

AN ABSTRACT OF THE THESIS OF

James Zan Cronan for the degree of Master of Arts

in General Science presented on 25 April 1974

Title: Heat Energy Exchange Between the Killdeer,

Its Eggs, and the Environment

Redacted for privacy

Abstract Approved: _____

Dennis L. McDonald

The vegetation surrounding a nest shades and insulates the incubating bird in addition to concealing it. The vegetative material that makes up a nest insulates the eggs from its warmer or cooler surroundings. Since a Killdeer builds a stone-lined nest on barren ground, both egg and adult are subject to more climatological variation than most other bird species and their eggs. In May and June, 1973, six nesting pairs studied at the Malheur National Wildlife Refuge were directly exposed to air temperatures (T_a s) as low as 0°C and to intense solar radiation.

At T_a s below 12°C , the maximum "dummy" egg temperature (T_e) recorded from five nests was 34°C as opposed to a maximum T_e of 37°C from nest #3 at 25°C T_a . This information suggests that at low T_a s, the Killdeers' heat output did not keep pace with the increased rate of heat loss from the eggs to the ground.

Three of four pair of Killdeers showed the lowest incidence of preening at T_{as} below 12°C . The movements involved in this interruptive behavior would tend to decrease the thickness of the birds' feather insulation. Thus the Killdeers may have foregone preening at low T_{as} in the interest of conserving body heat.

Data from five nesting pairs showed that the Killdeers began to open their mouths (increased evaporative cooling) and stand over their nests (increased convective cooling) at T_{as} between $25-29^{\circ}\text{C}$. The incidence of these thermoregulatory behaviors increased with increasing T_a (up to 40°C).

Between T_{as} of $28-38^{\circ}\text{C}$, two of four pairs spent less time standing when there was wind at ground level than they did when it was still. By sitting in response to air flow, the Killdeers were probably attenuating convective heat loss.

"Dummy" T_{es} from five nests ranged between $35-40^{\circ}\text{C}$ when the Killdeers were standing. The fact that the eggs were always in the birds' shadow explains why lethal T_{es} ($43-45^{\circ}\text{C}$) were never reached. The rate of radiant and conductive heat input from the ground and air must have been sufficient to prevent T_{es} from dropping below 35°C .

Heat Energy Exchange between the Killdeer,
its Eggs, and the Environment

by

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A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Arts

Commencement June 1974

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Date thesis is presented 25 April 1974

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ACKNOWLEDGEMENTS

I wish to thank Dennis McDonald for constructing the transmitters, for his help in planning the study, and for reviewing the thesis drafts. Tom Haislip was kind enough to help me with the experimental plan for a Killdeer nest site selection study that was never successfully completed. Most of the statistical analysis was done by Randy Spry. An unsponsored research grant from the Oregon State University Computer Center made his job much easier. Richard Holbo of the Oregon State University Forest Research Laboratory suggested how I might measure air temperature and wind speed. Also I am grateful to the personnel at the Malheur National Wildlife Refuge and to Denzel Ferguson, Director of the Malheur Environmental Field Station, for their cooperation and support.

TABLE OF CONTENTS

	Page
I. INTRODUCTION.....	1
Previous field studies of avian thermoregulation.....	1
The nesting environment, the nest location and construction, and the nesting behavior of Killdeer.....	2
Purpose of the study.....	3
II. MATERIALS.....	4
III. METHODS.....	7
Preliminary observations.....	7
Equipment setup.....	7
Data collection.....	12
Dummy egg calibration.....	15
IV. RESULTS.....	16
Percent occurrence of three interruptive behaviors versus T_a	16
Percent occurrence of three incubation behaviors versus T_a	16
Percent occurrence of three incubation behaviors versus wind speed.....	24
T_e versus T_a	30
V. DISCUSSION.....	37
Theoretical avian bioenergetics.....	37
Percent occurrence of three interruptive behaviors versus T_a	42
Percent occurrence of three incubation behaviors versus T_a	43
Percent occurrence of three incubation behaviors versus wind speed.....	47
T_e versus T_a	49

	Page
VI. CONCLUSION.....	52
BIBLIOGRAPHY.....	53
APPENDIX.....	55
GLOSSARY.....	56

LIST OF TABLES

Table	Page
I. The seven Killdeer nesting behaviors studied in relation to T_a and wind speed.....	8
II. The six Killdeer nests in this study.....	14
III. Percent occurrence of three interruptive behaviors versus T_a for five nests.....	17

LIST OF FIGURES

Figure		Page
1	The blind.....	5
2	The sun shield.....	6
3	The transistor radio beside a Killdeer nest.....	9
4	A Killdeer in the sit-with-mouth-open position.....	10
5	A Killdeer in the stand-with-mouth-open position.....	11
6	A cut-away view of the blind.....	13
7a-e	Percent occurrence of three incubation behaviors versus T_a for five nests.....	18
8a-d	Percent occurrence of three incubation behaviors versus wind speed for four nests.....	25
9a-e	T_e versus T_a for five nests.....	31
10	The theoretical relationship between the heat exchange of a Killdeer and T_a under laboratory conditions.....	40
11	The theoretical relationship between the heat exchange of a Killdeer and T_a under natural conditions.....	46

Heat Energy Exchange between the Killdeer, its Eggs, and the Environment

I. INTRODUCTION

Previous Field Studies of Avian Thermoregulation

One of the pioneering works in the field of avian thermoregulation is Baldwin and Kendeigh's "Physiology of the Temperature of Birds" which was published in 1932. Since that time many investigations have been undertaken in an attempt to understand the responses of birds to heat and cold stress. The following are recent examples of field studies in avian thermoregulation.

Ricklefs and Hainsworth (1969) pointed out that the flask-shaped nest of the Cactus Wren shields the birds from the intense solar radiation of the Sonoran desert. These investigators discovered that the wrens tended to position their nest entrances toward the prevailing winds (convective cooling) and they tended to leave nestling fecal sacs in the nest (evaporative cooling). As a result of these adaptations, nest air temperatures were never found to be more than 4°C above air temperature (T_a) outside the nest.

By way of contrast, nests of the Masked Booby on the Galapagos Islands are simply shallow depressions on barren ground. Therefore the incubating birds are exposed to both direct and reflected solar radiation. Bartholomew (1966) noted the following booby behaviors during the hottest part of the day: standing over the nest, drooping the wings away from the body, elevation of the feathers, and fluttering the gular area (i.e., the throat) with the mouth open. All these behaviors were thought to have a thermoregulatory function since they would facilitate

body heat dissipation by convection or, in the case of gular flutter, by evaporation.

The Nesting Environment, the Nest Location and Construction, and Nesting Behavior of the Killdeers

The Killdeers (Charadrius vociferus) that nest at the Malheur National Wildlife Refuge in southeastern Oregon encounter environmental conditions similar to those faced by the booby. The early summer climate of this area, which lies within the northwestern boundary of the Great Basin desert, is characterized by minimal rainfall and by daytime T_a that often exceed 32°C . However during the night and early morning the T_a sometimes reaches freezing.

Beside similarities in the nesting environment, the location and construction of Killdeer and Masked Booby nests is also comparable. Commonly a Killdeer pair will build their nest along the side of a road. The roads provide suitable nesting territories because they are free of vegetation and are elevated above the surrounding grass and sagebrush. Thus the birds can easily see approaching predators. In addition, the loose stones that form the road surface make it easy for the Killdeers to dig out a shallow nest hole with their feet. Sometimes the nest is nothing more than a depression but usually the nest wall is covered with light-colored, flat stones and the base is thinly lined with grass.

Incubation begins as soon as the first egg of the four-egg clutch is laid. During the day, the average attentive period (i.e., the period one bird remains at the nest) for both sexes is 50 minutes; however it can vary from 15 minutes to 4 hours or more. Generally, an incubator

will not leave the nest unless a potential predator approaches. Then the bird will attempt to lead the intruder away from the well-camouflaged eggs by walking slowly or feigning a broken wing. The eggs hatch on about the 25th day of incubation. Since the chicks are precocial, the Killdeer family can abandon the nest within a day's time. The preceding natural history information is based on the work of Bunni (1959) and on my own observations.

Purpose of the Study

Because the Killdeer nest in unsheltered areas, they are good subjects for a quantitative study of the relationships between T_a , wind speed, and nesting behaviors. Also these nesting birds provide an ideal opportunity to investigate the role of the incubating parent in maintaining proper egg temperature (T_e) because Killdeer eggs are exposed to greater variations in environmental temperatures than the eggs of most other birds.

II. MATERIALS

The blind used in this study was about 2.5 m long by 1 m wide by 1.5 m high. Its steel water pipe framework was fitted with a water resistant cotton cover. A slit in front to accomodate a 30x spotting scope was the blind's only opening (Fig. 1).

T_{as} were measured with a single channel, battery-powered thermistor thermometer. The unit consisted of an indicating meter connected to a sensing probe by a 2 m cord. The meter was graduated in 1°C intervals. Comparisons with a laboratory thermometer showed that the instrument was accurate to $\pm 1^{\circ}\text{C}$. The probe was inserted in an 8 cm high sun shield in order to obtain T_{as} at the height of a nesting Killdeer (Fig. 2).

A fast-registering cup anemometer was used to measure wind speed. Its factory calibrated meter was graduated in 1 mph ($45 \text{ cm}(\text{sec})^{-1}$) intervals.

T_{es} were detected by using a Killdeer egg shell that contained a centrally-located temperature transmitter encased in silicone glue. The transmitter circuit, which consists of a thermistor, capacitor, transistor, mercury battery, and a coiled wire antenna, is completely described by MacKay (1970) (also see Southwick, 1973). The rate of the clicking signal it emits is directly proportional to temperature.

The maximum transmission range to an AM radio of the two "dummy" eggs used in this study was 0.5 m. The transistor radio was connected to an on-off switch and earphone by wires so that it could be operated and listened to from the blind.



Figure 1 - The blind with spotting scope in place. Please note the sun shield in the lower right hand corner of the photograph. The pole at the left of the photograph supported the cup anemometer.



Figure 2 - The sun shield with the temperature sensing probe in place.

III. METHODS

Preliminary Observations

The first and perhaps most difficult step of the field work was to locate a nest. This task was accomplished by driving down a Refuge road until a Killdeer was seen. Then the bird was observed with 7x binoculars at a distance of at least 100 m. If the Killdeer had been incubating, it would usually return to the nest within 5 minutes. Then the location of the nest could be determined by noting the position of the seated bird relative to a landmark on the road (e.g., a large stone).

During the first few weeks of the field work, I continued to watch the Killdeers from the car after they had returned to their nests. As a result of these observations, I chose seven nesting behaviors to study in relation to T_a and wind speed (Table 1).

Equipment Setup

The day before a particular incubating pair was to be studied, a "dummy" egg was placed in their nest and one egg was removed and placed in an incubator. Then the transistor radio was buried beside the nest and the wires connected to it were strung out along the road (Fig. 3). The blind was set up 40 m away at the end of the radio wires.

About 15 minutes before an observation period was to begin the sun shield with the thermometer probe was placed 2 m from the blind on a surface similar to the one on which the nest was located. Also the cup anemometer was attached to a pipe that stood 1 m above the blind. Then I entered the blind with the following equipment: meters to register T_a

TABLE I

The Seven Killdeer Nesting Behaviors Studied in Relation to Air Temperature (T_a) and Wind Speed

The code for these behaviors that is used in the text is given in the right hand column.

DESCRIPTION	CODE
1) Sit with mouth closed	sit-mc
2) Stand with mouth closed	stand-mc
3) Sit with mouth open* (See Fig. 4)	sit-mo
4) Stand with mouth open* (See Fig. 5)	stand-mo
5) Preening	pr
6) Pecking at the ground	pk
7) Movement from the sit to stand position followed by resettling on the eggs	re

* The mouth open behavior was interpreted as a sign of an increased evaporation rate by either panting or gular flutter.



Figure 3 - The transistor radio positioned beside a Killdeer nest. The receiver was buried before a nest was studied.



Figure 4 - A Killdeer in the sit with mouth open position



Figure 5 - A Killdeer in the stand with mouth open position

and wind speed, a stopwatch, the 30x spotting scope, and a notebook (Fig. 6).

Data Collection

Nests were usually studied for two 2 hour observation periods per day for at least 2 days. Each 2 hour period was divided into thirty 4 minutes subperiods. Behavioral and environmental data were obtained within each subperiod as follows:

- 1) first 15 seconds - Windspeed was estimated to the nearest mph.
- 2) next 90 seconds - Preening, pecking, or resettling behaviors were noted if they were seen more than once. The other incubation behaviors had to be observed for more than 10 seconds before they were recorded.
- 3) next 15 seconds - Windspeed was again recorded.
- 4) next 30 seconds - T_a was recorded to the nearest 1°C .
- 5) next 60 seconds - T_e data was obtained by recording the number of transmitter clicks per minute.
- 6) last 30 seconds - Preparations were made for the next subperiod.

When the study of an incubating pair was completed, their egg was placed back in the nest. In all, data were obtained from six nests. Table II indicates where these nests were located and when they were studied.



Figure 6 - A cut-away view of the blind. The meters to register T_a and wind speed were mounted on a board that lay across the arms of the chair.

TABLE II

The six Killdeer Nests in this Study

This table shows the nest characteristics and when and for how long the nests were studied.

NEST NO.	LOCATION	CONSTRUCTION	DATES STUDIED	NO. OF 4 MIN SUBPERIODS
2	Roadside	Stones	28-30 May	150
3	Barren Ground	Wood Chips	21-23 May	210
7	Roadside	Stones	6-8 June	150
10	Roadside	Stones	11-17 June	165
11	Roadside	Stones	19-25 June	225
13	Roadside	Stones	23-27 June	<u>135</u>
TOTAL				1035

"Dummy" Egg Calibration

Both "dummy" eggs were calibrated in order to convert the T_e click rate data to $^{\circ}\text{C}$. This was done at 1 week intervals by placing the eggs in a water bath and counting the number of clicks per minute at 27, 29, 31, 33, 35, 37, and 39°C . Eggs #1 and #2 were calibrated four and three times respectively. Calibration regression analysis of this T_e versus click rate data (Snedecor and Cochran, 1968 p. 159) showed that when T_e was estimated to the nearest 0.1°C , the standard error for both eggs was $\pm 0.7^{\circ}\text{C}$. Because of this relatively large error, the T_e s were rounded off to the nearest 1.0°C .

IV. RESULTS

Percent Occurrence of Three Interruptive Behaviors versus T_a

Table III shows in what percent of the subperiods (n) each of three incubation interruptive behaviors (resettling, preening, and pecking) occurred in each of four T_a categories. Because of insufficient data, results for nest #7 were not included in the table. The fact that the occurrence rate for these behaviors is low makes it difficult to detect any trends in the results. However, it does appear that there is a direct relationship between the incidence of preening and T_a for four of the five nests.

Percent Occurrence of Three Incubation Behaviors versus T_a

Figure 7 a-e indicates in what percent of the subperiods each of three incubation behaviors (sit-mc, sit-mo, and stand-mo) occurred in each of four T_a categories. The results from five nests show that the Killdeer began panting and standing at T_a s between 25-29°C. In addition the figure shows that the incidence of stand-mo is directly related to T_a whereas the incidence of sit-mc decreases with increasing T_a . The occurrence rate of sit-mo does not vary predictably with T_a . It is not possible to show any trends for nest #13 because data were obtained in only one T_a category.

Figure 7 a-e also indicate that there was considerable inter-nest difference in the percent occurrence of the incubation behaviors in any one T_a category. For instance between 30-34°C the incidence of stand-mo

TABLE III

Percent Occurrence of Three Interruptive Behaviors versus T_a for Five Nests

The percent occurrence of Killdeer resettling (re), preening (pr), and pecking (pk), within (n) subperiods at four air temperature (T_a) categories. Results are shown for five pair of birds.

AIR TEMPERATURE (°C)	NEST #2			NEST #3			NEST #10			NEST #11			NEST #13		
	re	pr	pk	re	pr	pk	re	pr	pk	re	pr	pk	re	pr	pk
2-11	10	5	0	0	0	5	0	0	2	0	2	10	5	0	0
	n = 21			n = 19			n = 62			n = 42			n = 20		
12-21	14	0	3	7	7	8	9	0	0	4	8	12	5	5	3
	n = 36			n = 83			n = 22			n = 49			n = 40		
22-31	3	19	4	3	16	12	6	0	0	3	18	3			
	n = 68			n = 91			n = 32			n = 40					
32-41	0	11	0				5	0	0	0	19	6	2	14	11
	n = 19						n = 45			n = 72			n = 64		

Figure 7 a-e. The percent occurrence of three Killdeer incubation behaviors (sit-mc, sit-mo, and stand-mo) within (n) subperiods at four air temperature (T_a) categories. The total percent occurrence of the three incubation behaviors in any one T_a category sometimes exceeds 100% because more than one incubation behavior could be recorded in any one subperiod. Results are shown for five pair of birds.

NEST #2

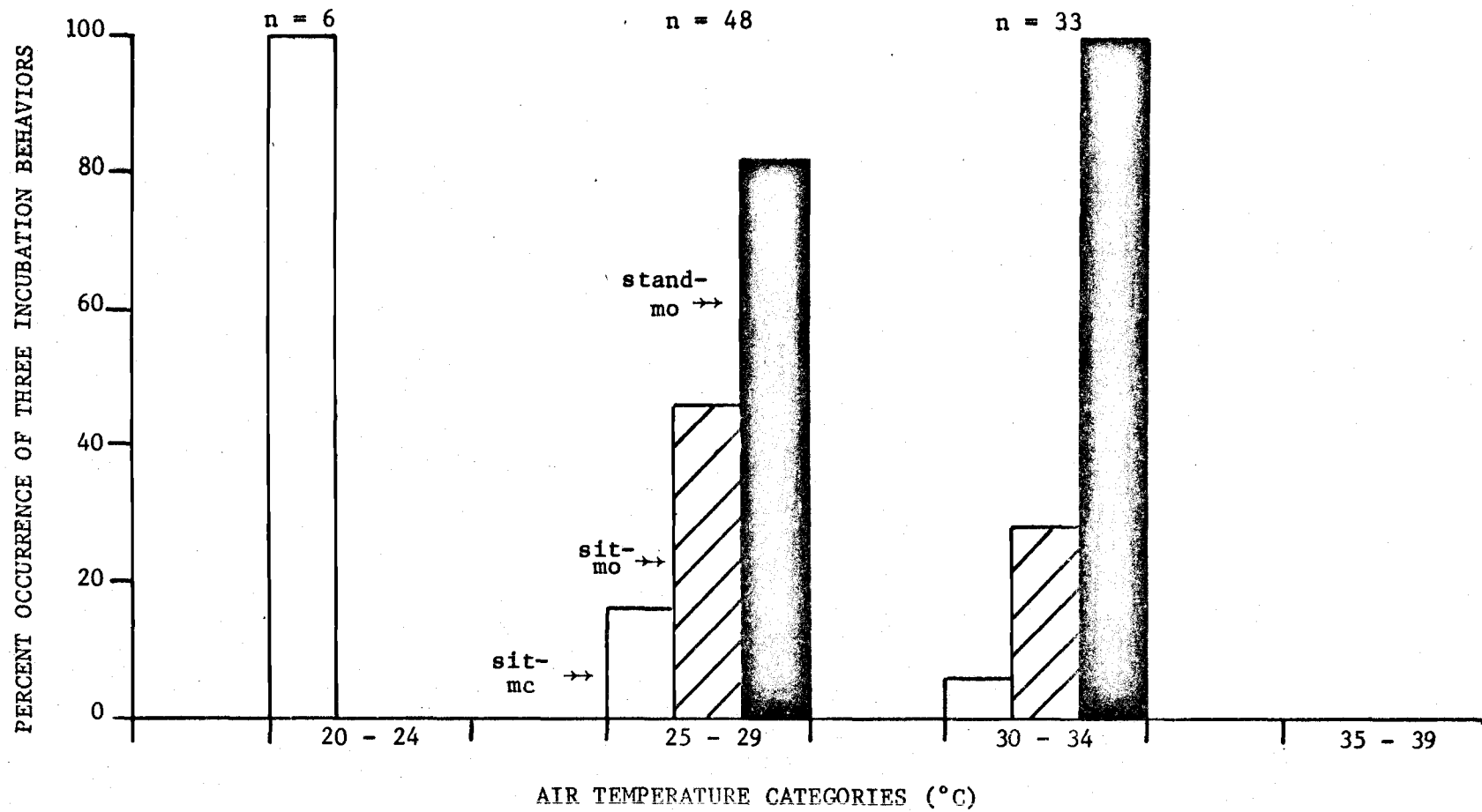


Figure 7a

NEST #3

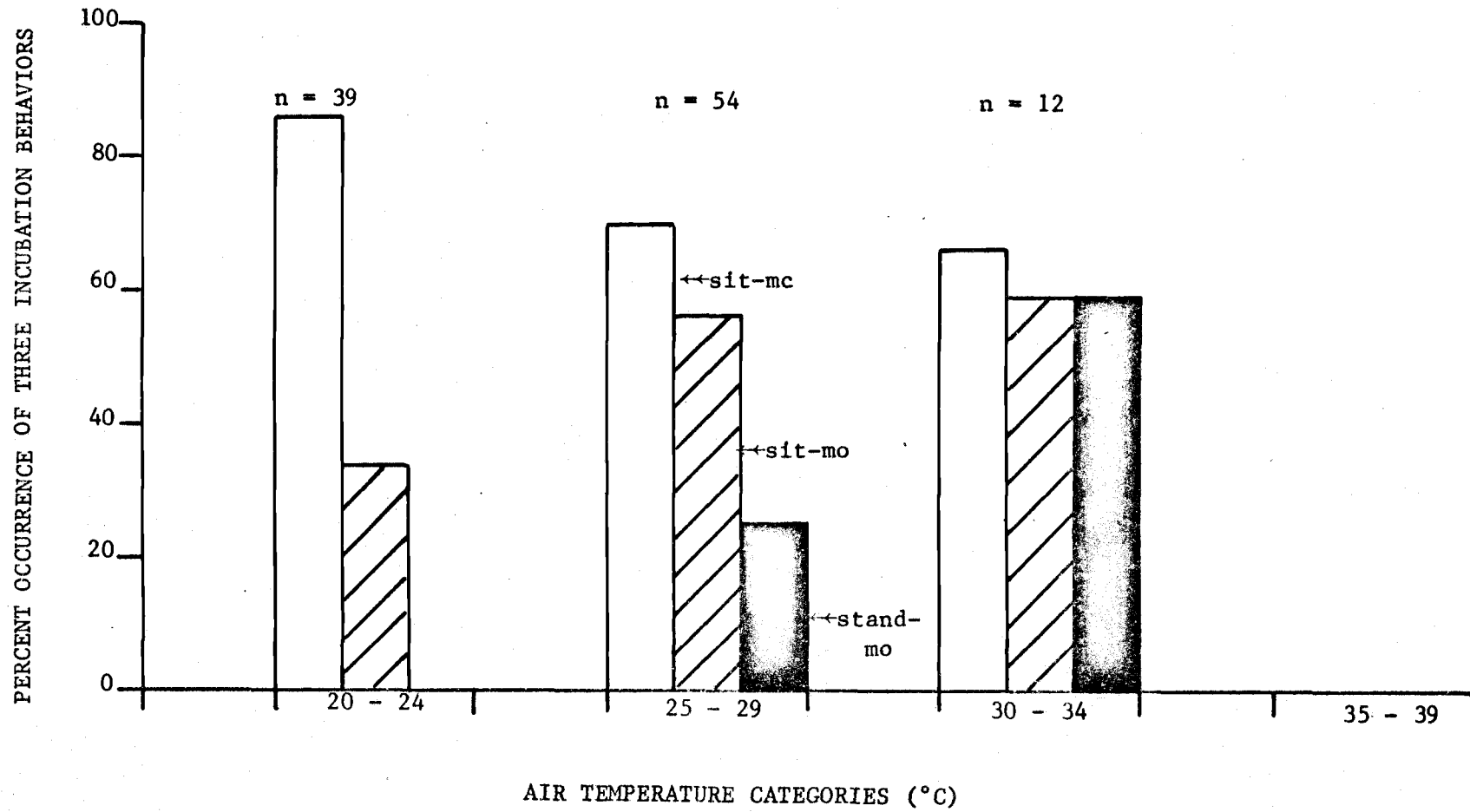


Figure 7b

NEST #7

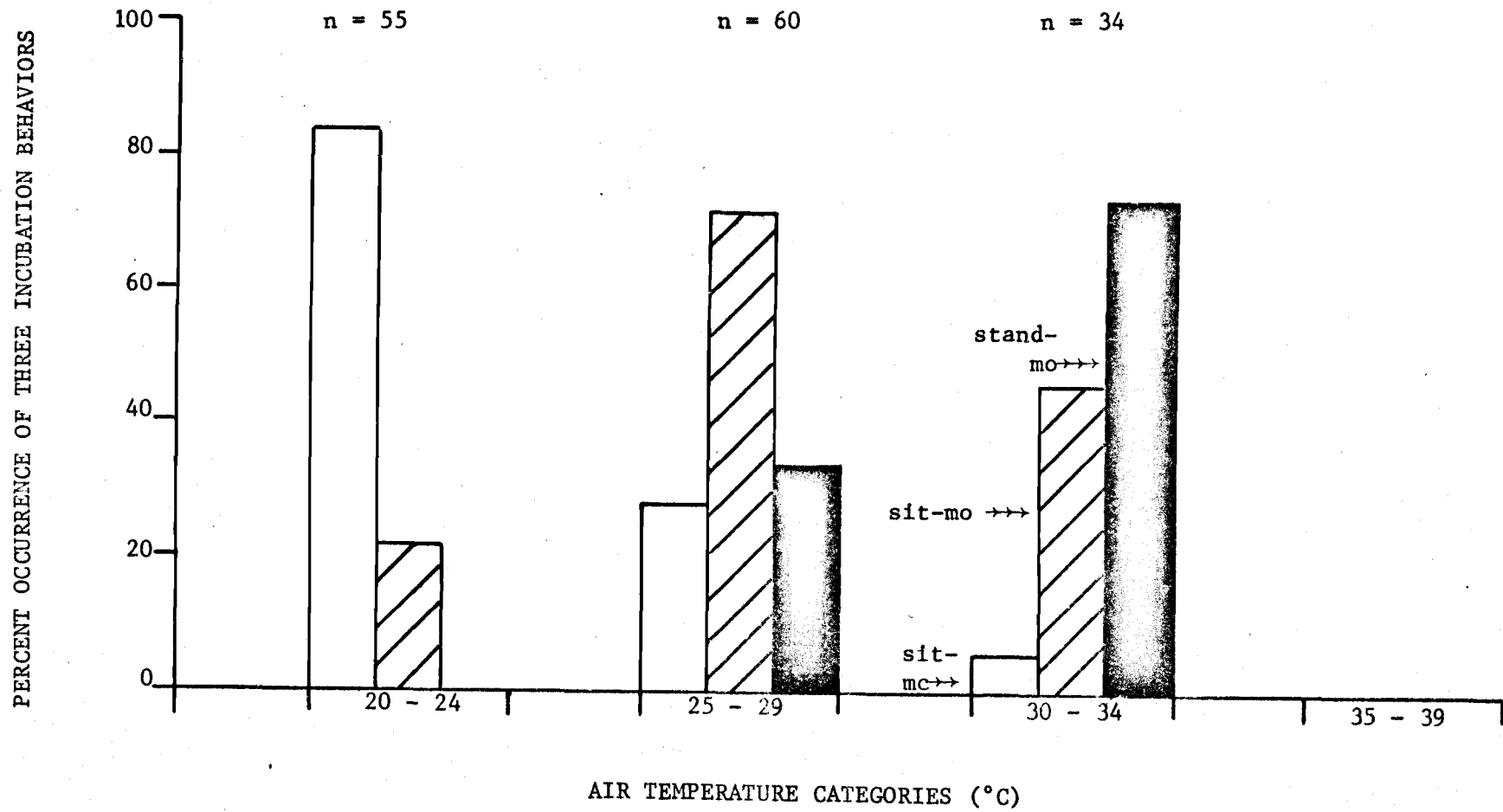


Figure 7c

NEST #10

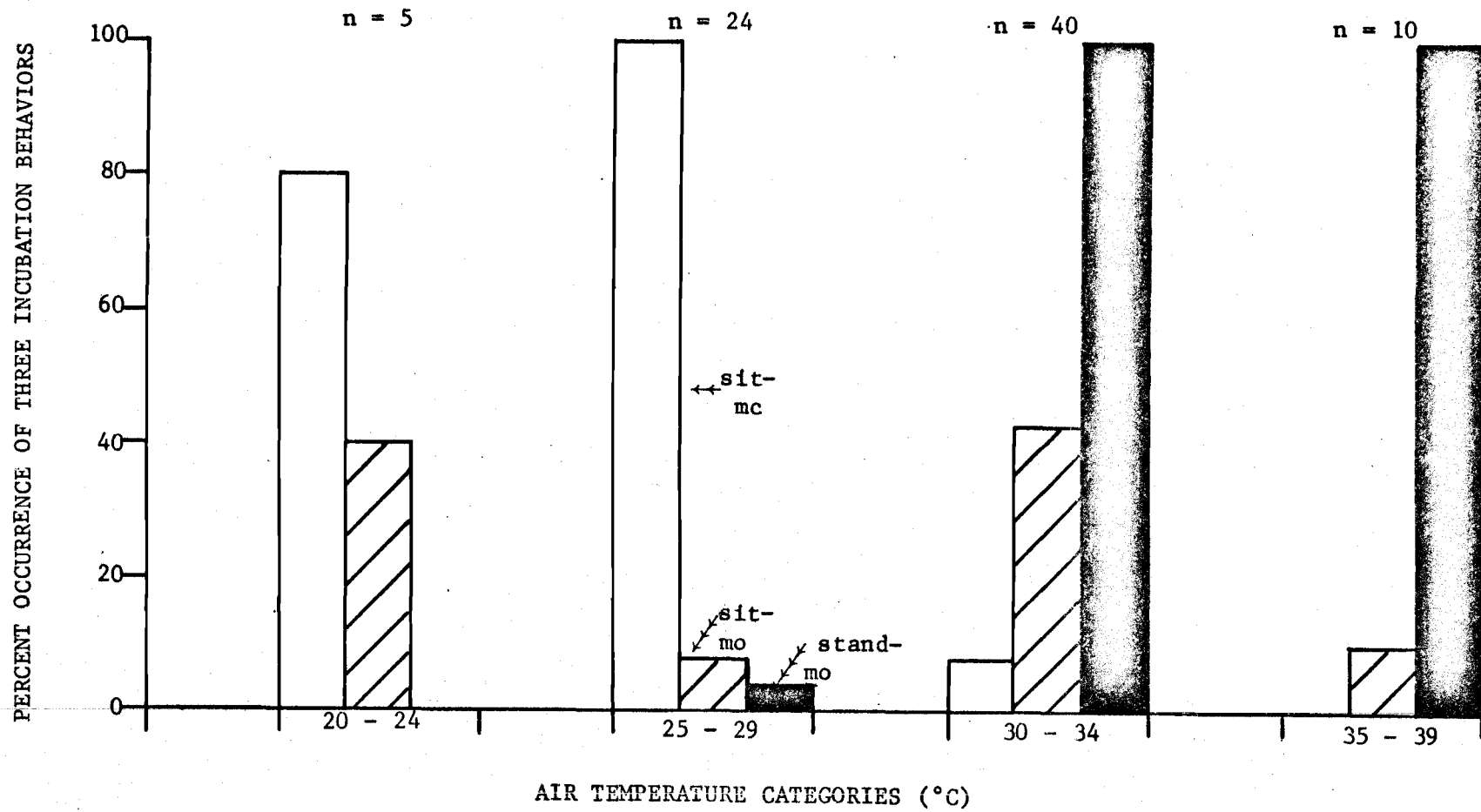


Figure 7d

NEST #11

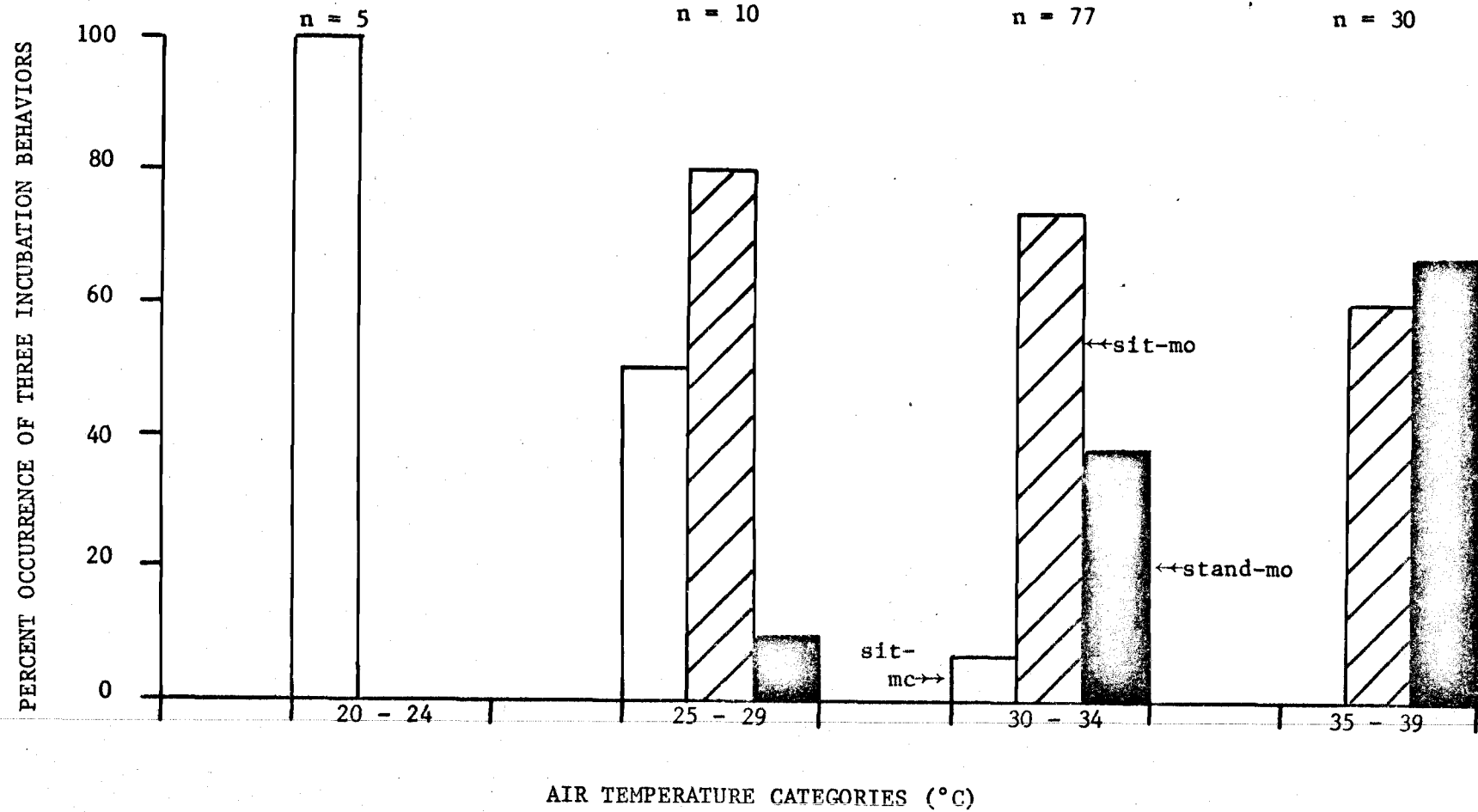


Figure 7e

was 59% and the incidence of sit-mc was at 65% for Nest #3. However, for Nest #2, stand-mo was at 100% while the incidence of sit-mc was only 6%.

Percent Occurrence of Three Incubation Behaviors versus Wind Speed

Figure 8 a-d indicates in what percent of the subperiods each of three incubation behaviors (sit-mc, sit-mo, and stand-mo) occurred in six wind speed categories at T_a s between 28-38°C. It also shows how many subperiods were observed at each °C within this T_a range. For two of the nests (#10 and #11) there is a nonuniform increase and decrease in the incidences of sit-mc and stand-mo respectively with increasing wind speed. The graph for Nest #3 shows the inverse relationship to Nest #10 and #11. The incidence of sit-mc is consistently low and the incidence of stand-mo is consistently high at all wind speeds for Nest #2. Data from Nest #7 and #13 do not contribute to a better understanding of Killdeer incubation behavior - wind speed relationships because these nests were rarely observed at the higher wind speed categories. Therefore, results from these nests are not included in Figure 8 a-d.

Figure 8 a-d. The percent occurrence of three Killdeer incubation behaviors (sit-mc, sit-mo, and stand-mo) within (n) subperiods at six wind speed categories at air temperatures between 28 and 38°C. The number of subperiods observed at each °C within this range is shown at the bottom of the figures. Results are shown for four pair of birds.

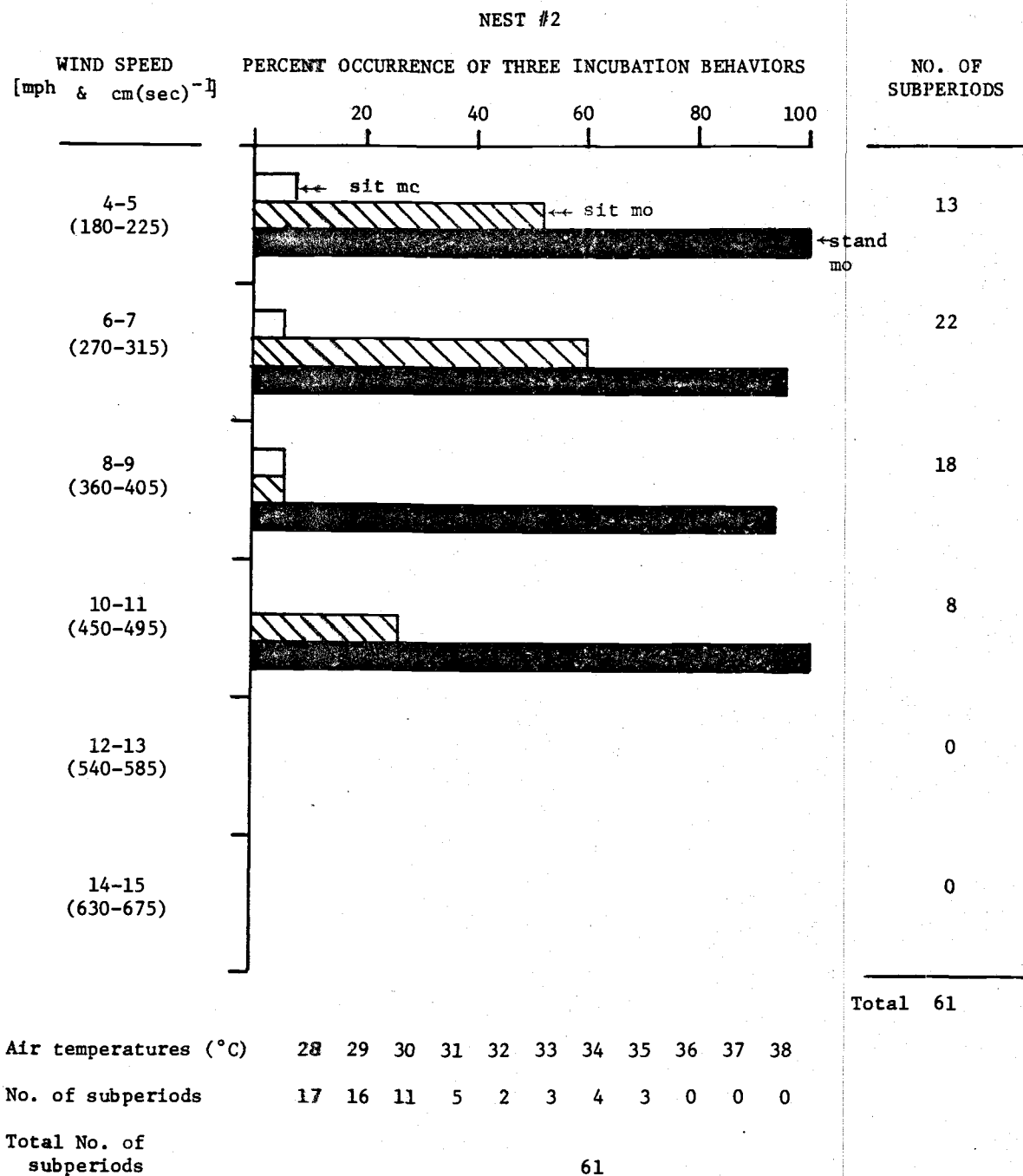
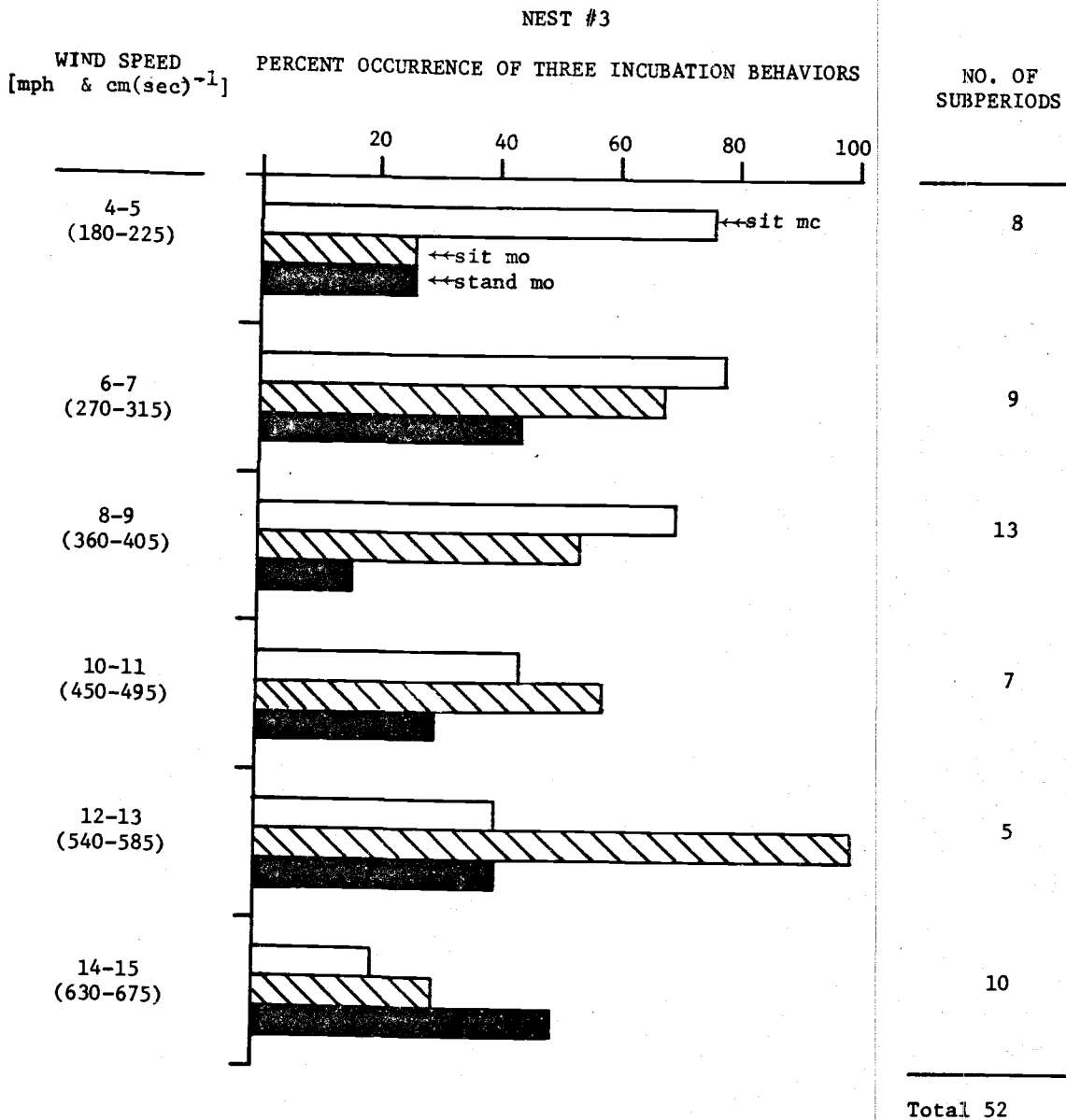


Figure 8a



Air temperatures (°C)	28	29	30	31	32	33	34	35	36	37	38
No. of subperiods	21	20	9	1	1	0	0	0	0	0	0
Total no. of subperiods	52										

Figure 8b

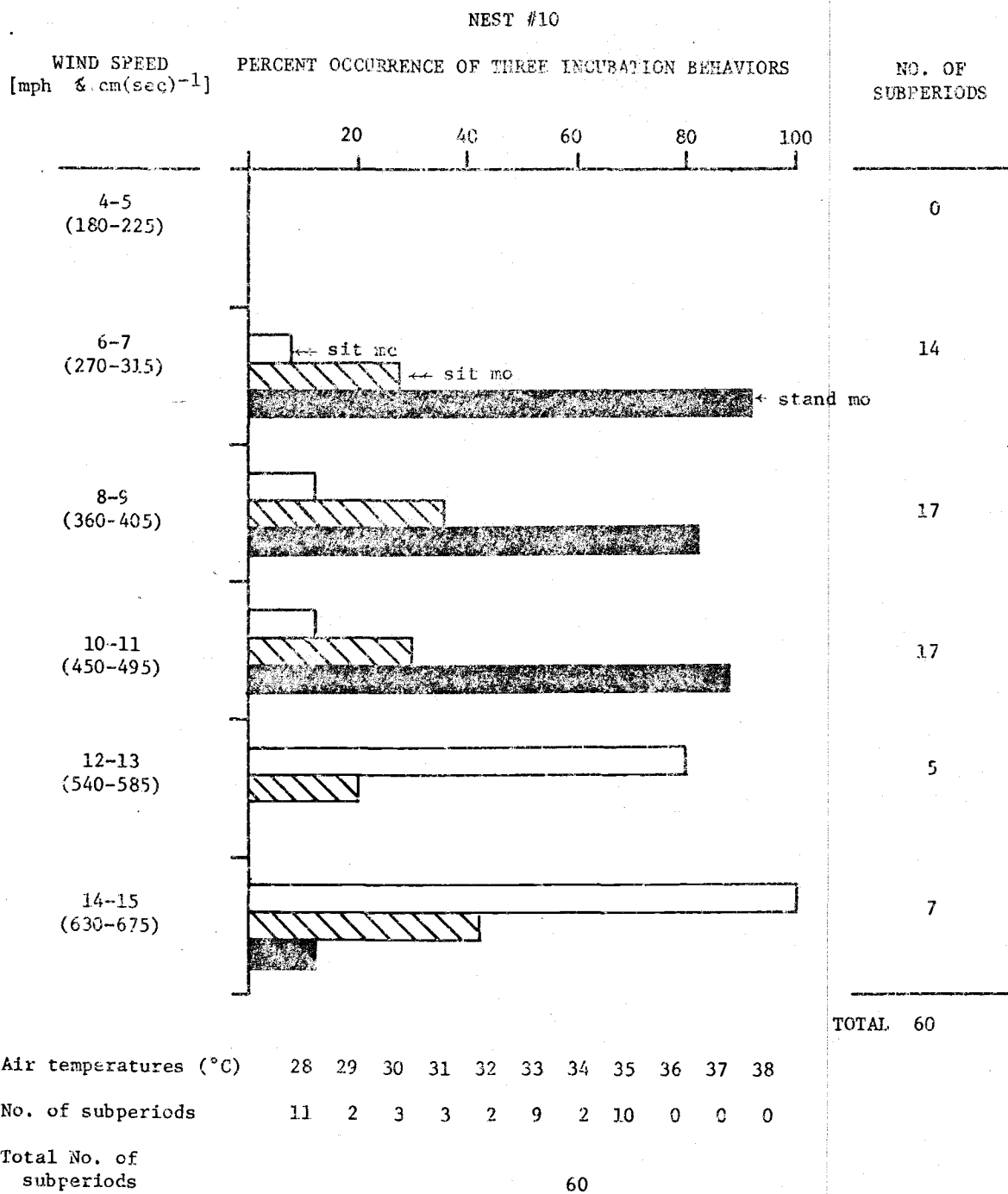


Figure 8c

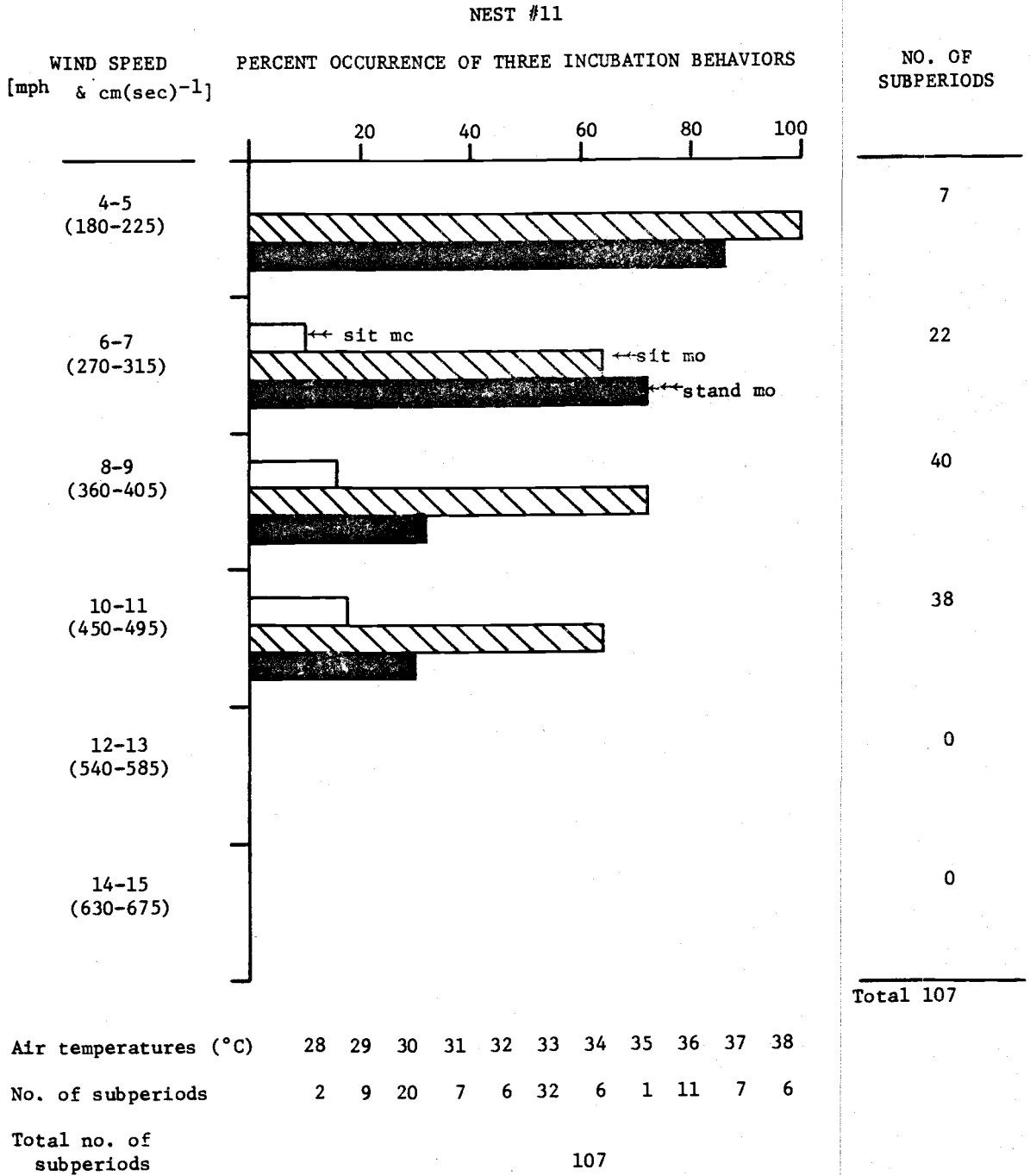


Figure 8d

T_e versus T_a

A comparison of the five regression lines in Figure 9 shows that the relationship between T_a and T_e for the five nests is similar. T_e data was not collected for Nest #7. The fact that the slope of each of these regression lines is significantly different from zero ($p < 0.001$) indicates that T_e was not independent of T_a .

Figure 9 a-e. The relationship between the temperature of a "dummy" Killdeer egg (T_e) and air temperature (T_a). Results are shown for five Killdeer pairs. A filled-in point indicates that more than three subperiods were observed at that particular $T_e - T_a$ combination. Δ indicates that a bird was standing over the nest for at least part of the subperiod(s). 0 indicates that a bird was sitting on the nest.

NEST #2

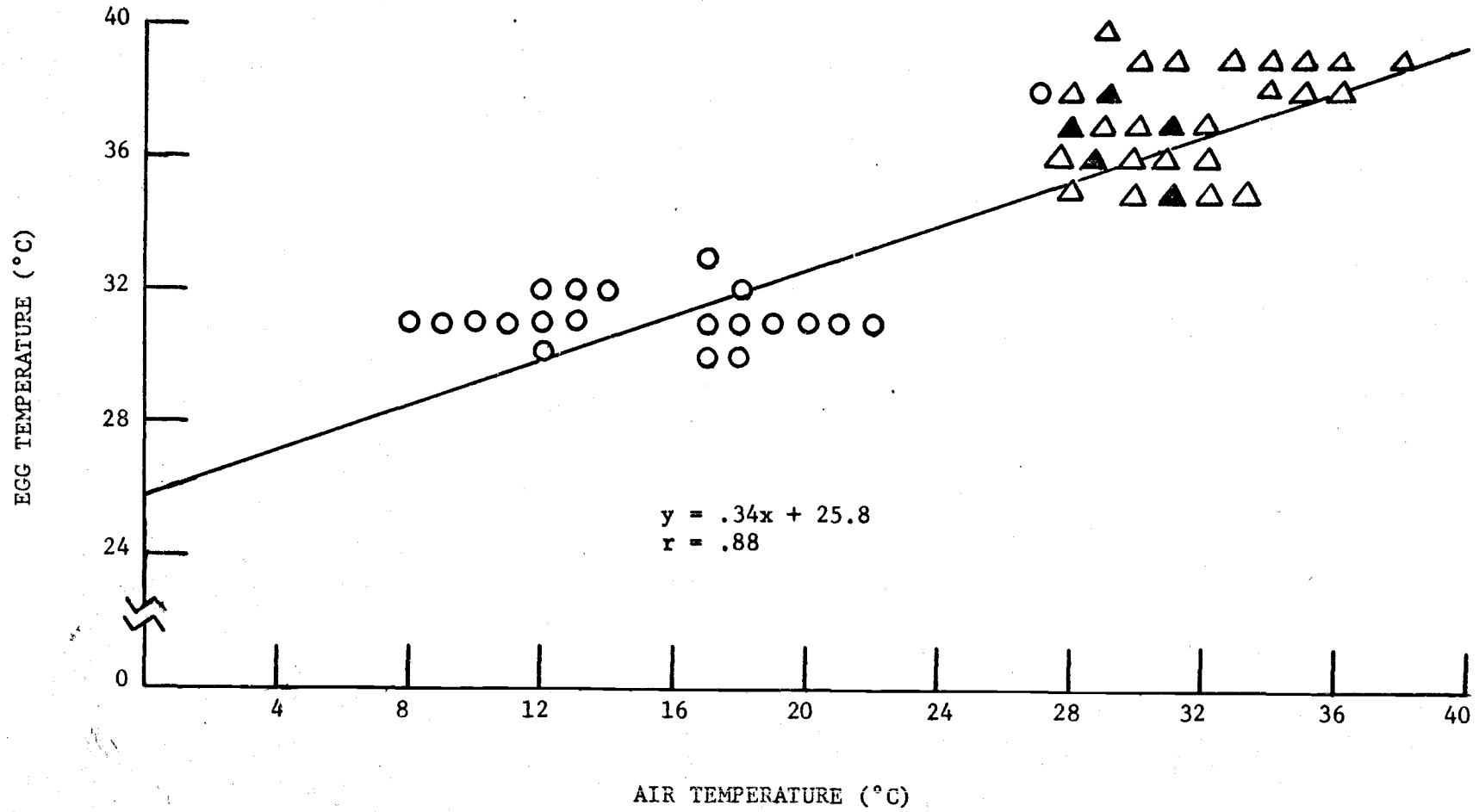


Figure 9a

NEST #3

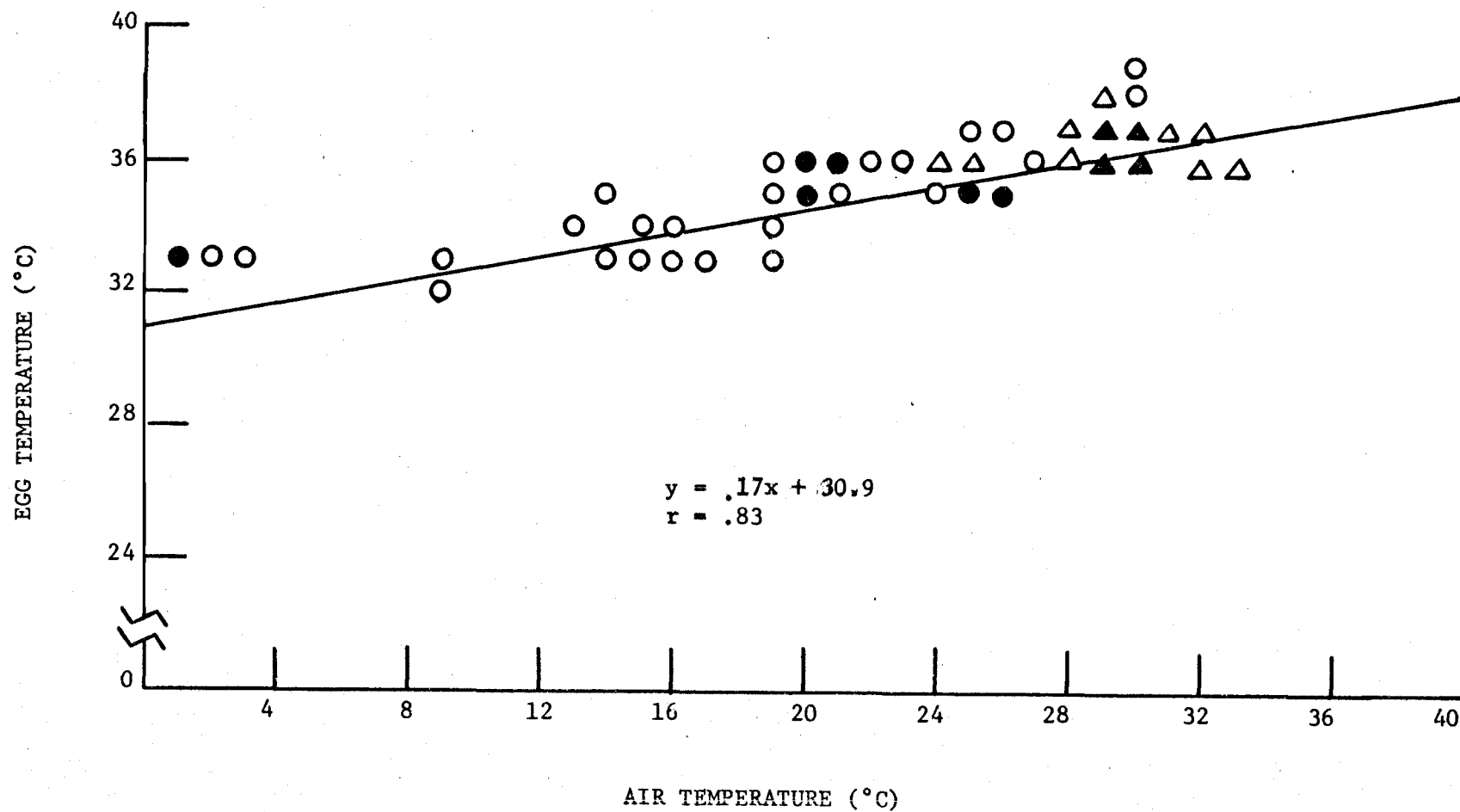


Figure 9b

NEST #10

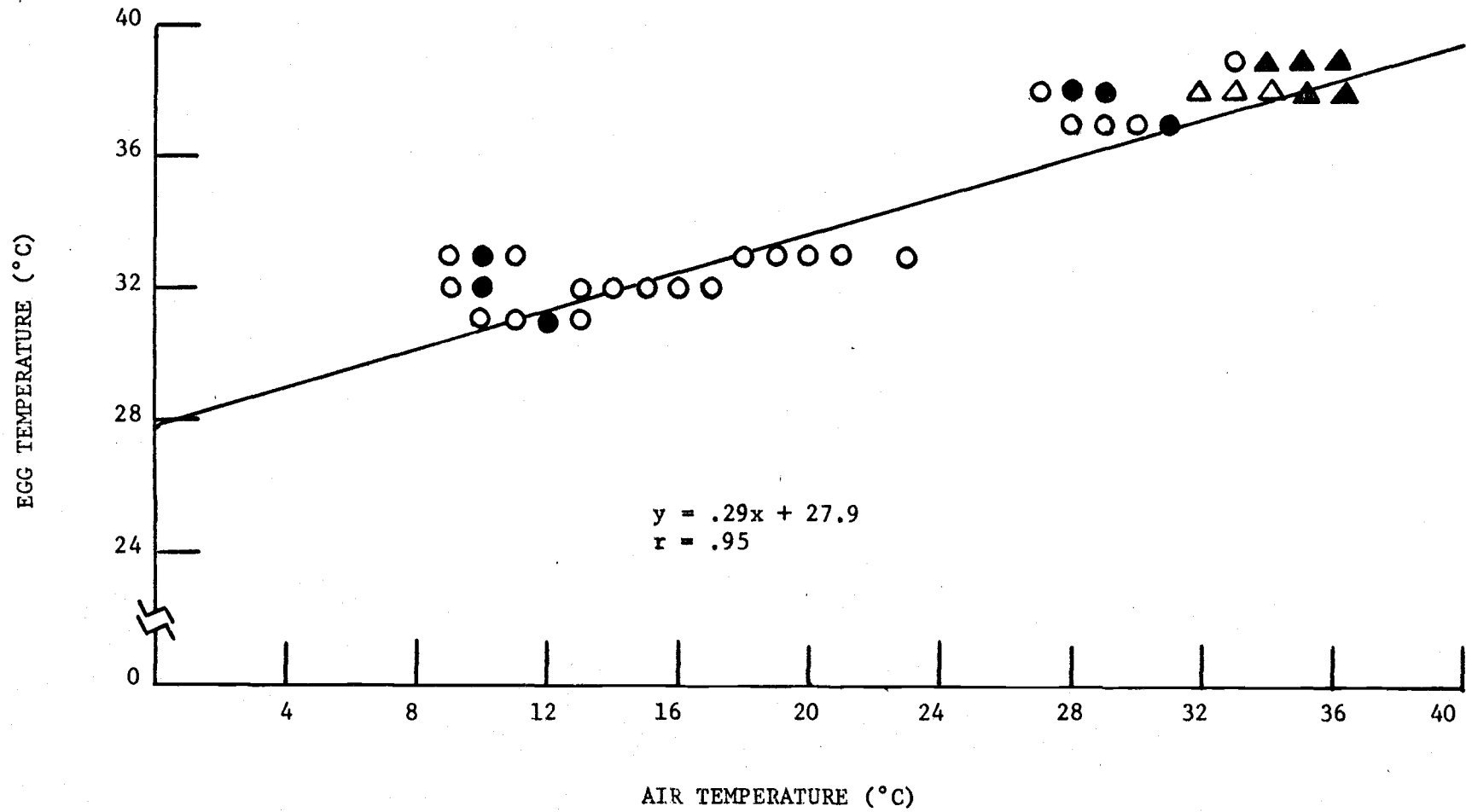


Figure 9c

NEST #11

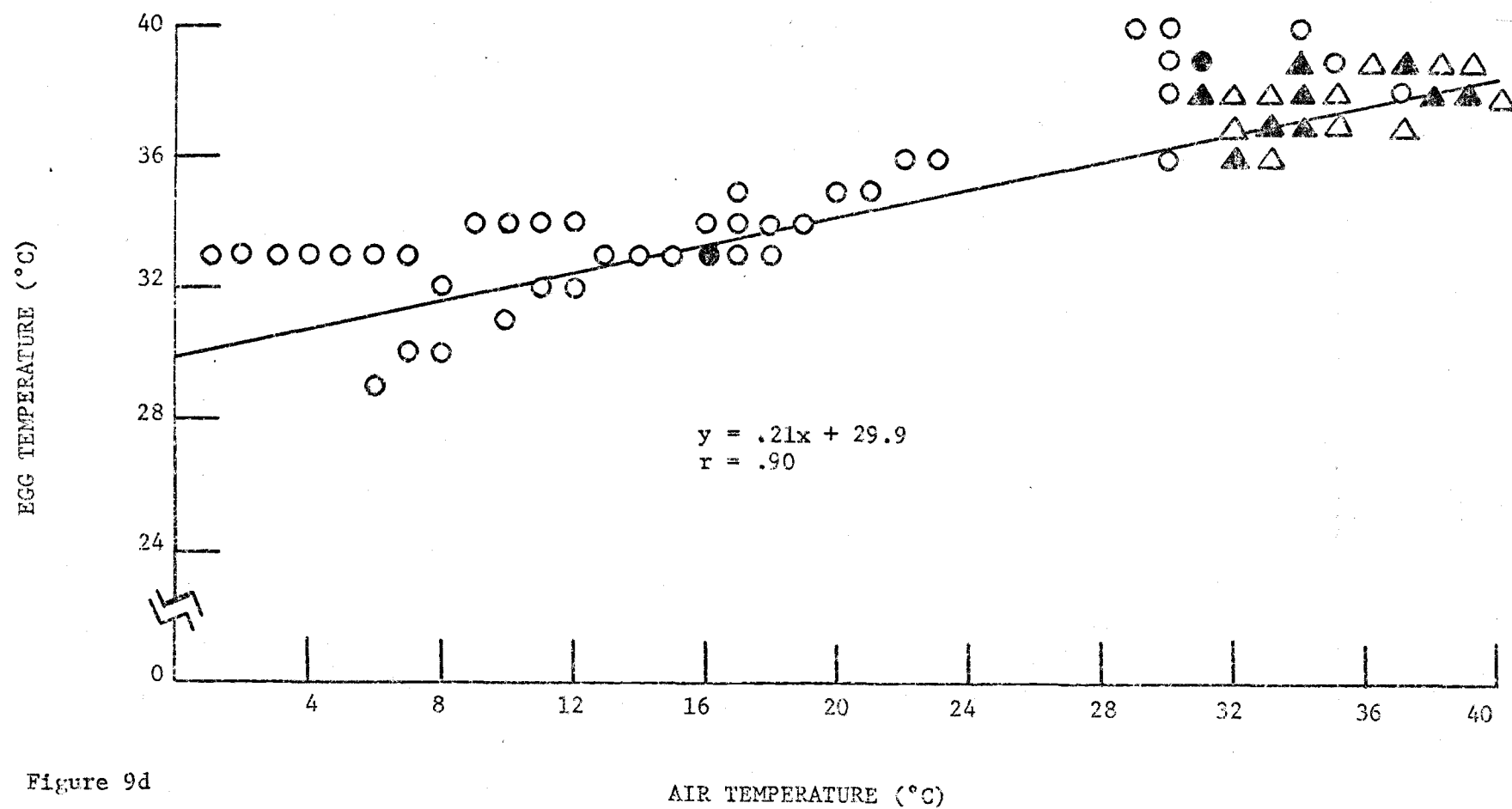


Figure 9d

NEST #13

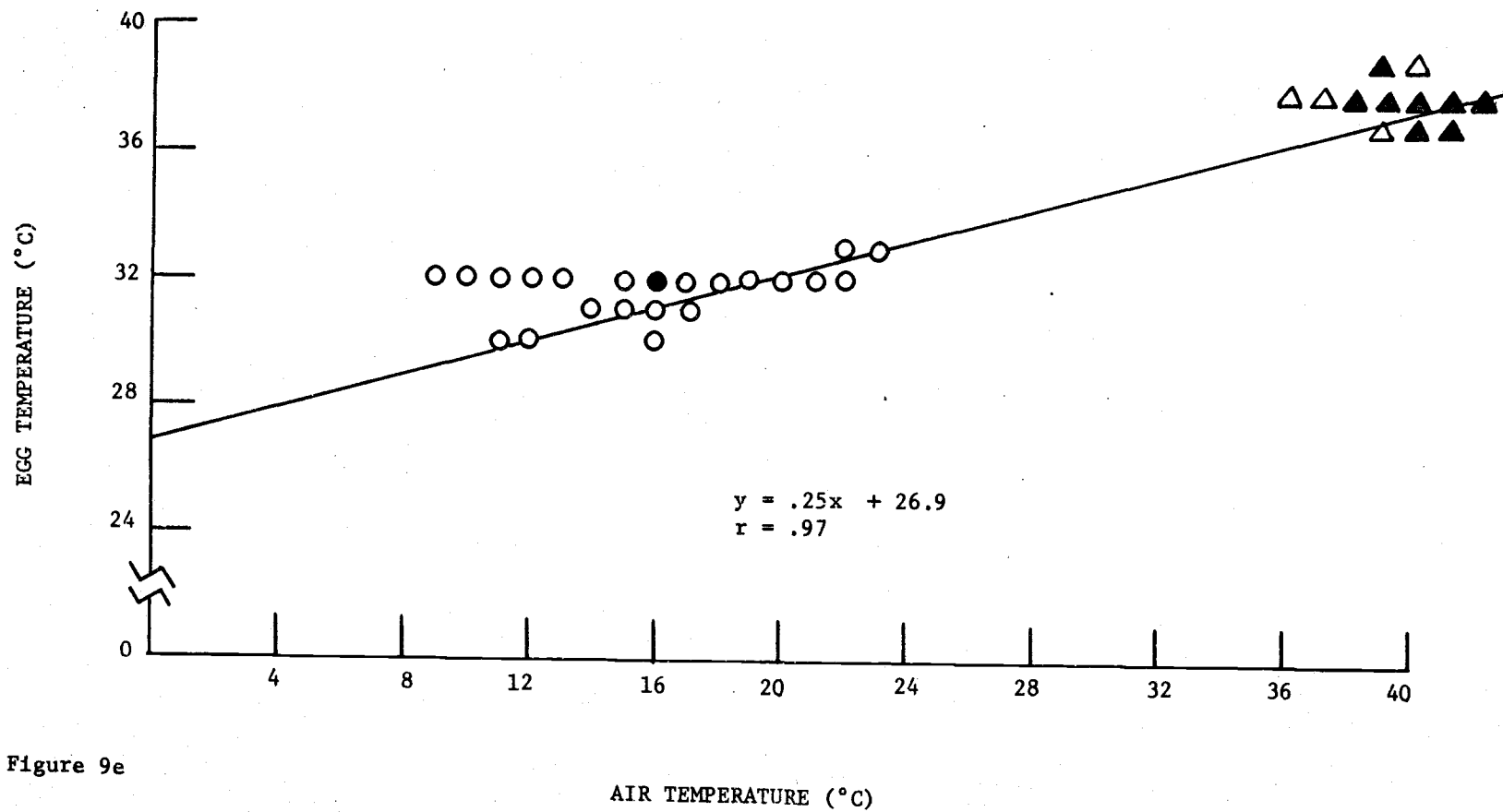


Figure 9e

V. DISCUSSION

Theoretical Avian Bioenergetics

Before attempting to explain the results of this study, some background information on avian bioenergetics must be presented. For the moment, assume that Killdeer are incapable of generating body heat. Then the only way they could maintain a body temperature (T_b) of 41.5°C would be if the T_a was exactly 41.5°C . If there was a drop in T_a , the rate of heat loss from the bird could be predicted by using Newton's law of cooling:

$$\frac{dH}{dt} = c(T_b - T_a) \quad (1)$$

which says that the change in heat content per change in time is equal to a cooling constant times the difference between T_b and T_a (Lasiewski, Weathers, and Bernstein, 1967).

Herreid and Kessel (1967) showed that the thermal conductance (C) of 13 species of Alaskan birds could be predicted by the equation:

$$\log C = 0.66 - 0.52 \log W \quad (2)$$

where W is weight in g and C is measured in $\text{cal}(\text{g} \cdot \text{hr} \cdot ^\circ\text{C})^{-1}$. After comparing conductance data from 40 bird species, Lasiewski, Weathers, and Bernstein proposed a similar conductance - weight relationship.

If we assume that the weight of an average Killdeer is 81g (Bunni, 1959), then its C would be about $0.6 \text{ cal}(81\text{g} \cdot \text{min} \cdot ^\circ\text{C})^{-1}$.

By using this value in equation 1, one can obtain a line that indicates the theoretical rate of heat loss from a Killdeer at T_a s between 0 and 41.5°C (Fig. 10).

Of course Killdeer, and all other organisms, do generate heat because the metabolic processes necessary to sustain life are not completely efficient. The physiologist's measurement of an animal's minimum heat production is the standard metabolic rate (SMR) which is taken when the animal is resting, post-absorptive, and not subject to environmental stresses.

After reviewing the results of 26 laboratory studies, Lasiewski and Dawson (1967) proposed the following SMR - weight relationship for non-passerine birds:

$$\log M = \log 78.3 + 0.723 \log W \quad (3)$$

where M is heat production in kcal(day)⁻¹ and W is weight in kg. The predicted SMR for a Killdeer would be about 9 cal (81g · min)⁻¹ (Fig. 10).

Birds and mammals are homeothermic (i.e., they can maintain a constant T_b) under most environmental conditions. This means that the dissipation of heat from these animals must occur at the same overall rate it is produced. This heat energy balance between the animal and the air can be expressed in this way:

$$\text{Heat produced} = \text{Heat lost} \quad (4)$$

$$M = C(T_b - T_a) \quad (5)$$

(Tracy, 1972).

Bunni has shown that an adult Killdeer's T_b is about 41.5°C. This is all the additional information necessary to show that a quiescent Killdeer should be in thermal equilibrium at an T_a of about 26.5°C (point x, Fig. 10).

$$9 \text{ cal}(81\text{g} \cdot \text{min})^{-1} = 0.6 \text{ cal}(81\text{g} \cdot \text{min} \cdot ^\circ\text{C})^{-1} (41.5-26.5^\circ\text{C}) \quad (6)$$

(from Kendrick 1969!)

Figure 10 - The theoretical relationship between the heat exchange of a Killdeer and air temperature (T_a) under laboratory conditions. The slope of the solid diagonal line (i.e., the thermal conductance (C)) represents the rate of heat loss from an 81 g bird at T_a s between 0 and 26.5°C. It also shows how fast a Killdeer would have to increase its metabolic rate at T_a s below 26.5°C in order to maintain a constant body temperature (T_b). The horizontal line shows that an 81 g bird metabolizing 9 cal(81g · min)⁻¹ (i.e., its standard metabolic rate (SMR)) can maintain a constant T_b between about 26.5 and 40°C. These two T_a s are referred to as the lower critical temperature (T_{lc}) and upper critical temperature (T_{uc}) of the Killdeer's thermoneutral zone. The dashed line beyond the thermoneutral zone indicates that a bird must increase its metabolic rate to support an increased evaporation rate (i.e., panting or gular flutter) at T_a s above 40°C.

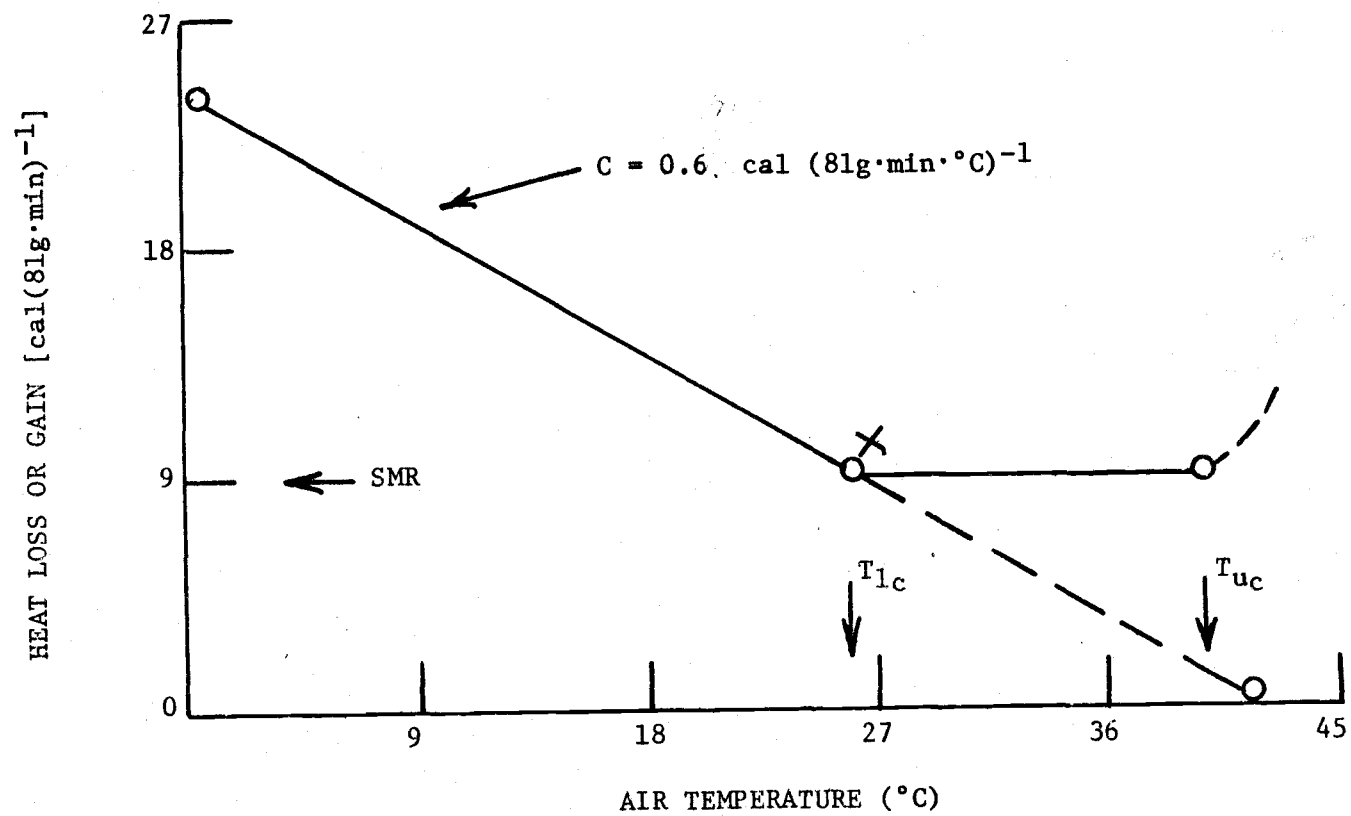


Figure 10

The 26.5°C T_a is known as the lower critical temperature (T_{lc}). At T_a s below the T_{lc} , the Killdeer can no longer depend on their insulation to prevent a drop in T_b . They must increase their metabolic rate to match the increased rate of heat loss (Fig. 10).

At T_a s greater than 26.5°C , the Killdeer would increase their C so that the rate of heat gain does not exceed heat loss. As Tracy (1972) points out, this means that C is not a constant; its value is dependent on conduction, convection, and radiation coefficients (h_k , h_c , and h_r respectively) as shown in these more detailed energy balance equations:

$$\begin{aligned} \text{Heat produced} &= \text{Heat loss to skin} = \\ \text{Heat loss to radiating surface through feathers} &= \end{aligned} \quad (7)$$

Heat loss to air

$$\begin{aligned} M &= h_k(T_b - T_s) + h_c(T_b - T_s) = \\ h_k(T_s - T_r) &= h_c(T_r - T_a) + h_r(T_r^4 - vT_a^4) + E \end{aligned} \quad (8)$$

where $h_c(T_b - T_s)$ is convective heat loss from body to skin by blood flow, T_r is the temperature of the radiation surface (i.e., the outer feathers), v is a variable dependent on humidity, and E is evaporative heat loss by exhaling.

Percent Occurrence of Three Interruptive Behaviors versus T_a

Porter and Gates (1969) tell us that for birds:

$$h_k = \frac{K_f}{d_f} \quad (9)$$

where K is feather conductivity and d_f is plumage thickness. This equation indicates that the value of the bird's conduction coefficient would increase as a result of any behavior that lead to a decrease in plumage thickness. Thus one would predict that the occurrence rate of such behaviors would be lowest when there was a large gradient between T_s and T_r (i.e., at low T_a).

It could be that the performance of pecking and resettling resulted in a marginally significant heat loss from the Killdeers because the incidence of these behaviors was lowest in the lowest T_a category in three of the five nests (Table III, p. 17). The fact that the Killdeers on four nests clearly spent less time preening at the lower T_a s suggests that net heat loss resulting from this behavior could have been more significant than it was from the other interruptive behaviors. The birds on the fifth nest (#10) did not preen at any T_a .

Interestingly enough Baerends et al (1970) found that for Herring Gulls, the incidence of resettling and preening was actually greater at lower T_a . Resettling was observed for an average of 4.0 and 2.4 minutes per 30 minutes while preening was observed for an average of 0.7 and 0.4 minutes per 30 minutes at T_a s of less than 14°C and greater than 18°C respectively. From a bioenergetic standpoint, these results

are difficult to understand.

Percent Occurrence of Three Incubation Behaviors versus T_a

Many authors including Bartholomew, Lasiewski, and Crawford (1968) have shown that birds begin to increase their breathing rate (i.e., they pant or flutter their gular area) only when the T_a of the metabolic chamber is raised to a level approaching their T_b (i.e., at about 40°C). This change in behavior is necessary because when a temperature gradient between the bird and no longer exists, evaporation is the only remaining avenue of heat loss (eq.8). The T_a at which a bird must increase its metabolic rate to support the demands of an increased breathing rate is known as the upper critical temperature (T_{uc}) (Figure 10, p.40). Physiologists refer to the region between the T_{lc} and the T_{uc} as the thermoneutral zone.

The T_{uc} s of the ten nesting Killdeers reported on in Figure 7a-e, p. 18 were well below 40°C. For example on 8 June a Killdeer on Nest #7 began panting when the T_a reached 25°C at 4 hours past dawn (there was a clear sky and no wind).

This information suggests that metabolism was not the only source of heat available to the birds. A more complete energy equation for the nesting Killdeers takes into account the additional energy sources of solar, skylight, and infra-red (IR) radiation:

$$\begin{aligned} \text{Heat gain} &= \text{Heat loss or gain to radiating surface} = \\ &\text{Heat loss or gain to environment} \end{aligned} \quad (10)$$

$$\begin{aligned} S + s + r(S + s) + M &= h_k(T_s - T_r) = \\ h_c(T_r - T_a) + h_r(T_r^4 - T_a^4) + h_r(T_r^4 - T_g^4) + h_k(T_r - T_g) + E \end{aligned} \quad (11)$$

where S is direct solar radiation, s is skylight radiation, $r(S + s)$ is reflected solar and skylight radiation, and $h_k(T_r - T_g)$ is heat loss or gain by conduction from the sitting bird to or from the ground (Priestly, 1957, Porter and Gates, 1969, and Heppner, 1970).

By 4 hours past dawn the radiation level must have been sufficiently intense to raise the average T_r of the Killdeer on Nest #7 well above the T_a . As a result of this positive gradient, there would have been considerable heat loss from the plumage by convection and radiation. However since the Killdeer's average T_r was probably about equal to its T_s , it is likely that none of this dissipated heat was a byproduct of metabolism. The bird had to start panting since, in the absence of a $T_s - T_r$ gradient, it could no longer lose internal heat by conduction through the plumage.

Figure 11 shows how the amount of radiant energy this Killdeer was absorbing at a T_{uc} of 25°C can be estimated. Its T_{lc} would have had to been about 11.5°C if one assumes that 13.5°C is a valid estimation of the width of the Killdeer's thermoneutral zone (Fig. 10, p. 40). If this Killdeer was maintaining a constant T_b , it would have been gaining and losing about $17 \text{ cal}(81\text{g} \cdot \text{min})^{-1}$. This rate of heat input is nearly twice that attributed to the bird's SMR. Absorbed radiant energy from the sources indicated in equation 11 must have contributed the additional $8 \text{ cal}(81\text{g} \cdot \text{min})^{-1}$.

By noon on that same day when the T_a had reached 30°C , the Killdeer was panting 100% of the time. At that point it is likely that the T_r of the bird's outer feathers exposed to the sun was approaching 80°C (Marder, 1973).

Figure 11 - The theoretical relationship between the heat exchange of a Killdeer and T_a under natural conditions. At 4 hours past dawn on 8 June a Killdeer on Nest #7 began panting when the T_a reached 25°C (i.e., its T_{uc} was 25°C). Assuming a 13.5°C wide thermoneutral zone, this means that the bird was gaining and losing about $17 \text{ cal}(81\text{g} \cdot \text{min})^{-1}$. The $8 \text{ cal}(81\text{g} \cdot \text{min})^{-1}$ heat input above the SMR can be attributed to absorbed radiant energy.

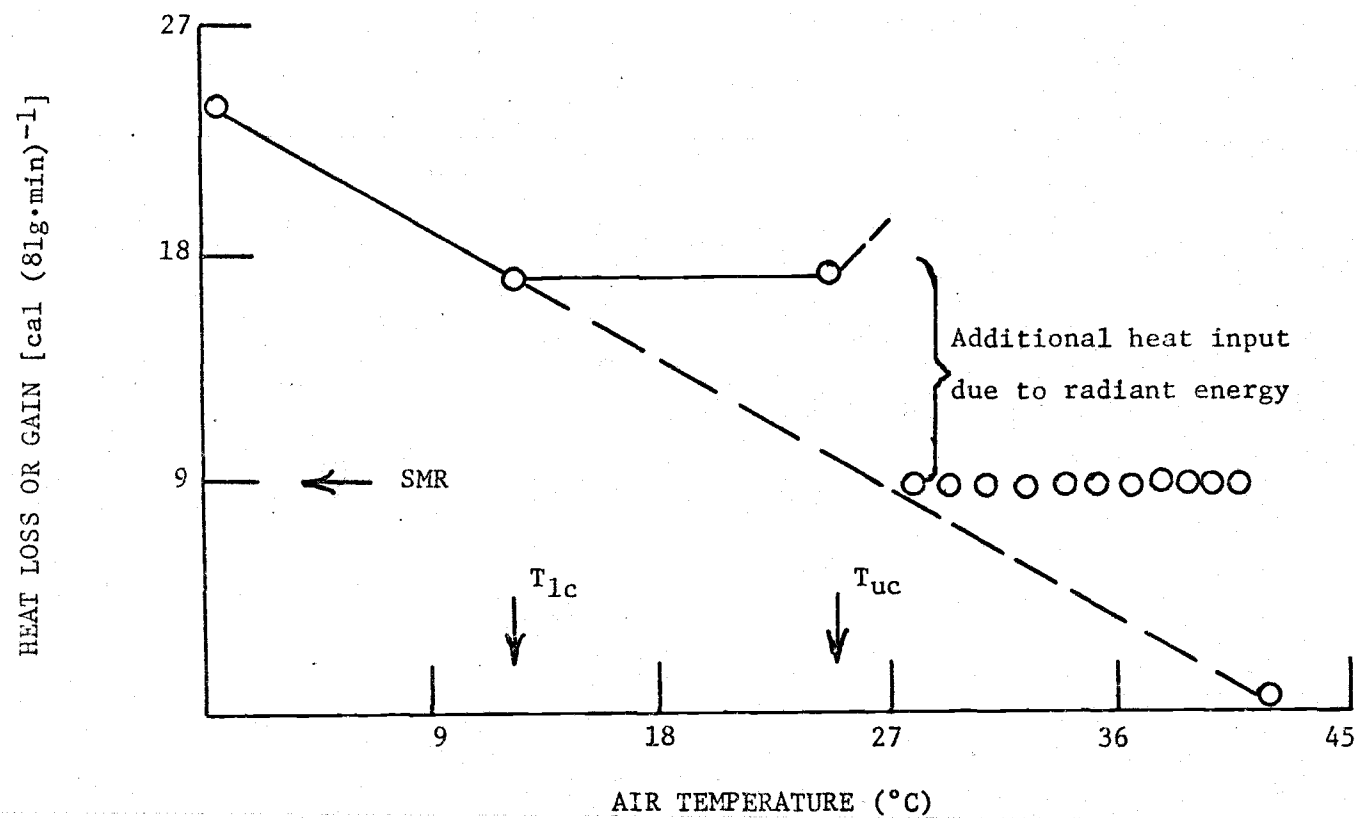


Figure 11

As a result there would have been conductive heat flow from the plumage into the body. The increase in the Killdeer's panting response was certainly an attempt to rid itself of this incoming heat.

Also under these conditions, the Killdeer was standing about 50% of the time. In that position the bird's belly, legs, and feet would have been shaded from direct radiation and would not have been in contact with the ground. If the T_r of these areas was even slightly less than the T_g then some conductive body heat loss to the plumage could have occurred. Also if the T_g was greater than the belly and leg T_r of the sitting Killdeer, then the bird would have avoided some conductive but not radiant heat gain by standing (eq. 11, p. 43).

Percent Occurrence of three Incubation Behaviors versus Wind Speed

It was noted in the results section that the relationship between the incidence of the incubation behaviors and T_a showed a lot of interest variation. Factors such as differences in individual tolerance to heat stress and day to day changes in the degree of cloud cover were probably the sources of some of this variation. In addition, it is likely that differences in wind speed among nests altered the Killdeers' responses to various heat loads.

Drent (1970) found that wind speed had a drastic effect on Herring Gull thermoregulatory behavior. At a radiation level of $1.0 \text{ cal}(\text{cm}^2 \cdot \text{min})^{-1}$, a bird panted 100% of the time at wind speeds less than $250 \text{ cm}(\text{sec})^{-1}$ (5.5 mph) while it did not pant at all at wind speeds greater than $400 \text{ cm}(\text{sec})^{-1}$ (8.8 mph).

The following equation will be useful in explaining Drent's

results:

$$h_c = A_c \left(k \frac{V^{1/3}}{D^{2/3}} \right) \quad (12)$$

where A_c is the surface area subject to convective heat loss, V is wind speed, D is the body diameter, and k is a constant dependent on the shape and roughness of the body and on the direction of the wind impinging on the body (Porter and Gates, 1969 and Heppner, 1970). With an increase in wind speed of $150 \text{ cm}(\text{sec})^{-1}$ the value of the gull's convection coefficient would have increased. And if we assume there was a positive gradient between T_r and T_a (eq. 11, p. 43), then the rate of heat loss from the bird would have also increased. By decreasing its evaporation rate (i.e., by decreasing the percent time panting to zero), the gull was attempting to re-establish its heat energy balance.

For Nest #10 and #11 in this study, there was no clear-cut relationship between sit-mo and wind speed at T_a s between 28 and 38°C (Fig. 8, p. 25). However the incidence of sit-mc did increase with increasing wind speed. At successively higher wind speeds equation 12 suggests that Killdeer would spend more time sitting relative to standing in order to regulate convective heat loss by reducing the amount of surface area (A_c) exposed to air flow.

The increase in the occurrence rate of both sit-mc and sit-mo did not take place until wind speeds reached $360 \text{ cm}(\text{sec})^{-1}$ (8 mph) for Nest #11 and $540 \text{ cm}(\text{sec})^{-1}$ (12 mph) for Nest #10. At lower wind speeds measured at 2.5 m one would not expect to see this change in behavior because the frictional effect of the surface would preclude any significant air flow at the height of a nesting Killdeer. Gates (1971) says that a $450 \text{ cm}(\text{sec})^{-1}$ (10 mph) wind at 2 m may blow at only $45 \text{ cm}(\text{sec})^{-1}$

at 10 cm.

In the case of Nest #3, the incidence of sit-mo actually decreased with increasing wind speed. It could be that the expected relationship did not show up because not enough data was taken at warmer T_a s. This contention is supported by the fact that, even at lower wind speeds, stand-mo was never observed to be the dominant behavior.

The occurrence rate of stand-mo for Nest #2 did not vary from about 100% at wind speeds up to $495 \text{ cm}(\text{sec})^{-1}$ (11 mph). The fact that this nest, unlike the others, was located in a sheltered area at the base of a roadbed may explain why the incidence of sit-mo was independent of wind speed.

T_e versus T_a

The heat energy equation for an egg less than 10 days old (i.e., one incapable of producing its own heat) under normal incubation conditions would be:

$$\text{Heat input to egg} = \text{Heat loss or gain from egg} \quad (13)$$

$$KM = h_c(T_r - T_{na}) + h_r(T_r^4 - vT_{na}^4) + h_r(T_r^4 - T_g^4) + h_k(T_r - T_g) + E \quad (14)$$

where KM is that fraction of the incubator's metabolic heat absorbed by one egg, T_r is the temperature of the egg's radiating surface, and T_{na} is the nest T_a .

At first glance it is not apparent how equation 14 could be useful in analyzing the relationship between T_e and T_a since T_a is not in any of the equation's terms. This difficulty can be overcome. Assume that T_g is proportional to T_a . So as T_a decreases, net heat loss from the eggs through the poorly-insulated nest to the ground would increase

if the incubator did not increase its heat input to the clutch.

Figure 9b, page 33, shows that at a T_a of 25°C , nest #3's maximum "dummy" T_e was 37°C . However at T_a s less than 12°C , the maximum T_e attained for any of the nests was 34°C . This information suggests that there was an increase in net heat loss from the eggs at low T_a .

By way of contrast, Drent found that the Herring Gulls, which build a grass-lined nest on the ground, were able to maintain a T_e of 37°C at T_a s as low as 12°C . That is, the slope of their T_e versus T_a regression line is equal to zero and the y-intercept is 37°C . A comparison of the regression equations in Figure 9 shows that Nest #3's regression line most closely approaches that of the Herring Gulls. This result is consistent with the fact that of all five Killdeer nests, only Nest #3 was made with wood chips which is a better insulating material than stone (Table II, p. 14).

The triangles of Figure 9, page 31, indicate that the incubating Killdeers were standing over the eggs during many of the subperiods observed at T_a s above 24°C . It has already been shown that this behavior was beneficial to the adults in that it would have increased convective heat loss. Apparently the standing position would not have been injurious to the embryos since when it was performed at T_a s up to 41°C , dummy T_e never exceeded 40°C . A lethal T_e of $43\text{--}45^\circ\text{C}$ (Rol'nik, 1970) was never reached because the nests were always in the standing Killdeers' shadow.

Since the minimum "dummy" T_e recorded while the birds were standing was only 35°C , it appears that the growth rate of the embryos would not have been seriously retarded. Heat input by radiation from the

ground, nest air, and the bird and by conduction from the ground must have been sufficient to prevent significant heat loss from the eggs (eq. 14).

VI. CONCLUSION

The results of this study show that the nesting Killdeer were behaviorally adapted to the high temperatures and intense solar radiation characteristic of the desert biome. That is, they regulated their percent time panting (or fluttering their gular area) and standing according to the heat load. These thermoregulatory behaviors allowed the Killdeer to avoid serious hyperthermia (i.e., a lethal T_b of about 45°C).

The roads seemed to provide suboptimal nesting habitat for the Killdeer in terms of excessive heat loss from the eggs during the cold early morning hours. "Dummy" T_{es} as low as 29°C were detected from incubated nests built on a stone substrate. This information suggests that embryonic development was retarded as a result of insufficient nest insulation. However it is not possible to comment on the extent of this retardation since 1) the optimal incubation temperature for Killdeer is not known and 2) T_{es} were not taken throughout a 24 hour period.

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APPENDIX

GLOSSARY

C	thermal conductance
E	heat loss by evaporation
h_c	convection coefficient
h_k	conduction coefficient
h_r	radiation coefficient
M	heat gain by metabolism
sit-mc	sit-with-mouth-closed behavior
sit-mo	sit-with-mouth-open behavior
stand-mo	stand-with-mouth-open behavior
T_a	air temperature
T_b	body temperature
T_e	egg temperature
T_g	ground temperature
T_{lc}	lower critical temperature
T_{na}	nest air temperature
T_r	radiating surface temperature (i.e., the temperature of the outer feathers)
T_s	skin temperature
T_{uc}	upper critical temperature