation in metabolic rate even without its fur. Hahn's work would have been more informative if he had examined more than two preweaning ages and compared the width of the thermal neutral zone of shaven and unshaven rats.

Hissa (1968) examined many aspects of thermoregulatory development which will not be reviewed here (e.g., shivering thermogenesis, myelinization, brown fat sensitivity to noradrenalin). Pelage was a minor topic. He measured metabolic rates while gradually lowering T_A of lemmings and hamsters with fur and with fur removed at several preweaning ages and two acclimation temperatures. Fur removal had no effect on 13-14 day old hamsters. At 17-19 days of age fur removal increased the slope (more negative) of metabolism on T_A below the lower critical temperature (LCT) but did not affect the LCT. In addition to the effect on the slope, 22-24 day old hamsters with fur had a LCT 2°C lower than those without fur when raised at 12°C; and 1.5°C lower when raised at 23°C. The lemming is a more precocious species and its fur changes less dramatically during postnatal ontogeny. Hissa concluded that it is of little importance before 10 days of age. After 10 days, removal of fur results in a higher LCT and a greater change in metabolic rate for decreases in T_A below LCT.

Poczopko (1969) measured the cooling and rewarming rates of the core (rectal) and skin (four sites) in young rabbits 1 hr to 17 days of age, alone or huddled with siblings in a nest. He also monitored diurnal temperature variations below, within and 1 to 2 cm above sibling huddles in nests in outdoor enclosures. Poczopko concluded that the "scanty pelage" provides little insulation before 8 days of age. However, even 2-day-olds exhibit some vasomotor control that reduces the rate of heat loss. The apparent effectiveness of vasomotor control improves from 2 to 8 days of age, but after 8 days its relative importance diminishes as the contribution of the fur increases.

Mount (1964) applied several of the previously described approaches. Mount compared the O_2 consumption, skin and rectal temperature in shaven and unshaven neonatal pigs over a range of environmental temperatures. Mount found vasomotor control to be very important, effecting 28% of the total increase in insulation as T_A fell from 38 to 5 ^oC. The tissue layer provided a maximum of 20%. The rest of the insulation was provided by the fur and boundary layer of air. Mount estimated the contribution of the fur to be at most only 15% of the total body insulation. Furthermore it was most important for the youngest ages -- newborn pigs have only about 1% body fat by weight. Even though the amount of hair per unit area increased with age, the relative contribution of fur to total insulation decreased as the pigs rapidly fatten. This is an interesting contrast to the situation of (apparently) most mammals like the rabbit whose fur gradually becomes a most important source of insulation.

Not until 1983 was the relation between changes in fur characteristics and changes in insulation during ontogeny specifically studied. McClure and Porter (1983) used a heat transfer model based on engineering theory (Conley, 1983, described in earlier section) to examine the fur of neonatal cotton rats. In addition, they applied a sensitivity analysis to elucidate the fur characteristics and interacting components that were responsible for the observed changes in the insulation of the fur. For cotton rats, the model predicted that the radiant and conductive conductivities changed in a compensatory manner as the fur grows. Consequently, there was no change in the overall conductivity. As fur density increased with the eruption of new hair follicles, radiation per unit thickness decreased and conduction increased (consistant with Skuldt et al. 1975). Fewer follicles erupted near the age of weaning, but the rat continued to grow; therefore, hair density decreased; radiation transfer became more important and conduction less. The sensitivity analysis was consistant with the findings of Scholander et al. (1950) that insulation was well predicted by fur depth, but density also had a small effect.

The most recent work on pelage ontogeny is by Timisjarvi et al. (1984). This team examined temperature profiles of reindeer pelt samples in various wind conditions and varified these results with some similar measurments on live calves and adults. Timisjarvi and colleagues also used scanning electron microscopy to study the structure of the fur. The youngest calves had only one rather wool-like fur type (i.e. no distinct guard and under fur). In cross-section these hairs had many hollow spaces resembling the guard hairs (but not the underfur) of the adults. Such a hollow hair structure could reduce the conductivity of the hair shafts; however, previous studies (e.g., Cena and Montieth, 1975b) suggested that conduction along the hairs has little effect on the overall heat transfer through the fur, anyhow. Temperature gradients were steeper for calf fur under all conditions, suggesting that the fur of the adult provided better insulation. Because calves maintained the same skin and rectal temperatures as adults, they must suffer a greater heat loss than the adults. Replacment of the calf fur begins about one month of age and is completed by four or five months.

Much less work has been published on ontogenetic changes in fur insulation than has been published on seasonal changes. Although considerable interest has been shown in neonates' ability to produce heat (Hill, 1983), rather few studies have attempted to quantify mechanisms by which neonates conserve heat. The next chapter is a contribution to alleviate some of this deficiency for the genus *Peromyscus*.

REAEARCH REPORT: THE DEVELOPMENT OF PELAGE INSULATION AND ITS RELATION TO HOMEOTHERMIC ABILITY IN *PEROMYSCUS LEUCOPUS*

INTRODUCTION

Two of the most important factors involved in determining a neonatal endotherm's ability to thermoregulate are its ability to produce heat and its ability to retain heat (insulation). Many researchers have studied the metabolic capabilities of young mammals (Chew and Spencer, 1967; Hill, 1976; Heath et al., 1977; McClure and Randolph, 1980; Webb, 1984), but only a qualitative examination of the pelage insulation has usually been made. The effect of removing the fur on thermoregulation has been examined in neonatal rats (Hahn, 1955), lemmings and hamsters (Hissa, 1968). Hill (1976), examining development of thermoregulation in *Peromyscus leucopus*, determined a metabolic index of insulation [$I= (T_b - T_a)/\dot{V}_{02}$] for neonates between birth and weaning. Only recently have researchers specifically and quantitatively examined the ontogeny of fur thermal properties: McClure and Porter (1983), in the precocial cotton rat (*Sigmodon hispidus*); and Webb and McClure (in review) in the altricial wood rat (*Neotoma floridana*).

The studies on *Sigmodon* and *Neotoma* employ a model based on heat transfer engineering theory to estimate heat losses through animal fur (Kowalski, 1978; Kowolski and Mitchell, 1979). These studies report the insulation of the fur as it lies naturally, i.e. not piloerected. Neonates may be able to increase their total pelage insulation 10 to 15 percent over these reported values if they are capable of pilomotor responses (Hammel, 1955).

In this report I apply an empirical method to measure directly the maximum pelage insulation (fully piloerected dorsal fur) during ontogeny of a small altricial rodent, _Peromyscus leucopus_. The objective of this work is to determine whether or not pelage insulation may be a characteristic that limits neonatal thermoregulation. By utilizing Hill's (1970, 1976) metabolic data on _P. leucopus_ neonates, I assess the relative importance of pelage insulation and surface-specific whole-body insulation. Furthermore, I compare the effects that metabolic capacity and pelage insulation development have on homeothermic ability, as well as estimate their combined effect.

Four terms are used to describe the overall characteristics of the pelts. First, the pelt thickness is the distance from the subdermal surface to the average height of the tallest hairs. Second, the effective thermal conductivity (k_e', W cm^{-1} $^{o}C^{-1}$) describes the ease with which heat moves through the pelt _per unit thickness_ of the pelt. (The superscript prime indicates that the assumptions of isotropic and homogeneous heat flow are not met and the subscript "e" indicates that the heat flow may be brought about by other mechanisms in addition to conduction.) Conductivity is defined by the rearranged Fourier equation, $k = q'' \times \Delta x/\Delta T$, where q'' is the heat flux, Δx is the thermal conductive thickness of the test material and ΔT is the temperature difference across the material. The effective conductivity is computed in the same way as the conductivity for pure conduction (Incropera and DeWitt, 1985). The third term is thermal conductance (U, $W\ cm^{-2}\ {}^{o}C^{-1}$). This is the heat flux necessary to maintain a 1 °C temperature gradient across the full thickness of the pelt; that is, $U = q''/\Delta T$ (Incropera and DeWitt, 1985). It describes the ease with which heat moves across the <u>entire thickness</u> of the pelt. Finally, the pelt will be discussed in terms of its insulation (I), which by definition is the inverse of conductance (1/U; Incropera and DeWitt, 1985).

MATERIALS AND METHODS

Colony

Most of the experimental animals were the progeny of 28 pairs of Peromyscus leucopus wild-caught in the Rose Lake Wildlife Research Area, Clinton Co., Michigan, during the spring and summer of 1983. A few experimental animals were the offspring of several first-generation, laboratory-born mice which were added to the breeding colony to replace wild-caught mice that died or did not breed after two pairings. All animals were housed in plastic cages (13 cm deep by 18 cm by 28 cm) on a photoperiod of 15:9 light:dark with lights on at 6 A.M., E.S.T. Food (Purina Mouse Breeder Blocks) and water were provided *ad libitum*. Wood shavings and cotton were provided for bedding and nesting.

A parental pair was allowed to raise its first litter to the average age of weaning, 20 days. This first litter and litters whose parity were known to be greater than six were not used in the experimental design. Therefore, parents were known to be experienced and parity effects on development were minimized for the experimental litters.

Nests were checked daily for births. The day a litter was discovered was considered day 0. On day 3 or 4, litters were culled to a standard size of four pups. Litters with fewer than three pups were not used. (Only two pups in the experimental design were from litters which had three pups.)

A 3 by 3 balanced lattice (Cochran and Cox, 1950) was used to stucture the assignment of treatments (litter ages). Blocks were assigned randomly to breeding pairs of mice. Treatments (litter ages) were assigned randomly within each block to the order of litters produced by a pair. This procedure insured that treatment replicates were assigned randomly and to different parental pairs (Table 1).

Table 1. 3X3 balanced lattice design plan. Treatments correspond to days of age, blocks (BLK) to parents. Three blocks are required for one complete replicate of the 9 treatments. The complete design requires four replicates of each treatment. DOB= date of birth, WC= wild caught, F-1 = first generation lab reared.

Table 1

Parents F DOB	M DOB	BLK	Days of Age			Date Block Completed
			Replicate I			
WC 4-83,	WC 4-83	1	8	6	4	11-83
WC 4-83,	WC 4-83	2	10	14	12	11-83
WC 8-83,	WC 8-83	3	20	18	16	5-84
			Replicate II			
WC 7-83,	WC 7-83	4	16	10	4	11-83
Information	Missing	5	12	6	18	6-84
F-1 8-83,	WC 7-83	6	14	20	8	5-84
			Replicate III			
WC 7-83,	WC 7-83	7	4	20	12	1-84
WC 7-83,	WC 7-83	8	16	14	6	11-83
WC 7-83,	WC 7-83	9	8	10	18	12-83
			Replicate IV			
WC 7-83,	WC 7-83	10	18	14	4	1-84
F-1 7-83,	F-1 7-83	11	20	6	10	2-84
F-1 7-83,	WC 7-83	12	16	8	12	3-84

Pelt Preparation

When a litter reached the assigned treatment age, all members were killed by cervical dislocation. The carcasses were then stored in a freezer. The frozen carcasses were thawed slightly to facilitate skinning. Care was taken to avoid stretching the pelt. Once the pelt was freed, it was mounted onto a frame, cooled in a freezer and then frozen in liquid nitrogen. The frozen pelts were lyophilized for 12 hours at an ambient pressure of 10 μm Hg and coil temperature of -50 °C. To assess shrinkage, the distance between points marked with permanent ink on the dermis was measured before freezing and after drying. Pelts which shrank measurably or cracked in the area to be tested were discarded and replaced with ones from siblings.

The fur of a dried pelt was cleaned with isopropynol, and Instant Dry Shampoo (Four Paws Products, Ltd), using cotton swabs and a soft toothbrush to remove oil and body fluids which may have soiled the fur during skinning.

Finally, a rectangular section (ranging from 1.5 by 2 cm to 3 by 3 cm) was trimmed from the mid-dorsal region of the pelt. This sample was always at least 0.5 cm larger than the heat flux meter in both dimensions (Figure 2). The fur on this pelt sample was piloerected by blowing an airstream opposite to the natural lay of the hair or by lifting the fur with a small, soft brush. Pelt samples were stored in a desiccator with Drierite until their thermal properties were tested.

Measurements

Thickness measurements of the pelt were made with the jaws of dial calipers to the nearest 0.01 cm. The average of at least three measurements was recorded. Heat transfer data were collected using the apparatus shown in Figures 1 and 2. The principles by which this apparatus operates are similar to the ASME "Northrop Method" (Wilkes, 1952).

For testing, a pelt sample was placed between the two sets of thermocouples and the ventral surface was adhered medially to the heat flux meter (RdF part no. 20451, see appendix for specifications) with a highly conductive heat sink compound (Sylvania ECG 424) and laterally to the guard area of the hot plate with double-sided transparent tape. The T2 set of thermocouples was positioned among the tips of the guard hairs (Figure 2).

To standardize the humidity among tests, the apparatus was enclosed within an acrylic box containing indicator Drierite during a run. Air was pumped through a drying column and into the box to facilitate mixing and replacement of the moist air originally present. During this process the heat sink was left suspended one to several millimeters above the copper walls, so that the air within the fur could dry. About 10 to 15 minutes were allowed for the air to dry before the heat sink was locked snuggly against the copper spacers within one millimeter of the tips of the longest hairs. In a few trials, the heat sink may have been in

Figure 1. Hot Plate Apparatus in Perspctive. Dimensions in cm: length by width by height. A) Acrylic box with silicon rubber seal around bottom edge: 13.5by 8.0 by 9.0 inner dimensions. B) Styrofoam base: 7.5 by 7.0 by 3.0.

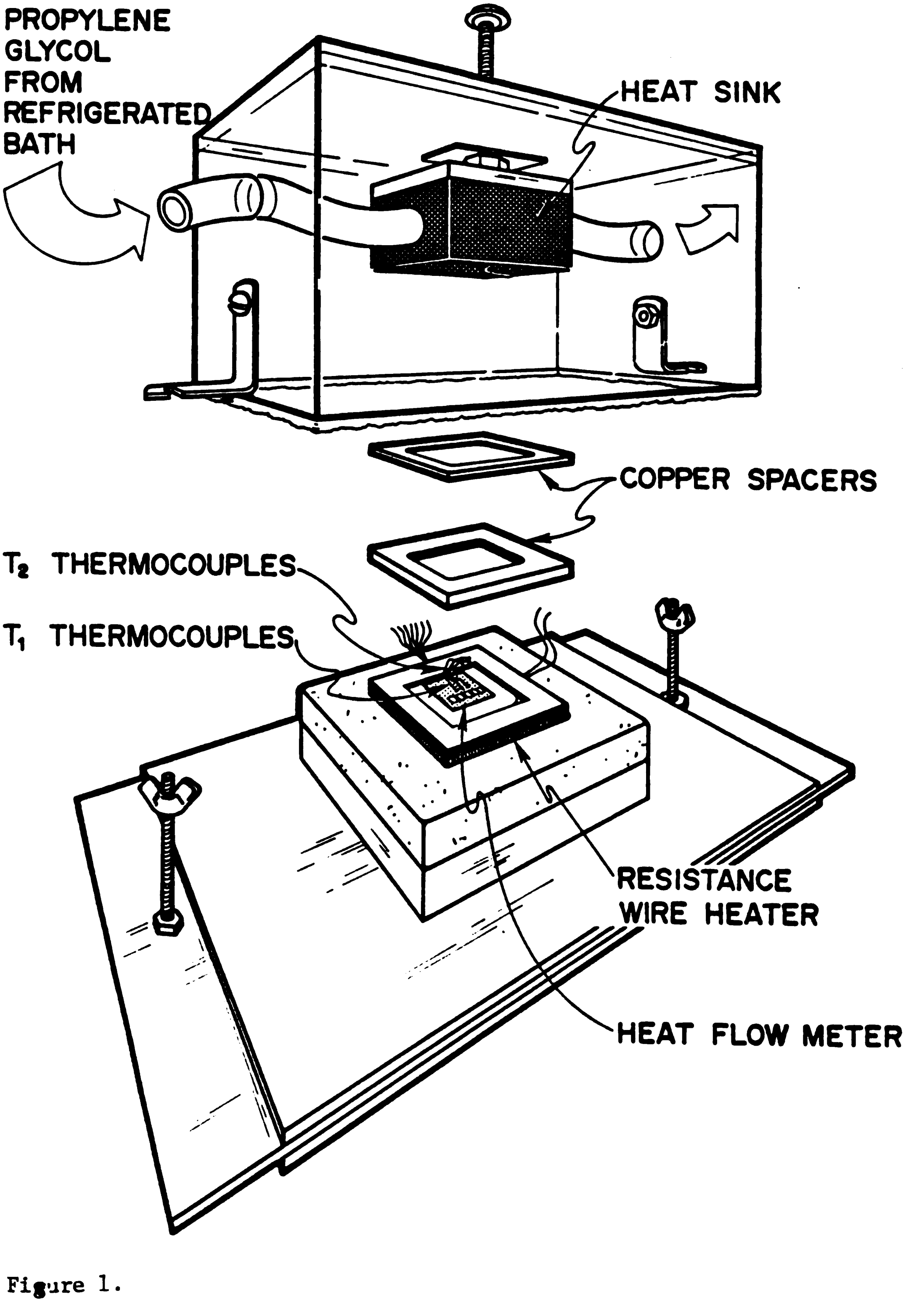
PROPYLENE GLYCOL FROM REFRIGERATED BATH
HEAT SINK
COPPER SPACERS
T_2 THERMOCOUPLES
T_1 THERMOCOUPLES
RESISTANCE WIRE HEATER
HEAT FLOW METER

Figure 1.

Figure 2. Cross section of Hot Plate Apparatus. (Dimensions in cm: length by width by height.) Brass heat sink: 4.0 by 4.0 by 2.5. Copper spacers of various thicknesses: 3.0 by 2.6 inner dimensions. Heat flux meter: 1.6 by 1.6 by 0.035, thermopile area: 1.4 by 0.25. Copper-constantan welded thermocouples (T1, T2), wire diameter: 0.00076, thermojucntion diameter: < 0.003. Resistance-wire heater: 4.0 by 4.0 by 0.45. Hot plate sample area: 3.0 by 2.6. Lateral thermocouples in each set are approximately 0.5 cm apart and are involved in measuring ΔT. The middle thermocouples measure the absolute temperature below the pelt (T_1) and among the guard hair tips (T_2).

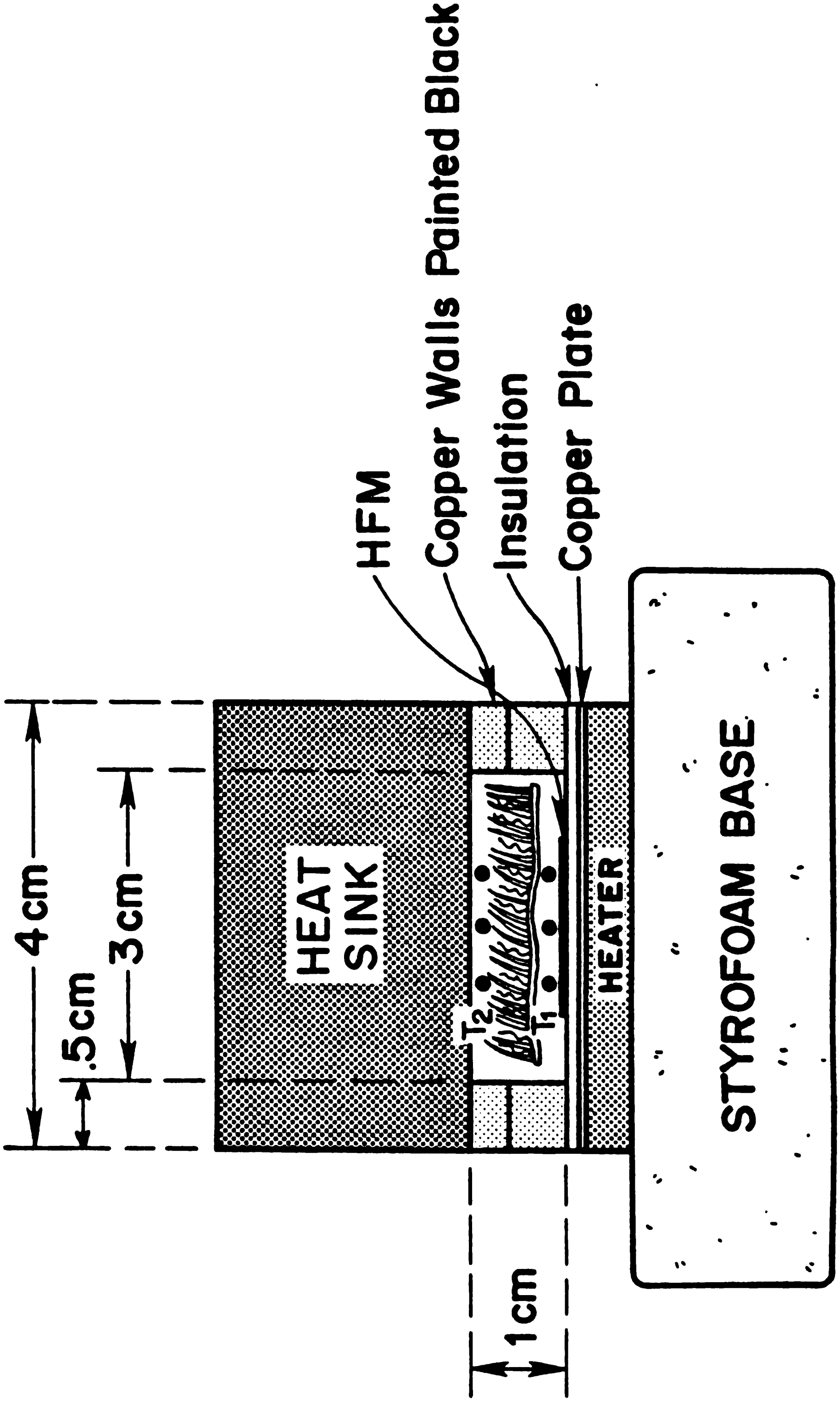
HFM
Copper Walls Painted Black
Insulation
Copper Plate
HEAT SINK
HEATER
STYROFOAM BASE
T_2
T_1
4cm
3cm
.5cm
1cm

Figure 2.

contact with the hair tips.

Two consecutive trials were run on each pelt: one in which the temperature difference across the pelt was nominally 1 °C and the other, nominally 5 °C. The order of the two trials was randomly determined.

One pair of thermojunctions in the T1 set and one pair in the T2 set were configured in a circuit such that the emf produced across the entire circuit was proportional to the difference between the average temperature beneath the pelt sample and the average temperature among the guard hair tips, ΔT (Figure 2,3). The emf was recorded continuously on one channel of a four-channel polygraph (Grass model 7) equipped with a low-level DC preamplifier (model 7P1) and a DC driver amplifier (model 7DAC). Another pair of thermojunctions measured the absolute temperatures below the pelt (T_1) and among the guard hair tips (T_2). These temperatures along with inner-wall temperatures, the temperature of the heat sink surface facing the fur (T_{HS}), the air temperature within the acrylic box and the bath temperature were recorded using a Honeywell Electronik 15 recording potentiometer calibrated for copper-constantan thermocouples with a precision of 0.5 °C.

The temperature measured at the T2 position should not be confused with an estimate of the radiant surface temperature (T_R) of the fur. Ambient air temperatures may not accurately reflect the T_R of an animal's surface as measured by infrared radiography (Hill et al., 1974).

Figure 3. Diagram of Thermocouple circuit used to determine ΔT. Open circles = electro-thermal junctions. Broken lines = constantan wire. Solid lines = copper wire. The emf measured across electro-thermal junctions in parallel is equal to the average emf produced by each junction. The emf measured across electro-thermal junctions in series is equal to the net emf between the two junctions. Therefore, the emf measured by the polygraph across the entire circuit diagrammed above is equal to the difference between the average emf at T_1 and the average emf at T_2 and is proporitonal to ΔT.

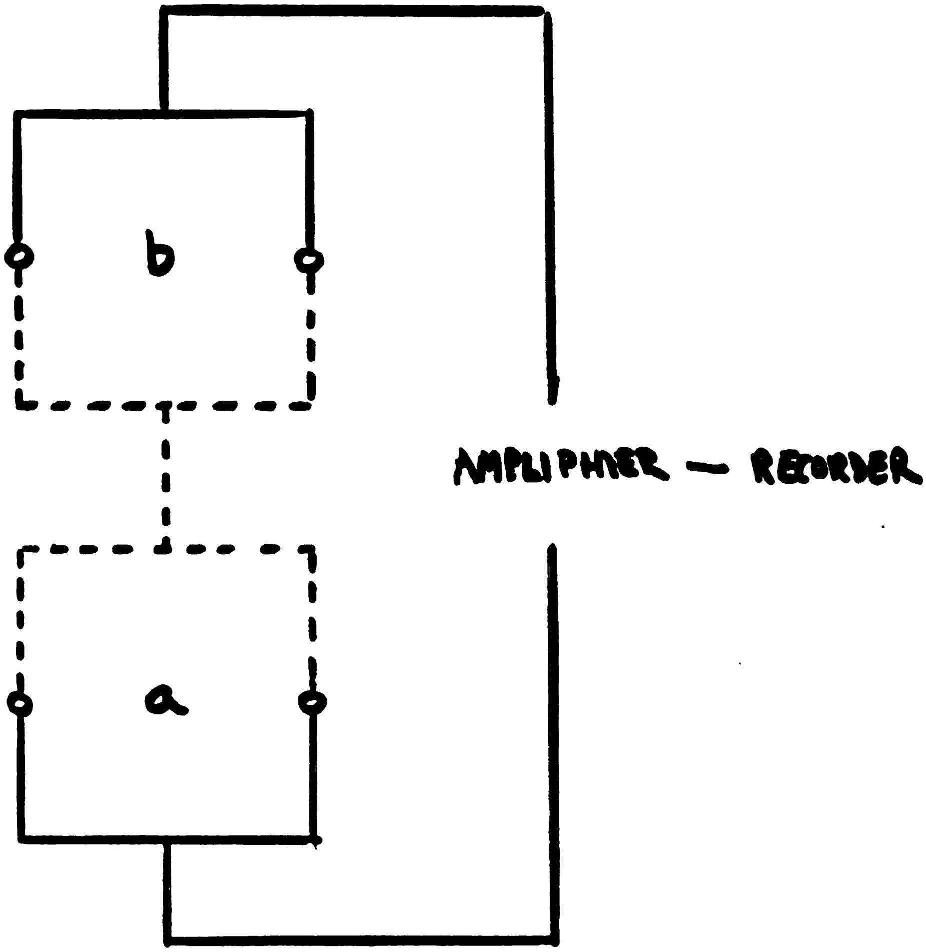

Figure 3.

However, T_R is not the desired temperature for this research. The radiant surface is an irregular one and, therefore, Δx varies from point to point (Figure 10). Averages could be used, but the computed values of insulation and conductivity would not include the effect of the layer of air trapped between the tips of the guard hairs and the tips of the under fur. Because I define the insulating unit of the pelt as all that is contained between the immaginay plane which rests on the tips of the tallest, erected guard hairs and the subdermal surface (Figure 10); the boundary temperatures needed are the temperatures of the lower dermal surface (T1) and of the air at the tips of the tallest hairs (T2).

A five thermopile heat flux meter (HFM, manufactured by RdF, Corp. and described by Hager (1965)) was used to measure the heat flux (q") across the pelt sample. The HFM produces an emf proportional to the heat flow through the meter averaged over the area of the thermopiles (i.e. heat flux). This emf was recorded continuously during an experiment on a second polygraph channel identical to the one used to record the ΔT emf.

The ΔT was controlled by varying the current from a 30V, 3A DC power supply (Schlumberger, model SP-2710) to the heater. The subdermal temperature, T_1, was controlled at a temperature between 31 and 33 °C (near that of the skin of an adult, homeothermic mouse; Conley,1983; also, unpublished data on neonatal <u>Sigmodon</u> and <u>Neotoma</u>, Webb, personal communication) by varying the temperature of the fluid flowing through the heat sink.

The "state" of the system was assessed by monitoring ΔT and q". The data were collected when no measurable change occurred in ΔT and q" for at least 10 minutes, i.e., after steady-state was obtained.

After the second trial, the apparatus was disassembled and the pelt sample removed, with care being taken not to disturb the position of the T2 set of thermocouples. The distance between T1 and T2 (Δx) was then measured with dial calipers to the nearest 0.01 cm.

Calibration of Apparatus Components

Before the apparatus was assembled, thermocouples signals were recorded on the Honeywell recorder, read to the nearest 0.1 ^{o}C, and calibrated against an NBS mercury-in-glass thermometer to the nearest 0.05^{o}C in an insulated, stirred water bath (AppendixA). The heat flux meter was calibrated by the manufacturer (Appendix C) and has a nominal sensitivity of 2.5 mV/(Watt cm^{-2}).

At the end of each trial, the Grass polygraph sensitivity was calibrated against three inputs of known voltages from a Leeds and Northrop galvinometer-potentiometer. The potentiometer was itself periodically tested with a Hewlett-Packard digital microvolt multimeter (Appendix A). The resulting calibration voltage pen deflections were measured with an Apple II digitizing tablet (avg. coefficient of variation = 0.0054). Each pen deflection was measured three times, and the average was used to calculate a distance-to-voltage conversion factor. The strip-chart records of the ΔT and q" pen deflections were similarly measured with the digitizing tablet. These distances were converted into voltages using the calculated conversion factors. The resulting voltages were converted into temperatures by using reference tables from the National Bureau of Standards for copper-constantan thermocouples or into heat fluxes by using the HFM calibration values provided by the manufacturer. The agreement between ΔT and (T_1-T_2) suggests that the accuracy of the ΔT measurement was better than 0.1 ^oC [$(T_1-T_2)= 0.04 +0.99(\Delta T)$, $r^2= 0.99$, $N= 62$].

Controls

To estimate the accuracy of the apparatus in measuring thermal conductivity, I compared my test results on a standard material, cork, to the conductivity values predicted by its density (Armstrong World Industries, Inc., Lancaster, PA. which used ASTM-method C-518, appendix). For my experiments, the cork was tested after at least 12 hr of desiccation. The T2 thermocouples were attached to the cold side of the cork sample with transparent tape and pressed into the cork surface with a blunt probe. The nominal mean temperature of the cork during the test was 24° C. The temperature difference was nominally 5° C (the condition I expected the most measurable error). The sample was approximately one mm smaller in all dimensions than the space enclosed between the hot and cold plates, i.e., the sample did not contact the walls or the heat sink. All procedures and test conditions were as similar to those for pelt experiments as possible, with the exception of mean temperature (which corresponded to the mean temperature of cork in the tests by Armstrong Indust.). In comparison to the results of Armstrong Indust., my apparatus overestimates thermal conductivity by about 15 percent (Appendix Table 2).

A second control experiment was run on each cork sample to assess the magnitude of heat flow that is not normal to the hot and cold plates. In these tests another heat flux meter of the same type previously described was adhered to the cold surface of the cork with heat-sink compound and transparent tape directly above the meter on the hot surface. The T2 set of thermocouples was taped to the upper surface of the second heat flux meter. A difference in heat flux measured by the two meters was assumed to be due to the heat flowing along a horizontal temperature gradient and to differences in meter calibrations. The latter were ruled out, because there was no difference in heat fluxes determined from the meters' signals when they were separated by only a thin layer of heat-sink compound or heat-sink compound and the T1 thermocouples. These results suggest that the accuracy of my apparatus to measure one diminsional heat flux varies with sample thickness, but on average is better than 85% (Appendix Table 3).

Another control was run to assess the variation introduced among experiments on pelts by variation in piloerection. Three pelts, each from a different age group (8, 10 and 14 days), were tested on three consecutive trials with ΔT nominally 5 °C and T_1 nominally 31 °C. Between each trial the fur was depressed and re-erected. The coefficients of variation among these trials were 6, 1 and 5 % for the 8-, 10- and 14-day-olds, respectively (Appendix Table 4).

Finally, the effect of free convection on heat transfer through the fur was examined with two approaches: first by an experimental procedure and then by a mathematical one. The experimental analysis of convective heat transfer was rather simple. A pelt sample was prepared and mounted in the apparatus as for effective conductivity tests. Once the apparatus-pelt system reached steady-state heat transfer conditions, the entire apparatus was inverted, so that now the cold plate was below the hot plate and the fur was oriented with its hairs pointing downward. Reversing the temperature gradient should prevent the bouyancy effects that effect free convection; therefore, the difference in steady-state heat flux between the two orientations should be the heat flux due to convective transfer. The second approach involved a complicated analysis of diminsionless groups (eg. Raleigh and Nusslet) and their correlations with heat transfer by convection through porous media better than 85% (Appendix Table 3).

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(Somerton and Knight, manuscript). Neither analysis suggested that free convection was occurring within the fur layer during experiments.

Statistical Analysis

The main ANOVA to test for treatment (age) effects was run on BMDP program 4V, "ANOVA for Repeated Measures." (Note there were two trials or "measures", one in which $\Delta T=1\ ^{o}C$ and a second in which $\Delta T=5\ ^{o}C$, for each replicate.) The ANOVA was run for each dependent variable (pelt thickness, k_e',U). This ANOVA also tests for trial differences. Separate one-way ANOVA were also run for each of the two trials.

Student-Newman-Keuls pair-wise comparisons (SNK) were run by SPSS9 on data sets for which significant treatment effects were found by the ANOVA. The SNK tested for pairs of age classes that were significantly different at the 0.05 level.

Multiple regression analysis (SPSS9 "New Regression" and SAS4.2 "MARQUART, NLIN") was used to fit curves to the data for qualitative description of the thermal development of the pelts. Correlation coefficients, prediction equations and significance of the regressions were also determined from SPSS9 and SAS4.2.

RESULTS

The results of the two trials, $\Delta T = 1\ ^{o}C$ and $\Delta T = 5\ ^{o}C$, differ significantly (ANOVA, $P<0.05$). The conductance (U), and the effective conductivity are greater when $\Delta T = 1\ ^{o}C$ than when $\Delta T = 5\ ^{o}C$. Because separate main (one-way) ANOVA and pair-wise comparisons were performed for each of the two trials, the difference between trials does not affect the results of these subsequent analyses. For regression analysis the data for the two trials were averaged because separate plots for the two trials parallel each other and were only slightly distinguishable. Furthermore, the standard deviations on the means overlapped more than 50%. The small difference between the trials is likely spurious, but otherwise, presently unexplainable. The main one-way ANOVA's indicated that a significant difference occurs among age groups for all dependent variables.

Because the form of the growth curve is not known *a priori*, three regression models were fit to the data: linear, quadratic and cubic. Cubic regressions best descibed all data sets.

Dorsal Pelt Thickness

Prior to 4 days of age, hair on the dorsal pelt of *Peromyscus leucopus* is apparent only under magnification. At 4 days of age, sparse hairs are evident to the unaided eye, but the fur depth accounts for less than half of the thin pelt thickness (tissue thickness = 0.07 cm, pelt thickness = 0.13 cm).

The overall-F of the regression descibing pelt thickness as a function of age (Figure 4) and each of the coefficients in the model are significant ($P < 0.05$, $r^2=0.99$). The dorsal pelt thickness increases linearly ($r^2=0.98$) from 0.13 cm at 4 days of age to 0.98 cm at 16 days of age at an average rate of 0.07 cm per day. From day 16 to weaning there is no net change in thickness. All age pairs were significantly different in pelt thickness (SNK, $P \leqslant 0.05$) except 18-and 20-day-olds and 16- and 20-day-olds.

Dorsal Pelt Effective Conductivity

The relationship between effective thermal conductivity of the dorsal pelt and age (Figure 5) is not significant ($P > 0.05$, $r^2= 0.68$). However, in a pair-wise comparison, k_e' at 4 days is significantly different from k_e' of all other age groups ($P \leqslant 0.05$). Between 4 and 6 days of age, k_e' nearly doubles from 3.68 to 6.11×10^{-4} W cm^{-1} $^{o}C^{-1}$, but after 6 days it changes little with a mean (k_e') of 6.64×10^{-4}.

Dorsal Pelt Thermal Conductance

The cubic regression which describes the dorsal pelt conductance as a function of age (Figure 6) and all of its coefficients are significant ($P < 0.05$, $r^2= 0.95$). Pair-wise comparisons reveal that 4 day olds are significantly different from all other age groups ($P \leqslant 0.05$). Four and 6, 8 and 12, and at $\Delta T = 5$ ^{o}C ,10 and 14 days are the successive age groups for which U differs significantly. Conductance is not significantly different among the pelts

Figure 4. Dorsal pelt thickness as a function of age. Thickness= $-0.27 + 0.093(\text{Age}) - 0.000071(\text{Age})^3$. $r^2 = 0.99$. $P < 0.05$.

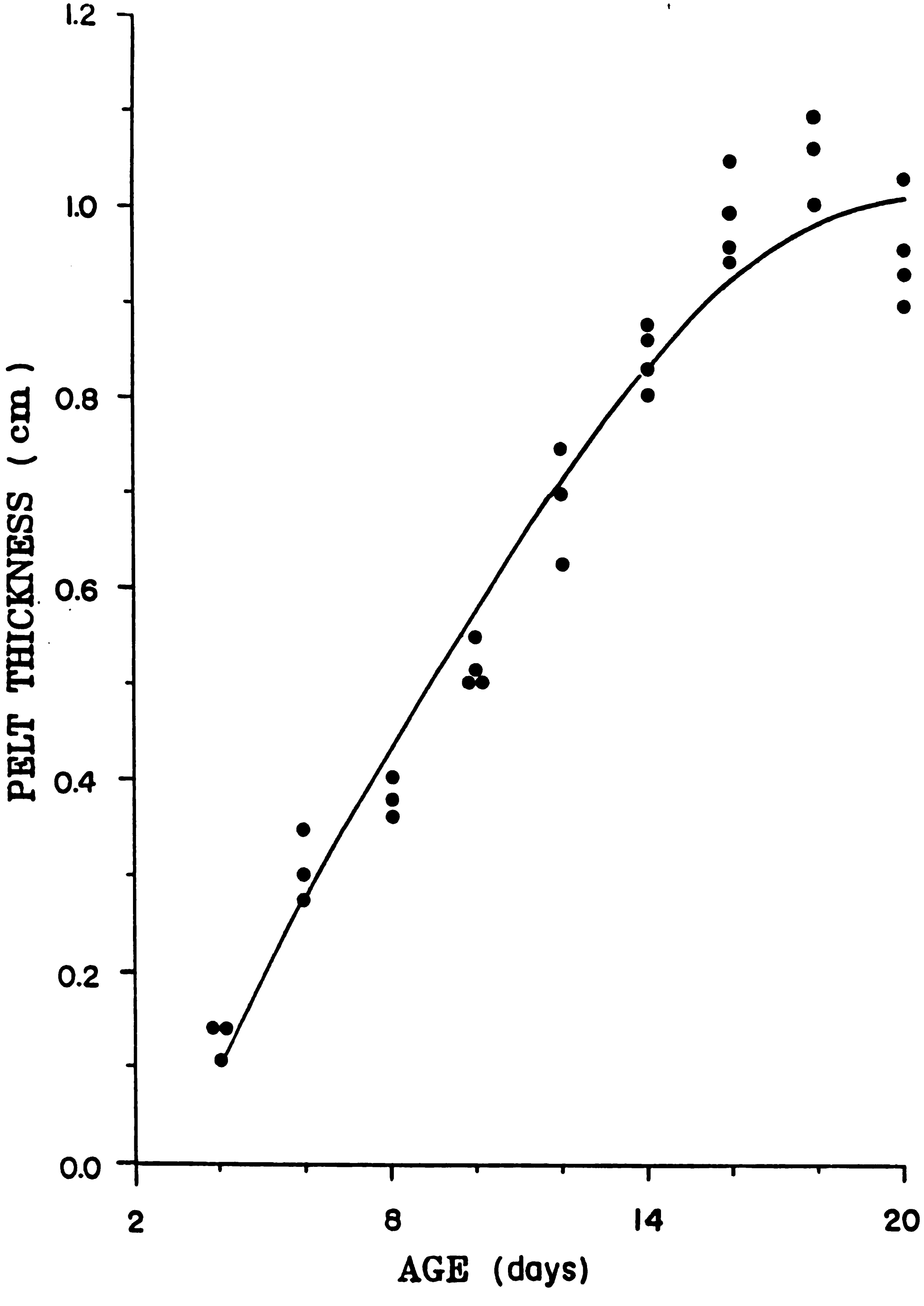

Figure 4.

Figure 5. Dorsal pelt effective thermal conductivity (k_e') as a function of age. Open circles represent results of tests for which ΔT = 1 °C and closed circles, 5 °C. Some points have been displaced laterally for clarity.
$k_e' = (-1.76 + 1.96(\text{Age}) - 0.14(\text{Age})^2 + 0.00335(\text{Age})^3) \times 10^{-4}$.
$r^2 = 0.68$. $P > 0.05$.

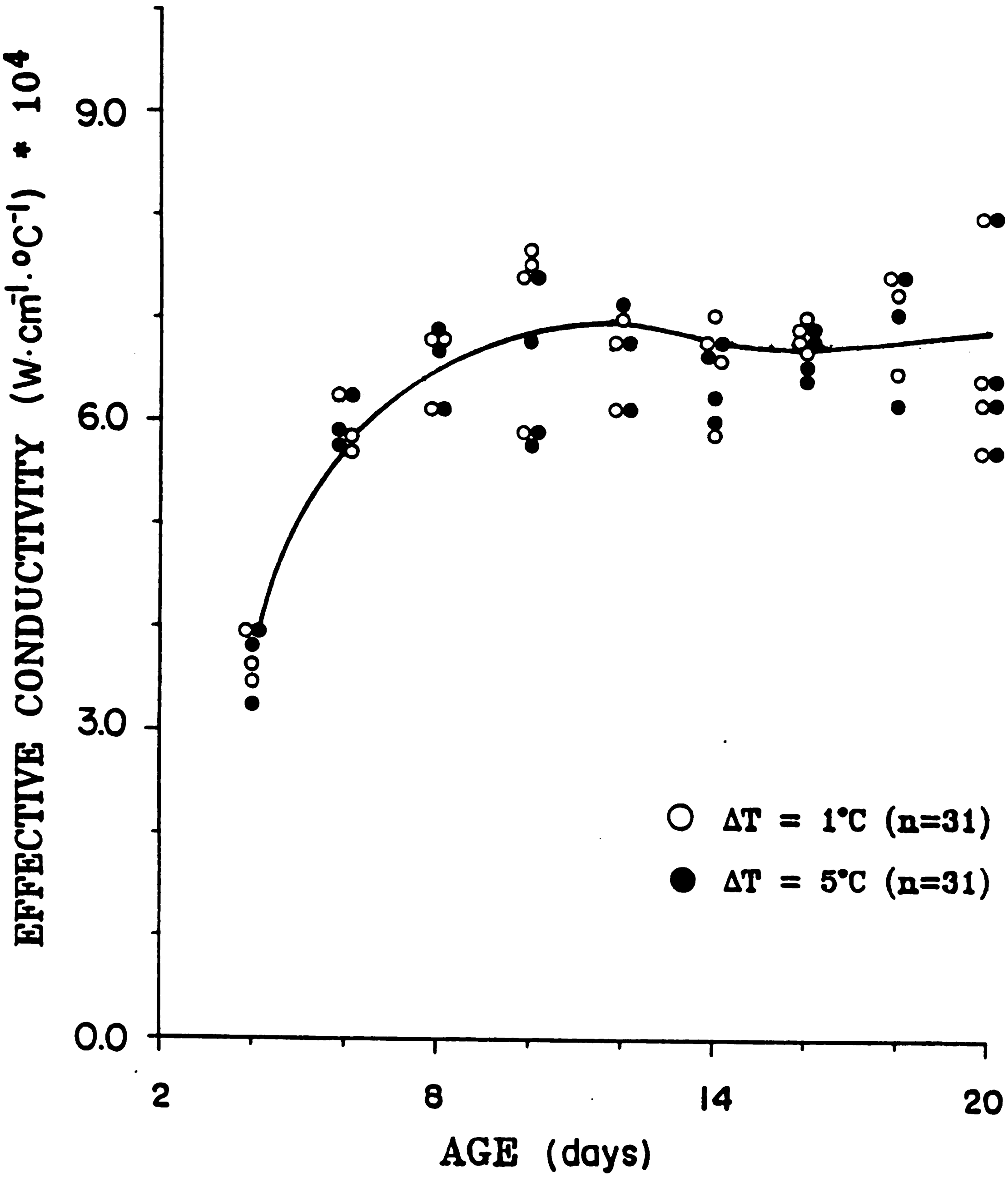
EFFECTIVE CONDUCTIVITY (W·cm⁻¹·°C⁻¹) * 10⁴
9.0
6.0
3.0
0.0
2
8
14
20
AGE (days)
○ ΔT = 1°C (n=31)
● ΔT = 5°C (n=31)

Figure 5.

Figure 5. Dorsal pelt effective thermal conductivity (k_e') as a function of age. Open circles represent results of tests for which $\Delta T = 1$ °C and closed circles, 5 °C. Some points have been displaced laterally for clarity.

$k_e' = (-1.76 + 1.96(\mathrm{Age}) - 0.14(\mathrm{Age})^2 + 0.00335(\mathrm{Age})^3) \times 10^{-4}$.

$r^2 = 0.68$. $P > 0.05$.

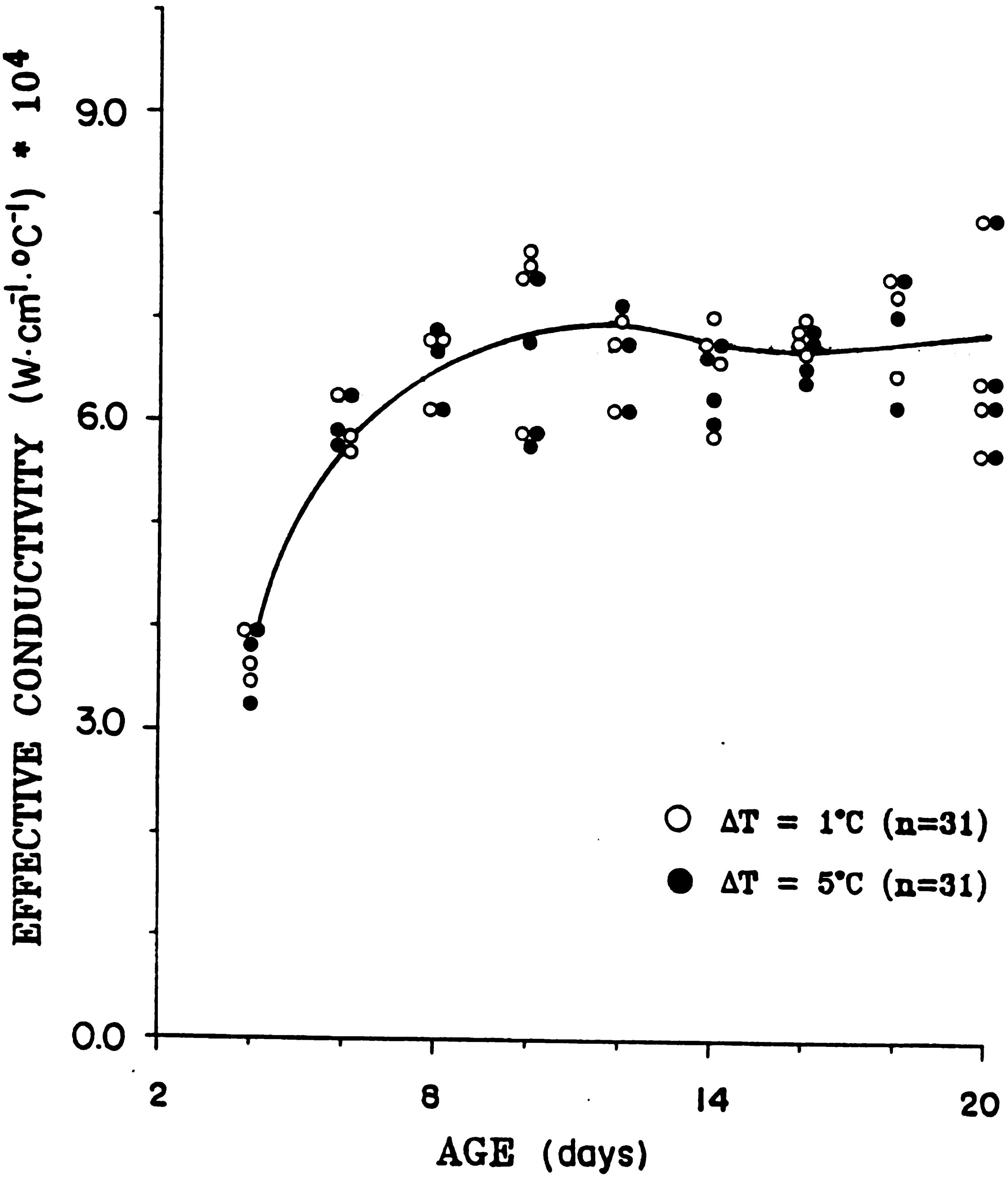
EFFECTIVE CONDUCTIVITY (W·cm⁻¹·°C⁻¹) * 10⁴
9.0
6.0
3.0
0.0
2
8
14
20
AGE (days)
○ ΔT = 1°C (n=31)
● ΔT = 5°C (n=31)

Figure 5.

Figure 6. Dorsal pelt conductance (U) as a function of age. Open circles represent results of tests for which ΔT = 1 °C and closed circles, 5 °C. Some points have been displaced laterally for clarity. The solid line is the regression on the data:

$U = (3.30 - 0.22(Age) + 0.00022(Age)^3) \times 10^{-3}$. $r^2 = 0.95$.

$P < 0.05$. The broken line is the predicted conductance:

$U_p = \bar{k}_e' / \text{pelt thickness}$.

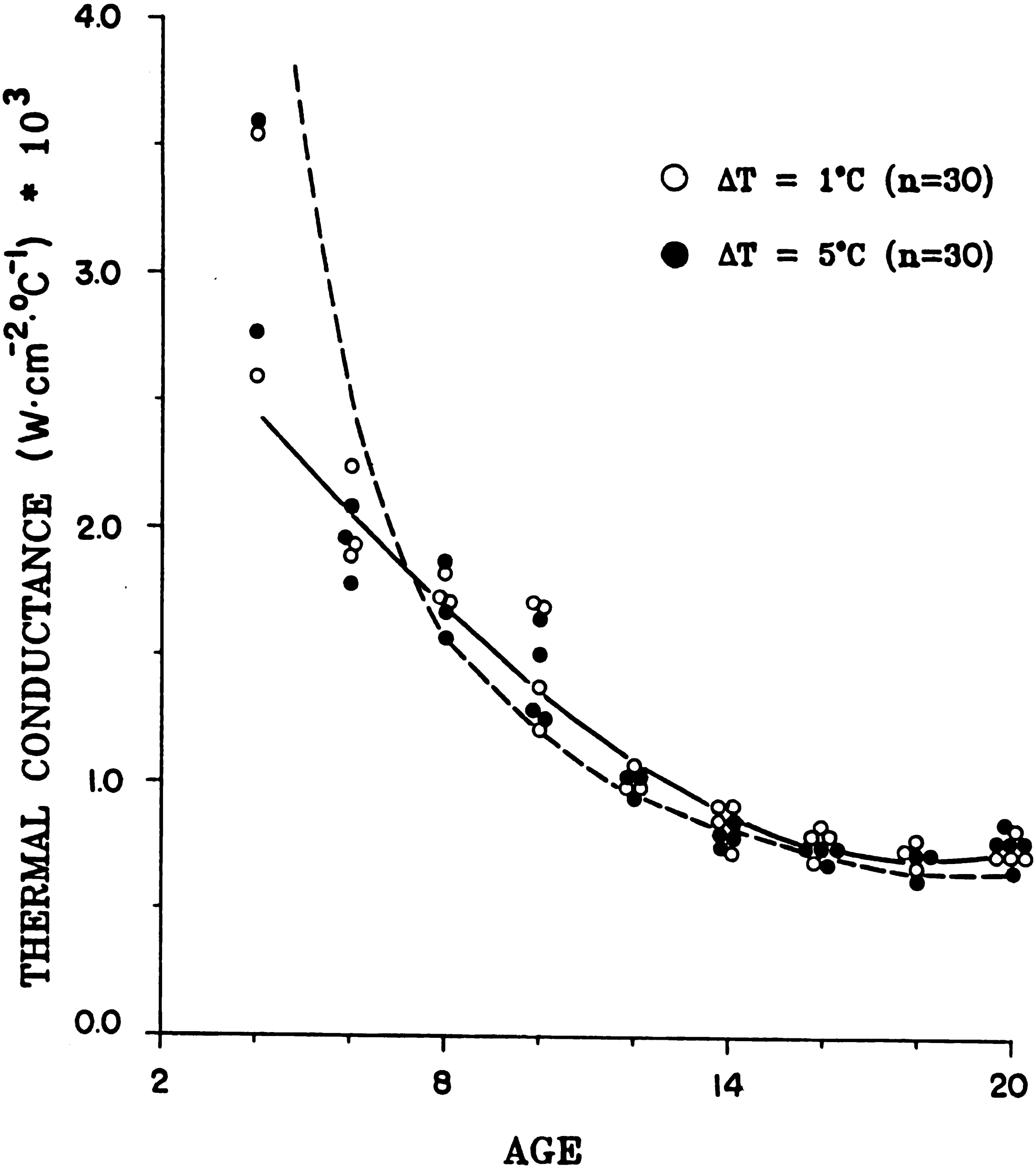
THERMAL CONDUCTANCE (W·cm⁻²·°C⁻¹) * 10³
4.0
3.0
2.0
1.0
0.0
2
8
14
20
AGE
○ ΔT = 1°C (n=30)
● ΔT = 5°C (n=30)

Figure 6.

Figure 7. Dorsal pelt insulation (I) as a function of pelt thickness (PTH). Open circles represent results of tests for which $\Delta T = 1$ °C and closed circles, 5 °C. Some points have been displaced laterally for clarity. The solid line is the regression on the data:

$I = (3.97 - 7.87(PTH) + 40.22(PTH)^2 - 22.72(PTH)^3) \times 10^2$.

$r^2 = 0.99$. $P < 0.05$. The broken line is the predicted insulation: $I_p = PTH/\bar{k}_e'$.

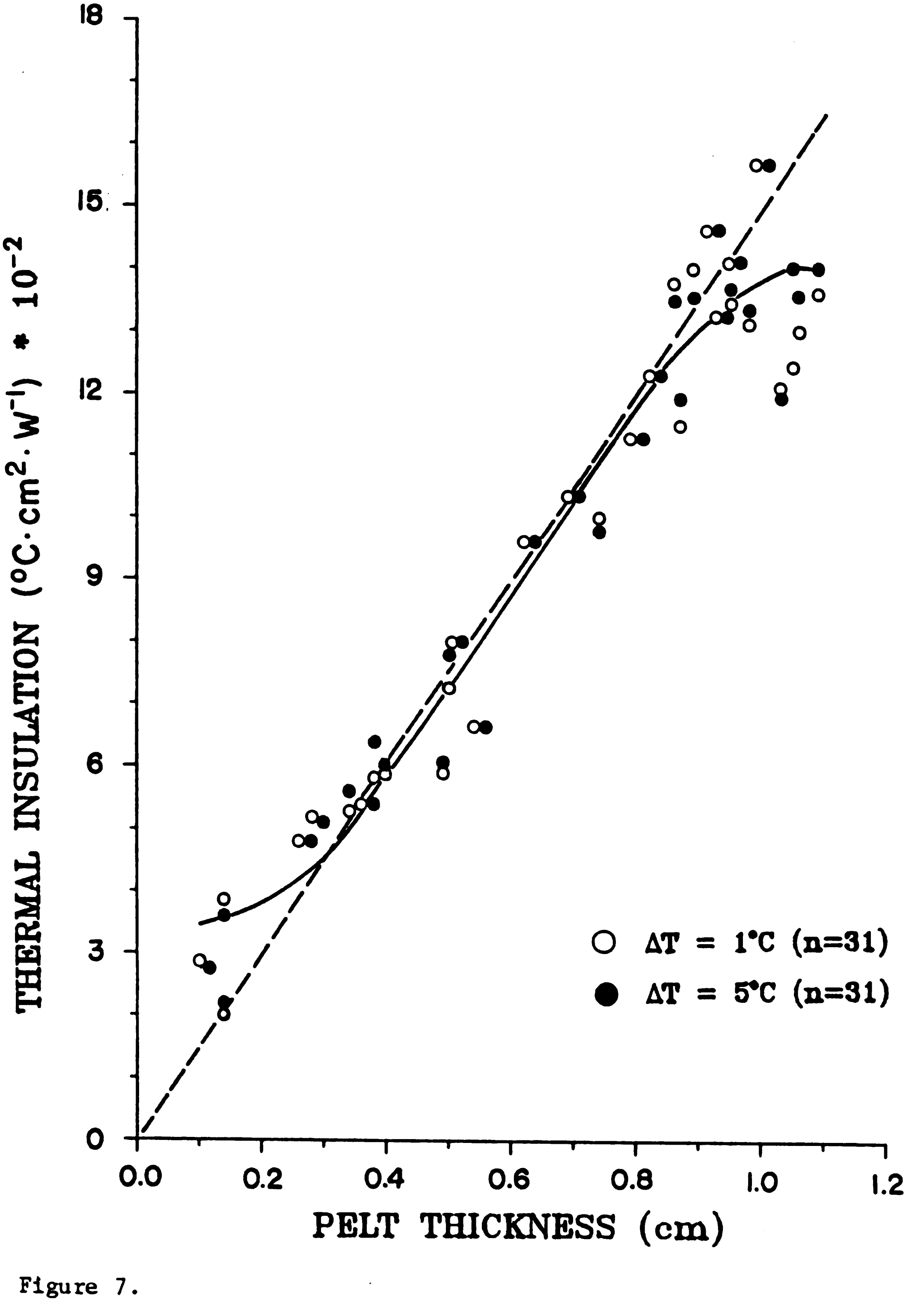
THERMAL INSULATION (°C·cm²·W⁻¹) * 10⁻²
PELT THICKNESS (cm)
0
3
6
9
12
15
18
0.0
0.2
0.4
0.6
0.8
1.0
1.2
○ ΔT = 1°C (n=31)
● ΔT = 5°C (n=31)

Figure 7.

of 14- to 20-day-old mice. At $\Delta T = 1$ °C, 10-day-olds are also not significantly different from any older age groups. The maximum mean U is 3.68×10^{-3} W cm^{-2} °C^{-1} at 4 days of age, but decreases rapidly to 8.29×10^{-4} W cm^{-2} °C^{-1} by 14 days of age. Insulation (1/U) is a linear function of pelt thickness between 0.25 and 0.85 cm pelt thickness ($r^2=0.98$, $P<0.05$), but a cubic regression best describes all the data (Figure 7).

Appendix Table 5 summarizes the means and standard deviations for all of the results.

DISCUSSION

Pelt Thickness

The fur of 4-day-old Peromyscus is not even as thick as that of newborn Sigmodon (McClure and Porter, 1983) or Neotoma (Webb and McClure, in review). As in P. leucopus, the rate of fur growth in Sigmodon and Neotoma is more rapid after 4 days of age than prior to 4 days. After day 4, the pelage of Neotoma grows linearly, as does that of P. leucopus (Figure 4). However, the fur continues to develop as a linear function of age through weaning in the altricial Neotoma, whereas fur growth slows and perhaps even stops before weaning in both the precocious Sigmodon and the altricial Peromyscus. The general pattern of development of the pelt thickness (or fur depth) in the altricial P. leucopus appears to be more similar to that of the precocial Sigmodon than the altricial Neotoma.

Effective Thermal Conductivity

Although the pelt thickness of neonatal *Peromyscus leucopus* changes dramatically during postnatal development from 4 to 16 days of age, the effective thermal conductivity only changes between 4 and 6 days of age. The conductivity of the 4-day-old's pelt primarily reflects the conductivity of the dried tissue layer (dermis, epidermis and perhaps some thin layer of subdermal muscle), because the tissue accounts for more than half of the total pelt thickness at 4 days. At 6 days the tissue layer on the pelt sample is slightly thinner and the fur is much longer than that of the 4-day-old's pelt. Now the fur accounts for more than half of the pelt thickness. The effect of the dried tissue layer is to reduce pelt k_e'. Because lyophilizing tissue removes water with minimal shrinkage, air is trapped in the intra- and intercellular spaces effecting the low tissue k_e' of the 4-day-olds. However, after 6 days of age the tissue is thin relative to the fur; therefore, the effect of the tissue on the pelt k_e' is small. (In order to estimate the effect of the skin on whole-pelt k_e', the k_e' of the skin was assumed to be the same for all pelts and equal to the k_e' measured for two 4-day-olds' pelts when the T2-set of thermocouples was in contact with the epidermis. The pelt k_e' is approximately 11% lower than fur k_e' at day 6, 8% at 12 and 5% at 18. Once the pelt has developed a noticeable layer of fur, k_e' does not change with age (Figure 5).

Sigmodon (McClure and Porter, 1983) and *Neotoma* (Webb

Effective Thermal Conductivity

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Sigmodon (McClure and Porter, 1983) and *Neotoma* (Webb and McClure, in review) furs also show no change in the effective thermal conductivity during postnatal development. The furred pelts of *P. leucopus* ($\geq$ 6 days of age) have k_e's nearly twice that which is estimated for fur alone from *Neotoma* and *Sigmodon*, but similar to the pelt k_e' of lemmings (6.0 X 10^{-4} W cm^{-1} $^{o}C^{-1}$), red foxes (7.2 X 10^{-4}), and some rabbits (4.7 to 5.6 X 10^{-4}; Scholander et al., 1950).

Conductance

Conductance largely reflects the changes seen in pelt thickness as a function of age because it describes a characteristic of the entire thickness of the pelt. If k_e' is constant (equal to the mean, $\bar{k}_e'$), then conductance is predicted to be a hyperbolic function of thickness ($U_p=\bar{k}_e'$/thickness).The correspondence between the measured conductance and the U predicted by the pelt thickness data (Figure 6.) suggests that thickness is the most important determinant of insulation during the ontogeny of *P. leucopus*. Furthermore, the result of a reciprocal transformation of the predicted U as a function of thickness is linear (predicted insulation in Figure 5). Previous authors have also observed the same, close relationship between pelt insulation and pelt thickness in ontogenetic studies (McClure and Porter, 1983; Webb and McClure, in review), interspecific studies (Scholander et al., 1950) and studies on the seasonal changes in fur (Hart, 1965; Johnson, 1977; Jacobson, 1980). The insulation of the 18-day-old *P.*

leucopus is comparable to that which Scholander et al. (1950) found for a rat and an arctic shrew, 1480 °C cm^{-2} W^{-1}.

A deviation from the predicted I in Figure 7 can occur only if there is a change in k_e'. A change in k_e' between 0.10 and 0.25 cm (which corresponds to 4 and 6 days of age) has already been discussed. At the other extreme of Figure 7, no change occurs in I as pelt thickness increases from approximately 0.85 cm to approximately 1.10 (roughly corresponding to 14 to 20 days of age, Fig. 4). Other fur characteristics must be changing to effect greater k_e's that compensate for the thicker pelts of older mice. A decrease in fur density as fewer hair follicles rupture with age and surface area continues to increase could be an explaination. This change in k_e' may not have been perceived in the conductivity data because of variation in Δx. A similar deviation from the predicted increase in insulation with thickness is apparent for the thicker pelts in Scholander et al. (1950) interspecific study. Perhaps under more natural conditions with wind and/or solar radiation the insulative benefits of these thicker furs would be evident.

The importance of pelage insulation relative to the surface-specific whole-body insulation in P. leucopus is illustrated in Figure 8. [For this figure, Hill's (1970, 1976) metabolic insulation index, °C g ccO_2^{-1} hr^{-1}, was converted into a term with the same units as used for pelt insulation in this study. Units of mass were converted into

Figure 8. Surface-specific whole-body and dorsal pelt insulation as functions of age. The solid line connects mean values of whole body data (Hill, 1976) and the broken line, dorsal pelt data. The overall-F on the regression for the differences is not significant. $\Delta I = 6.32 + 0.02(\text{Age})$. $r^2 = 0.02$.

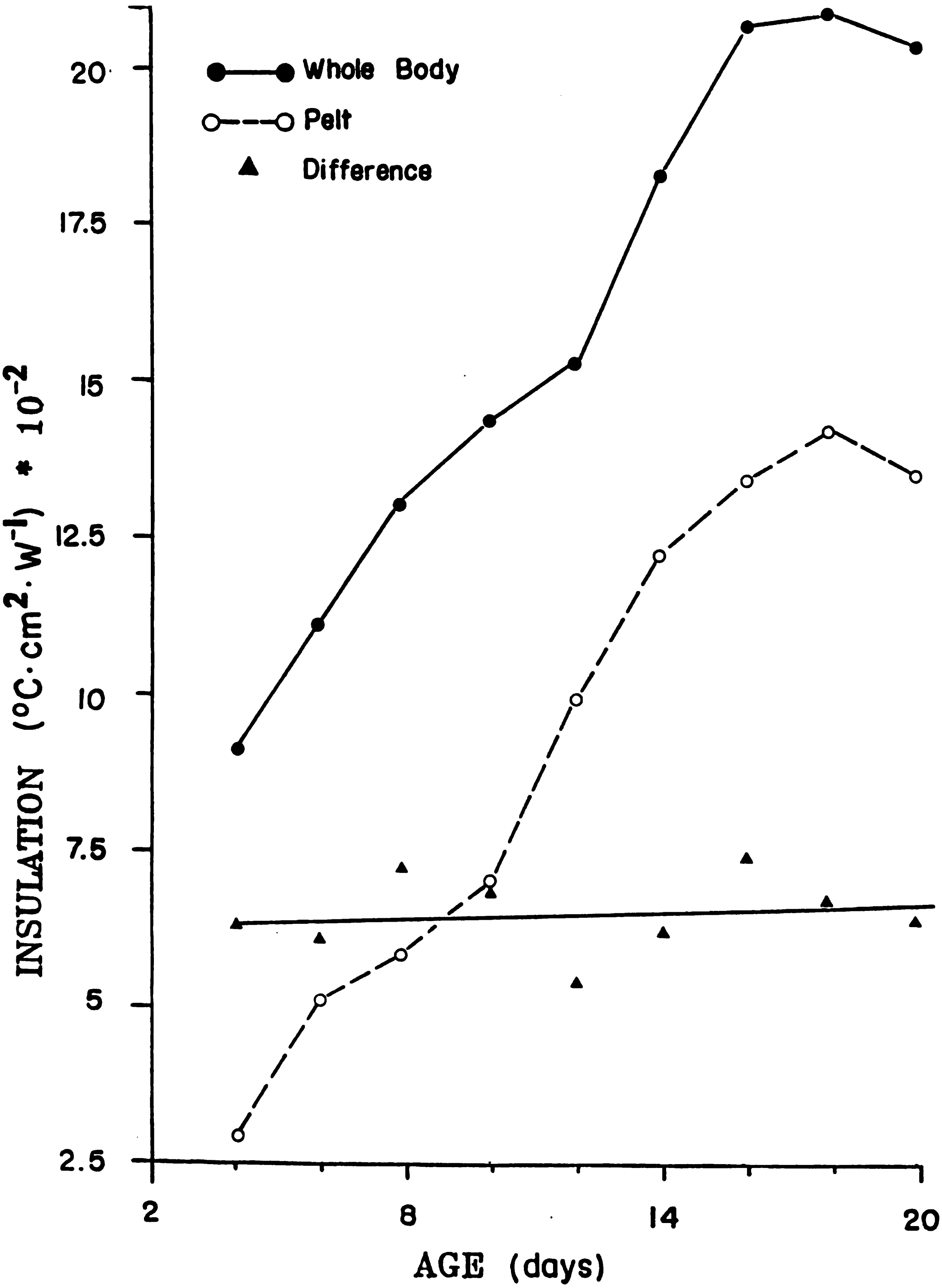
Whole Body
Pelt
Difference
INSULATION ($^oC\cdot cm^2\cdot W^{-1}$) * 10^{-2}
20
17.5
15
12.5
10
7.5
5
2.5
2
8
14
20
AGE (days)

Figure 8.

units of area by using the Meeh equation, $SA = 10(\text{mass})^{.67}$. The accuracy of this conversion is unknown for neonatal P. leucopus.] At 4 days of age the skin and sparse hairs can provide no more than 30% of the total insulation, but between 4 and 16 days of age the surface-specific whole-body insulation only doubles whereas the pelt insulation increases more than four fold, so that by 16 days of age it is responsible for 66% of the neonates' total insulation.

The increase in surface-specific whole-body insulation during postnatal development is entirely explained by the development of the pelt insulation, because the difference between mean pelt and surface-specific whole-body insulation does not increase as insulation increases with age (Figure 8). Futhermore, the development pattern of the surface-specific whole-body insulation resembles that of the pelt. These data suggest that in a free convective environment, changes in other factors during post-natal development (such as surface area to volume ratio, boundary layer, and peripheral vasomotor control) are negligible or compesatory. Had the net effect of other mouse characteristics been important, the difference between total body and pelage insulation would increase with age and the developmental patterns would not have corresponded as well.

Mean maximum metabolic rates of individual P. leucopus neonates were converted from Hill's (1970, 1976) $ccO_2\ g^{-1}\ hr^{-1}$ values to $W\ cm^{-2}$. The Meeh equation, $SA = 10(\text{mass})^{.67}$, was used to convert units of mass to units of area. The fur conductance data from the present study are estimates of the minimum metabolism necessary for a neonate to maintain its subdermal temperature (T_{SD}) 1 °C warmer than the ambient temperature (T_A) at the outer margin of the fur. Therefore, the peak metabolic rate of a neonate divided by the minimum pelt conductance provides an estimate of the maximum temperature difference an individual can maintain across its piloerected pelt.

By utilizing peak metabolism and minimum pelt conductance, 4 day old _P_. _leucopus_ could generate a 1.5 °C temperature difference between the subdermal and the ambient temperature near the outer margin of the fur. Therefore, 4-day-old pups could maintain a 31 °C T_{SD} at T_As near 29 °C (Figure 9). This agrees well with Hill's (1976) conclusion that 30 °C is the lowest T_A at which 4-day-olds can thermoregulate for more than 2 hours (these pups maintained a core temperature of about 35 °C). By 16 days of age the mouse is so well insulated that peak metabolism can elevate T_{SD} 20 °C above the T_A at the fur tips (Figure 9). According to Hill (1976), individual 16-day-olds can thermoregulate for more than 2 hours at 5 °C. Hill's estimate is even lower than that which this study predicts (11 °C, Figure 9) when T_{SD} is assumed to be 31 °C. The difference may reflect the effect of a boundary layer between the location at which Hill measured T_A in the chamber and the mouse's fur and/or that 16- to 20-day-olds can effect T_{SD}s below 31 °C in responce to cold by vasomotor control in deeper tissues

Figure 9. Lowest ambient temperature (T_A) at which neonates can maintain a T_{SD} of 31 °C by utilizing peak metabolism and minimum pelt conductance. T_A= 31°C - ((W cm^{-2})/(W cm^{-2} °C)). ●——● metabolism and conductance normal for age. ○——○ constant 4-day-old mouse metabolism and conductance normal for age. ▲----▲ metabolism normal for age and constant 4-day-old mouse conductance.

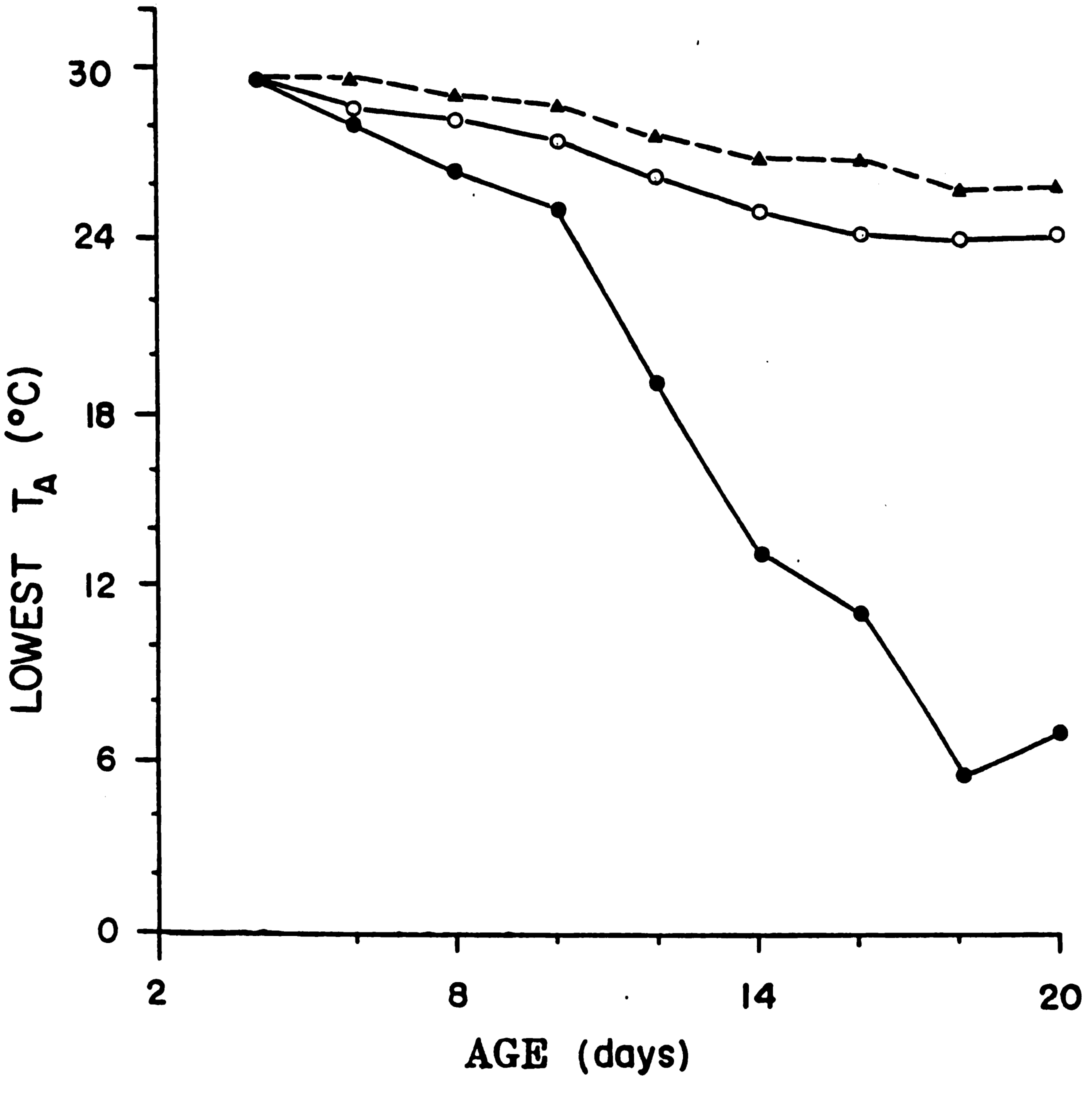

Figure 9.

(Irving, 1972).

The relative importance of the change in thermogenic capacity and pelt insulation on the development of homeothermic capabilities in *P. leucopus* was assessed by holding either the peak metabolism or pelt conductance constant and estimating the corresponding maximum ΔT for individuals at different ages. The results are illustrated in Figure 9, where $T_A = 31^\circ C - \Delta T$. A mouse with the metabolic potential of a 4-day-old and the pelage of a 16-day-old can maintain a maximum temperature difference across its pelt of 7 °C, but in the reversed case, only 4 °C. Considering that the normal 16-day-old can produce a 20 °C ΔT, both characteristics contribute substantially to the homeothermic capability of an individual. However, the changes in insulation alone permit a high body temperature (T_B) at lower T_As than do the changes in peak metabolism alone at all preweaning ages (Figure 9). Therefore, this simplistic model suggests that the development of the pelage may be more important than the development of thermogenic capacity in the ontogeny of homeothermy in *P. leucopus*.

Qualitatively, the pattern of homeothermy development closely follows that of pelage insulation on a day-by-day basis. According to Hill (1976), "acquisition of homeothermic capabilities [by individuals] ... proceeds relatively slowly between birth and 10 days of age, accelerates between 10 and 14, and appears to slow between 14 and 18." This statement is also an accurate description of the development of the dorsal pelt insulation (Figs. 7 and 8). This close coupling may further reflect the importance of the pelage to thermoregulation or a general pattern of post-natal development in P. leucopus. It would be interesting to see if many other physiological and morphological charateristics develop similarly.

Neonates even as young as 4 days can maintain high T_{B}s and respond homeothermically to decreases in T_A down to 0 °C when huddled with siblings in the nest (Hill, 1976). Therefore, the amount of pelage insulation is not important in determining when young mice begin thermoregulating in a natural situation. However, a reduction in pelt conductance effected by increased thickness results in a decreased lower-critical temperature and reduced cost of thermoregulation at T_As below the lower critical temperature. This may allow the neonates to tolerate longer periods of maternal inattentiveness and direct more energy to growth and development. The rate with which the pelage develops also influences the age at which a mouse can become independent of the nest and siblings and thermoregulate as an individual. The age at which Peromyscus leucopus are first observed to spend time outside of the nest, 16 days (Vestal et al., 1980; Hill, 1983), corresponds to the age at which the fur has finished its dramatic development, providing 95 - 100% of the pelage insulation that will develop before weaning and 66% of the total body insulation.

IMPLICATIONS FOR FUTURE RESEARCH

This research quantifies the insulative effect of pelage on the thermoregulatory ability of individual, neonatal Peromyscus leucopus in a metabolic chamber under free convective conditions. This research points out the importance of fur as a charateristic which limits the environments in which a neonate may remain homeothermic. However, this thesis only begins to answer questions about the neonate in its natural environment. Such developmental questions may be approached in two ways; one may study the maturation of function or function during maturation. When I determined the maximum ΔT at which neonates (with the appropriate insulation and metabolic capacity) could maintain a high T_B, I was examining how well the insulation could function during development. However, to understand how the insulation does function during postnatal ontogeny, one must have a comprehensive understanding of the neonates' natural enviroment. This requires nest microclimatology and a study of the interaction between the development of fur insulation and huddling with siblings and parents. Such studies cannot be represented by merely a static snap-shot, but must reflect the component of time. To understand the development of mature function, one must know how the fur insulation functions in the neonate relative to the adult in the environment of the adult. Therefore, the microclimate of the adult must be well understood. Then one must study the effectiveness of the neonates' and adults' fur in various wind and radiant conditions.

A quantified understanding of the mechanisms of heat transfer through the fur under various environmental conditions will enhance our resolution of the differences in pelage insulation when comparing individuals from an ontogenetic series or from different species. My research suggests that in the nest free convection is not an important mechanism of heat transfer through the fur layer at any age during post-natal ontogeny in *P. leucopus*. However, it will be difficult to ascertain with empirical studies whether free convection could ever effect a significant amount of heat transfer through fur. A mechanistic model in preparation by Somerton and Knight relates free convection to fur characteristics such as density, diameter and length. Mechanistic models as used by McClure, Porter and colleagues (EZFUR) are also invaluable for separating conduction and radiation in the fur because the technology for empirically quantifying these coupled processes is expensive or unavailable.

The EZFUR model does not deal with wind or solar radiation. Therefore, it is not applicable to many environments. This model needs to be adapted with a submodel that relates the effect solar radiation to direct and diffuse insolation and fur charateristics such as coat color (Walsberg, 1983), density and depth; and with a submodel that relates the effect of wind penetrance to wind speed, temperature and fur properties (Tregear, 1965; Lentz and Hart, 1960). A complete model will greatly facilitate studies of fur functional maturation as well as fur function during maturation. This model would not replace the need for or interest in empirical experimentation, but would provide a standard means of processing biological data to reveal higher resolution than is otherwise readily available. With this model other more complex and interactive projects (such as the interaction of the ontogeny of homeothermy and fur with season, latitude and altitude) will not be as intimidating.

My research suggests that the changes in fur insulation during post-natal development can account for all of the observed change in surface-specific whole-body insulation. This supports Scholander's (1955) view. However, because my methods examined only flat samples of the dorsal fur, I have no direct evidence of the magnitude of body size effects on the rate of heat transfer. By employing heated taxidermic mounts one can elucidate the effects of changes in size and shape relative to changes in the fur during ontogeny. Furthermore, these mouse models could be used to investigate the development of fur (and size and shape) in nests under various environmental conditions (as will be needed for the wind and solar radiation submodels for EZFUR).

Finally, the deviation from the insulation predicted by fur thickness at older ages may be an interesting phenomenon. A similar deviation can be found in Scholander's (1950) interspecific data. The larger species with thicker fur have less insulation than is expected for the thickness of their fur. This deviation implies that the effective conductivity is greater for the larger species and the older neonates. Why would an animal evolve or develop a thicker coat which has less insulation than a thinner coat may have? Scholander's and my experiments, as most experiments on fur insulation, were performed under no-wind/no-sun conditions. Advantageous fur characteristics which reduce wind penetrance and capture solar radiation may not be reflected in typical insulation studies. Tregear (1964) observed that furs with higher densities have lower conductances in wind than do less-dense furs. In still air, the effective conductivity of fibrous materials decreases with density, because radiant heat transfer decreases. Then at high densities, the effective conductivity increases because of an increase in conductive heat transfer (Skuldt et al., 1975; Owens-Corning Fiberglass, personal comm.). It is possible that the large species, like polar bears, have a much more dense coat than do most species. This would be of considerable advantage in the arctic winter wind, but appears as a relatively inefficient insulator in still-air experiments. In the older neonatal mice, the relatively reduced insulation is more likly a result of decreased fur density (as surface area continues to increase but number of hairs does not) effecting more radiant heat transfer. The relationships among coat color, density, solar radiation and wind during ontogeny, among species and environments could keep several scientists busy with exciting research for a long time.

APPENDICES

APPENDIX A

Calibrations

Thermocouple calibrations

Honeywell channel numbers 2, 3, 4, and 5:

NBS= $-0.49 + 1.01(Tc)$, $r^2 > 0.99$

Honeywell channel numbers 6 and 7:

NBS= $-0.55 + 1.01(Tc)$, $r^2 > 0.99$

Leeds and Northrop Galvinometer calibrations

HPDDM= $-1.79 + (LN)$, $r^2 = 1.00$

APPENDIX B

Controls

Table 2. Cork conductivity control results. Predicted values are the results of Armstrong, Inc. (ASTM Method C-518). The MEAN conductivities are the results of this study. The test thickness (dx) is in cm; density, in g cm^{-3}; conductivity, in W cm^{-1}. The percent difference (% Diff) is the difference between the measured (MEAN) and the predicted values divided by the predicted.

dx	density	predicted* conductivity	MEAN conductivity	N	SDEV	% Diff
0.09	0.19	0.000466	0.000485	2	0.000013	4
0.25	0.23	0.000502	0.000598	3	0.000048	19
0.39	0.26	0.000531	0.000684	3	0.000066	29
0.64	0.48	0.000756	0.000870	2	0.000080	15

* $k = 2.82 + 9.87(\text{density})$, $r^2 > 0.99$. (Armstrong)

APPENDIX B cont.

Table 3. Test for lateral heat loss through cork. The test thickness is in cm; density, in g cm^{-3}; q"1 is the heat flux through the HFM below the test material (W cm^{-2}) and q"2 is the heat flux through the HFM above the test material. The percent difference (% Diff) is the absolute difference between q"1 and q"2 divided by q"2. *This sample was more rigid than others; therefore, it was difficult to get good contact between the cork sample and the HFMs.

dx	density	q"1	q"2	% Diff
0.09	0.19	0.0150	0.0151	0.7
0.25	0.23	0.0105	0.0099	5
0.39	0.26	0.0062	0.0050	19
0.64	0.48	0.0064	0.0034*	46*

Table 4. Repeated piloerection results. Age is in days; dx, in cm; k_e',in W cm^{-1} ^oC. Means, standard deviations and covariances were determined for three consecutive trials of compressing and re-erecting the fur on one pelt of each age.

AGE	dx	MEAN k_e'	SDEV	COVAR
8	0.36	0.000570	0.000035	6%
10	0.50	0.000666	0.000009	1%
14	0.80	0.000692	0.000033	5%

Documents

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Q-116-02

MICRO-FOIL™ HEAT FLOW SENSOR

CALIBRATION

RdF PART NO. 20451-3

SERIAL NO. 208

Output at 70°F: 0.831 microvolts/Btu-Ft^{-2} -Hr^{-1}

Polarity: (For heat flow into surface)
White - Positive (+)
Red - Negative (-)

Temperature Multiplication Factor: See Attached Graph

*Thermal Resistance: 0.012 °F/Btu-Ft^{-2} -Hr^{-1} (Typ)

*Heat Capacity: 0.05 Btu-Ft^{-2}/°F (Typ)

Response Time: 0.400 sec (62% response to step change) (Typ)

*Thermal resistance is the temperature difference between front surface and rear mounting surface of the sensor per unit of heat flow through the sensor. Heat capacity is the amount of heat required to raise the mean temperature of the sensor 1°F. Typical values of these two properties are given primarily to indicate sensor capabilities and are required for heat flow calculations only in very rare instances.

BY: Marlon P Marshall RdF 20 CORP

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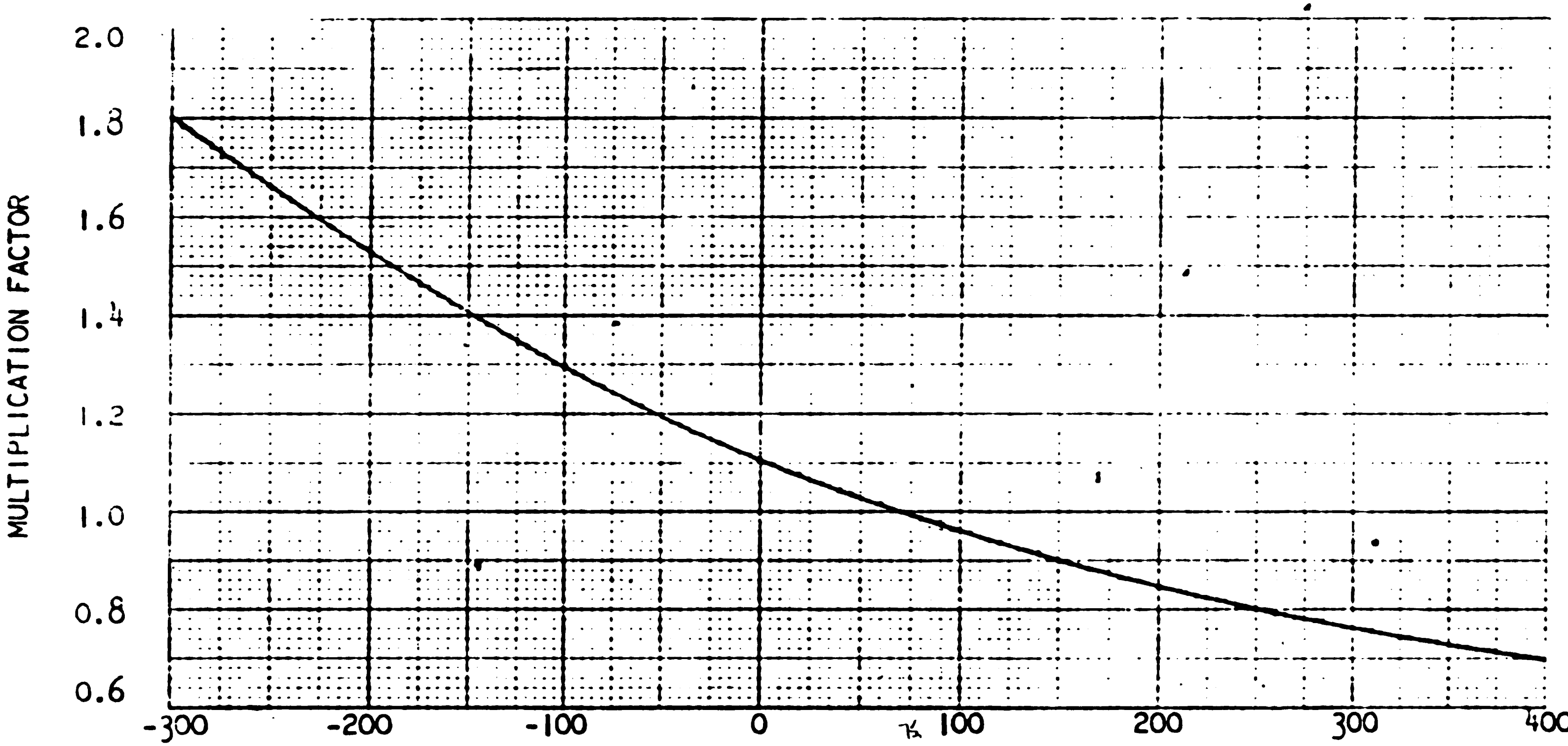
APPENDIX C cont.



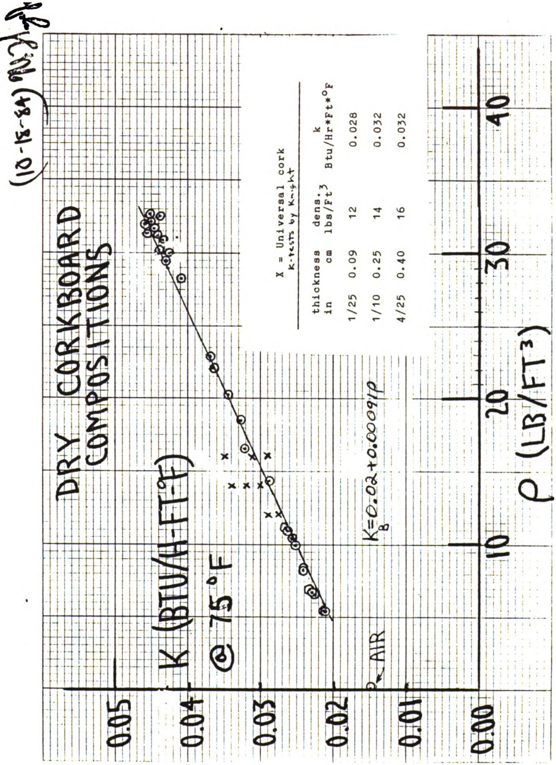
SURFACE TEMPERATURE, DEGREES FAHRENHEIT

MICRO-FOIL HEAT FLOW SENSOR

OUTPUT MULTIPLICATION FACTOR VS RECEIVING SURFACE TEMPERATURE
(70°F BASE)

RdF CORPORATION
HUDSON, NEW HAMPSHIRE

APPENDIX C cont.



APPENDIX D

Data

Table 5. Means and standard deviations on the means. Age is in days, N is replicates, pelt thickness in cm, k_e' in W cm^{-1} °C, U in W cm^{-2} °C, I in °C cm W^{-1}. Trial dT conditions are indicated as (1°C) and (5°C).

Table 5

AGE	4	6	8	10	12	14	16	18	20
N	3	3	3	4	3	4	4	3	4
Pelt Thickness	0.13	0.30	0.38	0.51	0.69	0.84	0.98	1.05	0.95
SDEV	0.02	0.04	0.01	0.03	0.06	0.03	0.05	0.05	0.06
$k_e'(1\ ^oC) \times 10^4$	3.66	6.23	6.74	6.77	6.72	6.58	7.02	7.17	6.61
SDEV	0.21	0.41	0.05	1.00	0.34	0.50	0.27	0.64	0.89
$k_e'(5\ ^oC) \times 10^4$	3.69	5.98	6.57	6.48	6.68	6.42	6.68	6.89	6.59
SDEV	0.39	0.23	0.40	0.78	0.52	0.35	0.22	0.64	0.99
$U(1\ ^oC) \times 10^4$	37.0	20.2	17.5	14.9	10.2	8.39	7.68	7.24	7.49
SDEV	11.9	1.90	0.69	2.38	0.51	0.77	0.25	0.50	0.51
$U(5\ ^oC) \times 10^4$	36.6	19.4	17.0	14.3	10.1	8.19	7.31	6.95	7.46
SDEV	9.37	1.48	1.43	1.88	0.38	0.60	0.24	0.52	0.63
$I(1\ ^oC) \times 10^{-2}$	2.90	4.97	5.73	6.84	9.85	12.0	13.0	13.9	13.4
SDEV	0.92	0.45	0.22	1.14	0.48	1.20	0.42	0.99	0.86
$I(5\ ^oC) \times 10^{-2}$	2.85	5.17	5.90	7.11	9.92	12.3	13.7	14.4	13.5
SDEV	0.73	0.40	0.49	0.91	0.38	0.92	0.45	1.11	1.10

APPENDIX E

Pelt Boundaries

Figure 10. Pelt boundaries. Broken line follows radiant surface. Solid line with closed circles marks the upper pelt-boundary where T2-thermocouples were placed. Solid line with open circles marks the lower pelt-boundary where the T1-thermocouples were placed.

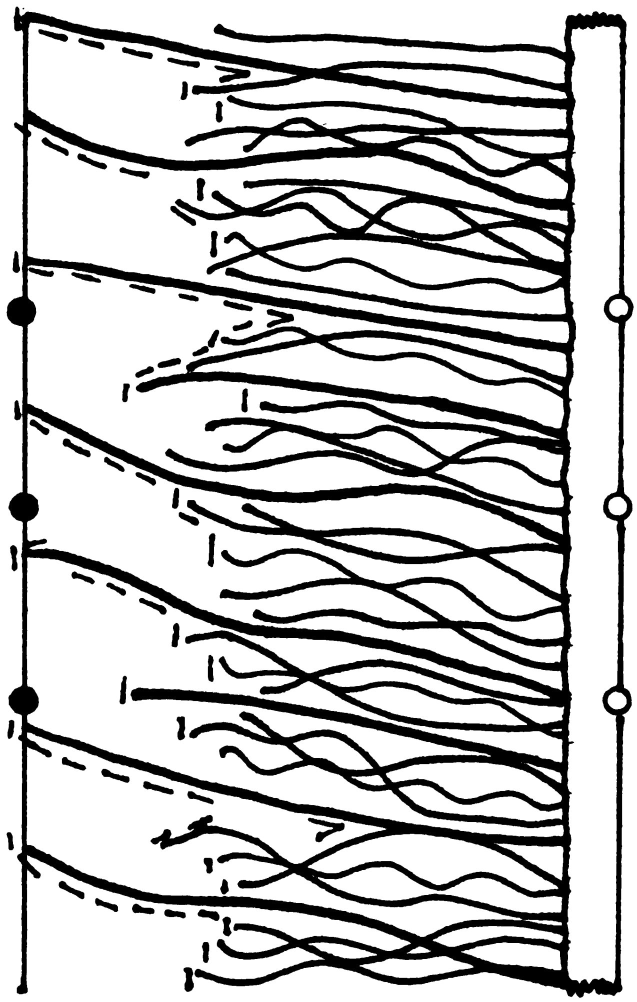


Figure 10.

LIST OF REFERENCES

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