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CHARADRIUS ALEXANDRINUS,

TO AN INLAND SALT PLAIN

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ADAPTATIONS OF THE SNOWY PLOVER,

CHARADRIUS _ALEXANDRINUS_,

TO AN INLAND SALT PLAIN

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ADAPTATIONS OF THE SNOWY PLOVER, *CHARADRIUS ALEXANDRINUS*, TO AN INLAND SALT PLAIN

INTRODUCTION

The snowy plover, *Charadrius alexandrinus*, is a small (30 to 40 g) member of the Charadriidae. It normally inhabits areas of high saline content--sea coasts and inland salt plains (Bent, 1929; Rittinghaus, 1961). In these areas, particularly the latter, the bird is often exposed to stressful thermal and osmotic conditions. My objectives were to examine ecological, behavioral, and physiological characteristics that allow this species to survive in the salt flats environment.

The results and conclusions of this study are presented in a series of three papers. The first, prepared in the style of The Southwestern Naturalist, is a detailed description of the Great Salt Plains along with selected aspects of the bird's natural history that relate to survival on the salt flats. The snowy plover's ability to tolerate salt water and to conserve water are treated in the second paper, which was prepared for an ornithological journal, The

Auk. Finally, in the third paper, written for The Condor, the thermal ecology of the nest and associated adult behaviors are discussed.

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PAPER I

NATURAL HISTORY OF THE SNOWY PLOVER ON THE GREAT SALT PLAINS, OKLAHOMA

NATURAL HISTORY OF THE SNOWY PLOVER
ON THE GREAT SALT PLAINS, OKLAHOMA

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ABSTRACT. The snowy plover, _Charadrius alexandrinus_, inhabits a salt flats in northwestern Oklahoma that is hot and windy. Evaporation is high, vegetation is lacking, and the salinity of the standing water is beyond the bird's tolerance. The plover survives by obtaining non-saline water through its insectivorous diet, restricting its activity range to areas near water, and standing in the water when ambient temperatures are high.

The snowy plover, _Charadrius alexandrinus_, is a wide-ranging species found on six continents (see Rittinghaus, 1961, for range map). Bent (1929) characterized it as primarily a coastal bird with some inland populations on alkaline flats. In the Eastern Hemisphere snowy plovers are associated with salty areas including inland salt flats in Hungary, North Africa, and central Asia (Rittinghaus, 1961).

No extraordinary physiological mechanisms have been found for this species (Purdue and Haines, 1974), which prompts the question of how the bird survives in inland, fresh water-poor habitats where it is exposed to the extremes of a continental climate. This study (1) describes such an inland area and (2) discusses how the adult plovers cope with their environment. The thermal ecology of the nest and related parental behavior is presented elsewhere (Purdue, 1974).

The habitat.--The Great Salt Plains, Alfalfa County, Oklahoma, originally covered an area of approximately 43 mi^2 (Ortenburger and Bird, 1933). In 1941 an impoundment flooded 32% of the salt flats. Even so, a vast area of unvegetated salt flats remains; it intergrades into the surrounding prairie through a series of grass islands and peninsulas (Fig. 1). My study area, picked because of accessibility and the exclusion of the general public, was in the northwest portion of the salt plains. An area of 49 ha was staked out; this consisted primarily of bare salt flats with two water courses (one constant and one intermittent) and grass islands at the periphery (Fig. 1).

The weather.--The Corps of Engineers, in connection with a nearby study of its own, maintained a weather station about 200 m S of the study area outlined in Fig. 1. Another station, 11 km ESE, was maintained at the Great Salt Plains dam. Both stations kept maximum and minimum daily temperatures, daily wind, and daily evaporation from a pan 4 feet in diameter. A third weather station in Cherokee, 10 km WSW of the study area, only maintained daily maximum and minimum temperatures. Comparison of matched values for the three stations shows the effect of the salt flats on weather. Two-factor (month and locality) analysis of variance tests were used to determine statistical differences.

The daily maximum and minimum temperatures in the normally vegetated areas, at Cherokee and at the dam, were essentially the same (Fig. 2), but thermal conditions on the salt flats were somewhat moderated. On the flats the maximum temperatures in the summer averaged about 2° C cooler and the minimum temperatures about 4° C warmer than the surrounding localities. The water table under the salt flats is usually less than 1 m below the surface, so the flats act like a large body of water in moderating thermal conditions. Even though maximum temperatures are slightly lower on the salt flats, the lack of shade exposes the plovers (and other animals) to intense solar radiation. Temperatures in the sun commonly are above 40° C during the summer months and, thus, are potentially stressful.

Both wind and evaporation are greater on the salt flats than at the dam (Fig. 3). The vast, flat expanse of the salt plains offers no topographical obstacles or vegetation to slow the movement of air. Of course, the wind is an important factor in the greater evaporation on the flats.

Standing water.--The water standing and coursing through the salt flats varies considerably in salinity (Ortenburger and Bird, 1933). In 1972 and 1973 a series of samples was taken from water on and near the study site (Fig. 1). Chloride concentration was measured with an Aminco-Cotlove chloride titrator. Na^+ and K^+ concentrations were determined with a flame photometer (Baird Atomic Model KY-2). Conductivity was measured with a conductivity meter (Radiometer Model CDM 2e) and reported as condosity (molar NaCl equivalent). Notable differences existed between the constant and intermittent streams in 1972 (Table 1). The four stations along the constant flow water course had condosity values ranging from 312 mM at Station #1, which is actually just outside the salt plains, to greater than 1000 mM from all stations on the flats (Stations #2 through #4). In contrast the intermittent streams were considerably saltier. Station #5 was on the study site, while Station #6 was just to the south; Station #7 was far to the south on the opposite side of the Great Salt Plains (Stations 2-5 are shown in Fig. 1). All 1972 samples from on the flats had condosities greater than 2000 mM, and two values were greater than 4000 mM. Heavy rains occurred in the spring in 1973 which resulted in a shift of water courses so that

Station #5 had a constant flow. There was a corresponding decrease in its salinity in 1973 so that condosity and other measurements were comparable to the original flowing stream.

Briefly stated, the salt flats present a habitat that is potentially stressful from both thermal and osmotic aspects. High ambient temperatures and evaporation tend to force the birds to utilize body water in evaporative cooling. The water thus expended must be replaced; however, the only available free water on the salt flats has salinities that are beyond the tolerance limits of the plovers (Purdue and Haines, 1974). It is therefore pertinent to know what the plovers do to avoid these potentials.

Sources of food and water.--Along the coasts the snowy plover feeds on crustateans and other small marine organisms (Bent, 1929; Rittinghaus, 1961), but inland, where marine invertebrates are absent, it is mainly insectivorous. On the Great Salt Plains, insect diversity is low but the numbers of individuals are high (Ortenburger and Bird, 1933). The plover's diet can be divided into three main categories. First, huge numbers of Bledius, a burrowing staphylinid beetle, occur on the flats proper. Plovers are commonly seen, sometimes several hundred meters away from water, running from burrow to burrow probing for the inhabitants. Second, flies--mainly of the genus Ephydra--often form dense bands closely paralleling the fresher water courses. They are absent from the extremely saline pools.

The snowy plover exhibits a peculiar foraging behavior in which it starts at the edge of a fly aggregation and runs through it with the bill open, scoop-like. The flies in the path of the bird disperse in the manner of water splashed by a high-speed truck as it fords a river. Presumably the plover traps one or more of the scattering flies in its mouth, because it quickly snaps its bill shut and ceases its charge, only to dart into the band of flies again a few seconds later. This foraging behavior has not been described previously even though Fisher (1893) reported snowy plovers feeding on dense aggregations of *Ephydra*.

The third major food source for the plovers is the insects blown onto the salt flats from the surrounding vegetated areas. Wind speed over the plains is often high (Fig. 3), and a wide variety of insects such as grasshoppers, leaf hoppers, lepidopterans, and beetles are carried onto the flats by the wind. Often they became debilitated, probably because of thermal and osmotic stress, and were easy prey for the birds. Tiger beetles (*Cicindela* sp.) are common around the grassy islands at the edge of the salt flats, and, though not debilitated, they are eaten on occasion. Ortenburger and Bird (1933) also noted that snowy plovers utilize wind-borne insects.

The insectivorous diet is not only important as food but also as a source of water. As mentioned before, most if not all of the free water on the flats exceeds the salinity tolerance of the bird. The plovers do not fly to fresh water off the flats; I visited numerous fresh water pools that were near but outside the study area and never observed snowy plovers at them. Color-banded individuals were consistently located in the same small areas on the salt plains, either on their feeding or nesting territories (maintained as reported by Rittinghaus, 1961). These observations suggest that the plovers do not travel to fresh water sources. Also, careful observations obtained by following color-marked individuals for several hours at a time indicate that the birds rarely drink the saline water in the area. The only definite case of such drinking occurred when I held a mist-netted bird overnight without food or water. Upon release the next morning it ran immediately to the constantly flowing (less saline) stream and drank.

These negative observations on the use of free water for drinking purposes do not prove that insects constitute the chief water source. However, in laboratory tests Purdue and Haines (1974) showed that this may be the case since plovers maintained their body weights on a diet of mealworm larvae and no free water. Bartholomew and Cade (1963) list several desert species of birds that are capable of obtaining adequate water from their food. Similarly, the long-billed marsh wren (<u>Telmatodytes palustris greseus</u>) living in extensive salt marshes on the Georgia coast can maintain body weight on a mealworm diet free of drinking water (Kale, 1967).

Snowy plovers apparently do not depend on the water of the salt flats for drinking, but they do utilize water courses as feeding sites. Their prey, which in part inhabit the stream edges, apparently provide the plover a major portion of its body water.

Use of standing water in thermoregulation.--Plovers are frequently exposed to high ambient temperatures on the salt flats. Behavior that counteracts the potential thermal load includes standing in or near the saline water.

I marked off a transect along the flowing water course, and, on 8 separate days in 1972 and 1973, I either walked the transect once an hour or used a spotting scope every 15 minutes between 1000 and 1800 hours (thus avoiding the peaks in foraging activity). The number of plovers standing or resting along the stream was counted, converted into number of birds per kilometer, and compared to the ambient temperature (taken 5 cm above the substrate away from the water). Though there was a difference between the two observational methods (walking was more accurate than the sighting technique), the data showed the same trends and were pooled (Fig. 4). There was a statistically significant positive regression between number of birds in the water and ambient temperature. This simple behavior is highly advantagous because it allows the plovers to use the saline water in evaporative cooling rather than their own water, which, of course, would have to be replaced.

Restriction of activities.--In general snowy plovers are restricted to the water courses on the salt plains. I made several extended hikes across the flats and tended to find plovers only around water--the only apparent difference in the habitat. This is borne out in the pattern of nest placement (Fig. 1). With one exception nests were located in bands paralleling the constantly flowing stream. The 300 x 400 m "panhandle" of the study area extended south from the water course. Despite thorough searching I found only one nest (#13) in this area during the 1972 season.

When a nest was found I measured the distance to the nearest flowing water (Table 2). All but two nests were within 200 m of the water. Seven were within 50 m, but these were the least successful. High water subsequent to heavy rains accounted for failures as did nest predation by a common crow, Corvus brachyrhynochos, that occasionally flew above the stream and spotted nearby nests. Thus, a paradoxical situation existed in that the plovers tended to locate their nests close to water, yet nests away from the water were more successful.

Snowy Plovers in Europe (Rittinghaus, 1961) and California (Bent, 1929) nested in grassy areas. Much sparse grassland was available around the periphery of the Great Salt Plains, yet I found no nests in it. All were on the flats proper. Similarly Rittinghaus (1961) and Bent (1929) reported that nests are generally located by or in debris.

Rittinghaus, in particular, observed nests well protected, especially from above. Boyd (1972) found in Kansas that nests are "often" located next to debris--once inside a goose skeleton. At the Great Salt Plains only 42% of the nests were next to any kind of debris at all and most of these were afforded virtually no protection from weather or predation due to the scanty size of debris. Driftwood, cow chips, etc., were scattered over the salt flats, yet they were not utilized by the plovers. Perhaps the debris was not as abundant as in areas where previous studies on this species were done and did not present truly alternative nest sites for the birds.

Conclusion.--The snowy plover lives in a habitat that is potentially dangerous in terms of thermal stress and dehydration. The species joins other xeric-adapted birds such as the horned lark, *Eremophila alpestris* (Trost, 1972), and columbid birds (MacMillen and Trost, 1966) that depend upon food selection, restricted activity range, and timely maintenance behavior for survival.

This study, part of a doctoral dissertation, was made possible through the cooperation of the Great Salt Plains National Wildlife Refuge manager, Mr. Ronald Sullivan, and his staff. In addition, special recognition is due to Dr. Charles C. Carpenter, the late Mrs. Grace Porter, Dr. Anthony A. Echelle, and Mrs. Joretta Purdue for being, respectively, major professor, landlady and friend, critical reviewer, and typist-in-residence.

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TABLE 1

Analysis of water samples taken from the Great Salt Plains, Oklahoma

Station	Date	Cond.[a]	Na^{+a}	K^{+a}	Cl^{-a}
#1	11 Apr 72	312	162	3	143
#2	16 Mar 72	1175	1105	2	1127
	11 Apr 72	1225	1214	3	1188
	7 Jun 72	1600	1567	5	1508
	13 Sep 72	1320			1584
#3	16 Mar 72	1225	1180	2	1180
	6 Apr 72	1175	1148	2	1138
	13 Sep 72	1100			1186
	31 May 73	940			936
#4	16 Mar 72	1270	1176	4	1170
	11 Apr 72	1325	1290	3	1272
	7 Jun 72	1500	1452	5	1436
	13 Sep 72	1350			1448
#5	16 May 72	3470	3219	4	3429
	7 Jun 72	3755	3842	7	3957
	31 May 73	920			959
	31 May 73	790			825
	13 Jun 73	1550			1899

TABLE 1--Continued

Station	Date	Cond.[a]	Na^{+}[a]	K^{+}[a]	Cl^{-}[a]
	16 Mar 72	3550	3310	5	3434
	6 Apr 72	4312		7	5098
#6	11 Apr 72	3850	4029	4	4167
	7 Jun 72	2650	2657	6	2735
#7	23 Mar 72	4225		5	5156

[a]Conductivity (Cond.) is in terms of condosity (mM NaCl equivalent). Na^{+}, K^{+}, and Cl^{-} are in terms of mEq/l.

TABLE 2

Nest locations for snowy plovers with respect to nearest water and nesting success

Distance to nearest water (m)	Number of nests	Number of successful nests	Percent success
1 - 50	7	2	28.6
51 - 100	5	2	40.0
101 - 150	3	2	66.7
151 - 200	4	2	50.0
201 or greater	2	2	100.0
Totals	21	10	47.6

Mean distance to nearest water = 128.3 m

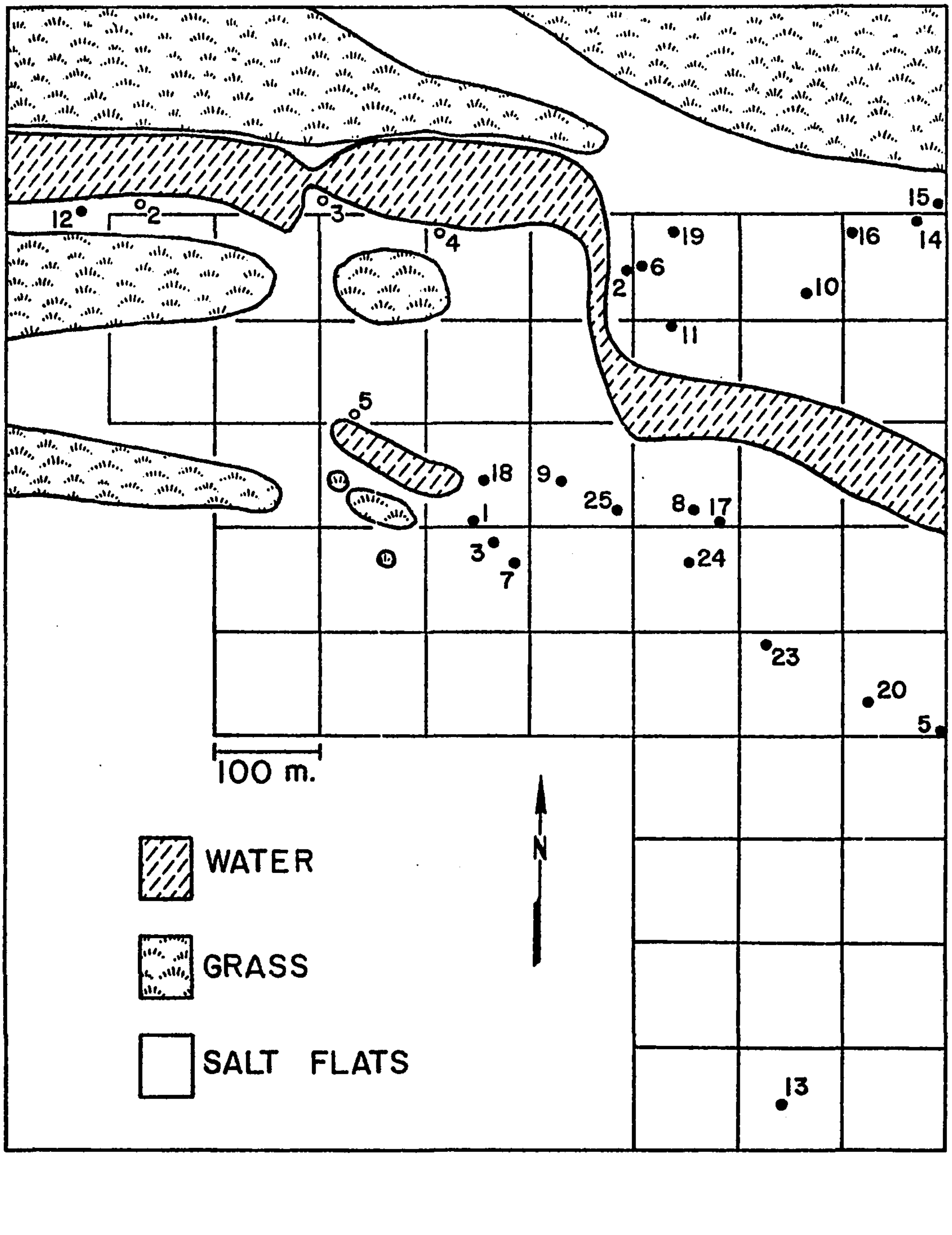
Figure Legends

Fig. 1. Map of study area on Great Salt Plains. Numbered dots are nest locations in 1972. Numbered open circles are water sample stations.

Fig. 2. Mean maximum (Tmax) and minimum (Tmin) air temperatures from three localities on or near the salt flats. The letter "S" indicates significant difference between means ($P < .05$).

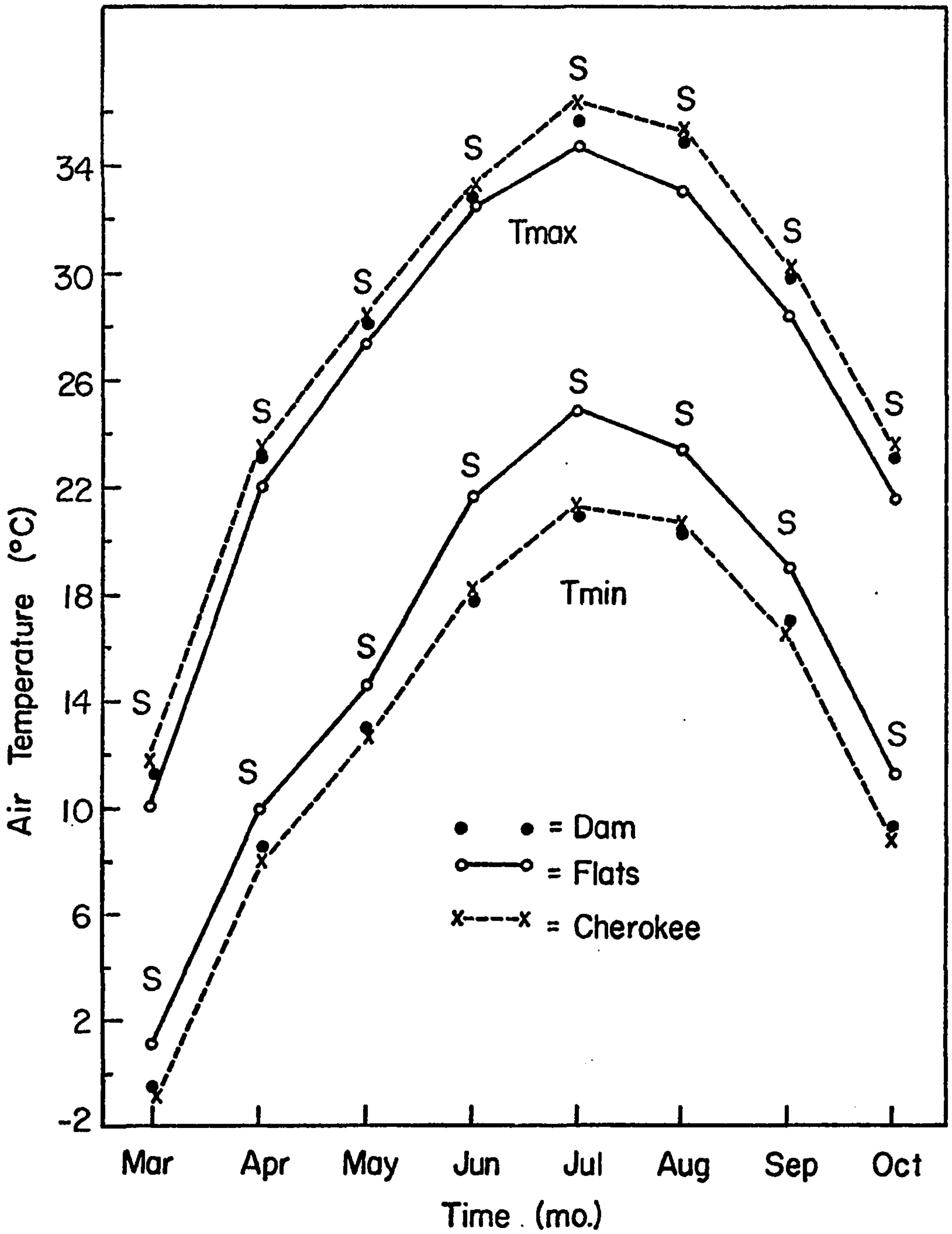
Fig. 3. Comparisons of wind velocity and evaporation rate between weather stations on the salt flats and near the Great Salt Plains dam. The letter "S" indicates significant difference between means ($P < .05$); "NS" nonsignificant.

Fig. 4. Effect of air temperature (T_A) on number of Snowy Plovers standing or resting in water between 1000 and 1800 hours.



12
2
3
4
19
6
16
15
14
2
10
11
5
18
9
25
8
17
1
3
7
24
23
20
5
13
100 m.
N
WATER
GRASS
SALT FLATS

Figure 1



Air Temperature (°C)
34
30
26
22
18
14
10
6
2
-2
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Time (mo.)
Tmax
Tmin
S
= Dam
= Flats
= Cherokee

Figure 2

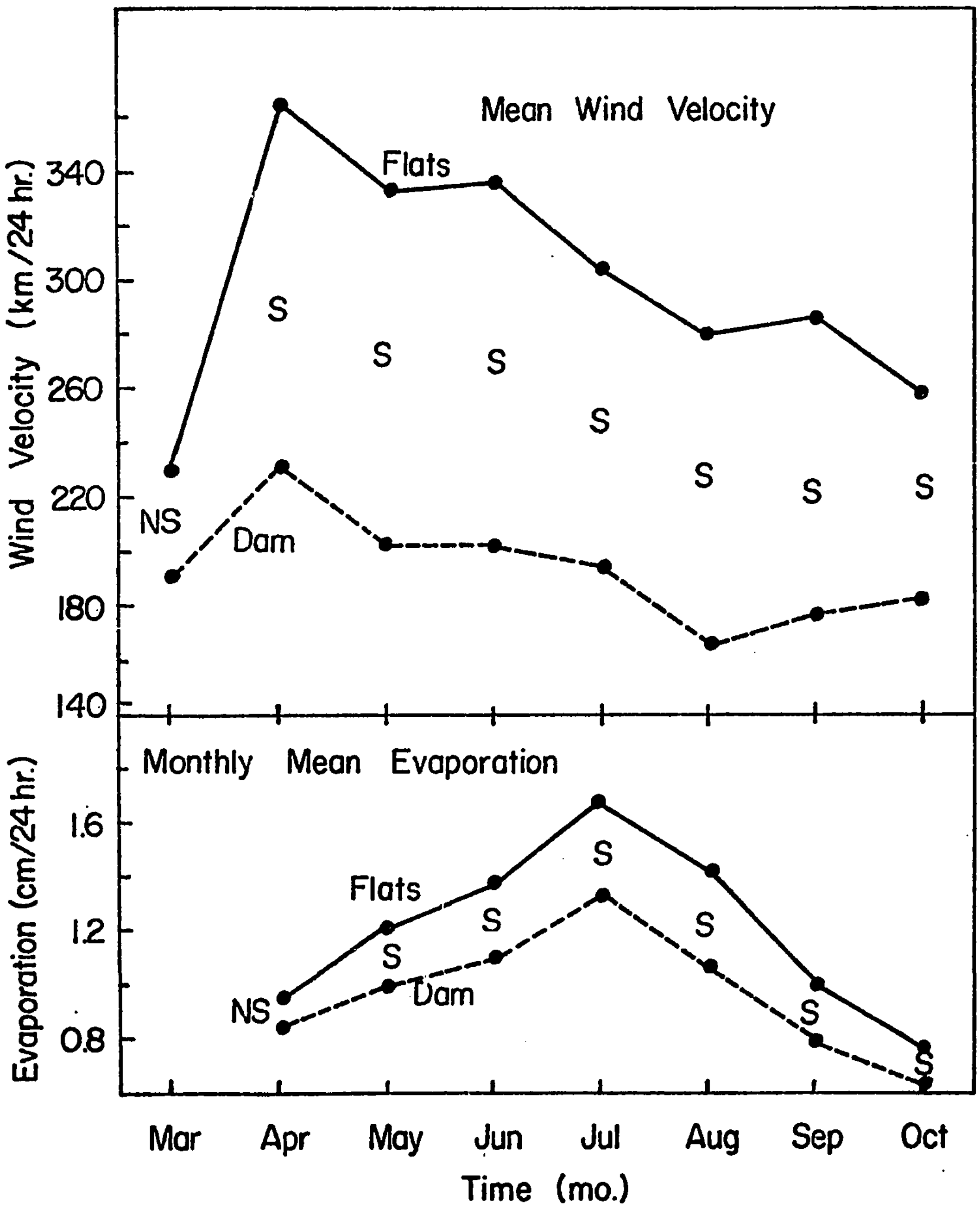

Mean Wind Velocity
Flats
Dam
NS
S
Wind Velocity (km/24 hr.)
340
300
260
220
180
140
Monthly Mean Evaporation
Evaporation (cm/24 hr.)
1.6
1.2
0.8
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Time (mo.)

Figure 3

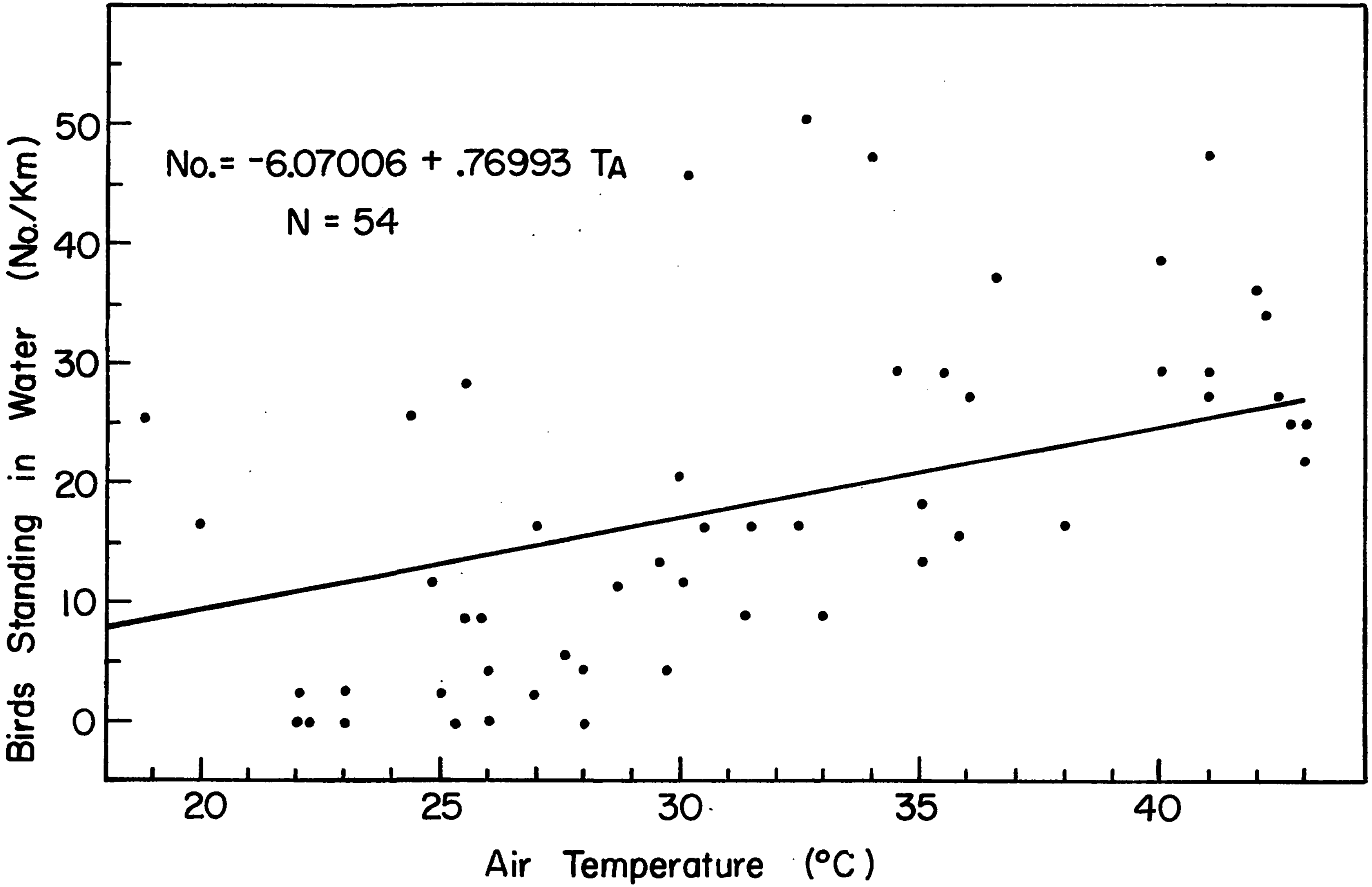

No.= -6.07006 + .76993 T_A
N = 54
Birds Standing in Water (No./Km)
0
10
20
30
40
50
20
25
30
35
40
Air Temperature (°C)

Figure 4

PAPER II

SALT WATER TOLERANCE AND WATER TURNOVER IN THE SNOWY PLOVER

SALT WATER TOLERANCE AND WATER TURNOVER IN THE SNOWY PLOVER

James R. Purdue

The Snowy Plover (*Charadrius alexandrinus*) is a small shorebird (30-40 g) commonly inhabiting areas of high salinity (Bent 1929, Rittinghaus 1961). One such area is the Great Salt Plains in northwestern Oklahoma. This is a large, barren, salt-encrusted flat where the plover lives and breeds in abundance. The standing water on the salt plains, ranging in chloride concentration from 825.0 to 5156.0 mEq/l, is osmotically stressful to most organisms, yet the Snowy Plover centers its activities around many of these pools and watercourses (Purdue 1974a). The purpose of this study was to determine if the plover has extraordinary physiological capability for handling hyperosmotic salt water. Its natural history and thermal ecology on the Great Salt Plains are treated elsewhere (Purdue 1974a, 1974b).

For comparison certain tests were also conducted on two other shorebirds, the Killdeer (*Charadrius vociferus*) and the Semipalmated Sandpiper (*Calidris pusillus*). The former species breeds in normally vegetated areas around the salt plains, but it is seldomly encountered on the salt flats, while the latter only migrates through the area on its way to breeding grounds in the north. Individual sandpipers, however, often spend several days or more foraging around the saline waters on the salt flats.

Methods

Birds were mist-netted or trapped on the salt flats and taken to laboratories at the University of Oklahoma, Norman, Oklahoma, where they were acclimated to experimental conditions for at least 2 weeks, fed ground Purina Cat Chow (protein, 30%; fat, 8%; water, 9.5-12%), and provided tap water *ad libitum*. I conducted five experiments to determine salt water tolerance: three on Snowy Plovers, and one each on Killdeer and Semipalmated Sandpipers (Fig. 1). Daily maintenance of body weight was the criterion for tolerance. Inverted bottles or graduated cylinders introduced water into small drinking cups. The shorebirds had considerable difficulty in learning to use rodent watering tubes, but a few birds finally did and were used for tests at higher concentrations. This procedure was necessary to avoid a slight upward shift in salt concentration due to evaporation from the drinking cups. Environmental conditions in the test chambers varied slightly between experiments due to the need to cooperate with other investigators; differences between tests are given in Fig. 1.

Another test on Snowy Plovers was conducted at 33° C, a vapor pressure deficit of 21-27 mm Hg, and a photoperiod of 13 hr light and 11 hr dark (L:D=13:11). Mealworms were fed <u>ad libitum</u> to a series of plovers deprived of any free water and body weight was monitored daily.

Tritiated water turnover experiments were conducted at 25° C (L:D=11:13, vapor pressure deficit = 17 mm Hg) and 40° C (L:D=11:13, vapor pressure deficit = 48 mm Hg) on Snowy Plovers, Killdeer, and Semipalmated Sandpipers. The birds, which were in a steady state as indicated by constancy of their body weight throughout the run, were injected intraperitoneally with 50 µl of 0.52 µ Ci/µl tritiated water (THO). At least two blood samples (10 to 25 µl plasma) were taken from the brachial vein within 4 hours of injection and subsequently single samples were taken daily. Each sample was centrifuged; the plasma was transferred to a toulene/butyl PBD/PBDO scintillation solution and counted (Beckman LS-133). Half life (T 1/2) was determined from the slope of the linear regression between the log of the cpm/ml plasma at time [t] x body weight at time [t] ÷ cpm/ml plasma x body weight at time [0] and time (t) in days. The equation for determining the fraction of water exchanged daily (λ) is:

$$\lambda = \frac{\ln 2}{T\ 1/2}$$

Total water content was estimated from the following relationship:

$$V_{H_2O} = \frac{cts_i}{A_o e^{-\lambda t} \cdot cts_t}$$

where V_{H_2O}= total water content in ml, cts_i = cpm/ml injected, t = time in days, A_0 = zero intecept of the plot of log At and t, and cts_t = cpm/ml at time (t). Daily water turnover was determined by the following equation:

$$\dot{V}_{H_2O} = V_{H_2O} \cdot \lambda$$

where $\dot{V}_{H_2O}$ = daily water turnover in ml/da. Both V_{H_2O} and $\dot{V}_{H_2O}$ were relativized by dividing by body weight. All statistical tests (significance of regression coefficients and analysis of variance) were done in accordance with Sokal and Rohlf (1969).

Results

<u>Salt water tolerance</u>.--The Snowy Plover (Fig. 2) and the Semipalmated Sandpiper (Fig. 4) were able to maintain or gain body weight at salinities of 0.2 to 0.25 M NaCl. At 0.3 M significant weight loss occurred in both species, but weight loss was slow and the birds survived for more than a week. Weight loss in the Snowy Plover (Fig. 2) was precipitous at 0.4 M and death would have resulted if the birds had not been given fresh water. In the sandpiper (Fig. 4) weight loss at 0.35 M and 0.4 M was not as precipitous as in the Snowy Plover, but it was considerably more rapid than at 0.3 M.

The Killdeer (Fig. 3) did not maintain its weight at salinities above 0.1 M, and weight loss was precipitous at only 0.2 M. Variability was great for the 0.2 M values, and the regression coefficient was not significant; however, there was a significant difference between days. Overall, the sandpiper and the Snowy Plover were about equal in ability to tolerate salt water, perhaps with the sandpiper being slightly better. The Killdeer was by far the least capable in this respect.

Water content.--Water constituted 69.6% and 72.8% of the body weight of Snowy Plovers in two separate tritiated water experiments (one at 25° C and one at 40° C) in which the birds were provided with tap water ad libitum. In a third test a group provided with 0.25 M NaCl was dehydrated to 62% (Table 1). The latter figure is significantly different ($P < .05$) from the other two according to the Student-Newman-Kauls a posteriori test which was used to isolate the deviant group indicated in a single-level analysis of variance (Sokal and Rohlf 1969). No difference was found between tap-watered birds kept at 25° C and those at 40° C.

Semipalmated Sandpipers contained less water than Snowy Plovers held at comparable environmental conditions. A two-way analysis of variance for temperature and species indicated a significant difference between species ($P < .05$) but not between temperatures. These sandpipers were in migration when captured in the middle of May and since the experiment was conducted only 20 days later, they still may have had migratory fat which would have decreased the percentage of body water. In contrast, the Snowy Plovers which showed decreased water content (those drinking 0.25 M NaCl) had been in captivity for several months. One Semipalmated Sandpiper (not included in Table 1) which was held in captivity for several months had a water content of 67.6%, a figure in line with Snowy Plovers held at comparable conditions (40° C). A single Killdeer held at 40° C also was similar in water content (67.2%).

Fluid consumption.--Fluid consumption was measured during the salt tolerance tests on Snowy Plovers (Fig. 5). Consumption was 20% of body weight per day when the birds were given distilled water. At moderate salinities, i.e., those that the plovers can tolerate for several days (Fig. 2), there was a dramatic increase in fluid intake. At 0.4 M NaCl, the point of precipitous weight loss, fluid intake diminished sharply.

Although water turnover rates (Table 1) subjected to one- and two-way analysis of variance tests revealed no statistically significant differences between species or within given species under the different conditions, both the Snowy Plover and the Semipalmated Sandpiper bordered on significantly increased turnover with increased ambient temperature: 43% at 25° C and 48% at 40° C for the plover and 54-57%, respectively, at comparable temperatures for the sandpiper. A slightly larger sample size probably would have confirmed this. A series of three Snowy Plovers on 0.25 M NaCl had slightly less turnover than plovers on tap water at the same temperature. A single Killdeer, held at 40° C, turned over 46% of its body weight each day.

Mealworm larvae were provided ad libitum as the only source of both food and water (Fig. 6) to a series of Snowy Plovers which were maintained at 33° C (see Fig. 1 for other environmental conditions). After an initial drop in weight during the first day, the birds maintained or increased their weight. The decrease in sample size as the experiment proceeded was due to the investigator's shortage of mealworms rather than any lack of ability by the bird to maintain weight.

Discussion

The salt tolerance of the Snowy Plover, Killdeer, and Semipalmated Sandpiper does not appear to be exceptional when compared to other species of birds. Bartholomew and Cade (1963) listed the following species as being able to tolerate salinities in excess of 0.3 M: *Taeniopygia castanadis*, three subspecies of *Passerculus sandwichensis*, and *Melospiza melodia cooperi*. Subsequently, MacMillen and Trost (1966) found that *Zenaida asiatica* and *Scardafella inca*, two common doves of the southwestern deserts of the United States, can withstand 37.5-50% sea water (equivalent to approximately 0.2 to 0.3 M NaCl). Three species of quail could not withstand more than 0.3 M NaCl (McNabb 1969). Agelaius phoeniceus tolerates up to 0.3 M NaCl (Hesse and Lustick 1972) while Amphispiza bilineata tolerated 0.4 M (Smyth and Bartholomew 1966) and Spizella breweri tolerated 0.55 M (Ohmart and Smith 1971). Frings and Frings (1959) found that two species of albatross could not survive in captivity until artificial sea water was provided. However, surprisingly little work has been reported on the salt tolerance of charadriiform birds even though their extrarenal salt glands are generally well developed and much studied. Hughes (1970) kept more than half of her sample of Larus glaucescens at constant weight when provided with 100% sea water (approximately 0.6 M NaCl) which is well beyond the limits tolerated by the three species I examined.

Staaland (1967) examined over 20 species of charadriiform birds for the size and function of nasal salt glands. He found that relative size of the gland was correlated with concentrating ability and ecology. Diversity of salt glands within the Charadriidae was evidenced by Pluvialis apricaria with a nasal gland (mg) to body weight (g) ratio of 0.3 while Charadrius hiaticula had a ratio of 0.7. My dissections suggest that the salt gland of the Snowy Plover is slightly smaller than that of Actis hypoleuos (diagramed in Staaland, 1967), which had a ratio of 0.6. The size of the Killdeer's salt gland, as revealed by dissection, is relatively smaller than the Snowy Plover's.

This evidence supports the salt tolerance findings in that the Snowy Plover has a moderately developed salt gland and a correspondingly intermediate ability to handle high osmotic loads. The Killdeer with a relatively smaller gland displayed reduced salinity tolerance.

The Snowy Plover's level of fluid consumption at various salt concentrations (Fig. 5) is intermediate between Batholomew and Cade's (1963) drinking patterns A and B. In pattern A, birds drink increasing amounts of water with increasing salinity until an upper limit is reached (0.4 M in this case) and consumption ceases. For pattern B, consumption is about the same across the entire range of salinities. According to Hesse and Lustick (1972) Red-winged Blackbirds (Agelaius phoeniceus) also had drinking characteristics which resembled both patterns A and B. Lustick (1970) suggested that the increase in drinking of tolerable salt water over distilled water may be the result of birds seeking salt.

Seemingly there is a disparity when one compares the water consumption and turnover results from two sets of data (Fig. 5 and Table 1). When provided distilled water ad libitum, the birds maintained body weight with consumption at 20% of body weight per day (Fig. 5), but daily water turnover, as determined through tritiated water studies, yielded values ranging from 43-48% (Table 1). The turnover values include water obtained by drinking as well as water preformed in food and produced through oxidative metabolism, while data from water consumption studies include only drinking water. Thus the difference between consumption of distilled water ad libitum (20%) and tritiated water turnover (43-48%) can be reconciled.

These two tests indicated that Snowy Plovers have similar water requirements to those of other avian species of similar body weight. Bartholomew and Cade (1963) compiled drinking water values for many bird species and showed a dramatic increase in relative water consumption for birds weighing 30 to 40 g or less. The Snowy Plover, which is in this weight class, fits in the pattern reported by Bartholomew and Cade.

Even though the Snowy Plover was not spectacular in its ability to tolerate salt or reduce water turnover, it does maintain body weight when fed mealworms, a substitute comparable to its natural food (Fig. 6). Its food, as discussed by Purdue (1974a), consists of flies, beetles, and other insects that are found on the salt plains. Insects, like other animals, have high water contents. Thus the insectivorous diet coupled with water-conserving behaviors, such as standing in pools during hot weather (Purdue 1974a), allows the Snowy Plover to avoid drinking the saline solutions that occur on the salt plains. Among other birds, Long-billed Marsh Wrens (Telmatodytes palustris) are also capable of survival on a diet of mealworms and no free water

(Kale 1967); several passerine species and the Budgerygah (Melopsittacus undulatus) can maintain body weight when fed dry seeds (Bartholomew 1972); and two dove species from the North American deserts manage to live on succulent plants (MacMillen and Trost 1966).

Thus, the Snowy Plover is another bird, such as the Horned Lark (Eremophila alpestris) (Trost 1972), and columbiid species (MacMillen and Trost 1966), that has limited physiological capacities, yet lives in a water-poor environment. To survive in these habitats the birds eat succulent foods and depend on appropriate maintenance behavior.

Acknowledgments

Thanks are due to Mr. Ronald Sullivan, manager of the Great Salt Plains National Wildlife Refuge, for his cooperation. Dr. Anthony A. Echelle critically reviewed the manuscript. The advice of Dr. Charles C. Carpenter, my major professor for the doctoral dissertation of which this paper is a part, and Mrs. Joretta Purdue, wife and editorial assistant, are appreciated.

Summary

A series of water-related experiments showed that Snowy Plovers do not have any outstanding physiological capabilities for dealing with the potential thermal and osmotic stresses of the Great Salt Plains, Oklahoma. Snowy

Plovers and Semipalmated Sandpipers failed to maintain body weight when given 0.3 M NaCl *ad libitum*. Killdeer did even more poorly by rapidly losing weight on 0.2 M. These salt water tolerance values are limited when compared to other, particularly marine, birds that can drink full strength sea water.

As shown by two different methods of determining water turnover, the Snowy Plover is no better at conserving water than other birds in its weight class. However, plovers without drinking water were able to maintain their weight when furnished mealworm larvae *ad libitum*. Thus, the insectivorous diet as well as maintenance behavior of the birds is essential for their survival on the salt flats.

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TABLE 1

Mean water content and daily water turnover for Snowy Plovers, Semipalmated Sandpipers, and Killdeer. Parenthetical numbers are standard errors. Drinking fluid was provided *ad libitum*

	N	Temp. (^{o}C)	Mean Body Wt. (g)	Water Content	Daily Water Turnover
Snowy Plover (Tap water)	4	25	33.7	69.59 (± 1.85)	43.32 (± 1.05)
	4	40	32.2	72.75 (± 1.07)	48.45 (± 3.31)
Snowy Plover (.25 M NaCl)	3	25	34.0	62.26 (± 2.56)	39.01 (± 1.73)
Semipalmated Sandpiper (Tap water)	3	25	24.3	58.50 (± 3.05)	54.45 (± 4.08)
	3	40	22.5	55.93 (± 2.42)	56.55 (± 7.29)
Killdeer (Tap water)	1	40	71.1	67.16	46.25

Figure Legends

Fig. 1. Schedule of salt water tolerance tests for Snowy Plovers, Killdeer, and Semipalmated Sandpipers. Gaps indicate periods when birds were supplied tap water *ad libitum*. Environmental conditions: A, temperature 33° C, vapor pressure deficit 21-27 mm Hg, L:D=13:11; B, temperature 25° C, vapor pressure deficit 17 mm Hg, L:D=11:13.

Fig. 2. Effect of salt water *ad libitum* on body weight of Snowy Plovers. N = sample size at beginning of test, * = significant regression coefficient ($P < .05$), NS = nonsignificant coefficient regression.

Fig. 3. Effect of salt water *ad libitum* on body weight of Killdeer. Abbreviations same as for Fig. 2 except Δ = significant difference between days ($P < .05$), but nonsignificant regression coefficient.

Fig. 4. Effect of salt water *ad libitum* on body weight of Semipalmated Sandpipers. Abbreviations given in Fig. 2.

Fig. 5. Fluid consumption of Snowy Plovers at concentrations of NaCl. Ranges are indicated by length of vertical lines, means by horizontal lines, and standard error either side of mean by darkened block. D. W. means distilled water.

Fig. 6. Snowy Plovers maintained on mealworms *ad libitum* with no free water. Sample sizes in parentheses.

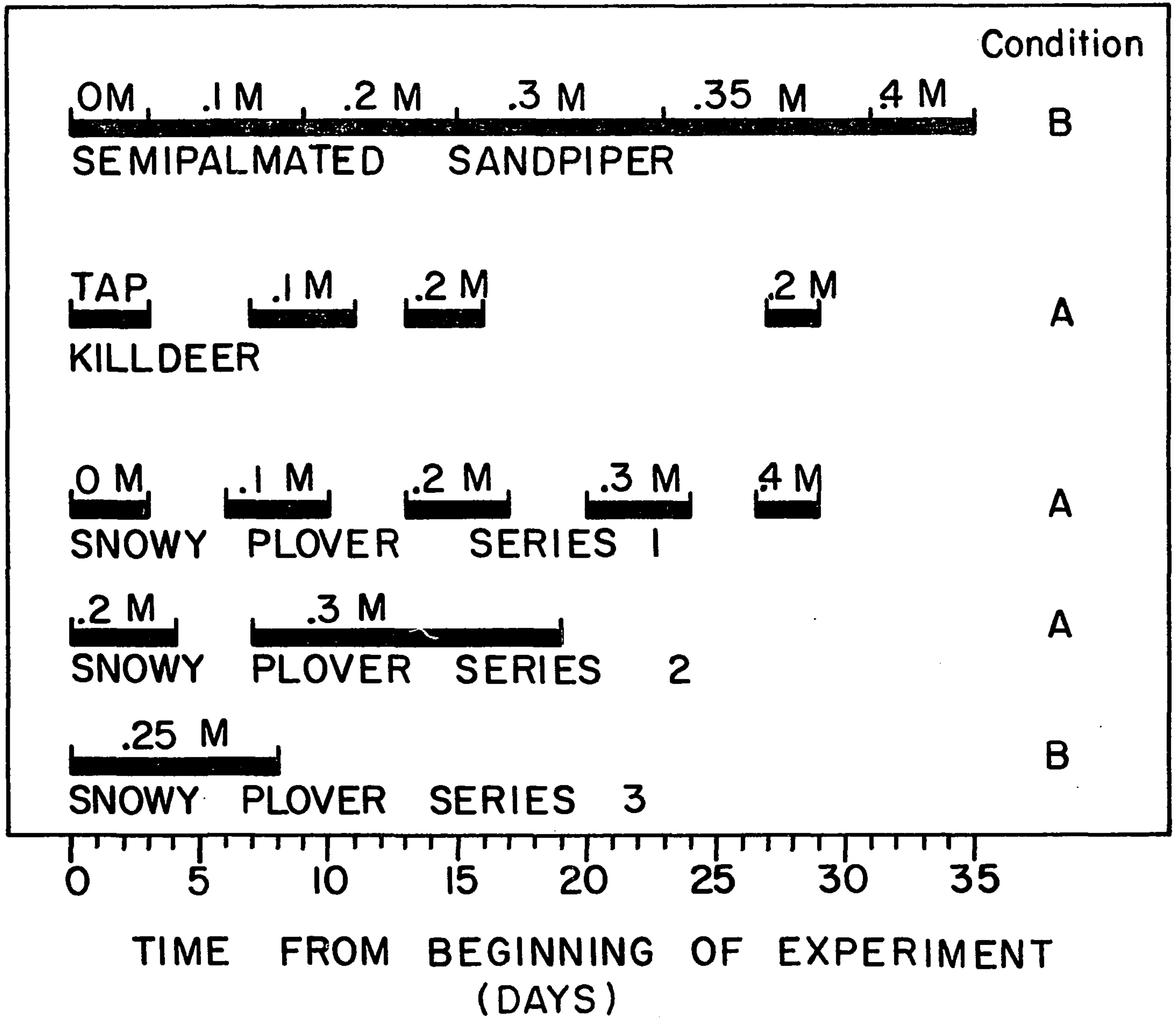
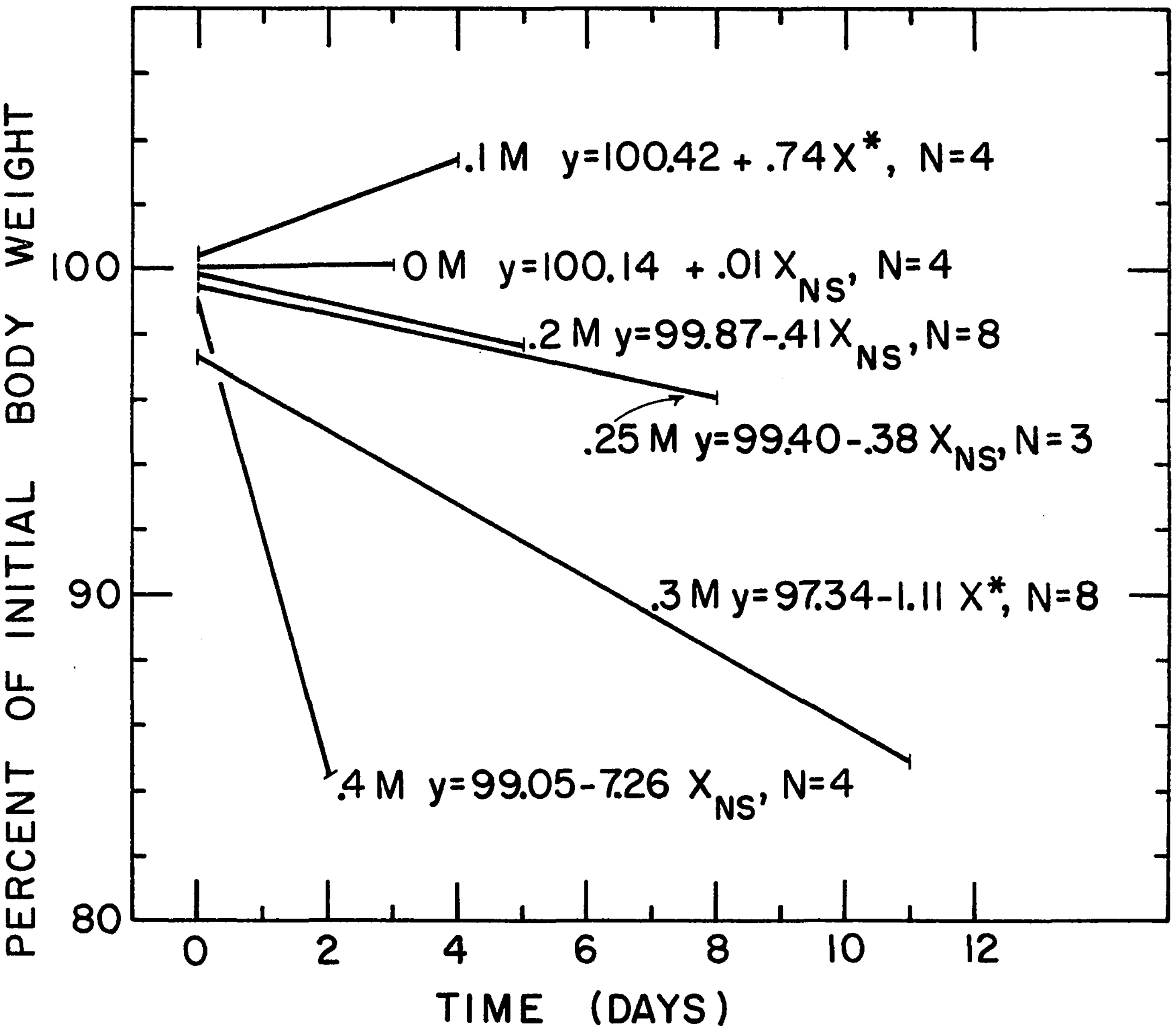
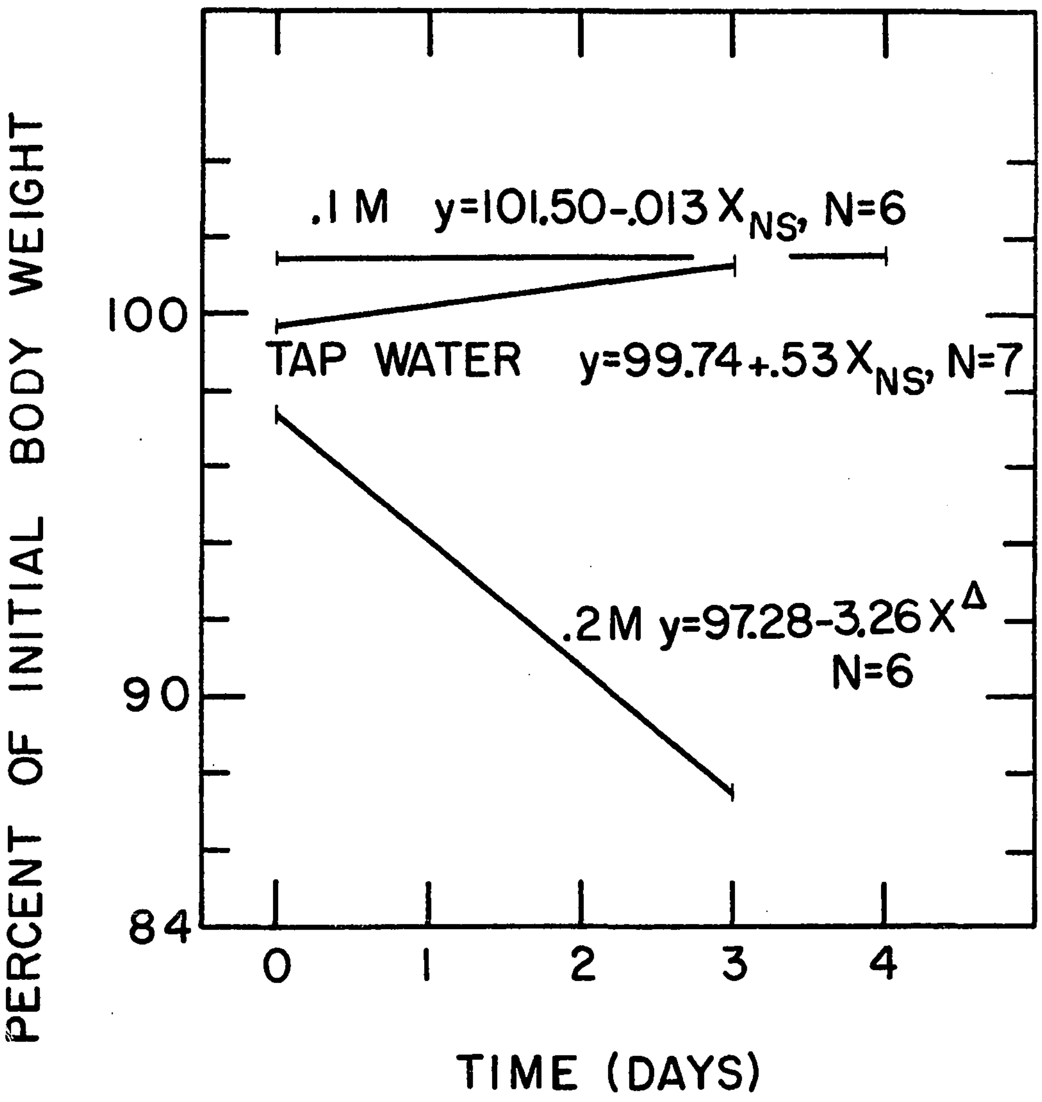

Condition
0M .1 M .2 M .3 M .35 M .4 M
SEMIPALMATED SANDPIPER
B
TAP .1 M .2 M .2 M
KILLDEER
A
0 M .1 M .2 M .3 M .4 M
SNOWY PLOVER SERIES 1
A
.2 M .3 M
SNOWY PLOVER SERIES 2
A
.25 M
SNOWY PLOVER SERIES 3
B
0 5 10 15 20 25 30 35
TIME FROM BEGINNING OF EXPERIMENT
(DAYS)

Figure 1



PERCENT OF INITIAL BODY WEIGHT
100
90
80
0
2
4
6
8
10
12
TIME (DAYS)
.1 M y=100.42 + .74 X*, N=4
0 M y=100.14 + .01 X_NS, N=4
.2 M y=99.87-.41 X_NS, N=8
.25 M y=99.40-.38 X_NS, N=3
.3 M y=97.34-1.11 X*, N=8
.4 M y=99.05-7.26 X_NS, N=4

Figure 2



PERCENT OF INITIAL BODY WEIGHT
100
90
84
.1M y=101.50-.013X NS, N=6
TAP WATER y=99.74+.53X NS, N=7
.2M y=97.28-3.26X Δ
N=6
0
1
2
3
4
TIME (DAYS)

Figure 3

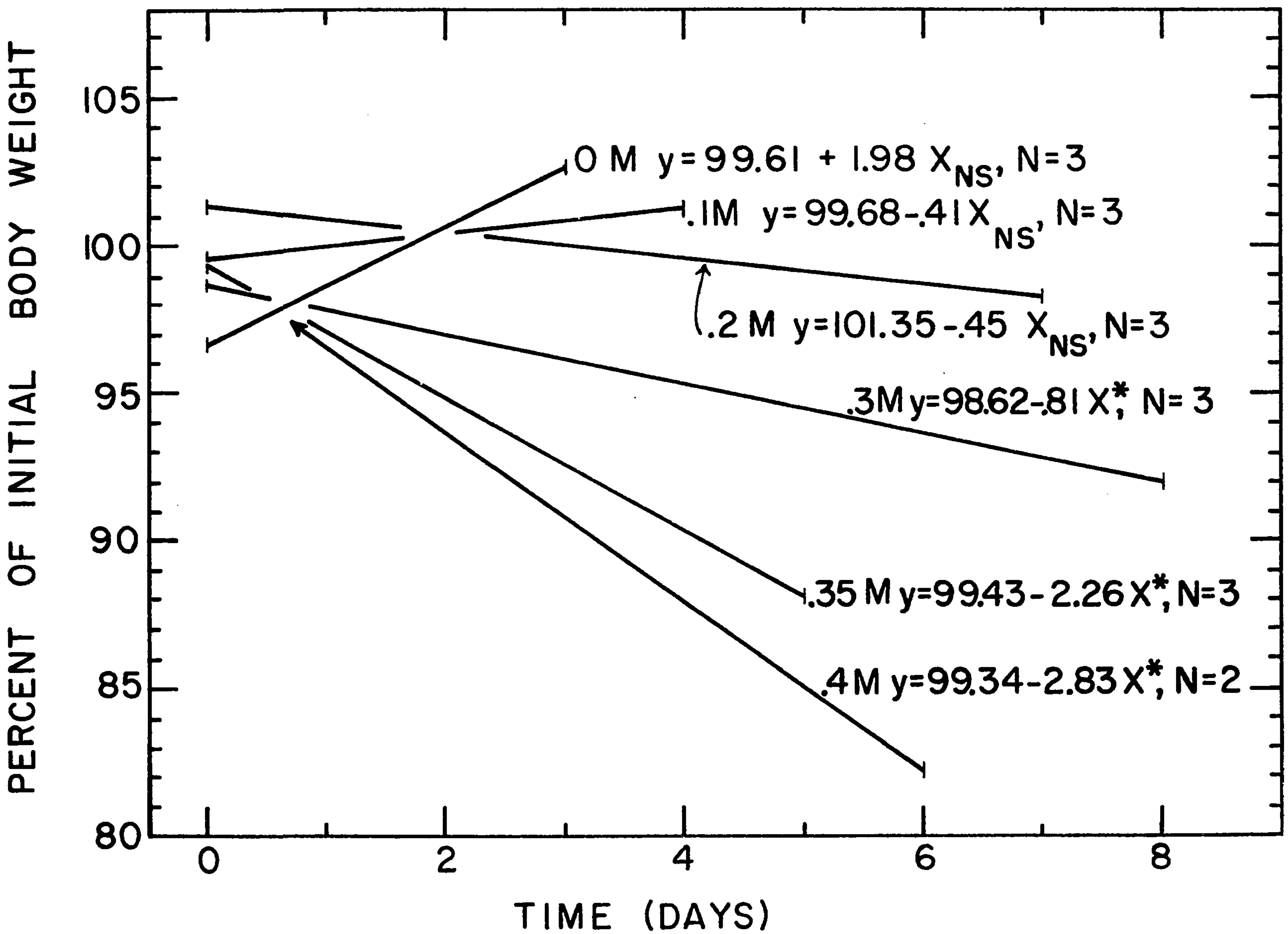

PERCENT OF INITIAL BODY WEIGHT
105
100
95
90
85
80
0
2
4
6
8
TIME (DAYS)
0 M y=99.61 + 1.98 X_NS, N=3
.1M y=99.68-.41X_NS, N=3
.2 M y=101.35-.45 X_NS, N=3
.3M y=98.62-.81 X*, N= 3
.35 M y=99.43-2.26X*, N=3
.4M y=99.34-2.83X*, N=2

Figure 4

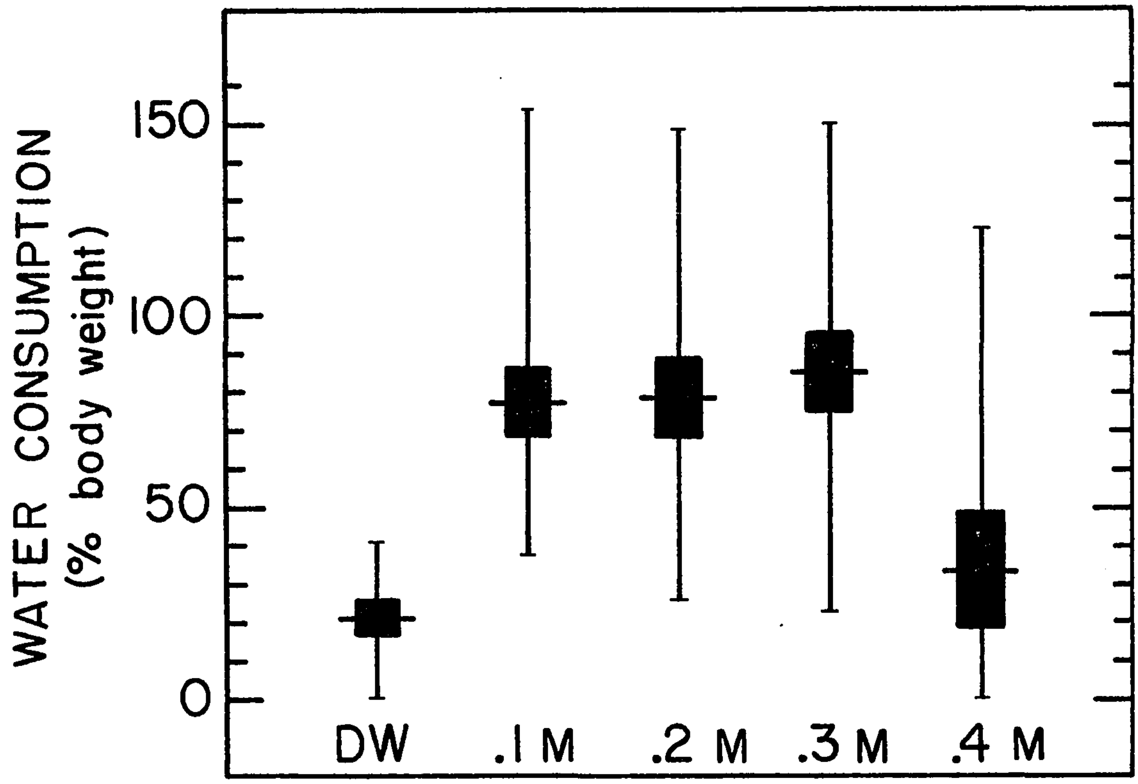
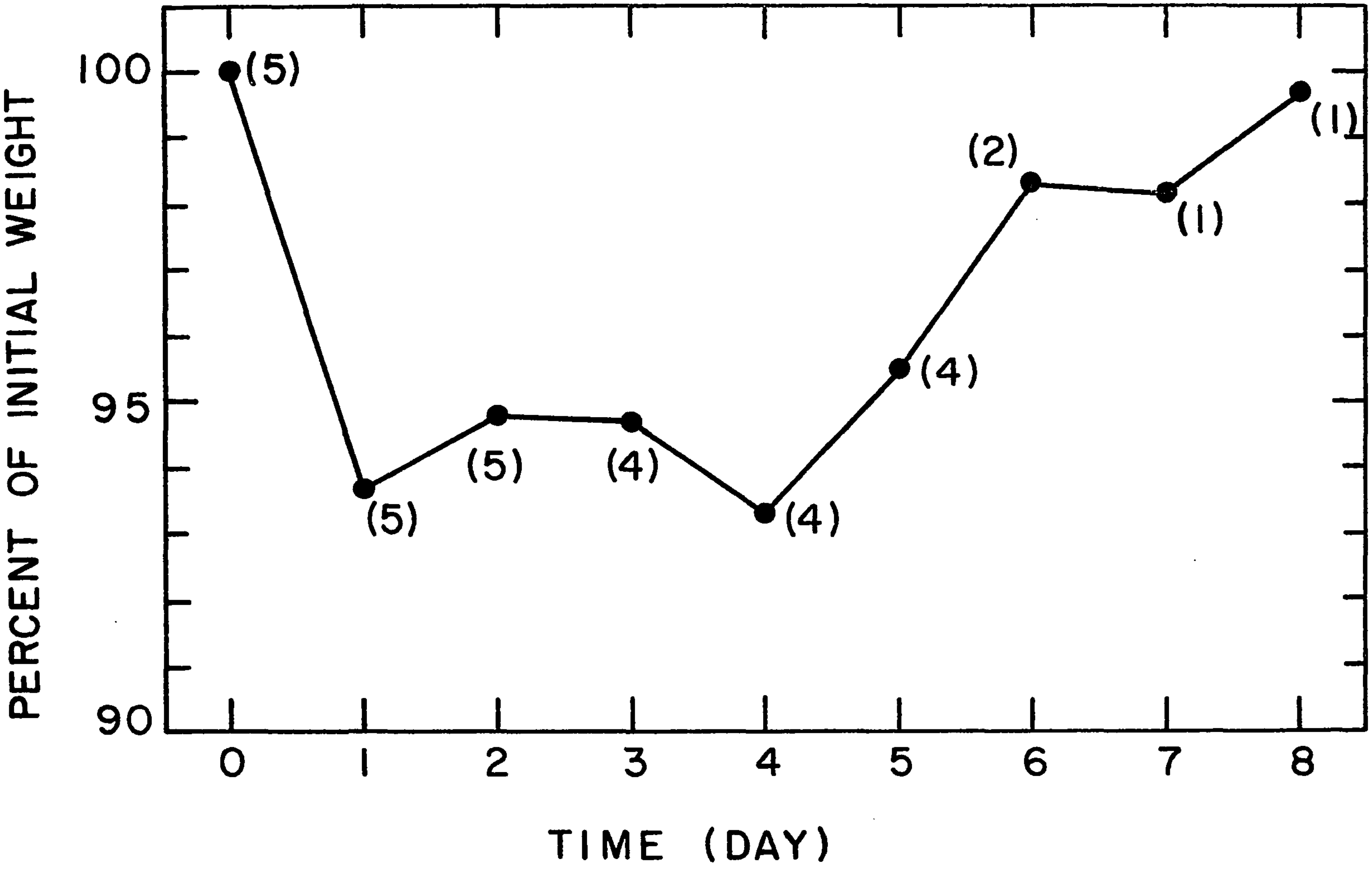


Figure 5



PERCENT OF INITIAL WEIGHT
100
95
90
0
1
2
3
4
5
6
7
8
(5)
(5)
(5)
(4)
(4)
(4)
(2)
(1)
(1)
TIME (DAY)

Figure 6

PAPER III

THERMAL ENVIRONMENT OF THE NEST AND RELATED PARENTAL BEHAVIOR IN SNOWY PLOVERS, *CHARADRIUS ALEXANDRINUS*

THERMAL ENVIRONMENT OF THE NEST AND RELATED PARENTAL BEHAVIOR IN SNOWY PLOVERS, CHARADRIUS ALEXANDRINUS

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Snowy Plovers (*Charadrius alexandrinus*) usually nest in bare, unvegetated habitats (Bent 1929). One such area is the Great Salt Plains, Alfalfa County, Oklahoma, where daily maximum temperatures are commonly above 40° C during the breeding months. The nests are simple scrapes on slight elevations and are highly exposed since the nearest vegetation (prairie grassland) is often several hundred meters away (Purdue 1974). Likewise plovers on the Great Salt Plains typically locate their nests away from any driftwood or debris, thus depriving the eggs of thermal moderation from such sources. Incubation studies on other charadriiform species have been conducted in cool (Norton 1972) and mild (Drent 1970) climates. Except for Howell and Bartholomew's work (1962), little has been done with charadriiform birds breeding in hot climates. My purposes here are to characterize the thermal environment in which Snowy Plover eggs are maintained on the Great Salt Plains of northwestern Oklahoma and to relate this to the behavior of the parents.

METHODS

A series of strategically placed thermistors were used to measure the temperatures of the nest environment (fig. 1). One egg was removed from each of several nests and replaced with another containing an implanted thermistor. This sensing egg was prepared by drilling a small hole in the side, extracting a small amount of fluid and replacing it with formaldehyde, inserting a thermistor (Yellow Springs Instruments No. 402) so that the sensing tip was positioned in the middle of the egg, and sealing with Duco cement.

A second, identically prepared temperature-sensing egg was placed on the substrate outside but near the nest. For some nests a flattened thermistor (Yellow Springs Instruments No. 409) was attached to a supporting wire and positioned through the cluster of eggs so that it would sense the temperature at the top of the eggs (brood patch temperature if an adult bird were incubating). Air temperature was monitored with a thermistor (Yellow Springs Instruments No. 401) placed a few meters from the nest with the sensing tip 5 cm above the substrate. All thermistor leads were connected to a monitoring device (Yellow Springs Instruments Tele-thermometer) in an automobile up to 100 m away. Readings were made every 10 minutes mostly during daylight hours (fig. 2). Once every 60 to 90 minutes surface temperature was measured around the nest with a Barnes I.R. Field Thermometer. Air movement was measured with a small, windmill-type anemometer placed on the substrate.

The automobile also served as an observation blind from which adult behavior was observed with binoculars or spotting scope; thus I was able to associate moment-to-moment changes in parental behavior with temperature readings. A continuous log was maintained which emphasized parental activities around the nest, particularly presence or absence, sitting or standing, and transference of incubation duties. Subsequently, this record was split into 5-minute segments and scored. If a bird was present for more than 50% of the 5-minute period, the nest was considered attended. Scores were then accumulated and related to appropriate factors (time since initiation of incubation, air temperature, and time of day). These data were treated statistically with replicated goodness of fit (G-statistics) for determining significant differences and _a posteriori_ tests for finding deviant groups by simultaneous testing procedures (Sokal and Rohlf 1969). Six nests representing a total of 207 hours were so analyzed (figs. 4-6). Brood-patch temperature and incubation behavior were related to given air temperatures by noting whether the attending bird was sitting or standing over the eggs at the various temperatures.

RESULTS AND DISCUSSION

In a review of incubation in birds Drent (1973) reported that several species show positive correlations between internal egg temperature and air temperature while other species do not. Temperatures of Snowy Plover eggs on the Great Salt Plains show a strong correlation with air temperature (fig. 3)--to the extent that to assign a "representative measurement" (Drent 1973) of egg temperature independent of air temperature for the plover would be arbitrary. Two factors contribute to this observation. First, only diurnal observations were made, and brooding behavior was frequently interrupted by activities such as foraging, picking around the nest, and egg turning. Such activities probably do not occur at night; thus, nocturnal egg temperatures probably would be higher than air temperature and the correlation with air temperature would be reduced. Russell (1969) demonstrated this for desert-dwelling doves. Second, the use of a dead egg to characterize egg temperatures does not allow for the effect of embryonic heat production. Drent (1970), using a respirometer on Herring Gull (*Larus argentatus*) eggs, found that after the 14th day embryonic heat production played a significant role in elevating egg temperature above that of the air immediately in contact with the egg.

My data from dead eggs show that lethal conditions occur on the salt flats and that parental incubation behavior moderates fluctuation in egg temperature. The maximum temperature recorded for eggs outside the nest was 48° C as compared with 43° C for eggs in the nests. The latter temperature lasted only briefly toward the end of a period when the parents had not attended the nest. Eggs outside the nest more closely parallel ambient temperatures than do eggs in the nest (fig. 4). Eggs in the nest became cooler than unattended eggs when the air temperature rose to about 33° C. Also, the former are cooler than ambient conditions at air and surface temperatures of 38-39° C; this does not occur in unattended eggs. Thus, there was a striking contrast between the temperatures of unprotected eggs, which roughly paralleled ambient conditions, and of the protected eggs which were less affected by the weather.

Several adult behaviors affect egg temperatures. As with other species (Drent 1970), time devoted to the eggs increases with duration of incubation (fig. 5).

Time of day is also correlated with incubating attentiveness (fig. 6). Plovers were quite attentive most of the day, but a distinct decrease occurred in late afternoon. This coincided with a major foraging period just before nightfall. No comparable decrease occurred in the early morning hours which represented a second major foraging period. Kendeigh (1952) found a drop in attentiveness during the daylight hours for House Wrens (Troglodytes aedon), but it was not as sharp as that shown in fig. 6. Norton (1972), working with Arctic-breeding sandpipers, also found decreased attention during the day.

Attentiveness is significantly reduced when the ambient temperature is between 31° and 40° C (fig. 7), a thermally moderate range for most birds. At moderate temperatures the adults can be away from the nest with little thermal danger to the eggs. Attentiveness is maximal at temperatures of 41-45° C, which probably are near lethal conditions. This agrees with von Haartman's (1956) observations on several other species of birds. Similarly, Howell and Bartholomew (1962) found that when a Sooty Tern (Sterna fuscata) nest is exposed to intense midday heat, the adults are extremely tenacious in staying with their eggs.

Moderate air temperatures and late afternoons, both of which correspond with diminished nest attention, often occur simultaneously. Also, the first third of the incubation period tends to be early in the season, increasing the likelihood of moderate thermal conditions. Thus the factors correlated with nest attentiveness in the Snowy Plover are not independently related.

At high temperatures the adults of many species of birds stand over the nest so that a shadow falls on the eggs; Boyd (1972) and Rittinghaus (1961) have reported this for the Snowy Plover. Fig. 8 clearly indicates that the frequency of standing is a function of ambient temperature. At air temperatures above 41° C standing occurs more frequently than sitting while fig. 8 also shows that there is no significant increase in the temperature at the top of the eggs. Brood patch temperature remained essentially constant throughout the range of external air temperatures. In 1958 Walters recorded brood patch temperatures in Snowy Plovers with a mercury bulb thermometer placed in a position comparable to the thermistors used in this study. His mean of 40.8° is somewhat higher than the means I obtained, but readings above 40° C were common in my study.

Both male and female Snowy Plovers incubate the eggs (Walters 1958, Rittinghaus 1961). Fig. 9 indicates that the duration of a parental shift is related to the external thermal environment. At cool and moderate air temperatures shifts are long--often more than 16 hrs. In hot weather the shifts are much shorter, and at air temperatures above 40° C the shifts are less than 1 hr long. Boyd (1972) showed convincingly that during hot weather Snowy Plovers apply moisture collected in their breast feathers from nearby pools to the egg surfaces. He reported similar behavior for Killdeer (Charadrius vociferus). Increases in this behavior may account for the reduced shift duration at high air temperatures (fig. 9).

Drent (1973) concluded that behaviors such as standing over the eggs and wetting the eggs with external water are merely for adult thermoregulation, and that any benefit for the eggs is coincidental. However, analysis of the temperatures at the top of the plover's eggs indicate that standing may be, at times, more effective than setting in keeping the eggs cool. With air temperatures greater than 36° C, 53 measurements at times when adults were standing over the eggs showed a mean egg temperature of 39.58° C, while 63 comparable readings taken when the parents were sitting had a mean of 40.07° C. Analysis of variance indicated a significant difference between these two means at the .05 level. These figures, coupled with the greater incidence of standing at higher air temperatures (fig. 8) imply that standing may be an efficient way to keep the eggs from overheating, especially when combined with egg wetting.

However the above effect may be tempered by wind. Purdue (1974) showed that the unvegetated salt flats receive much more wind action than the surrounding grasslands. Fig. 10 shows a statistically significant negative relationship between the incidence of standing over the eggs and wind speed when air temperatures are greater than 36° C. This relationship may be the result of at least two non-exclusive factors. First, at high velocity, winds carry along the substrate surface many sand and salt particles which can be quite abrasive. Second, high wind speed would break up the boundary layer of air surrounding the eggs and at high temperatures increase the transfer of heat to the eggs. By sitting on the eggs during this time the parental bird protects the eggs from both hazards. White-winged Dove (Zenaida asiatica) in the southwestern American desert, presumably with limited standing water for breast wetting, sat tightly on the eggs when ambient temperatures were extremely high (Russell 1969). In both the doves and the plovers, heat from the eggs was probably transferred to the adult via the brood patch.

In conclusion, the Snowy Plover nests in an area where eggs can be exposed almost daily to lethal thermal conditions. The parental birds respond with a variety of incubating behaviors which are finely tuned to ambient conditions, thus maintaining a suitable thermal environment for the eggs.

SUMMARY

The thermal environment of the eggs of Snowy Plovers was measured by placing thermistors in eggs and in strategic positions around the nest. Eggs which were outside the nest and therefore not receiving adult attention attained much higher, presumably fatal, temperatures while eggs inside the nest were kept cooler. Egg temperatures were positively correlated with air and surface temperatures, but thermal extremes were moderated by parental behavior.

Time spent on the nests by the adults was correlated with several interrelated factors. Nest attention increased

during the latter two-thirds of the incubation period and during times of high air temperature. Nest attention diminished in late afternoon, a period of peak foraging activity and moderate temperatures. The duration of each shift at the nest was reduced at high air temperatures while the amount of time spent standing rather than sitting over the nest increased. High wind speeds reduced the latter tendency.

ACKNOWLEDGMENTS

Thanks are due to Mr. Ronald Sullivan, manager of the Great Salt Plains National Wildlife Refuge for his assistance, as well as to Dr. Charles C. Carpenter, my major professor; Dr. Anthony A. Echelle, my critical reviewer, and Joretta Purdue--my wife, typist, and literary critic. This is a portion of a doctoral dissertation for the Department of Zoology, University of Oklahoma.

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Figure Legends

FIGURE 1. Schematic diagram of placement of thermistors in and near Snowy Plover nests. T_A measures air temperature, T_{EN} temperature of egg, T_{EON} temperature of egg out of the nest, T_{BP} temperature on top of eggs, and T_S surface temperature.

FIGURE 2. Distribution of observations throughout the day. Data pooled for entire study.

FIGURE 3. Effect of air temperature on egg temperature.

FIGURE 4. Effect of parental behavior on egg temperature. See figure 1 for abbreviations.

FIGURE 5. Effect of duration of incubation on adult attentive behavior. Horizontal line indicates homogeneous groups according to STP test (see text).

FIGURE 6. Effect of time of day on adult attentive behavior. See figure 5 for explanation.

FIGURE 7. Effect of air temperature on adult attentive behavior. See figure 5 for explanation.

FIGURE 8. Effect of air temperature on standing behavior and temperature on top of eggs.

FIGURE 9. Effect of air temperature on duration of parental shift.

FIGURE 10. Effect of wind on standing over the nest.

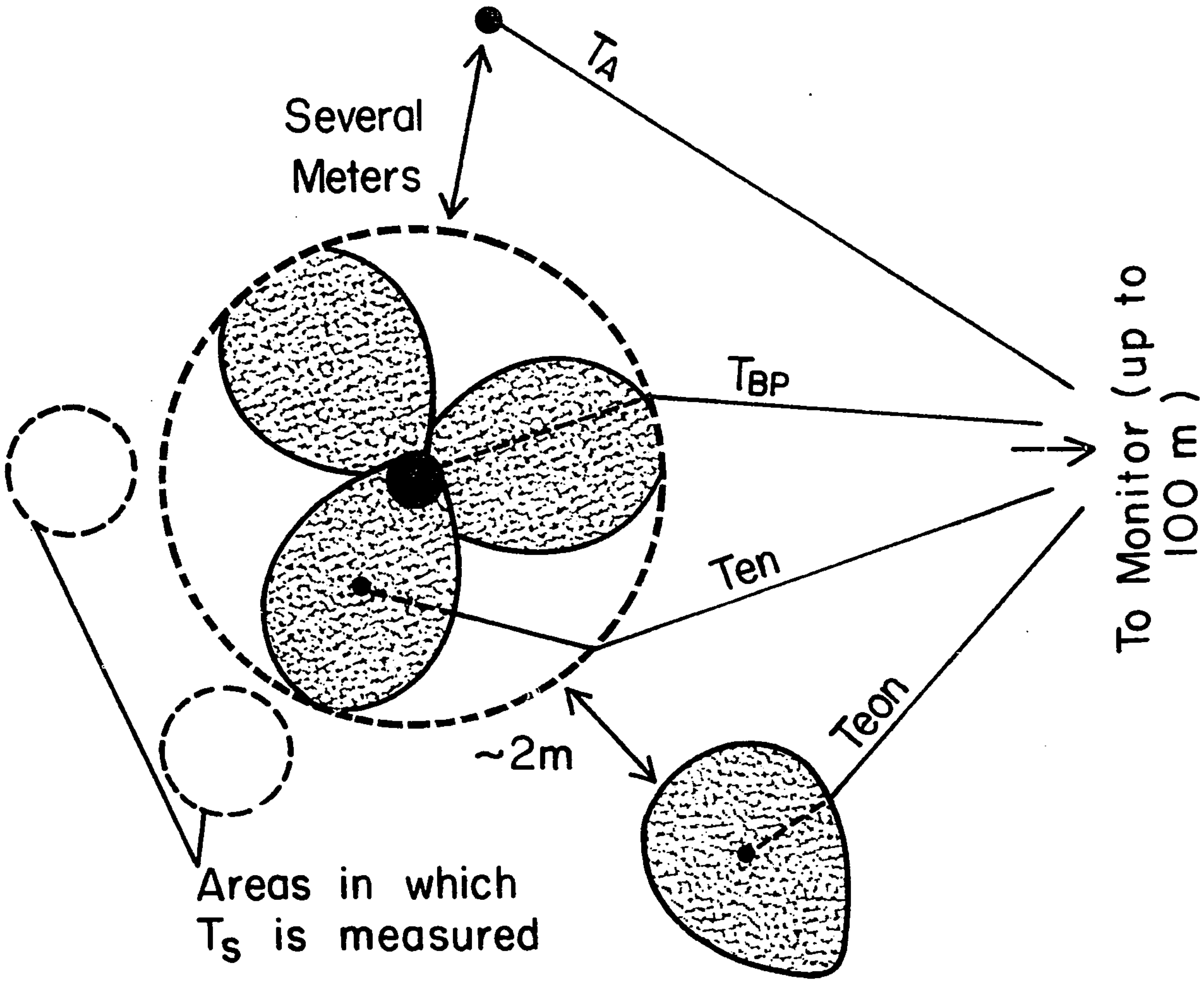
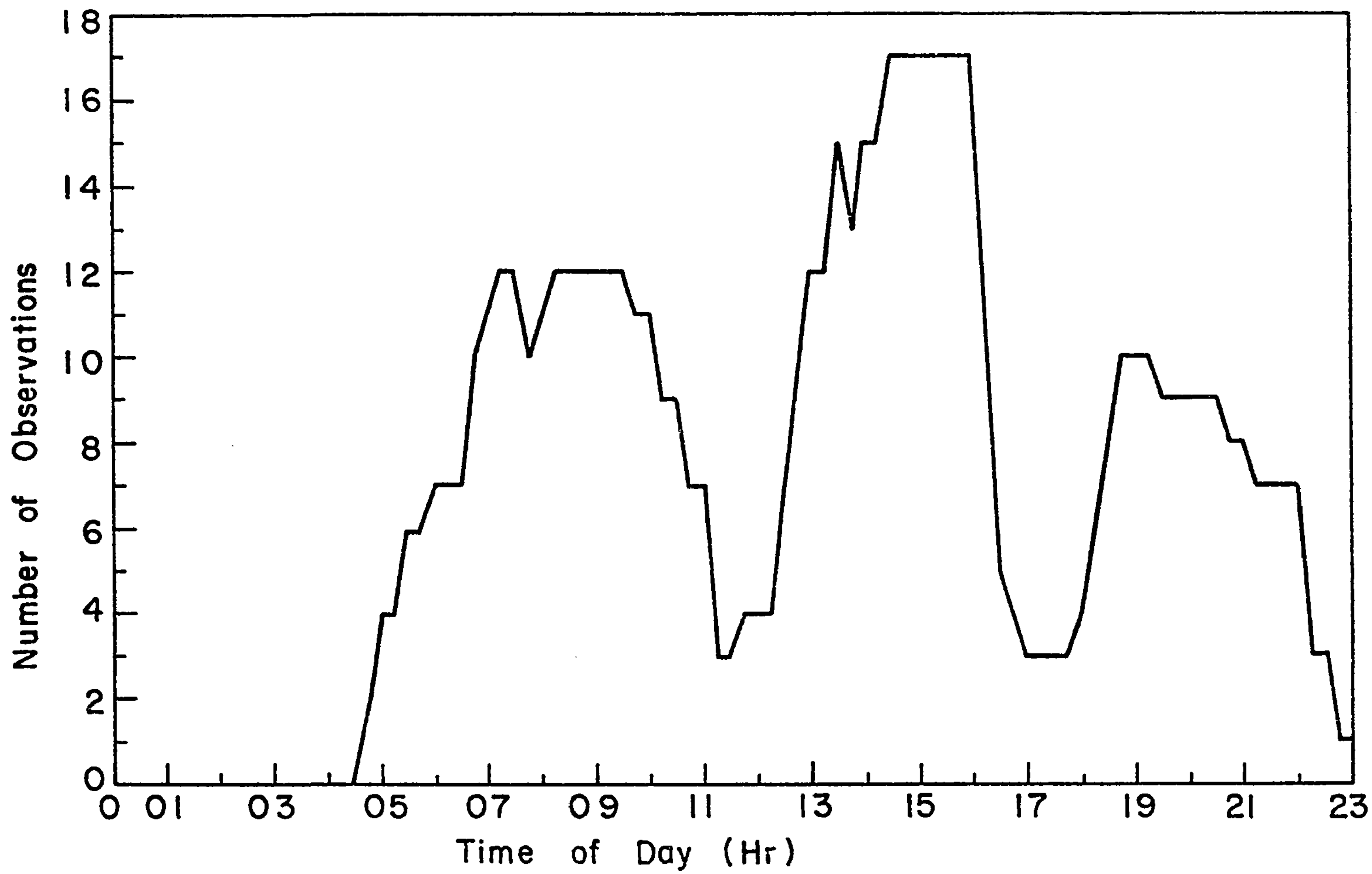
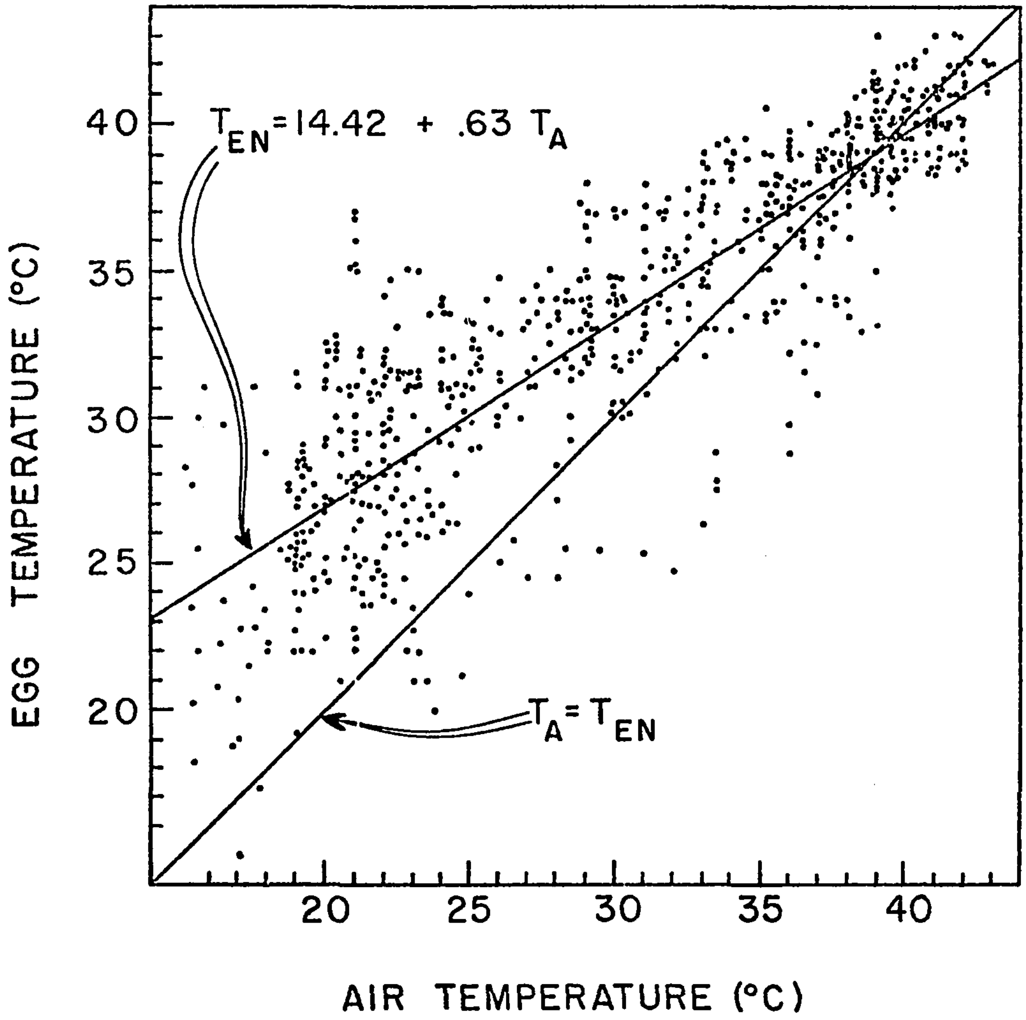

T_A
Several
Meters
T_{BP}
Ten
Teon
To Monitor (up to
100 m)
~2m
Areas in which
T_S is measured

Figure 1



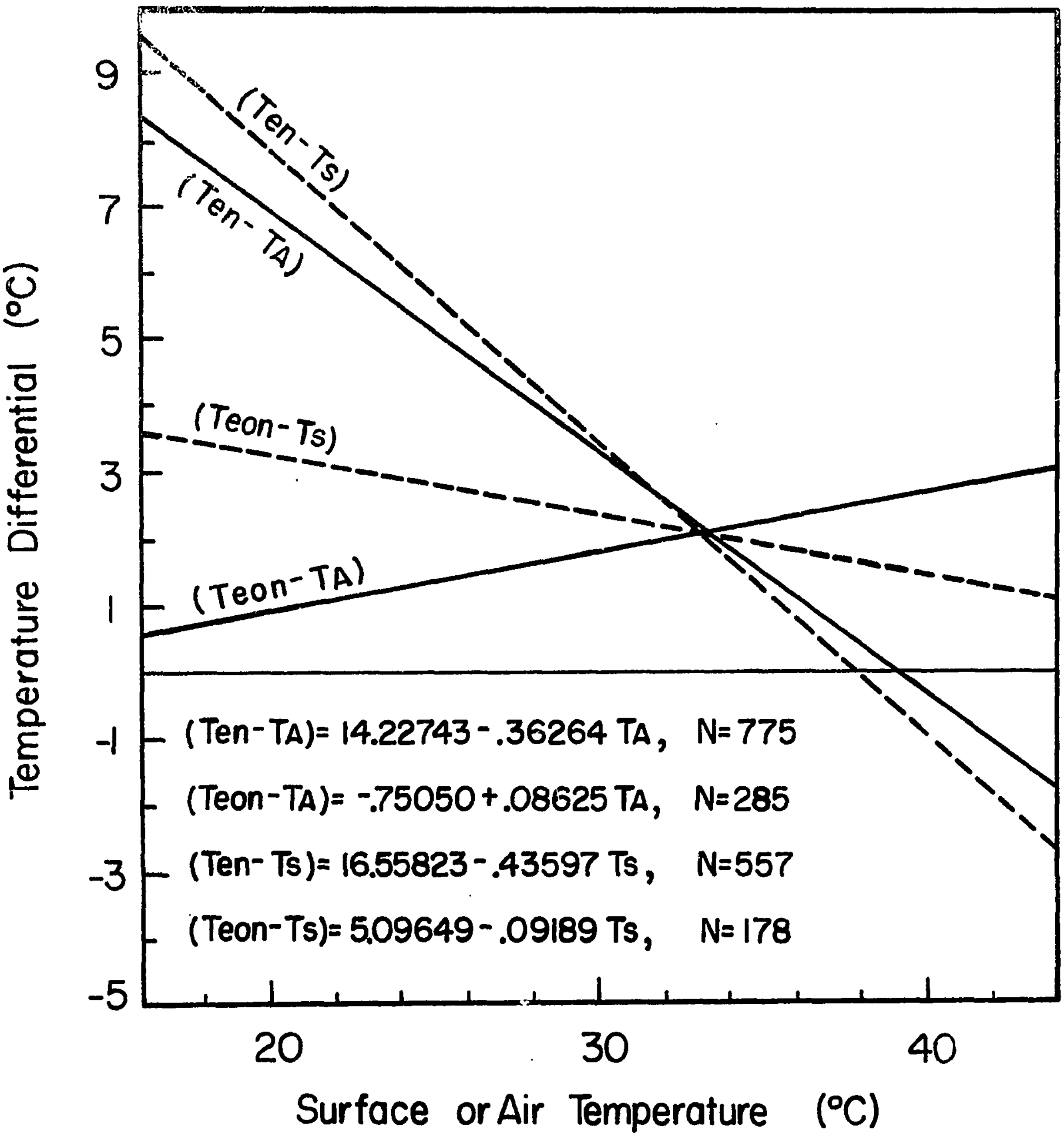
Number of Observations
0
2
4
6
8
10
12
14
16
18
0
01
03
05
07
09
11
13
15
17
19
21
23
Time of Day (Hr)

Figure 2



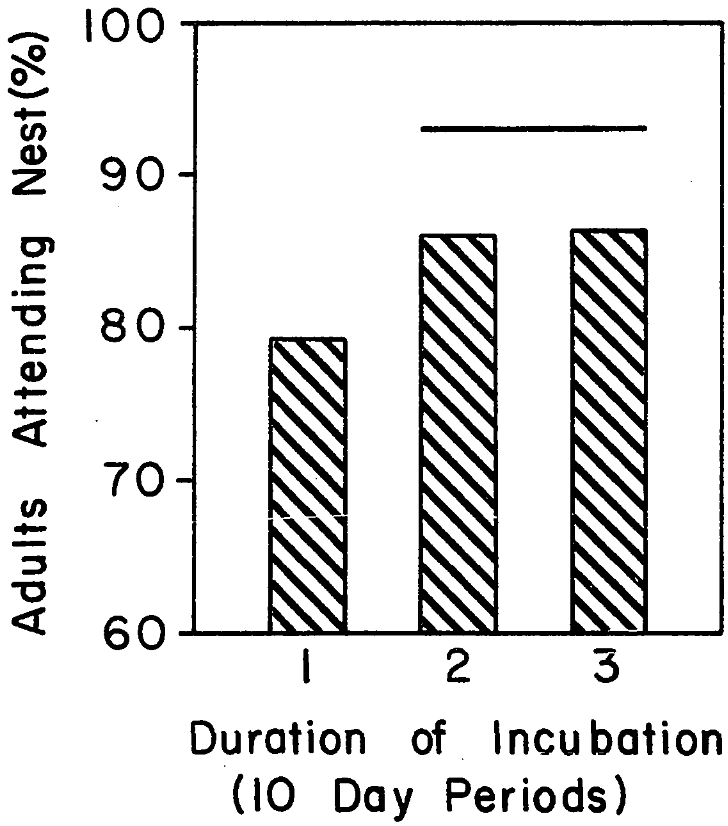
T_{EN}=14.42 + .63 T_A
T_A=T_{EN}
EGG TEMPERATURE (°C)
AIR TEMPERATURE (°C)
20
25
30
35
40

Figure 3



(Ten-Ts)
(Ten-TA)
(Teon-Ts)
(Teon-TA)
9
7
5
3
1
-1
-3
-5
(Ten-TA)= 14.22743 -.36264 TA, N=775
(Teon-TA)= -.75050 + .08625 TA, N=285
(Ten-Ts)= 16.55823 -.43597 Ts, N=557
(Teon-Ts)= 5.09649 -.09189 Ts, N=178
20
30
40
Temperature Differential (°C)
Surface or Air Temperature (°C)

Figure 4



100
90
80
70
60
Adults Attending Nest (%)
1
2
3
Duration of Incubation
(10 Day Periods)

Figure 5

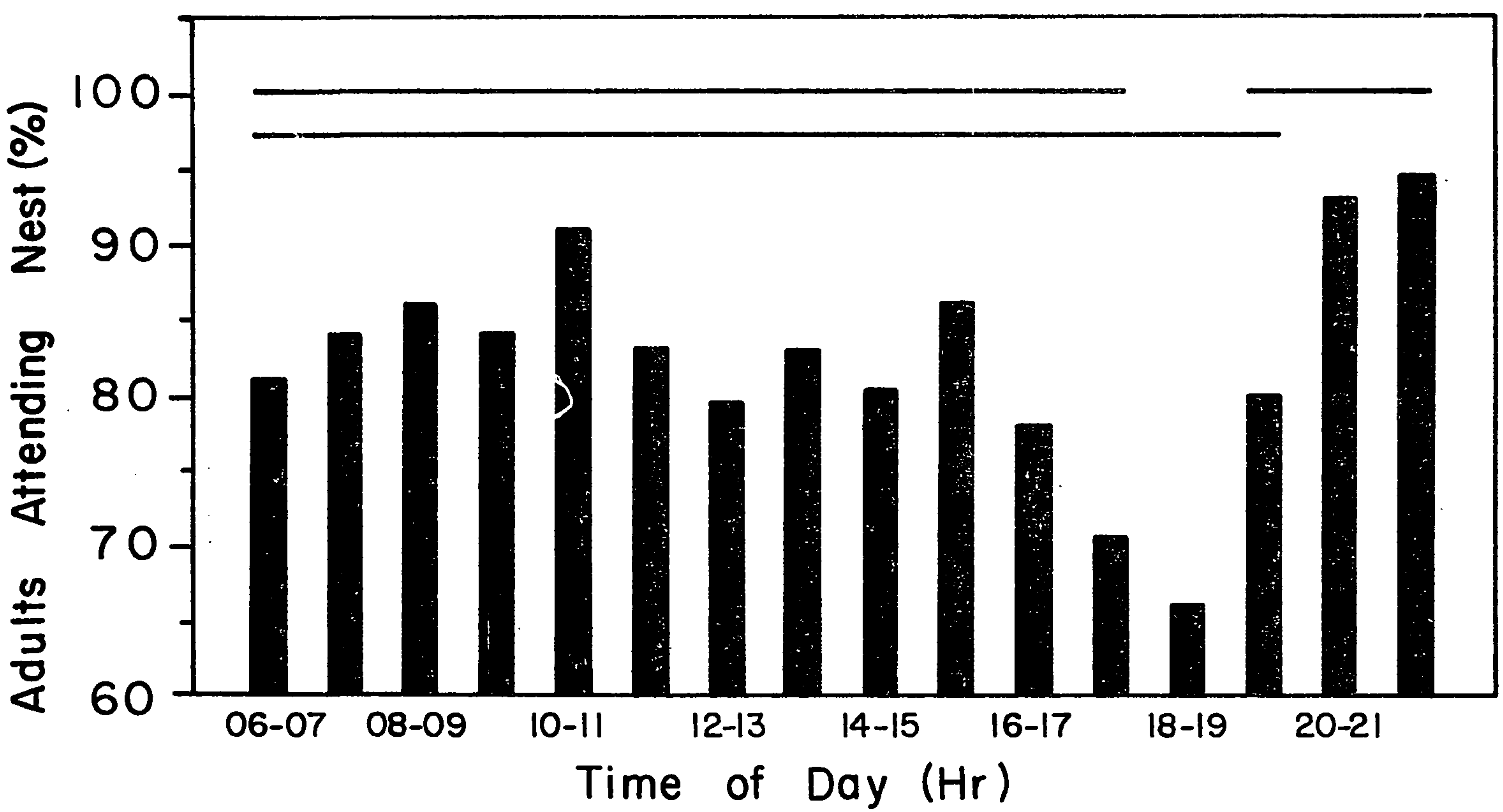

100
90
80
70
60
Adults Attending Nest (%)
06-07
08-09
10-11
12-13
14-15
16-17
18-19
20-21
Time of Day (Hr)

Figure 6

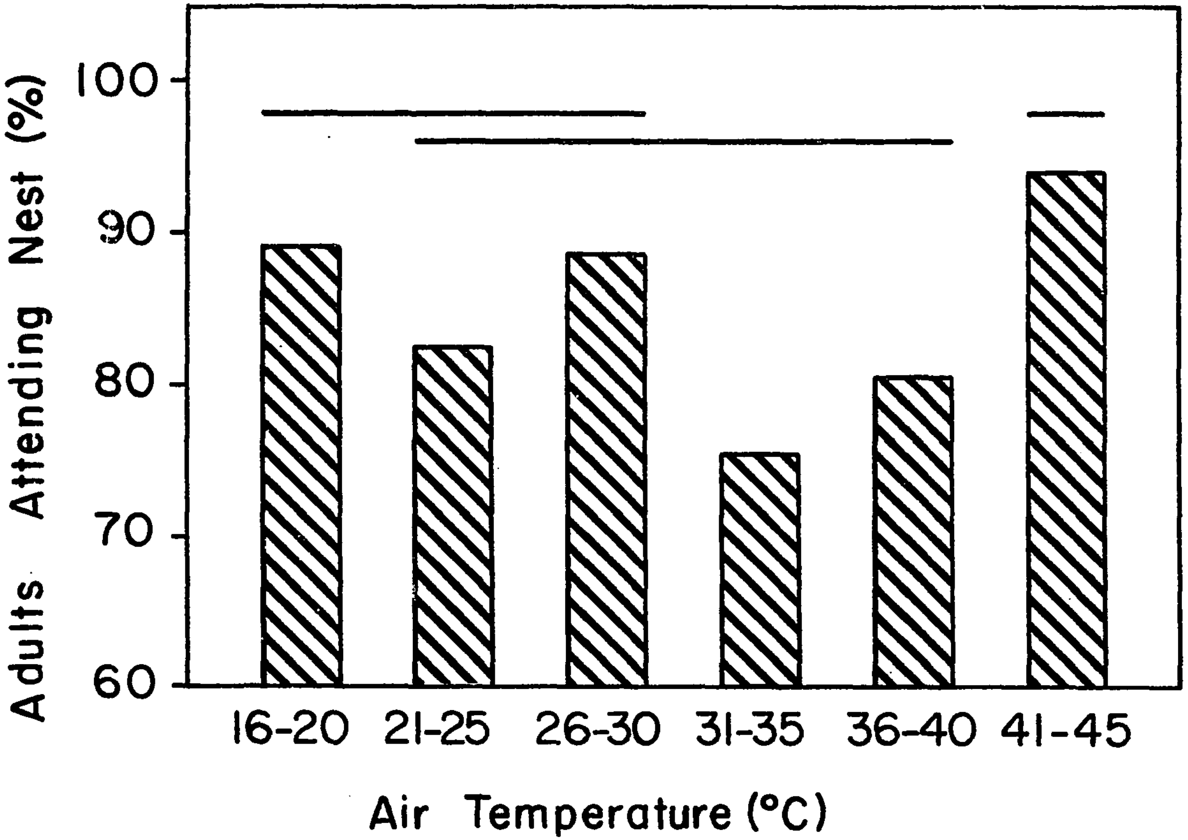

Adults Attending Nest (%)
100
90
80
70
60
16-20
21-25
26-30
31-35
36-40
41-45
Air Temperature (°C)

Figure 7

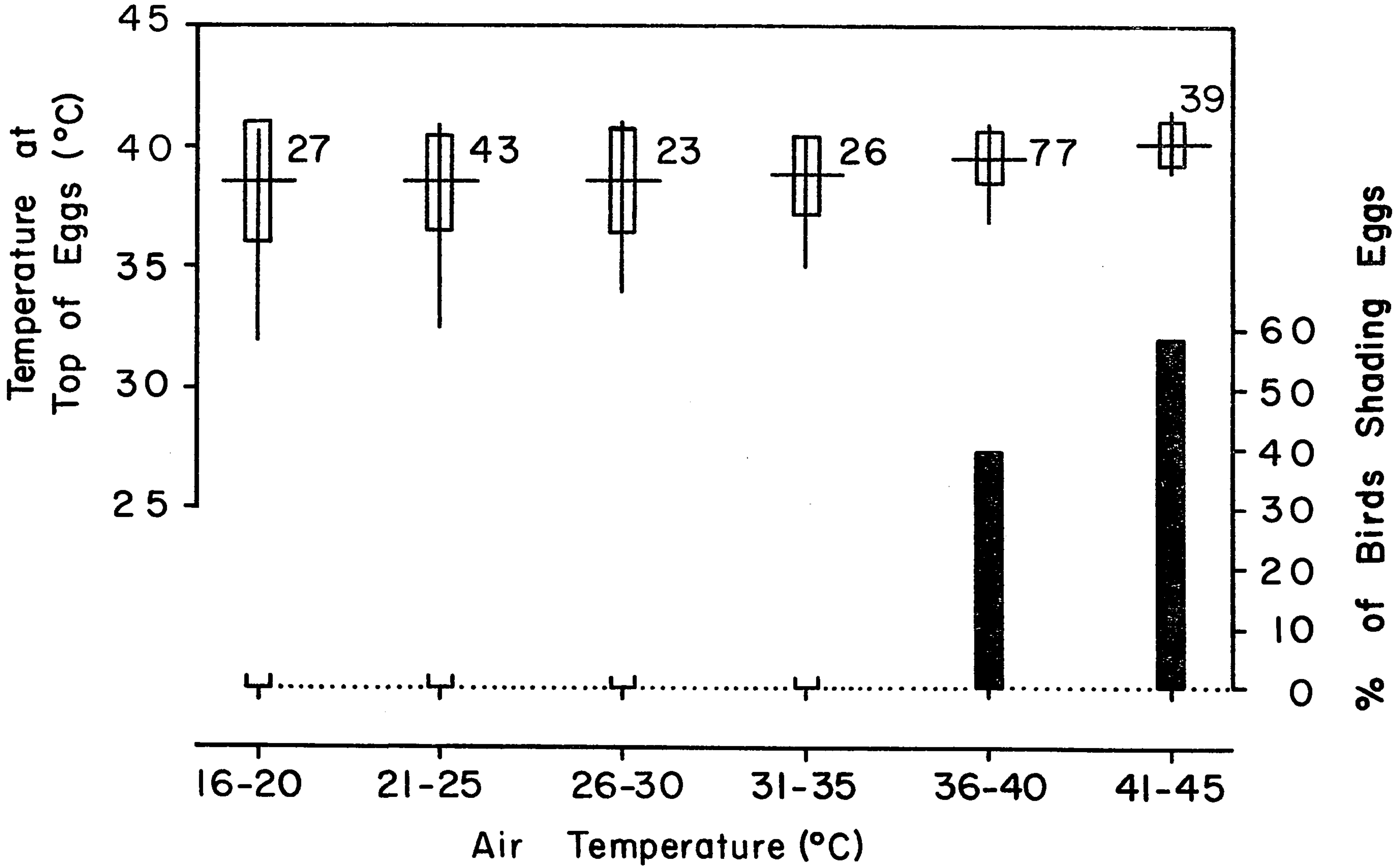

Temperature at
Top of Eggs (°C)
45
40
35
30
25
27
43
23
26
77
39
60
50
40
30
20
10
0
% of Birds Shading Eggs
16-20
21-25
26-30
31-35
36-40
41-45
Air Temperature (°C)

Figure 5

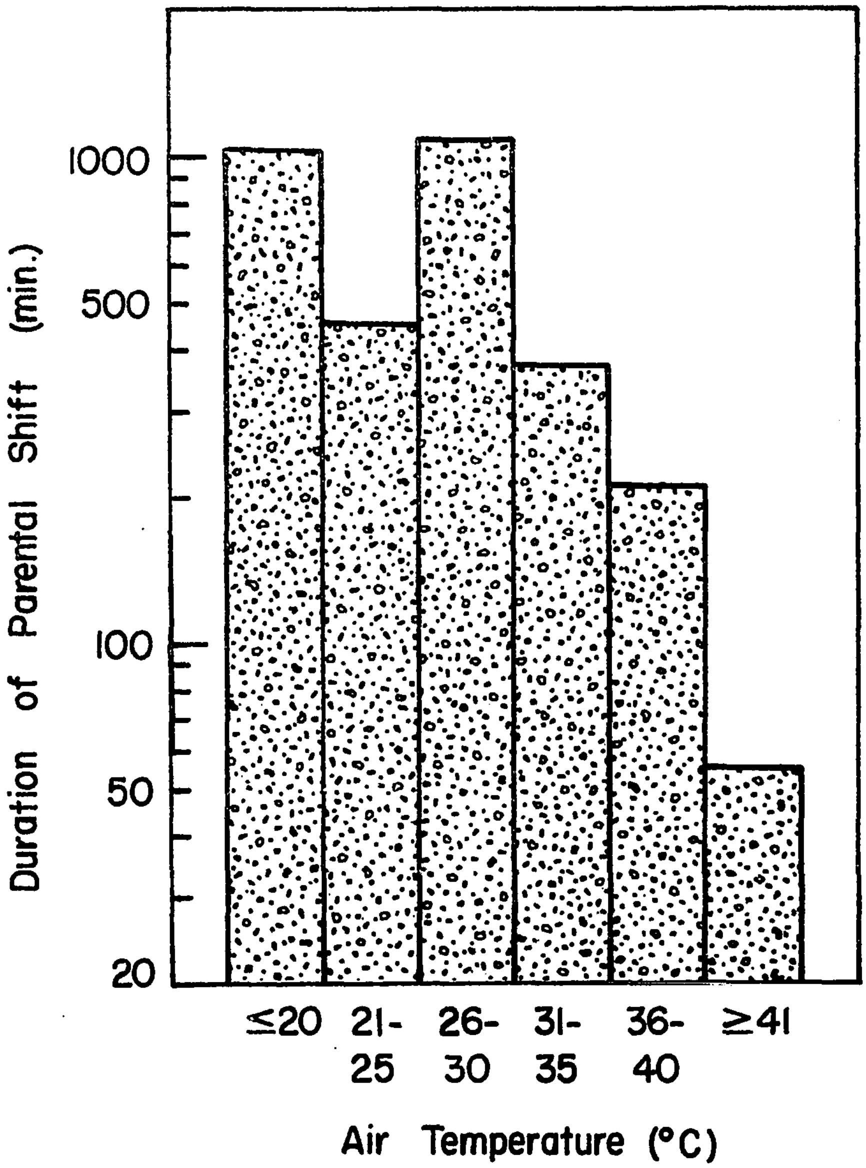
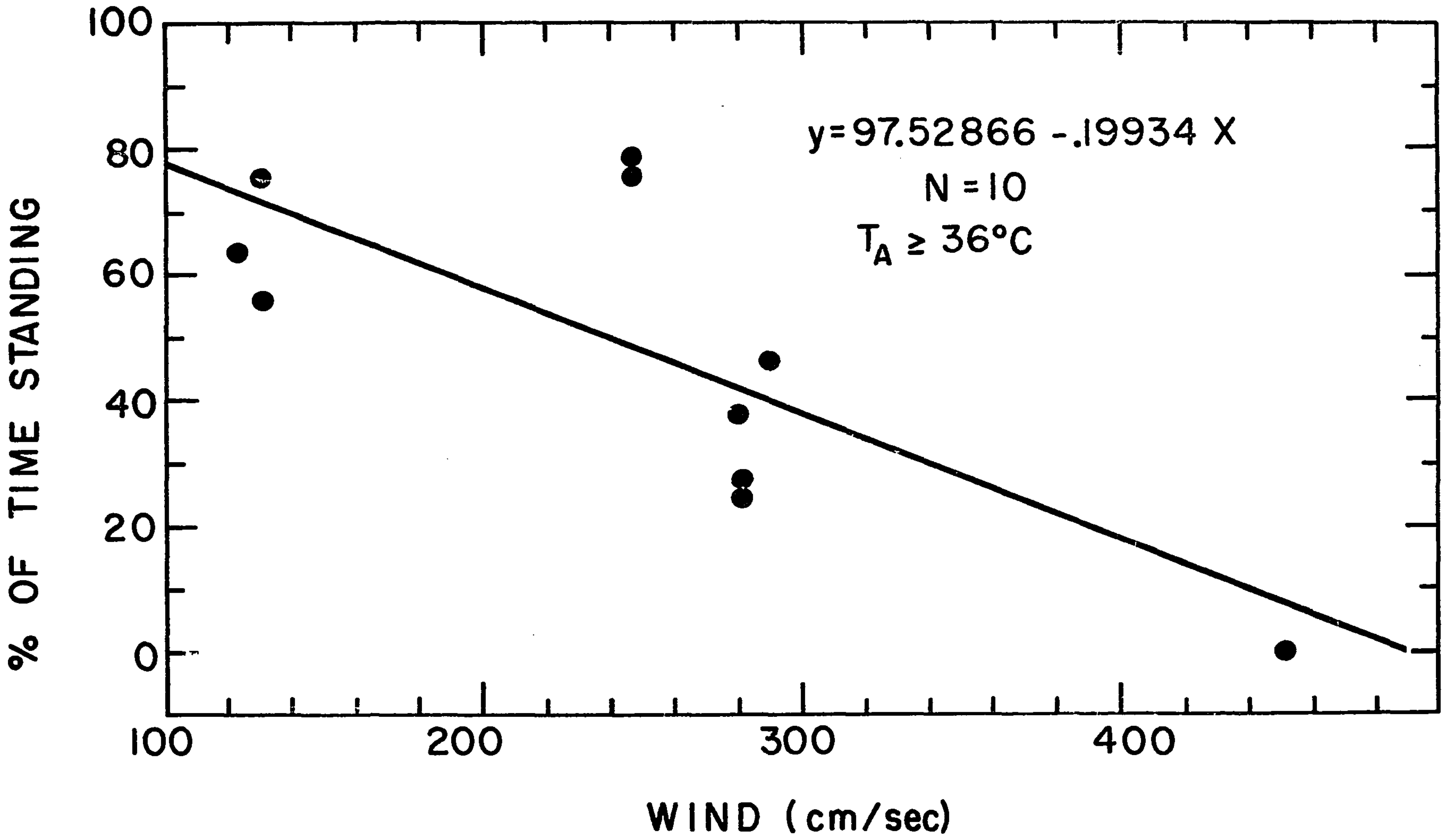

Duration of Parental Shift (min.)
1000
500
100
50
20
≤20
21-25
26-30
31-35
36-40
≥41
Air Temperature (°C)

Figure 9


y=97.52866 -.19934 X
N = 10
$T_A \geq 36°C$
% OF TIME STANDING
WIND (cm/sec)
100
80
60
40
20
0
100
200
300
400
Figure 10