

NESTING BEHAVIOR OF LACTATING NORWAY RATS

NESTING BEHAVIOUR OF LACTATING NORWAY RATS:
INFLUENCE OF DAMS' CHOICE OF TEMPERATURE AND PUP-ASSOCIATED STIMULI

BY

JAMES EDWARD JANS, B.A., M.A.

A Thesis

Submitted to the School of Graduate Studies
in Partial Fulfilment of the Requirements
for the Degree
Doctor of Philosophy

McMaster University

September 1980

DOCTOR OF PHILOSOPHY, (1980)

MCMASTER UNIVERSITY

(Psychology)

Hamilton, Ontario

TITLE: Nesting Behavior of Lactating Norway Rats: Influence of Dams'
Choice of Temperature and Pup-Associated Stimuli

AUTHOR: James Edward Jans, B.A., (University of Manitoba); M.A. (-
University of Maryland)

SUPERVISOR: Dr. M. Leon

NUMBER OF PAGES: xiii, 159

Abstract

Norway rat dams show an intermittent pattern of contact with their young during the first two weeks postpartum. Previous research has shown that one important factor influencing the length of the intermittent contacts (or nest bouts) is the body temperature of the dam. Dams tend to terminate nest bouts when their body temperature rises, and over the first two weeks postpartum nest bout durations decrease, as the dam experiences an elevation in body temperature during a nest bout both more frequently and more rapidly. In the present series of studies, the analysis of the pattern of mother-young contact is extended to include an investigation of the thermal environment that the dam herself chooses to nest in and the consequences of this choice for the pattern of nesting behaviour. Further, not only are nest bout durations considered in these studies, but also nest bout frequencies and interbout intervals.

It was shown that when dams were allowed to choose from a wide range of surface temperatures they placed their pups on a warm surface (approximately 32°C) and seemed to prefer to spend time between nest bouts on a fairly warm surface (approximately 24 - 26°C). In comparison to dams that were not given a range of temperatures to choose from, dams that established a warm nest site and spent time between nest bouts on a warm surface showed much shorter nest bout durations, a higher frequency of nest bouts (although the frequency of nest bouts that were long enough for milk delivery to occur was similar between groups), and longer durations between nest bouts. While the

short nest bout durations were most probably due to the fact that the dams were more likely to experience a fairly rapid rise in temperature during nest bouts, it was necessary to test separately whether the temperature that the dams preferred between nest bouts or the warm temperature at which the pups were maintained contributed to the higher frequency of nest bouts and the prolonged durations between nest bouts. It was found that if dams were forced to spend all interbout intervals on a fairly warm surface (approximately 26°C), they showed much longer intervals between nest bouts which were typically accompanied by a slow decline in the dam's body temperature. Maintaining the pups at a warm temperature during the dam's absence produced prolonged intervals between nest bouts in which milk delivery could occur and also a much higher frequency of nest bouts.

While previous investigations had assumed that the pups play a passive role in the determination of nest bout termination, it was found in the present investigation that the pups played both passive and active roles in the overall pattern of nesting. It was shown that dams maintain contact with pups if the pups are cold. Pups might also play a more active role in maintaining contact with the dam by attaching to the dam's nipples soon after contact is established, because failure to attach to the nipples soon after contact was established frequently led to rapid nest bout termination. Finally, it was found that pups could actively curtail interbout intervals by emitting ultrasonic vocalizations. While ultrasonic vocalizations are typically emitted only when the pups are subjected to some stress, and thus may not be important in a controlled laboratory situation, this

finding is of particular significance, as it indicates that the pups are not merely passive recipients of maternal care, but rather are capable of actively altering the pattern of nesting behaviour.

Acknowledgements

The completion of this thesis would not have been possible without the assistance and encouragement of several people. Drs. B.G. Galef, S. Siegel, and S.F.H. Threlkeld provided questions and commentary that were both stimulating and challenging. Dr. M. Leon supervised the research, provided financial support for animals and apparatus, and showed continuing interest in the data. Drs. M. Daly and M. Wilson offered several helpful suggestions and were always willing to listen, discuss, and encourage. Mr. E.A. Mitchell not only built and repaired most of the apparatus, but also provided numerous lively discussions. Ms. B. Pitt quickly and efficiently typed the majority of the manuscript, and Ms. W. Tasker skilfully typed the final modifications. Ms. M. Keane provided technical assistance with skill, efficiency, and a smile.

Throughout the entire venture there was Barbara. Typing, reading, drawing figures, mating animals, discussing, and encouraging were only a few of the ways in which she helped. Most important was the love and the happiness that she provided at all times. Finally, there was the arrival of Jennifer, who has added a new dimension of happiness to our lives.

TABLE OF CONTENTS

	PAGE
Introduction	1
Section I: Female Choice of Nest Site Temperature	1
Experiment 1. Surface temperature choice of female rats.	7
Experiment 2. Surface temperature choice for nesting of lactating female rats.	13
Experiment 3. Pup skin temperature when maintained in a nest in a 16°C ambience	20
Discussion	23
Section II: Dam Choice of Nest Site Temperature: Effect on the Nesting Pattern on Day 10 Postpartum	25
Experiment 4. Nesting pattern of day 10 postpartum dams that are allowed to select from a wide range of temperatures	25
Experiment 5. Nesting pattern of day 10 postpartum dams that are forced to spend interbout intervals on either a warm, cool, or unmanipulated floor surface ..	63
Experiment 6. Rate of maternal temperature decline during interbout intervals when dams are forced to spend interbout intervals on either a warm or unmanipulated floor surface	90
Discussion	99
Section III: Effects of the Pups on the Nesting Pattern on Day 10 Postpartum	102
Experiment 7. Nesting pattern of day 10 postpartum dams whose pups are either warmed, cooled, or unmanipulated during interbout intervals	103
Experiment 8. Effect of pup temperature, vocalizations, and ability to attach to the dam's nipples on the termination of interbout intervals and the maintenance of nest bouts	126

Summary and General Discussion	145
Appendix A	150
References	157

LIST OF FIGURES

	PAGE
Figure 1: Average chosen surface temperatures of nonlactating, Day 4 postpartum, and Day 10 postpartum female rats as a function of whether nest material was present or not. Symbols represent the mean temperature choices and bars represent the standard errors of the means.	10
Figure 2: Average chosen surface temperatures of Day 4 postpartum and Day 10 postpartum female rats (a) and average surface temperatures at which pups were placed by Day 4 postpartum and Day 10 postpartum female rats (b) as a function of whether nest material was available or not. Symbols represent the mean temperatures and bars represent the standard errors of the means.	15
Figure 3: The percentage of time when not in contact with the pups (IBI time) spent in each of the four sections of the thermocline by Experimental and Control dams. Symbols represent the mean percentages and bars represent the standard errors of the means.	30
Figure 4: The percentage of nest bouts terminated with a visit to each of the four sections of the thermocline by Experimental and Control dams. (a) illustrates the percentage of visits after all nest bouts and (b) illustrates the percentage of visits after nest bouts of at least 10 min duration. Symbols represent the mean percentages and bars represent the standard errors of the means.	35
Figure 5: The percentage of nest bouts immediately preceded by a visit to each of the four sections of the thermocline by Experimental and Control dams. (a) illustrates the percentage of visits before all nest bouts and (b) illustrates the percentage of visits before nest bouts of at least 10 min duration. Symbols represent the mean percentages and bars represent the standard errors of the means.	37
Figure 6: The distributions of interbout interval durations between all nest bouts for Experimental and Control dams. ..	40
Figure 7: The distributions of interbout interval durations between nest bouts of at least 10 min duration for Experimental and Control dams.	42

Figure 8: Mean interbout interval durations for Experimental and Control dams. (a) illustrates interbout interval durations between all nest bouts and (b) illustrates interbout intervals between nest bouts of at least 10 min duration. Superimposed bars represent the standard errors of the means. 44

Figure 9: Mean percentage of time that Experimental and Control dams spent with their pups. Superimposed bars represent standard errors of the means. 48

Figure 10: Distributions of all nest bout durations for Experimental and Control dams. 50

Figure 11: Distributions of nest bout durations for Experimental and Control dams when only nest bouts of at least 10 min duration are considered. 52

Figure 12: Mean nest bout durations for Experimental and Control dams. (a) illustrates the mean duration of all nest bouts and (b) illustrates the mean duration of nest bouts of at least 10 min duration. Superimposed bars represent standard errors of the means. 55

Figure 13: Mean frequencies of nest bouts for Experimental and Control dams. (a) illustrates the frequencies of all nest bouts and (b) illustrates the frequencies of nest bouts of at least 10 min duration. Superimposed bars represent the standard errors of the means. 57

Figure 14: The distributions of interbout interval durations between all nest bouts for dams exposed to either a warm, cool or unmanipulated floor during IBI. 67

Figure 15: The distributions of interbout interval durations between nest bouts of at least 10 min duration for dams exposed to either a warm, cool, or unmanipulated floor during IBIs. 69

Figure 16: Mean interbout interval durations for dams exposed to either a warm, cool, or unmanipulated floor during IBIs. (a) illustrates the mean durations between all nest bouts and (b) illustrates the mean durations between nest bouts of at least 10 min duration. Superimposed bars represent the standard errors of the means. 72

Figure 17: Mean percentage of time spent with pups for dams exposed to either a warm, cool, or unmanipulated floor during IBIs. Superimposed bars represent the standard errors of the means. 75

- Figure 18: The distributions of all nest bout durations for dams exposed to either a warm, cool, or unmanipulated floor during IBIs. 77
- Figure 19: The distributions of nest bout durations for dams exposed to either a warm, cool, or unmanipulated floor during IBIs when only nest bouts of at least 10 min duration are considered. 80
- Figure 20: Mean nest bout durations for dams exposed to either a warm, cool, or unmanipulated floor during IBIs. (a) illustrates the mean durations for all nest bouts and (b) illustrates the mean durations for nest bouts of at least 10 min duration. Superimposed bars represent standard errors of the means. 82
- Figure 21: Mean frequencies of nest bouts for dams exposed to either a warm, cool, or unmanipulated floor during IBIs. (a) illustrates the frequencies of all nest bouts and (b) illustrates the frequencies of nest bouts of at least 10 min duration. Superimposed bars represent standard errors of the means. 84
- Figure 22: Mean weight gain of pups whose dams were exposed to either a warm, cool, or unmanipulated floor during IBIs. Superimposed bars represent standard errors of the means. 87
- Figure 23: (a) Mean IBI durations for dams exposed to either a warm or unmanipulated floor during IBIs. Superimposed bars represent standard errors of the means. (b) Mean rate of maternal temperature decline during IBIs following nest bouts accompanied by a rise in maternal temperature for dams exposed to either a warm or unmanipulated floor during IBIs. Superimposed bars represent standard errors of the means. 92
- Figure 24: (a) Mean duration until maximum temperature decline during IBIs for dams exposed to either a warm or unmanipulated floor during IBIs. Superimposed bars represent standard errors of the means. (b) Mean rate of maternal temperature decline until maximum temperature decline during IBIs for dams exposed to either a warm or unmanipulated floor during IBIs. Superimposed bars represent standard errors of the means. 94
- Figure 25: Sample traces of maternal temperature during a nest bout and succeeding IBI for dams exposed to either a warm or unmanipulated floor during IBIs. 96

- Figure 26: Distributions of interbout interval durations between all nest bouts for dams whose pups were either warmed, cooled, or unmanipulated during IBIs. 106
- Figure 27: Distributions of interbout interval durations between nest bouts of at least 10 min duration for dams whose pups were either warmed, cooled, or unmanipulated during IBI. 108
- Figure 28: Mean IBI durations for dams whose pups were either warmed, cooled, or unmanipulated during IBIs. (a) illustrates mean durations between all nest bouts and (b) illustrates mean durations between nest bouts of at least 10 min duration. Superimposed bars represent standard errors of the means. 110
- Figure 29: Distributions of all nest bout durations for dams whose pups were either warmed, cooled, or unmanipulated during IBIs. 112
- Figure 30: Distributions of nest bout durations for dams whose pups were either warmed, cooled, or unmanipulated during IBIs when only nest bouts of at least 10 min duration are considered. 115
- Figure 31: Mean nest bout durations for dams whose pups were either warmed, cooled, or unmanipulated during IBIs. (a) illustrates mean durations for all nest bouts and (b) illustrates mean durations for nest bouts of at least 10 min duration. Superimposed bars represent standard errors of the means. 117
- Figure 32: Mean frequencies of nest bouts for dams whose pups were either warmed, cooled, or unmanipulated during IBIs. (a) illustrates frequencies of all nest bouts and (b) illustrates frequencies of nest bouts of at least 10 min duration. Superimposed bars represent standard errors of the means. 120
- Figure 33: Mean percentage of time spent with pups by dams whose pups were either warmed, cooled, or unmanipulated during IBIs. Superimposed bars represent standard errors of the means. 122
- Figure 34: (a) Floor plan of entire apparatus for switching litters during dam's absence. (b) Side view of antechamber, nest area, and nest tray. 129
- Figure 35: Mean latency to return to nest area for dams returning to either warm vocalizing, cool vocalizing, warm nonvocalizing, or cool nonvocalizing pups. Superimposed bars represent standard errors of the means. 134

- Figure 36: Number of dams that returned to either warm vocalizing, cool vocalizing, warm nonvocalizing, or cool nonvocalizing pups and stayed with the pups for 10 min. 137
- Figure 37: Mean latency to return to the nest area for a 10 min nest bout for dams returning to either warm vocalizing, cool vocalizing, warm nonvocalizing, or cool nonvocalizing pups. Superimposed bars represent standard errors of the means. 139
- Figure 38: Average core temperatures of dams exposed to either (a) cold (4°C), (b) control (22°C), or (c) warm (28°C) ambiances over a 2 hr testing period. Core temperatures were measured every 15 min and all dams were tested on three occasions: once when nonlactating, once on Day 4 postpartum, and once on Day 10 postpartum. Symbols represent the mean core temperatures and bars represent the standard errors of the means. 153

Introduction

During the first two weeks of life Norway rats depend on their mother for warmth, nutrition and elimination (Wiesner and Sheard, 1933). Contact with the mother during these two weeks is intermittent, and episodes of maternal care (nest bouts) are separated by interbout intervals (IBIs), during which the dam is absent from the nest (Grota and Ader, 1969; Plaut, 1974).

While the number of nest bouts per 24 hour period does not change systematically throughout the first two weeks postpartum, the duration of nest bouts progressively decreases, resulting in an overall decline in mother-litter contact time (Grota and Ader, 1969; Plaut, 1974). The decrease in the duration of mother-litter contact has been observed in both wild and domestic strains of Rattus norvegicus (Hughes, Harlan and Plaut, 1978). As nest bout durations decrease, the amount of time that maternal care is available to the pups must also decrease. Whatever factors are responsible for limiting nest bout duration, then, are also, in essence, responsible for limiting the amount of time that maternal care is available to the pups.

The pups appear to play a limited active role in the termination of nest bouts, as the pups will remain attached to the dam's nipples as long as the nipples are proffered (Wakerley and Lincoln, 1971). Further, nest bouts are not terminated contingent upon

milk delivery, as dams with sealed nipples show the same pattern of nesting as normal dams (Leon, Croskerry and Smith, 1978).

Croskerry, Smith and Leon (1978) have proposed that thermal cues play an important role in limiting nest bout duration. They suggested that when the dam initiates a nest bout, she joins a huddle, occluding her ventrum as she comes in contact with the pups, thereby reducing her ability to dissipate heat, and eventually suffers an increase in body temperature. It is this rise in maternal temperature which limits the duration of nest bouts. Factors which influence the rate of rise of maternal temperature during any given nest bout will influence its duration. These factors include ambient temperature, pup temperature at bout onset, dam temperature at bout onset, and the surface area to mass ratio of the huddle.

Measurements of the dam's ventral and core temperatures under various thermal conditions indicate a strong correlation between the rate of maternal temperature rise and the alacrity with which dams terminate nest bouts (Leon et al., 1978). For example, Leon et al. (1978) showed that dams spent less time with their pups and were more prone to rapid elevations in maternal temperature when the ambient temperature was 26°C than when the ambient temperature was 22° or 18°C. They also showed that maternal temperature rose more quickly and dams had shorter nest bouts when the pups were maintained at warm rather than cool temperatures. Pup temperature contributes to the termination of maternal nest bouts insofar as it changes the rate of maternal temperature rise. Woodside, Pelchat and Leon (1980) also showed that artificially raising maternal temperature curtailed nest bout duration.

Moreover, heavy dams, or those with large litters also showed shorter nest bouts, presumably because the huddle formed by these dams and litters has a lower surface area to mass ratio than those formed by small dams and their litters or dams with small litters (Croskerry, 1975).

Leon et al. (1978) note that an increase in maternal temperature is not necessarily the only factor influencing the termination of nest bouts. Hunger, thirst and the need to eliminate on the part of the dam are other probable factors which may serve to limit nest bout duration. The dam's thermal state, however, becomes an increasingly important factor over the first two weeks postpartum. Woodside et al. (1980) found that, on average, only approximately 20% of nest bout terminations are accompanied by a rise in maternal temperature on Day 4 postpartum; by Day 10 postpartum, however, over 90% of nest bout terminations are accompanied by a rise in maternal temperature.

Dams are particularly sensitive to the acute thermal effects of huddling with their offspring because their heat production is chronically elevated, and this elevation is enhanced over the course of lactation. The chronically elevated maternal temperature, coupled with the additional acute increase in heat retention when a dam joins the huddle, causes the dam to experience a further increase in maternal heat load that cannot be diminished by autonomic thermoregulatory mechanisms alone. Maternal temperature rises further, and only the behaviour of nest bout termination halts the rise in maternal temperature. As mothers proceed through lactation, they become more

and more vulnerable to the consequences of an acute increase in heat load. Jans, Marlatt and Leon (unpublished observations; see Appendix A) found that dams had consistently higher temperatures on Day 10 than on Day 4 of lactation, and, in turn, had consistently higher temperatures on Day 4 than when not lactating. Further, when exposed to a warm ambient temperature (28°C), the dams showed the largest rise in temperature on Day 10 postpartum.

Not only does temperature have a potent effect on the moment-by-moment mother-litter interaction, it also has important consequences for the survival of the young at extreme temperatures. Pennycuik (1964) showed that if dams and their litters were maintained at an ambient temperature of 34°C , the dams abandoned their litters. Further, at 16°C , if dams were not given access to nest material, then their young could not survive in spite of a considerable increase in mother-litter contact (Menich and Leon, unpublished observations).

A problem that arises because of the laboratory oriented nature of previous studies is that rat dams, when given the opportunity, may avoid the thermal limitation of their nest bouts by placing themselves in an area cool enough to preclude an acute rise in maternal temperature. Perhaps, if the dams were given a choice in the laboratory, they would place their pups on a cool, as opposed to a warm surface, and thus would be less likely to experience an acute rise in temperature and consequently could spend more time with their litters. Indeed, if dams are forced to care for cool pups or nest in a cool ambience they do not experience an acute rise in body temperature and do not have thermally limited bouts with their young (Leon et al., 1978).

Evidence from several previous investigations indicate that dams employ various behavioral strategies which potentially modify the thermal environment. For example, Sturman-Hulbe and Stone (1929) placed heaters near established nests and found that dams transported their pups to a new location. Further, Kinder (1927) presented dams with nest material and measured the quality of nests built in various ambient temperatures. She found that dams used similar quantities of nest material in all ambiances. Nests built in a warm ambience (approximately 27°C), however, were typically only a loose ring of material around the pups, while nests in cooler ambiances were invariably larger and fully enclosed.

Dams also alter the quality of their nests throughout lactation (Rosenblatt and Lehrman, 1963; Brewster, 1978). That is, dams initially build a well-constructed, completely enclosed nest. As the pups develop, however, the dam gradually breaks down the walls of the nest, so that by the end of the second week of lactation, the nest is merely an open bowl. Thus, as lactation progresses and the dam becomes more likely to experience an elevation of temperature during a nest bout, she also removes a source of heat insulation by breaking down the nest (Rosenblatt and Lehrman, 1963; Brewster, 1978).

Given 1) that the temperature (whether in terms of ambience or in terms of how warm the pups are maintained) at which dams nest influences the amount of time which the dam can spend with the pups and may also influence not only the growth rate but also the survival of the young; and 2) that dams employ various behavioural strategies to modify the thermal environment, a crucial point in the analysis of

mother-young interaction in this species is to determine the temperature at which dams choose to locate their nests. The first series of studies in this investigation focusses on this problem.

In a second group of studies, the influence of the choice of nest site temperature on the pattern of mother-young contact is determined, and in the third section factors relating to the role of the pups in the initiation and maintenance of nest bouts under these conditions is assessed.

Experiment 1

Mother rats could circumvent the thermal limitation on the amount of time that they can spend with their pups by choosing an environment which is cool enough to preclude a rise in body temperature when with their pups. If that were the case, then thermal considerations would not be a primary determinant of mother-young contact under most conditions. If, to the contrary, dams preferred to be in an area that is warm enough to ensure that their temperature reliably rises upon contact with the young, then one could conclude that temperature could play an important role in the determination of maternal contact time. I therefore tested dams for their temperature preference on a thermal gradient. Since the effective temperature that dams experience will be dependent on whether or not they have an insulating nest around them, I allowed dams to choose their preferred temperature either with or without nest material present. Dams were tested on Day 4 postpartum and Day 10 postpartum to determine whether their thermal preference changes over the course of lactation.

The response of these dams was also compared to that of non-lactating females to determine whether the thermal "set point" of female rats changes when they are lactating. The thermal set point is a body temperature that is defended behaviourally and physiologically by the animal. Since dams have chronically elevated body temperatures, it is possible that their thermal set point is also elevated. If that

were the case, then dams would prefer the same or higher temperatures than non-lactating females. If, on the other hand, the thermal set point of dams is unchanged, then one would expect dams to prefer temperatures on the thermocline lower than those preferred by non-lactating female rats because a low temperature would allow the dams to lose heat and thereby lower their body temperature.

Method

Subjects

Sixteen nonlactating and 32 lactating Wistar rats served as subjects in this experiment. Subjects were allocated to one of 6 independent groups of 8 in a 2 x 3 design: nest material vs no nest material x Day 4 postpartum vs Day 10 postpartum vs nonlactating.

Apparatus

All subjects were tested on a thermocline, which had the appearance of a long enclosed runway (166 cm x 16 cm x 14 cm) with a 0.6 cm (1/4 in) thick copper floor. Holes (0.7 cm diameter) in the clear Plexiglas lid allowed access for thermometers to measure floor temperature. An electric heating coil was attached to the copper floor, at one end, and the other end was submerged in an ice bath. Fluctuations in temperature were kept to a minimum by periodically adding ice to the bath. The temperature ranged from a mean of 11.66°C (standard error = 0.61) at the cold end to 32.44°C (standard error = 0.07) at the warm end.

The thermocline was divided by aluminum plates along the long axis into four equal compartments (41.5 cm x 16 cm x 14 cm). The rats

could easily pass between compartments through a 5.7 cm diameter hole in each of the dividers. Purina lab chow and water were available at all times in each compartment. Nest material was available to half of the subjects; sixteen strips of newspaper (58.4 cm x approximately 3.2 cm) were placed in each compartment when appropriate. The mean weight of the nest material was 60.53 g (standard error = 0.35).

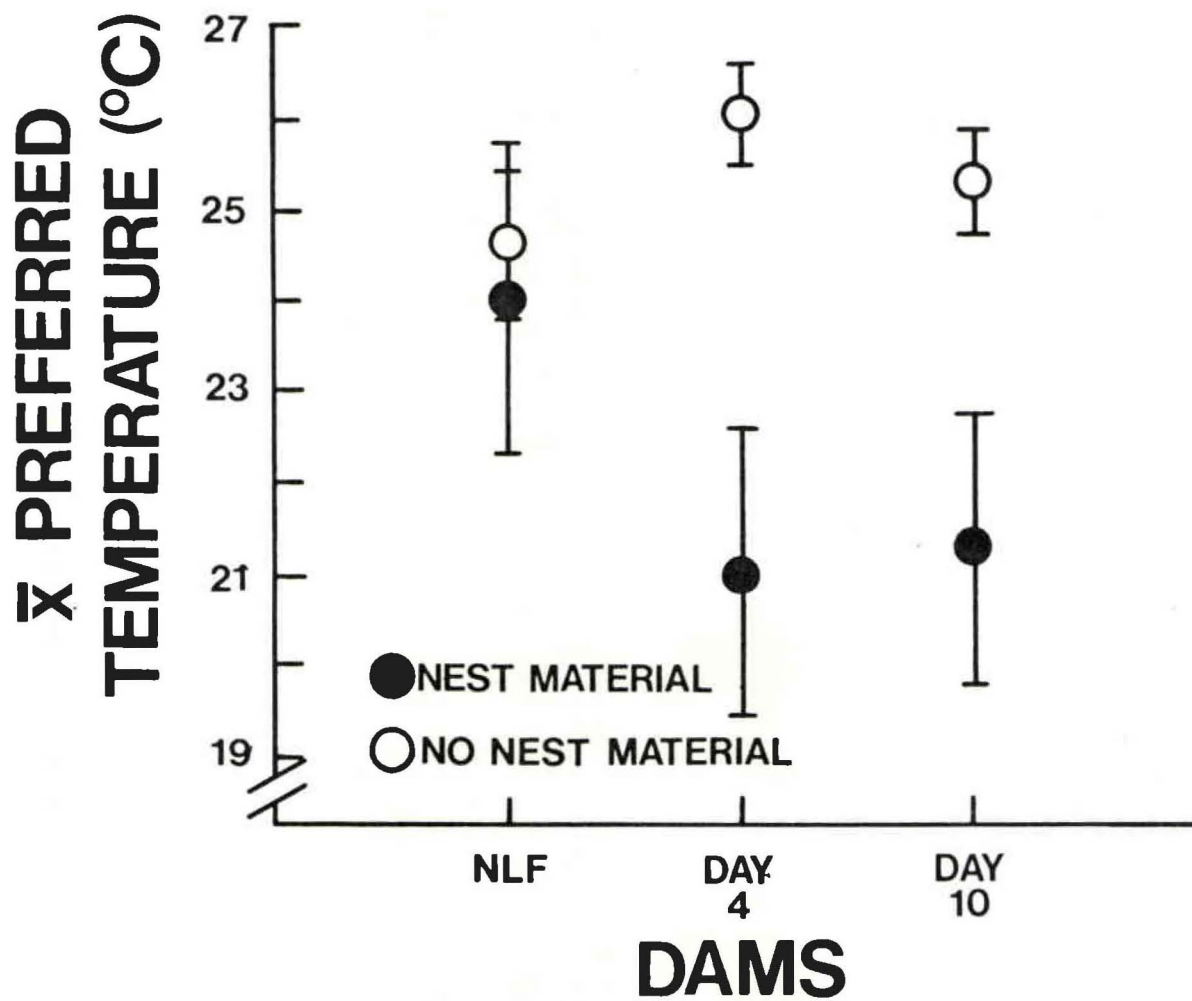
Procedure

The rats were tested individually for a three hour period. On the day of testing, food, water, and nest material (if applicable) were placed in the thermocline and the two extreme temperatures were recorded. The rat was then placed in one end of the thermocline and observed occasionally during the test period. The extreme temperatures were monitored throughout the three hour period. Almost all of the rats settled in a particular spot within one hour, and all were settled within two hours. After three hours the rat was removed and the floor temperature at which she had settled was recorded. The apparatus was thoroughly cleaned with warm water before the next animal was tested.

Results

The mean temperatures chosen by dams are shown in Figure 1. There was no statistically significant difference among the mean temperatures at which the three types of female settled ($F < 1.0$; $df = 2,42$; $p > .05$). The presence or absence of nest material, however, clearly reduced the temperature at which the females settled ($F = 10.35$; $df = 1,42$; $p < .01$). Although this effect was more obvious in the lactating groups, the interaction between type of female and the

Figure 1: Average chosen surface temperatures of nonlactating, Day 4 postpartum, and Day 10 postpartum female rats as a function of whether nest material was present or not. Symbols represent the mean temperature choices and bars represent the standard errors of the means.



presence of nest material was nonsignificant ($F = 1.78$; $df = 2,42$; $p > .05$).

Discussion

The results indicate that lactating rats, regardless of the stage of lactation, chose to sit at a temperature between 24° and 26°C , a temperature well within the range that would force up their body temperature when they come into contact with their young. It therefore appears that nest bout duration would normally be thermally limited if, in fact, dams choose to place their pups at such a temperature. These data also suggest that mother rats have an elevated thermal set point relative to their nonlactating counterparts, since the dams did not move to a cool area.

The presence of nest material substantially altered the lactating dams' choices in terms of both average choice and variability of choices, while the nonlactating group was not influenced by the nesting material to the same extent. All of the rats, whether lactating or not, with the exception of two nonlactating females that were in a cool area, matted their nest material and did not actually build nests, but it seems likely that the insulating nest material effectively raised the temperature at which they stayed.

Experiment 2

No pups were present in the previous experiment and it seemed possible that the added ability of lactating rats to conserve heat that would be afforded by pup contact might provoke them to move to a cooler area than if the pups were absent. I therefore determined the possibility that the pups could alter the preferred temperature of lactating rats. Gelineo and Gelineo (1952) had previously found that most rat dams placed their pups in nests built in a relatively cool environment (14.5 - 18.5°C). There are, however, at least two problems with their study. First, food and nest material were available only in one section of the apparatus and most of the rats chose to build their nests in that section. Second, several females were placed in the apparatus at one time, and typically nested close to one another. Nesting close together conserves heat and could have raised the effective temperature at which they stayed. The present experiment eliminated these two problems.

Method

Subjects

Sixteen Day 4 postpartum and 16 Day 10 postpartum lactating rats and their litters served as subjects in this experiment. Litters were routinely reduced to eight pups on the day of birth. Subjects were allocated to one of 4 independent groups of 8 in a 2 x 2 design:

nest material vs no nest material x Day 4 postpartum vs Day 10 postpartum.

Procedure

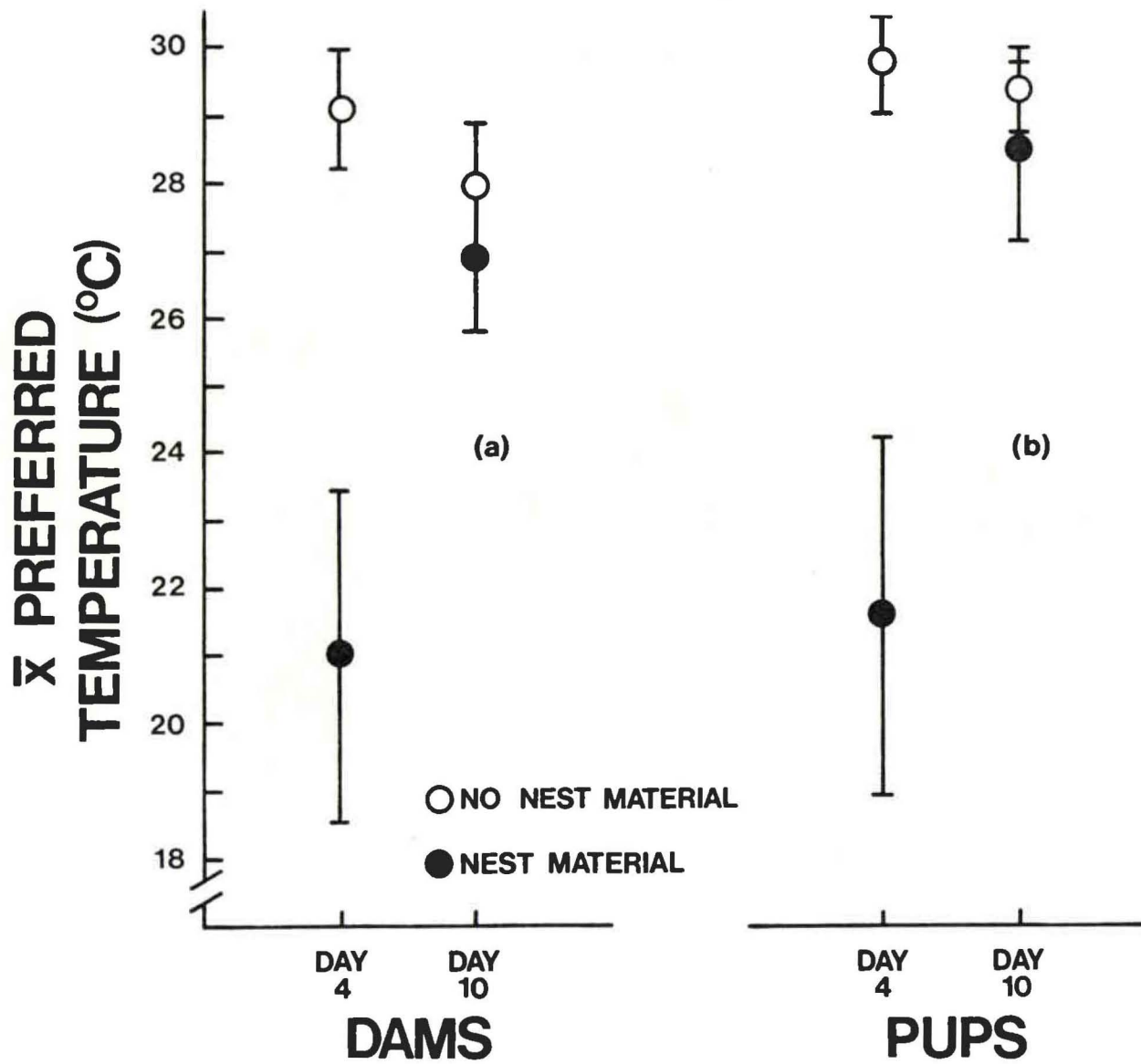
Tests took place in the same thermocline and with the same procedure described in Experiment 1 except that the pups were introduced into the apparatus with the mother. If the dams settled at a temperature different from the temperature at which she placed the pups, both temperatures were recorded. Again, almost all rats settled in a spot within 1 hour and all were settled within two hours.

Results

The mean chosen temperatures of the dams are shown in Figure 2a. As in Experiment 1, there was no statistically significant difference between the preferred temperatures of dams over the course of lactation ($F = 2.61$; $df = 1,28$; $p > .05$). The presence of nest material again reduced the temperature at which the females settled ($F = 9.63$; $df = 1,28$; $p < .01$). Nest material in this situation, however, affected the two groups differentially (Days x Nest material Interaction, $F = 5.65$; $df = 1,28$; $p < .05$).

The mean temperatures at which the pups were placed are shown in Figure 2b. In all cases the mean temperature at which the pups were placed was slightly higher than the mean temperature at which the dams chose to settle. There was a significant main effect for the age of the pups ($F = 4.28$; $df = 1,28$; $p < .05$); specifically, Day 10 pups were usually placed on a warmer surface than were Day 4 pups. Nest material reduced the temperature at which pups were placed ($F = 8.32$; $df = 1,28$;

Figure 2: Average chosen surface temperatures of Day 4 postpartum and Day 10 postpartum female rats (a) and average surface temperatures at which pups were placed by Day 4 postpartum and Day 10 postpartum female rats (b) as a function of whether nest material was available or not. Symbols represent the mean temperatures and bars represent the standard errors of the means.



$p < .01$), and affected the two groups differentially (Days postpartum x Nest material interaction: $F = 5.35$; $df = 1,28$; $p < .05$).

The presence of nest material produced two differences between the Day 4 and Day 10 dams, as is shown in Table 1. First, the Day 4 dams were slightly more likely to build a nest (i.e., 5 of 8 Day 4 dams built nests while 3 of 8 Day 10 dams built nests), and second, all of the Day 4 dams that built nests did so on cooler surfaces than the Day 10 dams that built nests.

Discussion

As in Experiment 1, the dams showed fairly consistent temperature preferences. When nest material was not present dams chose to settle between 25.2°C and 33.0°C , and nine of the 16 rats chose temperatures in the more restricted range of $28 - 32^{\circ}\text{C}$. Recall that the majority of dams without pups in Experiment 1 chose to stay at temperatures within a $24 - 26^{\circ}\text{C}$ range. In the present experiment, mothers continued to stay in warm areas and placed their pups in even warmer areas. These data clearly show that the pups did not induce their mothers to move to a cooler area for their interaction.

When nest material was available in the present experiment, the average temperature choice and the variability of choices were again affected, due to the fact that some dams used the nest material while others did not. When Day 10 dams did not build a nest they behaved similarly to the Day 4 dams that did not build nests; they placed their pups on a warm surface. For both groups, building an insulating nest apparently allowed the dams to care for the young in a cool

Table 1

Numbers in table refer to temperatures at which dams settled dependent upon whether the dams built nests or not. Data from Experiment 2; pups and nest material present.

	Days Postpartum	
	Day 4	Day 10
Constructed a nest	13.3°C	21.7°C
	15.2	23.6
	16.1	29.0
	17.0	
	20.0	
Ignored nest material	24.5°C	25.7°C*
	29.8	26.6 *
	31.6	27.3 *
		30.3
		30.9

*Indicates dams placed pups on a warmer surface, but settled themselves on the temperature indicated in the Table.

temperature, though the temperatures chosen by the Day 10 dams were not as cool as those chosen by the Day 4 dams. It is of interest to note here that the Day 4 nests had high walls and were fully enclosed, while the Day 10 nests were bowl-shaped with low walls and open at the top. The Day 10 females presumably had less insulation with such nests and the effective temperature at which they sat may have been comparable to Day 4 dams.

Considering the results of both Experiments 1 and 2 then, most of the dams in the present experiment placed their pups on a surface that was actually warmer than the surface upon which the dams themselves chose to settle. Even when nest material was available, half of the dams ignored the nest material and placed their pups on a warm surface. Of the eight dams that built nests, seven located their nests on a surface which was cooler than the surface upon which the dams in Experiment 1 chose to settle. Because the nest insulates the pups from the surrounding environment (King, 1963), dams that build nests may, in fact, be placing their pups in a warm area (at least warmer than the actual floor surface area). By simply measuring the temperatures of pups kept in a nest in a cold environment, it should be possible to determine whether dams that choose to build a nest on a cold surface are, in fact, creating a warm thermal environment for their young.

Experiment 3

In the previous experiment, dams given a choice of temperatures at which to place their pups either put the litter on a warm surface or built a nest at a somewhat lower temperature and then placed the young in the nest. It is possible that the latter group were avoiding the thermal consequences of huddling with their young by placing them in a cool thermal environment. Alternatively, the insulating properties of the nest might be such that although ostensibly at a cool temperature, these dams provided their young with a thermal environment warm enough to make the dams vulnerable to the acute thermal effects of huddling with them. These possibilities were investigated in the present experiment by exposing dams with litters and nest material to a somewhat more complete cool environment (air, rather than just floor, temperature was lowered) and the effective temperature at which dams came in contact with their pups was determined.

Method

Subjects

Twelve lactating Wistar rats and their litters, routinely reduced to eight pups at birth, served as subjects.

Apparatus

Dams and pups were left in their home cages (constructed of polypropolyne; inside dimensions: 35.6 cm x 31.1 cm x 16.5 cm) and given the same amount of nest material as the dams in Experiment 2.

The cages were placed in an environmental chamber (GPI, Inc.) maintained at 16°C and 50% relative humidity. This temperature was chosen because it closely approximates the mean temperature chosen by the 5 Day 4 postpartum dams that built nests in Experiment 2. Pup temperatures were measured with a YSI telethermometer (model 43 TA), using probe #403.

Procedure

Six dams and their litters were tested on Day 4 and 6 were tested on Day 10 postpartum. Dams and litters were placed in the environmental chamber on the day prior to testing to allow the dams to habituate to the new environment and to build nests.

The first step in the testing procedure was to carefully take apart the nest. Four pups were then removed and their skin temperatures quickly measured as a reflection of the effective nest temperature. As it was, the first temperature was always representative of the remaining pup temperatures.

Results

The mean pup skin temperature for the Day 4 pups was 34.15°C (standard error = 0.21), and 33.74°C (standard error = 0.11) for the Day 10 pups. Although the Day 10 pups were slightly cooler, there was no statistically significant difference between the groups ($t = 1.71$; $df = 10$; $p > .05$).

There was little apparent difference between the groups in the type of nest constructed. All of the Day 4 nests were tightly constructed and fully enclosed. The Day 10 nests were as well

constructed as Day 4 nests, except that one nest was not covered at all, and another was only loosely constructed.

Discussion

The pup temperature data indicate that the effective temperature at which mother-young contact takes place, even in a cool ambience, is relatively warm; warm enough, in fact, to virtually guarantee that the temperature of the dam will rise acutely when she comes in contact with the pups (Leon et al., 1978), thus limiting the duration of her nest bouts by a thermal mechanism.

Summary and Discussion of Section I

Without nest material or pups, most lactating dams chose a floor temperature between 24 and 26°C, a choice similar to that of nonlactating rats. Given that lactating rats have higher body temperatures than nonlactating rats, the fact that they did not seek out a cool area suggests that dams have an elevated thermal set point.

Adding nest material to the temperature choice situation disrupted the consistency of temperature choices. This was because several dams matted the nest material over the floor surface and thereby insulated themselves from the floor temperature. Thus, although these data may not provide further information as to the surface temperature preference of dams, they do at least indicate that the dams do not consistently choose a particular position. That is, it might be argued that the dams with no nest material consistently settled between 24°C and 26°C merely because there was some feature other than temperature which attracted the dams. If this were the case, it would be expected that the dams with nest material would choose the same location; they did not.

In Experiment 2, it was shown that when no nest material was available, all dams placed their pups on a warmer surface than the dams themselves prefer. Even when nest material was available, half of the dams failed to build nests and showed the same behaviour as animals with no nest material. Further, the dams that chose a cool temperature also built nests. In Experiment 3, it was shown that the nest serves to maintain the pups at a warm temperature, even in a cool ambience.

It seems reasonable to suggest, then, that the dams do not attempt to avoid a thermal limitation of the duration of their nest bouts. Although this statement is equally true for the Day 4 dams, the evidence is perhaps more striking for the Day 10 dams, since 90% of all nest bout terminations are accompanied by a rise in maternal temperature on Day 10 postpartum (Woodside et al., 1980).

Section II

Experiment 4

Limiting the amount of time that a dam spends with the pups during any individual nest bout does not necessarily mean that the dam limits the total amount of contact that she has with the pups. The dam could also limit the amount of time that she spends away from the pups and increase the number of nest bouts that she initiates.

Dams with warmed pups have been shown to have shorter, but more frequent, nest bouts than dams with normal pups (Leon et al., 1978). In this case, there was no difference in the total amount of mother-litter contact over a 24 hr period between the dams with warmed pups and the dams with normal pups. Thus, dams with warmed pups must have spent, on average, less time away from their pups between nest bouts.

Again, however, the point can be raised that both experimental and control dams in the Leon et al. (1978) study were restricted in terms of choosing, not only a nesting temperature, but also the temperature at which they stayed between nest bouts. That the temperature experienced by dams between nest bouts may be an important consideration is suggested by the fact that the majority of dams in Experiment 1 showed a clear and consistent temperature preference (24 - 26°C). Further, in Experiment 2, several of the dams that placed their pups at the warm end of the thermocline actually settled down between 24°C and 27°C themselves.

In all previous experiments on nesting behaviour, dams were not able to choose a temperature at which to stay between nest bouts (i.e. during IBIs). If the duration of the IBI is dependent on the rate at which the body temperature of dams declines, then the temperature at which dams stay during that time will, in large measure, determine their rate of heat loss and temperature decline. Dams may, therefore, be able to alter the rate of heat loss during the IBI, alter the duration of that interval, and thereby increase or decrease both the number of nest bouts and the total daily nest time.

In the present experiment, the nesting behaviour and behaviour during IBIs of dams free to choose temperatures along a thermal gradient were measured over a 24 hr period. If dams minimize the time during IBIs, they would be expected to go to a cool area in order to lose heat and be able to return quickly to the pups.

Method

Subjects

Twelve Day 10 postpartum rats with litters, routinely reduced to 8 pups at birth, served as subjects.

Procedure

Subjects were tested on the thermocline, described in Experiment 1, over a 24 hr period. Purina lab chow and water were available in each of the 4 compartments of the thermocline, but no nest material was available.

To monitor the movements of the dams, 20 photocells were mounted 4.5 cm from the floor and spaced 7.0 cm apart along the long

axis of the thermocline. The photocells were connected to a 20 pen Esterline-Angus chart recorder, so that breaking a photocell beam deflected one of the pens. The dams' movements during the test period were then transcribed from the Esterline-Angus chart and analyzed.

From the transcription of the Esterline-Angus data, it was possible to determine the total duration of mother-litter contact, nest bout durations, nest bout frequency, IBI durations, the amount of time spent in the various sections of the thermocline, and the movements of the dams during IBIs.

The subjects were divided into two groups of 6. For the Experimental group, the thermocline was operative, so that the floor temperature varied from, on average, 11.6°C (standard error = 0.13) to 32.12°C (standard error = 0.17). With no nest material the dams in the Experimental group were expected to (and actually did) locate their nests at the warm end of the thermocline, as in Experiment 2. During IBIs, then, dams could select from a wide range of temperatures.

In order to assess whether the Experimental dams were responding to the temperature gradient, or whether they were responding to some other aspect of the situation, the thermocline was not operative for the Control group. The floor temperature over the entire thermocline for the Control group approximated room temperature, with a mean of 22.48°C (standard error = 0.16). A small (16 cm x 10 cm) piece of black construction paper was placed over what would have been the warm end of the thermocline had the thermocline been operative. This induced the Control dams to nest in the same location as the

Experimental dams, and thus the two groups had the same area to select from during IBIs.

For convenience, the warm end of the thermocline, or what would have been the warm area (for the Control group), will be referred to hereafter as the "nest area." Further, the four sections of the thermocline will be referred to as Sections 1 through 4, with Section 1 being the coolest section and Section 4 the warmest. Thus the nest area is located in Section 4.

Dams and their pups were placed at the center of the thermocline, with half of the subjects in each of the two groups being placed on either side of the divider between Sections 2 and 3. This allowed the dams to choose a site for nest location. All dams moved their pups to the nest area within two hours, save one, and that one did so after three and one half hours. Analysis of the data began one hour after the dams had moved all of their pups to the nest area.

Dams and pups were removed 24 hr after being introduced to the thermocline. Because the dams varied in the amount of time before they moved their pups, the total time for data collection also varied; the mean time was 1291.42 min (standard error = 16.35).

For all measures, save the total amount of mother-young contact, two separate analyses have been performed. In the first, all nest contacts were included in the analysis, regardless of the duration of the contact. In the second analysis, however, nest contacts of less than 10 min duration were eliminated from the analysis. This division was used following Wakerley and Lincoln's (1971) report that the minimum time between pup attachment to the dam's nipples and milk

ejection is 10 min. Thus, any mother-young contact of less than 10 min duration probably does not constitute an episode in which milk is delivered to the young, and is probably functionally distinct from contacts of 10 min or more.

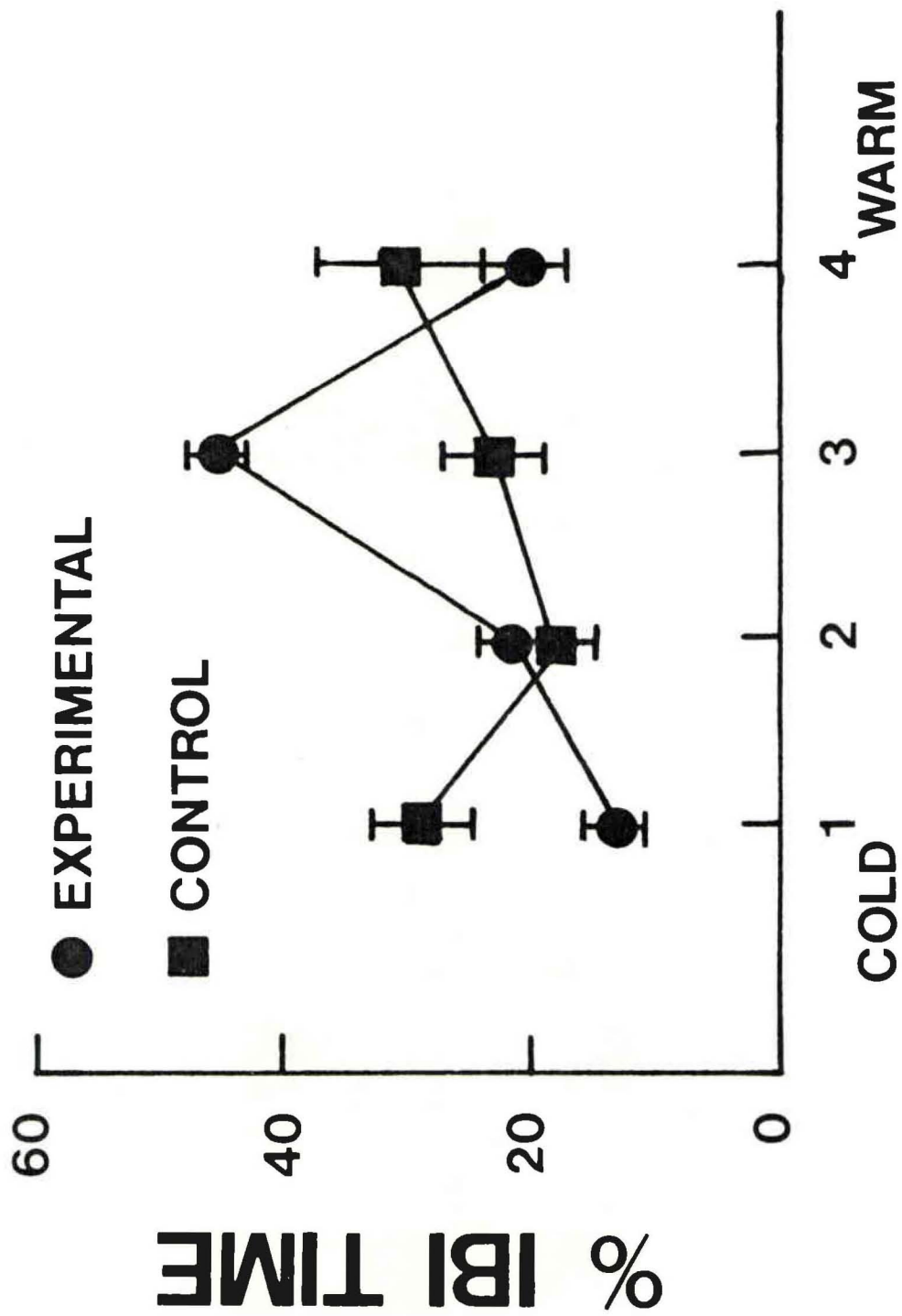
Results

Behaviour during IBIs

The major question of this study concerns whether the Experimental dams have shorter IBIs than the Control dams. Whether they do have shorter IBIs or not, however, it is also important to determine whether the Experimental dams may have adopted a strategy which would minimize the time spent away from the pups. By avoiding warm areas and spending more time in cool areas during IBIs, the Experimental dams should be able to reduce their elevated body temperatures and consequently reduce the duration of IBIs. Relative to the Control dams, then, if the Experimental dams attempt to minimize IBI time, they should spend a greater proportion of IBI time in Section 1 of the thermocline.

The mean proportions of time spent in each of the four sections of the thermocline, when dams were not in contact with the pups, and the associated standard errors of the means are shown for both groups in Figure 3. Winer (1962) has suggested that an arcsin transformation of data expressed as proportions is appropriate, as the means and variances of such data are related. Analysis of the transformed data revealed no main effect for Groups ($F < 1.0$; $df = 1,10$; $p > .10$) and a main effect for Sections ($F = 3.72$; $df = 3,30$; $p < .05$). Most

Figure 3: The percentage of time when not in contact with the pups (IBI time) spent in each of the four sections of the thermocline by Experimental and Control dams. Symbols represent the mean percentages and bars represent the standard errors of the means.



SECTION

important, however, is that the Groups x Sections interaction was significant ($F = 6.57$; $df = 3,30$; $p < .01$), indicating that the two groups differed in their usage of the available area during IBIs. The difference between the two groups was most pronounced in the proportion of IBI time spent in Sections 1 and 3. It was expected that if the Experimental dams attempted to minimize time spent away from the pups, they would spend more time than the Control dams in Section 1. The Experimental dams, in fact, spent much less time than the Control dams in Section 1, however, suggesting that the Experimental dams did not use this means to minimize time away from the pups.

The proportion of IBI time spent in Section 3 by the Experimental dams is about twice that of the Control dams. Further, the Experimental dams spent over twice as much time in Section 3 than in any other section of the thermocline. The temperature range of Section 3 was approximately 21°C to 26°C . Recall that most dams in Experiment 1 of the present investigation settled between 24°C and 26°C . The temperature range preferred by the dams in Experiment 1, then, represents the warmest part of Section 3.

To test whether the Experimental dams in the present study spent an inordinate amount of time in the $24 - 26^{\circ}\text{C}$ range, a comparison of the proportion of time spent in the area comprising the $24 - 26^{\circ}\text{C}$ range was made between the Experimental and Control dams. The Experimental dams spent one-third of their total IBI time in the $24 - 26^{\circ}\text{C}$ range ($\bar{x} \pm \text{S.E.} = 33.33 \pm 4.1\%$). The average for the Control dams, for the same area, was significantly lower ($\bar{x} \pm \text{S.E.} = 10.2 \pm 2.0\%$; $t = 4.66$; $df = 10$; $p < .01$).

To further emphasize the point that the Experimental dams spent a fairly large proportion of their IBI time on a warm surface, the total proportion of IBI time spent on a surface of 22.5°C or warmer (a range of surface temperatures that the Control dams never experienced) was determined and found to be, on average, 60.42% (standard error = 5.34%). Thus, the Experimental dams spent the majority of their IBI time on a surface that was warmer than the Control dams ever experienced.

Although the Experimental dams spent most of their IBI time on a relatively warm surface, they might have either preceded nest bouts or begun IBIs with visits to a cool area. Such behaviour would have increased maternal heat loss and allowed the dams to return to the pups with a curtailed IBI. Therefore, to determine whether the Experimental dams were visiting any particular area of the thermocline either just before or just after nest bouts, chi-square analyses were performed on the data using the position of Control dams before and after nest bouts as expected values. The data were analysed for all nest bouts, regardless of duration, and for nest bouts of at least 10 min duration. As will be seen, both analyses yielded similar results.

Expected values were obtained by first determining the proportion of Control dams' nest bouts which were either preceded or terminated with a visit to each of the sections of the thermocline. These values were then multiplied by the Experimental dams' mean number of nest bouts, yielding an expected value for each section of the thermocline. The percentage of visits to each section following nest bouts, regardless of the duration of the nest bouts, are shown for both

the Experimental and Control groups in Figure 4a. Comparable data for nest bouts of at least 10 min duration are shown in Figure 4b.

There are three features of Figure 4 which deserve attention. First, it is clear that discarding nest bouts of less than 10 min duration had very little effect on the distributions of visits. Second, there is very little apparent difference between the Experimental and Control dams in the proportion of times that they visited each of the sections following a nest bout. The only point at which the groups diverge is in the proportion of times that they visit Section 2 after all nest bouts. The chi-square analyses revealed that the Experimental dams were not likely to visit any particular section more often than the Control dams after nest bouts (all nest bouts: $X^2 = 5.17$; $p > .10$; nest bouts ≥ 10 min: $X^2 = 1.14$; $p > .10$). The third feature of note in Figure 4 is that the Experimental dams showed no particular preference for any section following nest bouts, although they were not very likely to stay in Section 4.

The percentage of visits immediately prior to nest bouts are shown for both groups in Figures 5a and b. Data for all nest bouts, regardless of duration, are shown in Figure 5a and data for nest bouts of at least 10 min duration are shown in Figure 5b. It is clear from Figure 5 that the two groups are very similar in their distributions of visits to sections prior to nest bouts (all nest bouts: $X^2 = 0.39$; $p > .10$; nest bouts ≥ 10 min: $X^2 = 1.14$; $p > .10$). As with the proportion of visits to sections following nest bouts, discarding nest bouts of less than 10 min duration had very little effect on the distributions of visits to sections preceding nest bouts, and neither group showed a

Figure 4: The percentage of nest bouts terminated with a visit to each of the four sections of the thermocline by Experimental and Control dams. (a) illustrates the percentage of visits after all nest bouts and (b) illustrates the percentage of visits after nest bouts of at least 10 min duration. Symbols represent the mean percentages and bars represent the standard errors of the means.

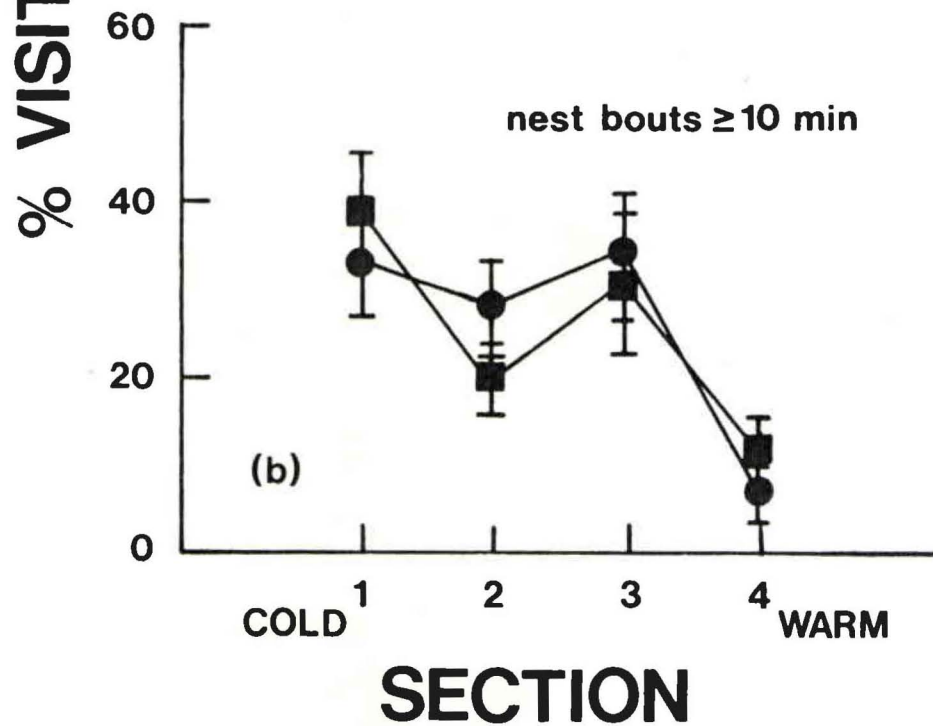
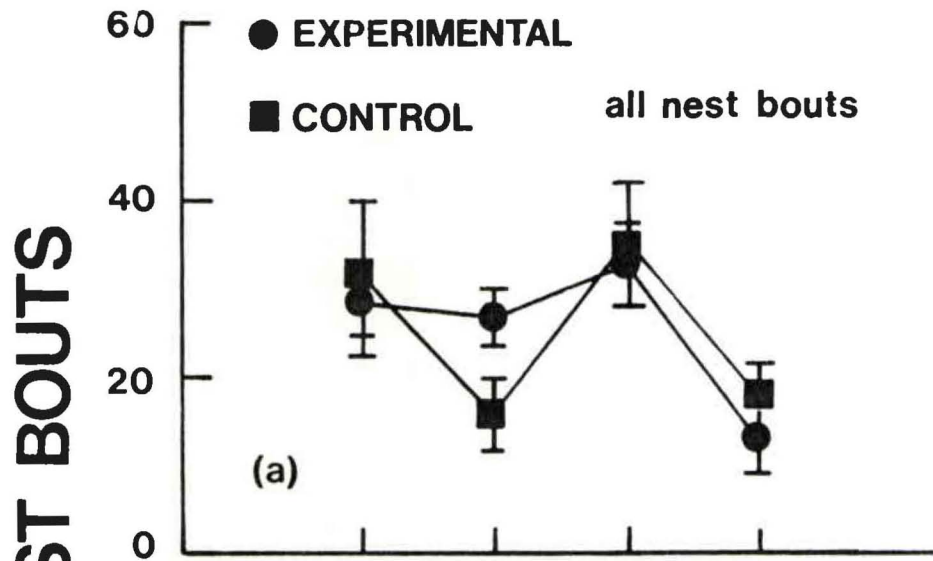
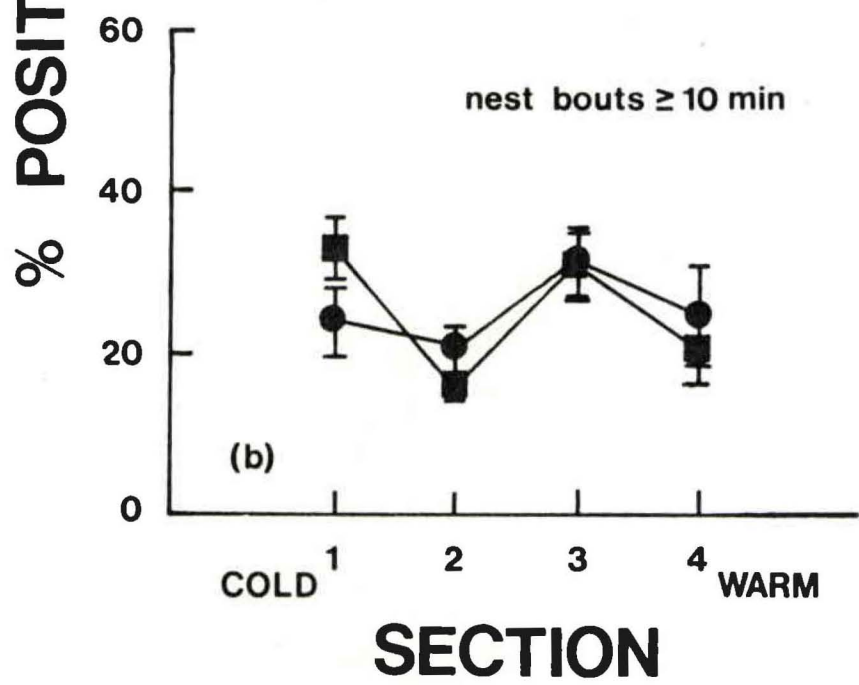
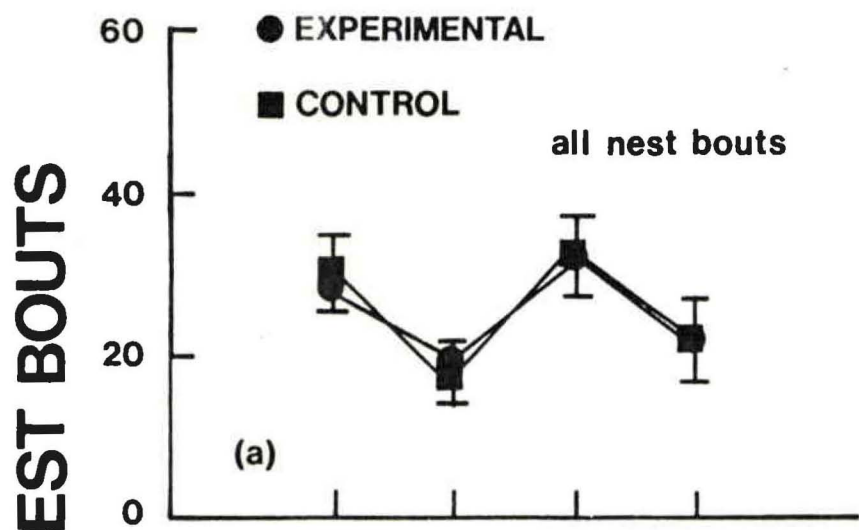


Figure 5: The percentage of nest bouts immediately preceded by a visit to each of the four sections of the thermocline by Experimental and Control dams. (a) illustrates the percentage of visits before all nest bouts and (b) illustrates the percentage of visits before nest bouts of at least 10 min duration. Symbols represent the mean percentages and bars represent the standard errors of the means.



strong tendency to visit any particular section immediately prior to a nest bout.

The above data indicate that the Experimental dams did not attempt to limit IBI durations by visiting the cool section of the thermocline. IBI durations are considered next.

The distributions of IBI durations between all nest bouts are shown for both groups in Figure 6. These distributions are statistically different (Kolmogorov-Smirnov test; $D_{\min} = .150$; $p < .025$; Siegel, 1956; Table M), due primarily to the fact that the Control dams have a higher proportion of IBIs of less than 10 min duration.

When nest contacts of less than 10 min duration are not counted as nest bouts, and are thus included in the measure of IBI duration, the difference between the Experimental and Control groups is magnified. The distributions of IBIs between nest bouts of at least 10 min duration are shown in Figure 7. The difference between these distributions is again statistically significant (Kolmogorov-Smirnov test; $D_{\min} = .256$; $p < .005$); the Experimental dams are more likely to have long IBIs than the Control dams.

The mean IBI durations and the associated standard errors of the means for both groups are shown in Figures 8a and b. Figure 8a shows IBI durations between all nest contacts and Figure 8b shows IBI durations between nest bouts of at least 10 min duration.

When considering IBIs between all nest contacts, the Experimental dams had a slightly longer mean IBI duration than the Control dams, but the difference is not statistically significant ($t =$

Figure 6: The distributions of interbout interval durations between all nest bouts for Experimental and Control dams.

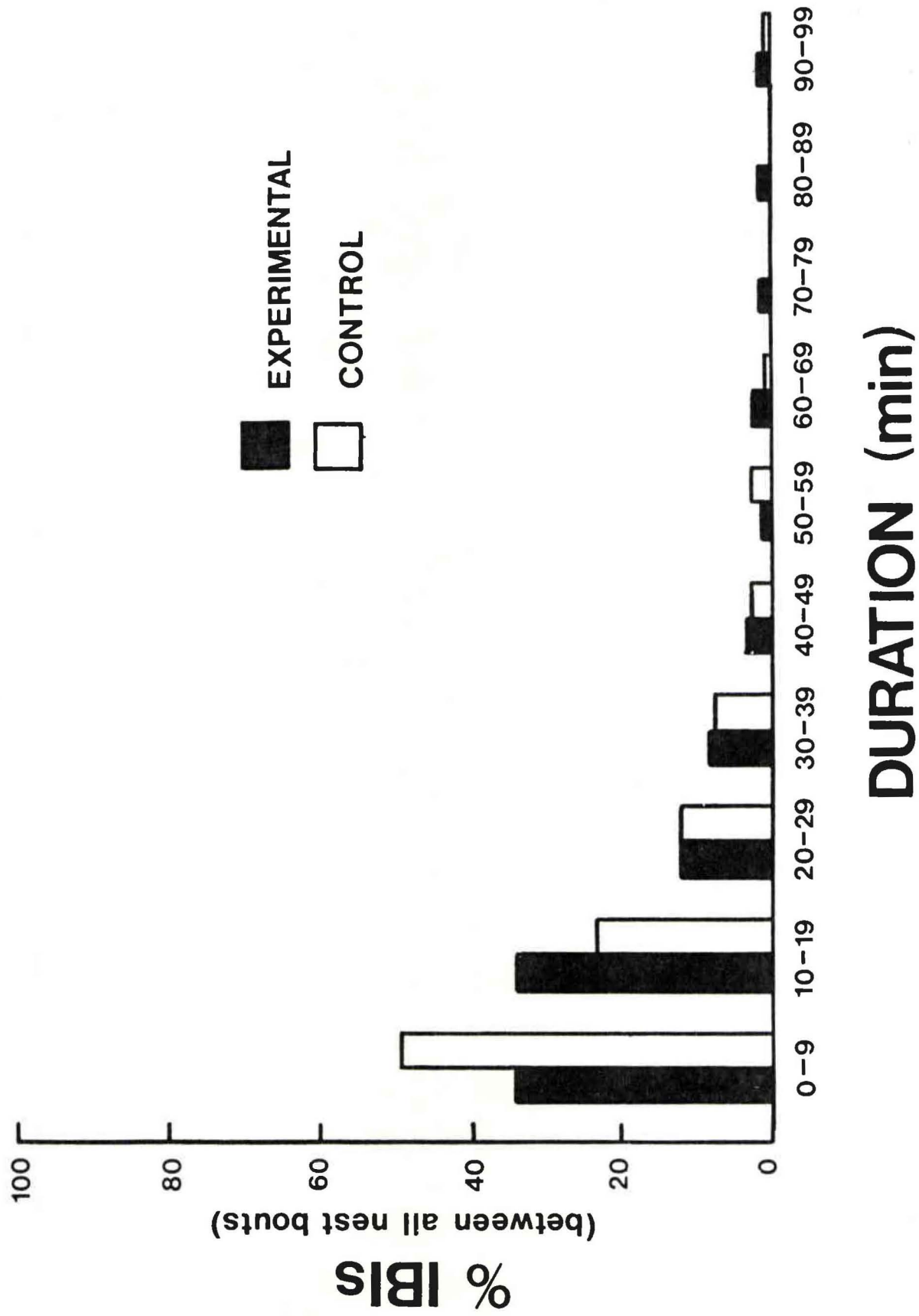


Figure 7: The distributions of interbout interval durations between nest bouts of at least 10 min duration for Experimental and Control dams.

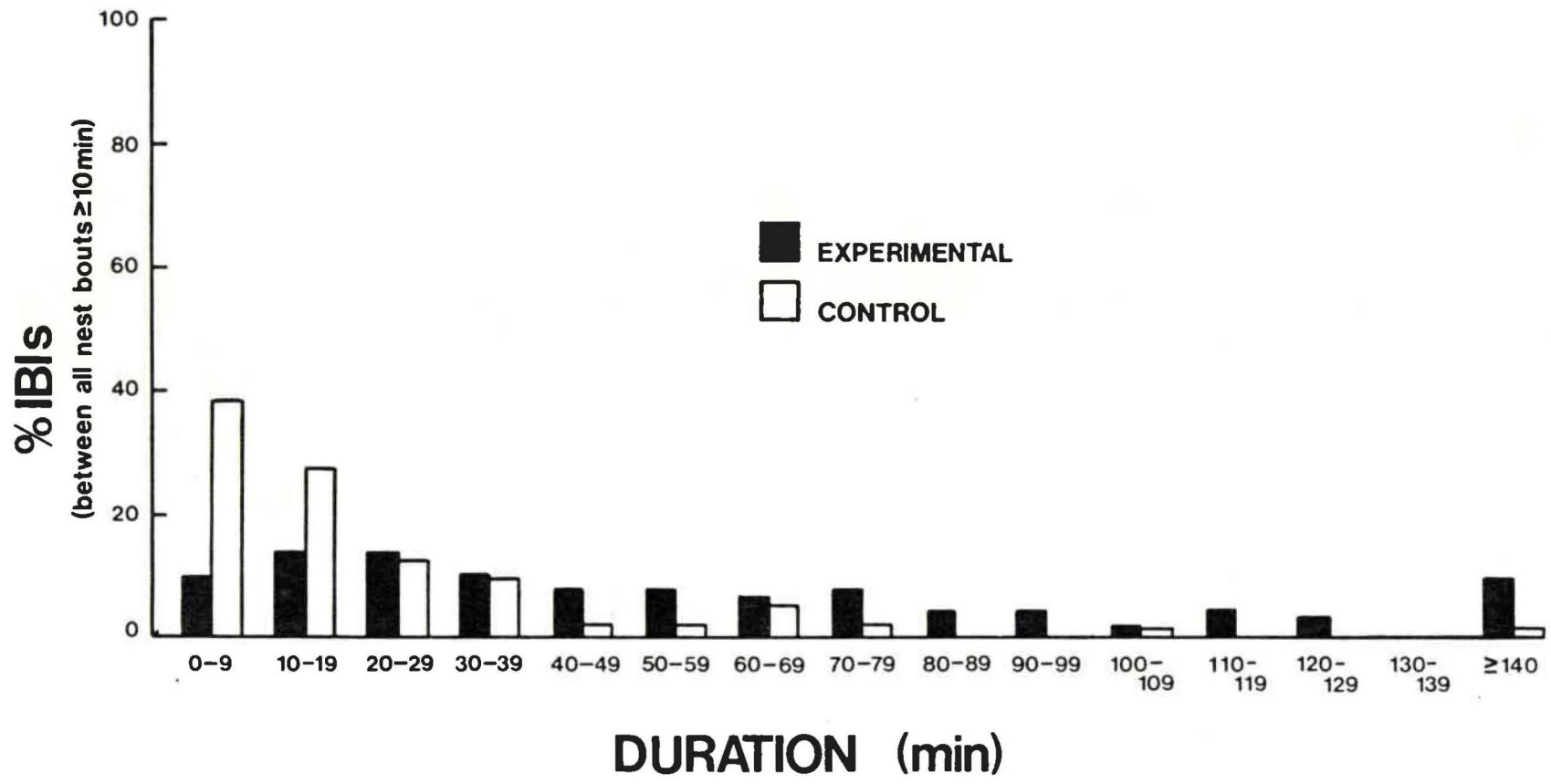
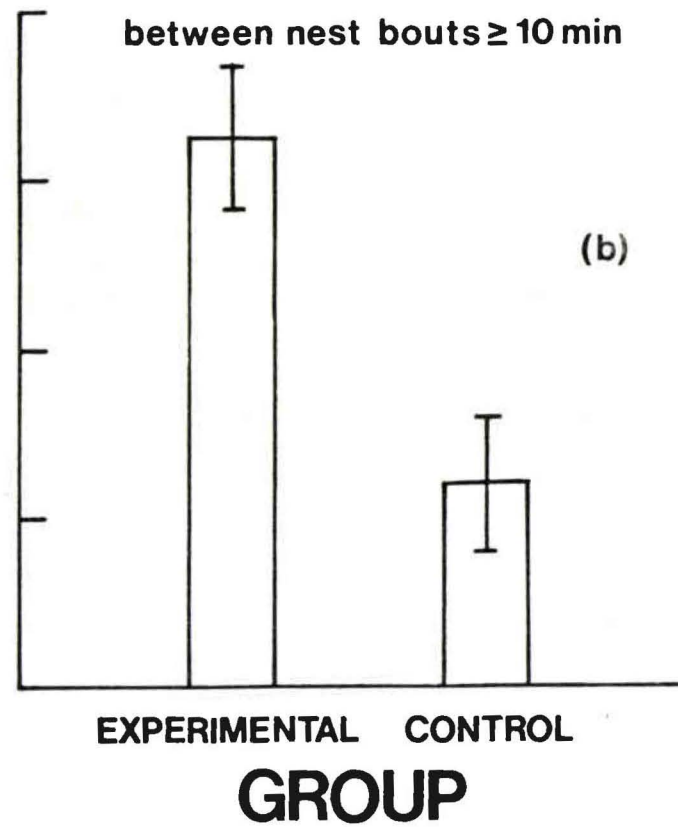
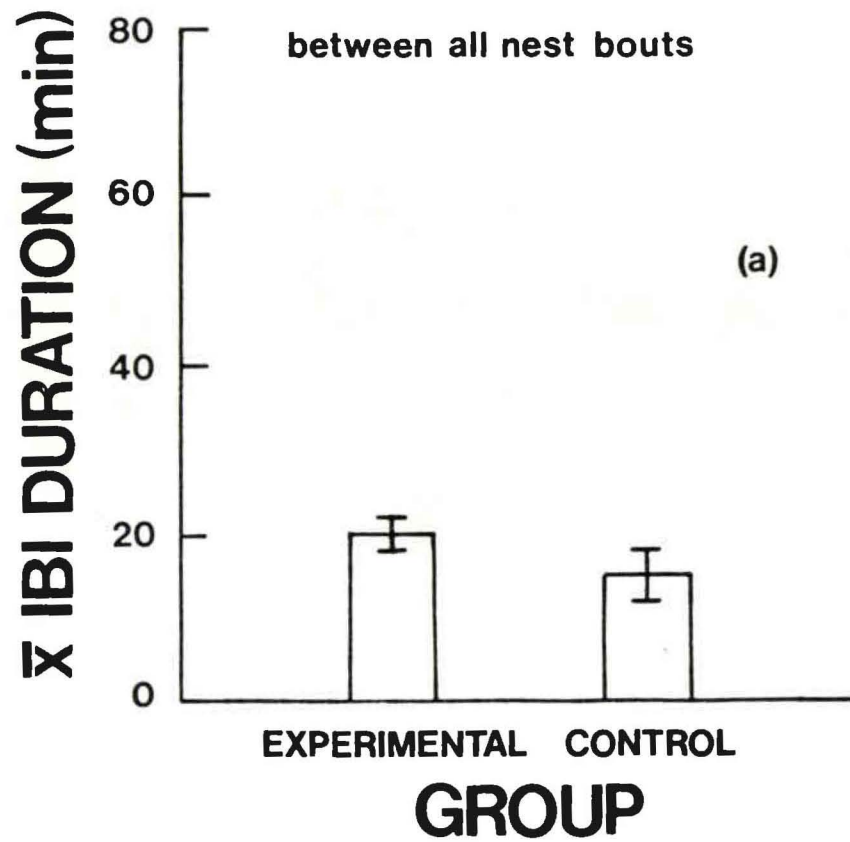


Figure 8: Mean interbout interval durations for Experimental and Control dams. (a) illustrates interbout interval durations between all nest bouts and (b) illustrates interbout intervals between nest bouts of at least 10 min duration. Superimposed bars represent the standard errors of the means.



1.41; $df = 10$; $p > .05$). For nest contacts of at least 10 min duration, however, the mean IBI for the Experimental dams is more than twice as long as the mean for the Control dams ($t = 20.22$; $df = 10$; $p < .01$). Parametric analysis may not be completely appropriate here, as IBI durations are apparently not normally distributed (Figures 6 and 7). Nonparametric analysis, however, reveals similar effects (between all nest bouts $U = 9$; $p = .0898$; between nest bouts ≥ 10 min; $U = 2$; $p = .0043$).

Discussion of IBI behaviour

It is clear that the Experimental dams did not reduce their IBI durations relative to the Control dams. When dams are allowed to choose from a wide range of temperatures during IBIs, they spend very little time on a cool surface and, in fact, seem to prefer a fairly warm surface. From these data it seems evident that the dams do not seek out a cool area during IBIs which might allow them to return to their pups more quickly than if they stay on the relatively warm surface that they prefer. In fact, relative to dams that are not allowed to choose from a range of temperatures during IBIs (the Control dams), the Experimental dams actually spent longer periods of time away from the pups.

There was no indication that either Experimental or Control dams showed a tendency to initiate or terminate a nest bout with a visit to any particular section of the thermocline. In the case of the Experimental dams, at least, these findings suggest that the dams did not use the available temperatures in order to quickly reduce their body temperatures either immediately before or immediately after nest

bouts. These findings also suggest that the dams did not attempt to minimize the amount of time spent away from their pups.

Mother-young contact

Because the total amount of time for which data were collected varied between animals, it was necessary to convert the data to a percentage of the total available time spent with the pups. The mean percentage of mother-litter contact and the associated standard error of the mean for the Experimental and Control groups are shown in Figure 9. As is evident, the Control dams spent twice as much time with their pups as the Experimental dams. The difference was statistically significant ($t = 4.70$; $df = 10$; $p < .01$), although the variance ratio was perhaps too high (5.57). A log transformation however, reduced the ratio to 1.35, and yielded a similar result ($t = 5.03$; $df = 10$; $p < .01$). Further, it should be noted that there was no overlap between the two groups in the percentage of mother-litter contact, such that the largest percentage of contact in the Experimental group was less than the smallest percentage of contact in the Control group.

The distributions of all nest bouts, regardless of duration, for the Experimental and Control groups are shown in Figure 10. The distributions are clearly different, with the Experimental dams showing a stronger tendency toward short nest bout durations (Kolmogorov-Smirnov test; $D_{\min} = 0.165$; $p < .01$). Eliminating nest bouts of less than 10 min reveals similar results, as shown in Figure 11, although the effect is perhaps slightly greater (Kolmogorov-Smirnov test; $D_{\min} = 0.231$; $p < .01$).

Figure 9: Mean percentage of time that Experimental and Control dams spent with their pups. Superimposed bars represent standard errors of the means.

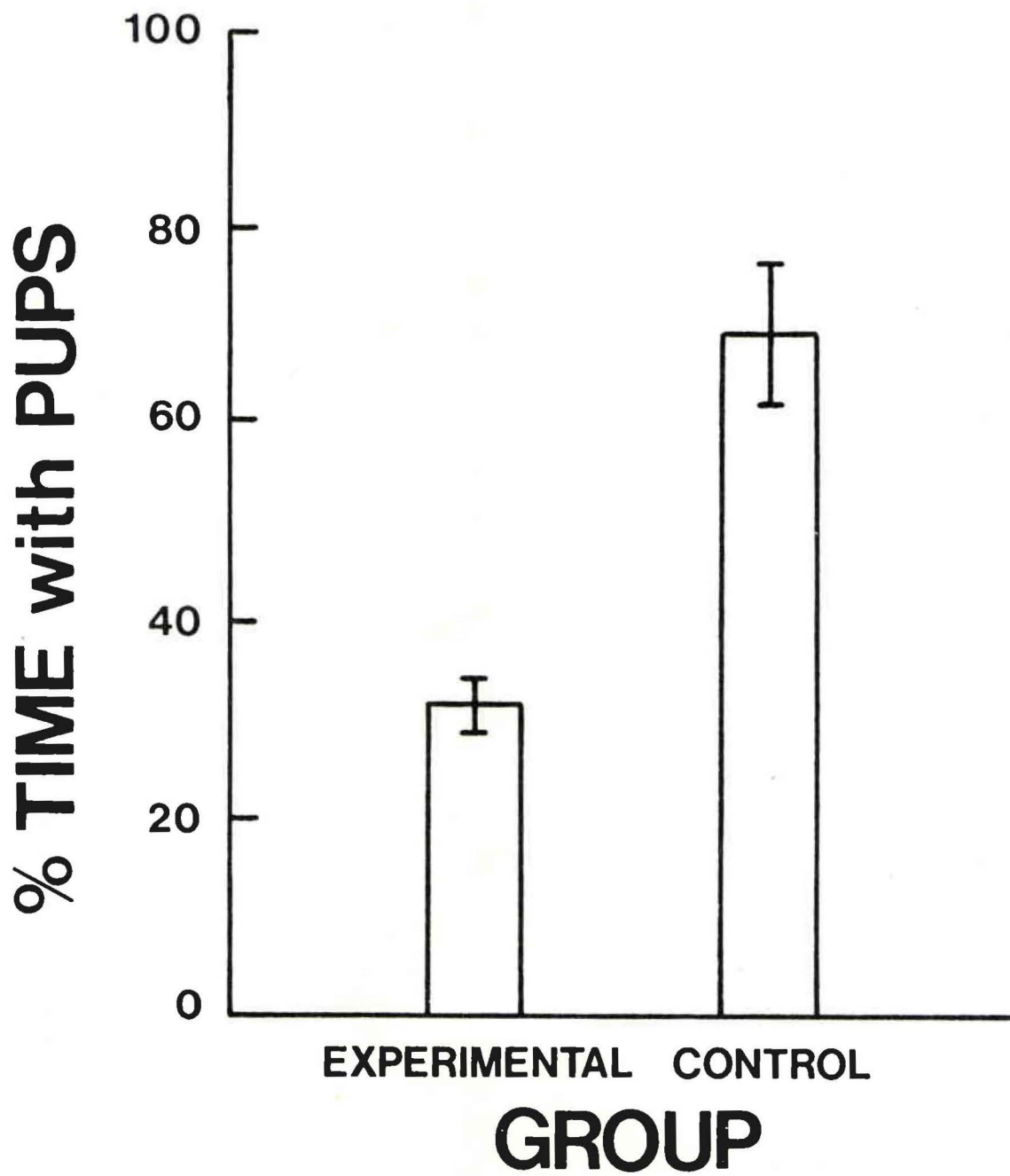


Figure 10: Distributions of all nest bout durations for
Experimental and Control dams.

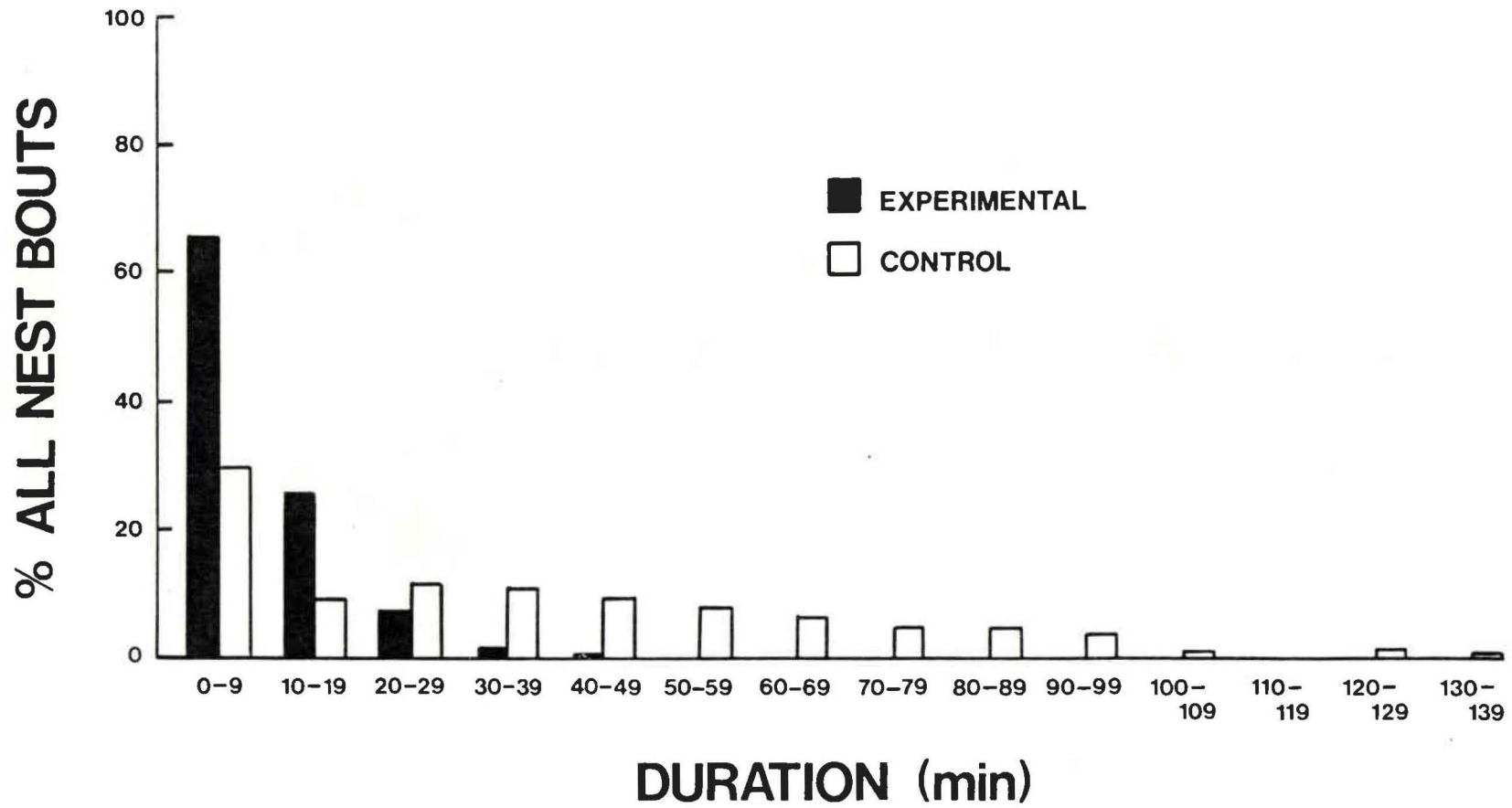
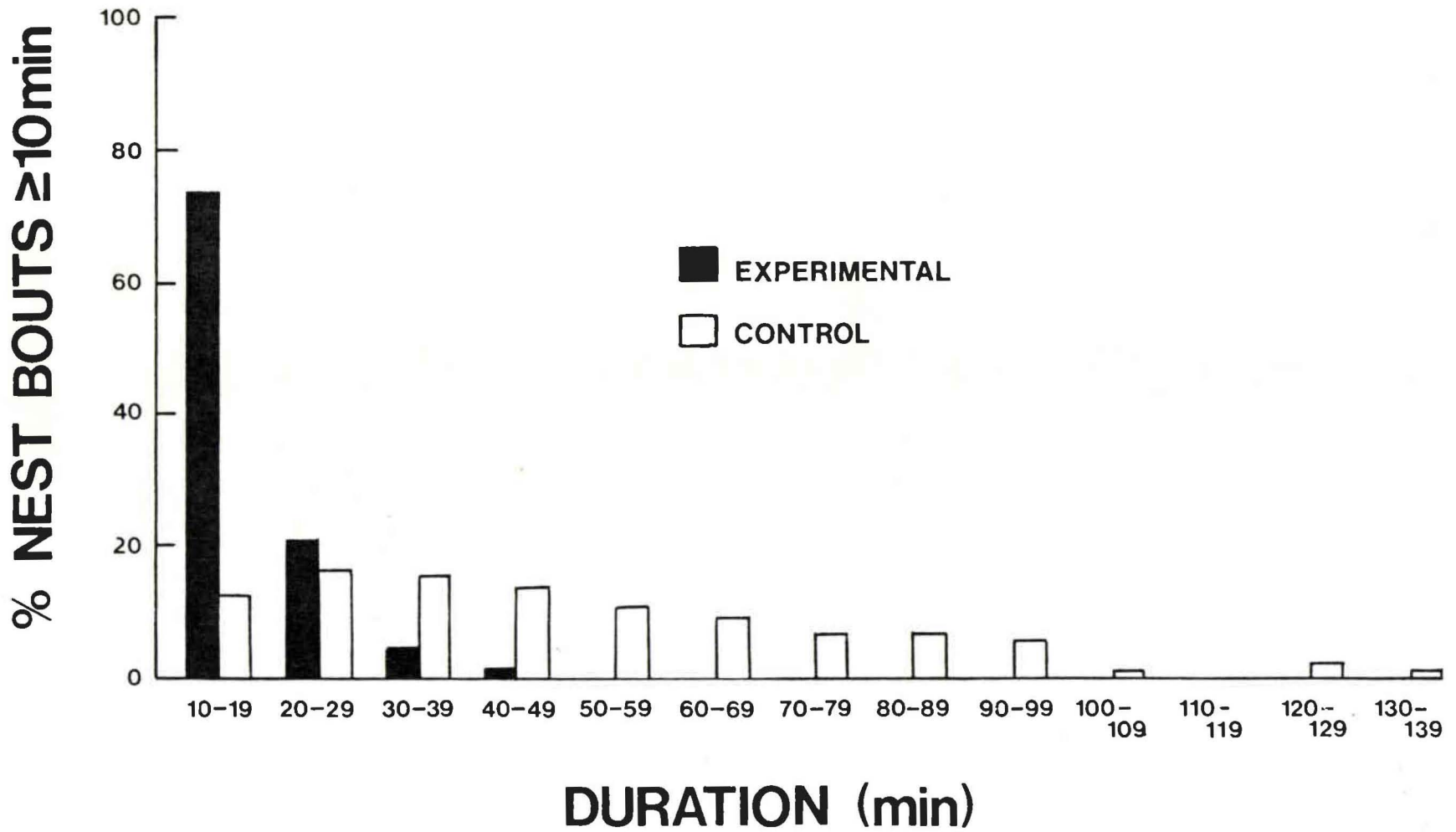


Figure 11: Distributions of nest bout durations for Experimental and Control dams when only nest bouts of at least 10 min duration are considered.



The mean nest bout durations and the associated standard errors of the means are shown in Figures 12a and b. Figure 12a shows the mean nest bout durations for all nest contacts, while Figure 12b shows the mean nest bout durations when only nest bouts of at least 10 min are considered.

Again, it is clear that the Experimental dams had shorter nest bouts than the Control dams. Because the variances of the two groups were markedly different (Figures 12a and b), and because nest bout durations apparently were not normally distributed (Figures 10 and 11), it seemed inappropriate to test for a difference between the groups with a parametric statistic, such as t . As with the percentage of mother-litter contact, however, each of the mean nest bout durations for dams in the Experimental group were shorter than each of the mean nest bout durations for dams in the Control group. Thus, a nonparametric statistic, such as the Mann-Whitney U, indicates that the difference between the groups is statistically significant ($U = 0$; $p < .01$).

The mean number of nest bouts, regardless of the duration of the nest bout, and the associated standard errors of the means for the two groups are shown in Figure 13a. The Experimental dams had almost twice as many nest bouts as the Control dams. The difference was significant ($t = 4.63$; $df = 10$; $p < .01$). When nest bouts of less than 10 min duration are eliminated, however, this effect is reversed, as seen in Figure 13b, although the difference in this case is not statistically significant ($t = 1.73$; $df = 10$; $.10 > p > .05$). Thus, while the total number of mother-litter contacts was higher for the Experimental dams, the number of contacts in which milk delivery could

Figure 12: Mean nest bout durations for Experimental and Control dams. (a) illustrates the mean duration of all nest bouts and (b) illustrates the mean duration of nest bouts of at least 10 min duration. Superimposed bars represent standard errors of the means.

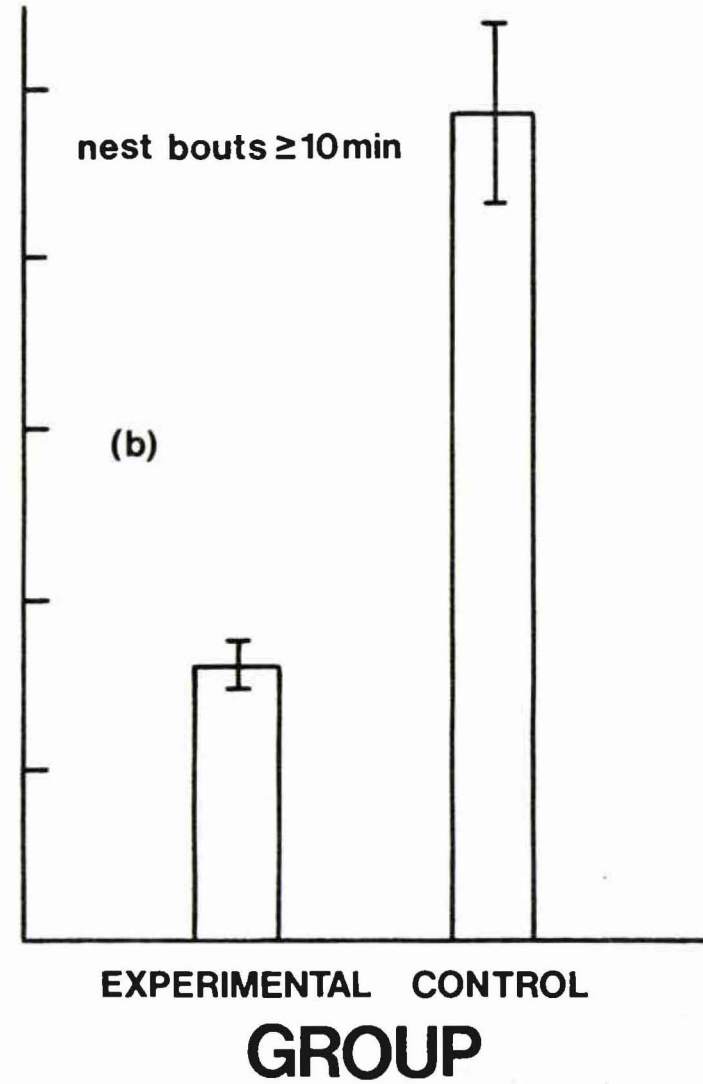
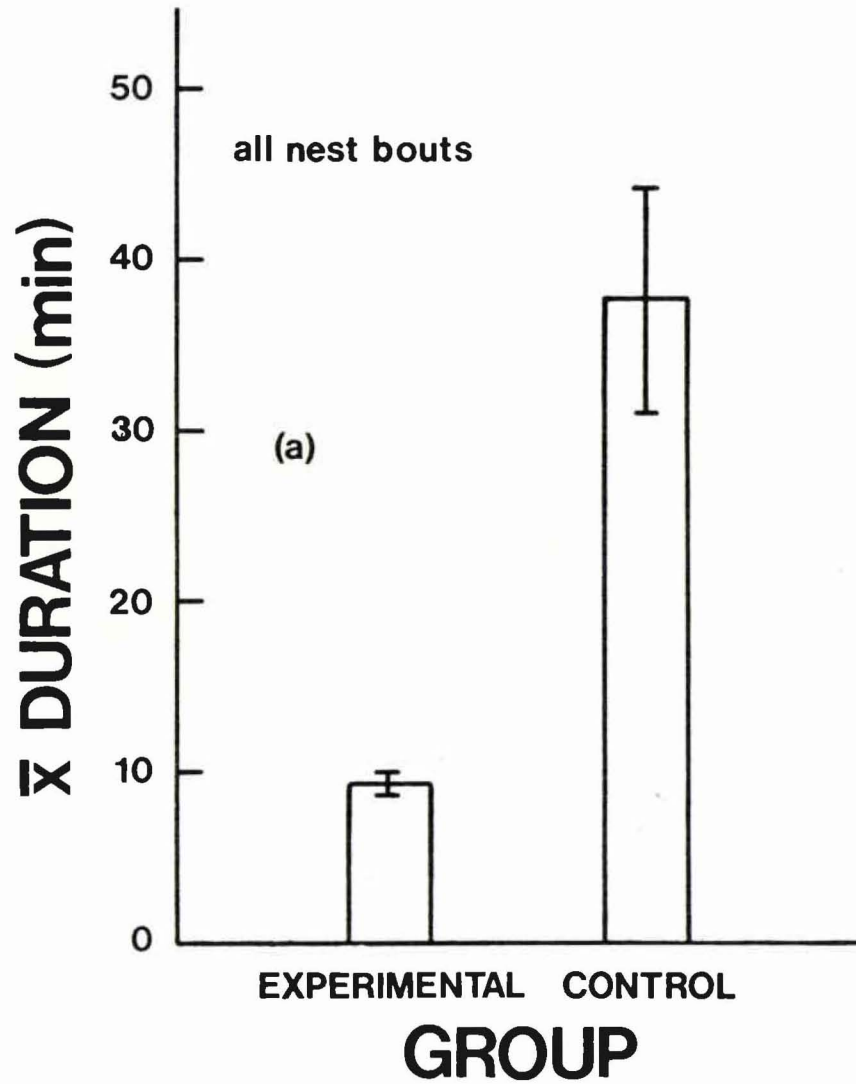
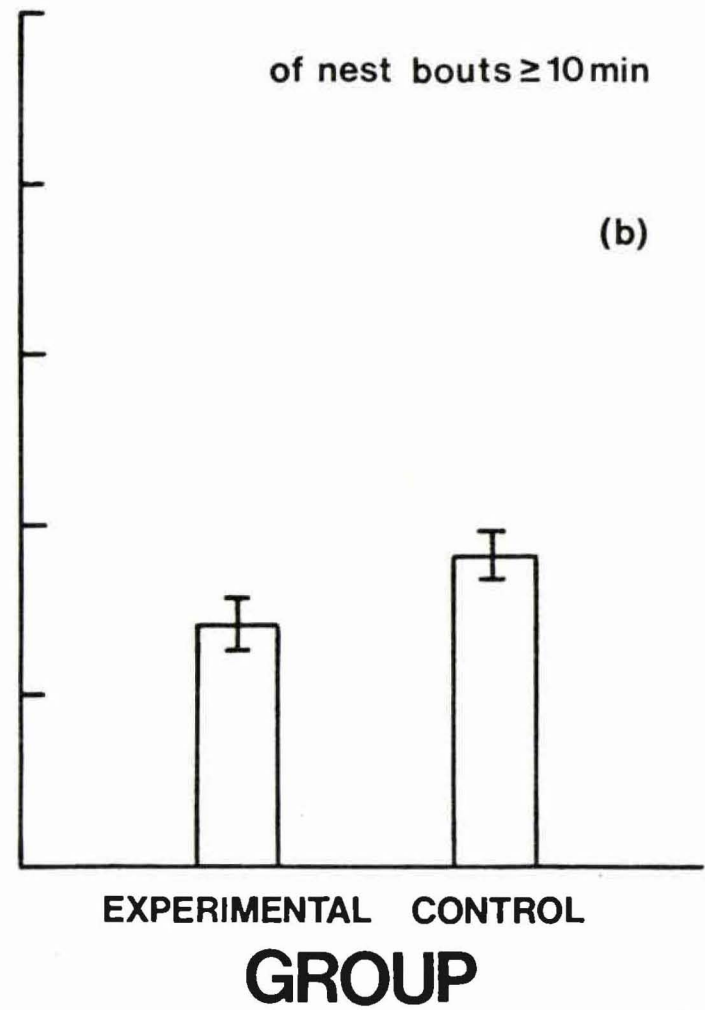
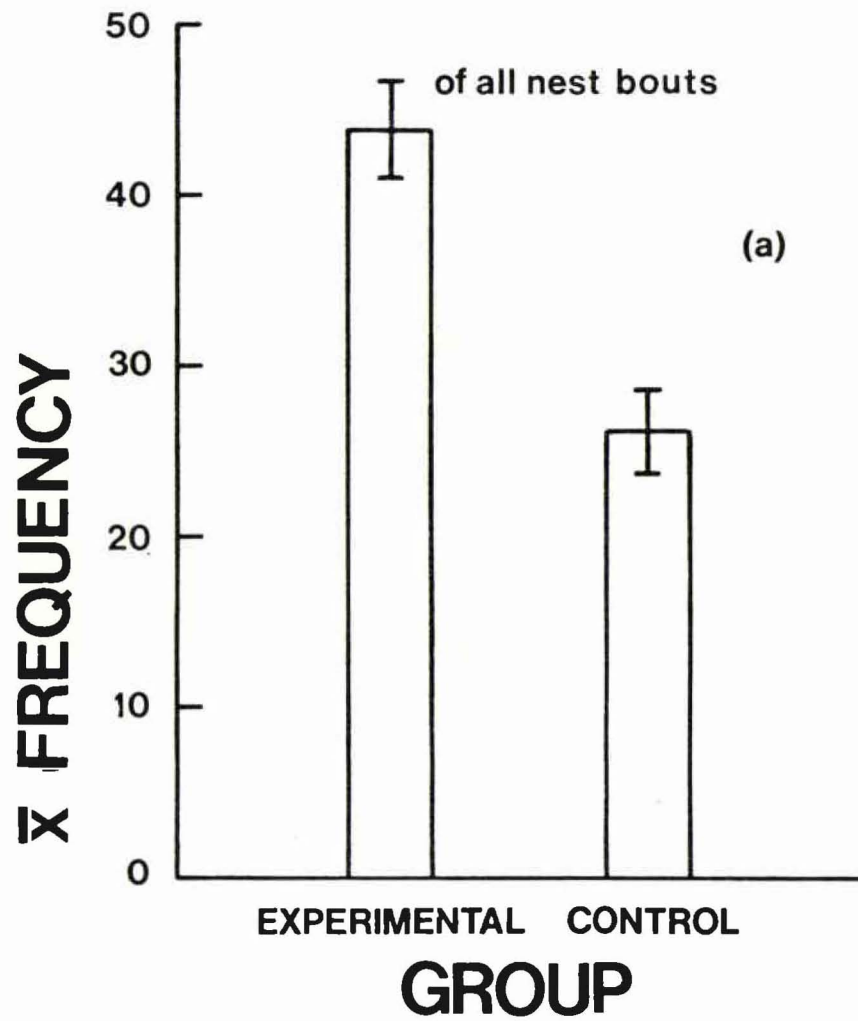


Figure 13: Mean frequencies of nest bouts for Experimental and Control dams. (a) illustrates the frequencies of all nest bouts and (b) illustrates the frequencies of nest bouts of at least 10 min duration. Superimposed bars represent the standard errors of the means.



occur (Wakerley and Lincoln, 1971) is similar between the two groups.

Discussion of mother-young contact

The Experimental dams in the present experiment had shorter, more frequent contacts with their pups than did Control dams. The difference in the frequency of nest bouts in the present study seems to be due to a much higher frequency of contacts of less than 10 min duration. The end result was that nesting on a preferred warm surface not only reduced the duration of individual nest bouts, it also reduced the total amount of mother-litter contact.

By choosing to nest on a warm surface, then, the dams self-imposed a situation in which the amount of time that they could spend with their pups was reduced. Although the amount of time that nutrition and warmth were available to the pups may have been reduced, it should be noted that the Experimental pups were probably not as dependent as the Control pups on the dam for warmth, as they were resting on a much warmer surface than the Control pups. Moreover, the Experimental pups had only slightly fewer opportunities to obtain nutrition from the dam in bouts greater than 10 min. Thus, although the Experimental dams spent only half as much time with their pups as the Control dams, it may have been without detriment to the pups.

Summary of Experiment 4

In the present experiment, dams with their litters were exposed to a thermal gradient for a period of 24 hr. All dams placed their pups at the warm end of the gradient (approximately 32 - 33°C), which represents a confirmation of the finding in Experiment 2 of the present

report. It is clear, then, that with no nest material available dams prefer to establish a fairly warm nest site.

On the basis of the findings of Croskerry et al. (1978), Leon et al. (1978), and Woodside et al. (1980), it was expected that establishing a warm nest site would limit the duration of individual nest bouts. In fact, it was found that the average nest bout duration for dams nesting in the warmth was less than half of that for dams nesting on a cooler surface (approximately 22°C). Further, over the entire 24 hr period the dams that nested on a warm surface had only about half as much contact with their pups as dams that nested on a cooler surface. Dams clearly do not attempt to maximize the time that they spend with their pups.

It was also found that dams on the thermal gradient spent a large proportion of their time away from their pups on a surface of 24 - 26°C, confirming the results of Experiments 1 and 2. It was suggested that spending a large proportion of time on such a temperature was unlikely to allow a rapid reduction in the dams' body temperatures and would thus result in longer average IBI durations.

In fact, dams on the thermal gradient had longer intervals between nest bouts in which milk delivery could occur than did dams that were on a constant temperature surface. But IBIs between all nest contacts, whether milk delivery could have occurred or not, were very similar between the two groups. Dams on the thermal gradient, however, were not as likely to show IBIs of less than 10 min duration.

Further measurements revealed that dams on the thermal gradient did not attempt to use the cold end of the gradient, either before or

after nest bouts, in order to reduce their body temperatures and thus limit the amount of time that they could spend away from their pups.

Because the dams on the thermal gradient did not seem to use the cold end of the thermocline in order to limit IBI durations, and because they spent a larger proportion of time during IBIs on a fairly warm surface, it seems reasonable to suggest that these two findings account for the longer IBI durations shown by these dams. Apparently, then, dams do not appear to minimize the amount of time that they spend away from their pups.

There is, however, one other factor which may have been important: the temperature of the pups. Pups on a surface of 32°C would, undoubtedly, retain their body heat for a longer period of time than would pups on a surface of 22°C . In the dam's absence, then, pups on the warmer surface would expend less energy, and would not require nutrition or warmth as quickly as pups on the cooler surface. It is conceivable that the dams on the thermal gradient in the present experiment were not needed at the nest site as much as the dams on the constant surface temperature, and thus spent longer periods of time away from the nest.

There are, then, two possible reasons for why dams on the thermal gradient showed longer IBI durations: 1) the dams spent a larger proportion of time on a warm surface and thus their body temperatures, which were elevated at nest bout termination, declined slowly; 2) the pups' rate of energy expenditure in the dams' absence was slowed due to the warm floor surface, and thus were not as much in need of the dams. The first possibility will be tested in the

following experiment. Factors relating to the pups will be tested in Section III of this investigation.

Experiment 5

Lactating rats choose to spend a large proportion of their IBI time on a fairly warm surface, and also tend to spend long periods of time away from their pups. While it has been suggested that the duration of IBIs may be dependent upon the rate at which maternal body temperature falls, no direct test of the hypothesis has yet been made.

Since the rate of heat loss is dependent upon the temperature gradient between the dam and her surroundings, it may be possible to alter the duration of IBIs by changing floor surface temperatures. By exposing dams to different floor surface temperatures during IBIs, while at the same time holding the temperature of the nest site constant across conditions, it should be possible to assess the importance of the rate of maternal heat loss and, thereby, maternal body temperature decline experienced during IBIs in determining IBI duration. In this case, the rate of pup energy expenditure during IBIs should be constant across conditions, and thus any differences in IBI durations could be attributed to the thermal gradient that exists between dams and their environment.

Method

Subjects

Eighteen lactating Wistar rats, with litters routinely reduced to 8 pups on the day of birth, were used as subjects.

Apparatus

A cage that had been developed for the continuous recording of maternal behaviour (Croskerry, Smith, Leon, and Mitchell, 1976) was modified to suit the purposes of the present experiment. The cage (61.0 cm x 30.5 cm x 15.25 cm) contained two rocking trays (30.5 cm x 11.4 cm) at either end. When the dam sat at one end of the tray, the entire tray tilted, a microswitch at the opposite end was displaced, and a running time meter was operated. When the dam stepped off the tray, the timer stopped.

The trays were divided in half so that the mother and pups occupied one half while the other half was covered and could be weighted to counterbalance the weight of the pups. Within the entire area of the cage, then, there were two nesting areas (15.25 cm x 11.4 cm) and a large floor area (38.1 cm x 30.5 cm). For the purposes of the present experiment, one nesting area was blocked off so as to be inaccessible to the dam.

The floor area was covered with 3.2 mm copper plate. Beneath the copper plate was a coiled tube (Tygon plastic tubing; 4.9 mm inside diameter), which allowed continuous circulation of water. Running cold or hot water through the tube resulted in cooling or warming of the floor area independently of the nest areas. A continuous record of the dam's nesting activity was obtained as described in Experiment 4.

Procedure

Dam and pups were placed in the apparatus on Day 9 postpartum and removed on Day 11 postpartum. Testing took place between 0900 hrs on Day 10 and 0900 hrs on Day 11 postpartum. The initial 24 hr period

from Day 9 until Day 10 was an habituation period. Purina lab chow and water were available continuously.

Subjects were tested under one of three conditions. Under the first condition (Unmanipulated), no water was passed through the tubes, and thus the surface temperatures of the floor and nest areas were the same. Under the second condition (Cool), cold water flowed under the floor area. Relative to the Unmanipulated dams, then, dams under the Cool condition experienced a cooler floor surface during IBIs. Under the third condition (Warm), warm water flowed under the floor area, so that these dams experienced a warmer floor surface during IBIs than either the Unmanipulated or Cool dams.

Because of fluctuations in room and water temperatures, the floor temperatures were not static. The average floor temperatures and the associated standard errors of the means were $16.80 \pm 0.36^{\circ}\text{C}$, $21.13 \pm 0.13^{\circ}\text{C}$, and $26.48 \pm 0.41^{\circ}\text{C}$ for the Cool, Unmanipulated, and Warm conditions, respectively. Further, there was no overlap among the three distributions of floor temperatures.

To be sure that the nesting area temperature was not influenced by the floor temperature, nesting area temperatures were measured both immediately before and immediately after testing. The temperatures were very similar across all conditions. The temperatures of the nesting areas were about 1°C higher after testing than before testing, presumably due to the presence of the dam and pups. The mean temperatures and the associated standard errors of the means before testing were: Warm, $21.02 \pm 0.34^{\circ}\text{C}$; Unmanipulated, $21.18 \pm 0.18^{\circ}\text{C}$; Cool, $21.02 \pm 0.22^{\circ}\text{C}$. After testing, the temperatures were: Warm,

$22.18 \pm 0.17^{\circ}\text{C}$; Unmanipulated, $22.33 \pm 0.08^{\circ}\text{C}$; Cool $22.12 \pm 0.07^{\circ}\text{C}$.

Total nest time, nest bout durations, nest bout frequency, and IBI durations were recorded for the 24 hr period. In addition, pup weight change was measured to determine the effects on the pups of different IBI durations, if they occurred.

Results

The first question to be addressed is whether the floor temperature that the dams experienced during IBIs influenced the duration of those IBIs. The distributions of IBIs between all nest bouts (regardless of nest bout duration) are shown in Figure 14. Comparable distributions for IBIs between nest bouts of at least 10 min duration are shown in Figure 15. In both figures, it is clear that dams in the Warm group are not as likely as dams in either of the other groups to have IBIs of less than 10 min duration, and are more likely to have longer IBIs (i.e., longer than 60 min between all nest bouts and longer than 80 min between nest bouts ≥ 10 min). The differences between the Warm group and the Unmanipulated and Cool groups are statistically significant in both analyses (Kolmogorov-Smirnov test; between all nest bouts: Warm-Unmanipulated, $D_{\min} = 19.2$, $p < .025$; Warm-Cool, $D_{\min} = 22.2$, $p < .005$; between nest bouts ≥ 10 min: Warm-Unmanipulated, $D_{\min} = 26.8$, $p < .01$; Warm-Cool, $D_{\min} = 26.1$, $p < .01$). The distributions of the Unmanipulated and Cool groups were not significantly different in either analysis (between all nest bouts:

Figure 14: The distributions of interbout interval durations between all nest bouts for dams exposed to either a warm, cool or unmanipulated floor during IBI.

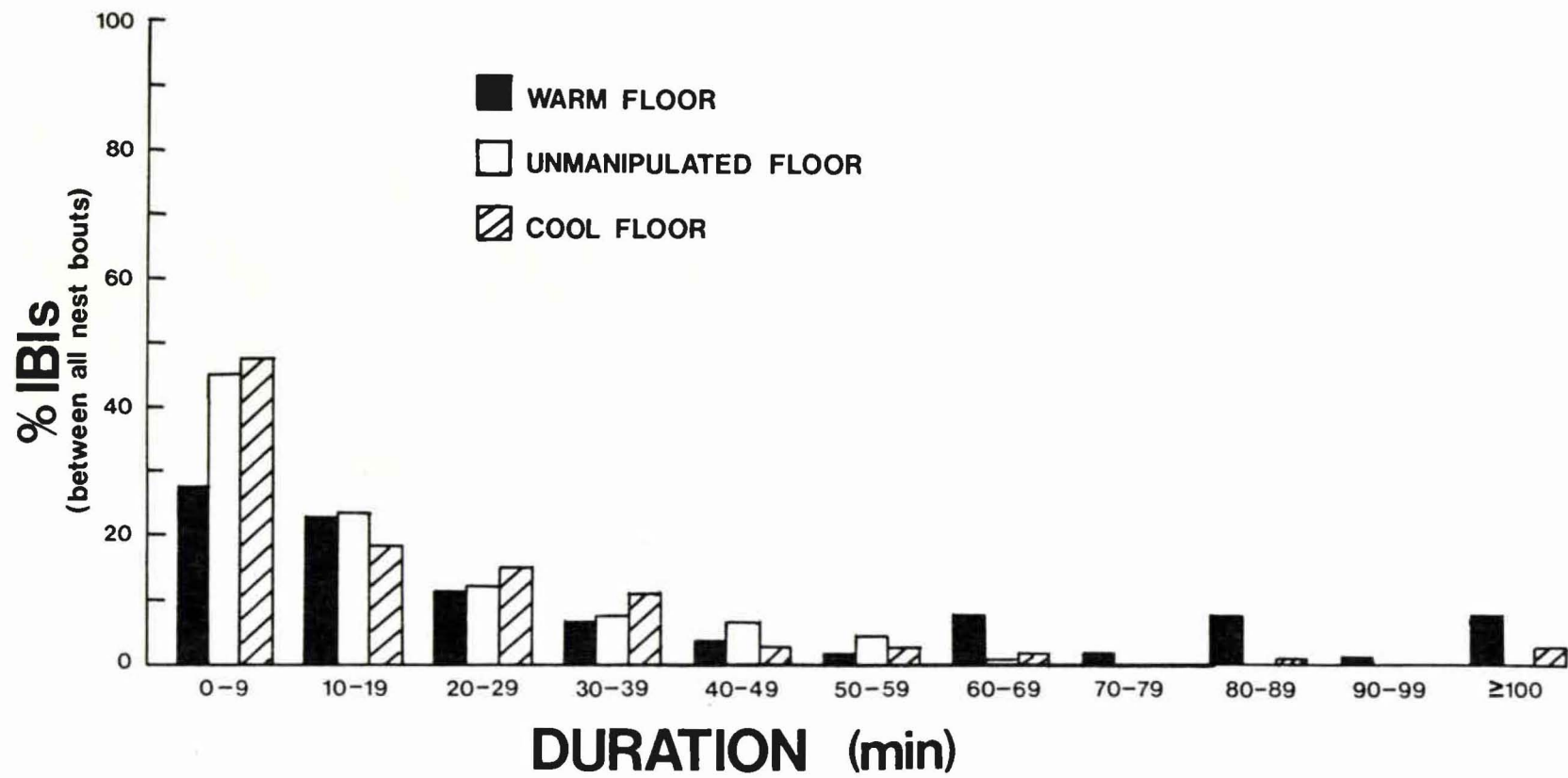
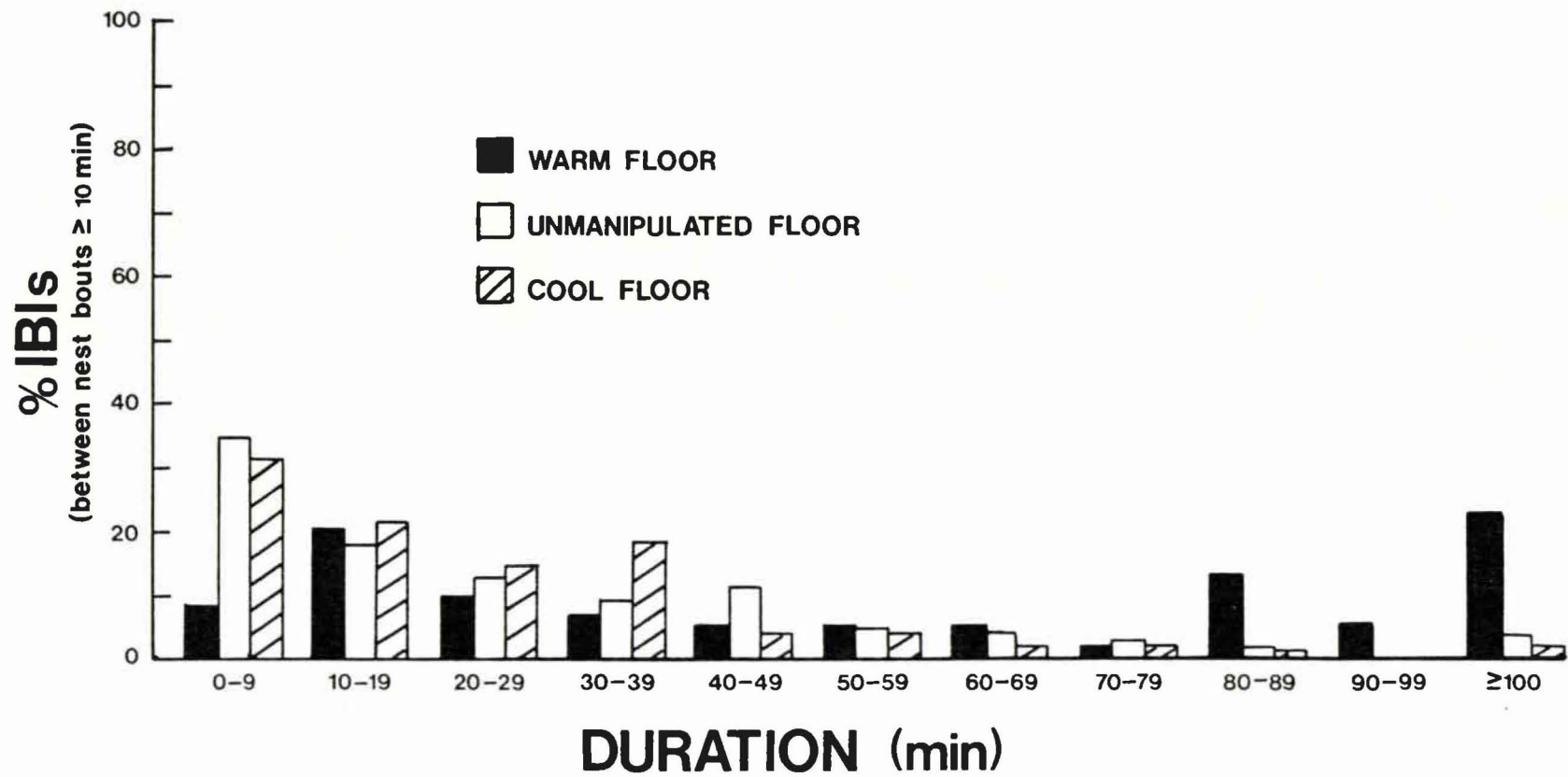


Figure 15: The distributions of interbout interval durations between nest bouts of at least 10 min duration for dams exposed to either a warm, cool, or unmanipulated floor during IBIs.



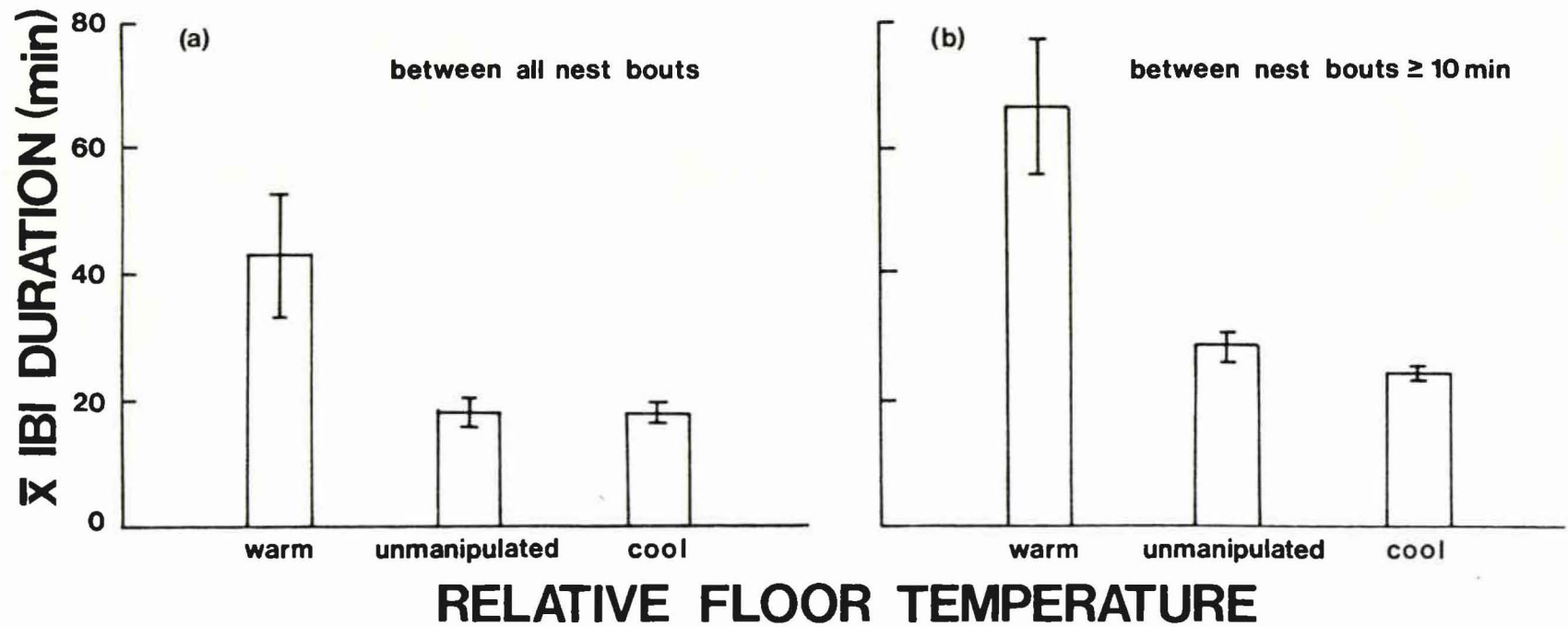
$D_{\min} = 16.2$; between nest bouts ≥ 10 min: $D_{\min} = 19.7$; both p 's $> .05$).

The mean IBI durations between all nest bouts and the associated standard errors of the means are shown for all three groups in Figure 16a. Because IBI durations were not normally distributed, and because variances were apparently nonhomogeneous, a nonparametric analysis (Kruskal-Wallis H statistic) was performed on the data. There was an overall difference among the three groups ($H = 10.33$; $p < .01$). Post hoc comparisons revealed that dams in the Warm group had longer IBI durations than dams in both the Unmanipulated and Cool groups (Mann-Whitney U test; both U 's = 1; $p = .0022$). There was no statistically significant difference between the Unmanipulated and Cool groups ($U = 14$; $p = .2944$).

The results for IBIs between nest bouts of at least 10 min duration were similar to those for IBIs between all nest bouts. The mean IBI durations between nest bouts ≥ 10 min and the associated standard errors of the means are shown for all groups in Figure 16b. As with the previous analysis, there was an overall difference among the three groups ($H = 12.32$; $p < .01$). Post hoc comparisons revealed statistically significant differences between the Warm group and both the Unmanipulated and Cool groups (both U 's = 0; $p = .0011$), while the Unmanipulated and Cool groups were not significantly different ($U = 9$; $p = .0898$).

It is evident that dams under the Warm condition had longer IBI durations than either of the other two groups of dams. The effects of

Figure 16: Mean interbout interval durations for dams exposed to either a warm, cool, or unmanipulated floor during IBIs. (a) illustrates the mean durations between all nest bouts and (b) illustrates the mean durations between nest bouts of at least 10 min duration. Superimposed bars represent the standard errors of the means.



the floor surface temperature apparently are not linear, however, as the Unmanipulated and Cool groups had very similar IBI durations.

The next question to be addressed is whether there was any effect on the total amount of mother-litter contact. The mean percentage of mother-litter contact and the associated standard error of the mean for each of the three groups is shown in Figure 17. Dams in the Warm group typically spent less time with their pups than dams in either of the Unmanipulated or Cool groups, and there is only a very slight difference between the Unmanipulated and Cool groups.

Analysis of variance revealed an overall effect of floor temperature on total mother-litter contact ($F = 5.67$; $df = 2,15$; $p < .025$), and post hoc paired comparisons revealed statistically significant differences between the Warm group and both the Unmanipulated and Cool groups (Tukey (a) test, both p 's $< .05$). The Unmanipulated and Cool groups did not differ significantly (Tukey (a) test; $p > .05$).

Given that dams under the Warm condition had longer IBI durations and showed a tendency to spend less time with their pups overall the question is whether dams under the Warm condition had a similar number of nest bouts as the other dams, but of shorter duration, or whether dams in the Warm group simply had fewer nest bouts.

The distributions of nest bout durations for each of the three groups are shown in Figure 18. Kolmogorov-Smirnov tests indicated that the distributions for all three groups were similar (Warm-Unmanipulated: $D_{\min} = 16.9$; Warm-Cool: $D_{\min} = 17.0$; Unmanipulated-

Figure 17: Mean percentage of time spent with pups for dams exposed to either a warm, cool, or unmanipulated floor during IBIs. Superimposed bars represent the standard errors of the means.

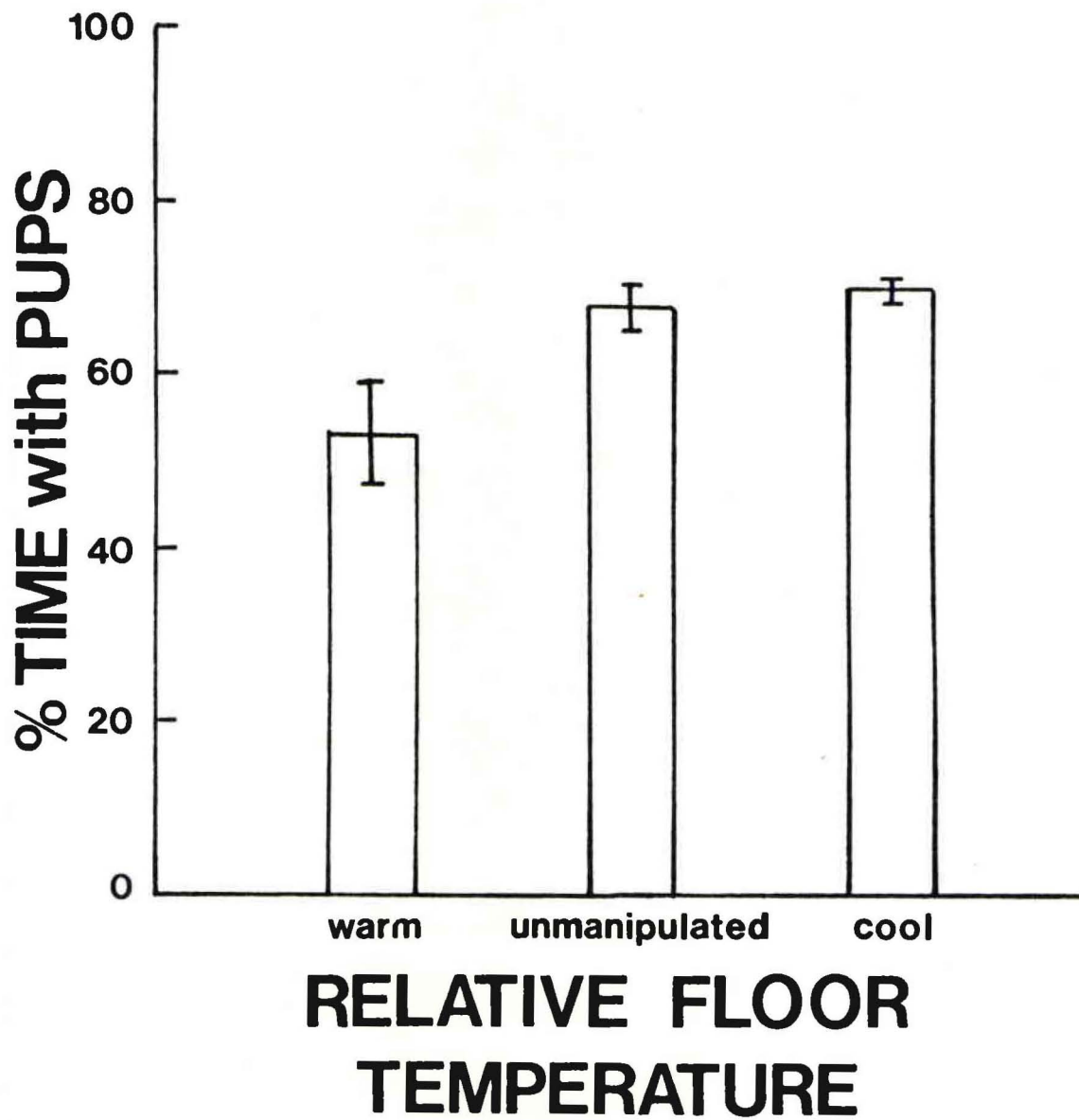
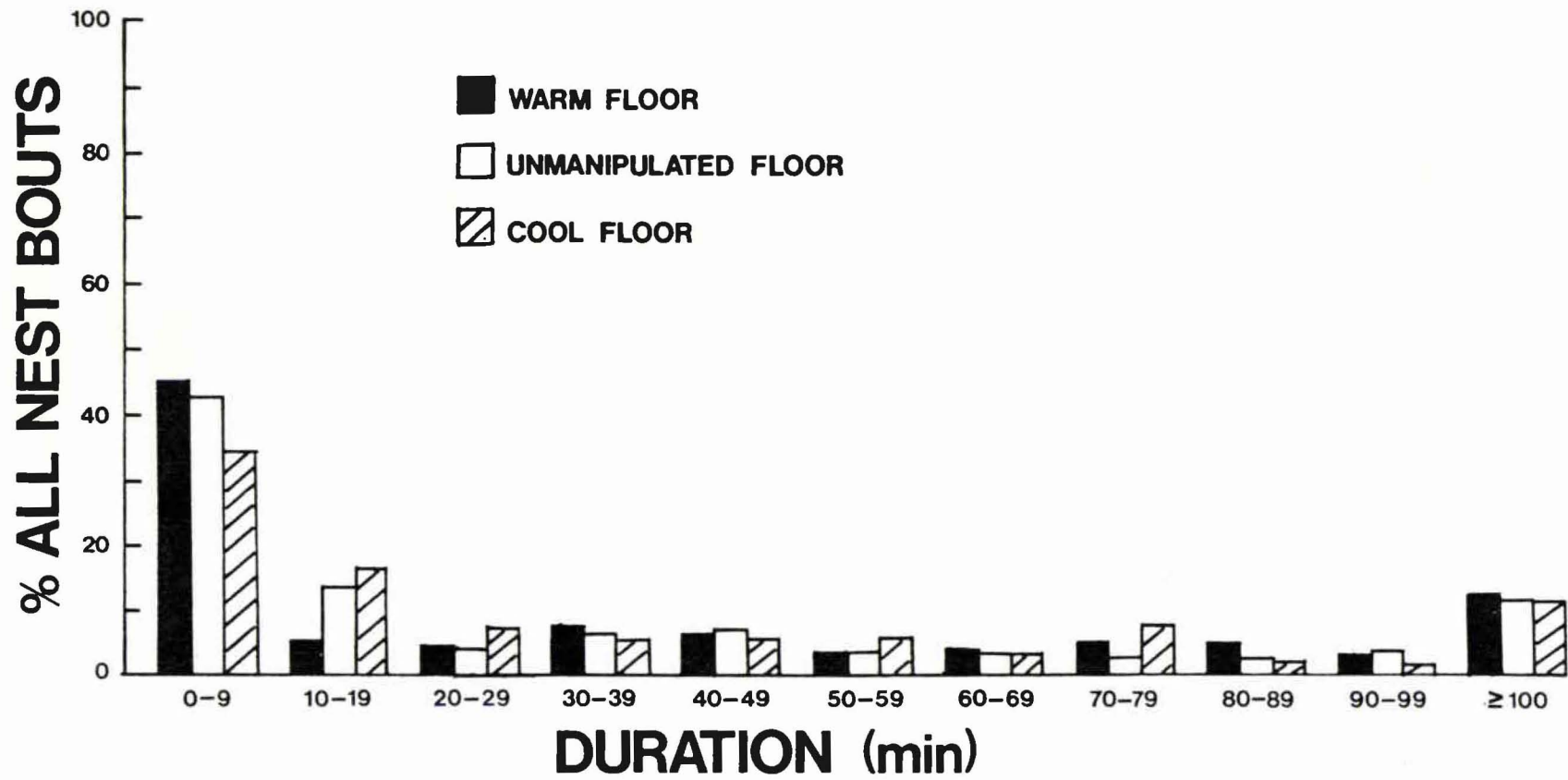


Figure 18: The distributions of all nest bout durations for dams exposed to either a warm, cool, or unmanipulated floor during IBIs.



Cool: $D_{\min} = 15.3$; all p 's $> .05$). When only nest bouts of at least 10 min duration are considered, there were again no statistically significant differences between the three distributions (Kolmogorov-Smirnov tests; Warm-Unmanipulated: $D_{\min} = 22.6$; Warm-Cool: $D_{\min} = 22.1$; Unmanipulated-Cool: $D_{\min} = 19.6$; all p 's $> .05$; Figure 19).

The mean nest bout durations and the associated standard errors of the means, when all nest bouts are considered, are shown in Figure 20a. Because nest bout durations were not normally distributed (Figure 18), a nonparametric analysis was performed, indicating that the nest bout durations were not significantly different ($H = 0.74$; $p > .10$). When nest bouts of at least 10 min duration were considered, there was, again, no statistically significant effect among the three groups ($H = 2.33$; $p > .10$; Figure 20b).

Dams under all three conditions had similar nest bout durations. Dams under the Warm condition, however, had less total contact with their pups, and spent longer periods away from their pups than dams under the Unmanipulated and Cool conditions. Of necessity, then, dams under the Warm condition must have had fewer nest bouts than the other dams. Figure 21a shows the mean frequencies for all nest bouts, and Figure 21b shows the mean frequencies of nest bouts of at least 10 min duration. In both cases, dams under the Warm condition have the fewest number of nest bouts, and dams under the Cool condition have slightly more nest bouts than dams under the Unmanipulated condition. When nest bouts of all durations are considered, however, the distributions of nest bout frequencies are not significantly different among the three groups ($H = 4.15$; $p > .10$). Eliminating nest

Figure 19: The distributions of nest bout durations for dams exposed to either a warm, cool, or unmanipulated floor during IBIs when only nest bouts of at least 10 min duration are considered.

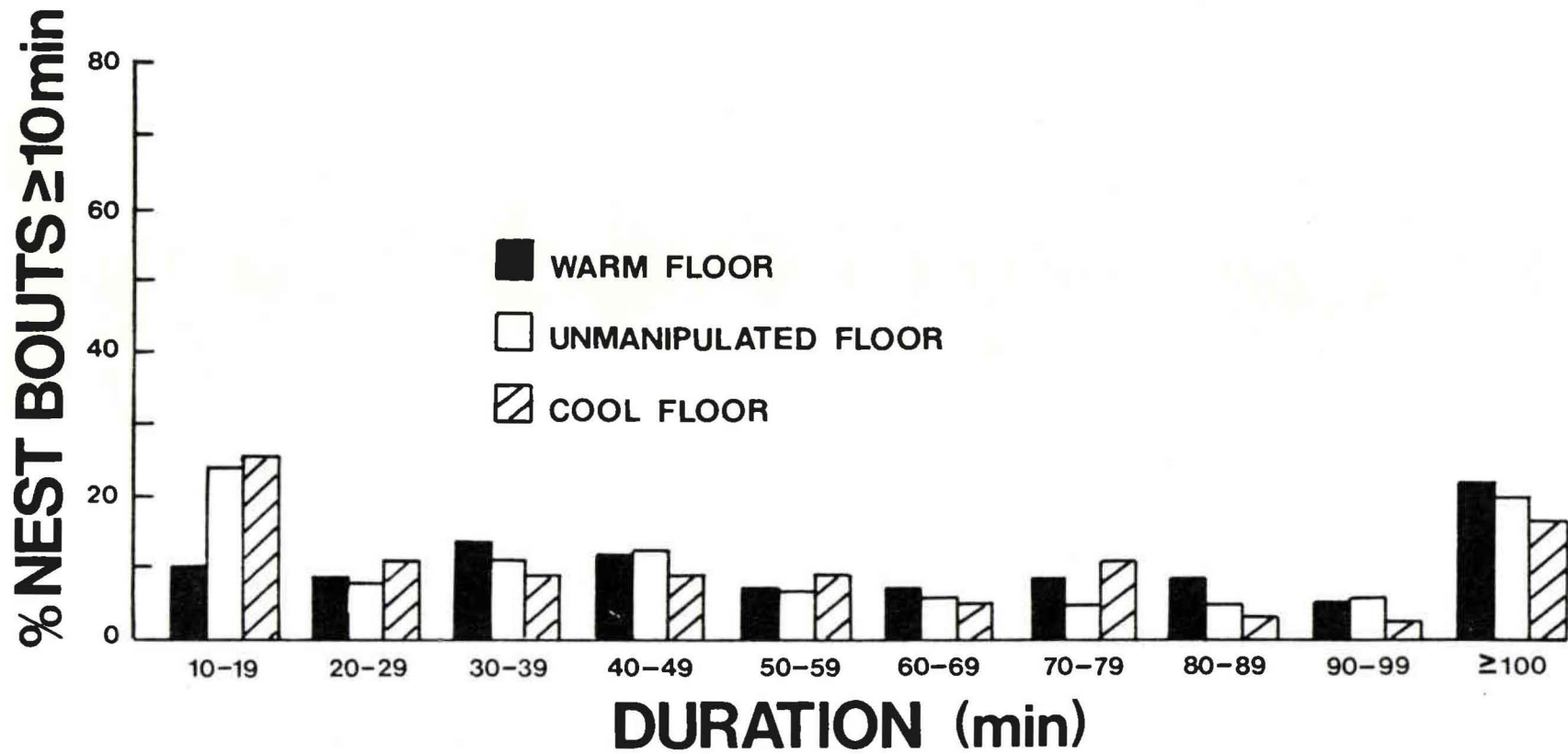


Figure 20: Mean nest bout durations for dams exposed to either a warm, cool, or unmanipulated floor during IBIs. (a) illustrates the mean durations for all nest bouts and (b) illustrates the mean durations for nest bouts of at least 10 min duration. Superimposed bars represent standard errors of the means.

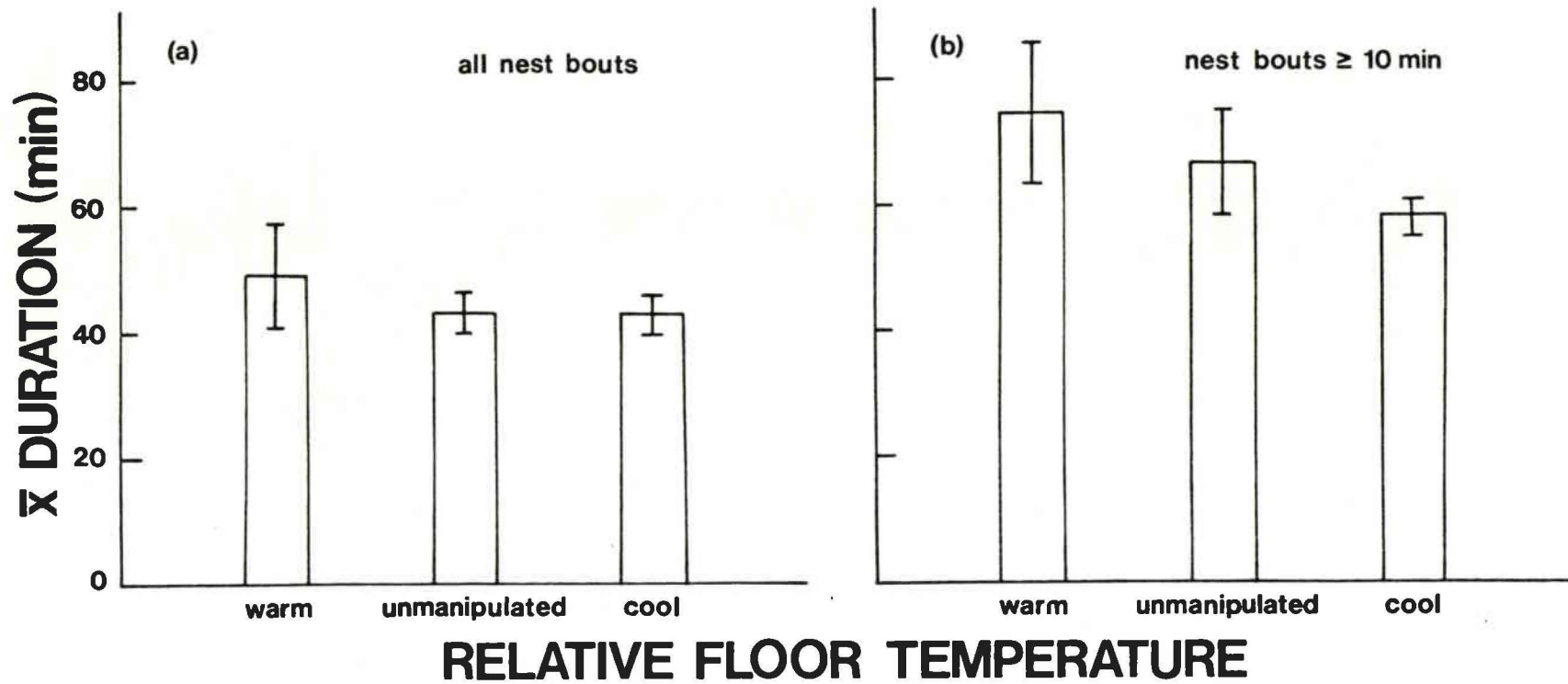
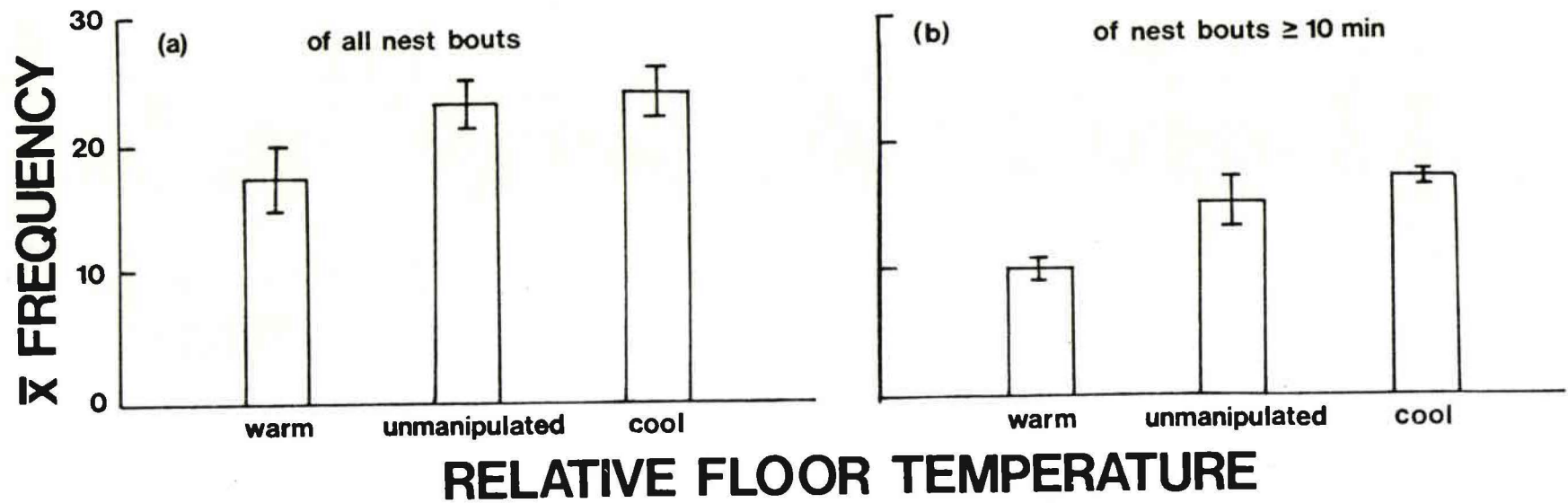


Figure 21: Mean frequencies of nest bouts for dams exposed to either a warm, cool, or unmanipulated floor during IBIs. (a) illustrates the frequencies of all nest bouts and (b) illustrates the frequencies of nest bouts of at least 10 min duration. Superimposed bars represent standard errors of the means.



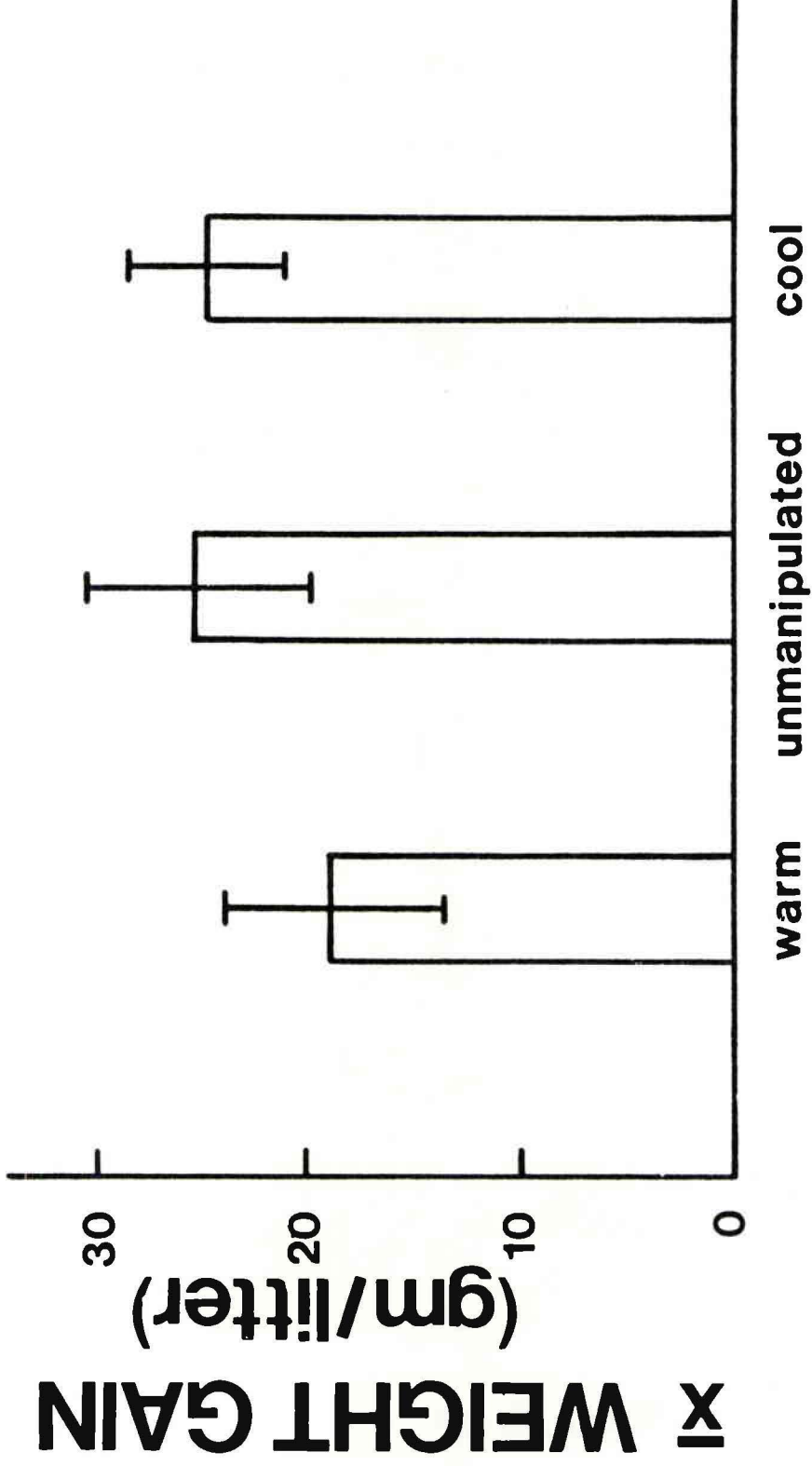
bouts of less than 10 min duration yields a statistically significant effect on the distributions of nest bout frequencies ($H = 8.86$; $p < .025$), which is accounted for by the fact that dams in the Warm group have fewer of such nest bouts than dams in both the Unmanipulated ($U = 5.5$; $p < .0325$) and the Cool ($U = 0$; $p = .0011$) groups. The difference between the Unmanipulated and Cool groups was nonsignificant ($U = 13$; $p = .2424$).

Although dams under the Warm condition spent approximately the same amount of time with their pups during each nest bout as dams under the Unmanipulated and Cool conditions, they had fewer contacts with their pups, resulting in less total mother-litter contact. Nevertheless, the pups appeared to suffer no ill effects of the shorter contact time. The mean weight gains and the associated standard errors of the means for litters under all three conditions are shown in Figure 22. Although litters under the Warm condition gained slightly less weight than litters under either of the other conditions, there was no statistically significant differences among the three groups ($F < 1.0$; $df = 2,15$, $p > .10$).

Discussion

The present experiment has demonstrated that the floor surface temperature that dams experience during IBIs influences the amount of time that dams will spend away from their pups. Dams that experienced a warm floor temperature during IBIs spent much longer periods away from their pups, with little or no detriment to the pups, than did dams that experienced cooler temperatures.

Figure 22: Mean weight gain of pups whose dams were exposed to either a warm, cool, or unmanipulated floor during IBIs. Superimposed bars represent standard errors of the means.



RELATIVE FLOOR TEMPERATURE

That the effects of floor temperature on IBI duration are not necessarily linear is indicated by the lack of a statistically reliable difference between dams exposed to the Unmanipulated and Cool conditions. Perhaps the lack of effect of a further reduction in floor temperature lies in the fact that IBI durations of both the Unmanipulated dams in the present experiment and the Control dams of Experiment 4 were markedly skewed towards short durations. In fact, most IBIs for both groups (whether between all nest bouts or nest bouts of at least 10 min duration) were less than 20 min in duration. In order for a statistical difference to have been observed, then, dams under the Cool condition would have had to have shown an overwhelming majority of IBIs of less than 20 min duration. Thus, the lack of an observed difference between the Unmanipulated and Cool groups may be, at least partially, attributed to a statistical "floor" effect.

In addition to the statistical limitation, however, there also may be a physical limitation imposed upon the dam. Specifically, dams must eat, drink, groom, and eliminate during IBIs. These are probably obligatory behaviours, and thus dams may not choose to (or even be able to) restrict the amount of time that they engage in these activities.

The most important finding in the present experiment, however, is that dams that experienced a warm floor surface during IBIs showed longer IBI durations. These data provide strong support for the suggestion that the prolonged IBIs shown by the dams on the thermal gradient in Experiment 4 was, at least partially, due to the fact that these dams spent a larger proportion of their IBI time on a warm surface.

Experiment 6

The results of Experiment 5 indicate that IBIs are prolonged if the dam is exposed to a warm floor surface, presumably because body temperatures decline more slowly during IBIs. One difficulty with this interpretation is that there was no direct evidence in Experiment 5 that the dams' rates of temperature decline were actually altered. Dam body temperature was directly measured in the present experiment.

Method

Subjects

Twelve lactating rats and their litters, routinely reduced to 8 pups at birth, served as subjects.

Apparatus

Subjects were tested in the cages described in Experiment 5, under the Warm and Unmanipulated conditions.

Procedure

On Day 7 postpartum dams were implanted with a YSI #44003A thermistor in the peritoneal cavity. Dam and pups were placed in the experimental cages on Day 9 postpartum, and dam core temperature and nesting behaviour were monitored, via a Beckman Polygraph (model 1700), from 0900 hrs on Day 10 through 0900 hrs on Day 11 postpartum. Six animals were allocated to each of the two conditions (Warm and Unmanipulated).

Results

IBI durations and the rate of maternal temperature decline during IBIs were measured for all nest bouts accompanied by a rise in maternal temperature. These data are shown in Figures 23a and b. As is clear from Figure 23a, IBIs following a nest bout accompanied by a rise in maternal temperature were much longer for dams that experienced a warm floor surface ($U = 0$; $p = .0011$). Further, dams under the Warm condition showed a much slower rate of temperature decline during such IBIs (Figure 23b; $t = 2.50$; $df = 10$; $p < .025$).

It was noted that dams under both conditions did not terminate IBIs when the decline in maternal temperature reached a maximal point. That is, maternal temperature fluctuated somewhat during IBIs, and dams did not always return to the nest when the minimum body temperature, for that particular IBI, was reached. For this reason, the time until the maximum decline in body temperature was reached during an IBI and the rate of temperature decline were also measured. These data are shown in Figures 24a and b. Again, dams under the Warm condition showed longer durations until the maximum decline was reached (Figure 24a; $U = 0$; $p = .0011$), and also a slower rate of decline (Figure 24b; $t = 2.43$; $df = 10$; $p < .025$).

A sample trace recording of maternal body temperature under each of the experimental conditions during an individual nest bout and IBI are shown in Figure 25. The figure illustrates both the prolonged IBI duration and the slower rate of temperature decline of dams under the Warm condition. The figure also shows that dams did not return to the nest when the maximum decline in temperature had been reached.

Figure 23: (a) Mean IBI durations for dams exposed to either a warm or unmanipulated floor during IBIs. Superimposed bars represent standard errors of the means. (b) Mean rate of maternal temperature decline during IBIs following nest bouts accompanied by a rise in maternal temperature for dams exposed to either a warm or unmanipulated floor during IBIs. Superimposed bars represent standard errors of the means.

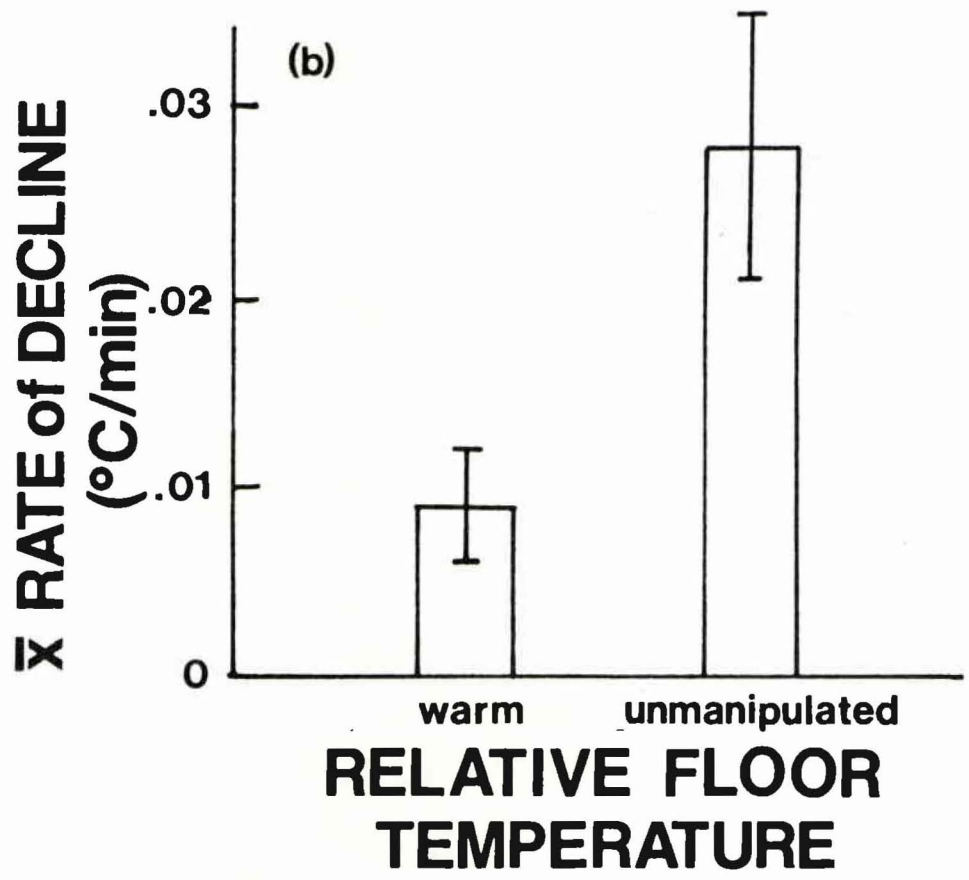
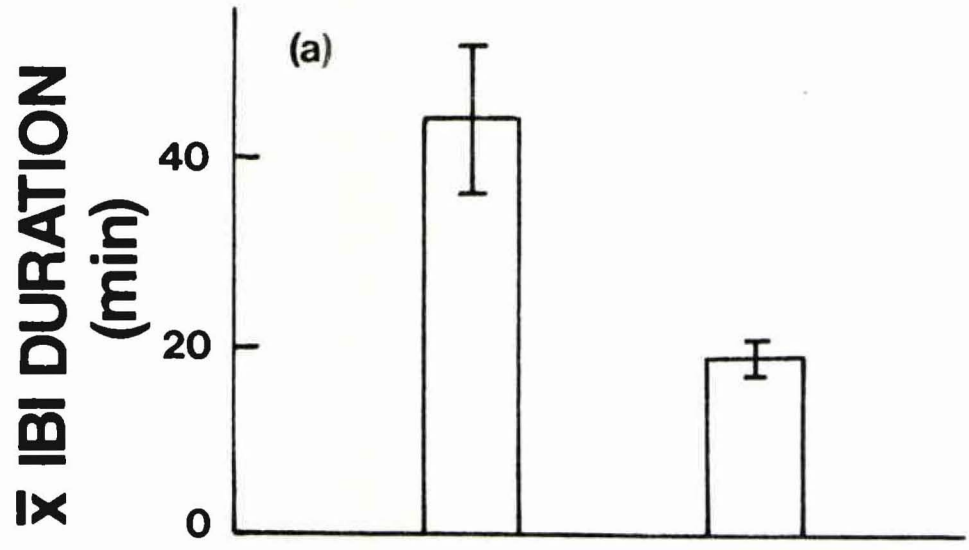


Figure 24: (a) Mean duration until maximum temperature decline during IBIs for dams exposed to either a warm or unmanipulated floor during IBIs. Superimposed bars represent standard errors of the means. (b) Mean rate of maternal temperature decline until maximum temperature decline during IBIs for dams exposed to either a warm or unmanipulated floor during IBIs. Superimposed bars represent standard errors of the means.

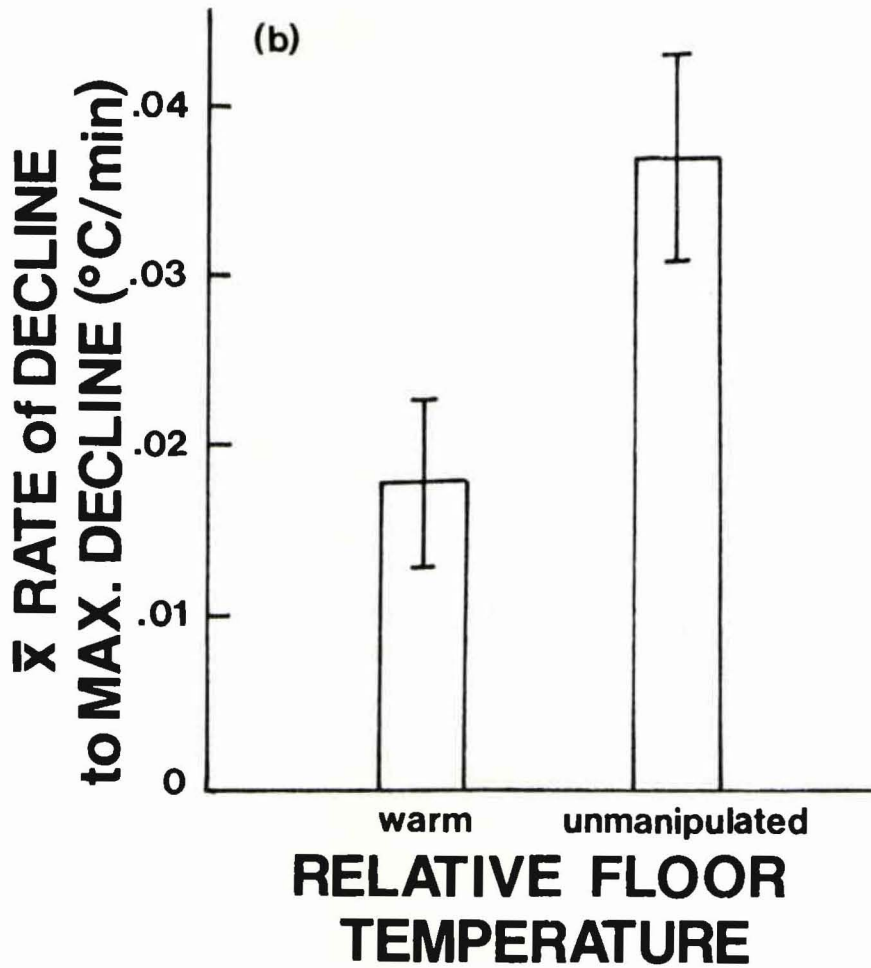
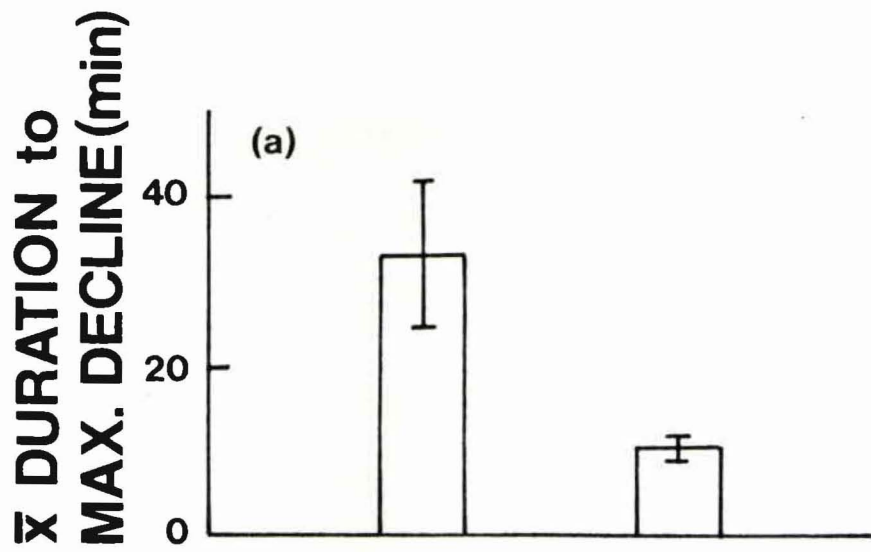
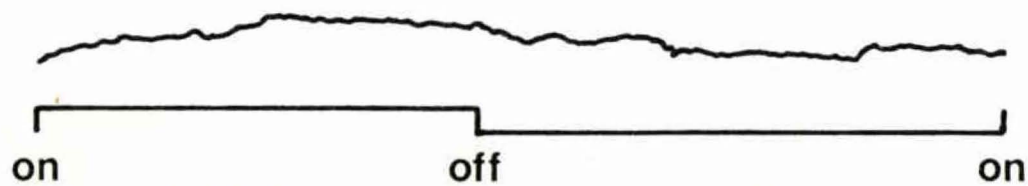


Figure 25: Sample traces of maternal temperature during a nest bout and succeeding IBI for dams exposed to either a warm or unmanipulated floor during IBIs.

WARM FLOOR

NEST BOUT
off 38.44 °C
on 38.09 °C



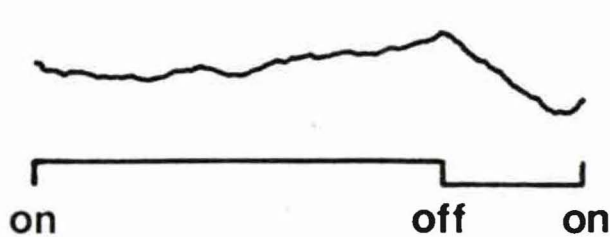
IBI
38.44 °C off
38.19 °C on

NEST BOUT
47 min

IBI
56 min

UNMANIPULATED FLOOR

off 38.30 °C
on 38.02 °C



38.30 °C off
37.67 °C on

NEST BOUT
43 min

IBI
15 min

Discussion

It is clear from the present experiment that prolonged IBIs are at least accompanied by a slow rate of maternal temperature decline. That the rate of temperature decline is not the sole factor in determining the duration of IBIs is indicated by the fact that dams frequently extend IBIs beyond the point at which their temperatures have reached a maximum decline.

Discussion of Section II

Experiment 4 is the first investigation of the pattern of nesting behaviour of lactating rats in which the dams were allowed to select both the temperature at which the pups were maintained and the temperature(s) that the dams themselves experienced between nest bouts. Thus, through the selection of temperatures, the dams in Experiment 4 could control the amount of time that they spent with their pups, and thereby control the amount of maternal care that they delivered to their pups. When dams were allowed to select temperatures while nesting, the pattern of nesting behaviour was substantially altered. For example, under normal laboratory conditions (i.e. a room temperature of approximately 21 - 22°C), the dams in both Experiment 4 (the Control group) and Experiment 5 (the Unmanipulated group) spent approximately 70% of the time with their pups. Dams that could control the temperatures that they experienced spent less than 35% of their time with their pups.

It was perhaps surprising that the Experimental dams of Experiment 4 neither maximized the amount of time that they could spend with their pups by nesting in a relatively cool area, nor minimized the amount of time that they could spend away from the pups by moving to a relatively cool area, rather than spending a large proportion of their IBI time resting on a relatively warm surface. It may be that the limited amount of time that rats are geared to spend with their young allows them to have sufficient time to forage for the greatly increased amount of food that they require to adequately nurture their offspring.

Three major differences were found in the pattern of nesting behaviour between dams that could choose the temperatures at which they nested and spent their IBIs and dams that were exposed to a constant floor surface temperature (Experiment 4): 1) the Experimental dams had much shorter nest bouts; 2) the Experimental dams had longer IBIs, particularly between nest bouts of at least 10 min duration; and 3) the Experimental dams showed a higher frequency of nest bouts in which milk delivery probably did not occur (i.e. nest bouts < 10 min).

The shorter nest bouts can be attributed to the fact that the body temperatures of these dams probably rose more rapidly during nest bouts than did the temperatures of the Control dams. In support of this statement is the fact that Woodside (1978) showed that over 90% of all nest bout terminations on Day 10 postpartum are accompanied by elevations in maternal temperature, and that Leon et al (1978) showed that dams experienced an elevated rate of temperature rise when pups were maintained at a warm temperature. Taking the above two findings together, it is very likely that the Experimental dams in Experiment 4 had rapid elevations of their body temperatures which caused them to have shorter nest bouts than the Control dams.

The prolonged IBI durations shown by the Experimental dams may be attributed, in part, to the fact that dams spent a large proportion of their IBI time resting on a relatively warm floor surface. Indeed, it was shown in Experiment 5 that when dams were forced to spend all of their IBI time on a warm surface, the IBI durations were markedly prolonged. It was also shown, in Experiment 6, that these prolonged

IBI durations were accompanied by a reduced rate of maternal temperature decline during the IBI.

While it has been shown here that the temperature that a dam experiences during an IBI is an important factor in determining IBI duration, it should be noted that the IBI duration data of Experiments 4 and 5 are not directly comparable. First, dams that were forced to spend all of their IBI time on a warm floor surface showed prolonged durations between all nest contacts. Dams that spent most, but not all, of their IBI time on a warm floor surface showed only a slight prolongation of IBI durations between all nest contacts. Second, both groups showed substantial prolongation of IBIs between nest bouts in which milk delivery could occur, but the Experimental dams of Experiment 4 showed a much higher frequency of short (< 10 min) nest bouts during these IBIs. That is, the high frequency of short nest bouts contributed to the prolongation of IBIs between nest bouts in which milk delivery could occur. The dams in Experiment 5 did not show a high frequency of short nest bouts.

At least one important difference between the experimental conditions of Experiments 4 and 5 was that the Experimental pups of Experiment 4 were maintained at a much warmer temperature than were the pups of Experiment 5. The purpose of Section III is to assess the contribution of the pups to the control of the nesting pattern.

Section III

That the temperature that the dam experiences during IBIs is an important factor in determining IBI durations is clear. To say that it is the sole factor, however, would be presuming that the dam is the only active participant in the determination of the nesting pattern, and that the pups are merely passive recipients of maternal care.

Given that the pups of Experiment 4 were maintained at a much warmer temperature than the pups of Experiment 5, and that a high frequency of short (< 10 min) nest bouts contributed to the prolongation of IBIs in Experiment 4 but not in Experiment 5, it is conceivable that the pups might play an important role in determining either the duration of IBIs or whether a particular nest bout is terminated before milk delivery can occur.

The next two experiments are concerned with elucidating the role of the pups in controlling the pattern of nesting behaviour. Experiment 7 investigates whether a manipulation of pup thermal state affects the pattern of nesting behaviour while Experiment 8 investigates the role of more specific pup-related cues in controlling maternal nesting patterns.

Experiment 7

In the following experiment, pup temperature is manipulated during the dam's absence. If pup thermal state contributes to the determination of IBI duration, then pups kept warm in their dams absence should allow the dam to remain away from the pups for longer periods than when the pups are allowed to cool during IBIs.

Method

Subjects

Eighteen lactating Wistar rats and their litters, routinely reduced to eight pups at birth, served as subjects.

Apparatus

The cages used for monitoring mother-young contact in Experiment 5 were used again here.

Procedure

For all subjects, a solenoid valve (Ascoelectric Ltd., Model #110) was connected to a Tygon plastic tube (inside diameter: 1.6 mm) coiled under the nest box, allowing for a periodic flow of water. Subjects were divided into three groups of six, the primary feature distinguishing the groups being the temperature of the water allowed to flow under a 3.2 mm copper plate lining the floor of the nest box.

Upon termination of a nest bout, the solenoid was operated allowing the flow of either warm (Warm condition) or cool (Cool condition) water. Under the Unmanipulated condition no water flowed, although the solenoid was operated at nest bout termination as it was

under the Warm and Cool conditions. The Unmanipulated condition in the present experiment, then, was the same as the Unmanipulated condition of Experiment 5.

Upon initiation of a nest bout, the solenoid valve closed, preventing further water flow; thus, water flowed under the nest box floor only in the dam's absence. Relative to pups under the Unmanipulated condition, during IBIs, pups under the Warm condition should have cooled more slowly, and pups under the Cool condition should have cooled more quickly.

With warm water flowing under the nest box floor, the floor temperature of the nest was raised approximately 1°C in 10 min and 2°C in 20 min. After 24 hr of continuous flow, however, the floor temperature was raised to only 26.2°C . With cool water, the floor temperature of the nest was decreased approximately 1°C in 10 min and 2°C in 20 min. After 24 hr of continuous flow the floor temperature was 17.4°C . Floor temperatures of the cages were similar among conditions and were not altered by even 24 hr of continuous flow of either warm or cold water.

As with the subjects in Experiment 5, dams and pups were placed in the apparatus at 0900 hr on Day 9 postpartum, and testing took place between 0900 hr on Day 10 postpartum and 0900 hr on Day 11 postpartum. Microswitches from the nest boxes were again connected to an Esterline-Angus chart recorder, to obtain a continuous record of nesting activity.

Results

The distributions of IBI durations between all nest contacts are shown in Figure 26. It is clear that all three distributions are very similar, and none of the comparisons revealed any statistically significant differences (Kolmogorov-Smirnov tests; Warm-Unmanipulated: $D_{\min} = 14.6$; Warm-Cool: $D_{\min} = 16.9$; Unmanipulated-Cool: $D_{\min} = 17.1$; all p 's $> .05$).

When IBIs between nest bouts of at least 10 min duration are considered, however, the Warm and Cool group distributions differ ($D_{\min} = 22.1$; $p < .05$), while the Unmanipulated group distribution differs from neither the Warm ($D_{\min} = 21.5$; $p > .05$) nor the Cool group distributions ($D_{\min} = 21.1$; $p > .05$). These data are illustrated in Figure 27.

The mean IBI durations and the associated standard errors of the means are shown in Figures 28a and 28b. IBI durations between all nest contacts are shown in Figure 28a. It is clear from the figure that differences among the groups are minimal ($H = 3.19$; $p > .10$). The analysis of IBI durations between nest bouts of at least 10 min duration, however, revealed an overall effect ($H = 7.83$; $p < .025$), as shown in Figure 28b. The Warm group differed from both the Unmanipulated ($U = 6$; $p = .0325$) and Cool ($U = 2$; $p = .0043$) groups, while the Unmanipulated and Cool groups were similar ($U = 11$; $p = .1548$).

The distributions of nest bout durations for all groups are shown in Figure 29. Here, there is no statistical difference between the Unmanipulated and Warm groups (Kolmogorov-Smirnov test; $D_{\min} =$

Figure 26: Distributions of interbout interval durations between all nest bouts for dams whose pups were either warmed, cooled, or unmanipulated during IBIs.

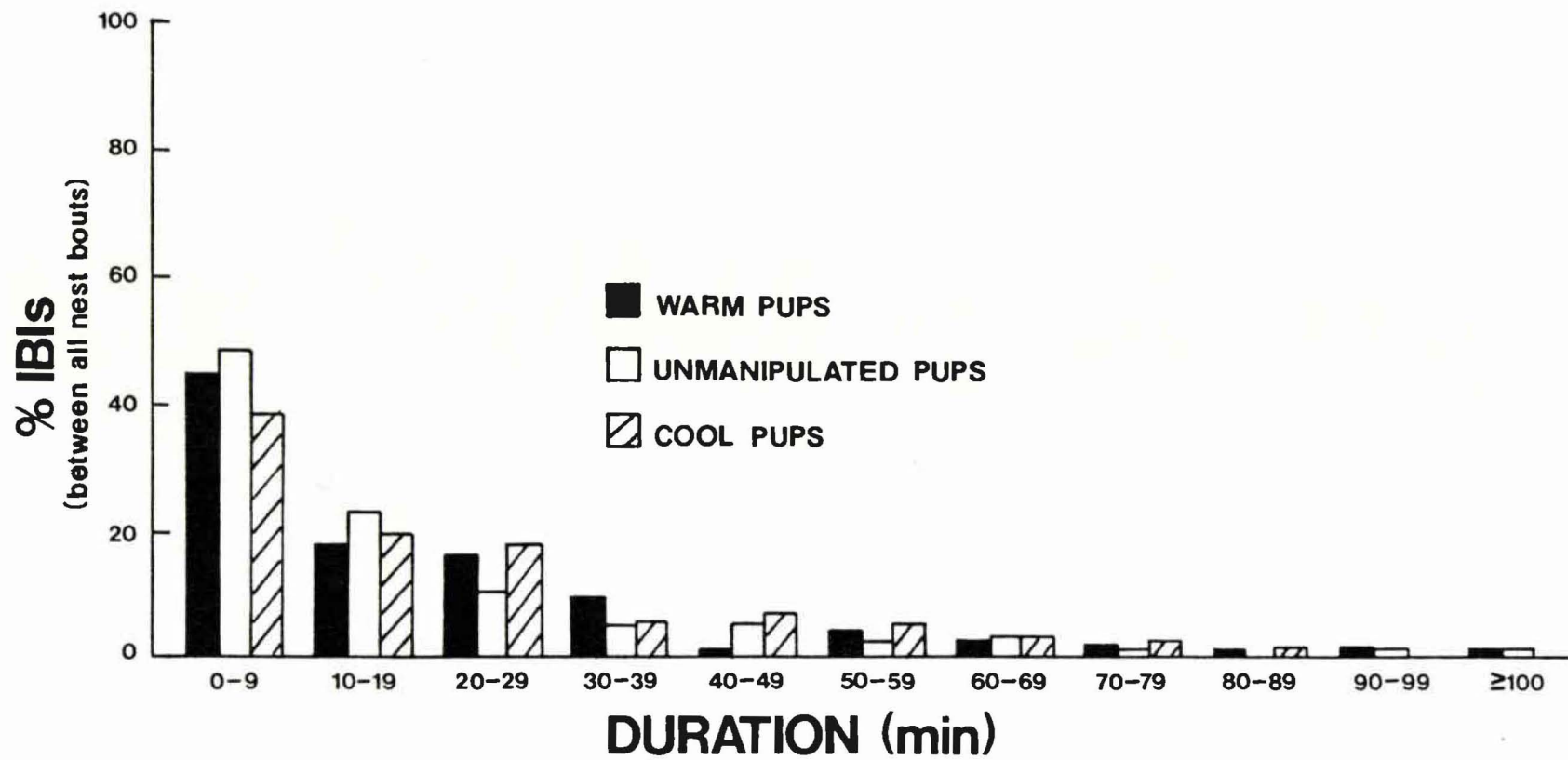


Figure 27: Distributions of interbout interval durations between nest bouts of at least 10 min duration for dams whose pups were either warmed, cooled, or unmanipulated during IBIs.

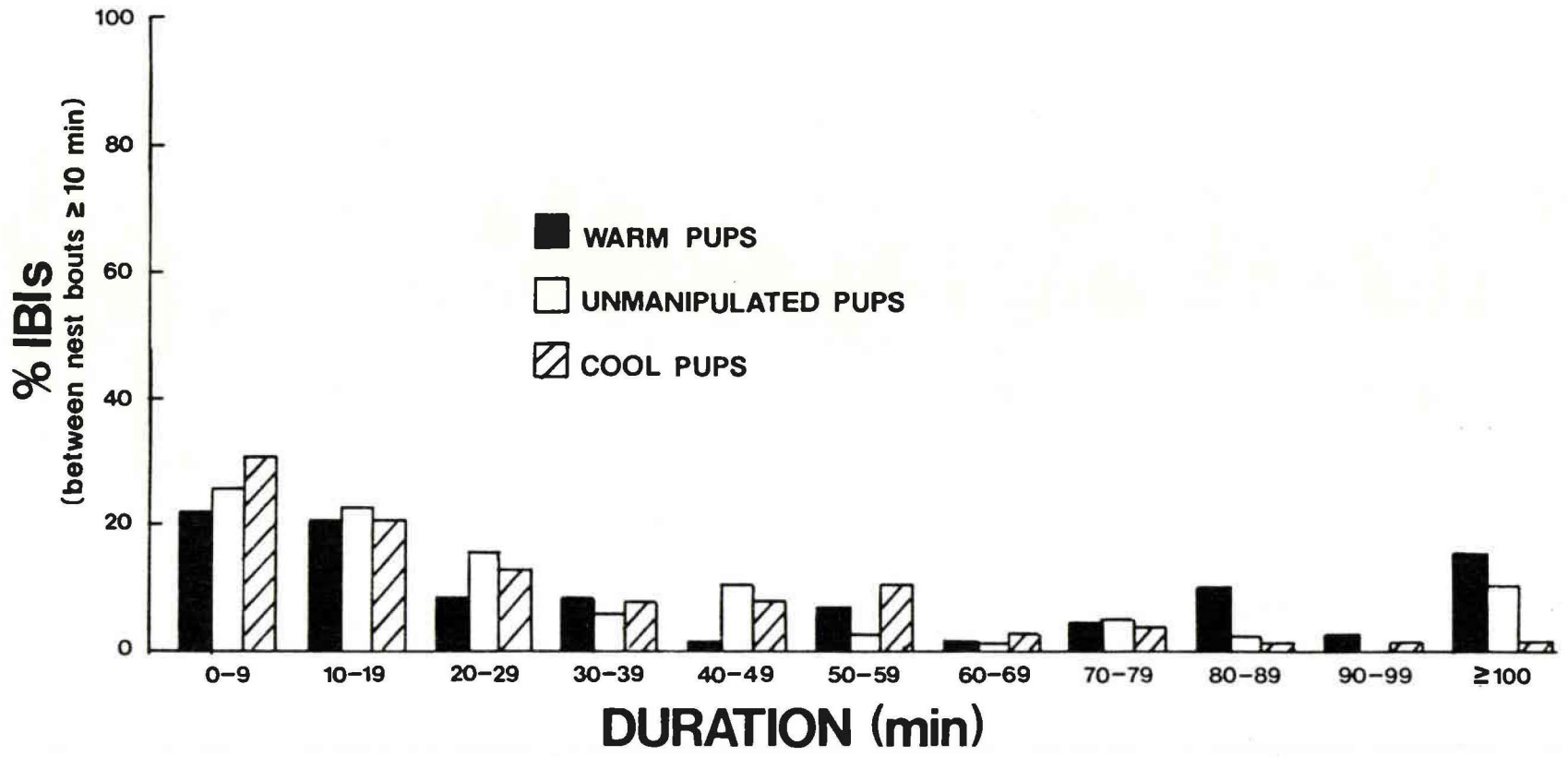


Figure 28: Mean IBI durations for dams whose pups were either warmed, cooled, or unmanipulated during IBIs. (a) illustrates mean durations between all nest bouts and (b) illustrates mean durations between nest bouts of at least 10 min duration. Superimposed bars represent standard errors of the means.

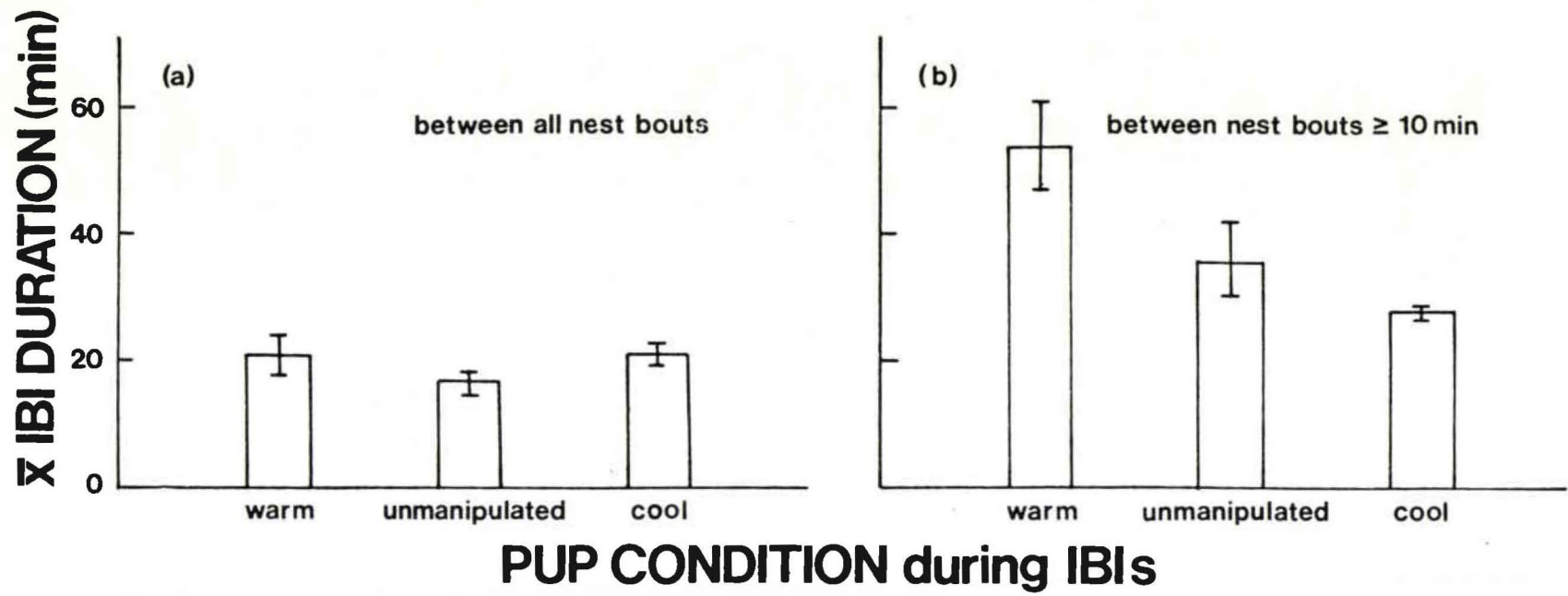
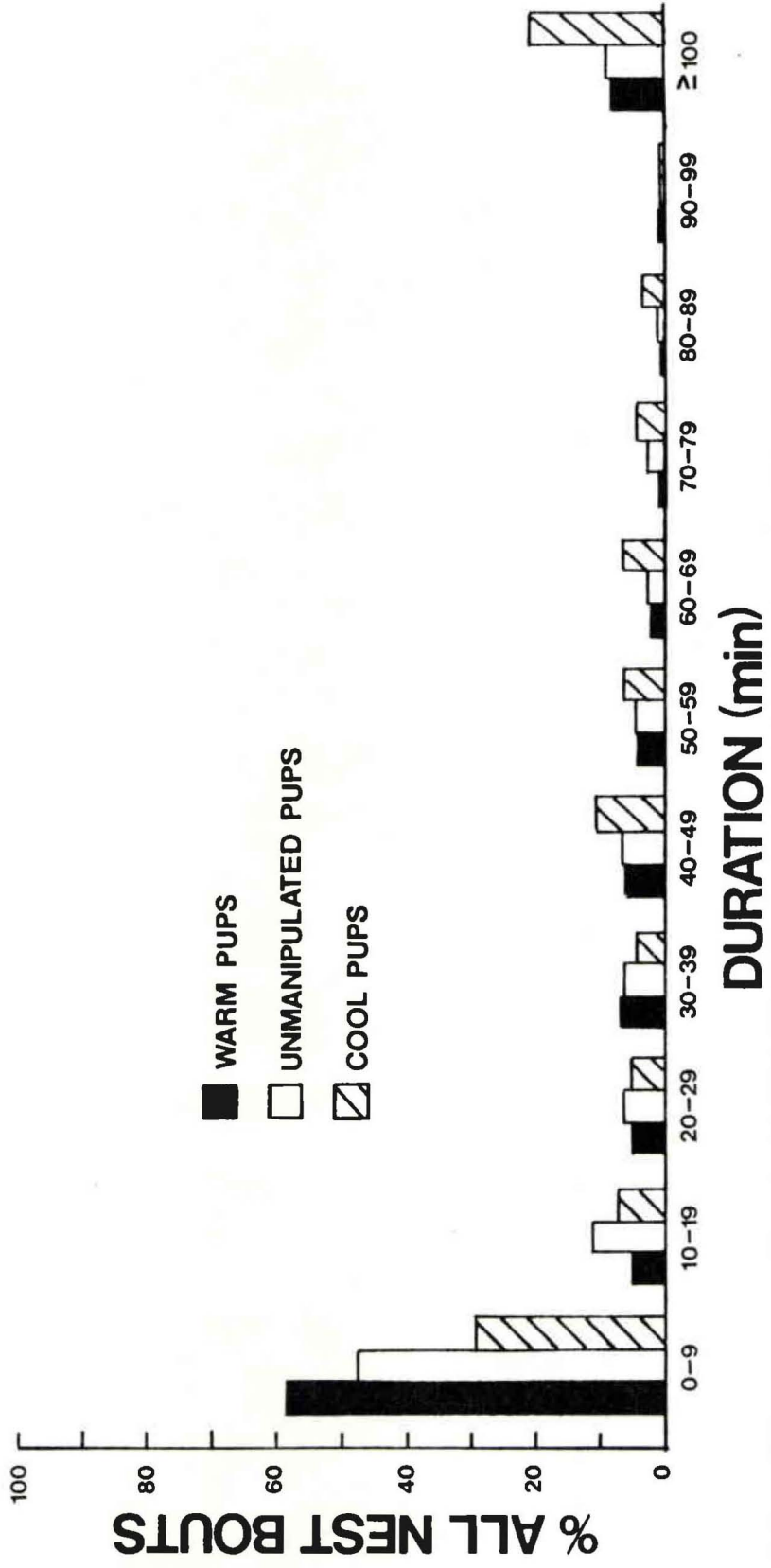


Figure 29: Distributions of all nest bout durations for dams whose pups were either warmed, cooled, or unmanipulated during IBIs.



14.6; $p > .05$), although the Warm group shows a higher proportion of nest bouts of less than 10 min. The Cool group differed significantly from both the Warm ($D_{\min} = 18.0$; $p < .025$) and Unmanipulated ($D_{\min} = 18.2$; $p < .025$) groups. These differences were due primarily to the low frequency of nest bouts of less than 10 min duration for the Cool group, relative to the Warm and Unmanipulated groups.

Eliminating nest bouts of less than 10 min duration from the analysis attenuates the differences between the groups. The distributions of nest bouts of at least 10 min duration are shown for all groups in Figure 30. Komogornov-Smirnov tests revealed no significant differences among the groups (Warm-Unmanipulated $D_{\min} = 21.5$; Warm-Cool: $D_{\min} = 22.1$; Unmanipulated-Cool: $D_{\min} = 21.2$; all p 's $> .05$).

The mean nest bout durations and the associated standard errors of the means, for all nest bouts, are shown in Figure 31a. It is clear from Figure 31a that the Cool dams showed much longer average nest bout durations than either the Warm or Unmanipulated dams. The analysis revealed statistically significant effects on nest bout durations ($H = 10.05$; $p < .01$), with the Cool group differing from both the Warm ($U = 2$; $p = .0043$) and Unmanipulated ($U = 1$; $p = .0022$) groups. The Unmanipulated and Warm groups were not significantly different ($U = 11$; $p = .1548$). The mean nest bout durations and the associated standard errors of the mean for nest bouts of at least 10 min duration are shown in Figure 31b. In this case, there was no overall effect on nest bout durations ($H = 3.14$; $p > .10$).

Figure 30: Distributions of nest bout durations for dams whose pups were either warmed, cooled, or unmanipulated during IBIs when only nest bouts of at least 10 min duration are considered.

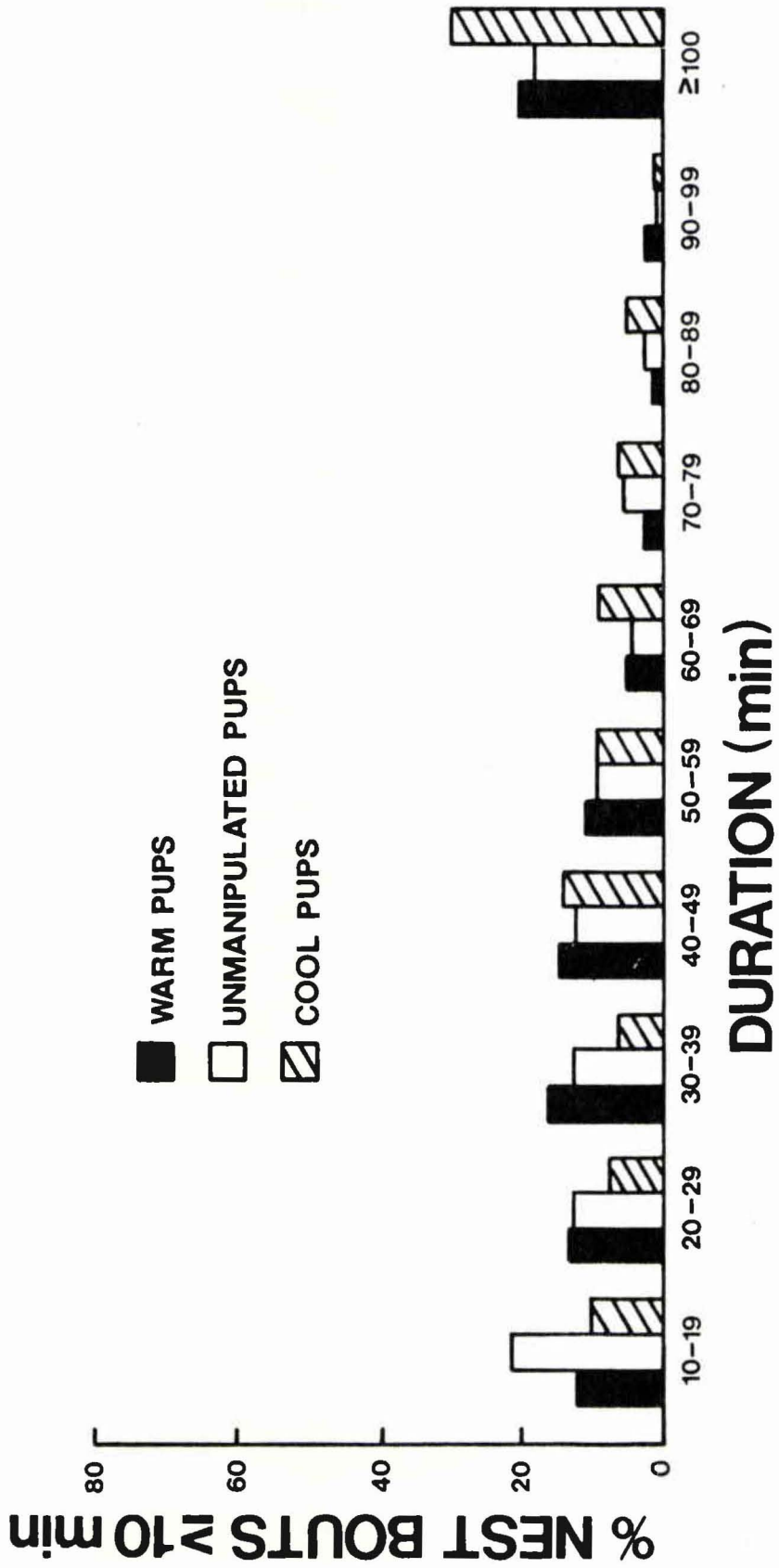
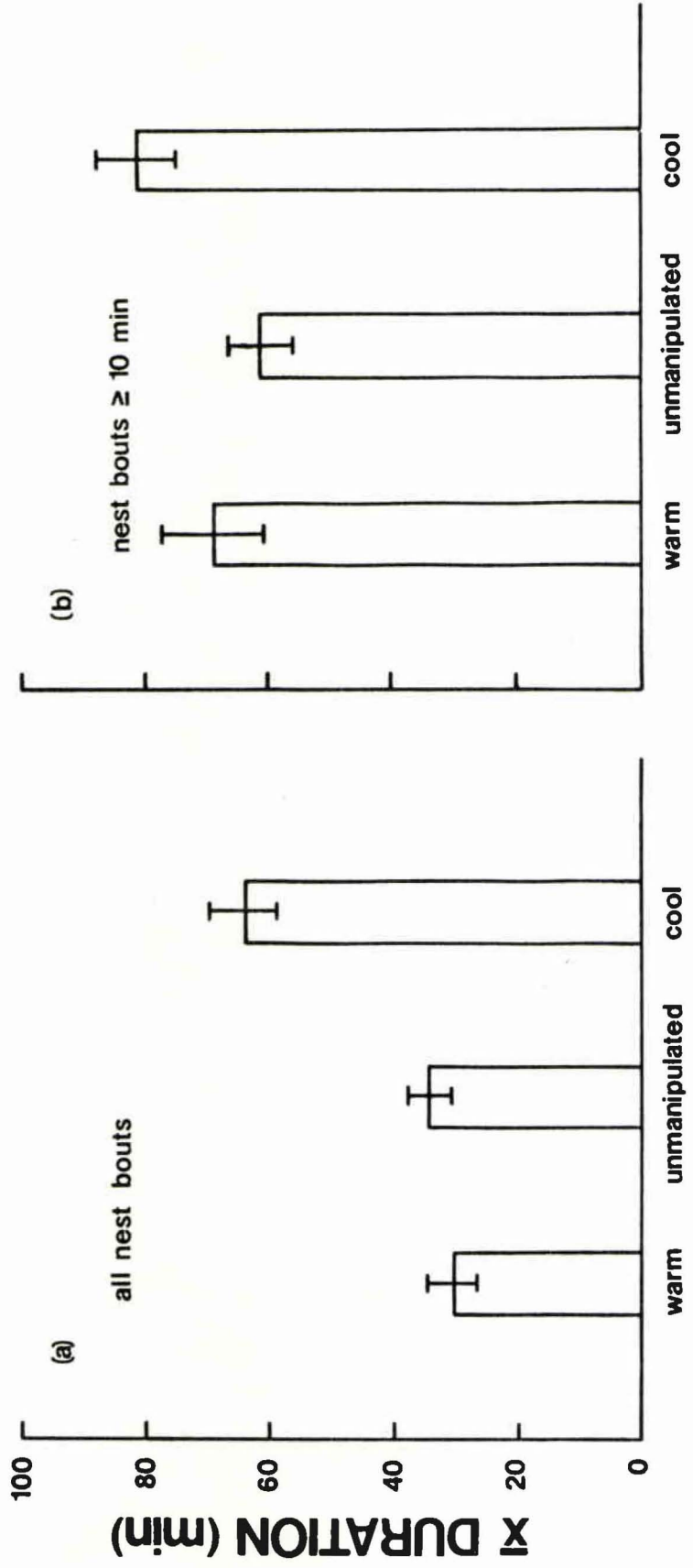


Figure 31: Mean nest bout durations for dams whose pups were either warmed, cooled, or unmanipulated during IBIs. (a) illustrates mean durations for all nest bouts and (b) illustrates mean durations for nest bouts of at least 10 min duration. Superimposed bars represent standard errors of the means.

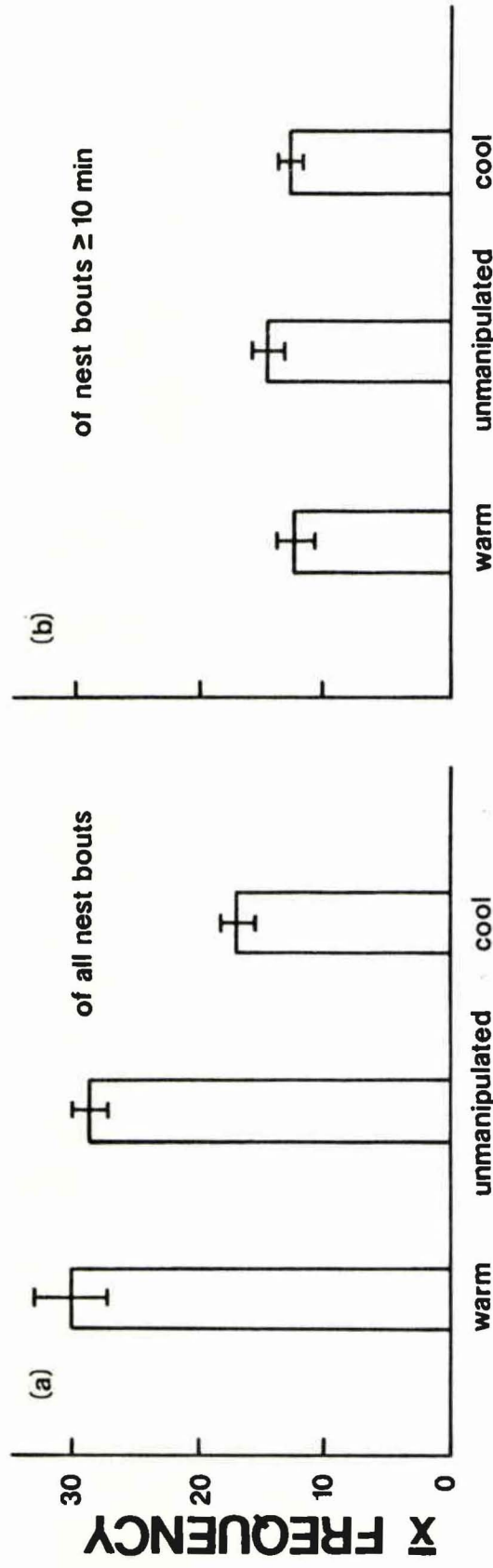


PUP CONDITION during IBIs

The mean frequencies of nest bouts, regardless of duration and the associated standard errors of the means are shown in Figure 32a. Comparable data for nest bouts of at least 10 min duration are shown in Figure 32b. There is an overall difference in the number of contacts with the pups (i.e. all nest bouts: $H = 10.28$; $p < .01$). The Cool group had significantly fewer contacts with their pups than either the Warm ($U = 2$; $p = .0043$) or Unmanipulated ($U = 0$; $p = .0011$) groups. While the Warm group had slightly more contacts with their pups than the Unmanipulated group, the difference was non-significant ($U = 13.5$; $p < .2424$). The frequencies of nest bouts of at least 10 min duration are similar among the three groups ($H = 1.51$; $p > .10$).

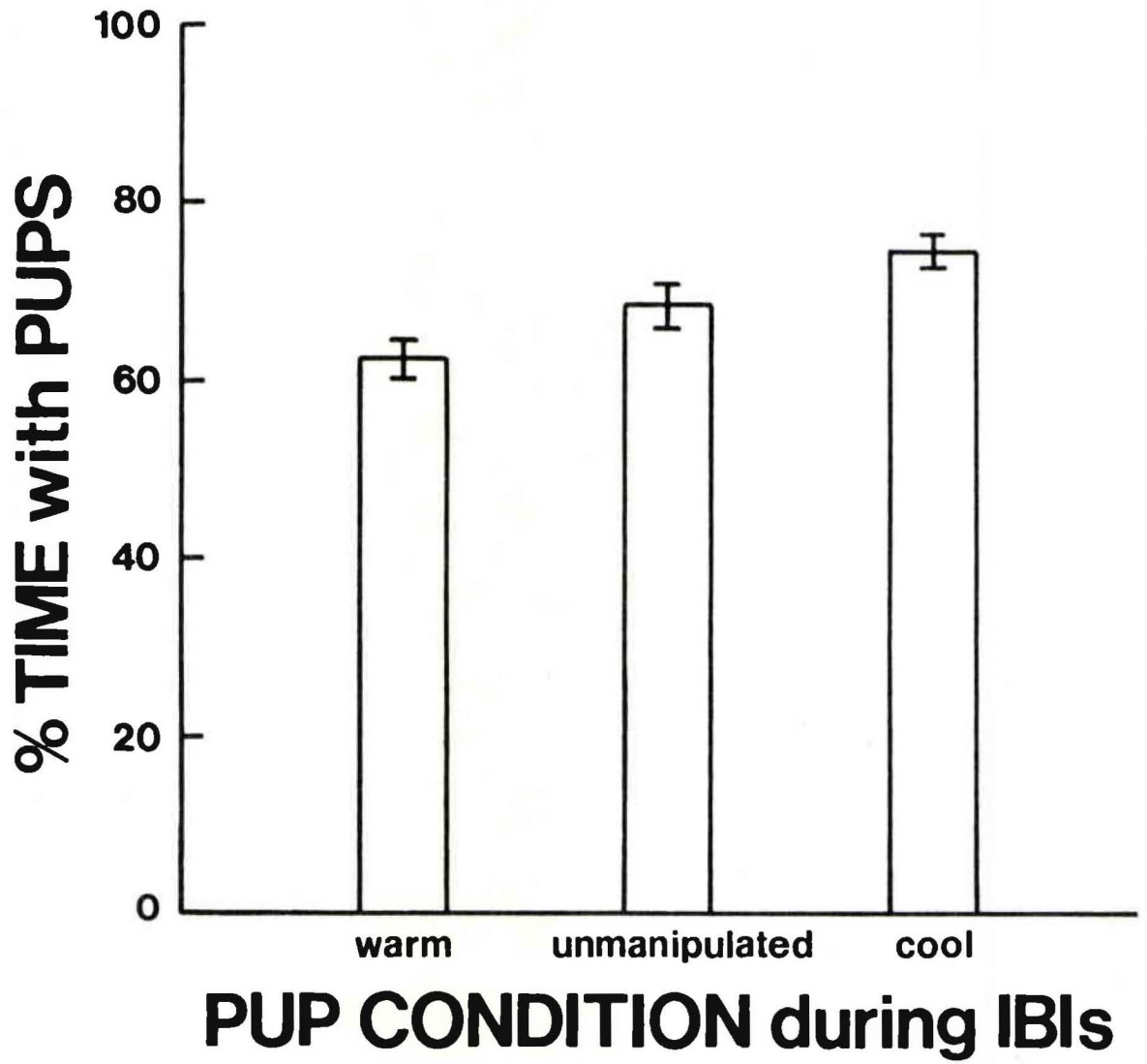
The mean percentages of total contact time are shown for all groups in Figure 33. Analysis of Variance revealed a statistically significant main effect on the total contact time ($F = 6.47$; $df = 2,15$; $p < .01$). Post hoc comparisons revealed that dams in the Warm group spent significantly less time with their pups than did dams in the Cool group (Tukey (a) test; $p < .01$), but dams in the Unmanipulated group were not significantly different from either the Warm or the Cool groups (Both p 's $> .05$). Nonparametric statistics revealed the same effects as the parametric analysis; there was an overall main effect ($H = 6.74$; $p < .05$), and paired comparisons showed that the Warm and Cool groups differed significantly ($U = 3$; $p = .0076$), while the Unmanipulated group differed from neither the Warm nor the Cool groups (both U 's = 9; $p = .0898$).

Figure 32: Mean frequencies of nest bouts for dams whose pups were either warmed, cooled, or unmanipulated during IBIs. (a) illustrates frequencies of all nest bouts and (b) illustrates frequencies of nest bouts of at least 10 min duration. Superimposed bars represent standard errors of the means.



PUP CONDITION during IBIs

Figure 33: Mean percentage of time spent with pups by dams whose pups were either warmed, cooled, or unmanipulated during IBIs. Superimposed bars represent standard errors of the means.



Discussion

The present data indicate that altering pup temperature between nest bouts is ineffective in influencing the duration of IBIs between all nest contacts. There is an effect, however, on the proportion of nest bouts in which milk delivery could not occur (nest bouts < 10 min), and consequently the duration of IBIs between nest bouts in which milk delivery could occur.

The effects of pup temperature follow two distinct courses. First, dams under the Warm pup condition showed the highest proportion of nest bouts of less than 10 min duration (although this proportion was not significantly different from that of the Unmanipulated dams). Because nest bouts of less than 10 min are included in the measure of IBIs between nest bouts of at least 10 min, dams under the Warm pup condition showed the longest durations between nest bouts in which milk delivery could occur. This pattern is similar to that shown by the Experimental dams of Experiment 4. Second, dams under the Cool pup condition showed the lowest proportion of nest bouts of less than 10 min duration, and consequently the average nest bout duration, when considering all nest contacts, was longest for this group. The duration of nest bouts in which milk delivery could occur, however, was not affected.

In both cases, the behaviour of the dams under the Unmanipulated pup condition was intermediate to that of the Warm and Cool groups. Further, it should be noted that the experimental conditions of the Unmanipulated group in the present experiment were

precisely the same as those of the Unmanipulated group in Experiment 5. It was expected, therefore, that the data from the two groups would be similar. In fact, the two groups were very much alike; the mean total mother-litter contact time, for example, differed by only 10 min. The point is raised here to emphasize that the nesting behaviour of dams under the Unmanipulated condition is clearly reliable and replicable across experiments.

It has been shown in the present experiment that manipulation of pup thermal state can alter the pattern of nesting behaviour. In the following experiment, the role of specific cues associated with the pups in influencing the dam's nesting behaviour will be investigated.

Experiment 8

It was shown in the previous experiment that the temperature of pups during IBIs can alter the pattern of nesting behaviour. The question now is by what mechanism dams respond to pup temperature. Of course, dams may simply monitor pup temperature, and return to and remain with the pups only when the pups have cooled to some extent. That is, the dam may initiate a nest bout and stay with the pups for an extended period of time (i.e. at least 10 min) only if the pups are sufficiently cool. Warm pups might produce a very sharp rise in the dam's temperature, forcing her to terminate the nest bout before milk delivery occurs. This explanation would account for both the prolonged IBIs between nest bouts of at least 10 min and the high proportion of nest bouts of less than 10 min duration observed in Experiments 4 and 7.

There is evidence, however, which indicates that the effect of a very rapid increase in maternal temperature might not account for the high proportion of nest bouts of less than 10 min duration. Woodside, Pelchat and Leon (1980), experimentally raised core temperatures of lactating rats by 1°C when on the nest. Raising the temperature took only 1 min, and the effect of raising the temperature this quickly was that dams terminated nest bouts much more quickly when heated than when not heated. The dams did not terminate the nest bout, however, until approximately 20 min after the onset of the heat. Thus, while a very rapid rise in maternal temperature produces a rapid termination of a

nest bout, the time course of the effect is such that it would probably not account for the high frequency of nest bouts of less than 10 min duration observed in the present series of studies.

Rather than the dam monitoring pup temperature, it is possible that the pups actively emit signals that influence the pattern of nesting behaviour. For example, rat pups emit ultrasonic vocalizations when cold (Okon, 1971), or when exposed to some other distress, such as rough handling (Noirot, 1968). These ultrasounds have been shown to initiate searching, retrieving, and transporting of pups by dams (Allin and Banks, 1972; Herrenkohl and Sachs, 1972; Brewster, 1978; Brewster and Leon, 1980). If ultrasounds produced by the pups induce the dam to return to the pups, it is conceivable that the warm pups of Experiments 4 and 7 were simply less likely to emit ultrasounds than were the other pups. IBIs could then have been extended in the case of dams whose pups were warm because the pups did not signal the dam to return.

There is at least one other behaviour that pups could emit that could conceivably influence the pattern of nesting behaviour. Teicher (personal communication) has shown that warm pups attach to the dam's nipples more slowly than cooler pups. In Experiments 4 and 7, then, dams with warm pups may have terminated nest bouts within 10 min simply because the pups did not attach to the dam's nipples. Thus, failure to attach to the nipples would also account for prolonged IBI durations between nursing episodes, as nest bouts of less than 10 min are included in the measure of IBI duration between bouts of at least 10 min.

The relative importance of pup temperature, pup vocalizations, and the ability of pups to attach to the dam's nipples on nest bout initiation and nest bout duration are assessed in the present experiment.

Method

Subjects

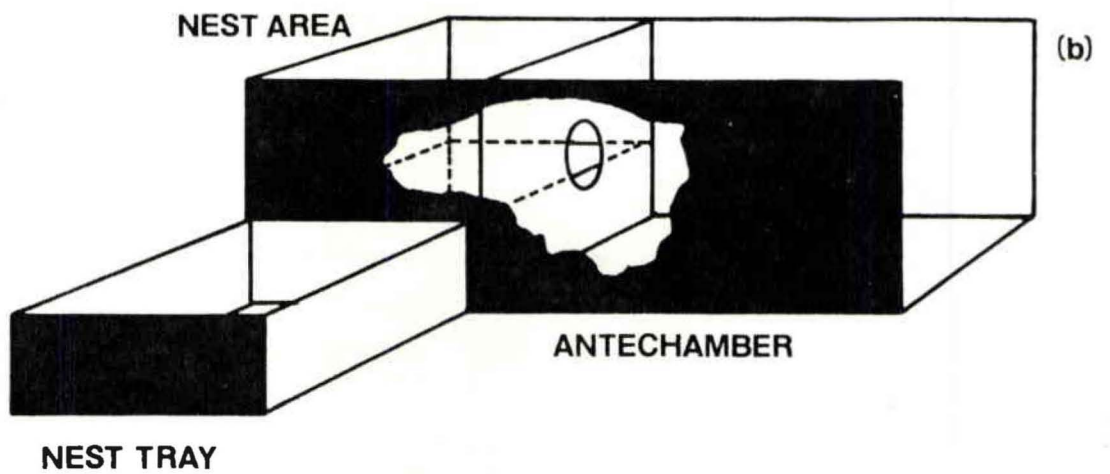
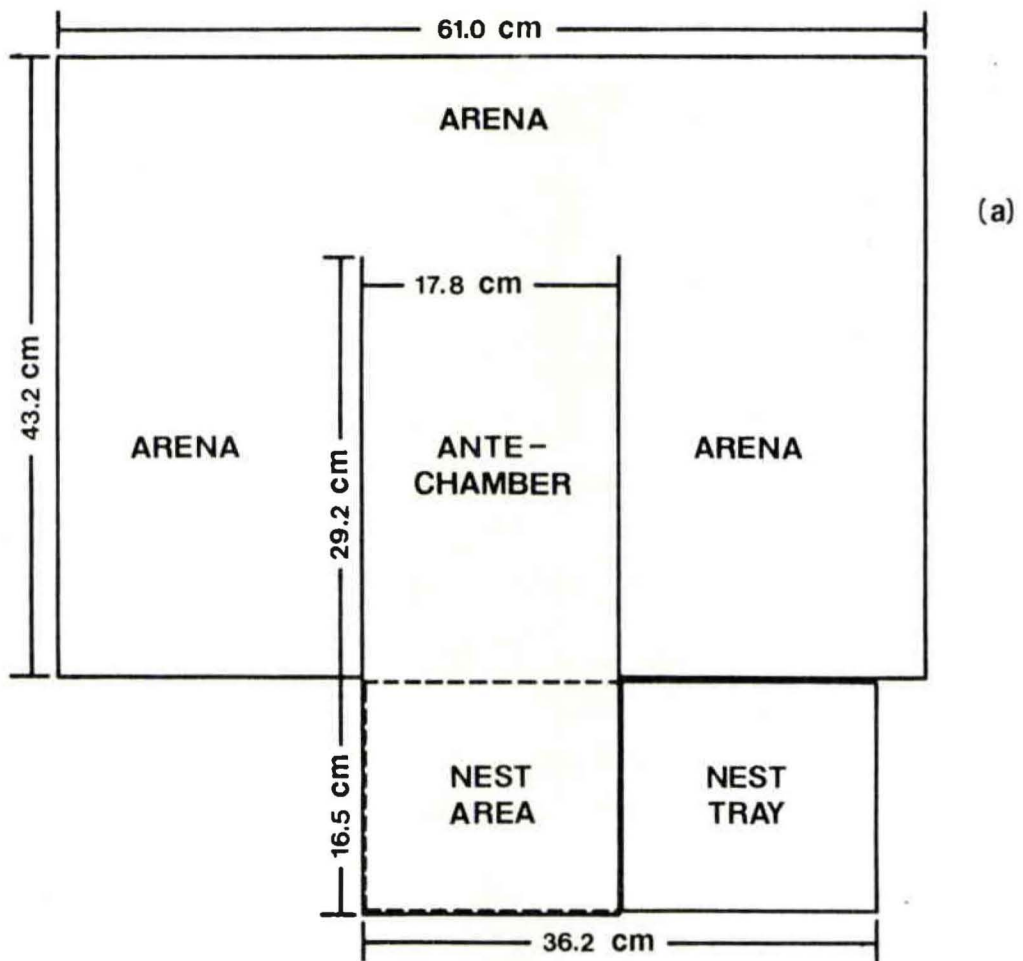
Twenty-four Day 10 postpartum lactating rats and their litters, routinely reduced to 8 pups on the day of birth, served as subjects. In addition, each of the litters used as subjects was paired with a second litter of the same age. The purpose of the latter litters is described below.

Apparatus

A cage was designed such that a nest tray could be easily slid back and forth, allowing the experimenter to present either of two nest boxes to a dam. The cage is illustrated in Figure 34.

There were three components to the cage: the nest area, the antechamber, and the arena. Dam and pups occupied the nest area and the dam could pass through the antechamber to the arena where Purina Lab chow and water were continuously available. A black 6.35 cm Plexiglas partition separated the nest area and antechamber. A 7.6 cm diameter hole in the centre of the partition allowed the dam to pass from the nest area to the antechamber. All sides of the nest area and antechamber were constructed of black, 6.35 mm Plexiglas while the arena was constructed of 1.27 cm plywood.

Figure 34: (a) Floor plan of entire apparatus for switching litters during dam's absence. (b) Side view of antechamber, nest area, and nest tray.



The arena was covered with hardware cloth and the antechamber was not covered. The nest area was covered with a hinged Plexiglas lid, so that dam and pups could be introduced or removed from the nest area without removing the hardware cloth from the top of the arena.

Further, because the nest area was completely external to the arena, a nest tray could be passed back and forth through the nest area during the dam's absence. The nest tray was twice as long as the nest area and was divided in half by a 15.3 cm x 5.7 cm Plexiglas partition. The partition, then, served to produce two separate nest boxes, one of which was enclosed by the nest area, and the other was completely external to the nest area and the larger arena.

Procedure

On the day prior to testing (Day 9 postpartum), the dam and litter were placed in the experimental cage, to familiarize the dam with the new environment. On Day 10, the experimenter entered the testing room at approximately 1000 hrs and waited for the dam to leave the nest area, which usually occurred by 1100 hrs.

The test began when the dam left the nest area. As soon as the dam stepped from the antechamber into the outer arena, the pups from the paired litter were placed in the external nest box and slid into the nest area. The experimental dam's pups were then removed from the now-external nest box. The latency to return to the nest area and, if the dam did not stay, the latency until the dam returned for a nest bout of at least 10 min duration, were recorded. After the dam had been in the nest for 10 min, the lid to the nest area was opened to determine if the pups were attached to the dam's nipples.

Subjects were divided into four groups of six. The feature distinguishing the four groups was the condition of the pups introduced into the nest area during the dam's absence. That is, the pups for each group were either cool and vocalizing, cool and nonvocalizing, warm and vocalizing, or warm and nonvocalizing.

Vocalizing, in this instance, indicated that the pups were producing ultrasonic vocalizations. The experimenter detected the ultrasounds through an ultrasonic receiver (Mini Bat Detector; QMC Instruments) tuned to transform ultrasounds at a frequency of 40 ± 3 kHz. Continuing ultrasound production was ensured by gently rolling the pups between the experimenter's hands. To ensure that the nonvocalizing pups did not produce ultrasonic or any other calls, pups were anaesthetized with .07 cc Equithesin (i.p.) prior to testing, and were monitored with the ultrasound receiver.

Both groups of vocalizing pups were removed from their dam at 0900 hrs. The nonvocalizing pups were removed from their dam and anaesthetised at 1000 hrs. The discrepancy in times when the pups were removed from their dams was necessary in order to equate, as well as possible, the temperatures of the pups when introduced into the nest area. Anaesthetised pups were found to lose heat more rapidly than awake pups, presumably because the anaesthetised pups could not actively huddle. Pup temperatures were measured with a YSI telethermometer (Model 43 TA; probe #403) at 1000 hrs and then ~~at~~ every 10 min until the test began.

The pups in the cool groups were placed in a small (15.25 cm x 11.4 cm x 5.1 cm) metal box and left exposed to a 22°C ambience.

Temperatures for the cool vocalizing pups varied between 30°C and 31.5°C, while temperatures for the cool nonvocalizing pups varied between 29.5° and 31.5°C. Both warm groups were placed in the same sort of metal box, but a 60 watt lamp was centered approximately 15 cm above the box. The lamp maintained the pups in both groups at 33.5 - 34.5°C.

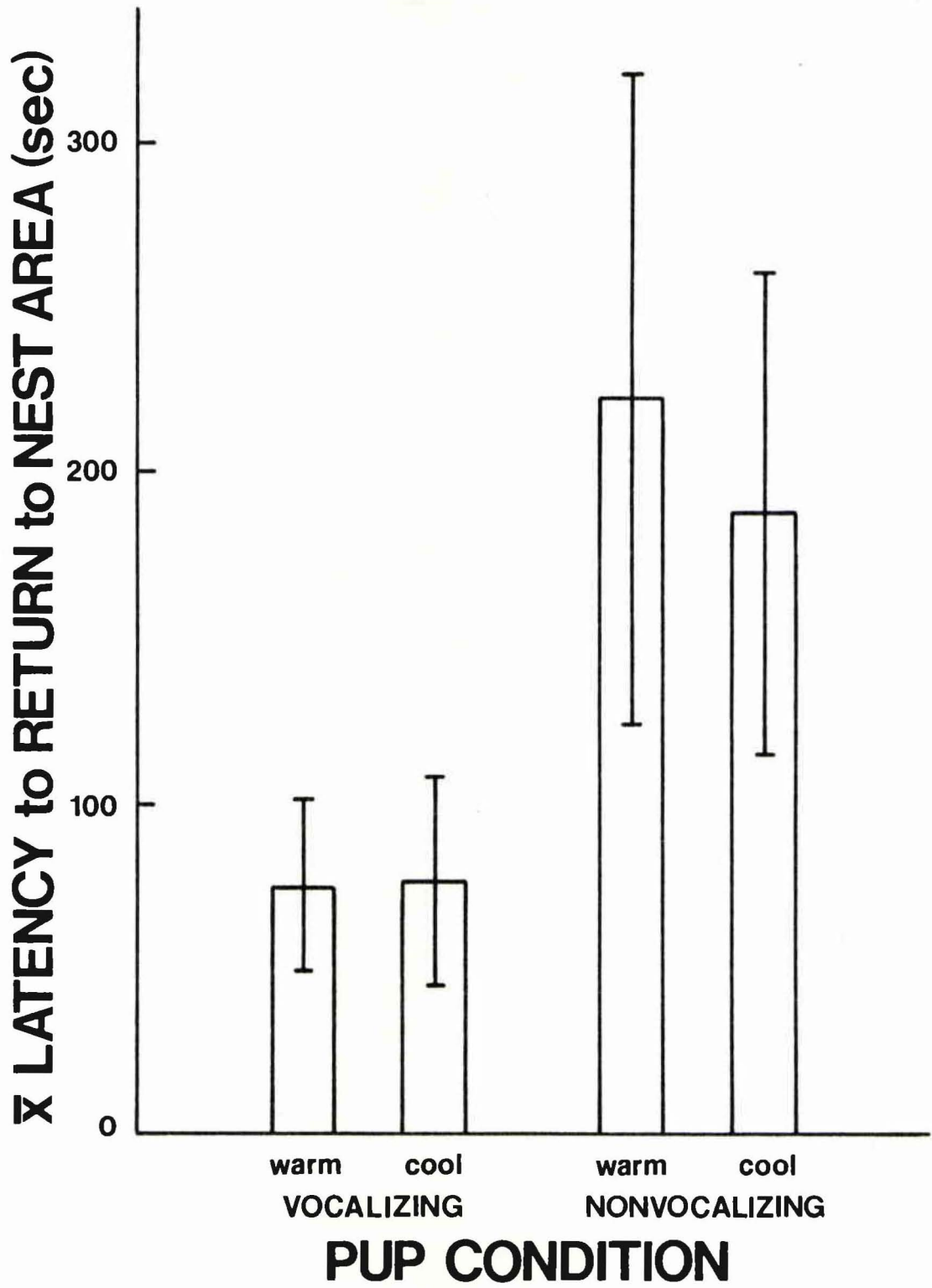
Latencies to return to the nest area were then analysed with a simple two-factor, independent groups, analysis of variance (temperature of pups; vocalizations). In addition, the importance of nipple attachment on the maintenance of mother-young contact could be assessed, as two of the four groups were incapable of attaching (the anaesthetised groups).

Results

The mean latencies to return to the nest after introducing the experimental pups to the nest area, and the associated standard errors of the means, are shown in Figure 35. It is clear from the figure that dams return to vocalizing pups more quickly than to nonvocalizing pups. The differences between returning to cool or warm pups whether the pups were vocalizing or not, were minimal.

As is clear from Figure 35, the variances differed markedly between the groups. The analysis of variance was, therefore, performed on the natural logarithm of the data points. There was an overall main effect for whether the pups were vocalizing or not ($F = 8.02$; $df = 1,20$; $p < .025$). The main effect for temperature of the pups and the interaction between vocalizations and temperature were both nonsignificant (Both F 's < 1.0 ; $df = 1,20$; $p > .10$).

Figure 35: Mean latency to return to nest area for dams returning to either warm vocalizing, cool vocalizing, warm nonvocalizing, or cool nonvocalizing pups. Superimposed bars represent standard errors of the means.



The number of dams in each group that stayed with their pups for 10 min after returning to the nest are shown in Figure 36. If the pups were cool, all dams stayed on the nest for 10 min, regardless of whether the pups were anaesthetised or not. Four of the six dams with warm unanaesthetised pups stayed for 10 min, and only one of the six dams with anaesthetised pups stayed for 10 min.

For both groups returning to cool pups, then, the latencies to return to the nest for a nest bout of at least 10 min duration are the same as those shown in Figure 35. These data are reproduced in Figure 37 with the mean latencies for dams to return to warm pups for a nest bout of at least 10 min duration. Dams with warm anaesthetised pups showed by far the longest latencies to return to the nest for at least 10 min. The two dams with warm nonanaesthetised pups that terminated their initial return to the nest before 10 min had elapsed are responsible for the large increases in the mean latency seen in this group.

It was necessary to perform a logarithmic transformation of these data before conducting the analysis. For these data, there was again an overall main effect for whether the pups were vocalizing or not ($F = 10.88$; $df = 1,20$; $p < .01$), as well as a main effect for the temperature of the pups ($F = 9.35$; $df = 1,20$; $p < .01$). The interaction was nonsignificant ($F < 1.0$; $df = 1,20$; $p > .10$). Post hoc comparisons revealed that the dams with warm anaesthetised pups returned more slowly than both groups with cold pups (Tukey (a); $p < .05$). The less conservative Tukey (b) procedure revealed that dams returned to warm anaesthetized pups more slowly than to warm

Figure 36: Number of dams that returned to either warm vocalizing, cool vocalizing, warm nonvocalizing, or cool nonvocalizing pups and stayed with the pups for 10 min.

No. DAMS that STAYED with PUPS 10 min

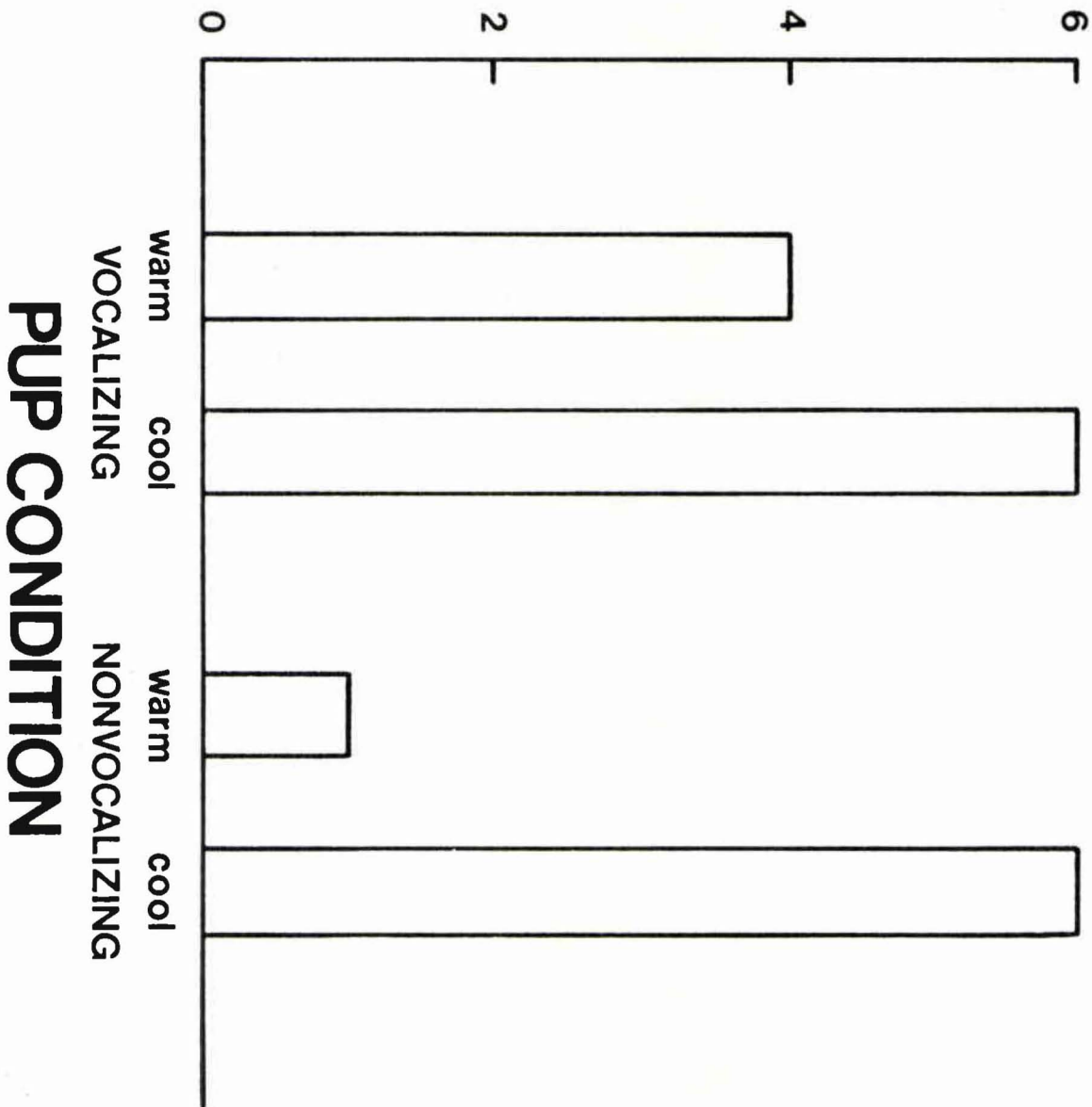
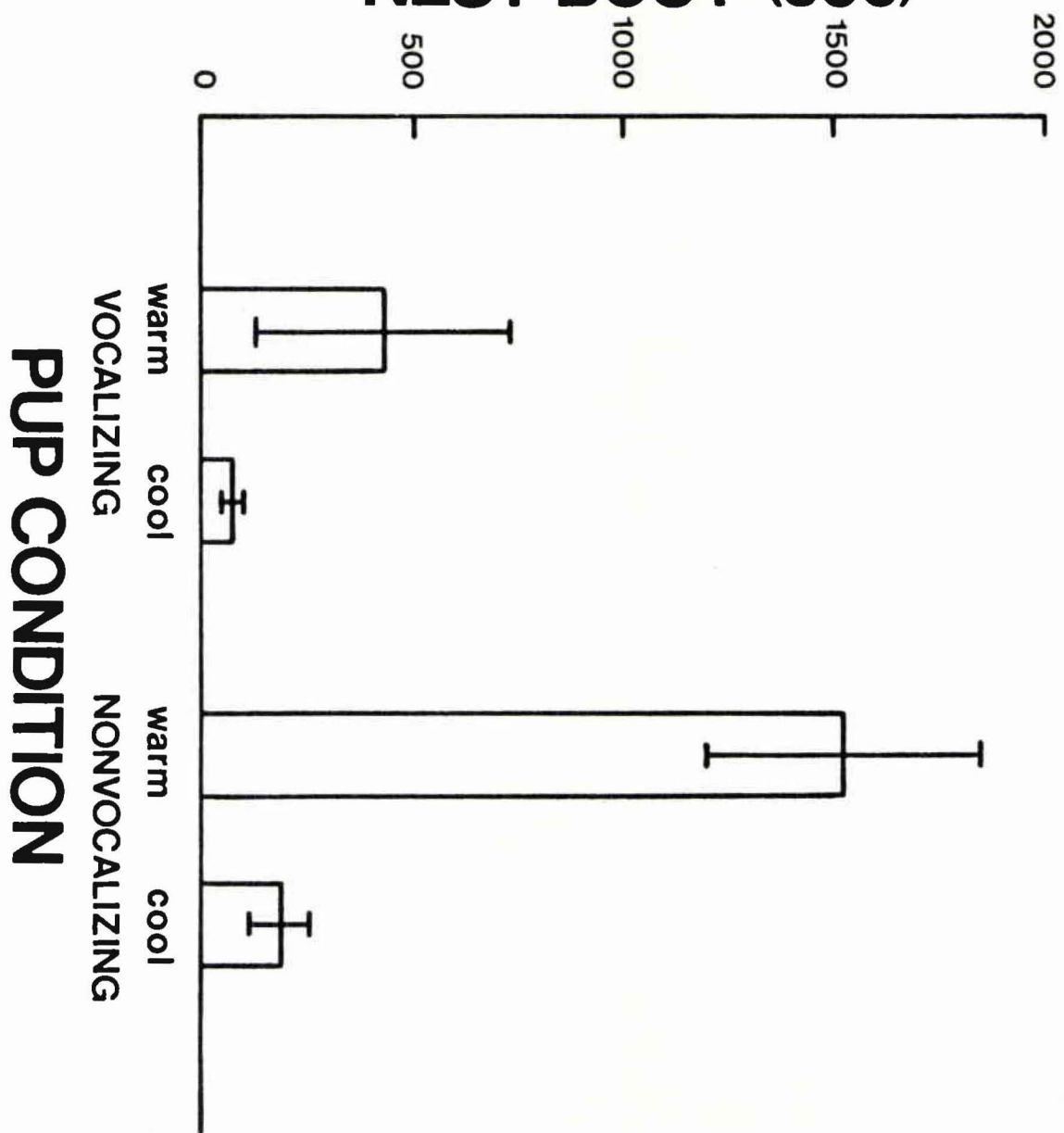


Figure 37: Mean latency to return to the nest area for a 10 min nest bout for dams returning to either warm vocalizing, cool vocalizing, warm nonvocalizing, or cool nonvocalizing pups. Superimposed bars represent standard errors of the means.

\bar{x} LATENCY to a 10 min NEST BOUT (sec)



nonanaesthetized pups ($p < .05$). None of the other comparisons were statistically significant.

Finally, when checked after the dams had eventually stayed on the nest for 10 min, all of the nonanaesthetized pups were attached to the dams nipples and, of course, none of the anaesthetized pups were attached.

Discussion

The results of the present experiment indicate that cues associated with the pups can control at least part of the dam's nesting behaviour. Consider first the dam's initial latency to return to the nest.

It is fairly clear that ultrasounding pups are more likely to prompt the dam to return to the nest than are nonultrasounding pups. That is, one half of the dams returning to vocalizing pups (i.e. 3 dams from each of the warm and cool groups) returned to the pups very quickly (within 35 sec), while the other 6 dams recorded latencies which were within the distribution of latencies shown by the dams returning to nonvocalizing pups.

In addition to the latency to return to the pups, other aspects of the behaviour of the dams differed depending upon whether they were returning to vocalizing or nonvocalizing pups. The behaviour of the dams returning to nonvocalizing pups was fairly stereotyped. The dams typically groomed, occasionally sniffing about the arena, and then returned to the nest. A few of the dams paused briefly at the food bowl before returning. There was no indication of distress or

excitement on the part of the dams, and all poked their heads into the nest area for 10 to 30 sec before entering.

Dams returning to vocalizing pups showed a slightly different pattern of behaviour. First, within 20 sec of the introduction of the pups to the nest area, all dams stopped short and perked their ears. Ultrasounds from the pups were detected by the experimenter throughout this 20 sec period. While 6 of these dams returned to the nest almost immediately, the other 6 resumed their activities, which again was typically grooming. All dams, however, when returning to the nest, did so without pausing outside the nest area as dams returning to nonvocalizing pups had done.

It seems clear, then, that the pups are capable of altering the pattern of nesting behaviour by emitting ultrasounds. How frequently the pups might emit ultrasounds, however, is open to question. For example, Hofer and Shair (1978) monitored pup ultrasonic vocalizations on Day 14 postpartum during the regular pattern of maternal care. They found that ultrasounds occurred most frequently during the 3 min period after arrivals and departures of the dam. Further, they found no increase in ultrasounds prior to the dam's arrival.

The findings of Hofer and Shair (1978), however, should not be taken to minimize the importance of the present data. Hofer and Shair found that under laboratory conditions the pups are not likely to emit ultrasounds. This may be due to the fact that pups in the laboratory are typically under very little stress. The present findings indicate that should the pups be stressed, and thus begin to emit ultrasounds, the vocalizations would prompt the dam to return to the nest fairly quickly.

One final observation with regard to the initial latency to return to the nest is that dams did not respond differentially to cool or warm pups, whether the pups were vocalizing or not. Apparently, then, dams do not simply monitor the temperature of the pups and return to the nest only when the pups have cooled.

While the temperature of the pups did not influence the initial latency to return to the nest, it did influence the duration of the nest bout. All dams returning to cool pups stayed with the pups for at least 10 min. If the pups were cool, then, whether they were also capable of nipple attachment or not was not a critical determinant of nest bout duration.

On the other hand, only 5 of the dams returning to warm pups stayed for 10 min. Of these 5 dams, 4 were with pups that were capable of nipple attachment. While this is not a statistically significant difference, it does suggest that if the pups are warm, nipple attachment becomes a relevant factor in maintaining mother-young contact. That is, while dams are less likely to stay with warm pups, as opposed to cool pups, for at least 10 min (and thus long enough for milk delivery to occur), the dams are even more unlikely to stay with pups for 10 min if the pups do not attach to her nipples.

In summary, then, there is both a passive and an active aspect to the pups' control over the nesting pattern. Considering the passive aspect first, dams will initiate nest bouts and stay with the pups (for at least 10 min) if the pups are cool. That is, if the pups are cool, there is no need for the pups to actively emit any signals to the dam. On the other hand, pups can actively influence the duration between

nest contacts by emitting ultrasonic vocalizations, and can also actively induce the dam to maintain contact by attaching to the dam's nipples.

Summary and General Discussion

The present series of studies have focussed predominantly on the effects of thermal factors on the pattern of nesting behaviour in the Norway rat. Previous investigations (Croskerry et al., 1978; Leon et al., 1978; Woodside et al., 1980) have shown that nest bouts are limited, at least partially, by a rise in maternal body temperature. The central finding of the present investigation was that when dams were allowed to freely select from a wide range of surface temperatures, and thus could control the likelihood of experiencing a temperature rise during a nest bout, as well as their rate of temperature decline between nest bouts, the amount of time that the dams spent in contact with their pups was sharply reduced.

But while previous investigations placed the onus for nest bout termination on the dam and assumed that the pups played a passive role, the present findings indicate that the pups can play both a passive and an active role in the control of the nesting pattern. Thus, there seems to be an interaction between cues associated with the pups and cues associated with the dam which determines whether a nest bout will be initiated, maintained, or terminated, and also determines the duration of IBIs.

There were three aspects of the dam's nesting pattern which were markedly different from the nesting pattern of control animals and which contributed to the reduction in mother-litter contact. First, nest bout durations were much shorter, presumably because the dams

placed their pups on a warm surface, and were thus more likely to experience a fairly rapid rise in temperature during nest bouts. Second, while the dams showed a similar frequency of nest bouts in which milk delivery could occur (nest bouts \geq 10 min), they also showed a much higher frequency of nest bouts in which milk delivery could not occur (nest bouts $<$ 10 min). Further experimentation indicated that maintaining the pups at a warm temperature during IBIs produced this high frequency of such short nest bouts, and that one possible contributing factor was the latency of the pups to attach to the dam's nipples.

The high frequency of short nest bouts also contributed to the third aspect of the nesting pattern - prolonged durations between nest bouts, particularly nest bouts of at least 10 min duration. That is, because the pups were warm, and perhaps also because the pups failed to attach to the dam's nipples, nest bouts were more frequently terminated within 10 min, thus increasing the time between nest bouts of at least 10 min duration. In addition, it was shown that the temperature that the dam experienced between nest bouts also contributed to the duration of IBIs, and that prolonged IBIs were associated with a slow rate of maternal temperature decline.

Finally, it was also found that pups could actively curtail IBIs by emitting ultrasonic vocalizations. While these ultrasounds may not play an important role in a laboratory situation, they are clearly of potential importance should the pups come under some stress.

Perhaps the most important implication of all of the above findings is that, at least on Day 10 postpartum, dams do not attempt to

maximize the amount of time that they spend with their pups. Indeed, it could be concluded that the dams attempt to maximize the total amount of time away from the pups. While the extra time away from the pups may not be important in the ad lib laboratory situation, it is a potentially important resource, as it allows the dam more time for foraging, and extra time for foraging is potentially beneficial to both dams and pups. It is clear from the present investigation that dams were able to purchase this resource by simply placing their pups on a warm surface.

Placing the pups on a warm surface may also help the dam perform her two most important pup-oriented functions: keeping the pups warm and feeding the pups. It is clear from the present investigation that dams can (and actually do) use the environment to keep the pups warm. Thus, the dams can fulfill one of her functions without devoting a great deal of time to the performance of that function. By keeping the pups warm during her absence, the dam also may be helping herself to perform the function of feeding the pups by not only allowing herself more time between nest bouts for foraging, but also if the pups are warm, they would presumably expend less energy during the dam's absence, and thus the overall growth of the pups may not be hindered by prolonged absences of the dam.

There is one other aspect of the feeding of the pups which should be noted. Although the dams that chose to nest on a warm surface had a frequency of nest bouts in which milk delivery could occur which was similar to that of control animals, the durations of such nest bouts were typically shorter than those of the control

animals. Given that Wakerley and Lincoln (1971) have shown that the time between successive milk ejections is fairly constant it is conceivable that these pups were not receiving as many milk deliveries as the control pups. Drewett and Trew (1978), however, have shown that the quantity of milk delivered per ejection within a nest bout decreases over successive ejections, and that the quantity delivered during the first ejection is almost twice that of any successive ejection. Thus, while it is possible that pups on the warm surface received fewer milk ejections, the absolute difference in terms of quantity of milk may have been minimal. It should also be noted, however, that both Wakerley and Lincoln (1971) and Drewett and Trew (1978) tested dams suckling pups at room temperature. An interesting question, then, is whether, in addition to the pattern of nesting, the timing of milk ejections also changes as a function of the temperature at which the dam suckles the pups.

From a wider perspective, it is probably best to consider the dams as being involved in a decision-making process while nesting (McFarland, 1977). McFarland (1977) has characterized animals as "optimizing agents", and has suggested that animals are capable of evaluating alternatives and maximizing, in terms of reproductive success, the combined value of the alternatives. Thermal factors, then, can be considered one class of factors involved in the dam's decision-making process while nesting.

Specifically, the dam must make several decisions concerning where to locate her nest, when to initiate nest bouts and when to terminate nest bouts. It has been shown in the present investigation

that surface temperature is an important factor in the decision of where to locate the nest. In a more natural situation, however, temperature would be only one factor among several (such as predator protection, accessibility to food, etc.) which the dam would have to evaluate in her decision. Similarly, while dam and pup temperatures have been shown to be important factors in the control of initiation and termination of nest bouts and IBIs, other factors such as predator avoidance, availability of food, the dam's need for food, etc., should also be evaluated by the dam before initiating or terminating nest bouts.

Appendix A

The Effects of Lactation and Ambient Temperature on Body Temperatures of Female Norway Rats

J. Jans, C. Marlatt, and M. Leon

McMaster University

Previous research has shown that female Norway rats have higher body temperatures when lactating than when nonlactating (Woodside, 1978). Further, Woodside and Woodside, Pelchat, & Leon (1980) showed that rats have higher body temperatures and are more likely to show a rise in core temperature when with their pups during the second postpartum week than during the first week.

The primary aim of the present experiment is to assess the effects of warm and cold ambient temperatures on dams' abilities to maintain their body temperature. Woodside's findings suggest that there should be differential effects of Day 4 postpartum, Day 10 postpartum, and when the dams are nonlactating. Specifically, lactating rats should show less ability to maintain their temperature in a warm ambient temperature than nonlactating rats, and this loss of ability to maintain body temperature should be more pronounced in the second week postpartum

Method

Subjects

Eighteen female Wistar rats served as subjects.

Apparatus

During the testing periods dams were housed individually in small (inside dimensions: 11.4 cm x 12.7 cm x 14.0 cm), wooden isolation boxes. Nine small air holes (0.6 cm diameter) provided some air circulation. Core temperatures were measured with a YSI telethermometer (Model 43TA), using YSI probe #428.

Procedure

The 18 female rats were divided into 3 groups of 6. Each group was tested in one of three environmental temperatures: Control (22.0°C), Warm (28.0°C), and Cold (4.0°C). The control environmental temperature is similar to that used in previous studies of nesting behaviour (e.g. Leon, Croskerry, and Smith, 1978). The warm temperature is similar to the mean temperature chosen by the dams in Experiment 2 of the present report (see Figure 2a; open symbols). It was not possible to test the Cold group dams in a temperature of about 16 - 18°C, which would have been similar to the mean temperature chosen by the nest-building dams of Experiment 2.

Each rat was tested twice during lactation (on Day 4 and Day 10 postpartum), and once when nonlactating. On the day of testing, rats were placed in an isolation box and moved to the appropriate environmental temperature: Control animals were placed on a counter in normal room temperature; Warm animals were placed in an oven (Thelco, Model 16); and Cold animals were placed in a refrigerator (Westinghouse Frost Free, Model 14). Dam core temperatures were measured every 15 min over a 2 hr period. Dams were then returned to their home cage until the next day of testing. Following testing on Day 10 postpartum,

the pups were removed from the home cage and the dams were tested 72 hr later, by which time they had stopped lactating.

Results

Core temperatures are plotted against time for the Cold Control, and Warm dams in Figures 38a,b, and c, respectively. The data were analysed with a three factor analysis of variance for one independent measure (ambient temperature) and two repeated measures (stage of lactation and time). The summary table for the analysis is shown in Table 2. As is shown in the table, all of the main effects, as well as the interactions between time and stage of lactation and time and ambient temperature, were statistically significant. Post hoc analyses revealed that the dams exposed to the warm temperature had consistently higher core temperatures than either the Control or Cold dams (Tukey (a); $p < .01$), but there was no difference between the Control and Cold dams (Tukey (a); $p > .05$). In addition, the dams had higher core temperatures on Day 10 postpartum than on Day 4 postpartum and, in turn, had higher core temperatures on Day 4 postpartum than when nonlactating (Tukey (a); all p 's $< .01$).

Discussion

As expected, all rats had higher body temperatures when lactating than when nonlactating, and were generally warmer on Day 10 than on Day 4 postpartum. Further, the Warm dams were less able to maintain their body temperatures on Day 10 than on Day 4 postpartum, and were most capable when nonlactating. These data confirm previous findings (Woodside, 1978; Woodside, Pelchat, and Leon, 1980).

Figure 38: Average core temperatures of dams exposed to either (a) cold (4°C), (b) control (22°C), or (c) warm (28°C) ambiances over a 2 hr testing period. Core temperatures were measured every 15 min and all dams were tested on three occasions: once when nonlactating, once on Day 4 postpartum, and once on Day 10 postpartum. Symbols represent the mean core temperatures and bars represent the standard errors of the means.

X CORE TEMPERATURE °C

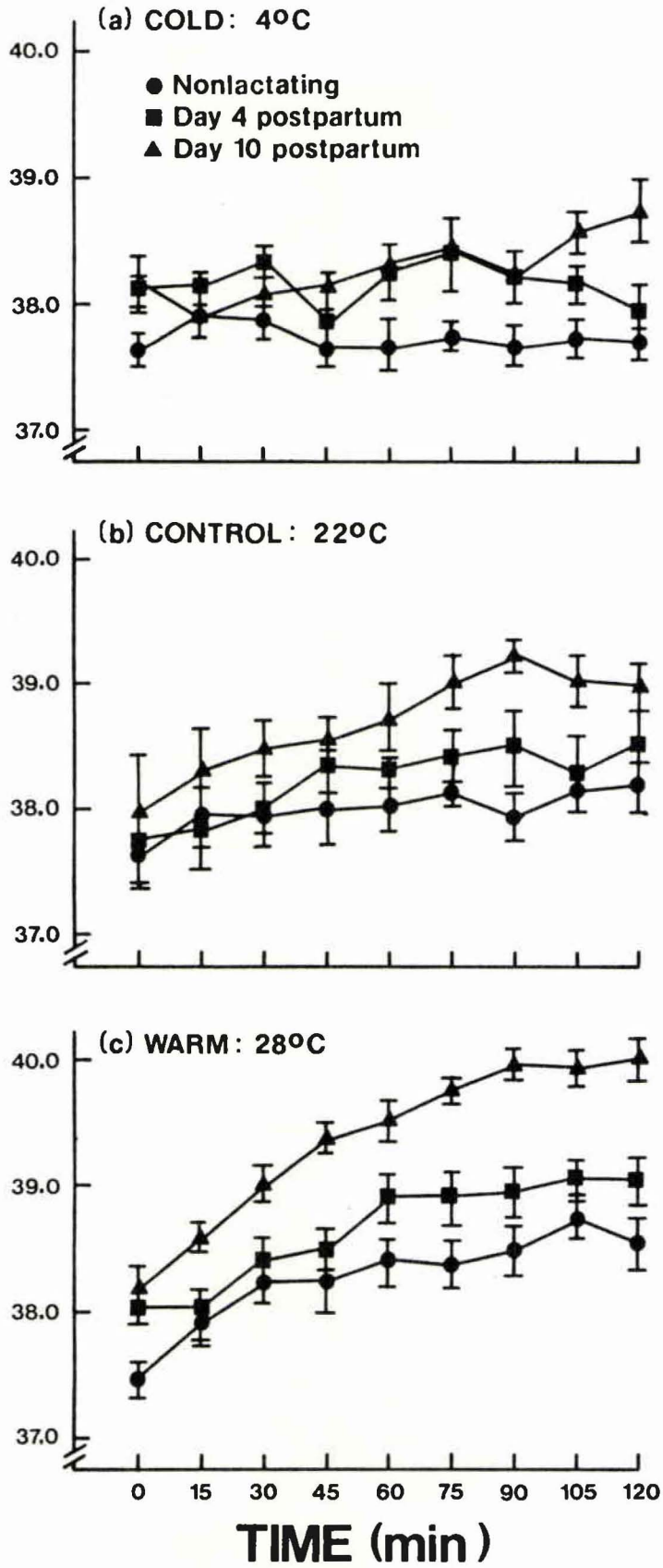


Table 2
Source table for analysis of variance

Source	SS	df	MS	F
Total	232.55	485		
Between Ss	58.99	17		
Temperature	40.43	2	20.22	16.31**
SwTemp	18.56	15	1.24	
Within Ss	173.45	468		
Days	50.49	2	25.25	28.06**
Days x Temp	6.45	4	1.61	1.79
Days x SwTemp	27.05	30	0.90	
Time	30.81	8	3.85	27.50**
Time x Temp	12.89	16	0.81	5.79**
Time x SwTemp	16.22	120	0.14	
Days x Time	5.87	16	0.37	4.63**
Days x Time x Temp	3.56	32	0.11	1.38
Days x Time x SwT	20.22	240	0.08	

**p < .01

The fact that the Control rats showed a rise in core temperature over time (especially on Day 10) is probably due to the small amount of air circulation in the isolation boxes. The boxes were quite small, and the air holes probably did not offer much circulation.

The most important point, however, is that the Warm rats showed less ability to maintain their body temperatures than either the Control or Cold rats. The warm ambient temperature was similar to the mean temperature chosen by the dams in Experiment 2 of the present report. Thus, establishing a nest in a warm ambient temperature would have the end result of decreasing the amount of time that the dams could stay with the pups per nest bout.

REFERENCES

- Allin, J. J. and Banks, E. M. Functional aspects of ultrasound production by infant albino rats (Rattus norvegicus). Animal Behaviour, 1972, 20, 175-185.
- Brewster, J. Transport of young in the Norway rat. Unpublished doctoral dissertation, McMaster University, 1978.
- Brewster, J. and Leon, M. Relocation of the site of mother-young contact: Maternal transport behavior in Norway rats. Journal of Comparative and Physiological Psychology. 1980, 94, 69-79.
- Croskerry, P. G. Normal prenatal and postnatal development of the Hooded rat and the effects of prenatal treatment with growth hormone. Unpublished doctoral dissertation, McMaster University, 1975.
- Croskerry, P. G., Smith, G. K., and Leon, M. A. Thermoregulation and the nesting behaviour of the rat. Nature, 1978, 273, 5660.
- Croskerry, P. G., Smith, G. K., Leon, L. N., and Mitchell, E. A. An inexpensive system for continuously recording maternal behaviour in the laboratory rat. Physiology and Behavior, 1976, 16, 223-225.
- Drewett, R. F. and Trew, A. M. The milk ejection of the rat, as a stimulus and a response to the litter. Animal Behaviour, 1978, 26, 982-987.
- Gelineo, S. and Gelineo, A. La temperature du nid du rat et sa signification biologique. Bulletin of Academic Serve. Science, 1952, 4, 197-210.

- Grota, L. J. and Ader, R. Continuous recording of maternal behaviour in Rattus norvegicus. Animal Behaviour, 1969, 17, 722-729.
- Herrenkohl, L. R. and Sachs, B. P. Sensory regulation of maternal behavior in mammals. Physiology and Behavior, 1972, 9, 689-692.
- Hofer, M. A. and Shair, H. Ultrasonic vocalization during social interaction and isolation in 2-week-old rats. Developmental Psychobiology, 1978, 11, 495-504.
- Hughes, C. W., Harlan, R. S., and Plaut, S. M. Maternal behavior of wild and domestic Rattus norvegicus recorded continuously in dual-chambered cages. Developmental Psychobiology, 1978, 11, 329-334.
- Kinder, E. F. A study of nest-building activity of the albino rat. Journal of Experimental Zoology, 1927, 47, 117-161.
- King, J. A. Maternal behavior in Peromyscus. In H. L. Rheingold (Ed.), Maternal behavior in mammals. New York: John Wiley & Sons, 1963.
- Leon, M., Croskerry, P. G., and Smith, G. K. Stimulus control of nesting behavior. Physiology and Behavior, 1978, 21, 793-811.
- McFarland, D. J. Decision making in animals. Nature, 1977, 269, 15-21.
- Noirot, E. Ultrasounds in young rodents: II. Changes with age in albino rats. Animal Behaviour, 1968, 16, 129-134.
- Okon, E. E. The temperature relations of vocalization in infant Golden hamsters and Wistar rats. Journal of Zoology, London, 1971, 164, 227-237.

- Pennycuik, P. R. The effects on rats of chronic exposure to 34°C. Australian Journal of Biological Sciences, 1964, 17, 245-260.
- Plaut, S. M. Adult-litter relations in rats reared in single and dual-chambered cages. Developmental Psychobiology, 1974, 7, 111-120.
- Rosenblatt, J. S. and Lehrman, D. S. Maternal behavior of the laboratory rat. In H. L. Rheingold (Ed.), Maternal behavior in mammals. New York: John Wiley & Sons, 1963.
- Siegel, S. Non-parametric statistics for the behavioral sciences. New York: McGraw Hill, 1956.
- Sturman-Hulbe, M. and Stone, C. P. Maternal behavior in the albino rat. Journal of Comparative Psychology, 1929, 9, 203-237.
- Wakerley, J. B. and Lincoln, D. W. Intermittent release of oxytocin during suckling in the rat. Nature, 1971, 233, 180-181.
- Wiesner, B. P. and Sheard, N. B. Maternal behaviour in the rat. London: Oliver and Boyd, 1933.
- Winer, B. J. Statistical principles in experimental design. New York: McGraw Hill, 1962.
- Woodside, B. Thermoendocrine influences on the duration of mother-litter contact in the Norway rat. Unpublished doctoral dissertation, McMaster University, 1978.
- Woodside, B., Pelchat, R., and Leon, M. Acute elevation of the heat load of mother rats curtails maternal nest bouts. Journal of Comparative and Physiological Psychology, 1980, 94, 61-68.