

CALIFORNIA STATE UNIVERSITY, NORTHRIDGE

A COMPARATIVE STUDY OF WATER LOSS IN TWO GEO-
GRAPHICALLY AND CLIMATICALLY ISOLATED POPULA-
TIONS OF THE COASTAL SIDE-BLOTCHED LIZARD,
UTA STANSBURIANA HESPERIS RICHARDSON

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Gary Stephen Thorpe

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ABSTRACT

A COMPARATIVE STUDY OF WATER LOSS IN TWO GEOGRAPHICALLY AND CLIMATICALLY ISOLATED POPULATIONS OF THE COASTAL SIDE-BLOTCHED LIZARD,
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Rates of evaporative water loss were obtained for two geographically and climatically isolated populations of Uta stansburiana hesperis Richardson under specified conditions of temperature, relative humidity and air flow. From these data, equations for the two populations predicting evaporative water loss were derived in an attempt to show: (1) habitat correlation of evaporative water loss and (2) differential, genetically-determined response patterns of evaporative water loss in respect to reproductive isolation.

In this study it was found that the rate of water loss in the two lizard populations did not differ significantly in relation to the effects of air temperature, relative humidity and convection.

INTRODUCTION

Water availability, of prime importance in the ecology of most reptiles, is possibly the most fundamental environmental feature affecting their dispersal. Although lizards are generally suited for life in warm regions, they are found from the Arctic Circle, as in the case of the common lizard Lacerta vivipara, to the sub-tropical and tropical regions where a diversity of representatives are found. In terms of water availability, lizard distribution ranges from the near marine or limnic, as in the case of Lophura amboinensis, to extreme xeric conditions as in the case of Uta stansburiana stejnegeri.

The major pathways of water loss in lizards includes that lost in feces and urine, through cutaneous and respiratory evaporation, and through evaporation from moist cloacal surfaces exposed during defecation. Cowles (1939, 1940, 1958), Cole (1943) and Bogert (1959) demonstrated that a direct correlation exists in reptiles between water loss and ambient temperature, and that lizards regulate their internal body temperature by ethological, structural and physiological means.

Ethological mechanisms for regulating body temperature in lizards include capturing solar radiation through basking, slowing the conduction of heat into the body from objects on which they rest by elevating the body and supporting themselves by the digits, escaping from intense solar rad-

iation by burrowing, and by quiescence during adverse winters (Templeton, 1960).

Structural and physiological mechanisms of temperature regulation include thermostatic color change, heat gained through metabolic processes, heat lost through respiratory and cutaneous evaporation of water and by partial estivation during hot summer days. Additional means of temperature regulation include heat loss or gain through conduction to or from the substrate, by conduction to or from the air and by radiation to or from other objects.

Desert lizards tend to exhibit only moderate physiological adaptations to maximal conditions of temperature stress, surviving primarily through behavioral responses. Cowles (1939) showed that, when subjected to substrate temperatures approaching 87 C, extremely thermophilic, diurnal lizards such as Sauromalus obesus, Dipsosaurus dorsalis dorsalis, Uma notata, Phrynosoma platyrhinos and Phrynosoma m'callii have internal temperatures ranging from 37 to 38 C. The coastal lizards Phrynosoma blainvilli blainvilli and Phrynosoma blainvilli frontale, and the high-desert species Crotaphytus collaris baileyi, Crotaphytus wislizenii and Crotaphytus silus, found in habitats of moderate temperature extremes, have internal temperatures approaching those of the thermophilic species. An internal temperature increase of only 2 C above this maximal range cause marked discomfort, while further increases caused eventual death in both groups.

Correlations between aridity of habitat and the rate of water loss have been demonstrated for a limited number of species. Claussen (1967) showed that at a temperature of 30 C, the rate of water loss in the sub-tropical iguanid, Anolis carolinensis, is greater than that in Uta stansburiana hesperis which inhabits semi-arid regions. He further suggests that a correlation exists between the rate of water loss and the availability of water in the natural habitats of these two lizards. Bentley and Schmidt-Nielsen (1966) compared cutaneous and respiratory evaporation rates in five species of reptiles from varied locales at 23 C and found that the total water loss from the desert lizard Sauromalus obesus was one-nineteenth that of the crocodilian Caiman sclerops.

Evolutionary mechanisms for adaptation are based upon hereditary variation within the species; however, hereditary variation in physiological characters in saurians have not been studied extensively. Such knowledge should form a basis for discernment of intra- and inter-specific relationships, variations within and among species and possible reasons for extensions of geographic range, since extension of the geographic range is dependent upon whether any new variation provides the adaptive capacity to occupy new environments.

The principal goal of this study is to determine rates of evaporative water loss for two geographically and climat-ically isolated populations of Uta stansburiana hesperis

Richardson under specified conditions of temperature, relative humidity and air flow, and to derive from these data, equations for the two populations predicting evaporative water loss, in an attempt to show: (1) habitat correlation of evaporative water loss and (2) sub-specific, differential genetically determined response patterns of evaporative water loss.

A null hypothesis, H_0 , is proposed such that for a variety of statistical tests, that the sample means of water stress of one population (Fallsvale)- μ_1 , are not significantly different from the sample means of the second population (Palm Springs)- μ_2 , at a confidence level of $\alpha = 0.05$. The rejection of the null hypothesis necessarily forces the acceptance of the alternate hypothesis- H_1 , such that the sample means of water stress are significantly different between the two populations at a 0.05 confidence level.

The treatments were designed so that adaptive behavioral responses to humid and thermal stress were held to a minimum. Any significant differences of water loss under experimental conditions between samples of the two isolated populations would support the conclusion that the two populations have evolved different capacities for water conservation.

ECOLOGY AND DESCRIPTION

According to L.M. Klauber (1939), the genus Uta is distributed throughout every life zone in western North America from Lower Sonoran to Transition and from ocean tide line to the yellow pine forests. North-south distribution limits extend from the State of Washington to the central Mexican plateau with eastward distribution encompassing the dry bajadas of the Great Basin region and into the southern Great Plains. Such a wide range of ecological habitats has resulted in genetic differences among lizard populations occupying distinct areas of this extensive range.

Stebbins (1954) recognized three subspecies of Uta stansburiana, two of which meet within the capture-limits of this study. These two subspecies are the desert side-blotched lizard- Uta stansburiana stejnegeri Schmidt and the coastal side-blotched lizard- Uta stansburiana hesperis Richardson.

The range of Uta stansburiana hesperis, the lizard under study in this project, extends from the San Joaquin Valley of central California to the coastal limits of Los Angeles County; extending as far south as Baja California (Smith, 1946).

The diagnostic characteristics for Uta stansburiana hesperis are: (1) uniform and small dorsal scales; (2) a

divided frontal scale; (3) two rows of postrostral scales and (4) a granular gular fold. For a complete description of this lizard see Smith (1946).

For most of the year these lizards are active and may be found during the day basking on rocks. During the winter they become dormant but may still emerge on relatively warm days.

The food consumed is similar for all species of Uta. Wood (1933) estimated that each lizard consumed approximately 9,000 insects per year and that consumption reaches a peak in August and a minimum in November, December and January. In captivity they feed readily upon flies and meal worms, especially during the warmer hours of the day when they are most active.

The enemies of the western Uta include various species of snakes and birds, and to a lesser extent white-footed mice and wood rats (Smith, 1946).

Studies by Tinkle (1961, 1962) and Jorgensen and Tanner (1963), using methods of minimum polygon and density probability functions to determine home range size, have shown average home range for juveniles to be 0.42 acres, for females 0.68 acres and for adult males 0.98 acres.

Further studies by Tinkle (1961) have shown that Uta populations are essentially annual with older individuals dying off after the breeding season. Consequently, an enlargement or shift of territory by some male individuals toward the end of summer is believed to be the probable

consequence of the death of an adjacent male. The result of this seasonal replacement and decline of the old generation is that movement into and out of the study area is negligible. Juveniles either mature within the parental home range or move in from sub-optimal positions to establish home ranges in the same area as the adults die.

Uta populations have three distinct features that may reflect the climatic history of the present study area. These distinct features may also reflect past distributional patterns which may be presently evidenced in intra-specific adaptations. These features are: (1) populations of Uta occur throughout the entire study area; (2) the two subspecies that occur in the study area are morphologically distinct and (3) the home range is under one acre and movement is virtually absent. With these factors in mind, it is likely that past distributions of Uta may have persisted for relatively long periods of time. If this is so, then it may be hypothesized that these past distributional patterns may be evidenced in the form of distinct differential potentials or capacities for water conservation among the two populations studied.

STUDY AREA

The first trapping site (Site 1) was located in the San Bernardino mountain range in Mountain Home Canyon, near the town of Fallsvale, California. Site 1 at 34°-05' latitude, 116°-56' longitude and at an elevation of 1.61 Km is in an east-west range of mountains approximately 158.4 Km east of the Los Angeles area. This mountain range constitutes the largest high mountain range in southern California, and includes Mt. San Gorgonio -the highest peak south of Mt. Whitney.

The forested areas of this mountain range are more extensive than elsewhere in southern California and have a rich fauna. The relative isolation of this mountain range from any other mountain range of similar altitude makes this trapping site desirable in terms of relative genetic isolation of the lizards found there.

Site 1 is on the Pacific side of this mountain range and is primarily Upper Sonoran to Transition in make-up. The following plant species found in the immediate trapping area are indicators for this particular zone type:

Alnus rhombifolia, Artemisia tridentata, Cercocarpus ledifolius, Eriodictyon trichocalyx, Juniperus occidentalis, Populus trichocarpa, Salix lasiolepis and Tetradymia canescens.

The climate of this area is characterized by moderately warm summers and moderately cold winters. As a result,

precipitation is abundant and increases with altitude, reaching a maximum between 1.5 and 2.0 Km. Above this level there is a decided decrease in precipitation corresponding to the further rise in elevation. Site 1 averages approximately 118 cm of rainfall annually, with most of the rain occurring from November through late March, with minimal amounts from April through October. Temperatures in the trapping area range below freezing in winters to the low thirties ($^{\circ}\text{C}$) for maximum summer extremes. Figure 1 illustrates trapping-site 1.

The second trapping site (Site 2) was located in the Colorado desert at the base of Mt. San Jacinto, near the town of Palm Springs, California. Site 2 at 33° - $50'$ latitude, 116° - $30'$ longitude and at an elevation of 0.3 Km is approximately 211.2 Km east of the Los Angeles area.

Site 2 is primarily Lower Sonoran in make-up. The following plant species found in the immediate trapping area are indicators for this particular zone type:

Larrea divaricata, Franseria dumosa, Encelia farinosa,
Dalea spinosa, Cercidium floridum and Chilops linearis.

The climate of this area is characterized by long, hot summers with 47 C being the average temperature between June and September, with temperatures of 56 C not being uncommon. In July, the hottest month, the mean daily temperature is 54 C with a diurnal range of approximately 29 C. Winter temperatures at Site 2 are relatively mild; in January, the coldest month, the mean daily temperature is

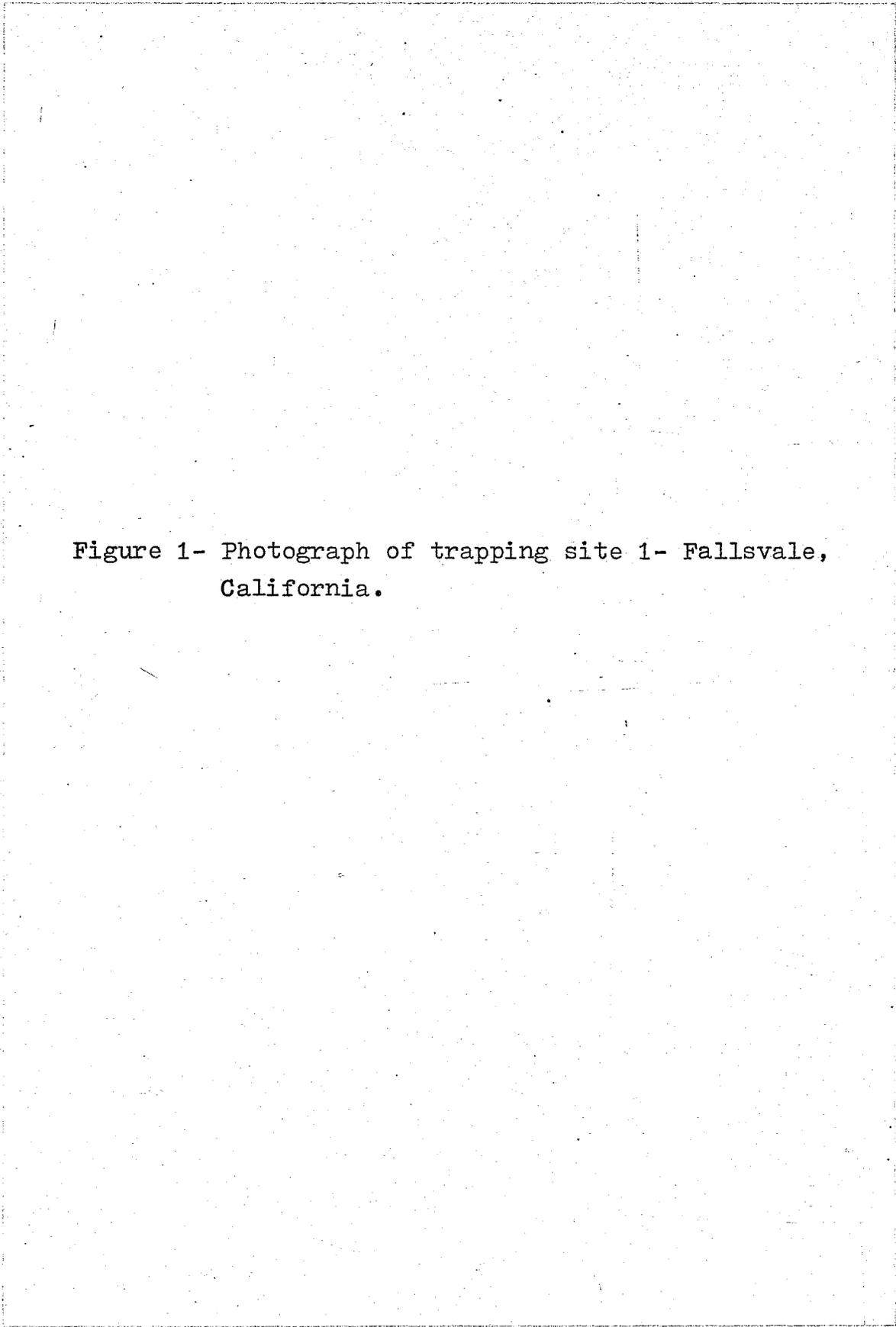


Figure 1- Photograph of trapping site 1- Fallsvale,
California.



32 C with a diurnal range of approximately 13 C. Freezing temperatures seldom occur in this trapping area.

The absolute humidity at Site 2 is very low throughout the year with the corresponding evaporative water rate being quite high. Rain is minimal in this area and what rain that does fall, comes in the form of convectional precipitation, in violent but short-lived thunderstorms. The mean annual precipitation for this area is 14.2 cm. Figure 2 illustrates trapping-site 2.

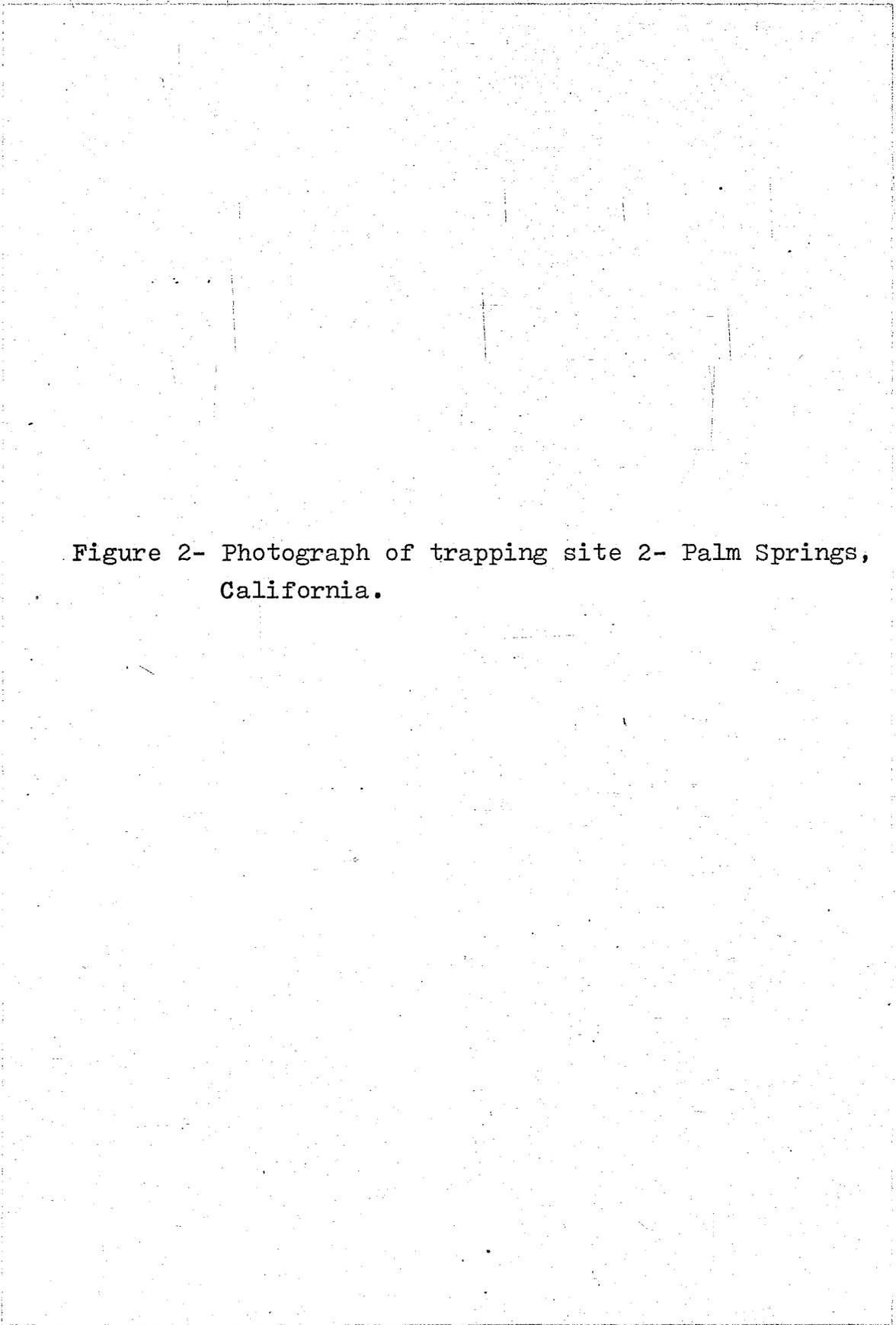


Figure 2- Photograph of trapping site 2- Palm Springs,
California.



METHODS AND MATERIALS

Thirty-four individuals of the coastal side-blotched lizard (*Uta stansburiana hesperis* Richardson) were collected at Site 1 (Fallsvale) from April through October, 1974. Thirty-one individuals of the same species were collected at Site 2 (Palm Springs) from November, 1974 through January, 1975. The trapping periods were chosen in an attempt to approximate equivalent air temperatures within the two distinct communities. This was done in an effort to minimize any factors associated with seasonal acclimation.

Air temperatures were recorded using a telethermometer, accurate to ± 0.5 C, at the exact position that the lizard had occupied prior to capture. The probe of the telethermometer was shaded from solar rays for all air temperature recordings. The date, time, and capture-site were recorded with each air temperature measurement. Substrate temperatures were taken approximately 5 millimeters beneath the soil surface. The substrate temperature was recorded at the exact position where each lizard was captured.

Relative humidity was determined by using a Casella whirling psychrometer with a readability of ± 0.5 C. Wind speed was determined by using a Dwyer hand-held anemometer in the vicinity of the capture site.

Four capture techniques were employed in this study. It was found that the technique used must vary to accommodate

varied terrestrial conditions. In other words, methods employed on desert sand do not necessarily work efficiently in mountain creek beds. The four techniques included: (1) noose method; (2) throw net; (3) fish net and (4) extension seizer- a commercial extension tool with expandable 'jaws'.

After capture, the internal body temperature of the lizard was determined by inserting the probe of the tele-thermometer into its cloaca. Each captured lizard was given an identification number, weighed with a field torsion balance and its approximate age determined. Sex was determined by the presence or absence of femoral pores, sexual dimorphic coloration and other characteristics listed by Smith, 1946. A collection of the field equipment used in this study is presented in Figure 3.

Part B: Laboratory Measurements

Lizards brought into the laboratory were individually kept in glass terraria provided with a sand substrate. Water and food, consisting of larvae of the lesser mealworm, Alphatobius diaperinus, were provided ad libitum. This diet kept them healthy judging by their general vigor and maintenance of body weight. Light cycles were set to match seasonal photoperiods and air temperature was maintained at approximately 22 C. Survival approached ninety percent and most lizards held or slightly increased their body weight while in captivity. The mean weight of the lizards used in this study was for the Fallsvale population 5.5 grams \pm 1.34

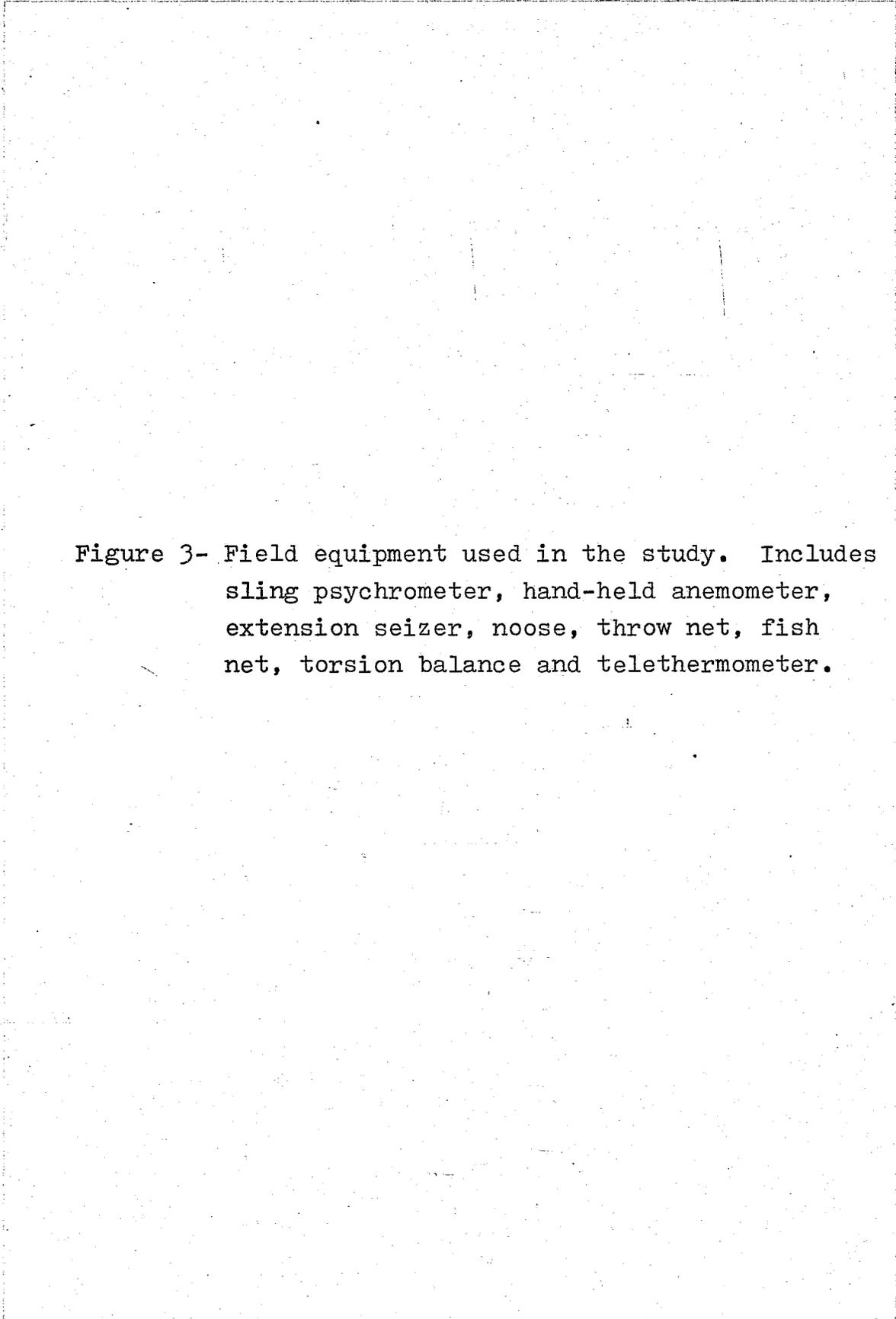


Figure 3- Field equipment used in the study. Includes sling psychrometer, hand-held anemometer, extension seizer, noose, throw net, fish net, torsion balance and telethermometer.



S.D., and for the Palm Springs population $5.1 \text{ grams} \pm 1.44$
S.D.

Prior to taking any of the measurements, each animal was placed in a container provided with moist paper towel-
ling for twenty-four hours. Food and drinking water were withheld during this period. This reduced defecation during the course of the experiment and allowed the lizard to attain a state of full or partial hydration. All measurements of water loss were completed within a week of capture to avoid the possibility of laboratory acclimation. During experimentation, all lizards were kept in total darkness to serve as a standard for comparison with previous studies (Claussen, 1967; Roberts, 1967; Templeton, 1960 and Warburg, 1965 a,b), and to reduce movements and activity associated with a photoperiodic rhythm.

Total evaporative water loss was determined in a system providing a constant flow of air. Air from a laboratory line was initially cleaned and dried by passing it through sulfuric acid and anhydrous calcium sulfate. Air flows of 10, 250, 500 and 850 cubic centimeters per minute were monitored to $\pm 5\%$ with a rotameter flow meter (Emerson Electric). The air was then passed through silica gel or bubbled through a concentrated salt solution (CaCl_2) or water to provide low, intermediate or high humidities respectively. Three B.O.D. cabinets (Precision Scientific) set at 16, 24 and 34 C were used to establish laboratory air

temperatures (Fig. 4).

Before experimentation, the cloaca of each animal was taped to prevent any possible weight loss by elimination of feces or urine; consequently any change in body weight was due to total water loss through both respiratory and cutaneous evaporation. The lizard was then weighed to the nearest 0.0001 gram using the Christian Becker analytical beam balance. After twenty-four hours in the B.O.D. cabinet, the lizard was removed and re-weighed. Total water loss was then calculated as the difference between original and final weight.

The ventilation rate of each animal during the experiment was determined by counting thoracic contractions. Aluminum foil was wrapped around the glass chamber, with a small 'peep' hole made for observations. With this 'peep' hole, one did not have to worry about light or movement of the experimenter causing changes in the ventilation rate due to alarm reactions. An activity level based on the following scale was subjectively determined for each lizard prior to removal of the lizard from the testing chamber:

1. Extremely active
2. Moderately active
3. Normal, non-moving
4. Less than normally active
5. Torpor
6. Death

After these measurements were made the initial body temperature was taken with the telethermometer.

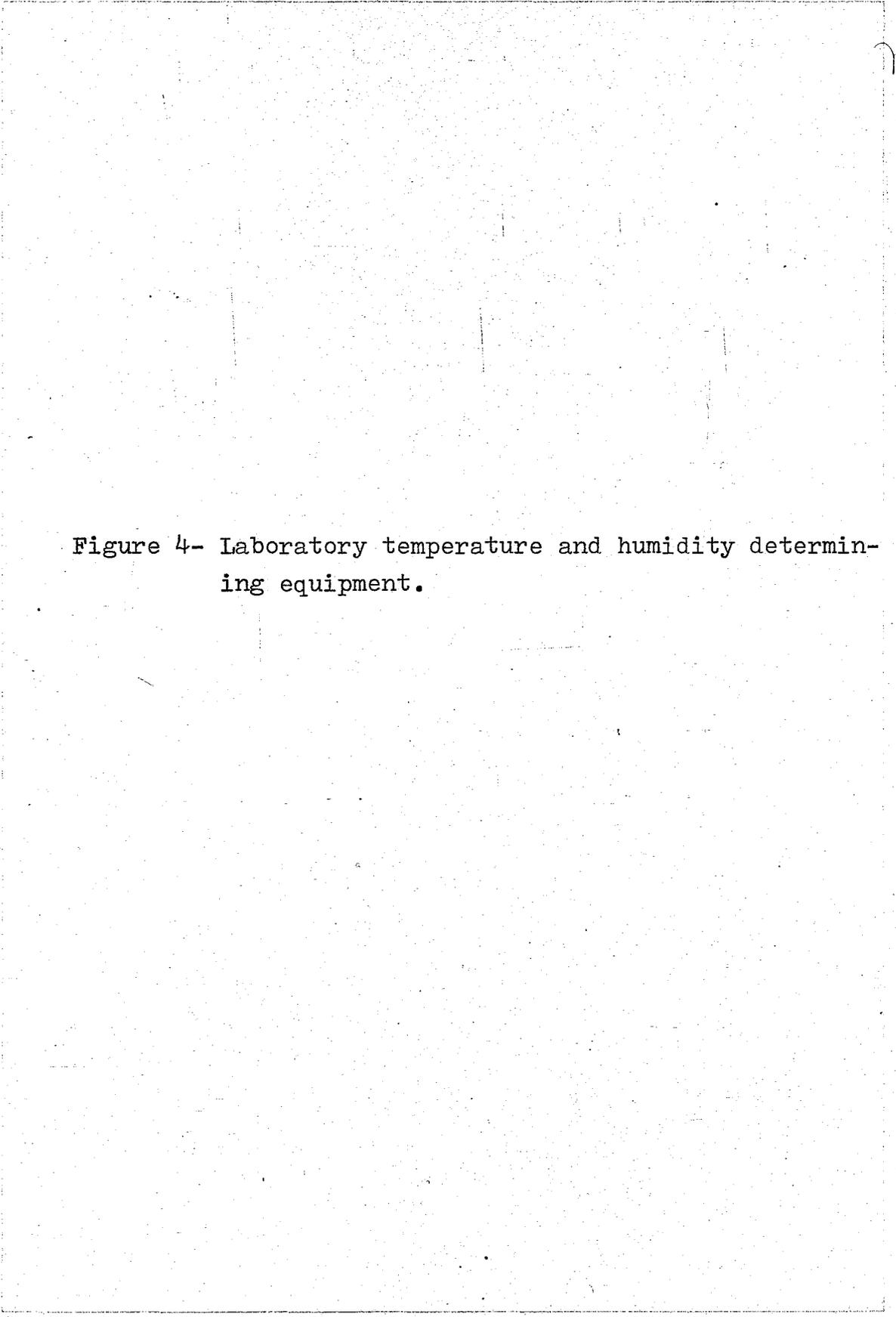
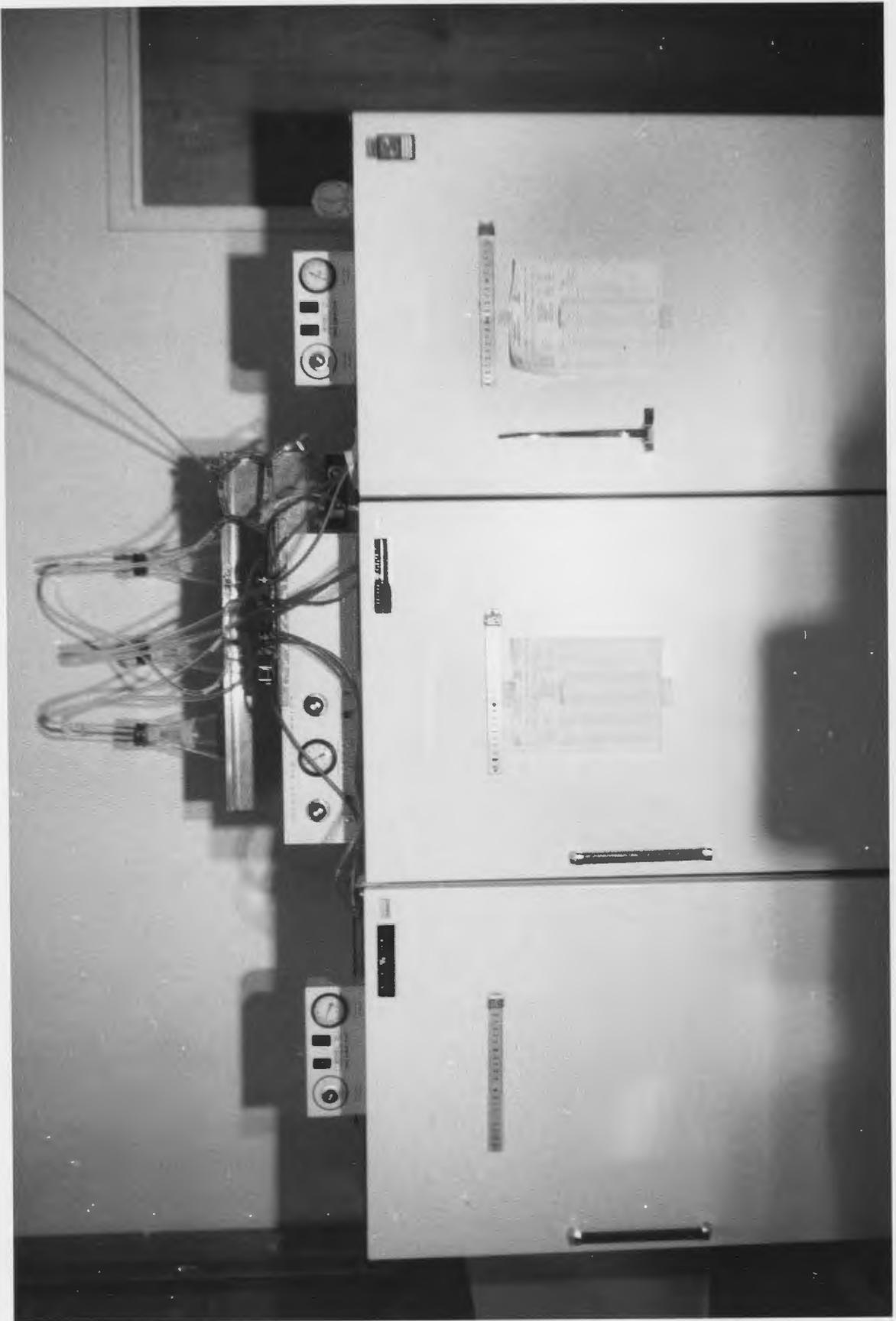


Figure 4- Laboratory temperature and humidity determining equipment.



All statistics were performed on the Control Data Corporation 3170 computer based at the California State University at Northridge campus. The computer programs used to analyze the data from this study were taken from Dixon (1971), and included the programs BMD03R- Multiple Regression with Case Combinations and BMD01R- Simple Linear Regression (One-Way Analysis of Covariance).

Percentage of initial body weight loss in 24 hours was calculated for each lizard based on the difference between initial body weight and body weight after treatment. Since defecation and urinary water loss were avoided, associated data must primarily reflect evaporative loss of water. Determination of activity level in response to specific laboratory conditions was subjective in nature and thus not amenable to statistical analysis.

RESULTS

Part A: Field Studies

In this study, field air temperatures, substrate temperatures and relative humidities were measured, along with the corresponding internal body temperatures of the lizards captured in the trapping area. Air temperatures, substrate temperatures and humidities in the habitats over the respective trapping periods are presented in Table 1.

Substrate temperatures as a function of air temperatures for both trapping areas are presented in Figure 5. A definite correlation exists for this function as evidenced by correlation coefficients of 0.96 for the Fallsvale site and 0.93 for the Palm Springs site; the increased values of the substrate temperatures being explained through the nature of specific heat of soil.

Body temperatures as a function of air temperatures for both trapping areas are presented in Figure 6. A logical increase in body temperature with a corresponding increase in air temperature was evident in both populations. Correlation coefficients of 0.89 for the Fallsvale site and 0.83 for the Palm Springs site support this relation. The higher body temperatures, when compared to the isotherm ($X=Y$), reveal the heliothermic nature of Uta stansburiana hesperis over the limited air temperature spans in this study.

Table 1- The micro-climates at Fallsvale and Palm Springs over the respective trapping periods. All temperatures are rounded to the nearest 1 °C.

Site	Air Temperature °C			Substrate Temp. °C	Relative Humidity	Internal Body Temp. °C
	Avg. Max.	Avg. Min.	Avg.			
September						
1) Fallsvale	24	6	16	43	40	31
2) Palm Springs	40	24	32	66	21	--
October						
1) Fallsvale	25	7	16	40	46	33
2) Palm Springs	32	16	24	59	36	--
November						
1) Fallsvale	11	-14	3	22	51	--
2) Palm Springs	27	10	18	49	41	34
December						
1) Fallsvale	5	-19	-1	9	64	--
2) Palm Springs	21	6	11	40	39	32
January						
1) Fallsvale	8	-18	0	15	68	--
2) Palm Springs	22	6	14	40	36	32

Site	Air Temperature °C			Substrate Temp. °C	Relative Humidity	Internal Body Temp. °C
	Avg. Max.	Avg. Min.	Avg.			
April 1974						
1) Fallsvale	14	-7	6	26	52	29
2) Palm Springs	31	13	22	41	38	--
May 1974						
1) Fallsvale	19	2	10	31	45	31
2) Palm Springs	35	17	25	47	31	--
June 1974						
1) Fallsvale	27	5	16	40	41	34
2) Palm Springs	42	22	32	68	21	--
July 1974						
1) Fallsvale	26	7	17	46	35	33
2) Palm Springs	42	24	33	72	17	--
August 1974						
1) Fallsvale	26	6	16	37	39	35
2) Palm Springs	42	23	33	74	16	--

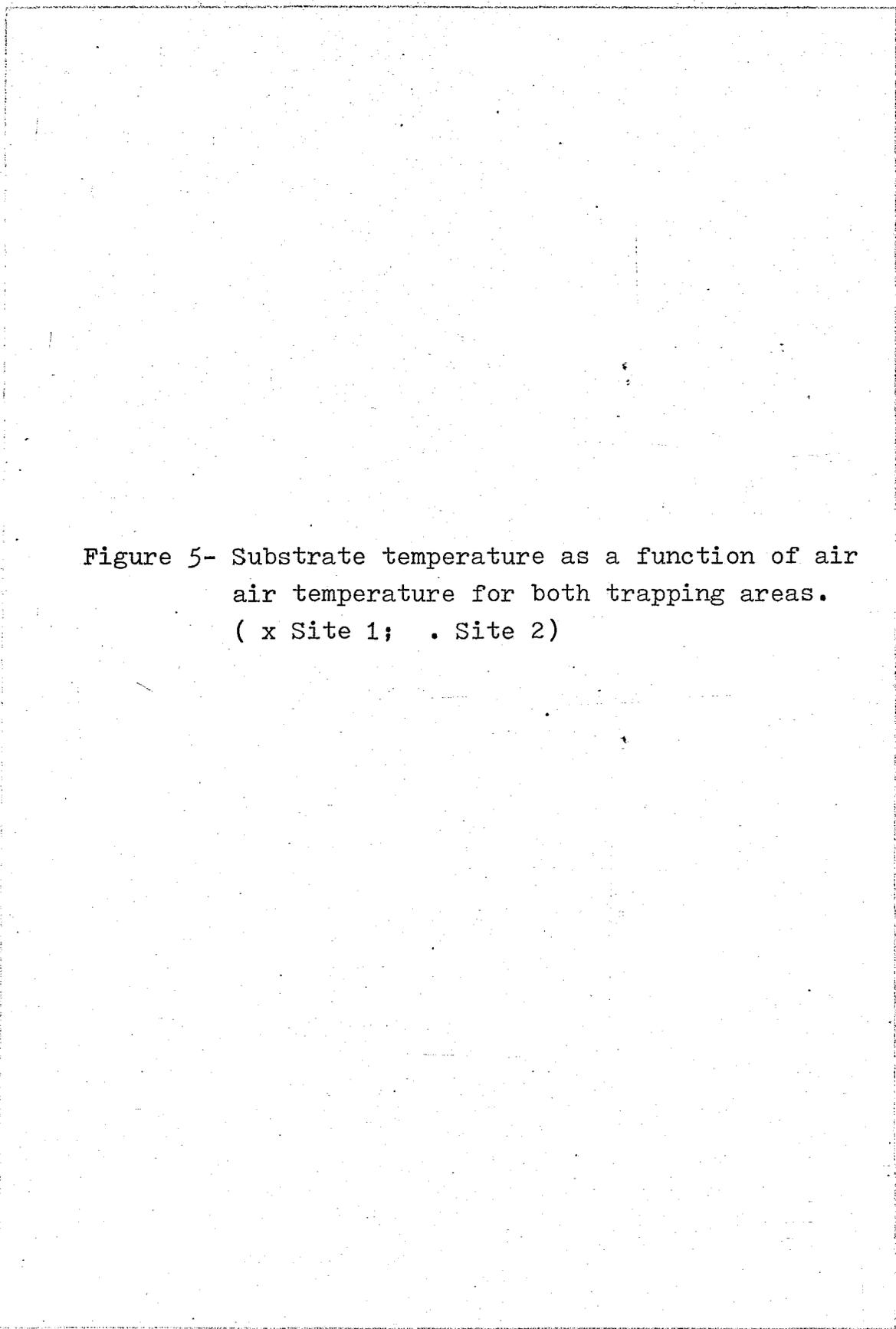


Figure 5- Substrate temperature as a function of air
air temperature for both trapping areas.
(x Site 1; . Site 2)

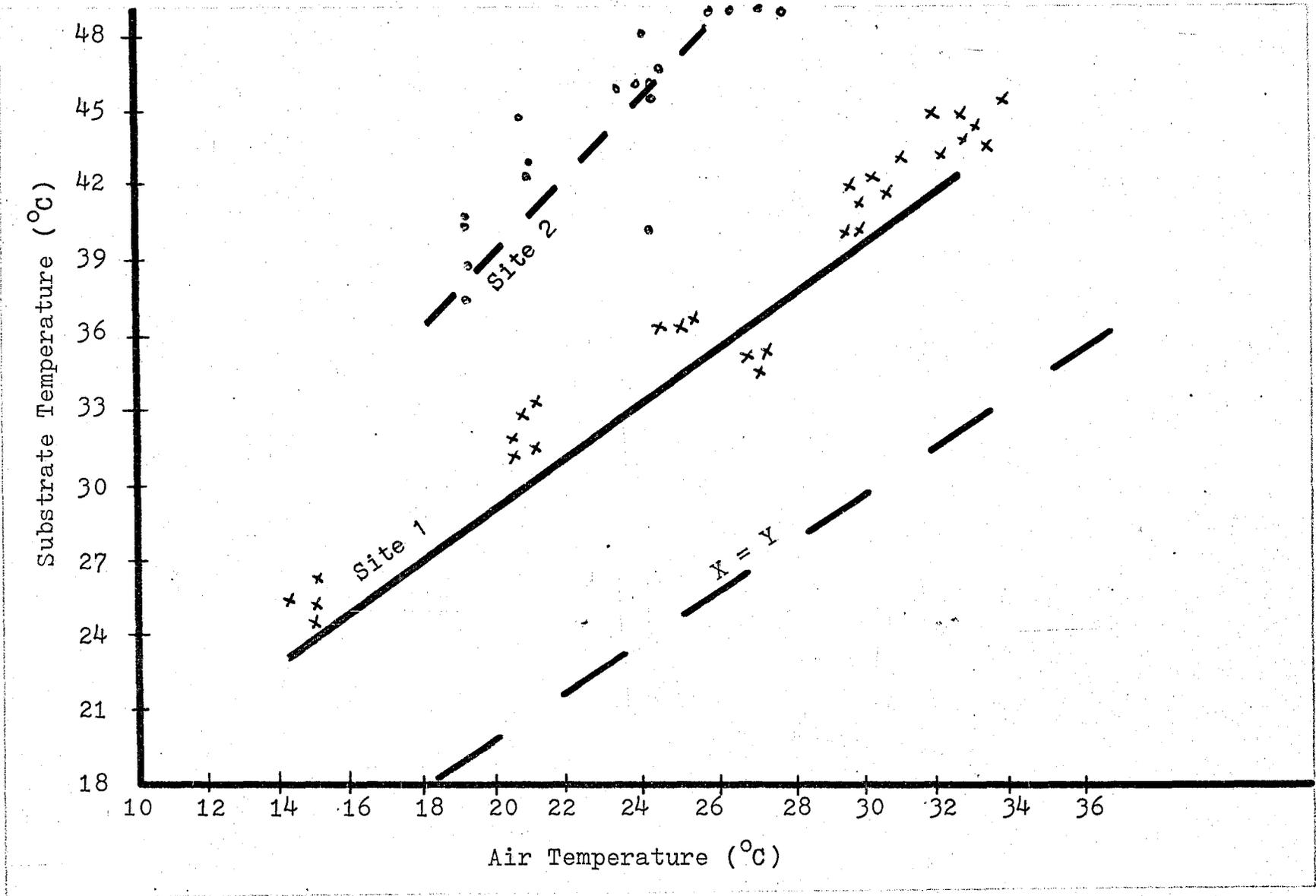
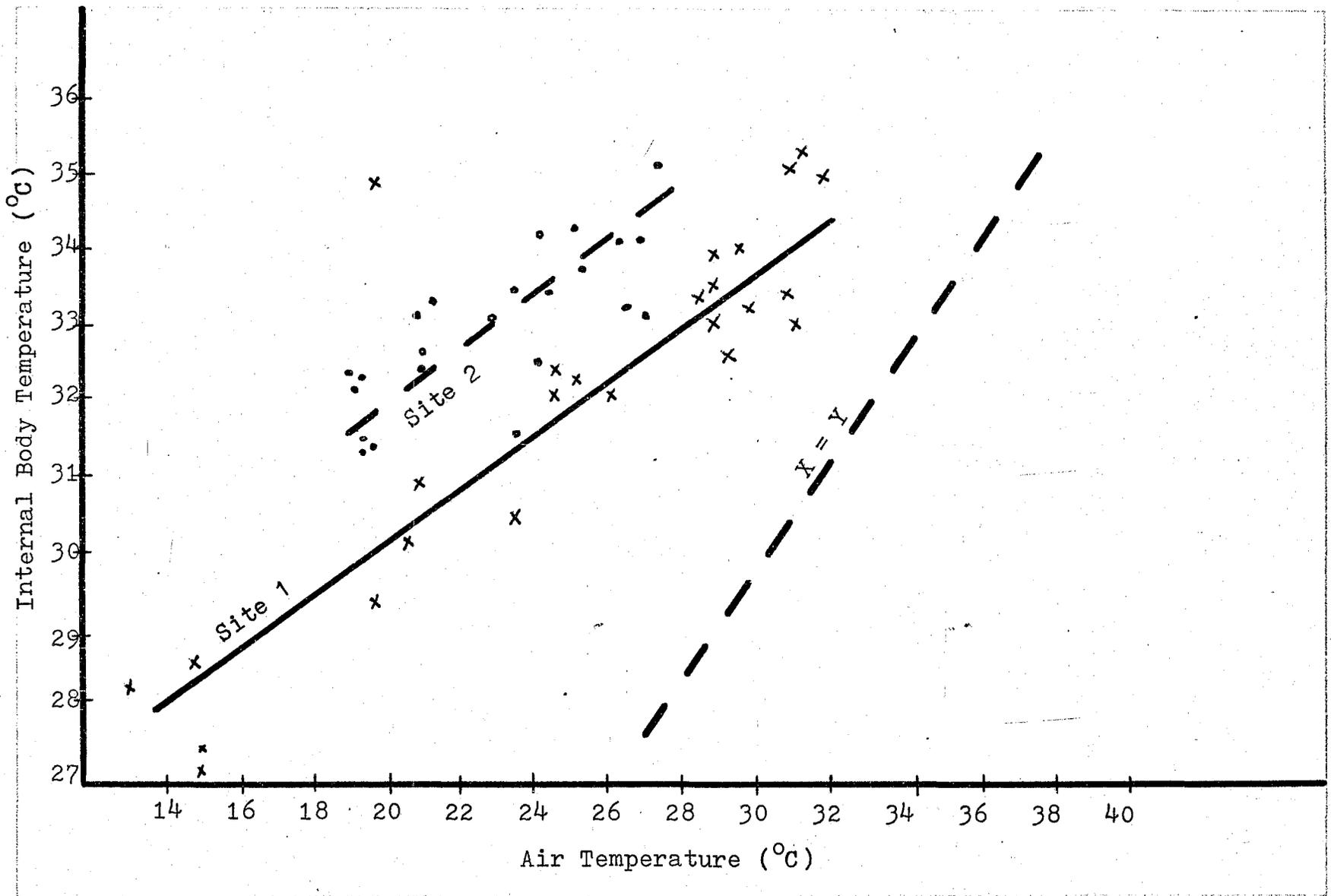


Figure 6- Body temperature as a function of air temperature for both trapping areas.
(x Site 1; . Site 2)



Part B: Laboratory Studies.

Data from laboratory studies of two populations of Uta stansburiana hesperis Richardson, isolated from each other in terms of geographic and climatic barriers, are summarized and presented in Table 2. The data were evaluated by multiple regression with case combination, treating the variables air temperature (C), relative humidity (%) and convection (cc/min) as independent variables and the rate of water loss ($\text{mg} \cdot \text{gm}^{-1} \cdot \text{hr}^{-1}$) as the dependent variable. Consideration of only three independent variables provided equations with a multiple correlation coefficient of 0.75 for Site 1 (Falls-vale) lizards and a value of 0.82 for Site 2 (Palm Springs) lizards, with respective standard errors of estimate of 0.15 and 0.12. This represents only a small decrease in correlation coefficient and a small increase in standard error of estimate. The equation for water loss in Site 1 lizards is:

$$\text{mg H}_2\text{O} \cdot \text{gm}^{-1} \cdot \text{hr}^{-1} = -0.303 + 0.024X_1 - 0.001X_2 + 0.0002X_3$$

and for Site 2 lizards:

$$\text{mg H}_2\text{O} \cdot \text{gm}^{-1} \cdot \text{hr}^{-1} = -0.286 + 0.023X_1 - 0.002X_2 + 0.0002X_3$$

where X_1 is air temperature, X_2 relative humidity and X_3 convection. All coefficients are highly significant, with standard errors and an analysis of variance of the multiple regression presented in Table 3.

Table 2- Evaporative Water Loss, Internal Body Temperature, Ventilation Rate and Activity Level means of the two populations of lizards under varied laboratory conditions.

Site	Air Temp.	%Rel. Humid.	Cnvctn. Rate	n	%Body Wt. Loss	Evap. Water Loss	s ²	Int. Body Temp	Vent. Rate	Activity Level
1	16	50	250	2	0.060	0.025	0.00	16.1	5	5
2	16	50	250	2	0.125	0.006	0.00	16.0	3	5
1	24	7	10	4	0.415	0.173	0.002	24.7	11	2
2	24	7	10	3	0.866	0.207	0.007	24.8	12	2
1	24	7	250	3	0.933	0.387	0.004	24.5	9	2
2	24	7	250	3	0.866	0.360	0.005	24.3	11	2
1	24	7	500	2	0.920	0.385	0.000	24.6	9	2.5
2	24	7	500	3	0.887	0.370	0.013	24.5	10	2.5
1	24	7	850	3	1.107	0.460	0.000	25.1	11	2
2	24	7	850	2	1.020	0.425	0.001	24.1	12	1.5
1	24	50	10	2	0.755	0.315	0.001	24.2	14	2.5
2	24	50	10	2	0.420	0.175	0.004	24.3	15	2.5
1	24	50	250	2	0.590	0.245	0.005	24.1	13	3
2	24	50	250	2	0.840	0.280	0.005	24.2	12	3
1	24	50	500	2	1.055	0.440	0.006	24.8	17	1.5
2	24	50	500	3	0.990	0.413	0.014	24.6	14	3
1	24	50	850	2	0.755	0.315	0.007	24.6	17	3
2	24	50	850	3	0.703	0.293	0.022	24.5	12	2.5
1	24	84	10	2	0.515	0.215	0.011	25.5	13	3.5
2	24	84	10	2	0.215	0.090	0.004	25.7	18	4

Site	Air Temp.	%Rel. Humid.	Cnvctn. Rate	n	%Body Wt. Loss	Evap. Water Loss	s ²	Int. Body Temp.	Vent. Rate	Activity Level
1	24	84	250	3	0.550	0.230	0.015	24.9	16	2.5
2	24	84	250	2	0.325	0.135	0.004	24.9	14	4
1	24	84	500	2	0.550	0.230	0.000	24.1	11	3.5
2	24	84	500	2	0.480	0.200	0.006	24.7	16	3.5
1	24	84	850	2	0.970	0.405	0.004	25.2	14	3.5
2	24	84	850	2	0.600	0.250	0.010	24.5	14	3.5
1	34	7	10	3	1.270	0.530	0.027	34.3	29	1
2	34	7	10	3	1.077	0.447	0.005	34.3	28	1
1	34	7	250	3	1.703	0.710	0.055	34.1	27	1
2	34	7	250	3	1.426	0.590	0.022	34.3	31	1
1	34	7	500	2	1.110	0.465	0.024	34.3	29	1
2	34	7	500	3	1.216	0.503	0.021	35.1	28	1
1	34	7	850	2	1.580	0.660	0.001	34.3	27	1
2	34	7	850	2	1.150	0.755	0.011	34.3	29	1.5
1	34	50	10	2	1.055	0.440	0.017	34.3	33	1
2	34	50	10	2	0.967	0.400	0.004	35.2	32	1.5
1	34	50	500	2	0.790	0.330	0.017	34.9	26	1.5
2	34	50	500	2	1.055	0.440	0.017	34.5	31	1.5
1	34	50	850	2	1.835	0.765	0.013	34.8	31	2.5
2	34	50	850	2	1.789	0.740	0.010	34.8	32	1.5

TABLE 3

STANDARD ERRORS OF REGRESSION COEFFICIENTS

	Variable	Coefficient	Std. Error
Site 1	Air Temperature	0.02412	0.00433
Site 2	Air Temperature	0.02283	0.00362
Site 1	Relative Humidity	-0.00116	0.00075
Site 2	Relative Humidity	-0.00198	0.00066
Site 1	Convection	0.00021	0.00007
Site 2	Convection	0.00025	0.00025

ANALYSIS OF VARIANCE OF THE MULTIPLE REGRESSION

I. Site 1- Fallsvale

Source of Variation	df	F _s	F _{.05(3,43)}
a) Due to regression	3	17.89	2.84
b) Deviation about regression	43		
Coefficient of Determination 0.555			

II. Site 2- Palm Springs

Source of Variation	df	F _s	F _{.05(3,43)}
a) Due to regression	3	29.51	2.84
b) Deviation about regression	44		
Coefficient of Determination 0.668			

In terms of intra-specific correlation of water loss between these two populations, a null hypothesis H_0 was established such that $\rho_1 = \rho_2$, with the alternate hypothesis H_1 such that $\rho_1 \neq \rho_2$ at $P \leq 0.05$. A test of homogeneity among two correlation coefficients, as outlined by Sokal and Rohlf (1969), was performed given the coefficients of determination of 0.555 for Site 1 lizards and 0.668 for Site 2 lizards (Table 3). A value of 0.474 for determined X^2 was compared to established χ^2 values of

$$\chi^2_{.50(1)} = 0.455$$

$$\chi^2_{.10(1)} = 2.706$$

with the result that we do not have sufficient evidence to reject the null hypothesis of no heterogeneity among the multiple correlation coefficients ($P > 0.1$).

A test of significance for the multiple regressions in terms of explaining some of the variation of the dependent variable (evaporative water loss) in terms of the variation of the independent variables (air temperature, relative humidity and convection) was performed. A null hypothesis was established such that $\beta = 0$; that is, that the sample value of b comes from a population with a parametric value of $\beta = 0$ for the regression coefficient. A determined value of $F_s = 17.89$ for Site 1 lizards (Table 3) was compared to established F values of:

$$F_{.05(3,43)} = 2.84$$

$$F_{.001(3,43)} = 6.60$$

with the result that a large and significant portion of the variance of the dependent variable has been explained by regression on the independent variables- X_1 , X_2 and X_3 . Comparable F_s values for Site 2 lizards (Table 3) point to the same conclusion.

Correlations between initial body weight and the total evaporative water loss at two ambient temperatures (24 and 34 C) at low relative humidity (7%) produced equations (Table 4) with correlation coefficients such that correlation could not be demonstrated; coefficients between -0.5 and +0.5 not being significant (Sokal and Rohlf, 1969). Figures 7 and 8 present a graphic interpretation of these relationships.

The effects of air temperature, relative humidity and convection on the rate of water loss for the two populations are shown in Figs. 9 and 10. Using the Student-t distribution, homogeneity among the treatment sample means is demonstrated at the 0.05 significance level and is presented in Table 5.

In all lizards studeid, a direct correlation existed between the mean ventilation rate and air temperature: at the higher air temperature, lizards breathed faster (Figs. 11 and 12). Inter-population ventilation rates were found to be not significantly different ($P > 0.05$) (Table 6).

TABLE 4- Regression equations of initial body weight (gms) as a function of the total evaporative water loss ($\text{mg}\cdot\text{gm}^{-1}\cdot 24 \text{ hrs}^{-1}$) at two ambient temperatures at low relative humidity.
Y = dependent variable, total evaporative water loss
X = independent variable, initial body weight

TABLE 4

24 C, 7% Rel. Humid.

Site 1 $Y = 0.629 + 0.031X$ $r = 0.163$

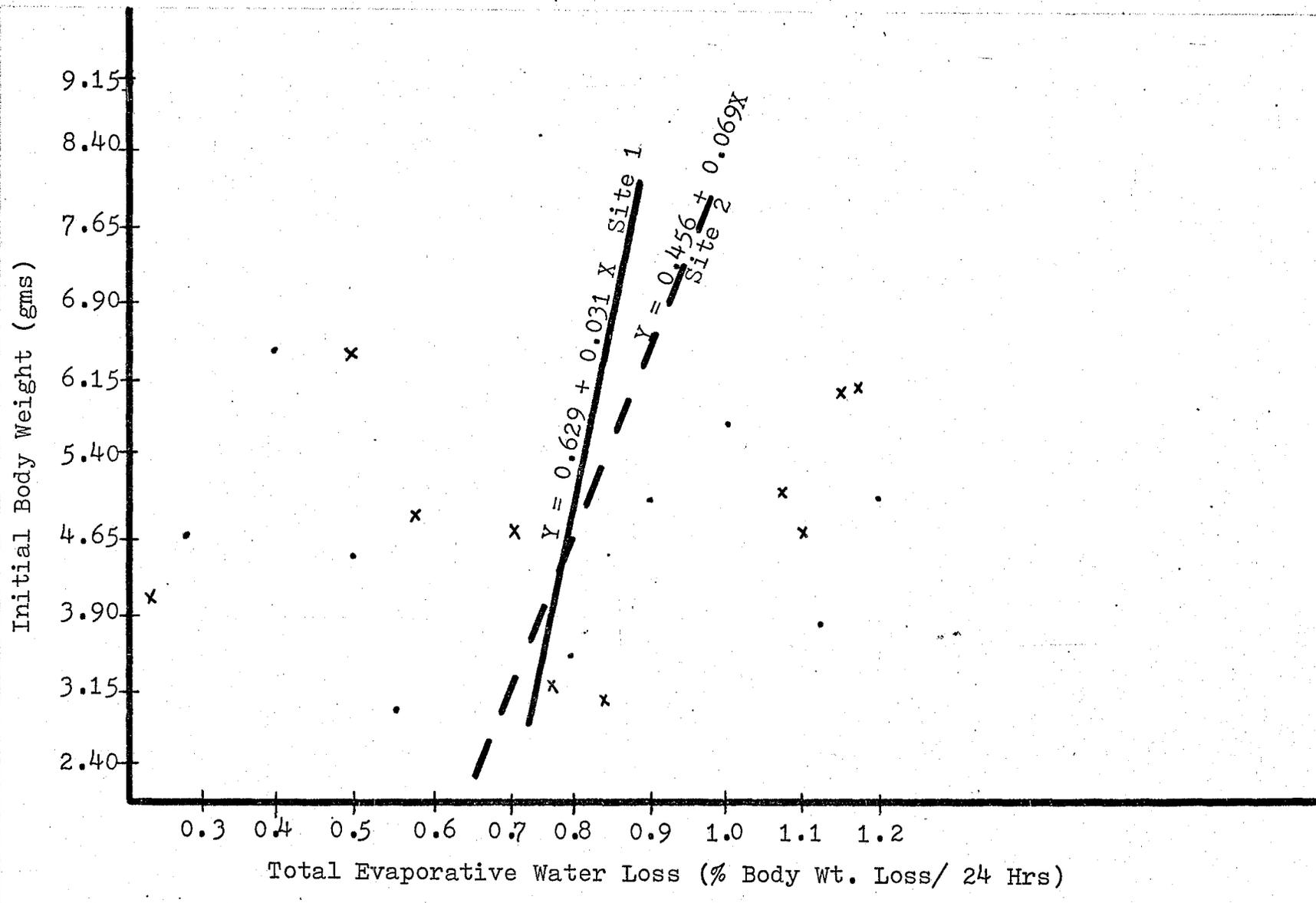
Site 2 $Y = 0.456 + 0.069X$ $r = 0.291$

34 C, 7% Rel. Humid.

Site 1 $Y = 2.067 - 0.105X$ $r = -0.299$

Site 2 $Y = 1.748 - 0.119X$ $r = -0.355$

Figure 7- Linear regression of percentage weight loss as related to body weight of Site 1 and Site 2 lizards at 24 C and 7% relative humidity. (. Site 1; x Site 2)



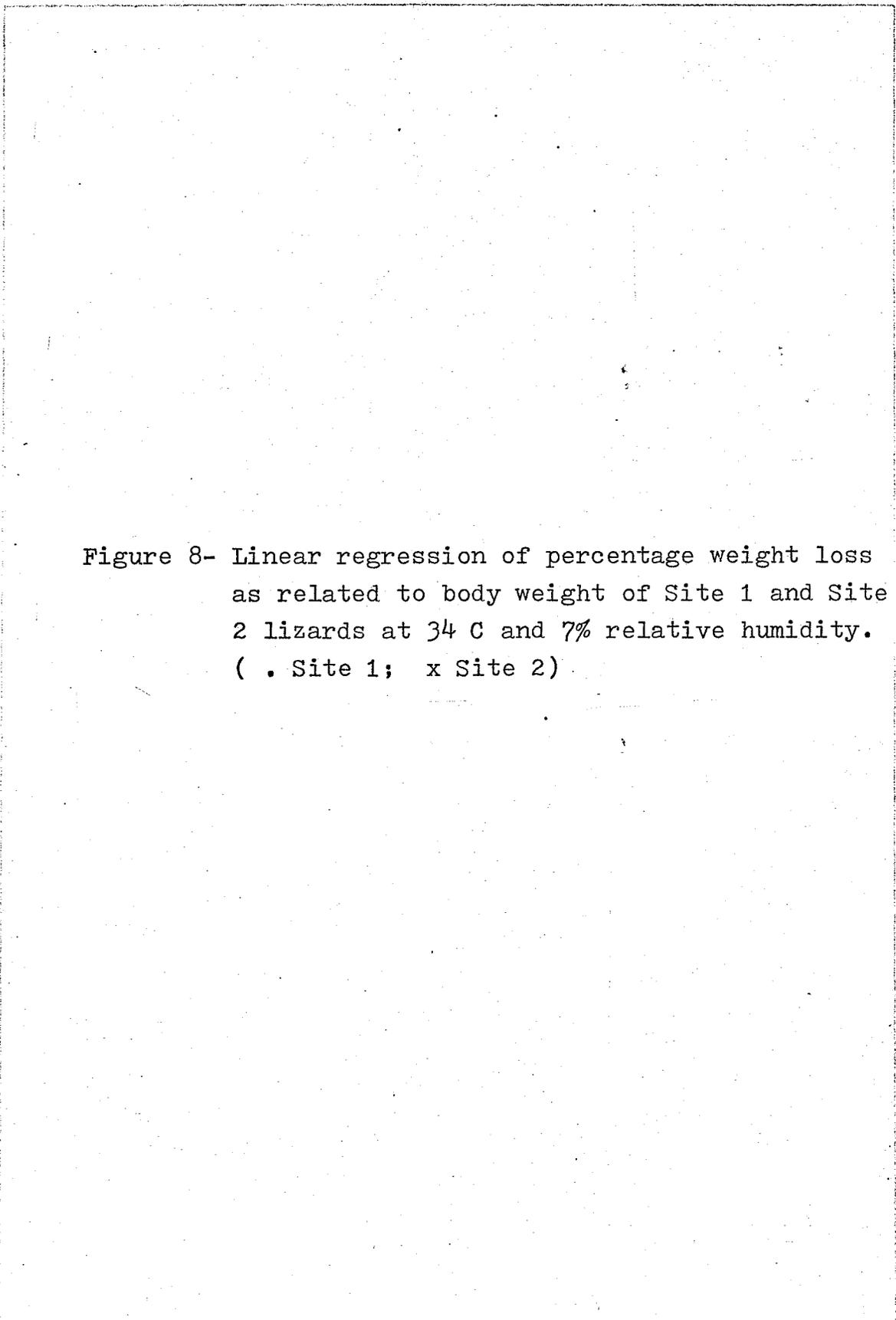


Figure 8- Linear regression of percentage weight loss as related to body weight of Site 1 and Site 2 lizards at 34 C and 7% relative humidity. (. Site 1; x Site 2)

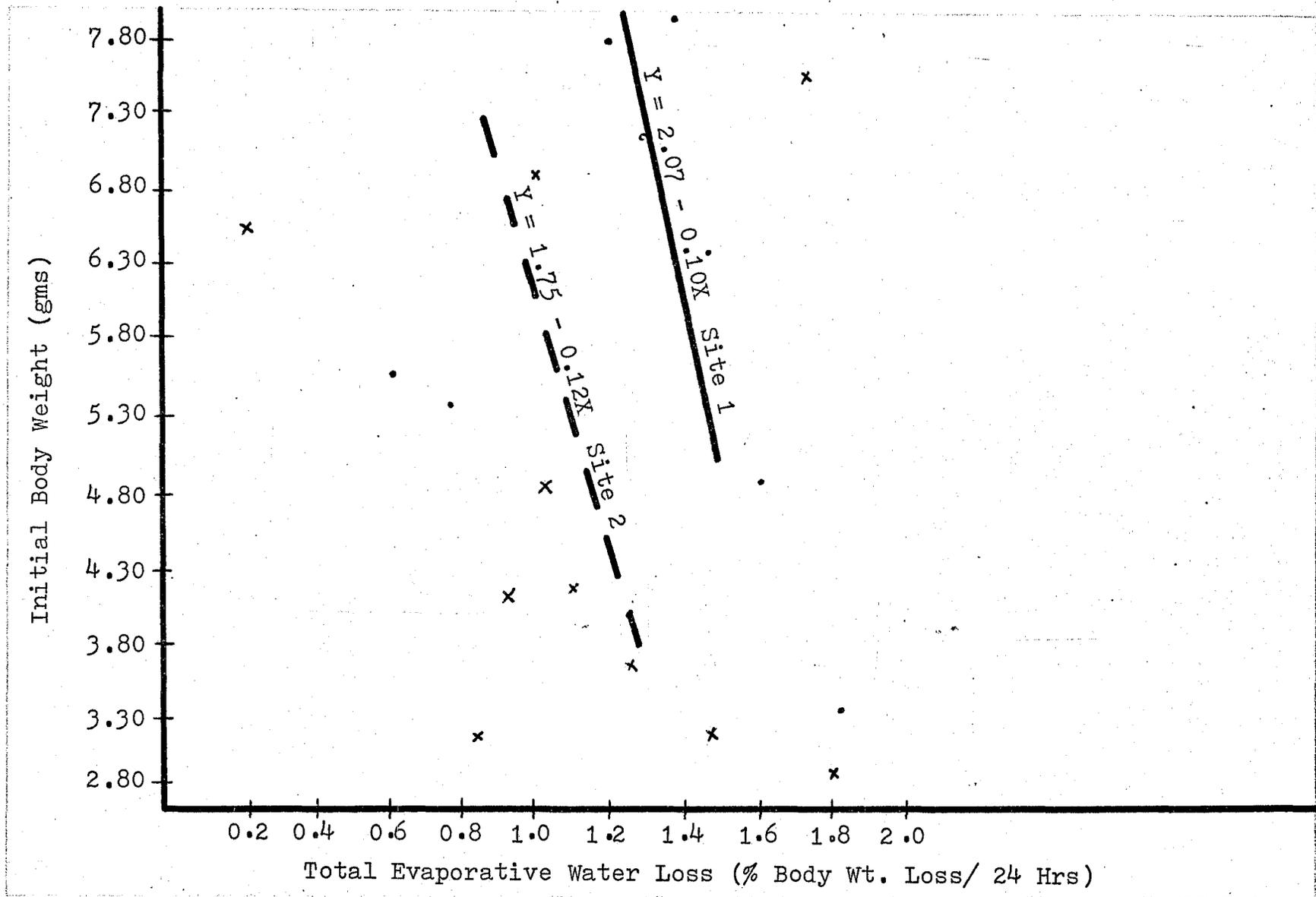
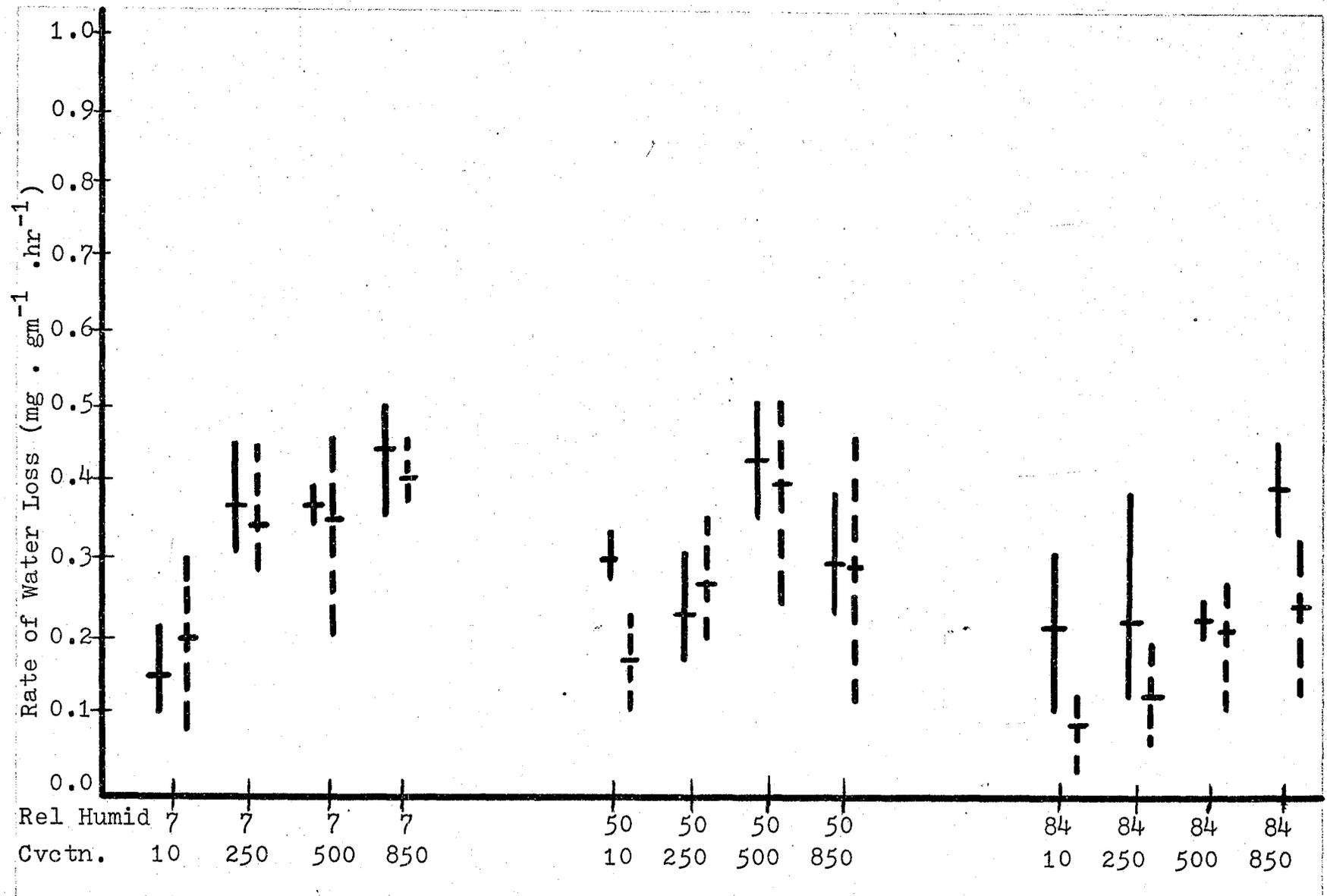


Figure 9- The effects of relative humidity and convection on the rate of water loss at 24 C. The range is represented by the vertical line; the mean by the horizontal line. Solid line represents Fallsyale population; dashed line represents Palm Springs population.



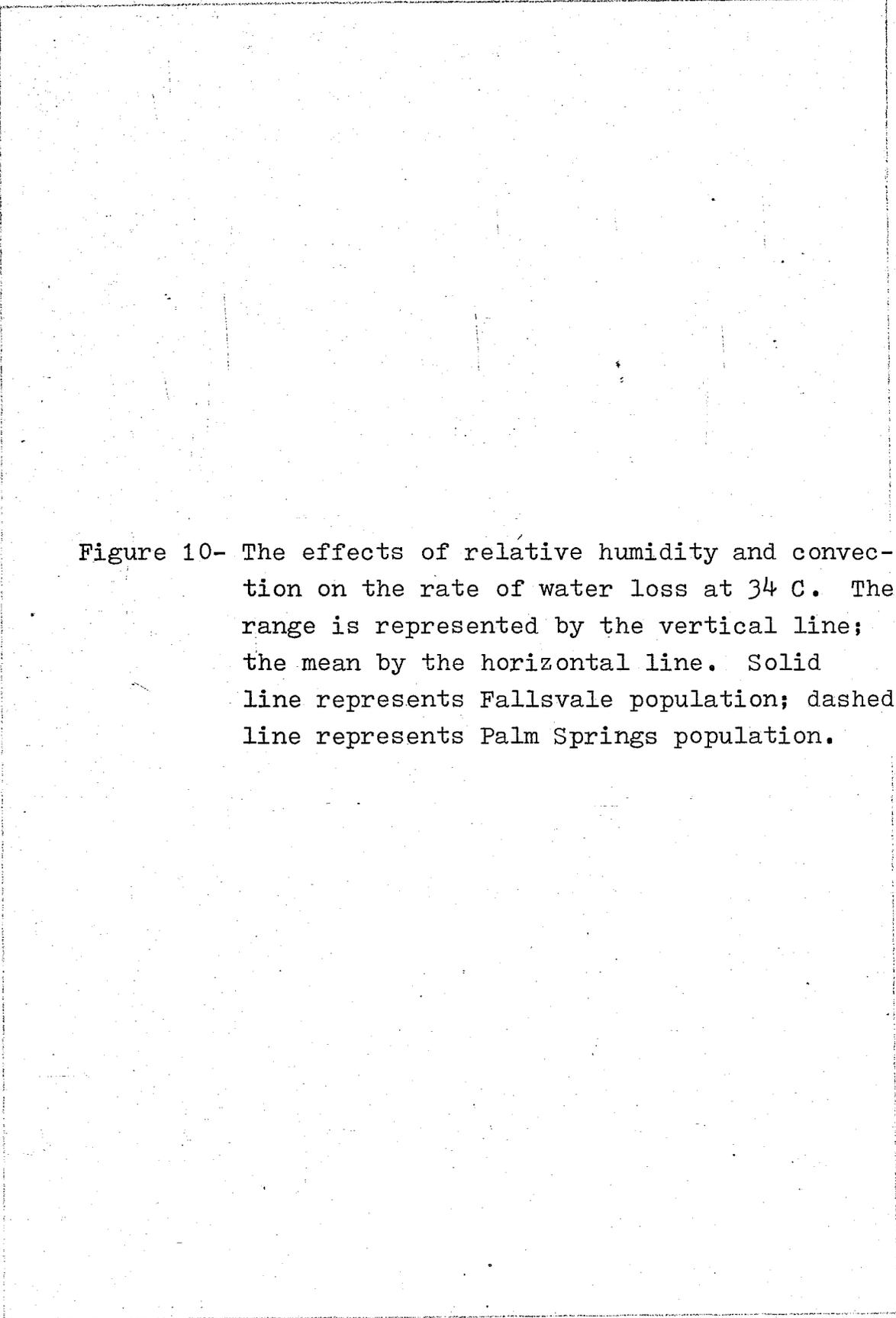


Figure 10- The effects of relative humidity and convection on the rate of water loss at 34 C. The range is represented by the vertical line; the mean by the horizontal line. Solid line represents Fallsvale population; dashed line represents Palm Springs population.

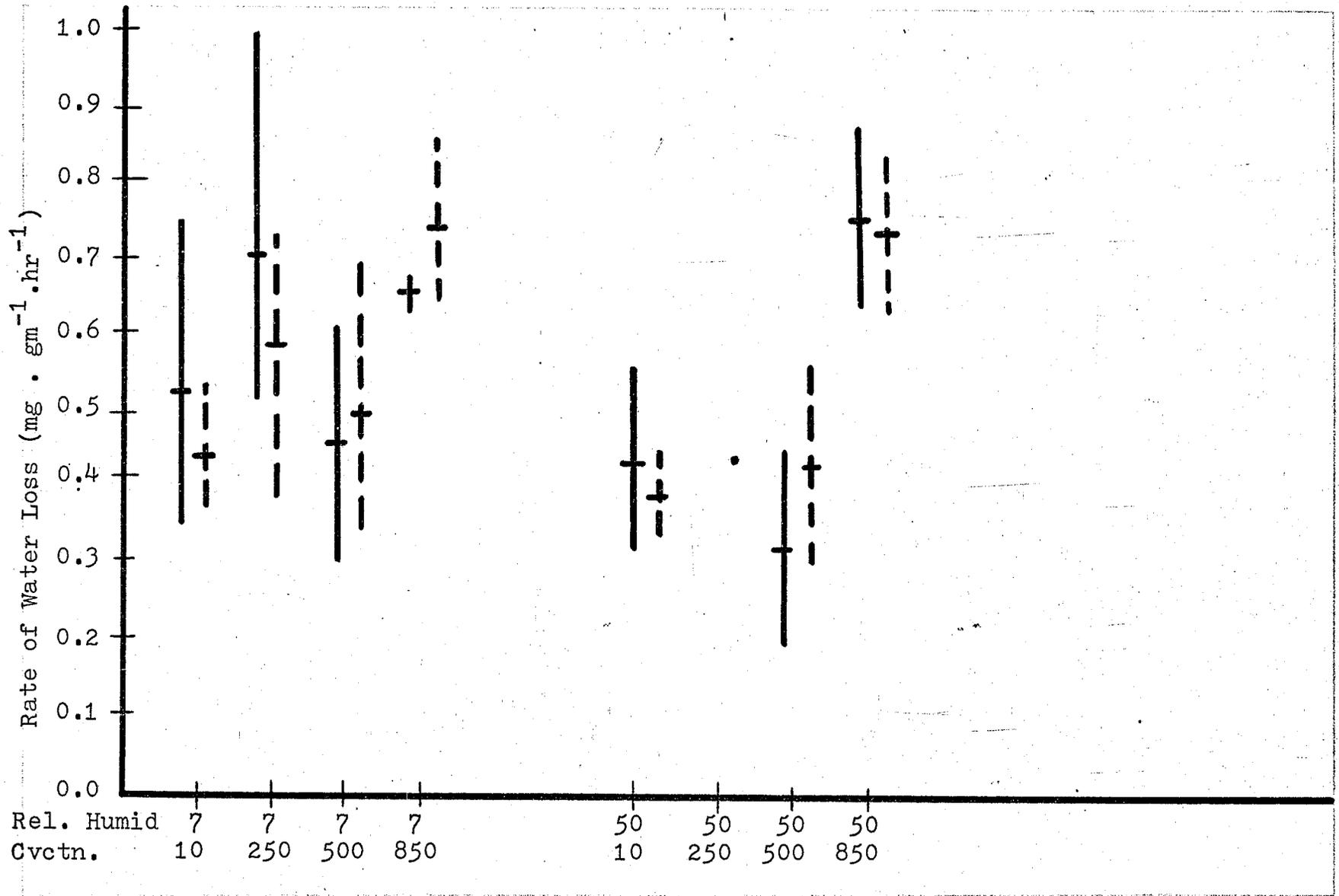


TABLE 5- A Student-t test of the hypothesis that two population sample means for evaporative water loss- under varied environmental conditions- come from populations with equal μ .

TABLE 5

Air Temp.	Rel. Humid.	Convectn. cc/min	Total # of runs	df	Observed t_s	Expected $t_{.05}(df)$
24	7	10	7	5	0.708	2.571
24	7	250	6	4	0.500	2.776
24	7	500	5	3	0.179	3.182
24	7	850	5	3	0.714	3.182
24	50	10	4	2	2.800	4.303
24	50	250	4	2	0.493	4.303
24	50	500	5	3	0.182	3.182
24	50	850	5	3	0.185	3.182
24	84	250	5	3	1.050	3.182
24	84	500	4	2	0.545	4.303
24	84	850	4	2	1.845	4.303
34	7	10	6	4	0.806	2.776
34	7	250	6	4	0.594	2.776
34	7	500	5	3	0.281	3.182
34	7	850	4	2	1.234	4.303
34	50	10	4	2	0.055	4.303
34	50	500	4	2	0.854	4.303
34	50	850	4	2	0.234	4.303

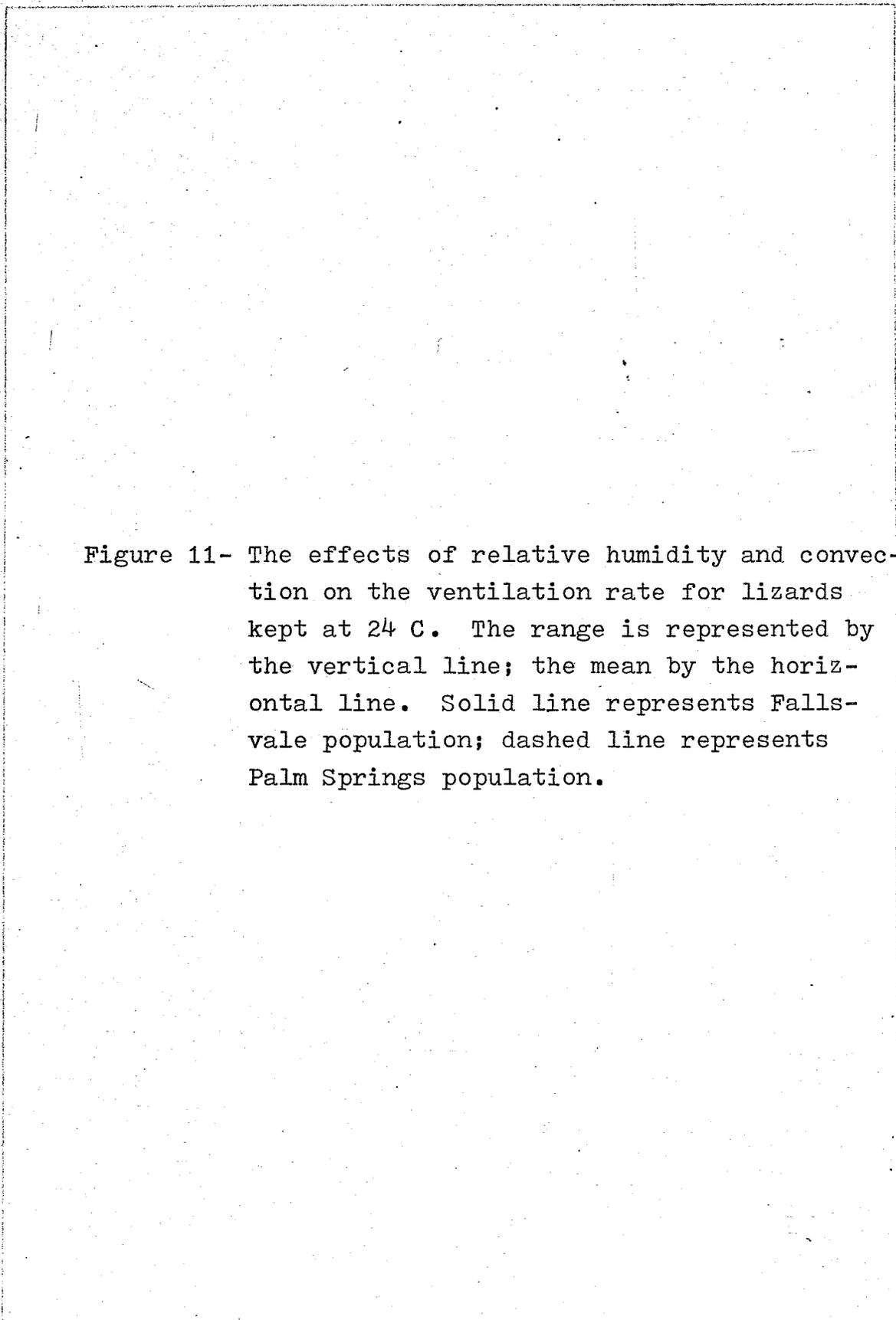


Figure 11- The effects of relative humidity and convection on the ventilation rate for lizards kept at 24 C. The range is represented by the vertical line; the mean by the horizontal line. Solid line represents Falls-vale population; dashed line represents Palm Springs population.

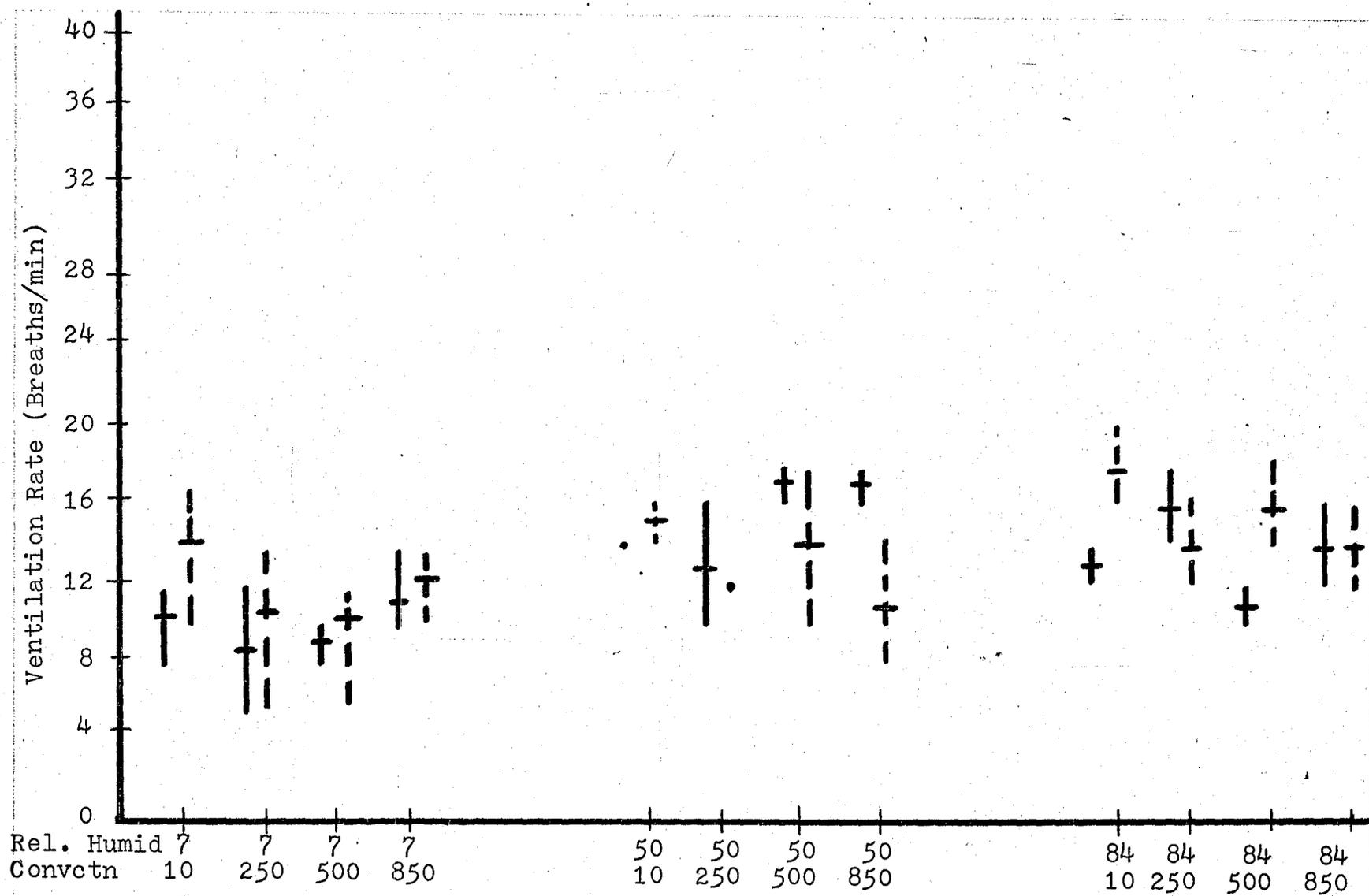


Figure 12- The effects of relative humidity and convection on the ventilation rate for lizards kept at 34 C. The range is represented by the vertical line; the mean by the horizontal line. Solid line represents Fallsvale population; dashed line represents Palm Springs population.

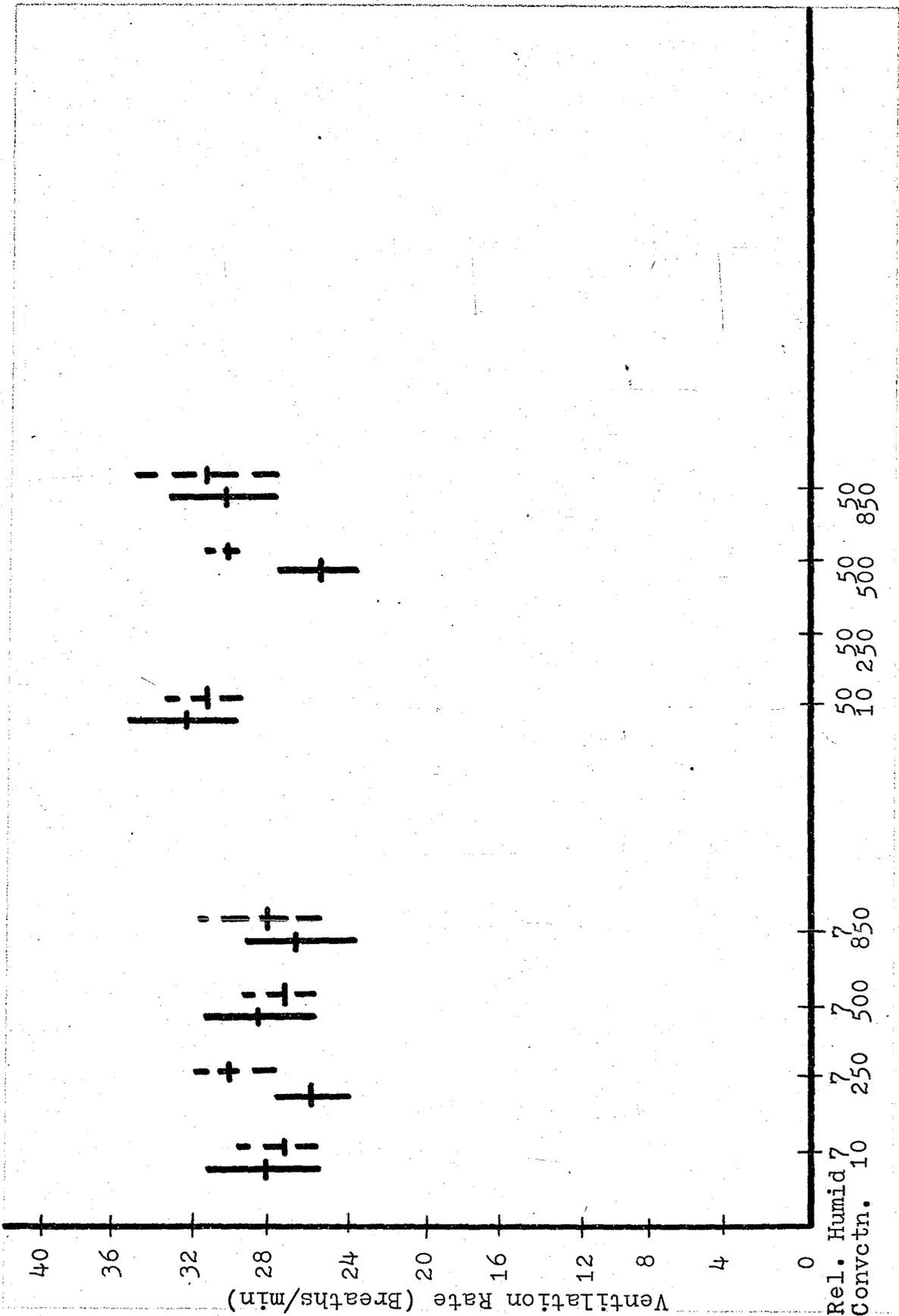


TABLE 6- A Student-t test of the hypothesis that the two population sample means for ventilation rate- under varied environmental conditions- come from populations with equal μ .

TABLE 6

Air Temp. °C	Rel. Humid. %	Convctn. Rate cc/min	Total # of runs	df	Observed t_s	Expected $t_{.05(df)}$
24	7	10	7	5	1.49	2.57
24	7	250	6	4	0.82	2.77
24	7	500	5	3	0.47	3.18
24	7	850	5	3	0.38	3.18
24	50	10	4	2	1.41	4.30
24	50	250	4	2	0.47	4.30
24	50	500	4	2	1.20	2.77
24	50	850	5	3	3.28*	2.77
24	84	10	4	2	3.16	4.30
24	84	250	5	3	1.24	3.18
24	84	500	4	2	3.16	4.30
24	84	850	4	2	0.00	4.30
34	7	10	6	4	0.39	2.77
34	7	250	6	4	2.60	2.77
34	7	500	5	3	0.50	3.18
34	7	850	4	2	0.66	4.30
34	50	10	4	2	0.39	4.30
34	50	500	4	2	3.16	4.30
34	50	850	4	2	0.28	4.30

* Significant

If convection is considered to have little or no influence on the ventilation rate, then the difference between the ventilation rate means between 7 and 50 percent and 50 and 84 percent relative humidity at 24 C are found to be not significantly different ($P > 0.05$). The difference between the ventilation rate means between 7 and 84 percent relative humidity were found to be significant ($P < 0.05$). Ventilation rate means were found to be significantly different ($P < 0.05$) between 7 and 50 percent relative humidity at 34 C air temperature; Table 7, an 'a posteriori' Student-Newman-Keuls test demonstrates this argument.

In all lizards studied, a direct correlation existed between the mean internal body temperature and the environmental factors of air temperature and relative humidity (Figs. 13 and 14). Inter-population body temperatures were found to be not significantly different ($P > 0.05$) (Table 8). If convection is considered to have a relatively minor effect on internal body temperature, then the difference between the internal body temperature means between 7 and 50 percent relative humidity at 24 C are found to be not significantly different ($P > 0.05$). The difference between internal body temperature means between 7 and 84 percent and 50 and 84 percent relative humidity were found to be significant ($P < 0.05$). Internal body temperature means were found to be significantly different ($P < 0.05$) between 7 and 50 percent relative humidity at 34 C air temperature; Table 9, an 'a posteriori' Student-

TABLE 7- Multiple comparisons among ventilation rate means at various relative humidities at constant air temperatures (convection rate assumed to have no significant influence): a Student-Newman-Keuls test.

TABLE 7

	24 C				34 C			
	df	SS	MS	F _s	df	SS	MS	F _s
Y-Y _{among}	2	168	84		1	73	73	
Y-Y _{within}	55	1318	24	3.50	32	336	10.5	6.95

$$F_{.05}(2,55) = 3.17$$

$$F_{.05}(1,32) = 4.17$$

LSR* R.H.
(7%--84%) = 3.78
Observed range = 4.06
Significant

LSR R.H.
(7%--50%) = 2.33
Observed range = 3.04
Significant

LSR (7%--50%) = 3.10
Observed range = 2.48
Significant

LSR (50%--84%) = 3.33
Observed range = 1.58
Not Significant

Air Temperature 24 24 24
Relative Humidity 7 50 84

Significant

Air Temperature 34 34
Rel. Humidity 7 50

Significant

*LSR- Least Significant Range

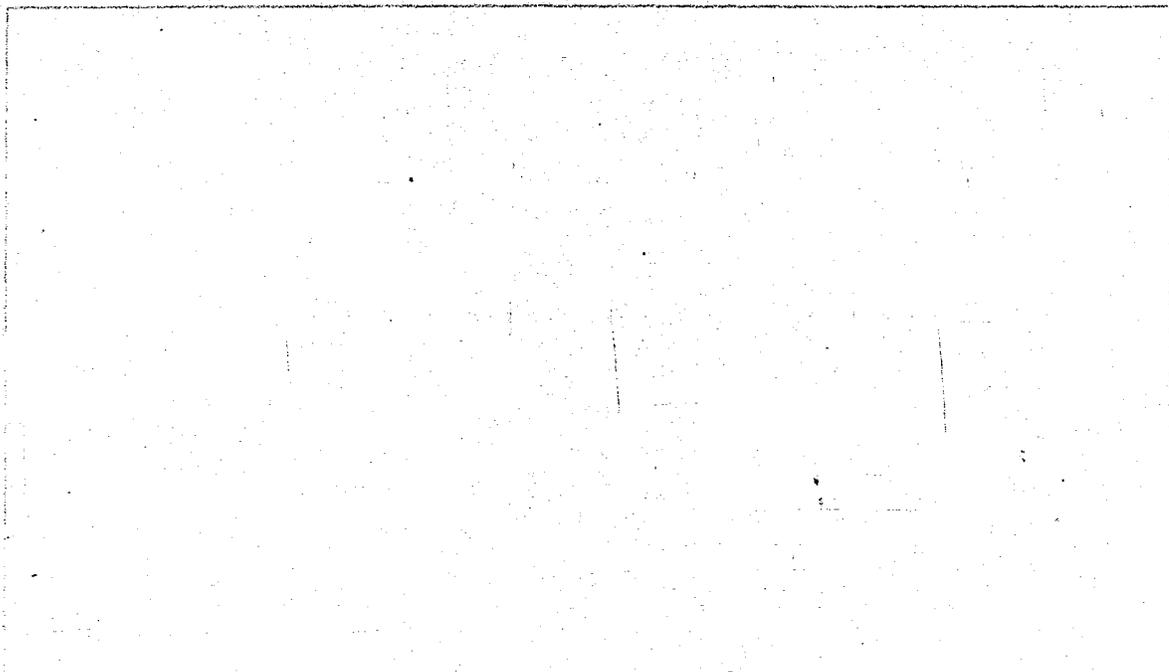
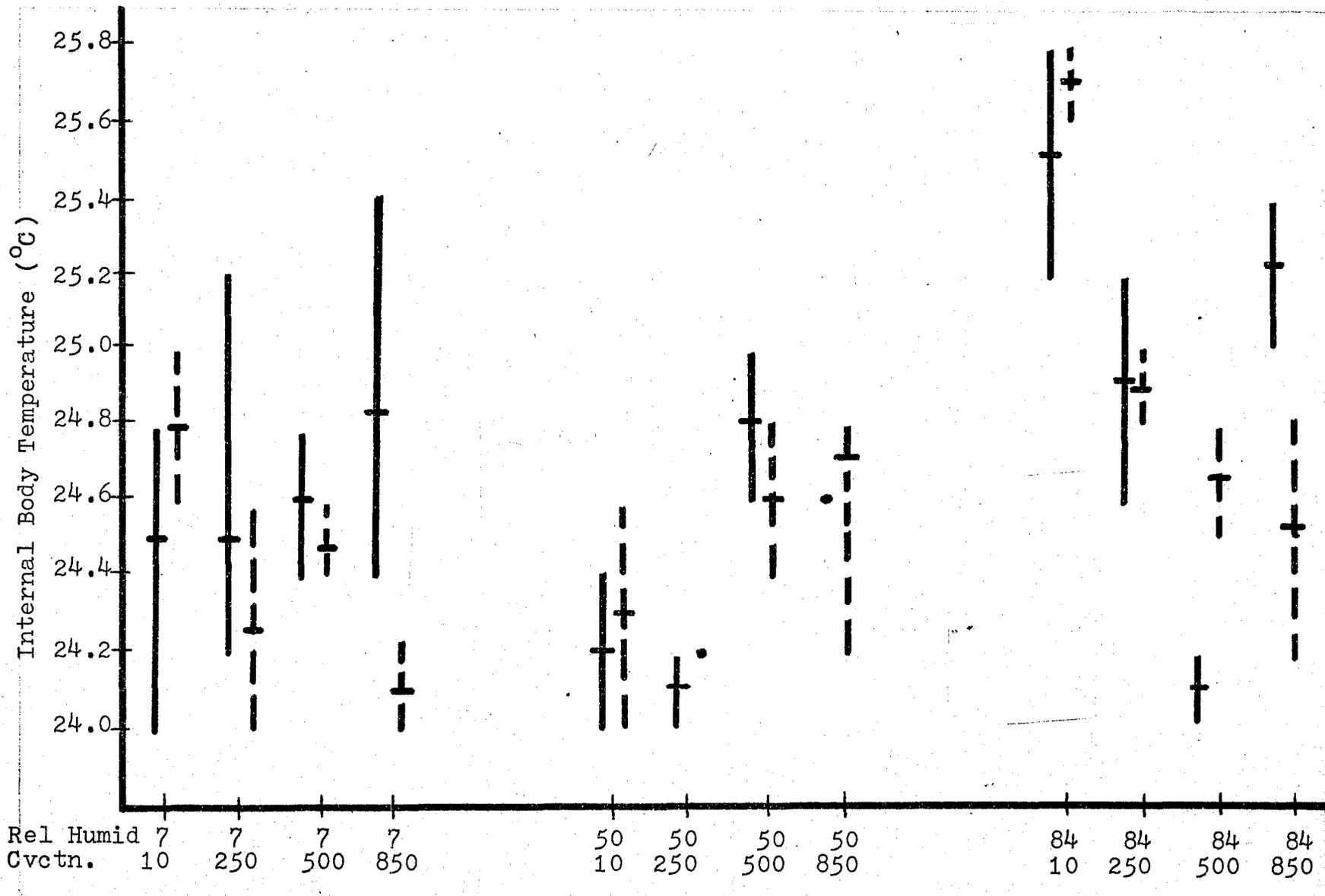


Figure 13- The effects of relative humidity and convection on the internal body temperature for lizards kept at 24 C. The range is represented by the vertical line; the mean by the horizontal line. Solid line represents Fallsvale population; dashed line represents Palm Springs population.



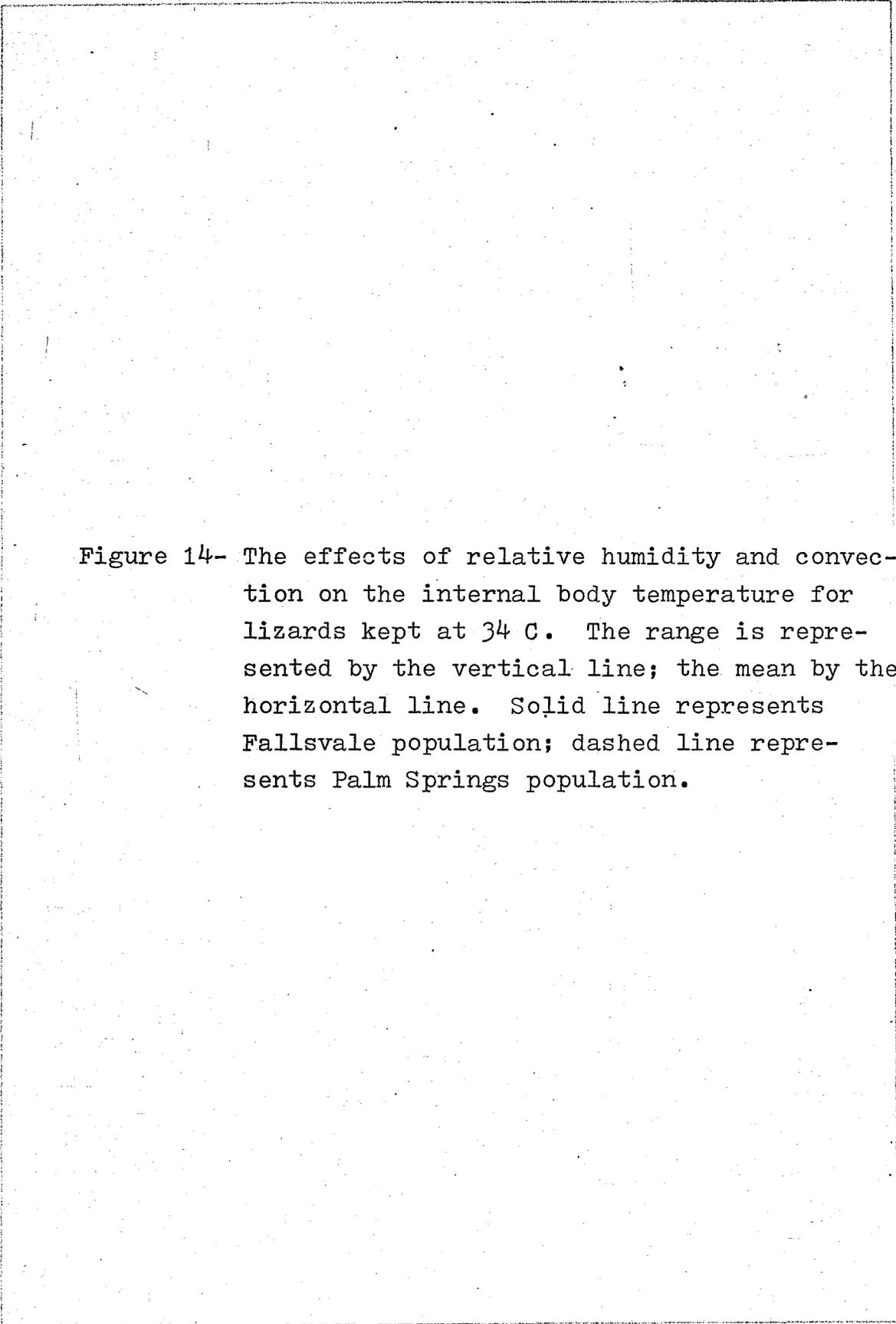


Figure 14- The effects of relative humidity and convection on the internal body temperature for lizards kept at 34 C. The range is represented by the vertical line; the mean by the horizontal line. Solid line represents Fallsvale population; dashed line represents Palm Springs population.

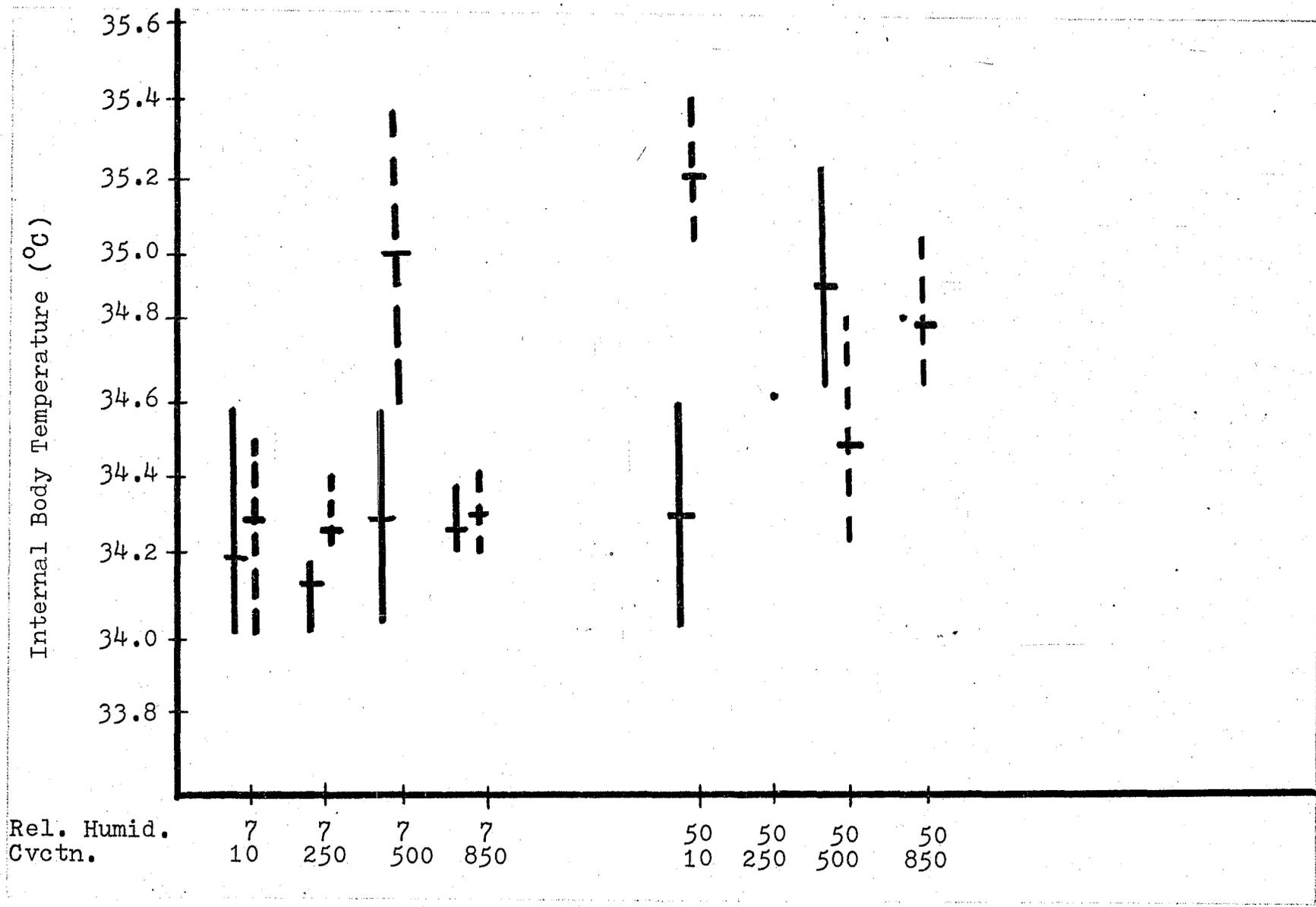


TABLE 8- A Student-t test of the hypothesis that the two population sample means for internal body temperature- under varied environmental conditions- come from populations with equal μ .

TABLE 8

Air Temp. °C	Rel. Humid. %	Convctn. Rate cc/min	Total # of runs	df	Observed t_s	Expected $t_{.05}(df)$
16	50	250	4	2	1.43	4.30
24	7	10	7	5	0.33	2.57
24	7	250	6	4	0.75	2.77
24	7	500	5	3	0.80	3.18
24	7	850	5	3	2.44	3.18
24	50	10	4	2	0.39	4.30
24	50	250	4	2	1.43	4.30
24	50	500	5	3	0.94	3.18
24	50	850	5	3	0.54	3.18
24	84	10	4	2	0.89	4.30
24	84	250	5	3	0.15	3.18
24	84	500	4	2	3.97	4.30
24	84	850	4	2	2.75	4.30
34	7	10	6	4	0.15	2.77
34	7	250	6	4	2.59	2.77
34	7	500	5	3	4.49*	3.18
34	7	850	4	2	0.00	4.30
34	50	10	6	4	3.53*	2.77
34	50	500	4	2	1.33	4.30
34	50	850	4	2	0.00	4.30

* Significant

TABLE 9- Multiple comparisons among internal body temperature means at various relative humidities at constant air temperatures (convection rate assumed to have no significant influence): a Student-Newman-Keuls test.

TABLE 9

	<u>24 C</u>				<u>34 C</u>			
	df	SS	MS	F _s	df	SS	MS	F _s
Y-Y _{among}	2	2	1		1	1	1	
				15.63				13.16
Y-Y _{within}	55	11			32	5	0.076	
F _{.05(2,55)}	= 3.17				F _{.05(1,32)} = 4.17			
LSR [*] R.H. (7%--84%)	= 0.19				LSR(7%--50%) = 0.19			
Observed range	= 0.38				Observed range = 0.36			
Significant					Significant			
LSR(7%--50%)	= 0.16							
Observed range	= 0.14							
Not Significant								
LSR(50%--84%)	= 0.17							
Observed range	= 0.52							
Significant								
Air Temperature	24	24	24		Air Temperature	34	34	
Relative Humidity	7	50	84		Relative Humidity	7	50	
	Significant				Significant			

*LSR- Least Significant Range

Newman-Keuls test, demonstrates this argument.

In Figures 15 and 16, the effects of air temperature, relative humidity and convection of subjective activity levels are shown. Owing to the determination of subjective activity levels, statistical analysis becomes impractical and meaningless.

Figure 15- The effects of relative humidity and convection on the subjective activity level for lizards kept at 24 C. The range is represented by the vertical line; the mean by the horizontal line. Solid line represents Fallsvale population; dashed line represents Palm Springs population.

- 1-- Extremely active
- 2-- Moderately active
- 3-- Normal, non-moving
- 4-- Less than normally active
- 5-- Torpor
- 6-- Death

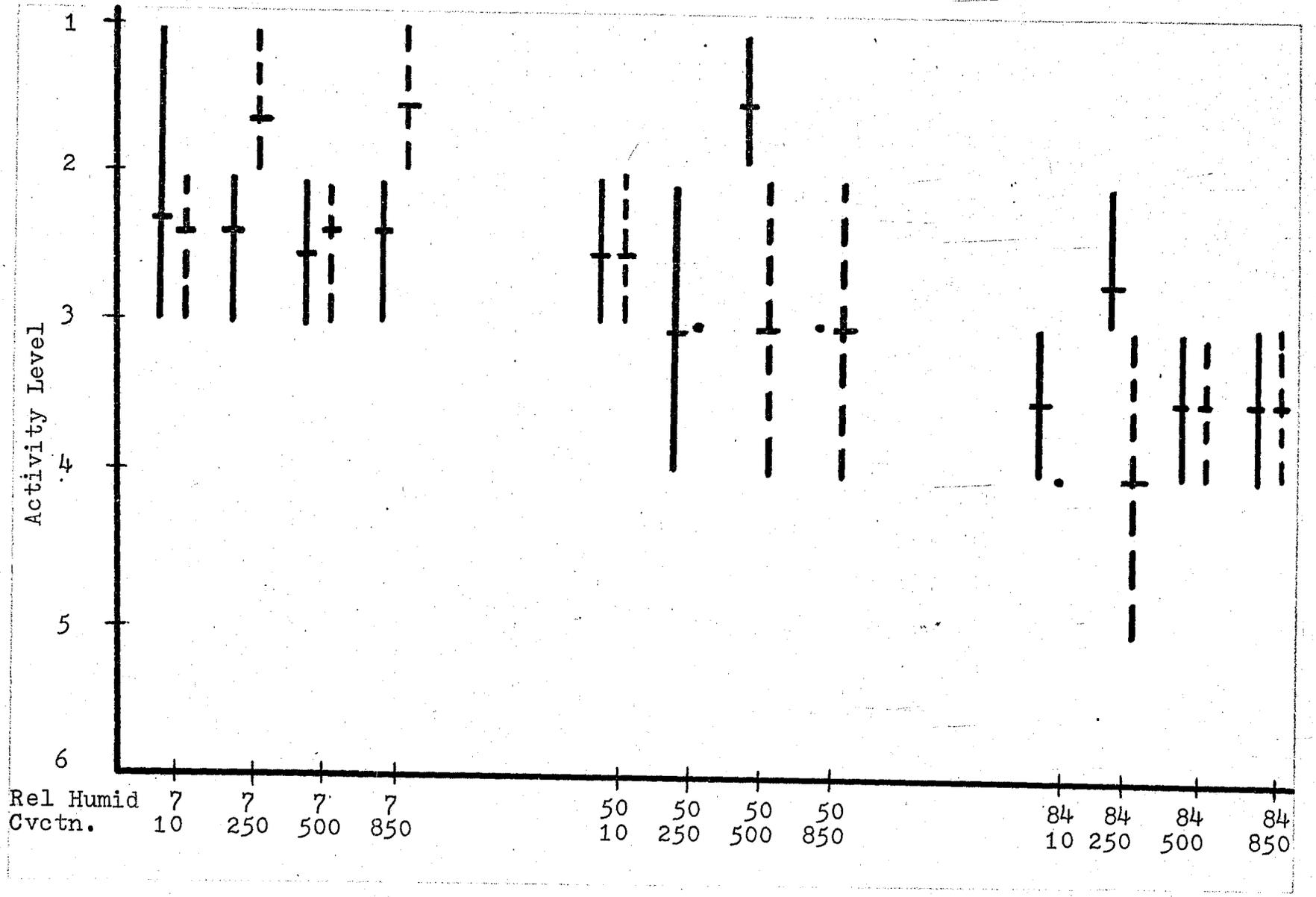
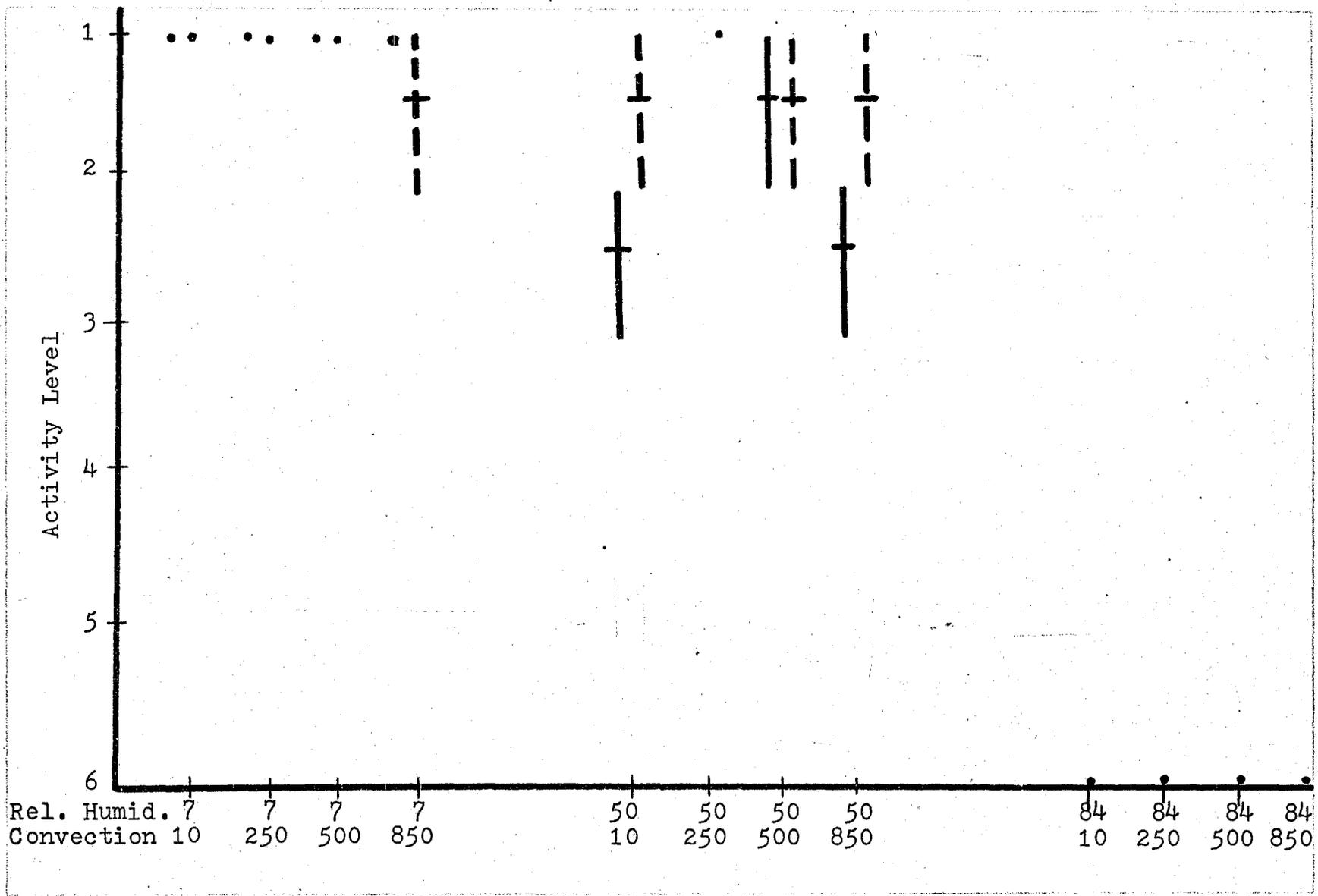


Figure 16- The effects of relative humidity and convection on the subjective activity levels for two populations of lizards kept at 34 C. The range is represented by the vertical line; the mean by the horizontal line. Solid line represents Fallsvale population; dashed line represents Palm Springs population.

- 1-- Extremely active
- 2-- Moderately active
- 3-- Normal, non-moving
- 4-- Less than normally active
- 5-- Torpor
- 6-- Death



DISCUSSION

Claussen (1967) working with Uta stansburiana hesperis Richardson and Anolis carolinensis found "no correlation between the rate of evaporative water loss (% of initial wt. loss/ hr.) and the initial weight of the lizards for either species". The data in this report, comparing the evaporative water rates intra-specifically, agree with those of Claussen. These results differ from those of Warburg (1965a) who, working with the Australian lizards- Tiliqua rugosa (Gray) (Scincidae) and Amphibolurus barbatus Cuvier (Agamidae), found an inverse relationship between body weight and percentage weight loss. Warburg however failed to give correlation coefficients to support this conclusion.

Roberts (1967) reported that the extent of water and weight conservation at low temperatures and high humidities are of considerable significance in determining survival. Carnivorous lizards that are active can replenish water losses from water in food, when food is available. For field animals at times of low food availability however, water is probably scarce. Lizards though can ethologically compensate by going underground into burrows where temperatures become moderate and humidities increase. She further reported that, at 35 C in dry air, the evaporative loss from Uta stansburiana hesperis Richardson was at a rate of 1.80 percent of body weight per day as compared to values ranging

from 1.07 to 1.70 in this study. Whether water loss can be minimized to the extent that dehydration is less a potential problem than breakdown of tissue or other assorted starvation factors has yet to be determined. Metabolic water becomes of value in this respect when water loss by the lizard is minimal. In field lizards, the lower body temperatures of winter active Uta's may be of some significance in the conservation of both water and energy.

Although in all lizards studied a direct relationship existed between the mean ventilation rate and air temperature (Figs. 11 and 12), a considerable degree of variation was evident among different animals and in the same animal under given sets of environmental conditions. Templeton (1960) reported that at air temperatures below 44 C, the ventilation pattern is primarily diphasic in pattern. A lizard breathing in this manner, under relatively low thermal stress conditions, retains inspired air for a short time before expelling it- the length of time the air is retained being inversely related to the ventilation rate. This is contrasted with a monophasic pattern, evident under conditions of thermal stress, in which inspired air is not retained, but quickly expired, ie. panting.

With increase of air temperature from 24 to 34 C, with the consequent and proportional increase in internal body temperature (Fig. 14), evaporative cooling is augmented by a subsequent increased capacity of air to hold more water

vapor as it becomes warmer. Above panting initiation temperatures, these two processes (evaporative cooling and air capacity) fail to adequately dissipate metabolic heat, with the additional heat being dissipated by panting.

Homogeneity between the two populations was determined using a Student-t test of the sample ventilation rate means (Table 6). The influence of relative humidity on the ventilation rate was investigated through the use of a Student-Newman-Keuls test (Table 7). It is shown in this report that at 24 C, the only significant difference ($P < 0.05$) noted in ventilation rates is between the extremes of relative humidity- 7 and 84%, while at the higher air temperatures a significant difference ($P < 0.05$) is noted between the low and intermediate relative humidities- 7 and 50%. This would lead to the conclusion that, assuming a constant relative humidity, higher air temperatures have a more pronounced effect on ventilation rates and that relative humidity plays a more decisive role in influencing ventilation rates and their associated response patterns at higher air temperatures.

In general, the lizards exposed to relatively lower air humidities were capable of maintaining lower internal body temperatures than those lizards exposed to relatively more humid air (Figs. 13 and 14); the efficiency of thermoregulation being related to the evaporative water rate. Internal body temperatures of Uta's measured at an environmental temperature of 24 C and 7% relative humidity had

sample means that averaged 0.53 C above the ambient air temperature, while at 24 C and 84% relative humidity, the sample means averaged 0.93 C above the ambient air temperature. The values at 34 C--7% relative humidity and 34 C--50% relative humidity were 0.35 and 0.74 respectively.

Figures 13 and 14 show that Uta populations are heliothermic; at the temperatures used in this study, the internal body temperatures were always higher than the corresponding air temperatures. An ambient temperature is eventually reached, referred to as the thermoregulation temperature, at which point the internal body temperature from then on does not exceed air temperature. At about this temperature the animal begins to control body temperatures by panting. Monophasic ventilation patterns, as evidenced through the frequency and degree of thoracic contractions as compared with abdominal contractions, were not evident in this study. This temperature, unique for each species, is the result of both physiological and behavioral adaptations. Cowles and Bogert (1944), working with desert reptiles, have shown that internal body temperatures above the thermoregulation temperature are the result of radiation, convection and conduction; the primary factor involved in the capacity-limits for thermoregulation being primarily circulation (Bartholomew and Tucker, 1963; Strelnikow, 1944).

While for all lizards studied, correlations did exist in respect to response patterns for various combinations of

environmental factors, inter-population differences were found to be not significant ($P > 0.05$) (Tables 8 and 9).

Lizards, being obligatory ectotherms, accomplish thermoregulation primarily by behavioral mechanisms. According to St. Girons and St. Girons (1956), the strictly physiological thermoregulatory mechanisms serve only auxiliary roles under field conditions. The internal body temperatures obtained in the field in this study when compared to internal body temperatures obtained under laboratory conditions—holding ethological mechanisms to a minimum—agree with the conclusions of St. Girons and St. Girons (Figs. 6, 13 and 14).

Rodgers (1953), working with Sceloporus graciosus, found that the internal body temperature reflected environmental differences related to time of day, season and microhabitat. Additional pathways of thermoregulation which include heat loss or gain through conduction and/or radiation, also influence internal body temperatures; the relative contribution of each pathway being a function of the ethology and ecology of the particular population.

Soule (1963), working with nine species of desert lizards, finds that a certain amount of tolerance is advantageous to ectotherms living in thermally diverse habitats: the greater the tolerance to body temperature fluctuations, the less time expenditure for thermoregulation. Metabolic processes, with their associated thermal limitations, how-

ever, serve to define tolerance limits. The specific range of eurythermy and the specific optimal temperature ranges of thermochemical processes, are then seen as varying from one ecotype to the next: the more diverse and complex the habitat, the greater the tolerance limits.

Bogert (1949a,b) studying species of Cnemidophorus and Sceloporus, found that congeneric species living in widely separated geographic regions and diverse habitats have similar thermoregulatory temperatures. It can then be concluded that whatever genetically determined differences exist in response patterns among the two populations to internal body temperatures- which are ultimately linked with evaporative water loss rates- have either been obscured by tolerance and response overlap and/or that such differences were not significant at the established levels in this report.

SUMMARY

1. Air temperature has the greatest influence on evaporative water loss; approximately a ten times greater effect when compared to relative humidity, and a ten to one-hundred times greater effect when compared to convection.
2. Insufficient evidence to reject the null hypothesis of no heterogeneity among the multiple correlation coefficients ($P > 0.05$) in terms of intra-specific correlation of water loss between the two populations.
3. A large and significant portion of the variance of the dependent variable in the multiple regression for the two populations has been explained by regression on the independent variables.
4. Correlation could not be demonstrated between initial body weight and the total evaporative water loss at two ambient temperatures (24 and 34 C) and low relative humidity (7%).
5. Homogeneity between the two sample means in terms of the effects of air temperature, relative humidity and convection on the rate of water loss, was demonstrated.
6. A direct correlation exists between the mean ventilation rate and air temperature. Inter-population ventilation rates were found to be not significantly different ($P > 0.05$).
7. The difference between the ventilation rate means between 7 and 50 percent and 50 and 84 percent relative

humidity at 24 C were found to be not significantly different ($P > 0.05$).

8. The difference between the ventilation rate means between 7 and 84 percent relative humidity at 24 C were found to be significantly different ($P < 0.05$).

9. Ventilation rate means were found to be significantly different between 7 and 50 percent relative humidity at 34 C ($P < 0.05$).

10. A direct correlation existed between the mean internal body temperature and the environmental factors of air temperature and relative humidity.

11. Inter-population body temperatures were found to be not significantly different ($P > 0.05$) under specified laboratory conditions.

12. The difference between the internal body temperature means between 7 and 50 percent relative humidity at 24 C were found to be not significantly different ($P > 0.05$).

13. The difference between internal body temperature means between 7 and 84 percent and 50 and 84 percent relative humidity were found to be significantly different at 34 C ($P < 0.05$).

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