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NEST INSULATION: ENERGY SAVINGS TO BROWN LEMMINGS USING A WINTER--ETC(U)

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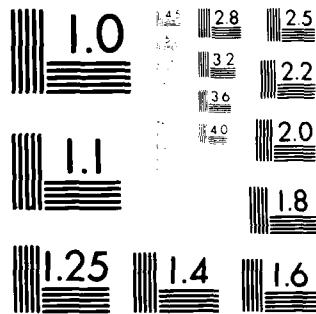
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Nest insulation: energy savings to brown lemmings using a winter nest.

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10 Timothy M. Casey

Running head: Nest insulation and lemming energetics

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ABSTRACT

Energy metabolism of brown lemmings in summer pelage with and without real or artificial nest material was measured over long periods at several air temperatures. Resting metabolism of lemmings at $T_a = -16^\circ\text{C}$ was higher than that of lemmings which had nests. At higher T_a the difference between resting metabolism of animals with and without nests decreased and was similar at $T_a = 20^\circ\text{C}$. The energy savings by reduction of heat loss of resting lemmings translates into a ca. 50% decrease in the average metabolic rate. The energy saved at rest is equivalent to a reduction in thermal conductance of roughly 40%. Independent estimates of energy savings due to nest insulation by analysis of cooling curves of a lemming model with and without a nest suggest a 45% change in thermal conductance. Baby lemmings huddled in a nest had equilibrium body temperatures four to five times higher than isolated nestlings outside the nest. These data suggest that there is a substantial energy savings at ecologically relevant air temperatures. If the insulative value of the nest is similar whether the animal is in summer or winter pelage, these data suggest that lemmings could exhibit thermoneutral levels of resting metabolism while in large nests at subnivalian air temperatures typical of Barrow, Alaska during the winter.

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INTRODUCTION

Brown lemmings (Lemmus trimucronatus) are active throughout the year on the Arctic tundra despite mean air temperatures (T_a) ranging from +5 in summer to about -30°C in winter. During more than 6 months of the year the tundra is totally snow covered and lemming activity is confined to the subnival environment, the air space formed between the snow and the frozen ground (Benson, 1969).

The subnival environment, in non-Arctic habitats, is often dramatically warmer than the macroenvironmental air temperatures because snow provides effective insulation and the ground temperature is usually at or above freezing. In the Arctic, however, the ground is composed of permafrost whose mean temperature is about -18°C (Brewer, 1958). Consequently, T_a in the subnival environment of the Arctic tundra is routinely about 15 to 20°C below 0°C during the late winter and early spring (Kelley & Weaver, 1969). Moreover, subnival air temperatures vary dramatically depending on the depth of snow cover (MacLean et al, 1974).

During the winter, lemmings build straw nests at the surface of the ground (Scholander et al, 1950a) which they utilize during inactive periods. These nests undoubtedly have energetic significance since they provide insulation and therefore retard rates of heat loss for their occupant (s). At present, there are little empirical data to assess the energy savings to lemmings provided by their nest. The present study investigates the significance of nest insulation to the energetics of brown lemmings by measurement of oxygen consumption and cooling rates of living lemmings, and cooling rates of an artificial model with and without the nest.

MATERIALS AND METHODS

This study was conducted from July to October 1976, and July 1977, at the Naval Arctic Research Laboratory, Barrow, Alaska. Lemmings used in this study

were obtained from an animal colony maintained at the laboratory consisting of locally captured individuals and their offspring. Animals were housed indoors under natural photoperiod at T_a of about 10°C .

Lemmings were placed inside an airtight plexiglass box equipped with inlet and outlet ports. Inside the plexiglass box was a smaller sheet metal nest box having two partitions. Food (Purina rat chow and carrots) was placed in one partition and the other was either left empty or provided with approximately 25 g of cotton in strips for nest material. In two cases, winter nests were collected from the tundra and provided in place of the cotton.

Oxygen consumption was continuously monitored using a Beckman G-2 paramagnetic oxygen analyzer. Water vapor was absorbed prior to gas analysis by passing the air stream through a column of drierite. Flow rates were measured with a Matheson 603 flow meter calibrated with a Brooks Dual GC mass flow controller (Model 5840). Air flow rates were approximately 1.2 liters/min. Gas values are converted to STP.

The plexiglass chamber was placed in a large constant temperature cabinet where air temperature was controlled ($\pm 1^\circ\text{C}$). Air temperature was monitored using a 30 gauge copper-constantan thermocouple attached to a portable potentiometer (Omega Inst. Co.). Lemmings were exposed to a photoperiod of 24 hr. light and 0 hr. dark.

Animals were run for 8-18 hours with no nest material and then given either cotton or a real nest and measurements continued for 8 to 16 hours. Occasionally the sequence was reversed, i.e. nest material first, followed by no nest material to insure that initial high values in $\dot{V}O_2$ were the result of the absence of a nest.

An independent estimate of nest insulation was obtained using a lemming model. A solid woods metal cast of a skinned lemming carcass was plated with a thin layer of copper. The woods metal was then melted out of the inside of the

copper shell by drilling small holes in the model and immersing it in boiling water. When cool, the skin of the lemming was fitted to the model and stitched together with surgical silk. The model was supplied with a 30 gauge copper-constantan thermocouple in the center of the body cavity. Details for the model building process are given by Bakken and Gates, (1975). The model was heated to approximately 40°C in a small oven after which it was placed in the center of a nest sitting on a large patch of tundra turf, or directly on the turf, and allowed to cool. The turf, nest and model were placed inside a wind tunnel chamber similar to the one described by Gessamen (1972). Body and air temperature were recorded on a Honeywell multipoint recorder. Cooling curves reported here were made in still air, since there is probably little air movement within a nest under the snow.

Cooling curves of lemming nestlings were measured by inserting a 36 gauge cu-cn thermocouple (enamel insulated to the tip) into the back of the throat. Nestlings were held by the nape of the neck between thumb and forefinger, which caused them to gape. Temperatures were read to $\pm 0.2^{\circ}\text{C}$ on an Omega portable laboratory thermometer at intervals timed with a stopwatch. Individuals were placed singly into glass beakers lined with paper towel. The nest boxes used for these experiments are similar to those described by Hill (1972). Air temperature inside the constant temperature chamber used in these experiments was 0°C.

RESULTS

Behavior: In the respirometer, lemmings having access to a real nest arranged themselves in a ball with the anterior dorsal surface of the back protruding from the top of the nest. The major portion of the nest was arranged around and below them. They couldn't completely surround themselves with the nest material but there was a loose covering of grass surrounding the dorsal surface.

Nests were placed in nestboxes because they were old, dry and very fragile. If the lemmings were given only a nest without a nestbox, the nest would invariably fall apart within a few hours. In the field, however, nests appeared to be woven into the grassy substrate and often could not be removed intact due to substrate attachment.

The lemmings which were given strips of cotton began to fashion the cotton into a nest as soon as it was introduced into the respirometer. During inactive periods the lemmings were completely enclosed within a dome shaped cotton nest similar in shape to nests constructed on the tundra. [see MacLean et al., (1974) - their fig. 1].

Resting Oxygen Consumption: At an air temperature of 20°C the mean rates of mass specific oxygen consumption ($\dot{V}O_2$) were similar for animals with and without nest (fig. 1). At lower air temperatures the resting oxygen consumption of animals having nest material was lower than the $\dot{V}O_2$ of those without it, and the difference increased as T_a decreased (figure 1). At $T_a = 0^\circ\text{C}$, $\dot{V}O_2$ of lemmings with nests was about 28% lower than that of lemmings without nests and the difference increased to 43% at $T_a = -16^\circ\text{C}$, a temperature which approximates winter air temperatures in the subnival environment (Kelly & Weaver, 1969). Results for lemmings given real nests instead of cotton ones show a similar reduction in resting metabolism compared to lemmings without nests (figure 1). The change in overall thermal conductance (slope of $\dot{V}O_2$ vs. T_a from fig. 1) under these conditions, $-.138 \text{ ml } O_2(\text{g h } ^\circ\text{C})^{-1}$ to $-.084 \text{ ml } O_2(\text{gh}^\circ\text{C})^{-1}$ or .054, is approximately 40%.

Maximum Oxygen Consumption: There was only a slight difference in maximum continuous rates of oxygen consumption of animals with and without nests. At $T_a = -16^\circ\text{C}$ the $\dot{V}O_2$ max was 11.6 ml O_2/gh (± 1.73 S.D.) for lemmings without a nest and 9.55 ± 2.04 for animals with a nest, yielding a $\dot{V}O_2$ max 18% lower for animals with nests. At $T_a = 0$, $\dot{V}O_2$ max was 8.87 ± 1.37 for lemmings without nests and 7.81 for lemming with nests.

Average Metabolic Rate: The average metabolic rate, the mean value of long term measurements, includes both resting and active metabolism (fig. 2). It therefore provides a more realistic value of the energy cost of an animal at a given air temperature (see Morrison & Grodzinski, 1975). Animals having nesting material have an average $\dot{V}O_2$ 40% lower than those without nests at $T_a = -16^\circ\text{C}$ and the difference in $\dot{V}O_2$ decreased to an insignificant amount at $T_a = 20^\circ\text{C}$ (fig. 3).

Activity patterns: The lemmings in this study exhibited a regular cyclic activity. In most cases the period was about 4 hours and was not modified by air temperature, time of day, or the presence or absence of nest material. These data are similar to the cyclic activity patterns of lemmings reported by Fisher and Needler (1957) and by Coady (1975).

Cooling curves: The cooling rate of the lemming model was reduced when placed inside the nest. Fig. 4 shows a typical comparison of cooling curves of the lemming model with and without a nest. Six nests (mass $28.1\text{g} \pm 7.6$ S.D., length $18.5\text{ cm} \pm 2.7$, width $17.0\text{ cm} \pm 3.5$, height $7.7\text{ cm} \pm 2.1$) were collected from the tundra for analysis of cooling curves. Mean cooling rate for the model inside six nests was $.0412^\circ\text{C}/\text{min.}^\circ\text{C} \pm .0041$ S.D. as compared to a cooling rate of $.077^\circ\text{C}/\text{min.}^\circ\text{C}$ for the model without the nest. The equilibrium temperature of the model (see Bakken, 1976) equalled the air temperature. The model duplicated the surface area and pelage of a lemming and differed substantially from a real lemming only in its heat capacity. The average change in cooling rate was $.036^\circ\text{C}/\text{min.}^\circ\text{C}$ or 46.6%. The change in cooling curves of the model with or without a nest reflects the change in overall thermal conductance (Morrison and Tietz, 1957; Bakken, 1976) and is of similar magnitude to the values predicted by $\dot{V}O_2$ data.

Cooling of sucklings: The relation of body temperature to time in individual lemmings (ages 2, 3, and 4 days) isolated in beakers and of the same animals huddled with siblings in a cotton nest is shown in figure 5. In isolated

individuals, the rate of cooling decreases with age. There is a substantial decrease in the rates of cooling of the same animals when huddled with siblings in the nest. By 4 days of age they are able to maintain a body temperature 20°C above the air temperature for at least an hour and have stopped cooling 30 minutes after the mother was removed (fig. 5). The isolated four day olds continue to cool and their cooling rates are essentially linear on semi logarithmic coordinates.

DISCUSSION

Although conditions in the present study do not totally match the micro-environment, it is obvious that there is a substantial energetic advantage to lemmings which utilize a nest, particularly at low air temperatures (fig. 1). This change in $\dot{V}O_2$ at low T_a for animals with and without nests is analogous to the seasonal shift in thermal conductance of larger animals which results from change in fur depth (Irving et al., 1955). In both cases the rates of heat loss are retarded by added insulation, in the former case behaviorally, and in the latter, morphologically. The magnitude of the change in conductance (40 to 50%) is not surprising since nest walls are several cm thick and in still air the thickness of the insulator is a major determinant of rates of heat flow through it (see Bakken, 1976).

Both collared lemmings and brown lemmings show seasonal change in insulation (Scholander et al., 1950b, Hart and Heroux, 1955; Coady, 1975; Casey et al., 1978). The adult lemmings used in this study were probably in summer pelage as judged by the estimated thermal conductance values of animals without nests (fig. 1). Whether in summer or winter pelage, the energy savings provided by nest insulation should be additive. Therefore, animals in winter pelage which occupy a nest should have lower oxygen consumption at a given T_a than reported in this study. For example, if thermal conductance of a lemming in winter is .080 ml $O_2 \cdot g^{-1} h^{-1} \cdot ^\circ C$, (Scholander et al., 1950b) its resting $\dot{V}O_2$ without a nest at T_a of $-16^\circ C$ ($\dot{V}O_2 = C [T_b - T_a]$)

would be about 4.4 ml O₂/g/hr. If the same reduction of $\dot{V}O_2$ is assumed for the animal in winter pelage as a result of being in the nest (i.e. conductance reduced by .054 - see results) its conductance becomes 0.026 ml O₂(g.h.°C)⁻¹. Under these circumstances the lemmings could be at basal levels of $\dot{V}O_2$ at air temperatures of -16°C as predicted by Scholander et al. (1950a). Consequently, there should be a strong selective pressure for nest building by lemmings due to the energy savings which would result throughout the winter and spring.

Scholander et al (1950a) report that two different sized lemming occur on the tundra and interpret this dichotomy as the difference between individual and colonial nests. A more recent study by MacLean et al., (1974) suggests that large nests are built by reproductively active females while the smaller nests may be built by other members of the population. These authors postulate that the large well insulated nests may be built as much for the benefit of the off spring as for the female. This argument is reasonable and may be illustrated by looking at the previous calculation. If the combination of a winter pelage and a large nest reduces thermal conductance of a lemming to 0.026 ml O₂ (g.h.°C)⁻¹, a lemming having this conductance would be at thermoneutral metabolism at a Ta of -35°C. Since the subnivian environment at Barrow is usually not colder than about -20°C (Kelly and Weaver, 1969), this much insulation should not be needed for an individual lemming. Moreover, as pointed out by MacLean et al., a larger nest would take longer to warm up after the lemming enters and allow less time to profit from it between foraging bouts.

A large nest will cool more slowly than a small one, and this, is highly beneficial to baby lemmings, because the cooling rates of the nestlings will be slowed. The metabolism of nestlings is directly proportional to their body temperature (Hissa, 1968; Chew & Spencer, 1967). A decreased cooling rate will mean a greater amount of time at high body temperatures and therefore at high rates of heat production. Huddling of nestlings will also retard their cooling

rate (Pearson, 1960; Gebczynski, 1975). The heat produced by nestlings in turn retards the cooling of the nest. As a result, if insulation is great enough, the combined metabolism of the huddled nestlings may be sufficient for them to maintain high body temperatures indefinitely. Four day old lemmings have stable body temperatures about five times higher than the equilibrium T_b of isolated individuals of the same age (fig. 4). Hill (1975), and Gebczynski (1975) also report elevated T_b of baby mammals in the nest for long periods when the mother is absent. These data suggest that body temperatures of nestlings are not entirely dependent upon metabolic heat from their mothers, but rather depend to an important extent on the added insulation afforded by huddling and the nest. A large nest will allow the mother increased time for foraging under circumstances where the young would freeze without it, particularly up to about day 7 before which the capacity of lemmings to maintain high body temperatures without added insulation is limited (Morrison et al., 1954; Hissa, 1968; Casey, in preparation). Without a well insulated nest, young lemmings exposed to T_a 's of -20°C would freeze to death in minutes. Therefore, it is not surprising that large nest size is associated with successful reproduction of lemmings during sub-zero weather in the early spring (MacLean et al., 1974).

These data can not be applied to energetics of brown lemmings in the field until more aspects of the ecology of lemmings in winter are understood. The nests utilized in this study were winter nests and, at present, information of winter activity of lemmings and the extent and duration of their nest occupancy is scant (see MacLean et al., 1974). Moreover, there are no microclimate data currently available concerning winter lemming nests.

During the summer, data are available for activity patterns and nest occupancy of lemmings in the field (Banks et al., 1975). However, the nests of lemmings in summer are built underground and the energetic significance of such nests has not been examined. In addition, the ADMR's of free-ranging lemmings on the tundra obtained from D_2^{18} studies are markedly higher than those of

lemmings confined in respirometers in the laboratory with ad libitum food available (Peterson et al, 1976). The higher field values presumably reflect increased costs associated with foraging and locomotion. If there is a reduction in resting energy metabolism for lemmings occupying summer nests, the discrepancy between laboratory and field studies of ADMR will be even greater, attaching even greater significance to energetic cost of activity in lemmings.

It is not unreasonable to suggest that there will be some energy savings associated with nest occupancy during the summer. The animals will be in a less exposed area, away from the wind. The ground temperature increases due to prolonged solar radiation, and summer lemming nests often have a carpet of fine grass clippings which should reduce heat transfer from animals to ground by conduction (Strecker and Morrison, 1952). However, if the insulative capacity of underground lemming nests is similar in magnitude to that of a winter nest, the energy savings to a lemming will not be as great as in the winter since energy savings are increased as air temperature decreases (fig. 1).

The change of location and nesting pattern of brown lemmings during the summer and winter may relate to predator-prey interactions. During the summer, the winter nests are particularly conspicuous to avian predators such as the snowy owl and pomerine jaeger, which only occur on the tundra during that season. It is unclear whether there is a change in insulative capacity of a winter nest on the surface of the ground compared to a summer nest under-ground but there is obvious survival value in moving below ground by decreasing the incidence of predation.

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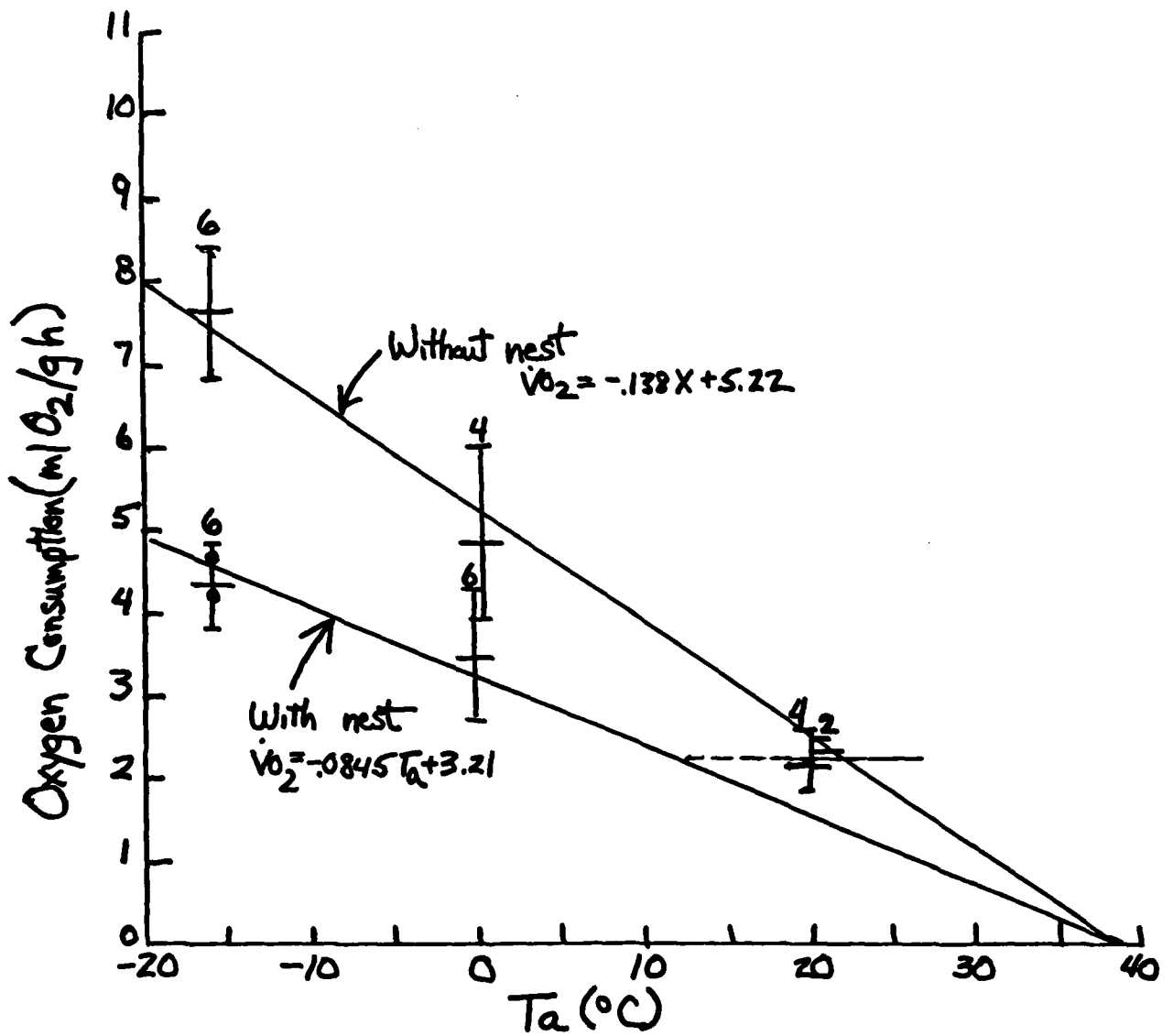
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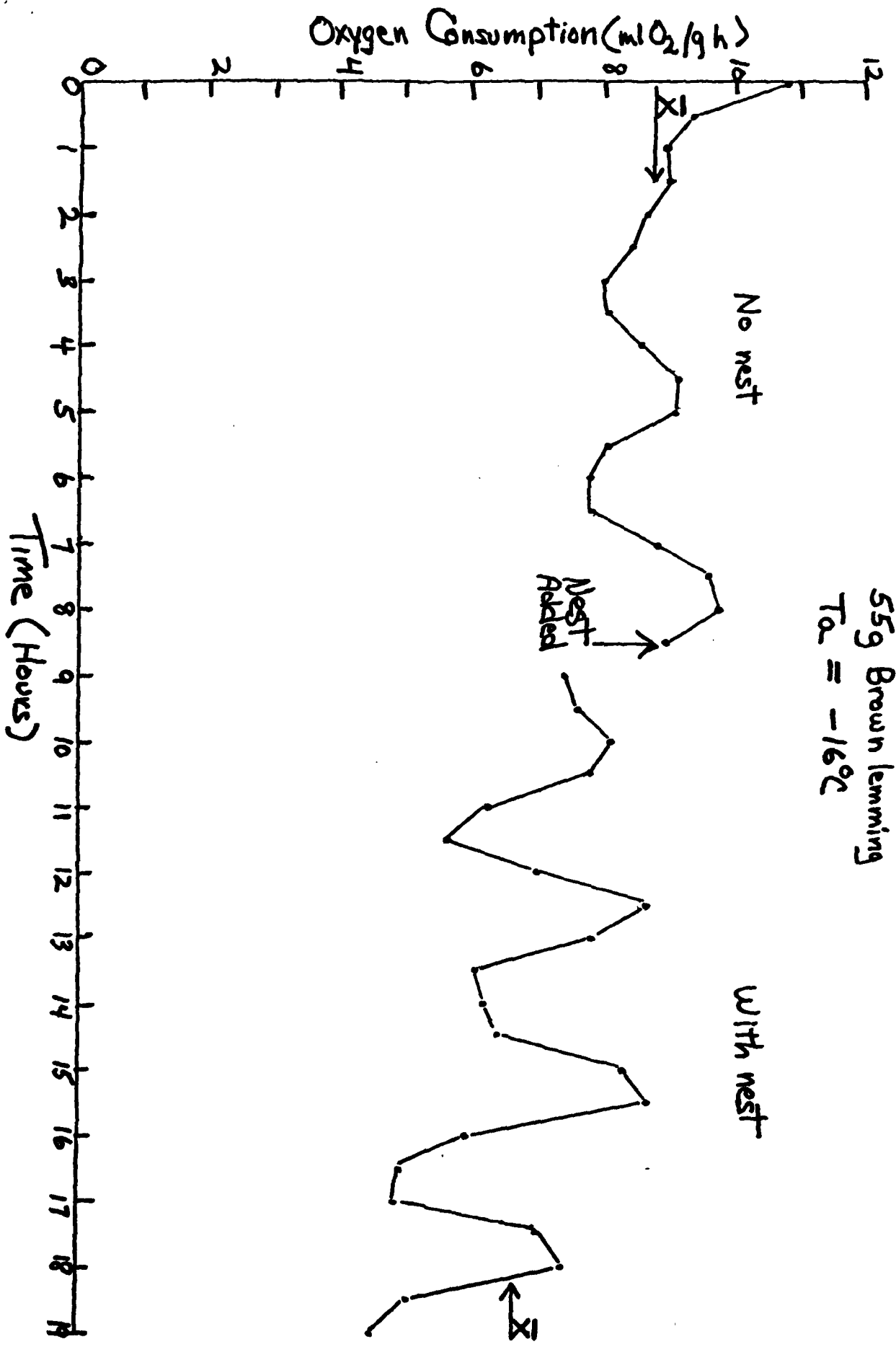
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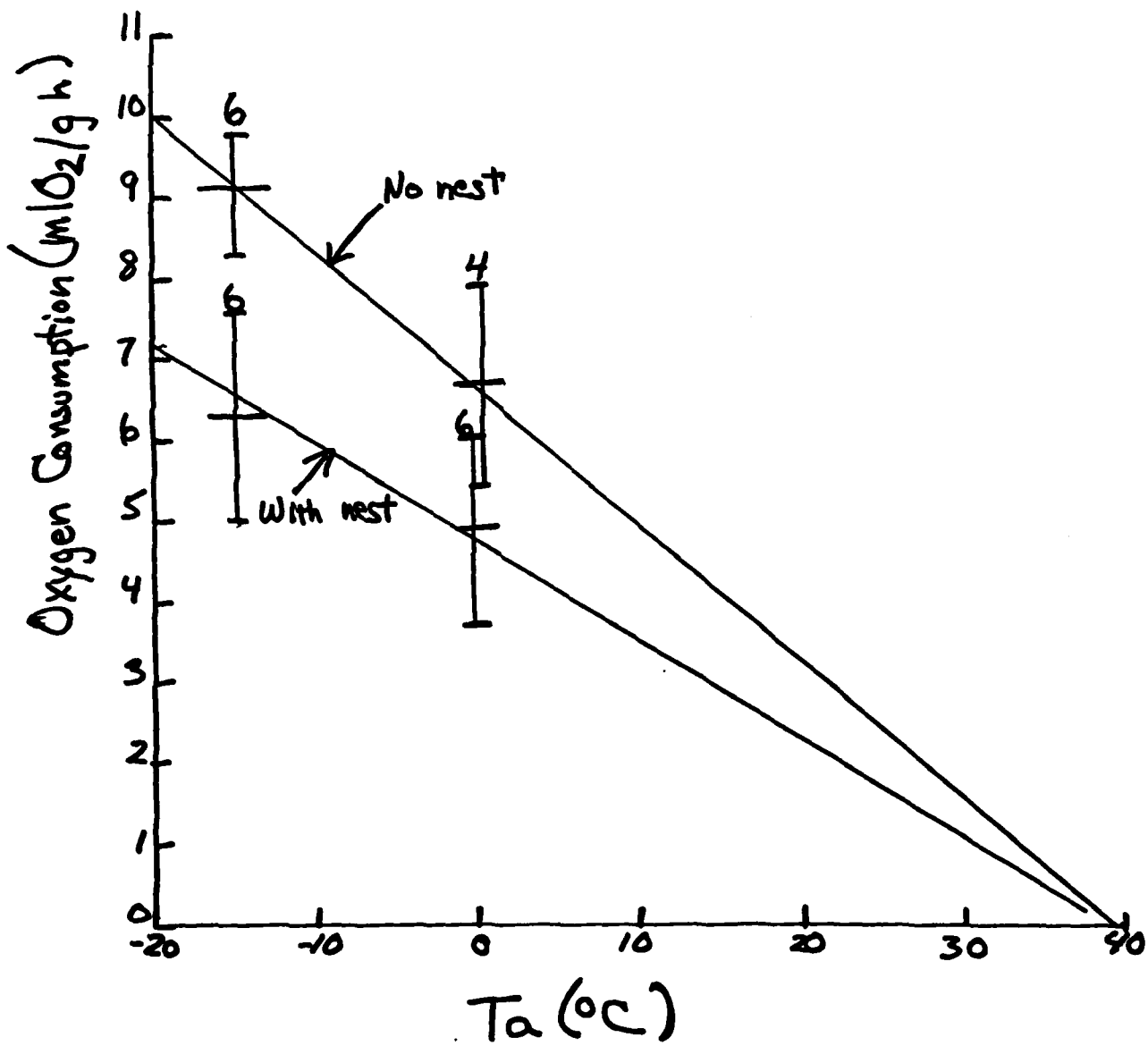
- Figure 1. Mean rates of resting oxygen consumption of brown lemmings at several air temperatures with and without nest material in the respirometer. Vertical lines represent \pm 1st standard deviation, numbers indicate sample size. Closed circles at $T_a = -16^\circ\text{C}$ represent data using lemming nests collected on the tundra in place of cotton nest material.
- Figure 2. Oxygen consumption of a 55g, male brown lemming at $T_a = -16^\circ\text{C}$ without nest material and after nest material is added (at arrow). Average rates for the entire period with and without nest are indicated by the symbol \bar{x} .
- Figure 3. Average rates of oxygen consumption (including both rest and activity) for brown lemming at T_a 's of 0 and -16°C with and without nest material in the respirometer. Symbols as in figure 1.
- Figure 4. Cooling curves of 2, 3 and 4 day old baby lemmings isolated in glass beakers or huddled in a cotton nest with three siblings, $T_a = 0^\circ\text{C}$.
- Figure 5. Cooling curves in still air of lemming model on a patch of tundra turf and enclosed within a lemming nest collected at Point Barrow, Alaska.

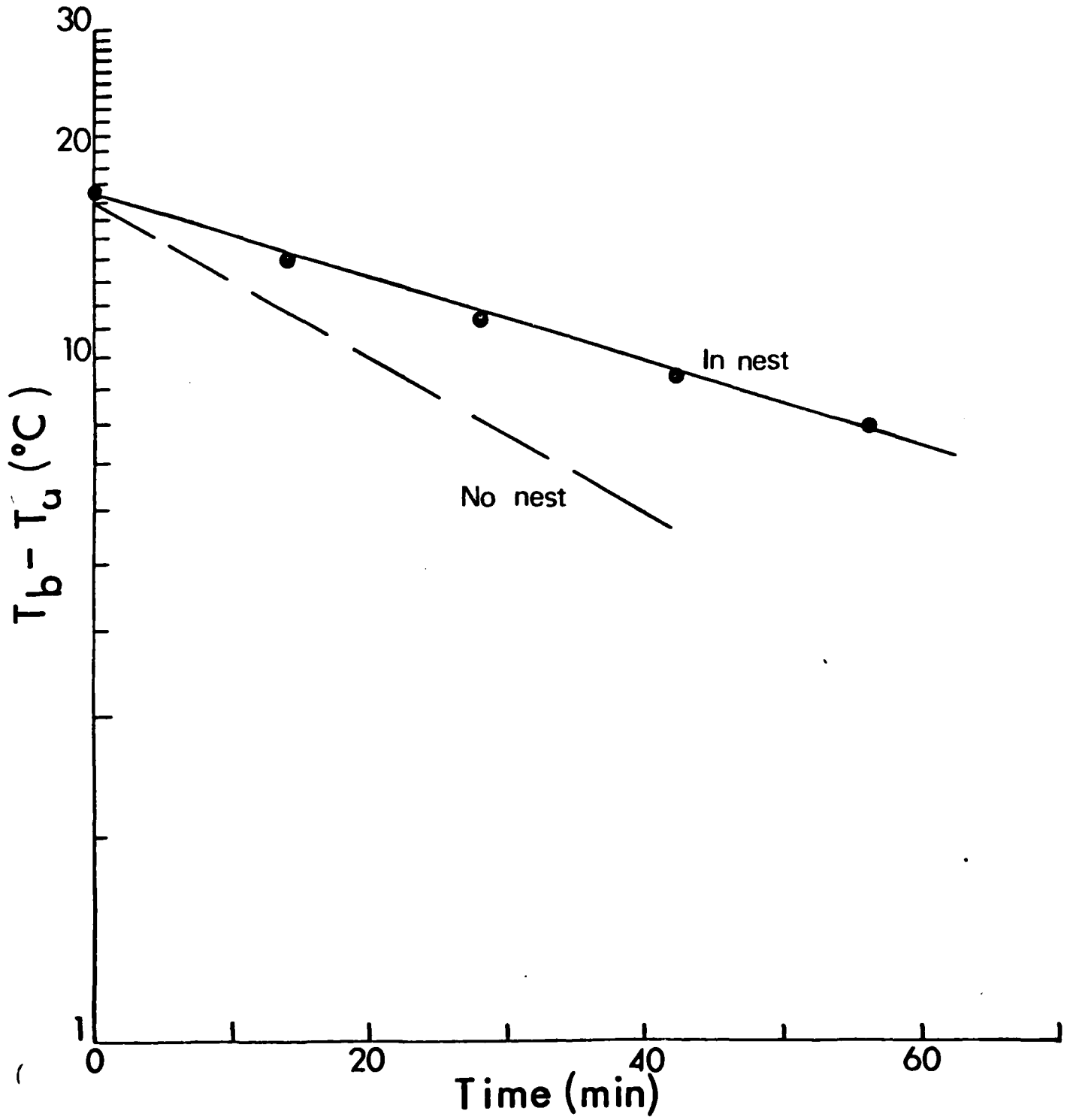
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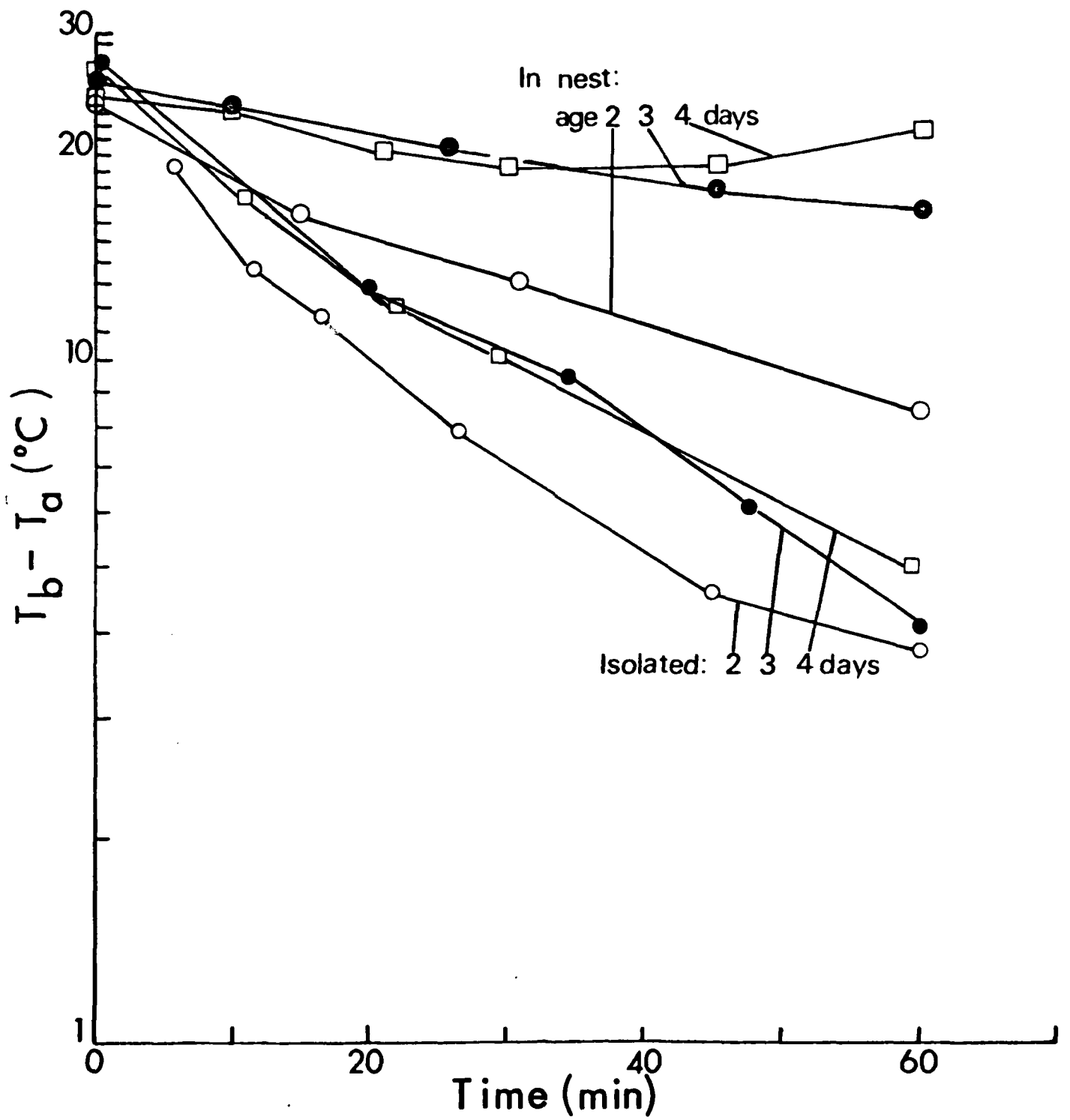
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