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ECOLOGY OF INCUBATION IN WILSON'S PLOVER
(CHARADRIUS WILSONIUS)

A DISSERTATION SUBMITTED TO
THE FACULTY OF THE DIVISION OF BIOLOGICAL SCIENCES AND THE
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BY

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TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS	ii
LIST OF TABLES	vii
LIST OF ILLUSTRATIONS	viii
INTRODUCTION	1
Chapter	
I. STUDY AREAS AND BREEDING BIOLOGY OTHER THAN INCUBATION	7
Introduction	7
Nesting Habitat and Study Areas	8
Results	13
Territory Establishment	13
Nest Site Selection	15
Nest site location	15
Nest site fidelity	17
Egg Laying	21
Starting Dates	21
Laying Intervals	24
Egg-laying behavior	24
Relaying	25
Eggs	26
Physical description	26
Clutch Size	27
Incubation	28
Start of Incubation	28
Feeding on Fiddler Crabs During Incubation	30
Hatching	32
Incubation Period	32
Events at Hatching	33
Hatching Intervals	33
Hatching Dates	34
Hatching Success	34
Causes of Nest Failure	39
Effect of Rain and Nest Site on Hatching Success	41
Chicks	43
Departure from the nest	43
Brooding	44
Habitat Used by Chicks	45
Fledging success	47
Adoption	48
Weight at Hatching	50
Discussion	50

Nesting Habitat	50
Territory Establishment	50
Nest Site Selection	52
Egg-laying	56
Eggs	59
Incubation	62
Feeding during Incubation	63
Hatching	64
Chicks	71
Summary	73
 II. DIVISION OF LABOR DURING INCUBATION BY PAIRS	79
Introduction and Methods	79
Results	81
Discussion	89
 III. MALE INCUBATION	94
Introduction	94
Methods	94
Results	96
Discussion	102
 IV. FACTORS AFFECTING INCUBATION BEHAVIOR	106
Introduction	106
Data Collection and Reduction	109
Data Analysis	114
Results	116
Regression Analysis of Incubation Behavior	116
Effect of Air Temperature on Incubation Time	116
Other factors affecting Incubation Time	121
Effect of Air Temperature on Mean Absence	122
Other Factors Affecting Mean Absence	125
Effect of Air Temperature on Mean Incubation Bout Length	126
Other Factors Affecting Mean Incubation Bout Length	128
Survivorship Analysis of Incubation Behavior	128
Survivorship Analysis of Incubation Bout Durations	128
Survivorship Analysis of Absence Durations	143
Survivorship Analysis of Parental Shift Lengths	154
Effect of Air Temperature on Shading Time	162
Posture on the nest during Shading	166
Effect of Sun on Orientation on the Nest	166
Discussion	168
Effects on Incubation Time, Incubation Bouts, and Absences	168

Survivorship of Incubation Bouts, Absences, and Parental Shifts	172
Shading Time	175
Solar Orientation of the Incubating Bird . .	175
Conclusions	177
 V. EGG AND NEST TEMPERATURES	180
Introduction	180
Materials and Methods	181
Results	184
Diurnal patterns of T(E), T(N), and T(A) . .	184
Factors Affecting Egg & Nest Temperature . .	206
Factors Affecting Variance in T(N) during the Day	222
Rate of Change in Temperature of Uncovered Eggs	225
Heated Egg Experiment	227
Discussion	231
 VI. CONCLUSIONS AND A THERMOREGULATORY MODEL OF INCUBATION	240
Summary of Factors Affecting Incubation Behavior and Egg and Nest Temperatures	240
Incubation in the Context of the Breeding Season	245
Adaptations of Shorebirds to Nesting in a Hot Environment	249
A Thermoregulatory Model of Incubation	255
Previous models	255
A Proposed Thermoregulatory Model of Incubation	262
Assumptions	263
Conclusions	264
 Appendix	
A. ELAPSED TIMES AND DISTANCES BETWEEN RENESTS . . .	276
B. EGG-LAYING TIMES AND INTERVALS	277
C. HATCHING INTERVALS	278
D. KNOWN AND POTENTIAL EGG PREDATORS IN THE STUDY SITES	279
E. BRIEF DESCRIPTIONS OF WILSON'S PLOVER DISPLAYS .	280
F. FEEDING RATES ON FIDDLER CRABS, 1979	283
BIBLIOGRAPHY	285

LIST OF TABLES

Table	Page
1. Hatching Success Estimates	38
2. Diurnal Division of Labor and Parental Shift Lengths in 1980	83
3. Division of Labor in Territory Defense by Pair 23-79	88
4. Time budgets of pairs and lone male with chicks .	100
5. Transformed Incubation Time Regressions	118
6. Transformed Mean Absence Regressions	123
7. Transformed Mean Incubation Bout Regressions . . .	127
8. Transformed Shading Time Regressions	163
9. Orientation of Incubating Bird Relative to Sun, Pair 21	168
10. Factors Affecting Daytime Mean T(N), 1980	220
11. Factors Affecting C.V. of T(N) during day, 1980 .	223
12. Heated Egg Experiment, 31 May 1981, Pavement Nest	231
13. Factors Affecting Components of Incubation Behavior and Egg and Nest Temperature	242
14. Adaptations of Shorebirds to Incubation in Hot Climates	250

LIST OF ILLUSTRATIONS

Figure	Page
1. Number of nests having vegetation in 8 directions. . .	19
2. Distribution of nest starts in 1979 and 1980.	23
3. Distribution of hatching dates in 1979 and 1980. . . .	36
4. Incubation time in Pairs and Lone Males.	98
5. Quadratic Regression of incubation time on air temperature for Wilson's Plover pairs, 1980.	120
6. Regression of mean absence on air temperature for 1980 pairs.	125
7. Regression of mean incubation bout length on air temperature for 1980 pairs and males.	130
8. Plots of incubation bout survival.	133
9. Survivorship plots of incubation bout duration by sex. .	136
10. Flow Diagram of Incubation Bouts and Absences. . . .	139
11. Survivorship plots of incubation bouts at three temperature ranges.	142
12. Survival of incubation bouts grouped by stage of incubation.	145
13. Survivorship of absence durations.	148
14. Survivorship of absence durations grouped by sex and by type. .	151
15. Survivorship of absence durations grouped by stages of the incubation period.	153
16. Survivorship of absence durations at low, moderate, and high air temperature.	156
17. Survivorship of Parental Shift Durations.	159

18. Survivorship of parental shift durations by sex, temperature and stage of incubation.	161
19. Regression of transformed shading time on air temperature, and shading posture.	165
20. T(E), T(N), & T(A) in Nest on Soil, 29 May 1981. .	187
21. T(E), T(N), & T(A) in Nest on Pavement, 30 May 1981.	190
22. Plot of T(E) vs. T(N) with fitted regression lines.	193
23. Mean T(N) & T(A), Day and Night, during study period in 1980.	196
24. Diurnal patterns of T(N) & T(A) at two nests in 1980.	199
25. Comparison of Night T(N) before and after clutch completion, Nest 18-80.	202
26. T(N) & T(A) for Pair and Single Incubators, 1980.	205
27. Plot of T(E) vs. T(A) with fitted regression lines.	208
28. Plot of T(N) vs. T(A) with fitted regression lines.	211
29. Plot of T(E) vs. time of day for soil nest showing parental behavior.	213
30. Plot of T(E) vs. time of day for pavement nest showing parental behavior.	216
31. Plots of T(N) & T(A) showing nest attendance. . .	219
32. Rate of Change in Temperature of Uncovered Egg vs. T(A).	229
33. Incubation time vs. air temperature for two species.	259
34. Predicted Maximum Absence Length, Minimum Incubation Time, and Metabolic Rate.	267

INTRODUCTION

Incubation in birds is not as simple as it looks. What appears to be a monotonous, undemanding process of sitting on the eggs until they hatch actually involves a complicated interplay of the behavior of the parents, the development of the embryo, and the effect of the environment on both the parents and the eggs. A complete study of the adaptations of this "fundamental adaptive unit" (Bartholomew and Dawson 1979) of parents and eggs must include behavioral, physiological, and ecological data on each of its interrelated members.

Incubation is commonly defined as "the process by which the heat necessary for embryonic development is applied to the egg" (Beer 1964). After studying incubation in a hot climate, I propose a more general definition: the process by which egg temperature is regulated within the limits of embryonic development. The concept of regulation is needed rather than simply warming, because in hot climates successful incubation requires cooling eggs as well as warming them. Indeed, cooling is more critical than warming. Chicken embryos (Lundy 1969) and gull embryos (Bennett et. al 1981) are much more quickly killed by high than low tem-

peratures. Birds incubating in hot climates in exposed nests must alternately warm and cool their eggs, while at the same time regulating their body temperature within permissible limits. At high air temperatures these species must both cool the eggs and themselves. Many species breeding in hot climates practice bisexual incubation, which can reduce the heat load on each parent. Incubation behavior is much more complicated in bisexually incubating birds than in single-sex incubators, because there are patterns of nest relief and division of labor that are absent in single-sex incubators.

This study is an examination of the ecology of incubation in Wilson's Plover (*Charadrius wilsonius*), a monogamous shorebird with bisexual incubation that nests on the ground in hot environments. Thus incubation is more complex than in single-sex incubators, but its study was facilitated by good visibility of nests, simple habitat, and few within and between species interactions in this species. The study of division of labor was greatly facilitated by the sexual dimorphism in plumage that exists in Wilson's Plover. Both body size and egg size in Wilson's Plover are relatively small for shorebirds (65 g and 12 g respectively). This small size results in a relatively low thermal inertia and high surface/volume ratio compared to larger shorebirds, which should result in a large effect of climate on incubation behavior. Data were collected simultaneously on the behavior of the parent at the nest, climatic conditions, and

nest and egg temperatures, making it possible to analyze correlations and effects between the different elements of the "fundamental adaptive unit" of incubation.

Incubation can also only be understood in the context of the breeding season as a whole, since it is only one stage in a process beginning with courtship and ending with fledged young. The amount of energy expended on incubation by each sex must be compared to their energy expenditure on other activities and in other stages of the breeding season. Monogamous birds are generally expected to share the energy expenditure over the breeding season, but since only the female lays eggs, the male must spend more energy than the female on some other activity to balance her expenditure on egg-laying (Trivers 1972). Selection should also favor increasing lifetime reproductive output, so life expectancy and lifetime fecundity must also be taken into account in analyzing any one breeding season. Tropical shorebirds are characterized by reduced clutch size, low nesting success, and long life expectancy (see below), so the energy expended on any one nest may be less important in tropical shorebirds than in shorter-lived arctic or temperate species.

An important feature of this study is that sample sizes, both in terms of the amount of data collected and the number of different breeding pairs studied, are large enough to detect patterns of variability between days, between pairs, and through the breeding season. I collected over 1600 hours of behavioral samples on 29 incubating pairs in the

three years of the study, including data on 11 pairs in 1979, 16 pairs in 1980, and 2 pairs in 1981. Nest and air temperature were recorded concurrently with parental behavior on 36 whole days at 10 nests in 1980, and egg, nest, and air temperatures were recorded with parental behavior for 15 hours at 2 nests in 1981. Some studies of incubation in shorebirds (e.g. Ashkenazie and Safriel 1979) take the approach of studying one or a few incubating pairs exhaustively, assuming that their adaptations are typical of the species. The between-pair variability ignored by this approach not only makes the results less valid, but the variability itself can show the degree of flexibility possible in different aspects of incubation. Those aspects that are the most constrained should vary less between pairs than less constrained aspects. For example, incubation itself must have a very strong selective advantage, because all birds (including Megapodes) regulate egg temperature in some way. At the other extreme, barring any sexual dimorphism in body size or brood patches, in bisexual incubators the parents should be about equally effective as incubators, so the division of labor during incubation could show a great deal of between-pair variability without affecting the regulation of egg temperature. Because the present study includes data on so many different pairs, it is possible to draw conclusions about the relative level of constraints placed on dif-

ferent aspects of incubation, and different aspects do appear to be constrained in varying degrees.

Chapter 1 includes data on the breeding biology of Wilson's Plover outside of incubation itself. Chapter 2 documents the patterns of division of labor by the sexes in 1980, and these were found to vary considerably between pairs. Chapter 3 (published in Auk 98: 835-838) concerns the incubation patterns at four nests at which one parent incubated alone (the male in three cases), showing that the division of labor during incubation is even more flexible than it appeared from the examination of pairs in Chapter 2. Chapter 4 examines the effects of environmental factors on several aspects of incubation behavior. Almost all aspects examined were strongly dependent on air temperature in some way, but differences between pairs were unimportant. Responses to the environment did depend on the number of parents incubating, and in some cases to the type of substrate under the nest. Chapter 5 reports on patterns of nest and egg temperatures in Wilson's Plover, and these patterns also depended on air temperature and substrate under the nest. However, there was no difference in these patterns between pair and single incubators, suggesting that egg temperature is under tighter constraints than patterns of incubation behavior. Chapter 6 contains a summary of factors affecting incubation behavior and egg & nest temperatures, and an evaluation of incubation in Wilson's Plover in the context of the breeding season. It also contains conclusions about

the adaptations that make incubation in a hot climate by Wilson's Plover successful. The main adaptation used by shorebirds nesting at the Salton Sea in California was belly-soaking (Grant 1979), but this was used only rarely by Wilson's Plover. Instead, Wilson's Plover uses a cooling mechanism not seen in shorebirds at Salton Sea, gular flutter. Chapter 6 also includes an extension of the model by Scholander et al. (1950) on body temperature regulation in endotherms to the regulation of egg temperature by parental behavior in birds. The proposed model is more general than the model of incubation by White and Kinney (1974), since it applies to both bisexual and single-sex incubators.

CHAPTER I

STUDY AREAS AND BREEDING BIOLOGY OTHER THAN INCUBATION

Introduction

This chapter contains information about the breeding season as a whole in Wilson's Plover, providing a context into which the more detailed study of incubation will be placed. For many species of birds, including most shorebirds, the material in this chapter is available from published sources. For Wilson's Plover, the only full-length article ever published (Tomkins 1944) is mainly a description of breeding displays, so most of the results in this chapter have never been reported before. The value of this chapter goes beyond providing a context for incubation and filling a gap in the literature on this species, however. Information on the breeding biology of all tropical shorebirds is very sketchy compared to temperate and arctic species, although their breeding biology appears to be very different from that of temperate and arctic species (see below).

The chapter begins with a description of study sites, nesting habitat, and nest sites. The choice of nest site is important in this species, because it has effects on hatching success (this chapter), incubation behavior (Chapter 4), and egg temperatures (Chapter 5). Territory establishment is described, and it is done mostly by the male. Renesting

and nest initiation dates are quantified, and egg size and clutch size. All of these are related to the energy balance of the female and division of labor. The periods of clutch completion (between the laying of the first and last eggs) and hatching (between the hatching of the first and last chicks) are described, and incubation during clutch completion appears to have the consequence of asynchronous hatching in this species. Estimates of hatching success are given, and they are about as low as in most other tropical shorebirds. Activities of the parents and chicks are described, and the tending behavior of this species is discussed. Ways in which the breeding biology of Wilson's Plover differs from that of other plovers are discussed.

Nesting Habitat and Study Areas

Wilson's Plover breeds from Virginia south along the Atlantic and Gulf coasts, and along both coasts of Central and South America as far south as Peru on the west and Brazil on the east (Blake 1979). I studied the breeding of Wilson's Plover at two sites on the coast of Texas, where they are migratory, but many of the more southern populations are resident.

In 1979 the study area was Laguna Atascosa National Wildlife Refuge, Cameron County, Texas. This 45,000 acre wildlife refuge is located on a former delta of the Rio Grande River, about 25 miles (42 km) north of Brownsville. The eastern edge of the refuge is the Laguna Madre, a shallow

body of water about 7 mi (12 km) wide that lies between the mainland and South Padre Island, which is on the Gulf of Mexico. Soils on the refuge are mostly saline, clayey, and poorly drained, and they may be flooded with salt water during hurricanes. Salt may also be blown into the refuge attached to dust during dry years, which occurred in the 1950's, killing many trees. The Gulf of Mexico has very little tide, so there no real tidal flats.

Wilson's Plovers nested on areas of the refuge called "salt flats", sparsely vegetated, low, level areas with a soil classified as "Sejita silty clay loam" (Williams et al. 1977). Salinity of this soil is high (35-70 mmhos/cm), and permeability is low (0.5 - 1.5 cm/hr). The original vegetation of the salt flats was probably 75% Shoregrass, *Monanthochloe littoralis*, and other grasses, including Gulf Cordgrass, *Spartina spartinae*. Under intense grazing pressure, the water table rises as the grasses are removed, a salt crust forms, and the grasses are gradually eliminated and replaced by halophytes (Williams et al. 1977). These halophytes include Sea Ox-eye Daisy (*Borrichia frutescens*), Saltwort (*Batis maritima*), two species of Glasswort (*Salscornia bigelovii* and *S. virginica*), Sea lavender (*Limonium nashii*) and Seepweed (*Suaeda conferta*) (Fleetwood 1967). The perennial Glasswort (*S. virginica*) was more common and was the species found near plover nests, while the annual Glasswort (*S. bigelovii*) tended to grow by itself in otherwise bare areas. The areas where most salt flats were

located, Units 2 & 3 of the refuge, were intentionally overgrazed during the 1950's to produce better goose forage (R. Stratton, pers. comm.). Thus it is likely that overgrazing made the salt flats better habitat for plovers, since they prefer open areas (see below).

A key element of the salt flats as plover habitat appears to be the fiddler crabs, with *Uca subcylindrica*, probably the most common species. Fiddler crabs are very common on the salt flats, with burrows every meter or so, and plover nests are often near several burrows. Many fiddler crabs built a vertical tunnel of soil around the entrance to their burrow, probably to try to keep rain water out, and after heavy rains thousands of fiddler crabs migrated to higher ground. Fiddler crabs are an important part of the diet of Wilson's Plovers (see Appendix F).

Wilson's Plover was studied in 1980 on Matagorda Island, Aransas National Wildlife Refuge, Calhoun County, Texas. This is a barrier island, about 33 mi (55 km) long, located about 115 mi (192 km) southwest of Houston and 46 mi (77 km) northeast of Corpus Christi. The study area was the U. S. Air Force Matagorda Island Bombing and Gunnery Range until it was taken over by the U. S. Fish & Wildlife Service in the early 1970's. Wilson's Plover nested in two habitats on the island, on the gulf beach and on the bay side. No nests were found on the beach, but plovers that appeared to be nesting were seen there several times, and a chick was found with its parents on the upper part of the beach on 17 June.

Wilson's Plovers were more common on the bay side of the island, which is a low area of salt flats and salt marshes on Espiritu Santo Bay. Since it is a barrier island rather than a former delta, the soils at Matagorda Island are much more permeable than at Laguna Atascosa. Most of the salt flats used by Wilson's Plovers on Matagorda Island are on "Haplaquents" soil, which is saline (20-50 mmhos/cm), but relatively permeable (5 - 15 cm/hr) (Mowery and Bower 1978). The salt flats on Matagorda adjoin the bay and are frequently inundated, so they have probably always been dominated by halophytes, rather than losing grass via overgrazing. Shoregrass, Saltwort, Glasswort, Sea Ox-eye Daisy, and Sea Lavender are present as at Laguna Atascosa, but one nest was near Smooth Cordgrass (*Spartina alterniflora*) and Red Mangrove (*Rhizophora mangle*), which are rare or absent at Laguna Atascosa. Fiddler crabs are as common as at Laguna Atascosa, with *Uca panacea* possibly the most common species, but they did not build tunnels or migrate as they did at Laguna Atascosa, probably because there was less flooding.

Three other areas of the Texas coast were examined briefly for Wilson's Plovers during the breeding season. On Mustang Island, which is the second barrier island south of Matagorda Island, public use of the beach is intense and no Wilson's Plovers were seen there. Several Wilson's Plovers were seen feeding on the bay side of the island, which has less public use, and some probably breed there. On North Padre Island, immediately south of Mustang Island, public

use probably also interferes with beach nesting, and the bay side of the island has large barren dunes that had no plovers on them. There might be suitable nesting habitat right at the edge of the Laguna Madre, which was inaccessible. On South Padre Island there was also intense beach use by humans, as well as dune use by three-wheeled motorcycles, and no plovers were seen in these areas. Wilson's Plovers were seen at an isolated clump of small dunes right at the edge of the Laguna Madre, where a group of four adult birds displayed to me, as if there were nests in the area. In general, human use on other parts of the coast seemed to eliminate the beach nesting I saw on Matagorda, but the nesting on the less-used bay side and on the mainland probably occurs at other places on the coast.

Other authors have reported mainly beach nesting by Wilson's Plover. In Georgia, this species is reported to nest in sand dunes and in open areas of sandy islands (Tomkins 1944). In Texas, they are reported to nest in "broad open sand flats . . . and low spaces between dunes within sound of the surf" (Oberholser 1974). Howell (1930) reports nests are made in Florida "in sand or in a shell heap on the higher part of the beach." Bent (1929) reported some nests found in "higher portions of beaches" on "dry, sandy plains," and also on a shell bank near mangrove seedlings. One report of use of a salt flat habitat is from Merritts Island, Florida, where nests were found in Glasswort and

Saltwort clumps around water holes (Bent 1929).

Other bird species breeding in the same habitat in both study areas include the Least Tern (*Sterna albifrons*), Willet (*Catoptrophorus semipalmatus*), American Avocet (*Recurvirostra americana*), Black-necked Stilt (*Himantopus mexicanus*), Common Nighthawk (*Chordeiles minor*), and (rarely) Snowy Plover (*Charadrius alexandrinus*). Killdeer (*C. vociferus*), Horned Lark (*Eremophila alpestris*), and Eastern Meadowlarks (*Sturnella magna*) bred nearby in drier, grassier habitats.

Results

Territory Establishment

I first arrived at Laguna Atascosa on 11 April and at Matagorda Island on 17 April. It is possible that many territories had already been established by this time, and in fact nesting had begun at both sites by those dates (see below). However, most pairs seemed to be in the process of establishing territories. Territorial chases were common, and parallel walks (see Appendix E) were seen on Matagorda on 17 and 18 April, indicating boundaries were being established.

Territorial fights involved long chases flying a few meters above the ground, which made it difficult to determine territorial boundaries. Some idea of territory size can be inferred from the distance between the closest simultaneous nests. The closest such nests were Nests 9-80 and

10-80, which were 35.5 m apart on a salt flat, but they were partially separated by a slight rise. Nests 17-80 and 26-80 were 39.3 m apart, but on opposite sides of a road, and Nests 18-79 and 20-79 were 64 m apart along a road. At Nest 15-79 the male defended the nest as far as 88 m from the nest along a road. The road nesting at Laguna Atascosa, and to some extent the runway nesting at Matagorda, produced long, narrow territories that mainly included the road or runway. Thus the distance defended along the road could not be used as the radius of a circular territory. This may also explain why road and runway nests tended to be so far apart (300 m or more). If the territory is essentially two-dimensional it is much longer than a circular territory of the same area.

Most territorial fights were between males, but fights between neighboring territory holders were rare. Most fights appeared to be between a territory holder and an intruder. The parallel walk, which is most likely to occur in a balanced encounter between two neighbors, was only seen at the beginning of the breeding season, and at the end when mobile territories were defended around chicks. During most of the breeding season neighbors appeared to either respect each other's territorial boundaries, or to tolerate intrusions by neighbors. The female, who was most often on the nest in the middle of the day, did not always leave the nest to chase intruders, but the male might chase them if he were in the area.

Nest Site Selection

Nest site location

Nest site location showed consistent patterns at each study site, but the patterns were slightly different at the two study sites. The main pattern was to nest in a fairly open area, but next to at least one clump of vegetation. Only 1/58 nests found in the two years had no plant stems within 0.5 m of the nest cup, while 4 nests had only tiny stems near the nest (about 1 cm tall). The other 53 nests all had plants near the nest, and some were almost encircled by plants, although there was always one clear approach.

At Laguna Atascosa there was a strong tendency to nest on roads. In the salt flats, the roads were elevated about 1 m to keep them from flooding, and were made of either crushed shell, caleche (a white porous rock), or river gravel. There was usually vegetation both in the center strip of the road and at both edges of the road, and this is where the nests were found, but not where this vegetation was dense. There were 21/29 nests found on roads, and of the 8 nests found off roads, 7 were within 10 m of a road (mean 4.5 m), and 1 was 33 m from a road (Nest 25-79). This sample is probably biased because roads were used to look for nests. When attempts were made to find nests away from roads, including attempts using a blind, no other nests were found. Many of the salt flats were under water several times during the breeding season, so most if not all nests there would

have been flooded. Of the 21 nests on roads, 9 were on gravel, and 12 on other types of roads.

On Matagorda Island, the tendency to nest on man-made substrates was less pronounced than at Laguna Atascosa, but it was still present. There were also 29 nests found, and 13 were on concrete or asphalt pavement used by the Air Force as runways and aprons. There were roads similar to those at Laguna Atascosa, but only 1 nest (17-80) was found next to a road, in gravel. The abandoned runways and aprons had very little human use, and the plovers nested in sections where grass and weeds were growing through cracks in the pavement. The runways with the most grass and the least grass had only 1 nest each, and the other pavement nests were either on the apron (3 nests) or on the 2 runways with intermediate amounts of vegetation.

There were 15 nests on soil on Matagorda, but only 4 were within 12 m of a road (mean 9.0 m), and the rest were 20 - 108 m from the nearest road. Thus 52% of the nests at Matagorda were off roads, compared to only 28% at Laguna Atascosa. This suggests that the predominance of road nesting at Laguna Atascosa is an unusual occurrence brought about by flooding, since vast amounts of pavement were available at Matagorda, yet it was used for less than half of the nests.

The most common nest site on soil at both study areas was at the edge of a bare salt flat, in a clump of halophytic vegetation. A nest was often near more than one species of plant. The most common species near nests was Glasswort (9

nests 1979, 7 nests 1980), followed closely by Shoregrass (7 nests 1979, 8 nests 1980), Saltwort (11 nests 1979, 4 nests 1980), and less often Seepweed (5 nests 1979, 2 nests 1980) and Sea Ox-eye Daisy (2 nests 1979, 3 nests 1980). The location of the vegetation relative to the nest and to compass direction was recorded in 1980 for all nests, and the number of nests with vegetation in 8 compass directions is shown in Figure 1. The distribution of vegetation around the nests differed significantly from random ($Q = 17.3$, d.f. = 7, $P < 0.02$). There is a predominance of nests with vegetation on the south and southwest sides, which is where both the sun and the wind tend to come from on Matagorda Island.

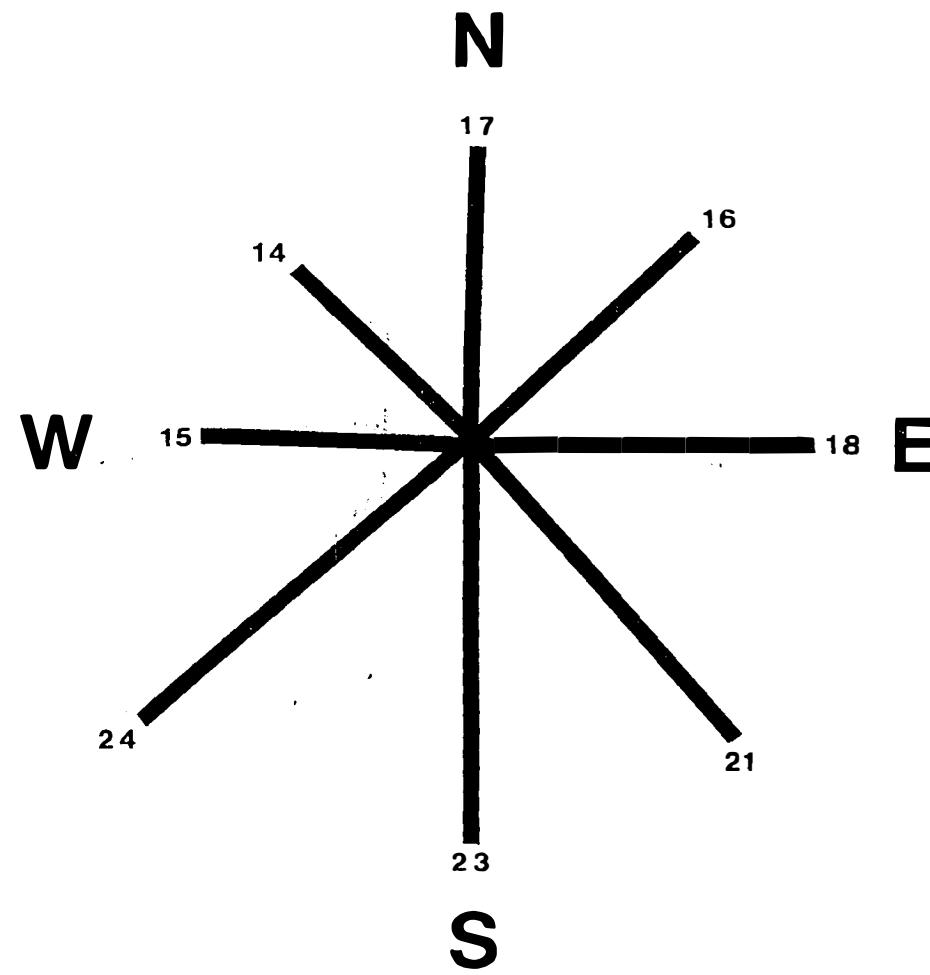
Nests did not tend to be particularly close to open water, although no nest was more than 0.5 km from it. Parents used open (fresh) water for drinking and bathing, but it did not appear to be necessary next to the nest. The risk of flooding might account for this, especially at Laguna Atascosa. Matagorda Island was narrow enough (1.5 mi, 2.5 km) that birds could fly to either the gulf or the bay very easily. Consequences of this distance from water will be discussed in Chapter 6.

Nest site fidelity

There are two types of nest site fidelity, between renests in the same breeding season and between two or more breeding seasons. Of the first type, there were 2 definite renests in 1979 and 6 in 1980, and all were located in the

FIGURE 1: Number of nests having vegetation in 8 directions.

The number of nests with vegetation near the nest in each of 8 compass directions is shown for the 29 nests found in 1980. The distribution differs significantly from random ($Q = 17.3$, d.f. = 7, $P < 0.02$).



same habitat type as the first nest. Distances from the first to the second nest are given in Appendix A, and the mean was 54.7 m, or 40.0 m without one long distance. This is close enough to be essentially within the same breeding territory. When the pair from Nest 9-80 chose a spot for a renest, Nest 25-80, it was farther from the nearest neighbor, Nest 10-80, than Nest 9-80 had been.

In the second type of nest site fidelity, there were 2 nests found at Matagorda in 1981 that involved birds banded in 1980. A nest was found near 5-80 that was attended by male 5-80 and a new mate. She did not resemble female 5-80 without bands, since female 5-80 had a very dark breast band and she was very pale. The 1981 nest was 40.6 m from Nest 5-80, on the same strip of salt flat next to a road, under a similar clump of vegetation. This was the soil nest used for egg temperature measurement (see Chapter 5). Nest 5-80 hatched successfully. A nest was also found in 1981 attended by both members of pair 6-80, which had been a successful nest on soil next to a clump of Smooth Cordgrass, but the chicks may have been lost to flooding right after hatching. In 1981, the pair moved 303 m to a clump of grass on one of the runways, a completely different substrate. This was the pavement nest used for egg temeprature measurement (see Chapter 5). The nest was well-sheltered compared to many runway nests. The birds had lost some of their

color bands, so I put a trap on the nest to check band numbers, and both members of the pair entered the trap. This never occurred in 1979 or 1980. Pair 2-80 was still together in 1981, and appeared to be nesting or to have chicks near the sites of Nests 2-80 and 26-80, but no nests or chicks were found.

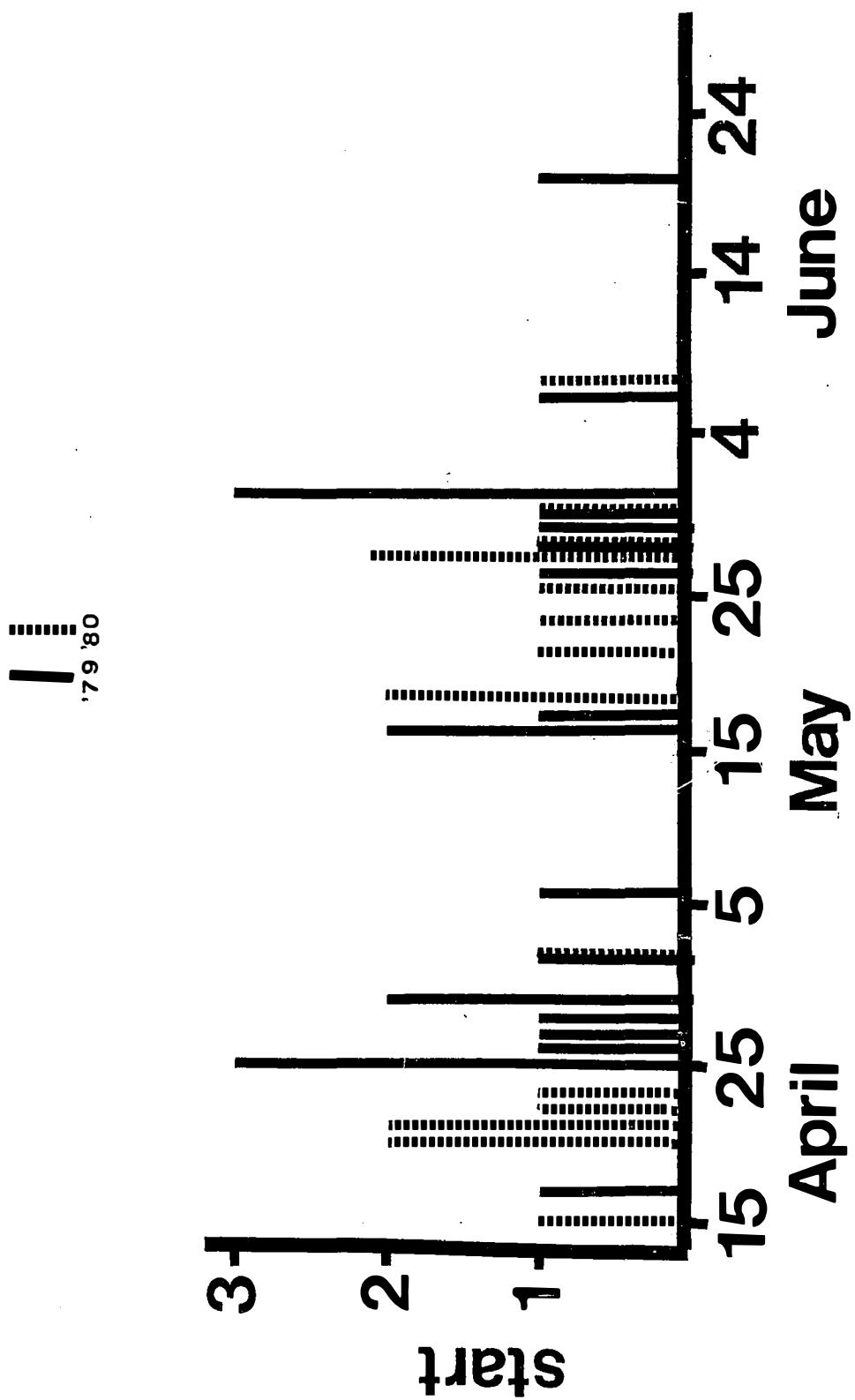
Egg Laying

Starting Dates

The distribution of nest initiation dates in the two years of the study are shown in Figure 2. The earliest start in the nests I found was 15 April (Nest 2-80 by back-dating), and the latest start was 19 June (Nest 29-79). However, a young chick was found on 1 May 1979, so there must have been a nest started by at least 1 April, before I arrived in the study area. A chick was also seen in another area on 10 May 1979, so at least 2 such early nests were successful. In 1980, chicks were not seen until those from Nest 2-80 were found on 13 May, so either breeding did not start before 15 April, or no chicks were produced that I saw. One Killdeer chick was found on 6 May.

In 1979, there were peaks of egg-laying between 25-29 April and 26-31 May, about a month apart, and in 1980 there were similar peaks a few days earlier, 21-23 April and 18-30 May. The spacing of one month suggests that many of the

FIGURE 2: Distribution of nest starts in 1979 and 1980.



later nests were renests after the first nest failed (see below).

Laying Intervals

Data on laying intervals are available for 7 nests, and are shown in Appendix B. The underlined times are exact (from movies) and the others are estimates based on nest checks. Time to lay the complete clutch of 3 eggs averaged 119.4 hr at 5 nests, with roughly equal intervals of about 50-60 hr between eggs, for a total of almost exactly 5 days to lay the clutch.

Laying intervals in Wilson's Plover are given by Bent (1929) as "a day often intervened between the laying of eggs, once an interval of two days occurred and in one nest the third egg was laid on the ninth day after the first." Thus the last egg is usually laid on the fifth day, or 4 days after the first egg, but this is obviously approximate.

Egg-laying behavior

Egg-laying was only observed once, at Nest 1-80. The pair had been scrape-making 17 and 18 April, and on 20 April they were scrape-making, did a scrape-exchange, and a precopulatory display (without copulation) (see Appendix E). The female's belly was visibly swollen. On 21 April the female worked on the scrape (which was in pavement), tossed bits of nest material over her shoulder, then the male scraped, then the female returned and the male did part of the scrape exchange. Shortly after she came to the nest she crouched

over the scrape, her tail quivered, her vent enlarged, and the egg popped out at 1136. She poked it with her bill, crouched over it, and at 1138 she stood up, tossed some nesting material, and then settled on the egg. Then it was left in the sun for a few minutes (to dry?) and the female rolled it under her with her at 1143. She left the nest for 30 sec at 1150, the male came at 1151, and a scrape exchange and precopulatory sequence followed, which the female ended by going to the nest at 1159. The male sat and stood over the egg for brief periods between 1222 and 1400, interspersing that with tossing nest materials over his shoulder. The laying of the third egg in Nest 18-80 was not observed directly, but time-lapse samples were made of the nest, and the female had been at the nest (with 4 brief absences) for 54 min before the egg was laid at 1626. Before that the male had been incubating on and off since the movie began, at 0735 that morning.

Relying

Days between starts, and between failure and start, are shown in Appendix A for 8 renests. The mean time between starts was 31 days, which is the same as the time between peaks in nest starts (Figure 2). Thus the gap in nest starts probably represents the time when nesting birds were either incubating their first clutch, or not yet ready to lay their second. The time from nest failure to the start of a new nest was at least 5 days, and up to 13 days, with

one figure of 49 days (which could have included another nesting attempt). Nest 2-80 was a special case, since its first nest was successful, and it is discussed below under adoption.

Eggs

Physical description

I measured 75 eggs in 1980, and they averaged 35.21(1.22) x 25.84(0.50) mm, with standard deviations in parentheses. Extremes were 38.30 x 25.30 mm, 34.40 x 26.80 mm, 32.25 x 26.00 mm, and 35.40 x 24.65 mm. Egg length, with a coefficient of variation of 3.45%, was almost twice as variable as breadth (CV = 1.95%). Length and breadth were not closely related (covariance = -0.09, correlation = -0.15). Mean weight of 14 eggs was 12.01 g, and all but 3 were weighed in the first half of incubation.

Bent (1929) gave averages for 66 Wilson's Plover eggs, and they were 35.7 x 26.2 mm, which is slightly higher than my sample. Extremes of 38.5/31.5 in length and 27/25 mm in breadth are similar to my sample. Schoenwetter (1967) gives 12.4 g for egg weight in Wilson's Plover.

There was no consistent pattern in the volume of first and second clutches. Using the formula of volume = length x (breadth)² from Schoenwetter (1967), without a constant since I am comparing within a species, second clutches had 111.4%, 104.2%, 99.6%, and 99.2% of the volume of first

clutches in the four cases in which it was measured. Laying order was only known at a few nests in 1980, and at Nest 1-80, the later eggs were shorter and had less volume than the first (37.40×26.10 , 35.35×26.55 , 35.20×26.45 mm). The third egg in Nest 18-80 was longer than the others, but it was narrower, so it had less volume. In Nest 23-80, the second egg was both longer and more voluminous than the first, and in Nest 28-80 the second egg was shorter but more voluminous than the first. Thus there is no consistent pattern in egg size with laying order in this sample.

Clutch Size

Complete clutch size was 4 at 1 nest, 3 at 45 nests, and 2 at 5 nests (mean 2.92). Most of the clutches of 2 were late in the breeding season, starting between 30 May and 7 June. However, since only 1 of the nests with 2 eggs hatched (Nest 28-80), some of them may have been deserted before clutch completion, or had lost an egg before I found the nest.

Clutch size appears to be the same in this species in other areas. Bent (1929) reports it as "ordinarily three eggs, often only two, and very rarely four." Howell (1930) reported clutch size in Florida as "usually 3 or 4, rarely 5," but no one else has reported a clutch of 5. The commonest description is "eggs 2-4, usually 3" (Oberholser 1974).

Incubation

Environmental factors affecting total incubation time are analyzed in Chapter 4, and nest and egg temperatures are analyzed in Chapter 5. Division of labor during incubation is discussed in Chapter 2. This section concerns the periods of clutch completion and hatching, and feeding during incubation.

Start of Incubation

Most precocial birds are not reported to incubate before the clutch is complete, but this depends on the definition of incubation. It is often qualified as 'effective' or 'regular' incubation, meaning incubation that actually warms the eggs, or that has a regular pattern. Another sense is that of applying enough heat to begin development of the eggs, the result of which is observed in asynchronous hatching. In Texas, environmental heat would be sufficient to begin development of an unattended egg, and possibly to kill the embryo from overheating. Thus it is more biologically important to determine how much incubation, in the sense of temperature regulation, occurs during clutch completion, even though it may not be 'effective' or 'regular'.

After the first egg was laid in Nest 1-80, the male crouched over the egg for 1 - 5 min periods interspersed with nest construction and absences for the next 2 hr. He was on the egg only about 30 - 40% of this period. Between 22 and 25 hr after the egg was laid, on the morning of the

next day, he was on the egg 19% of the time, almost all of it standing, without incubation by the female. No bird was at the nest at 1445 that day, and the male came to the nest at sunset for about 20 min, with frequent egg-rolling, but then he left again. The following morning, the second egg was in the nest. Between 0851 and 1231, incubation was more regular, with male/female incubation time of 42%/19%, with longer bouts by the male (up to 32 min) and only 3 min of standing over the egg. Between 1731 and 2100 that day, male/female incubation was 66%/2%, and the following day, male/female incubation was 36%/14% for the whole day, with 2 eggs all day. This low total of 50% was erratically distributed, with highest totals in the morning (57%) and afternoon (83%, all male), and lowest at midday (36%) and evening (27%). The birds may have been warming the eggs in the morning, since they were probably not incubated overnight, and keeping them from overheating in the afternoon, when temperatures peak. Incubation is clearly not 'regular' when there are 1 or 2 eggs.

At Nest 18-80, attendance and nest temperature records began when there were 2 eggs, and the third egg was laid on the first afternoon of the sample. There was little warming of eggs on the previous night (Ch. 5), and the male incubated alone 30% of the morning and 76% of the midday periods before the third egg was laid in the afternoon. The next day there was a fairly regular incubation pattern, with male/female incubation times of 24%/46% in the morning,

0%/97% at midday, 58%/30% in the afternoon, and 64%/0% in the evening.

Thus incubation becomes regular in Wilson's Plover at clutch completion, but the eggs appear to require some temperature regulation prior to clutch completion. Standing over the eggs at midday might not only keep them from overheating, but also slow their development.

Feeding on Fiddler Crabs During Incubation

At several nests in 1979, parents were observed to feed on fiddler crabs near their nests, especially at Nest 23-79. Although this probably did not constitute all of their feeding time, since they could also feed away from the nest, fiddler crabs are large prey and could be a significant food source. I counted the number of crabs caught when this was visible, and the results are shown in Appendix F. All samples in which more than one crab was caught are shown, and there were only a few samples when one crab was caught. When crabs were available several were usually caught. The area around Nest 23-79 was particularly good for catching fiddler crabs: on one day, 14 June 1979, Pair 23-79 caught a total of 8 crabs, an unbanded pair caught 13 crabs, and a Willet family was also catching crabs in the same area. This was an island of salt flat habitat created by a spillway cut, surrounded by grassland. This may have concentrated both the crabs and the birds that catch them on the small area of salt flat.

Wilson's Plovers catch fiddler crabs using a feeding technique that I never saw used by the other shorebirds feeding on them (Black-bellied Plover, Long-billed Curlew, Willet). The Wilson's Plover stands very still looking for a crab to catch, cocking its head so that one of its eyes can see the crab directly. It runs at the crab very rapidly, with its head still cocked. It catches the crab by a leg with its bill, and the plover shakes its head from side to side. This causes the crab's body to break off from the leg in the bird's bill. The bird swallows or drops the detached leg or claw, picks up the crab by another leg, and repeats this process until the crab is a legless carapace. Then the carapace is swallowed whole. The plover must judge as it is handling the crab whether it will be able to swallow it, and some birds must overestimate their swallowing ability. I found fiddler crab carapaces on the ground with all legs removed, probably the result of a plover that processed a carapace it could not swallow. The plover probably regurgitates the shell later, but I never saw this.

The feeding rates in Appendix F, especially those for the lone males (26-79 and 29-79), must approach the maximum possible rate for this species. Handling time is considerable, a minute or more to eat one crab. The lone males, especially 26-79, were very efficient feeders, catching many crabs in very little time. Male 26-79 did this by flying to an area about 50 m from the nest, a section of road with a

white shell surface. The crabs may be easier to see on a light background, because he always caught one or more crabs on these brief trips before he returned to the nest. Using this technique he caught 8 crabs one day and 12 crabs another day, which could be most of the food he would need that day.

I did not analyze the energetic content of the crabs, but analyses of fiddler crabs of similar size are available (Cammen et al. 1980). The crabs that I caught were all *Uca subcylindrica*, and I estimate that one of them could contain more than 3.6 KCal or 15 KJ of energy. Even if only a fraction of that is utilized, that is quite a bit of energy for a bird weighing 60 g. Semipalmated sandpipers (about 30 g) need about 150 - 200 KJ a day during incubation (Ashkenazie and Safriel 1979).

Hatching

Incubation Period

At Nest 18-80, the third egg was laid at 1626 on 30 May, and the last egg hatched at 1942 on 24 June, which was 25 days 3 hr later. Incubation periods were determined less accurately at other nests: 25-27 days at 29-79, >25 days 0 hr at 12-79, >23 days 10 hr at 26-79, >24 days 4 hr at 19-80, and 24 - 26 days at 10-79. The incubation period in Wilson's Plover is given by Bent (1929) as 24 - 25 days.

Events at Hatching

Starring or cracking was not looked for before hatching. One egg in Nest 2-80 felt cracked on the evening of 11 May, and the chicks hatched the next day. Pipping was noted 2 hr before hatching in one egg in Nest 26-79. Several chicks were found halfway out of eggs, with the large end of the shell gone. The parents appeared to be very prompt in removing the shells from the nest. The parent always flew with the piece of shell and dropped it far from the nest. Parents usually tried to remove any foreign object from the vicinity of the eggs, so this is probably not a specialized response to hatching eggs.

Hatching Intervals

Hatching intervals were determined at 7 nests, and are shown in Appendix C. Two nests, 10-79 and 29-79, hatched three chicks in less than 19 hr, and 2 chicks hatched in Nest 17-80 only 4.5 hr apart. The other nests had an interval of about 24 hr between 2 chicks, and either a shorter interval between the other 2 chicks, or no third chick. The long interval was not always in the same position, however.

In the nests in which the third egg failed to hatch, the parents usually incubated for another day before they deserted it. At Nest 17-80, time-lapse samples showed that regular incubation continued 24 hr after the second chick hatched, and there was a parent on the nest 24 and 48 hr after the second chick hatched in Nest 3-79. The last egg

in Nest 13-80 was cool when checked 16 hr after the second chick was found, but the chick could have hatched up to 13 hr before I found it.

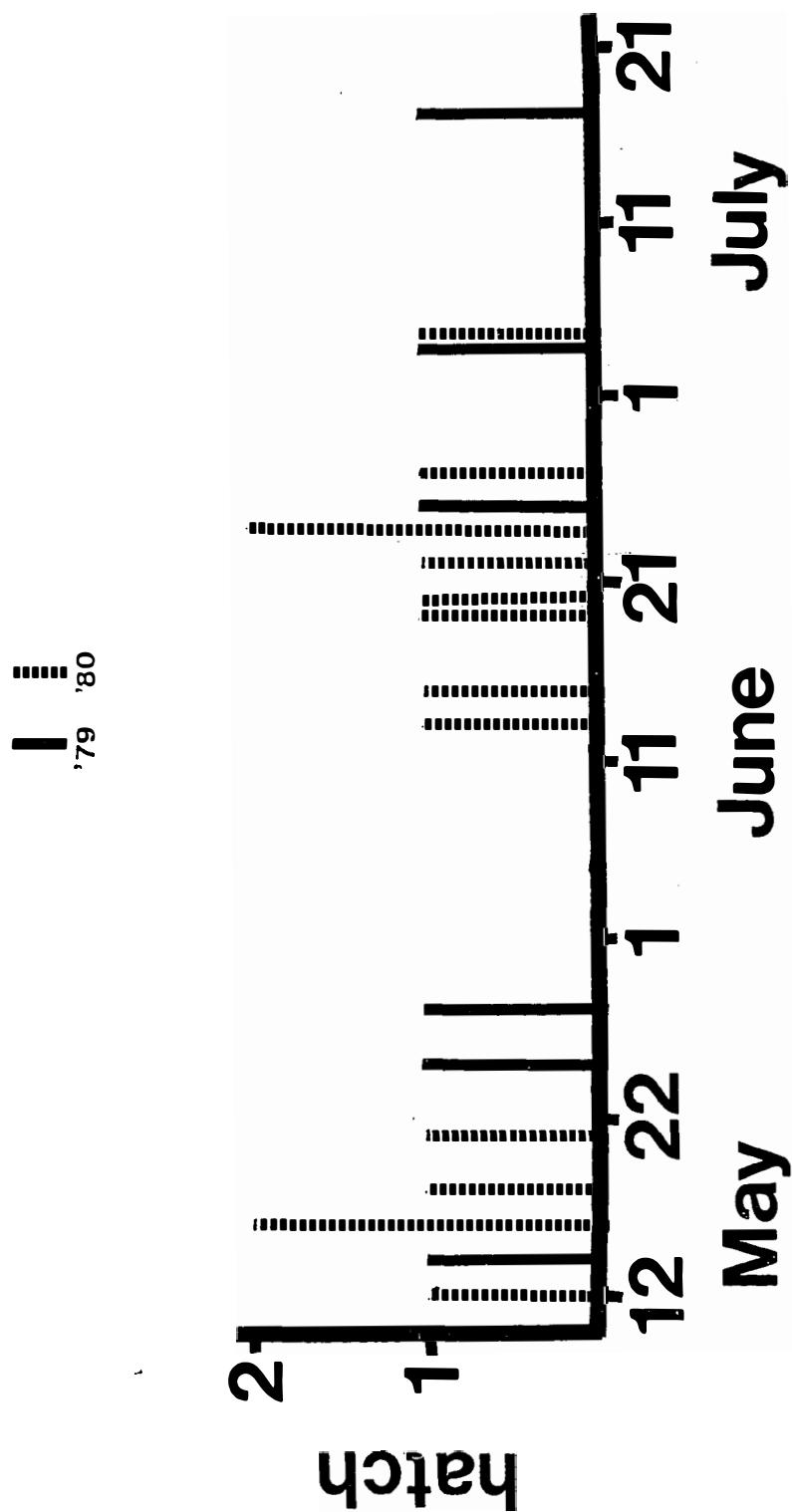
Hatching Dates.

Dates on which hatch began in both years are shown in Figure 3 for the 20 nests that hatched. Not surprisingly, peaks in hatching dates fall about 30 days after peaks in nest starts, since that is the time required for clutch completion and incubation (5 + 25 days). Both nest starts and hatching were slightly later in 1979 than in 1980. The separation of the first and second peaks in hatching dates is sharper than the separation in starting peaks. No nests hatched between 28 May and 25 June in 1979, or between 21 May and 13 June in 1980.

Hatching Success.

Hatching success in both years of the study is shown in Table 1. Three estimates are given: proportion of nests producing at least 1 chick (proportion of successful nests = PSN); proportion of eggs laid that hatched (egg hatching success), and the probability (based on exposure) that an egg present at the start of incubation will hatch, using the method of Mayfield (1961, 1975). As can be seen in the table, the first two estimates agree closely, especially in 1979, but that the Mayfield estimate is lower than the others in both years. The first two estimates probably overes-

FIGURE 3: Distribution of hatching dates in 1979 and 1980.



timate the actual hatching success, because some nests that failed were never found (Mayfield 1961), but the Mayfield estimates can underestimate the true hatching success if their assumptions are violated (Green 1978).

One of the assumptions of the Mayfield estimate, that nest mortality is constant over all days and all nests, appears to be violated in two ways in the present sample of Wilson's Plover nests. One violation is that PSN was higher in the second half of the breeding season than in the first half in both years. In 1979, PSN was 21% (3/14) for nests found before 1 June, and 50% (3/6) for nests found after that date. In 1980, PSN was 36% (5/14) for nests found before 1 June, and 75% (9/12) for nests found after that date. No dramatic decrease in nest predators was noted around 1 June, but there was less rain after that date (see below). The other violation was that hatching success appeared to be related to nest substrate (see below).

If the conventional estimates of hatching success are too high, and the exposure estimates are too low, the best estimate is probably somewhere between the two. In 1979, this range is 20 - 30%, and in 1980 the range is 33 - 54%. Since the ranges for the two years almost overlap, whether hatch-

TABLE 1
HATCHING SUCCESS ESTIMATES

	Year	
	1979	1980
NESTS		
Number found	29	29
Failed during clutch compl.	5	0
Human disturbance	2	1
Outcome unknown	2	2
Net number	20	26
Number hatching chicks	6	14
Number destroyed	14	12
PSN (Proportion successful nests)	.300	.538
EGGS		
Number hatched	17	34
Number laid	57	75
Left in nest after hatch	1	5
Lost during incubation	0	8
Egg hatching success	.298	.453
EXPOSURE		
Nest-days	230	385
Egg-days	-	1086
Nest survival probability	.208	.453
Hatching probability	.940	.870
Egg survival probability	1.0	.831
Overall nesting success	.196	.328

ing success really was higher in 1980 cannot be determined from such a small sample. It is clear, though, that hatching success is near the bottom of the range of values reported for other shorebirds (see Discussion).

Causes of Nest Failure.

The main causes of nest failure were flooding, predation by mammals, and probably predation by snakes. Known and potential nest predators present in the study sites are listed in Appendix D. Nest 1-79 was found under water after rain, and Nests 22-79 and 27-79 showed signs of flooding (mud stuck to deserted eggs). Coyote sign was found near several deserted nests: tracks at Nests 23-79, 8-80, and 20-80, and scats at Nests 28-79 and 9-80. Surprisingly, a coyote scat was found right next to Nest 27-80 one morning, but the nest was intact. Feline tracks (without claw marks) about 32 mm (1.3 in) long were found near Nest 25-79 after it was found partly destroyed, and they were about the size of Jaguarundi tracks (Murie 1954). I had seen a small yellow-brown cat in the same area the night before with short ears and a long tail, and this also fits the description of a Jaguarundi, not a Bobcat (Murie 1954). The eggs were first found partly eaten at about 1900 hours, with one egg gone and one half gone. The next morning at about 1100 all the eggs were gone, a hole was dug near the nest, and the tracks were found. The tracks did not follow mine to the nest.

There were signs of cattle near several disturbed and destroyed nests at Matagorda in 1980. Cattle signs were found near Nests 10-80, 12-80, 14-80, and 24-80 when they were found destroyed, and one egg in Nest 12-80 was crushed. One egg disappeared from Nest 16-80 after something, probably a cow, bumped into the camera that was filming the nest and chewed the flag marking the nest. The flags had also been chewed at Nests 10-80 and 14-80, and I watched a cow do this at another nest. The cows appeared to be attracted to any strange object, and they were seen eating styrofoam floats on the beach. I tried to place the flag far enough from the nest to prevent a cow that was chewing it from trampling the nest, but another member of the herd could always step on the nest. The dogs on Matagorda did not usually go onto the salt flats, but their tracks look almost identical to coyote tracks, and dogs may have eaten some 1980 nests. Dogs were thought to be the main cause of egg loss in a mainland population of Killdeer in Ontario (Nol 1980).

Small rodents sometimes destroy eggs by making a small hole in them and removing the contents (Maxson and Oring 1978), and this may have happened in 2 deserted nests in 1979. The egg left in Nest 3-79 on 15 May was found with a small hole and the contents gone on 21 May, with ants cleaning up what was left of the contents. One of the 4 eggs deserted in Nest 4-79 on 5 May was also found empty with

ants on 21 May, but the other eggs appeared to be full, and all the eggs were gone on 28 May. A similar fate probably befell the egg left in Nest 16-80 on 20 May, which had ants on it on 22 May. This type of egg predation was not recorded at attended nests.

This only accounts for 14 of the 26 nests lost in both years: 3 flooded, 5 Coyote, 1 Jaguarundi, and 5 cattle. At the other 12 failed nests, there was no sign of any animal and no eggshells, which probably rules out the Raccoon and the Striped Skunk as predators (Rearden 1951), and the Great-tailed Grackle and Laughing Gull as well, since these species usually leave the eggshells in or near the nest. Of course, it is possible that the shells blew or were washed away from some nests before they were checked, but that is unlikely. Snakes are the potential predator least likely to leave a sign, and Indigo and Rat Snakes, Racers and Rattlesnakes are all known egg eaters. There could also have been cases of Coyote and Bobcat predation in which no sign was left. I suspect that in at least some cases, nest desertion preceded predation, although some deserted nests lasted a long time before being preyed upon (see above).

Effect of Rain and Nest Site on Hatching Success

Although only a few nests were definitely flooded, nests tended to disappear around the time of heavy rains. In 1979, there were 12 days during the breeding season that had rain of 2.5 mm (.10 in) or more at the Brownsville Airport

(NOAA 1979). Since I often could not get to nests until 2 days after rain because the roads were impassable, there were 21 days during the 93-day breeding season with either rain or the day after (sometimes it rained on two consecutive days). Of the 14 nest losses, 9 came on one of these 21 days (64%), which is significantly more than the 23% of failures that would fall on those days if their distribution was random with respect to rain ($\chi^2 = 10.4$, $P < 0.001$). In 1980, there were 9/81 days either with rain or the day after, with amounts of 21.8 - 26.2 mm (0.86 - 1.03 in) of rain at Port O'Connor (NOAA 1980). There were 4/12 (33%) failures associated with rain, but only 11% are expected under the null hypothesis, and this difference is also statistically significant ($\chi^2 = 5.6$, $P < .025$). The significance of these results must be qualified by the fact that unequal numbers of nests were at risk on different days of the breeding season.

The distribution of days with rain was skewed towards the beginning of the breeding season, and this may be one cause of the lower nesting success at the beginning of the breeding season. In 1979, 97.5 mm (3.84 in) fell before 4 June and only 53.3 mm (2.1 in) fell after that date, although there were 6 days with rain in each period. In 1980, 150.1 mm (5.91 in) of rain fell before 1 June, and 0 mm fell after that date. The normal total for May is 100.6 mm at Victoria, but normally 84.1 mm falls in June.

Nest site also appeared to have an effect on hatching

success. In 1979, 5/14 (36%) of nests on roads hatched, while only 1/6 (17%) of nests off roads hatched, and the one that hatched was close to the road (Nest 12-79). Gravel roads had a higher PSN than other sites, with 4/8 (50%) PSN compared to 2/12 (17%) for other substrates. The center strip of gravel roads was the most successful site (3/3 or 100%), compared to 3/17 (18%) successful in other sites. At Matagorda in 1980, pavement nests had higher success (8/12 or 67%) than soil nests (6/14 or 43%). In the second half of the breeding season, this difference was even more pronounced: 6/6 or 100% success on pavement vs. 2/6 or 33% success on soil. Sample sizes would have to be larger to be sure of these trends.

Chicks

Departure from the nest.

The chicks are wet and still have an egg tooth at hatching. They usually took some steps out of the nest within 1 hr of hatching. Since the last chick could hatch up to 40 hr after the first, the first chick might have to spend more than a day near the nest, unless the off-duty parent cared for it elsewhere. Right after hatching the chicks would crouch next to the eggs when I checked the nest, but within a few hours they began to hide in vegetation near the nest when I checked it. The older chicks appeared to feed in the vegetation near the nest during the day, and return to the

nest occasionally to be brooded, while their younger siblings were hatching.

Departure from the nest occurs soon after hatching, at least when the last egg hatches in the morning. At Nest 29-79, the third egg hatched at about 0645 on 18 July, and the nest was at the edge of a road. The male (the female was gone; see Chapter 3) led the two older chicks north in the road, away from me, at 0729, but he returned to the nest when the youngest chick failed to follow. He brooded the youngest chick, and the two other chicks also returned to the nest. He led them out again at 0802, when the youngest went a short distance from the nest and stopped, and the male returned to it again. This leading and return was repeated at 0812, but the youngest was gradually moving away from the nest, and it was following the others by 0856. By 1200 the family had reached a curve in the road about 100 m from the nest, and at 1649 they had left the road and were in some vegetation at the edge of a nearby pond. The male returned to the nest 5 times while the family was moving away from me, showing that he could not count.

Brooding

Little brooding was observed after the chicks left the nest, partly because it was so difficult to watch chicks that were out of the nest. Sometimes a parent and some chicks would disappear into some vegetation, and the parent might be brooding the chicks, but they might also be feed-

ing. Male 29-79 brooded his chicks for a total of only 14 min in a sample of 2 hr made the day the chicks left the nest (see Chapter 3). If there were two parents attending there probably would have been more brooding than this. Pair 21-79 did no brooding that I could see during 5 hr when the chicks were 1 - 6 (probably 2 - 3) days old, but some brooding could have taken place out of sight. An unmarked pair with young chicks did no brooding during 10 hr of observation (see Chapter 3), and it was less likely that I missed some brooding in that case. It was probably so warm during the day that young chicks rarely required brooding, although they were probably brooded at night. Even night temperatures were mild, with a normal minimum of 25° C. during the breeding season.

Either the parent or the chick could initiate brooding. The parent initiated it by walking up to the chick and crouching near it, and then raising one wing when the chick approached. Chicks would also go up to parents and try to get under them.

Habitat Used by Chicks.

In all cases that chicks were seen feeding (not moving from one area to another), they were in a low wet area in a salt flat, usually in a clump of Saltwort. Saltwort tends to grow in the wetter, lower areas of the salt flats (pers. obs.). The chicks were all but invisible when they were in this vegetation, and they appeared to be catching small ani-

mal prey at the base of the plants. The chicks would run singly across bare areas between one clump of Saltwort and another, usually at intervals of 1 hr or more. At the end of the day the whole family often moved to another area together, with both parents attending. When the family was not moving, only one parent usually attended the chicks while the other parent was out of sight. The attentive parent did not stay especially near the chicks or lead them, but it usually spent a large part of its time alert or displaying (Pair 21-80 and Unmarked Pair, see Chapter 3). The only time I saw a parent actively call to and lead chicks was when the chicks from Nest 29-79 were leaving the nest. The tending strategy appeared to be inactive (*sensu* Walters 1980), and sometimes it was difficult to tell which adult was caring for the chicks if there were several adults in the same area.

Parents usually defended a territory around the chicks when other plovers were nearby. Male 29-79 defended a territory at the edge of a pond against another male that was also caring for chicks, and the two males did parallel walk displays together. Parallel walks were also seen between Male 23-80 and the male of the Unmarked pair that had chicks near that nest.

The areas used by the chicks for feeding were not usually near the nest, since nests were not always near wet areas. Pairs nesting on roads usually led their chicks away from roads, which has obvious adaptive value since chicks freeze

when threatened by man. Male 26-79 flew to a wet area about 100 m directly away from the road on the day after his chicks had hatched, and his chicks were probably near the spot to which he flew. Males 29-79 and 21-79, also road nesters, also moved about 100 m and off the road with their chicks, but Pair 12-79 was seen only 10 - 20 m from its nest with chicks. However, Nest 12-79 was at the edge of a salt flat that contained suitable feeding areas for chicks. Pair 2-80 moved only about 30 m from its nest with its chicks after hatching, also because suitable habitat was nearby. Pair 6-80 was found with its chicks about 30 m from its nest on the day after hatch, stranded on high ground after flooding caused by heavy rain.

Fledging success.

No broods were followed to fledging, but fledging success appeared to be fairly low. Pair 12-79 had lost a chick when seen two weeks after hatching, and only 1 chick from Nest 2-80 was seen 2 weeks later (see below). The only families seen with 3 chicks had young chicks. One pair was seen with 1 large chick and 3 small chicks, which could have been the result either of double-brooding or of adoption.

Chicks are vulnerable to bad weather when they are young (Bennett and Dawson 1979). The 3 chicks from Nest 6-80 were found near their nest the day after hatching, and only the largest chick was dry. The 2 smaller chicks were quite wet and probably had trouble thermoregulating. There had been

heavy rain the day before. Time to fledging is not known, but it is about a month in other plovers (Bent 1929).

Adoption

Although adoption is not nearly as common in shorebirds as in some anatids such as Canada Geese, it does occur, and one definite case was found in Wilson's Plover. Pair 2-80 was seen with its chicks the day after hatching, but the next day they led them out of sight down the road (14 May). Pair 2-80 was seen near Nest 6-80 on 19 May, and they acted like they had no chicks, although Nest 6-80 was in the direction the family had been walking on 14 May. On 29 May, Female 2-80 displayed to me as I walked near the site of another nest that was about 150 m from Nest 2-80, and on 30 May the pair acted like it had a nest near their previous nest. In fact, Nest 26-80 was found nearby on 2 June, and it had been started on about 28 May. At the time I assumed the chicks from Nest 2-80 had died, since I did not see them with their parents.

I was surprised on 3 June to see one of the banded chicks from Nest 2-80 near Nest 26-80, and at first I assumed its parents were caring for it. It became apparent that an unbanded pair was caring for it, especially when the male of the unbanded pair brooded it briefly. This other pair defended a territory adjacent to that of Pair 26-80. It is not clear when the adoption occurred. If it occurred soon after hatching, the chicks may have remained with the

unbanded pair while the parents were near Nest 6-80. However, the adoption could also have occurred after the parents brought the chick(s) back to their former territory in preparation for making Nest 26-80. Individual recognition is not known between shorebird chicks and parents, so there may not be a critical period for adoption as there is in anatids. Pair 2-80 was technically double-brooded, but it did not actually care for its chick to fledging.

Once I knew that adoption was possible, I watched closely when I released a chick from an unknown nest that I caught and banded on 23 June. The chick ran away from me towards a group of adults that had been giving me broken-wing displays (see Appendix E), where it was joined by another chick, and a pair of adults came up to it and the female brooded it. Another female came up to the female with the chicks, and squatted next to her as if she were trying to initiate brooding. The male of the pair did not drive off this other female immediately, but he did drive off the many other adults that approached his mate. It appeared that some of the other adults were actively trying to brood the chicks.

Adoption in Wilson's Plover was reported by Bent (1929), but not under natural conditions. One newly hatched chick and two eggs were exchanged for the eggs in a nest, and the female began brooding the chick a few minutes after she returned to the nest.

Weight at Hatching

There were 20 chicks banded in 1980, mostly within 1 - 2 days of hatching. The 19 banded within 2 days of hatching had a mean weight of 9.3 g (range 7.0 - 10.7 g), and 1 3-day-old chick weighed 12.0 g. No chicks were recaptured to check growth rates, partly because most were never seen again, and partly to avoid disturbing the family.

Discussion

Nesting Habitat

The apparent discrepancy between past and present nesting habitat of Wilson's Plover is probably related in part to increasing human use of beaches. Wildlife refuges on the Atlantic coast now report this species as rare where it was once supposed to be common (Bent 1929). It is possible that Wilson's Plovers breed on salt and mud flats on the Atlantic coast without attracting notice, since travel in such areas is difficult. The greater tidal reach on the Atlantic may make salt flats unsuitable for nest sites, however. A survey of the breeding status of this species in the U.S. is needed, especially on the Atlantic coast.

Territory Establishment

The pattern of nests spaced far apart and little territorial fighting is fairly typical of other reports of nest spacing in Wilson's Plover. Tomkins (1944) gives few details of territory size, but he mentions two nests about 150 ft (46 m) apart, and states that "a plover territory is

seldom much smaller than a circle roughly one hundred feet in radius." Bent (1929) states that "Wilson's Plover might almost be said to nest in colonies," but that nests are "never nearer than 20 yards apart," which is not very close by colonial standards. Baynard (in Bent 1929) found a "colony of at least 50 pairs nesting on a bank of white sand, probably half a mile long," but I doubt that anywhere near that number of nests were actually found, since that would allow only 50 linear feet of sand bank per nest. Wilson's Plovers tend to congregate around humans near their nests, giving the impression there are far more nests in the immediate area than there actually are. Part of the colonial association may be that Wilson's Plover nests are sometimes found at the edge of Least Tern colonies, but there are usually only a few Wilson's Plover nests per colony (pers. obs.).

Other plovers also tend to space nests far apart. In the Little Ringed Plover, nests are mostly spaced more than 185 m, with a minimum of 56 m (Simmons 1956), and in the Killdeer mean distance is 244 m with a minimum of 14 m (Mace 1971). Minimum distances between nests are 8 - 18 m in Kittlitz's Sandplover (C. pecuarius) (Hall 1958), and in the White-fronted Sandplover (C. marginatus), most nests are more than 46 m apart (Shewell 1951). Average distance between 17 Snowy Plover nests in Kansas was 85 m, with the 2 closest pairs 15 and 20 m apart, and 10 pairs less than 60 m apart (Boyd 1972) Piping Plover nests are spaced a mean of

52 m apart, with a range of about 3 m - 200 m apart (Cairns 1977). Mean nest spacing in C. bicinctus in New Zealand with a minimum spacing of 4 - 5 m (Phillips 1981).

Some authors also give estimates of territory size, but these seem to be less useful than nest spacings since they are somewhat subjective. Cairns (1977) estimates territories of 500 - 8,000 m² in the Piping Plover, Mace (1971) estimates 885 m² for the Killdeer, Mason (1947) estimates 625 - 880 m² for the Ringed Plover, and Sluiters (1938) estimates 5,000 m² for the Little Ringed Plover. However, in some cases close-nesting neighbors are tolerated (Graul 1973, Hall 1958), so it is difficult to define the size of the defended area. Tolerance of some intruders was also noted in Wilson's Plover, especially by the female while incubating. The amount of feeding done on territory and the local breeding density probably affect the territory size a great deal, so there may not be a typical figure for each species.

Nest Site Selection

Road nesting is a fairly unusual pattern in other plovers. Killdeer have been reported to nest on railroad beds in a few instances (Bunni 1959:118 and references therein). In Minnesota, Lenington (1975) found Killdeer nests on asphalt near vegetation in an abandoned parking lot, and near railroad tracks. Five of six Killdeer nests found by Cronan (1974) in Malheur National Wildlife Refuge in Oregon

were along roads, however. Most roads outside of wildlife refuges probably have too much human use to be potential nest sites. Other species nested in roads at Laguna Atascosa: I found a Snowy Plover nest with 2 eggs in the middle strip of a caleche road that was also used by Wilson's Plovers, and I found a Killdeer nest with 4 eggs in the middle strip of a caleche road in a dry grassy area not used by Wilson's Plovers. Nighthawks probably also nested on roads at Laguna Atascosa, and both Nighthawk and Least Tern nests were found on runways at Matagorda. Thus road nesting was fairly common near salt flats, but it may not be in other habitats, or where roads are used more.

The roads through the salt flats at Laguna Atascosa were normally only driven once a week by a staff member doing a survey, and sometimes on weekends, so they had very light use. At Matagorda there was probably no regular driving on the runways, and an occasional illegal airplane landing (the runways were closed) was always made on the least vegetated runway, which had only one nest on it. There was an increase in human activity at Matagorda in 1980, when an oil company began drilling at the other end of the island. This apparently reduced the number of Least Terns nesting on the runways (J. Shelton, pers. comm.), but appeared to have less effect on the Wilson's Plovers.

Nests on roads are farther apart than nests on soil. The closest simultaneous road nests were 64 m apart, while the closest off-road nests were 35.5 m apart. The other road

nests were all at least 300 m from the closest active nest. This spacing could reduce the chance that a nest predator hunting along the road would find more than one nest, or it might be that the parents defend a longer territory when it is narrow. Road nesters usually only challenged birds that were in or near the road, and rarely chased birds that were near the nest but off the road.

Wilson's Plovers in Georgia seek unobstructed nesting sites: "Usually nests are not near thick vegetation, and shelter from view is not liked" (Tomkins 1944). Most nests are placed "close to a piece of drift-trash or similar low windbreak," (Tomkins 1944), but not next to vegetation. Snowy Plovers also tend to nest next to an object, not always plant stems (Boyd 1972), but Rittinghaus (1961) felt that shelter from view from above was an important nest site characteristic, and an object was not necessary. Piping Plovers do not tend to nest near either objects or stems in Nova Scotia (Cairns 1977), but Killdeer tend to nest near objects (Bunni 1959), and Mountain Plovers often nest near cow dung (Graul 1975). The possibility that objects or plants near the nest help the parents relocate the nest is discounted by Maclean & Moran (1965), who feel that their function is more likely camouflaging the nest by disrupting its outline, or shielding it from view from aerial predators.

The preponderance of plant stems on the south and southwest sides of Wilson's Plover nests suggests that they may

shade the eggs during parental absences, especially in the afternoon when temperatures peak. In several nests the eggs were in the shade of the plants in the afternoon, and observations on shaded and unshaded eggs show that unshaded eggs heat to over 41° C. in full sun, while shaded eggs tend to stay near shaded air temperature, which is usually lower than that. The function as a windbreak is suggested by Tomkins (1944), and several Wilson's Plover eggs were found that had apparently been blown out of nests on pavement. Shorebirds at the Salton Sea do not nest near plant stems (Grant 1979). Nesting near vegetation in a hot environment could reduce wind velocity, which may be important in cooling the eggs (see Chapter 5).

Although there is fairly high nest site fidelity in plovers, both in renests and from year to year (Wilcox 1959, Lenington and Mace 1978, Rittinghaus 1961), there is also some adaptability in nest site selection, and previously unused areas are occupied in some cases (Tomkins 1944, Wilcox 1959). It would seem to be adaptive to learn that a certain substrate tends to be unsuccessful, yet there was only one pair in the present study (Pair 6-80) that moved from a soil substrate to pavement. There was one other possible nest site switch, since Nest 28-79, a road nest, was near Nest 1-79, a flooded soil nest, and may have been made by the same pair. Since the plovers may not have the time or energy to experiment with every nesting substrate, they may remain on the one they have tried before, since another

could be even less successful. It would be very interesting to see if offspring of road and pavement nesters nested on roads and pavement, but no nests were found in 1981 that involved chicks banded in 1980.

Egg-laying

Given the mild climate in Texas, it is surprising that egg-laying did not begin earlier than April. There were at least 2 nests started in early April in 1979, but most pairs appeared to wait until late April to begin egg-laying. Breeding schedules of plovers in much more northerly locations are not very different from that of Wilson's Plover in Texas. Nest starts of *alexandrinus* in Germany had a similar bimodal distribution, with the first peak at 5 May and the second at 15 May, (Rittinghaus 1961:48). Piping Plovers in southern Nova Scotia begin laying in mid-April and stop in mid-June (Cairns 1977), as do Killdeer in Michigan (Bunni 1959). Nest starts in *montanus* in Colorado range from 17 April to 15 June (Graul 1975). Since temperatures in Texas are milder, there must be some reason why nesting does not begin earlier in Texas.

Migration could not be a reason, since the Texas plovers probably only migrate as far as Mexico, and they may return to Texas in March, which is when they arrive in Georgia (Tomkins 1944). The weather in April is neither terribly colder nor more or less rainy than May in Texas. The lowest temperature during the study was 35° F. in April near Mata-

gorda, while the minimum in April 1979 near Laguna Atascosa was 53° F., but these are not very cold. Perhaps day length is too short prior to April, or food is less available in Texas before April. The simplest explanation may be that Wilson's Plovers do not need to start breeding before April in order to produce enough young each year.

Although the timing of the start of laying is puzzling, the end of laying seems to be related to the drying trend in June and July in Texas. No rain fell after 21 May in 1980, and most of the ponds were dried up by the end of June on Matagorda, while this drying up occurred in mid-July at Laguna Atascosa in 1979. Laying stopped earlier in 1980 than 1979, possibly because the rain stopped earlier. There would be little feeding habitat for the chicks if all the ponds dried up, and they are also used by the parents for bathing, drinking, preening, and some feeding. Also, it gets so hot in Texas, beginning in June, that thermoregulation of both eggs and adults must become very difficult during incubation. Belly-soaking occurred at a few nests in 1980 (see below), but without ponds there would be no place to wet the belly.

Laying intervals in other plovers are similar, although some species lay more rapidly. Of the species that also have 3-egg clutches, Snowy Plovers average 96 hr (4 days) between first and third eggs, with a range of 18-72 hr (mean 46 hr) between any 2 eggs (Ritterhaus 1961). This is one day faster than Wilson's Plover, but Boyd (1972) reported

that Snowy Plovers take 5 days to lay a complete clutch.

Mountain Plovers average about 53 hr (range 28-108 hr) between eggs (Graul 1975).

Of plovers with 4-egg clutches, Piping Plovers lay eggs at about 48-77 hr intervals, taking 6-7 days to complete the clutch (Cairns 1977, Wilcox 1959). Killdeer lay 4 eggs in 3.3-4.1 days, or about 1 egg every 24 hr, which is twice as fast as Wilson's Plover (Bunni 1959). Least Sandpipers lay eggs just as rapidly, about every 29.6 hr (Miller 1977). The Black-bellied Plover has 36 hr intervals, or 4.5 days for 4 eggs (Hussell and Page 1976). In the polyandrous Dotterel (*Eudromias morinellus*), 24 - 36 hrs elapse between successive layings (Nethersole-Thompson 1973), and laying intervals in the Eurasian Golden Plover (*P. apricaria*) are 48 - 60 hrs (Bannerman 1961:209).

Since laying intervals are difficult to determine accurately, and most of the species studied occasionally had longer intervals, these data mainly show that laying intervals in most plovers fall into the range of 46 - 60 hr, with shorter intervals in vociferus, *P. squatarola*, and *E. morinellus*. The latter species is polyandrous, but there is no obvious reason why the other two species should have short laying intervals. In *montanus*, which has a rapid multi-clutch mating system (Graul 1973), laying intervals are long, although clutches could be laid more rapidly if they were short. Most laying intervals in calidridine sandpipers are shorter than those in plovers, about 24 - 30 hr (Miller 1977).

In Wilson's Plover, the time between failure and starting a new nest is fairly long compared to other plovers. In the Killdeer, 4 pairs which lost their first clutch all started replacements within 7 days of the loss (Bunni 1959). In the Snowy Plover, 3 renests began 4-7 days after the first clutch was destroyed (Rittinghaus 1961), and 1 renest started only 2-4 days after the loss of the previous clutch (Boyd 1972). Two Piping Plover renests began about 5 days after nest destruction (Cairns 1977).

The sample of time between renests in wilsonius is small, however, and it may be biased towards long intervals. Rain inhibits the start of laying in some species of birds (Immelman 1971, Graul 1975), and there were at least 2 days with rain between all but one of the failures and renests observed. Rain did not fall before Nest 23-79 was started, but heavy rain fell the day before Nest 14-79 failed, and this may have delayed the start of Nest 23-79 until the soil dried out.

Eggs

Egg weights in the Charadriinae range from 6.8 g in C. collaris to 33.0 g in P. apricaria, so egg weight in wilsonius falls in the lower half of this range. Proportional egg weight (female body weight divided by egg weight) ranges from 14% in E. morinellus to 22% in wilsonius, with one higher figure of 28% in modestus. Thus wilsonius has a high

proportional egg weight, but several species are almost as high, and the reduced clutch size reduces the proportional clutch weight. The arctic species *hiaticula* and *semipalmatus*, which are slightly smaller than *wilsonius*, have proportional egg weights of 19% and 21% respectively. Since they have 4-egg clutches, their respective proportional clutch weights are 77% and 85%, compared to only 65% in *wilsonius*. (Table 1, Graul 1973).

Miller (1979) also found no consistent pattern in total volume between first and second clutches in the Least Sandpiper, but he did find a tendency for later eggs to be longer. He also found little correlation between length and breadth, and more variability in length than breadth.

The problem of the upper limit of 4 on clutch size in the *Charadrii* is too complex to be discussed here, and has recently been discussed elsewhere (Maclean 1972, Walters 1980). The reduction in clutch size below 4 in tropical species is more relevant, since it occurs in *wilsonius*, and it appears to be an easier question to answer.

All Nearctic and Palearctic plovers have a clutch size of 4, while all of those in the tropics except *cinctus* have a clutch size of 3 or 2 (Maclean 1972). The reduction in clutch size towards the equator is a very general phenomenon in birds, both between populations within species and between species within genera (Lack 1968, Welty 1975). Several differences between the polar and equatorial regions have been proposed as ultimate factors in this reduction.

Shorter daylight in the tropics gives the parents less time to gather food for nestlings (Hesse in Klomp 1970, Lack 1954), and lower adult mortality in non-migratory populations might allow fewer young per year to be produced in those populations (Klomp 1970). Food for the nestlings may be harder to obtain in the tropics (Ricklefs 1970), and higher nest predation in the tropics could select for reduced clutch size to facilitate relaying (Oring and Knudson 1972).

Few data are available to test these hypotheses in shorebirds, but one comparison has recently been published (Summers and Hockey 1980). The White-fronted Plover (C. marginatus) nesting in South Africa was compared to published information on the closely related hiaticula, which nests in Greenland and northern Europe. Based on banded birds, the life expectancy of the resident marginatus is 7.5 years, compared to 3.5 - 4 years for the migratory hiaticula, using the method of Grosskopf (1964). In South Africa, marginatus lays 2 eggs up to 5 times per year, while hiaticula in the arctic lays 4 eggs, usually once per year (Bannerman 1961). Proportional clutch weight is 37% in marginatus and 77% in hiaticula. Nest success probability (Mayfield 1961) is 30% in marginatus, while nesting success in arctic hiaticula is probably much higher. Other arctic shorebirds hatch 70 - 96% of eggs laid (Ricklefs 1969), and closely related semi-palmatus hatched 100% of nests in two studies (5/5 nests on Baffin Island, Sutton and Parmalee 1955, and 3/3 nests in

Alaska, Williamson et al. in Ricklefs 1969). Laying intervals are 2 - 4 days in *marginatus*, compared to about 36 hr in *hiaticula*.

Based on these data, several of the hypotheses on clutch size reduction may apply to plovers. Adult life expectancy is twice as long in the resident tropical species, but nesting success is much lower in the tropical species. More clutches per year are laid in the tropics, and the long laying intervals in *marginatus*, suggest that food to the female may be limited during egg-laying. Faced with low probability of nesting success, the tropical strategy may be to lay fewer eggs repeatedly, investing less in each clutch. In the longer breeding season, apparently enough chicks can be raised to balance the relatively low adult mortality, in spite of the low nesting success and small clutch size.

Incubation

The irregular incubation during clutch completion is not quantified in many studies, presumably because it is not considered important. Thus regular incubation is reported to begin with clutch completion in the Snowy Plover (Rittinhaus 1961, Boyd 1972), the Piping Plover (Cairns 1977), Killdeer (Bunni 1959), and Black-bellied Plover (Hussell and Page 1976). Quantitative results for several arctic sandpipers show a gradual increase in percentage of nests seen covered as the clutch is completed. In the Least Sandpiper the figures are 27%, 40%, 61%, and 99% for 1, 2, 3, and

4-egg clutches (Miller 1977). In marginatus, visits to the nest during clutch completion are made by both sexes together, and they take turns standing over the eggs for brief periods (Summers & Hockey 1980).

The high amount of incubation during clutch completion in wilsonius compared to other plovers could be related to the hot climate in Texas, since most of it occurred during the hottest part of the day, when the eggs may have needed cooling. Since the female does little incubation during clutch completion, presumably because she is feeding to get energy to produce eggs, and the male spends some time in courtship and territorial defense, there may be an upper limit on the amount of incubation during clutch completion. Part of the increase in incubation towards the end of clutch completion could be due to an increase in the female's share of incubation, as it is in the present study.

Feeding during Incubation

The foraging behavior of Wilson's Plover was studied by Strauch and Abele (1979) on their wintering range, on the Pacific coast of Panama. Based on the analysis of stomach contents, Wilson's Plover food items are 96% crustaceans (33% Uca sp.), 3% ants, and 1% polychaete worms. In contrast, Collared Plovers (C. collaris) in the same areas eat 50% insects, and 27% crustaceans, their diet overlapping 10 - 20% with that of Wilson's Plover. Semipalmated Sandpipers (C. semipalmatus) eat 82% polychaete worms, overlapping only

4% in diet with Wilson's Plover. Thus the diet of Wilson's Plover is specialized on crustaceans in both Texas in the summer and Panama in the winter. Although data on diets of other plovers in Texas was not collected, Wilson's Plover appeared to have little diet overlap with them in the summer, as it did in the winter in Panama. Wilson's Plovers eat significantly larger prey than the other two plovers in Panama, and probably in Texas as well.

Hatching

The incubation period of about 25 days in *wilsonius* is in the middle of the range of other plovers, from 23 days in *semipalmatus* (Witherby et al. 1943) to 29 days in *montanus* (Graul 1975). The shortest incubation periods might be expected to be in the arctic, where the breeding season is shortest, but aside from *semipalmatus* most arctic plovers have fairly long incubation periods (e.g. 26 - 27 days in *P. squatarola*, Hussell and Page 1976). Incubation periods are longer when only one sex incubates, as in *montanus* (Graul 1973), and the 25 - 28 days for *E. morinellus* (Nethersole-Thompson 1973).

Incubation periods in plovers can be different in different areas, and in different nests in the same area. Incubation period of *vociferus* in Michigan is 25.1 days (Bunni 1959), but on a sandy peninsula (Long Point, Ontario), it is 27 days (Nol 1980). Incubation period of *alexandrinus* in Germany is 26.3 days (Rittinghaus 1961), and in Kansas it is

25.5 days (Boyd 1972). Incubation periods were longer than normal at some nests of *montanus* (Graul 1975) and *melodus* (Cairns 1977) that were subjected to disturbance. In the present study, one nest at which the male incubated alone for most of the period may have had a longer than normal incubation period, between 25 and 27 days (Nest 29-79).

Hatching intervals are somewhat longer in *wilsonius* than in most other plovers, or at least their distribution seems skewed towards longer intervals. A clutch of 3 in *alexandrinus* hatches in a mean of 14 hr, range 4 - 24 hr, in Kansas (Boyd 1972), and most hatch in a total of 12 - 15 hr, range 5 - 48 hr, in Germany (Rittinghaus 1961). The 3 eggs *montanus* hatch in a mean of 7 hr, range 3 - 41 hr, and the 4 eggs of *vociferus* have been reported to hatch in a mean of 20 hr, range 4.5 - 38.9 hr (Bunni 1959), or within 6 - 16 hr (Davis 1943). The eggs of *melodus* hatch within 4 - 8 hr of each other in most cases, with intervals up to 45 hr (Cairns 1977), so most clutches of 4 hatch in a total of 12 - 24 hr in that species. The clutch of 4 in *P. apricaria* hatches in 6 - 36 hr (Nethersole-Thompson in Bannerman 1961), and in *P. squatarola*, 4 eggs hatch in 24 - 48 hr (Hussell & Page 1976). Both eggs hatched on the same day in one nest of *marginatus* (Summers & Hockey 1980).

The importance of hatching synchrony in shorebirds has been questioned by some authors (Hussell & Page 1976, Miller 1977). If asynchrony were strongly selected against, why does some incubation occur during clutch completion? The

lowest mean hatching interval reported for plovers, 7 hr in *montanus*, occurs in a species that often delays incubation until after clutch completion (Graul 1973). If a certain minimum amount of incubation is needed during clutch completion, this still does not explain an increase in incubation time during this stage.

One possible answer is that nest predation can be higher at unincubated nests than at incubated ones (Miller 1977), and there is more parental investment at risk as more eggs are laid. Incubation time may increase as eggs are laid to protect this increasing investment, even though this probably increases hatching asynchrony later. As found in the present study and most other studies, the parents will usually continue incubating long enough for any viable chicks to hatch. Hatching asynchrony prevents the older chicks from moving to a feeding area until the later chicks hatch, but most shorebird chicks probably catch little food in their first day or two, and there is usually yolk left in their stomachs to nourish them in the first few days (Welty 1975).

Hatching success in Wilson's Plover, between 20 - 54%, is lower than the reported hatching success for most temperate and arctic shorebirds. Percent successful nests was 70% and 53% in two years in Colorado in *montanus* (Graul 1975), and for *alexandrinus* in Oklahoma PSN was 73% and 38% in two years (Grover 1979), while in Kansas this species had PSN of 60% and 56% in two years (Boyd 1972). Egg hatching success

in Germany for *alexandrinus* was 95% over several years (Rittinghaus 1961), while egg hatching success for *melodus* was 79% and 72% in two years in Nova Scotia (Cairns 1977), and 91% over several years on Long Island (Wilcox 1959). For *vociferus*, 87% (26/30) of nests in Michigan hatched (Bunni 1959), while only 46% (12/26) hatched in Minnesota (Mace 1971). In *hiaticula*, 36% of eggs hatched in Germany (Laven 1940), but hatching success is probably higher in the arctic (see above). As noted above, reported hatching success for arctic sandpipers and plovers fall in the 70 - 96% range (Ricklefs 1969).

Reported hatching success for tropical plovers and lapwings are much lower than the figures for arctic and temperate breeders. In New Zealand, only 20% (8/40) of the nests of *bicinctus* hatched (Phillips 1981), and in Australia, 20% (8/40) of the nests of *alexandrinus* hatched (Hobbs 1972). In Africa, the Blacksmith Plover (*Vanellus armatus*) had a nest hatching probability (Mayfield 1961) of only 17% (3/12 nests hatched), and the Long-toed Lapwing (*V. crassirostris*) had a nest hatching probability of 30% (3/6 nests hatched) (Walters 1980). In Venezuela, the Chilean Lapwing (*V. chilensis*) had a nest hatching probability of 21% (6/15 nests hatched) (Walters 1980). The range of 17 - 30% for other tropical Charadrii is very similar to the results of the present study, and shows that low hatching success is a general phenomenon in tropical Charadrii, occurring in North and South America, Africa, Australia, and New Zealand.

One reason that has been proposed for the lower hatching success in shorebirds closer to the equator is an increase in terrestrial predators, especially snakes and mammals (Oring and Knudson 1972). Of the egg-eating snakes seen near nests in Texas, only the Racer and the Rat Snake occur very far north of Texas, and these do not occur north of the U.S. (Conant 1975). Most of the mammalian nest predators have wider distributions, although not reaching into the Arctic, but they appear to be more common farther south. Many of them are nocturnal, and the nights are longer in the summer closer to the equator, giving them more time to hunt. The severe hail storms that can destroy almost all the ground nests in the Great Plains (Boyd 1972, Graul 1975) were not seen in Texas, and there may be fewer such weather-caused nest failures farther south. More data on nest predators are obviously needed in all habitats.

Aside from nest destruction due to hail mentioned above, rain is not usually reported as being associated with nest failures in studies of shorebird breeding. Rain was associated with lower hatching success in V. armatus, which had low hatching success in the rainy season and much higher hatching success in the dry season (Walters 1980). The areas around the nests of V. chilensis were sometimes flooded, but the nests were placed on unflooded rises (Walters 1980). The low soil permeability and high water table in the study areas of wilsonius may make flooding a more serious problem than in other plovers.

The higher hatching success of road and pavement nests compared to soil nests is probably related to the lower risk of flooding, but there are probably other differences as well. Since roads are a relatively new habitat type, predators may be less likely to search for nests on them. Nest camouflage was better on gravel roads than on soil, and if a pavement nest was in a grass clump it could be well hidden also. Roads and pavement do not show human tracks the way soil does, so fewer predators may have followed my tracks to the road and pavement nests. One possible advantage of road nests was that certain roads were preferred sites for catching fiddler crabs, probably because they could be caught when they were crossing the road with no burrow nearby (see above and Appendix F). Some road nesting pairs were the only pairs to feed in significant amounts near their nests. Cronan (1974) thought that Killdeer in Oregon nested along roads because they were free of vegetation, elevated and thus giving a better view of approaching predators, and they provided a soft substrate for scraping. The first two arguments could also apply to Wilson's Plover, but the roads (and especially the pavement) in Texas were generally a harder substrate than the soils nearby.

Roads and pavement must have their disadvantages as nest sites as well, however. Coyotes were seen several times at Laguna Atascosa trotting along roads with their noses to the ground, and they and other predators might find nests this way. There is always the risk of the nest being run over by

a vehicle, although only one nest, a nest of *vociferus* at Matagorda, was run over during the study. Humans find road nests more easily than soil nests, since the incubating bird usually stays on the nest longer at the approach of a car than at the approach of a person walking. Another disadvantage is that roads are more dangerous for chicks than for eggs, and the chicks must be led away from the nesting territory. At Matagorda the cows fed more on pavement than on the salt flats, since they prefer eating grass on the pavement, and some pavement nests had the problem of eggs rolling out of the nest. Incubation behavior was different at pavement and soil nests (see below), with shorter absences at pavement nests than at soil nests, presumably because the pavement was hotter (see Chapter 4). Lenington (1975) noted that a pair of *vociferus* nesting on asphalt was the only pair that brooded its chicks during the heat of the day, probably for the same reason.

In most studies of shorebird breeding all the nests are on the same substrate, so comparisons between substrates are not possible, or sample size is too small to permit a comparison. One comparison has been made between *vociferus* nesting on Long Point, Ontario, which had a nest hatching success of 29%, while 12 nests on the mainland nearby had a nest hatching success of 64%, both calculated by the Mayfield (1961) method (Nol 1980). Gulls and Raccoons ate most of the nests lost at Long Point, while dogs were thought to have been the main nest predator on the mainland.

Chicks

In many shorebird species, the family leaves the nesting territory as soon as all the chicks are dry, and the family does not return to the nesting territory again. None of the families of *wilsonius* were found in their nesting territories after hatching, and there are no reports of return to the nesting territory in *alexandrinus*, which also may have a fairly mobile territory around the chicks (Rittinghaus 1961, Boyd 1972, Warriner and Warriner 1977). Families become progressively farther away from the nest site as the chicks get older in *montanus*. (Graul 1975).

In at least two plover species, the family regularly returns to the nesting territory for brooding at night, spending the day in a feeding territory. This has been reported for *vociferus* in Minnesota (Lenington 1980) and for *melodus* in Nova Scotia (Cairns 1977). The advantage of returning to the nesting territory is probably that it is less likely to be flooded than the feeding territory, which is next to water in *vociferus* and on sand flats in *melodus*. Some of the *vociferus* families spent several days on their nesting territory while the feeding territory was flooded (Lenington 1980).

Resident plovers and lapwings, which often hold the same territory for most or all of the year, are reported to remain in the nesting territory with the chicks. This is presumably what occurs in *marginatus* in South Africa, al-

though few chicks were observed (Summers and Hockey 1980).

In V. crassirostris, there are permanent territories with a mean size of 2200 m² on aquatic vegetation in which the chicks and adults feed, but the adults tend to feed away from the chicks (Walters 1980). In V. chilensis, the territories were larger (1.5 - 5 ha) and in some cases the feeding area was separated from the nesting area, and chicks foraged in the nesting territory in V. armatus, although the adults sometimes fed elsewhere (Walters 1980). One tropical species is similar to alexandrinus: the Crowned Lapwing (V. coronatus) is only territorial until hatching, after which the chicks are attended as they move about but are not defended from conspecifics (Walters 1980).

The merging of two broods has been reported in two plover species. This occurred once in alexandrinus in Kansas, apparently permanently, (Boyd 1972), and temporary "creches" of up to 7 chicks cared for by one adult were observed in melodus (Cairns 1977). The creches usually involved older chicks and non-feeding behavior, and during feeding the families were distinct (Cairns 1977). The latter author felt that individual recognition of chicks by parents of chicks was possible in melodus, although the willingness of alexandrinus parents to brood tern chicks was thought by Rittinghaus (1961) to show the absence of such recognition in that species. There are no other reports of suspected individual recognition in shorebirds.

One case of permanent adoption has been reported in *vociferus*. A 12-day-old chick which was being cared for by its father was fought over and ultimately adopted by another adult after the father developed a lame foot (Lenington 1975). There was no evidence that either parent in Pair 2-80 was injured, but I did see what looked like adults fighting over chicks (see above). One possible advantage in adopting a presumably unrelated chick is if experience in raising chicks increases future fledging success. In Canada Geese, families remain together through the winter, and larger families are dominant to smaller ones (Raveling 1970), so adoption makes more sense in geese than in shorebirds.

Summary

1. This chapter contains data on the breeding biology of Wilson's Plover, *Charadrius wilsonius*, which were collected during field work in April - July 1979, April - June 1980, and May - June 1981 at two sites on the coast of Texas. There were 64 nests found, and 1600 hrs of behavioral data were collected on 29 nesting pairs, using both observational methods and time-lapse movie cameras.
2. Territory establishment, seen mainly in April, involved horizontal threats and chases, which often involved aerial chases a few meters above the ground. Most territorial activity was done by

males. Parallel walks occurred in some balanced encounters, Most nests were spaced far apart, and less fighting was seen after nesting began. The closest active nests were 36 m apart, but most nests were more than 100 m from their nearest neighbor.

3. All nests were found in a salt flat habitat, either on the salt flat or on roads or pavement near the salt flat. Most nests except those on pavement were near fiddler crab burrows, and fiddler crabs were an important prey of adults. All but a few nests were next to at least one clump of vegetation, and more nests had vegetation to the south of the nest than in other directions. The significance of these nest site patterns is discussed.
4. Pairs often renested after a nest was lost, and all renests were in the same habitat patch with the same mate, with the second nest a mean of 55 m from the first. Two nests were found in 1981 with birds banded in 1980: one male had nested near his 1980 nest with a new mate, and one pair had nested 300 m from its 1980 nest, on a different substrate.

5. Egg-laying began in early April in 1979, and in mid-April in 1980, but the first peak of egg-laying came in late April in both years. A second peak of egg-laying came in late May or early June, and most were probably renests. Laying ended slightly earlier in 1980 than in 1979, possibly because it stopped raining in late May in 1980. The timing of the breeding season is discussed, especially its relatively late start.
6. Eggs were laid at about 60 hr intervals, and about 5 days were required to lay 3 eggs. Relaying began 5 - 13 days after the first clutch was lost, but these periods may have been extended because of rain. These are similar to laying intervals in other plovers, but relaying is usually more rapid.
7. Mean weight of eggs was 12.0 g, and mean dimensions were 35.2 x 25.8 mm. There was no consistent trend in egg size with laying order, nor in total clutch volume in first and second clutches, and egg length and egg breadth were not closely correlated.
8. Mean clutch size was 2.92, with 88% of completed clutches having 3 eggs. Ancestral clutch size was probably 4 in *Charadrius*, and reasons for a reduction in clutch size in *wilsonius* are dis-

cussed. The main reasons are thought to be low nesting success, which requires frequent relaying, and possibly low adult mortality.

9. Incubation during clutch completion is quantified at several nests, and it was done mostly by the male, with an erratic pattern that became more regular near the end of the period. The diurnal distribution of this incubation (more at midday) suggests that its main function may be to protect the eggs from overheating. Possible reasons for the commonly observed increase in incubation time during clutch completion are discussed in light of the fact that this probably causes hatching asynchrony. It is suggested that protection of the eggs from weather and predation may offset the disadvantage of asynchronous hatching.
10. Incubation period was exactly 25 days 3 hr at one nest, and about 24 - 26 days at several other nests. At one nest at which the male incubated alone it was slightly longer, 25 - 27 days.
11. Three eggs hatched over a period of 8 - 40 hr, with intervals between 2 eggs of 1 - 28 hr. This is slightly more asynchronous than some other plovers, and the adaptive significance of hatching synchrony is discussed.

12. Hatching success was 20 -30% in 1979 and 33 - 54% in 1980, with known losses due to flooding, Coyotes, cattle, and a Jaguarundi. Snakes were probably the main unknown predator. This relatively low hatching success is discussed in relation to the life histories of temperate and tropical shorebirds.
13. Nest failures were associated with rain, and nests on roads or pavement had a higher hatching success than nests on soil. Hatching success was also higher near the end of the breeding season in both years of the study, probably because less rain fell later in the season. Road nests may have had higher success because they were less likely to be flooded than soil nests.
14. Chicks were led from the nest as soon as the youngest was dry, usually to a clump of vegetation near a pond, where the chicks fed in the vegetation. It was almost impossible to follow the activities of the chicks because they spent almost all of their time in cover.
15. The parents were not very active in tending the chicks, and were only seen to call to them and lead them when leaving the nest. Usually one parent stayed near the chicks while the other parent

was out of sight. The parent near the chicks made little attempt to stay close to them, although it usually spent a large part of its time being alert and defending a territory around the chicks against conspecifics. Fledging success appeared to be low, since older broods rarely contained 3 chicks, and often only 1 chick was seen. The significance of this tending strategy is discussed.

16. One case of adoption of a banded chick is described. The adoptive parents cared for it on a territory adjacent to that of the parents, who had started a second nest. One additional case of adults trying unsuccessfully to adopt a chick is described, and the significance of adoption is discussed.

CHAPTER II

DIVISION OF LABOR DURING INCUBATION BY PAIRS

Introduction and Methods.

Sex roles during incubation are usually omitted from studies of the breeding biology of monogamous shorebirds, either because the sexes are indistinguishable, or because equal sharing of incubation is assumed. Because unequal parental investment by the sexes could lead to competition for mates and polygamy, monogamy implies equal parental investment by the sexes (Trivers 1972). However, unequal division of labor could favor polygamy without actually producing it, so this logical transposition is not strictly true, but it is still a useful starting point for analyzing division of labor. When data on division of labor are presented, they are usually based on brief observations on one or a few pairs, assuming that it varies little within or between pairs. Even the commonly made observation that males in monogamous species do a larger share of incubation during clutch completion or hatching has only been quantified in a few shorebirds (Miller 1977, Mundahl 1977). As discussed in the next chapter, knowledge of the division of labor during breeding in monogamous species is essential to an understanding of the evolution of polygamous mating systems. The costs and benefits of polygamy can only be fully

measured by comparison to a closely related monogamous species. Enough data on division of labor during incubation in Wilson's Plover were collected to estimate the flexibility of division of labor in the population. From the standpoint of the evolution of polygamy, the flexibility itself could be more important than the actual division, since different forms of polygamy involve very different divisions of labor.

The methods of data collection and reduction are the same as given in Chapter 4, and will not be repeated here. Data from 1980 were used and not data from 1979, because there is a significant diurnal pattern in the division of labor, and the 1980 data covered all periods of the day much more evenly than the 1979 data. The 1980 data were used for calculating parental shift lengths on the assumption that parental shifts shorter than one minute (the time-lapse sampling interval) were both unlikely, never having been seen during direct observation, and relatively unimportant if they occurred, because most shifts were much longer than one minute. The measure of male share of incubation is: male incubation time / total incubation time, calculated over whole days (except for time period analyses) to take diurnal variations into account. Parental shift length is the time between successive nest reliefs, when either the male relieves the female or the female relieves the male. One parental shift usually contains several incubation bouts and absences, all by the same bird.

The variable of male share was not normally distributed,

and the arcsine distribution failed to make it normally distributed (KSLTEST procedure, SAS Institute 1979). For this reason, non-parametric tests were used to analyze male share. Kruskal-Wallis one-way ANOVA was used when there were more than two independent groups compared (pairs and incubation stages) (SAS Institute 1979), and Friedman two-way ANOVA was used when the groups were related (Siegel 1956), using two-tailed probabilities in both cases. When there were two independent groups compared, the Mann-Whitney U test with the normal approximation was used (SAS Institute 1979), and the Wilcoxon matched-pairs signed-ranks test (Siegel 1956) was used to compare paired data, both with one-tailed probabilities. Independent groups were assumed for incubation stages because in most cases, the same pair was not sampled in all three stages. Survivorship analysis (Hull and Nie 1979) was used on the durations in minutes of parental shifts.

Results

Division of labor during daylight incubation is shown in Table 2 for 13 pairs in 1980. Male share of daylight incubation ranged from 7% in Pair 6-80 to 79% in Pair 1-80. The stage of incubation (clutch completion, middle, and hatching) is shown for each sample, and some of this between-pair variance in male share is due to variance between stages. Male share was consistently higher during clutch completion and during hatching than during the middle stage. This pat-

tern was found in Pair 18-80, which was sampled in all three stages, and also between two stages in Pairs 19-80 and 17-80. This difference between stages was highly significant over all pairs (Kruskal-Wallis $H = 18.2$, d.f. = 2, $P = 0.0001$). In addition, male share of incubation during clutch completion (63%) was significantly higher than during the middle stage (30%) (Mann-Whitney $z = 3.7$, $P = 0.0001$). During hatching male share rose to 41%, and this difference is also significant compared to the middle stage (Mann-Whitney $z = 2.3$, $P = 0.01$). For this reason, further analysis of the male share data was done only on data from the middle stage. The amount of time spent incubating, or incubation time, did not vary significantly between pairs, except Pair 1-80 was only on the nest 53% of the time. Incubation time for the other pairs ranged from 70 - 88%, so the pairs were dividing up roughly equal amounts of incubation time in very different ways.

Median survivorship of male and female parental shifts is also shown in Table 2, and female shifts were longer in all pairs except Pairs 18-80 and 19-80 during clutch completion, and Pair 17-80 during hatching. Small sample sizes probably prevented this difference from being significant in all but four pairs, and two of the significant differences are during hatching (Pairs 18-80 and 25-80). Thus although males increase their share of incubation during hatching, the pattern of longer female shifts appears to persist from the middle stage into the hatching stage. Over all pairs,

TABLE 2

DIURNAL DIVISION OF LABOR AND PARENTAL SHIFT LENGTHS IN 1980

Pair	Stage ^a	Male Share	Male Shift (min)	Female Shift (min)	N ^b
1-80	C	79%	-	-	2
2-80	M	51%	59.1	93.7	5
3-80	M	28%	70+	300+	2
5-80	M	15%	175+	825+	5
6-80	M	7%	80+	775+	3
10-80	M	10%	100+	650+	3
11-80	M	17%	175+	525+	3
16-80	M	16%	123.6	341.7	4
17-80	M	16%	-	-	1
17-80	H	78%	100.0	71.3	1
18-80	C	56%	475+	300.0	2
18-80	M	21%	4.2	65.0	1
18-80	H	44%	16.2	33.2 ^c	3
19-80	C	59%	350+	175.0	1
19-80	M	30%	34.1	125.8 ^c	5
21-80	M	46%	54.4	153.8	4
22-80	M	13%	37.5	650+ ^c	3
25-80	H	23%	27.5	65.3 ^c	3
26-80 ^d	M	45%	42.4	126.7	6
28-80	M	38%	28.8	45.0	3

^a C = Clutch completion, M = middle stage, H = hatching.

^b N = sample size in whole days (approx. 14 hr each)

^c Significant difference in shift survival between sexes ($P < 0.05$).

^d Renest by Pair 2-80.

females had significantly longer parental shifts than males (median survivorship 88.9 min vs. 39.1 min, Lee-Desu D = 20.5, $P < 0.0001$).

After accounting for the differences between incubation stages in the division of labor, there is still significant variation between pairs, and most of the incubation is done by the female in all but a few pairs. For the middle stage of the incubation period, male share of incubation differed very significantly between pairs (Kruskal-Wallis H = 63.9, d.f. = 12, $P < 0.0001$). Male share of incubation was consistently high in Pair 2-80 (51%) and in the renest by the same pair (26-80, 45%) later in the same breeding season. The only other pairs in which the male did more than a third of the incubation were Pair 21-80 (46%) and Pair 28-80 (38%). Females used belly-soaking in both pairs, and male 28-80 was the only male to use belly-soaking, and this may be related to the increased male share in these pairs (see Chapter 6). Male share in the other pairs ranged from 7% to 30%, all much less than 50%.

Male share of incubation differed significantly between different time periods each day, and this pattern was not

correlated with daily fluctuations in air temperature. Mean male share was 24% between 0700-1030, 13% between 1031-1400, 18% between 1401-1730, and 41% between 1731-2100, which is significantly different over the four periods (Friedman $\chi^2 = 15.0$, d.f. = 3, $P < 0.01$). The difference between male share in the first three periods (18%) and in the last period (41%) is also highly significant (Wilcoxon matched-pairs $T = 13$, $N = 13$, $P = 0.01$). The sharp increase in male share in the last time period is due to the fact that many males came to the nest during this period, and remained on the nest until nightfall.

If this diurnal pattern were correlated with temperature, male share should be different in the two middle periods of the day compared to the first and last periods, because air temperatures peak in the two middle periods. There was no significant difference between male share of incubation in four ranges of air temperature (Kruskal-Wallis $H = 6.0$, d.f. = 3, $P = 0.11$), and there was no significant linear regression of male share of incubation on air temperature. In a few pairs, male share was higher at the beginning of a three-day movie sample, but this trend was not significant over all pairs (Friedman $\chi^2 = 2.0$, d.f. = 2, $P = 0.5$). There was also no difference between male share of incubation when it was raining compared to periods with no rain (Mann-Whitney $z = 1.7$, $P = 0.09$).

The imbalance of the daylight division of labor raises the question of which sex incubates at night, since it lasts about 10 hr, and the nest is incubated (see below). Males

were usually on the nest at nightfall, and males were found on the nest in 4/5 checks made between 2100 and 2200. The one female found on the nest at this time was being trapped, which probably disturbed the normal pattern. In movie samples made in 1980, females were on the nest at first light on 33/39 days, and males were on the nest at last light on 38/55 days. Thus the female might relieve the male any time between last light (usually 2030) and first light (usually 0615). In 1981 at Matagorda Island I made time-lapse movies at night (2200 - 0600 hrs) at 3 nests, using an electronic flash and a timer that triggered the camera at 17 - 25 min intervals. In every frame that a bird was visible, the bird faced the camera and could be sexed, and it was always the male. At dawn the orientation of the bird on the nest changed, and it could not be sexed accurately, but it looked like the female. Thus the changeover appears to occur just before dawn. This would nearly equalize the time spent on the nest per day by each sex. Two of the males in the 1981 movies were banded and studied on Nests 5-80 and 6-80, and in 1980 they had daylight incubation shares of only 15% and 7% respectively (Table 2).

The division of labor in behaviors other than incubation could also be unequal, and if the male did a larger share this could also balance the division of labor over the whole breeding season, as is expected in monogamous breeding systems (Trivers 1972). Territory defense was too rare at most nests to make a meaningful estimate of its division of labor,

but at Nest 23-79, territory defense was common enough over a four-day period to make a comparison possible. This nest was in an "island" of salt flat habitat created by a spill-way cut at Laguna Atascosa, and it was surrounded by grass-land habitat not used by shorebirds. The spatial isolation of the habitat probably explains why Pair 23-79 had frequent territorial conflict with an unmarked pair of Wilson's Plovers with three young chicks, and a pair of Willets with a chick.

Territory defense at Nest 23-79 is shown in Table 3. The male spent 2.0 - 7.5% of his time displaying, which was active territory defense, including chases, parallel walks, puffed-breast displays, and broken-wing displays (given to Willets) (see Appendix E). He spent 8 - 17% of the samples alert, which was also part of territory defense. The female spent less time displaying (0 - 2.2%), less time alert (1 - 11%), and more time incubating than the male in all four samples, which totalled 29.2 hr. The male also had more bouts of displaying than the female in every sample, indicating he was more likely to respond to intruders, but the female had longer mean display bouts than the male in two samples. This indicated that once she responded to an intruder the bout might be long. The female sometimes displayed with the male, joining him in a parallel walk at one point.

Male share of incubation in these four samples ranged from 10.6% on 10 June to 28.3% on 14 June, and male share of

TABLE 3

DIVISION OF LABOR IN TERRITORY DEFENSE BY PAIR 23-79

Date	Sex	OOS	Incubate	Alert	Display	No. bouts	Mean bout (min)	Time
6/9	M	.183	.145	.112	.032	15	.71	1308-
	F	.039	.641	.112	.020	5	1.3	1836
6/10	M	.209	.063	.088	.075	18	1.6	1419-
	F	0	.529	.011	.015	7	.82	1750
6/14	M	.422	.190	.173	.027	10	1.7	0841-
	F	0	.482	.026	.022	5	2.7	1854
6/16	M	.517	.142	.083	.020	8	1.1	1236-
	F	0	.712	.021	0	0	0	1936

OOS = Proportion of time bird was out of sight during sample.

territory defense ranged from 55.1% of 14 June to 100% on 16 June. Willets were the main intruders except on 14 June, when it was the Wilson's Plovers with chicks. Territory defense took much less time than incubation, but it was probably more energy-intensive as well. Territory defense may also involve some risk of bodily harm, although I did not actually see a Willet jab at a plover. I did see Willets jab each other, and one Willet picked up another by the neck, so a Willet could be a dangerous adversary to the much smaller plover. The most likely reason for the high level of territory defense in this pair is the high level of feed-

ing on fiddler crabs in its territory (Chapter 1 and Appendix F). This made the territory attractive to Willets and other Wilson's Plovers.

Discussion

As discussed above, sex roles during incubation are often omitted from studies of breeding biology of shorebirds.

Sexes are dimorphic in most *Pluvialis* species, and the Golden Plover (*P. dominica*) on St. Lawrence Island is reported to have a diurnal pattern of male by day (0700 to 1900) and female by night (which is still light) (Sauer 1962). The Eurasian Golden Plover (*P. apricaria*) usually changes places on the nest every 4 - 5 hr, but at some nests the male incubates most of the day, and the female could be on at night (Bannerman 1961:211). A "male by day, female by night" pattern is also found in several arctic sandpipers, including the Least Sandpiper (Miller 1977), the Western Sandpiper (*C. mauri*) (Holmes 1971). Stilt Sandpiper (Jehl 1973), and the Dunlin (*C. alpina*) (Jehl 1973). Mundahl (1977) trapped 5 Killdeer on their nests at night, and all were male. Daytime incubation is shared roughly equally in Killdeer (Mundahl 1977, Bunni 1959). In the Snowy Plover, Boyd (1972) found through automatic recording that the female incubated most of the day at 3 nests, with the male on the nest for 2 periods of 1 - 1.5 hr each in the morning and late afternoon. The sex of the bird incubating at night could only be determined for 3 nights, and in all cases it was the female,

not the male as in Wilson's Plover and Killdeer. Because Boyd's equipment only recorded arrivals and departures at the nest, and because it was so complex (one bird had a magnet glued on its back that registered when it passed under a coil), his results are less reliable than those for Wilson's Plover and Killdeer. Rittinghaus (1961) watched 12 Snowy Plover nests for 1 day each (0915 - 2115), and found that the female incubates most of the day, and the male always comes to the nest before nightfall, with a mean male share of 34%. In the Chestnut-banded Sandplover (*Charadrius pallidus*), only females were seen on the nest during the day, and almost all birds seen on the nest in the late evening were males (Jeffery and Liversidge 1951). Only the female was seen incubating during the day in *bicinctus* in New Zealand (Phillips 1981), so the male incubated at night if at all. The "female by day, male by night" pattern probably also exists in the Greenshank (*Totanus nebularia*) (Nethersole-Thompson in Bannerman 1961). In the Mountain Plover only one parent incubates most nests, since this species has a rapid multi-clutch mating system (Graul 1973).

An explanation for the "male by day, female by night" pattern in many arctic shorebirds is proposed by Miller (1977). The energetic demands of incubation are greater during the colder night, and the female is better able to incubate then because she is larger (in many sandpipers). Food is probably more available during the day, since most invertebrates are inactive at low temperatures, so the

female can regain energy lost in egg production by feeding during the day. Similar reasoning can apply to the "female by day, male by night" pattern, although most plovers do not show sexual dimorphism in size. Mundahl (1977) proposes that night incubation by male Killdeer enables the female to "feed, seek shelter, or reduce energy expenditure," and that risk of predation to the incubating bird might be greater at night than during the day. This investment by the male could thus balance the investment by the female in the eggs (Trivers 1972). The argument on relative energy expenditure of day and night incubation requires data on the energetic costs of incubation, which are not available for Wilson's Plover. Night incubation requires warming the eggs, even in Texas (Chapter 5), and day incubation requires little warming. The energetic costs of cooling the eggs are unknown, but Wilson's Plover uses both panting and gular flutter when incubating during the hottest part of the day. Gular fluttering has never been reported in any Charadriiformes, but it is a very efficient means of dissipating heat in other birds (Dawson and Hudson 1970), so the costs of daytime incubation may be relatively low.

Foraging and predation may also be factors in the diurnal division of labor in Wilson's Plover. Audubon (1840) reports that Wilson's Plover "feeds as much by night as by day," and its eyes are large relative to its head size. The prey of Wilson's Plover (invertebrates) is probably more active in the cooler evening and night than during the day,

so by incubating in the evening and at night the male may enable the female to gather more food than she could at other times. On the subject of predation, many of the potential predators on adults are nocturnal mammals, and the paler breast band of the female could make her less conspicuous than the male to diurnal predators.

The explanation for the higher male share of incubation during clutch completion is probably that the female is expending a great deal of energy on egg production at that time, which limits the amount of time she can spend incubating. Incubation during clutch completion is somewhat irregular in Wilson's Plover (Chapter 1), as it is in most shorebirds, and the male is able to do most of it in spite of fairly high levels of courtship and territory defense during this period (Chapter 1). The increase in male share of incubation during the hatching stage has been explained by Miller (1979) as a reduction in female share because of her earlier energy expenditure on egg-laying. It is also possible that this increase reflects the change in parental shift patterns at hatching (Chapter 4), when shifts become shorter in both sexes. This may be related to the rapid removal of eggshells, which is probably facilitated by short parental shifts, or possibly to the off-duty parent caring for the first-hatched chicks near the nest. The main point is that there are reasons for more equal sharing of incuba-

tion during hatching that have nothing to do with the energy balance of either parent.

In conclusion, male share of incubation is significantly higher during the clutch completion and hatching stages of incubation compared to the middle stage. During the middle stage, most males did less than a third of the incubation done by the pair, and there was a significant variation in male share of incubation between pairs. Male share was significantly higher during the evening than during the rest of the day. Parental shift length was longer in females than in males in all pairs during the middle stage, and this pattern was reversed in two pairs during clutch completion and one pair during hatching. There was no difference in male share of incubation that was related to air temperature. The preponderance of female incubation in most pairs may be balanced by the male incubating all night (found at 3 nests), and by the male taking a greater share of territorial defense (found at 1 nest). The "female by day. male by night" division of labor that appears to exist in this species could be related to changing energetic costs of incubation, diurnal changes in food availability, or possibly to diurnal changes in risk of predation.

CHAPTER III

MALE INCUBATION

Introduction

Male incubation, defined as exclusive incubation by the male, is thought to be a necessary step in the evolution of polyandry from monogamy in birds. When the female has time to gather more food, she can lay clutches more rapidly, which may be an advantage under certain conditions (Emlen and Oring 1977, Graul 1973). Polyandry is then possible if the female can mate with other males for successive clutches.

This is the first report of male incubation in Wilson's Plover, a strictly monogamous shorebird (Tomkins 1944 and unpubl. data). Males incubated alone at three nests for a total of 31 days of incubation, documented by 215 hr of behavioral samples at these three nests. At 14 other nests in 1980, the males' average share of daylight incubation was 27% (range 7-44%), which is significantly less than 50% ($t = 5.21$, $df = 13$, $P = 0.0002$, using arcsine transformation).

Methods

Nesting behavior of Wilson's Plovers was studied during two breeding seasons at two locations on the coast of Texas. In 1979 450 hr of behavioral observations were made at 15

nests at Laguna Atascosa NWR, Cameron County, Texas. Focal-animal samples (Altmann 1974) were made on both parents at a nest, dividing their behavior into feeding, displaying (including all social behavior), preening, incubating, alert standing, and out of sight. Data were analyzed using the CRESCAT system (Kaye 1977). In 1980, time-lapse movie samples at 1-minute intervals were made of 900 hr of parental behavior at 15 nests on Matagorda Island, Aransas NWR, Calhoun County, Texas. The movies were analyzed with an editor with a frame counter. Using time checks on the film, single frames were converted to instantaneous samples (Altmann 1974) of behavior at the nest. Behavior was classified as sitting on eggs, standing over eggs, standing near nest, or out of sight. Nests were numbered consecutively each year, and pair number corresponded to nest number (e.g. Nest 29-79 was the 29th nest found in 1979, and male 29-79 was the male incubating on that nest). At least one parent was color banded at each nest, and the sexes could always be distinguished by plumage. Incubation period was 25 to 26 days, and active nests were found between 5 April (young chicks seen 1 May) and 17 July. Data presented here show incubation time, defined as the estimated percent of daylight hours spent incubating, by each parent and by males alone after female disappearance. Incubation time was transformed using the arcsine transformation (Winer 1971) for all statistical tests.

Results

In 1979, males incubated alone at the last two active nests of the season, 26-79 and 29-79. Female 26-79 disappeared between day 10 and day 18 of incubation, while I was not watching the nest. From 28 June (day 18) onward, I watched this nest for 52 hr during all periods of the day, and saw only the male incubating. All three eggs hatched in this nest on 6 July, and the chicks were led away by the male and not seen again.

For comparative purposes, average incubation time, as percent of time spent incubating, is shown in Figure 4 a for 9 nests at which both parents incubated. The females were on the nest about 60% of the time, and the males about 20% of the time, between 0700 and 1730. Between 1731 and 2100, the females' incubation time decreased and the males' increased, so that each was about 40%. Total incubation time for the day was 76%. Figure .4 b shows incubation time for Nest 26-79, before and after female disappearance. Total incubation time for this nest before disappearance was 89%, and male incubation time was 28%, but after disappearance the male incubated 73% of the time, which is similar to the average for pairs.

At Nest 29-79, the female was seen on the nest on the afternoons of days 7, 9, and 11 of incubation, but not on the afternoon of day 10 (1 July). She was not seen on or near the nest during 97.5 hr of observation between days 14 and 26 of incubation. Figure 4 c shows incubation time for

FIGURE 4: Incubation time in Pairs and Lone Males.

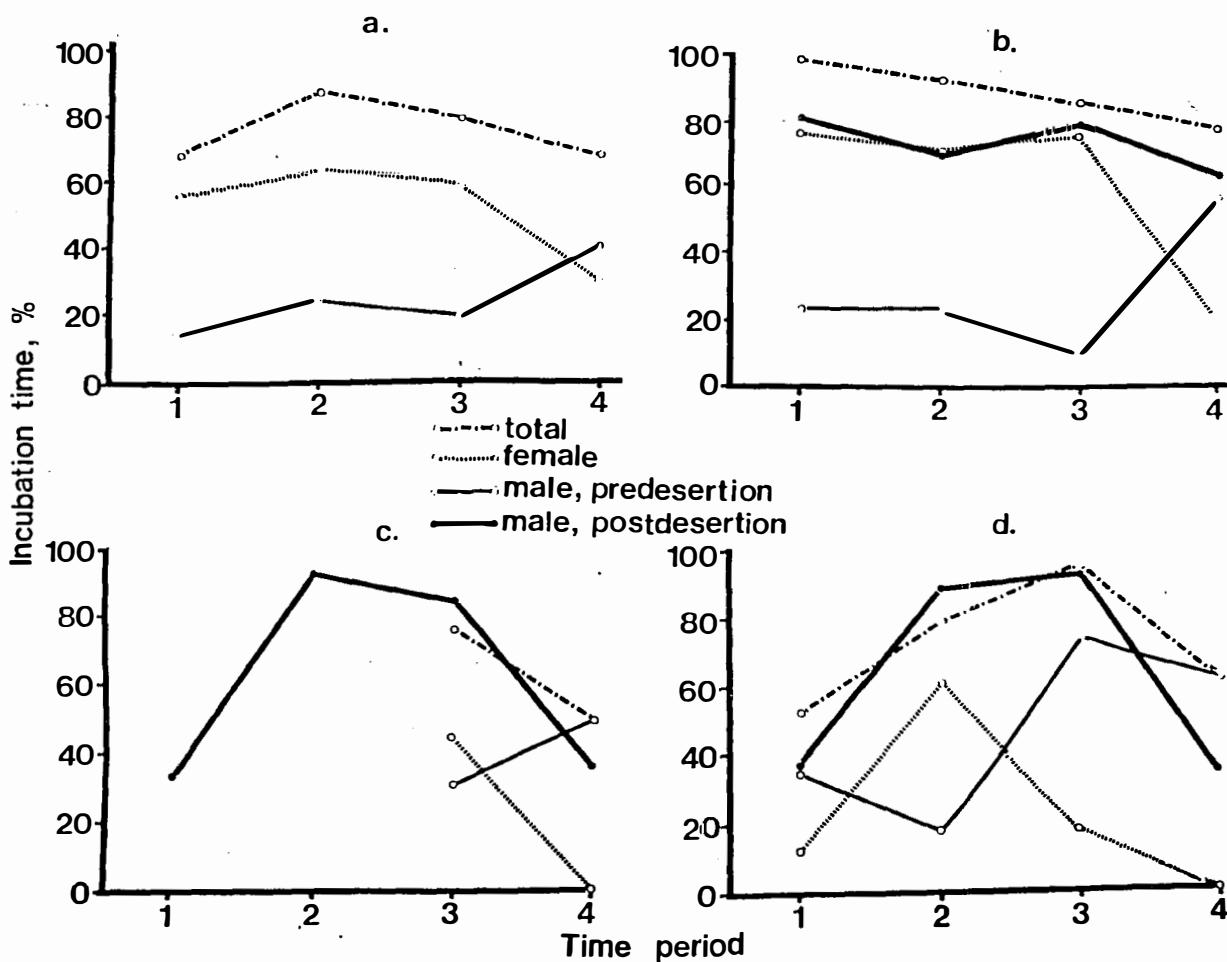
Incubation time, % of time spent incubating, for Wilson's Plover. Time period 1 = 0700 - 1030, 2 = 1031 - 1400, 3 = 1401 - 1730, 4 = 1731 - 2100.

a : Average times for 9 nests at which both parents incubated (1979 data).

b : Nest 26-79 before and after female disappearance.

c : Nest 29-79 before female disappearance (1401-2100 only) and after disappearance.

d : Nest 29-80 before and after female disappearance.



this nest before and after female disappearance. During 9.5 hr of observation prior to her disappearance, total incubation time was 65% and male incubation time was 41% (data available only for 1401-2100). After her disappearance the male's incubation time increased to 60% during this period, but he had had unusually low incubation time between 0700-1030 and 1731-2100. He made long trips away from the nest at these times, presumably to feed. Since this nest also hatched successfully, on 17 July, none of his absences led to lethal heating of the eggs.

Male 29-79 was seen with his chicks a few times after hatching. He led them to one of the few marshes remaining in the area, where he defended a territory around the chicks at the edge of the water. Table 4 shows time budgets for two intact pairs with young chicks, and for male 29-79 when his chicks were two days old. Male 29-79 fed more near the chicks, was alert less and displayed less near the chicks, and was out of sight more than the total for intact pairs. He spent only 21% of the sample attending the chicks (alert, display, and brood), compared to 50-80% for the intact pairs. This reduction in time spent attending the chicks may have been the result of his incubating alone for 12 days.

One case of male incubation occurred on Matagorda Island in 1980. At Nest 29-80, the female was trapped and experimentally removed from the nest on the morning of day

TABLE 4
TIME BUDGETS OF PAIRS AND LONE MALE WITH CHICKS

Pair	Sex	Alert	Dis-display	Brood	Feed	Other	OOS	N
21-79	M	10	8	0	0	2	80	315
	F	34	49	0	1	0	16	
Unknown	M	21	6	0	4	6	63	613
	F	30	1	0	12	10	47	
29-79	M	5	5	11	33	9	37	125

Other = Fly, preen and rest.

OOS = Out of sight, usually away from chicks.

N = Sample size in min.

Pair 29-79: female out of sight throughout sample.

17 of incubation (12 June), and returned on the morning of day 18. She did not come to the nest during the rest of day 18, and was not seen again. In time-lapse samples made throughout days 22-24 of incubation, the male incubated alone. Hatching began the next day, 20 June, and all three eggs hatched. Figure 4 d shows incubation time for this nest on day 16, before removal, and for the male alone on days 22-24 of incubation. (Incubation time at the start of day 16 was somewhat reduced, as it was at most nests, by the recent placing of the camera.) Male 29-80 had higher incubation time than most males prior to the female's

disappearance, and his incubation time after disappearance was almost identical to that of male 29-79 when he was alone (Figure 4 c). Before female removal, total daily incubation time was 71%, and male incubation time was 48%. The male alone incubated 58% of the time on day 22 (which had a camera-placement effect similar to that on day 16).

One other removal experiment was done in 1980. The male was removed from Nest 21-80 on the morning of day 16 (9 June) of incubation, and returned on the morning of day 17. During his absence the female incubated 75% of the time, and he first incubated at 1703 on the day of his return. He was on the nest 42% of the time between then and nightfall, with no incubation by the female after 1703. This is a normal male incubation time for this period (Figure 4 a), but the female usually incubates as well. Each of the removed birds lost 10 g (15% of their body weight) during 24 hr of captivity, so it is surprising that male 21-80 undertook a normal load of incubation only 9 hr after his release. I made 15.5 hr of focal-animal samples on pair 21-80 on days 21-23 of incubation, and average daily incubation time for the pair after removal was 81%, compared to 88% before removal. Female incubation time was 66%, compared to 49% before the removal. One egg disappeared from this nest during days 21-23, one egg hatched, and one egg was left in the nest. The two eggs in the nest on day 24 floated high in water, indicating both were close to hatching.

Discussion

Males of many species of shorebirds in which both sexes incubate are reported to take an increasing share of incubation as it proceeds, and this has been shown statistically for the Least Sandpiper (*Calidris minutilla*) (Miller 1977). However, exclusive male incubation has only been documented in a few species of monogamous shorebirds. The best documented case of male incubation is the Killdeer (*C. vociferus*). In a study of 39 Killdeer nests, Bunni (1959) reported exclusive male incubation at 3 nests, lasting for 2, 9, and 11 days per nest before hatching. All three were second nests at the end of the breeding season, which appears to be when male incubation occurs in Wilson's Plover. Male incubation sometimes occurs for briefer periods before hatching in the Least Sandpiper (Miller 1977) and in the Dunlin (*Calidris alpina*) (Soikkeli 1967). Only one parent incubates at most nests of the polygamous Mountain Plover (*C. montanus*), and this species has a diurnal incubation pattern (Graul 1975, Fig. 4) very similar to that of males 29-79 and 29-80 (Figure 4 c & d).

Male incubation leads to female emancipation and the possibility of additional clutches, but it does not follow that male incubation is the result of selection for female emancipation. Other selective pressures could produce male incubation, and selection for female emancipation might begin after male incubation existed. One hypothesis is that the female deserts because she is in worse condition than

the male due to the stress of egg-laying, and her chance of survival would decrease if she did not desert (Graul 1973, Ashkenazie and Safriel 1979). This hypothesis has not been tested directly on known pairs, but Ashkenazie and Safriel (1979) showed that random samples of female Semipalmated Sandpipers (*Calidris pusilla*) decreased in weight more rapidly than similar samples of males as the season progressed. They also estimated that females had 15% higher energy requirements than males during the breeding season, due mainly to egg-laying. Another hypothesis is that there is an advantage to uniparental care at the end of the breeding season. An increase in the local food supply caused by the removal of one of the parents has been proposed by Pitelka (1959) as a possible advantage of uniparental care. This theory predicts that either sex could desert, but only females appear to desert in Wilson's Plover and Killdeer. However, these two hypotheses are not mutually exclusive. There could be an advantage to the female in deserting, and an advantage to the reproductive success of the pair in uniparental care. No data are available to isolate these hypotheses, and they are difficult to test separately since both are related to the food supply.

Male incubation in Killdeer is thought to follow female desertion (Bunni 1959), but the possibility that missing females died rather than deserting cannot be ruled out, since the females were not seen after they stopped incubating. However, there were three other broods of Wilson's

Plovers seen at the end of the breeding season in 1979 in addition to 26-79 and 29-79, and all three were also cared for by lone males. Since these were the only cases of mate loss seen that year, I suspect that they were the result of desertion rather than the coincidence of five female deaths. Female desertion after hatching is common in several monogamous shorebirds, including the Killdeer (Lenington 1980).

In conclusion, the absence of one parent caused the remaining parent (three males and one female) to increase its incubation time significantly (paired $t = -3.34$, $df = 3$, $P = 0.022$), but it also caused a significant decrease in total incubation time at the nest (paired $t = 3.52$, $df = 3$, $P = 0.019$), apparently without reducing hatching success. Thus the division of labor during incubation in Wilson's Plover is highly flexible, allowing the male to do all the incubation for up to 12 days (male 29-79), and for the female to do all the incubation for at least 1.3 days (female 21-80). This flexibility pre-adapts this species for the evolution of polygamy, especially polyandry (Emlen and Oring 1977). Sequential polyandry and simultaneous polygyny have been reported in the Snowy Plover (C. alexandrinus) (Warriner and Warriner 1978) and sequential polyandry and possible polygyny have been reported in the Mountain Plover (Graul 1973). In addition, the results show that in the morning and evening, incubation time can be as low as 34% (Figure 4 c & d) without causing hatching failure. The

question of why pairs normally incubate more than this minimum is discussed in Chapter 6.

Male incubation should be looked for in other monogamous shorebirds at the end of the breeding season, because it could have been overlooked in earlier studies. To test hypotheses about male incubation, estimates of changes in food availability through the breeding season are needed, as are successive weighings of known pairs through the breeding season, and data on breeding success of lone males and pairs. Ideally, data on the fates of absent females should be collected.

CHAPTER IV

FACTORS AFFECTING INCUBATION BEHAVIOR

Introduction

Wilson's Plover is a small, ground-nesting, monogamous shorebird that practices bisexual incubation. Bisexual incubation is defined as incubation by both sexes alternately (Skutch 1957). Because Wilson's Plover nests on the ground on exposed salt flats in hot climates, both the parents and the eggs are exposed to large temperature fluctuations during the incubation period (23° to 41° C. at my study site in Texas). Incubation behavior should show thermoregulatory responses to these extremes of temperature, and thus air temperature should have a large effect on incubation behavior.

However, it should also be possible for two parents sharing incubation to keep the nest incubated virtually all the time, since in so many bird species one sex incubates alone. If one parent can manage to incubate 60-80% of the time on its own (Skutch 1962), incubation time could approach 100% if shared roughly equally by two birds. This line of reasoning, and data on the Herring Gull (*Larus argentatus*), a bisexual incubator, led White and Kinney (1974) to conclude that bisexual incubation should be essentially constant, with a parent on the nest almost all the time, independent

of air temperature. Herring Gulls incubate about 98% of the time independent of air temperature, and regulate egg temperature by adjusting their "tightness of sit" (Drent 1970), or degree of contact between eggs and brood patch.

One problem with the prediction of near-constant incubation by bisexually incubating birds is that it assumes that the energetic costs of incubation, and the time and energy required for self-maintenance, are about the same for different species. If the energetic costs of incubation were higher in a bisexual incubator than in a single-sex incubator, or time required for self-maintenance were higher in the bisexual incubator, the prediction might not hold. Bisexual incubation could be an advantage in stressful environments where costs of incubation are high, because the cost is spread over two adults rather than one. Under such circumstances each incubating parent might not be able to incubate half the time, and total incubation time might be less than 100%.

Another problem with the prediction of constant incubation by bisexual species is that it assumes the pair will incubate the maximum amount possible. This appears to be true for Herring Gulls (Drent 1970), but there are no single-sex incubators among the gulls for comparison. Perhaps the Herring Gulls are actually incubating the minimum amount necessary to ensure successful hatching of the eggs. This is suggested by the fact that in colonial nesters such as gulls, unattended eggs are quickly destroyed by neighbors

(Skutch 1957). Thus the minimum level of incubation time in gulls is probably set by social behavior, not by egg temperatures. Wilson's Plover is a non-colonial nester, and neighbors do not destroy unattended eggs, so incubation time is most likely to be constrained by egg temperature, which in most birds must be kept between about 32° and 42° C. to ensure hatching (Lundy 1969).

Asssuming that parents may incubate less than the maximum amount possible is comparable to the assumption made about lizard time budgets by Kiester and Slatkin (1974), that individuals will attempt to maximize the "free time" in their time budget. The "free time" is the time left over after all self-maintenance activities have been completed, and one of the main things it can be used for is social behavior.

If incubating Wilson's Plovers attempt to increase their time off the nest, they should incubate at least as much as is necessary to keep the eggs within the optimum temperature range for development, but not necessarily 100% of the time. This should result in a dip in incubation time when air temperatures are in the "thermal neutral zone", about 30 - 35° C., when egg temperatures should be stable without the egg being incubated (White and Kinney 1974). When air temperatures exceed this range, parental attendance should again be required to keep the eggs from overheating (Purdue 1976, Grant 1979, Maclean 1967). If the parents do not attempt to increase their time off the nest, incubation time should be more or less independent of air temperature.

Data Collection and Reduction.

Incubation behavior of Wilson's Plovers was studied during two breeding seasons at two locations on the coast of Texas. In 1979, 450 hr of behavioral samples were made at 15 nests at Laguna Atascosa National Wildlife Refuge, Cameron County, Texas. Focal animal samples (Altmann 1974) were made on both parents at a nest, using behavioral categories feeding, displaying, preening, incubating, alert standing, and out of sight. Data were reduced (converted from sequential records to calculated durations of behavioral states) using the CRESCAT system (Kaye 1977). An incubation bout is defined as an uninterrupted occurrence of incubation ("sessions", Skutch 1962, "attentive periods", Kendeigh 1952). There are 808 incubation bouts in the 1979 sample, and CRESCAT was used to calculate the time of day each bout started and its duration in minutes for each sex. They were re-sorted by start time using SAS (SAS Institute 1979), and lengths of absences were determined by subtracting the time of the end of one incubation bout from the time of the start of the next incubation bout. Five types of absences were classified: 1) between two male bouts, 2) between two female bouts, 3) between a male and a female bout (in that order) a female and a male bout, and 5) between bouts of a male incubating alone (see below). Incubation time was defined as the proportion of a time period that

either parent was sitting or standing on the nest (= "incubation constancy", Skutch 1962, "attentiveness", Kendeigh 1952). It was calculated with SAS using the formula of Skutch (1962): Incubation time = mean incubation bout length / (mean incubation bout length + mean absence length). Rather than using the whole day as the unit of analysis, as Skutch (1962) and Kendeigh (1952) did, I divided the daylight hours into four equal periods of 3.5 hr each: 0700-1030, 1031-1400, 1401-1730, and 1731-2100. In this way I hoped to preserve meaningful diurnal variation in air temperature, since mean daily air temperature is fairly constant in Texas in the summer but there is a pronounced diurnal pattern. Air temperature for each time period was determined from readings taken every 3 hr at Brownsville Airport (NOAA 1979), which is located about 50 km SSW of the study area. In order to make these air temperatures directly comparable with temperatures measured near the ground at the study site in 1980, I transformed them using a regression of 1980 air temperatures on temperatures from another airport in 1980 (see below). This regression was highly significant ($F = 326$, $r = 0.86$), and the transformation had no effect on the significance or R^2 value of regressions in which the transformed temperatures were used. The only effect was to change the coefficients of the regressions, making them more comparable to 1980 regressions. Using TV for temperature at Victoria (in °F.) and TM for temperature at Matagorda (in °C.), the equation (with

standard deviations in parentheses) is: $TM = -25.7(2.3) + 0.67(.03) TV.$

In 1980, time-lapse movie samples at 1-min intervals were made of 900 hr of parental behavior at 15 nests on Matagorda Island, Aransas National Wildlife Refuge, Calhoun County, Texas. The movies were analyzed frame-by-frame with a Goko MM-1 editor with a frame counter. Using time checks on the film, single frames were converted to point samples of behavior (Altmann 1974). The number of minutes per frame was calculated for each interval between time checks, and the clock time for each change of behavioral state was calculated by the formula: clock time = (number frames since time check) \times (minutes/frame) + (time at last time check), using a programmable calculator. Behavior was classified as: standing over eggs (eggs showing under bird), sitting on eggs (eggs not showing), standing near nest, or out of sight. Sexes were identified by plumage, and at least one parent was color banded at each nest. Days were divided into the four periods using the calculated clock times, and incubation time for each period was calculated by dividing the number of frames in which a bird was on the nest (sitting or standing) by the number of frames during the period. Mean absence was calculated as the mean length of absences (periods when the nest was uncovered) during the time period. Since the minimum recordable absence was 1 minute, this may be a biased estimate of the true mean absence length, but it was felt that the longer absences are the

most important ones to the parents and the eggs. Mean bout length was calculated as: mean bout = (incubation time x mean absence) / (1 - incubation time), since it was not calculated directly for 1980. Parental shift lengths, or the time between successive nest reliefs, were calculated from the 1980 data using SAS. It was assumed that shifts shorter than 1 minute were very unlikely (none that short were seen by direct observation) and that if they did occur and were unrecorded they were of minor importance, since most shifts were much longer than 1 minute (see below). Although the 1979 data was made in continuous samples rather than point samples, it was not used because shifts were often longer than the sampling periods in 1979.

Two additional components of incubation behavior were calculated that were not available from the 1979 data. Shading time was calculated as the (number of frames standing / total number of frames) for each incubation bout. Orientation on nest was scored by counting the number of frames in which the bird on the nest was facing the sun, lateral to the sun, or back to the sun, for 2 hr periods between 0700 and 1900. The lateral total was divided by two because there are two ways to be lateral to the sun, and the results were summed and the percent of time spent in each category was calculated for each time period. Grant (1979) used the same method of data reduction, except not with movies.

Air temperatures were recorded in 1980 near nests that also had movie samples being made of them. Temperature was measured with an Atkins No. 3 probe in a thin stainless steel sheath, which was placed about 5 m from the nest in a small clump of vegetation, about 5 cm off the ground. Nest temperature was measured simultaneously (see Ch. 5). Temperatures were recorded with an Atkins telethermometer connected to a Rustrak 2-channel strip-chart recorder powered by an automobile battery. Time checks were placed on the strip chart each time they were placed on the film, and the telethermometer was calibrated both before and after each 3-day movie sample with a mercury thermometer accurate to the nearest 0.1° C. The air temperatures were compared to air temperatures measured by the National Weather Service at Victoria Airport (NOAA 1980), about 100 km inland from Matagorda Island, and the temperatures I measured were usually 2 - 3° C. higher than those at Victoria. This regression was used in transforming the 1979 temperatures (see above). Additional weather data used from Victoria included: wind speed in knots, relative humidity, and rainfall in inches. Rainfall amounts were checked against daily totals for Port O'Connor, only 17 km from Matagorda on the coast of the mainland, and there was a good agreement with amounts in Victoria. Per cent possible sunshine was obtained from Corpus Christi Airport, 167 km SW of Matagorda, because this is not measured at Victoria.

Data Analysis

Analysis of the effects of various independent variables on mean incubation bout length, mean absence length, incubation time, and shading time were done using multiple regression and multiple stepwise regression techniques in SAS (SAS Institute 1979). Before analysis, mean incubation bout length and mean absence length were transformed to improve normality using the log transformation, and incubation time and shading time were transformed with the arcsine transformation (Winer 1971). After transformation the distribution of the variables did not differ significantly from the normal distribution (KSLTEST procedure, SAS). Orientation on the nest was analyzed without transformation using the Friedman 2-way analysis of variance (Siegel 1956). This non-parametric procedure was chosen because the question of interest was whether or not orientation was random with respect to the sun. The data were not precise enough to answer additional questions about orientation.

A different type of analysis was done on the durations of incubation bouts and absences in the 1979 data, and on parental shift durations in 1980, using the raw data rather than means taken over time periods. I did survival or life-table analysis of both incubation bouts and absences, using the SPSS program SURVIVAL (Nie and Hull 1979). This type of analysis has been used on behavioral data by S. Altmann (in prep.) on foraging behavior in baboons, by Fitzpatrick (1981) on foraging behavior in flycatchers, and by

Wiley and Hartnett (1980) on aggressive behavior in juncos. It has never before been used to analyze incubation behavior. It has two advantages over regression analysis: it does not assume that the variable is normally distributed, and it takes into account censored bouts (bouts which continued after the sample ended). It also can answer questions about the data that regression cannot, especially questions about the structure of the time budget. An examination of the hazard rate, which is the chance that a bout will end during a specified interval given it has survived up to that interval, will show whether the hazard rate changes with time or is independent of time. If the hazard rate is any power function of time, it has a Weibull distribution, which gives a numerical expression of the relationship between hazard rate and elapsed time (S. Altmann pers. comm.). This was done by a regression of $\ln(\ln(S(t))^{-1})$ on $\ln(t)$, where $S(t)$ is the probability that a bout will last at least t minutes. The slope of this line estimates the parameter β . The parameter a was calculated from: $a = \exp(-m/\beta)$ where m is the y-intercept of the regression. The parameter β is the shape parameter: for $\beta < 1$ the hazard rate is a decreasing power function of time, and for $\beta > 1$ the hazard rate is an increasing power function of time. The parameter a is the "characteristic time to failure" of the Weibull distribution, the 63rd percentile of the hazard rate distribution. This analysis was not done on the 1980 data because it was not obtained from continuous samples, as

the 1979 data was, and thus the data on bout lengths for 1980 are not precise to be used in survival analysis.

There were 808 incubation bouts recorded in 1979, and 759 of those were uncensored (recorded from beginning to end). Only uncensored absences were analyzed, because I felt that censored absences were likely to be the product of human disturbance and thus be somewhat unnatural. Various grouping variables were used to look for significant differences between the survival distributions of different groups. Grouping variables included sex (with lone males as a third sex), low/mid/high temperature, and stages of the incubation period. Survivorship distributions were compared using the Lee-Desu statistic D, which tests if two sets of data have the same survivorship distribution. The test statistic D has approximately the Chi-square distribution (Hull and Nie 1979).

Results

Regression Analysis of Incubation Behavior

Effect of Air Temperature on Incubation Time

Incubation time was significantly dependent on air temperature in both 1979 and 1980. Theoretical considerations, as well as an initial examination of the data, suggested that a curvilinear model was needed, since the response to temperature was strikingly nonlinear. In both years incubation time decreased with increasing air temperature up to

about 31° C., and above that point it increased with increasing air temperature. A quadratic multiple regression model in which there is a negative coefficient for temperature and a positive coefficient for $(\text{temperature})^2$ fit these data well. Multiple regression equations for the two years of the study are shown in Table 5.

Through stepwise regression I had found previously that pairs incubated significantly more than lone males at a given temperature. For this reason the regressions in Table 5 were done separately for pairs and males in each year. One problem with this separation is that because the lone males were incubating at the end of the breeding season, they only incubated when temperatures were high, so the full range of air temperatures is not shown in the data for males. As a result only the $(\text{temperature})^2$ term was significant in the regression equations for males, and the temperature term was excluded. The equation titled '1980 Means' used the 1980 pairs data with mean incubation time calculated for each time period for each pair. This was done because sample sizes were not equal on each pair in the original data, and this equalized sample sizes at four points per pair. However, this also had the effect of removing some of the unexplained variance in the regression model, because the R^2 value was higher for 1980 means.

The data points and the regression of incubation time on air temperature for 1980 pairs are shown in Figure 5. The same concave upwards curve resulted from the regression on

TABLE 5
TRANSFORMED INCUBATION TIME REGRESSIONS

Group	Intercept	Temp.	Temp. ²	R ²	F	P	N
1979 Pairs	42.89	-2.59	0.041	34%	11.2	.001	45
1980 Pairs	17.25	-1.01	0.017	46%	67.2	.001	157
1980 Means	16.83	-1.01	0.017	65%	49.3	.001	55
1979 Males	-1.65	-	0.0032	20%	5.4	.029	23
1980 Males	0.768	-	0.0011	21%	6.5	.017	26

Temperature term non-significant for lone males
(1979 Males and 1980 Males).

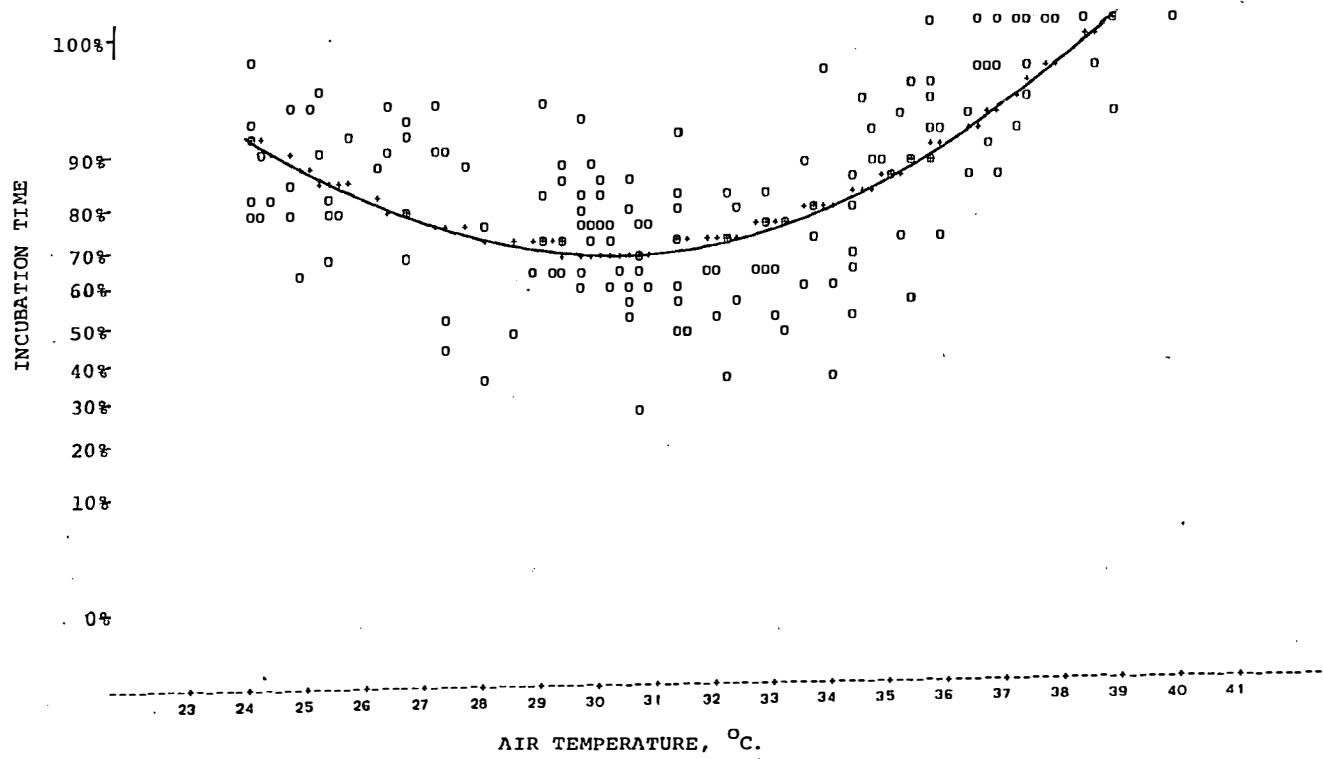
N = number of 3.5 hr time periods; for 1980 Means, each observation is the mean value for one time period over 2 - 6 days per pair.

the 1979 data, but the range of air temperatures was narrower. This dip in incubation time occurred exactly where it was predicted, in the "thermal neutral zone" (White and Kinney 1974) around 30° C.

The technique of dividing the daylight hours into four equal periods appears to have worked well for these data in showing the response of incubation time to air temperature. Air temperature must be one of the most important factors affecting incubation time in this species, since it explained 20 - 65% of the variance in the data. It is unlikely that this is due to common correlation with another

FIGURE 5: Quadratic Regression of incubation time on air temperature for Wilson's Plover pairs, 1980.

Original values of incubation time are shown on the Y-axis on the scale of the arcsine transformation. Symbols: 'O' = data point, curve is line fitted by quadratic multiple regression ($R^2 = 46\%$).



variable. Using longer time periods would eliminate some of the variance in temperature, while using shorter periods would increase the between-period variance in incubation time, so the 3.5 hr periods appear to be a useful compromise. Using shorter periods would also make it less likely that incubation time in one period is independent of incubation time in other periods.

Other factors affecting Incubation Time

No other independent variables were selected in stepwise regression. Other independent variables used were: relative humidity, percent possible sun, wind speed, rainfall, day of incubation, day of season, and day of sample (within each 3-day movie sample). In addition several dichotomous variables were not selected: whether the nest was successful or not, whether the nest was on pavement or soil (1980 only, see Ch. I), whether the period was near the beginning of a 3-day sample or not, absence or presence of rain, and amount of male incubation. It is possible that if some of the weather variables, especially wind, had been measured at the study site they would have had a significant effect on incubation time. One unmeasured variable was whether or not the sun was behind a cloud. Incubating birds often went to the nest when the sun was out, and left the nest when it was behind a cloud (see Chapter 5). Of course, sun also affects air temperature.

Effect of Air Temperature on Mean Absence

Mean absence also varied significantly with air temperature in both years of the study. The pattern of mean absence vs. temperature was the inverse of the incubation time-temperature relationship. The longer mean absences at moderate temperatures contributed to the dip in incubation time at moderate temperatures, although there was also a dip in mean incubation bout length at moderate temperatures (see below).

Regressions of mean absence on temperature are given in Table 6. As with incubation time, lone males differed significantly from pairs, so the regressions were done separately. Males had significantly longer absences than pairs. Note that the temperature coefficient is now positive and the (temperature)² term is negative, and that the R² figures are somewhat lower than for incubation time. The temperature term also dropped out of the model in the male regressions for the same reason as in incubation time.

A plot of data points with fitted curve is shown in Figure 6 for 1980 pairs. The longest absences are taken at moderate temperatures. Note that the slope of the regression line is steeper as it approaches high temperatures than as it approaches low temperatures. This is as expected because thermoregulation of the eggs is more critical in the 36-40° C. range than in the 24-28° C. range (Lundy 1969).

TABLE 6
TRANSFORMED MEAN ABSENCE REGRESSIONS

Group	Intercept	Temp.	Temp ²	R ²	F	P	N
1979 Pairs	-111.0	7.28	-0.12	21%	5.5	.007	43
1980 Pairs	-17.19	1.30	-0.02	40%	51.8	.001	156
1980 Means	-13.94	1.11	-0.02	48%	24.3	.001	55
1979 Males	6.88	-	-0.004	10%	2.5	.13	24
1980 Males	3.67	-	-0.001	13%	3.5	.07	25

Non-significant regressions shown for 1979 and 1980 Males for comparison purposes.

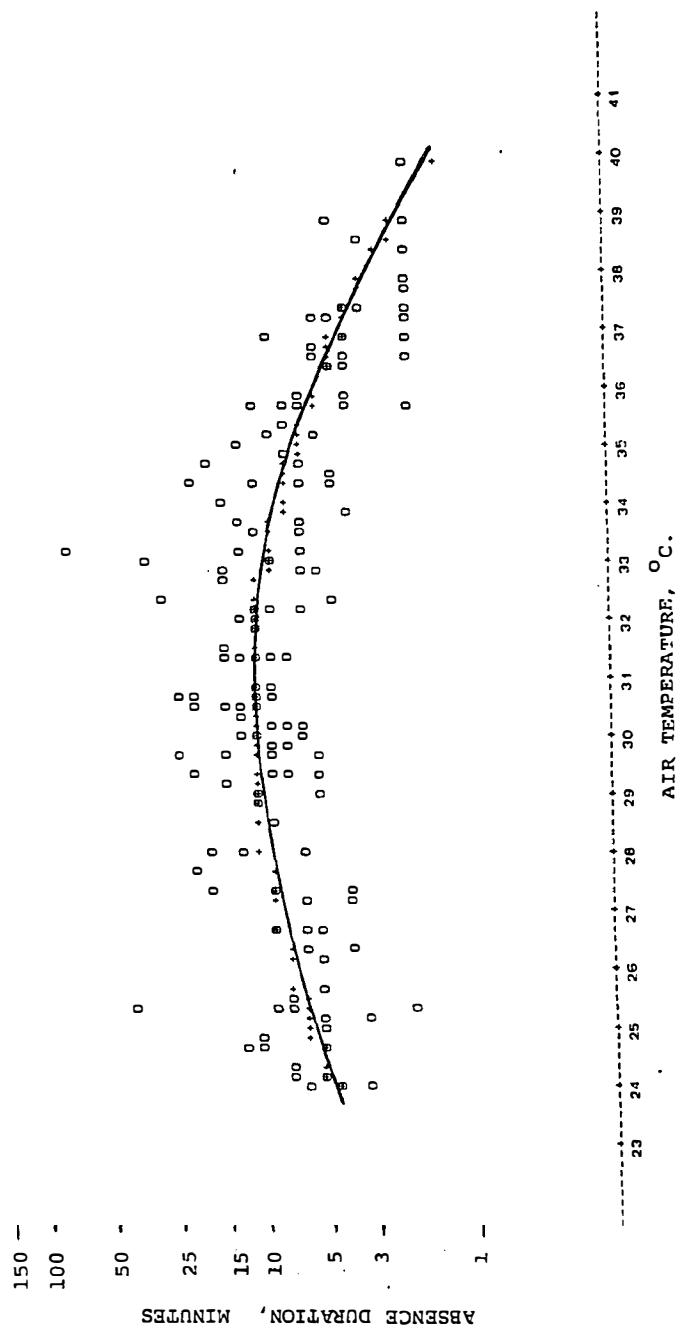
N = number of 3.5 hr time periods analyzed (means over 2 - 6 days for 1980 Means).

Other Factors Affecting Mean Absence

In stepwise regression of other independent variables on mean absences, one other variable was selected. This was a dummy variable that was 0 if the nest was on pavement, or 1 if the nest was on soil (1980 pairs data only). This had a coefficient of +0.256, indicating that absences were longer on soil than on pavement, and it explained an additional 2% of the variance (R^2 went from 48% to 50%). The shorter absences on pavement were probably caused by the fact that

FIGURE 6: Regression of mean absence on air temperature for 1980 pairs.

Mean absence on a log scale vs. air temperature for 1980 pairs. Data points = 'O', curve = line fitted by quadratic multiple regression ($R^2 = 40\%$).



the pavement gets hotter than the soil in the afternoon (pers. obs.), and the eggs might overheat on pavement if absences were too long (see Chapter 5). The retention of heat by pavement could possibly make longer absences possible later in the day, but this might occur after dark (see Ch. 5). The pavement usually still felt warm at nightfall.

Effect of Air Temperature on Mean Incubation Bout Length

Mean incubation bout length also varied significantly with air temperature. Although incubation time is determined by mean incubation bout length and mean absence length (see Methods), several different patterns of incubation bout length would be consistent with the above results. The observed response of incubation bout length to temperature in Wilson's Plover is in fact different from the response in other shorebirds, even though the responses to temperature of incubation time and mean absences are similar to those of other shorebirds (see below).

Regressions of incubation bout length differed from the above regressions in that pairs and lone males did not differ in the response of bout length to temperature. Thus the following regressions were not done separately for pairs and males, except that the data for 1980 means only include data on pairs.

Regressions of transformed mean incubation bout length on air temperature are shown in Table 7. Much less variance is explained by these regressions than the above regressions

(14 - 16%), except for 1980 pair means. Excluding the males from the 1980 data only raised the R^2 value from 16% to 18%, but when means were taken of the pairs data the R^2 value went up to 53%, or an improvement of 35%. This large improvement shows that some of the unexplained variance is due to variance between days over the same time period, since this variance was removed by taking means. A plot of this regression for 1980 data is shown in Figure 7.

TABLE 7
TRANSFORMED MEAN INCUBATION BOUT REGRESSIONS

Group	Intercept	Temp.	Temp ²	R ²	F	P	N
1979 Pairs& Males	49.98	-2.96	0.046	14%	6.0	.004	76
1980 Pairs& Males	20.82	-1.18	0.020	16%	15.3	.0001	162
1980 Pair Means	39.01	-2.50	0.043	53%	29.5	.0001	54

N = number of 3.5 hr time periods for which data were analyzed.

Although the increase in mean bout length with decreasing air temperature below about 31° C. is significant, it is not nearly as dramatic as the increase in mean bout length with increasing temperature above 31° C.. As with mean absence, the response to temperature has a steeper slope at high

temperature than at low temperature, possibly because thermoregulation of the eggs is more critical at high temperatures.

Other Factors Affecting Mean Incubation Bout Length

No other independent variables were selected in stepwise regression. For 1979 these were day of incubation and pair number, and for 1980 these were day of incubation, day of sample, per cent possible sun, wind speed, day of season, and pavement/soil. Survival analysis was found to be more successful than regression in identifying other sources of variance in incubation bout length (see below).

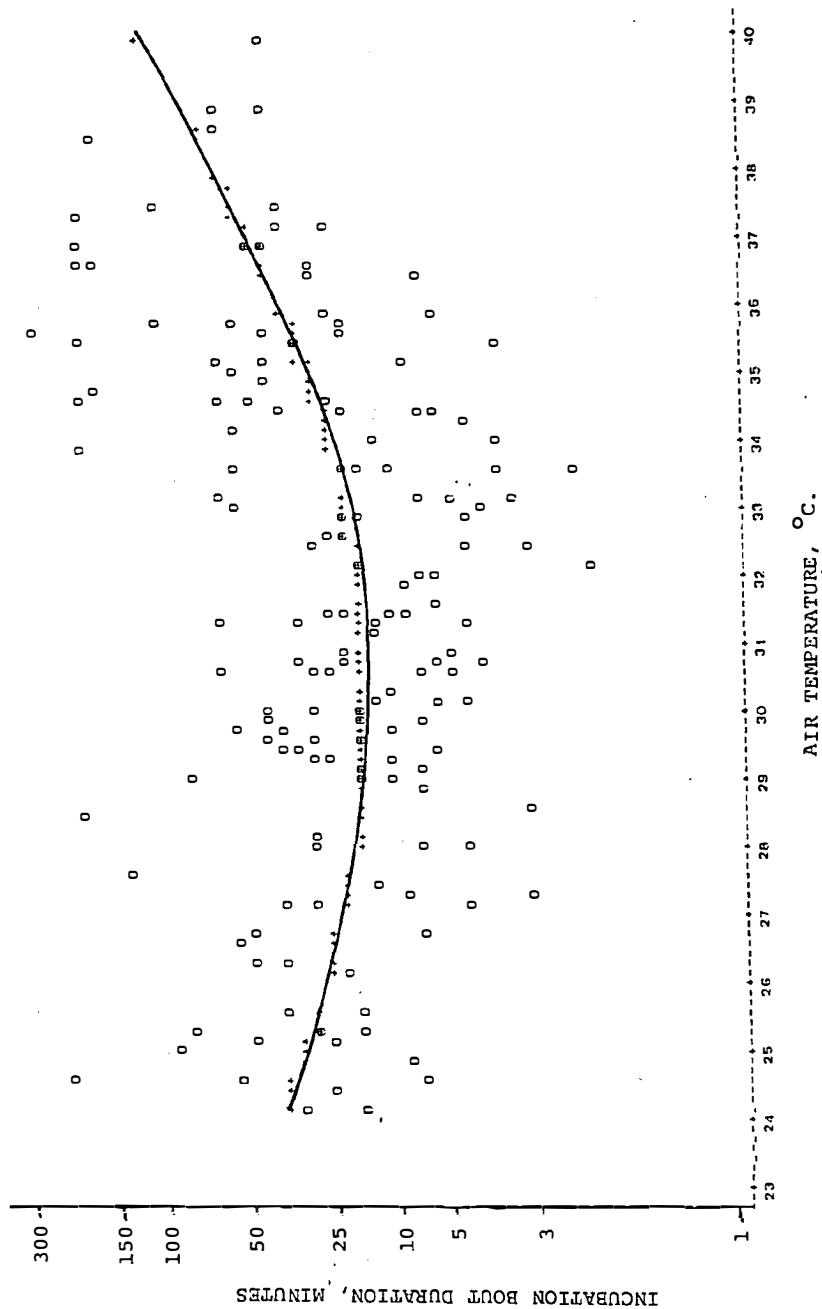
Survivorship Analysis of Incubation Behavior

Survivorship Analysis of Incubation Bout Durations

For this analysis, each incubation bout (or absence, see below) in the 1979 sample was treated as an individual whose life span was given by the duration of that incubation bout or absence. Censored incubation bouts were those which continued after my sample ended, but I excluded censored absences (see Methods). The log survivorship curve of incubation bout durations (Figure 8 a) is not perfectly linear, as it would be if the hazard rate (or chance a bout will end) were independent of the survival time. The curve departs from a straight line after about 20 minutes. An

FIGURE 7: Regression of mean incubation bout length on air temperature for 1980 pairs and males.

Mean incubation bout durations, on a log scale, plotted against air temperature, 1980 pairs and males. Data points = 'O', curve = line fitted by quadratic multiple regression ($R^2 = 16\%$).



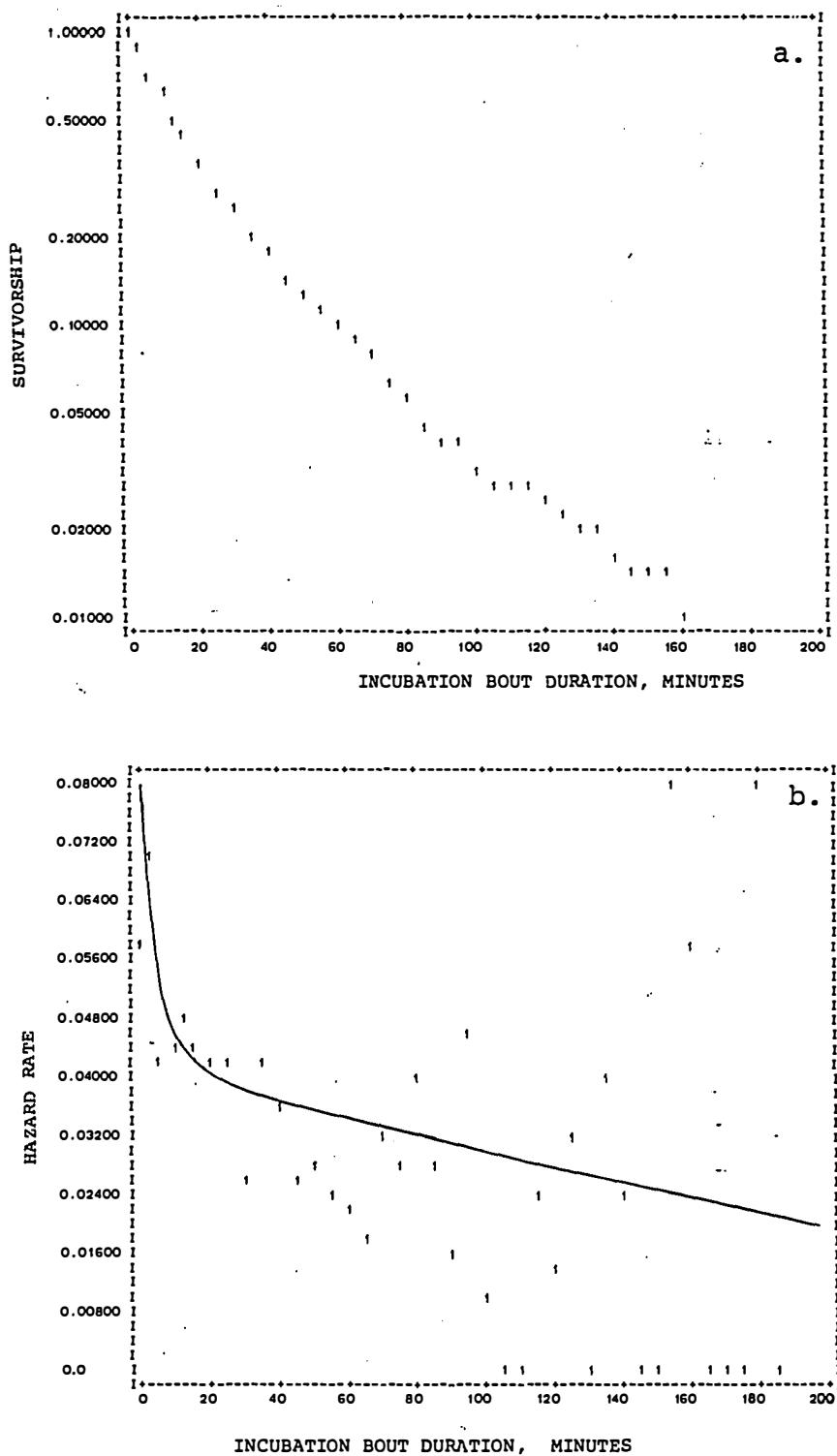
examination of the curve of hazard rate (Figure 8 b) shows that as expected, it is not independent of bout duration. Hazard rate decreases as bout duration increases. It appears that the hazard rate is a power function of time, which is the type of curve which can be fit by the Weibull distribution (S. Altmann in prep.) This is a general form of the exponential survival distribution, and the relevant parameters were found using the method of S. Altmann (in prep.) described above. I found that for incubation bouts β (shape parameter) = 0.759, which indicates the hazard rate is decreasing with time, and a (time to failure) = 18.6 minutes. The curve drawn on Figure 8 b shows the hazard rates predicted from the Weibull distribution. The predicted hazard rate descends steeply until about 30 - 40 minutes, and then it almost levels off beyond that point. This suggests that once an incubation bout has lasted beyond a certain time, its chance of ending is unrelated to how long it has continued, and it is likely to be ended by some external factor, such as the arrival of the partner near the nest. However, this transition in hazard rate at 30 - 40 min after the bout begins could also be related to an external factor affecting incubation bout length, such as air temperature.

Because regressions involving incubation behavior differed between pairs and lone males, incubation bout

FIGURE 8: Plots of incubation bout survival.

a: Log survivorship curve, or probability that a bout will last as long as the time (in min) on the X - axis.

b: curve of hazard rate vs. time surviving, predicted by Weibull distribution (see text).



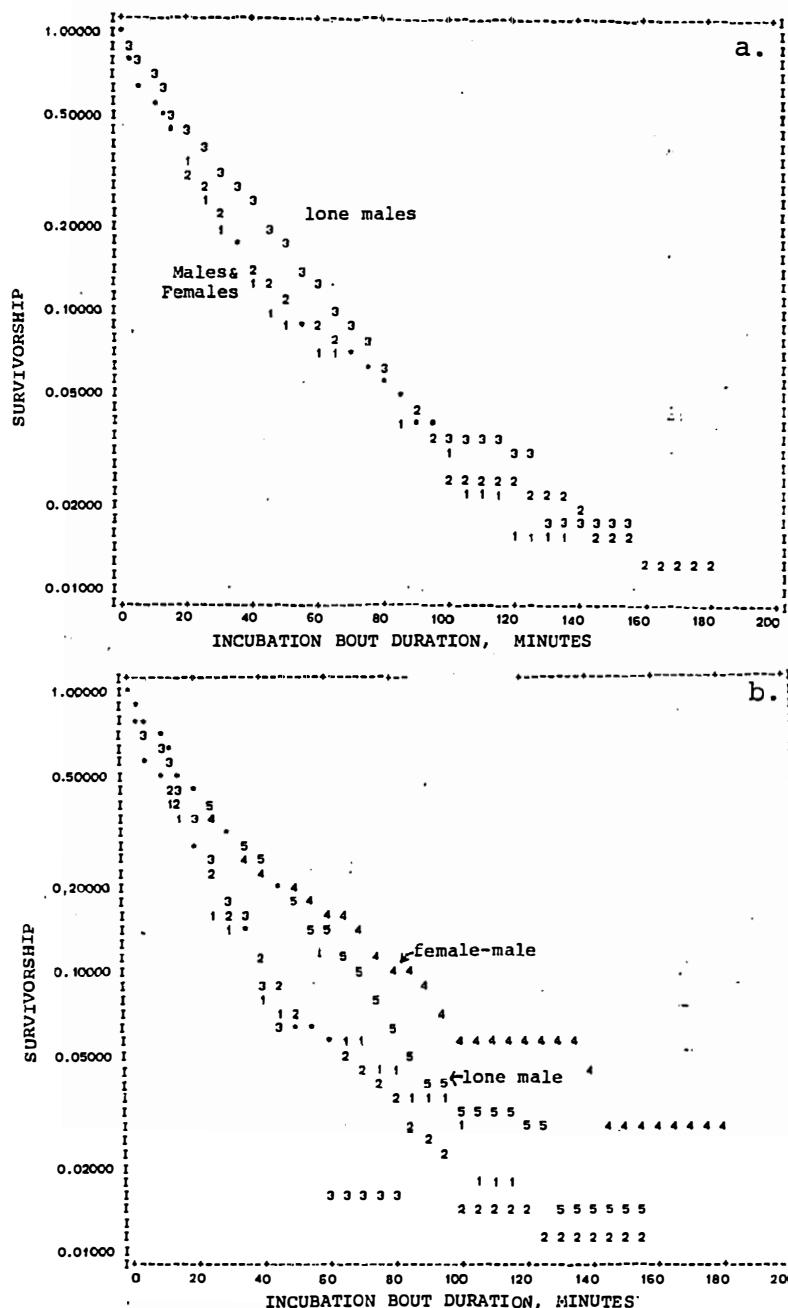
duration distributions were analyzed by sex, subdividing males into those in pairs and those incubating alone. The resulting log survivorship curves are shown in Figure 9 a. Overall the three categories have significantly different survivorship distributions ($D = 15.9$, $P = 0.0003$), but there was no difference in bout survivorship between males and females in pairs. Incubation bouts were significantly longer in lone males than in either males or females in pairs. The most likely explanation for this is that lone males had no partner to relieve them and thus shorten their incubation bouts. In further comparisons I analyzed pairs and lone males separately, as was done for most of the regression analysis.

Within each sex, incubation bouts were subdivided by the sex of the following incubator. Thus male bouts that were followed by male bouts were type 1, female bouts followed by a female bout were type 2, and male-female and female-male bouts were types 3 and 4 respectively. Lone males had only one type of bout, type 5. Figure 9 b. shows the log survivorship curves for the different types of incubation bouts, and the distributions of types differed significantly overall ($D = 37.6$, $P < 0.0001$). Not surprisingly, bouts by lone males had one of the longest median durations (Type 5, 16.2 min), significantly longer than male-male bouts in pairs (Type 1, 9.2 min, $P < 0.0001$). Female bouts that

FIGURE 9: Survivorship plots of incubation bout duration by sex.

a: Log survivorship vs. time surviving for incubation bout durations grouped by sex. Symbols: '1' = males in pairs, '2' = females in pairs, '3' = lone males. Distributions of males and females in pairs did not differ significantly, but other pairwise comparisons were significant.

b: Log survivorship of incubation bout durations grouped by type of bout, based on the sex of the preceding and following incubators. Symbols: In pairs: '1' = male-male bouts, '2' = female-female bouts, '3' = male-female bouts, '4' = female-male bouts. In lone males: '5' = lone male-lone male bouts. Several pairwise comparisons were significant (see text).



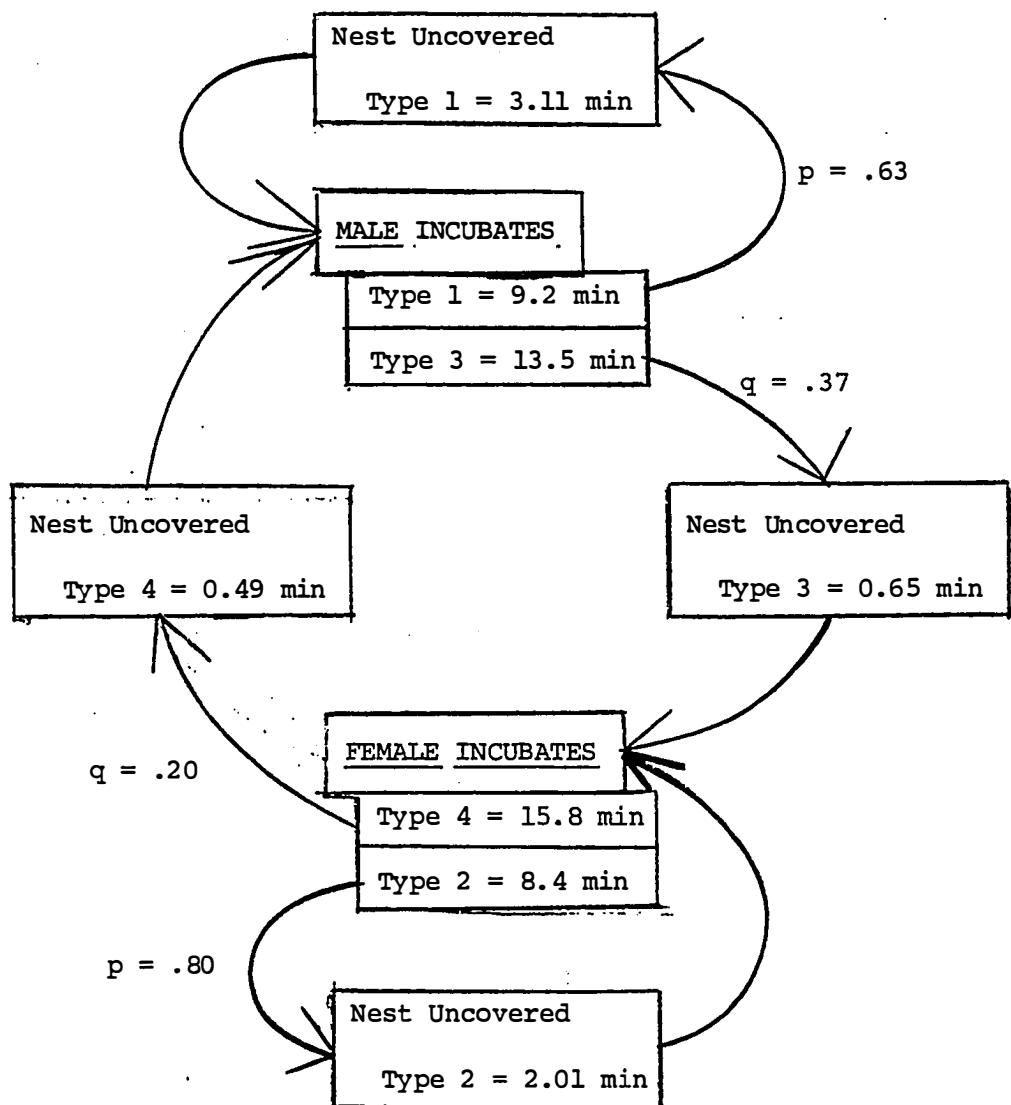
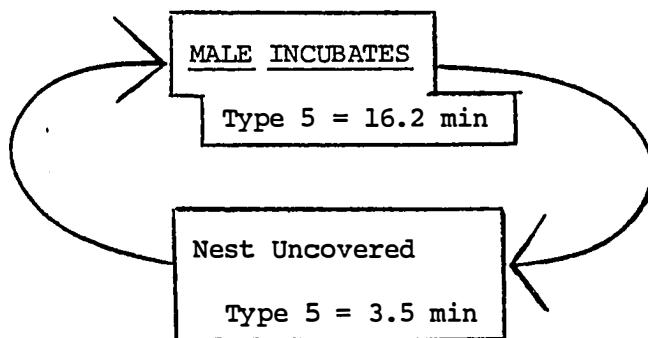
preceded a male bout were almost as long as Type 5 (Type 4, 15.8 min). These were much longer than female - female bouts, with a median of only 8.4 min (Type 2, $P = 0.0008$). The analogous comparison between male bouts (Type 3, 13.5 min vs. Type 1, 9.2 min) was in the same direction, but was not significant. One possible reason for the length of female-male bouts (Type 4) compared to female-female (Type 2) is that the male usually relieved the female on the nest in the late afternoon, when it was usually quite hot, and bouts are longer when it is hot (see above). An intriguing alternative is that the female anticipates the male's relief of her at a certain time of day, and stays on the nest longer than she normally would in expectation of relief.

Because these transitions are complex, they are diagrammed in Figure 10, along with the corresponding types of absences (discussed below) and the median duration of each type of bout and absence. The probability that any given male bout will be followed by a male or a female bout is shown, and the corresponding probabilities for female bouts are also shown. The reader should refer back to this diagram in the discussion that follows.

Survival of incubation bouts was compared at low temperature (below 31° C.), moderate temperature (31-33° C.), and high temperature, and the survivorship differed significantly for both pairs and males. Figure 11 a shows

FIGURE 10: Flow Diagram of Incubation Bouts and Absences.

Flow diagram of possible transitions during incubation in pairs (upper section) and lone males (lower section) in Wilson's Plover. The median survivorship of each type of bout or absence is given in minutes, and probabilities are shown: p = chance that a given bout by a sex will be followed by a bout by the same sex, and q = probability that it will be followed by a bout by the opposite sex. Significant differences exist between some of the durations (see text), and both bouts and absences differed significantly over all types.

P A I R SL O N E M A L E S

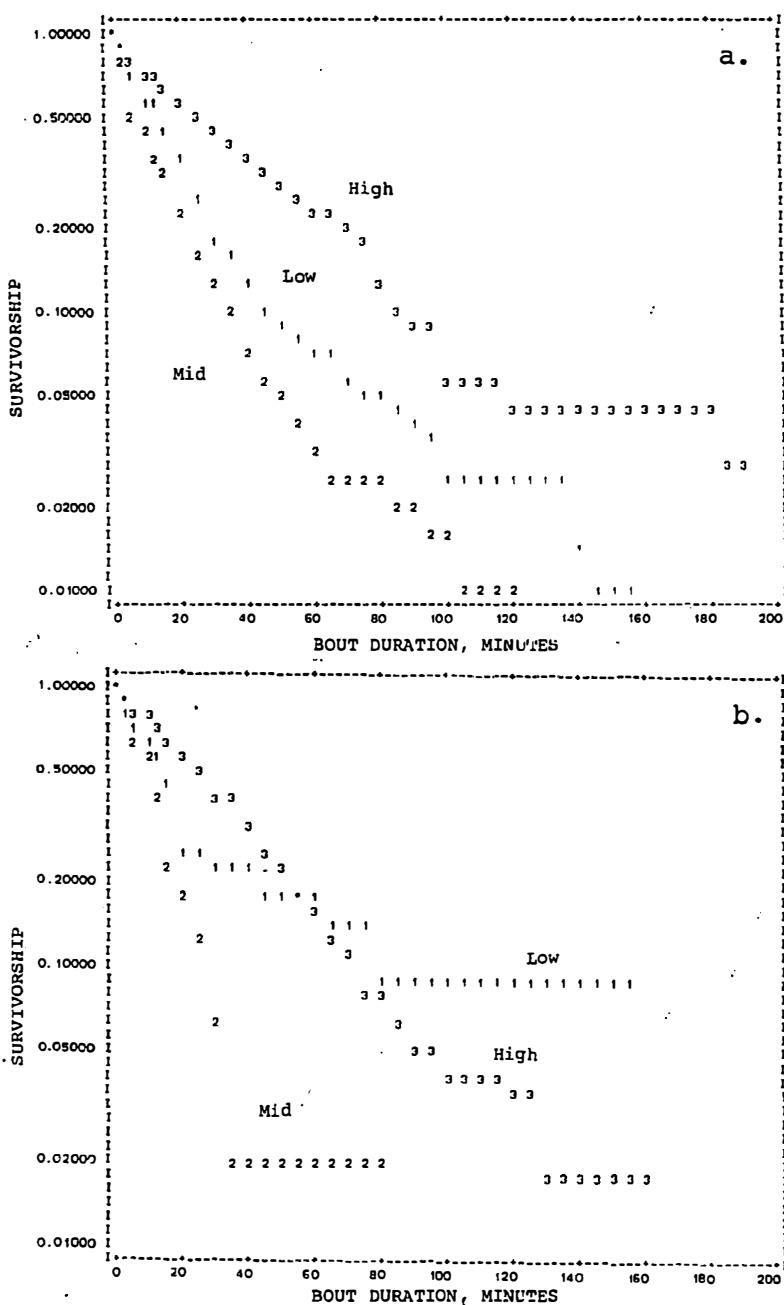
log survivorship for pairs and Figure 11 b shows log survivorship for lone males. The results are in agreement with the regression analysis above: incubation bouts by pairs were shorter at moderate temperatures than at low temperatures ($P = 0.0001$), and at high temperatures incubation bouts were significantly longer than at low or moderate temperatures ($P < 0.0001$ for both comparisons). The pattern was less clear-cut in lone males, but the distributions differed significantly overall ($D = 24.7$, $P < 0.0001$), and incubation bouts were significantly longer at high temperature than at moderate temperature ($D = 24.1$, $P < 0.0001$).

Survivorship of incubation bouts was compared at different stages of the incubation period as follows: clutch completion (days 0-2), middle stage (days 3-23), and hatching (days 24-26). Survivorship differed significantly in the three stages both for pairs ($D = 25.6$, $P < 0.0001$) and lone males ($D = 23.3$, $P = 0.001$). Pairwise comparisons were also significant in pairs, except between the first two stages. The log survivorship function for pairs is shown in Figure 12 a and for lone males in Figure 12 b. In both pairs and lone males the longest bouts occurred in the middle stage of incubation, with shorter bouts during clutch completion and hatching (no data on clutch completion in lone males). The distributions of bouts during the middle stage of incubation are similar in pairs and males, but during hatching the pairs have shorter bouts than the males. This is because during hatching the pairs change places at

FIGURE 11: Survivorship plots of incubation bouts at three temperature ranges.

a: Survivorship plots for pairs at '1' = low temperature (< 31° C.), '2' = moderate temperature (31-33° C.), and '3' = high temperature (> 33° C.)

b: Survivorship plots for lone males over the same temperature ranges with the same symbols.



the nest much more often than during the middle stage of incubation, which reduces the bout length, while changeovers are impossible for lone males. The reason for reduced bout length during clutch completion is that incubation has not reached the normal amount until the clutch is completed or soon after, and during this period many visits to the nest are brief and often interrupted by periods of nest construction (Chapter 1).

Survivorship Analysis of Absence Durations.

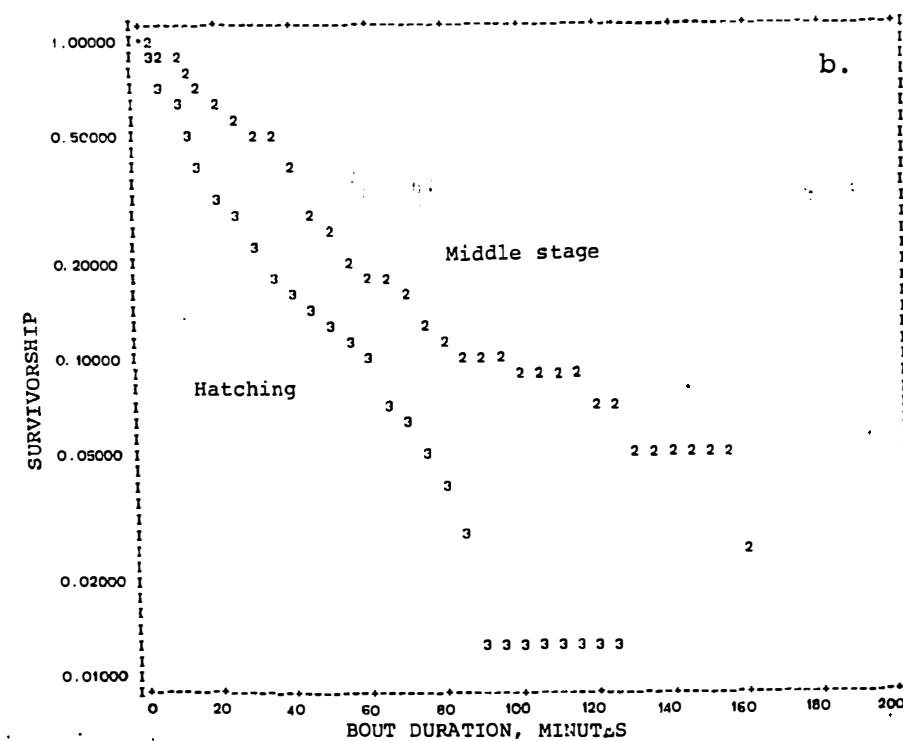
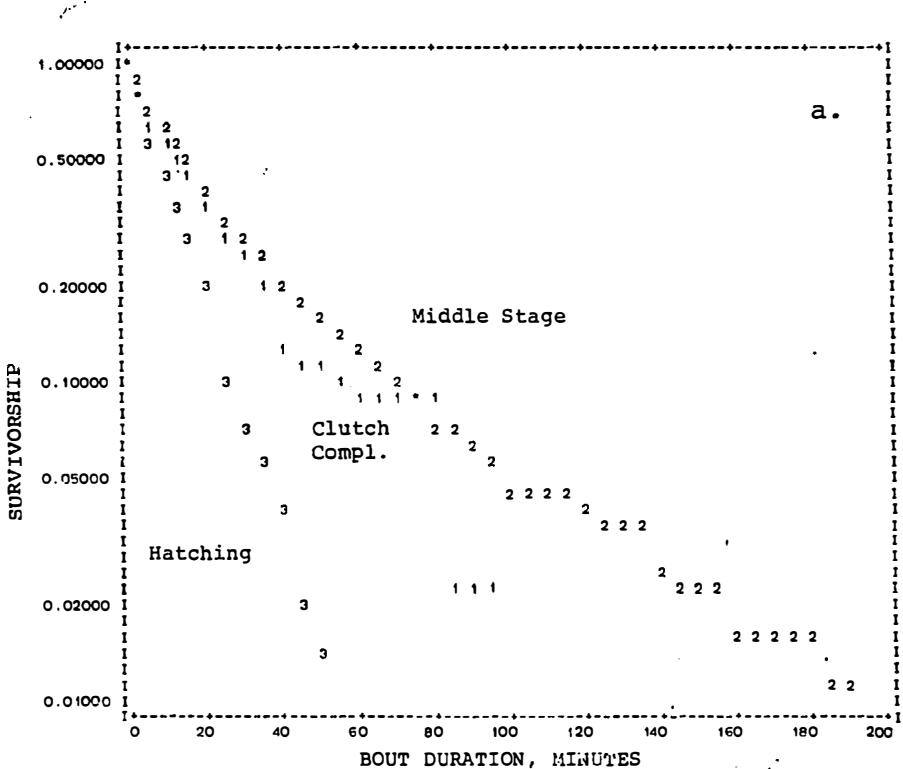
Log survivorship of absence durations is not strictly linear with respect to time (Figure 13 a). The slope of the curve begins to decrease at about 10 minutes. The hazard rate (Figure 13 b) decreases up to about 10 minutes and then levels off. Thus absences become more likely to continue the longer they have continued, as was also found for incubation bouts. As with bouts, this is probably due to the fact that absences occurred under varying conditions, conditions that affected absence length. The longer an absence continues, the more likely it is to be occurring under conditions that favor long absences (e.g. moderate air temperature). Survivorship of absences would have to be analyzed under more uniform conditions to see if they fit a negative exponential distribution. Only 14% of the absences lasted

FIGURE 12: Survival of incubation bouts grouped by stage of incubation.

a: Data for pairs for three stages.

b: Data for lone males for last two stages only.

Symbols: 1 = clutch completion (days 0-2), 2 = middle stage of incubation (days 3-23), and 3 = hatching (days 24-26).



past the 8 minute mark, so a vast majority of the absences were short. Most of the long absences occurred in the late afternoon when temperatures were in the 30 - 32° C. range, or the "thermal neutral zone" (White and Kinney 1974). as far as thermoregulation of the eggs was concerned. They were generally late enough in the day so that direct sun did not hit the eggs. Under these thermally unconstrained conditions, absences ranged up to 220 minutes for one lone male, and it is not surprising that hazard rate is independent of absence duration for long absences.

A Weibull distribution was also fit to the absence survivorship curve, and the resulting parameters were: $\beta = +0.65$, slightly higher than for bouts, and $a = 3.71$ min, much shorter than for bouts, as expected. This was used to calculate the predicted hazard rates in Figure 13 b.

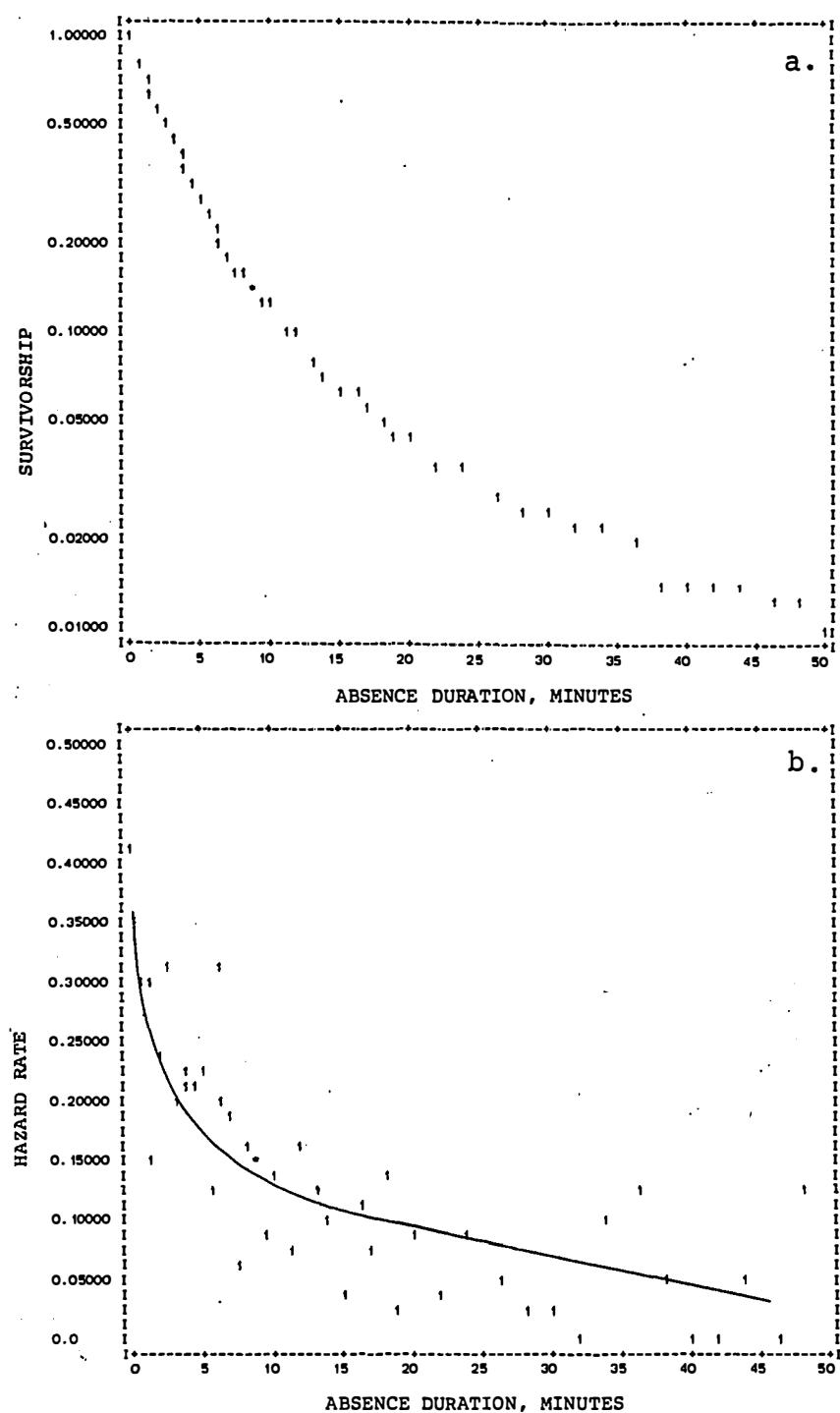
As for incubation bouts, I found that survival of absences differed significantly by sex (male, female, lone male). As a result the subsequent comparisons were done for pairs and males separately. The log survivorship curve for sexes is shown in Figure 14 a. The duration distributions differed significantly between the three sexes ($D = 30.1$, $P = 0.0001$), but there was no significant difference between males and females in pairs. Lone males had significantly longer absences than either sex in pairs.

Comparing absence survival by type (see Methods), I found that male-female (type 3) and female-male (type 4) were the shortest, with respective medians of 0.65 and 0.49

FIGURE 13: Survivorship of absence durations.

a: Log survivorship curve of absence durations vs. time surviving.

b: Plot of hazard rate vs. time surviving, with predicted hazard rate curve fitted by Weibull function (see text).



min. The next shortest absences were female-female (type 2), with a median of 2.01 min. Male-male absences in pairs (type 1) and lone male-lone male absences (type 5) were the longest with medians of 3.11 and 3.50 min respectively. The plot of log survivorship (Figure 14 b) shows that types 2, 3, and 4 had very similar survival, type 1 was longer, and type 5 was the longest, especially after about 12 min. These survival distributions differ significantly ($D = 68.9$, $P < 0.0001$).

Absence durations differed significantly between stages of the incubation period both for pairs ($D = 14.3$, $P = 0.0008$) and lone males ($D = 8.5$, $P = 0.0035$). Absences were longest during clutch completion, when incubation was generally erratic (see Chapter 1), shorter during the middle stage, and shortest during hatching, with all pairwise comparisons significant. The reduction in absence reduction during hatching agrees with the qualitative impression that the parents are unusually attentive to the eggs during this stage. Log survivorship plots grouped by stage are shown in Figure 15 a for pairs and Figure 15 b for lone males. The magnitude of the reduction in absence length during hatching was similar in pairs and lone males, although the males had longer absences than pairs in each stage.

In pairs, absence durations were significantly shorter at high temperature than at moderate and low temperatures

FIGURE 14: Survivorship of absence durations grouped by sex and by type.

a: Survivorship of absence durations grouped by sex. 1 = male in pairs, 2 = female in pairs, 3 = lone male.

b: Survivorship of absence durations grouped by type.
Symbols: In pairs: Type 1 = male-male absences, Type 2 = female-female absences, Type 3 = male-female absences, Type 4 = female-male absences. In lone males: Type 5 = male-male absences. The sexes refer to the incubator preceding and following the absence (see text).

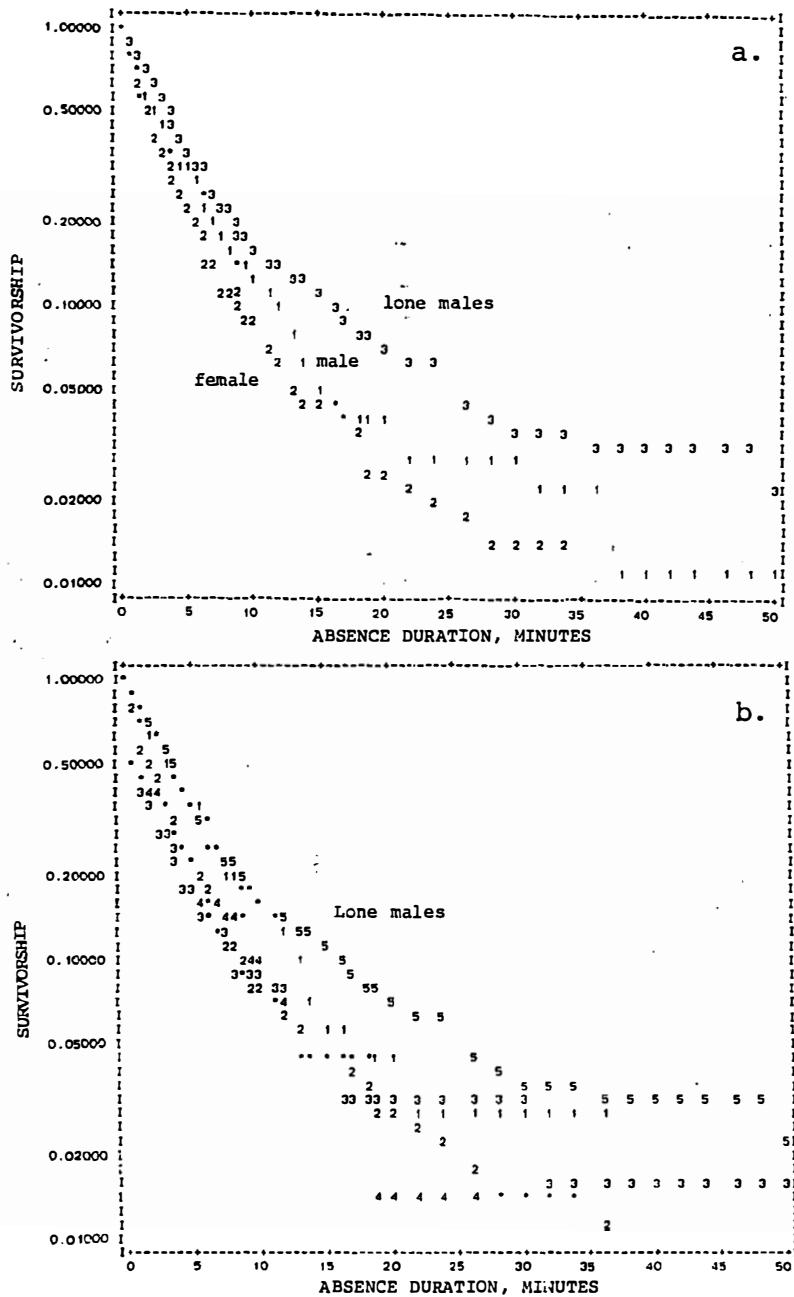
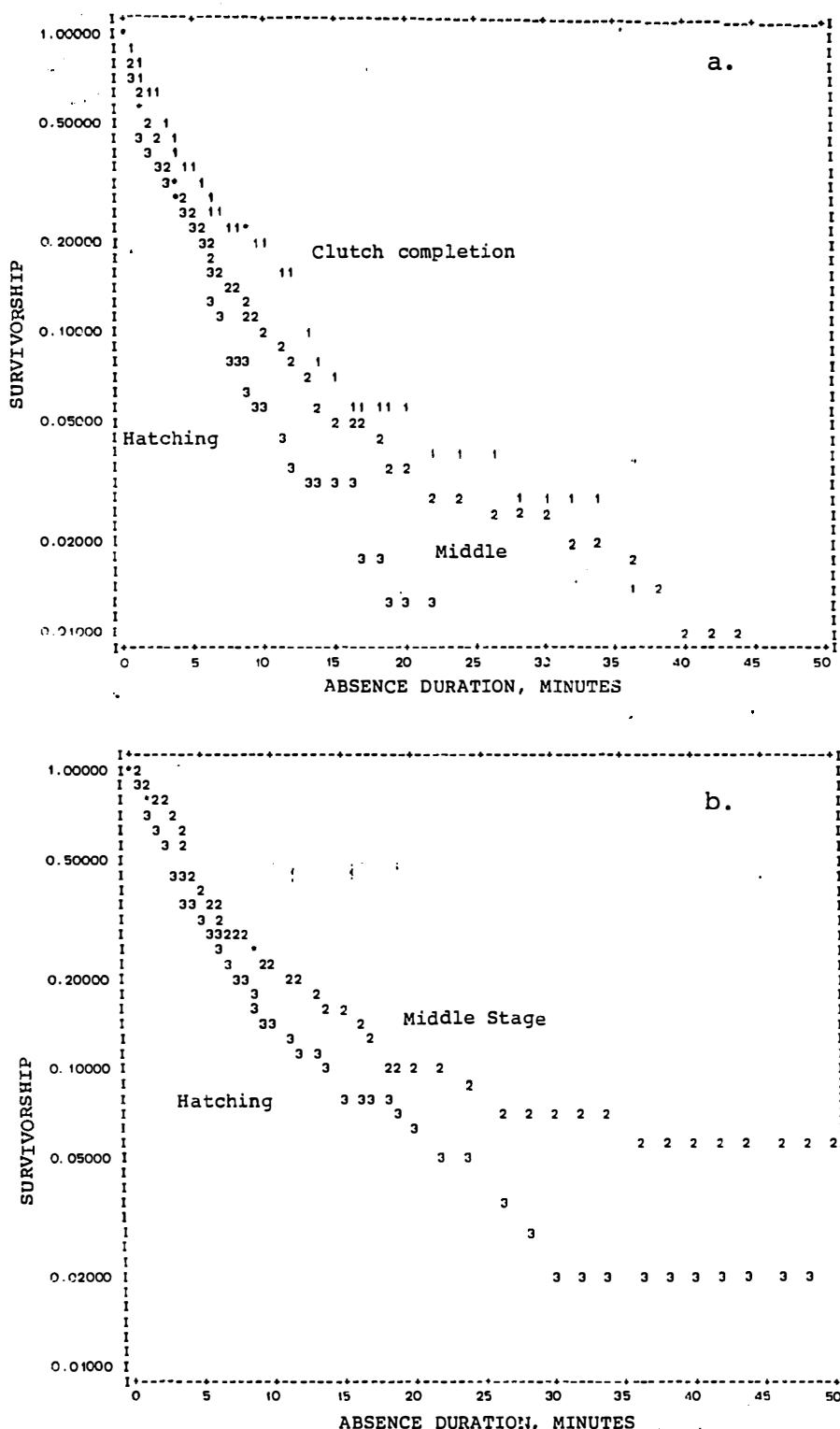


FIGURE 15: Survivorship of absence durations grouped by stages of the incubation period.

a: Log survivorship plot for pairs.

b: Log survivorship plot for lone males (no data for clutch completion).

Symbols: 1 = clutch completion (days 0-2), 2 = middle stage (days 3-23), 3 = hatching (days 24-26).



($D = 10.5$, $P = 0.004$). The distributions did not differ significantly in lone males. The log survivorship plot for pairs is shown in Figure 16 a, and the curve for high temperature is below the other curves up to about 7 minutes, and then it is above the other curves. As already mentioned, 86% of absences were shorter than 8 minutes, so this represents a few long absences that occurred in the high temperature group. Regression shows the effect of air temperature on absence more clearly than survivorship analysis. The regression of mean absence duration on air temperature was non-significant for lone males, as was the survivorship comparison. The log survivorship plot for lone males is shown in Figure 16 b.

Survivorship Analysis of Parental Shift Lengths

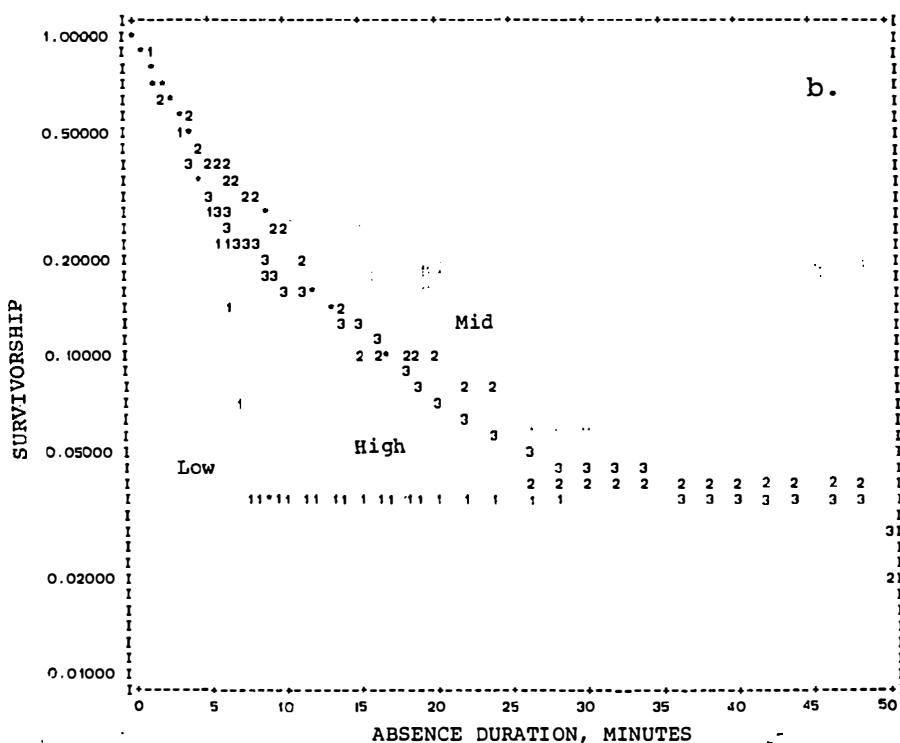
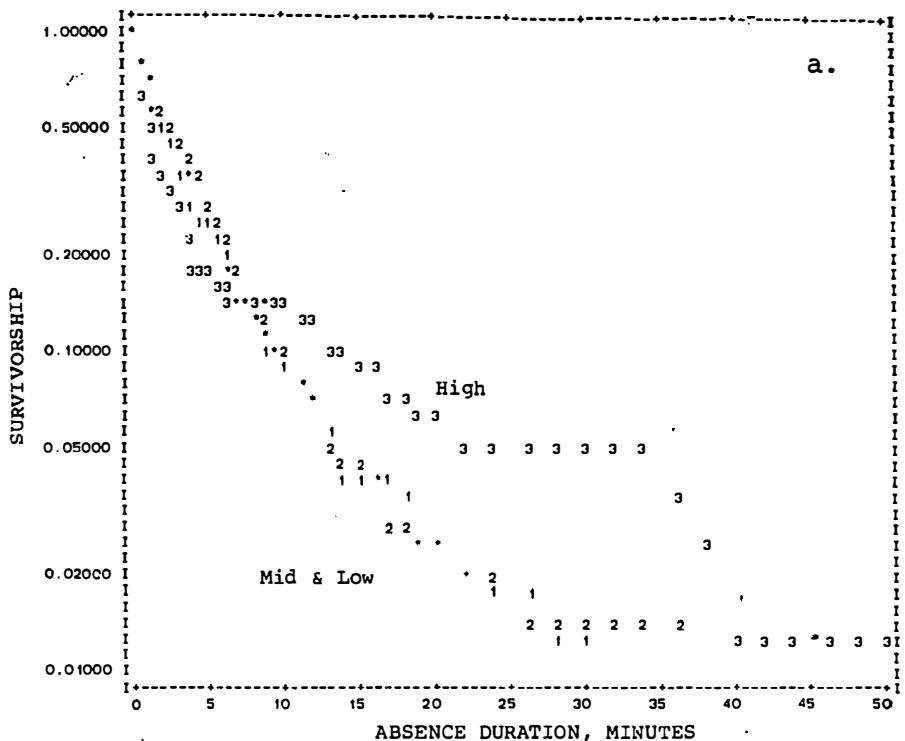
Each parent usually did more than one incubation bout and absence before being relieved by its mate, and thus the time between nest reliefs, or parental shift length, was longer than incubation bout lengths. A log survivorship plot of parental shifts is shown in Figure 17 a, and the longest shifts were over 850 min, when the female incubated all day at a few nests. As with incubation bouts and absences, the decrease in hazard rate with increasing shift duration shown in Figure 17 b could be due to shifts occurring under different conditions. The shape parameter β is 0.54 for shifts, and time to failure a is 143.2 min for shifts, much

FIGURE 16: Survivorship of absence durations at low,
moderate, and high air temperature.

a: Log survivorship plot for pairs.

b: Log survivorship plot for lone males.

Symbols: 1 = < 31° C., 2 = 31 - 33° C., 3 = > 33° C. The
distributions differed significantly for pairs only (see
text).



longer than for incubation bouts. As found in Chapter 2, shifts were significantly longer in females (Figure 18 a). When shift durations are compared by temperature ranges, there is a slight but significant decrease in shift duration above 33° ($D = 9.3$, $P = 0.01$), but no difference in shift duration between low and moderate temperatures. This is shown in Figure 18 b. Parental shift lengths were also compared between stages of the incubation period, shown in Figure 18 c. Shifts were longest during clutch completion (when the male did most of the incubation, Chapter 2), shorter during the middle stage, and shortest during hatching (when incubation bouts and absences were also short). As for incubation bouts during hatching, the log survivorship curve of shifts is the most linear during hatching, and thus closest to a negative exponential distribution. This indicates that something independent of shift duration causes shifts to end during hatching. The removal of egg-shells from newly hatched chicks was associated with shift change during hatching, and the relieving parent often came to the nest before the relieved parent left the nest. The dramatic reduction in parental shifts probably reduced incubation bout duration during hatching. Care of the first-hatched chicks may have also been involved in the changes in shifts at hatching, since they did not always stay in the nest.

FIGURE 17: Survivorship of Parental Shift Durations.

a: Log survivorship plot of parental shift durations.
Some shifts by females lasted all day (> 850 min).

b: Hazard rate vs. shift duration, with fitted Weibull curve (see text).

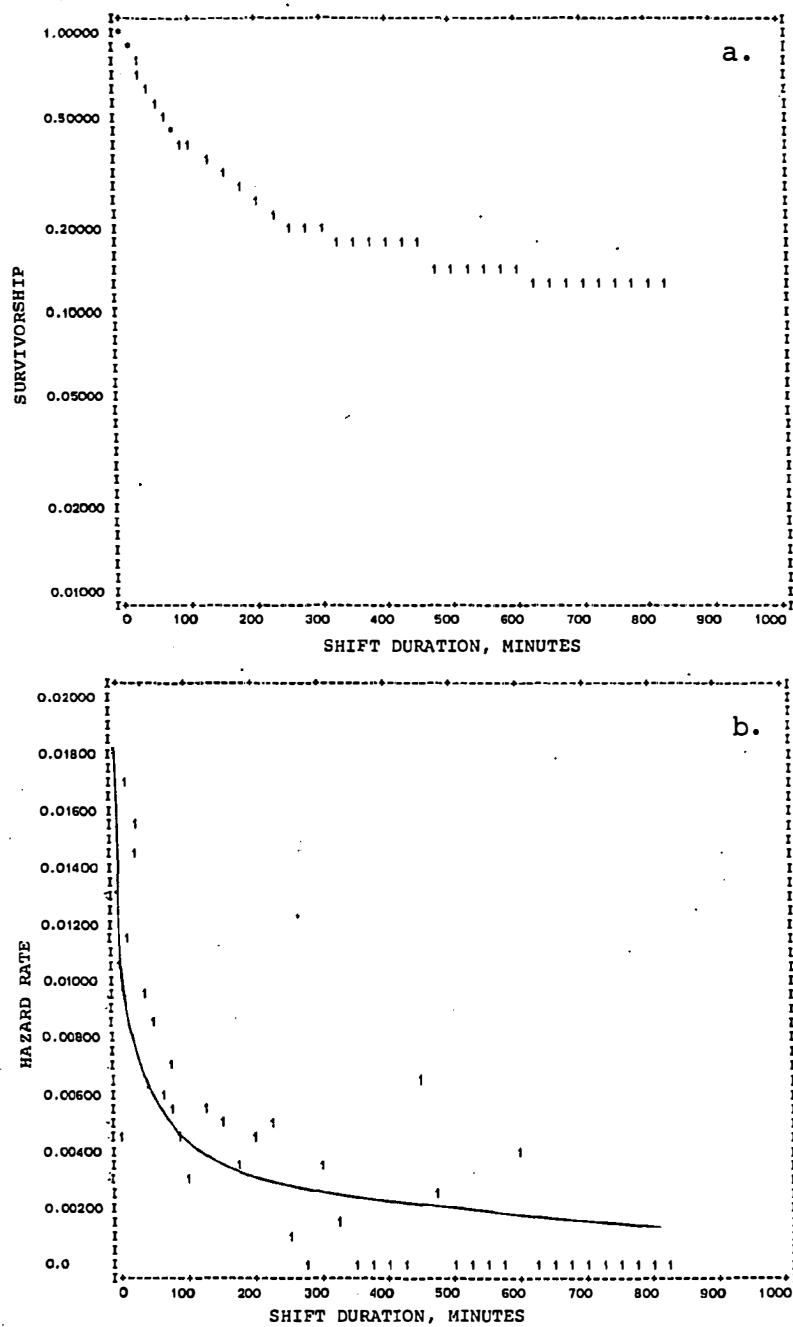
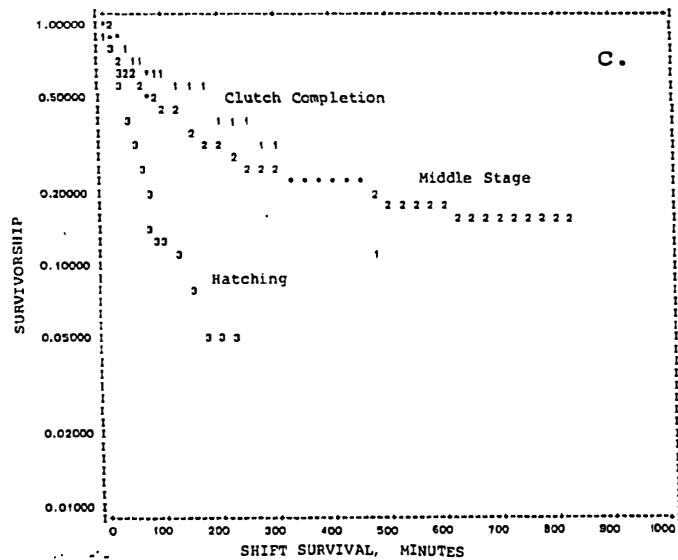
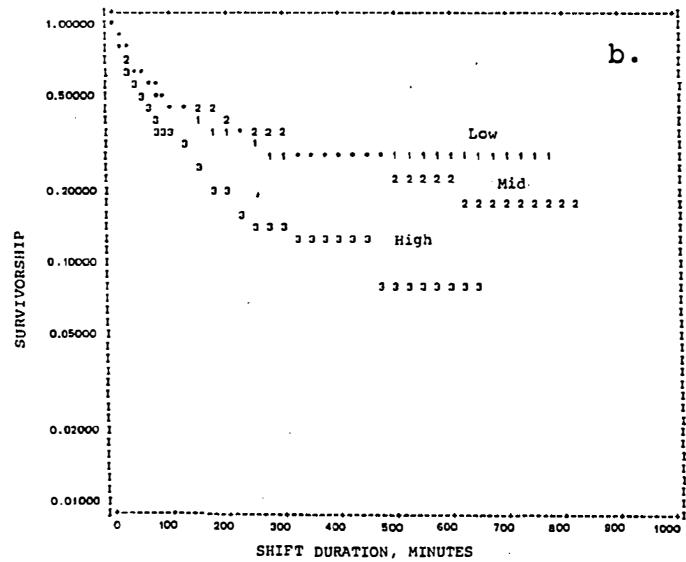
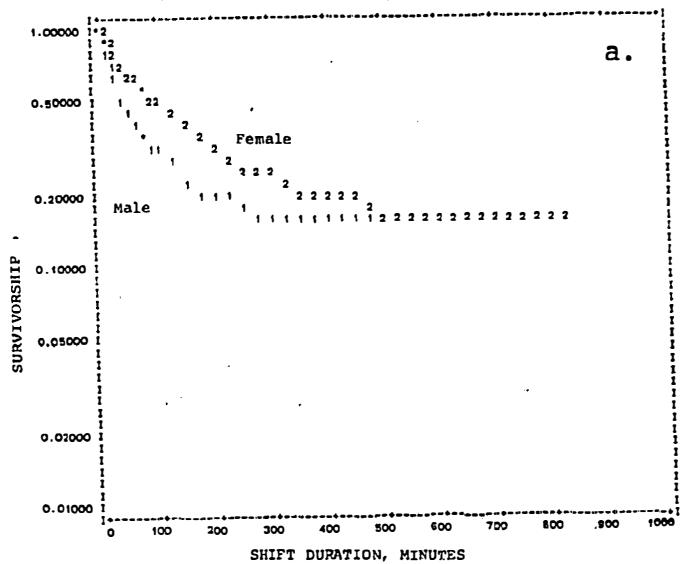


FIGURE 18: Survivorship of parental shift durations by sex, temperature and stage of incubation.

a: Log survivorship of parental shift durations grouped by sex. 1 = male, 2 = female. Females had significantly longer shifts than

b: Survivorship of parental shift durations grouped by air temperature. 1 = $< 31^\circ$, 2 = $31-33^\circ$, 3 = $> 33^\circ$. Shifts were slightly but significantly shorter at high temperature (see text).

c: Survivorship of parental shift durations grouped by stage of incubation. 1 = clutch completion (days 0-2), 2 = middle stage (days 3-23), 3 = hatching (days 24-26).



Effect of Air Temperature on Shading Time

Since shading time only includes time on the nest, it is less related to the time budgets of the parents than the preceding variables, and more related to the thermoregulation of the eggs and parent. Shading could affect the energy balance of the parent if it used more energy than sitting, but standing also probably helps to cool the parent.

Drent (1973) predicted that shading time should increase with increasing air temperature up to the point where egg temperature reached body temperature of the parent, and above that point shading time should decrease. The increase is caused by attempts to cool the eggs by radiation and convection by standing over them, and the decreased shading at very high temperatures is explained as cooling the eggs by contact with the parent. Since egg temperature is usually about 3° C. above air temperature (see Ch. V), and brood patch temperature is probably about 39° C. (Walters 1958), the inflection point should come at about 36-37° C.

Regressions of shading time on air temperature show that the pattern predicted by Drent (1973) is in fact found in this species. The inflection point occurs at about 36-37° C., and the regression is highly significant for all pairs studied. I analyzed pairs from near the end of the breeding season because the necessary temperature range did not exist

earlier in the season. Regression equations are given in Table 8.

TABLE 8
TRANSFORMED SHADING TIME REGRESSIONS

Pair	Dates	Intercept	Temp.	Temp ²	R ²	F	P	N
All	All	-56.91	3.17	-0.042	32%	28.6	.001	126
21-80	6/2-6/4	-154.9	8.90	-0.126	44%	5.6	.02	16
26-80	6/5-6/7 & 6/14-6/16	-70.31	3.90	-0.052	48%	22.0	.001	50
19-80	6/17-6/19	-44.35	2.42	-0.032	47%	12.5	.001	30

N = Number of incubation bouts for which data were analyzed.

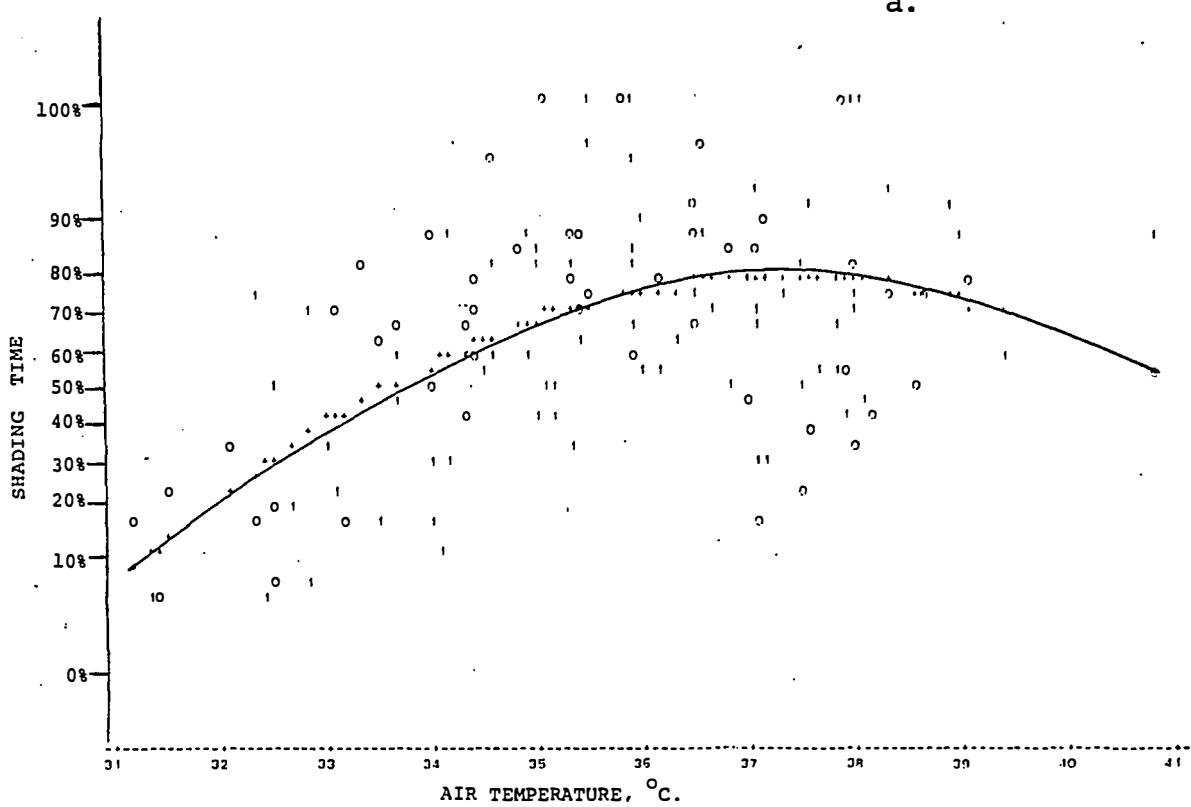
The regression of transformed shading time on air temperature is shown in Figure 19 a. The R² figures are quite high for shading time, 44% to 48% for the different pairs, which is what is expected since this is mainly a thermoregulatory response. The uniformity between pairs of the response to temperature suggests that between-pair variation was suppressed by a physical constraint, namely air temperature. No other variables were selected in stepwise regression on shading time. The independent variables tested were sex, pair, wind, day of incubation, and pavement/soil. (the dummy variable for pavement or soil under the nest).

FIGURE 19: Regression of transformed shading time on air temperature, and shading posture.

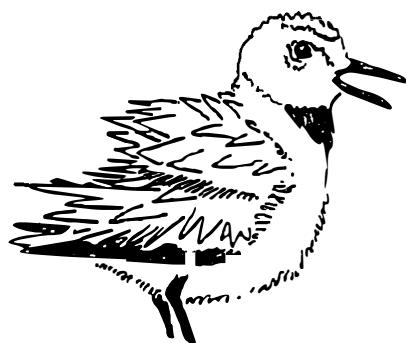
a: Regression of transformed shading time on air temperature at three nests. Symbols: 0 = male data point, 1 = female data point, curve = line fitted by quadratic multiple regression ($R^2 = 32\%$).

b: Posture used on nest during shading. Note erect crown and back feathers, exposed legs, air space above eggs, and open bill (panting). This bird was also using gular flutter.

a.



b.



Posture on the Nest during Shading

The posture on the nest during shading is shown in Figure 19 b for male 21-80. This drawing was traced from a photograph taken on 16 June 1980 at about 1430, when the air temperature was about 39°. The male had his crown and back feathers erect, which would help insulate him from heat, and he was standing completely clear of the eggs, with his legs exposed. His bill was open because he was panting, and he was also fluttering his gular area. When it was slightly cooler (around 36°) shading birds did not erect crown and back feathers, and they drooped their wings towards the ground.

Effect of Sun on Orientation on the Nest

This analysis differs from the others in that temperature is not involved, at least not directly. The hypotheses about solar orientation by incubating birds are related to the effect of solar radiation on the heat load of the bird, but different theories make opposite predictions. Incubating Nighthawks (*Chordeiles minor*) tend to face away from the sun during the heat of the day (Weller 1958), which would facilitate evaporative cooling via gular flutter, since this keeps the gular area in the shade. Lustick et al. (1978) explain the fact that incubating Herring Gulls (*Larus argentatus*) tend to face towards the sun on the basis of reflectivity of different parts of the plumage. By facing the sun

the birds expose more white feathers and fewer dark feathers to the sun, thus minimizing heat load. However, Herring Gulls do not use gular flutter (Drent 1970), so facing away from the sun may only apply to species that use it. Since Wilson's Plover uses gular flutter in Texas (pers. obs.), they are expected to face away from the sun. Some authors (e.g. Gochfeld 1978, Common Tern (*Sterna hirundo*)) find that facing into the wind occurs when the wind is strong, but that orientation is random at other times.

Data for one pair at one nest over 3 days shows that solar orientation does occur during the heat of the day in Wilson's Plover, with facing away from the sun predominating at that time (Table 9). Overall orientation is not significantly different from random (Friedman ANOVA, $\chi^2 = 1.33$, N.S.), but after 1100 the pattern is highly significant ($\chi^2 = 8.0$, $P = 0.0046$), with the most time spent tail to the sun, and the least spent facing the sun. During the time of maximum daily temperature, 1500-1700 hrs, almost all the time was spent tail to the sun. Local noon occurred at about 1320 hrs (daylight time and west of the meridian for Central Time), and since the latitude is fairly low in Texas (28° N.) orientation should not be too pronounced near noon because the sun is high in the sky. There appears to be a different pattern of facing the sun between 0700-1100, but it is nonsignificant ($\chi^2 = 4.0$, $P = 0.17$), and the reason for this pattern is not known.

TABLE 9

ORIENTATION OF INCUBATING BIRD RELATIVE TO SUN, PAIR 21

Hours	Mean Proportion of Time Spent:		
	Facing Sun	Lateral to Sun	Tail to Sun
7 - 9	0.68	0.18	0.13
9 - 11	0.48	0.31	0.22
11 - 13	0.11	0.39	0.50
13 - 15	0.07	0.43	0.50
15 - 17	0.03	0.04	0.93
17 - 19	0.11	0.20	0.69

Although wind speed and direction were not measured at the study site, winds were usually from the southwest on Matagorda Island. I detected no tendency to face the southwest in this sample.

Discussion

Effects on Incubation Time, Incubation Bouts, and Absences

Since these three components of incubation behavior are closely related, they are discussed here together. The results on the effect of air temperature on incubation time are not in agreement with the prediction of White and Kinney (1974), who predicted that bisexual incubating birds should incubate virtually all the time independent of air temperature.

An interesting question is whether the eggs would be harmed by more incubation. They probably would not be harmed. Because the function of incubation is assumed to be temperature regulation rather than warming, it is impossible to have too much regulation, although it is possible to have too much warming. Too little is known about rates of nest predation to say whether a nest is more likely to be found when a bird is on it than when no bird is on it.

The fact that both pairs and lone Wilson's Plovers reduce their incubation time at moderate temperatures indicates that either 1) the parent(s) are not able to maintain high incubation time uninterruptedly, or 2) the parents do not attempt to maximize their incubation time, instead keeping it above the minimum required for hatching. The zone of reduced incubation time (and of increased mean absence) corresponds to the "zone of stable regulation" (White and Kinney 1974) in which little parental attention is needed to keep egg temperature in the optimum range. Thus the parent(s) are reducing incubation time precisely when this reduction will hurt the eggs least. The fact that lone males incubate much more than males in pairs (see Ch. 3) shows that the pair probably could keep their incubation time high at all temperatures, and that for some reason they do not.

One explanation for the dip in incubation time is that it is to the parents' advantage to increase their time off the nest when this will not cause overheating or chilling of the

eggs. Time off the nest can be used for foraging, and one of the main prey of Wilson's Plover are fiddler crabs. Fiddler crab (*Uca* sp.) abundance varied dramatically between days (see Appendix F), related to flooding of the burrows. Under these conditions there would be an advantage to having time off the nest available for feeding. The days of Fiddler Crab abundance followed rains, and thus were relatively unpredictable. Another advantage of increasing time off the nest is that both birds could conserve energy for possible repeat nesting attempts, and the male could be in better condition if he is put in the position of incubating alone. It is possible that if pairs incubated more of the time, males would be unable to incubate alone. Thus the reduction in incubation time at moderate temperatures could have select as insurance for future contingencies.

Most of the available data on the response of incubation time, incubation bout duration and absence duration to air temperature are for single-sex incubators. Studies Kluijver (1950) and Kendeigh (1952), and a review by von Haartman (1956), show that the most common response to increasing air temperature is to decrease incubation bout length, and either increase absence length or hold it constant, causing decreased incubation time. Other patterns of response of incubation time to air temperature shown by von Haartman (1956) appear to be insignificant, involving a regression with a slope of +0.002 for one species (Wood Pewee, my calculation from Kendeigh's data). Afton (1980) shows that in

the anatids, in which only the female incubates, incubation time decreases with increasing air temperature. He also shows that this decrease is more pronounced in species with small eggs than in species with larger eggs.

One recent study of incubation did include data on bisexual incubators, however. Grant (1979) studied the responses of incubation bout duration and absence duration to air temperature in the Black-necked Stilt and American Avocet. For incubation bout duration he found that incubation bouts are short at low temperature, longest at moderate temperature, and short at high temperature for both species. This is exactly the opposite of the pattern found for incubation bout durations in Wilson's Plover. This difference is discussed in Chapter 6. Absence durations in the Black-necked Stilt and American Avocet show the same response to temperature as incubation bouts, which is the same response found in absences in Wilson's Plover. Thus Wilson's Plover differs from these two larger shorebirds in its pattern of incubation bout durations, but not in its pattern of absence durations. The response of incubation time to temperature was not shown directly by Grant (1979), but incubation time was reduced in early morning, when temperatures were moderate, and higher at other times of the day. Purdue (1976) found a reduction in incubation time at moderate air temperatures in the Snowy Plover in Oklahoma.

The regressions shown are not intended to apply outside the indicated temperature ranges. It is expected that

components of incubation behavior would show little or no response to temperature at lower or higher temperatures, when incubation time should be uniformly high. This appeared to occur in the few observations made at temperatures below 24° C., which were excluded from the regressions. This is discussed further in Chapter 6. The effects of errors in measurement on the regressions were considered, but it was felt that since the goal of the regression was expressing a relationship rather than accurate prediction, the potential error of 1 - 2° C. probably would not obscure the relationship.

Survivorship of Incubation Bouts, Absences, and Parental Shifts

In general, survivorship analysis gave results similar to those from regression analysis. It showed clearly the changes between stages of the incubation period, and between the sexes and the type of incubation bouts and absences. Incubation bouts, absences, and parental shifts were all shorter during the hatching stage than during the middle stage of incubation, which is in agreement with the qualitative impression that the parents are very attentive to the eggs during hatching.

The fact that the hazard rates of durations of incubation bouts, absences, and parental shifts all appear to fit the Weibull distribution suggests that there may be a biological explanation for this pattern. The Weibull distribution was first used to predict failure rates of machinery, a

situation in which many machines failed early, but the more reliable ones kept working for a long time. In animal behavior the Weibull distribution has been found in durations of feeding bouts and of agonistic bouts. In feeding bouts the explanation is that bouts are longer in larger food patches, and in agonistic bouts the bout lasts longer when the contestants are more evenly matched in fighting ability.

It is possible that measuring incubation behavior under varying environmental conditions produced the decrease in hazard rates that were observed, but this seems to be unlikely. The decrease in hazard rate persists in almost all the subgroups of incubation behavior that were analyzed. The explanation for the fit to the Weibull distribution of incubation bouts and parental shifts could be related to nest relief. The return of the partner might account for the decrease in hazard rate of incubation bouts: if a parent has been sitting on the nest a long time, it may continue to sit until it is relieved by its mate, if it has some way to anticipate relief. The decrease in hazard rate in parental shift duration may have a similar explanation: the longer a shift lasts, the more likely it is to be in a pair with little male incubation. The longest shifts were all by females, especially female 6-80 (see Chapter 2). The decrease in hazard rate in absence durations may have a different explanation: during shorter absences the parents tended to stay in the vicinity of the nest, while during

longer absences the parent almost always flew away from the nest (pers. obs.). Thus the longer the duration of an absence, the more likely it is to be away from the nest. Since flying involves energetic costs, and the bird was probably feeding away from the nest, once it reached the distant area it tended to stay there for some time, which would reduce the hazard rate of long absences.

As noted above, the differences between the pairs and the males in their incubation bouts' response to temperature and hatching illustrate the probable constraints on lone incubators. The lone males did not have as long bouts at high temperature, or as short bouts during hatching, because they are never relieved. Lone males also had the longest type of bout when the types were compared, suggesting that nest relief is an important factor limiting bout length in pairs. I saw a few cases in which the sitting bird stayed on the nest until the relieving bird approached the nest directly and gave the "nest-relief call", but in general the sitting bird seemed to leave the nest at the first sight of the relieving bird. The greater length of the female-male bouts compared to female-female bouts suggests that the female may have been anticipating relief by the male. Most males relieved at about the same time each afternoon, so the females could have been using cues of solar angle to anticipate his return. The lone males, with no relief, used a long bout - long absence pattern of incubation, which was successful in that both nests of lone males hatched in 1979.

Shading Time

The present results are the clearest expression to date of the relationship between shading time and air temperature that was predicted by Drent (1973). Previous results are qualitative (Maclean 1967) or simply show an increase in shading time with increasing air temperature (Purdue 1976). The high R^2 values of the shading time regressions are evidence for a thermoregulatory response, and the decreased standing at high temperatures are inconsistent with the theory that standing cools the parent rather than the eggs. There would be no reason for the parent to stand less at very high temperature if it were only trying to cool itself. Wilson's Plovers may use gular flutter, which has never before been reported in Charadriiformes (Dawson and Hudson 1970), to cool themselves while incubating at high air temperature (see Chapter 6).

Solar Orientation of the Incubating Bird

Solar orientation is related to shading the eggs, although the connection is not immediately obvious. I noticed in the field that Wilson's Plover is small enough relative to the size of the clutch that when it stands over the eggs the sun may hit them directly, especially if the bird is facing the sun. Putting the tail to the sun appeared to maximize the size of the bird's shadow, and the area in which to shade the eggs. Since solar orientation is most pronounced in the hottest part of the day, which is when

shading time is at or near its maximum, casting a large shadow on the eggs could be a function of solar orientation. Keeping the gular area in shadow could also be important, since the bird was also using gular flutter at high temperatures. Some sort of experimental manipulation would be necessary to test these hypotheses separately.

Since terns are relatively large compared to their two small eggs, the general lack of solar orientation in terns could be explained by the fact that they probably cast a large shadow whichever way they face. Terns do sometimes stand over eggs (Grant 1979), but are not known to use gular flutter. Grant (1979) reports that the Snowy Plover and Killdeer that he studied in California did not use gular flutter, but they did pant, which would also be more effective in the shade. All the shorebirds at Salton Sea except one tern show solar orientation during the heat of the day (Grant 1979).

Another reason for a lack of solar orientation in some studies is that it did not get hot enough during the study to observe it. Various other hypotheses have been proposed to explain the phenomenon, e.g. Cairns (1977) proposes that putting the back to the sun made it easier to see approaching predators. This would obviously only work for predators coming from that direction, so this is not very persuasive. Incubating birds frequently turn their heads. Reducing shadow size to reduce conspicuousness to predators is a more likely alternative explanation.

Conclusions

It appears that the main factor affecting all aspects of incubation behavior in Wilson's Plover is air temperature. Although it was sometimes fairly windy at both study sites, wind did not appear to have a significant effect. Although it was measured off the study site at an airport, which might not represent actual variation in wind at the nest, there was usually so much variance in incubation behavior explained by temperature that little more could have been explained by variance in wind. Variation in wind could be responsible for some of the between-day variance in incubation behavior, if it were measured more accurately. Another unmeasured source of between-day variance was feeding patterns, which might affect incubation behavior.

There is some evidence from incubation patterns that the effect of air temperature on egg temperature is more important in determining patterns than the effect of air temperature on the parents themselves. It could be stressful to incubate at the hottest part of the day, so the parent should stay off the nest then if it were trying to avoid thermal stress to itself. In birds nesting in hot climates that change places at the nest often during the hottest part of the day, the off-duty bird spends most of its time in the shade (Maclean 1967). This is discussed further in Chapter 6.

Another factor that appeared to affect the distribution of incubation bout lengths was the chance of nest relief. I

found that bouts by the female immediately preceding relief by the male were longer than other female or male bouts. Since the birds relieved each other at fairly consistent times each day, and they could perceive time of day from solar position, it is possible that the female anticipates relief by the male and waits for him to arrive. There is the complicating factor that this relief may occur at a hot part of the day when bouts are longer, however.

The importance of nest relief in the structure of the time budget of incubating parents is demonstrated by the incubation behavior of lone males. The lone males were consistently less able to adjust their incubation schedules to meet various contingencies than the pairs were, especially at high temperature and during hatching. Obviously a great deal of flexibility of scheduling is lost when only one parent is incubating.

Since the lone males incubated significantly more than they did when they had partners, it seems clear that pairs could keep the nest incubated almost all the time at all temperatures. The observed fact that pairs and males both reduce incubation time at moderate temperatures suggests that both pairs and males increase their time off the nest when the eggs are not in danger of overheating or chilling. The advantage of this is both to make the scheduling of incubation more flexible, and to include a buffer of time that can be used on days when there is extra time required for self-maintenance or incubation. By increasing their

time off the nest on an average day the birds would have extra time available on the non-average days.

CHAPTER V

EGG AND NEST TEMPERATURES

Introduction

In many species of birds, egg temperature during incubation varies between relatively narrow limits, and is essentially independent of air temperature (Drent 1975, White and Kinney 1974). However, in some birds egg temperatures fluctuate within wider limits (Bennett et al. 1981), and these fluctuations are positively correlated with shaded air temperature (Cronan 1974, Grant 1979, Purdue 1976). All of these species nest on the ground in hot climates, as Wilson's Plover does.

The present study was undertaken to determine the constancy of egg temperature and the relationship between egg and air temperature in Wilson's Plover, a species in which this has never been studied before. More data were collected on nest temperature than on egg temperature, to minimize disturbance of the parents and of the eggs. Nest temperature was found to be highly correlated with egg temperature in this species, so changes and patterns in nest temperature were used as an estimate of changes and patterns in egg temperature for comparative purposes. I also collected data on the behavior of the parents at the nest to study behavioral regulation of egg and nest temperature in this species.

In birds in which egg temperature fluctuates more than a few degrees each day, a study of the regulation of egg temperature must consider not only factors that tend to stabilize egg temperature (e.g. parental behavior) but also factors that cause it to fluctuate (e.g. changes in air temperature). The present study examined several aspects of parental behavior, including incubation time (% of time a parent was on the nest), shading time (% of time the bird on the nest stood over the eggs), and belly-soaking (coming to the nest with visibly wet belly feathers). Environmental variables studied included air temperature, wind speed, rainfall, and type of substrate under the nest. Rate of change in egg temperature of uncovered eggs was also calculated for comparison to patterns of nest attendance.

Materials and Methods

Wilson's Plovers were studied at Matagorda Island, Aransas National Wildlife Refuge, Calhoun County, Texas. I collected 39 days of continuous records of nest and air temperature at 13 nests in 1980, between 3 May and 24 June. In 1981 I collected records of egg, nest and air temperature at 2 nests on 2 days for a total of 15 hrs, at nests made by marked pairs I had studied in 1980. The study area is a barrier island on the coast of Texas, where Wilson's Plovers nest on both soil and pavement in a salt flat habitat. The study area is described in detail in Ch. 1. All temperatures are in degrees Celsius, T(E) stands for egg tempera-

ture, $T(N)$ stands for nest temperature, and $T(A)$ stands for shaded air temperature.

Temperatures were recorded with thermistor probes and telethermometers. In 1980, two Atkins telethermometers were connected to a Rustrak 2-channel strip chart recorder. Both probes contained No. 3 sensors, and the nest probe was a flat disk 11.5 mm diameter, 2.1 mm thick, enclosed in a 19.0 mm square of white fabric tape. This probe was placed in the bottom of the nest cup under the eggs, and the lead was fastened to the ground just outside the nest cup. Air temperature was recorded with a stainless steel probe (3.3 mm diameter, 109 mm long) which was placed parallel to the ground, 5 cm off the ground, in the shade of vegetation near the nest. The Rustrak recorder was powered by a 12 V truck battery. While temperatures were recorded, a time-lapse movie camera recorded behavior at the nest for three days. Time checks were made on the movie and the strip chart at least once a day. Details of the behavior sampling are given in Ch. 4. The equipment was removed from the field at the end of 3 days, the truck battery was recharged overnight, and the telethermometers were recalibrated against a mercury thermometer accurate to 0.1° C. at a range of temperatures using a water bath. Neither the time nor the temperature calibrations of the records varied significantly from the start to the finish of a record.

The strip chart records were digitized using an Apple II Plus microcomputer with a graphics tablet. Nest and air

temperatures were read every 15 min from the strip chart. Two records during which the parents repeatedly removed the probe from the nest were discarded, yielding over 2400 values each for nest and air temperature. Data were analyzed and plotted using SAS (SAS Institute Inc. 1979).

Data on nest and air temperature were also recorded directly in 1980, using a YSI telethermometer and a No. 423 probe in the bottom of the nest cup for T(N) and a No. 408 probe in the shade of the blind 5 cm off the ground for T(A). The blind was about 15 m from the nest. In 1981, the same YSI telethermometer was used to record T(E), T(N), and T(A) on 29 and 30 May. A No. 424 probe was placed with its tip near the center of an egg that had been incubated about a week, judging by its flotation in water, and the probe was glued in place with epoxy cement. T(N) was measured with a No. 408 probe in the bottom of the nest, and T(A) was measured with a No. 408 probe in the shade of vegetation 5 cm off the ground near the nest. Extension cables 25 m long were used, and temperatures and parental behavior were recorded from a blind. I recorded temperatures whenever they changed more than 0.5°, and I made a concurrent focal animal sample (Altmann 1974) of the behavior of the parent on the nest. Temperatures in the egg were measured in 2 nests, one on soil (that originally contained the egg) on 29 May, and one on pavement on 30 May (the egg with the probe was substituted for one of the eggs in that nest during measurement).

A dummy egg was constructed for a heated egg experiment from an empty eggshell (taken from an abandoned nest in 1979). The shell was strengthened with epoxy cement, cut in half, and the heating element from a car cigarette lighter was placed inside, and the halves glued together. A YSI No. 423 thermistor probe was inserted to monitor the temperature of the egg. The heating element was connected via an extension cable to two 6 V lantern batteries. Dummy egg temperature was regulated at about 45° C. by connecting and disconnecting the heating element from the batteries. Data collected in 1981 were also analyzed and plotted using SAS.

Mean $T(N)$, and its coefficient of variation (C.V.), were calculated from the 1980 data using SAS for four 3.5 hr daylight time periods each day, the same time periods that were used for analyzing incubation behavior. They were 0700-1030, 1031-1400, 1401-1730, and 1731-2100 CDT. The distribution of nest temperature was found not to differ significantly from normality, but the C.V. of $T(N)$ had to be transformed with the log transformation to achieve normality (using KSLTEST procedure in SAS).

Results

Diurnal patterns of $T(E)$, $T(N)$, and $T(A)$

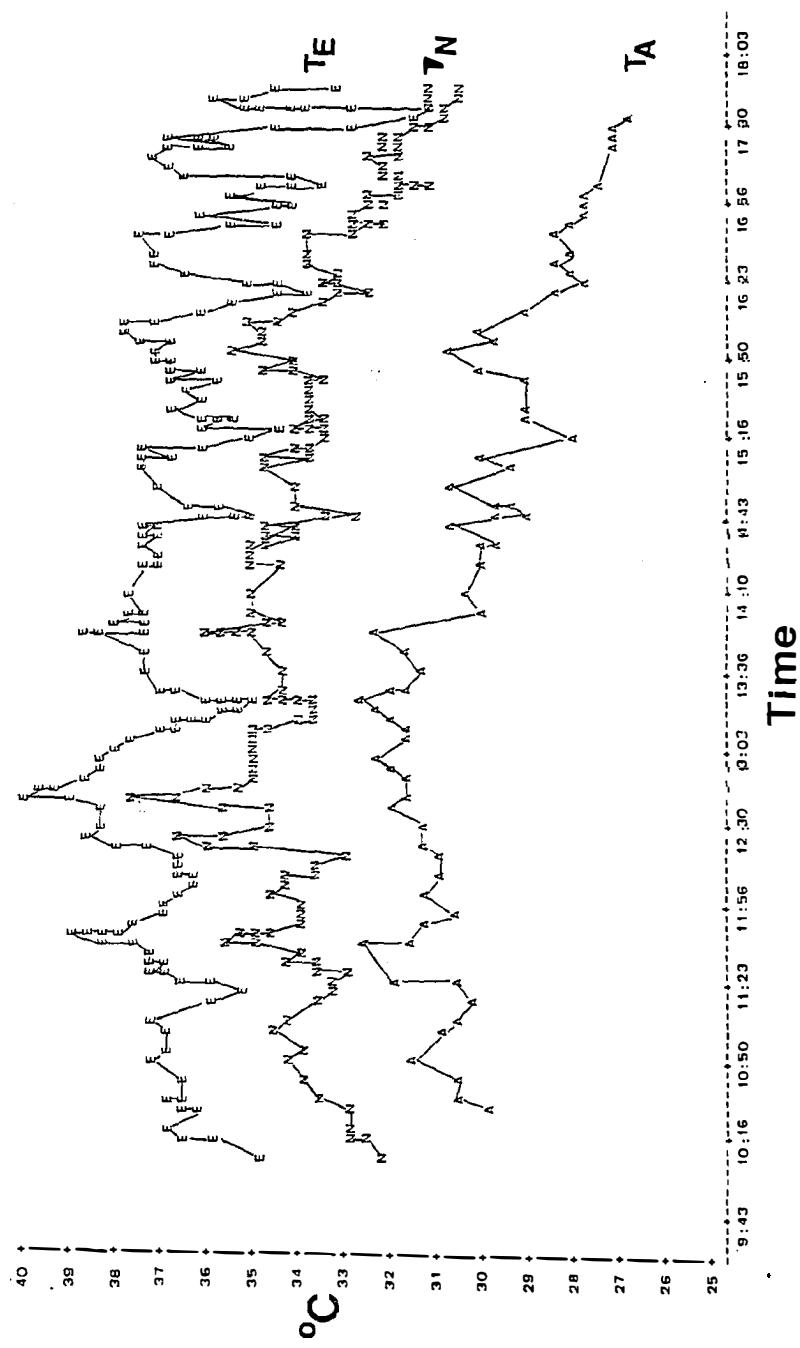
Temperatures at the soil nest on 29 May 1981 are shown in Figure 20 for the period 1007-1747 hrs. $T(E)$ was not regulated within narrow limits, ranging from a high of 39.9°

after an absence shortly after noon, to a low of 31.3° after an absence in the late afternoon. This day was abnormal because a thunderstorm was approaching in the afternoon. Dark clouds and thunder appeared at 1615 hrs, and the T(A) began to drop after 1400 hrs. On most days T(A) peaked later in the day, at 1500-1600 hrs. The approaching storm was probably partly responsible for the wide swings in T(E) in the afternoon. The parents regulated T(E) at about 36-37° during the midday period, and T(N) at 34-35°, values similar to those found in other birds (Drent 1975). T(N) was usually 2-3° below T(E), but its changes paralleled those of T(E) quite closely, probably because the eggs are so small (12 g.).

The same egg with the probe was put in a nest on pavement on 30 May and records were made between 1230-2000 hrs. The temperatures are shown in Figure 21, and the pattern of rising and falling temperatures is similar to that in the preceding figure, but there are some differences. No storm occurred on 30 May, and T(A) peaked between 1500-1645 hrs, about the normal time. T(A) was higher than on 29 May, due probably to the absence of a storm and the presence of pavement rather than soil under the nest. The spikes in T(A) were probably caused by sun flecks hitting the probe. T(E) had narrower limits on 30 May than on 29 May, with a high of 38.0° at 1630 hrs and a low of 33.8° during an absence at 1940 hrs. T(N) paralleled T(E) as it did the previous day, but at a few points T(N) was higher than T(E).

FIGURE 20: T(E), T(N), & T(A) in Nest on Soil, 29 May 1981.

Plot of egg temperature 'E E E', nest temperature 'N N N', and air temperature 'A A A' vs. time of day (1007 - 1747 hrs) at a Wilson's Plover nest on a soil substrate.



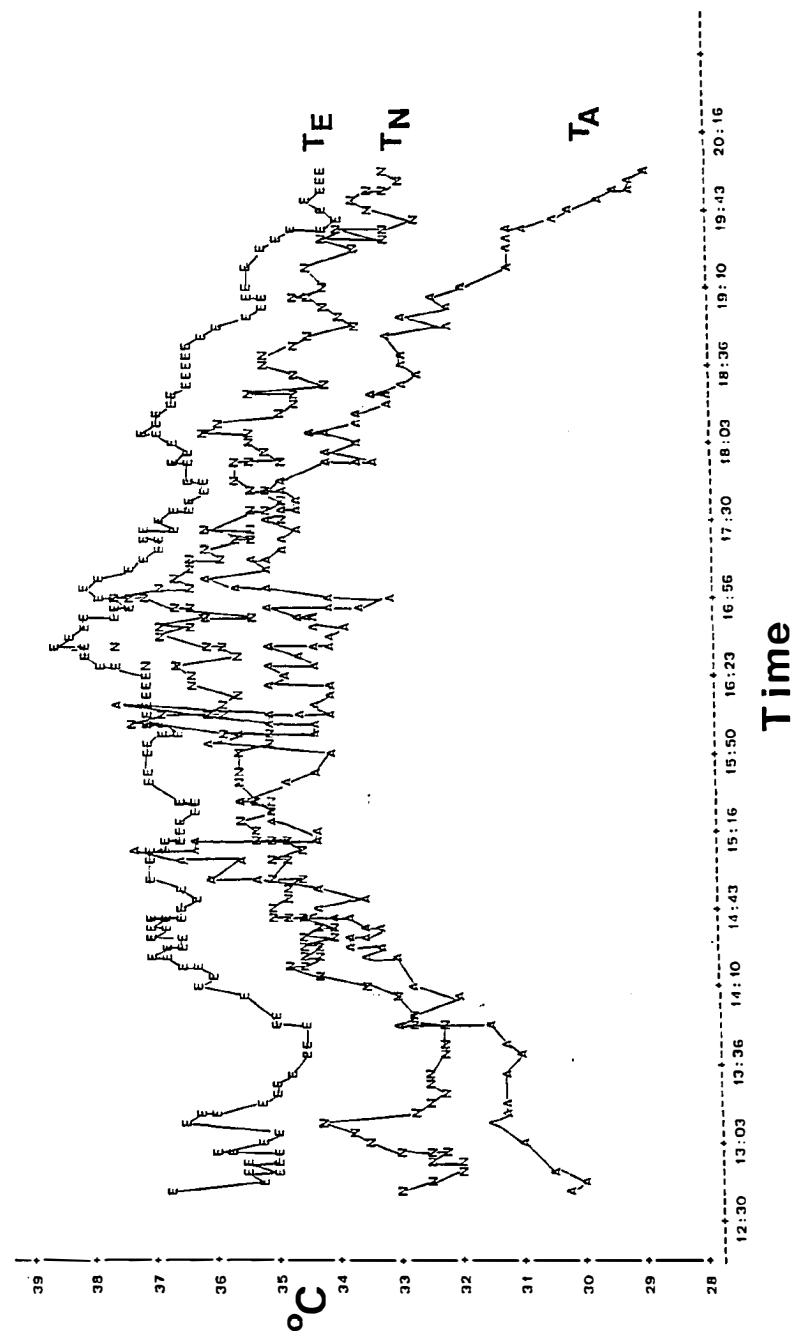
This was expected in the pavement nest, because the pavement is probably hotter than the eggs in the afternoon, and the T(N) probe was between the eggs and the pavement.

Comparing the point at which T(E) and T(N) began to drop each day, T(A) fell to 28.0° at 1800 hrs on 29 May, but not until 2000 hrs on 30 May. If a drop in T(A) triggers a drop in T(E) and T(N), one would expect this drop to occur at about the same T(A) on different days, even if this is reached at different times on different days. However, T(E) and T(N) were still being regulated at normal daytime levels when the sample ended on 29 May, although they did fall sharply during absences. On 30 May, T(E) only reached 34.0° after the male had been sitting for 10 min just before the end of the sample, well below the temperature at midday. The parents may either prevent T(E) from falling in the afternoon when a storm is approaching, or they may allow T(E) to fall at about the same time each day, rather than at a particular T(A) value. In either case this suggests that the fall in T(E), although correlated with a fall in T(A), may actually be caused by a change in parental posture on the nest rather than being caused directly by a change in T(A).

The close minute-to-minute relationship of T(E) and T(N) is confirmed by a regression of T(E) on T(N) for each sample, as shown in Figure 22. The slope of the regression

FIGURE 21: T(E), T(N), & T(A) in Nest on Pavement, 30 May 1981.

Plot of egg temperature 'E E E', nest temperature 'N N N', and air temperature 'A A A' vs. time of day (1230 - 2000 hrs) at a Wilson's Plover nest on pavement.

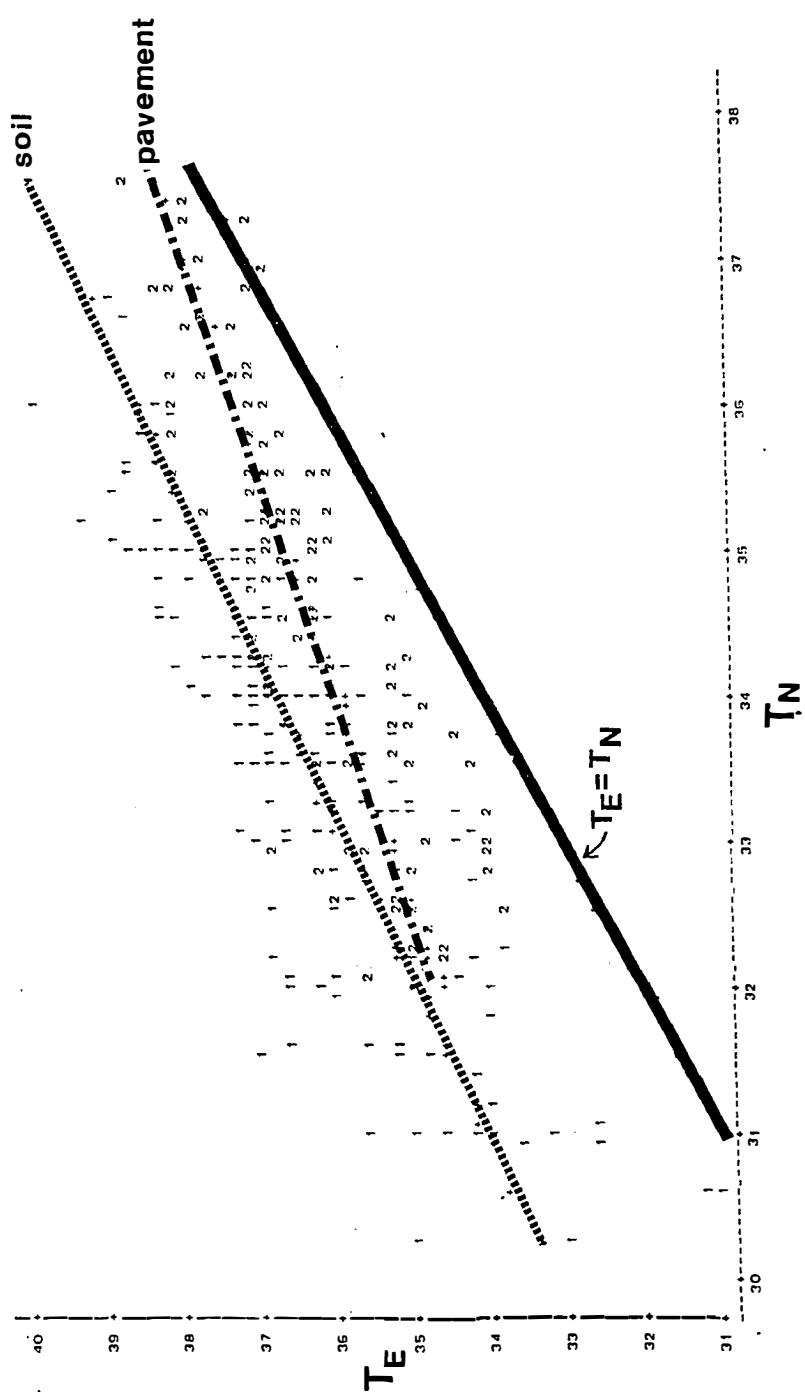


was slightly higher in the soil nest (sample=1) than in the pavement nest (sample=2). $T(E)$ was always greater than $T(N)$, except for the few points in the pavement nest. If the same trend continued at higher $T(N)$, $T(E)$ should be below $T(N)$ above about $T(N)=38^\circ$ at the pavement nest, but not until a much higher temperature was reached in the soil nest. $T(N)$ went above 38° on quite a few occasions in the 1980 data from pavement nests (see below). The regression equation for the soil nest was $T(E) = 6.93 + 0.88(T(N))$, $R^2 = 68\%$, $P < 0.0001$, and for the pavement nest it was $T(E) = 14.3 + 0.64(T(N))$, $R^2 = 68\%$, $P < 0.0001$. This shows that while $T(N)$ is not a perfect predictor of $T(E)$, it predicts enough of the variance in $T(E)$ (68% in my sample) to be useful for comparative purposes, which is how it will be used below.

Data on nest and air temperature collected in 1980 included both day and night records, and the data were continuous for 3 days so that different days can be compared at the same nest. Mean daily and nightly values of $T(N)$ and $T(A)$ increased sharply during the study period (3 May to 24 June), as shown in Figure 23 a and b for day and night means respectively. Deviations from the warming trend occurred on 14-16 May, which was a sample at a soil nest, Nest 5-80. It rained several times during the sample, which appeared to depress temperatures. The increase in mean night $T(N)$ between 29 and 31 May was associated with clutch completion

FIGURE 22: Plot of $T(E)$ vs. $T(N)$ with fitted regression lines.

Plot of $T(E)$ vs. $T(N)$ for the soil and pavement nests in 1981. Solid line is line of $T(E) = T(A)$, dashed line is regression line for soil nest, and dots and dashes are regression line for pavement nest.



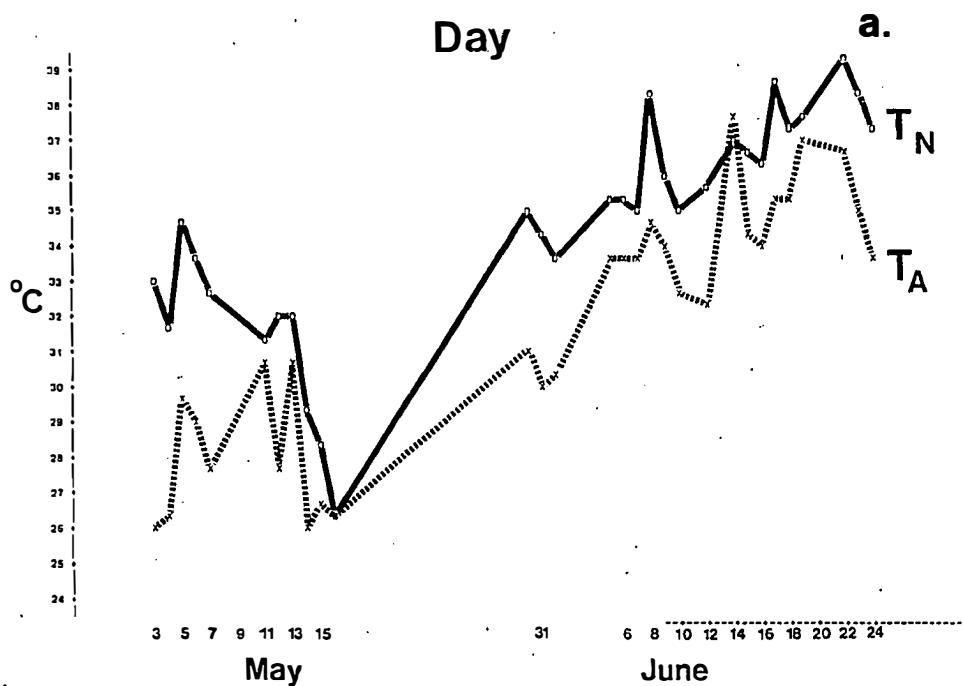
(see below) at Nest 18-80. Mean T(N) was unusually high both by day and by night on 8 June, which was the first day of the sample on Pair 21-80. Temperatures during these periods are shown in more detail below. The mean difference between T(N) and T(A) was greater at night than during the day (5.0° at night, 2.9° during the day), as expected because T(A) is lower at night. Mean day T(N) was significantly higher than mean night T(N) (day = 34.6°, night = 31.1°, $t = 22.2$, $P < 0.0001$).

Typical temporal patterns of T(N) and T(A) are shown in Figure 24 a & b for two different samples. Figure 24 a shows Nest 26-80, on soil, between 14 - 16 June, and Figure 24 b shows data from Nest 19-80, on pavement, for 17 - 20 June. Patterns of T(N) and T(A) were similar in all nests studied, except that both were lower earlier in the breeding season. Data from these two nests were chosen because they were complete records, and they were made during consecutive periods on different substrate types. T(A) was unusually high on 14 June, although T(N) was not higher than normal that day. Comparing Nest 26-80 to Nest 19-80, which were consecutive records but on soil and pavement respectively, night T(A) was slightly higher on pavement than on soil, although the data were not collected on the same nights. Also, T(A) appears to drop more sharply at dusk on soil than it does on pavement, although the difference is not as

FIGURE 23: Mean $T(N)$ & $T(A)$, Day and Night, during study period in 1980.

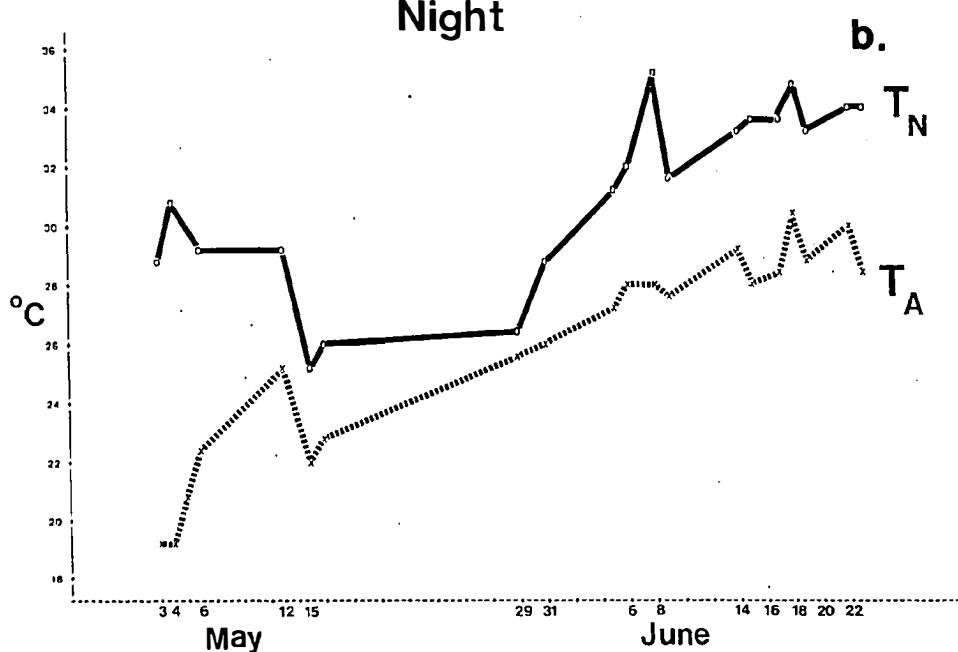
a: Daytime mean $T(A)$, dashed line, and mean $T(N)$, solid line, during the study period in 1980.

b: same means for night (2030 - 0630 hrs). Data are available for fewer nights than for days (see Methods).



Night

b.



marked as one might expect from the heat held by the pavement. The peak of $T(N)$ at midday was about the same at the two nests. Data collected on the same days would of course be necessary to make a more rigorous comparison of the thermal environment of soil and pavement nests.

A general feature of all the temporal patterns on $T(N)$ and $T(A)$ was that $T(N)$ rose with $T(A)$ in the morning, but $T(N)$ fell more slowly than $T(A)$ in the afternoon. The substrate is presumably warmer in the afternoon than in the morning, which may keep the nest warmer, but also the parents may be keeping $T(N)$ up by applying heat to the eggs in the afternoon. $T(N)$ was fairly constant at night, although there are occasional drops that were probably caused by parental absences. Use of a flash with a movie camera showed that nests are not incubated continuously at night (see Ch. 2), and the records of $T(N)$ at night showed that the nest was warmed at a mean of 92% of the points, so this is an estimate of incubation time at night.

Night incubation time appeared to be much less before clutch completion than after clutch completion, however. Nest 18-80 was studied from the night before the 3rd egg was laid until 2 nights after the 3rd egg was laid, and the night temperatures are shown in Figure 25 a and b. Figure 25 a shows the night before the 3rd egg was laid, and the nest was warmed in only 8% of the points. Figure 25 b shows

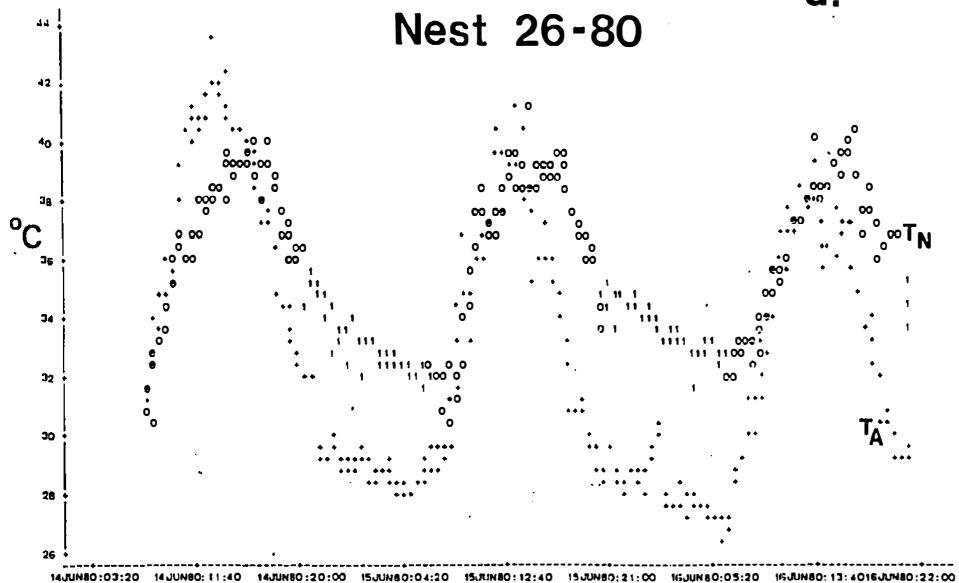
FIGURE 24: Diurnal patterns of $T(N)$ & $T(A)$ at two nests in 1980.

a: Nest 26-80, soil, 14 June - 16 June.

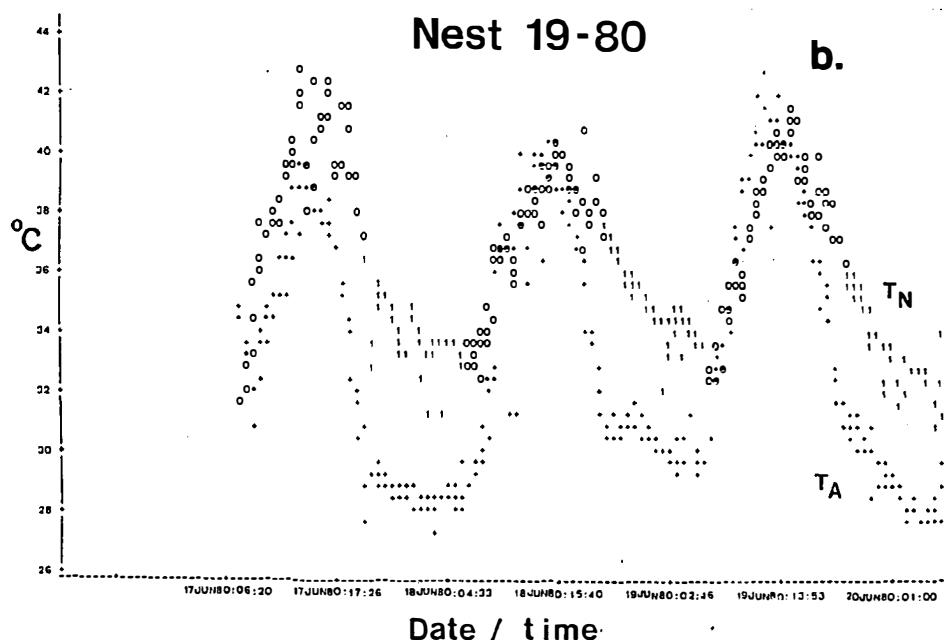
b: Nest 19-80, pavement, 17 June - 20 June.

Symbols: '0' = day $T(N)$, '1' = night $T(N)$, '+' = $T(A)$ (day and night).

a.



b.



the data for two nights later (data for the intervening night were not useable), and on this night the nest was warmed in 61% of the points. This is still less than the usual 92%, but clearly an increase. Nest 18-80 was incubated a normal amount on the day after the first night shown (see below), and T(N) was in the normal range during the day, so night incubation may be avoided during clutch completion to minimize the asynchronous hatching of the eggs.

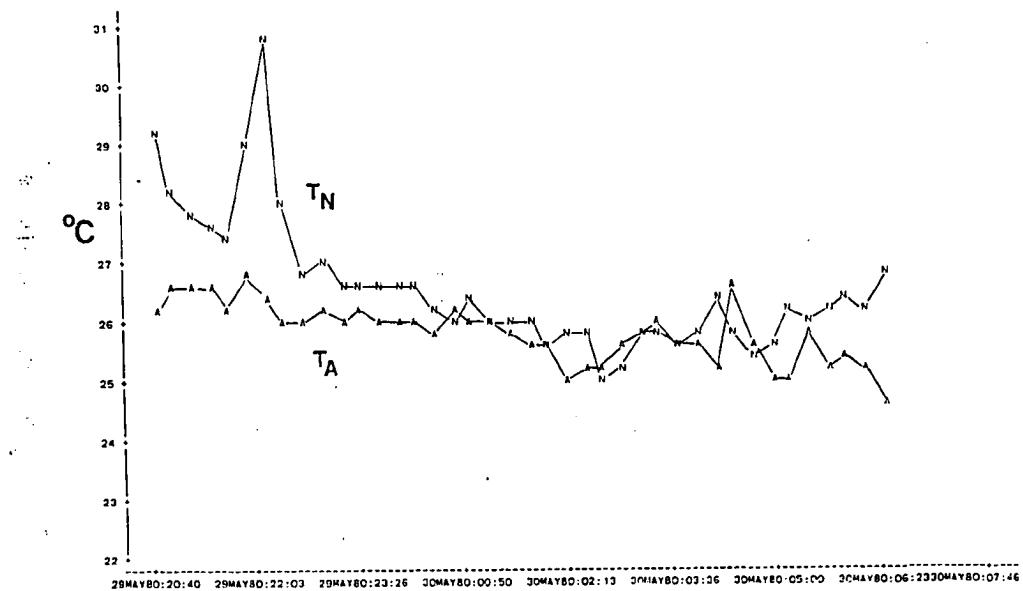
There appeared to be little difference between the diurnal temperature patterns of nests with pairs or lone incubators, although data are incomplete for one of the nests at which there was a lone incubator. The male was trapped at Nest 21-80 on the morning of 9 June, and he was kept in a cage and then released near the nest 24 hr later. The female was trapped at Nest 29-80 on the morning of 13 June, and released near the nest 24 hr later. Male 21-80 resumed incubation on the day of his release, but female 29-80 was not seen again (see Ch. 3 for details). Data on T(N) and T(A) for Nest 21-80 are shown before, during, and after male removal in Figure 26 a. There was one spike in T(N) before removal, which was associated with an absence (see below), and during the night before removal, T(N) was as high as 38.0° for part of the night, higher than any other T(N) recorded at night. It is possible that the nest

FIGURE 25: Comparison of Night T(N) before and after clutch completion, Nest 18-80.

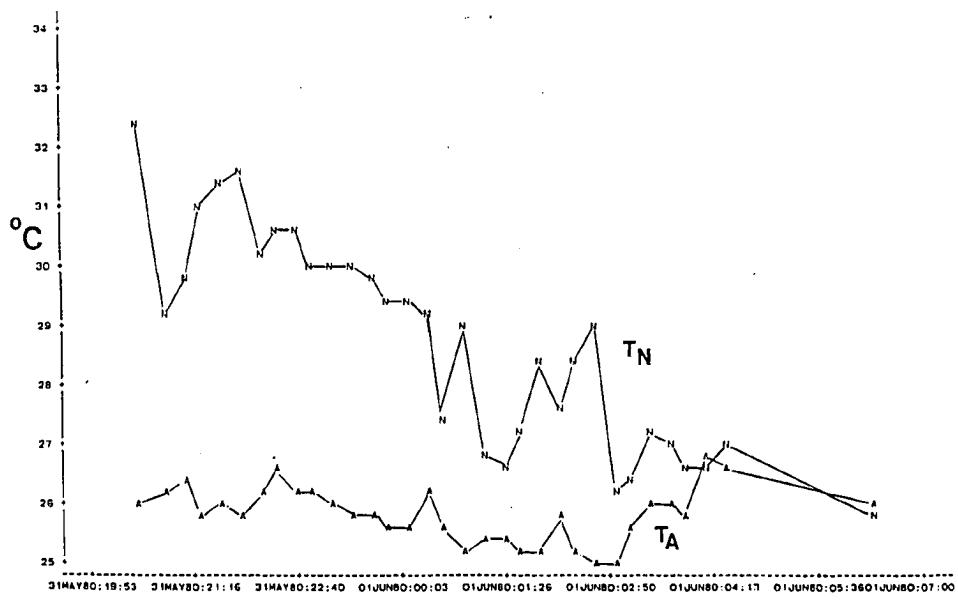
a: Night T(N) 'N', and T(A) 'A', for Nest 18-80 the night before clutch completion (29 May - 30 May).

b: Same graph for the same nest 2 nights after clutch completion.

a.



b.



Date / time

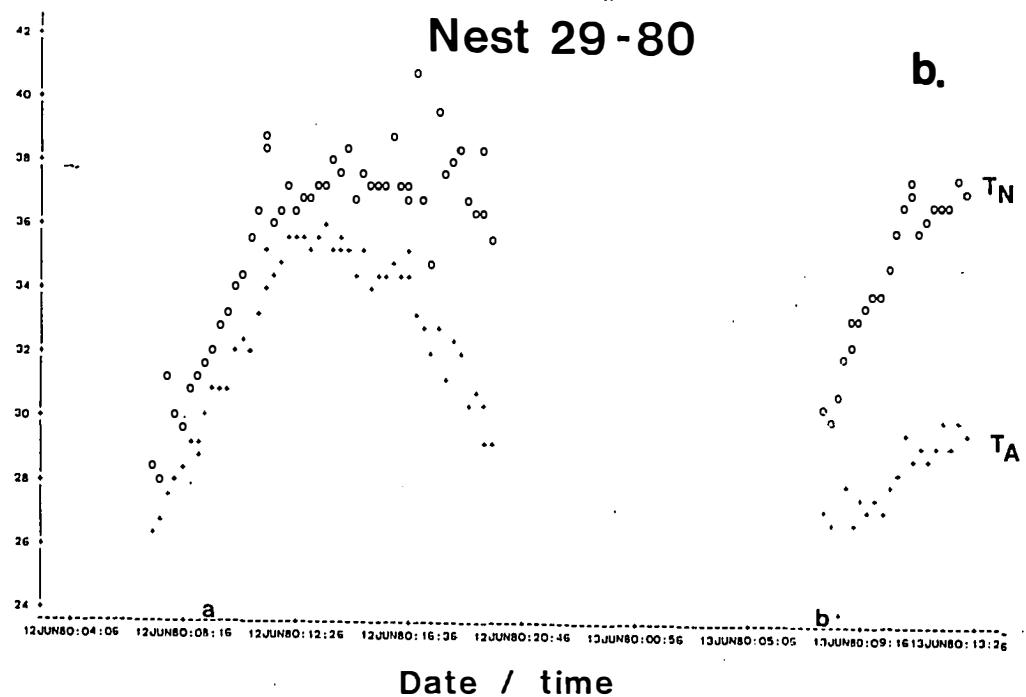
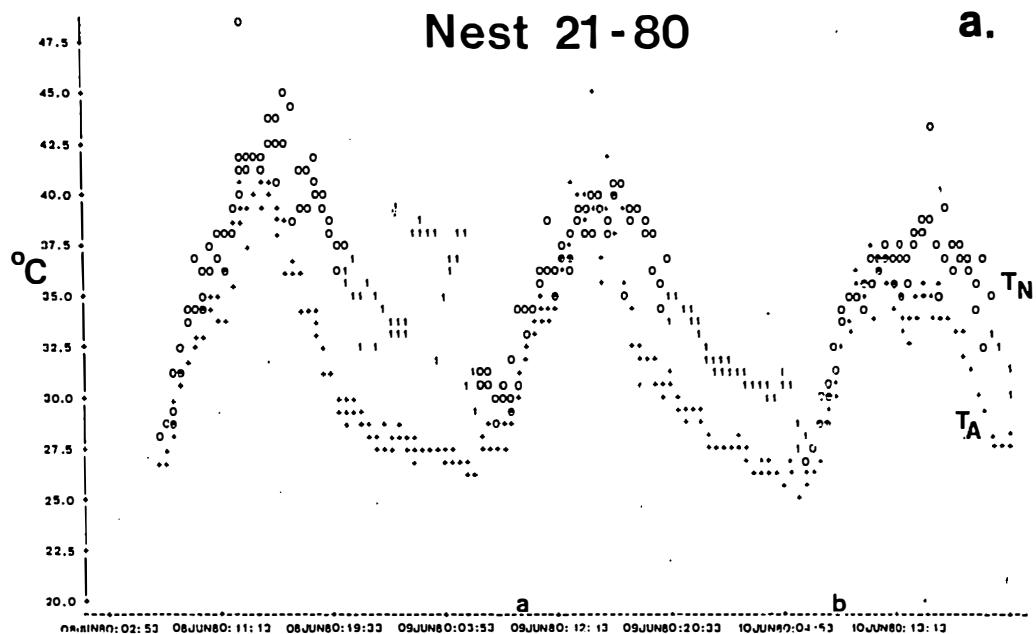
probe got moved on top of the eggs during this period, because in one of the discarded records the probe was seen on top of the eggs one day and it recorded a temperature of about 38°. The temperature is higher on top of the eggs because it is in contact with the brood patch, which usually has a temperature of about 40° (Drent 1975). After removal on 9 June, the female actually kept $T(N)$ below levels reached on the previous day, even though $T(A)$ was higher than on the previous day. The record of $T(N)$ for the night the female was alone shows that she must have incubated most of the night, because $T(N)$ stayed consistently above $T(A)$ until just before dawn. After the return of the male on 10 June, both $T(N)$ and $T(A)$ were lower than on the two previous days although there was one spike in $T(N)$. The male began incubating at about 1600. Female 21-80 used belly-soaking a few times, which cooled the eggs somewhat (see below), but it was a sporadic occurrence. Data for Nest 29-80 are shown in Figure 26 b, and data are only useable for the day of the removal and the morning of the day after removal, because the probe was not always in the nest. The patterns of $T(N)$ and $T(A)$ look similar to those in other nests.

The similarity of $T(N)$ patterns in pairs and lone incubators is not surprising, since it was shown in Ch. 3 that the lone incubators had high hatching success. If $T(N)$ fluctuated much more in lone incubators than in pairs, and

FIGURE 26: T(N) & T(A) for Pair and Single Incubators,
1980.

a: T(N) during day = '0' and at night = '1', and T(A) = '+', for Nest 21-80, 8 June - 10 June. The male was removed on the morning of 9 June ('a') and returned on the morning of 10 June ('b'), and he began incubating at about 1600 hrs on 10 June.

b: T(N) = '0' & T(A) = '+' for Nest 29-80, on 12 June after the female was removed ('a'), and T(N) for the morning of 14 June. The female was returned at point 'b' but was never seen again.



especially if T(N) reached higher levels in lone incubators, lower hatching success due to embryo death would be expected in lone incubators. Normal T(N) at night by female 21-80 is consistent with the observation that the incubation period is the same in lone incubators as in pairs, since it would be longer if night incubation were reduced.

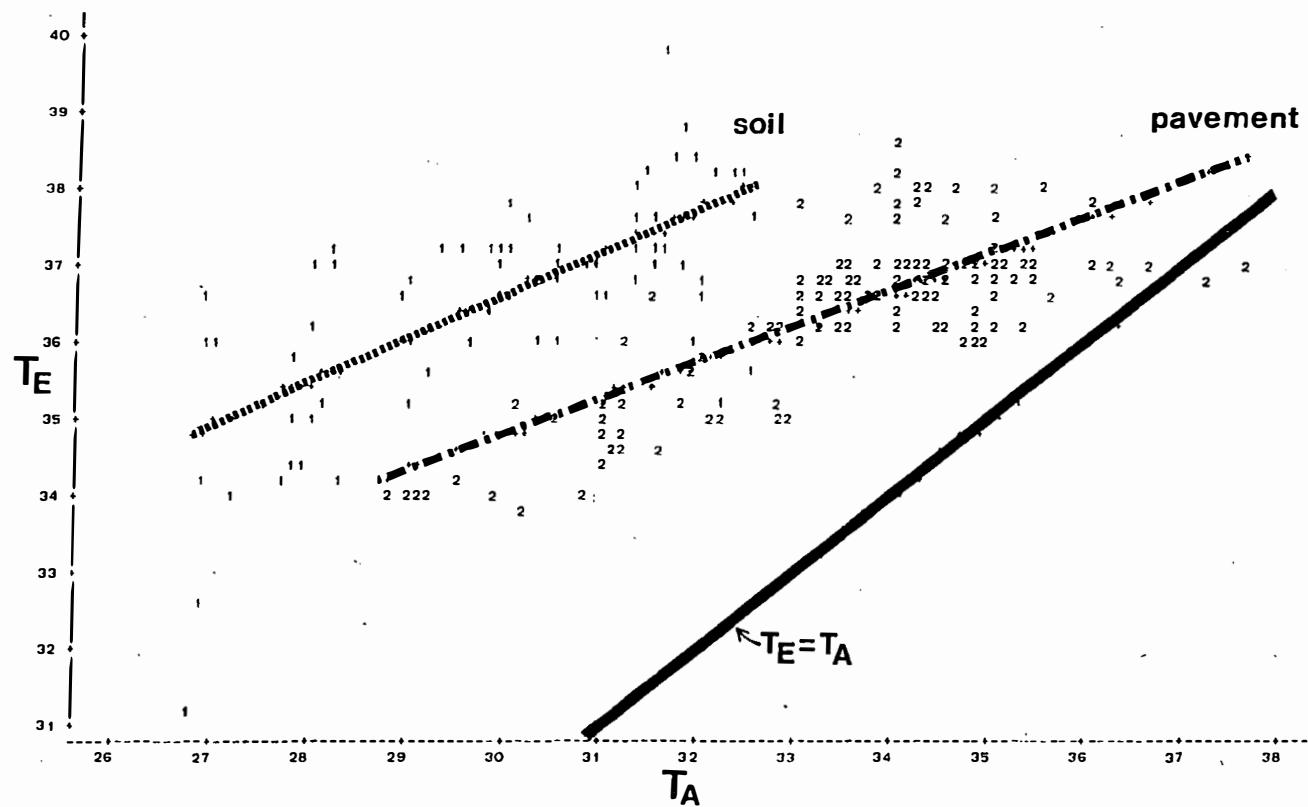
Factors Affecting Egg & Nest Temperature

There was a large effect of T(A) on both T(E) and T(N). Regressions of T(E) on T(A) are shown in Figure 27 for the soil and pavement nests, which had slightly different regressions. As with the regression of T(E) on T(N) shown above, in the regression of T(E) on T(A) had a higher slope in the soil nest than in the pavement nest. Regression equations were: soil nest, $T(E) = 19.8 + 0.56(T(A))$, $R^2 = 45\%$, $P < 0.0001$; pavement nest, $T(E) = 20.9 + 0.46(T(A))$, $R^2 = 58\%$, $P < 0.0001$. Note that T(E) was less than T(A) at two points in the pavement nest, and that the regression predicts $T(E) < T(A)$ for $T(A) > 38.7^\circ$ in the pavement nest, or 45° in the soil nest. A combination of two factors keeps T(E) above T(A): warming of the eggs by the parents, and also the warming of the egg by the sun during absences. An uncovered egg would become much hotter than the air if left very long.

Regressions of T(N) on T(A) are shown in Figure 28 a for day observations and Figure 28 b for night observations in

FIGURE 27: Plot of $T(E)$ vs. $T(A)$ with fitted regression lines.

Plot of egg temperature vs. air temperature for the soil and pavement nest in 1981. Solid line shows $T(E) = T(A)$, dashed line is for soil nest, and dots & dashes are regression line for pavement nest.



1980. Variation both between and within days is included, so the range of T(A) is broad, especially during the day. The regression equation for day values is $T(N) = 13.7 + 0.66(T(A))$, $R^2 = 63\%$, $P < 0.0001$, which predicts that T(A) will exceed T(N) when T(A) is above 40.3° . The night equation is similar, $T(N) = 14.9 + 0.62(T(A))$, but R^2 is lower (43%), $P < 0.0001$. It never got warm enough at night for T(A) to exceed T(N), and changes in the posture of the parent on the nest probably have a larger effect on T(N) at night than during the day, because it is cooler at night.

Parental behavior during the day had a clear and usually predictable effect on T(E) and T(N). T(E) in the soil nest is shown in Figure 29, with letters denoting the behavior of the parents at the time of each reading. The egg cooled during some absences ('X') and warmed during others; reasons for this are discussed below. As expected, the parent sitting on the eggs ('F' or 'M') warmed them if they were cool, or cooled them if they were warm (above 37°). Shading or standing over the eggs ('U' or 'O') began when T(A) was 32° , and generally it had the effect of reducing T(E) and T(N). The female sat on the eggs to cool them when they were very hot (peaks at 1148 and 1240 hrs), but she used shading to cool the eggs when they were less hot (e.g. at 1315 and 1440 hrs). The dark clouds and thunder at 1615 hrs were associated with a drop in T(E) of 4° while the male was off the nest. The male used shading once even after the thunder began, at 1710 hrs, and it reduced T(E).

FIGURE 28: Plot of $T(N)$ vs. $T(A)$ with fitted regression lines.

a: Plot of $T(N)$ vs. $T(A)$ for daytime 1980 data, with solid line showing $T(N) = T(A)$, and dashed line showing fitted regression line (equation in text). Symbols: 'A' = one observation, 'B' = two observations, etc.

b: Same graph for 1980 nighttime data.

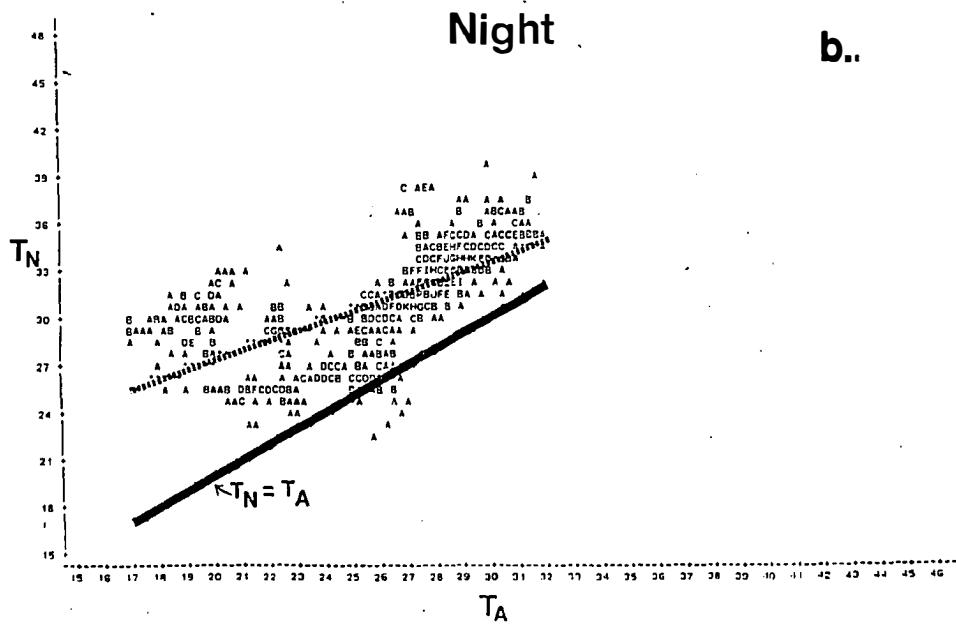
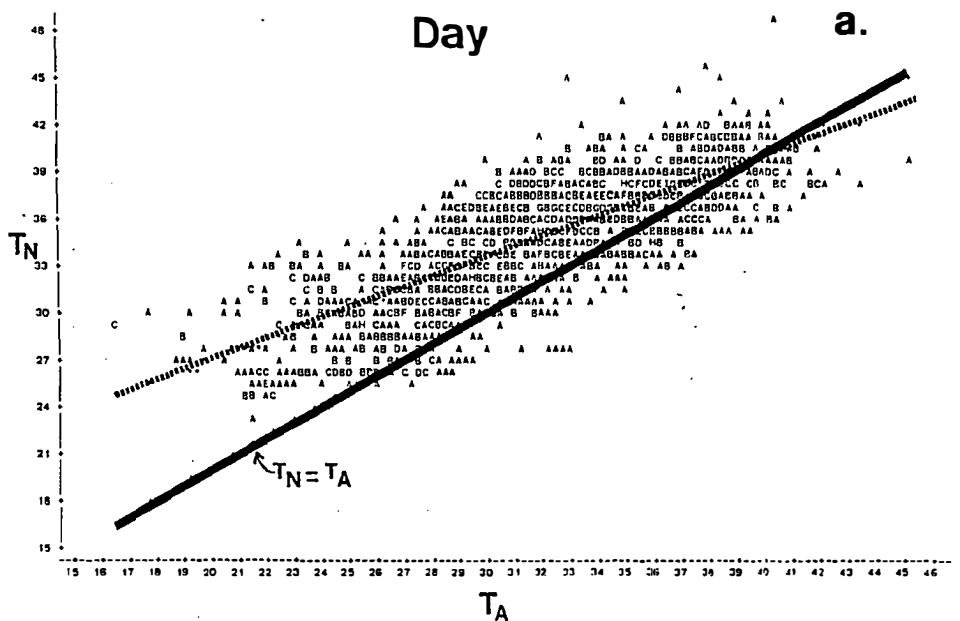
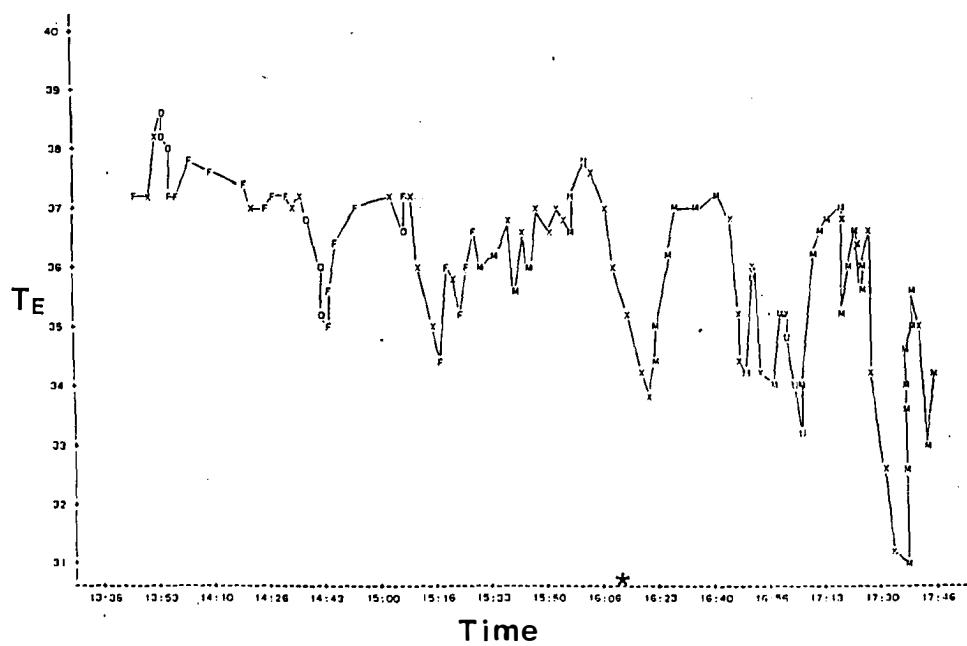


FIGURE 29: Plot of T(E) vs. time of day for soil nest showing parental behavior.

Plot of T(E) vs. time of day for soil nest, 29 May 1981. Letters denote behavior at the nest: 'M' = male sits on eggs, 'F' = female sits on eggs, 'U' = male shades eggs, 'O' = female shades eggs, 'X' = nest uncovered. Thunder began at 1615 hrs, rain at about 1900 hrs.

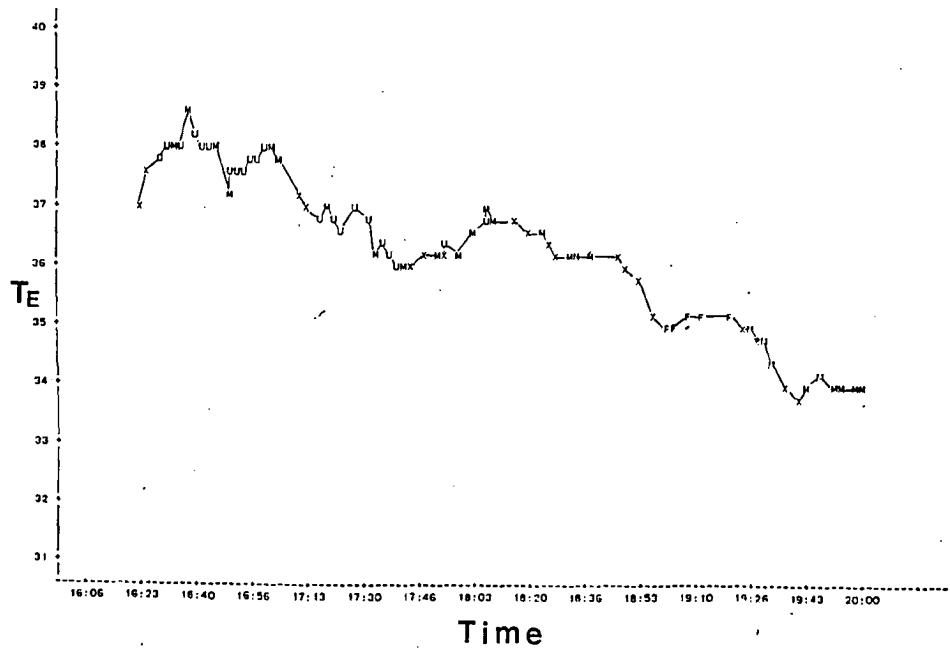
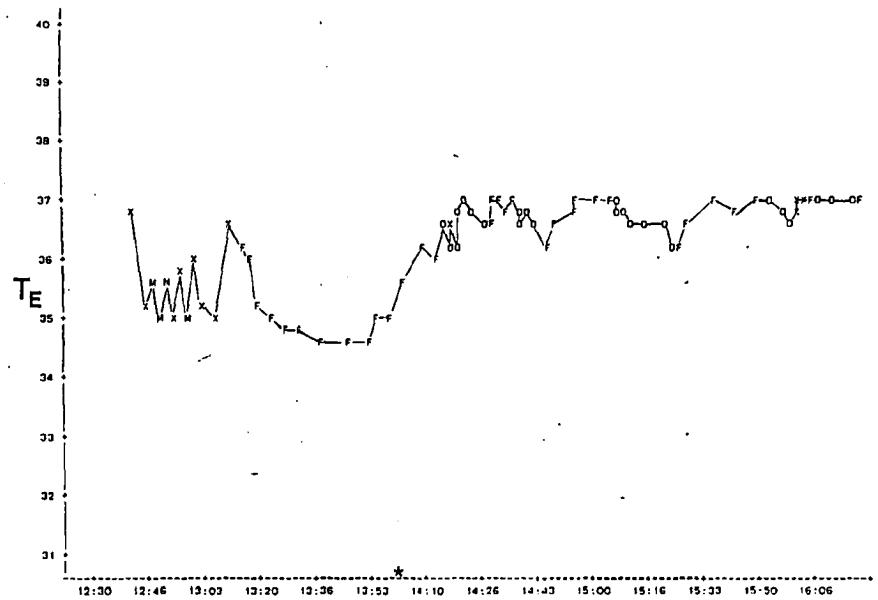


Data from the pavement nest on 30 May are shown in Figure 30, and there appears to be less minute-to-minute variation in T(E) than on 29 May, although the range was similar over the whole day. The female began to shade the eggs when T(A) was 33°, but shading only caused a slight drop in T(E) or T(N), in contrast to the drop it caused on the previous day in the soil nest. This could be due to three factors: T(A) was higher on 30 May, so the T(E)-T(A) gradient was smaller; pavement is hotter than soil at the same T(A) when the sun is out, as it was on 30 May; and the wind was lighter on 30 May than on 29 May. Several times on 29 May a small gust of wind caused an immediate drop in T(E) if the parent was standing over the eggs, so wind seems to be necessary for shading to cool the eggs. The sun was behind the clouds until 1400 hrs on 30 May, and after it came out, T(E) rose from 35° to 36.5°, while the female sat quietly on the eggs. She began to shade the eggs shortly thereafter. The presence or absence of direct sun was not recorded in the present study, but it also appeared to affect both T(E) and parental behavior at the nest.

Data on T(N) and T(A) were read directly from strip-chart records for two days in 1980, reading at every peak and trough of T(N) instead of every 15 min. The results are shown in Figure 31 a & b, showing the first day of the sample at Nest 18-80 and Nest 21-80 respectively. A broken

FIGURE 30: Plot of T(E) vs. time of day for pavement nest showing parental behavior.

Plot of T(E) vs. time of day for pavement nest, 30 May 1981, showing behavior at the nest: 'M' = male sits on eggs, 'F' = female sits on eggs, 'U' = male shades eggs, 'O' = female shades eggs, 'X' = nest uncovered. Point at which sun came out is marked.



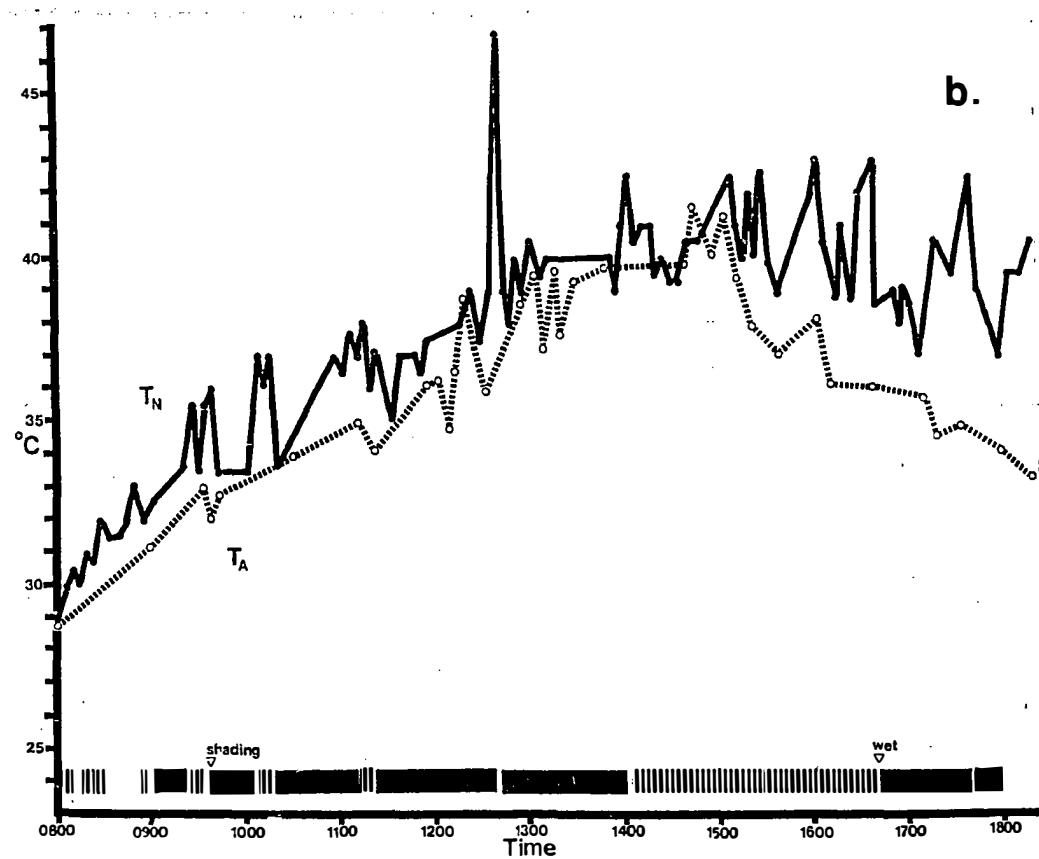
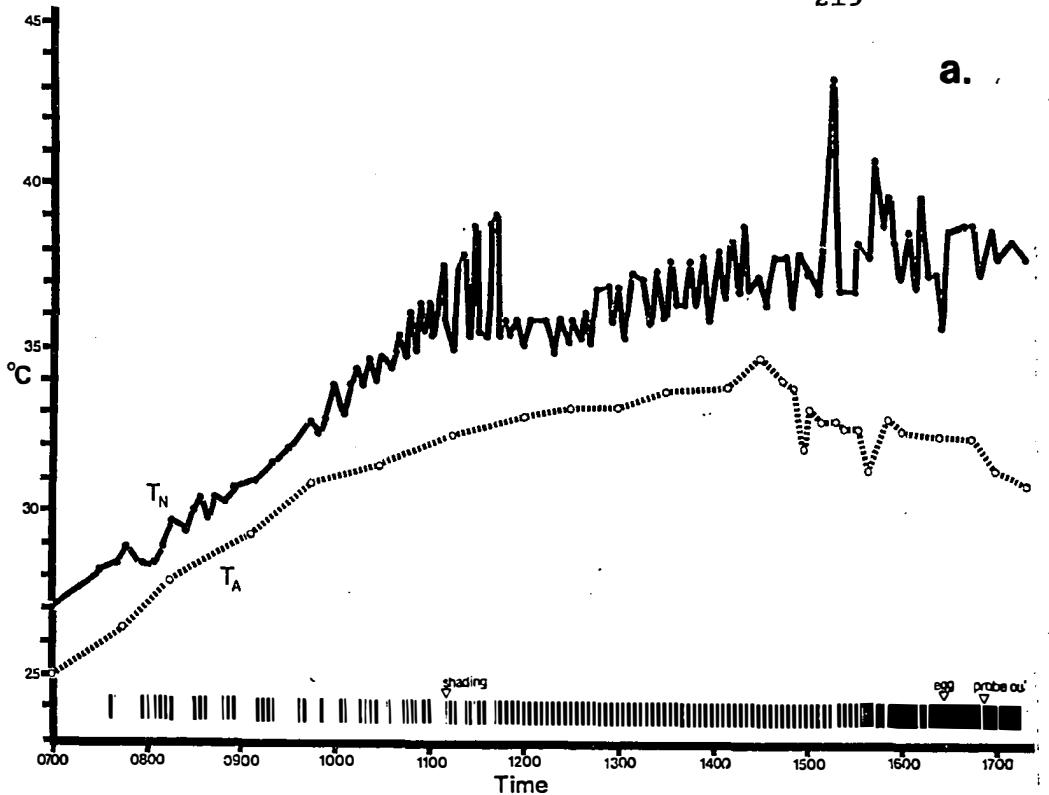
bar along the bottom shows when the male was on the nest, the solid bar when the female was on the nest, and no bar for absences. All the spikes in T(N) were associated with absences, when sun flecks may have hit the probe. Figure 31 a shows temperatures at Nest 18-80 on the day that the third egg was laid. The male incubated most of the day, which is typical of clutch completion (see Ch. 2), and the female came to the nest shortly before she laid the egg. This nest had been incubated very little the previous night (see above), yet it was incubated fairly continuously during the day. The daytime incubation was clearly necessary to keep the eggs from overheating. The male began shading the eggs at the normal T(A) of 32°, and shading alternated with sitting kept T(N) between 35 - 36° for most of the day. The nest appeared to cool during shading and warm during sitting, producing the variation shown between 1130 - 1500, when the male was on the nest continuously.

Data from Nest 21-80 on 8 June are shown in Figure 31 b, the day before the male was removed from this nest (see above). Both T(N) and T(A) were unusually high on this day. The parents' response to high T(A) and T(N) was to minimize the length and number of absences, since they have such a dramatic effect on T(N), and presumably a lesser but still significant effect on T(E). Another response by the female was to return to the nest with a wet belly, but this was not

FIGURE 31: Plots of $T(N)$ & $T(A)$ showing nest attendance.

a: Plot of $T(N)$, solid line, and $T(A)$, dashed line, vs. time of day at Nest 18-80 on 30 May 1980, the day the 3rd & last egg was laid. Broken bar along bottom = male on nest, solid black bar = female on nest, no bar = nest uncovered. Note regulation of $T(N)$ between 1130 and 1500 hrs.

b: Similar plot with same symbols for Nest 21-80 on 8 June 1980, before the male was removed. Note overall high temperatures and spikes in $T(N)$ during absences.



done until after T(A) and T(N) had peaked after 1600 hrs. Belly-soaking caused a drop in T(N), but only a temporary one. Wet belly feathers appeared to dry fairly quickly on the nest, usually within an hour.

Means of T(N) were calculated for 114 3.5 hr daylight time periods in 1980, and stepwise regression was used to identify significant predictors of mean T(N). As expected, most of the variance was explained by T(A), but there were other predictors. Table 10 shows the regression coefficients and R² values for these factors.

TABLE 10
FACTORS AFFECTING DAYTIME MEAN T(N), 1980

Variable	B value	R ² contribution	P
Intercept	17.8		
T(A)	0.64	67%	0.0001
Incubation time	-3.65	4%	0.001
Pavement/soil	-1.33	3%	0.0012
		TOTAL = 71%	

B value = partial regression coefficient from stepwise regression.

Mean T(N) was positively correlated with mean T(A), as expected, but it was also found that Mean T(N) was negatively correlated with incubation time. The significance of this correlation is unclear, because incubation time is high at both low and high T(A) (see Ch. 4). The results also show that T(N) was lower on soil than on pavement. This result is complicated by the fact that most of the pavement nests were studied late in the breeding season, when T(A) and T(N) were both higher (see Figure 23 a above). However, variance caused by T(A) had already been accounted for in the regression model, and a variable of the day of the breeding season was not selected by the stepwise regression procedure. Other variables not selected were: day of incubation, day of movie sample (1-3), wind speed, pair/single incubator, rainfall, and absence/presence of belly-soaking. The variable for belly-soaking included 12 periods during which belly-soaking occurred, and it was expected to reduce T(N). Belly-soaking was observed in Pairs 19-80, 21-80, 28-80, and 29-80, all of which were nesting on pavement. Only the female used belly-soaking, except in Pair 28-80, in which both sexes used belly-soaking. Of the 12 cases of belly-soaking, T(N) dropped in 10 cases, with a mean drop of 2.3° (range 0.5-5.2°). However, the drop in T(N) was temporary, and apparently it was not enough to affect the regression.

Factors Affecting Variance in T(N) during the Day

Because T(N) and T(E) show such a pronounced diurnal variation in Wilson's Plover, it is impossible to state a "normal" T(E) for this species, as has been done for other species (Drent 1973). Such measurements are probably only made during quiet incubation at midday. Thus to compare the degree of thermoregulation of the eggs the deviation of T(E) or T(N) from a "normal" value cannot be used. However, embryo development is abnormal if there are wide and frequent fluctuations of T(E), even if lethal levels are not reached (Lundy 1969). I chose the coefficient of variation (C.V.) of T(N), calculated over 3.5 hr daylight time periods, as a comparative index of thermoregulatory performance during that interval. The log transformation was used to achieve normality (see Methods).

Stepwise regression was used to find significant predictors of the coefficient of variation of T(N), and the results are shown in Table 11. Since T(A) is the main factor affecting T(N), as shown in the preceding section, it was expected that the C.V. of T(A) would be one of the main factors affecting the C.V. of T(N). However, incubation time was the first variable selected, with R^2 contribution of 19%, and C.V. of T(A) was selected second, with R^2 contribution of only 4%.

The results for incubation time were expected on the hypothesis that incubation regulates T(N) (and thus T(E)), and the C.V. of T(N) is lower at high incubation time. The

TABLE 11

FACTORS AFFECTING C.V. OF T(N) DURING DAY, 1980

Variable	B value	R ² contribution	P
Intercept	3.19		
Incubation time	-0.74	19%	0.0023
C.V. of T(A)	0.05	4%	0.0014
Day of incubation (1-22)	-0.016	5%	0.02
Pavement/soil	-0.30	3%	0.0008
Mean T(N)	-0.03	4%	0.013
Day of sample (1-3)	-0.12	3%	0.016
	TOTAL =	38%	

B value = partial regression coefficient from stepwise regression.

R² contribution = increase in total R² caused by adding that variable to the regression model.

fact that the C.V. of T(N) was positively correlated with the C.V. of T(A) shows that the parents are less than perfect regulators of T(N). T(N) fluctuated less as hatching approached, and this was a consistent trend through the incubation period, not an artifact produced by a few outliers (unpub. data). Reasons for this change are unclear, except that parents relieved each other at the nest more often as hatching approached (Ch. 4), which might improve regulation of T(N). Embryonic heat production is unlikely

to have any direct effect on $T(N)$. Data on sensitivity of chicken embryos of extreme temperatures shows that in general the embryo is less sensitive as hatching approaches (Lundy 1969), so the observed trend is unlikely to be related to embryo sensitivity. Variance in $T(N)$ was lower on soil than on pavement, as expected because the pavement often became so hot during the day. $T(N)$ varied less at high $T(N)$, a result that is in agreement with the finding that bird embryos are much more quickly killed by high temperatures than by low ones (Bennett et al. 1981). This also shows that the pavement/soil factor is unlikely to be an artifact, because the pavement nests were later in the season, when $T(N)$ was higher, yet they had greater C.V. of $T(N)$ than the soil nests. Finally, putting the movie camera and probes at the nest appeared to interfere slightly with the regulation of $T(N)$, since its C.V. went down as the sample progressed. Some pairs reduced their incubation time for a few hours after the equipment was left, but this factor was not a significant one in regressions on incubation time (see Ch. 4). This longer-term effect on $T(N)$ regulation could be due to poking at the foreign object in the nest (the probe), or some change in posture on the nest caused by the camera or the probe. Putting a dummy camera and probe at the nest a day or two before the sample began would probably eliminate this effect.

Other variables not selected in the stepwise regression procedure were: mean $T(A)$, day of breeding season,

pair/single incubator, absence/presence of belly-soaking, wind speed, and rainfall. Thus $T(N)$ did not fluctuate more in single incubators than in pairs, although sample size was small for single incubators. This confirms the conclusion drawn from examining the diurnal patterns of $T(N)$ above, which showed no apparent differences between pair and single incubators. Wind speed, which was measured at an airport and not at the study site, showed a non-significant negative correlation with the C.V. of $T(N)$, meaning that $T(N)$ was less variable when there was more wind. This agrees with the finding that parents use shading the eggs to regulate $T(E)$ and $T(N)$, and that shading only cools the eggs and nest when there is some wind (see Figure 30 above). This factor needs further study, using measurements made near the ground near the nests.

Rate of Change in Temperature of Uncovered Eggs

One function of incubation is to regulate egg temperature within the limits at which development occurs (Drent 1975), and the change in $T(E)$ that occurs when the nest is uncovered will determine how long the nest can remain unattended without exceeding those limits. Egg cooling rates are usually studied in an environmental chamber, and cooling rate has been found to vary inversely and logarithmically with egg weight (Drent 1975). Wilson's Plover eggs weigh 12 g, so their predicted cooling rate is about $2.0^{\circ}\text{ C.} / ^{\circ}\text{C. hr}$, where the degrees in the numerator refer to the drop in

$T(E)$, and in the denominator to one degree difference between $T(E)$ and $T(A)$. Cooling rates in a nest are often higher than the predicted rate, due to conductive and convective losses, especially for small eggs (Drent 1975). My measure of $T(A)$ did not integrate all the heat fluxes on an egg (as a model egg would), so I cannot compare my rates to the theoretical rate. Instead I have calculated rate of change in $T(E)$ in $^{\circ}\text{C.} / \text{min}$ and plotted it against $T(A)$ at the start of the absence, using data from 29 and 30 May 1981. Much less research has been done on egg heating rates than on cooling rates (Kendeigh 1973).

Rate of change in $T(E)$ during absences is shown in Figure 32 plotted against $T(A)$ at the start of the absence. Unlike the other regressions using data from these two nests, the regression was not significantly different at the two nests. The rate of change in $T(E)$ was positively correlated with $T(A)$: Rate = $-2.88 + 0.091(T(A))$, $r = 0.73$, although the rate variable was non-normal and no suitable transformation could be found. The Spearman Rank Correlation was slightly greater, $r = 0.78$, $P = 0.0001$. The lowest points on the $T(A)$ axis were late in the day on 29 May, when a thunder-storm was brewing, which explains the high cooling rate. The regression line crosses rate = 0 at $T(A) = 31.7^{\circ}$, which is exactly the point of minimum incubation time by the parents (see Ch. 4). This shows that the parents reduce their incubation time when the eggs need the least attention to stay within temperature limits, since at 31.7° the eggs

should neither cool nor heat when left unattended. This is what I had hoped to show in calculating the rate of change in $T(E)$, and this will be discussed further in Ch. 7.

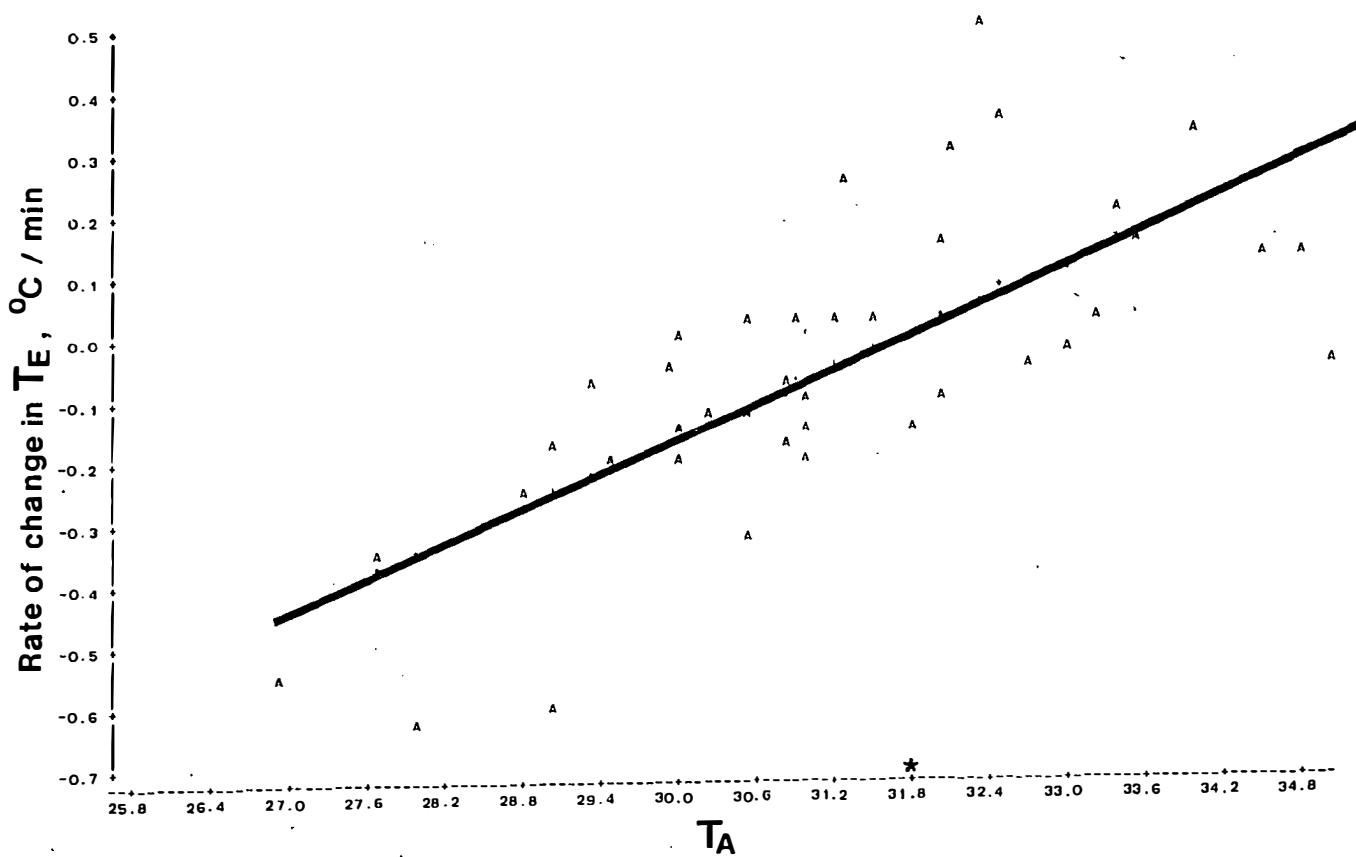
Heated Egg Experiment

One experiment was done in 1981 to see how a hot egg would affect incubation behavior during a period when eggs were not normally hot. The experiment was attempted at 3 different nests, but only at one did the parents and the weather cooperate to make the results useable. At one nest the male refused to go to the nest with wires coming out of it, although the female had done so.

The experiment was done in the morning, before the eggs normally warmed up to their daily maximum temperature, and before the parents normally began panting and shading the eggs, both of which usually began at $T(A) = 32^\circ$. This $T(A)$ was reached some time before noon, depending on the weather, but on the day of the experiment it was not reached by noon, so the day was somewhat cooler than usual. In a hotter climate at the Salton Sea in California, Grant (1979) could only do a similar experiment shortly after dawn. The experiment was done successfully on 31 May at the same nest at which temperatures were recorded on 30 May. Results are shown in Table 12. The largest change produced by the hot egg was an increase in the number of pokes from 0 to 15 per hr. During a poke the bird lifts slightly off the nest and pokes the eggs with its bill. Shading time increased from 0

FIGURE 32: Rate of Change in Temperature of Uncovered Egg vs. T(A).

Rate of change in $T(E)$, in degrees C. / min, is shown plotted against $T(A)$ for 42 absences observed on 29 and 30 May 1981. The regression line is shown by a solid line, and it did not differ significantly between the samples. The regression line crosses rate = 0 at 31.7° .



to 12% when the egg was heated, but shading did not begin right away. No absences were taken during the heating period, and it is possible that the egg was so much hotter than normal that the female was trying to cool it by contact with her brood patch. Poking the eggs might help in this process. Frequency of poking was not recorded in other data on incubation that I collected, so there are no other data to compare these to. Panting by the female began at $T(A) = 29.8^\circ$ at the end of the heating period, slightly below the normal starting point of 32° . The female left the nest soon after the end of the heating period, and the male came to the nest. The male began both panting and gular flutter 20 sec after he came to the nest, at $T(A) = 32.0^\circ$, and he continued both for 19 min, then stopped both. During these 19 min the egg cooled from 39.0° to 35.2° . He began warming the egg immediately after he stopped panting & gular flutter. Thus panting and gular flutter were correlated with egg cooling, but experiments are needed to see if they are used to dissipate excess heat from the eggs. The male relieved the female shortly after the end of the heating period, so the same bird was on the nest throughout the control and heating periods, but not the post-heating period.

TABLE 12

HEATED EGG EXPERIMENT, 31 MAY 1981, PAVEMENT NEST

Time	Period	T(A)	T(E)	Shade Time	Incub. Time	Pokes
0850-0950	control	25.0- 28.5°	35.0- 36.2°	0%	97%	0
0950-1100	heating	27.6- 29.8°	36- 50°	12%	100%	15
1100-1140	post- heating	29.2- 30.0°	35.2- 44.5°	21%	88%	3

Pokes = number of times during period that the bird stood up over the eggs and poked them.

Discussion

There are several problems that arise in trying to compare my results to those of similar studies on other birds. Temperature measurements have been taken in different parts of the egg and nest in different studies, egg size affects the measurements in several ways, and methods of data analysis differ. The embryo usually floats near the top of the egg early in development, so this could be considered the place to get the most "accurate" measure of temperature of development (Drent 1975). However, this would be very difficult to achieve in the small egg of Wilson's Plover, and the temperature differential between the center of the egg and the embryo should be much less in a small egg than in a large one. The temperature measured at the center of a

Herring Gull egg weighing 90 g (Drent 1970) is thus not comparable to the temperature measured at the center of a Wilson's Plover egg weighing 12 g. The larger egg also has a much larger thermal inertia, so changes in $T(E)$ in the two eggs are difficult to compare. Yet another difference is that embryonic heat production has a large effect on $T(E)$ in large eggs as hatching approaches, while the effect is usually not detectable in small eggs (Drent 1975).

On the subject of data analysis, some studies (e.g. Grant 1979) only include measurements of $T(E)$ taken after the bird has been sitting quietly on the nest for at least 30 min. This is a sort of equilibrium egg temperature, rather than the range of $T(E)$ that occurs under natural conditions of incubation. The present study includes measurements of $T(E)$ and $T(N)$ taken during both incubation bouts and absences. If data during absences are excluded from the regression of $T(E)$ on $T(A)$, the R^2 value drops at the soil nest (45% to 31%) but not significantly at the pavement nest (58% to 57%), and a significant relationship still exists at both nests. Thus this correlation is not an artifact of including data from absences, as Purdue (1976) implied. In fact, Grant (1979) found a significant positive correlation of $T(E)$ with $T(A)$ in all the species he studied, except one species at one study site only, in spite of his excluding data during absences.

Another problem in comparing studies of egg temperature, and also of incubation behavior, is that most effects occur

only under a certain range of environmental conditions.

Failing to find a particular correlation could simply mean that the range of environmental conditions necessary to produce the effect was not present in the study area, or not present in the data collected. All such studies are natural experiments and the investigator has no direct control over temperature or other variables. For example, the greatest effect of $T(A)$ on $T(E)$ occurs above about 30° , but most temperate zone breeding birds are never or rarely exposed to $T(A)$ higher than that. The Herring Gulls studied by Drent (1970) were exposed to a $T(A)$ range of $12 - 28^{\circ}$. At the other extreme, the Salton Sea appears to be so hot that this thermal neutral zone is passed through quickly early in the morning, so that little data can be collected during it (Grant 1979). The study area should be hot but not too hot if the full range of incubation behavior and egg and nest temperatures are to be observed.

Forewarned by these caveats, several other birds nesting on the ground in hot climates have $T(E)$ positively correlated with $T(A)$. These include the Snowy Plover (*Charadrius alexandrinus*) (Purdue 1976), Killdeer (*C. vociferus*), American Avocet (*Recurvirostra americana*), Black-necked Stilt (*Himantopus mexicanus*), Forster's Tern (*Sterna forsteri*), and Lesser Nighthawk (*Chordeiles minor*) (Grant 1979) and Killdeer (Cronan 1974). All but the nighthawk are in the Charadriiformes, and most birds making exposed nests on the ground in hot climates belong to that order. Most of the

birds in which $T(E)$ is independent of $T(A)$ either have well-insulated nests off the ground (e.g. House Wren, *Troglodytes aedon*, Kendeigh 1963) or have large, lined nests on the ground in cool climates (e.g. Herring Gull, Drent 1970). Data on $T(E)$ for birds which make better-insulated nests on the ground in hot climates (e.g. Horned Lark, *Eremophila alpestris*) are not available but would be very useful.

Purdue (1976) used unshaded air temperature in his study of Snowy Plover, but Grant (1979) found using similar equipment in a similar habitat that that unshaded $T(A)$ was about 4.4° above shaded $T(A)$. Thus 4.4 should be subtracted from $T(A)$ in the regression equation from Purdue (1976), $T(E) = 14.4 + 0.63(T(A))$, changing it to $T(E) = 11.7 + 0.63(T(A))$ to reflect the use of unshaded $T(A)$. Cronan (1974) reports a regression of $T(E) = 25.8 + 0.34(T(A))$ at one Killdeer nest, and slightly lower slopes at four other nests. Grant (1979) reports a regression for Killdeer of $T(E) = 25.6 + 0.36(T(A))$, very close to Cronan's regression, and for other species (American Avocet, Forster's Tern, Black-necked Stilt) he found slopes of similar magnitude at some study sites, and smaller slopes at others, the lowest being -0.056 for Forster's Tern at one location. Most of the species studied by Grant at the Salton Sea use belly-soaking frequently, and this may have affected the regression.

In waterfowl such as Canada Geese (*Branta canadensis*), $T(E)$ depends on $T(A)$ only during laying (Cooper 1978). The low range of $T(A)$ values, the large eggs, the large clutch

size, and the down that lines the nest and is put over the eggs presumably keeps $T(A)$ from affecting $T(E)$ at other times. There is also little effect of $T(A)$ on $T(E)$ after the laying period in the smaller Northern Shoveler (*Anas clypeata*) (Afton 1979). Mean daily $T(E)$ increased slightly during the incubation period in the Shoveler, probably due to embryonic heat production. Egg cooling rate during absences in the Shoveler was negatively correlated with mean $T(A)$ during the absence, which is the same as my result, because my cooling rates are negative and Afton's were positive. Drent (1970, Fig. 35) shows a graph of $T(E)$ & $T(N)$ vs. $T(A)$ for one Herring Gull nest over a 24 hr period, and $T(E)$ and $T(N)$ were essentially constant over a $T(A)$ range of 12 - 28°. Kendeigh (1963) found no significant change in $T(E)$ of a House Wren over a $T(A)$ range of 20 - 32°, but $T(N)$ increased significantly over the same range.

The diurnal fluctuations in $T(E)$ and $T(N)$ found in Wilson's Plover should result from the positive correlation of $T(E)$ with $T(A)$, but Purdue (1976) shows no daily patterns and Grant (1979) only shows them for some of the species, the Black-necked Stilt and Forster's Tern, and these were similar to the rise and fall found in the present study. Bennett et al. (1981) found that $T(E)$ in one Western Gull nest rose each day and each night, as in the present study, but in another nest the fluctuations in $T(E)$ were less marked and less regular. Howell (1979) made most of his observations on the Egyptian Plover (*Pluvianus aegyptius*)

between 1000 - 1730 hrs only, and $T(E)$ was fairly constant between those hours, but $T(N)$ rose and fell as the day progressed. Observations made on one night showed that $T(E)$ is lower at night than during the day in this species.

The observation that shading cools the eggs was made by Purdue (1976) for the Snowy Plover. The use of shading was also observed in Snowy Plover and in Killdeer at the Salton Sea by Grant (1979), but its effect on $T(E)$ was not investigated. Purdue (1976) found that when $T(A)$ was above 36° , shading time was lower when winds were very high. This was thought to be due to wind-blown sand hitting the parent. The importance of wind convection to egg cooling is stressed by Bennett et al. (1981): an exposed gull egg near vegetation with reduced convection becomes much hotter during the day than an exposed egg on open sand, with normal convection. Black-necked Stilt eggs heat very quickly when exposed at midday (Grant 1979).

I have not found a published study using variance of $T(E)$ or $T(N)$ as an index of thermoregulatory performance during incubation. The variance of $T(B)$, or body temperature, is used by Huey and Slatkin (1976) and others as an estimate of "thermal niche breadth" in lizards, and it is positively correlated with variance in air temperature. There are obvious parallels between regulation of $T(B)$, using metabolic and behavioral mechanisms, and the regulation of $T(E)$, using parental behavior at the nest. These parallels are discussed in Ch. 6.

Experiments with a heated egg were done by Grant (1979) at several Black-necked Stilt nests. He was mainly interested in eliciting belly-soaking, which the heated egg failed to do. He did not show the quantitative effect of the heating on incubation behavior, but it caused some birds to leave the nest. Drent et al. (1970) put heated eggs in Herring Gull nests, and found that the frequency of resetting, egg-shifting, nest building, and looking down was higher on hot eggs. Egg-shifting is the closest to what I called poking. Their impression was that the bird on hot eggs was "fidgety", an impression that I also had with Wilson's Plover. Franks (1967) presented hot eggs to incubating Turtle Doves (*Streptopelia risoria*) and found that hooking the bill over the egg, or shifting, increased when eggs were hot. Moving eggs with the feet, turning on the nest, and nest relief were also more common on hot eggs. In general, hot eggs seem to increase the frequency of behaviors that interrupt incubation, rather than increasing the frequency of behaviors that might cool the eggs. It is possible that the novel stimulus of hot eggs in a cool environment elicits an unusual response. It would be interesting to test an incubating bird with a hot environment but with cool eggs, but this would also be a novel stimulus. It is also possible that shading the eggs is triggered by neither high T(E) nor high T(A) directly. On several occasions I noticed that incubating birds stood when the sun came out

from behind a cloud, and sat when the sun went behind another cloud. Given the possible interactions with wind as well, it seems that egg-heating experiments are of limited value in determining the functions or proximate causes of incubation behavior.

In conclusion, egg and nest temperatures in Wilson's Plover are similar to those found in other birds, and their responses to air temperature are similar to those found in other birds nesting on the ground in hot climates. The type of substrate under the nest, soil or pavement, have significant effects on several aspects of egg and nest temperatures. There are no significant differences found between patterns of nest temperature in pairs compared to single incubators, or between periods in which belly-soaking occurred compared to those in which it did not occur. Overall the patterns of nest temperature are surprisingly consistent from nest to nest, except for the pavement/soil difference.

Several factors have a significant effect on the coefficient of variation in nest temperature, which was used as a comparative index of the regulation of egg temperature. The most significant is a negative correlation of the C.V. of $T(N)$ with incubation time, showing statistically that incubation has the effect of regulating nest temperature. An egg heating experiment showed that the main response to a hot egg is egg poking, and that the parent may dissipate the heat from the egg through its own body. The rate of change in $T(E)$ during absences is positively correlated with $T(A)$.

during the absence, and the rate is zero at $T(A) = 31.8^\circ$. This is the same $T(A)$ at which incubation time is minimal, and this correspondence is discussed in Chapter 6.

Several questions are raised by the results in this chapter that can best be answered by reference to other aspects of the breeding biology of this species. One question is why so many pairs chose to nest on pavement late in the breeding season, when the thermal environment seemed to be dangerous to the eggs. A hotter substrate might benefit the parents if it allowed them to reduce incubation time at night, but there did not appear to be dramatic differences between $T(N)$ in pavement and soil nests at night (Figure 24). Another question is how the parents regulate their body temperature while keeping the eggs cool, without belly-soaking frequently. Grant (1979) concluded that belly-soaking was the main mechanism used to cope with the hot environment at the Salton Sea by the birds nesting there. Another question is how the lone incubators managed to regulate $T(N)$ about as well as pairs, even though they had lower incubation time than pairs (Ch. 3). Finally, the increase in incubation bout length at high temperature (Ch. 4) is especially puzzling, since most shorebirds reduce incubation bout length at high temperature (Grant 1979). These questions are discussed below in Chapter 6.

CHAPTER VI

CONCLUSIONS AND A THERMOREGULATORY MODEL OF INUCBATION

Summary of Factors Affecting Incubation Behavior and Egg and Nest Temperatures.

The factors, or independent variables, which were found to have a statistically significant effect on different components and on egg and nest temperatures are shown in Table 13. All components were significantly affected by air temperature except division of labor, and division of labor was the only component that differed significantly between pairs. Since the two sexes appeared to be equally effective incubators, the division of labor was not expected to be under the same thermal constraints as other components of incubation, and the observed variability in division of labor bears out this expectation. Male share of incubation ranged from 7% to 51% in pairs (Chapter 2), and at three nests the male apparently did 100% of the incubation for up to 11 days (Chapter 3). Males did more incubation during clutch completion and hatching than during the middle stage, and males did more incubation after 1730 hours than before that time each day. At three nests the male probably incubated all night as well.

Incubation time was strongly correlated with air temperature, but the relationship was not linear. Incubation time

was minimal at moderate air temperature (31 -33° C.), and higher at both low and high temperature. Pairs had significantly higher incubation time than males at any given temperature. Absence duration was also correlated with air temperature in a non-linear way, reaching a maximum at moderate air temperatures, and absences were shorter at low and high temperatures. Absences were longer in lone males than in pairs at a given temperature. Absences were longest during clutch completion, shorter during the middle stage of incubation, and shortest during hatching. In both sexes, absences during nest relief were shorter than absences that did not involve nest relief. Male absences that did not involve nest relief were significantly longer than similar female absences.

Incubation bout duration showed the same response to air temperature as incubation time, with the minimum duration at moderate air temperatures and longer bouts at low and high temperature. Lone males had significantly longer incubation bouts than males in pairs in survival analysis, but this factor was not significant in regression analysis. Females had much longer incubation bouts before nest relief compared to when they were not relieved, suggesting that they may stay on the nest in anticipation of relief. Incubation bouts were longest during the middle stage of incubation, and shorter during clutch completion and hatching.

Parental shift length was affected by many of the same factors. Shifts by females were longer than shifts by

TABLE 13

FACTORS AFFECTING COMPONENTS OF INCUBATION BEHAVIOR AND EGG
AND NEST TEMPERATURE

Component	Factor(s)
1) Division of labor	Pairs, Stages of Incubation, Time Periods
2) Incubation time	Air temperature, pair/lone male
3) Absence length	Air temperature, pair/lone male, stages of incubation, nest substrate, sex
4) Incubation bout length	Air temperature, pair/lone male, stages of incubation, sex
5) Parental shift length	Air temperature, sex, stages of incubation
6) Shading time	Air temperature
7) Orientation on nest	Air temperature, solar angle
8) Egg temperature	Air temperature, nest substrate, parental behavior
9) Nest temperature	Air temperature, nest substrate, incubation time
10) C.V. of Nest temperature	Incubation time, C.V. of air temperature, stage of incubation, nest substrate, nest temperature, day of sample

males, even though incubation bout lengths did not differ between the sexes. This is because one shift usually contained several incubation bouts, and there could be more bouts of the same length in female shifts than in male

shifts. Parental shifts were shorter at high air temperature than at moderate or low air temperatures, and shifts were longest during clutch completion, shorter during the middle stage, and shortest during hatching. Thus absence length, incubation bout length, and shift length were all reduced during hatching.

Shading time was strongly affected by air temperature. Shading of the eggs began at about 32° C., reached a maximum at about 36° C., and dropped off above that temperature. Orientation to the sun on the nest was observed during the hotter part of the day, with the incubating bird putting its back to the sun. This probably makes panting and gular flutter more effective, and may help to keep the eggs in shade.

Egg and nest temperatures were strongly and positively correlated with air temperature. Because egg temperature is the most critical component of incubation in terms of embryo survival and development, it should show the least variability between groups, unless there were differences in hatching success. Thus the lone male incubators had significantly lower incubation time, longer absences, and longer incubation bouts than pairs, but their hatching success was at least as high as pairs. Nest temperature was the only component of incubation analyzed that did not differ between pairs and lone incubators, suggesting that it is in fact more tightly constrained than other components. Regressions of egg and nest temperature did vary according to nest

substrate, which affected nest microclimate. Variance in nest temperature was negatively correlated with incubation time, showing that incubation functions to regulate nest temperature. Variance in nest temperature was positively correlated with variance in air temperature and with nest temperature, and negatively correlated with day of incubation. Variance in nest temperature was lower on soil than on pavement. Variance in nest temperature decreased during the three-day time-lapse movie sample, suggesting that a reaction to the camera disturbed nest temperature regulation slightly.

In conclusion, division of labor by the sexes showed the greatest amount of variability of the components studied, showing large variations between different nesting pairs. Nest and egg temperatures showed the least amount of variability of the components, with no difference in nest temperatures between pairs and lone male incubators. Other components of incubation showed intermediate amounts of variability. This is interpreted as showing that egg and nest temperatures are under the tightest selective constraints because they are the most directly related to hatching success, while division of labor is the least constrained component, because it should have little effect on egg and nest temperatures, and on hatching success.

Incubation in the Context of the Breeding Season

Many aspects of incubation in Wilson's Plover are explainable in relation to one feature of its breeding biology: low hatching success, probably about 20 -40% (Chapter 1). Low hatching success has two consequences that in turn affect incubation patterns: nest site selection and frequent renesting.

Nest site selection by Wilson's Plovers in Texas is unusual in that roads and pavement are used much more frequently than in other plovers. Road and pavement nests have higher hatching success than soil nests, probably due to a lower risk of nest flooding on roads and pavement (Chapter 1). Wilson's Plover nests were also farther from water than those of many other shorebirds, which is probably also an adaptation to the risk of flooding. One consequence of nesting far from water is that belly-soaking is more difficult. At the Salton Sea, some Snowy Plovers nest so close to water that the incubating bird can wet its belly and return to the nest in 30 sec or less (Grant 1979). As discussed above, Wilson's Plover may have compensated for the rarity of belly-soaking by using gular flutter to cool itself during incubation. Road and pavement nesting could also affect rates of nest predation, as discussed in Chapter 1, but little is known of searching methods of nest predators.

Low hatching success also results in frequent renesting (making a new nest after one is lost) in Wilson's Plover.

Since any one nest has a low probability of success, several nesting attempts may have to be made before one is successful. To be able to renest, the female must be able to lay new eggs, and the pair must be able to continue incubation over a fairly long breeding season. One adaptation to renesting is the reduced clutch size, which is 3 in Wilson's Plover, compared to 4 in arctic and temperate plover species. The female invests less energy in each clutch, and she is able to replace them more rapidly, when clutch size is reduced. This reduces the energy drain of repeated renesting, making it more likely to be possible, and thus increases the chance that the pair will have at least one successful nest that season.

Renesting could also lead to energetic depletion of the female, even with reduced clutch size. The higher energetic demands on the female due to egg-laying may contribute to female desertion in arctic sandpipers (Ashkenazie and Safriel 1979). This may also explain why some females stopped incubating late in the breeding season in Wilson's Plover in 1979 (Chapter 3). The male may continue incubating alone rather than looking for a new mate because desertion occurred too late in the breeding season to remate and start a new nest.

Because renesting is common in Wilson's Plover, and because female desertion may occur at the end of the breeding season, division of labor earlier in the breeding season may be related to the possibility of renesting and female

desertion. Both sexes reduce incubation at moderate air temperatures (see above), and taking extra time away from the nest would help each parent be prepared for a possible renest, if the time is used for foraging. Whether the division of labor either leads to female desertion, or makes male incubation possible after female desertion, is more difficult to establish. If the female spent more energy on incubation than the male, this leaves the male in better condition to incubate alone, but it also makes female desertion more likely. If the male spends more energy on incubation than the female, she might be able to replace clutches faster, and female desertion might be less likely, but the male might not be able to incubate alone. Although the female spends more daylight hours incubating in most pairs, the energetic costs of incubating at different times are not known in this species. There does appear to be a marked diurnal pattern in food availability, which could affect the energy balance of the parents. Prey are more available in cooler parts of the day, when the male was usually on the nest and the female thus free to feed. Male and female energy balances could be about the same during incubation.

Male share of incubation is increased during clutch completion and during hatching in Wilson's Plover. During clutch completion the female needs time to forage since she is producing eggs, which is probably why the male does more incubation. During hatching, the female could decrease her share of incubation if she needed more time to forage

(Miller 1979), but there could also be advantages to more equal sharing of incubation during hatching. Shift length is sharply reduced (Chapter 4), so the parents were together at the nest much more often than usual. This probably facilitates eggshell removal, tending of newly hatched chicks, and finally departure from the nest. The family usually departs from the nest together soon after the last chick hatches.

Wilson's Plover generally fits the description of a tropical plover given by Summers & Hockey (1980) for C. marginatus. The reduced clutch size, low hatching success, and frequent renests are also found in that species. Whether Wilson's Plover also has the compensating advantage of long life expectancy is not known, but few potential predators on adults were seen in Texas, and the wintering range (Mexico) is not far away.

The adaptive significance of the flexibility of division of labor during incubation in Wilson's Plover may be that it enables one parent to complete nesting successfully if necessary. The last nest of the season may be the only chance by the pair to have chicks that year, since earlier nests probably failed. This flexibility would also be an advantage if ecological conditions changed, or breeding range of the species changed. Different ecological conditions could favor uni-parental care over bi-parental care, and could lead to the evolution of a polygamous mating system (Pitelka et al. 1974). The flexibility of the division

of labor in Wilson's Plover, especially if it exists in other monogamous shorebirds, is an explanation for the question of why polygamous mating systems are relatively common in shorebirds.

Adaptations of Shorebirds to Nesting in a Hot Environment

Successful incubation in an exposed nest in a hot climate requires adaptations that both keep the eggs from overheating, and keep the incubating parent(s) from overheating. These adaptations may function by either directly cooling the eggs and/or the parents, or they may reduce the exposure to heat of the eggs or the parent(s). Studies of other shorebirds nesting in hot climates show that most species exhibit a variety of behavioral modifications at high air temperature, which perform one or another of these functions. A summary of these adaptations is given in Table 14, along with the relevant findings on Wilson's Plover from the present study.

One of the most common responses of incubation to high air temperature is to increase incubation time, usually to near 100%. This was found in all the shorebirds nesting at the Salton Sea (Grant 1979), in the Snowy Plover in Oklahoma (Purdue 1976), and in the Egyptian Plover (Howell 1979). This was also found in Wilson's Plover. When air temperature exceeds body temperature of the parent, the parent may cool the eggs simply by sitting on them.

TABLE 14
ADAPTATIONS OF SHOREBIRDS TO INCUBATION IN HOT CLIMATES

Other Shorebirds	Function	Wilson's Plover	Function
1) Increased incubation time ^{a-c}	Protects eggs from heat	Same	Same
2) Shorter absences ^{a-c}	Reduces exposure of eggs to heat, sun	Same	Same
3) Shorter incubation bouts ^a	Reduces exposure of parent to heat, sun	Longer incubation bouts	Lower absence rate?
4) Shorter parental shifts ^{a,b}	Reduces exposure of parent to heat, sun	Slightly shorter shifts	Same
5) Standing over eggs ^{a,b}	Cools parent and eggs	Same	Same
6) Panting ^{a-c}	Cools parent	Same	Same
7) Putting back to sun	Cools parent (mouth in shade)	Same	Same
8) Belly-soaking ^{a,c}	Cools parent and eggs	Rare, nests far from water	Risk of floods?
9) No gular flutter	-	Common gular flutter	Cools parent

^a Grant 1979

^b Purdue 1976

^c Howell 1979

Absences, or periods when the nest is uncovered, become very short at high air temperatures in all the same species, including Wilson's Plover. Uncovered eggs heat to near lethal levels in a few minutes at high air temperature (Grant 1979, present study), so this adaptation is probably an essential one. However, the length of incubation bouts has no necessary direct effect on egg temperature, and Wilson's Plover differs from other shorebirds in this respect. Black-necked Stilts, American Avocets, Forster's Terns, Snowy Plovers, and Killdeers at the Salton Sea reduce incubation bout lengths at high air temperature (Grant 1979), but Wilson's Plover increases incubation bout lengths at high temperature. This difference could be related to patterns of parental shift length: in Wilson's Plover, shift length is shorter at high temperature, but not nearly as short as in other shorebirds. Median shift survival at over 33° C. is 46 min in Wilson's Plover, while average shift in Killdeer at high temperature at the Salton Sea is only 10 - 15 min (Grant 1979). Because of the restriction on absence length, most incubation bouts at high temperature are ended by nest relief, and if shifts are shorter, incubation bouts will be shorter. In the absence of a partner to relieve it, a Wilson's Plover incubating at high temperature stays on the nest rather than risking overheating of the eggs during an absence. Longer incubation bouts at high temperature also reduces the rate of absences per unit time, which could also protect the eggs from overheating.

Although long incubation bouts at high temperature may protect the eggs from overheating, they expose the parent to heat for a longer period of time. Parents off the nest can seek shade or water to cool themselves. One adaptation that could cool the parent on the nest is shading the eggs, which occurs in Wilson's Plover and in other plovers (Grant 1979, Purdue 1976). Shading could cool the parent by exposing its legs and shaded belly to convection, and also cool the eggs by convection in the shade. Shading cools the egg under some conditions in Wilson's Plover (see Chapter 5). However, shading would have little cooling value at very high air temperature, when egg temperatures were approached or exceeded, and in fact shading time decreases at very high air temperature in Wilson's Plover (Chapter 4). At very high air temperature the parent could cool the egg with its body, but the problem of how the parent then regulates its body temperature is aggravated. Larger shorebirds such as Avocets and Stilts do not use shading, presumably because they have such long legs (Grant 1979).

Shorebirds in hot environments use panting at high temperature, and this probably reduces body temperature (Grant 1979). The bill is opened and breathing rate is increased, and cooling is by evaporation, primarily from air sac surfaces. In Wilson's Plover panting begins at $T(A) > 32^\circ C$. Shorebirds at the Salton Sea (Grant 1979), and Wilson's Plover, also tended to put their backs to the sun when

incubating during the heat of the day. This would keep the mouth in the shade, and increase the efficiency of panting in cooling the parent. In Wilson's Plover it also increases the shadow size of the parent, and thus facilitates keeping all three eggs in the shade.

Both Grant (1979) and Howell (1979) consider belly-soaking or repeatedly coming to the nest with wet belly feathers, to be the most important adaptations of shorebirds to nesting in the hot climates they studied. It cools the parent and the eggs, and it occurs during the hot part of the day in all shorebirds nesting at the Salton Sea (Grant 1979), and in the Egyptian Plover in Ethiopia (Howell 1979). It also raises nest humidity, which may benefit the eggs (Grant 1979). Belly-soaking is associated with nesting near water, since the feathers must be re-wetted often. It may require short parental shifts, because in some shorebirds (e.g. Killdeer, Grant 1979) one parent wets its belly only when the other parent is on the nest. Wilson's Plover does not nest near water, probably because of the risk of flooding to the eggs (Chapter 1), and parental shifts do not decrease very much at high air temperature. Belly-soaking was only seen at four nests on pavement in 1980, and not commonly at those nests. Thus it could not be the main adaptation to incubating in a hot climate in Wilson's Plover.

There are other species of birds that nest on the ground in hot climates without short parental shifts and without

belly-soaking, and they are not shorebirds but nighthawks (*Chordeiles*, sp.). Common Nighthawks (*C. minor*) nest on runways near Wilson's Plovers on Matagorda Island, and Lesser Nighthawks (*C. acutipennis*) nest at the Salton Sea (Grant 1979). The Lesser Nighthawk female incubates through the heat of the day without relief by the male and without belly-soaking. Nighthawks use gular flutter, which is highly developed in that group, to regulate body temperature at high air temperature. In nighthawks, gular flutter achieves a higher degree of evaporative cooling than panting while using less energy than panting (Dawson and Hudson 1970). The gular area is lighter and thus easier to move than the thoracic cavity. Nighthawks are among the most efficient birds at regulating T(B) at high T(A), and gular flutter appears to be the key to this efficiency.

Although Wilson's Plover uses some belly-soaking, it resembles the nighthawks in that it uses gular flutter most of the time during the heat of the day. None of the shorebirds nesting at the Salton Sea appear to use gular flutter (Grant 1979), and gular flutter is not reported in Charadriiformes (Dawson and Hudson 1970), but it is very unlikely that Wilson's Plover is the only shorebird to use gular flutter. It is probably more common or better developed in Wilson's Plover than in other shorebirds. Gular flutter seems to replace belly-soaking as the key adaptation to nesting in a hot environment in Wilson's Plover.

Assuming that gular flutter helps parents regulate body temperature in Wilson's Plover, it may make road and pavement nesting more successful in this species. Roads and pavement had lower risk of nest flooding than soil nests (Chapter 1), but this advantage is often offset by the hotter nest microclimate. Belly-soaking was only seen at nests on pavement, so the parents used both gular flutter and belly-soaking on pavement.

Long incubation bouts and long parental shifts might make the nest less conspicuous to predators. They both reduce the arrival and departure rate of birds at the nest. Some predators might detect nest locations by detecting arrivals and departures at the nest, and nest predation is fairly high in Wilson's Plover (Chapter 1). The initial reason for a low level of belly-soaking in Wilson's Plover was more likely to be the flooding risk when nesting near water, which required other adaptations to make successful incubation possible in a hot climate.

A Thermoregulatory Model of Incubation

Previous models

Although incubation has been studied for many years, the precise effect of air temperature on incubation behavior has not been studied until recently. The general conclusion for single-sex incubators was that incubation time was reduced at high air temperature (von Haartman 1956). White and Kinney (1974) proposed a more specific model of the response of incubation time to air temperature in single-sex incubators,

based on thermoregulation of the eggs and foraging needs of the incubating parent.

White and Kinney (1974) studied incubation behavior in the Village Weaverbird, *Ploceus cucullatus*, a single-sex incubator that makes woven nests in trees. They conclude that the response of incubation time to air temperature in this species is best described by the negative hyperbolic curve shown in Figure 33 a. Incubation time is near 60% below about 30° C., and above that "release temperature" (White and Kinney 1974) it fell to zero by about 37° C. The curve was chosen empirically, as the one best fitting the data. The principal finding is that incubation time, calculated over one-hour periods, falls to zero at high air temperature. White and Kinney assume that as air temperature increases, it approaches egg temperature, and thus egg cooling rate during absences approaches zero. This is a consequence of Newton's law of cooling (see below). Thus the eggs need less warming, and less incubation time, at higher air temperatures. The female weaverbird is assumed to reduce her incubation time at high air temperature in order to increase her foraging time. The fact that she increases her foraging time as air temperature increases shows that at lower temperatures, her foraging time is limited by the time demands of incubation.

Thus there are sound theoretical reasons for predicting that incubation time will decrease with increasing air temperature, but the prediction made by White and Kinney that it

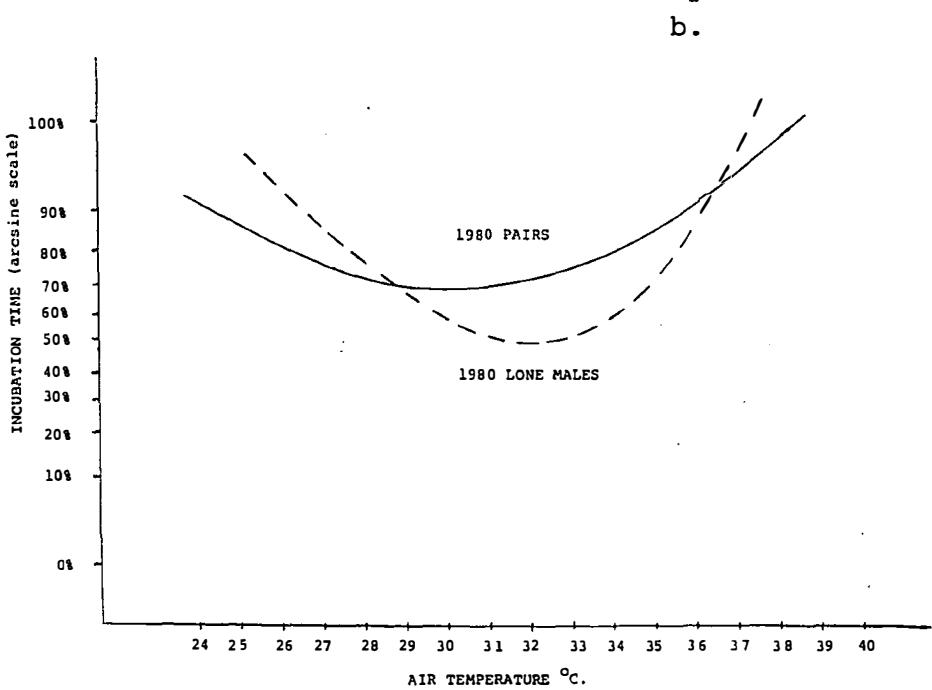
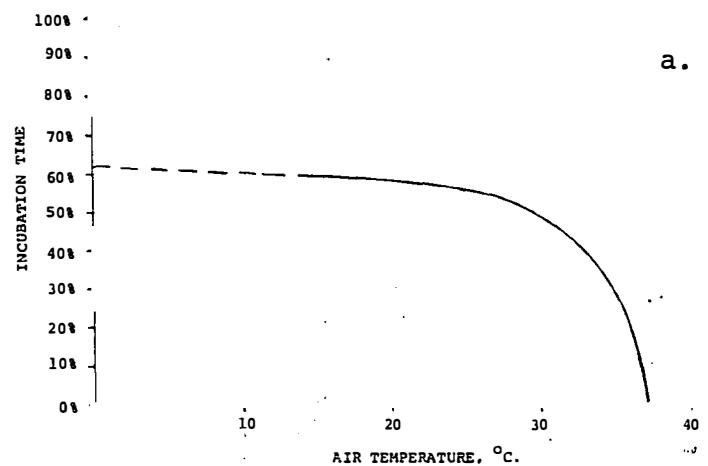
will literally fall to zero when air temperature reaches egg temperature is not as well established. In their own study, White and Kinney estimate incubation time from nest and egg temperature, and this method becomes less and less accurate as air temperature approaches egg temperature, because it relies on a drop in egg or nest temperature when the parent leaves the nest. Thus White and Kinney's data for the critical temperature range are unreliable. Also, Ward (1965) reports that another weaverbird that ceased incubating at high air temperature continues to make frequent short visits to the nest, which could be related to monitoring or regulating egg temperature. Thus the time and energy costs of incubation, as egg temperature regulation, probably do not fall to zero at high air temperature, although this is what White and Kinney imply.

White and Kinney attempt to apply this model, the negative hyperbolic curve, to incubation in all other single-sex incubators, but the attempt is unconvincing, and it includes erroneous references. They show the response of incubation time to air temperature in four other single-sex incubators based on data from other studies, but the critical temperature range above 30° C. is missing in all four studies, so drawing the curve down to zero incubation time is not justified. There is a decrease in incubation time with increasing air temperature in all four studies. White and Kinney also cite references in an attempt to show that other single-sex incubators also stop incubating at

FIGURE 33: Incubation time vs. air temperature for two species.

a: Incubation time vs. air temperature for the Village Weaverbird, from White and Kinney (1974). Incubation time was calculated over one-hour periods, and the curve was apparently extrapolated below 15° C. (dotted line). The curve was fit by Bartlett's three-group regression.

b: Incubation time vs. air temperature for Wilson's Plover, from the present study. Incubation time was calculated over 3.5 hr periods. The curves shown are for pairs in 1980 (solid line, fit by quadratic multiple regression) and lone males in 1980 (dashed line, fit by eye).



high air temperature, but only one of these is a correct reference, to a one-sentence anecdote about *Geospiza magnirostris* (Lack 1945), a single-sex incubator. Another bird referred to is the Red-billed Quelea (*Quelea quelea*) (Ward 1965), which also stops incubating at high air temperature, but it is a bisexual incubator. White and Kinney also refer to data on two other bisexual incubators when they cite Howell and Bartholomew (1962) in the same sentence. This paper concerns the Red-tailed Tropic Bird (*Phaethon rubricauda*) and the Red-footed Booby (*Sula sula*), and the only mention in that paper of a cessation of incubation at high air temperature involved one Tropic Bird nest, in which no eggs hatched. White and Kinney also cite this paper as showing that some birds shade their eggs at high temperature, although the one mention of shading involved only chicks.

White and Kinney discuss the effect of nest insulation on incubation time, and find that incubation time is lower in better-insulated nests. The Village Weaverbird, with a relatively well-insulated nest, only incubated 60% of the time, even at low air temperatures. In contrast, incubation time in Wilson's Plover, shown in Figure 33 b, was near 100% at air temperatures below about 24° C. The Wilson's Plover nest is an open cup on the ground, and thus is very poorly insulated. White and Kinney (1974) point out that single-sex incubators, such as the weaverbird, tend to have better insulated nests than bisexual incubators, such as Wilson's

Plover. The response of incubation time to temperature in Wilson's Plover shows a decrease with increasing air temperature, but above the "release point" found in the weaverbird, Wilson's Plover increases incubation time instead of decreasing it as in the weaverbird. It does not appear that White and Kinney knew of a curve such as this when they discussed bisexual incubation.

The discussion of bisexual incubation by White and Kinney is brief and oversimplified. They create a dichotomy between bisexual incubation, which they call "continuous" (the nest is incubated almost all the time), and single-sex incubation, which they call "intermittent" (incubation time varies with air temperature). There appears to be no precedent for this dichotomy in the literature, in particular not in the detailed review of modes of incubation by Skutch (1957), and there appears to be no basis for it. Birds in which one parent incubates and either fasts or is fed on the nest are termed "intermediate" mode by White and Kinney, and they are also assumed to have "continuous" incubation.

The only exceptions allowed by White and Kinney to "continuous" incubation by bisexual incubators is a reference to one sentence in Skutch (1957), but one of their other references (Ward 1965) shows that bisexual incubation can be just as "intermittent" as single-sex incubation. White and Kinney's main support for "continuous" incubation in bisexual incubators is the study of the Herring Gull by

Drent (1970), but that study did not include data collected at air temperatures above 28° C., and so it did not include data relevant to the problem. As discussed in Chapter 4, the minimum incubation time in the Herring Gull is probably set by the frequent nest predation by other Herring Gulls, not by air temperature. There is strong selection against "intermittent" incubation in the Herring Gull, but not in all bisexual incubators. The assumption of "continuous" incubation in all bisexual incubators is not supported by data, and needs to be re-examined.

A Proposed Thermoregulatory Model of Incubation

I propose that both single-sex and bisexual incubation may be "intermittent" under the right conditions, and that the dichotomy set up by White and Kinney (1974) is closer to a continuum. Incubation has many functions (Drent 1975). For simplicity incubation is assumed to have only one function: thermoregulation of egg temperature within the limits of normal development. Incubated egg temperatures are quite consistent in different species of birds (Drent 1975), and the temperature tolerances of embryos are similar in the few species that have been studied (Bennett et al. 1981), so there should be broad similarities in these temperature limits in different species.

Because this model only considers one function of incubation, it does not attempt to predict the actual amount of incubation time under a given set of conditions, but only an

approximate minimum incubation time at a given air temperature. Reducing incubation time below that minimum is assumed to reduce hatching success due to abnormal development or embryo death. Increasing incubation time above that minimum is assumed to have no effect on hatching success, as far as thermoregulation is concerned; any amount above the minimum is assumed to be equally effective in regulating egg temperature.

Assumptions

1. The function of incubation is to regulate $T(E)$.
2. Newton's Law of Cooling applies to uncovered eggs; since $T(E)$ is fairly constant, $dT(E)/dt$ should be proportional to $T(A)$.
3. There are upper and lower limits of $T(E)$ between which normal development of the embryo proceeds.
4. Egg thermoregulation does not require incubation bout length to depend on $T(A)$, so it is assumed to be independent of $T(A)$. There will be a minimum incubation bout length (time required to restore $T(E)$ to the normal value after an absence) but it should vary little with $T(A)$.

Conclusions

1. At any $T(A)$, $dT(E)/dt$ sets a maximum absence length: longer absences result in $T(E)$ exceeding the limits of normal development. This maximum absence length should be inversely proportional to $|dT(E)/dt|$, producing the curve shown in Figure 34 a.
2. Although the maximum absence length exists at any instant for the $T(A)$ at that instant, it would be infinite when $dT(E)/dt = 0$, not a very meaningful result. Also, incubation time can only be calculated over a time period, not at an instant. Thus the maximum absence time becomes the length of the time period used for analysis, as shown in Figure 34 a.
3. Using the formula Incubation time = mean incubation bout length / mean incubation bout length + mean absence length, incubation time should be inversely proportional to absence length, and thus should be directly proportional to $|dT(E)/dt|$, producing the curve shown in Figure 34 b. This is the minimum incubation time.
4. The exact shape of both curves depends on C, or the relative thermal conductance (or lack of insulation) of the nest. If the nest is better

insulated (lower C), minimum incubation time will be lower.

5. The shorter the time period used for analysis, the more pronounced will be the dip in minimum incubation time, dropping to zero if the time period is short enough.

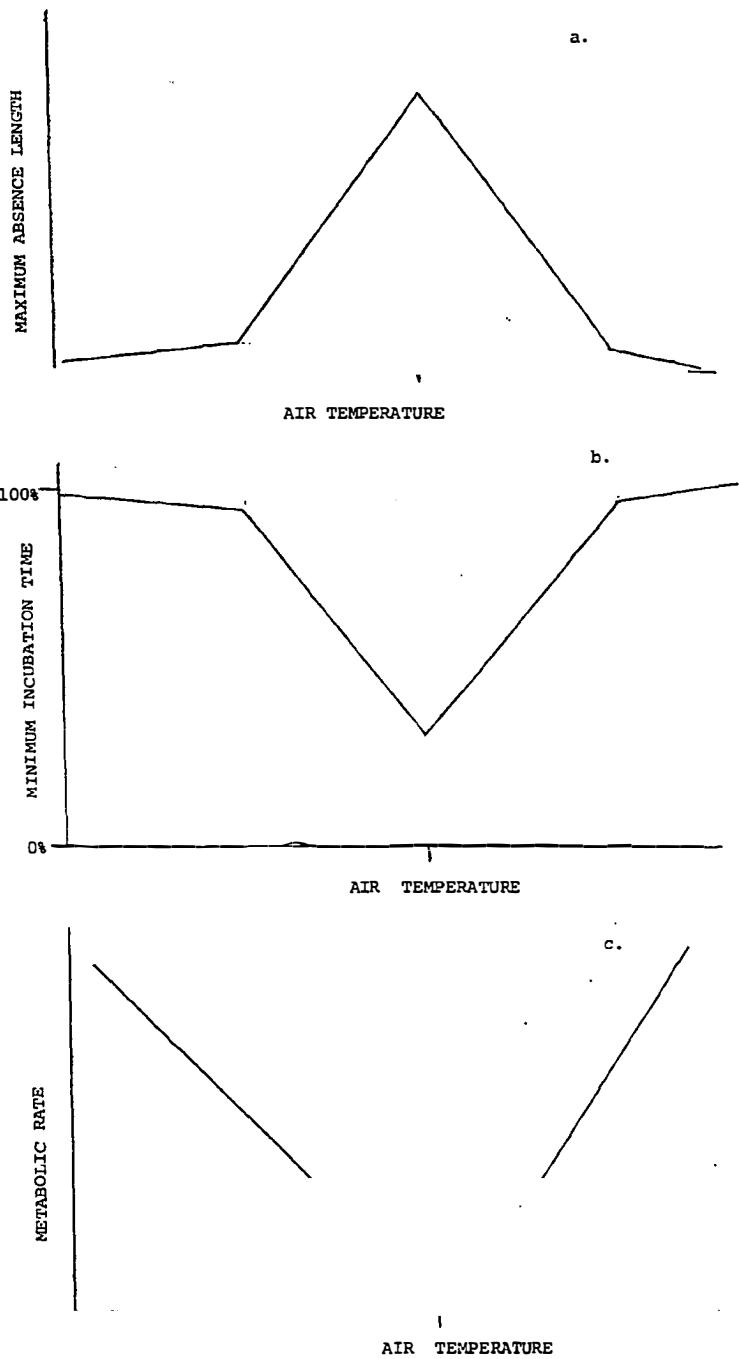
This approach to egg thermoregulation treats the egg as an extension of the parent's body core for practical purposes (Drent 1975). The regulation of body temperature in endotherms was modeled by Scholander et al. (1950), based on Newton's law of cooling and the assumption that the endotherm was simply an insulated heating element. The resulting curve of predicted minimum metabolic rate (Figure 34 c) is very similar to the curve of predicted minimum incubation time in Figure 34 b. This is because the function of incubation time in regulating egg temperature is analogous to the function of metabolism in regulating body temperature. There is a thermal neutral zone in which metabolic rate is minimal, and body temperature is maintained independent of air temperature by adjusting body insulation (Scholander et al. 1950). When air temperature falls below the lower critical temperature, metabolic rate must be increased to make up for heat lost to the environment (e.g. by shivering). The thermal neutral zone also has an upper critical temperature: when air temperature exceeds it, metabolic rate must increase to dissipate heat,

FIGURE 34: Predicted Maximum Absence Length, Minimum Incubation Time, and Metabolic Rate.

a: Predicted maximum absence length for incubating birds in relation to air temperature. Point marked is point of thermal equilibrium (see text).

b: Predicted minimum incubation time for incubating birds in relation to air temperature, with point of thermal equilibrium shown. Curve is inverse of maximum absence curve.

c: Predicted metabolic rate for endotherms at different air temperatures, based on model by Scholander et al. (1950).



e.g. by panting, sweating, or gular flutter. The same curve shows the amount of heat lost or gained by the body at different air temperatures, and the metabolic rate needed to maintain body temperature at different air temperatures. Measurements of metabolic rates in a variety of animals have shown that they agree closely with this predicted curve (Scholander et al. 1950). According to Calder (1974), the Scholander model "stimulated over two decades of comparative physiology, and remains a useful basis of analysis after its limitations are understood."

As with the body of an endotherm, eggs must have heat added to them when air temperature falls below the point of thermal equilibrium, and they must have heat removed from them (or they must be shielded from heat sources) when air temperature goes above that point. Egg temperature regulation is probably not as critical as body temperature regulation, but the required heat fluxes are the same. From the standpoint of the incubating parent, behaviors used to keep eggs warm at low temperatures, such as sitting tightly on the eggs, would also help to conserve their own body heat. Behaviors used to cool eggs at high air temperature, such as shading the eggs and belly-soaking, may also function to cool the body of the parent (Grant 1979). However, some birds, such as White-winged Doves (Russell 1969) and Lesser Nighthawks (Grant 1979), respond to high air temperature by sitting quietly on the eggs. In this

case the need of the eggs for cooling appears to be at odds with the need of the parent to cool its body, since it is unlikely that quiet sitting helps dissipate body heat. The nighthawk cools itself with gular flutter (Grant 1979), but apparently the dove does not (Russell 1969). The problem of egg temperature vs. body temperature regulation at high temperature deserves further study.

This model of incubation has made no assumption about the number of incubating parents or their requirements for foraging time, only about the physical properties of the nest and its microclimate. One problem with applying this model to different groups of birds is that not all species are exposed to the full range of air temperatures, so only part of it may apply to many species. Thus the common observation that incubation time decreases with increasing air temperature in most temperate zone single-sex incubators (von Haartman 1956) is explained by the left-hand portion of the curve in Figure 34 b., because in the temperate zone, air temperature rarely exceeds the point of thermal equilibrium.

Another problem with the predicted increase in incubation time at high air temperature is that it may not occur in well-insulated nests off the ground. The function of this increase is assumed to be to shield the eggs from heat or dissipate heat from the eggs. Eggs in a well-insulated nest may already be so well shielded from heat that the presence of the parent would add little shielding. All of the known

mechanisms of cooling eggs have only been observed in species making open nests on the ground, and might not work in a well-insulated nest. Shading the eggs or belly-soaking would be useless in such a nest, because they depend on convection and evaporation respectively for cooling. Dissipating the heat from the eggs through the body of the parent would be very difficult since the parent would also be well-insulated. Thus birds with well-insulated nests may cease incubating at high air temperature because there is little that incubation could do to reduce egg temperature in such nests. The frequent short visits to the nest made by the Red-billed Quelea at high air temperature (Ward 1965) could have involved moving the eggs in the nest, which is one behavior that could help keep down egg temperature, by distributing heat more evenly. Data are needed on the rate of change in egg temperature in well-insulated nests at high air temperature.

The number of incubating parents, and their foraging requirements, are some of the many possible reasons why birds should incubate more than the predicted minimum incubation time. If only one parent is incubating, and it must forage for itself, incubation time should be closer to the minimum than if two parents incubate in the same nest, or if the incubator can live on stored fat or food brought by its mate. As shown in Figure 33 b, incubation time was reduced in single incubators compared to pairs in Wilson's Plover. An increase in required foraging time should bring

incubation time closer to the predicted minimum for that nest. Other functions of incubation may also dictate higher incubation time. In the Herring Gull, protection of the eggs from intraspecific predation probably accounts for the high incubation time (Skutch 1957). Eggs may need higher incubation time to be protected from other predators, or from effects of climate other than temperature (e.g. rain, hail, wind, or wind-blown sand).

If the dip in incubation time is to occur, it is also necessary that increased time off the nest, which is the result of the dip in minimum incubation time, be of some use to the incubating parent, especially for foraging. Some birds feed only far from the nest, and only at low tide, so the ability to safely leave the eggs at moderate air temperature may be of no value to the bird, if food is too far away or unavailable. Thus the dip in incubation time should be more pronounced in birds that can feed at any time of day, and can feed fairly close to the nest, or can perform other maintenance activities near the nest (e.g. preening, bathing).

The advantage to the incubating bird(s) in increasing their time off the nest at moderate air temperature is that it gives them more time to forage or perform other self-maintenance activities. If the incubating parent(s) are getting just barely enough time to forage and otherwise maintain themselves, they might not be able to keep incubating during a sudden period of low food availability.

or bad weather. Since food availability and weather are never completely predictable, it would be to the bird's advantage to take extra time for self-maintenance when it is available, because conditions could become adverse suddenly. This is analogous to the argument about lizard time budgets made by Kiester and Slatkin (1974), that by foraging in the least possible time on average days, lizards will have extra time available on non-average days.

As noted above, this thermoregulatory model of incubation agrees with data on single-sex incubators, which for most species does not include data above about 30° C.. A decrease in incubation time with increasing air temperature is predicted up to that point, and that is what has been found (von Haartman 1956, White and Kinney 1974). No data are available that show an increase in incubation time at high air temperature in single-sex incubators, but this may have to do with nest insulation (see above).

Data from several studies of incubation in bisexual incubators agrees closely with the proposed model of incubation. The dip in incubation time at moderate air temperature (20 - 30° C.) was reported qualitatively for the Double-banded Courser *Rhinoptilus africanus* breeding in the Kalihari Desert by Maclean (1967). Purdue (1976) showed that the proportion of adults attending nests (comparable to but not the same as incubation time) was significantly reduced between 30 and 40° air temperature in the Snowy Plover in Oklahoma, compared to higher and lower temperature

ranges. Howell (1979) shows nest attendance at different air temperatures in the Egyptian Plover, and attendance was reduced when air temperature was near 30° compared to higher temperatures, but data are not shown for lower air temperatures. Grant (1979) also found a reduction in incubation time in the Snowy Plover at moderate air temperature compared to high temperature. In the Killdeer, incubation time was high at both low and high temperature, and was reduced at moderate temperature (Grant 1979).

Thus several shorebirds show the same response of incubation time to air temperature that is predicted by the model, and this response was found in Wilson's Plover as well (Chapter 4). An additional prediction of the model, that single-sex incubators should have incubation time closer to the minimum than bisexual incubators, is also verified by the data on Wilson's Plover (Chapter 4). Because lone incubators had high hatching success, they must have been incubating more than the minimum incubation time, but they were closer to the minimum than pairs, because they incubated significantly less than pairs. A comparison of nests in different microclimates (pavement and soil substrates) showed that this can affect absence duration, and similar differences should exist between nests with different insulative properties.

The proposed model is more general than the one of White and Kinney (1974), because it can apply to either bisexual or single-sex incubators. Available data show that the

model applies more fully to bisexual incubating species than to single-sex incubators, but more data are needed on single-sex incubators in hot climates. Experimental manipulations, such as removal of a parent, should be used to analyze conditions that affect the degree to which incubation time exceeds the minimum required by thermoregulation of the eggs. This approach could be extended to testing the effects of other functions of incubation on incubation time, such as predators and precipitation. The dip incubation time is expected to be most pronounced in species that feed near the nest at all times of day, with relatively uninsulated nests, and in species with single-sex incubation or an unequal division of labor in bisexual incubation.

One goal of such a model of incubation is to integrate it into a model of the evolution of mating systems in birds. By considering the physiological requirements of incubation, and establishing the minimum incubation requirements for egg thermoregulation in each species, it becomes possible to predict when single-parent care is possible, and when bi-parental care would have an advantage over single-parent care. It would be very difficult to establish theoretical minimum levels for other reproductive activities, such as territory defense or tending of chicks. When minima can be established, it is possible to make comparisons between groups and see by how much the minimum is exceeded in each group. Thus establishing minimum requirements for

incubation provides a comparative base for examining the effects of different ecologies on mating systems, and thus can help in the understanding of the evolution of mating systems.

APPENDIX A
ELAPSED TIMES AND DISTANCES BETWEEN RENESTS

Nests	Days Start-Start	Days Fail-Start	Distance (m)
2-79/29-79	51	49	157
14-79/23-79	25	7	38.4
3-80/20-80	30	<13	72.7
14-80/21-80	>16	5	43.5
7-80/22-80	>33	11	24.0
4-80/23-80	>37	13	49.0
9-80/25-80	>17	6	23.9
2-80/26-80	38	21	28.9

APPENDIX B
EGG-LAYING TIMES AND INTERVALS

Nest	Time of laying			Est. Intervals (hr)		
	Egg 1	Egg 2	Egg 3	1 - 2	2 - 3	1 - 3
1-80	<u>1136</u> (4/21)	1725(4/23)- 0830(4/24)	1909(4/25)- 1656(4/26)	54-69	-	104-128
18-80	-	1220(5/28)	<u>1626</u> (5/30)	-	>52	-
28-80	1600(6/7)	0745(6/9)- 0830(6/10)	-	36-64	-	-
1-79	1300(4/25)	1342(5/1)	1625(5/1)	-	-	>125
2-79	1540(4/25)	-	1300(5/1)	-	-	117
6-79	1542(4/27)	0922(5/1)	1700(5/2)	-	-	121
14-79	0930(5/6)	<u>1113</u> (5/7)	0802(5/11)	-	-	119

APPENDIX C
HATCHING INTERVALS

Nest	Time of hatch			Intervals (hrs)		
	Chick 1	Chick 2	Chick 3	1 - 2	2 - 3	1 - 3
3-79	1645(5/14)	0724- 1724(5/15)	none	15-27	-	-
10-79	0805(5/28)	0908(5/28)	1640(5/28)	1	7	8
26-79	1611(7/4)	1415(7/5)	1737(7/5)- 0845(7/6)	22	3-18	25-40
29-79	1130(7/17)	2000(7/17)	0645(7/18)	8.5	10.5	19
13-80	0700(5/16)	0715- 2020(5/17)	none	24-37	-	-
17-80	0710(5/18)	1132(5/18)	none	4.5	-	-
18-80	0917(6/23)	1609(6/23)	1942(6/24)	7	27.5	34.5

APPENDIX D

KNOWN AND POTENTIAL EGG PREDATORS IN THE STUDY SITES

Species name	Occurrence	No. Nests
Domestic cattle	M	5
Horse	M	?
Dog	M	?
Coyote (<i>Canis latrans</i>)	B	
Bobcat (<i>Lynx rufus</i>)	B	?
Raccoon (<i>Procyon lotor</i>)	B	
Western Diamondback Rattlesnake (<i>Crotalus atrox</i>)	B	?
Rat Snake (<i>Elaphe</i> sp.)	B	?
Laughing Gull (<i>Larus atricilla</i>)	B	
Great-tailed Grackle (<i>Quiscalus major</i>)	B	1?
Jaguarundi (<i>Felis eyra</i>)	L	1
Ocelot (<i>Felis pardalis</i>)	L	
Indigo Snake (<i>Drymarchon corais</i>)	L	
Racer (<i>Coluber constrictor</i>)	L	
Mexican Ground Squirrel (<i>Citellus mexicanus</i>)	L	?
Bridled Weasel (<i>Mustella frenata</i>)	L	
Striped Skunk (<i>Mephitis mephitis</i>)	L	

Occurrence: M = Matagorda, L = Laguna Atascosa, B = Both.

APPENDIX E
BRIEF DESCRIPTIONS OF WILSON'S PLOVER DISPLAYS

Scrape-exchange

Male makes scrape, which may become nest, by scraping out shallow cup with his feet. He usually makes several within his territory. The female approaches one while he is in it. As she approaches, the male steps out of the scrape with one wing facing her, droops this near wing towards the ground, "bows" his head, pointing his bill at the ground, and gives a call sounding like "moo".

Copulation sequence

The male approaches the female from behind, with his breast down and tail up in the air. If the female does not move away, he stands behind her and alternately kicks his legs up to his breast ("marking time"). If she has still not moved after about 1 min, he mounts her by jumping up on her back, and begins moving his feet on her back ("treading"). Then he grabs the nape of her neck with his bill and thrusts his

pelvis down, and this is presumably when cloacal contact occurs. The mount usually lasted a minute or more, and sometimes the pair fell over backwards together at the end.

Parallel Walk

During territorial fights, two birds, usually males, were sometimes each unable to chase off the other, and parallel walking resulted. The pair walks rapidly or runs parallel to each other, bodies horizontal, along a line that appears to divide their two territories. At the end of the line each turns away from the other and they repeat the display along the same line in the opposite direction. This was only seen during territory establishment and the chick stage.

Puffed-breast display

After successfully chasing off another Wilson's Plover, males often stood erect with breast feathers puffed out, partially covering the wings at the side. This was also used in a threatening context before a chase.

Broken-wing display

A common predator response of nesting shorebirds. Wilson's Plovers lie or crawl along the ground, beating their wings

on the ground, and give a buzzy call. Unlike many shorebirds (e.g. Killdeer), Wilson's Plover uses this almost exclusively when it has chicks, and not when it has eggs. The bird tries to lead the intruder away from the chicks.

Dummy-brooding

This was the most common response to humans near nests during incubation. The pair, or more often a group of 20 - 30 adults of both sexes, would gather around the intruder, standing and calling. Some members of the group, often females, would suddenly run behind a clump of vegetation and act as if settling on a nest, although there was no nest there. The bird would jump up a few minutes later, and repeat the display behind another clump of vegetation. This could distract predators, including humans, from the real nest.

APPENDIX F
FEEDING RATES ON FIDDLER CRABS, 1979

Pair	Sex	Date	Time	No. crabs	Percent feed	crabs/hr
3-79 ^a	M	5/14	0850-1850	3	23%	1.3
	F			5	16%	3.1
3-79 ^a	M	5/15	0724-1724	5	34%	1.5
	F			0	6%	0
23-79	M	6/8	1309-1717	11	34%	7.8
	F			0	3%	0
23-79	M	6/9	1308-1823	3	43%	1.3
	F			1	5%	3.1
23-79	M	6/10	1419-2049	8	30%	4.2
	F			0	7%	0
23-79	M	6/14	0841-1851	7	14%	5.1
	F			1	8%	1.2
Unbnd. ^b	M	6/14	0841-1851	4	4%	9.9
	F			9	12%	7.1
23-79	M	6/16	1236-1936	6	21%	4.1
	F			1	2%	6.9
23-79	M	6/18	1450-1702	2	13%	7.3
	F			0	7%	0
26-79 ^c	M	7/3	0706-1506	3	3%	11.5
26-79	M	7/4	0920-1920	8	5%	17.8
26-79	M	7/5	0907-1737	12	6%	23.6
29-79 ^c	M	7/16	0640-2028	3	1%	23.8
29-79	M	7/17	0801-2031	3	1%	42.9

- a During hatching
- b Attending young chicks near Nest 23-79
- c Males were incubating alone

BIBLIOGRAPHY

- Afton, A. 1979. Incubation temperatures of the Northern Shoveler. *Can. J. Zool.* 57: 1052-1056.
- 1980. Factors affecting incubation rhythms of Northern Shovelers. *Condor* 82: 132-137.
- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49: 227-267.
- Ashkenazie, S., & U. Safriel. 1979. Time-energy budget of the Semipalmated Sandpiper *Calidris pusilla* at Barrow, Alaska. *Ecology* 60: 783-799.
- Audubon, J. 1840. Birds of America, 1840-1844, vol. 5. New York, J. J. Audubon.
- Bannerman, D. 1961. The Birds of the British Isles, vol X. London, Oliver and Boyd.
- Bartholomew, G., & W. Dawson. 1979. Thermoregulatory behavior during incubation in Heermann's Gulls. *Physiol. Zool.* 52: 422-437.
- Bennett, A., W. Dawson, & R. Putnam. 1981. Thermal environment and tolerance of embryonic Western Gulls. *Physiol. Zool.* 54: 146-154.
- Bent, A. 1929. Life Histories of North American Shore Birds. Order Limicolae, Part 2, pp. 246-253. Washington, D.C., Bulletin of U.S. National Museum.
- Blake, E. 1977. Manual of Neotropical Birds, vol 1. Chicago, University of Chicago Press.
- Boyd, R. 1972. Breeding biology of the Snowy Plover at Cheyenne Bottoms Waterfowl Management Area, Barton County, Kansas. Unpublished M.S. thesis, Emporia, Kansas, Kansas State Teachers College.
- Bunni, M. 1959. The Killdeer, *Charadrius v. vociferus*, Linnaeus, in the breeding season: ecology, behavior, and the development of homioiothermism. Unpublished D.Sc. dissertation, Ann Arbor, Michigan, University of Michigan.

- Cairns, W. 1977. Breeding biology and behaviour of Piping Plover (*Charadrius melanotos*) in southern Nova Scotia. Unpublished M.S. thesis, Halifax, Nova Scotia, Dalhousie University.
- Calder, W. III. 1974. Consequences of body size for avian energetics. Pp. 86-151 in Avian Energetics (R. Paynter, Ed.). Pub. Nutall Orn. Club No. 15.
- Cammen, L., E. Seneca, & L. Stroud. 1980. Energy flow through the fiddler crabs *Uca pugnax* and *U. minax* and the marsh periwinkle *Littorina irrorata* in a North Carolina salt marsh. Amer. Midl. Natur. 103: 238-250.
- Conant, R. 1975. A Field Guide to Reptiles and Amphibians of Eastern and Central North America, 2nd ed. Boston, Houghton Mifflin Co.
- Cooper, J. 1978. The history and breeding biology of the Canada Geese of Marshy Point, Manitoba. Wildl. Monogr. No. 61.
- Cronan, J. Z. 1974. Heat energy exchange between the Killdeer, its eggs and the environment. Unpublished M.A. thesis, Corvallis, Oregon, Oregon State University.
- Davis, E. 1943. A study of wild and hand-reared Killdeers. Wilson Bull. 55: 223-233.
- Dawson, W., and J. Hudson. 1970. Birds. Pp. 224-310 in Comparative physiology of thermoregulation, vol. 1 (G. C. Whittow, Ed.). New York, Academic Press.
- Drent, R. H. 1970. Functional aspects of incubation in the Herring Gull. Behav. Suppl. 17: 1-132.
- 1973. The natural history of incubation. Pp. 262-311 in Breeding biology of birds (D. S. Farner, Ed.). Washington, D.C., National Academy of Sciences.
- 1975. Incubation. Pp. 333-420 in Avian Biology, vol. 5 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.
- Drent, R. H., K. Postuma, & T. Joustra. 1970. The effect of egg temperature on incubation behavior in the Herring Gull. Behav. Suppl. 17: 235-260.
- Emlen, S. T., & L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197: 215-223.

- Fitzpatrick, J. 1981. Search strategies of tyrant flycatchers. *Anim. Behav.* 29: 810-821.
- Fleetwood, R. 1967. Plants of the Laguna Atascosa National Wildlife Refuge. Harlingen, Texas, Bureau of Sport Fisheries and Wildlife.
- Franks, E. 1967. The responses of incubating Ringed Turtle Doves (*Streptopelia risoria*) to manipulated egg temperatures. *Condor* 69: 268-276.
- Gochfeld, M. 1978. Incubation behavior in common terns: Influence of wind speed and direction on the orientation of incubating adults. *Anim. Behav.* 26: 848-851.
- Grant, G. S. 1979. Avian incubation: Egg temperature, nest humidity, and behavioral thermoregulation in a hot environment. Unpublished Ph.D. dissertation, Los Angeles, California, University of California at Los Angeles.
- Graul, W. 1973. Adaptive aspects of the Mountain Plover social system. *Living Bird* 12: 69-94.
- 1975. Breeding biology of the Mountain Plover. *Wilson Bull.* 87: 6-31.
- Green, R. 1978. Do more birds produce fewer young? A comment on Mayfield's measure of nest success. *Wilson Bull.* 89: 173-175.
- Grosskopf, G. 1964. Sterblichkeit und Durchschnittsalter einiger Kuestenvoegel. *J. Orn.* 105: 427-449.
- Grover, P. 1979. Habitat requirements of charadriiform birds nesting on the salt flats at Salt Plains National Wildlife Refuge. Unpublished M.S. thesis, Stillwater, Oklahoma, Oklahoma State University.
- von Haartman, L. 1956. Der Einfluss der Temperatur auf den Brutrhythmus experimentell nachgewiesen. *Ornis Fenn.* 33: 100-107.
- Hall, K. 1958. Observations on the nesting sites and nesting behavior of the Kiihlitz's Sandplover *Charadrius pecuarius*. *Ostrich* 29: 113-125.
- Hobbs, J. N. 1972. Breeding of Red-capped Dotterel at Fletcher's Lake, Daretton, NSW. *Emu* 72: 121-125.

- Holmes, R. 1971. Density, habitat, and the mating system of the Western Sandpiper (*Calidris mauri*). *Oecologia* 7: 191-208.
- Howell, A. H. 1932. Florida Bird Life. Tallahassee, Florida, Florida Department of Game and Freshwater Fish.
- Howell, T. R. 1979. Breeding biology of the Egyptian Plover *Pluvianus aegyptius* (Aves: Glareolidae). Univ. Cal. Pub. Zool. Vol. 113.
- , & G. Bartholomew. 1962. Temperature regulation in the Red-tailed Tropic Bird and Red-tailed Booby. *Condor* 64: 6-18.
- Huey, R., & M. Slatkin. 1976. Costs and benefits of lizard thermoregulation. *Quart. Rev. Biol.* 51: 363-384.
- Hull, C., & N. Nie. 1979. SPSS Update: New procedures and facilities for Releases 7 and 8. New York, McGraw-Hill Book Co.
- Hussell, D., & G. Page. 1976. Observations on the breeding biology of Black-bellied Plovers on Devon Island, N.W.T., Canada. *Wilson Bull.* 88: 632-653.
- Immelman, K. 1971. Ecological aspects of periodic reproduction. Pp. 342-391 in *Avian Biology*, vol 1 (D. S. Farner & J. A. King, Eds.). New York, Academic Press.
- Jeffery, R., & R. Liversidge. 1951. Notes on the Chestnut-banded Sandplover. *Ostrich* 22: 68-76.
- Jehl, J. R., Jr. 1973. Breeding biology and systematic relationships of the Stilt Sandpiper. *Wilson Bull.* 85: 115-147.
- Kaye, K. 1977. CRESCAT: software system for the analysis of sequential or real-time data. Chicago, University of Chicago Computation Center.
- Kendeigh, S. 1952. Parental care and its evolution in birds. *Illinois Biol. Monogr.* 22 (1-3).
- 1963. Thermodynamics of incubation in the House Wren (*Troglodytes aedon*). *Proc. XIII Int. Orn. Congr.* pp. 884-904.
- Kiester, A. R., & M. Slatkin. 1974. A strategy of movement and resource utilization. *Theor. Pop. Biol.* 6: 1-20.

- Klomp, H. 1970. The determination of clutch-size in birds: A review. *Ardea* 58: 1-124.
- Kluijver, H. 1950. Daily routines of the Great Tit, *Parus major*, L. *Ardea* 38: 99-135.
- Lack, D. 1945. The Galapagos Finches (Geospizinae): A study in variation. *Occas. Pap. Calif. Acad. Sci.* 21: 27.
- 1954. The natural regulation of animal numbers. Oxford, Oxford University Press.
- 1968. Ecological adaptations for breeding in birds. London, Chapman and Hall.
- Laven, H. 1940. Beitrage zur Brutbiologie des Sandregenpfeifers, (*Charadrius hiaticula*) L. *J. Orn.* 88: 183-287.
- Lenington, S. 1975. Parental behavior in the Killdeer. Unpublished M.S. thesis, Minneapolis, Minnesota, University of Minnesota.
- 1980. Bi-parental care in Killdeer: An adaptive hypothesis. *Wilson Bull.* 92: 8-20.
- Lundy, H. 1969. A review of the effects of temperature, humidity, turning and gaseous environment in the incubator on the hatchability of the hen's egg. Pp. 143-176 in *The fertility and hatchability of the hen's egg* (T. C. Carter and B. M. Freeman, Eds.). British Egg Marketing Board Symposium No. 5. Edinburgh, Oliver and Boyd.
- Lustick, S., B. Battersby, & M. Kelty. 1978. Behavioral thermoregulation: orientation toward the sun in Herring Gulls. *Science* 200: 81-83.
- Mace, T. 1971. Nest dispersion and productivity of Killdeers (*Charadrius vociferus*). Unpublished M.S. thesis, Minneapolis, Minnesota, University of Minnesota.
- Maclean, G. L. 1967. The breeding biology and behaviour of the Double-banded Courser *Rhinoptilus africanus* (Temminck). *Ibis* 109: 556-569.
- 1972. Clutch size and evolution in the Charadrii. *Auk* 89: 299-324.

- Maclean, G., & V. Moran. 1965. The choice of nest site in the White-fronted Sandplover *Charadrius marginatus*. Vieillot. Ostrich 36: 63-72.
- Mason, A. G. 1947. Territory in the Ringed Plover. Brit. Birds 40: 66-70.
- Maxson, S., & L. Oring. 1978. Mice as a source of egg loss among ground-nesting birds. Auk 95: 582-584.
- Mayfield, H. 1961. Nesting success calculated from exposure. Wilson Bull. 73: 255-261.
- 1975. Suggestions for calculating nest success. Wilson Bull. 87: 456-466.
- Miller, E. 1977. Breeding biology of the Least Sandpiper, *Calidris minutilla* (Vieill.), on Sable Island, Nova Scotia. Unpublished Ph.D. dissertation, Halifax, Nova Scotia, Dalhousie University.
- Mowery, I., & J. Bower. 1978. Soil Survey of Calhoun County, Texas. Washington, D.C., Soil Conservation Service.
- Mundahl, J. T. 1977. Role specialization in the parental and territorial behavior of the Killdeer. Unpublished M.S. thesis, Logan, Utah, Utah State University.
- Murie, O. 1954. A field guide to animal tracks. Boston, Houghton Mifflin Co.
- Nethersole-Thompson, D. 1973. The Dotterel. London, Collins.
- Nol, E. 1980. Factors affecting the nesting success of the Killdeer (*Charadrius vociferus*) on Long Point, Ontario. Unpublished M.S. thesis, Guelph, Ontario, University of Guelph.
- NOAA (National Oceanic and Atmospheric Administration). 1979. Local Climatological Data, Brownsville, Texas. Asheville, North Carolina, National Oceanic and Atmospheric Administration.
- 1980. Local Climatological Data, Victoria, Texas. Asheville, North Carolina, National Oceanic and Atmospheric Administration.
- Oberholser, H. 1974. The bird life of Texas (E. B. Kincaid, Ed.). Austin, University of Texas Press.

- Oring, L. W., & M. L. Knudson. 1972. Monogamy and polyandry in the Spotted Sandpiper. *Living Bird* 11: 59-74.
- Phillips, R. 1981. Behavior and systematics of New Zealand plovers. *Emu* 80: 177-197.
- Pitelka, F. A. 1959. Numbers, breeding schedule, and territoriality in Pectoral Sandpipers of northern Alaska. *Condor* 61: 233-264.
- Pitelka, F. A., R. Holmes, & S. MacLean, Jr. 1974. Ecology and evolution of social organization in arctic sandpipers. *Amer. Zool.* 14: 185-204.
- Purdue, J. 1976. Thermal environment of the nest and related parental behavior of Snowy Plovers, *Charadrius alexandrinus*. *Condor* 78: 180-185.
- Raveling, D. 1970. Dominance relationships and agonistic behavior of Canada Geese in winter. *Behaviour* 37: 291-319.
- Rearden, J. D. 1951. Identification of waterfowl nest predators. *J. Wildl. Manage.* 15: 386-395.
- Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. *Smiths. Contr. Zool.* 9.
- 1970. Clutch size in birds: outcome of opposing predator and prey adaptations. *Science* 168: 599-600.
- 1974. Energetics of reproduction in birds. Pp. 152-292 in *Avian energetics* (R. Paynter Jr., Ed.). Pub. Nuttall Orn. Club No. 15.
- Rittinghaus, H. 1961. *Der Seeregenpfeifer (Charadrius alexandrinus L.)*. Wittenberg, Germany, A. Ziemsen Verlag.
- Russell, S. 1969. Regulation of egg temperatures by incubating White-winged Doves. Pp. 107-112 in *Physiological systems in semiarid environments* (C. Hoff and M. Riedesel, Eds.). Albuquerque, New Mexico, University of New Mexico Press.
- SAS Institute, Inc. 1979. *SAS User's guide*, 1979 edition. Cary, North Carolina, SAS Institute.
- Sauer, E. 1962. Ethology and ecology of Golden Plovers on St. Lawrence Island, Bering Sea. *Psychol. Forsch.* 26: 382-467.

- Scholander, P., R. Hock, V. Walters, F. Johnson, & L. Irving. 1950. Heat regulation in some arctic and tropical mammals and birds. Bio. Bull. 99: 237-258.
- Schoenwetter, K. 1967. Handbuech der Oologie, vol. 1. Berlin, Akademie Verlag.
- Shewell, E. 1951. Notes on the nesting of the White-fronted Sandplover, *Charadrius marginatus*, at Gamtoos River mouth in 1950. Ostrich 22: 117-119.
- Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. New York, McGraw-Hill Book Co.
- Simmons, K. 1956. Territory in the Little Ringed Plover, *Charadrius dubius*. Ibis 98: 390-397.
- Skutch, A. 1957. The incubation patterns of birds. Ibis 99: 69-93.
- 1962. The constancy of incubation. Wilson Bull. 74: 115-152.
- Sluiters, J. 1938. Bijdrage tot de biologie den kleinen Plevier (*Charadrius dubius curonicus*). Ardea 27: 123-151.
- Soikkeli, M. 1967. Breeding cycle and population dynamics of the Dunlin (*Calidris alpina*). Ann. Zool. Fenn. 4: 158-198.
- Strauch, J., Jr., & L. Abele. 1979. Feeding ecology of three species of plovers wintering on the Bay of Panama, Central America. Studies in Avian Biology 2: 217-230.
- Summers, R., & P. Hockey. 1980. Breeding biology of the White-fronted Plover (*Charadrius marginatus*) in the south-western Cape, South Africa. J. Nat. Hist. 14: 433-445.
- Sutton, G., & D. Parmalee. 1955. Breeding biology of the Semipalmated Plover on Baffin Island. Bird-Banding 26: 137-147.
- Tomkins, I. R. 1944. Wilson's Plover in its summer home. Auk 61: 259-269.
- Trivers, R. 1972. Parental investment and sexual selection. Pp. 136-179 in Sexual Selection and the Descent of Man, 1871-1971 (B. Campbell, Ed.). Chicago, Aldine-Atherton.

- Walters, J. 1957. Behavior during the egg-laying period in the Snowy Plover (Charadrius alexandrinus L.) and the division of labor during the nesting cycle (in Dutch with English summary). *Ardea* 45: 24-62.
- , 1958. On the temperature of the brood patches in the Snowy and Little Ringed Plovers (Charadrius alexandrinus and dubius) (in German with English summary). *Ardea* 46: 124-138.
- Walters, J. R. 1980. Evolution of parental care in lapwings. Unpublished Ph.D. dissertation, Chicago, Illinois, University of Chicago.
- Ward, P. 1965. The breeding biology of the Black-faced Dioch Quelea quelea in Nigeria. *Ibis* 107: 326-349.
- Warriner, J., & R. Warriner. 1978. Pajaro's Plovers. Point Reyes Bird Observatory 45: 4-5.
- Weller, M. 1958. Observations on the incubation behavior of a common nighthawk. *Auk* 75: 48-59.
- Welty, J. C. 1975. The life of birds, 2nd ed. Philadelphia, W. Saunders Co.
- White, F., & J. Kinney. 1974. Avian incubation. *Science* 186: 107-115.
- Wilcox, S. 1959. A twenty year study of the Piping Plover. *Auk* 76: 129-152.
- Wiley, R., & S. Hartnett. 1980. Mechanisms of spacing in groups of juncos: Measurements of behavioral tendencies in social situations. *Anim. Behav.* 28: 1005-1016.
- Williams, D., C. Thompson, & J. Jacobs. 1977. *Soil Survey of Cameron County, Texas*. Washington, D.C., Soil Conservation Service.
- Winer, B. 1971. Statistical principles in experimental design, 2nd ed. New York, McGraw-Hill Book Co.
- Witherby, H., F. Jourdain, N. Ticehurst, & B. Tucker. 1943. *The handbook of British birds*, vol. 4. London, Witherby Ltd.