To Yellow Peril
Hope it doesn't
keep you awake like
it kept me awake

Running
Water

AN ANALYSIS OF THE FALL OCCURRENCES AND NOCTURNAL ORIENTATIONS OF VAGRANT WOOD WARBLERS (PARULIDAE) IN CALIFORNIA

A DISSERTATION
SUBMITTED TO THE DEPARTMENT OF BIOLOGICAL SCIENCES
AND THE COMMITTEE ON GRADUATE STUDIES
OF STANFORD UNIVERSITY
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

By
David Francis DeSante
August, 1973

I certify that I have read this thesis and that in my opinion it is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Colin S Pittendrigh
(Principal Adviser)

I certify that I have read this thesis and that in my opinion it is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

H. Craig Heller

I certify that I have read this thesis and that in my opinion it is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Thomas M Cover
(Departments of Statistics and
Electrical Engineering)

Approved for the University Committee
on Graduate Studies:

Dean of Graduate Studies

ABSTRACT

AN ANALYSIS OF THE FALL OCCURRENCES AND NOCTURNAL ORIENTATIONS OF VAGRANT WOOD WARBLERS (PARULIDAE) IN CALIFORNIA

David Francis DeSante, Ph.D.
Stanford University, 1973

Immatures of most species of wood warblers characteristic of eastern North America occur regularly, although in very small numbers, on the Pacific Coast of California during fall migration. The purpose of this study is to present and test a mechanistic theory to account for this fall vagrancy in immature North American wood warblers.

The first part of this study is theoretical in approach. Based upon what is known of both the migratory behavior of wood warblers and distance-and-direction nocturnal migration, a generalized theory of the first fall migration of an immature warbler is presented. The possible errors in such a migration system are outlined in detail. All of the fall and winter occurrences of vagrant warblers in California are then analyzed in terms of the various species abundances and in terms of the locations and timing of the occurrences within the state to determine which of the possible errors inherent in the migration system of the immature warbler is responsible for the vagrant phenomenon. The result of this analysis is a strong indication that the misoriented warblers that reach California have followed a direction that is a mirror image, across the North-South axis, of the correct direction.

The second part of this study is experimental in approach. Over 500 nocturnal orientation experiments were conducted, by the "footprint" technique, on 24 California captured Blackpoll Warblers, one of the most common vagrant species. The data from these experiments are analyzed, by several new techniques, to determine whether vagrant Blackpoll Warblers are capable of demonstrating preferred directions, and, if so, what directions are chosen. The results of this analysis indicate that these birds do show directed behavior when placed into orientation cages under the clear night sky and, furthermore, that the entire sample of Blackpoll Warblers is directed in a consistant multimodal manner which appears to be symmetric to both the North-South and East-West axes. Such symmetry in orientation behavior is compatible with the theory that vagrant Blackpoll Warblers, when placed in orientation cages, display both the correct migratory direction and the mirror image of that direction as well as the 180° reverse of each of these directions. This 180° reverse orientation is considered to be a generalized adaptive response to adverse stress conditions such as arriving over unsuitable habitat at the termination of a migratory flight, encountering adverse weather or being captured and prevented from migrating.

A working hypothesis for mirror image misorientation in immature wood warblers is presented that is consistant with all of the results of this investigation. Immature warblers are assumed to learn the stationary point of the night sky (celestial North) as a reference point to which to relate their inherited migratory direction. This direction is defined in terms of (1) the angular deviation from the reference point and (2) the sense (right or left, clockwise or counterclockwise) with which that angular deviation is measured. Mirror image misorientation is then due to left-right confusion (mirror image equivalence) of that sense. The choice of the orientation (correct or mirror image) for the first actual migratory flight is either determined randomly or, more likely, is environmentally triggered by the wind direction. The orientation of this intial flight is reinforced so that the orientation of subsequent flights is determined by the orientation of the initial flight. When the warbler is captured, prevented from migrating and tested in an orientation cage over several nights, it displays a stress-induced alternation between the correct and the mirror image orientations.

Finally, several theoretical evolutionary implications of mirror image misorientation are discussed. It is concluded that mirror image misorientation is probably not unique to wood warblers but may be a potential

characteristic of all birds that utilize a distance-and-direction migration system.

Approved for publication:

By H. Craig Heller

Department of Biological Sciences

By ______________________________

Dean of Graduate Studies

to Rich Stallcup

who, more than any man alive, knows
the beauty and the magic that is the
wood warbler.

PROLOGUE

On September 17, 1971, a gray overcast day with light SSE winds, I captured one Tennessee Warbler, one Black-throated Blue Warbler, one Blackburnian Warbler, five Blackpoll Warblers and two American Redstarts. During the course of that day I saw an Ovenbird, another Redstart and at least two other Blackpoll Warblers. I spent that day on Southeast Farallon Island, a small granitic outcropping of less than 100 acres, sporting two trees and lying some 28 miles west of the Golden Gate Bridge, San Francisco, California. Those who are familiar with the ranges of these birds recognize them as being rather typical "eastern" warblers, species that could be expected in northeastern United States at that time of the year, some 2500 miles east of the Farallons. But those who have been searching the outer windbreaks of coastal Marin, Monterey or San Diego Counties each fall, precisely looking for such birds, may realize that such a day was not exceptional -- a good, but not extraordinary "vagrant day" on the Farallons.

Occurrences of such accumulations of "lost birds" have been noted each fall for the last eleven years. They have, of course, stimulated much excitement and speculation on the part of many West Coast "birders" and no little bit of skepticism among many museum ornithologists, particularly during the early years of the discovery of the seemingly incredible numbers of such birds, 1962-1965. Arm chair biologists have appraised the situation and offered explanations for the occurrences of these birds. Some of their theories are contradictory, most are incomplete and none are truly mechanistic in approach. It is the purpose of this dissertation to present a comprehensive theory for this phenomenon based upon the total accumulation of the occurrences of these birds in California, observations of these birds in the wild and the results of more than 500 orientation cage experiments on 24 individuals captured during the falls of 1969-1971.

ACKNOWLEDGMENTS

The success of this undertaking is due, in no small part, to the generous assistance of innumerable friends and colleagues. To all of them, I wish to express my sincere appreciation. In particular, however, I wish to thank several people, without whose help this project could not have been completed.

First, I wish to thank the many California field ornithologists who have devoted countless pleasurable hours in the field in search and discovery of vagrant warblers in California. It is upon their observations that the first part of this study is based. In particular, I thank Guy McCaskie and Rich Stallcup who, in some sense, pioneered the discovery of these birds.

To Dr. Peter Raven, whose confidence and enthusiasm allowed me to initiate this project, I owe a great deal of thanks.

The field work associated with this investigation could not have been completed without the hospitality of the Point Reyes Bird Observatory, in particular Dr. David Ainley, Jim Lewis, John Smail and Helen Strong, who permitted the use of their housing and facilities on Southeast Farallon Island.

I thank them sincerely. I also thank the U.S. Coast Guard for transportation to the Island. The completion of the field work in San Diego was made possible by Alan and Jean Craig, who generously opened their home and banding facilities to me. To them, I owe a great deal of thanks. I wish to thank Peter Egan, Henry Robert, Rich Stallcup and Robert Stewart for their assistance with some of the orientation experiments reported in this dissertation.

I thank the personnel of the Department of Computer Science, Stanford University, for the use of their facilities at the Stanford Artificial Intelligence Project. In particular I wish to thank Dr. Thomas Binford, Les Ernest, Dr. Cordell Green and Dr. John McCarthy.

A great deal of appreciation is owed to various members of the Department of Statistics, Stanford University, for the generous guidance and assistance that they provided in the statistical analysis of the data presented here. In particular, I wish to thank Dr. Thomas Cover, Dr. Bradley Efron, Dr. Rupert Miller, Dr. Lincoln Moses and Ann Varady for their help. To Dr. Moses, who freely gave so much of his valuable time and frienship, I wish to extend a personal message of thanks.

For many pleasurable, helpful discussions during the course of this investigation, as well as for the careful reading of this manuscript, I wish to thank my reading committee: Dr. Thomas Cover, Dr. Craig Heller and Dr. Colin

Pittendrigh. I especially wish to thank Dr. Phillip Sokolove for his constant encouragement and many timely comments. For technical assistance in the preparation of this manuscript, I wish to thank Dr. Daniel Bobrow and Dr. Jeff Rulifson of Xerox Palo Alto Research Center.

The financial support of this project was provided by National Institute of Health, Population Biology Training Grant, GM 00365, to Dr. Paul Ehrlich and by a Department of Biological Sciences, Stanford University, Bio-Fellowship. I thank both of these sources for their support.

Finally, to Janet Farness, I owe a debt of appreciation that I can never hope to repay. Not only did she give, so unselfishly, her time and help throughout every facet of this project, but she also undertook the task of typing this manuscript. For this service, alone, I am extremely grateful. But far above this physical task, I thank Janet for her constant kindness, understanding and love, without which, this project could not have been completed and without which, my life would have been empty.

Dave DeSante
Stanford University
Stanford, California
August 1973

TABLE OF CONTENTS

Page

Abstract..iv
Dedication..viii
Prologue..ix
Acknowledgments...xi
List of Tables..xvi
List of Figures...xxi
List of Appendices..xxiv

PART I - BACKGROUND

Chapter 1.
The extent of the problem - an introduction.......1-1

Chapter 2.
Previous suggestions on the occurrences of vagrant warblers in California - a review.........2-1

Chapter 3.
The present study - an introduction...............3-1

PART II - A THEORETICAL APPROACH

Chapter 4.
The wood warbler - a review.......................4-1

Chapter 5.
A generalized theory of distance-and-direction migration applicable to the immature wood warbler...5-1

Chapter 6.
Possible errors inherent in a distance-and-direction migration of an immature wood warbler...6-1

Chapter 7.
An analysis of the fall occurrences of vagrant wood warblers in California.......................7-1

Page

PART III - AN EXPERIMENTAL APPROACH

Chapter 8.
The orientation cage - an introduction............8-1

Chapter 9.
Experimental methods................................9-1

Chapter 10.
The digitization of the footprint data............10-1

Chapter 11.
The characterization of digitized data............11-1

Chapter 12.
Experimental results................................12-1

PART IV - SYNTHESIS

Chapter 13.
180° reverse orientation - a discussion...........13-1

Chapter 14.
Mirror image misorientation - a discussion........14-1

Chapter 15.
Summary and conclusions............................15-1

PART V - REFERENCE MATTER

Chapter 16.
Bibliography.......................................16-1

Chapter 17.
Appendices...17-1

LIST OF TABLES

Page

1-1. Warblers comprising an integral part of the California avifauna....1-4

1-2. Summary of the fall and winter occurrences of potential vagrant wood warblers in California....1-7

1-3. Summary of the fall and winter occurrences of definite vagrant wood warblers in California....1-9

1-4. Variation from year to year in the number of fall and winter occurrences of vagrant warblers in California....1-14

1-5. The North American wood warblers that have not been recorded in California in the fall or winter....1-16

1-6. Summary of the occurrences of vagrant warblers in Northern California according to location....1-19

1-7. Summary of the occurrences of vagrant warblers in Southern California according to location....1-20

1-8. Summary of the percentages of vagrant warbler occurrences in California according to location....1-21

1-9. Percentages of fall and winter Southern California vagrant warbler occurrences that are on the east side of the Sierra and higher southern California mountains....1-24

1-10. Ages of vagrant warblers examined in California during the fall....1-30

4-1. Primary fall migration routes of eastern wood warblers....4-5

LIST OF TABLES (CONT)

Page

4-2. A summary of some important characteristics of wood warblers....4-8

5-1. Factors necessary for a successful distance-and-direction migration for an immature wood warbler....5-11

6-1. Summary of possible orientation errors in the distance-and-direction migration of an immature wood warbler....6-2

7-1. Average arrival dates of Northern Species of vagrant warblers in California....7-3

7-2. Average arrival dates for Southern Species of vagrant warblers in California....7-7

7-3. Comparison of average arrival dates and distances flown for Northern and Southeastern vagrant warblers in California....7-9

7-4. Summary of predicted results of the analysis to distinguish between mirror image and simple misorientation....7-25

7-5. An analysis of the total number of occurrences of eastern warblers in California according to breeding range, population size and normal migration route....7-27

7-6. An analysis of the percentage of occurrences of eastern warblers in Northern California according to breeding range and migration route....7-30

7-7. An analysis of the percentage of occurrences of eastern warblers in the Interior of California according to breeding range and migration route....7-32

7-8. An analysis of the difference in average arrival dates between Southern and Northern California according to breeding range and migration route....7-33

LIST OF TABLES (CONT)

Page

7-9. An analysis of the occurrences of Southwestern vagrant warblers in California..........7-35

9-1. Capture data on all Blackpoll Warblers used in this study..................................9-4

10-1. Pearson product-moment coefficient of correlation, r, for two independent digitizations of the same 21 orientation traces of California captured Blackpoll Warblers.......................................10-15

11-1. Characteristics of various mode finding algorithms tested on 200 randomly produced circular distributions..........................11-7

11-2. Combinations of theoretical circular normal distributions used in testing the approximate multimodal analysis............................11-12

11-3. Summary of errors produced by the approximate multimodal analysis on mixtures of circular normal distributions...........................11-22

12-1. Summary of the weights of all California captured Blackpoll Warblers used in this study...12-2

12-2. Summary of activities of California captured Blackpoll Warblers tested in "footprint" orientation cages..............................12-6

12-3. Differences in mean activities between "fat" and "thin" California captured Blackpoll Warblers.......................................12-8

12-4. Mean differences in activities between three test periods for seven 1971 California captured Blackpoll Warblers...................12-12

12-5. Mean differences in activities between early and late night September, 1971, tests for California captured Blackpoll Warblers.........12-13

LIST OF TABLES (CONT)

Page

12-6. Mean difference in activities between the first and second night tested and between the first + second and third + fourth nights tested for California captured Blackpoll Warblers....12-17

12-7. Percentage of multimodal behavior displayed by California captured Blackpoll Warblers......12-20

12-8. Mean concentration about the mean vector for all unimodal data produced by California captured Blackpoll Warblers....12-27

12-9. Results of the Single Trace Analysis run on the summation of activities of each California captured Blackpoll Warbler..........12-57

12-10. Results of subjective clustering analysis on the distribution of mean directions of all 23 Northern California captured Blackpoll Warblers....12-67

12-11. Results of the Rao test on the distribution of primary and unimodal mean directions chosen by each California captured Blackpoll Warbler tested over many nights................12-71

12-12. Results of the Rao test on the distribution of directions avoided by California captured Blackpoll Warblers....12-77

12-13. Maximum negative mean values of the test statistic $X(\Psi) = \frac{F(\Psi) - F_O(\Psi)}{\sigma_O(\Psi)}$ and significance levels for California captured Blackpoll Warblers....12-90

12-14. Distribution of individual California captured Blackpoll Warblers over ten potential correct directions as determined by the test statistic $\overline{X}(\Psi)$....12-91

LIST OF TABLES (CONT)

Page

12-15. Maximum values and significance levels for two test statistics, $Z_1(\Psi)$ and $Z_2(\Psi)$, for California captured Blackpoll Warblers.........12-100

12-16. Distribution of individual California captured Blackpoll Warblers over ten potential correct directions as determined by the test statistics $Z_1(\Psi)$ and $Z_2(\Psi)$.......................12-102

13-1. Vanishing directions of fall migrants during early morning hours on Southeast Farallon Island...13-5

14-1. Distribution of unimodal or primary mean directions displayed by California captured Blackpoll Warblers.....................14-7

LIST OF FIGURES

Page

1-1. Map of California illustrating areas mentioned in the text....1-2

1-2. Fall and winter occurrences of definite vagrant wood warblers in California. The number of occurrences prior to 1962 as a function of the number of occurrences in the Interior....1-27

1-3. Fall and winter occurrences of definite vagrant wood warblers in California. The number of occurrences prior to 1962 as a function of the total number of occurrences....1-28

7-1. Some possible kinds of assortment between breeding and wintering ranges....7-14

7-2. Theoretical correct and mirror image migration routes for two hypothetical species of warblers. One is an Atlantic Coast migrant, the other a Gulf Coast migrant....7-16

8-1. Distribution and fall migration route of the Blackpoll Warbler....8-8

9-1. Example of assembled "footprint" orientation cage used in this study....9-10

9-2. Position of the lighthouse on Southeast Farallon Island in relation to the orientation cages....9-11

10-1. Examples of completed "footprint" orientation traces made by California captured Blackpoll Warblers under the clear night sky....10-2

10-2. Relationship between blackness and V values for the digitization of "footprint" data....10-9

10-3. Logarithmic relationship between blackness and V values for the digitization of "footprint" data....10-10

LIST OF FIGURES (CONT)

Page

10-4. Blackness wheels designed to digitize "footprint" orientation data....................10-12

10-5. Example of equipment and method for digitizing "footprint" orientation data........10-13

11-1. Results of the approximate multimodal solution of bimodal mixtures of theoretical circular normal distributions..................11-14

12-1. Mean weight as a function of time for twelve Blackpoll Warblers captured on Southeast Farallon Island, Sep. 17-22, 1971..............12-4

12-2. Mean activity as a function of time for seven Blackpoll Warblers captured on Southeast Farallon Island, Sep. 17-22, 1971 and tested on the same 30 nights...............12-10

12-3. Mean activity as a function of time for all Blackpoll Warblers tested during the entire three years of this study.......................12-15

12-4. Frequency distribution of $\Delta\Phi$, the difference between the mean direction of the primary mode and the mean direction of the secondary mode measured clockwise from the primary mode, for all bimodal traces produced by Blackpoll Warblers under clear night skies...............12-22

12-5. Examples of unimodal orientation data produced by a California captured Blackpoll Warbler, Bird 32, under the clear night sky and illustrating various concentrations, r_U, about the mean unimodal vector...................12-28

12-6 to 12-29. Orientation of Zugunruhe of California captured immature Blackpoll Warblers tested under the clear night sky. Birds number 21 to 44..........................12-31 to 12-54

LIST OF FIGURES (CONT)

Page

12-30. Vector diagram for the summation of activities of all tests on all California captured Blackpoll Warblers.................... 12-59

12-31. Distribution of mean directions obtained by the summation of activities of all tests of each Northern California captured Blackpoll Warbler (23 birds)............................ 12-63

12-32. Distribution of avoided directions for all 23 California captured Blackpoll Warblers that were tested over several nights........... 12-74

12-33. Distribution of preferred directions, $\Phi_n (n=1,4)$, according to the mirror image hypothesis.. 12-81

12-34. Probability density function, $P(\beta)$, for the uniform distribution for various values of θ.. 12-85

12-35. Some of the members of the family of diameter constant distributions, $P(\alpha)$, for which $P(\beta)$ is identical to $P(\beta)$ for the uniform distribution.................................. 12-88

12-36. Comparison of $F(\psi)$ for two unimodal distributions with $F_o(\psi)$ for the uniform distribution.................................. 12-93

14-1. Results of a visual mirror image stimulus discrimination test on pigeons................ 14-4

LIST OF APPENDICES

Page

I Data used for the calculation of predicted average arrival dates for eastern wood warblers..........17-1

II Environmental data for all nights on which California captured Blackpoll Warblers were tested.......................................17-2

III Digitized raw data for all orientation tests on all California captured Blackpoll Warblers........17-4

IV Conversion table for parameters of theoretical circular normal distributions.....................17-14

PART I

BACKGROUND

CHAPTER 1

THE EXTENT OF THE PROBLEM - AN INTRODUCTION

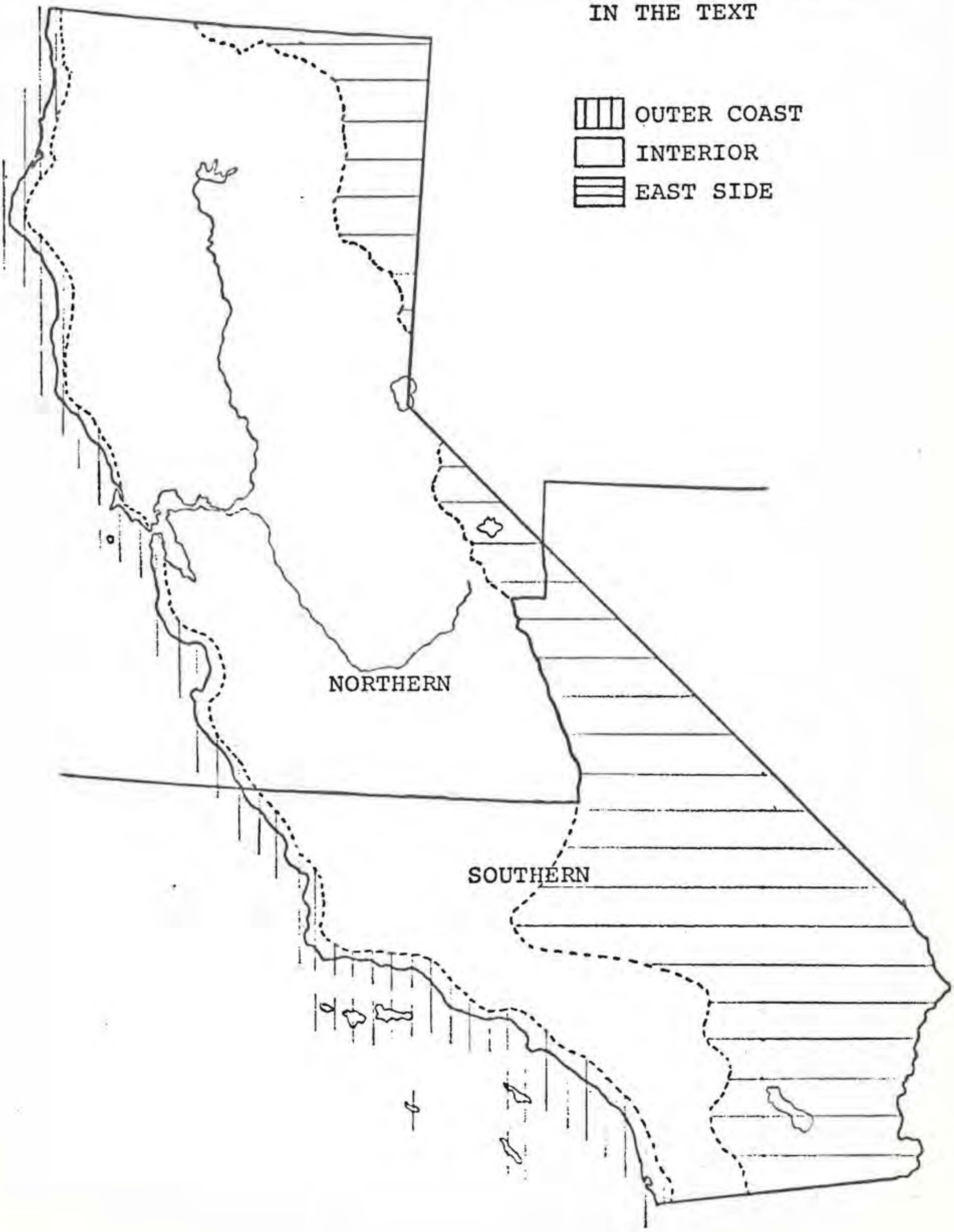
A vagrant bird in a given geographical area is defined as an individual of a population of birds that neither regularly breeds nor winters in that area and whose normal migration route between its breeding and wintering grounds does not pass through (or over) that area. The term "out-of-range" may be synonomous with vagrant. Thus, one may consider vagrant individuals but not, in the strictest sense, vagrant species. If, however, all of the individuals of a given species that occur in a given area must be vagrant individuals, then that species may be referred to as a vagrant species in the geographical area in question. For the purposes of this dissertation, the area in question is limited to the political area of the state of California. A map of California, showing areas referred to in this study, is presented in Figure 1-1.

Western Species

Fifty-four species of wood warblers (family Parulidae) are known to breed (or have bred) in North America north of Mexico and the West Indies [American Ornithologists' Union, 1957]. Only twelve of these fifty-four are known to breed or winter regularly in cismontane California in such numbers that they may be considered to comprise an integral

FIGURE 1-1

MAP OF CALIFORNIA
ILLUSTRATING AREAS MENTIONED
IN THE TEXT



part of the avifauna of the state [Grinnell and Miller, 1944]. These species, along with their basic seasonal roles in California, are presented in Table 1-1. Five of these species, the Audubon's, Black-throated Gray, Townsend's, Hermit and MacGillivray's Warblers are unique to the montane areas of the western cordilleras or to the Pacific Slope of North America and may properly be referred to as western species. All of these species, however, are represented by closely related species (or forms) in eastern North America and are thought to have differentiated in western North America as a result of glacial isolation during the Pleistocene [Mengel, 1964]. The eastern counterpart of the Audubon's Warbler is the Myrtle Warbler and extensive studies [Hubbard 1969, 1970] indicate that it may deserve only subspecific rank. It is basically an eastern species, breeding entirely east or north of the western cordilleras but is unique among eastern species in that it winters extensively on the Pacific Slope of North America including California. The origin of this Pacific Slope wintering range will be the subject of a future investigation; for the present, the Myrtle Warbler is included as one of our regular California species.

The remaining six species of western warblers breed (in one form or another) in both western and eastern North America. These species include the Orange-crowned, Nashville, Yellow and Wilson's Warblers, the Common

TABLE 1-1

WARBLERS COMPRISING AN INTEGRAL PART OF THE CALIFORNIA AVIFAUNA

I	<u>CISMONTANE SPECIES</u>		
	ORANGE-CROWNED WARBLER	BREEDS	WINTERS
	NASHVILLE WARBLER	BREEDS	*
	YELLOW WARBLER	BREEDS	*
	MYRTLE WARBLER		WINTERS
	AUDUBON'S WARBLER	BREEDS	WINTERS
	BLACK-THROATED GRAY WARBLER	BREEDS	*
	TOWNSEND'S WARBLER		WINTERS
	HERMIT WARBLER	BREEDS	*
	MACGILLIVRAY'S WARBLER	BREEDS	*
	YELLOWTHROAT	BREEDS	WINTERS
	YELLOW-BREASTED CHAT	BREEDS	*
	WILSON'S WARBLER	BREEDS	*
II	<u>DESERT OR DESERT MOUNTAIN SPECIES</u>		
	VIRGINIA'S WARBLER	BREEDS LOCALLY	*
	LUCY'S WARBLER	BREEDS LOCALLY	*
III	<u>PROBABLE NORMAL TRANSIENT SPECIES IN SOUTHEASTERN DESERTS</u>		
	NORTHERN WATERTHRUSH		*
	AMERICAN REDSTART	**	*

* Winters rarely or in very small numbers
** Has bred in the state

Yellowthroat and the Yellow-breasted Chat. It is to be expected that various eastern forms of all of these species have occurred in California in the fall as vagrant individuals. Since the racial identity of California occurring migrant (or vagrant) individuals of these species is impossible to ascertain in the field (and extremely difficult even in the hand), the number of vagrant occurrences of eastern representatives of these species in California cannot be determined. As a result, this dissertation will not be further concerned with these species.

Potential Vagrant Species

Two additional species, the Virginia's and Lucy's Warblers, breed locally in the deserts or desert mountains of southeastern California (Table 1-1). The normal wintering areas of both species lie in western Mexico, some distance to the southeast of their breeding grounds. Thus, although they may be expected to occur regularly as transients in extreme southeastern California, their occurrences in cismontane California may be due to vagrant individuals. These species therefore will be included in the present discussion.

If one connects the westernmost normal breeding location and the westernmost normal wintering location of each of the remaining forty species of North American wood warblers with a "straight" line (either a rhomb line of constant angle with respect to true north, or a great-circle line), one finds that this line will pass through California for only two species, the Northern Waterthrush and the American Redstart (Table 1-1). Both of these species regularly breed west to the Pacific Coast of British Columbia and regularly winter west to southern Baja California and northwestern Mexico. The line connecting these locations passes directly through the desert regions of southeastern California where these species may thus be expected to be normal transients. In addition, the Northern Waterthrush breeds west in Alaska to the Bering Sea. If we accept the possibility of a direct trans-Pacific flight for this species from Alaska to Baja, we find that it could occur as a normal transient in cismontane California as well as on the deserts. Nevertheless, some discussion of both of these species will be included in this dissertation with the hope of shedding some light as to the relative numbers of normal transients and vagrant individuals of these species in California. These species, along with the Virginia's and Lucy's Warblers, will be referred to as potential vagrant species. A summary of all of their known California fall and winter occurrences is presented in Table 1-2.

TABLE 1-2

SUMMARY OF THE FALL AND WINTER OCCURRENCES OF POTENTIAL VAGRANT WOOD WARBLERS IN CALIFORNIA

	Occurrences NORTHERN CALIFORNIA			Occurrences SOUTHERN CALIFORNIA			Occurrences ALL OF CALIFORNIA		
SPECIES	Total #	# of Winter	# Prior to 1962	Total #	# of Winter	# Prior to 1962	Total #	# of Winter	# Prior to 1962
Virginia's	15			238	7	9	253	7	9
Lucy's	6	1	1	27	2	2	33	3	3
Northern Waterthrush	57	1	14	98	17	13	155	18	27
American Redstart	188	5	11	426	66	45	614	71	56
Total Occurrences	266	7	26	789	92	69	1055	99	95
Total Species	4	3	3	4	4	4	4	4	4

Definite Vagrant Species

All of the remaining thirty-eight species of North American wood warblers, according to the definition presented above, could only occur in California as definite vagrant species. Of these thirty-eight species, thirty have occurred in California in the fall and winter for a total of 1776 occurrences. These data are summarized, species by species, in Table 1-3.

Three important points regarding the sources of these data must be discussed. First, the data have been obtained by an exhaustive search of the literature (all issues of Western Birds, formerly California Birds, 1970-present; all issues of American Birds, formerly Audubon Field Notes and before that, the Season of Audubon Magazine, 1940-present; all issues of the Condor, 1899-present; all issues of the Auk and the Wilson Bulletin 1940-present; Grinnell and Miller [1944]; Pyle [1961]; McCaskie and DeBenedictis [1966]), a search of the major ornithological collections of California, a search through the Daily Journal of the Point Reyes Bird Observatory; Farallon Island Station, and personal communication with most of the more active field ornithologists in California. As such, it is felt that the vast majority of the occurrences have been compiled and that any overlooked occurrences will not substantially alter the results of this discussion. A complete listing of the fall

TABLE 1-3

SUMMARY OF THE FALL AND WINTER OCCURRENCES OF DEFINITE VAGRANT WOOD WARBLERS IN CALIFORNIA

	Occurrences NORTHERN CALIFORNIA			Occurrences SOUTHERN CALIFORNIA			Occurrences ALL OF CALIFORNIA		
SPECIES	Total #	# of Winter	# Prior to 1962	Total #	# of Winter	# Prior to 1962	Total #	# of Winter	# Prior to 1962
Black-and-white	86	24	18	124	14	33	210	38	51
Prothonotary	2			7			9		
Worm-eating	3			2		1	5		1
Golden-winged				2		1	2		1
Blue-winged	1			2			3		
Tennessee	89	2	8	137	7	9	226	9	17
Parula	7			10	4		17	4	
Magnolia	28		1	35		3	63		4
Cape May	7			6		1	13		1
Black-throated Blue	37		5	54	1	6	91	1	11
Black-throated Green	5			24		2	29		2
Golden-cheeked	1						1		
Cerulean				2		1	2		1
Blackburnian	16			22			38		
Yellow-throated	1			2			3		
Grace's				2			2		
Chestnut-sided	25		2	18	2	1	43	2	3
Bay-breasted	3			9		1	12		1
Blackpoll	262		1	176	1	1	438	1	2
Pine	1			3			4		
Prairie	17			24	1		41	1	
Palm	279	28	13	140	25	4	419	53	17
Ovenbird	26			20	2	4	46	2	4
Louisiana Waterthrush				1		1	1		1
Kentucky	1						1		
Connecticut	3			1			4		
Mourning				1			1		
Hooded	4			5			9		
Canada	6			17		2	23		2
Painted Redstart				20	8	17	20	8	17
Total Occurrences	910	54	48	866	65	88	1776	119	136
Total Species	24	3	7	28	10	17	30	10	17

and winter occurrences of these species in California is available from the author by request.

Secondly, these data represent the total number of occurrences of individual birds rather than the total number of records where a single record could pertain to multiple individuals. The reason for this procedure is that two or more individuals of the same species at the same location (even the same tree) at the same time may each have arrived independently and, therefore, must be considered independently. Finally, the vast majority of the 2831 occurrences recorded in Tables 1-2 and 1-3 have been sight records. Nevertheless, at least one California taken fall specimen exists for all thirty-four species of vagrant warblers recorded in the fall or winter in California except for Yellow-throated (photograph on file at the San Diego Natural History Museum) and Blue-winged (description on file at the same place). The day in which all acceptable occurrences of vagrant birds must be accompanied by a specimen has, happily, disappeared in California. The vast majority of the records of these birds have been published in <u>American Birds</u> where it has been the policy of the Regional Editors (at least in California) to only publish records of vagrant birds if the record is accompanied by totally convincing details. The author, therefore, feels that the number of errors in identification in these records, if any, is negligibly small.

Number of Vagrant Occurrences

Several important results are immediately apparent from Table 1-3. The sheer magnitude of the total number of definite vagrant occurrences (1776) strongly suggests that something other than mere accident or chance is responsible for this phenomenon. It is also important to note that the number of occurrences varies widely among the 30 definite vagrant species; some of the rarer (e.g., Golden-cheeked Warbler, Kentucky Warbler, etc.) are represented by only a single occurrence while some of the more common (e.g., Blackpoll Warbler, Palm Warbler) are represented by well over 400 occurrences. Definite vagrant species occur commonly in both Northern and Southern California. (The definition of these areas is as shown in Figure 1-1.) Table 1-3 indicates that slightly more definite vagrant species have occurred in Southern than in Northern California (28 vs. 24) but with slightly fewer occurrences (866 vs. 910). These data, however, should not be construed to be absolute in any sense but to be only relative with regard to the number of observers, the time spent by observers in the field and the number of concentration points for observing these birds. Northern California occurrences, for example, may be biased on the high side because of the continual daily observations since 1968 on Southeast Farallon Island. Nevertheless, these data can be used to obtain relative species abundances in Northern and Southern California.

Thus, when one looks at the four potential vagrant species (Table 1-2), one finds them to be relatively more common in Southern than in Northern California (789 vs. 266 occurrences) than are the definite vagrant species.

Tables 1-2 and 1-3 also indicate that a relatively small number of individuals (9.4% and 6.7% respectively) have remained into (or were discovered during) the winter period which is arbitrarily defined as extending from December 17 - April 25. It is possible that some interpretive errors may be included here as some of the late December birds could have been extremely late fall migrants while some of the April birds could have been unusually early spring migrants. For the most part, however, these winter records represent individuals that have remained in a suitable wintering location (usually riparian riverbottoms) for an extended period of time. Most of the single-date winter records occur either in late December or April, times of high observer bias due to Christmas Bird Counts and the return of normal western spring migrants, both of which bring large numbers of observers out of hiding. It should be noted that all of the species that have occurred in the winter have occurred much more commonly during the fall and that the species with the most winter records are species with more northern normal winter ranges such as the Palm and Black-and-white Warblers and the American Redstart. In view of these facts it seems likely that all wintering individuals of vagrant warblers in California arrived in California as fall vagrants rather than as winter wanderers. As would be expected, there are more winter occurrences for Southern than for Northern California.

One of the most interesting facts shown in Tables 1-2 and 1-3 is that the vast majority of the known occurrences of these birds in California have been subsequent to 1962. For example, only 7.7% of the total occurrences of definite vagrant species were recorded prior to 1962 and only 17 of the 30 species were involved. The potential vagrant species were not recorded much more frequently, only 9.0% of their total occurrences being prior to 1962. At first glance, such data may be interpreted to mean that the vagrant phenomenon in California is of extremely recent origin. However, an alternative interpretation is tenable and will be presented below.

The number of vagrant warblers that have occurred in California since 1962 has shown a rather steady increase from year to year (Table 1-4). This may be interpreted as a result of the increased field efforts of the ever increasing number of observers specifically looking for these birds each fall. The rather abrupt increase noted in 1968 is a result of the establishment of a permanent censusing and banding operation by the Point Reyes Bird Observatory on Southeast Farallon Island. Nevertheless, some variation in the number of vagrant warblers does occur from year to year.

TABLE 1-4

VARIATION FROM YEAR TO YEAR IN THE
NUMBER OF FALL AND WINTER OCCURRENCES
OF VAGRANT WARBLERS IN CALIFORNIA

SPECIES	PRIOR TO 1962	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	TOTAL
Black-and-white	51	4	13	13	7	15	14	9	23	9	18	34	210
Prothonotary					1	1	2		2	1	1	1	9
Worm-eating	1						1		1		1	1	5
Golden-winged	1	1											2
Blue-winged			1	2									3
Tennessee	17	13		28	7	20	15	20	22	28	25	31	226
Virginia's*	9	35	13	28	17	23	10	16	11	17	13	61	253
Lucy's*	3		1	1	2	2	5	2	6	5	3	3	33
Parula		1	1	1	2	1	1	3	2	1	1	3	17
Magnolia	4	1	3	2	3	2	7	6	9	5	7	14	63
Cape May	1	2						3	1	2	3	1	13
Black-throated Blue	11	3	1	5	2	4	6	11	9	13	10	16	91
Black-throated Green	2		5	3		4	3		2	2	2	6	29
Golden-cheeked											1		1
Cerulean	1						1						2
Blackburnian		1	1	1		3	3	2	6	8	5	8	38
Yellow-throated									2			1	3
Grace's						1		1					2
Chestnut-sided	3	6	3	2	3	5	2	4	6	2	1	6	43
Bay-breasted	1			3		2	1	2	1		2		12
Blackpoll	2	11	8	28	21	20	29	37	71	40	80	91	438
Pine						1	1			1	1		4
Prairie		4	3	5	1	5	6		4	2	3	8	41
Palm	17	12	43	34	40	24	18	52	22	22	41	94	419
Ovenbird	4		4		2	2	2	6	4	7	3	12	46
Northern Waterthrush*	27	2	4	5	8	5	10	14	7	13	19	41	155
Louisiana Waterthrush	1												1
Kentucky												1	1
Connecticut			1	1				2					4
Mourning								1					1
Hooded							2	2			3	2	9
Canada	2				1		2	3	3		4	8	23
American Redstart*	56	28	32	60	30	25	47	47	64	63	55	107	614
Painted Redstart	17					1		2					20
TOTAL	231	124	137	222	147	166	188	245	278	241	302	550	2831

* Potential vagrant species

For example, both 1964 and 1972 were apparently excellent falls for vagrant warblers in California while 1970 was a rather poor year. These yearly variations are even more apparent in the case of individual species. Thus, 1968 was an excellent year for Palm Warblers but only an average year for Blackpolls while 1969 was an excellent year for Blackpolls but only a mediocre or poor year for Palm Warblers. A discussion of these variations will be presented in Part IV of this dissertation.

It is interesting at this time to list the eight species of North American wood warblers that have not been recorded in California during the fall or winter (Table 1-5). Six of these species are migratory in North America. They include three basically Mexican species that have a very limited breeding range in southwestern United States: the Colima, Olive and Red-faced Warblers. Also included are the extremely rare and local Bachman's and Kirtland's Warblers and the quite uncommon southeastern Swainson's Warbler. When these few species are contrasted to the 30 definite vagrant species that have been recorded in California in the fall, it is apparent that the vagrant phenomenon is extremely widespread among migratory wood warblers. There are only two non-migratory species of wood warblers in North America, the Olive-backed Warbler and the Ground-chat, and both are limited to the lower Rio Grande Valley of Texas.

TABLE 1-5

THE NORTH AMERICAN WOOD WARBLERS THAT HAVE NOT BEEN RECORDED IN CALIFORNIA IN THE FALL OR WINTER

MIGRATORY SPECIES	NON-MIGRATORY SPECIES
SWAINSON'S WARBLER	OLIVE-BACKED WARBLER
BACHMAN'S WARBLER	GROUND-CHAT
COLIMA WARBLER	
OLIVE WARBLER	
KIRTLAND'S WARBLER	
RED-FACED WARBLER	

As would be expected, neither of them have been recorded in California.

Localized Nature of Vagrant Occurrences

From the data presented in Tables 1-2 and 1-3 one might surmise that since definite or potential vagrant species of warblers occur rather uniformly in both Northern and Southern California, they might also occur rather uniformly across California from east to west. This, however, is not the case. Rather, they are extremely localized, being concentrated along the immediate coast of the state. In Figure 1-1, California is divided into three major longitudinal areas: 1) the Outer Coast, 2) the Interior and 3) the East Side. The Outer Coast includes the open waters of the Pacific, the various offshore islands and the immediate coast which is defined as all areas of the state on or west of the coastal slope of the outermost range of coastal mountains <u>and</u> less than ten miles inland from the actual coast. The Outer Coast, therefore, always extends inland for less than or equal to ten miles and, in some cases, for as little as two miles. The Interior includes all areas of California east of the Outer Coast and west of the easternmost crest of the Cascade, Sierra Nevada and higher southern California mountain axis. Finally, the East Side includes all of the remaining area of California, including all of the Great Basin and Great Basin mountain ranges, all of the deserts of southeastern California and the desert ranges, and the easternmost slopes of the Cascade, Sierra Nevada and higher southern California mountain axis.

The distribution of all of the occurrences of both definite and potential vagrant species among these areas is presented for Northern California in Table 1-6 and for Southern California in Table 1-7. The Outer Coast occurrences for Northern California are further divided to indicate the number of occurrences on the continuously censused Southeast Farallon Island. Presumably because of the unacceptable habitat and lack of food, no vagrant warbler has yet attempted to winter on the Farallons. Tables 1-6 and 1-7 are primarily presented for the sake of completeness. The most interesting data contained in these tables can be expressed in terms of the percentages of the total number of occurrences for each area (Table 1-8). The most outstanding feature of these data is, of course, the extremely localized nature of the "vagrant" occurrences. Over 91% of the Northern California occurrences of definite vagrant species are on the Outer Coast, that is, within ten miles of the ocean. Even this breakdown does not do full justice to the localized nature of these occurrences. The majority of the Northern California Outer Coast occurrences that are not on the Farallons are on Point Reyes, Marin County, or Point Pinos, Monterey County, only a few hundred

TABLE 1-6

SUMMARY OF THE OCCURRENCES OF VAGRANT WARBLERS
IN NORTHERN CALIFORNIA ACCORDING TO LOCATION

	TOTAL FALL AND WINTER OCCURRENCES						WINTER OCCURRENCES ONLY			
	OUTER COAST									
	S.E. FARALLON	OTHER	TOTAL	INTERIOR	EAST SIDE	TOTAL	OUTER COAST	INTERIOR	EAST SIDE	TOTAL
I DEFINITE VAGRANT SPECIES										
Black-and-white	8	53	61	25		86	9	15		24
Prothonotary		2	2			2				
Worm-eating		3	3			3				
Blue-winged		1	1			1				
Tennessee	26	50	76	13		89	2			2
Parula	2	5	7			7				
Magnolia	14	12	26	2		28				
Cape May	4	3	7			7				
Black-throated Blue	11	21	32	5		37				
Black-throated Green	2	3	5			5				
Golden-cheeked	1		1			1				
Blackburnian	9	6	15	1		16				
Yellow-throated		1	1			1				
Chestnut-sided	9	6	15	10		25				
Bay-breasted	1	2	3			3				
Blackpoll	101	156	257	4	1	262				
Pine		1	1			1				
Prairie	8	9	17			17				
Palm	93	171	264	15		279	24	4		28
Ovenbird	20	6	26			26				
Kentucky		1	1			1				
Connecticut	2	1	3			3				
Hooded	1	2	3	1		4				
Canada	3	3	6			6				
TOTAL	315	518	833	76	1	910	35	19		54
II POTENTIAL VAGRANT SPECIES										
Virginia's	5	6	11	1	3	15				
Lucy's		5	5	1		6	1			1
Northern Waterthrush	12	37	49	8		57		1		1
American Redstart	62	108	170	17	1	188	4	1		5
TOTAL	79	156	235	27	4	266	5	2		7
GRAND TOTAL	394	674	1068	103	5	1176	40	21		61

TABLE 1-7

SUMMARY OF THE OCCURRENCES OF VAGRANT WARBLERS IN SOUTHERN CALIFORNIA ACCORDING TO LOCATION

	TOTAL FALL AND WINTER OCCURRENCES				WINTER OCCURRENCES ONLY			
	OUTER COAST	INTERIOR	EAST SIDE	TOTAL	OUTER COAST	INTERIOR	EAST SIDE	TOTAL
I DEFINITE VAGRANT SPECIES								
Black-and-white	85	24	15	124	8	2	4	14
Prothonotary	5		2	7				
Worm-eating	2			2				
Golden-winged	1	1		2				
Blue-winged	2			2				
Tennessee	115	13	9	137	4	2	1	7
Parula	4		6	10	2		2	4
Magnolia	27	4	4	35				
Cape May	5		1	6				
Black-throated Blue	39	4	11	54	1			1
Black-throated Green	20	1	3	24				
Cerulean	1		1	2				
Blackburnian	20		2	22				
Yellow-throated	2			2				
Grace's	2			2				
Chestnut-sided	14		4	18			2	2
Bay-breasted	7		2	9				
Blackpoll	169	2	5	176	1			1
Pine	3			3				
Prairie	24			24	1			1
Palm	123	5	12	140	16	4	5	25
Ovenbird	11	5	4	20		1	1	2
Louisiana Waterthrush			1	1				
Connecticut	1			1				
Mourning	1			1				
Hooded	1	1	3	5				
Canada	15	2		17				
Painted Redstart	8	10	2	20	1	7		8
TOTAL	707	72	87	866	34	16	15	65
II POTENTIAL VAGRANT SPECIES								
Virginia's	214	13	11	238	3	4		7
Lucy's	23	1	3	27	1	1		2
Northern Waterthrush	32	9	57	98	10	4	3	17
American Redstart	203	32	191	426	9	3	54	66
TOTAL	472	55	262	789	23	12	57	92
GRAND TOTAL	1179	127	349	1655	57	28	72	157

TABLE 1-8

SUMMARY OF THE PERCENTAGES OF VAGRANT WARBLER OCCURRENCES IN CALIFORNIA ACCORDING TO LOCATION

	TOTAL FALL AND WINTER OCCURRENCES						WINTER OCCURRENCES ONLY			
	OUTER COAST									
	S.E. FARALLON	OTHER	TOTAL	INTERIOR	EAST SIDE	TOTAL	OUTER COAST	INTERIOR	EAST SIDE	TOTAL
I DEFINITE VAGRANT SPECIES										
Northern California	34.7	56.8	91.5	8.4	0.1	100.0	64.8	35.2	0.0	100.0
Southern California			81.6	8.3	10.0	100.0	52.3	24.6	23.1	100.0
TOTAL			86.7	8.3	5.0	100.0	58.0	29.4	12.6	100.0
II POTENTIAL VAGRANT SPECIES										
Northern California	29.7	58.6	88.3	10.2	1.5	100.0	71.4	28.6	0.0	100.0
Southern California			59.8	7.0	33.2	100.0	25.0	13.0	62.0	100.0
TOTAL			67.0	7.8	25.2	100.0	28.3	14.1	57.6	100.0
ALL VAGRANT SPECIES										
Northern California	33.6	57.2	90.8	8.8	0.4	100.0	65.6	34.4	0.0	100.0
Southern California			71.2	7.7	21.1	100.0	36.3	17.8	45.9	100.0
TOTAL			79.4	8.1	12.5	100.0	44.5	22.5	33.0	100.0

yards from the ocean in the isolated outer windbreaks of Monterey Cypresses! Table 1-8 indicates that the percentages of Southern California Outer Coast occurrences of definite vagrant species is somewhat lower than that for Northern California, about 82%. This is due to two reasons: (1) the absence of a continuously manned island observatory and (2) the presence of many carefully watched East Side desert oases which, like islands in an ocean, are extremely effective in concentrating migrant passerines in basically unsuitable habitat. It is interesting to note that the percentage of occurrences in the Interior is nearly identical in both Northern and Southern California, about 8.3%.

Table 1-8 further indicates that the percentage of winter definite vagrant occurrences on the Outer Coast of both Northern and Southern California is nearly 30% less than the total of fall and winter occurrences. The majority of the percentage increase occurs in Interior areas. This indicates that wintering vagrant warblers may tend to seek more sheltered, food rich areas removed some distance from the typically windy Outer Coast.

The potential vagrant species, also shown in Table 1-8 present an interesting contrast between Northern and Southern California. The percentages of Northern California occurrences in the various areas for these species are very similar to the percentages for definite vagrant species.

This would be expected if these birds are really vagrants in Northern California. In Southern California, however, the percentage of Outer Coast occurrences for potential vagrant species is reduced by about 20% compared to the definite vagrant species. The percentage increase is made up entirely by East Side occurrences, a result that would be expected if some of these birds are normal transients in the desert areas. To ascertain whether this effect occurs in each of the four potential vagrant species, the percentage of Southern California East Side occurrences for each of these species may be compared with the percentage for various definite vagrant species. These data are presented in Table 1-9. The species are arranged according to the percentage of Southern California East Side occurrences. To remove possible sample size errors, only species with over ten Southern California occurrences are included. The result is clear; only the Northern Waterthrush and American Redstart have a significantly high percentage of East Side occurrences in Southern California. The Virginia's and Lucy's Warblers, on the other hand, have a percentage of East Side occurrences that is comparable to such far-eastern definite vagrant species as Black-throated Blue, Blackburnian and Prairie Warblers. Thus, it appears that the occurrences of Northern Waterthrushes and American Redstarts on the East Side are augmented by numbers of normal transients through these areas but that the

TABLE 1-9

PERCENTAGES OF FALL AND WINTER SOUTHERN CALIFORNIA VAGRANT WARBLER OCCURRENCES THAT ARE ON THE EAST SIDE OF THE SIERRA AND HIGHER SOUTHERN CALIFORNIA MOUNTAINS

SPECIES	NO. OF OCCURRENCES IN S. CALIF.	NO. OF OCCURRENCES ON EAST SIDE	% OF OCCURRENCES ON EAST SIDE	
Northern Waterthrush*	98	57	58.2	Some normal transients on east side
American Redstart*	426	191	44.8	
Chestnut-sided	18	4	22.2	Only vagrants on east side
Black-throated Blue	54	11	20.4	
Ovenbird	20	4	20.0	
Black-throated Green	24	3	12.5	
Black-and-white	124	15	12.1	
Magnolia	35	4	11.4	
Lucy's*	27	3	11.1	
Painted Redstart	20	2	10.0	
Blackburnian	22	2	9.1	
Palm	140	12	8.6	
Tennessee	137	9	6.6	
Virginia's*	238	11	4.6	
Blackpoll	176	5	2.8	
Prairie	24	0	0.0	
Canada	17	0	0.0	

* Potential vagrant species

occurrences of Virginia's and Lucy's Warbler are not. (Nor are the occurrences of Black-and-white and Tennessee Warblers, species that need an angle of misorientation of less than 10° to reach southeastern California.) However, this in itself does not indicate that all Northern Waterthrushes and American Redstarts on the Outer Coast of Southern California are vagrant individuals. This will be further discussed below.

Vagrant Occurrences - A Recent Phenomenon?

The extreme paucity of occurrences of vagrant warblers prior to 1962 may be interpreted in light of the extremely localized nature of the occurrences of these birds, with fully 80% of all occurrences being on the Outer Coast. Personal communication with many observers who were active in California during the fifties and early sixties indicates that the Outer Coast was ornithologically neglected until the 1962 discovery of the large numbers of vagrants present in coastal San Diego and Marin Counties. Where were the observers looking during these years? Observations published in Audubon Field Notes during these years indicates that observers were looking in Interior areas such as the Berkeley Hills, the Los Angeles Basin and the Central Valley, areas where vagrant warblers are extremely scarce (only 8% of the occurrences are in Interior areas). If this is indeed the case, then the number of occurrences for any given species prior to 1962 should be proportional to the abundance of that species in Interior areas. This relationship is shown for all definite vagrant species for both Northern and Southern California in Figure 1-2. The result is clear; the more common a species is in the Interior the more often it was recorded prior to 1962. The larger slope for Southern California simply indicates a greater amount of observation there. The Pearson product-moment coefficients of correlation for these relationships are 0.946 for Northern California and 0.951 for Southern California.

On the other hand, if ornithological observations were not biased prior to 1962, then the number of occurrences of a given species prior to 1962 should be proportional to the total number of occurrences of that species in the state. This relationship is shown for all definite vagrant species for both Northern and Southern California in Figure 1-3. The correlation, if any, is very poor. The Pearson product-moment coefficients of correlation are 0.571 for Northern California and 0.472 for Southern California. Thus, it appears that the paucity of vagrant occurrences prior to 1962 was not due to a paucity of vagrants, but rather was due to a paucity of observers in localities favored by vagrants. Whether or not the actual number of vagrants is changing in California can only be determined by long-term

FALL AND WINTER OCCURRENCES OF DEFINITE VAGRANT WOOD WARBLERS IN CALIFORNIA. THE NUMBER OF OCCURRENCES PRIOR TO 1962 AS A FUNCTION OF THE NUMBER OF OCCURRENCES IN THE INTERIOR (AS DEFINED IN CHAPTER 1).

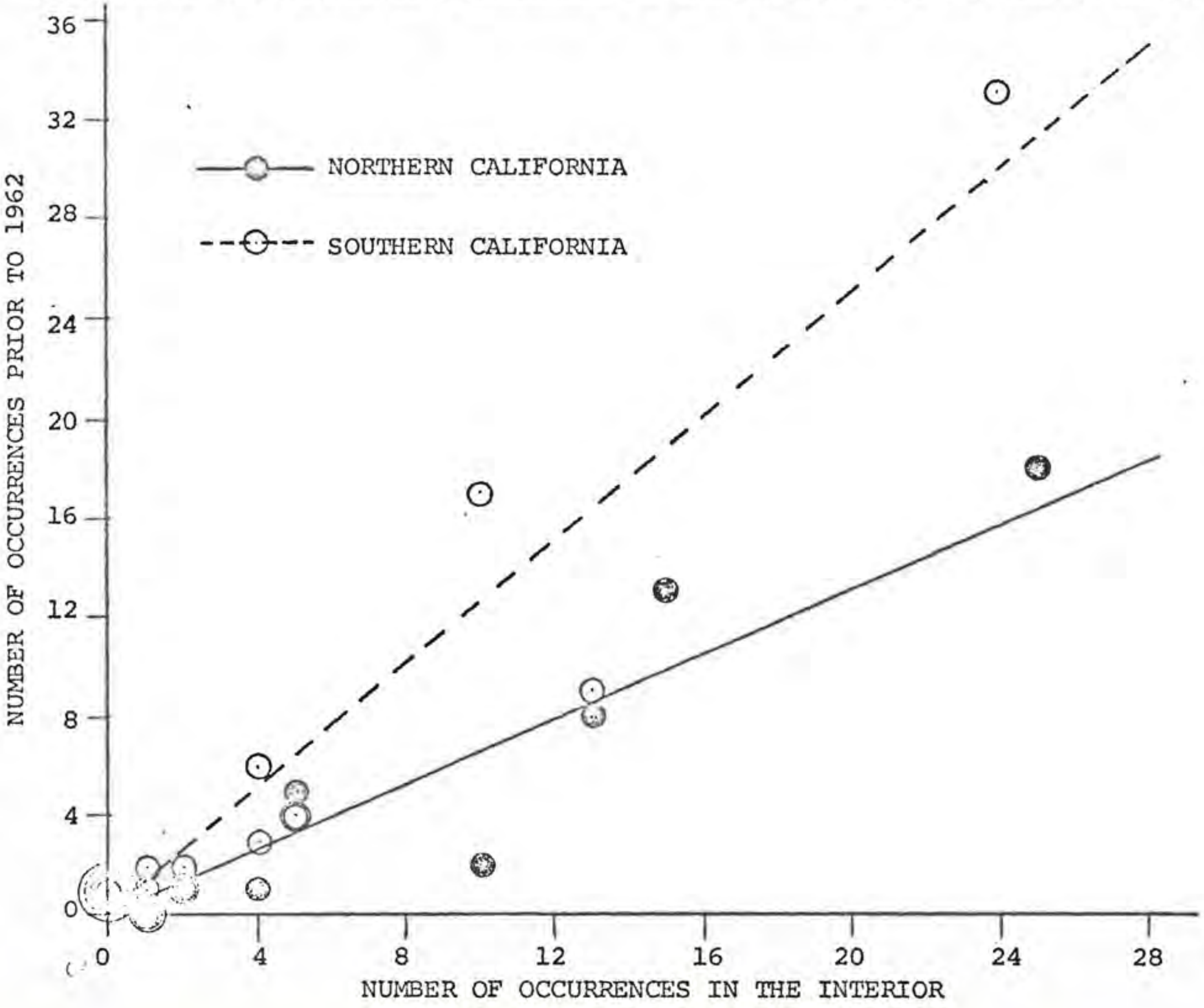
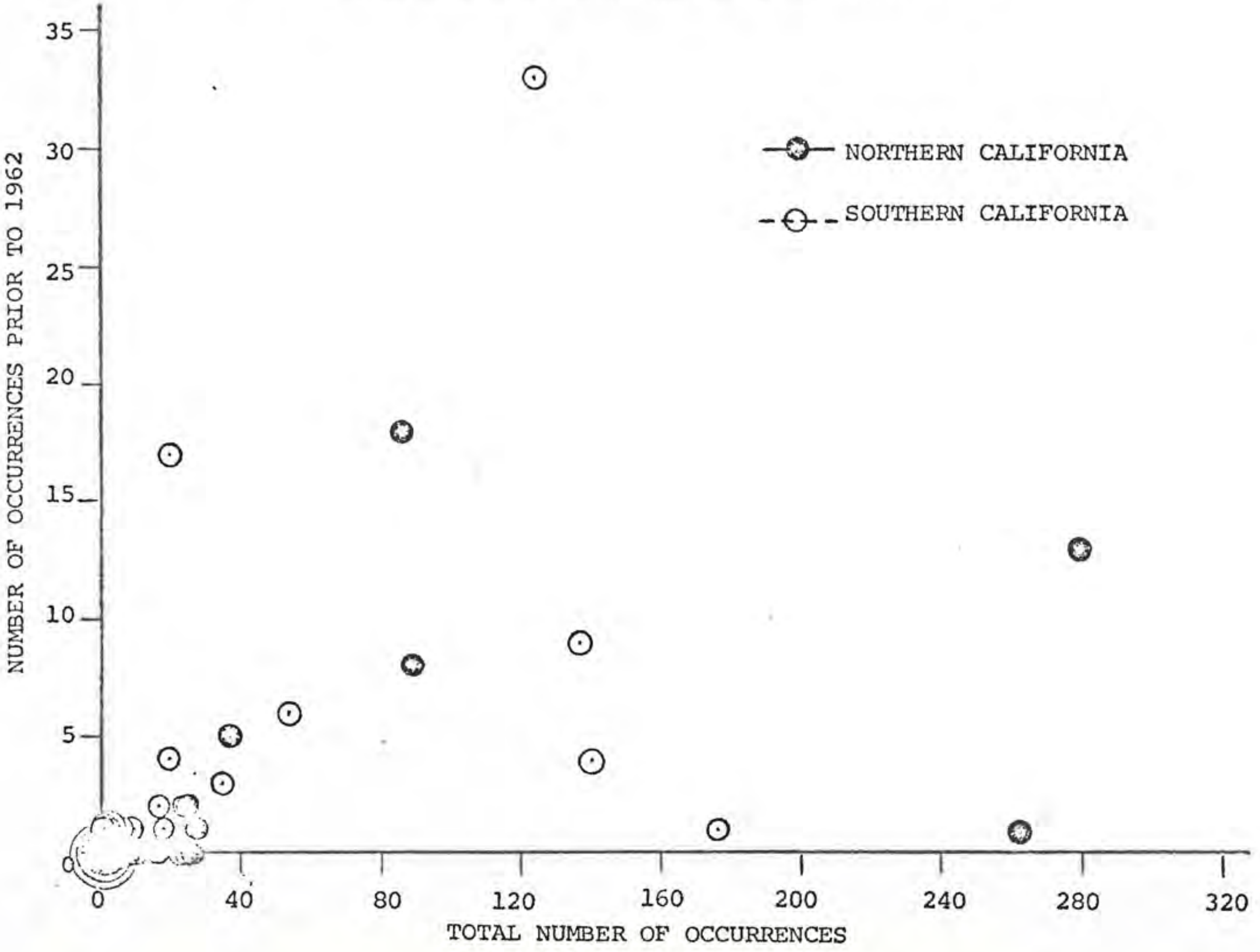


FIGURE 1-2

FIGURE 1-3

FALL AND WINTER OCCURRENCES OF DEFINITE VAGRANT WOOD WARBLERS IN CALIFORNIA. THE NUMBER OF OCCURRENCES PRIOR TO 1962 AS A FUNCTION OF THE TOTAL NUMBER OF OCCURRENCES



systematic censusing of a good vagrant location. Southeast Farallon Island may be ideal for this purpose.

Age of Vagrants

Age data has been obtained on 339 individual vagrant warblers examined in the hand on the Outer Coast of California and on 31 individuals examined in the hand in Interior or East Side areas (Table 1-10). Much of the coastal data have been obtained at Southeast Farallon Island and Palomarin Ranch near Bolinas, Marin County (both courtesy Of the Point Reyes Bird Observatory) and at Point Loma and near Imperial Beach, San Diego County (courtesy of Alan and Jean Craig and Virginia Cochran). Interior and East Side data are meager and have come from a variety of sources. All data have been obtained by the standard method of skull ossification [Stewart, 1972]. The percentage of immatures is very high among coastally captured individuals, between 86 and 91%. The uncertainty is due to the uncertainty of the skull ossification process during October and November [Stewart, 1972]. Of those species having a reasonable sample size, only the American Redstart (and possibly the Chestnut-sided Warbler) has a comparatively low percentage of immatures, about 75%. This indicates that some of the American Redstarts occuring along the coast may, like some of those occurring on the East Side, be normal transients. Note, however, that the Northern Waterthrush as

TABLE 1-10

AGES OF VAGRANT WARBLERS EXAMINED
IN CALIFORNIA DURING THE FALL

SPECIES	OUTER COAST			INTERIOR AND EAST SIDE			TOTAL		
	NUMBER EXAMINED	NUMBER OF IMMATURES	% IMMATURE	NUMBER EXAMINED	NUMBER OF IMMATURES	% IMMATURE	NUMBER EXAMINED	NUMBER OF IMMATURES	% IMMATURE
Black-and-white	10	9	90.0	2	2	100.0	12	11	91.7
Prothonotary				1	1	100.0	1	1	100.0
Worm-eating	1	1	100.0				1	1	100.0
Golden-winged	1	1	100.0				1	1	100.0
Blue-winged									
Tennessee	28	25-27	89.3-96.4	1	1	100.0	29	26-28	89.7-96.6
Virginia's*	9	8	88.9	3	2	66.7	12	10	83.3
Lucy's*	2	1-2	50.0-100.0				2	1-2	50.0-100.0
Parula	1	0	0.0				1	0	0.0
Magnolia	12	9-11	75.0-91.7	2	2	100.0	14	11-13	78.6-92.9
Cape May	4	4	100.0	1	1	100.0	5	5	100.0
Black-throated Blue	12	10	83.3				12	10	83.3
Black-throated Green	5	4-5	80.0-100.0				5	4-5	80.0-100.0
Golden-cheeked	1	1	100.0				1	1	100.0
Cerulean				1	1	100.0	1	1	100.0
Blackburnian	9	8	88.9				9	8	88.9
Yellow-throated	1	1	100.0				1	1	100.0
Grace's									
Chestnut-sided	14	10-11	71.4-78.6	2	2	100.0	16	12-13	75.0-81.3
Bay-breasted	2	2	100.0				2	2	100.0
Blackpoll	85	79-83	92.9-97.6				85	79-83	92.9-97.6
Pine									
Prairie	5	5	100.0				5	5	100.0
Palm	44	39-44	88.6-100.0				44	39-44	88.6-100.0
Ovenbird	11	10	90.9	1	1	100.0	12	11	91.7
Northern Waterthrush*	10	10	100.0	3	3	100.0	13	13	100.0
Louisiana Waterthrush				1	0	0.0	1	0	0.0
Kentucky	1	0-1	0.0-100.0				1	0-1	0.0-100.0
Connecticut	2	2	100.0				2	2	100.0
Mourning	1	1	100.0				1	1	100.0
Hooded	1	1	100.0				1	1	100.0
Canada	2	2	100.0	1	1	100.0	3	3	100.0
American Redstart*	65	48-49	73.8-75.4	12	8	66.7	77	56-57	72.7-74.0
Painted Redstart									
TOTAL	339	291-309	85.8-91.2	31	25	80.6	370	316-334	85.4-90.3
TOTAL IF AMERICAN REDSTART IS ELIMINATED	274	243-260	88.7-94.9	19	17	89.5	293	260-277	88.7-94.5

* Potential vagrant species

well as the Virginia's Warbler have high percentages of immatures on the Outer Coast, comparable to other vagrant species. This suggests that coastal occurrences of these species are most likely to be due to vagrant individuals. When the American Redstart data are eliminated because of the uncertainty of their vagrant status, the vagrant phenomenon on the Outer Coast of California is most certainly (89-95%) an immature phenomenon.

A very high percentage of immatures among normal transients, however, has been indicated for coastal California [Ralph, 1971; Stewart et al., in press] as well as for coastal locations in eastern North American [Robbins et al., 1959; Drury and Keith, 1962; Murray, 1966a; Phillips et al., 1966]. Some of these sources and others [Nisbet et al., 1963; Clench, 1969; Leberman and Clench, 1969], however, indicate that the percentage of immatures drops considerably as one moves more than ten miles inland. Table 1-10 indicates that this is the case for the American Redstart but not for most of the other species. When the American Redstart data are eliminated, the percentage of immatures occurring in Interior and East Side areas remains very high (89%). This supplies strong evidence that the vagrant phenomenon throughout California is primarily attributable to immature birds. Nevertheless, a few adult birds do occur.

Summary

The major characteristics of the fall vagrant warbler phenomenon in California may now be summarized. (1) It is a regularly occurring phenomenon that is very widespread among most species of migrant wood warblers. (2) Different species occur in widely varying numbers. (3) The number of occurrences of each species varies somewhat from year to year. (4) Most of the occurrences are concentrated along the Outer Coast of California but occurrences are frequent in both Northern and Southern California. (5) Most of the individuals involved are immature birds. (6) There is no positive indication that it is a very recently evolved phenomenon.

CHAPTER 2

PREVIOUS SUGGESTIONS ON THE OCCURRENCES OF VAGRANT WARBLERS IN CALIFORNIA - A REVIEW

Grinnell [1922] was among the first to speak of vagrant birds in California. He claimed that, because of the great mobility of birds, the occurrence of the "accidental" was to be expected. He postulated that the role of the "accidental" was one of pioneering, that is, of keeping the species aware of the possibilities for range expansion while simultaneously serving to relieve population pressures. While he thus attempted to explain the effect of the "accidental", he presented no mechanism as to the cause of the "accidental".

In the fall of 1962, field ornithologists discovered that the Outer Coast of California was a concentrating location for vagrant birds [Mans, 1963; Small, 1963]. Observations over the next few years verified the regular nature of these occurrences. Several characteristics of the vagrant phenomenon were soon established: that certain species, often those with more westerly breeding grounds, were more common in California than others; that the bulk of the occurrences were attributable to immature birds; and that the occurrences were concentrated along the Outer Coast of California [Chase and DeBenedictis, 1965; McCaskie and Pugh, 1965]. The idea then became prevalent that some of the more westerly breeding species (including among others, the Blackpoll Warbler, Northern Waterthrush and American Redstart) were establishing or utilizing a limited West Coast migration route. These birds were then referred to as rare migrants rather than as vagrants [McCaskie, 1967, 1968, 1969, 1970a; Chandik and Baldridge, 1968, 1969]. The remainder of the species were still classified as vagrants, or, in the case where they occurred annually, as regular vagrants. No explanation, however, was yet put forth as to the mechanism of these vagrant occurrences.

More detailed analyses of the vagrant phenomenon in California were made by Paxton [1965, 1967]. He left the question of any particular mechanism of vagrancy open but discussed the "oasis" effect of the Outer Coast and indicated a possible correlation between coastal vagrant occurrences and the presence of a high pressure area over the Great Basin or northern Rocky Mountains which would produce easterly winds. He did not, however, feel that the correlation was perfect. McCaskie [1966, 1967], on the other hand, claimed no correlation between the occurrence of vagrants and any local weather conditions in Southern California.

In the fall of 1967, Point Reyes Bird Observatory personnel found that the Farallon Islands, twenty-eight miles west of San Francisco, was an excellent location for concentrating vagrant warblers. Ralph [1968] discussed the Farallon and other Northern California occurrences of vagrant warblers through 1967 and concluded that all of these species, even the more regular ones, were most likely composed of vagrant individuals. He accounted for their occurrences by genetic or physiological aberrations in individual birds that resulted in the complete misdirection of the individual's migration. He further postulated that a random scattering of these birds was the most likely explanation for their occurrences and considered weather effects to be minimal.

The first comprehensive theory for California vagrant warbler occurrences was a theory of drift migration advanced by Bagg [1970]. Using Able's unpublished data on nocturnal passerine migration over Lake Charles, Louisiana, during the fall of 1969, and using daily weather maps for the same period, Bagg hypothesized that an easterly or southeasterly wind flow displaced birds from their normal migration route in Texas or Louisiana and carried them hundreds of miles westward or northwestward to interior points of California or Nevada. He then claimed that subsequent northeasterly winds drifted them to the California coast thereby accounting for the timing of the fall 1969 vagrant occurrences. In the following year Bagg [1971] reiterated this same claim, namely that vagrants reached the California coast by flying downwind. Objections were raised to this theory of drift migration by Chandik et al. [1971] and by McCaskie [1972], primarily on the grounds that many of

California's more common vagrant species (Blackpoll, Palm and Black-throated Blue Warblers) are very rare or casual in Texas to begin with. However, Able [1972] showed a good correlation between some of the fall 1971 California vagrant occurrences and easterly winds and again claimed that a major part of the California vagrant warbler occurrences were due to wind drifted migrants. This wind drift hypothesis was seemingly strengthened by evidence that local wind conditions were paramount in causing good landfalls of vagrant warblers on the Farallon Islands and the coast of Northern California [Chandik et al., 1971; DeSante and Remsen, 1973]. Nevertheless, wind drift alone fails to account for the very different abundances of the various vagrant species in California as were shown in Table 1-3. Why, for example, are there over 400 occurrences of the Palm Warbler as opposed to only 12 for the Bay-breasted Warbler when both species have rather similar ranges and would be expected to be influenced by wind drift in similar ways? Or why are there 91 occurrences of the Black-throated Blue Warbler and only 38 for the Blackburnian Warbler, again species with rather similar ranges? Why has the Prairie Warbler occurred 41 times while all other southeastern species have occurred less than 15 times? Such disparities strongly indicate that something other than wind drift is involved in the vagrant phenomenon.

A different approach to the vagrant phenomenon was attempted by Austin [1971]. He analyzed the timing of the California occurrences of fall (and spring) vagrant warblers and compared this timing to the timing of these species at comparable latitudes on the East Coast of North America. He divided the various vagrant species into four groups based upon their breeding ranges: Group 1 - species breeding east of 100° longitude and south of Canada; Group 2 - species breeding east of 100° but into Canada; Group 3 - species breeding west to the Rocky Mountains; Group 4 - species breeding west of the Rocky Mountains. The comparison of the arrival dates indicated that the birds of Group 1 averaged 36 days later in California than on the East Coast, Group 2 averaged 22 days later in California, Group 3 averaged 15 days later and Group 4 averaged only 5 days later in California than on the East Coast. Based on these data he concluded that the species of Group 4 are regular migrants in California. He thus reiterated the old claim that these birds are establishing or utilizing established migration routes down the West Coast. He applied this same result to several of the more common species of Group 3 but considered the remainder of the birds, because of the later nature of their occurrences in California than on the East Coast, to be truly vagrants. However, he provided no mechanism for this vagrancy except to quote the wind drift theories discussed above. What is incredible in all of this, is that he totally neglected to consider the fact that an eastern bird of Group 3 or 4 has at least three times as far to fly to reach the California coast than to reach the East Coast. Since he made no compensation for this increased distance in determining whether a bird was late, all of his conclusions based on timing must be considered to be invalid. Other criticism of this work can be found in DeBenedictis [1971] and McCaskie [1972].

Several analyses have been undertaken on individual species of the more common vagrant warblers in California. Pulich and Phillips [1953] hypothesized a desert flight line for the American Redstart based on the rather large number of occurrences in the lower Colorado River Valley. Root [1962] doubted a west coast migration route for this species. McCaskie [1970b], however, indicated that this species is a regular transient both on the deserts and along the coast of California. Data presented in Chapter 1 of this dissertation indicates that this may be true for some individuals, but I believe that many of the coastal (at least) American Redstarts are vagrants.

An excellent analysis of the California occurrences of the Northern Waterthrush was presented by Binford [1971]. He considered all of the coastal individuals of this species to be vagrants but indicated that many of the East Side occurrences were due to regular transients. These conclusions agree well with the data presented in Chapter 1.

In addition, he hypothesized that the Sierra Nevada serves as an effective barrier to westward migrating vagrants tending to concentrate them on its eastern flank. Subsequent flights tend to carry the birds across the Sierra and Central Valley so that they concentrate next on the Outer Coast. Such a hypothesis can explain the extreme paucity of vagrant occurrences in the Sierra and Central Valley. Unfortunately he supplies no mechanism for this westward vagrancy.

McCaskie [1970c] has analyzed the California occurrences of the Blackpoll Warbler. He discusses and rejects the hypotheses of random scattering, the establishment of a West Coast migration route, a direct line flight from Alaska to California and wind drift. He favors the hypothesis of a "mirror-image" reversed migration based primarily upon radar data showing the occurrences of 180° reversed migrations. Under his hypothesis, the vagrant Blackpoll Warbler, instead of migrating first eastward and then southward, migrates "first westward and then southward", a hypothesis analogous to that proposed by Rabøl [1969a] in explaining the westward vagrancy of several Old World warblers (Sylvidae). However, neither McCaskie nor Rabøl present any mechanism to account for such a reversed migration except to quote possible correlations between reversed migration and high temperatures during the fall [Baird et al., 1959; Nisbet, 1962]. It will become apparent from Part II of this study that McCaskie has confused 180° reversed migration and true mirror image migration.

The most recent comprehensive analysis of vagrant warblers in California is provided by DeBenedictis [1971] who has made several valuable contributions to this subject. First, he has shown that the pattern of species abundance in California can be largely explained by the size of the source populations. This result indicates that the vagrant phenomenon may be common to all species of warblers and not a special characteristic of certain species. He has also shown that the next most likely factor determining the relative species abundances in California is the amount of deviation from the normal migration route necessary to get each species to California. He notes, however, that this does not explain the relative abundance of certain exceptionally numerous species in California -- the Palm, Black-throated Blue and Prairie Warblers. He further claims that the pattern of abundance of these vagrants is "the result of passive phenomenon -- the failure of organisms to be perfect navigators". Unfortunately, he does not provide any insight into the cause of this failure. Finally he presents valid criticism of Grinnell's [1922] claim that vagrant birds are in some sense "pioneers". This aspect of the problem will be further discussed in Part IV of this dissertation.

CHAPTER 3

THE PRESENT STUDY - AN INTRODUCTION

It is clear from the preceding chapter that none of the previous "explanations" of the vagrant warbler phenomenon in California are completely satisfactory. Several of the preceding theories are inconsistant within themselves, most are contradictory to one another and, more importantly, none are truly mechanistic in their approach. The purpose of the present study is to present and test a comprehensive, mechanistic theory of vagrancy in immature North American wood warblers.

The present study is basically divided into two major parts. The first is theoretical in its approach. Based upon what is known of the migratory behavior of wood warblers and upon what is known of nocturnal migration in general and "distance-and-direction" nocturnal migration in particular, a generalized theory of the first fall migration of an immature warbler is presented. Next, all of the possible errors in such a system are outlined in detail. Finally, all of the fall and winter occurrences of vagrant wood warblers in California are analyzed in terms of the various species abundances and in terms of the locations and timing of the occurrences within the state to determine which of the possible errors inherent in the migratory system of the immature warbler is responsible for the vagrant phenomenon.

The second part of this study is experimental in its approach. Over 500 nocturnal orientation experiments, using the "footprint" technique [Emlen and Emlen, 1966], were conducted on 24 individual California captured Blackpoll Warblers, one of the most common vagrant species. The data from these experiments are analyzed to determine whether Blackpoll Warblers are capable of demonstrating preferred directions, and, if so, to determine what directions are chosen. These results are then used to test the theoretically proposed mechanism of vagrancy.

During the early stages of this experimental program, it became apparent that many of the Blackpoll Warblers showed multimodal behavior, either during a single night's experiment, or, more often, over several night's tests. Mathematical and statistical techniques for handling such multimodal circular data are not available in the literature. Therefore several new techniques are presented.

The concluding part of this study is a discussion of the mechanism of vagrancy in immature wood warblers in terms of its evolutionary implications. The possibility of its general applicability to other groups of birds is discussed. Finally, a brief discussion of fall vagrancy in adult birds is presented.

PART II

A THEORETICAL APPROACH

CHAPTER 4

THE WOOD WARBLER - A REVIEW

The wood warblers, with very few exceptions, form a compact, easily recognized group of small, brightly-colored, active, insectivorous birds of the family Parulidae. This family, which also includes the nectar-eating bananaquits and conebills [Peters, 1968], forms a single group in the broad assembledge of New World nine-primaried oscines [Austin, 1961]. This assembledge is indeed a large one, and, in addition to the Parulidae, includes the various icterids (Icteridae), tanagers (Thraupidae) and New World finches (Fringillidae) as well as several small, rather obscure, neotropical groups. The closely related nature of all of these birds is attested to by the difficulty of classifying many of the "borderline" genera. Some systematists have suggested lumping all New World nine-primaried oscines into one or a few great "families", a scheme apparently based on the assumption that they are all of common ancestry, an unprovable proposition at best [Griscom and Sprunt, 1957]. Regardless of the overall details of classification, it is generally recognized that the complex of New World nine-primaried oscines is of relatively recent neotropical origin [Mayr, 1946]. The wood warblers themselves have received extensive treatment by Chapman [1917], Bent [1953] and Griscom and Sprunt [1957].

About half of the approximately 109 species of wood warblers are migratory, breeding in temperate areas of North America and wintering, for the most part, in the neotropics. This migratory assembledge is characterized by a relatively high degree of sexual dimorphism, and, in many species, by the presence of a rather distinct alternate or breeding plumage, especially in males. In contrast, the sedentary tropical members of the family are generally sexually monomorphic and never exhibit a specialized breeding plumage. These differences are presumably a direct effect of migratory behavior and the resulting annual necessity of establishing a temporary breeding territory.

The large number of closely related species among these migratory warblers may be considered to be indicative of a high degree of adaptive radiation within the group and may attest to a very recent origin of many of the forms. In fact, several writers [Mengel, 1964; Hubbard, 1969] have proposed theories of speciation in certain of these forms as a result of glaciation during the latter part of the Pleistocene. While such theories of speciation are, no doubt, well founded, they neglect to consider the role of migration and the effect of selection on the winter grounds and, thus, are incomplete. It is hoped that some of the ideas presented in this dissertation will be considered by future investigators of speciation in North American wood warblers.

Some characteristics of the migratory behavior of North American wood warblers are important for the development of this discussion. It is well known that all wood warblers are predominantly or exclusively nocturnal migrants. The advantage of nocturnal migration in passerines is apparently due to the immediate necessity for food rather than sleep at the culmination of a migratory flight [Lincoln, 1950]. A vast amount of data from banding operations and radio and TV tower kills indicates that warblers are capable of storing large quantities of subcutaneous fat during their migratory period. This fat serves as fuel for the long migratory flights [Odum et al., 1961] and it is this fat that must be replenished during the stopovers in migration. These stopovers have been estimated for various passerines to range from about 1.5 to 5.5 days [Stack and Harned, 1944; Borror, 1948; Wolfson, 1954; West and Peyton, 1972; DeWolfe et al., 1973]. Apparently the length of the stopover time is less during the latter part of a bird's spring flight than at other times [Lincoln, 1950] a result that may be correlated with the relative day length available for feeding and resting. An average stopover time for wood warblers during the course of a fall overland migration may be estimated to be about four days.

As pointed out by Mengel [1964], warblers are considerably more abundant, widespread and diversified in eastern deciduous forest or northern coniferous forest habitats (eastern species) than in western montane forest habitats (western species). The migration routes of western species generally follow the NW-SE axis of the major western cordilleras from montane breeding grounds in western North America to montane wintering grounds in Mexico or northern Central America. None of the western species need to habitually make an overwater crossing during the course of their migration (although some may cross the Gulf of California from southern Baja to western Mexico [DeSante, MS]). The use of landmarks, such as mountain masses, as an aid to navigation may therefore be important in western species. In marked contrast most individuals of virtually all eastern species make an extensive overwater crossing. Only the Pine Warbler which winters entirely in southeastern U.S. and the Orange-crowned Warbler (basically a western species) are the exceptions. Thus, a navigation system that can operate without the use of landmarks (such as a celestial or geophysical system) is of paramount importance for eastern species.

The location of this overwater crossing can be conveniently used to divide the eastern warblers into three groups (Table 4-1). The first group includes species that tend to migrate southward to the Gulf Coast of United States, and then make an overwater crossing to eastern or southern Mexico, Central America or northwestern South America. These species tend to avoid the South Atlantic

TABLE 4-1

PRIMARY FALL MIGRATION ROUTES* OF

EASTERN WOOD WARBLERS

TRANS-GULF (SOUTHWARD)	TRANS-ATLANTIC (SOUTHEASTWARD)	
TO CENTRAL AMERICA OR NW SOUTH AMERICA	TO WEST INDIES OR NE SOUTH AMERICA	BOTH TRANS-GULF AND TRANS-ATLANTIC
PROTHONOTARY	BACHMAN'S	BLACK-AND-WHITE
WORM-EATING	ORANGE-CROWNED**	SWAINSON'S
GOLDEN-WINGED	CAPE MAY	PARULA
BLUE-WINGED	BLACK-THROATED BLUE	MYRTLE
TENNESSEE	BLACKPOLL	YELLOW-THROATED
NASHVILLE	KIRTLAND'S	PINE**
YELLOW	PALM	OVENBIRD
MAGNOLIA	CONNECTICUT	NORTHERN WATERTHRUSH
BLACK-THROATED GREEN		LOUISIANA WATERTHRUSH
CERULEAN		YELLOWTHROAT
BLACKBURNIAN		AMERICAN REDSTART
CHESTNUT-SIDED		
BAY-BREASTED		
KENTUCKY		
MOURNING		
YELLOW-BREASTED CHAT		
HOODED		
WILSON'S		
CANADA		

* Data obtained from Chapman [1917], Bent [1953], American Ornithologists' Union [1957], Griscom and Sprunt [1957], Bond [1961] and Robbins et al. [1966].

** Does not make an overwater crossing.

Coast of the United States and the West Indies and include the majority of the eastern warblers. Evidence for such a trans-Gulf migration route has been supplied by Lowery [1945] and Stevenson [1957]. I will refer to species that primarily use this route as "Gulf Coast" species.

A second group includes species that tend to migrate <u>southeastward</u> to the Atlantic Coast of eastern or southeastern United States or Florida and then make an overwater crossing to the West Indies or northeastern South America. These species tend to avoid the Gulf Coast of the United States as well as mainland Mexico and Central America. Strong evidence for such a route in the Blackpoll Warbler has been put forth by Nisbet [1970] over prior objection to such a route by Murray [1965]. I will refer to species primarily using this route as "Atlantic Coast" species. A third group may be defined which includes several, often widely-distributed, species of eastern warblers which appear to regularly use both the trans-Gulf and the trans-Atlantic route, although different populations are most likely involved [Taylor, 1972].

Displacement experiments on wintering Northern Waterthrushes in Venezuela showed that 100% (of 4) adults returned from displacements of 10-65 kilometers while 100% (of 14) immatures did not return [Schwartz, 1963]. If, as is likely, such behavior is typical of wood warblers, then it can be assumed that immature warblers on their first fall migration do not navigate in the strictest sense of the word (i.e., bicoordinate navigation) but follow a "distance-and-direction" or "simple orientation" type of migratory system. The details of such a migratory system will be outlined in the following chapter. A summary of the important characteristics of wood warblers that were discussed in the present chapter is presented in Table 4-2.

TABLE 4-2

A SUMMARY OF SCME IMPORTANT CHARACTERISTICS OF WOOD WARBLERS

NEW WORLD, NINE-PRIMARIED OSCINES OF RELATIVELY RECENT NEOTROPICAL ORIGIN

MORE WIDESPREAD, COMMON AND DIVERSE IN EASTERN NORTH AMERICA

NOCTURNAL MIGRANTS CAPABLE OF STORING LARGE QUANTITIES OF SUBCUTANEOUS FAT

MOST INDIVIDUALS OF ALL EASTERN SPECIES (EXCEPT PINE AND ORANGE-CROWNED WARBLERS) MAKE AN OVERWATER CROSSING:

A] "TRANS-GULF" TO CENTRAL AMERICA OR NORTHWESTERN SOUTH AMERICA

or

B] "TRANS-ATLANTIC" TO THE WEST INDIES OR NORTHEASTERN SOUTH AMERICA

IMMATURES APPARENTLY USE A "DISTANCE-AND-DIRECTION" TYPE OF ORIENTATION ON THEIR FIRST FALL MIGRATION

CHAPTER 5

A GENERALIZED THEORY OF DISTANCE-AND-DIRECTION MIGRATION APPLICABLE TO THE IMMATURE WOOD WARBLER

The differences between true bicoordinate or goal navigation and simple distance-and-direction or compass orientation have been outlined by many authors and succinctly summarized by Matthews [1968]. The fundamental difference lies in the fact that a bird using true navigation is capable of correcting for displacement from either its migration route or its "home", whereas a bird using simple orientation is not. True navigation, therefore, involves some "knowledge" of the coordinates of its "home" or goal location, some "knowledge" of the coordinates of its present or "release" location, and the ability to determine and follow a route between the two locations. On the other hand, simple orientation involves only the ability to successfully follow a given compass direction for a given distance.

Experiments designed to show true navigation include a multitude of work on homing pigeons summarized by Wallraff [1967] as well as a formidable array of experiments involving the displacement of adult birds from their breeding or wintering grounds summarized by Matthews [1968]. Despite the success of these experiments in indicating an amazing ability to return to the "home" location in a relatively short period of time, no single mechanism or even the use of any single cue accounting for bicoordinate navigation can be considered to be unambiguously proven [Griffin, 1969; Bellrose, 1972; Schmidt-Koenig, 1972; Wagner, 1972; Walcott, 1972].

Evidence that migrating birds use a true bicoordinate navigation system in passing between their breeding and wintering grounds is likewise circumstantial. It is based primarily upon the well known ability of adult birds to faithfully breed in the exact same location (even the same tree!) and to return to the exact same wintering location year after year [Dorst, 1962]. Supplementary evidence has been supplied by experiments showing that adult birds have the ability to return to their proper breeding or wintering grounds after being artificially displaced from their normal migration route [Rupple, 1944; Bellrose, 1958; Perdeck, 1958, 1967; Wolff, 1970]. These experiments have also shown the <u>inability</u> of immature birds to correct for these displacements. As clearly discussed by Matthews [1968], these experiments indicate that the immature bird maintains its original direction and proceeds for roughly the appropriate distance before terminating its migration. Thus has come the generally accepted hypothesis that immature birds, at least in their first fall migration, use a distance-and-direction type of simple orientation while adults make use of some (as yet unknown) mechanism of true navigation. The displacement experiments on Northern

Waterthrushes, quoted in the preceding chapter [Schwartz, 1963], indicate that this hypothesis may quite accurately apply to North American wood warblers. In contrast to the above widely accepted idea, Evans [1968] and Rabøl [1969b, 1970] have indicated that certain immature passerines, primarily Old World warblers (Sylvidae), may be capable of correcting for artificial or wind displacements. I do not feel, however, that their techniques or sample sizes provide conclusive evidence to support their claims.

Fortunately, a great deal more is known about the possible mechanism and cues used by birds utilizing a distance-and-direction migration system than is known about true navigation. In distance-and-direction migration, the distance that a bird migrates is fundamentally dictated by the length of time that the bird is "physiologically ready" to migrate. This "physiological readiness" is expressed in a nocturnal passerine migrant in two ways: (1) by the timing and duration of a nocturnal migratory urge which may be expressed in a captive individual by nocturnal restlessness or Zugunruhe and (2) by the timing and duration of the ability to store subcutaneous fat, the fuel for migratory flights. Gwinner [1972] has conclusively shown that the timing and duration of this "physiological readiness" is based, at least in long distance migrants, on an endogenous circannual rhythm. He has further indicated that the duration of this physiological readiness roughly corresponds to the length of time necessary for the bird to complete its migration to its winter range. Emlen [1969a] has indicated that in the Indigo Bunting, a nine-primaried New World oscine, this physiological readiness may be controlled by the experimental manipulation of the bird's photoperiod. There is, therefore, every reason to believe that the distance of the first fall migration of the immature wood warbler may likewise be controlled by an endogenous temporal rhythm.

The direction that a distance-and-direction migrant chooses for its first fall migration is apparently genetically inherited. However, the bird must be able to relate this inherited direction to its external environment (the surface of the earth) by means of some reference point or external cue. Considerable evidence is available to show that diurnal migrants can use the time-compensated position of the sun as an effective solar compass, even if they cannot use it as a means of true navigation [Matthews, 1968; Griffin, 1969; Bellrose, 1972; Schmidt-Koenig, 1972; Walcott, 1972]. The ability of nocturnal migrants to determine their appropriate migration direction by means of celestial cues has been indicated in a variety of species [Kramer, 1949; Sauer and Sauer, 1960; Hamilton, 1962a, b; Sauer, 1963; Mewaldt et al., 1964; Emlen, 1967a]. It was conclusively proven, however, when Emlen [1967b] showed that Indigo Buntings that demonstrated directional preferences under the night sky, continued to orient correctly under an artificial planetarium sky set for local conditions, reversed their directions when the north-south axis of the planetarium sky was reversed 180°, and lost their ability to orient when the planetarium stars were turned off and the dome was diffusely illuminated.

Emlen then devised experiments to isolate the cues used in celestial orientation. His early experiments along these lines met with little success but did show the important result that Indigo Buntings were not relying upon a bicoordinate navigation system (as claimed by Sauer and Sauer [1960] for three Old World warblers) nor were they employing a time-compensated star compass such as required for simple sun compass orientation [Emlen 1967c]. Instead they seemed to be responding to Gestalt stimuli provided by the star pattern alone. In a more recent series of very elegant experiments, Emlen [1969b, 1970a, 1972] has provided strong evidence that the stationary point of the rotating star sphere (celestial north) serves as the reference point or external cue to which an Indigo Bunting relates its migratory direction, and that this reference point is learned during the first month or two of the young bunting's life. Emlen has hypothesized [1972] that the immature buntings are predisposed to respond to the apparent rotational motion of the night sky but come to concentrate their attention on areas of relatively slow rotation, thereby coming to rely upon the circumpolar sky area. I prefer to state this hypothesis in an alternate way, namely, that the immature bunting's sightings of the night sky, at various times during a single night and at various times over several nights, tend to be imprinted upon the bird's memory but that consistant reinforcement of this imprinting only occurs over that area of the sky where the amount of movement is small, that is, over the circumpolar area.

The fact that various New World, nine-primaried, nocturnally migrating oscines have been shown to be able to orient their migratory activity according to celestial cues does not prove that these birds are incapable of using other cues. Griffin [1969] has pointed out that the occurrence of migratory orientation under and, in some circumstances, inside of an opaque overcast has been conclusively shown by many adequate radar studies. In the same paper, he discusses various non-celestial cues that could be useful for simple orientation including visual cues from the earth's surface, inertial navigation, acoustic cues, air currents and a sensitivity to the earth's magnetic field. Of these various possibilities, only the last has received considerable experimental attention. Recent data provide strong evidence that at least some birds, including Ring-billed Gulls [Southern, 1969, 1972], pigeons [Keeton, 1971, 1972] and European Robins [Wiltschko, 1972], are capable of directional response with respect to the earth's magnetic field. Wiltschko [1972] has, in addition, provided an intriguing hypothesis that these birds can use the angle between the gravity vector and the magnetic field direction as a reference point for north. Whether North American nine-primaried oscines are capable of using geomagnetic information has not been proven, and, in the case of the Indigo Bunting, has been doubted by Emlen[1970b]. Nevertheless, the question should not be considered to be settled.

It may be reasonable to assume that, if magnetic cues are used by an immature warbler to determine a reference point, these cues may be learned in a way analogous to the way in which the immature bunting learns the celestial reference point. With either celestial or magnetic cues, therefore, the orientation of migration for an immature warbler may be a combination of an inherited direction and a learned reference point to which the inherited direction is related. Whether celestial north or magnetic north may be the reference point for the immature warbler does not substantially effect the arguments I wish to pursue. Therefore, for the time being, let us concentrate on celestial cues.

Emlen [1969a] has pointed out that since migration is a two way journey, we must expect the seasonal reversal of the preferred migratory direction. The migratory direction may, therefore, be considered as a line on a compass having both positive and negative vector directions. The positive direction, D^+, may be considered to be the forward or fall migratory direction while the negative direction, D^-, may be considered to be the reverse or spring migratory direction. The relationship between the two directions for some birds (but certainly not for all species) may be approximately $D^-=D^++180°$. Emlen [1969a] showed that, for the Indigo Bunting, the choice of the sign of the preferred direction is solely dependent upon the physiological state of the bird and is not a function of environmental factors such as the particular sky pattern. While we may accept this as applying to the overall seasonal direction of migration (that is south or north, + or -), a wealth of radar and observational data clearly shows the existence of occasional and, at times, substantial reversed migration [Nisbet and Drury, 1968; Eriksson, 1970; Richardson 1970, 1971, 1972]. These must be considered to be relatively short-term effects and are most likely correlated with the wind direction, an environmental factor. A growing body of evidence [Lowery and Newman, 1966; Gauthreaux and Able 1970; Richardson 1970, 1971, 1972] indicates that most passerines consistantly tend to fly downwind. That such behavior may be energetically, if not evolutionarily, advantageous can be surmised if one imagines the energy expenditure vs. progress curve of an eight gram warbler flying into a thirty knot headwind. It is important to realize that the acceptance of downwind migration does not necessarily imply that the birds' migrations are entirely controlled by the wind directions but rather could imply that winds not aligned with the inherited migratory direction tend to inhibit migration while winds aligned with the proper migratory direction tend to stimulate migration. Thus, while the ultimate timing of the bird's migration depends on the timing of its physiological readiness, the proximate timing of individual flights depends upon environmental factors.

The wind or other weather factors may not be the only environmental factors influencing the proximate timing of migration. It is also likely that the actual fat accumulation of an individual bird must reach some theshold level to be sufficient to initiate a night's flight. This threshold is very likely to be variable throughout the migratory period. Since the actual fat accumulation is dependent to some extent upon the quantity and availability of food, it can also be considered to be an environmental variable.

In summary, the following conditions may be necessary for the successful distance-and-direction migration of an immature wood warbler. If the nature, timing and duration of the warbler's physiological migratory readiness is correct and if it has inherited the correct direction and has correctly learned the external reference point to which to relate its direction, and furthermore if it has been able to find sufficient food to store fat and has been exposed to and chosen the correct winds, then the warbler will complete its migration at some point within the winter range of the species and, therefore, will have completed a successful migration. A summary of these factors, physiological, inherited, learned and environmental, necessary for a successful distance-and-direction migration for an immature wood warbler is presented in Table 5-1.

TABLE 5-1

FACTORS NECESSARY FOR A SUCCESSFUL DISTANCE-AND-DIRECTION MIGRATION FOR AN IMMATURE WOOD WARBLER

FACTOR	TYPE
CORRECTLY TIMED "MIGRATORY READINESS" OF THE PROPER DURATION	PHYSIOLOGICAL
CORRECT MIGRATORY DIRECTION	INHERITED
CORRECT SIGN (FORWARD OR REVERSE, SPRING OR FALL) TO THE MIGRATORY DIRECTION	PHYSIOLOGICAL
CORRECT REFERENCE POINT FROM WHICH TO RELATE THE MIGRATORY DIRECTION	LEARNED
WINDS IN ROUGHLY THE CORRECT DIRECTION	ENVIRONMENTAL
SUFFICIENT FOOD TO ACCUMULATE THE NECESSARY QUANTITIES OF SUBCUTANEOUS FAT	ENVIRONMENTAL

CHAPTER 6

POSSIBLE ERRORS INHERENT IN A DISTANCE-AND-DIRECTION MIGRATION OF AN IMMATURE WOOD WARBLER

The fundamental factors controlling the distance-and-direction migration of an immature wood warbler were outlined in the previous chapter. The various possible errors that could arise in such a migratory system may now be investigated. First of all, it is important to note that since the distance-and-direction type of migratory system is not a time-compensated system, errors in the timing or duration of the physiological readiness for migration will not directly affect the orientation of the warbler's first migration. They will, however, directly affect the location where the bird will attempt to winter since such errors directly affect the distance flown. For example, errors in the duration of the warbler's migratory readiness could cause the bird to winter either north or south of its normal winter range depending upon whether the duration is too short or too long.

A summary of the possible direction or orientation errors inherent in the first fall migration of an immature warbler is presented in Table 6-1. As shown in this Table, errors in orientation may be classified into two main types: (1) errors producing <u>disorientation</u> and (2) errors producing <u>misorientation</u>. These two types of errors are fundamentally different in both mechanism and result but, unfortunately,

TABLE 6-1

SUMMARY OF POSSIBLE ORIENTATION ERRORS IN THE DISTANCE-AND-DIRECTION MIGRATION OF AN IMMATURE WOOD WARBLER

I ERRORS PRODUCING DISORIENTATION

MECHANISM	RESULT	TIMING
FAILURE TO INHERIT ANY DIRECTION	FLIES IN RANDOM DIRECTIONS OR DRIFTS DOWNWIND	LATE
FAILURE TO LEARN ANY REFERENCE POINT TO WHICH TO RELATE THE INHERITED MIGRATORY DIRECTION	FLIES IN RANDOM DIRECTIONS OR DRIFTS DOWNWIND	LATE

II ERRORS PRODUCING MISORIENTATION

MECHANISM	RESULT	TIMING
FAILURE TO INHERIT THE CORRECT MIGRATORY DIRECTION.	SIMPLE MISORIENTATION: FLIES IN INCORRECT DIRECTION (ALL DIRECTIONS ARE POSSIBLE)	ON TIME
FAILURE TO EXHIBIT THE CORRECT SIGN (FORWARD OR REVERSE, FALL OR SPRING) TO THE MIGRATORY DIRECTION	180° REVERSE MISORIENTATION: FLIES IN REVERSE (180°) DIRECTION FROM CORRECT DIRECTION	ON TIME
FAILURE TO RELATE THE MIGRATORY DIRECTION TO THE REFERENCE POINT BY THE CORRECT SENSE (POSITIVE OR NEGATIVE, CLOCKWISE OR COUNTER-CLOCKWISE, RIGHT OR LEFT)	MIRROR IMAGE MISORIENTATION: FLIES IN MIRROR IMAGE (WITH RESPECT TO THE AXIS OF THE REFERENCE POINT, THE N-S AXIS) OF CORRECT DIRECTION.	ON TIME
FAILURE TO LEARN THE CORRECT REFERENCE POINT TO WHICH TO RELATE THE INHERITED MIGRATORY DIRECTION	SIMPLE MISORIENTATION IF INCORRECT REFERENCE POINT IS STATIONARY: FLIES IN INCORRECT DIRECTION (ALL DIRECTIONS ARE POSSIBLE)	ON TIME
	REFERENCE POINT MISORIENTATION IF INCORRECT REFERENCE POINT IS NON-STATIONARY: FLIES IN INCORRECT ARCS (ALL ARCS ARE POSSIBLE)	SOMEWHAT LATE

have often been used interchangeably in many of the previous studies discussed in both Chapters 2 and 5. In order to alleviate this confusion, I now define *disorientation* to be the *inability of an individual to consistantly follow any direction*. As such, disorientation may be considered to be the opposite or lack of orientation. I then define *misorientation* to be the *inability of an oriented bird to follow the correct direction*. Misorientation, therefore, simply implies an incorrect orientation.

Disorientation errors may arise by one or both of two mechanisms: (1) the failure of the individual warbler to have inherited any direction or (2) the failure of the bird to have learned a reference point to which to relate its inherited direction. A warbler that has no inherited direction but has learned a reference point will be capable of following a given direction for an entire night's flight (or more) but will have no predisposition to choose any particular direction. It is likely that such a bird would fly for a given night in a certain randomly chosen direction and then fly, on subsequent nights, in other independent randomly chosen directions. The path of such a bird may be likened to a diffusion process with a jump distance of a single night's flight, perhaps 200 miles. Such a bird would appear to be oriented on a given night's flight but will be disoriented over several night's flights. If, however, the bird imprints on and reinforces the directions randomly chosen on the first few flights, its behavior would change from disorientation to orientation (or misorientation).

If a warbler fails to learn a reference point to which to relate its inherited direction, it will always be disoriented. It will be able to follow a given randomly chosen direction only as long as its inertial guidance system (if any) allows it to maintain its course. It is likely that each night's flight will begin in some randomly chosen direction and soon decay into some kind of arc or spiral-like curve. In the absence of any inertial guidance system, each night's flight will appear totally erratic and haphazard.

The path of a disoriented warbler, as just presented, may be oversimplified due to the lack of consideration of the wind. As summarized in Chapter 5, most passerine migrants tend to fly downwind. It, therefore, seems likely that a disoriented warbler, either one that has no inherited direction or one that is unable to relate its direction to a reference point, will simply drift downwind at whatever direction the wind takes on each night of its flight. Statistically, the distribution of such birds, during and after their fall migration, will be determined entirely by the distribution of wind directions on their breeding ranges and over their subsequent wind drifted migration routes.

Another important result of disorientation concerns the timing of a disoriented bird along its wind drifted route.

Since the bird's migration path over many night's flights will not approximate a straight line (unless the wind is consistantly in the same direction) it will take the bird longer to reach any randomly chosen point away from its starting point than if it had flown there in a straight line. Thus, the timing of arrival at any location away from the starting point will average later for a disoriented than for an oriented bird.

Table 6-1 indicates that misorientation errors can arise by any one of four mechanisms. The first is straightforward: the failure of the individual warbler to inherit the correct migratory direction. The result is equally straightforward, the bird simply follows an incorrect orientation. It should be noted that any and all directions are possible for any given individual warbler, although as pointed out by DeBenedictis [1971], smaller angles of misorientation may be more likely than larger angles. Errors of this type will be referred to as simple misorientation.

A second mechanism of misorientation is the failure of an individual warbler to exhibit the correct sign (that is forward or reverse, fall or spring) to its migratory direction. Such an error will cause the bird to follow the reverse or spring migratory direction on its first fall flight. Many species of birds, including most warblers, have nearly identical spring and fall migratory routes. In these species, the spring direction is roughly 180° reversed from the fall direction. Errors of this type will, therefore, be referred to as _180° reversed misorientation_.

The third mechanism of misorientation is more subtle. Two pieces of information are necessary in order to relate an inherited direction to an external compass reference point: (1) a certain angle and (2) a sense to that angle, either positive (clockwise or right) or negative (counterclockwise or left). A wrong angle gives rise to the simple misorientation discussed above. The wrong sense, however, gives rise to a special kind of misorientation that causes the bird to follow a direction that is a mirror image (across the axis of the compass containing the reference point) of the correct direction. If the reference point is assumed to be celestial north, this error will cause the immature warbler to follow the mirror image, across the N-S axis, of the correct direction. Thus, an immature warbler that should fly SE (135° measured clockwise from true north) will fly SW (135° measured counterclockwise from true north). Errors of this type will be referred to as _mirror image misorientation_. Two important boundary conditions concerning mirror image misorientation should be pointed out. First, if the correct direction of an individual warbler is due north or south (actually any multiple of 180° or pi radians away from the reference point) mirror image misorientation decays into correct orientation. Second, if the correct direction lies due east or west (actually any odd multiple of 90° or pi/2 radians away from the reference point) mirror image misorientation becomes identical to 180° reversed misorientation.

One final characteristic is common to all three of these types of misorientation, the timing of the misoriented bird. Since the migration route of such a bird will roughly approximate a straight line, it will arrive at any point a given distance from its starting point at the same time that an oriented bird on the correct route would arrive at this same distance from its starting point, provided they both started at the same time. These types of misoriented birds, therefore, arrive <u>on time</u>, a basic characteristic by which they can be distinguished from disoriented birds.

A fourth mechanism of misorientation is the failure of an individual warbler to learn the correct reference point to which to relate its inherited direction. If the incorrect reference point is non-celestial and stationary with respect to the correct reference point, the result will be <u>simple misorientation</u>, identical and undistinguishable from the simple misorientation caused by inheriting an incorrect migratory direction. However, any celestial reference point other than the correct one (celestial north) will be non-stationary and will move, both during the course of a single night and over the course of several nights. The path of such a misoriented warbler will, therefore, be a series of arcs, the curvature of which will be proportional to the distance that the incorrect celestial reference point is removed from celestial north. The behavior of such a warbler will, therefore, resemble disorientation in that it will tend to arrive somewhat late at any given distance from its starting point. This type of misorientation will be referred to as *reference point misorientation*.

CHAPTER 7

AN ANALYSIS OF THE FALL OCCURRENCES OF VAGRANT WOOD WARBLERS IN CALIFORNIA

As was shown in the preceding chapter, the timing of the occurrences of vagrant warblers can provide a basic test to distinguish between disoriented and most kinds of misoriented birds. I now propose to carry out this test by comparing the actual average arrival dates of the various vagrant species in California with predicted average arrival dates in California based upon the migration schedule of these birds on their normal migration routes.

To facilitate this analysis, I have grouped the various vagrant species according to their breeding ranges. The birds fall naturally into three groups: (1) Northern Species breeding extensively or entirely in Canada, (2) Southeastern Species breeding in eastern United States but only marginally or not at all into Canada and (3) Southwestern Species breeding in southwestern United States or northern Mexico.

The actual average arrival dates of vagrant warblers in California was simply calculated as the mean of all dated occurrences of each species in California. Winter records were not included in this calculation because it was assumed that these birds arrived during the fall and had been present for some time. When a fall occurrence extended over several days, the first day the bird was found was used as the arrival date. The actual average arrival dates for Northern Species are presented in Table 7-1 along with the number of dated occurrences (sample size) for each species. The species are further divided into potential and definite vagrant species as defined in Chapter 1.

The predicted average arrival dates of Northern Species were calculated by the following method. The average arrival date for each species on its normal migration route was calculated as the mean of banding data obtained at Island Beach, New Jersey [Murray, 1966a] or, for the two species where this data was unavailable (American Redstart and Blackburnian Warbler), as the median of observational data at Baton Rouge, Louisiana [Lowery, 1960]. Each species was then assumed to be uniformly distributed over its entire breeding range and the geographical center of mass of the breeding range was determined by graphical means. This determination was made from breeding ranges as defined by Bent [1953], American Ornithologists' Union [1957], Griscom and Sprunt [1957] and Robbins et al. [1966]; the last proved most useful in this regard. The location of the geographical center of the breeding range was then transferred to a large globe and the shortest distances (great circle distances) between the geographical center of the breeding range and Island Beach, New Jersey (or Baton Rouge, Louisiana) and Morro Bay, California were measured for each species. Morro Bay was chosen for this calculation

TABLE 7-1

AVERAGE ARRIVAL DATES OF NORTHERN SPECIES OF VAGRANT WARBLERS IN CALIFORNIA

	PREDICTED ARRIVAL DATE*	ACTUAL ARRIVAL DATE		DIFFERENCE (DAYS)
		DATE	SAMPLE SIZE	
POTENTIAL VAGRANT SPECIES				
Northern Waterthrush	SEP 12	SEP 16	131	+4
American Redstart	SEP 20	SEP 20	486	0
DEFINITE VAGRANT SPECIES				
Black-and-White	SEP 28	OCT 3	163	+5
Tennessee	SEP 29	OCT 2	211	+3
Magnolia	OCT 7	SEP 30	63	-7
Cape May	OCT 9	OCT 3	13	-6
Black-throated Blue	OCT 23	OCT 15	87	-8
Black-throated Green	OCT 10	OCT 21	29	+11
Blackburnian	OCT 10	OCT 4	38	-6
Chestnut-sided	OCT 6	SEP 28	41	-8
Bay-breasted	OCT 11	OCT 13	12	+2
Blackpoll	SEP 28	SEP 29	398	+1
Palm	OCT 25	OCT 21	348	-4
Ovenbird	OCT 3	OCT 2	43	-1
Connecticut	SEP 29	SEP 25	4	-4
Mourning	SEP 30	OCT 3	1	+3
Canada	SEP 29	OCT 5	23	+6
UNWEIGHTED SPECIES AVERAGE				-0.53
WEIGHTED SPECIES AVERAGE			2091	-0.18

*Based on the timing of normal migrants in New Jersey (Murray, 1966a) or Louisiana (Lowery, 1960), distances calculated from the geographical center of the breeding range, and a rate of migration of 50 miles per day.

because it is roughly central to all of the California vagrant warbler occurrences. These distances can be assumed to represent the average distances that each species of warbler must fly to reach Island Beach (or Baton Rouge) and Morro Bay.

In terms of the above mentioned parameters, the predicted average arrival date for a vagrant warbler in California, t_V, can be calculated by

$$t_V = t_N + (d_V - d_N) \cdot R \qquad (7-1)$$

where t_N is the average arrival date for that species at a point on its normal migration route (Island Beach or Baton Rouge), d_V and d_N are the distances between the geographical center of the species breeding range and Morro Bay and Island Beach (or Baton Rouge) respectively, and R is the average rate of migration for oriented (or misoriented) individuals of that species. For the purposes of this calculation, R has been chosen to be 50 miles/day. This value is based upon the assumption that an individual warbler makes a full night's flight of 200 miles (8 hours at 25 MPH) every fourth night. This estimate is in agreement with stopover times discussed in Chapter 4 and known flight speeds for migration [Lincoln, 1950; Eastwood, 1967]. It also agrees well with the differences in arrival dates for fall migrating warblers between St. Louis, Missouri [Anderson and Bauer, 1968] and Baton Rouge, Louisiana

[Lowery, 1960]. These data, when used in formula (7-1) above, predict an R between 44.2 and 55.3 miles/day.

The data used in the calculation of the predicted average arrival date for vagrant species are presented in Appendix I, while the predicted average arrival dates themselves are shown in Table 7-1 for Northern Species. The differences between the predicted and actual average arrival dates (+ means the species is late, - means the species is early) are seen to be very small for both potential and definite vagrant species. In fact, the unweighted species average difference is only -0.53 days while the weighted (by sample size) species average difference is -0.18 days. If the potential vagrant species are eliminated because of possible contamination of the data by normal transients in California, the unweighted species average difference becomes -0.87 days while the weighted species average difference becomes -0.61 days, still within a single day. The obvious conclusion, therefore, is that Northern Species of fall vagrant warblers occur <u>on time</u> in California and are primarily comprised of misoriented rather than disoriented individuals. This is in direct opposition to at least one published account that fall vagrant warblers in California are late [Austin, 1971]. Of course a Black-throated Blue Warbler arriving in California in mid-October seems late compared to western warblers migrating through California in August and September, and also seems late compared to mid-

September arrival dates of Black-throated Blue Warblers on the East Coast. However, when one remembers that it has flown some 1700 miles further to reach California, it turns out not to be late but to be on time.

The analysis just presented cannot unambiguously prove that <u>all</u> individuals of Northern Species are misoriented. A very few inordinately late occurrences are on record for nearly all species of vagrants that have reached California. Such records can only be attributed to disoriented birds. However, considering the relatively large sample sizes for most species, a few very late records do not materially change the average arrival date, nor, negate the conclusion that most of the occurrences are caused by misoriented birds.

Average arrival dates for Southeastern Species on their normal migration routes are difficult to obtain since most species breed throughout eastern United States, making it impossible to distinguish locally breeding or hatched individuals from true migrants arriving from further north. As a result, accurate predicted arrival dates in California cannot be obtained for Southeastern Species by the method outlined above.

However, an indication of the timing of these species can be obtained by comparing their average arrival dates in California (Table 7-2) and distance flown to reach California with the average arrival dates and distance flown

TABLE 7-2

AVERAGE ARRIVAL DATES FOR SOUTHERN SPECIES OF VAGRANT WARBLERS IN CALIFORNIA

	AVERAGE ARRIVAL DATE	SAMPLE SIZE
I SOUTHEASTERN SPECIES		
Prothonotary	OCT 6	9
Worm-eating	OCT 19	5
Golden-winged	NOV 15	2
Blue-winged	SEP 19	3
Parula	OCT 9	14
Cerulean	OCT 13	2
Yellow-throated	OCT 9	3
Pine	OCT 11	4
Prairie	OCT 3	40
Louisiana Waterthrush	AUG 17	1
Kentucky	NOV 21	1
Hooded	OCT 2	9
II SOUTHWESTERN SPECIES		
Virginia's	SEP 19	126
Lucy's	OCT 1	30
Golden-cheeked	SEP 9	1
Grace's	OCT 3	2
Painted Redstart	SEP 27	15

for Northern Species which have already been shown to be on time. This comparison is presented in Table 7-3. The values shown in this table are the averages over all species, weighted by the sample size of each species. Based on the sample of Northern Species, the predicted average arrival date for the sample of Southeastern Species is October 4. The actual arrival date of this sample is October 6, only two days later. Implicit in this analysis, however, is the assumption that both groups of species begin migrating at the same time, an assumption open to some criticism since Southeastern Species are known to begin breeding before Northern Species. Bent [1953], however, supplies considerable egg date data to indicate that this difference is only 7-10 days between the latitudes in question. Even if this difference in breeding schedules is carried over into differences in the timing of the initiation of migration, the average arrival dates of Southeastern Species in California (maximum 9-12 days late) are not as late as would be expected if the sample were entirely comprised of disoriented individuals. It, therefore, seems likely that the sample of Southeastern Species is primarily comprised of misoriented individuals but contains a few very late, disoriented individuals (for example, the Golden-winged Warblers and Kentucky Warbler shown in Table 7-2 as well as one each Northern California December Prothonotary and Worm-eating Warbler). Furthermore

TABLE 7-3

COMPARISON OF AVERAGE ARRIVAL DATES AND DISTANCES FLOWN FOR NORTHERN AND SOUTHEASTERN VAGRANT WARBLERS IN CALIFORNIA

	AVERAGE ARRIVAL DATE*	AVERAGE DISTANCE FLOWN (MILES)*	PREDICTED ARRIVAL DATE**	DIFFERENCE (DAYS)
NORTHERN SPECIES	OCT. 2	1878	–	–
SOUTHEASTERN SPECIES	OCT. 6	1982	OCT. 4	+2

* Average over all species weighted by the sample size of each species

** Based on Northern Species and assuming both groups begin migrating at the same time it is likely that the later average arrival date for Southeastern Species than for Northern Species is attributable to fewer misoriented birds in the Southeastern sample rather than more disoriented birds.

Very little is known of the migration schedules of the Southwestern Species. Their average arrival dates are presented in Table 7-2 primarily for the sake of completeness. However, the dates shown do not suggest the occurrence of substantial numbers of late birds. In summary, it can be concluded that the vast majority of the occurrences of vagrant warblers in California are due to misoriented rather than disoriented individuals.

The next step of this analysis is to determine which of the various mechanisms of misorientation is responsible for the large number of vagrant occurrences in California. First, consider 180° reversed misorientation. Simple inspection of the breeding ranges of the various species of vagrant warblers that have occurred in California indicates that very few (if any) of the records of Northern or Southeastern Species could even remotely be attributable to this mechanism of misorientation. For example, six species of Northern warblers, the Tennessee, Cape May, Bay-breasted, Blackpoll, Palm and Connecticut Warblers, have breeding ranges that lie entirely north of the latitudes of California. It is, therefore, impossible for 180° reversed migration to cause any individuals of these species to reach

California in the fall and yet some of our commonest vagrant species are included among them. An additional ten species of Northern warblers breed within the latitudes of California only in an extension of their ranges down the Appalachian Plateau. Any individuals of these species to reach California by 180° reversed misorientation must have a nearly due east normal migration route. While such a route cannot be disproven for Atlantic Coast migrants (See Table 4-1), it can be argued against in the case of the Black-throated Blue Warbler, the most likely candidate for such a route. If Black-throated Blue Warblers reached California by 180° reversed misorientation from the Appalachians, these Black-throated Blues would be of the well marked race "cairnsii"; none of these have yet been detected in California. 180° reversed misorientation cannot be ruled out for Atlantic Coast migrant individuals of species breeding south to the Gulf of Mexico, although, again, it seems highly unlikely. Among Southwestern species, only the Painted Redstart is a reasonable possiblity. In summary, while 180° reversed migration could possibly account for a very few cases of vagrant warbler occurrences in California, it cannot be responsible for the vast majority of the occurrences and, in particular, cannot account for <u>any</u> occurrences of several of the most common vagrant species.

It thus appears that the vast majority of the occurrences of vagrant warblers in California are due to forward misorientation errors in individual birds. As shown in Chapter 6, these errors could either be due to the bird's inheriting a wrong direction for its first fall migration or learning a wrong stationary reference point to which to relate its inherited direction (simple misorientation), or by the bird's relating its direction to the reference point with the wrong sense (mirror image misorientation). In the former case an individual warbler could have any direction (although some may be more likely than others), while in the latter case the bird is constrained to a single misorientation direction, namely the mirror image across the N-S axis of the correct direction. If one knew exactly the correct directions for all individuals of a given species, then it would be a simple matter to determine whether the mirror images of these directions could produce vagrant individuals in California. Unfortunately these correct directions are not well known even when the breeding and winter ranges are well defined. This uncertainty regarding the correct directions stems from two sources. First, the basic migration routes of many species, surprisingly, are not entirely determined. For example, recall the debate over the existence of a trans-Atlantic route originating from New England for the Blackpoll Warbler [Murray, 1965; Nisbet, 1970]. Secondly, even in those cases where the basic migration route is well defined, correct directions for individual birds remain unknown because, in the absence of considerable capture-recapture data on monotypic species, there is no way of knowing how the individuals assort on their wintering grounds. Three of the many possible kinds of assortment are illustrated in Figure 7-1: (a) positive assortment, in which individuals from the western part of the breeding range winter in the western part of the winter range; (b) negative assortment, in which individuals from the western part of the breeding range winter in the eastern part of wintering range; (c) random assortment, in which birds from the western part of the breeding range winter randomly throughout the winter range. Because of these uncertainties, any exact calculation of the correct direction, the mirror image direction or the angle of misorientation must be equally uncertain.

Despite the drawbacks just mentioned, there does exist an analysis of California vagrant warbler occurrences that will provide strong evidence for the type of misorientation involved. The basis of the analysis is the comparison of the relative species abundances, the locations of occurrence and the local timing between Atlantic Coast and Gulf Coast eastern vagrant species. The various species are grouped into these catagories according to their migration routes as shown in Table 4-1. To eliminate possible contamination of the data by the occurrences of some normal transients, the Northern Waterthrush and American Redstart are not included in this analysis.

FIGURE 7-1

SOME POSSIBLE KINDS OF ASSORTMENT BETWEEN
BREEDING AND WINTERING RANGES

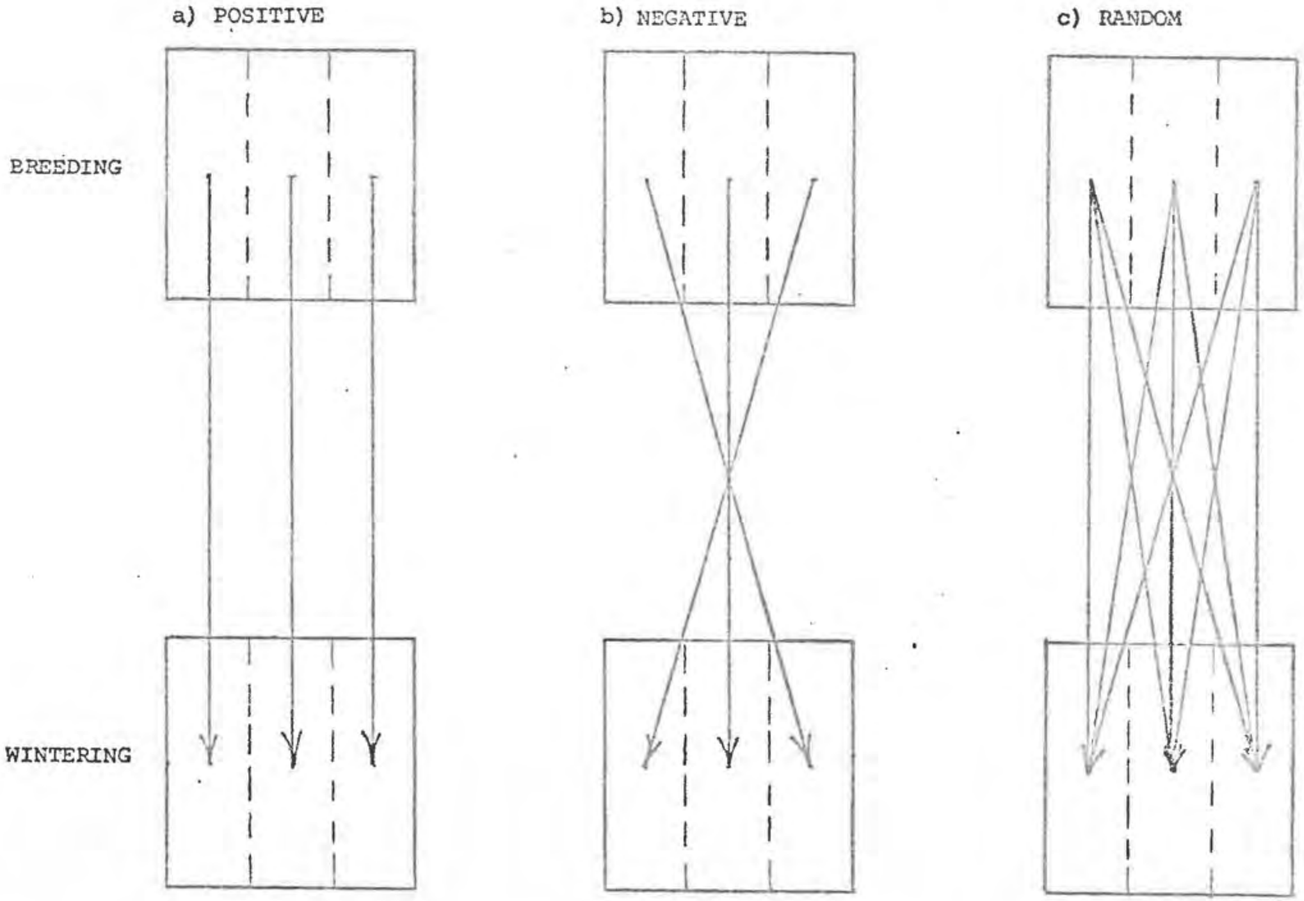
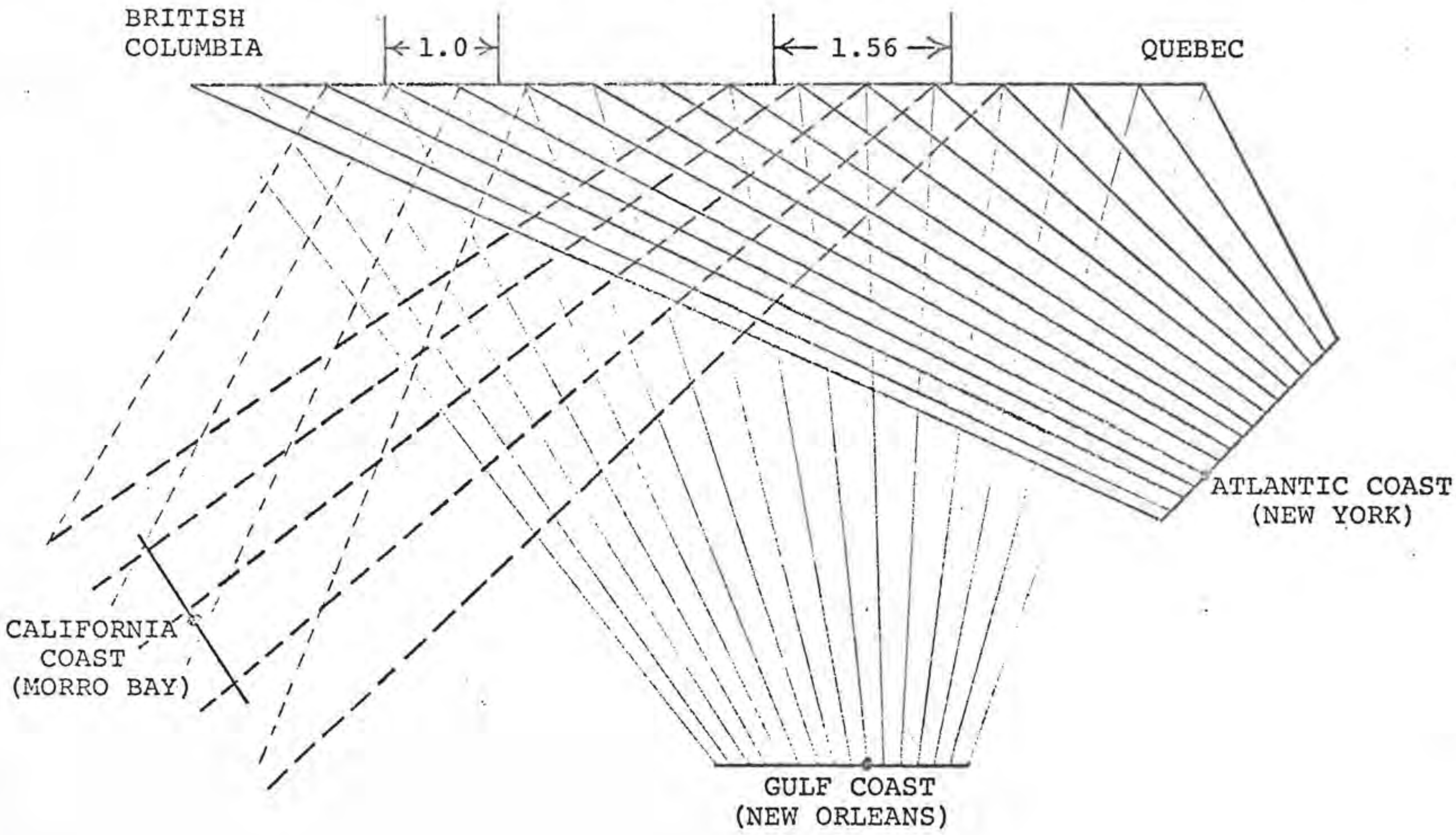


Figure 7-2 shows an E-W line drawn across part of the breeding ranges of two hypothetical species of Northern warblers. The line is drawn to scale on a Mercator Projection of part of North America. The only parts of the Mercator Projection shown in the figure are the California coast between Sonoma and San Diego Counties, the Gulf Coast between Texas and Florida and the Atlantic Coast between Maryland and Nova Scotia. Morro Bay, New Orleans and New York are as indicated. The breeding ranges are assumed to extend across Canada from central British Columbia to central Quebec at 55° N latitude. Now assume that the two species have identical breeding ranges, identical total population sizes, uniform population densities across the breeding range and equal tendencies to be misoriented either by a simple or a mirror image mechanism. Next assume that one species is of the Atlantic Coast type of migrant and that individuals of this species positively assort along the migration front between Maryland and Nova Scotia. The correct migration routes for individuals of this species are shown in bold lines. Such a migration pattern may fairly accurately represent the Blackpoll Warbler. Finally assume that the other species is of the Gulf Coast type of migrant and that individuals of this species also positively assort along a migration front between Texas and Florida. The correct migration routes for individuals of this species are shown in fine lines. This migration pattern may represent

FIGURE 7-2

THEORETICAL CORRECT (SOLID LINES) AND MIRROR IMAGE (DASHED LINES) MIGRATION ROUTES FOR TWO HYPOTHETICAL SPECIES OF WARBLERS. ONE IS AN ATLANTIC COAST MIGRANT (BOLD LINES), THE OTHER A GULF COAST MIGRANT (FINE LINES). LOCATIONS SHOWN ARE TO SCALE ON A MERCATOR PROJECTION OF NORTH AMERICA. (SEE TEXT FOR FULL EXPLANATION.)



the Tennessee Warbler. Mirror image routes for individuals from part of the ranges of each species are shown in dotted lines, bold for the Atlantic Coast species and fine for the Gulf Coast species.

Two important points become apparent from this figure from geometrical considerations alone. First, mirror image vagrants of the Atlantic Coast species that could occur in California originate from further east in the breeding range than do California mirror image vagrants of the Gulf Coast species. Second, mirror image vagrants of the Atlantic Coast species that could reach California are drawn from a distance that is 1.56 times as long as the distance from which Gulf Coast vagrants could be drawn. If we define this distance as D, we can state that $D_A=1.56D_G$. This indicates that 1.56 times as many Atlantic Coast vagrants as Gulf Coast vagrants should occur in California for species having identical breeding ranges and identical total population sizes.

In actuality, the ratio of occurrences of Atlantic Coast species to Gulf Coast species, T_A/T_G, may be greater than 1.56 for several reasons. First, the actual population density of most species of Northern warblers tends to decrease from east to west across their Canadian breeding grounds. This is probably due to a more eastern evolution and adaptation of these species and a subsequent spread westward [Mengel, 1964]. As a result, potential mirror image vagrants of Atlantic Coast species will tend to be drawn from higher density breeding grounds than Gulf Coast mirror image vagrants. Second, there is likely to be a distribution of correct directions having some standard deviation or spread, S, from each point along the line across the breeding range rather than just a single correct direction as shown in Figure 7-2. This spread of correct directions will have the effect of increasing the distance across the breeding range from which mirror image vagrants could be drawn to reach California, that is of increasing D. It can be shown by graphical means that, for a given spread of correct directions from each point across the breeding range, the increase in D_A is greater than the increase in D_G. This is because the rate of change of the correct directions, as one moves across the breeding range, is greater for Gulf Coast species than for Atlantic Coast species. Or, stated another way, the correct directions of the Atlantic Coast species are more nearly parallel than are the correct directions of Gulf Coast species. This is also the basic reason why $D_A > D_G$ with only a single correct direction at each location. Stated mathematically, the geometry of the situation is such that

$$D_A > D_G$$

and, as S increases, D_A and D_G both increase but

$$\Delta D_A > \Delta D_G.$$

A final reason why T_A/T_G may be greater than 1.56 concerns species with more eastern breeding ranges. As the western limit of a species breeding range moves further east, the probability that the species will be unable to supply mirror image vagrants to California increases. However, since Atlantic Coast species originate from further east, this probability increases faster for Gulf Coast than Atlantic Coast species. The effect of these various factors is probably multiplicative. Thus, actual ratios of T_A/T_G may be expected to vary anywhere between 2 and 8, but will always be greater than 1, if mirror image misorientation is the operative mechanism causing vagrant warblers to reach California.

If, on the other hand, simple misorientation is the predominant mechanism causing vagrant warblers to reach California, it can be shown that T_A/T_G will be less than or equal to 1, that is, there will always be as many or more occurrences of Gulf Coast species than of Atlantic Coast species. If simple misorientation is operative and all angles of misorientation are equally probable, then $T_A/T_G=1$ provided that the total number of birds in the source population is the same for both Atlantic Coast and Gulf Coast species. As pointed out by DeBenedictis [1971], however, the number of misoriented birds could decrease as the angle of misorientation increases simply because, with greater angles of misorientation, a bird will arrive at areas further removed from its normal range, that is, areas in which it is more likely to be ill adapted for survival. Thus, selection should be stronger against large angles of misorientation than against small angles. If this is indeed the case, then simple misorientation should produce more occurrences of Gulf Coast species than Atlantic Coast species simply because the angles of misorientation necessary to produce vagrants in California are substantially less for Gulf Coast than for Atlantic Coast species having identical breeding ranges (See Figure 7-2). In this case, therefore, $T_A/T_G<1$. In summary, the ratio of the total number of fall vagrant occurrences between Atlantic Coast and Gulf Coast species provides a powerful test to isolate the mechanism of misorientation. It must be stressed, however, that this test can only be used to compare Atlantic and Gulf Coast species that have similar breeding ranges and population sizes.

Three additional tests can be derived from Figure 7-2 that have the desirable property of being independent of the total population sizes. These tests deal with the location and timing of the vagrant occurrences within the state and, like the above test, basically involve a comparison of Atlantic Coast and Gulf Coast species. The first test considers the occurrences along a roughly N-S line through California and utilizes the percentage of the vagrant occurrences that have been in Northern California. The test statistic is the percentage of Northern California occurrences for Atlantic Coast species divided by the percentage of Northern California occurrences for Gulf Coast species: $\%N_A/\%N_G$.

The logic behind this test is as follows. Let us assume that the distribution of birds across the normal migration front of either an Atlantic Coast or Gulf Coast species is not uniform, as shown in Figure 7-2, but is a unimodal distribution having a mean located somewhere near the midpoint of the migration front. Such a distribution will result if the individuals located at any given point along the line through the breeding range of the species exhibit a unimodal distribution of correct directions having a reasonably large angular deviation from the mean. (An angular deviation of ±10° is perfectly adequate and completely realistic in this regard.) If this is indeed the case, then the distribution of mirror image vagrants along a Pacific Coast migration front will likewise be unimodal and will also have its mean located somewhere near the midpoint of the migration front. The migration front will, of course, be much wider for the mirror image distribution than for the correct distribution since the mirror image directions are diverging while the correct directions are converging. It is furthermore obvious from Figure 7-2 that the mean of the mirror image distribution for Atlantic Coast species will intersect the Pacific Coast at a point further north than will the mean of the Gulf Coast species' mirror image distribution. It follows, therefore, that the percentage of occurrences in Northern California for an Atlantic Coast mirror image vagrant will be greater than that for a Gulf Coast mirror image vagrant provided that both species have similar breeding ranges. Thus, if mirror image misorientation is the controlling mechanism, $\%N_A/\%N_G>1$. This ratio is seen to be independent of the total population sizes.

If, on the other hand, simple misorientation is the controlling mechanism for vagrancy, the result will be different. If all angles of misorientation are equally probable, then the vagrant distributions will be uniform for both Atlantic Coast and Gulf Coast species so that $\%N_A/\%N_G=1$. Or, if smaller angles of misorientation are preferred, $\%N_A/\%N_G<1$ since Gulf Coast species need a smaller angle of misorientation to reach any point in California than do Atlantic Coast species. Again these ratios are independent of the total population sizes.

A second test that is independent of population sizes is provided by the location of vagrant occurrences along an E-W line across California. It is obvious from Figure 7-2 that the directions taken by Gulf Coast mirror image vagrants that reach California are more nearly N-S than are the directions taken by Atlantic Coast mirror image vagrants that reach California. Therefore, the probability of a mirror image vagrant stopping in the Interior of California will be greater for Gulf Coast than for Atlantic Coast species since the long axis of California is closer to N-S than to E-W. If the test statistic is defined to be the percentage of Interior occurrences for Atlantic Coast species divided by the percentage of Interior occurrences for Gulf Coast species, we find that $\%I_A/\%I_G<1$ if mirror image misorientation is the operative mechanism.

If, on the other hand, simple misorientation is the controlling mechanism and all angles of misorientation are equally probable, $\%I_A/\%I_G=1$. If smaller angles of misorientation are preferred, $\%I_A/\%I_G>1$. This results from the fact that, for equal angles of misorientation, Gulf Coast species must originate from further east in their breeding range, than Atlantic Coast species. As such, the Gulf Coast species will have a route that is more perpendicular to the long axis of the state and will, therefore, have a smaller probability of occurring in the Interior.

The final test, also independent of the total population size, is also based on the probable direction that Gulf Coast and Atlantic Coast species must fly to reach California for each mechanism of misorientation. As shown above, if mirror image vagrancy is operative, the flight path of Gulf Coast vagrants will be more nearly parallel to the long axis of California than the flight path of Atlantic

Coast vagrants. This indicates that the difference in timing between Northern and Southern California should be greater for Gulf Coast vagrants than for Atlantic Coast vagrants. The test statistic here is $\Delta t_A - \Delta t_G$ where Δt is the difference (in days) in the average arrival dates between Southern and Northern California. If mirror image vagrancy is operative $\Delta t_A - \Delta t_G$ should be negative. On the other hand, if simple misorientation is operative and all angles of misorientation are equally probably, $\Delta t_A - \Delta t_G$ should equal 0. Or, if smaller angles of misorientation are preferred $\Delta t_A - \Delta t_G$ will be positive. This is because, in this case, the average Atlantic Coast vagrant will originate from further west than the average Gulf Coast vagrant, just the opposite from the case for mirror image misorientation. A summary of the predicted results of all four of the tests just described is presented in Table 7-4.

Now each of these tests can be applied to the actual data. For the purposes of these tests I have assumed that species utilizing both the Gulf Coast and Atlantic Coast migration routes (Table 4-1) are more likely to behave as Gulf Coast species than as Atlantic Coast species although they should perhaps be somewhat intermediate in character. This would be expected if positive assortment occurs across the migration front, a reasonable assumption. These species are indicated by an asterisk (*) in the Tables that follow so that the validity of this assumption can be ascertained.

TABLE 7-4

SUMMARY OF PREDICTED RESULTS OF THE ANALYSIS TO
DISTINGUISH BETWEEN MIRROR IMAGE AND SIMPLE MISORIENTATION

THE BASIS OF THIS ANALYSIS IS A COMPARISON OF VAGRANT OCCURRENCES
BETWEEN ATLANTIC COAST*, A, AND GULF COAST*, G, SPECIES

			SIMPLE MISORIENTATION	
		MIRROR IMAGE MISORIENTATION	ALL ANGLES EQUALLY PROBABLE	SMALLER ANGLES MORE PROBABLE THAN LARGER ANGLES
I	TOTAL NUMBER OF OCCURRENCES IN CALIFORNIA = T	$T_A/T_G>1$	$T_A/T_G=1$	$T_A/T_G<1$
II	% OF OCCURRENCES THAT ARE IN NORTHERN CALIF = %N	$\%N_A/\%N_G>1$	$\%N_A/\%N_G=1$	$\%N_A/\%N_G<1$
III	% OF OCCURRENCES THAT ARE IN THE INTERIOR = %I	$\%I_A/\%I_G<1$	$\%I_A/\%I_G=1$	$\%I_A/\%I_G>1$
IV	DIFFERENCE IN AVERAGE ARRIVAL DATES BETWEEN SOUTHERN AND NORTHERN CALIFORNIA = Δt	$\Delta t_A-\Delta t_G<0$	$\Delta t_A-\Delta t_G=0$	$\Delta t_A-\Delta t_G>0$

* SEE CHAPTER 4 FOR DEFINITION.

Table 7-5 presents the analysis of the total number of occurrences of eastern species in California. In order to compare species having similar breeding ranges, the species are divided into four groups: (I) Northern Species breeding west of the western cordilleras, (II) Northern Species breeding west to the eastern base of the western cordilleras, (III) Northern Species breeding west to south-central Canada and (IV) Southeastern Species. Accurate data on the total population sizes of these various species are, unfortunately, unavailable. As a rough approximation, I have divided the species into two groups: (1) fairly common to abundant species and (2) uncommon to rare species. These classifications were taken, unaltered, from Robbins et al. [1966]. Within each group, the species are arranged according to an increasing angle of misorientation which is defined as the minimum angle necessary to bring the westernmost individual of each species to Morro Bay, California. The results of this analysis are straightforward. Within each group, the Atlantic Coast species are always more common as vagrants in California than are the Gulf Coast species, even though they usually have a greater angle of misorientation. The ratio T_A/T_G varies from 1.94 in the case of Blackpoll/Tennessee Warblers to 41.00 in the case of Prairie/Kentucky Warblers. The average T_A/T_G for the five groups in which comparisons can be made varies from 2.25 to 8.50. The total group average

TABLE 7-5

AN ANALYSIS OF THE TOTAL NUMBER OF OCCURRENCES OF
EASTERN WARBLERS IN CALIFORNIA ACCORDING TO BREEDING RANGE,
POPULATION SIZE AND NORMAL MIGRATION ROUTE

		FAIRLY COMMON TO ABUNDANT SPECIES			UNCOMMON TO RARE SPECIES		
	ANGLE OF MISORIENTATION	TOTAL OCCURRENCES (T)		RATIO	TOTAL OCCURRENCES (T)		RATIO
		ATLANTIC	GULF	T_A/T_G	ATLANTIC	GULF	T_A/T_G
I NORTHERN SPECIES BREEDING WEST OF WESTERN CORDILLERAS							
TENNESSEE	10°		226	1.94			
MAGNOLIA	19°		63	6.95			
BLACKPOLL	23°	438		-			
AVERAGE		438	144.5	3.03			
II NORTHERN SPECIES BREEDING WEST TO EASTERN BASE OF WESTERN CORDILLERAS							
BLACK-AND-WHITE*	11°		210	2.00			
OVENBIRD*	22°		46	9.11			
BLACK-THROATED GREEN	26°		29	14.45			
BAY-BREASTED	31°		12	34.92			
PALM	34°	419		-			
MOURNING	35°					1	4.0-13.0
CAPE MAY	37°				13		-
CANADA	41°		23	18.22			
CONNECTICUT	58°				4		-
AVERAGE		419	64.0	6.55	8.5	1	8.50
III NORTHERN SPECIES BREEDING WEST TO SOUTH-CENTRAL CANADA							
CHESTNUT-SIDED	52°		43	2.12			
BLACKBURNIAN	56°		38	2.39			
BLACK-THROATED BLUE	78°	91		-			
AVERAGE		91	40.5	2.25			
IV SOUTHEASTERN SPECIES							
LOUISIANA WATERTHRUSH*	31°					1	-
PARULA*	47°		17	2.41			
PINE*	53°		4	10.25			
BLUE-WINGED	57°					3	-
GOLDEN-WINGED	60°					2	-
HOODED	64°		9	4.56			
YELLOW-THROATED*	65°		3	13.67			
PROTHONOTARY	68°		9	4.56			
WORM-EATING	71°					5	-
KENTUCKY	74°		1	41.00			
CERULEAN	79°		2	20.50			
PRAIRIE	93°	41		-			
AVERAGE		41	6.4	6.38		2.7	-

* Gulf Coast and Atlantic Coast migrant

is found to be 5.34. These results agree very well with the predicted T_A/T_G for mirror image misorientation: $T_A/T_G>1$, probably between 2 and 8. This analysis, therefore, supplies a strong indication that mirror image misorientation rather than simple misorientation is the operative mechanism accounting for eastern vagrant warblers in California. It also supplies an immediate explanation for DeBenedictis' [1971] "exceptionally numerous" species (Palm, Black-throated Blue and Prairie Warblers). It should also be noted that species utilizing both the Gulf Coast and Atlantic Coast migration routes do indeed behave similarly to the remainder of the Gulf Coast species although the T_A/T_G ratios may average slightly less than the average for all Gulf Coast species. This is also in agreement with the previous prediction.

Objections could be raised against the preceding analysis on the basis that the resulting T_A/T_G ratios could be accounted for by differences in the total population size of the various species. For example, Robbins et al. [1966] considers the Blackpoll Warbler (438 occurrences) to be an abundant species while the Tennessee (226 occurrences) and Magnolia (63 occurrences) Warblers are only rated as common, suggesting that population size rather than migration direction could account for the number of vagrant occurrences. And yet the Palm Warbler (419 occurrences) is only considered by Robbins to be fairly common while the

Black-and-white Warbler (210 occurrences), Ovenbird (46 occurrences), Black-throated Green (29 occurrences) and Canada (23 occurrences) Warblers are all considered to be common, indicating that population size is not the controlling factor in this group of species. In order to overcome any uncertainty due to population sizes, the other proposed tests must now be considered.

Table 7-6 presents the analysis of the percentage of occurrences of eastern warblers in Northern California as a function of breeding range and migration route. In three out of the four groups with similar breeding ranges, as well as in the grand total for all species, the ratio $\%N_A/\%N_G$ is greater than 1, as predicted for mirror image misorientation. This ratio may be expected to decrease as the breeding range is moved further east or south since all such birds should be considerably more common in Southern than in Northern California. However, it should always remain above 1. Such a decrease is noticeable in Groups III and IV. The discrepancy in Group III is primarily due to an inordinately large number of Northern California occurrences for the Chestnut-sided Warbler. No explanation is available for this discrepancy at this time but we should remember that the percentage of adult Chestnut-sided Warblers was also inordinately high (Table 1-9). Regardless of this one exception, the results presented in Table 7-6 supply further

TABLE 7-6

AN ANALYSIS OF THE PERCENTAGE OF OCCURRENCES
OF EASTERN WARBLERS IN NORTHERN CALIFORNIA
ACCORDING TO BREEDING RANGE AND MIGRATION ROUTE

	OCCURRENCES						
	ATLANTIC COAST SPECIES			GULF COAST SPECIES			RATIO
	TOTAL	N.CAL.	%N.CAL. ($\%N_A$)	TOTAL	N.CAL.	%N.CAL. ($\%N_G$)	$\%N_A/\%N_G$
I NORTHERN SPECIES BREEDING WEST OF WESTERN CORDILLERAS							
TENNESSEE				226	89	39.4	
MAGNOLIA				63	28	44.5	
BLACKPOLL	438	262	59.8				
TOTAL	438	262	59.8	289	117	40.5	1.48
II NORTHERN SPECIES BREEDING WEST TO EASTERN BASE OF WESTERN CORDILLERAS							
BLACK-AND-WHITE*				210	86	41.0	
OVENBIRD*				46	26	56.5	
BLACK-THROATED GREEN				29	5	17.2	
BAY-BREASTED				12	3	25.0	
PALM	419	279	66.6				
MOURNING				1	0	0.0	
CAPE MAY	13	7	53.8				
CANADA				23	6	26.1	
CONNECTICUT	4	3	75.0				
TOTAL	436	289	66.3	321	126	39.3	1.69
III NORTHERN SPECIES BREEDING WEST TO SOUTH-CENTRAL CANADA							
CHESTNUT-SIDED				43	25	58.1	
BLACKBURNIAN				38	16	42.1	
BLACK-THROATED BLUE	91	37	40.7				
TOTAL	91	37	40.7	81	41	50.6	0.80
IV SOUTHEASTERN SPECIES							
LOUISIANA WATERTHRUSH*				1	0	0.0	
PARULA*				17	7	41.2	
PINE*				4	1	25.0	
BLUE-WINGED				3	1	33.3	
GOLDEN-WINGED				2	0	0.0	
HOODED				9	4	44.4	
YELLOW-THROATED*				3	1	33.3	
PROTHONOTARY				9	2	22.2	
WORM-EATING				5	3	60.0	
KENTUCKY				1	1	100.0	
CERULEAN				2	0	0.0	
PRAIRIE	41	17	41.5				
TOTAL	41	17	41.5	56	20	35.7	1.16
GRAND TOTAL	1006	605	60.1	747	304	40.7	1.48

* Gulf Coast and Atlantic Coast migrant

evidence that mirror image misorientation is the controlling mechanism of vagrancy in eastern warblers.

The results of the third test are presented in Table 7-7. It should be noted that the test statistic used, the percentage of Interior occurrences, includes only occurrences in the Interior of California as defined in Chapter 1. It does not include records on the East Side of the Sierra and higher Southern California mountains. The reason for this is that these mountain masses tend to concentrate westward flying migrants in the desert oases lying along their eastern flank, in a manner similar to the way the ocean concentrates westward flying migrants at "oases" of trees along the Outer Coast. Occurrences on the East Side, therefore, will not necessarily be representative of birds having a more N-S orientation. Interior occurrences, however, will be representative of a more N-S orientation since westward flying vagrants will tend to overfly this area [Binford, 1971]. Again, the results are straightforward; the ratio $\%I_A/\%I_G$ is found to be less than 1 for all four groups of species, exactly as predicted for mirror image misorientation.

The results of the final test are presented in Table 7-8. As would be expected in fall migration, the vast majority of the species occur later in Southern than in Northern California. However, Gulf Coast species generally show a greater difference in this timing than do Atlantic

TABLE 7-7

AN ANALYSIS OF THE PERCENTAGE OF OCCURRENCES
OF EASTERN WARBLERS IN THE INTERIOR** OF CALIFORNIA
ACCORDING TO BREEDING RANGE AND MIGRATION ROUTE

	OCCURRENCES						
	ATLANTIC COAST SPECIES			GULF COAST SPECIES			RATIO
	TOTAL	INT.	%INT. ($\%I_A$)	TOTAL	INT.	%INT. ($\%I_G$)	$\%I_A/\%I_G$
I NORTHERN SPECIES BREEDING WEST OF WESTERN CORDILLERAS							
TENNESSEE				226	26	11.5	
MAGNOLIA				63	6	9.5	
BLACKPOLL	438	6	1.4				
TOTAL	438	6	1.4	289	32	11.1	0.12
II NORTHERN SPECIES BREEDING WEST TO EASTERN BASE OF WESTERN CORDILLERAS							
BLACK-AND-WHITE*				210	49	23.3	
OVENBIRD*				46	5	10.9	
BLACK-THROATED GREEN				29	1	3.4	
BAY-BREASTED				12	0	0.0	
PALM	419	20	4.8				
MOURNING				1	0	0.0	
CAPE MAY	13	0	0.0				
CANADA				23	2	8.7	
CONNECTICUT	4	0	0.0				
TOTAL	436	20	4.6	321	57	17.8	0.26
III NORTHERN SPECIES BREEDING WEST TO SOUTH-CENTRAL CANADA							
CHESTNUT-SIDED				43	10	23.3	
BLACKBURNIAN				38	1	2.6	
BLACK-THROATED BLUE	91	9	9.9				
TOTAL	91	9	9.9	81	11	13.6	0.73
IV SOUTHEASTERN SPECIES							
LOUISIANA WATERTHRUSH*				1	0	0.0	
PARULA*				17	0	0.0	
PINE*				4	0	0.0	
BLUE-WINGED				3	0	0.0	
GOLDEN-WINGED				2	1	50.0	
HOODED				9	2	22.2	
YELLOW-THROATED*				3	0	0.0	
PROTHONOTARY				9	0	0.0	
WORM-EATING				5	0	0.0	
KENTUCKY				1	0	0.0	
CERULEAN				2	0	0.0	
PRAIRIE	41	0	0.0				
TOTAL	41	0	0.0	56	3	5.4	0.00
GRAND TOTAL	1006	35	3.5	747	103	13.8	0.25

* Gulf Coast and Atlantic Coast migrant

** As defined in Chapter 1.

TABLE 7-8

AN ANALYSIS OF THE DIFFERENCE IN AVERAGE
ARRIVAL DATES BETWEEN SOUTHERN AND NORTHERN CALIFORNIA
ACCORDING TO BREEDING RANGE AND MIGRATION ROUTE

AVERAGE ARRIVAL DATES

	ATLANTIC COAST SPECIES				GULF COAST SPECIES				
	SAMPLE SIZE	S.CAL.	N.CAL.	DIFF. (Δt_A)	SAMPLE SIZE	S.CAL.	N.CAL.	DIFF. (Δt_G)	$\Delta t_A - \Delta t_G$
I NORTHERN SPECIES BREEDING WEST OF WESTERN CORDILLERAS									
TENNESSEE					211	OCT 6	SEP 27	+9	
MAGNOLIA					63	OCT 3	SEP 25	+8	
BLACKPOLL	397	OCT 4	SEP 27	+7					
WEIGHTED AVERAGE	397			+7.00	274			+8.77	-1.77
II NORTHERN SPECIES BREEDING WEST TO EASTERN BASE OF WESTERN CORDILLERAS									
BLACK-AND-WHITE*					163	OCT 3	OCT 3	0	
OVENBIRD*					43	OCT 13	SEP 24	+19	
BLACK-THROATED GREEN					29	OCT 23	OCT 11	+12	
BAY-BREASTED					12	OCT 19	SEP 26	+23	
PALM	248	OCT 24	OCT 20	+4					
MOURNING					1	OCT 3	-	-	
CAPE MAY	13	OCT 5	OCT 2	+3					
CANADA					23	OCT 12	SEP 13	+29	
CONNECTICUT	4	SEP 27	SEP 25	+2					
WEIGHTED AVERAGE	265			+3.92	270			+7.81	-3.89
III NORTHERN SPECIES BREEDING WEST TO SOUTH-CENTRAL CANADA									
CHESTNUT-SIDED					41	OCT 6	SEP 22	+14	
BLACKBURNIAN					38	OCT 6	OCT 3	+3	
BLACK-THROATED BLUE	87	OCT 17	OCT 13	+4					
WEIGHTED AVERAGE	87			+4.00	79			+8.71	-4.71
IV SOUTHEASTERN SPECIES									
LOUISIANA WATERTHRUSH*					1	AUG 17	-	-	
PARULA*					14	OCT 20	SEP 29	+21	
PINE*					4	OCT 13	OCT 5	+8	
BLUE-WINGED					3	SEP 22	SEP 13	+9	
GOLDEN-WINGED					2	NOV 15	-	-	
HOODED					9	OCT 16	SEP 14	+32	
YELLOW-THROATED*					3	OCT 17	SEP 21	+26	
PROTHONOTARY					9	OCT 3	OCT 16	-13	
WORM-EATING					5	SEP 15	NOV 10	-56	
KENTUCKY					1	-	NOV 21	-	
CERULEAN					2	OCT 13	-	-	
PRAIRIE	40	SEP 29	OCT 9	-10					
WEIGHTED AVERAGE	40			-10.00	47			+6.85	-16.85
TOTAL WEIGHTED AVERAGE	789			+4.77	670			+8.24	-3.47

* Gulf Coast and Atlantic Coast migrant

Coast species. The test statistic $\Delta t_A - \Delta t_G$ is seen to be negative for each group, again exactly as predicted for mirror image misorientation and not as predicted for simple misorientation. The total weighted average differences, 8.24 days for Gulf Coast species and 4.77 days for Atlantic Coast species represent differences in distance travelled of 412 and 239 miles respectively, assuming a rate of migration of 50 miles/day. Considering that the straight line distance between Northern California (Southeast Farallon Island) and Southern California (San Diego) is 440 miles, the above differences in distance travelled are quite reasonable.

In summary, the relative species abundances in California, the relative locations of occurrences of vagrant warblers in California, both along a N-S and an E-W axis, and the relative timing in Northern and Southern California all supply very strong evidence that mirror image misorientation rather than simple misorientation is the operative mechanism causing eastern warblers to occur in California.

Finally we may consider the occurrences of the Southwestern Species of warblers in California. The numbers of occurrences for both Northern and Southern California are shown in Table 7-9 for the five species that have occurred in the state. If simple misorientation were operative and all angles of misorientation were equally probable, then we

TABLE 7-9

AN ANALYSIS OF THE OCCURRENCES OF SOUTHWESTERN VAGRANT WARBLERS IN CALIFORNIA

	NORTHERN CALIFORNIA			SOUTHERN CALIFORNIA		
		ANGLE OF MISORIENTATION* FROM			ANGLE OF MISORIENTATION** FROM	
SPECIES	NUMBER OF OCCURRENCES	AVE. CORRECT DIRECTION	AVE. MIRROR IMAGE DIRECT.	NUMBER OF OCCURRENCES	AVE. CORRECT DIRECTION	AVE. MIRROR IMAGE DIRECT.
Virginia's	15	127°	61°	238	69°	3°
Lucy's	6	136°	74°	27	92°	30°
Golden-cheeked	1	141°	77°	0	126°	62°
Grace's	0	152°	76°	2	126°	50°
Painted Redstart	0	161°	77°	20	136°	52°

* To San Francisco
** To San Diego

would expect roughly similar numbers of occurrences for all species except the Golden-cheeked Warbler since the other four species are all regarded as common by Robbins et al. [1966]. This however is not the case. Table 7-9 indicates that the Virginia's Warbler is extremely frequent in Southern California, in fact, about 10 times as frequent as either the Lucy's Warbler or the Painted Redstart, the next most frequent species. Table 7-9 does indicate, however, that some correlation exists between the number of occurrences in Northern or Southern California and the average angle of simple misorientation necessary for each species to reach Northern or Southern California. (For the purposes of this calculation, Northern California occurrences were assumed to be at San Francisco while Southern California occurrences were assumed to be at San Diego. The angles of misorientation were then calculated from the line joining the geographical centers of the breeding and winter ranges.) Such a correlation would be expected if simple misorientation were operative and smaller angles of misorientation were preferred. Nevertheless, the correlation presents some serious problems, the outstanding one being that a large difference in the frequency of occurrences exists between a 69° angle of misorientation (238 occurrences) and a 92° angle of misorientation (only 27 occurrences). This would indicate a very inexact migration behavior for the Virginia's Warbler. If this is typical of other species of warblers, then we would expect far more occurrences of Northern species than there actually are since most of these species need angles of misorientation that are considerably less than 60° (See Table 7-5). Thus, the simple misorientation model is not very satisfying in explaining the occurrences of Southwestern Species.

A far better correlation can be obtained if we compare the number of occurrences at each location to the necessary angle of misorientation from the average _mirror image direction_ of each species. For example, Table 7-9 shows that the average mirror image direction of the Virginia's Warbler passes within 3° of San Diego but is removed by 61° from San Francisco. There is little wonder that the species is so frequent in Southern California! Only the Painted Redstart appears to be more common than it should be if mirror image misorientation is the operative mechanism of vagrancy in this group. Yet only three of the 20 occurrences of this species have been subsequent to 1962, the time during which nearly all of the occurrences of the remaining species were recorded. It is likely, therefore, that the rather large number of occurrences of this species prior to 1962 is an artifact of the extremely obvious nature of this bird. Any casual observer of birds could easily overlook hundreds of Grace's, Lucy's or Virginia's Warblers without once missing a Painted Redstart.

In summary, it appears that mirror image misorientation can account for the California fall occurrences of the Southwestern as well as the eastern species of warblers. It can, therefore, be concluded that mirror image misorientation is a widespread phenomenon among all migratory species of wood warblers.

PART III

AN EXPERIMENTAL APPROACH

CHAPTER 8

THE ORIENTATION CAGE - AN INTRODUCTION

For a long time, the only methods available to researchers studying migratory orientation were either marking and displacing migrants and awaiting recoveries of these birds or releasing captured birds and recording their vanishing directions. The first method was cumbersome and very slow in producing results; the second method had the disadvantage that a given individual could only be tested once. It was, therefore, a significant advance when Kramer [1949] discovered that certain caged passerines manifested directional tendencies in their cages that were appropriate for the particular migratory season. In particular, Kramer discovered that certain nocturnal migrants were capable of orienting their nocturnal migratory restlessness or Zugunruhe when placed in circular cages exposed to the night sky. Such cages have come to be known as orientation cages.

The requirements for the design of an orientation cage and just what such a device attempts to measure must now be examined. First of all, the orientation cage must be placed in a known direction with respect to the external environment. Secondly, the cage must be designed so that all potential directional tendencies that the birds might show are equally probable. Thus, an orientation cage should be circular. Next, the bird must be exposed to some consistant set of potential directional cues. Placing the cage under the clear night sky or in a planetarium accomplishes this purpose. Finally some means must be available for recording the directional choices made by the birds. Several techniques have been developed to accomplish this task.

Kramer [1949] originally designed a drum-shaped cage, less than one meter in diameter, with a transparent bottom. The experimenter would lie below this "Kramer" cage and observe the general headings of a bird over short periods of time. This method, however, is extremely time consuming. Only one bird can be tested at a time, and many of the decisions as to heading are unduly subjective. Refinements of this technique utilizing automatic recording devices such as microswitch perches, electronic counters or continuous chart recorders have been developed by numerous workers [Farner and Mewaldt, 1953; Merkel and Fromme, 1958; Mewaldt and Rose, 1960; Sauer, 1963]. All of these methods, however, basically utilize the same principle: a bird is placed in the center of a circular series of perches or pedals each connected to a counter. Each time the bird moves from the center of the cage to one of the peripheral perches it activates a recording. In order for these recordings to be truly representative of a directional choice, it is necessary that the bird return to the center of the cage after each jump. Workers who have appreciated this last point have attempted to separate the peripheral perches by dividers or have even enclosed them in separate small cages open only to the central perch [Aagaard and Wolfson, 1962]. The continual chart recording of such orientation data has the distinct advantage that directional responses may be obtained as a function of time. The basic disadvantage of all of these methods of automatic recording is the expense of such units. This severely limits the number of birds that can be tested simultaneously and thereby limits the statistical significance of the results. In addition, the number of recording perches have usually been few: 8, 12 or 16. This severely limits the resolution of the preferred direction, particularly if a bird's response is multimodal.

An ingenious method of recording orientation data has more recently been developed by Emlen and Emlen [1966]. The bird is placed on a pad impregnated with black indelible ink in the center of an inverted cone of white absorbent paper. Each time the bird jumps or flutters up the side of the cone, it leaves a permanent footprint record of its directional response. The slope of the cone is 45°, a slope that effectively prevents the bird from remaining on the cone. After each jump, the bird slides back to the ink pad in the center of the cage. Thus consistant directional responses are assured. The advantages of this technique are many: simplicity, low cost, portability and the independence from cumbersome electrical or mechanical gear. In addition, many birds can be tested simultaneously thereby increasing the probability of obtaining statistically significant results. Two disadvantages of this method are that the data cannot be analyzed as a function of time except by replacing blotters at certain intervals, and that the resulting "footprint" data must be digitized, a laborious, time-consuming and somewhat subjective task.

Vagrant warblers in California may be most readily captured on Southeast Farallon Island. Transporting oneself to the island, however, is an uncertain proposition at best and landing equipment on the island is a difficult, hazardous task. Thus, simplicity and portability of orientation equipment was a primary concern in this study. For these reasons, the Emlen "footprint" technique was chosen as the sole method of obtaining orientation data.

The questions that may be answered by orientation data collected by the "footprint" technique may now be examined. The most basic question is whether vagrant warblers in California are comprised of disoriented or misoriented individuals. This question can be answered by showing whether or not California captured vagrant warblers are capable of displaying directional behavior when placed into an orientation cage and tested under the clear night sky. However, even if an individual shows significantly directed behavior on a single night's test, it cannot be assumed that this individual will not be disoriented in the wild. A bird that has learned the correct reference point to which to relate an inherited migratory direction, but that has failed to inherit any direction may still be a disoriented individual. It will be capable of following a given direction for an entire night's flight but will have no predisposition to choose the same direction night after night. If such a bird is placed in an orientation cage on several successive nights, it should show significantly directed behavior on each night, but no significantly directed behavior over all of the nights. It is, therefore, necessary to test a given individual over many nights in order to eliminate the possibility that disorientation is responsible for the occurrences of vagrant warblers in California.

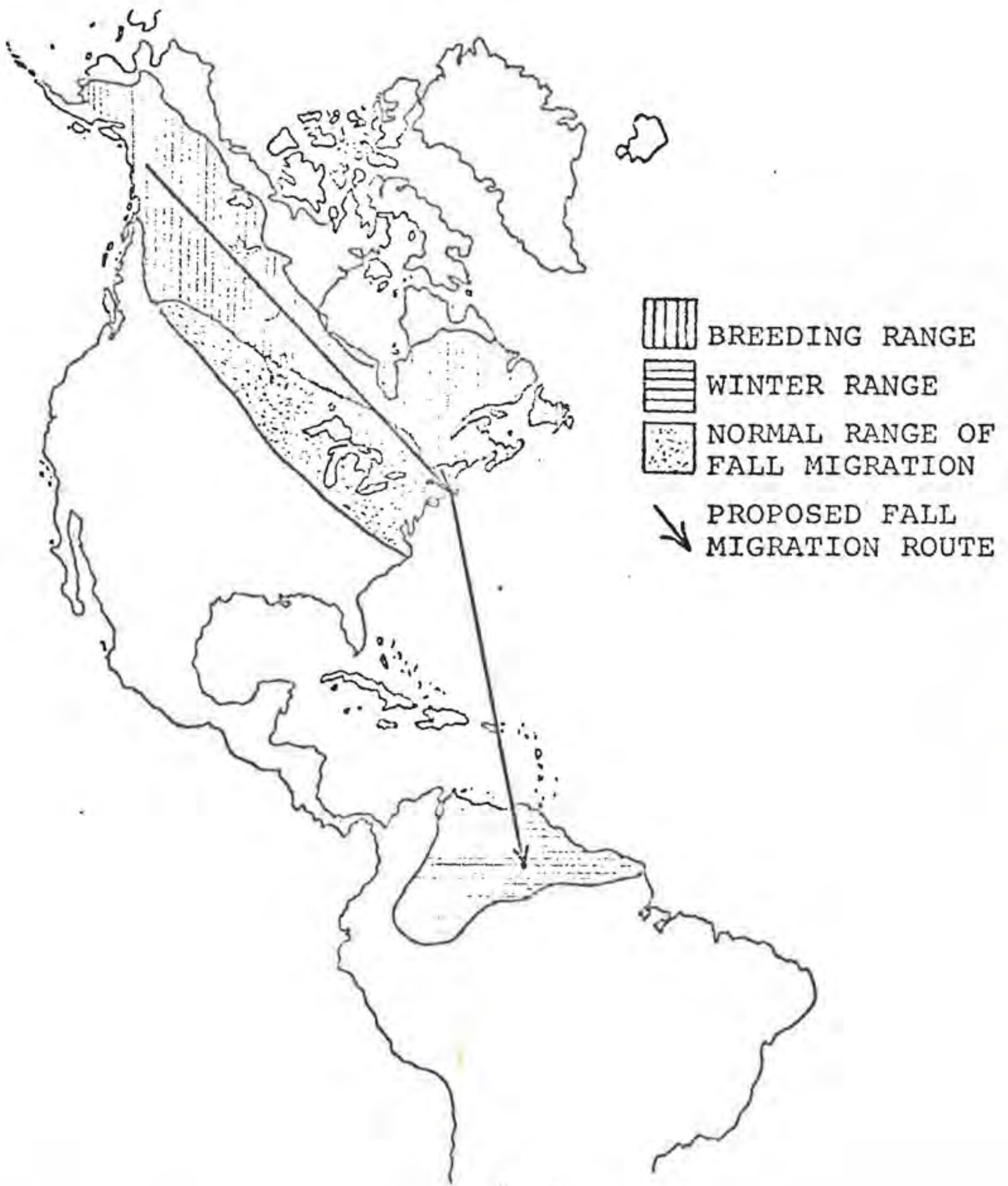
If it is found that each bird tested is significantly directed over many nights, then it can be assumed that these birds are misoriented individuals. It would then be desirable to determine whether the mechanism involved is simple misorientation or mirror image misorientation. To answer this question, a good estimate of the mean directions shown by several different individuals of the same species must be obtained. If simple misorientation is operative and all angles of misorientation are equally probable, then a wide range of mean directions would be expected among different individuals of the same species. If, on the other hand, simple misorientation is operative and certain angles of misorientation are preferred, then the mean directions of various individuals would be expected to be similar. This same result, however, will also occur if mirror image misorientation is the operative mechanism. To differentiate between the last two hypotheses, the preferred direction of the entire sample of a given species must be examined. If this direction is not a reasonable mirror image direction, simple misorientation may be assumed to be operative. If, however, this direction is a reasonable mirror image direction, then a strong indication, although not a conclusive proof, that mirror image misorientation is the controlling mechanism will have been obtained. It is thus apparent that a reasonably large sample size of a single species is needed in order to determine the mechanism of misorientation. Three years of effort produced such a sample size for only the Blackpoll Warbler (Dendroica striata). As a result, only the Blackpoll Warbler orientation data is included in the experimental part of this dissertation.

There are several additional reasons why the Blackpoll Warbler is an excellent experimental species with which to test various hypotheses regarding the mechanism of fall vagrant warbler occurrences. First, the correct fall migration route of the Blackpoll Warbler is probably better known than that of any other North American wood warbler.

Based on an analysis of 140,000 warblers killed during nocturnal migration at 135 locations in eastern North America, a systematic sample of migrant warblers obtained over six or more years at 14 eastern banding stations, and the results of extensive radar tracking along the Atlantic Coast, Nisbet [1970] has detailed the fall migration route of the Blackpoll Warbler. A representation of Nisbet's proposed route is presented in Figure 8-1. Second, the correct ESE transcontinental migration route of this species, as shown in Figure 8-1, appears to be a fairly uniform characteristic of the entire population of Blackpoll Warblers. This suggests the important result that a single mirror image misorientation direction (WSW) will also be characteristic of all populations of this species. This characteristic, therefore, will considerably simplify the interpretation of orientation data gathered on vagrant individuals of this species.

FIGURE 8-1

DISTRIBUTION AND FALL MIGRATION ROUTE
OF THE BLACKPOLL WARBLER
(AFTER NISBET, 1970)



CHAPTER 9

EXPERIMENTAL METHODS

Capture of Experimental Birds

Although the Blackpoll Warbler is the most abundant definite vagrant warbler in California, the bird is by no means common. One or more Blackpoll Warblers can usually be found on about half of the days during their peak migratory period, September 15-October 15, if one diligently searches certain favored coastal "oases" such as are present at Point Reyes, Marin County, Point Pinos, Monterey County, or Point Loma, Imperial Beach or Otay, San Diego County. The capture of these birds, however, is another matter. They usually occur in isolated windbreaks of very dense cypress or tamerisk trees and generally remain high enough in the foliage that normal mist netting operations fail to capture them. In addition, most of the vagrant locations are on private lands where an extensive mist netting operation is impractical.

Fortunately, Blackpoll Warblers occur most abundantly on Southeast Farallon Island where, since 1968, the Point Reyes Bird Observatory has established a continuously manned field station. The island has three trees, two Monterey Cypress (Cupressus macrocarpa) with overlapping canopies growing on the leeward side of one of the Coast Guard houses and a nearly prostrate Monterey Pine (Pinus radiata) growing along the windward side of a small hill. Needless to say, the majority of the arboreal landbirds that arrive on the island soon gravitate to one of these trees. The first arrival location on the island, however, is, as often as not, around the lighthouse located atop the 343 foot hill that occupies the majority of the island area. Accordingly, these preferred locations are all well supplied with the tools to capture landbirds. The two cypress trees are surrounded by two 12-meter and two 6-meter, 36-mesh mist nets. Beneath the trees sits a water-baited house trap, 8' x 8' x 4'. The prostrate pine is completely enclosed by a large Heligoland trap while a variable number of mist nets and another house trap are present near the light atop the hill. Five years of records indicate that fully 75% of the vagrant warblers found on the island can be captured. Accordingly, I based my operations on Southeast Farallon and was present there between October 1-15, 1969, September 1 - October 14, 1970 and September 15 - October 29, 1971.

Twenty-four Blackpoll Warblers were used in the course of this investigation. Twenty-two of them were captured on Southeast Farallon. The remaining two were captured, quite fortuitously, at Palomarin Ranch, Bolinas, Marin County (only 18 miles from Southeast Farallon), and at Point Loma, San Diego County. The following data were taken on all captured birds: date, time and location of capture, age (by skull ossification), weight, fat, wing length and any presence of molt. The amount of fat and the degree of skull ossification were subjective measurements based on the generally used increasing scale of 0, trace, 1, 2, 3. In the case of skull ossification, a 3 class represents complete ossification. I often modified the basic classes with + and - modifiers. In addition, I often took tail, culmen and tarsus measurements, recorded plumage characteristics and attempted to sex the individuals by means of a combination of wing length and plumage characteristics. I do not, however, believe that the sex data are completely reliable. Finally, to facilitate the identification of individual birds, each bird was banded with a small numbered plastic color band. A summary of the capture data for all 24 Blackpoll Warblers is presented in Table 9-1. It is important to note that this sample of 24 Blackpoll Warblers was entirely comprised of immature birds.

Maintenance of Experimental Birds

Because of their very small sizes, extremely active and nervous behavior and insectivorous diet, wood warblers are notoriously difficult to keep in captivity. The problems are even more acute when full grown warblers are taken from the wild. The most critical time in keeping such a bird is the breaking in period, generally about the first 48 hours of captivity. If the bird survives this time it can usually be kept indefinitely although subsequent periods of molt

TABLE 9-1

CAPTURE DATA ON ALL BLACKPOLL WARBLERS USED IN THIS STUDY

BIRD NUMBER	LOCATION	DATE	TIME	AGE	SKULL OSSIFICATION	WEIGHT (grams)	FAT	WING LENGTH (mm)	MOLT	SEX
21	Bolinas	Sep. 9,1969	1000	Imm.	2	10.8	0	73.0	0	M
22	S.E. Farallon	Oct. 5,1969	1800	"	3-	11.0	1-	72.5	0	U
23	"	Oct. 6,1969	1600	"	1	12.0	1	73.5	0	M
24	"	Sep.21,1970	1010	"	1+	12.3	T-	74.5	0	M
25	"	Oct. 1,1970	1300	"	2	14.8	2-	76.0	0	M
26	"	Oct. 3,1970	0815	"	1+	11.8	0	75.5	0	M
27	"	Oct. 3,1970	1230	"	1+	11.7	1	70.5	0	F
28	"	Oct. 4,1970	1845	"	2	14.1	2-	71.0	0	F
29	"	Oct.12,1970	0900	"	2	11.2	T-	69.0	0	F
30	Point Loma	Oct.27,1970	1145	"	2	17.3	3-	75.5	0	M
31	S.E. Farallon	Sep.17,1971	1300	"	1+	13.1	1	75.5	0	M
32	"	Sep.17,1971	1500	"	T+	11.8	T	72.0	0	F
33	"	Sep.17,1971	1700	"	1	10.9	T	74.5	0	M
34	"	Sep.17,1971	1800	"	T+	11.1	T-	70.0	0	F
35	"	Sep.21,1971	0830	"	1+	10.2	T	69.0	0	F
36	"	Sep.21,1971	0900	"	1	11.4	1-	69.0	0	F
37	"	Sep.21,1971	0900	"	1+	11.3	T-	74.0	0	M
38	"	Sep.21,1971	1530	"	1	12.3	1	75.0	0	M
39	"	Sep.21,1971	1630	"	T	12.3	1	75.0	0	M
40	"	Sep.22,1971	1130	"	1	10.9	T	68.0	0	F
41	"	Sep.22,1971	1130	"	1	12.1	1-	69.5	0	F
42	"	Sep.22,1971	1200	"	1	10.3	0	71.5	0	F
43	"	Oct. 4,1971	1830	"	2+	10.6	0	74.0	0	M
44	"	Oct.11,1971	0915	"	2	13.0	1+	75.0	0	U

present additional difficulties. During the course of this investigation, I developed a technique of housing and feeding that resulted in a better than 90% survival rate in wild captured wood warblers of all species. Fortunately, Blackpoll Warblers are comparatively robust and sluggish warblers and, as such, are easier to keep than smaller more active species such as Wilson's Warblers or American Redstarts. Only three Blackpoll Warblers were lost during the breaking in period, two that were never tested and bird number 22 of the present study.

A summary of the successful technique for keeping wood warblers in captivity is as follows. The birds were placed, immediately after the capture data were recorded, into small holding cages, the dimensions of which were between 8" x 8" x 8" and 12" x 12" x 8". A freshly captured bird was always placed alone into a holding cage or into a cage containing an already well broken in bird. Two freshly captured birds were never placed into the same cage. Furthermore, it was found inadvisable to keep more than two birds in a single cage. Each cage was supplied with two perches so that the birds could jump from one to the other without having to flutter against the walls or bottom of the cage. All parts of the cage that were open to light, except the back side, were kept covered with a white bedsheet to prevent frantic activity when a person was working around the cages. The back side of the cage which was open to light faced a blank wall. The birds were not allowed a view of trees or bushes or they would continually beat themselves against the back side of the cage in an attempt to reach them. The cages were kept out of the wind, and, when possible, in a heated room.

Warblers, especially during migration, have voracious appetites. It was quite common for a recently captured 11 gram Blackpoll Warbler to eat over 100 "large" mealworms in a single day! A freshly captured bird was placed into a cage already supplied with food. Water, however, was not added until the second day in captivity since open containers for water were used. Otherwise the birds would become soaked in a matter of minutes as a result of their initial escape efforts. Food was placed against the back side of the cage since that was the direction the birds generally faced. The following diet was found to be adequate to keep warblers in good health for extended periods of time: an abundance of "large" mealworms, strained yolk of hard-boiled eggs, a commercially available soft-billed bird food mixture, small quantities of moist ripe fruit (e.g., oranges), water and commercially available liquid vitamins. Of course the mealworms made up the bulk of the diet. Fresh food was placed in the cages daily. During the breaking in period, I found it desirable to place the mealworms in a shallow dish and also to place a few on top of the egg and soft-billed bird food mixture. The birds seemed to respond more quickly to freely crawling mealworms than to a mass of worms contained in a deeper feeding dish. They also learned to pick up the strained egg as they picked up mealworms out of it. Once the birds were broken in, however, the mealworms were placed in a deeper dish from which they could not escape.

All birds in the course of this study were maintained under the natural photoperiod at the particular locality where they were kept. On Southeast Farallon, the birds were maintained in a heated room with a large west-facing window. At Stanford University, the birds were kept in a west-facing greenhouse having an opaque east side. In San Diego, the birds were kept on a west-facing outdoor patio, well sheltered from the wind. The weight and subjective fat content of each bird were monitored about every second day that the birds were kept in captivity. These measurements were taken, as often as was possible, during the middle or late afternoon. This was done, not only to obtain data on the timing of the physiological readiness for migration, but also to monitor the health of the captive birds.

Orientation Tests on Experimental Birds

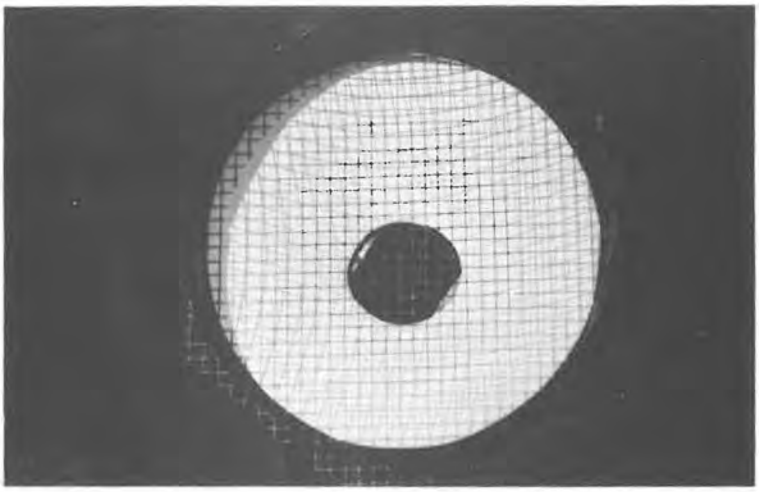
Orientation data were obtained by the "footprint" technique as developed by Emlen and Emlen [1966]. The orientation cage rested on the rim of a two quart aluminum pudding pan, in the center of which was placed a thin piece of sponge cloth moistened with black printer's ink. The walls of the cage were made from a white desk blotter which was cut, formed and stapled into a funnel of slope 45°. The top diameter of this funnel was about 37 cm. while the bottom diameter was 10.7 cm. This shape was obtained by cutting out of the flat desk blotter a disk with an outer radius of 25.7 cm. and an inner radius of 7.6 cm. For the purposes of cutting, the blotters were held between two pieces of plywood and cut, 125 at a time, by means of a band saw. Staple lines were marked on the flat blotters at an angular distance of about 256°. The actual assembly (stapling) was done at the location of testing. A blotter paper weight of 240 pounds per 1000 sheets was found to be sufficient to maintain the shape of the funnel on exceedingly humid nights (as are common on Southeast Farallon). The top of the cage was formed by a square piece of one-half inch mesh hardware cloth to which was attached a circular shield of sheet metal, 37 cm. in diameter and 8.6 cm. high. The inside of this shield was painted flat black. The purpose of this shield was to effectively block out of the bird's view all objects on the horizon and to eliminate any horizon glow caused, for example, by the lights of a distant city. In accomplishing this purpose, the lower 45° of the sky is, of course, blocked from the view of the bird when it is standing on the sponge cloth in the center of the cage. This angle decreases to 30° when the bird jumps up the side of the cage. An example of an assembled orientation cage is shown in Figure 9-1.

Winds on Southeast Farallon during orientation tests usually averaged 10 knots and occasionally reached 24 knots with gusts of over 30 knots. In order to keep the orientation cages from blowing away, each one was individually set up inside of a strong corrugated cardboard produce box, the bottom of which was opened and weighted with rocks.

Orientation tests were conducted at three locations:
(1) Southeast Farallon Island, 37°45'N, 123°0'W,
(2) Stanford University campus 37°23'N, 122°12'W and
(3) Point Loma 32°39'N, 117°17'W. The exact location of testing on Southeast Farallon was on a concrete foundation of a destroyed Coast Guard installation on the south sea terrace near East Landing. This location was favorable for two reasons. First, it was far enough removed from the lighthouse atop the hill that the birds could not directly see the light and yet close enough to the light so that the diverging beam did not brighten the vicinity of the orientation cage. This situation is schematically shown in Figure 9-2. Second, this location was on the leeward side of the island and allowed more ease in setting up the orientation tests on nights of extremely high winds. The location of the tests at Stanford University was on a remote area of the campus removed as far as possible from the

FIGURE 9-1

EXAMPLE OF ASSEMBLED "FOOTPRINT" ORIENTATION
CAGE USED IN THIS STUDY
(SEE TEXT FOR DETAILS)

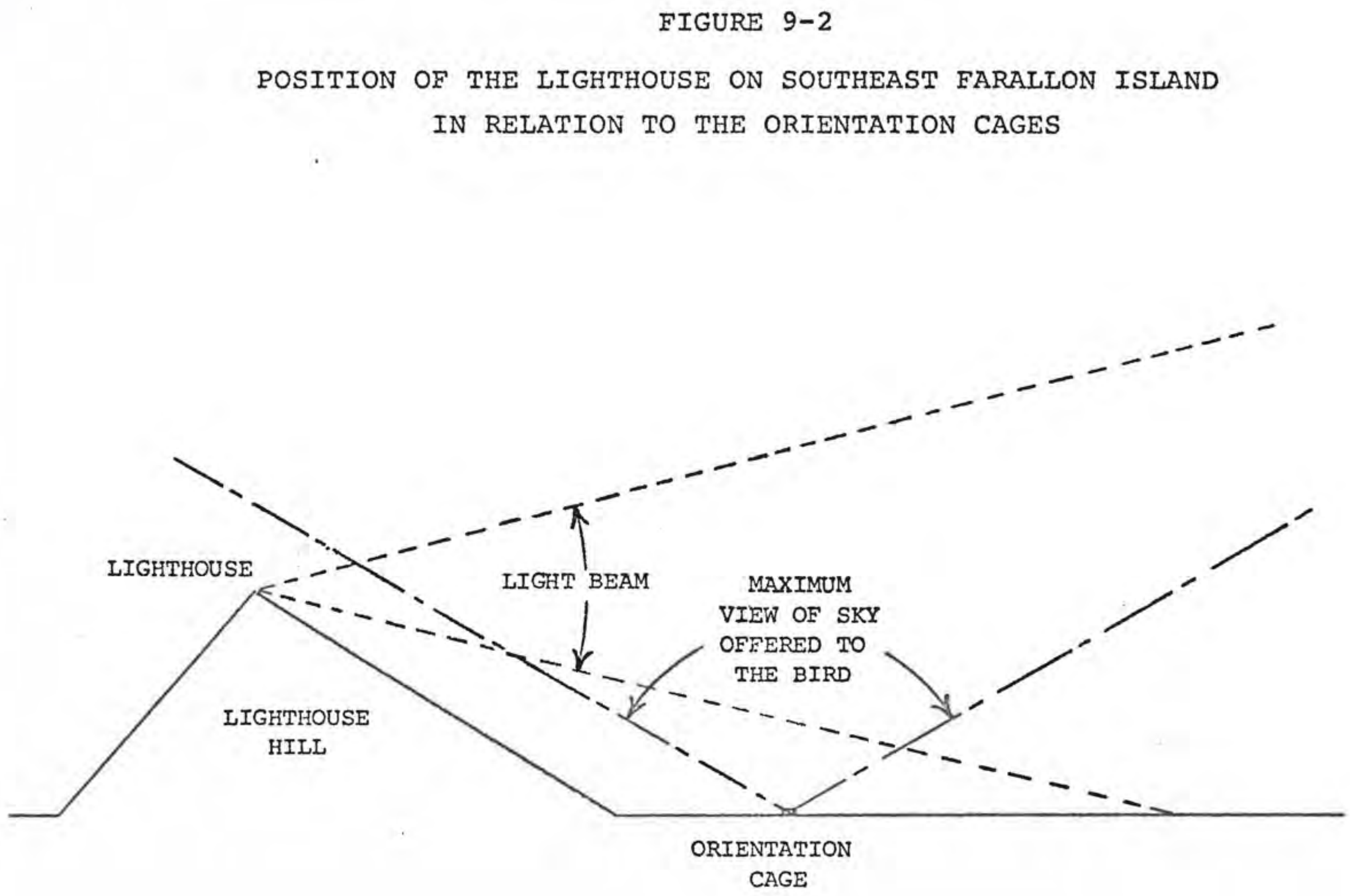


TOP VIEW

SIDE VIEW

FIGURE 9-2

POSITION OF THE LIGHTHOUSE ON SOUTHEAST FARALLON ISLAND
IN RELATION TO THE ORIENTATION CAGES



lights of Stanford and Palo Alto. The location on Point Loma was at the Cabrillo National Monument removed as far as possible from the lights of San Diego.

In order to reduce the number of variables present in the test data, all tests were conducted on clear, or at least mostly clear, nights. Because of the possibility of a disruptive phototactic response by birds toward the moonlit part of the orientation funnel, all tests were conducted on moonless nights or before the moon had risen or after it had set. During the course of the experiments in 1969, it was discovered (on Blackpoll Warblers as well as on many other species of warblers) that the vast majority (often 100%) of the total activity of a given bird on a given night was produced within the first hour of testing. Accordingly, all of the 1970 and 1971 data as well as 2 of the 16 1969 data were based on tests of exactly one hour duration. Thus a total of 507 of the 521 Blackpoll Warbler tests presented in this dissertation are one hour tests. In an attempt for consistancy I tried to begin each test between 90 and 105 minutes after local sunset, a time by which all of the sunset glow has disappeared from the west and the stars are in full brightness. However, because of the influence of the moon, there are only 12 consecutive nights during each lunar cycle in which a one hour test at this time of the night can be run. Since several of the nights during these 12 day cycles were liable to be overcast, especially on

Southeast Farallon where low overcast or coastal fog actually predominates, and I desired to obtain a reasonable sample size for each test period, I often had no choice but to begin tests later in the night, after the moon had set.

The procedure used in conducting a "footprint" orientation test was simple and straightforward. The blotting paper funnels were stapled, an ID number was marked on each one along with the date of the test and a small mark was made for north. The position of the test apparatus (staple line and seam line of the shield) with respect to north was continuously varied so that it would not influence, in a consistant manner, any directional choices the birds might make. The sponge cloths were then inked with a qualitatively constant amount of printer's ink. This inking was faithfully repeated every night for every orientation cage to insure that the amount of ink and its viscosity were consistant for all birds and for all tests. The cages were then set up. The birds were then removed from their holding cages by the light of a very dim head lantern (two layers of masking tape were placed over the light), placed in holding bags and transported in the dark to the orientation cages. The birds were then quickly placed into the orientation cages and the cages were aligned by eye with Polaris, true north. The exact location of the particular orientation cage, within the array of cages, into which a given bird was placed was varied in a nearly random manner from night to night. The species and band number were recorded for each bird to correspond to the ID number of the particular orientation funnel into which each bird was placed. The birds were then left for exactly one hour.

While the birds were in the orientation cage, the following environmental data were recorded: date, time of test, wind direction and velocity, percentage and location of any cloud cover and ambient temperature. Any unusual environmental effects were also noted such as the presence of searchlights, any excessive horizon glow or an inordinately hazy or smog-filled sky. A summary of these environmental data for each test night is presented in Appendix II. When the hour was up, the birds were taken from their orientation cages in the same order that they were put in and returned in the dark to their specific holding cages. The orientation funnels were then picked up and spread out in a safe place to dry overnight. The pans with the inked sponge cloths were stacked and stored in a shaded location to prevent the ink from drying out. On the following day, when the orientation funnels had dried, the staple lines were marked with light pencil, the species name and band number were recorded on each funnel, and the funnels were unstapled. They were then ready for analysis.

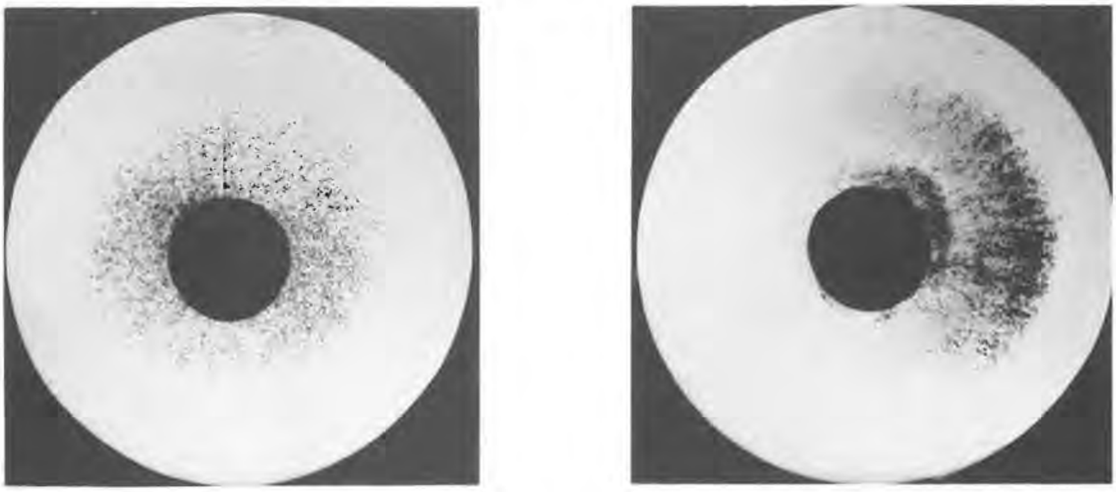
CHAPTER 10

THE DIGITIZATION OF THE FOOTPRINT DATA

A visual inspection of the completed orientation traces usually supplies a good indication of the amount and directionality of a given bird's activity on a single night. Examples of completed orientation traces for Blackpoll Warblers are shown in Figure 10-1a-c. Figure 10-1a, for example, shows a nearly uniform distribution of medium activity. Figure 10-1b shows an apparently unimodally directed distribution of high activity. Figure 10-1c shows an apparently bimodal distribution of medium activity directed in approximately 180° opposite directions. For statistical purposes, however, it is necessary to digitize the footprint data, thereby translating them into numerical form. Emlen and Emlen [1966] accomplish this digitization as follows: first, the trace is subdivided into 24 equal 15° sectors; next, the amount of activity in each sector is evaluated by directly comparing the density of the footprints (blackness) with densities on a reference scale that has been designed to depict 20 equally increasing increments of activity. Thus, each 15° sector is given a numerical value from 1 to 20 that defines the amount of activity in arbitrary activity units. Such a method is entirely subjective and could introduce subjective bias into the statistical analysis. I, therefore, expended

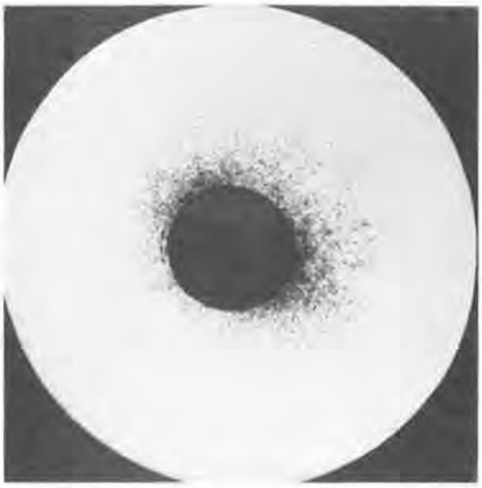
FIGURE 10-1

EXAMPLES OF COMPLETED "FOOTPRINT" ORIENTATION TRACES
MADE BY CALIFORNIA CAPTURED BLACKPOLL WARBLERS
UNDER THE CLEAR NIGHT SKY



a. NEARLY UNIFORM DISTRIBUTION OF MEDIUM ACTIVITY; BIRD 40; TRACE 629; 9/26/71

b. APPARENTLY UNIMODAL DISTRIBUTION OF HIGH ACTIVITY; BIRD 32; TRACE 414; 10/20/71



c. APPARENTLY BIMODAL DISTRIBUTION OF MEDIUM ACTIVITY; BIRD 40; TRACE 630; 9/27/71 considerable effort in an attempt to digitize the footprint data by non-subjective means.

The first approach that I tried involved the use of a specially designed optical densitometer to scan the footprint data. The procedure used was as follows. First, each trace was photographed with High Contrast Copy Film in a standard manner under uniform illumination. The negatives were then placed in a high quality enlarger and the image was projected downward onto a specially designed disk that rotated at a constant angular velocity. A series of five photocells were arranged along the radius of the rotating disk and were masked in such a manner that they responded to a small (5.5°) sector of the projected trace. The output of the photocells as they scanned the projected trace was then automatically plotted on a constant velocity X-Y recorder. The speed of the recorder was coordinated with the angular velocity of the rotating disk so that a constant distance along the X-axis corresponded to 360° around the projected trace. Average values of blackness at any point on the trace could then be read directly off of the Y-axis of the chart recording. To avoid the effects of external lighting, the entire apparatus was housed in a black box.

Unfortunately, this method did not supply the accuracy needed to correctly digitize the data. Errors stemmed from two sources. First, the illumination supplied by the enlarger was not uniform over the entire field and more importantly, was not uniform over time. Second, the photocells were not sensitive enough to resolve traces that displayed few but well directed footprints. High sensitivity photocells were available but unfortunately had very slow response times. This necessitated a very slow rate of angular velocity for the disk making the digitization of a large number of traces impractical. The method, however, has considerable feasibility but requires inordinately expensive equipment.

The second approach that was attempted involved fully seven months of concentrated effort. Through the kindness of the personnel at Stanford University's Artificial Intelligence Project (A.I.), I was given access to the computerized Hand-Eye facilities. The "Eye" of the Hand-Eye facility consisted of a specially designed television camera that was connected to an analog-digital converter in such a way that the voltage output of the television camera was digitized to 6-bit information at 320 points along each of 240 TV scan lines. This array of 76,800 6-bit data points was then inputted directly into a PDP-10 computer located in the same room. This digitization therefore produced one out of 64 potential darkness levels for each of the 76,800 points in the TV image.

The method whereby the TV "Eye" digitized the data contained on an orientation trace was as follows. First, a mapping program was constructed that mapped each of the

76,800 TV scan data points into one of 1440 bins; if the data fell outside of the trace, it was ignored. These bins corresponded to 180 two degree divisions around the orientation trace times 8 radial divisions of 3/4" each within every two degree sector. Thus, the footprint data could be digitized with respect to how high the bird jumps up the funnel as well as with respect to the direction the bird jumps. The 6-bit TV data was then averaged over each bin and over all 8 radial bins in each two degree interval to produce an average blackness for each interval. Reference values of "white" and "black" were obtained for each bin by allowing the TV "Eye" to see first a clean white blotter and then a flat black blotter. The difference between the average "white" and average "black" values for each bin were then set equal to 63 and the actual value of blackness was interpolated between these extremes. This method effectively compensated for the shading that is inherent in a TV image. This shading results from the fact that electrons hit the outer edges of the TV image at a more oblique angle than at the center thereby losing energy and producing an apparent darkening of the image near the periphery. This effect is most noticeable when the TV is looking at a uniformly white piece of blotter paper.

Since the white blotter paper upon which the orientation traces were made tends to discolor with age, a method was developed to compensate for this effect. The blackness of six small squares around the outer periphery of the trace (where the bird had left no marks) were averaged to get an average value of "white" for that trace. All of the values of "white" for the individual bins were then adjusted by the average value of "white" for that particular trace. All of these refinements were incorporated into a rather complicated series of computer programs that I wrote.

When the method was perfected, it was found to be capable of producing an extremely accurate digitized representation of the footprint data. However, a series of hardware problems continually plagued the technique and defied correction by software methods. The first was an unpredictable but anomolously high noise to sensitivity ratio at certain areas in the TV scan where the shading underwent fairly rapid change. This had the effect of producing unreliable data over these small areas. The second problem was also concerned with the shading which did not remain constant over time but rather fluctuated unpredictably. This instability was so great, at times, that reproducible values of "white" could not be obtained even one minute apart. In the end, the entire method had to be discarded. However, the effort was not entirely wasted. Enough good data was obtained on a fairly large sample of different traces to allow the construction of a series of standard 15° sectors each having an accurately determined value of blackness. The digitization of all of the

Blackpoll Warbler data presented in this dissertation was then accomplished by a subjective comparison of the blackness of a given 15° sector to the blackness of the non-subjectively determined standards.

The scale of standard blackness values was, like the scale used by Emlen, composed of increasing increments of blackness. Unlike Emlen's scale, however, it was not composed of <u>equally</u> increasing increments of blackness. It was felt that Emlen's method loses critical resolution, especially at lower end of the scale, since it has been suggested that the human eye detects differences in intensity acccording to the <u>logarithm</u> of the intensity rather than according to the intensity itself. It was therefore decided to create experimentally a scale of standards that most closely fitted the limits of resolution of my own eyes since I was to be doing all of the digitization. To accomplish this, a linear scale of values, V, was produced in which the range of blackness corresponding to any particular V value was proportional to some constant percentage of the mean blackness for that V value. Such a scale was then laid out by finding 15° sectors on actual traces that had been digitized by the TV "Eye" that had these mean blacknesses. Inspection of this scale by eye quickly indicated whether it was too coarse, that is, my eyes were capable of perceiving smaller differences in blackness than those indicated by the scale, or too fine, that is, my eyes could not readily distinguish the differences in blackness between adjacent V values. The scale finally chosen was one in which the range of blackness for any V value corresponded to 15% of the mean blackness for that V value. This scale fitted my eyes very nicely, that is, I could readily perceive the difference in blackness between adjacent V values but the differences were relatively small. This method, of course, could not be extended to very small blacknesses because it would produce an infinite number of V values as the blackness approached zero. The bottom end of the scale (V values below 10) was, therefore, based on an actual count of the number of dots present in the particular 15° sector. This scale produced 34 V values ranging in blackness from 0.040 at V=1 to 58.605 at V=34. Pure white, that is no marks, corresponded to a blackness of 0.0 while pure uniform black corresponded to 63.0. These represent, of course, the limits of the 64 possible 6-bit numbers produced by the TV "Eye". During the course of this investigation, no single 15° sector was ever found to have a blackness value greater than 37.3. As a result, only 31 V values were actually used. A plot of the mean blackness for each of the 31 V values is presented in Figure 10-2. At this point, I was curious to see how closely the V values corresponded to the logarithm of the mean blacknesses. Figure 10-3 shows these same data plotted on a log scale. The values clearly fall on a straight line

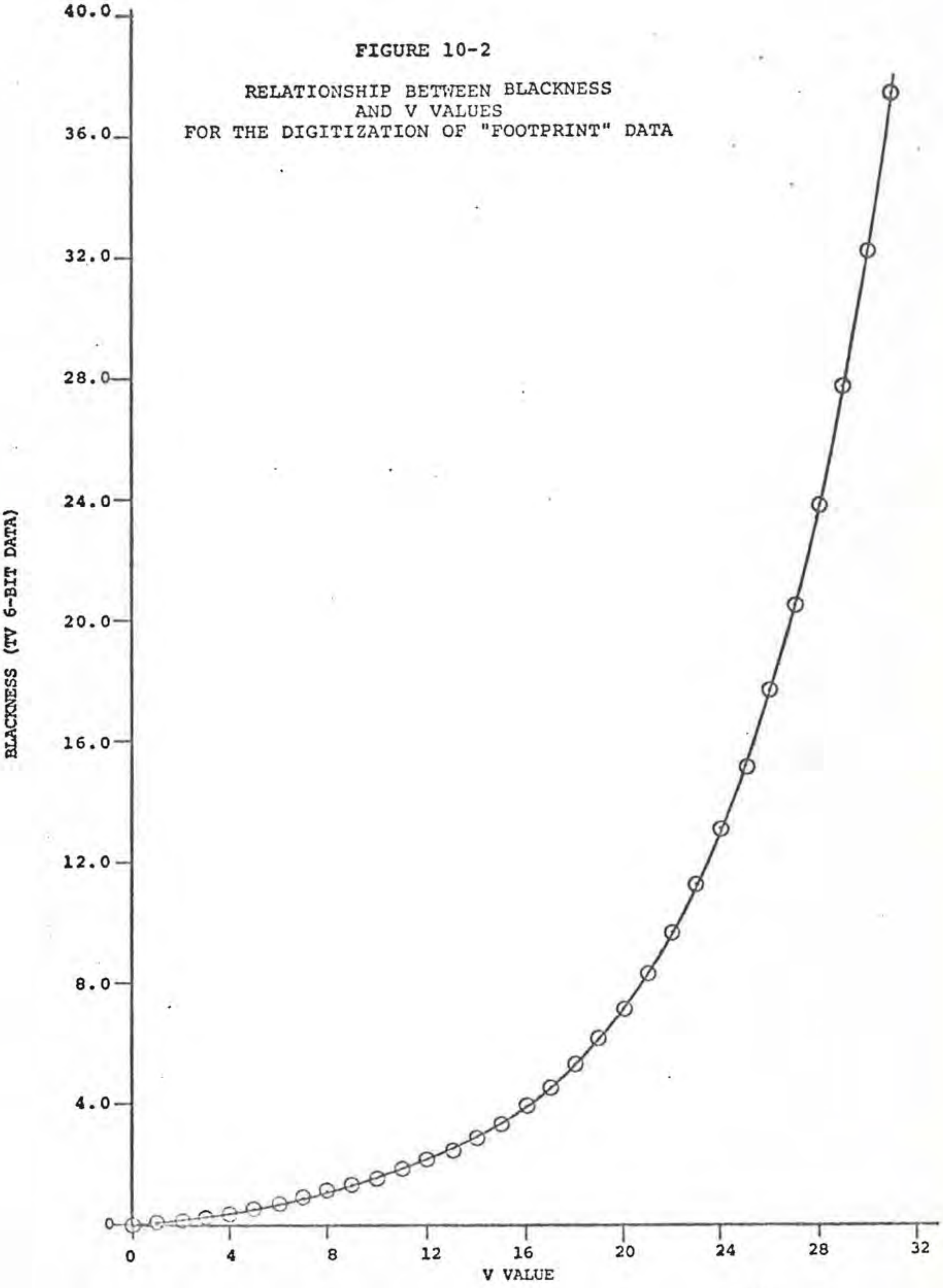
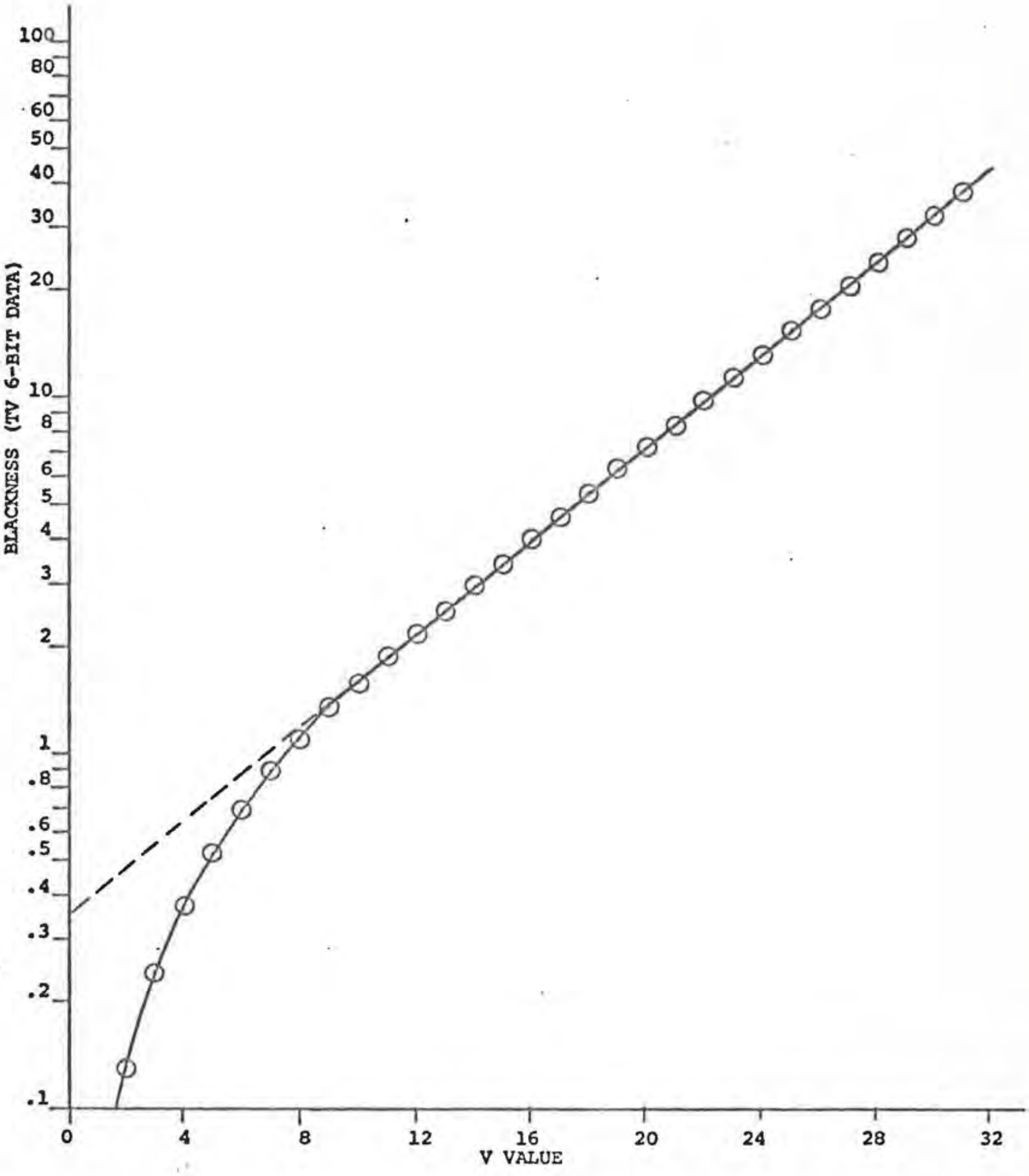


FIGURE 10-2

RELATIONSHIP BETWEEN BLACKNESS
AND V VALUES
FOR THE DIGITIZATION OF "FOOTPRINT" DATA

FIGURE 10-3

LOGARITHMIC RELATIONSHIP BETWEEN BLACKNESS AND V VALUES
FOR THE DIGITIZATION OF "FOOTPRINT" DATA



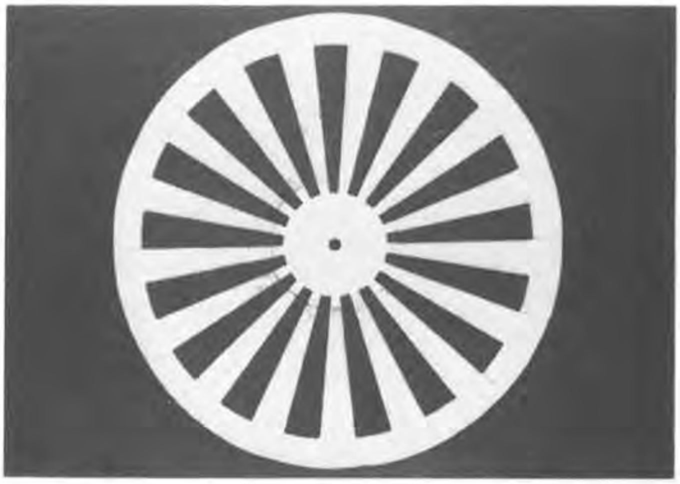
down to V=10 supplying experimental evidence that my eyes, at least, do perceive differences in blackness according to the logarithm of the blackness rather than according to the blackness itself.

To facilitate the comparison of the 15° sectors of a real trace with the standards, two blackness wheels were constructed. These wheels consisted of a circular array of alternating 15° spaces and 15° spokes. (Note that 15° sectors on the conical trace correspond to 10.625° sectors on the flattened trace.) Fifteen degree sectors were then cut from actual orientation traces in such a manner that the average blackness of each 15° sector, as determined by the TV "Eye", very closely approximated the mean value of blackness for each V value. These 31 sectors were then glued onto the spokes of the blackness wheels in order of increasing V. The actual blackness wheels used in the digitization of all of the data presented in this dissertation are shown in Figure 10-4.

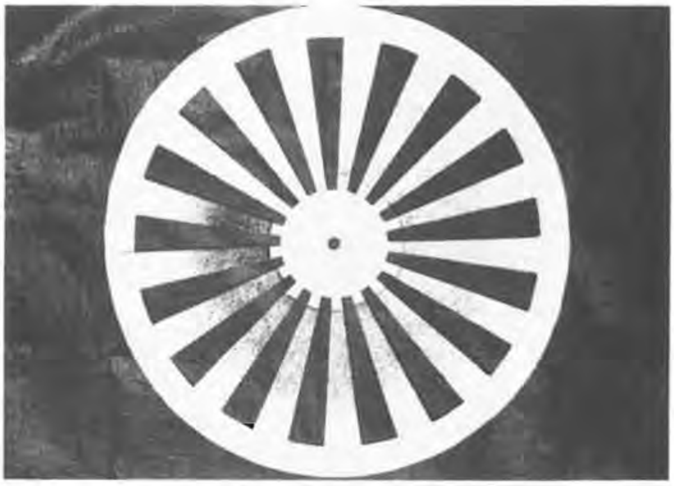
A special vacuum easel, designed to facilitate the actual digitization of the traces, was constructed out of plywood and plexiglass (Figure 10-5a). An orientation trace was held firmly in place by the easel after being carefully aligned by means of the starting line and alignment circles that were drawn on the easel (Figure 10-5b). The angular position of the end point of the flattened trace (staple line), AC, was then recorded by means of the scale drawn on

FIGURE 10-4

BLACKNESS WHEELS DESIGNED TO DIGITIZE
"FOOTPRINT" ORIENTATION DATA
(SEE TEXT FOR DETAILS)



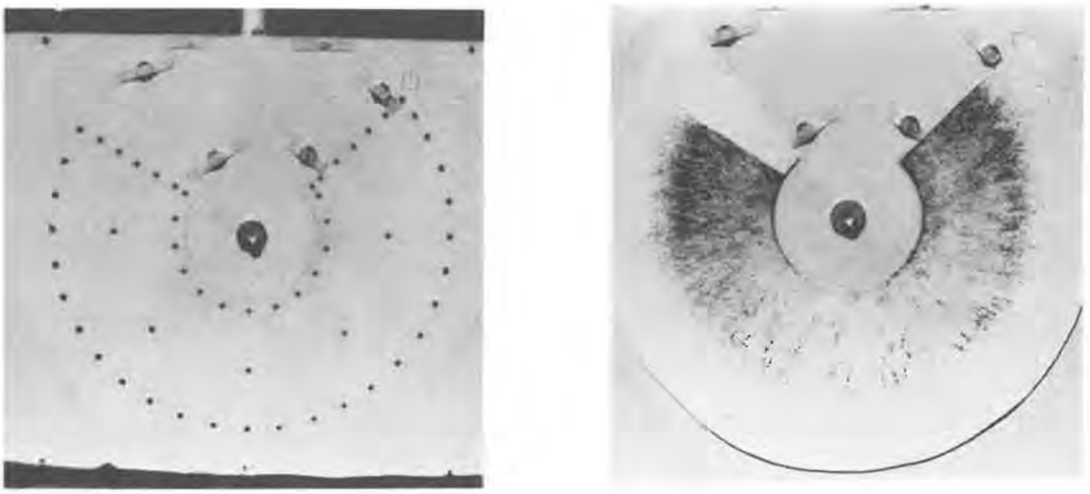
a. WHEEL #1: V VALUES FROM 1 TO 17



b. WHEEL #2: V VALUES FROM 18 TO 31

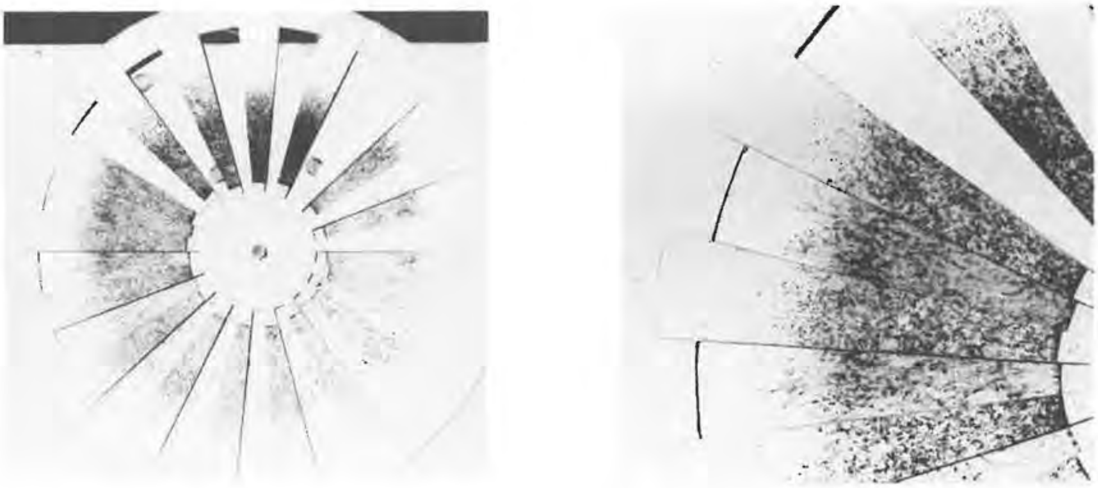
FIGURE 10-5

EXAMPLE OF EQUIPMENT AND METHOD FOR
DIGITIZING "FOOTPRINT" ORIENTATION DATA
(SEE TEXT FOR DETAILS)



a. SPECIALLY CONSTRUCTED VACUUM EASEL FOR HOLDING ORIENTATION TRACES

b. VACUUM EASEL WITH TRACE ALIGNED AND HELD IN PLACE



c. VACUUM EASEL WITH TRACE AND APPROPRIATE BLACKNESS WHEEL IN PLACE

d. DIGITIZATION OF 23rd 15° SECTOR. A COMPARISON IS SHOWN WITH V=26 and V=27 ON BLACKNESS WHEEL.

the easel. Similarly the angular position of true north, AN, was also recorded by means of the scale on the easel. The exact position of true north, NOR, relative to the start of each actual trace could then be computed as

$$NOR = 360.0 \cdot AN/AC \qquad (10-1)$$

The appropriate blackness wheel was then placed over the trace (Figure 10-5c) and rotated until the V value was found that best corresponded to the blackness of the first 15° sector of the trace. This procedure was continued until all twenty-four 15° sectors were satisfactorily digitized (Figure 10-5d).

The method outlined above was laborious and time-consuming, especially considering that over 500 traces had to be digitized. Nevertheless, I felt that the effort was worth the trouble since I felt that an extremely accurate digitization was being obtained for each trace. To test the reproducibility of the digitization, about 4% of the digitized traces were set aside and redigitized after about a week had passed. The Pearson product-moment coefficient of correlation, r, was then computed for each of the 21 traces that were digitized twice. These data are presented in Table 10-1 and indicate a very high degree of correlation between the two digitizations.

This method of digitization produces a series of 24 integer values for V, one for each 15° sector. These V values can be converted to the arbitrary blackness values

TABLE 10-1

PEARSON PRODUCT-MOMENT COEFFICIENT OF CORRELATION, r, FOR TWO INDEPENDENT DIGITIZATIONS OF THE SAME 21 ORIENTATION TRACES OF CALIFORNIA CAPTURED BLACKPOLL WARBLERS

TRACE NUMBER	r
225	0.971
250	0.974
275	0.982
300	0.985
325	0.989
350	0.979
375	0.997
400	0.922
425	0.935
450	0.927
475	0.972
498	0.983
523	0.984
550	0.981
575	0.987
600	0.969
625	0.925
650	0.979
675	0.977
700	0.994
724	0.993
AVERAGE	0.972

according to the curve shown in Figure 10-2. It would be desirable, however, if the arbitrary blackness values corresponded to some estimate of the activity that had a more real physical basis. To accomplish this, the number of jumps that 21 different individual warblers of 6 species made on single night tests was determined by listening to the activity of each bird during an entire one hour test. The 21 traces produced by these birds were then digitized by the method outlined above and the total blackness was calculated for each trace. The Pearson product-moment coefficient of correlation, r, was determined for this sample and found to be $r=0.853$ which indicates that the amount of blackness produced during a single night's test is significantly correlated with the total number of jumps made by the individual warbler during that test ($P<.01$). The conversion factor, F, defined as the amount of blackness produced/jump, was then calculated for all 21 individual birds and the mean of this value was obtained: $\overline{F}=0.28635$ blackness units/jump. This conversion factor was then used to convert the V value for each 15° sector into an activity value, A, equal to the estimated number of jumps in that 15° sector. The digitized footprint data were then ready for statistical analysis. A computer listing of all of the digitized raw data used in this dissertation is presented in Appendix III.

CHAPTER 11

THE CHARACTERIZATION OF DIGITIZED DATA

Once the footprint data had been digitized into 24 V_i values corresponding to the 15° sectors, these V_i values were entered into the Stanford Computation Center's IBM 360 computer. These data were then converted, by the method described in Chapter 10, into 24 activity values, A_i, which corresponded to the number of jumps in each 15° sector. At this point, an empirical circular distribution of the activity had essentially been created. To facilitate the understanding of these data, it is necessary to characterize each empirical circular distribution by a small number of parameters that, as completely as possible, describe the bird's behavior during a given test. If it is suspected that the empirical distributions are unimodal, that is have a single preferred direction, three parameters are of interest: (1) a parameter, AT, that is a measure of the total amount of activity that the bird has produced during the test; (2) a parameter, Φ, that is a measure of the preferred direction in which the bird has oriented its activity; (3) a parameter, r, that is a measure of the concentration of activity about the preferred direction.

The total amount of activity, AT, that the bird has produced on a given night, may be unambiguously represented by the total number of jumps that the bird made during that test:

$$AT = \sum_{i=1}^{24} A_i \quad . \qquad (11\text{-}1)$$

The calculation of the preferred direction of the empirical circular distribution, however, is not as unambiguous. Two different measures of the preferred direction may be considered. The first is called the empirical mean direction, Φ, which is defined as the direction that points toward the center of mass of the circular distribution. It is calculated as the direction of the mean vector or vector sum of the distribution by the following familiar equations:

$$X = \frac{1}{AT}\sum_{i=1}^{24} A_i \cdot \sin \alpha_i \qquad (11\text{-}2)$$

$$Y = \frac{1}{AT}\sum_{i=1}^{24} A_i \cdot \cos \alpha_i \qquad (11\text{-}3)$$

$$\Phi = \tan^{-1} (X/Y) \qquad (11\text{-}4)$$

where α_i is the midpoint of each 15° sector. The second measure of preferred direction may be called the mode direction, M, and is defined as that direction where A_i is a maximum:

$$M = \alpha_i \qquad (11\text{-}5)$$

for that i where A_i is a maximum. If A_i reaches its maximum value in two or more 15° sectors, M may be estimated as the mean of these various α_i. It should be noted that if the empirical circular distribution displays axial symmetry, Φ=M. If the empirical circular distribution is not axially symmetric, the difference Φ-M may be used as a measure of the skew in the distribution.

Corresponding to each of these measures of the preferred direction of the empirical distribution, a measure of the concentration about that preferred direction can be calculated. Corresponding to the mean direction, Φ, the mean vector length, r, is given by:

$$r = \sqrt{X^2 + Y^2} \quad . \qquad (11\text{-}6)$$

It should be noted that if the distribution is perfectly uniform, that is, all sectors have equal activities, r=0 and Φ does not exist. On the other hand, if the distribution is perfectly concentrated, that is, all of the activity lies in a single 15° sector, r=1 and $\Phi=\alpha_i$ of that sector. Thus, for all cases:

$$0 \leq r \leq 1 \quad . \qquad (11\text{-}7)$$

Corresponding to the mode direction, M, the mode intensity, I, is given by:

$$I = A_i/AT \qquad (11\text{-}8)$$

for that i where A_i is a maximum. In this case, it should be noted that if the distribution is perfectly uniform, I = 1/24 = 0.0417, while if the distribution is perfectly concentrated, I=1. Thus, for all cases:

$$0.0417 \leq I \leq 1 \quad . \qquad (11\text{-}9)$$

It is logical to ask which is the better estimate of the preferred direction, the mean direction or the mode direction. Both have interesting physical meanings. The mode direction is the direction that the bird chooses most often. On the other hand, the mean direction is the direction defined by the location, with respect to the starting point, at which the bird would end up if it were allowed to jump, unconstrained by a cage, A_i times in each direction α_i. This last characteristic is exactly what should be measured in order to determine what direction Blackpoll Warblers have followed to reach California. Thus, like most other researchers in the field of bird orientation, I have chosen the mean direction as the best estimate of the preferred direction shown by an individual bird when tested in an orientation cage.

As mentioned previously, however, visual inspection of the footprint data indicated that many of the birds appeared to prefer two or more directions during a single night's test. At present, no statistical methods are available for dealing with empirical multimodal circular distributions. I have developed an approximate method which may be of interest to workers in this field. This method, therefore, is outlined in detail.

It is first necessary to ask what constitutes a mode in an empirical circular distribution. Theoretically any sector, i, located at α_i, could be considered to represent a mode if its activity, A_i, is greater than the activity of each of the sectors on either side, that is, if

$$A_i > A_{i+1} \quad \text{and}$$
$$A_i > A_{i-1} \quad .$$

For an empirical circular distribution with i=24, one could expect a maximum of 12 modes. It seems likely, however, that such a distribution could be due to chance fluctuations, noise, in the measurements of A_i. It is, therefore, necessary to develop a method of mode finding that produces modes that are more likely to be real manifestations of the behavior of the birds rather than manifestations of noise in the measurements. Considering the size of the orientation funnel and the size of a Blackpoll Warbler, it seems likely that a single jump by such a bird could produce marks in at least two 15° sectors. Such behavior was confirmed by directly observing birds in orientation cages from beneath the cage. It was felt, therefore, that the least stringent mode finding algorithm should be that the activities of each of three adjacent 15° sectors, the peak, should be greater than the activities of each of two adjacent 15° sectors, the valleys, on each side of the peak. Such a mode finding algorithm was referred to as the three peak - two valley criterion, abreviated 3P-2V. Other more stringent mode finding algorithms that were derived included 3P-3V, 4P-2V, 4P-3V and a combination of either 3P-3V or 4P-2V.

It was decided to test these various mode finding algorithms on randomly produced circular distributions of data. It was felt that if the particular mode finding algorithm indicated a high percentage of multimodal distributions on randomly produced data, it was too weak. On the other hand, if the algorithm indicated a very small percentage of multimodal distributions, it was too strong. Each algorithm, therefore, was tested on 200 empirical circular distributions produced by the Stanford University's random number generator. These results, along with the characteristics of each mode finding algorithm, are presented in Table 11-1. An intuitive interpretation of these results suggested that algorithm number 5, the combination of the 3P-3V and 4P-2V algorithm, was the best candidate. Therefore, this mode finding algorithm was used on all of the data presented in this dissertation.

This mode finding algorithm was then programmed and applied by computer to all of the 508 active Blackpoll Warbler traces. It calculated the number of modes present on each trace as well as the extent and location (in terms of 15° sectors) of the peak of each mode when two or more modes were found on a single trace. The peak of a given mode was defined as the entire extent of the trace between the minimum sized valleys necessary to satisfy the particular mode finding algorithm. Of these 508 traces, 3 (0.6%) were found to have 3 modes, 183 (36.0%) were found to

TABLE 11-1

CHARACTERISTICS OF VARIOUS MODE FINDING ALGORITHMS TESTED ON 200 RANDOMLY PRODUCED CIRCULAR DISTRIBUTIONS

	ALGORITHM*	MINIMUM EXTENT OF A MODE	NO. OF POSSIBLE MODES PER TRACE	% TRIMODAL	% BIMODAL	% UNIMODAL	% NO MODES	% MULTIMODAL
1	3P - 2V	75°	4	10.0	30.5	46.5	13.0	40.5
2	3P - 3V	90°	4	0.5	8.0	51.0	40.5	8.5
3	4P - 2V	90°	4	2.0	16.0	53.0	29.0	18.0
4	4P - 3V	105°	3	0.0	2.5	28.5	69.0	2.5
5	Either 2 or 3	90°	4	3.0	24.5	54.5	18.0	27.5

* See text for explanation

have 2 modes, 322 (63.4%) were found to have 1 mode and none were found that contained no modes. If the trace was found to be unimodal, the unimodal analysis described above was used; however, if the trace was found to be multimodal, the approximate multimodal analysis, described below, was used. This entire procedure, incorporated into a single computer program, is referred to as the Single Trace Analysis.

The approximate multimodal analysis is now reduced to the problem of finding suitable estimates for the parameters of each mode. For example, if the distribution is found to be bimodal, five parameters are unknown: the total activity, AT_1, the mean direction, Φ_1, and the concentration about the mean direction, r_1, of the first mode and the mean direction, Φ_2, and the concentration about the mean direction, r_2, of the second mode. The total activity of the second mode, AT_2, can be easily obtained since $AT_2=AT-AT_1$. A rigorous solution to this problem can be obtained by choosing the correct underlying theoretical circular distribution for each mode, creating a theoretical mixture of the two distributions and iterating for the five unknowns. Since there exists no a priori knowledge of the form of the underlying theoretical distribution for the orientation behavior of a Blackpoll Warbler, and since each distribution is composed of only 24 data points it is felt that such an approach is hopeless.

An approximate solution to this problem, therefore, was obtained by means of the following two simplifying assumptions: (1) that all of the activity contained in the peak of each mode, that is in the extent between the valleys, belongs exclusively to that mode and (2) that the measure of concentration of activity about the mean, r, for each mode is related to the mode intensity, I, of that mode as if each mode fitted a circular normal or von Mises distribution. The density function of such a distribution is given as

$$f(\alpha) = \frac{1}{2\pi \cdot I_0(\kappa)} \cdot e^{\kappa \cdot \cos(\alpha - \theta)} \qquad (11\text{-}10)$$

where θ is the angle where $f(\alpha)$ takes its maximum value, κ is a parameter of concentration and $I_0(\kappa)$ represents the "Bessel function of purely imaginary argument of order zero" [Batchelet, 1965].

Based upon the above assumptions, the parameters of each mode, k, were calculated as follows. The proportion of the activity in each mode, PA_k, was determined as the activity in the peak of mode k divided by the sum of the activities in the peaks of all modes. The activity of each mode, AT_k, was then given by

$$AT_k = PA_k \cdot AT \quad . \qquad (11\text{-}11)$$

This method effectively considers all of the activity in the peak of a given mode to belong exclusively to that mode but proportions the activities of the valleys according to the activities of the adjacent peaks. The mean direction of each mode, Φ_k, was simply calculated as the vector sum of all of the activity contained in the peak of that mode. Thus, the valleys were effectively ignored as far as the calculation of the mean direction of each mode was concerned. The measure of concentration of activity about the mean for each mode, r_k, was determined from the mode intensity of that mode, I_k, by means of the table presented in Appendix IV. The value of I_k was calculated as

$$I_k = A_i/AT_k \qquad (11\text{-}12)$$

where i represents the particular 15° sector in the peak of the mode in question that contains the maximum activity.

The many assumptions involved in the approximate multimodal analysis just described do not lend much confidence that the method is capable of producing reliable results. It was therefore decided to test the method on bimodal mixtures of theoretical circular normal distributions having known parameters. It was felt that if the approximate multimodal analysis produced good results on circular normal distributions, it should produce reasonably meaningful results on empirical circular distributions.

The procedure for carrying out this test was as follows. Equation (11-10) was solved for $f(\alpha_i)$ for 24 values of α_i beginning at α_i=7.5° and increasing by 15° intervals. This produced a discreet distribution of data similar in format to that obtained from digitized orientation traces. This procedure was repeated for all combinations of $\theta=0°$, $100°$, $120°$, $140°$, $160°$, $180°$ and $\kappa=0.40828$, $1,159832$, 2.87129. These κ values correspond to values of ρ for the theoretical circular normal distribution (which are perfectly analagous to r for empirical circular distributions) of $\rho=0.20$ (weak concentration about the mean), 0.50 (medium concentration), 0.80 (strong concentration) respectively [Batchelet, 1965]. The mixtures of circular normal distributions were obtained by adding, at each α_i, the appropriate value of $f(\alpha_i)$ according to each of the combinations shown in Table 11-2. In addition, each $f(\alpha_i)$ was weighted, before adding, according to one of five combinations of the activities of each component of the mixture, $A'_1:A'_2$. These five combination were $A'_1:A'_2=50:50$, 60:40, 70:30, 80:20 and 90:10. This method, therefore, produced a total of 225 (45x5) mixtures of circular normal distributions, each having known values of A'_1, θ_1, ρ_1 and A'_2, θ_2, ρ_2 with the restriction that $A'_1+A'_2=100$. The Single Trace Analysis program was then run on all 225 of these mixtures and produced experimental AT_k, Φ_k, r_k values which could be directly compared to the known A'_k, θ_k, ρ_k values for each mode, k, of each mixture. This comparison, however, was extremely complicated because of the large number of variables involved.

To make the comparison simple and meaningful, the following procedure was employed. The experimental values

TABLE 11-2

COMBINATIONS OF THEORETICAL CIRCULAR NORMAL DISTRIBUTIONS USED IN TESTING THE APPROXIMATE MULTIMODAL ANALYSIS

COMBINATION	$\Theta_1(°)$	ρ_1	$\Theta_2(°)$	ρ_2
1	0	0.2	100	0.2
2	0	0.2	100	0.5
3	0	0.2	100	0.8
4	0	0.2	120	0.2
5	0	0.2	120	0.5
6	0	0.2	120	0.8
7	0	0.2	140	0.2
8	0	0.2	140	0.5
9	0	0.2	140	0.8
10	0	0.2	160	0.2
11	0	0.2	160	0.5
12	0	0.2	160	0.8
13	0	0.2	180	0.2
14	0	0.2	180	0.5
15	0	0.2	180	0.8
16	0	0.5	100	0.2
17	0	0.5	100	0.5
18	0	0.5	100	0.8
19	0	0.5	120	0.2
20	0	0.5	120	0.5
21	0	0.5	120	0.8
22	0	0.5	140	0.2
23	0	0.5	140	0.5
24	0	0.5	140	0.8
25	0	0.5	160	0.2
26	0	0.5	160	0.5
27	0	0.5	160	0.8
28	0	0.5	180	0.2
29	0	0.5	180	0.5
30	0	0.5	180	0.8
31	0	0.8	100	0.2
32	0	0.8	100	0.5
33	0	0.8	100	0.8
34	0	0.8	120	0.2
35	0	0.8	120	0.5
36	0	0.8	120	0.8
37	0	0.8	140	0.2
38	0	0.8	140	0.5
39	0	0.8	140	0.8
40	0	0.8	160	0.2
41	0	0.8	160	0.5
42	0	0.8	160	0.8
43	0	0.8	180	0.2
44	0	0.8	180	0.5
45	0	0.8	180	0.8

of AT_k, Φ_k, r_k for each mode, k, were converted to the parameters of theoretical circular normal distributions, A'_k, θ_k, κ_k. The discreet distribution of the mixture of these circular normal distributions was then obtained by the method outlined above. This distribution was then plotted by computer along with the discreet distribution of the original mixture of theoretical circular normal distributions. A simple visual comparison of the two curves was then made. If the approximate multimodal solution in the Single Trace Analysis was exact, the two curves would be identical. If the approximate solution was inexact, the differences between the curves would show the type and magnitude of the error. A few representative plots from the 225 that were produced are shown in Figure 11-1a-h.

It was found that, on the whole, the approximate multimodal solution produced surprisingly accurate results on mixtures of circular normal distributions. A summary of the errors obtained for each of the parameters are shown for various conditions in Table 11-3. In general, the calculated mean directions were quite accurate, especially as the difference between the actual mean directions of the modes approached 180° where the solution was exact. In all other cases, the difference between mean directions was somewhat overestimated. If the two modes had approximately equal concentrations, the approximate multimodal solution produced excellent results with respect to both the activity

FIGURE 11-1.

RESULTS OF THE APPROXIMATE MULTIMODAL SOLUTION OF BIMODAL MIXTURES OF THEORETICAL CIRCULAR NORMAL DISTRIBUTIONS
(SEE TEXT FOR FULL EXPLANATION)

0 = Original bimodal mixture
1 = Approximate multimodal solution
* = Both original mixture and approximate solution

a. $A'_1 = 50 \quad \theta_1 = 0° \quad \rho_1 = 0.8$

$A'_2 = 50 \quad \theta_2 = 100° \quad \rho_2 = 0.8$

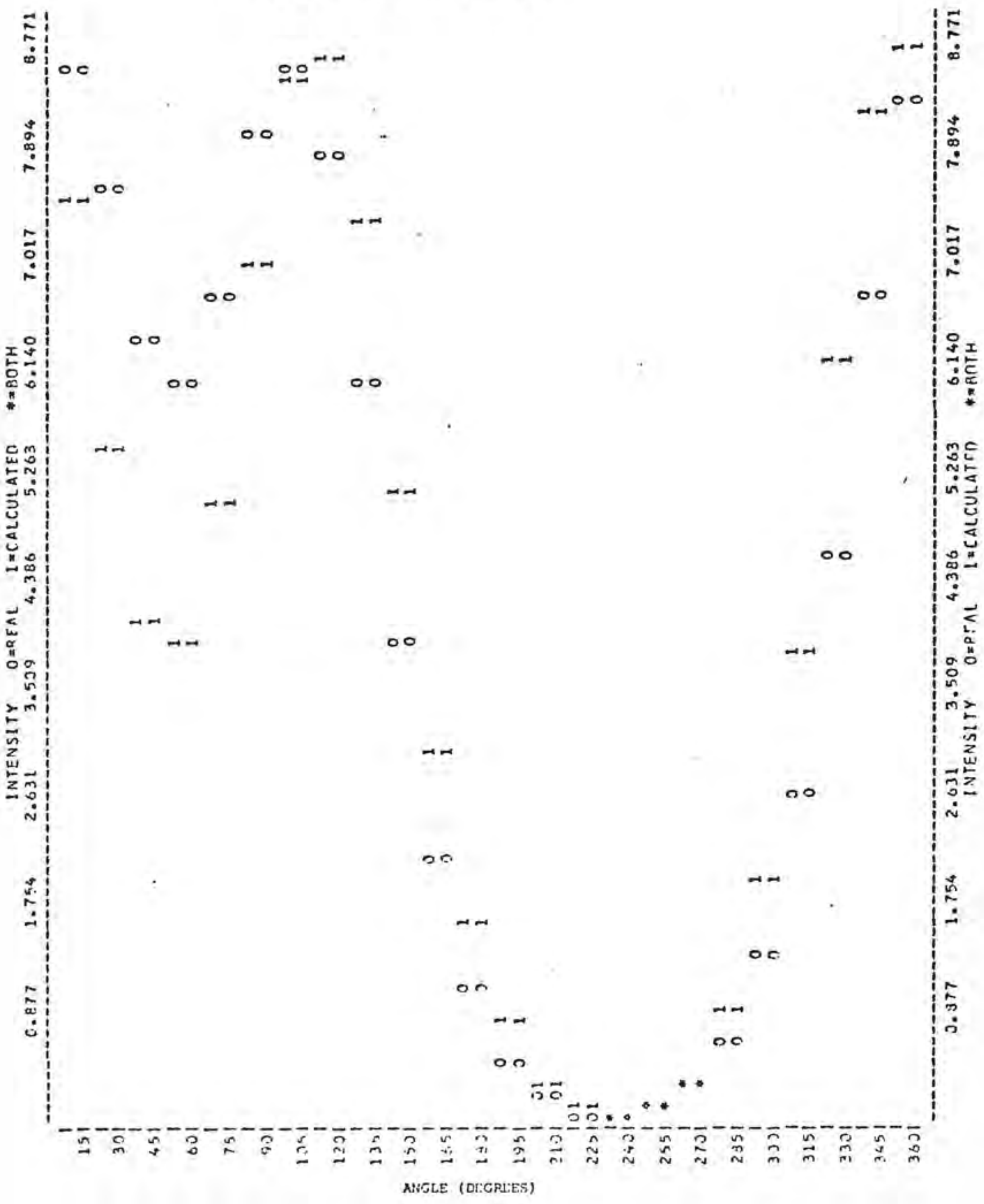


FIGURE 11-1 (CONT)

RESULTS OF THE APPROXIMATE MULTIMODAL SOLUTION OF BIMODAL MIXTURES OF THEORETICAL CIRCULAR NORMAL DISTRIBUTIONS (SEE TEXT FOR FULL EXPLANATION)

0 = Original bimodal mixture
1 = Approximate multimodal solution
* = Both original mixture and approximate solution

b. $\lambda'_1 = 50$ $\theta_1 = 0°$ $\rho_1 = 0.8$

$\lambda'_2 = 50$ $\theta_2 = 140°$ $\rho_2 = 0.8$

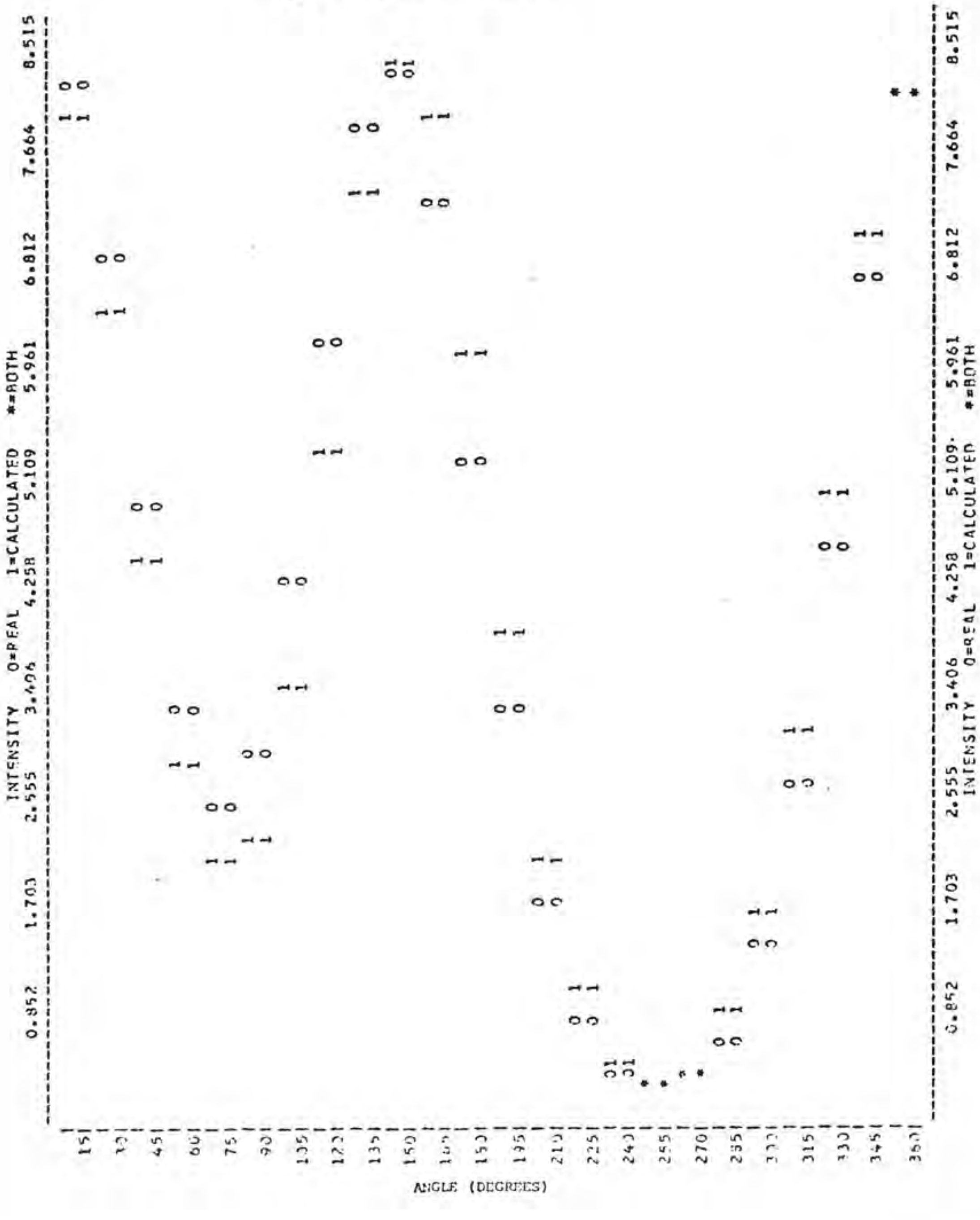


FIGURE 11-1 (CONT)

RESULTS OF THE APPROXIMATE MULTIMODAL SOLUTION OF BIMODAL MIXTURES OF THEORETICAL CIRCULAR NORMAL DISTRIBUTIONS
(SEE TEXT FOR FULL EXPLANATION)

0 = Original bimodal mixture
1 = Approximate multimodal solution
* = Both original mixture and approximate solution

c. $A'_1 = 50$ $\theta_1 = 0°$ $\rho_1 = 0.8$

$A'_2 = 50$ $\theta_2 = 180°$ $\rho_2 = 0.8$

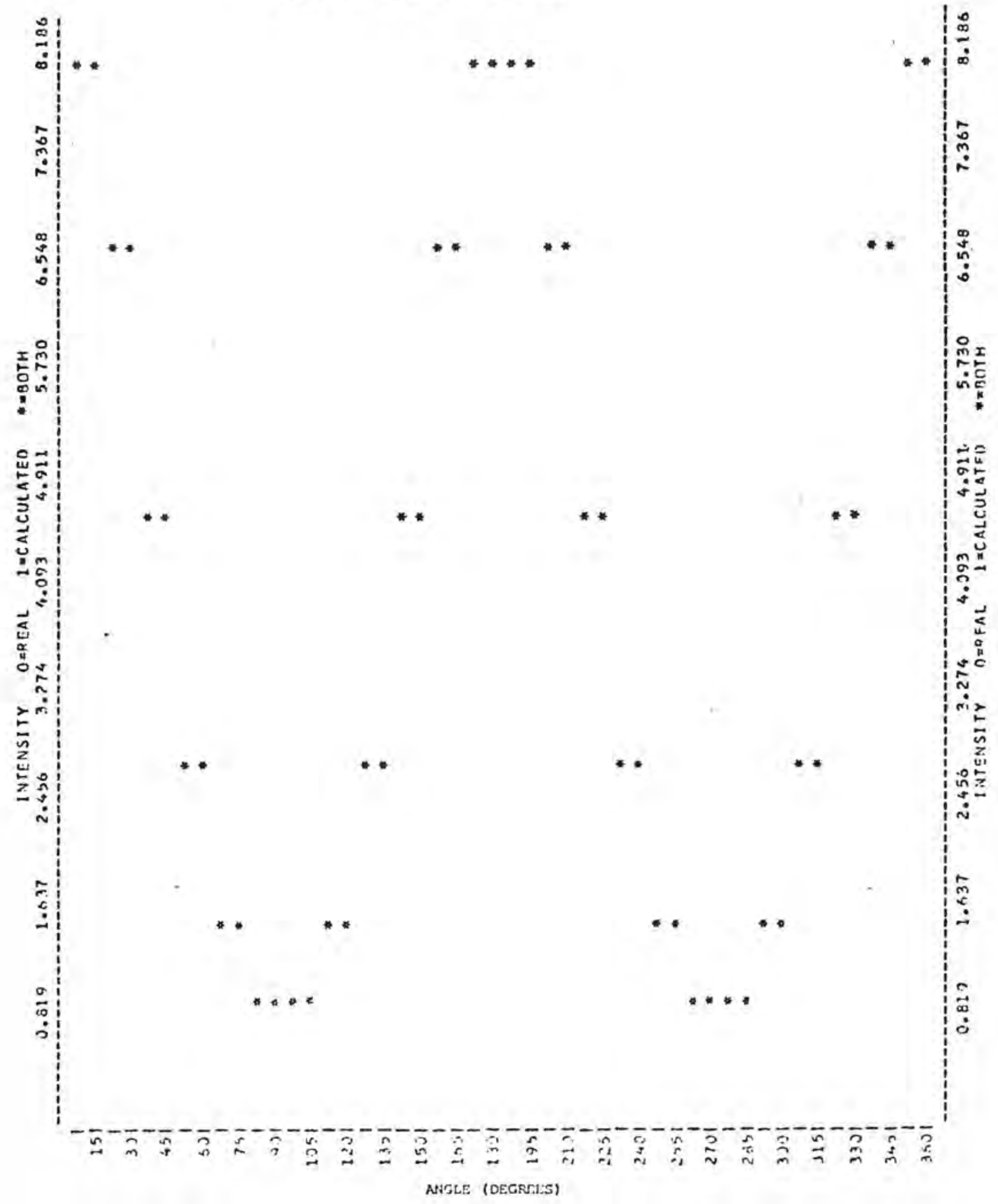


FIGURE 11-1 (CONT)

RESULTS OF THE APPROXIMATE MULTIMODAL SOLUTION OF BIMODAL MIXTURES OF THEORETICAL CIRCULAR NORMAL DISTRIBUTIONS (SEE TEXT FOR FULL EXPLANATION)

0 = Original bimodal mixture
1 = Approximate multimodal solution
* = Both original mixture and approximate solution

d. $A'_1 = 70$ $\theta_1 = 0°$ $\rho_1 = 0.5$
$A'_2 = 30$ $\theta_2 = 160°$ $\rho_2 = 0.2$

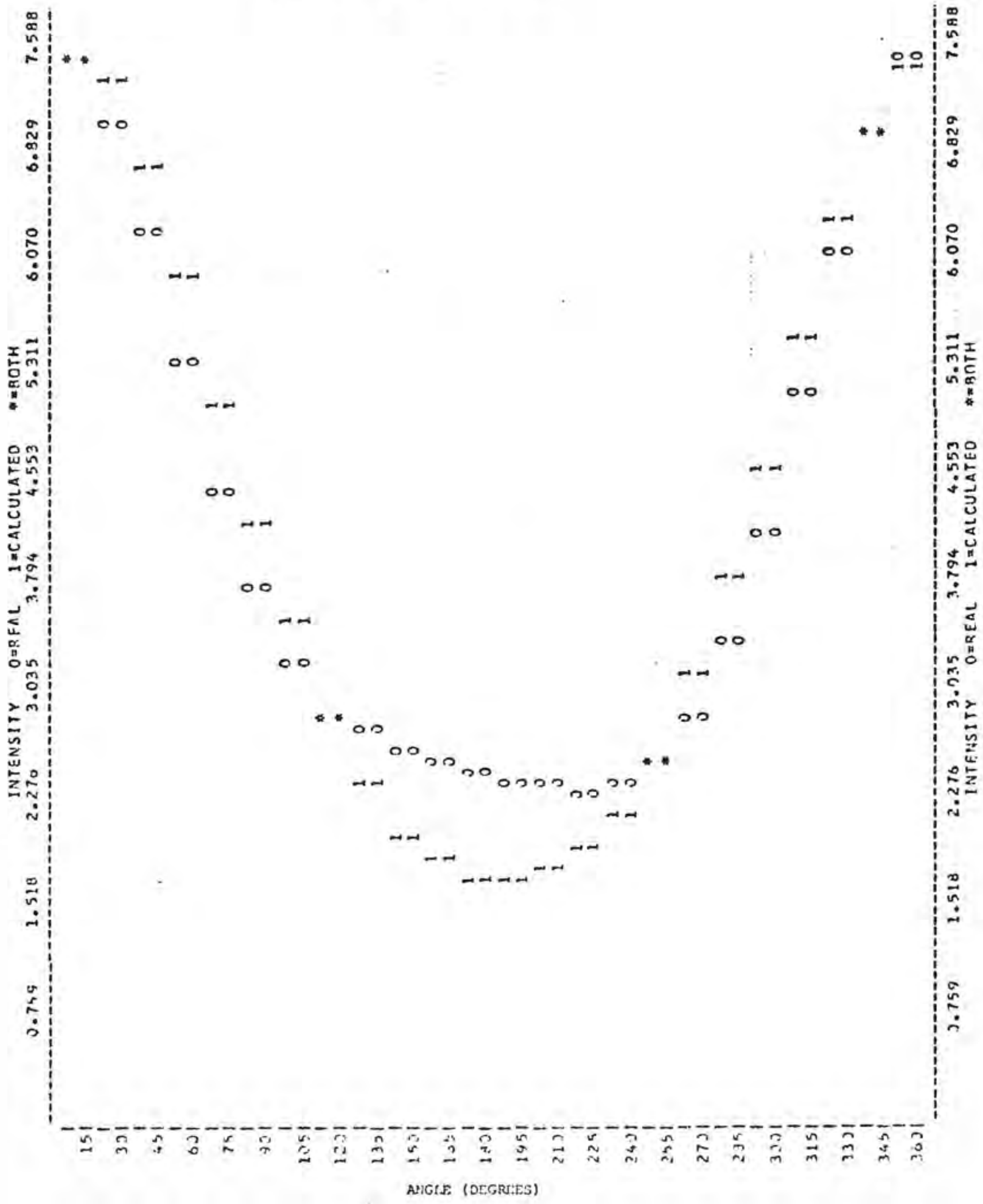


FIGURE 11-1 (CONT)

RESULTS OF THE APPROXIMATE MULTIMODAL SOLUTION OF BIMODAL MIXTURES OF THEORETICAL CIRCULAR NORMAL DISTRIBUTIONS
(SEE TEXT FOR FULL EXPLANATION)

0 = Original bimodal mixture
1 = Approximate multimodal solution
* = Both original mixture and approximate solution

e. $A'_1 = 70$ $\theta_1 = 0°$ $\rho_1 = 0.5$

$A'_2 = 30$ $\theta_2 = 160°$ $\rho_2 = 0.5$

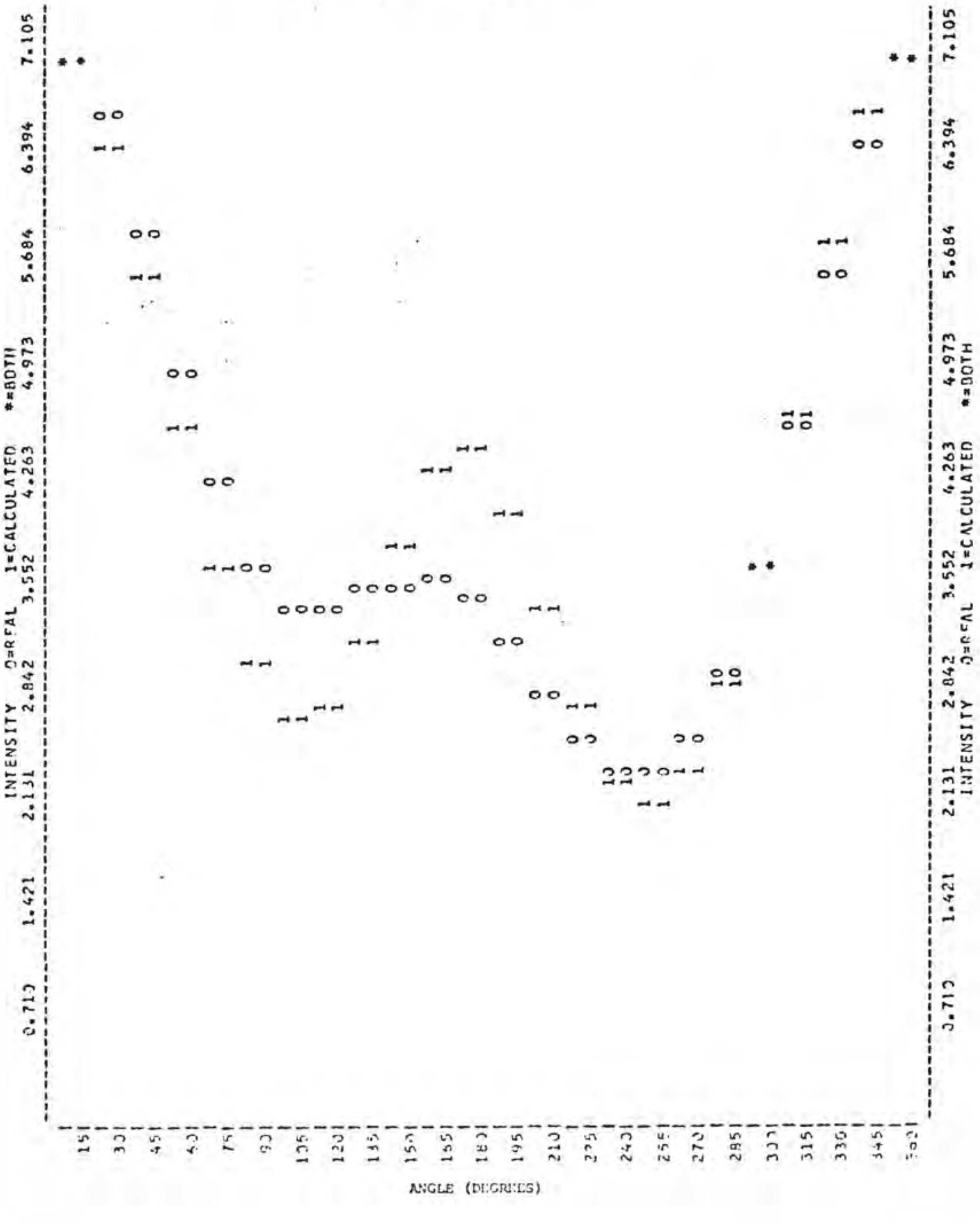


FIGURE 11-1 (CONT)

RESULTS OF THE APPROXIMATE MULTIMODAL SOLUTION OF BIMODAL MIXTURES OF THEORETICAL CIRCULAR NORMAL DISTRIBUTIONS
(SEE TEXT FOR FULL EXPLANATION)

0 = Original bimodal mixture
1 = Approximate multimodal solution
* = Both original mixture and approximate solution

f. $A'_1 = 70 \quad \theta_1 = 0° \quad \rho_1 = 0.5$

$A'_2 = 30 \quad \theta_2 = 160° \quad \rho_2 = 0.8$

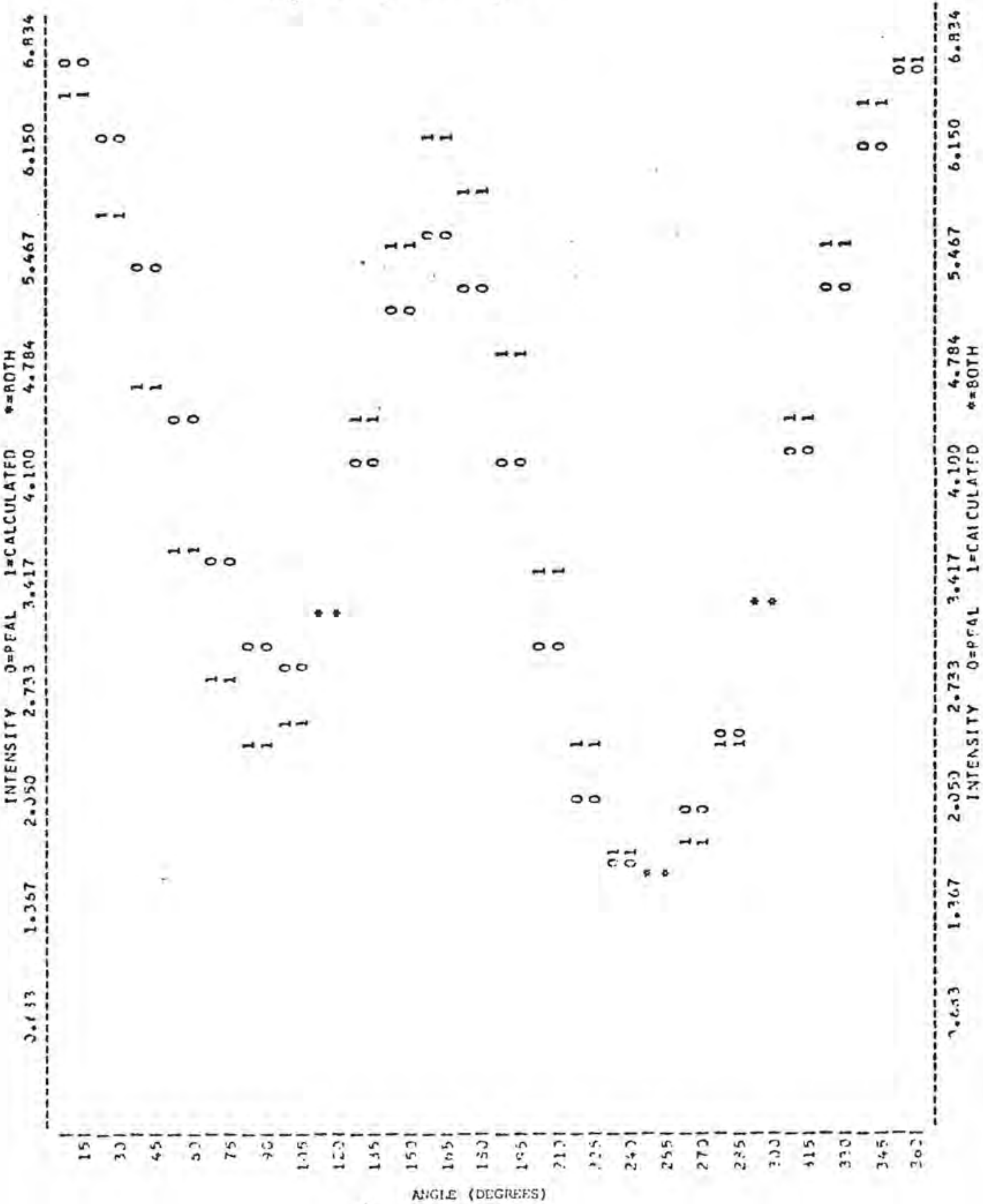


FIGURE 11-1 (CONT)

RESULTS OF THE APPROXIMATE MULTIMODAL SOLUTION OF BIMODAL MIXTURES OF THEORETICAL CIRCULAR NORMAL DISTRIBUTIONS (SEE TEXT FOR FULL EXPLANATION)

0 = Original bimodal mixture
1 = Approximate multimodal solution
* = Both original mixture and approximate solution

g. $A'_1 = 80$ $\theta_1 = 0°$ $\rho_1 = 0.2$
$A'_2 = 20$ $\theta_2 = 140°$ $\rho_2 = 0.8$

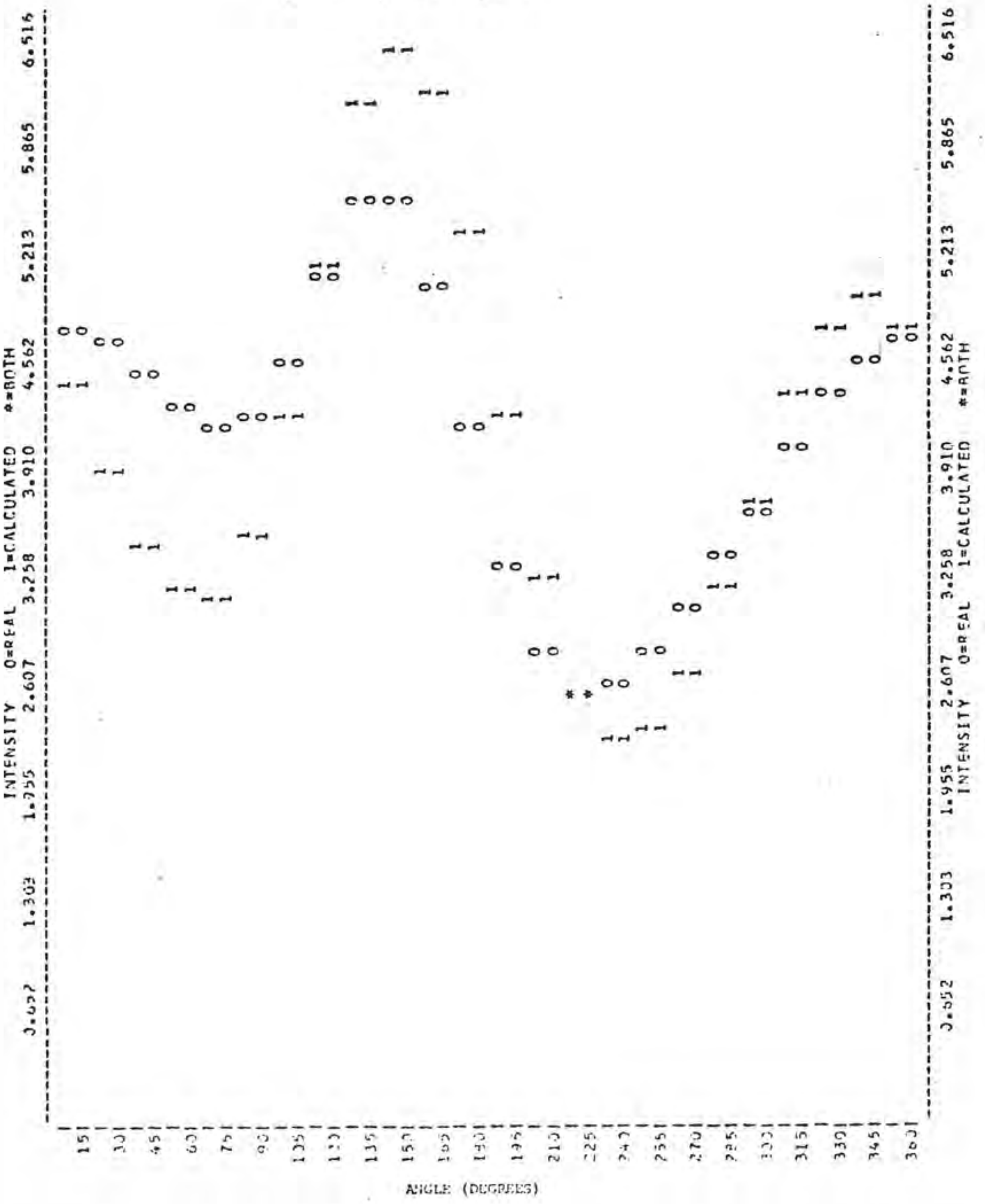


FIGURE 11-1 (CONT)

RESULTS OF THE APPROXIMATE MULTIMODAL SOLUTION OF BIMODAL MIXTURES OF THEORETICAL CIRCULAR NORMAL DISTRIBUTIONS (SEE TEXT FOR FULL EXPLANATION)

0 = Original bimodal mixture
1 = Approximate multimodal solution
* = Both original mixture and approximate solution

h. $A'_1 = 80$ $\theta_1 = 0°$ $\rho_1 = 0.2$

$A'_2 = 20$ $\theta_2 = 180°$ $\rho_2 = 0.8$

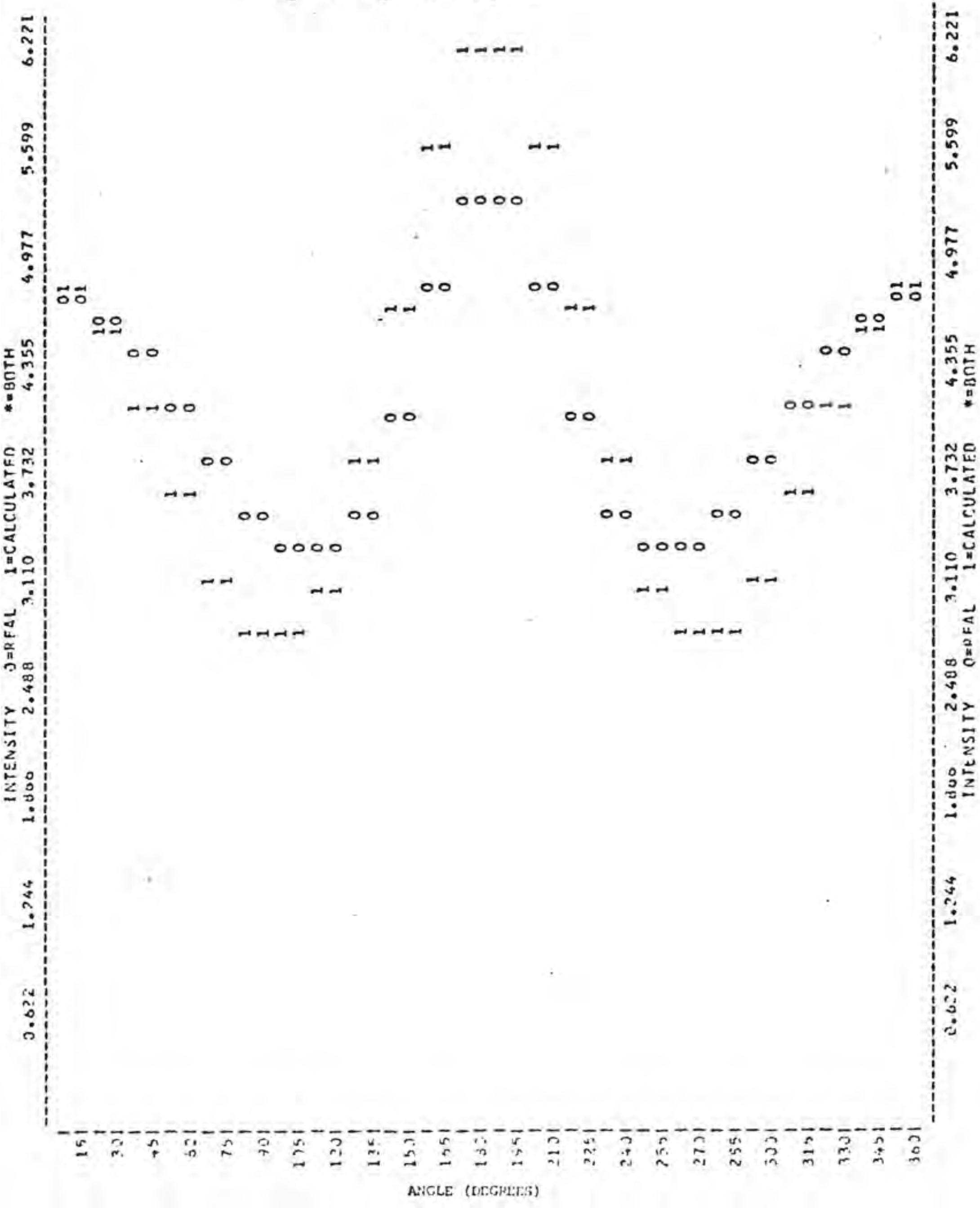


TABLE 11-3

SUMMARY OF ERRORS PRODUCED BY THE APPROXIMATE MULTIMODAL ANALYSIS ON MIXTURES OF CIRCULAR NORMAL DISTRIBUTIONS

PARAMETER	CONDITION	ERROR
MEAN DIRECTION, ϕ_k	$\Theta_1 - \Theta_2 = 180°$	NONE
	$\Theta_1 - \Theta_2 \simeq 140°$	SMALL, < 10°
	$\Theta_1 - \Theta_2 \simeq 100°$	MEDIUM, ≃ 12°
	$\Theta_1 - \Theta_2 < 90°$	MODE FINDER GENERALLY FAILS TO DISTINGUISH MODES
ACTIVITY, A_k	$\rho_1 \simeq \rho_2$	VERY SMALL, < 4%
	$\rho_1 < \rho_2$	A_1 UNDERESTIMATED, GENERALLY < 14%
	$\rho_1 > \rho_2$	A_1 OVERESTIMATED, GENERALLY < 14%
CONCENTRATION, r_k	$\rho_1 \simeq \rho_2$	VERY SMALL, < 4%
	$\rho_1 < \rho_2$	r_1 RATHER BADLY OVERESTIMATED BUT r_2 GOOD
	$\rho_1 > \rho_2$	r_1 GOOD BUT r_2 RATHER BADLY OVERESTIMATED

and concentration of each mode. The activity of relatively flat modes, however, was generally underestimated while the activity of sharp modes was generally overestimated. In contrast, the concentration of flat modes was quite seriously overestimated but the concentration of sharp modes was generally quite good. Therefore, it was decided that the approximate multimodal solution could not necessarily produce a reliable estimate for the parameter of concentration, r_k. It was furthermore decided that the activities, AT_k, could generally be used, at least to determine which was the primary mode, while the mean directions, Φ_k, could always be trusted to be reasonably good estimates of the actual mean directions.

One final important result became apparent while creating the mixtures of theoretical circular normal distributions used to test the approximate multimodal analysis. This was the fact that all mixtures of two circular normal distributions whose mean directions differed by less than 90° produced unimodal distributions even when the concentration around each mean direction was very high, $r=0.80$. This finding effectively placed a lower limit on the resolution of any approximate multimodal analysis based on a mode finding technique.

CHAPTER 12

EXPERIMENTAL RESULTS

The Weights of Blackpoll Warblers Captured in California

Weight and fat data were taken about every other day during the period of captivity on all California captured Blackpoll Warblers. An inspection of these data indicated that weight and fat were very well correlated with each other, increases in weight being accounted for by increases in the fat level. Because these fat levels were subjectively determined, weight data alone are used in the remainder of this discussion.

A summary of the maximum weight attained by each Blackpoll Warbler, the date this maximum weight was first attained, and the average weight of each individual during the entire time that it was kept in captivity is presented in Table 12-1. These data indicate that birds that attained higher maximum weights generally averaged fatter than birds that attained lower maximum weights. All individuals except five, the three 1969 birds and birds number 27 and 29 (1970), attained 3-fat levels (bulging). Both the average weight and the maximum weight attained averaged higher in both 1970 and 1971 than in 1969. These results are highly significant (P>.98). Similarly, both the average weight and the maximum weight attained averaged higher in 1971 than in 1970. These results, however, are not as significant

TABLE 12-1

SUMMARY OF THE WEIGHTS OF ALL CALIFORNIA CAPTURED BLACKPOLL WARBLERS USED IN THIS STUDY

	BIRD NUMBER	DATES OF CAPTIVITY	WEIGHT AT CAPTURE	MAXIMUM WEIGHT OBTAINED	DATE OF MAXIMUM WEIGHT	AVERAGE WEIGHT	NUMBER OF WEIGHINGS
I 1969							
	21	Sep. 9-Sep.23	10.8	12.7	Sep.14	11.87	7
	22	Oct. 5-Oct. 6	11.1	11.1	Oct. 5	11.10	1
	23	Oct. 6-Oct.12	12.0	12.8	Oct. 9	12.30	6
	Mean		11.30	12.20	Sep.29	11.76	
	Std. dev.		0.62	0.95		0.61	
II 1970							
	24	Sep.21-Nov. 7	12.3	25.5	Oct.22 *	20.04	25 **
	25	Oct. 1-Nov. 7	14.8	25.2	Oct.22 *	21.42	17 **
	26	Oct. 3-Nov.11	11.8	25.3	Oct.22 *	19.76	19 **
	27	Oct. 3-Nov. 3	11.7	14.6	Oct.16	12.85	15
	28	Oct. 4-Nov. 7	14.1	22.7	Oct.27 *	16.84	17
	29	Oct.12-Nov. 7	11.2	14.5	Oct.27	13.86	12
	30	Oct.27-Nov. 8	17.3	17.3	Oct.27	13.94	7
	Mean		13.31	20.73	Oct.23	16.96	
	Std. dev.		2.04	5.09		3.48	
III 1971							
	31	Sep.17-Nov. 9	13.1	23.6	Oct.23	17.22	19
	32	Sep.17-Nov.19	11.8	28.8	Oct. 7 *	24.81	29 **
	33	Sep.17-Oct.28	10.9	28.3	Oct.24 *	20.65	19 **
	34	Sep.17-Nov.19	11.1	23.8	Nov.13	18.31	24
	35	Sep.21-Nov.11	10.2	22.5	Oct.26	17.65	23
	36	Sep.21-Nov.19	11.4	25.5	Oct.28 *	18.42	28
	37	Sep.21-Nov.19	11.3	24.6	Oct. 8	21.69	27 **
	38	Sep.21-Nov.17	12.3	29.8	Oct.11 *	22.52	21 **
	39	Sep.21-Nov.19	12.3	21.6	Nov.16	15.92	25
	40	Sep.22-Nov.19	10.9	28.0	Oct.26 *	22.80	27 **
	41	Sep.22-Nov.19	12.1	28.8	Oct.26 *	21.66	27 **
	42	Sep.22-Nov.15	10.3	18.5	Nov. 7	15.13	20
	43	Oct. 4-Nov.13	10.6	25.0	Oct.26	17.22	19
	44	Oct.11-Nov.11	13.0	23.0	Oct.28	16.85	13
	Mean		11.52	25.13	Oct.26	19.35	
	Std. dev.		0.90	3.28		2.96	

* Fat birds based on criterion that maximum weight attained is greater than mean maximum weight for that year

** Fat birds based on criterion that average weight is greater than mean average weight for that year

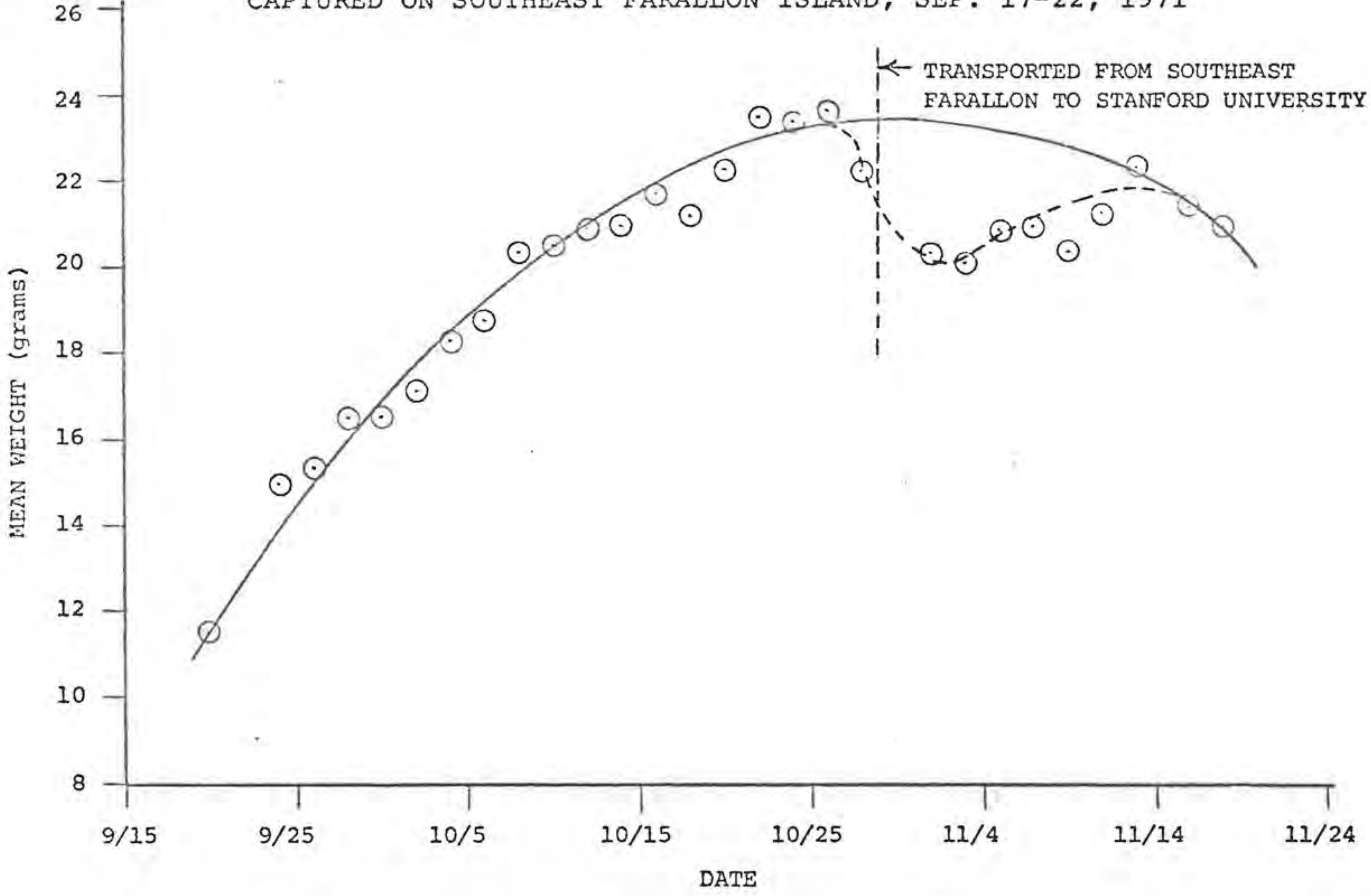
(P=.942, P=.707 respectively). These differences can be attributed to improvements in the experimental maintenance of captive warblers over the three years.

An attempt was made to classify individuals as either "fat" or "thin" on the basis of the mean weight of each year. All of the 1969 birds were classified as "thin". Of the 1970 and 1971 birds, the classification "fat" was based on the criterion that the maximum weight attained was greater than the mean maximum weight for that year. Another classification was based on the criterion that the average weight was greater than the mean average weight for that year. These "fat" birds are indicated in Table 12-1 for each criterion by "*" or "**".

As indicated in Table 12-1, 12 Blackpoll Warblers were captured between September 17 and 22, 1971. All of these individuals, birds 31-42, were captured on Southeast Farallon and probably represent the single most homogenous group of birds obtained. The mean weight of these 12 birds is plotted in Figure 12-1 as a function of time. The capture dates and weights were averaged to obtain the starting point of the curve. A rather smooth curve was obtained that apparently resulted in a peak weight of about 23.7 grams around November 1. The sharp drop in weight that occurred October 26-November 1 was apparently due to the stress of transporting these birds from Southeast Farallon to Stanford University. Although this actual journey

FIGURE 12-1

MEAN WEIGHT AS A FUNCTION OF TIME FOR TWELVE BLACKPOLL WARBLERS CAPTURED ON SOUTHEAST FARALLON ISLAND, SEP. 17-22, 1971



occurred on October 29, the birds were readied for this journey by being placed in a few crowded cages on October 25. The boat to the island, however, was delayed by three days because of heavy seas and inclement weather.

Murray [1966b] indicated that the maximum weights attained by fall migrant immature Blackpoll Warblers on the Atlantic Coast are 21.9 grams (New Jersey) and 21.5 grams (Massachusetts). The higher maximum weights attained by captive Blackpoll Warblers in this study are probably due to the lack of energy expenditure in obtaining food and the inability to initiate migratory flights. The sample of experimental birds reached a weight of 20-22 grams between October 9-17 indicating that they were potentially capable of initiating a long overwater flight at approximately the same time that wild individuals on the Atlantic Coast initiate their overwater flight. There is, therefore, no indication that the sample of California captured experimental birds are in any way abnormal with respect to the physiology that controls weight and fat production.

The Nocturnal Activities of Blackpoll Warblers Captured in California

The nocturnal activities of experimental birds were recorded as jumps/test according to the method outlined in Chapter 10. A summary of these data for all 24 California captured Blackpoll Warblers is presented in Table 12-2. It

TABLE 12-2

SUMMARY OF ACTIVITIES OF CALIFORNIA CAPTURED BLACKPOLL WARBLERS TESTED IN "FOOTPRINT" ORIENTATION CAGES

BIRD	NO. OF TESTS	TOTAL ACTIVITY (jumps/test)	MEAN ACTIVITY (jumps/test)	STANDARD DEVIATION
21	7	569.69	81.38	65.66
22	1	53.71	53.71	-
23	8	459.39	57.42	55.36
MEAN OF 1969 BIRDS			64.17	15.02
24	28	2112.02	75.43	55.53
25	21	741.28	35.30	35.75
26	23	5304.71	230.64	202.36
27	18	754.66	41.93	34.93
28	20	1319.73	65.99	86.01
29	15	1709.96	114.00	70.37
30	9	911.15	101.24	60.56
MEAN OF 1970 BIRDS			94.93	66.34
31	24	2126.25	88.59	83.66
32	31	7040.89	227.13	208.43
33	22	501.65	22.80	24.53
34	31	6204.61	200.15	135.74
35	25	2752.15	110.09	152.30
36	31	412.02	13.29	16.65
37	31	654.35	21.11	23.13
38	29	1375.49	47.43	28.94
39	30	626.96	20.90	18.84
40	30	5413.53	180.45	160.00
41	30	1552.64	51.75	67.42
42.	27	2451.35	90.79	125.34
43	16	395.81	24.74	31.84
44	14	438.66	31.33	23.00
MEAN OF 1971 BIRDS			80.75	72.97
MEAN OF ALL 24 BIRDS			82.82	65.34
MEAN OF 23 BIRDS TESTED ON SEVERAL NIGHTS			84.10	66.51

is apparent from these data that the average activity varies widely among the 24 individuals tested, ranging from a low of about 13 jumps/test for bird 36 to a high of about 231 jumps/test for bird 26. The mean average activity for all 24 birds was found to be 82.82±65.34 jumps/test. This represents an average rate of jumping of about 1.4 jumps/minute for one hour tests. The mean average activities for individuals tested during each of the three years of the duration of this study is also presented in Table 12-2. None of the differences between various years are found to be statistically significant ($P<.77$ for all differences).

What accounts for the wide variation in average activity among the various individuals? It was felt that the average activity of a given individual might be correlated with the individual's weight, with fatter birds showing more activity. To test this hypothesis, the mean average activity of "fat" birds was compared to the mean average activity of "thin" birds, these classifications having been defined above. A summary of the results of this test are presented in Table 12-3. While there is a tendency for "fat" birds to have higher average activities than "thin" birds, the differences obtained by any of the criteria used are not found to be highly significant ($P<.924$ for all three criteria).

TABLE 12-3

DIFFERENCES IN MEAN ACTIVITIES BETWEEN "FAT" AND "THIN" CALIFORNIA CAPTURED BLACKPOLL WARBLERS

	"FAT" BIRDS			"THIN" BIRDS					
CRITERION*	N	MEAN AVE. ACTIVITY (jumps/night)	STANDARD DEVIATION	N	MEAN AVE. ACTIVITY (jumps/night)	STANDARD DEVIATION	DIFFERENCE (jumps/night)	"t" STATISTIC	SIGNIFICANCE P
1	10	95.02	84.31	14	74.10	49.37	20.92	0.766	.774
2	9	99.12	87.86	15	73.04	48.27	26.08	0.944	.822
3	8	108.87	88.57	16	69.79	48.08	39.08	1.483	.924

* CRITERION 1: "Fat" birds are those whose maximum weight attained was greater than the mean maximum weight attained for all birds tested that year.**

CRITERION 2: "Fat" birds are those whose average weight is greater than the mean average weight for all birds tested that year.**

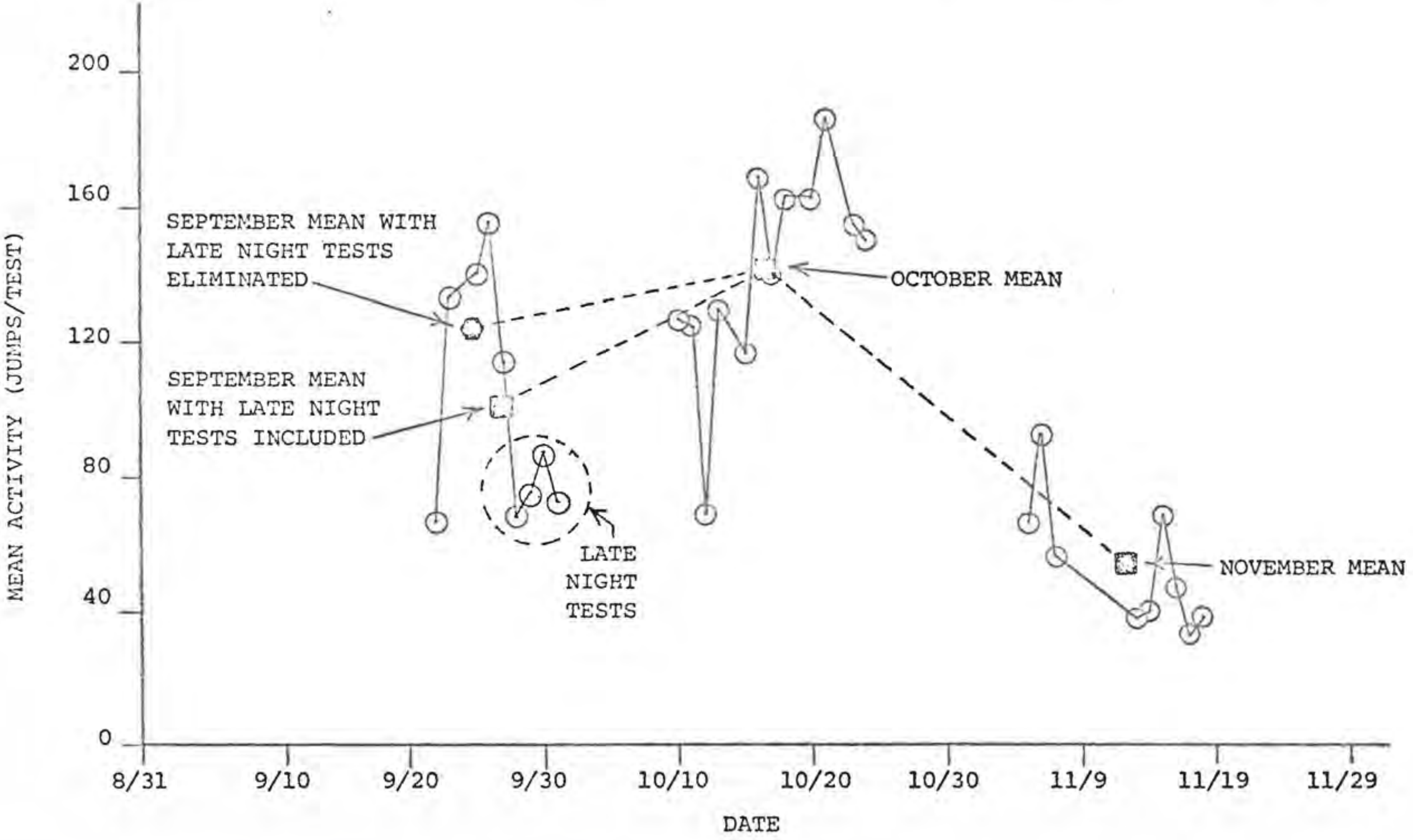
CRITERION 3: "Fat" birds are those that satisfy both Criteria 1 and 2.

** All 1969 birds are considered thin.

Table 12-2 also indicates that the standard deviation of the average activity of a given bird tested over many nights is very high. It is interesting to inquire into possible reasons for this high variability in the activity of a single individual. It is reasonable to assume that the nocturnal activity of captive Blackpoll Warblers may vary during the migration period, increasing to a peak at the height of the season and then decreasing as the physiological readiness for migration wanes. To test this hypothesis, the activities of single night tests can be examined as a function of season for each of the experimental birds. The fact that many of the birds were only tested over part of the migratory season, coupled with the fact that the activities of different individuals varied widely, makes the analysis of this entire collection of data uncertain. A consistant sample of seven individuals can be found, however, that were all captured on Southeast Farallon between September 17-22, 1971 and that were all tested on the same 30 nights. A plot of the mean activity of these 7 birds as a function of the date of testing is presented in Figure 12-2. The dates of testing can be arranged into three groups: (1) September (September 22-October 1), (2) October (October 10-24) and (3) November (November 5-18). The means of each of these three periods for all seven birds are shown in Figure 12-2 and indicate that this sample does indeed show peak activity during the

FIGURE 12-2

MEAN ACTIVITY AS A FUNCTION OF TIME FOR SEVEN BLACKPOLL WARBLERS CAPTURED ON SOUTHEAST FARALLON ISLAND SEP. 17-22, 1971 AND TESTED ON THE SAME 30 NIGHTS



October period. To test whether the differences between the three periods are significant, a matched pairs t-test was run on the mean of the differences between test periods for the individual birds. These data are presented in Table 12-4a. Only the difference between October and November activities was found to be highly significant $(P=.972)$.

It should be pointed out that four of the 30 tests on each bird, because of constraints caused by moonlit nights and temporary fog, were initiated very late at night (well after midnight). These four nights occurred September 28-October 1, all in the first test period. All of these nights appeared to produce mean activities well below the mean activity of that test period (Figure 12-2). It is, therefore, interesting to determine whether this apparent difference is significant. Accordingly, the matched pairs t-test was run on these seven birds as well as on the entire sample of 12 birds (which included the sample of 7) tested on these nine September nights. The mean of the differences in the mean activities of individual birds between the 5 tests run before midnight (early) and the 4 tests run after midnight (late) was determined. These data are presented in Table 12-5. A real difference between early and late night tests is indicated but the difference is not highly significant for either sample $(.91<P<.94)$.

TABLE 12-4

MEAN DIFFERENCES IN ACTIVITIES BETWEEN THREE TEST PERIODS FOR SEVEN 1971 CALIFORNIA CAPTURED BLACKPOLL WARBLERS

SAMPLE SIZE	PERIODS OF COMPARISON	MEAN DIFFERENCE IN ACTIVITY (jumps/night)	STANDARD DEVIATION	"t" STATISTIC	SIGNIFICANCE P
a. ALL 9 SEPTEMBER TESTS USED					
7	Oct. vs. Sep. 1971	37.37	169.55	0.583	.709
7	Oct. vs. Nov. 1971	94.81	105.64	2.374	.972
7	Sep. vs. Nov. 1971	54.65	129.58	1.116	.846
b. ONLY 5 EARLY NIGHT SEPTEMBER TESTS USED					
7	Oct. vs. Sep. 1971	19.22	188.42	0.270	.602
7	Oct. vs. Nov. 1971	94.81	105.64	2.374	.972
7	Sep. vs. Nov. 1971	75.45	156.45	1.276	.875

TABLE 12-5

MEAN DIFFERENCES IN ACTIVITIES BETWEEN EARLY AND LATE NIGHT SEPTEMBER, 1971, TESTS FOR CALIFORNIA CAPTURED BLACKPOLL WARBLERS

SAMPLE SIZE	COMPARISON	MEAN DIFFERENCE IN ACTIVITY (jumps/night)	STANDARD DEVIATION	"t" STATISTIC	SIGNIFICANCE P
12	Early vs. late nights	24.46	58.01	1.460	.914
7	Early vs. late nights	43.40	66.44	1.728	.933

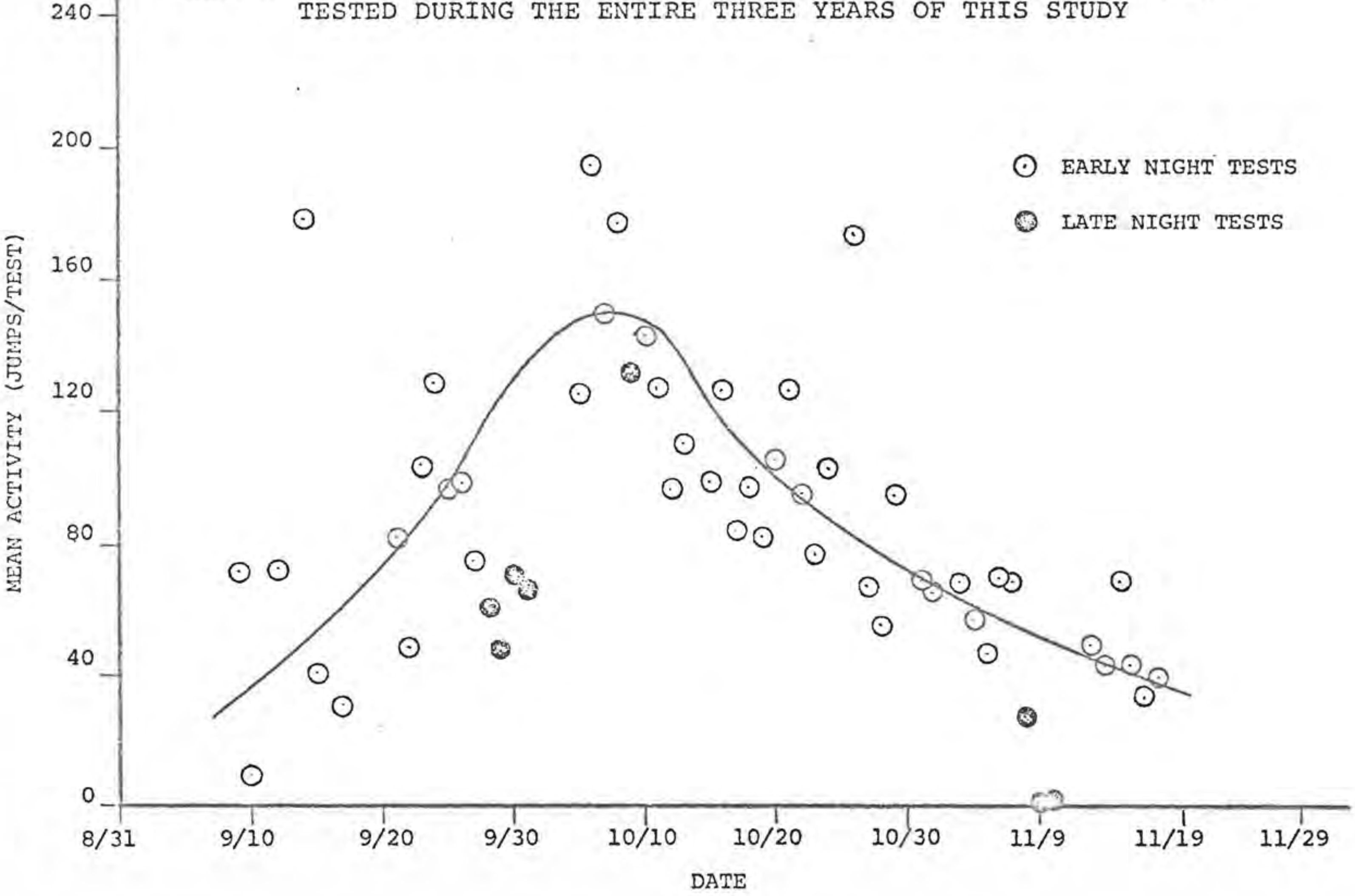
In view of this finding, it is desirable to recalculate the matched pairs t-test for the three test periods using only the 5 early September nights (since all October and November tests were run well before midnight). These data are presented in Table 12-4b. It is apparent that the difference in activity between September and October is decreased but the difference between September and November is increased. However, the October-November difference still remains the only significant one.

The average activity of all birds tested during all three years is plotted as a function of the time of year in Figure 12-3. Nights on which tests were conducted after midnight are indicated by filled circles. It should be pointed out that conclusions based on these data must be made with caution since the number of birds tested on each night was not constant. Nevertheless, there appears to be a trend toward a peak of activity occurring about October 6 followed by a fairly smooth decline. This corresponds extremely well with the time at which Blackpoll Warblers on the Atlantic Coast initiate their long overwater flight, a time when they should exhibit their peak migratory activity. Thus, there appears to be nothing abnormal about the timing of the migratory readiness in this sample of vagrant California captured Blackpoll Warblers.

One final point concerning the nocturnal activities of captive individuals placed in "footprint" orientation cages

FIGURE 12-3

MEAN ACTIVITY AS A FUNCTION OF TIME FOR ALL BLACKPOLL WARBLERS TESTED DURING THE ENTIRE THREE YEARS OF THIS STUDY



seemed worth investigating. It was felt that the activities of freshly caught birds might not be truly representative of Zugunruhe behavior but might simply represent frantic efforts to escape from the orientation cage. If such were the case, the activities of birds tested for the first night might be significantly higher than their activities on subsequent nights. On the other hand, it was felt that a bird placed in an orientation cage for the first time might be in a state of shock and produce very little or no activity. Accordingly, the mean differences in activity for individual birds between the first and second night of testing, and between the first plus second and third plus fourth nights of testing were tested for significance by the matched pairs t-test. The results of this analysis are shown in Table 12-6. These data indicate that no significant difference in activity exists between the first and second night's test (P=.746) nor between the first plus second and third plus fourth night's tests (P=.684). It is therefore likely that the nocturnal activity of freshly captured birds is truly representative of Zugunruhe and, as such, can confidently be included in an analysis of the directionality of this behavior.

TABLE 12-6

MEAN DIFFERENCE IN ACTIVITIES BETWEEN THE FIRST AND SECOND NIGHT TESTED AND BETWEEN THE FIRST + SECOND AND THIRD + FOURTH NIGHTS TESTED FOR CALIFORNIA CAPTURED BLACKPOLL WARBLERS

SAMPLE SIZE	COMPARISON	MEAN DIFFERENCE IN ACTIVITY (jumps/night)	STANDARD DEVIATION	"t" STATISTIC	SIGNIFICANCE P
23	1st vs. 2nd night	-20.67	146.91	-0.675	.746
23	1st + 2nd vs. 3rd + 4th nights	-22.99	227.41	-0.485	.684

The Directionality of Blackpoll Warblers Captured in California

It is now appropriate to inquire into the heart of this investigation, that is, to pose the question: Do California captured Blackpoll Warblers exhibit preferred directions when tested in orientation cages under the clear night sky, and, if so, what are those directions? This is the basic question that prompted the initiation of the experimental part of this dissertation. If this question can be answered then this investigation will have been successful.

Visual inspection of the orientation traces produced by Blackpoll Warblers, such as were shown in Figure 10-1a-c, during the three years of field work associated with this investigation, led me to believe that the birds were indeed capable of exhibiting directionality on a given night. However, as the investigation proceeded, the consistancy of the directionality expressed by a given individual, and by different individuals, became an increasingly elusive problem. The basic difficulty arose when it became apparent that a given bird, even during a single test, seemingly indicated the expression of more than one direction. A method of resolving the problem of multimodal behavior, at least as far as the directions are concerned, was presented in Chapter 11. This method, which included a mode finding algorithm and both a unimodal and an approximate multimodal analysis, has been called the Single Trace Analysis.

As a starting point, therefore, the number of modes chosen on single night's tests by the various Blackpoll Warblers can be examined. A summary of these data, for all 24 individuals, is presented in Table 12-7. Of the 508 tests displaying some activity, 186 or 36.6% were found to show multimodal behavior according to the mode finding algorithm used in the Single Trace Analysis. Multimodality, therefore, does appear to be a relatively frequent phenomenon in orientation tests on California captured Blackpoll Warblers. Multimodality is also found to be a relatively regular phenomenon among all of the individuals tested. For example, the mean of the percentage of multimodality shown by individual birds tested on several nights (23 birds), was found to be 35.5±13.7%. The standard deviation is, therefore, only 38.7% of the mean value. On the other hand, the average activity of these same 23 individuals can be seen from Table 12-2 to be 84.1±66.5 jumps/test. In this case, the standard deviation turns out to be 79.1% of the mean value. Thus it appears that this sample of Blackpoll Warblers shows only half as much variability in their multimodality than they show in their total activity.

The preceding discussion, therefore, indicates that multimodal behavior is a relatively common and consistant phenomenon among California captured Blackpoll Warblers tested in "footprint" orientation cages. However, the

TABLE 12-7

PERCENTAGE OF MULTIMODAL BEHAVIOR
DISPLAYED BY CALIFORNIA CAPTURED
BLACKPOLL WARBLERS

BIRD	NUMBER OF ACTIVE TESTS	NUMBER PRODUCING MULTIMODAL DATA	% MULTIMODALITY
21	7	0	0.00
22	1	1	100.00
23	7	2	28.57
24	28	8	28.57
25	20	7	35.00
26	23	7	30.43
27	17	11	64.71
28	20	6	30.00
29	15	8	53.33
30	9	3	33.33
31	23	7	30.43
32	31	10	32.26
33	21	5	23.81
34	31	7	22.58
35	23	7	30.43
36	29	10	34.48
37	30	13	43.33
38	29	8	27.59
39	30	14	46.67
40	30	18	60.00
41	30	14	46.67
42	24	8	33.33
43	16	5	31.25
44	14	7	50.00
TOTAL	508	186	36.61

AVERAGE/BIRD

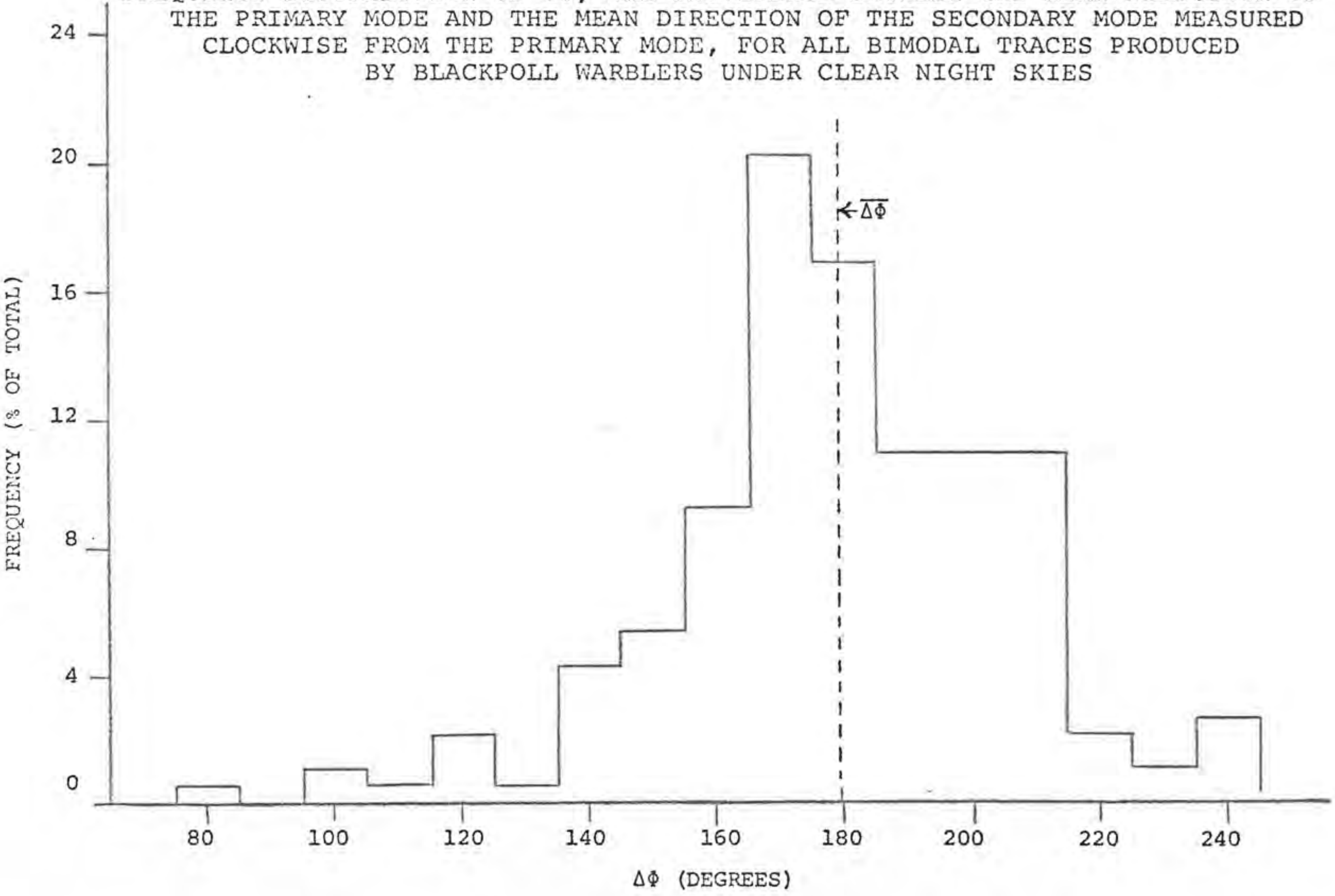
1) ALL BIRDS	38.20 ± 18.82%
2) ELIMINATING BIRD 22	35.51 ± 13.75%

question remains: Is it a real phenomenon attributable to the behavior of the birds, or is it merely an artifact of the test procedure or subsequent analysis? To answer this question, the relationship between the various modes exhibited in each one hour test can be examined. Of the 186 tests that produced multimodality, 183 (98.4%) were found to be bimodal, while only 3 (1.6%) were trimodal. The angular relationship between the primary and secondary modes in each of these 183 bimodal traces can, therefore, be examined. Primary modes are defined as those modes that contain over 50% of the total activity of the trace (as determined by the approximate multimodal solution). Thus, the statistic $\Delta\Phi$, which is defined as the difference (in degrees) between the mean direction of the primary mode and the mean direction of the secondary mode measured clockwise from the primary mode, can be calculated. Because of the characteristics of the mode finding algorithm used in the Single Trace Analysis, the value of $\Delta\Phi$ cannot be much less than 90° nor much greater than 270° since the mode finder is unable to differentiate between modes that are much less than 90° apart.

The distribution of $\Delta\Phi$ at ten degree intervals between 70° and 240° is shown in Figure 12-4. An obvious peak is seen to occur in the neighborhood of 170-180°. The mean value of $\Delta\Phi$ for all 183 bimodal traces is found to be $179.2 \pm 27.0°$. A one sided t-test shows that this value does

FIGURE 12-4

FREQUENCY DISTRIBUTION OF ΔΦ, THE DIFFERENCE BETWEEN THE MEAN DIRECTION OF THE PRIMARY MODE AND THE MEAN DIRECTION OF THE SECONDARY MODE MEASURED CLOCKWISE FROM THE PRIMARY MODE, FOR ALL BIMODAL TRACES PRODUCED BY BLACKPOLL WARBLERS UNDER CLEAR NIGHT SKIES



does not differ significantly from 180° (P=.662). Similarly, the mean value of $\Delta\Phi$ for all of the 131 bimodal traces obtained during 1971 is found to be 178.5±26.7°, while the $\overline{\Delta\Phi}$ for the 52 bimodal traces obtained in 1969 and 1970 is 180.8±28.0°. Again, one sided t-tests show that these values do not differ significantly from 180° (P=.737 and P=.581 respectively). These results, therefore, supply very strong evidence that the bimodality exhibited by California captured Blackpoll Warblers in "footprint" orientation cages is an expression of a given direction and the 180° opposite direction. Such behavior has been occasionally indicated by previous studies on bird orientation [Sauer and Sauer, 1960] and has been referred to as conflict orientation. However, the present study is the first to show that conflict orientation indeed represents two modes of behavior that are exactly 180° apart.

It is important to note, however, that the fact that bimodal behavior is oriented in 180° opposite directions does not eliminate the possibility that such behavior is an artifact of the test apparatus itself. Furthermore, the fact that birds can distinguish 180° opposite directions while inside of a circular orientation cage does not indicate in any way that the birds are capable of utilizing directional cues from outside of the cage. In fact, the ability of a bird to produce a unimodally directed trace during a one hour test does not prove that the bird is a well oriented individual, capable of directional behavior based on external cues. The bird could simply begin jumping in a given randomly chosen direction and continue jumping in that direction for the duration of the hour. It could maintain the given direction (or its 180° reverse) by means of an inertial guidance system or, simply by the internal characteristics of the cage itself. Stated in statistical terms, an active bird jumping in an orientation cage is making a series of directional choices (each jump may be considered to represent a choice on the part of the bird), but we have no a priori knowledge of the independence of any of the choices (or jumps). Any valid statistical treatment necessitates some knowledge of the number of independent events, N, which is not necessarily equal to the number of jumps or to the amount of activity, A. This is a very important point that far too few researchers in the field of bird orientation fully appreciate.

Emlen [1969b] proposed a procedure for determining a relative measure of the independence of consecutive jumps made by Indigo Buntings in "footprint" orientation cages. This procedure was to place a translucent glass lid over the orientation cage and to record, by direct visual observation from below the cage, the directions of sequential jumps made by the bird. Independence of jumps was indicated when the mean directional distance between pairs of jumps for various orders of pairs approximated 90° or when the autocorrelation coefficient approached zero. This method presupposed that the individual was behaving in a uniform manner with respect to directionality. Emlen claimed that this was a reasonable assumption since the bird was prevented from seeing any directional cues external to the cage. This method was attempted with various species of warblers in the present study but was found to be unsuccessful for two reasons: (1) the activity of the birds dropped drastically if it did not cease entirely when the translucent lid was placed on the cage and (2) with such a small amount of activity there was no indication that the birds were behaving uniformly. It was, therefore, my opinion that the question of the independence of jumps could not be rigorously resolved and that the only way of demonstrating significantly oriented behavior was by considering the results of many independent tests on the same individual (or a few tests on many individuals if it is suspected that all individuals would have identical orientations). Nevertheless, the fact that a given bird is capable of producing a directed trace on a single night does supply an indication that the bird is at least predisposed to directionality. With the above considerations in mind, the directionality of single night's tests may now be examined.

As shown in Chapter 11, a good measure of the concentration of activity around the preferred direction of a unimodal circular distribution is given by the length of the resultant vector, r, of the vector sum. When a distribution is multimodal, an estimate of r can be obtained for each mode based upon the mode intensity, I, of that mode. This estimation of r is based on the assumption that all of the activity in the peak (eliminating the valleys) of each mode belongs entirely to that mode and that the distribution around the peak approximates a circular normal distribution. This method, therefore, does not allow extensive overlapping of the various modes. As was shown in Chapter 11, such a method of multimodal analysis usually resulted in an overestimation of r especially if the modes were weakly concentrated about the preferred direction. To avoid conclusions based on such overestimations of r, this discussion will be limited at this time to the values of r obtained on unimodal traces, r_U.

The number of traces indicating unimodal behavior is presented, for each of the 24 California captured Blackpoll Warblers, in Table 12-8 along with the mean value, $\bar{r}_U$, for the unimodal traces produced by each of these birds. The average value of $\bar{r}_U$ over all 322 of these tests was found to be $\bar{r}_U$=0.554 while the average value of $\bar{r}_U$ over the 23 individuals that produced unimodal data was $\bar{r}_U$=0.547. These values of $\bar{r}_U$ are certainly indicative of well directed behavior. For example, the series of traces shown in Figure 12-5a-d (all produced by Blackpoll Warbler #32)

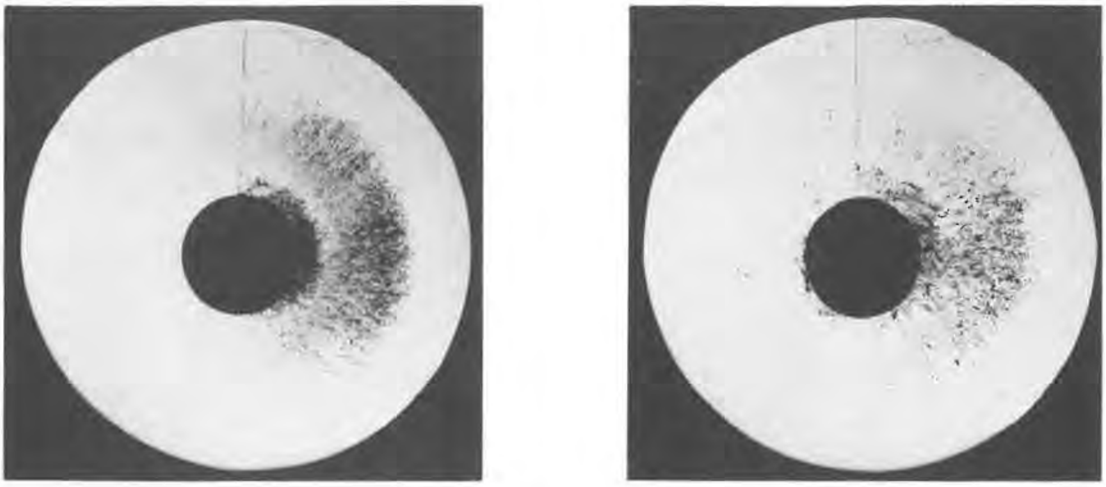
TABLE 12-8

MEAN CONCENTRATION ABOUT THE MEAN VECTOR FOR ALL UNIMODAL DATA PRODUCED BY CALIFORNIA CAPTURED BLACKPOLL WARBLERS

BIRD	NUMBER OF TESTS PRODUCING UNIMODAL BEHAVIOR	MEAN CONCENTRATION ABOUT THE MEAN VECTOR r_u
21	7	.394
22	0	--
23	5	.350
24	20	.519
25	13	.733
26	16	.494
27	6	.614
28	14	.628
29	7	.506
30	6	.503
31	16	.493
32	21	.505
33	16	.722
34	24	.357
35	16	.473
36	19	.720
37	17	.657
38	21	.491
39	16	.653
40	12	.623
41	16	.663
42	16	.416
43	11	.693
44	7	.382
TOTAL	322	.554
AVERAGE/BIRD		.547 ± .123

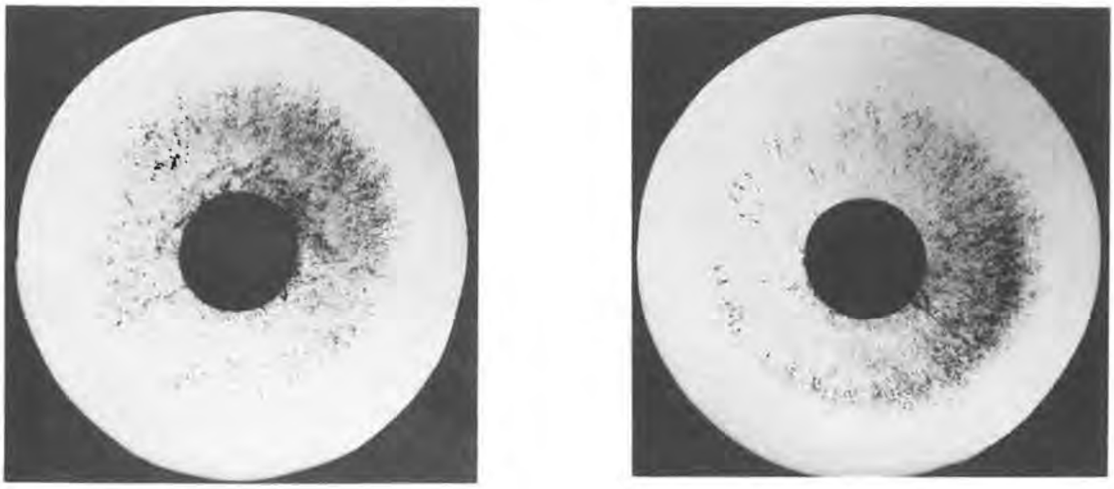
FIGURE 12-5

EXAMPLES OF UNIMODAL ORIENTATION DATA PRODUCED BY A CALIFORNIA CAPTURED BLACKPOLL WARBLER, BIRD 32, UNDER THE CLEAR NIGHT SKY AND ILLUSTRATING VARIOUS CONCENTRATIONS, r_u, ABOUT THE MEAN UNIMODAL VECTOR



a. $r_u = 0.767$
TRACE 415; 10/21/71

b. $r_u = 0.681$
TRACE 412; 10/17/71



c. $r_u = 0.490$
TRACE 413; 10/18/71

d. $r_u = 0.334$
TRACE 417; 10/24/71

display r_U values of 0.767, 0.681, 0.490 and 0.334 respectively. However, whether or not such values of r_U indicate statistically significant directionality depends, of course, on the number of independent choices, N, made by the bird. The Rayleigh test provides a simple and powerful method of statistically distinguishing between unimodally directed behavior and uniform behavior if the number of independent choices involved is known. The test statistic for the Rayleigh test is

$$Z = N \cdot r^2 \quad . \qquad (12\text{-}1)$$

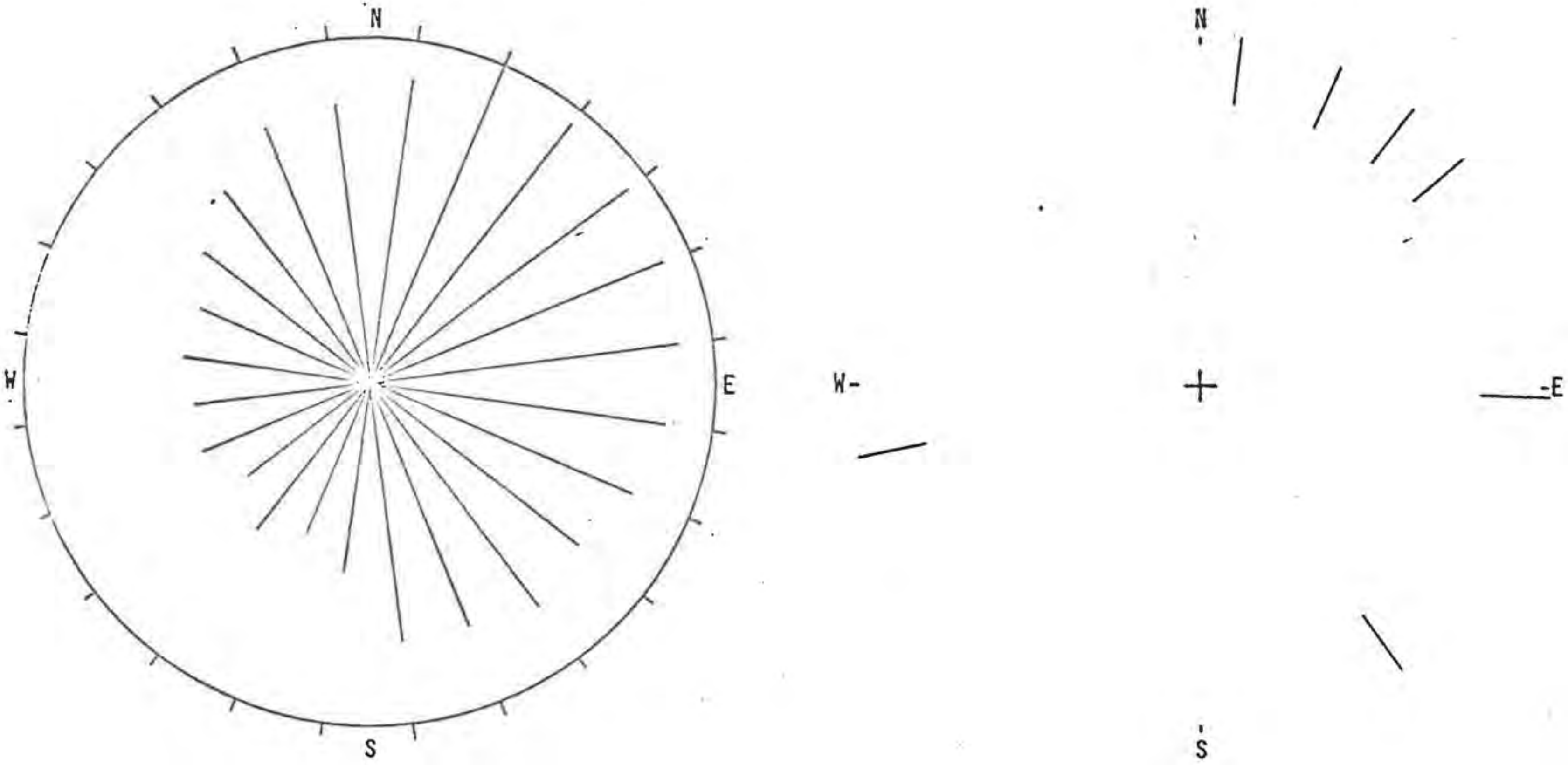
The null hypothesis of the uniform distribution (P_{RAY}) can then be tested by examination of a table of critical values of Z as presented in Batschelet [1965, 1972]. These tables indicate that the average unimodal Blackpoll Warbler trace, having r_U=0.547, will be significantly directed (P_{RAY}<.05) if the number of independent choices, N, is at least 9.75. The average number of jumps per unimodal test for the sample of California captured Blackpoll Warblers was found to be 99.05. This result indicates that if, on the average, only one out of every 10 jumps represents an independent choice, the average unimodal trace would be significantly directed (P_{RAY}<.05). Emlen [1969b] indicated that, for Indigo Buntings, independence of jumps was approached, on the average, by every fourth jump and assured by every eighth jump. If Blackpoll Warblers behave similarly when placed into orientation cages, then there exists a very strong indication that they are capable of significantly directed behavior over the course of a single night's test, at least when their behavior is unimodally directed. As pointed out in Chapter 8, however, the fact that a bird is capable of significantly directed behavior on a single night's test, does not prove that the bird is not disoriented. To demonstrate truly oriented behavior it is still necessary to examine the results of several nights' tests on a given individual.

There are two basic methods of presenting the results of several orientation experiments on a given individual. The first is to sum all of the activities in each 15° sector over all of the tests on that individual thereby producing a single composite distribution. Since the location of true north was varied with respect to the 15° sectors from night to night, it is first necessary to transform the raw data so that the first 15° sector extends from true north to 15°, the second from 15° to 30°, etc. Then the indicated summation can be acomplished. It should be noted that this method, in effect, weights each night's test according to the total activity produced that night. The resulting composite distributions for each of the 24 individual Blackpoll Warblers are shown as vector diagrams in Figures 12-6a to 12-29a. The radius of each diagram represents the maximum number of jumps in any single 15°

FIGURE 12-6

ORIENTATION OF ZUGUNRUHE OF A
CALIFORNIA CAPTURED IMMATURE BLACKPOLL
WARBLER TESTED UNDER THE CLEAR NIGHT SKY

BIRD NUMBER 21



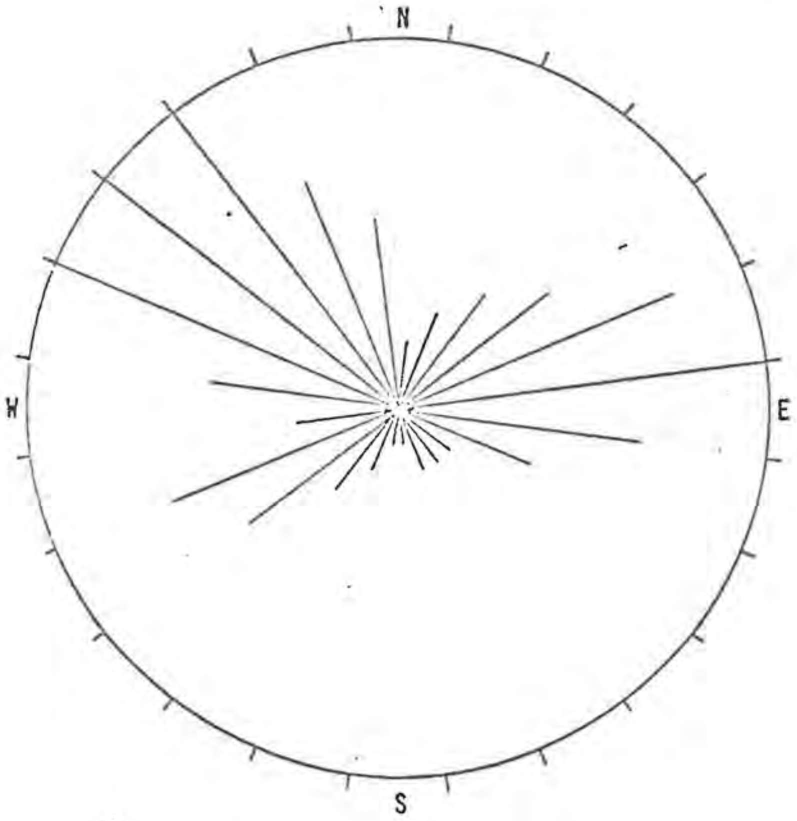
a. VECTOR DIAGRAM OF THE SUMMATION OF ACTIVITIES OF ALL TESTS. THE RADIUS, R, REPRESENTS THE MAXIMUM NUMBER OF JUMPS IN ANY ONE 15° SECTOR. R= 32.1

b. DISTRIBUTION OF NIGHTLY MEAN DIRECTIONS. UNIMODAL AND PRIMARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS SOLID LINES. SECONDARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS DASHED LINES.

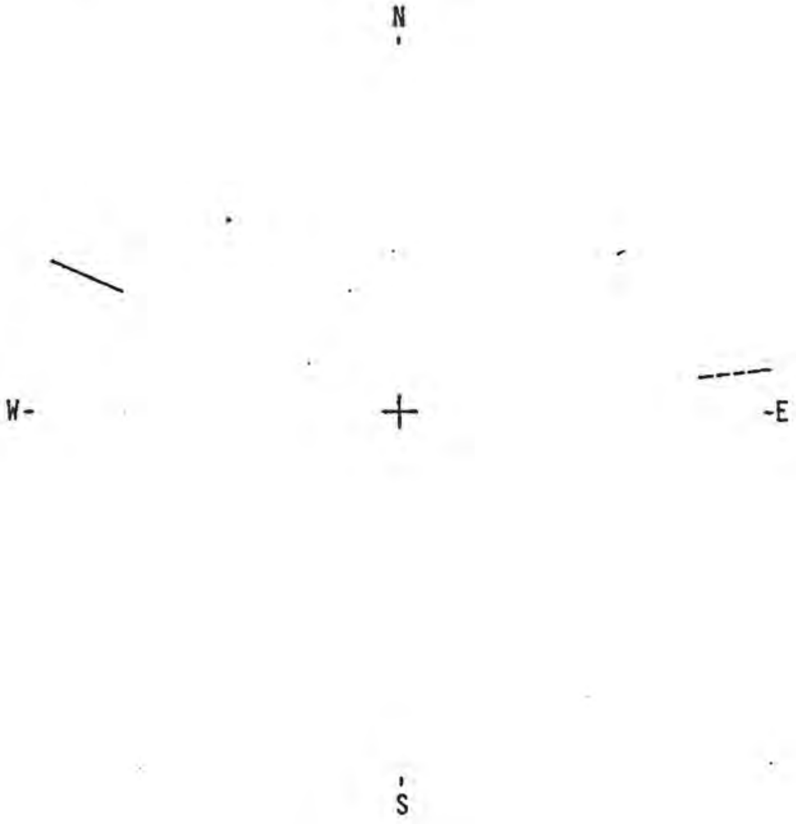
FIGURE 12- 7

ORIENTATION OF ZUGUNRUHE OF A
CALIFORNIA CAPTURED IMMATURE BLACKPOLL
WARBLER TESTED UNDER THE CLEAR NIGHT SKY

BIRD NUMBER 22



a. VECTOR DIAGRAM OF THE SUMMATION OF ACTIVITIES OF ALL TESTS. THE RADIUS, R, REPRESENTS THE MAXIMUM NUMBER OF JUMPS IN ANY ONE 15° SECTOR. R= 4.6

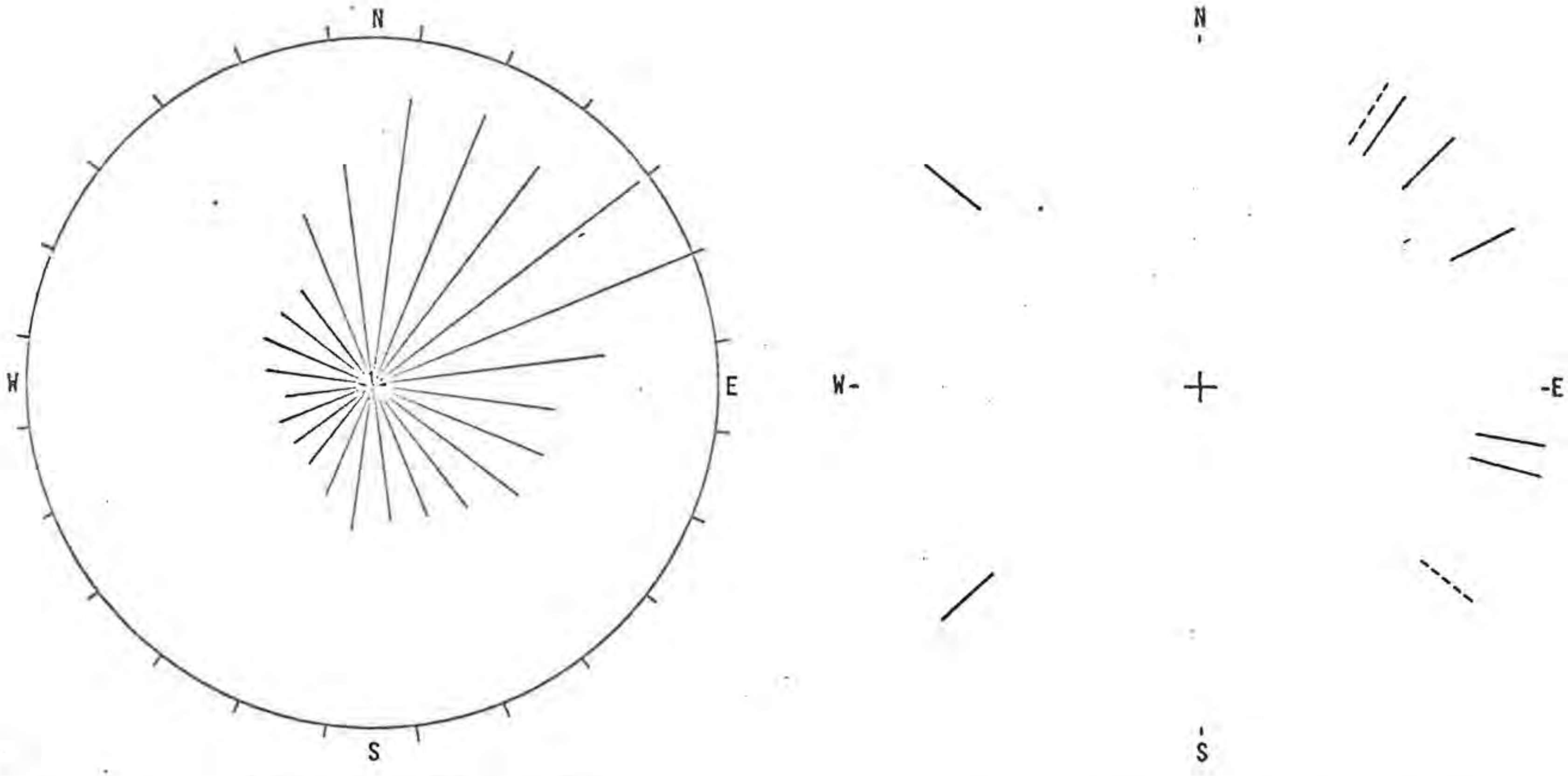


b. DISTRIBUTION OF NIGHTLY MEAN DIRECTIONS. UNIMODAL AND PRIMARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS SOLID LINES. SECONDARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS DASHED LINES.

FIGURE 12-8

ORIENTATION OF ZUGUNRUHE OF A
CALIFORNIA CAPTURED IMMATURE BLACKPOLL
WARBLER TESTED UNDER THE CLEAR NIGHT SKY

BIRD NUMBER 23



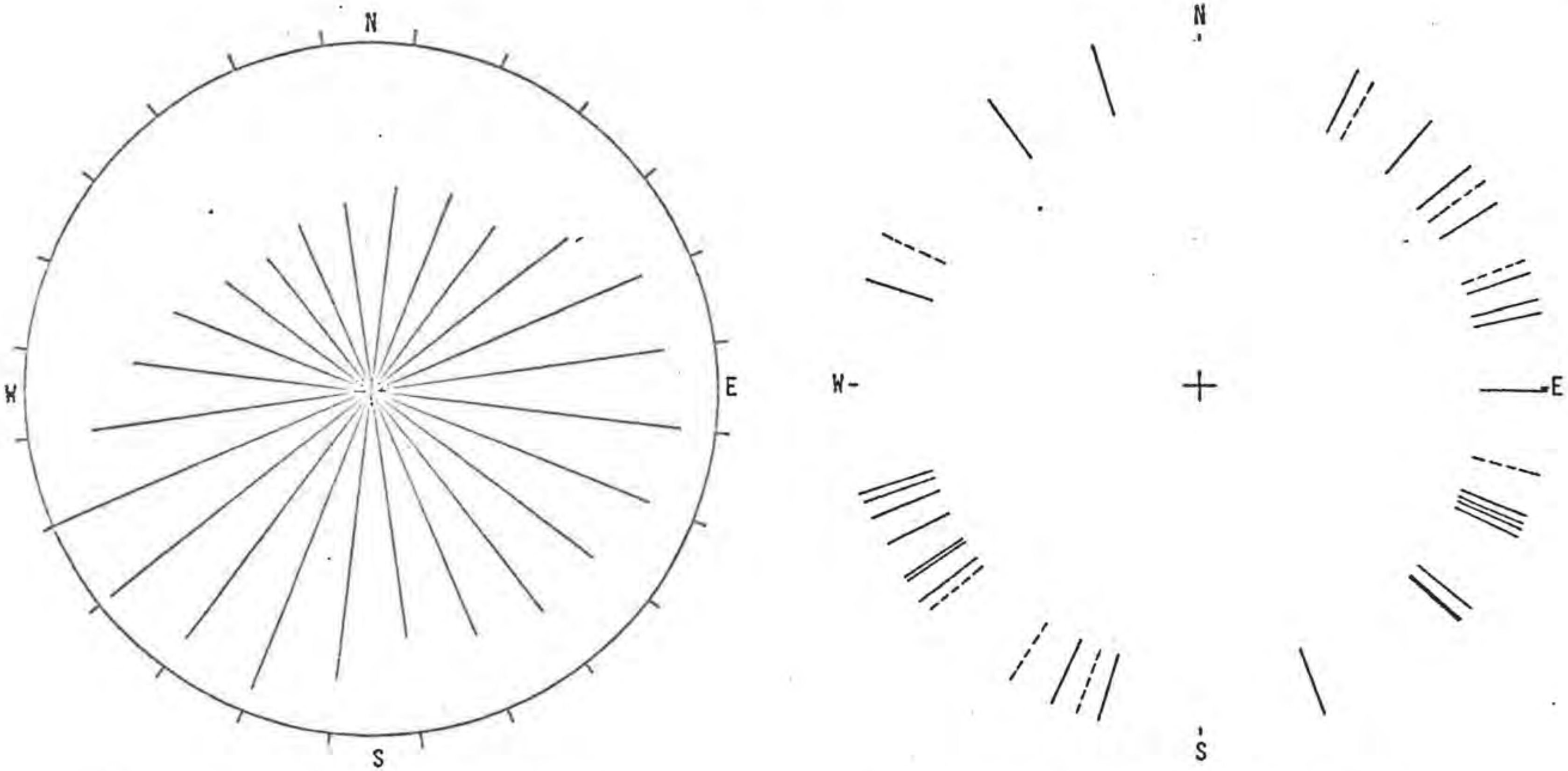
a. VECTOR DIAGRAM OF THE SUMMATION OF ACTIVITIES OF ALL TESTS. THE RADIUS, R, REPRESENTS THE MAXIMUM NUMBER OF JUMPS IN ANY ONE 15° SECTOR. R= 36.4

b. DISTRIBUTION OF NIGHTLY MEAN DIRECTIONS. UNIMODAL AND PRIMARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS SOLID LINES. SECONDARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS DASHED LINES.

FIGURE 12-9

ORIENTATION OF ZUGUNRUHE OF A
CALIFORNIA CAPTURED IMMATURE BLACKPOLL
WARBLER TESTED UNDER THE CLEAR NIGHT SKY

BIRD NUMBER 24



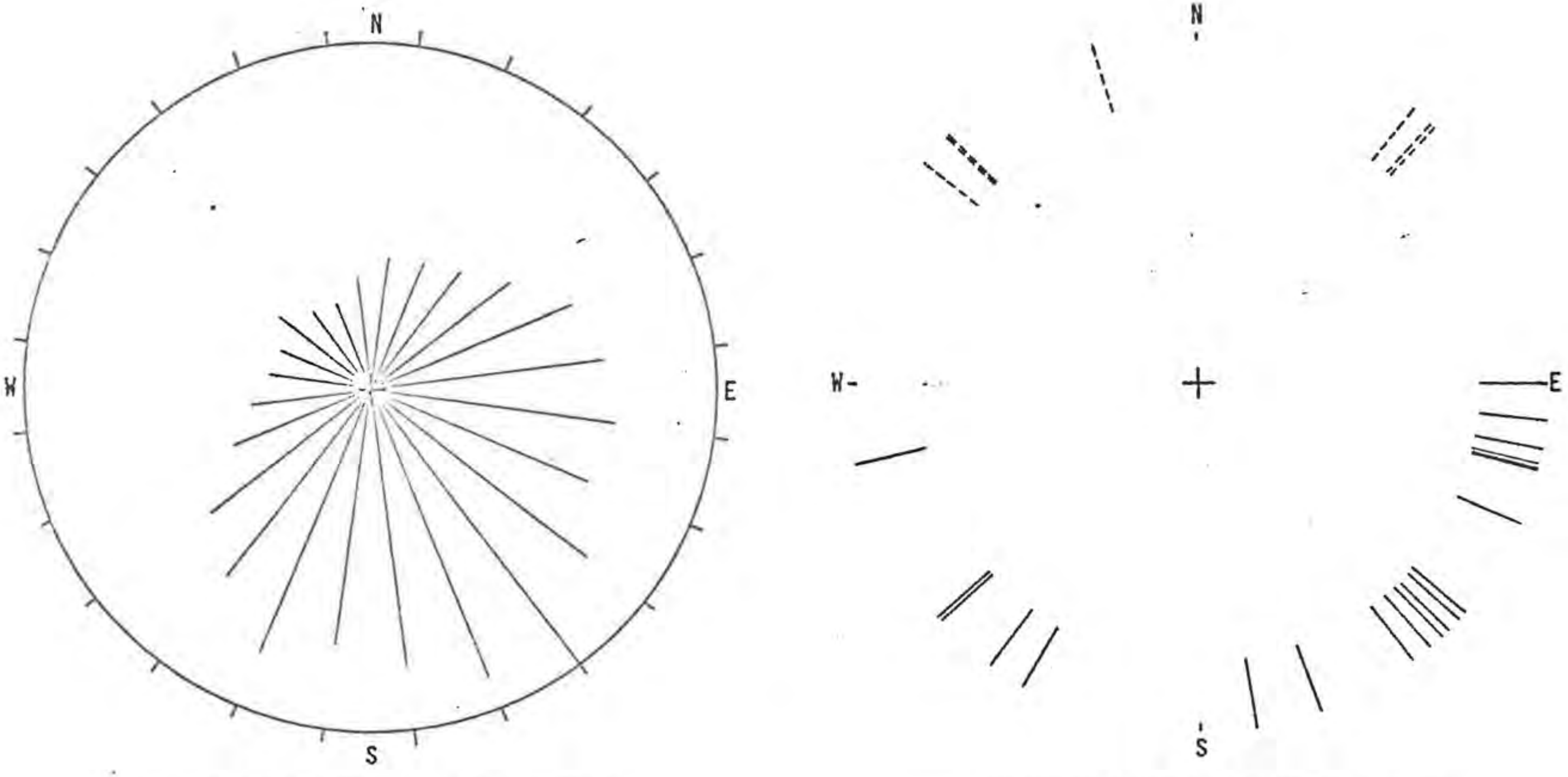
a. VECTOR DIAGRAM OF THE SUMMATION OF ACTIVITIES OF ALL TESTS. THE RADIUS, R, REPRESENTS THE MAXIMUM NUMBER OF JUMPS IN ANY ONE 15° SECTOR. R= 115.7

b. DISTRIBUTION OF NIGHTLY MEAN DIRECTIONS. UNIMODAL AND PRIMARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS SOLID LINES. SECONDARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS DASHED LINES.

FIGURE 12-10

ORIENTATION OF ZUGUNRUHE OF A
CALIFORNIA CAPTURED IMMATURE BLACKPOLL
WARBLER TESTED UNDER THE CLEAR NIGHT SKY

BIRD NUMBER 25



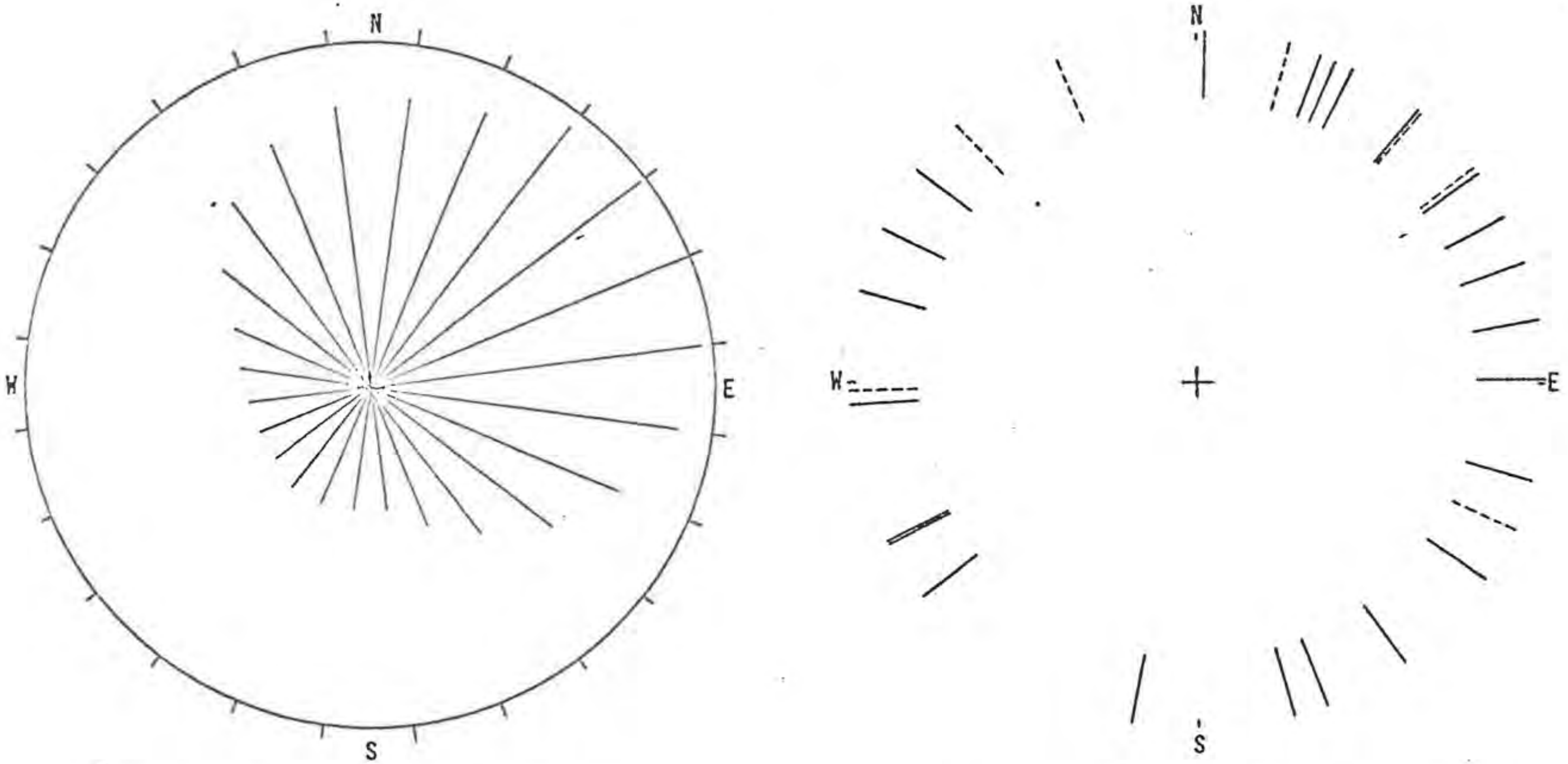
a. VECTOR DIAGRAM OF THE SUMMATION OF ACTIVITIES OF ALL TESTS. THE RADIUS, R, REPRESENTS THE MAXIMUM NUMBER OF JUMPS IN ANY ONE 15° SECTOR. R= 54.9

b. DISTRIBUTION OF NIGHTLY MEAN DIRECTIONS. UNIMODAL AND PRIMARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS SOLID LINES. SECONDARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS DASHED LINES.

FIGURE 12-11

ORIENTATION OF ZUGUNRUHE OF A
CALIFORNIA CAPTURED IMMATURE BLACKPOLL
WARBLER TESTED UNDER THE CLEAR NIGHT SKY

BIRD NUMBER 26



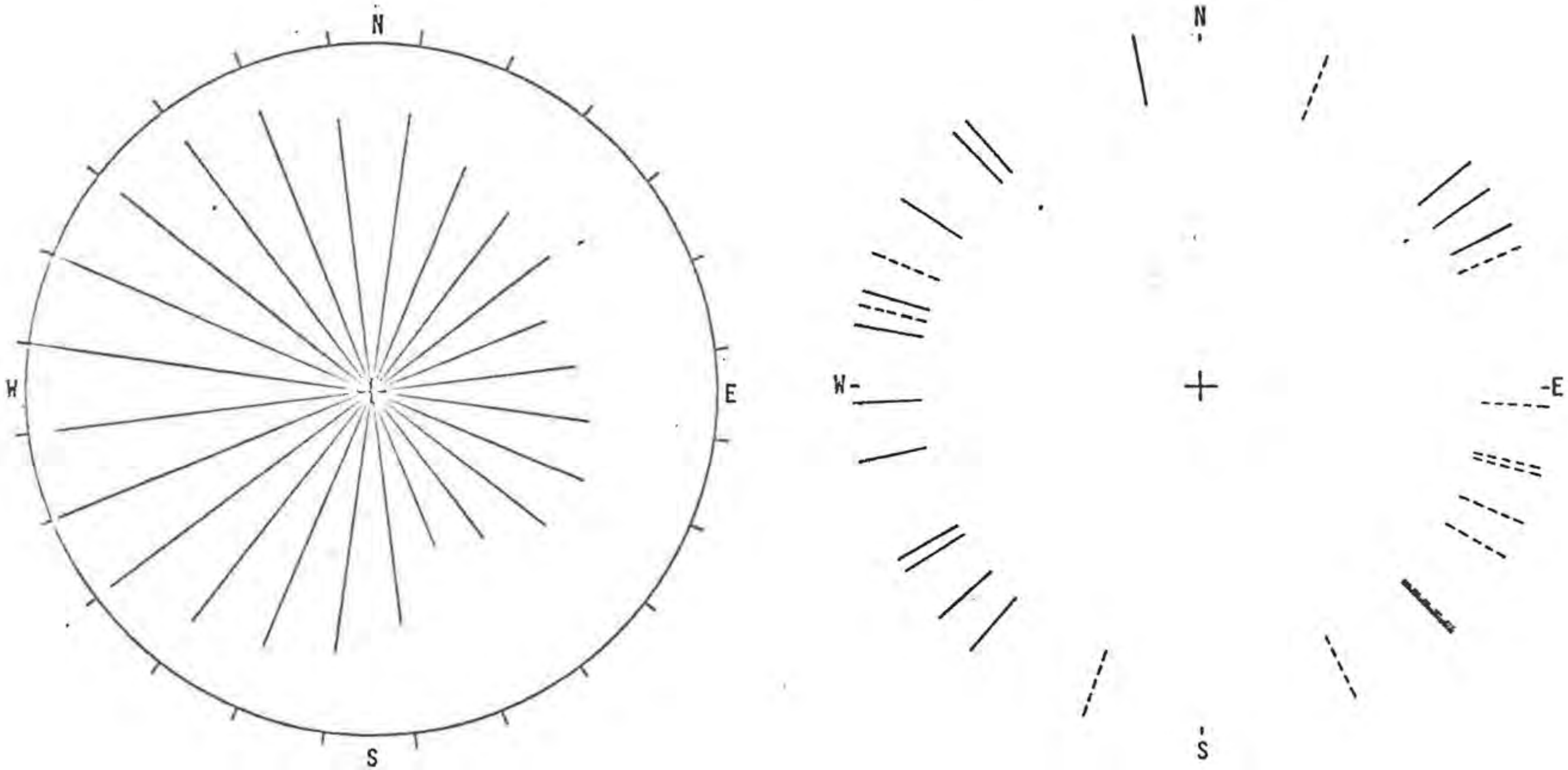
a. VECTOR DIAGRAM OF THE SUMMATION OF ACTIVITIES OF ALL TESTS. THE RADIUS, R, REPRESENTS THE MAXIMUM NUMBER OF JUMPS IN ANY ONE 15° SECTOR. R= 346.7

b. DISTRIBUTION OF NIGHTLY MEAN DIRECTIONS. UNIMODAL AND PRIMARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS SOLID LINES. SECONDARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS DASHED LINES.

FIGURE 12-12

ORIENTATION OF ZUGUNRUHE OF A
CALIFORNIA CAPTURED IMMATURE BLACKPOLL
WARBLER TESTED UNDER THE CLEAR NIGHT SKY

BIRD NUMBER 27



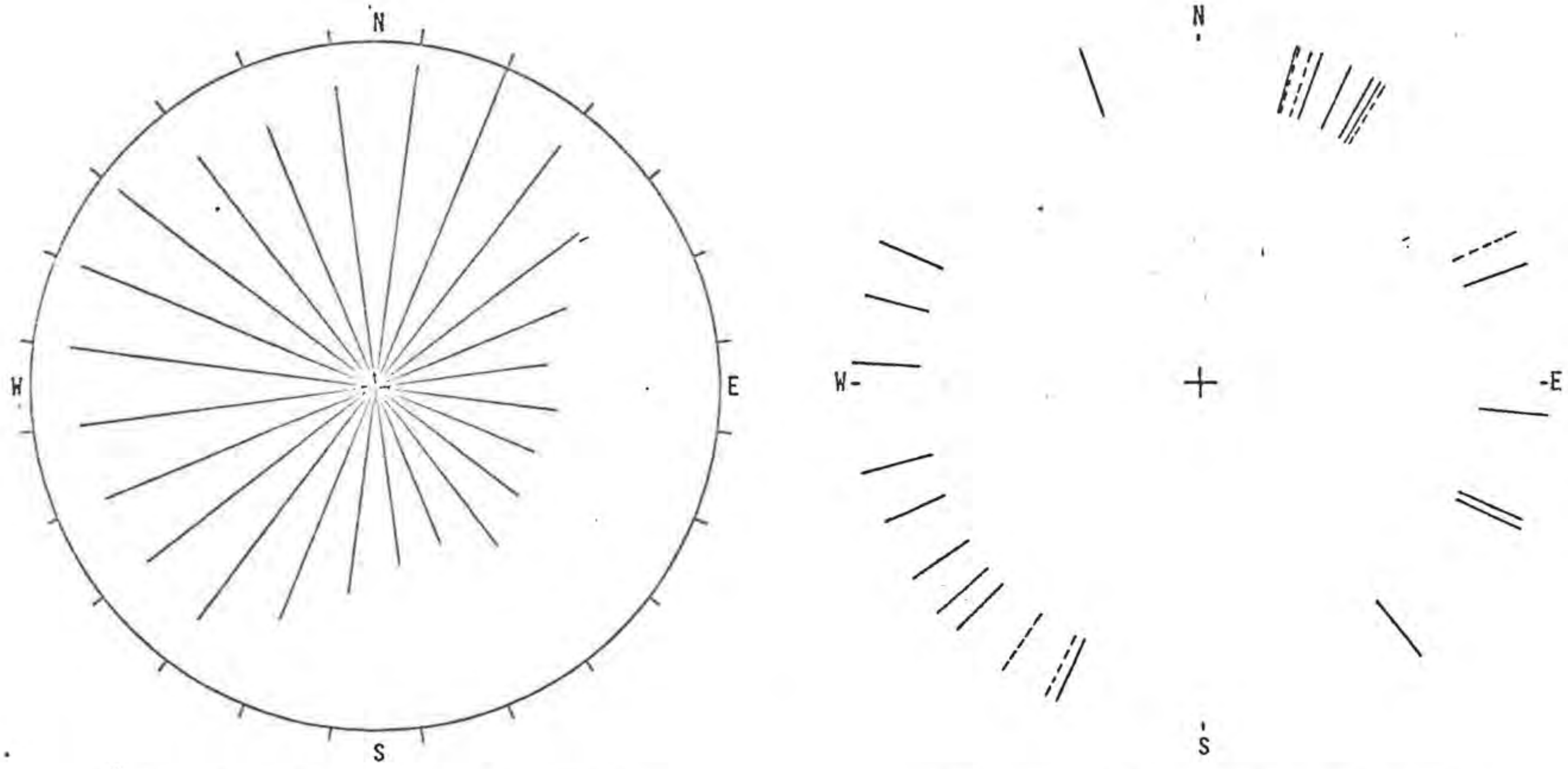
a. VECTOR DIAGRAM OF THE SUMMATION OF ACTIVITIES OF ALL TESTS. THE RADIUS, R, REPRESENTS THE MAXIMUM NUMBER OF JUMPS IN ANY ONE 15° SECTOR. R= 40.4

b. DISTRIBUTION OF NIGHTLY MEAN DIRECTIONS. UNIMODAL AND PRIMARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS SOLID LINES. SECONDARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS DASHED LINES.

FIGURE 12-13

ORIENTATION OF ZUGUNRUHE OF A
CALIFORNIA CAPTURED IMMATURE BLACKPOLL
WARBLER TESTED UNDER THE CLEAR NIGHT SKY

BIRD NUMBER 28



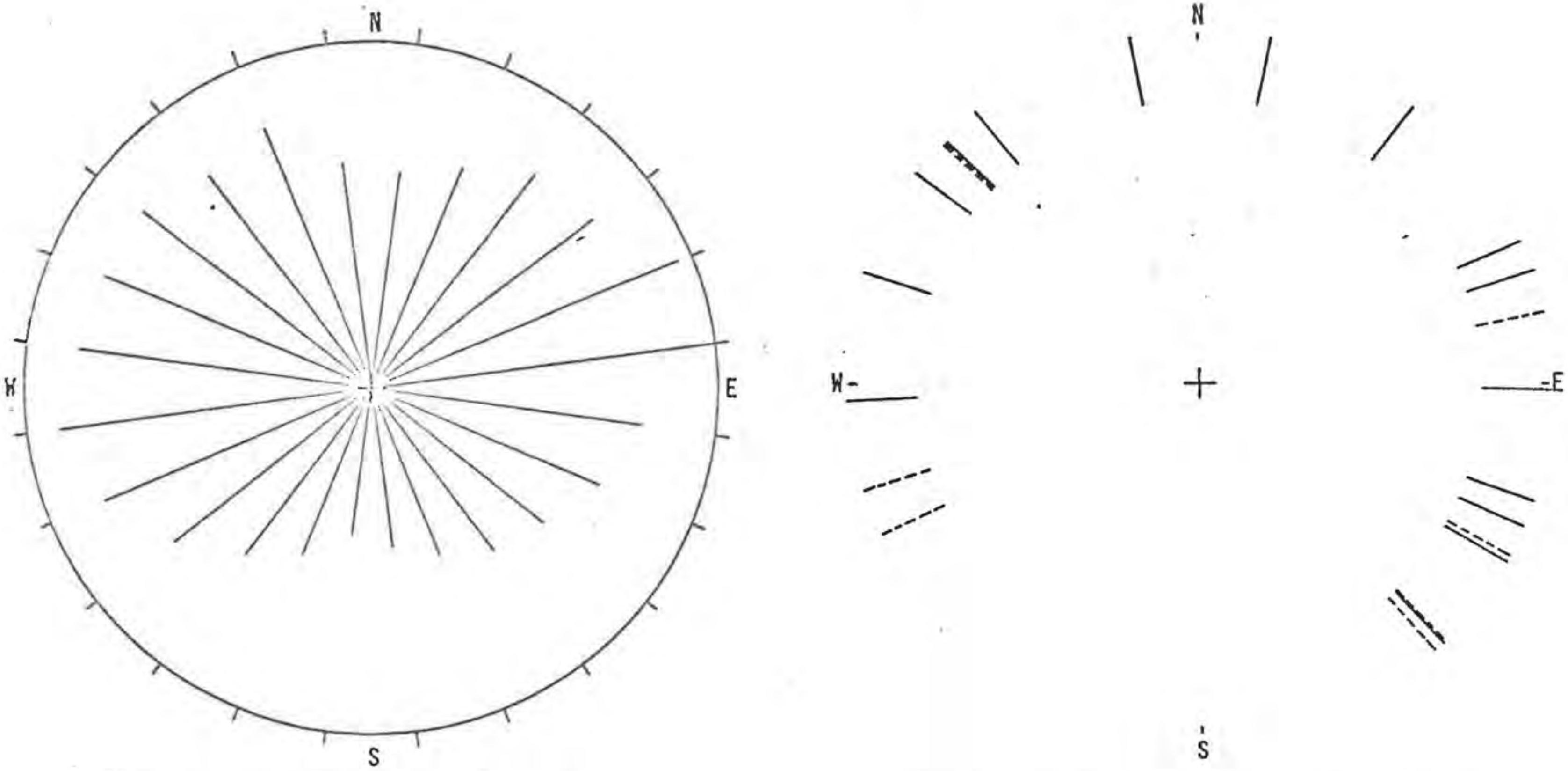
a. VECTOR DIAGRAM OF THE SUMMATION OF ACTIVITIES OF ALL TESTS. THE RADIUS, R, REPRESENTS THE MAXIMUM NUMBER OF JUMPS IN ANY ONE 15° SECTOR. R= 72.3

b. DISTRIBUTION OF NIGHTLY MEAN DIRECTIONS. UNIMODAL AND PRIMARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS SOLID LINES. SECONDARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS DASHED LINES.

FIGURE 12-14

ORIENTATION OF ZUGUNRUHE OF A
CALIFORNIA CAPTURED IMMATURE BLACKPOLL
WARBLER TESTED UNDER THE CLEAR NIGHT SKY

BIRD NUMBER 29



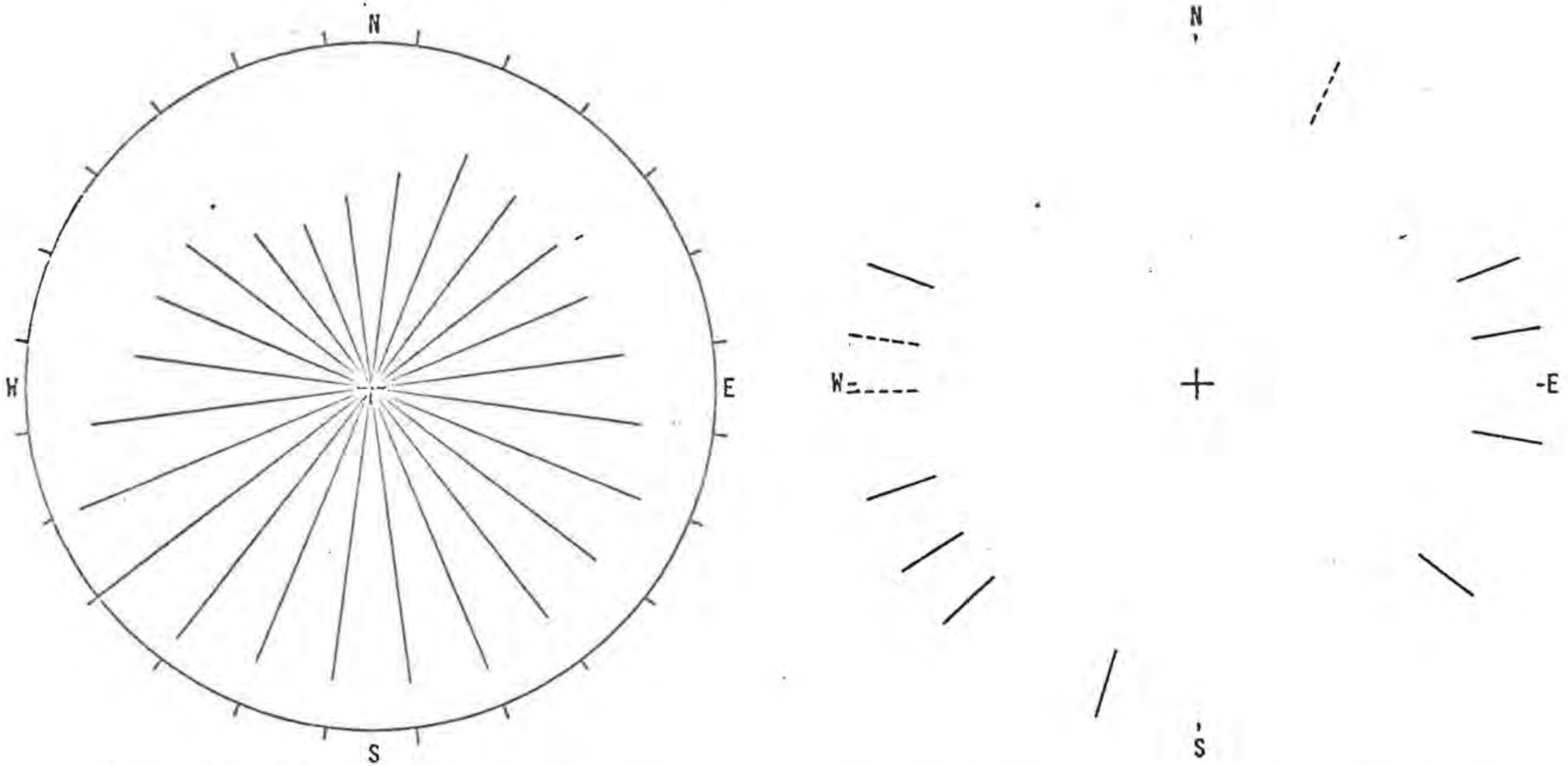
a. VECTOR DIAGRAM OF THE SUMMATION OF ACTIVITIES OF ALL TESTS. THE RADIUS, R, REPRESENTS THE MAXIMUM NUMBER OF JUMPS IN ANY ONE 15° SECTOR. R= 97.0

b. DISTRIBUTION OF NIGHTLY MEAN DIRECTIONS. UNIMODAL AND PRIMARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS SOLID LINES. SECONDARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS DASHED LINES.

FIGURE 12-15

ORIENTATION OF ZUGUNRUHE OF A
CALIFORNIA CAPTURED IMMATURE BLACKPOLL
WARBLER TESTED UNDER THE CLEAR NIGHT SKY

BIRD NUMBER 30



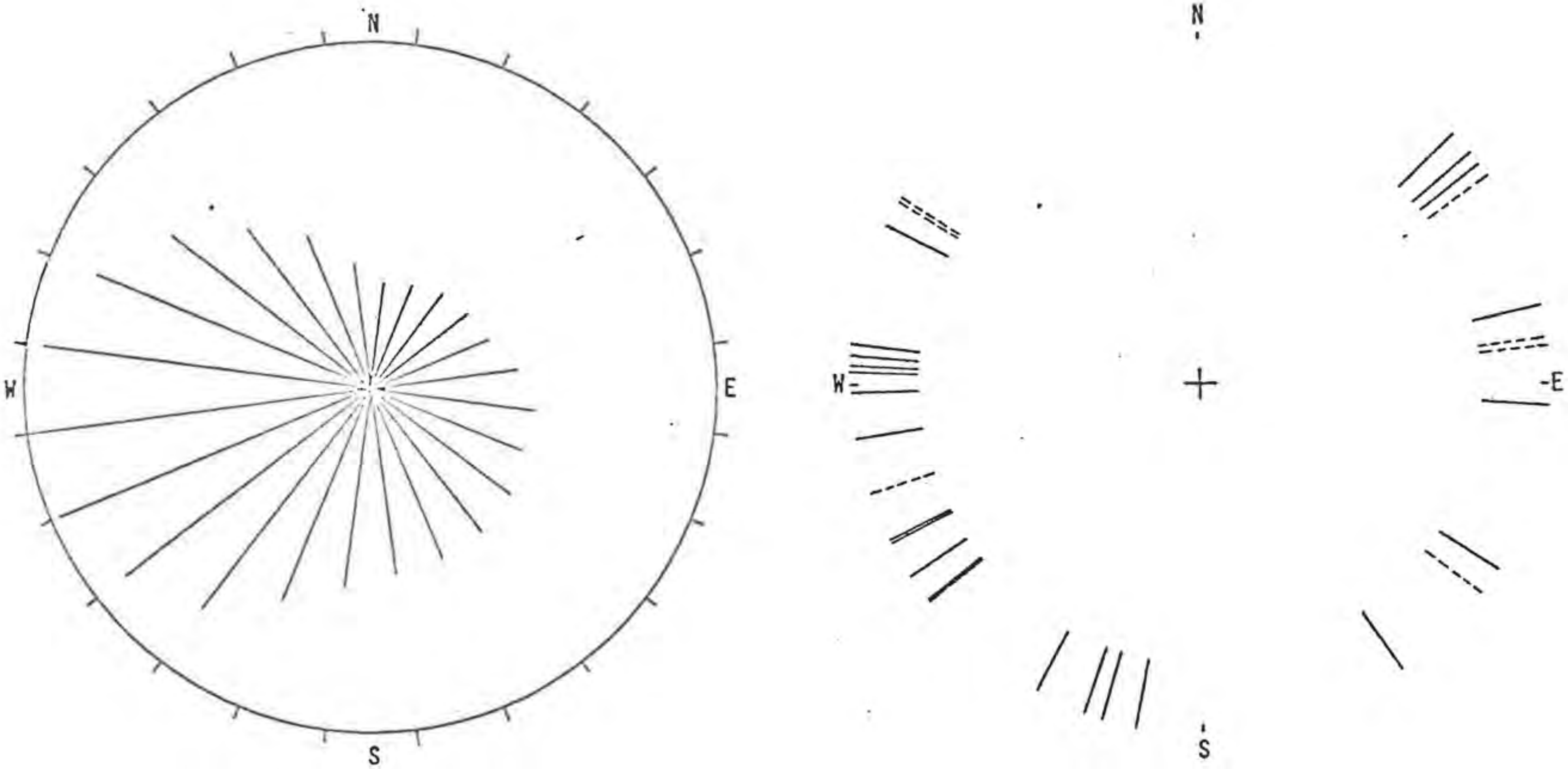
a. VECTOR DIAGRAM OF THE SUMMATION OF ACTIVITIES OF ALL TESTS. THE RADIUS, R, REPRESENTS THE MAXIMUM NUMBER OF JUMPS IN ANY ONE 15° SECTOR. R= 49.0

b. DISTRIBUTION OF NIGHTLY MEAN DIRECTIONS. UNIMODAL AND PRIMARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS SOLID LINES. SECONDARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS DASHED LINES.

FIGURE 12-16

ORIENTATION OF ZUGUNRUHE OF A
CALIFORNIA CAPTURED IMMATURE BLACKPOLL
WARBLER TESTED UNDER THE CLEAR NIGHT SKY

BIRD NUMBER 31



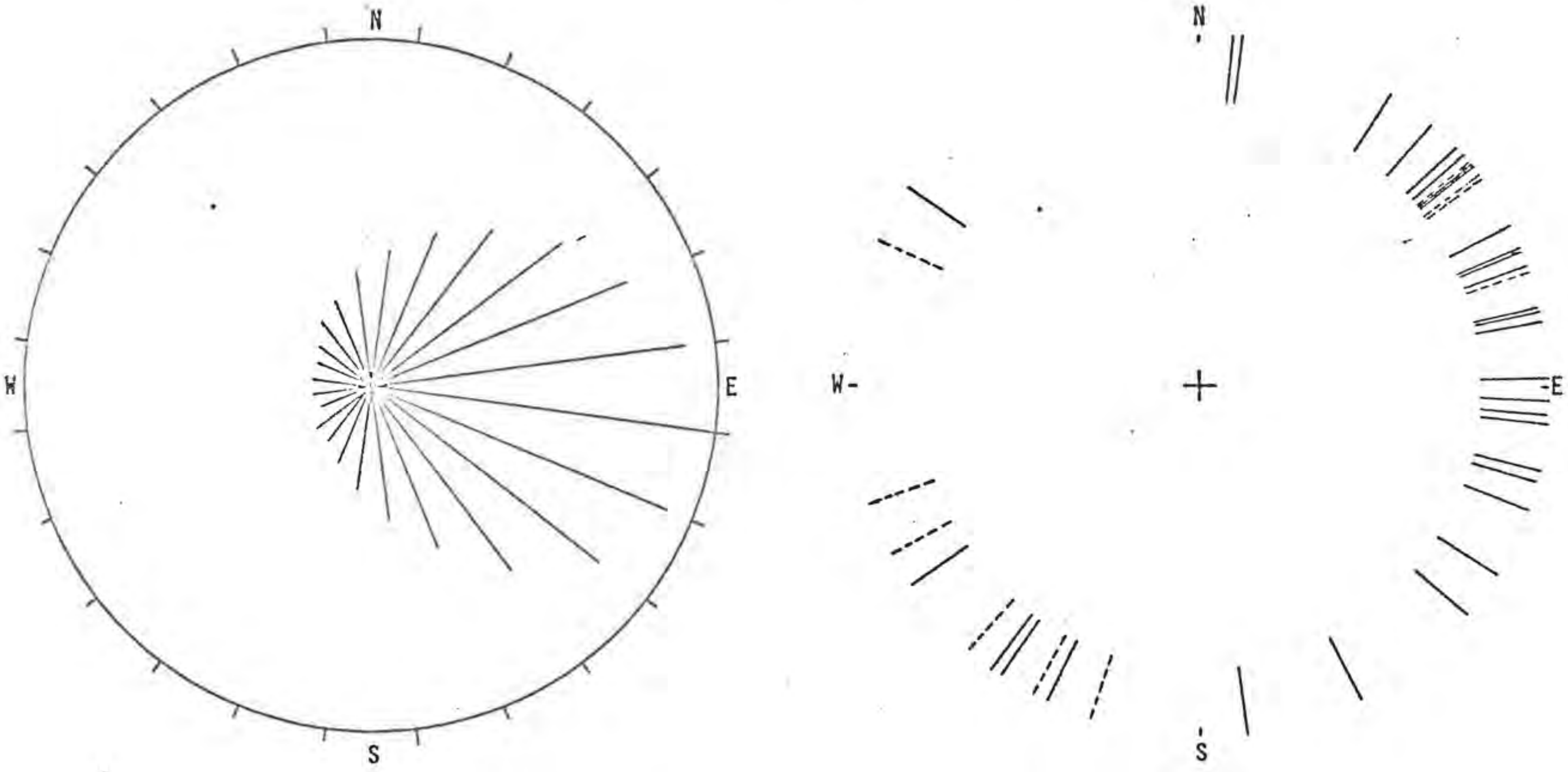
a. VECTOR DIAGRAM OF THE SUMMATION OF ACTIVITIES OF ALL TESTS. THE RADIUS, R, REPRESENTS THE MAXIMUM NUMBER OF JUMPS IN ANY ONE 15° SECTOR. R= 148.1

b. DISTRIBUTION OF NIGHTLY MEAN DIRECTIONS. UNIMODAL AND PRIMARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS SOLID LINES. SECONDARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS DASHED LINES.

FIGURE 12-17

ORIENTATION OF ZUGUNRUHE OF A
CALIFORNIA CAPTURED IMMATURE BLACKPOLL
WARBLER TESTED UNDER THE CLEAR NIGHT SKY

BIRD NUMBER 32



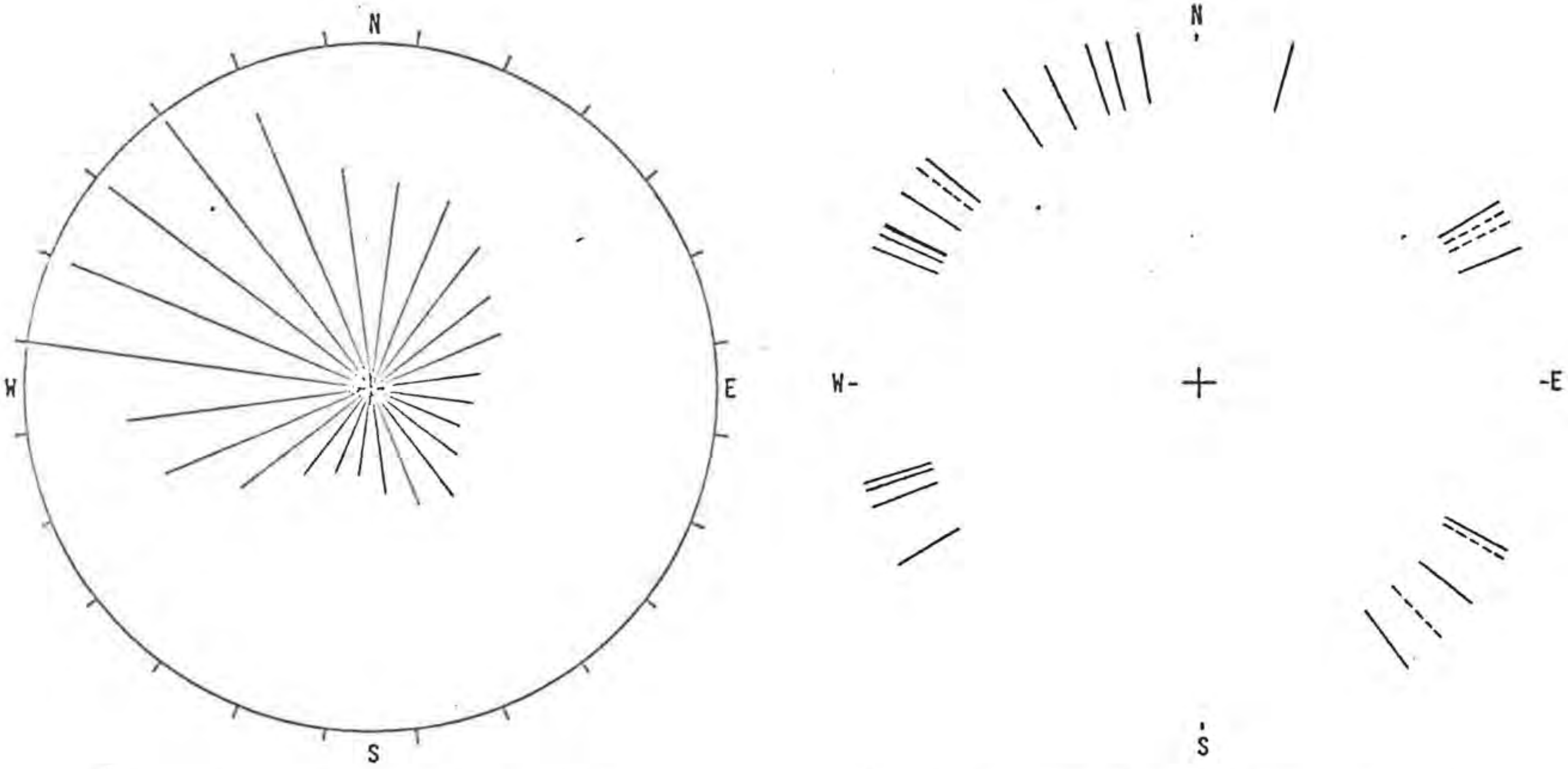
a. VECTOR DIAGRAM OF THE SUMMATION OF ACTIVITIES OF ALL TESTS. THE RADIUS, R, REPRESENTS THE MAXIMUM NUMBER OF JUMPS IN ANY ONE 15° SECTOR. R= 637.1

b. DISTRIBUTION OF NIGHTLY MEAN DIRECTIONS. UNIMODAL AND PRIMARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS SOLID LINES. SECONDARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS DASHED LINES.

FIGURE 12-18

ORIENTATION OF ZUGUNRUHE OF A
CALIFORNIA CAPTURED IMMATURE BLACKPOLL
WARBLER TESTED UNDER THE CLEAR NIGHT SKY

BIRD NUMBER 33



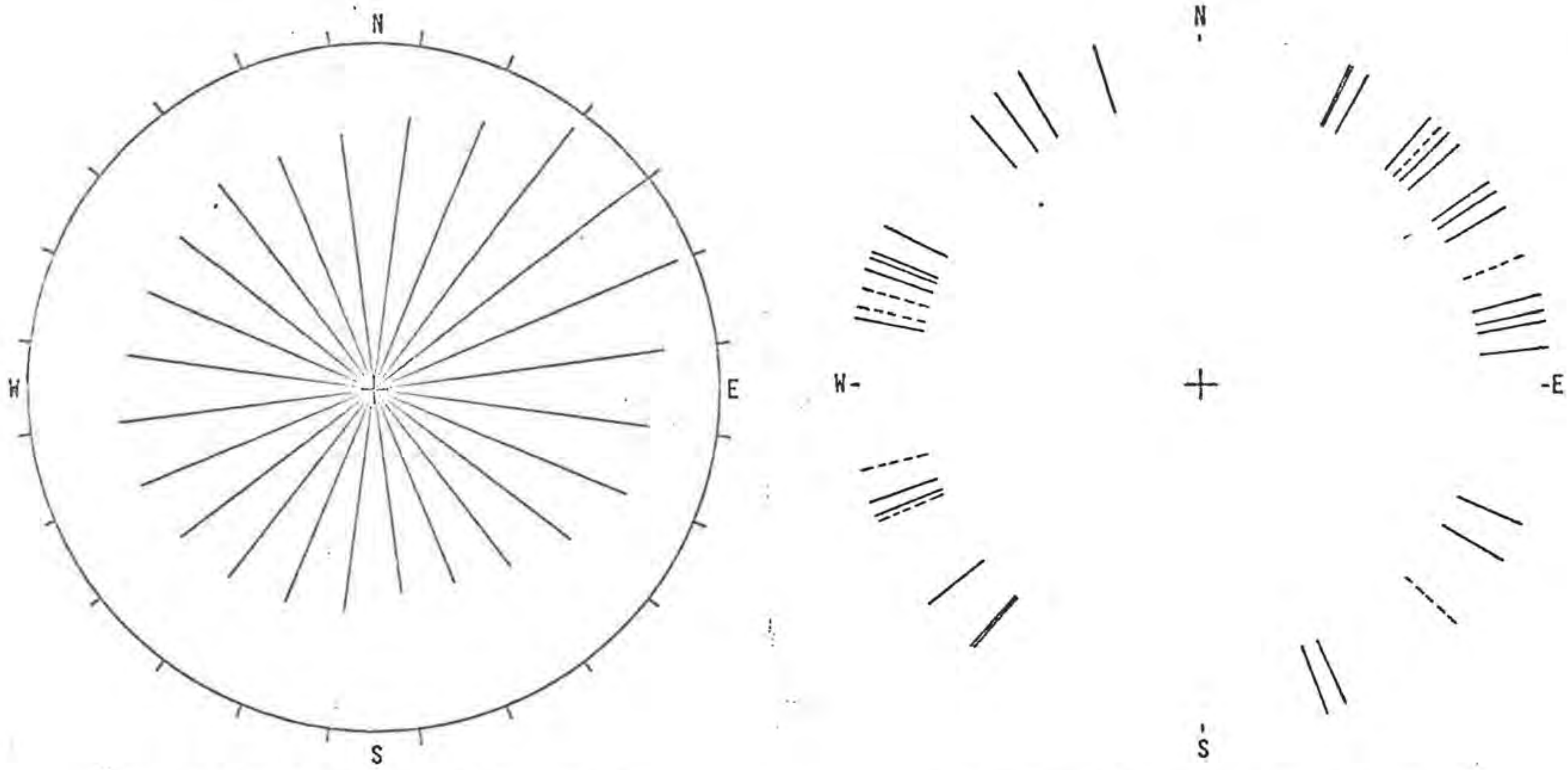
a. VECTOR DIAGRAM OF THE SUMMATION OF ACTIVITIES OF ALL TESTS. THE RADIUS, R, REPRESENTS THE MAXIMUM NUMBER OF JUMPS IN ANY ONE 15° SECTOR. R= 38.2.

b. DISTRIBUTION OF NIGHTLY MEAN DIRECTIONS. UNIMODAL AND PRIMARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS SOLID LINES. SECONDARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS DASHED LINES.

FIGURE 12-19

ORIENTATION OF ZUGUNRUHE OF A
CALIFORNIA CAPTURED IMMATURE BLACKPOLL
WARBLER TESTED UNDER THE CLEAR NIGHT SKY

BIRD NUMBER 34



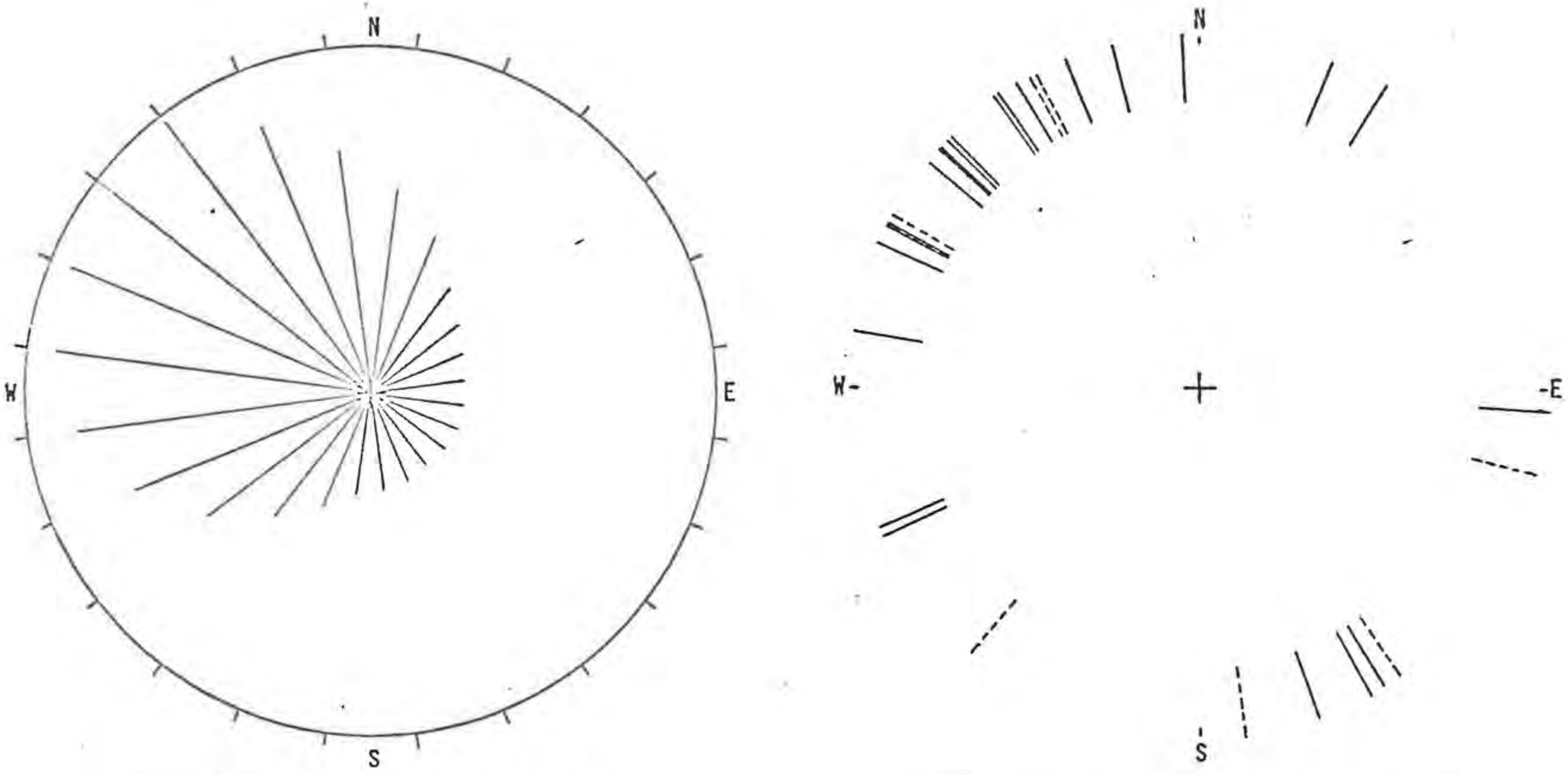
a. VECTOR DIAGRAM OF THE SUMMATION OF ACTIVITIES OF ALL TESTS. THE RADIUS, R, REPRESENTS THE MAXIMUM NUMBER OF JUMPS IN ANY ONE 15° SECTOR. R = 338.6

b. DISTRIBUTION OF NIGHTLY MEAN DIRECTIONS. UNIMODAL AND PRIMARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS SOLID LINES. SECONDARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS DASHED LINES.

FIGURE 12-20

ORIENTATION OF ZUGUNRUHE OF A
CALIFORNIA CAPTURED IMMATURE BLACKPOLL
WARBLER TESTED UNDER THE CLEAR NIGHT SKY

BIRD NUMBER 35



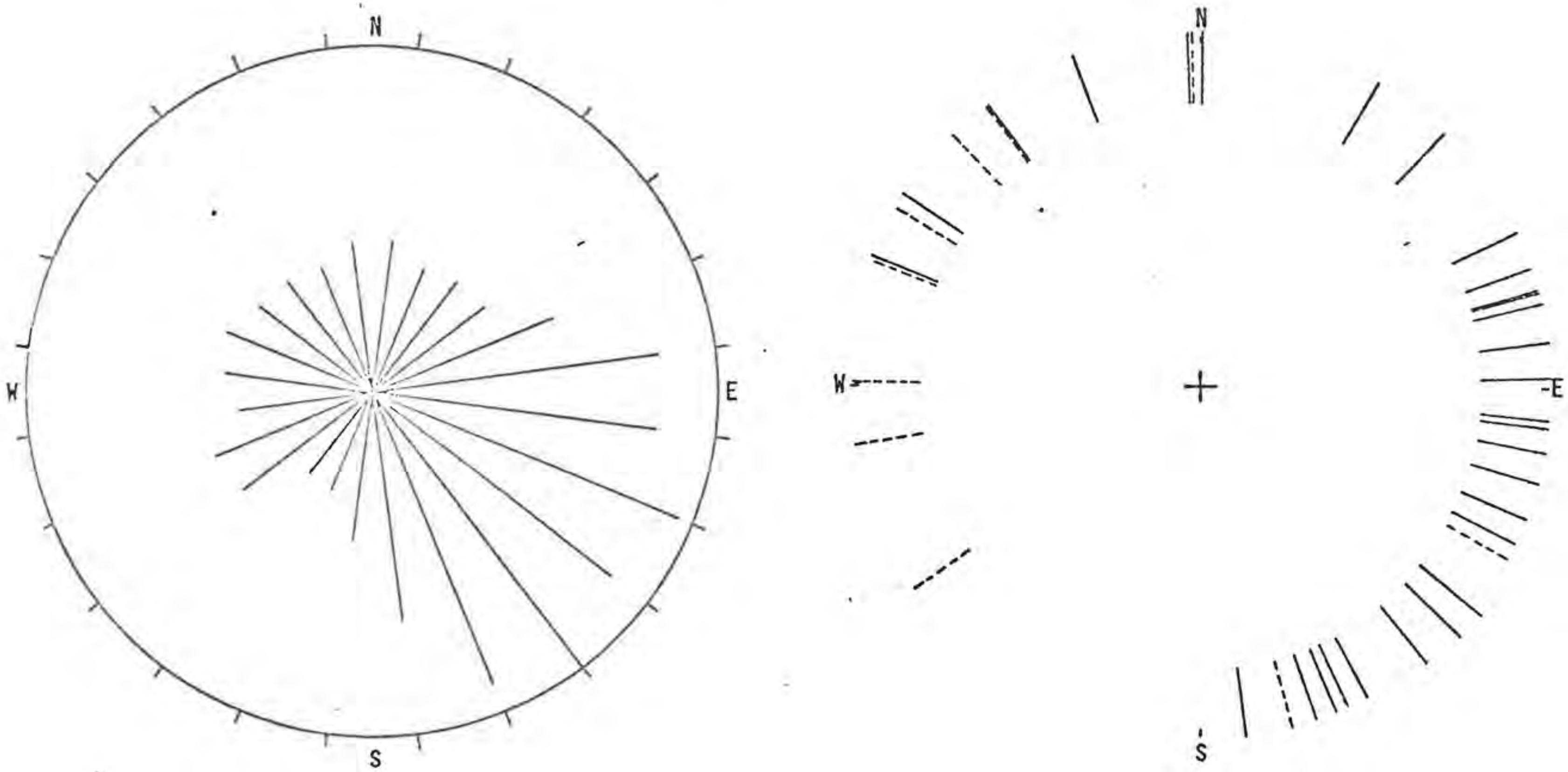
a. VECTOR DIAGRAM OF THE SUMMATION OF ACTIVITIES OF ALL TESTS. THE RADIUS, R, REPRESENTS THE MAXIMUM NUMBER OF JUMPS IN ANY ONE 15° SECTOR. R=212.8

b. DISTRIBUTION OF NIGHTLY MEAN DIRECTIONS. UNIMODAL AND PRIMARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS SOLID LINES. SECONDARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS DASHED LINES.

FIGURE 12-21

ORIENTATION OF ZUGUNRUHE OF A
CALIFORNIA CAPTURED IMMATURE BLACKPOLL
WARBLER TESTED UNDER THE CLEAR NIGHT SKY

BIRD NUMBER 36



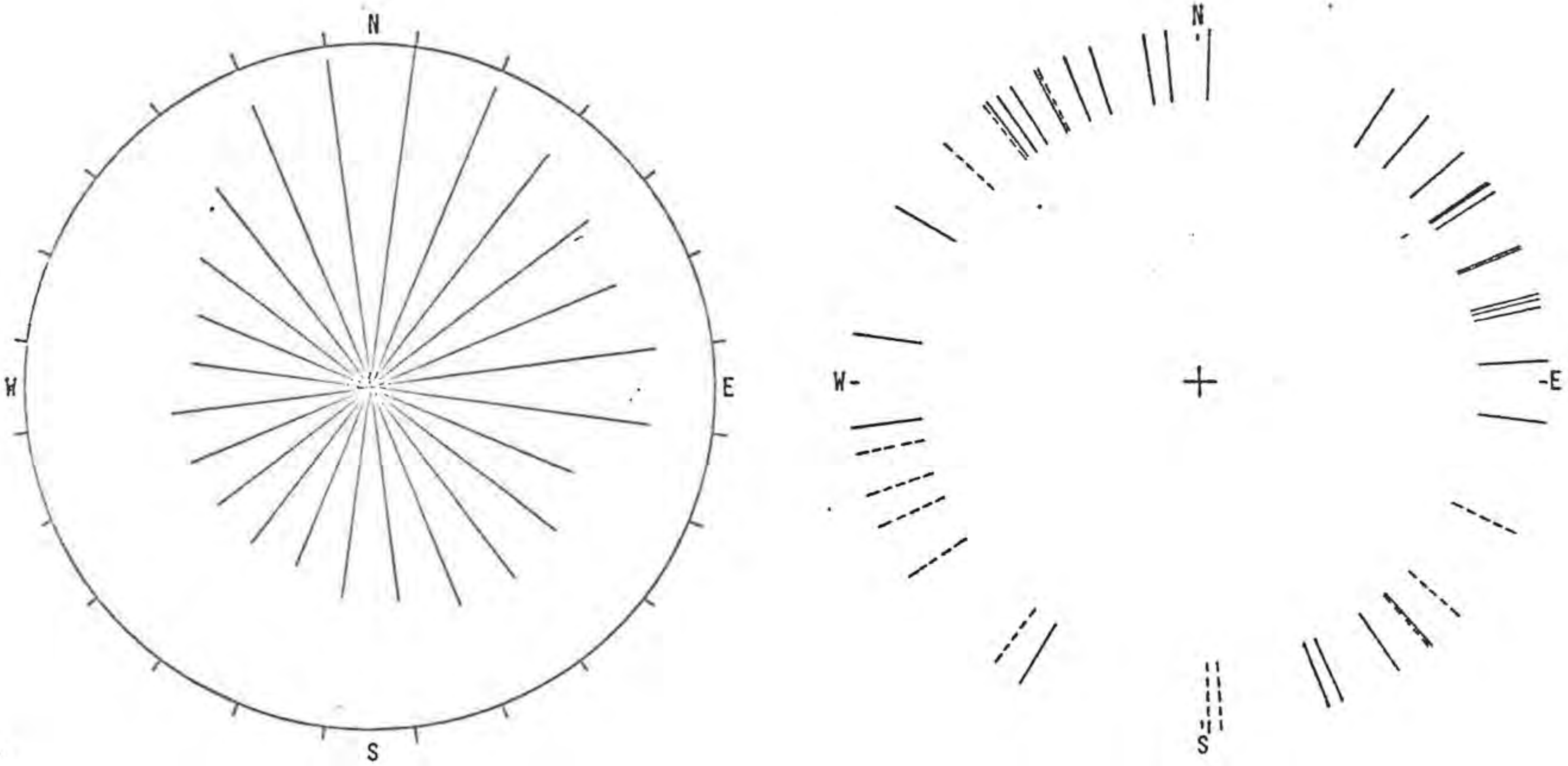
a. VECTOR DIAGRAM OF THE SUMMATION OF ACTIVITIES OF ALL TESTS. THE RADIUS, R, REPRESENTS THE MAXIMUM NUMBER OF JUMPS IN ANY ONE 15° SECTOR. R= 30.7

b. DISTRIBUTION OF NIGHTLY MEAN DIRECTIONS. UNIMODAL AND PRIMARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS SOLID LINES. SECONDARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS DASHED LINES.

FIGURE 12-22

ORIENTATION OF ZUGUNRUHE OF A
CALIFORNIA CAPTURED IMMATURE BLACKPOLL
WARBLER TESTED UNDER THE CLEAR NIGHT SKY

BIRD NUMBER 37



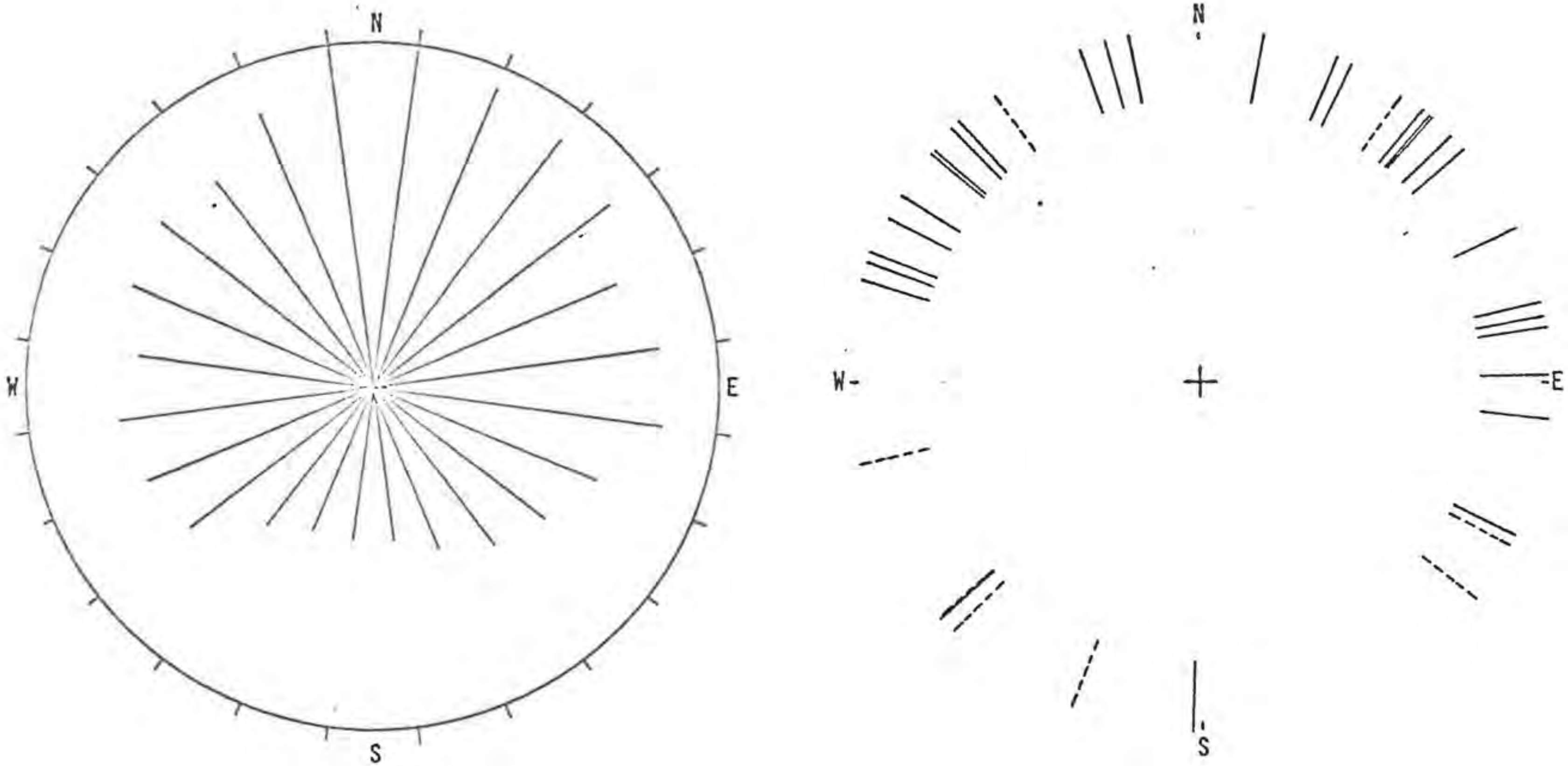
a. VECTOR DIAGRAM OF THE SUMMATION OF ACTIVITIES OF ALL TESTS. THE RADIUS, R, REPRESENTS THE MAXIMUM NUMBER OF JUMPS IN ANY ONE 15° SECTOR. R= 37.7

b. DISTRIBUTION OF NIGHTLY MEAN DIRECTIONS. UNIMODAL AND PRIMARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS SOLID LINES. SECONDARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS DASHED LINES.

FIGURE 12-23

ORIENTATION OF ZUGUNRUHE OF A
CALIFORNIA CAPTURED IMMATURE BLACKPOLL
WARBLER TESTED UNDER THE CLEAR NIGHT SKY

BIRD NUMBER 38



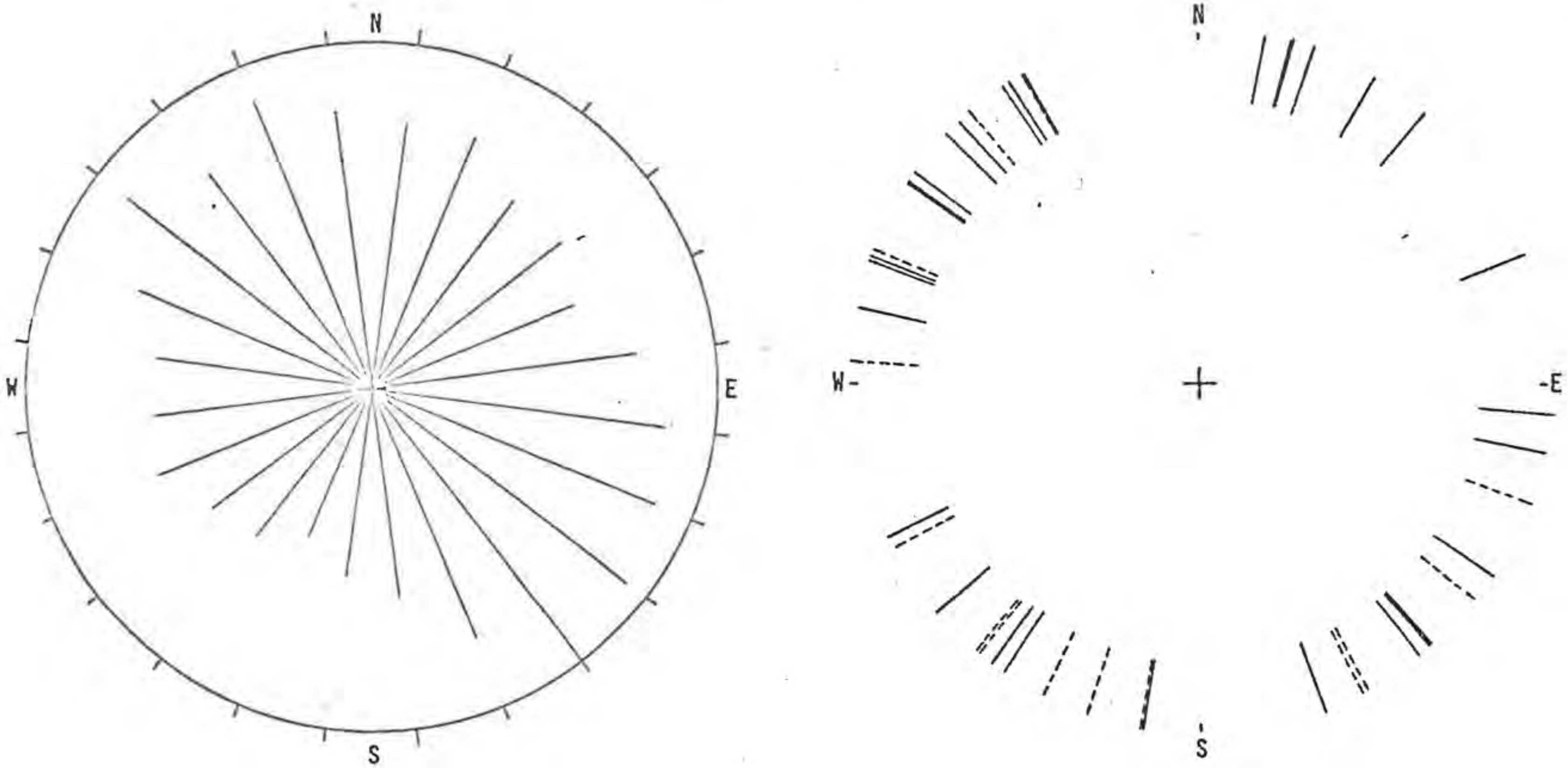
a. VECTOR DIAGRAM OF THE SUMMATION OF ACTIVITIES OF ALL TESTS. THE RADIUS, R, REPRESENTS THE MAXIMUM NUMBER OF JUMPS IN ANY ONE 15° SECTOR. R= 77.8

b. DISTRIBUTION OF NIGHTLY MEAN DIRECTIONS. UNIMODAL AND PRIMARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS SOLID LINES. SECONDARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS DASHED LINES.

FIGURE 12-24

ORIENTATION OF ZUGUNRUHE OF A
CALIFORNIA CAPTURED IMMATURE BLACKPOLL
WARBLER TESTED UNDER THE CLEAR NIGHT SKY

BIRD NUMBER 39



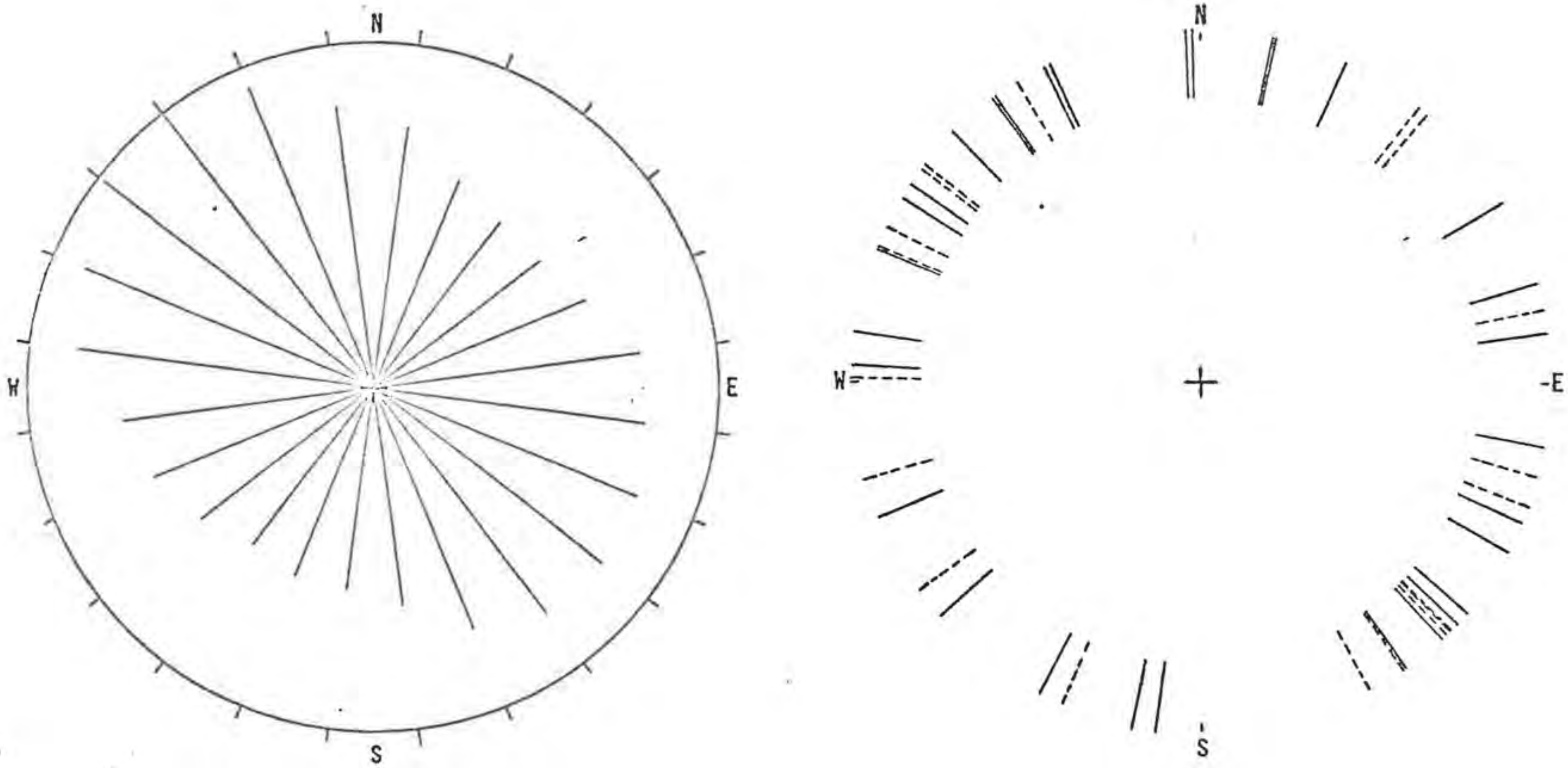
a. VECTOR DIAGRAM OF THE SUMMATION OF ACTIVITIES OF ALL TESTS. THE RADIUS, R, REPRESENTS THE MAXIMUM NUMBER OF JUMPS IN ANY ONE 15° SECTOR. R= 34.9

b. DISTRIBUTION OF NIGHTLY MEAN DIRECTIONS. UNIMODAL AND PRIMARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS SOLID LINES. SECONDARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS DASHED LINES.

FIGURE 12-25

ORIENTATION OF ZUGUNRUHE OF A
CALIFORNIA CAPTURED IMMATURE BLACKPOLL
WARBLER TESTED UNDER THE CLEAR NIGHT SKY

BIRD NUMBER 40



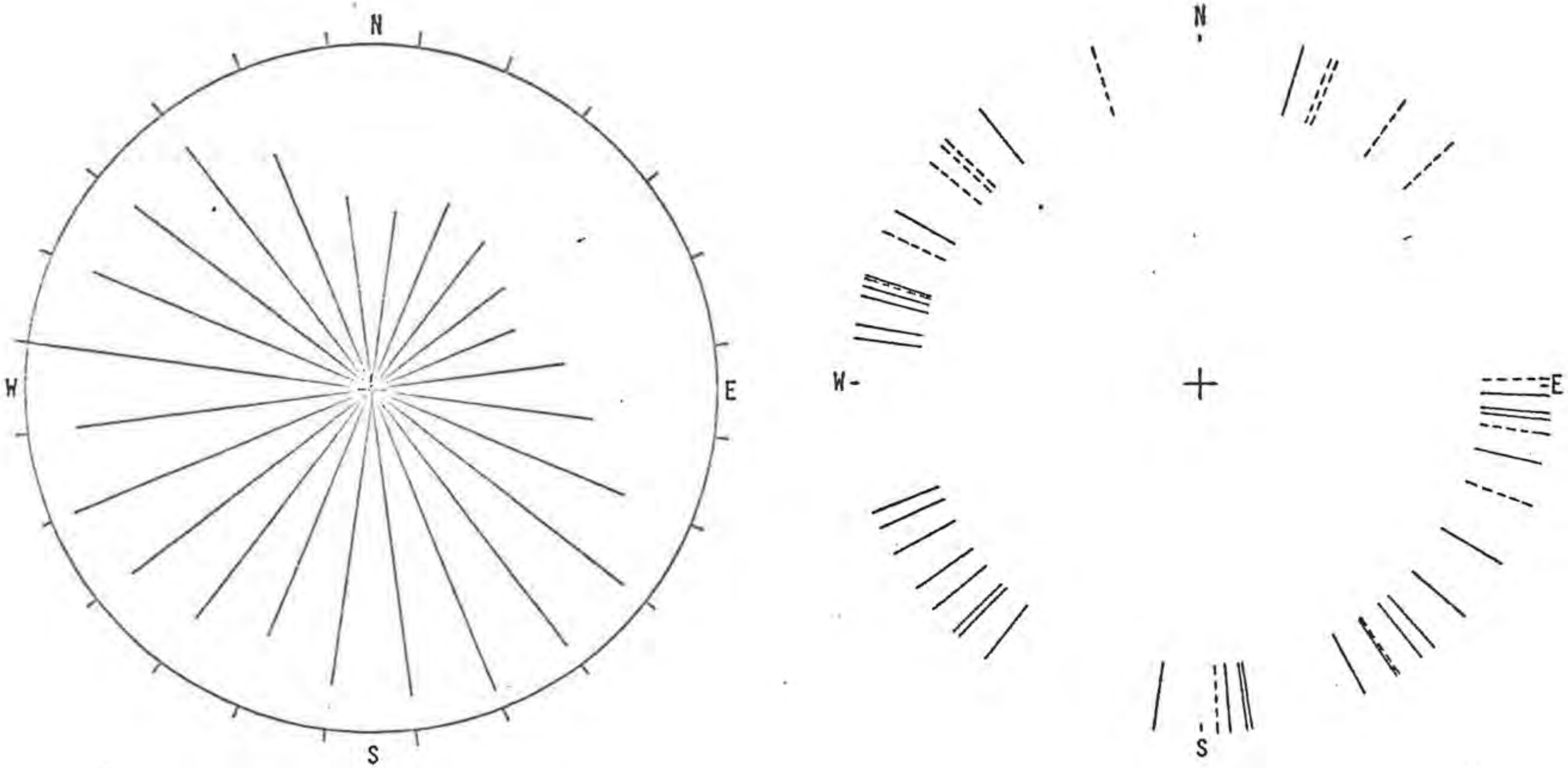
a. VECTOR DIAGRAM OF THE SUMMATION OF ACTIVITIES OF ALL TESTS. THE RADIUS, R, REPRESENTS THE MAXIMUM NUMBER OF JUMPS IN ANY ONE 15° SECTOR. R=293.7

b. DISTRIBUTION OF NIGHTLY MEAN DIRECTIONS. UNIMODAL AND PRIMARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS SOLID LINES. SECONDARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS DASHED LINES.

FIGURE 12-26

ORIENTATION OF ZUGUNRUHE OF A
CALIFORNIA CAPTURED IMMATURE BLACKPOLL
WARBLER TESTED UNDER THE CLEAR NIGHT SKY

BIRD NUMBER 41



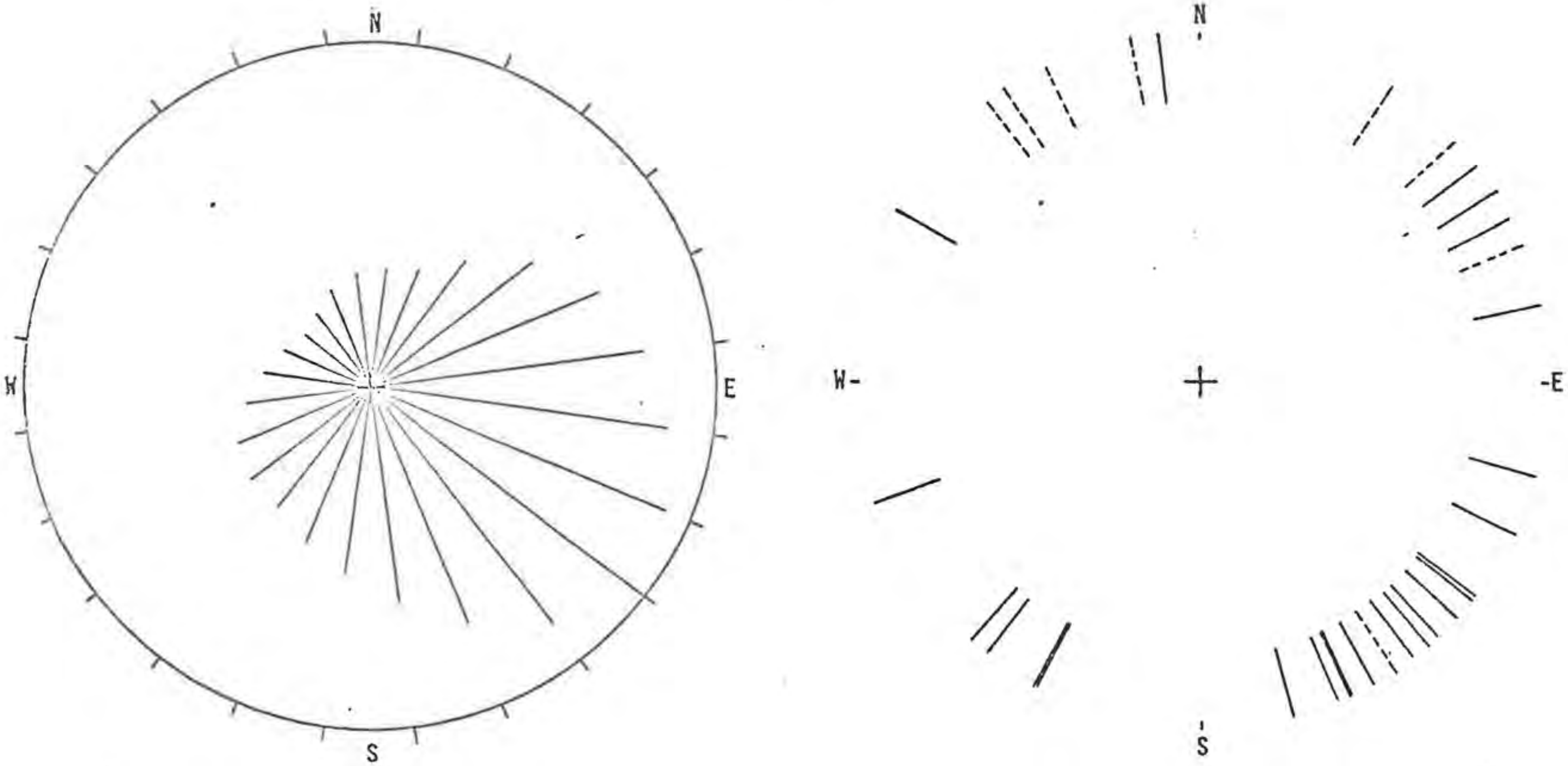
a. VECTOR DIAGRAM OF THE SUMMATION OF ACTIVITIES OF ALL TESTS. THE RADIUS, R, REPRESENTS THE MAXIMUM NUMBER OF JUMPS IN ANY ONE 15° SECTOR. R= 82.9

b. DISTRIBUTION OF NIGHTLY MEAN DIRECTIONS. UNIMODAL AND PRIMARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS SOLID LINES. SECONDARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS DASHED LINES.

FIGURE 12-27

ORIENTATION OF ZUGUNRUHE OF A
CALIFORNIA CAPTURED IMMATURE BLACKPOLL
WARBLER TESTED UNDER THE CLEAR NIGHT SKY

BIRD NUMBER 42



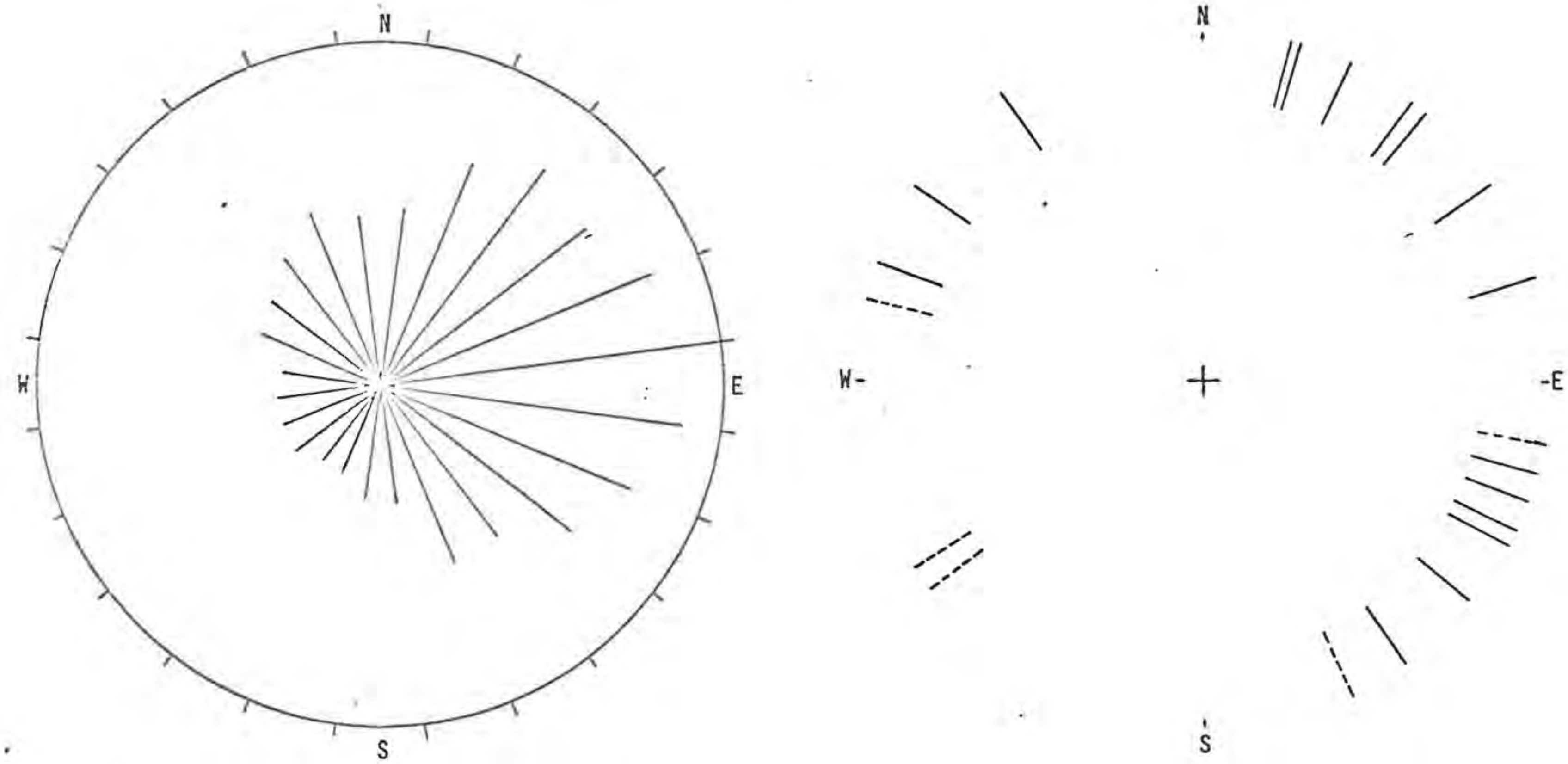
a. VECTOR DIAGRAM OF THE SUMMATION OF ACTIVITIES OF ALL TESTS. THE RADIUS, R, REPRESENTS THE MAXIMUM NUMBER OF JUMPS IN ANY ONE 15° SECTOR. R=189.3

b. DISTRIBUTION OF NIGHTLY MEAN DIRECTIONS. UNIMODAL AND PRIMARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS SOLID LINES. SECONDARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS DASHED LINES.

FIGURE 12-28

ORIENTATION OF ZUGUNRUHE OF A
CALIFORNIA CAPTURED IMMATURE BLACKPOLL
WARBLER TESTED UNDER THE CLEAR NIGHT SKY

BIRD NUMBER 43



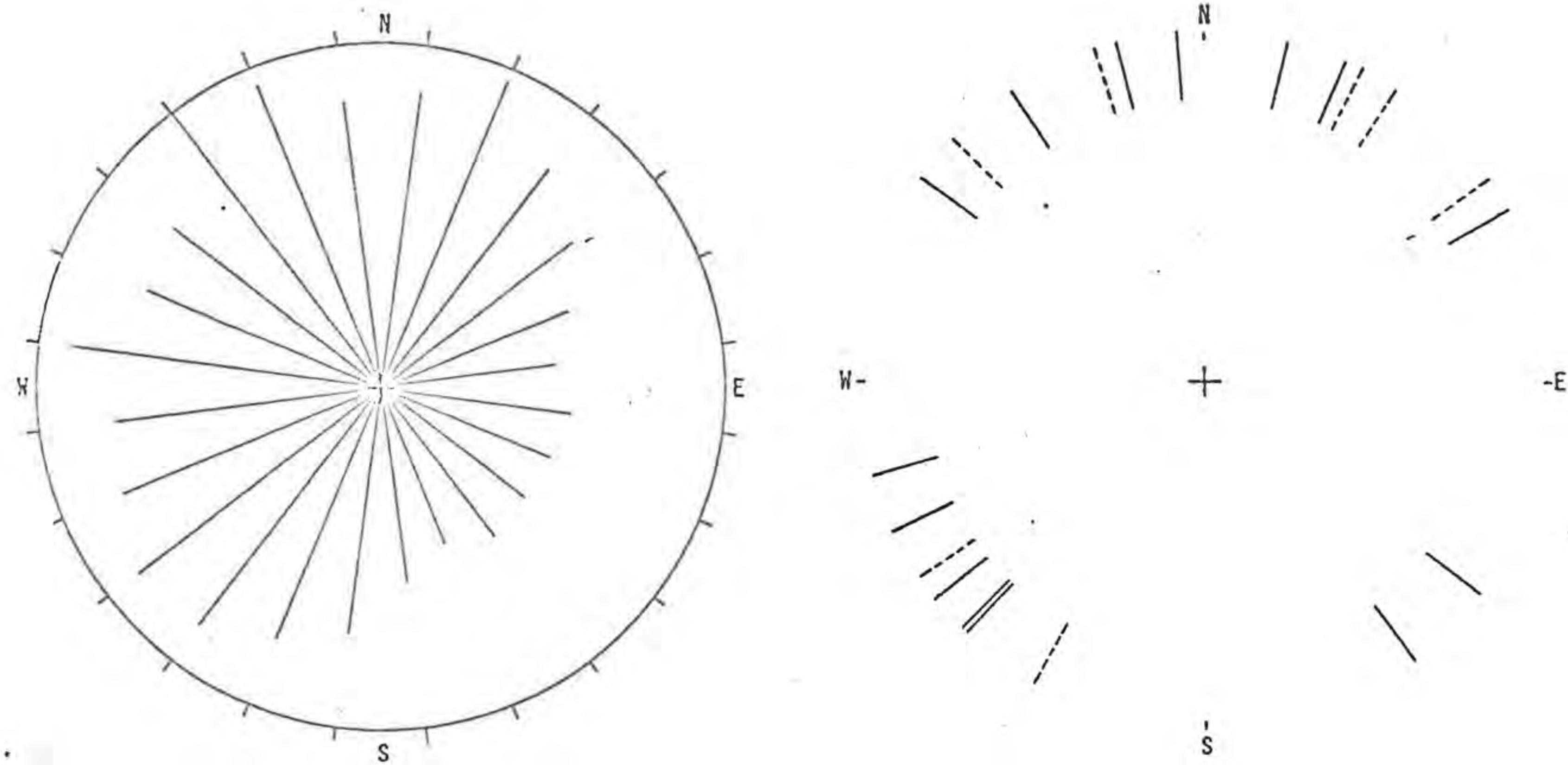
a. VECTOR DIAGRAM OF THE SUMMATION OF ACTIVITIES OF ALL TESTS. THE RADIUS, R, REPRESENTS THE MAXIMUM NUMBER OF JUMPS IN ANY ONE 15° SECTOR. R= 30.2

b. DISTRIBUTION OF NIGHTLY MEAN DIRECTIONS. UNIMODAL AND PRIMARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS SOLID LINES. SECONDARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS DASHED LINES.

FIGURE 12-29

ORIENTATION OF ZUGUNRUHE OF A
CALIFORNIA CAPTURED IMMATURE BLACKPOLL
WARBLER TESTED UNDER THE CLEAR NIGHT SKY

BIRD NUMBER 44



a. VECTOR DIAGRAM OF THE SUMMATION OF ACTIVITIES OF ALL TESTS. THE RADIUS, R, REPRESENTS THE MAXIMUM NUMBER OF JUMPS IN ANY ONE 15° SECTOR. R= 24.3

b. DISTRIBUTION OF NIGHTLY MEAN DIRECTIONS. UNIMODAL AND PRIMARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS SOLID LINES. SECONDARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS DASHED LINES.

sector.

The second method of presenting the results of several orientation experiments on a given individual is to subject each night's data to the Single Trace Analysis and plot, on a circular diagram, the resulting mean directions. This method, in contrast to the summation of activities method, weights each direction equally, regardless of the activity or the concentration about the mean. The resulting circular diagrams for all 24 Blackpoll Warblers are presented in Figures 12-6b to 12-29b. The mean directions for unimodal data as well as the primary mean directions for multimodal data are shown as solid lines while the secondary mean directions for multimodal data are shown as dashed lines.

Inspection of the composite distributions obtained by the summation of activities method and shown in Figures 12-6a to 12-29a indicates that the majority of the California captured Blackpoll Warblers show some consistant directionality when tested over several nights. Some of the individuals show apparent bimodal behavior. Birds number 29 (Figure 12-14a), 39 (Figure 12-24a) and 40 (Figure 12-25a) are particularly well marked examples of this phenomenon. As perhaps expected, these bimodal directions appear to be approximately 180° apart from each other.

To obtain numerical data as to the preferred directions chosen by each bird and the amount of directionality shown by each bird, the composite distribution for each bird can be subjected to the Single Trace Analysis. These results are presented in Table 12-9. The first finding is that 10 of the 24 birds (41.7%) display multimodal behavior in their composite distributions. This value is in close agreement with the percentage of multimodal traces obtained on single night's tests (36.6%) but, as would be expected, is somewhat higher. Furthermore, all of the 10 multimodal individuals are bimodal and $\overline{\Delta\Phi}$, the mean difference between the primary and secondary mean directions (measured clockwise) is 175.7±23.2°. A one sided t-test, furthermore, indicates that this value does not differ significantly from 180° (P=.718).

As an estimate of the concentration around the preferred direction that is displayed by Blackpoll Warblers tested over several nights, the 14 unimodally directed birds can be examined. The mean r_U for these individuals is found to be $\overline{r}_U=0.226$, a value indicative of some degree of directionality. The minimum number of independent choices necessary for the mean unimodal bird to be significantly directed ($P_{RAY}<.05$) may be obtained from equation (12-1) for $r=0.226$ and is found to be $N=58.6$. Since the mean unimodally directed bird produced about 1854 jumps over all of its tests, $P_{RAY}<.05$ can be obtained if independence of jumps is achieved, on the average, once in every 32 jumps. Furthermore, since the average unimodal individual produced 90.10 jumps/night, significant ($P_{RAY}<.05$) unimodal behavior

TABLE 12-9

RESULTS OF THE SINGLE TRACE ANALYSIS RUN
ON THE SUMMATION OF ACTIVITIES OF EACH
CALIFORNIA CAPTURED BLACKPOLL WARBLER

BIRD	NUMBER OF MODES	MODE NUMBER	TOTAL ACTIVITY	% ACTIVITY IN EACH MODE	MEAN DIRECTION $\Phi(°)$	CONCENTRATION ABOUT THE MEAN UNIMODAL VECTOR r_U	DIFFERENCE BETWEEN PRIMARY AND SECONDARY DIRECTIONS FOR BIMODAL INDIVIDUALS $\Delta\Phi(°)$
21	1	1	569.69	100.00	60.0	.160	
22	2	1	53.71	60.44	292.8		150.9
		2		39.56	83.7		
23	1	1	459.39	100.00	53.7	.270	
24	2	1	2112.02	52.87	75.5		165.9
		2		47.13	241.4		
25	1	1	741.28	100.00	146.9	.272	
26	1	1	5304.71	100.00	48.1	.265	
27	1	1	754.66	100.00	281.2	.131	
28	2	1	1319.73	59.86	252.0		134.9
		2		40.14	26.9		
29	2	1	1709.96	50.77	274.6		170.0
		2		49.23	84.6		
30	1	1	911.15	100.00	180.4	.104	
31	1	1	2126.25	100.00	243.7	.234	
32	1	1	7040.89	100.00	91.9	.408	
33	2	1	501.65	88.26	319.3		190.3
		2		11.74	149.6		
34	2	1	6204.61	66.85	58.8		175.5
		2		33.15	234.3		
35	1	1	2752.15	100.00	300.2	.338	
36	1	1	412.02	100.00	121.9	.211	
37	1	1	654.35	100.00	38.9	.058	
38	1	1	1375.49	100.00	10.8	.147	
39	2	1	626.96	59.97	307.3		178.9
		2		40.03	126.2		
40	2	1	5413.53	57.00	309.2		176.3
		2		43.00	125.5		
41	2	1	1552.64	58.45	303.5		196.2
		2		41.55	139.7		
42	1	1	2451.35	100.00	123.4	.293	
43	1	1	395.81	100.00	70.8	.272	
44	2	1	438.66	51.28	10.4		217.9
		2		48.72	228.3		

MEAN r_U FOR SAMPLE OF 14 UNIMODALLY DIRECTED BIRDS .226

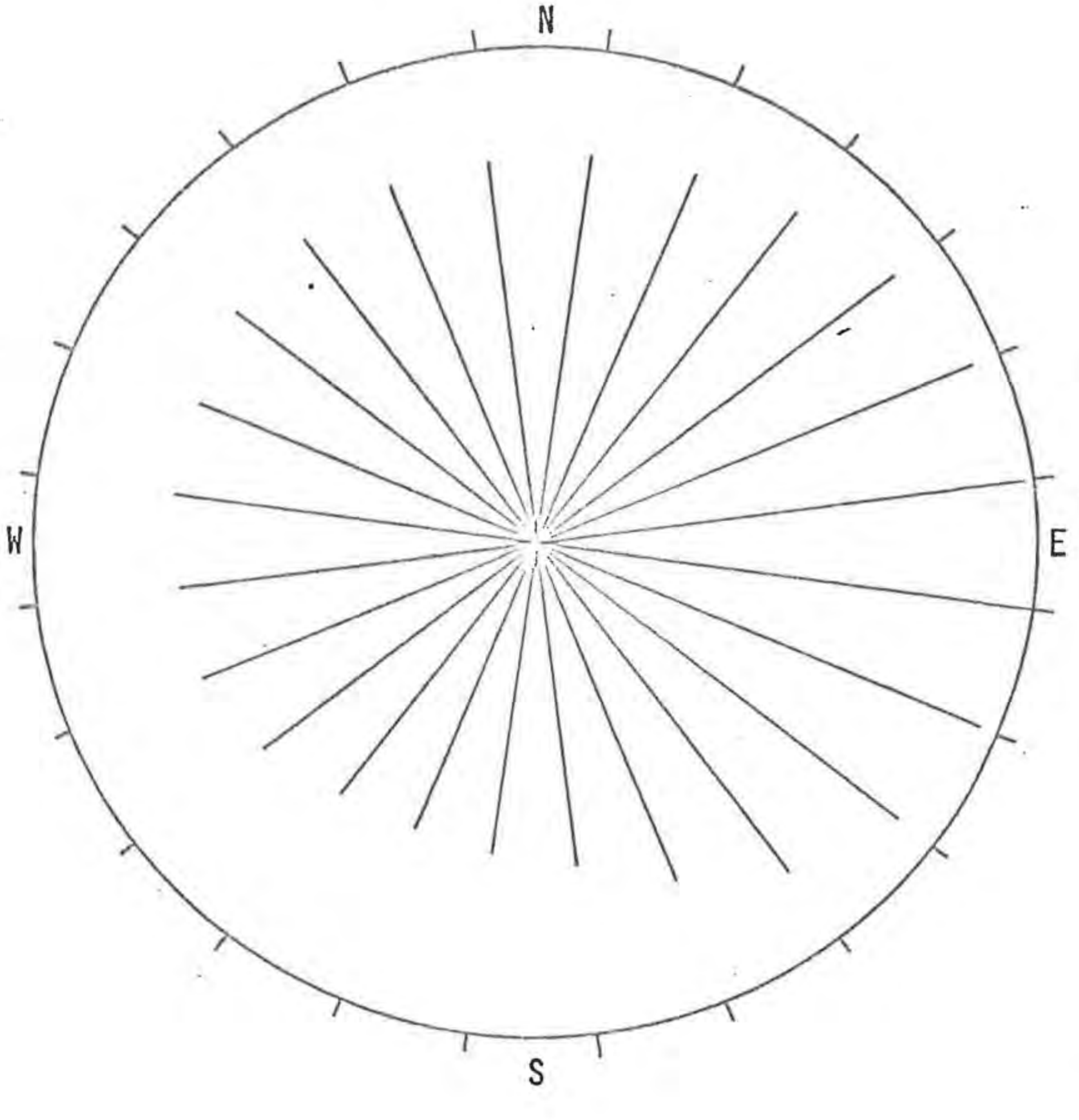
MEAN $\Delta\Phi$ FOR SAMPLE OF 10 BIMODALLY DIRECTED BIRDS 175.7 ± 23.2

is indicated if each bird made, on the average, only 3 independent choices each night! There is, therefore, a strong indication that Blackpoll Warblers captured in California are capable of consistantly directed behavior over many successive nights of testing in "footprint" orientation cages. Hence, Blackpoll Warblers captured in California are not disoriented individuals.

The next step of this analysis is to inquire whether the sample of 24 Blackpoll Warblers captured in California displays a common misorientation direction. Considering the widely scattered directions indicated in Table 12-9, this hypothesis seems doubtful. Nevertheless, all of the activities in each 15° sector for all of the tests on all of the birds can be summed to produce a single composite distribution representative of the combined activities of all 24 California captured Blackpoll Warblers. These data are shown in the vector diagram in Figure 12-30 and appear to indicate some small degree of directionality. If this distribution is subjected to the Single Trace Analysis, it is found that the distribution is indeed unimodal with a mean direction of 67.3° and a concentration about the mean, r_U=0.084. If the single San Diego captured individual, bird number 30, is eliminated from this summation and the remaining 23 Northern California birds (all but one of which were captured on Southeast Farallon, the single exception, bird number 21, having been captured at Bolinas, only 18

FIGURE 12-30

VECTOR DIAGRAM OF THE SUMMATION OF ACTIVITIES OF ALL TESTS ON ALL CALIFORNIA CAPTURED BLACKPOLL WARBLERS. THE RADIUS, R, REPRESENTS THE MAXIMUM NUMBER OF JUMPS IN ANY ONE 15° SECTOR. R=2416.5



miles from Southeast Farallon, virtually the closest mainland point to the island) are included, a more uniform sample may result. Nevertheless, there is little difference in the result: the Single Trace Analysis still indicates a unimodal distribution, now with a mean direction of 66.0° and a concentration about the mean, r_U=0.086. The Rayleigh test, with N=24 or 23, indicates that the resulting distribution is not, in either case, significantly different from a uniform distribution (P_{RAY}>>.10). It therefore appears that this sample of Blackpoll Warblers does not have a statistically significant common unimodal misorientation direction.

Nevertheless, it may be interesting to examine the mean direction obtained by this summation of all of the California captured Blackpoll Warbler traces, 67.3° or ENE. It is obvious that Blackpoll Warblers could not reach California by following an ENE direction from their breeding range. However, they could reach California by following the 180° reverse of this direction, 247.3° or WSW. If this direction is followed back to the breeding grounds of the Blackpoll Warbler it is found that the California captured individuals should, on the average, originate in central Ontario or even Quebec. More interestingly, it is found that the mirror image, with respect to the N-S axis, of this WSW direction is 112.7° or ESE. Such a direction may be the approximately correct migratory direction for the passage of the Blackpoll Warbler across continental North America [Nisbet, 1970]. This intriguing coincidence prompts us to examine the data in more detail.

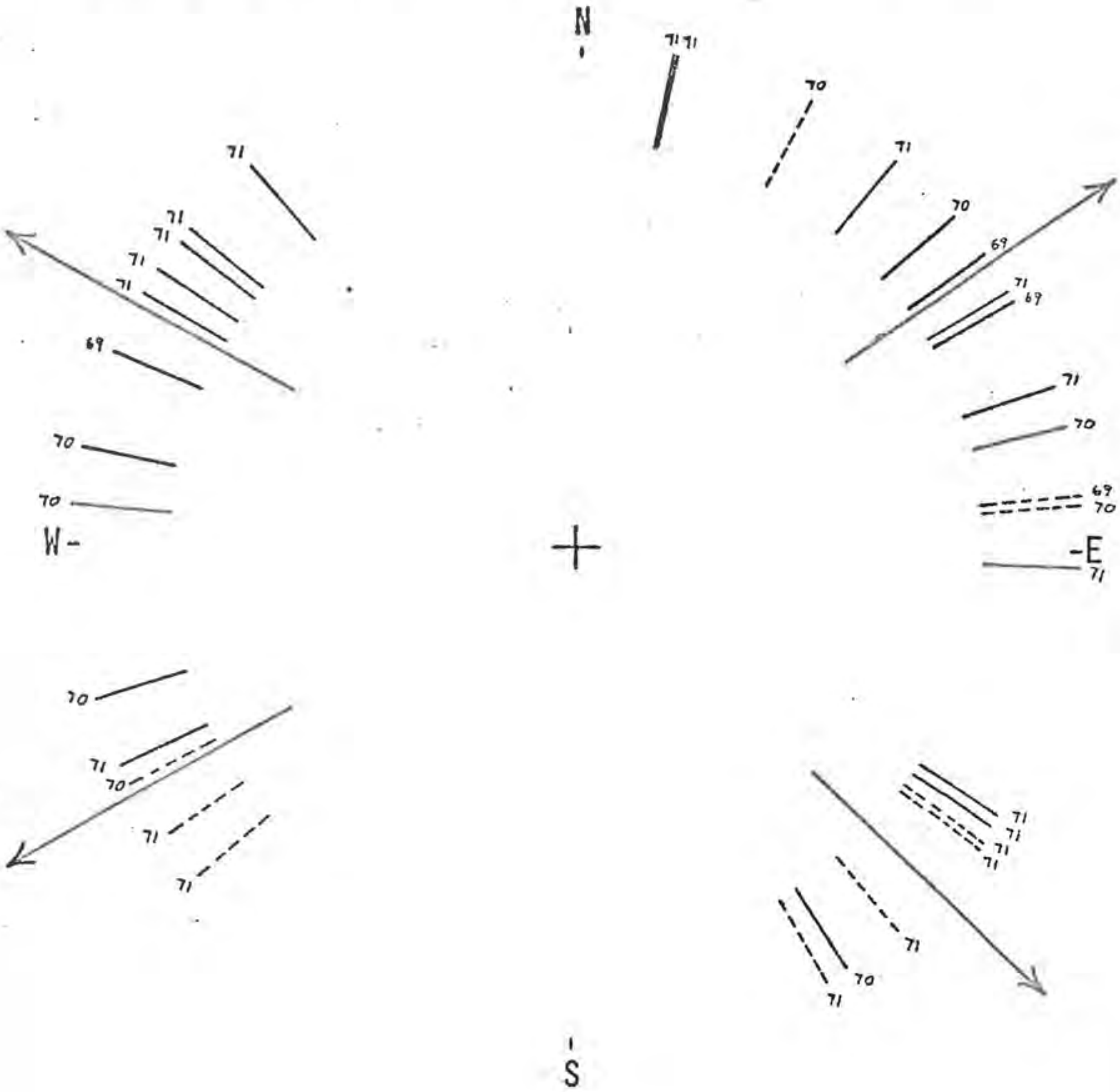
The summation of activities method of analysis just presented, while simple and straightforward, may represent an oversimplification of the data. First of all, this technique weights the data according to the total activity of each bird on each night. Thus, the behavior of extremely active birds on more active nights may effectively mask any underlying behavior of less active birds on less active nights. Secondly, the fact that the summation of all Blackpoll Warbler data is not significantly unimodally directed according to the Rayleigh test does not eliminate the possibility that it is significantly multimodally directed. This is because the Rayleigh test cannot distinguish multimodal behavior from uniform behavior. Furthermore, if the resulting distribution is multimodal and the mean directions of the modes lie much closer than 90° from each other, the mode finding algorithm used in the Single Trace Analysis will fail to differentiate them. In view of these shortcomings in the summation of activities method, it is worthwhile to attempt a second method of analysis of the data.

The mean directions obtained by the Single Trace Analysis for the summation of data for each individual Blackpoll Warbler were presented in Table 12-9. The mean directions of all 23 Northern California individuals can be plotted on a circular diagram in the manner that Figures 12-6b to 12-29b were created. These data are shown in Figure 12-31. The first glance at these data indicates that this sample of birds produces mean directions spread nearly entirely around the compass. However, closer inspection reveals the presence of concentrated clumps of mean directions and large gaps where no mean directions are found. It is, therefore, desirable to test whether this distribution of mean directions differs significantly from a uniform distribution. The Rayleigh test, however, is likely to be inadequate for this purpose since it is only powerful when the alternative to the uniform distribution is a unimodal one. The distribution shown in Figure 12-31, however, appears to be multimodal.

A powerful statistical test to ascertain the presence of directionality in a circular distribution of points (or the location of mean vectors) regardless of whether the distribution is unimodal or multimodal has been derived by Rao [1969] and summarized by Batchelet [1972] and will be referred to as the Rao test. The theory behind this test is very simple. If a circular distribution of N points is perfectly uniform, the difference (in degrees) between adjacent points, T_i, will be constant, 360/N. If, on the other hand, the distribution of N points is not uniform but exhibits distinct clusters of points, then T_i will be quite

FIGURE 12-31

DISTRIBUTION OF MEAN DIRECTIONS OBTAINED BY THE SUMMATION OF ACTIVITIES OF ALL TESTS OF EACH NORTHERN CALIFORNIA CAPTURED BLACKPOLL WARBLER (23 BIRDS). UNIMODAL AND PRIMARY MULTIMODAL MEAN DIRECTIONS ARE SHOWN AS SOLID LINES. SECONDARY MULTIMODAL DIRECTIONS ARE SHOWN AS DASHED LINES. LONG ARROWS REPRESENT THE MEAN DIRECTIONS OF EACH OF THE FOUR MAJOR CLUMPS OF DIRECTIONS. SMALL NUMBERS REFER TO THE YEAR IN WHICH THE BIRD WAS TESTED.



variable, some T_i being very small and other T_i being quite large. In all cases however:

$$\sum_{i=1}^{N} T_i = 360 \quad . \qquad (12\text{-}2)$$

The Rao test, in effect, compares the real distribution with the uniform distribution by using, as a test statistic, the absolute value of the difference between the real T_i and 360/N. If the sum of this statistic over all N is sufficiently large, then the null hypothesis of the uniform distribution can be rejected. Specifically, the test statistic used in the Rao test is:

$$U = \frac{1}{2} \cdot \sum_{i=1}^{N} \left| T_i - \frac{360}{N} \right| \quad . \qquad (12\text{-}3)$$

In using the Rao test, it must be remembered that while there are 33 mean directions represented in the distribution, 10 of them are secondary directions. These have already been shown to be significantly correlated to the corresponding primary directions by being, on the average, 180° opposite to them. As a result, there are only 23 independent directions, corresponding to the number of individual birds involved. When the Rao test is performed on the data illustrated in Figure 12-31, it is found that U=158.93 for N=23 which results in a strong indication that the distribution of mean directions for the sample of

Northern California Blackpoll Warblers is not a uniform distribution (P=.058). Furthermore, when the Rayleigh test is performed on these data, it is found that $r_U=0.289$ for N=23 and $P_{RAY}>.10$. The combined results of these two tests, therefore, provide strong evidence that the distribution is indeed multimodally directed.

There now exists the problem of deciding how the various mean directions shown in Figure 12-31 are clustered. Since there exists no a priori method for solving this problem some subjective guesses must be made. If the distribution is bimodal, then there should be two major gaps in the distribution that effectively isolate the modes. Figure 12-31 indicates that there are indeed two large gaps, one located near south and the other near north. These gaps effectively divide the distribution into an eastward and a westward mode. If all of the mean directions are weighted equally and the vector sum of each mode is computed, it is found that the mean directions for each mode are 82.4° and 276.0° respectively. It is now logical to inquire whether these two mean directions bear any interesting relation to each other, in particular, whether they could be mirror image directions. It is found that indeed they are and, furthermore, that the calculated mirror image axis lies at 359.2°, within 1° of true north!

It is also interesting to note that the two next largest gaps in the distribution shown in Figure 12-31 lie near east and west. If these gaps are considered to be real, they would effectively partition the distribution into four modes, NW and SW and NE and SE. When clustered in this manner, the four modes have an interesting property. The NW and NE modes are composed of 100% and 76.9% primary or unimodal mean directions respectively, while the SW and SE modes are composed of only 40.0% and 42.9% primary or unimodal mean directions respectively. The mean direction of each of these four resulting modes may be computed by vector summation. The results are presented in Table 12-10 and illustrated on Figure 12-31 by the long arrows. As perhaps expected, the opposite modes are found to be approximately 180° removed from each other and are therefore considered to represent 180° reversed directions. As such, all of the SE mean direction can be transformed into the NW mode by adding 180° to each of them, and all of the SW mean directions can be transformed into the NE mode by the same method. The mean NE and NW directions can then be calculated. They are found to be 56.3° and 305.4° respectively. The calculated mirror image axis for this case turns out to be 0.9°, again within 1° of true north! These results are also presented in Table 12-10.

Such symmetry displayed by the mean directions of the four quadrants would, of course, be expected if the distribution were uniform. However, there would be no reason to expect such symmetry from a multimodal

TABLE 12-10

RESULTS OF SUBJECTIVE CLUSTERING ANALYSIS
ON THE DISTRIBUTION OF MEAN DIRECTIONS OF ALL
23 NORTHERN CALIFORNIA CAPTURED BLACKPOLL WARBLERS

	ALL BIRDS (23)			1969-70 BIRDS (9)			1971 BIRDS (14)		
	NUMBER OF VECTORS	MEAN DIRECTION	DIFFERENCE	NUMBER OF VECTORS	MEAN DIRECTION	DIFFERENCE	NUMBER OF VECTORS	MEAN DIRECTION	DIFFERENCE
NE CLUSTER	13	54.9°		7	61.8°		6	46.9°	
SW CLUSTER	5	239.9°		2	246.7°		3	235.4°	
DIFFERENCE NE→SW (clockwise)			185.0°			184.9°			188.5°
NE CLUSTER (TRANSFORMING SW)	18	56.3°		9	62.9°		9	49.8°	
NW CLUSTER	8	298.5°		3	282.9°		5	307.9°	
SE CLUSTER	7	133.3°		1	146.9°		6	131.1°	
DIFFERENCE NW→SE (clockwise)			194.8°			224.0°			183.2°
NW CLUSTER (TRANSFORMING SE)	15	305.4°		4	293.9°		11	309.6°	
MIRROR IMAGE AXIS		0.9°			358.4°			359.7°	
CORRECT DIRECTION	15	125.4°		4	113.9°		11	129.6°	
VAGRANT DIRECTION	18	236.3°		9	242.9°		9	229.8°	

distribution unless it were an underlying characteristic of the distribution. And it has already been shown that the distribution is very likely multimodal. In addition, the fact that the same basic mirror image symmetry of the distribution can be obtained by considering either the two largest or the four largest gaps supplies further evidence that the symmetry is real.

A physical meaning can now be suggested for each of the four modes. The SE mode may be considered to be the correct direction of migration for the Blackpoll Warbler, the direction the bird follows in crossing continental North America to reach the Atlantic Coast. The experimentally determined value of 125.4° (Table 12-10) may be a good approximation to this correct direction. The NW mode is the 180° reverse of the correct direction. The SW mode is the mirror image across the N-S axis of the correct direction and is the direction followed by vagrant individuals that reach California. This direction is called the vagrant direction. The NE mode is, of course, the 180° reverse of the vagrant direction. It is interesting to note that Northern California Blackpoll Warblers tend to prefer the 180° reverse directions rather than the forward directions. This phenomenon will be further discussed in Part IV of this dissertation.

Table 12-10 also includes separate analyses of the 1971 sample of 14 Northern California Blackpoll Warblers along with the combined 1969-1970 sample of 9 birds. In both of these cases the results produced are entirely consistant with the hypothesis just presented. The calculated mirror image axes are found to lie at 359.7° (1971) and 358.9° (1969-1970). The correct directions are found to be 129.6° (1971) and 113.9° (1969-1970). Again, these are very likely to be good approximations to the actual correct directions flown by wild Blackpoll Warblers.

It is now be apparent from Figure 12-31 why the summation of activities method produced a unimodal vector sum lying in the NE quadrant. The eight NW directions very nearly cancel the seven SE directions since they are approximately 180° apart, leaving 13 NE directions and 5 SW directions. Thus, the unimodal direction of 66° may indeed be a valid, but highly oversimplified, estimate of the average direction of the sample of 23 Northern California Blackpoll Warblers.

There is one serious problem with the above hypothesis. If all vagrant Blackpoll Warblers reach California by following the mirror image vagrant direction, why are 11 out of 23 individuals (47.8%) oriented on the correct direction (or its 180° reverse) when placed in "footprint" orientation cages? The answer lies, I believe, in the hypothesis that all vagrant Blackpoll Warblers actually display both the correct and the vagrant directions as well as the 180° reverses of each. If the directional preferences of the various birds on any given night are distributed randomly between the correct and vagrant directions, and the activities on any given night are allowed to vary widely but randomly with respect to the correct and vagrant directions, then it would be expected that the summation of activities method on individual birds would produce the result that about 50% of the birds would favor the correct direction while 50% of the birds would favor the vagrant direction. This is exactly the result described above.

If this hypothesis is correct, then the distribution of mean nightly directions for each individual bird should be multimodal and all four preferred modes should appear. Simple visual inspection of the distribution of mean nightly directions for each of the 24 birds (Figures 12-6b to 12-29b) supplies strong evidence that they are not unimodally distributed. In all cases the mean directions appear to be scattered nearly entirely around the compass. The Rao test may then be applied to each distribution in order to determine if the distributions are significantly (multimodally) directed. The results of this test are presented for each individual in Table 12-11. To insure independence, of course, only the primary and unimodal mean directions were used. Table 12-11 indicates that 10 of the 23 birds tested over several nights (43.5%) show significant directionality ($P<.05$). Interestingly, of the 17 birds that were tested on 17 or more nights, 10 (58.8%) are found to be

TABLE 12-11

RESULTS OF THE RAO TEST ON THE DISTRIBUTION OF PRIMARY AND UNIMODAL MEAN DIRECTIONS CHOSEN BY EACH CALIFORNIA CAPTURED BLACKPOLL WARBLER TESTED OVER MANY NIGHTS

BIRD	N	U*	P**	
21	7	119.01	>>.10	
22	1	--	--	
23	7	136.61	>>.10	
24	28	147.78	>.10	
25	20	207.10		<<.01
26	23	105.30	>>.10	
27	17	165.91		<.05
28	20	131.60	>.10	
29	15	117.30	>>.10	
30	9	129.40	>>.10	
31	23	167.73		<.05
32	31	170.49		<.01
33	21	168.67		<.05
34	31	166.67		<.05
35	23	180.63		<.01
36	29	150.66	>.10	
37	30	153.90	>.05	
38	29	166.25		<.05
39	30	140.60	>.10	
40	30	112.30	>>.10	
41	30	165.00		<.05
42	24	172.60		∿.01
43	16	160.70	>.05	
44	14	132.83	>.10	
TOTAL			13	10
TOTAL IF ELIMINATE ALL BIRDS WITH N<17			7	10

* RAO STATISTIC
** SIGNIFICANCE

significantly directed (P<.05) while none of the 6 birds tested on less than 17 nights are significantly directed. It therefore appears that if multimodal behavior is suspected, relatively large sample sizes (at least 17 tests) must be available in order to obtain significant results from the Rao test. Sample sizes of this order have rarely been reported in the literature of orientation cage experiments.

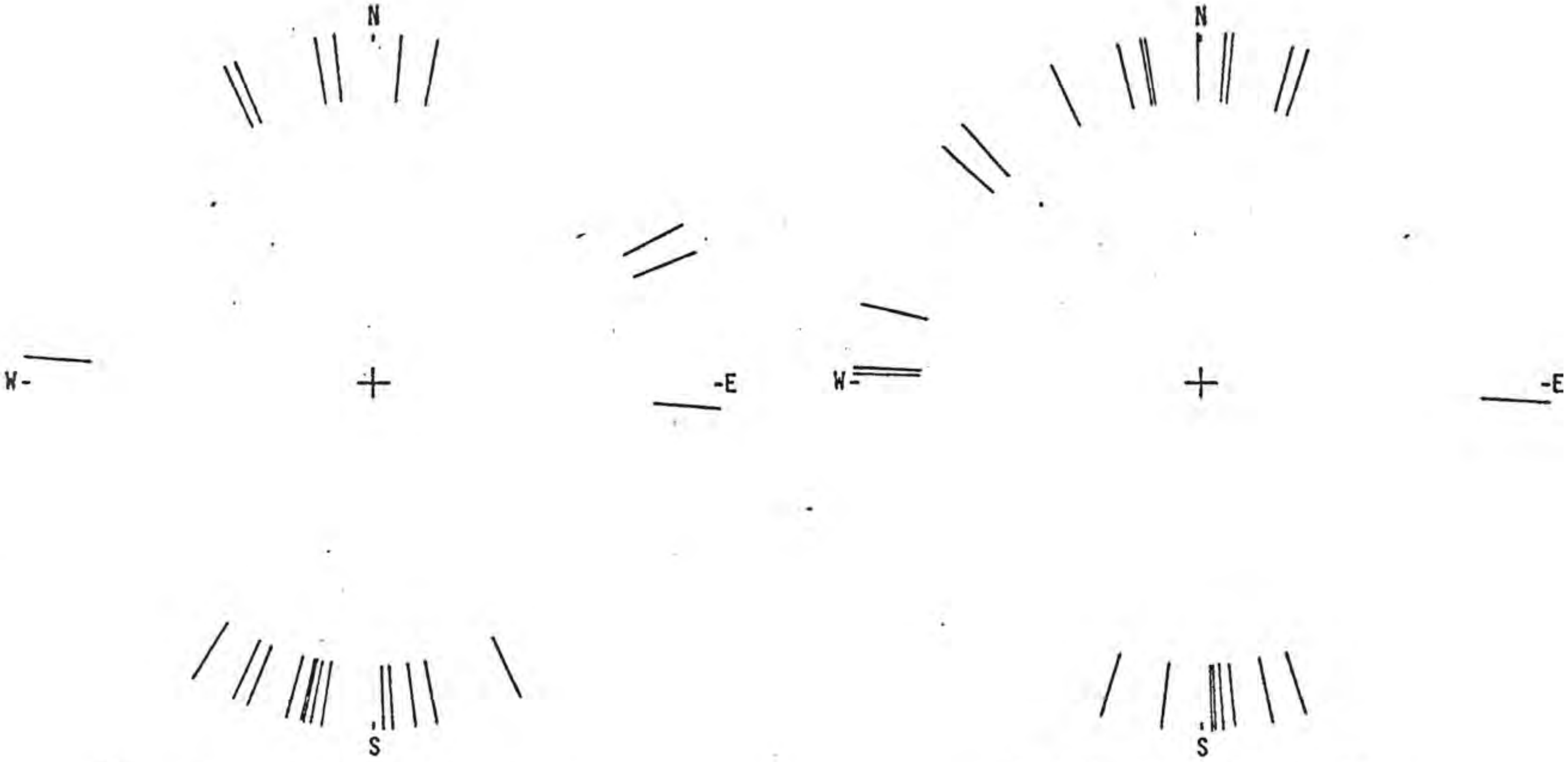
This analysis of the distribution of mean directions of single night tests for a given individual supplies strong evidence that California captured Blackpoll Warblers do exhibit several well directed modes of acitivity. Unfortunately, simple visual inspection of the data is incapable of determining the preferred direction of these modes since there is no straightforward method to isolate them. In some cases, bird 42 (Figure 12-27b) for example, the modes appear to be represented by fairly distinct clusters of mean directions. In most cases, however, it is difficult to decide what constitutes a cluster.

There is, however, an unambiguous piece of useful information available from the distribution of mean nightly directions for each individual bird: the largest gap between any two adjacent mean directions. This gap may be considered to be largest area, in angular coordinates, consistantly avoided by each individual bird over all of its tests. As such, the midpoint of this gap may be considered to be a measure of the primary avoided direction of that bird. If the preferred modes of all of the California captured Blackpoll Warblers display a common directionality, then we would expect that the distribution of the primary avoided direction for all birds would be directed. For example, if the sample of Blackpoll Warblers were all unimodally directed in the same direction, then the sample would be expected to show a single primary avoided direction that would, in general, be 180° removed from the preferred unimodal direction. If, for another example, a sample of Blackpoll Warblers were all bimodally directed in identical 180° opposite directions, then that sample could be expected to display two primary avoided directions. They would be 180° removed from each other and orthogonal to the axis of the preferred bimodal direction.

The distribution of the actual, experimentally determined, primary avoided directions for the sample of 23 Blackpoll Warblers that were tested on several nights is shown in Figure 12-32a. It is obvious from these data that the birds very clearly avoid both north and south. There is also an indication that east and west are avoided, although to a lesser degree than north and south. If this is indeed the case then the sample must show four preferred modes and they must lie generally near NE, SW, NW and SE. This is essentially the same result that was obtained previously on the entire sample. For this conclusion to be valid, the

FIGURE 12-32

DISTRIBUTION OF AVOIDED DIRECTIONS FOR ALL 23 CALIFORNIA CAPTURED BLACKPOLL WARBLERS THAT WERE TESTED OVER SEVERAL NIGHTS (SEE TEXT FOR FULL EXPLANATION)

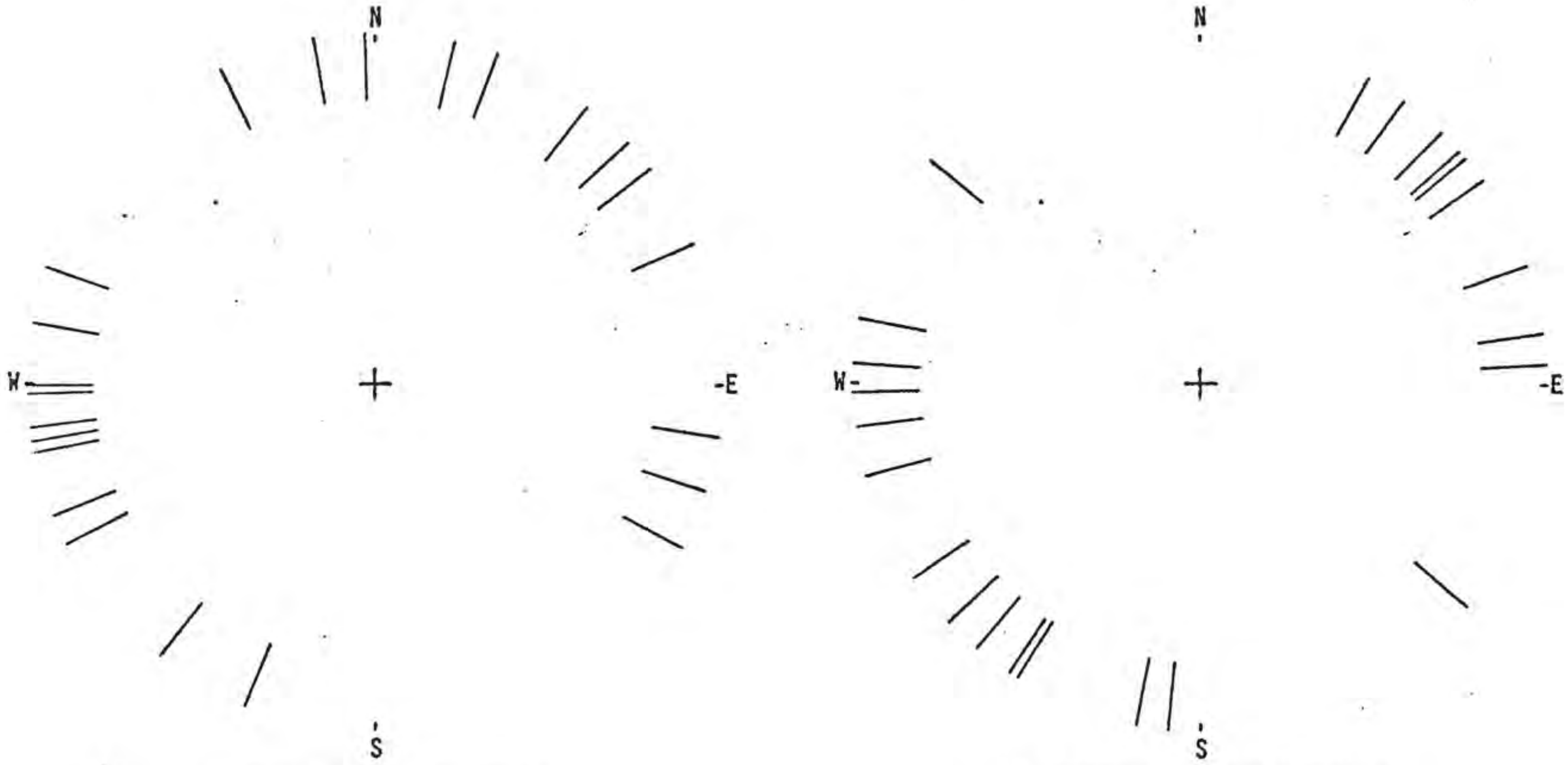


a. PRIMARY AVOIDED DIRECTIONS

b. SECONDARY AVOIDED DIRECTIONS

FIGURE 12-32 (CONT)

DISTRIBUTION OF AVOIDED DIRECTIONS FOR ALL 23
CALIFORNIA CAPTURED BLACKPOLL WARBLERS THAT WERE TESTED
OVER SEVERAL NIGHTS
(SEE TEXT FOR FULL EXPLANATION)



c. TERTIARY AVOIDED DIRECTIONS

d. QUATERNARY AVOIDED DIRECTIONS

distribution of these primary avoided directions must be non-uniform. This distribution was therefore subjected to a Rao test with the result, given in Table 12-12, that the distribution of primary avoided directions for all birds is significantly directed ($P<.01$).

Continuing the same line of reasoning, it is clear that if all individuals in the sample of Blackpoll Warblers are bimodally directed in a consistant manner, then the distribution of secondary avoided directions (the second largest gap on the distribution of mean directions for a given individual tested over many nights) for these individuals will also tend to be directed. These data are shown in Figure 12-32b which indicates that this distribution may indeed be directed and perhaps in the same manner that primary avoided directions are directed, that is, at N, S, E, and W. The results of the Rao test on the secondary avoided directions, shown in Table 12-12, does indeed indicate that they are significantly directed ($P<<.01$). Furthermore, the results of the Rao test on the combination of primary and secondary avoided directions indicates that this combination is significantly directed ($P<<.01$). This supplies conclusive evidence that the primary and secondary avoided directions are indeed directed in the same way. At this point there exists a strong indication that each individual of the sample of Blackpoll Warblers is at least bimodally directed in two of the

TABLE 12-12

RESULTS OF THE RAO TEST ON THE DISTRIBUTIONS OF DIRECTIONS AVOIDED BY CALIFORNIA CAPTURED BLACKPOLL WARBLERS

	N	U*	P**
PRIMARY	23	184.37	<<.01
SECONDARY	23	188.27	<<.01
TERTIARY	23	124.77	>>.10
QUATERNARY	23	153.88	<.10
PRIMARY & SECONDARY	46	194.11	<<.01
PRIMARY, SECONDARY & TERTIARY	69	150.80	<.05
PRIMARY, SECONDARY & QUATERNARY	69	141.47	>.10
PRIMARY, SECONDARY, TERTIARY & QUATERNARY	92	138.36	>.10

* RAO STATISTIC
** SIGNIFICANCE

possible four modes and that these four modes tend to be the same for all birds in the sample.

Continuing the analysis it is found that the distributions of tertiary and quaternary avoided directions are not significantly directed by themselves but that the distribution of the combination of the primary, secondary and tertiary avoided directions is significantly directed ($P<.05$). Finally, it is found that the distributions of the combinations of the primary, secondary and quaternary, and the primary, secondary, tertiary and quaternary avoided directions are not significantly directed. These data are also presented in Table 12-12. The distribution of the tertiary and quaternary avoided directions are presented in Figures 12-32c and d.

What does all this mean? The simplest explanation for these results is that each Blackpoll Warbler is usually directed in three of four possible modes and that the four modes are the same for all Blackpoll Warblers in the sample. It is reasonable to ask why each bird usually shows only three of the four possible modes rather than all four. The answer lies, I believe, in the assumption that each bird displays considerable angular deviation, from night to night, in the mean direction of each mode. If the two most preferred modes for each bird, that is, the modes that occur the greatest number of times over many night's tests, happen to be two adjacent modes (as is likely to happen 2/3 of the time if the number of times each mode is chosen is randomly distributed), then it is likely that the angular deviation in the mean directions obtained for each mode from night to night will cause the modes to coalesce. If this happens, then the largest gap between these two modes is likely to be smaller than gaps found within the least well directed mode. Thus, only three avoided directions will tend to be consistantly directed in the sample since the fourth will occur more or less at random somewhere in the least well directed mode for each bird. This is exactly the effect indicated in the data in Table 12-12. In addition, it is very important to note that Figures 12-32c, d unambiguously show that the vagrant modes are the least well directed modes!

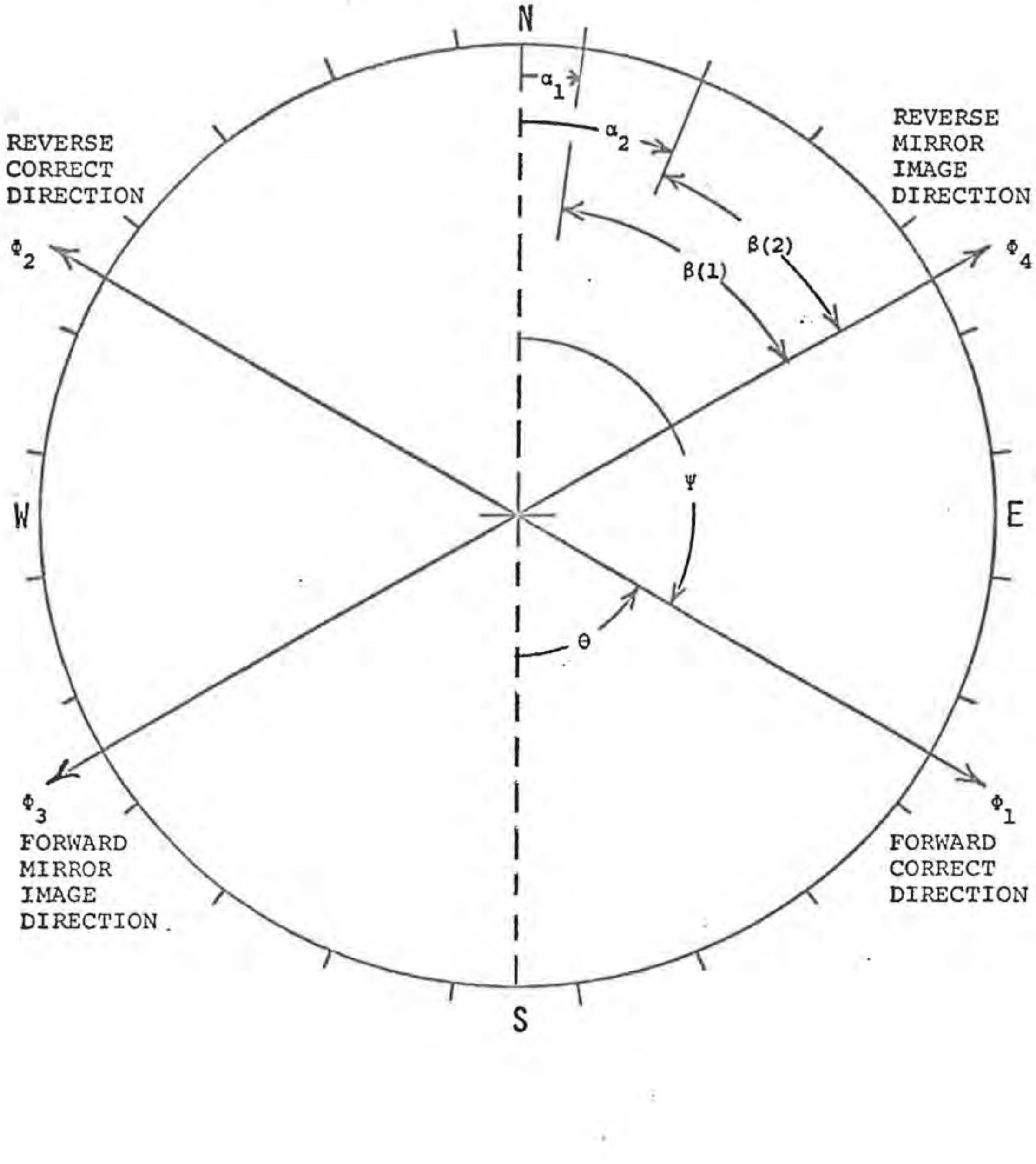
This problem of the coalescence of adjacent heavily preferred modes will become more severe as the two modes approach each other. It will be least severe if the modes are all 90° apart. Since there exist empirical data to indicate that N and S are avoided more often than E and W (Figure 12-32a, b), it can be assumed that the modes are located closer to E and W than to N and S. Again, this is qualitatively consistant with the results shown for the entire sample in Figure 12-31.

A working hypothesis for the orientation of California captured Blackpoll Warblers, consistant with all of the results obtained thus far can now be formulated. Assume that vagrant Blackpoll Warblers reach California by following a misorientation direction that is a mirror image, across the N-S axis, of the correct direction. Assume further that the correct direction is approximately ESE or somewhere around 110° or 120°. Finally assume that when such a Blackpoll Warbler is captured on the Outer Coast of California and tested over many clear nights in a "footprint" orientation cage, it is capable of consistantly displaying not only the mirror image vagrant direction but also the correct direction as well as the 180° reverse directions of both the mirror image vagrant direction and the correct direction. While the activity of a given night's test on such a bird may be unimodally directed or bimodally directed in 180° opposite directions, the activity over many nights will be distributed according to an "X" pattern that will be axially symmetric with respect to both the N-S and E-W axes.

Dr. Lincoln Moses, of the Statistics Department, Stanford University, has developed a method to directly test this hypothesis [Moses and DeSante, MS]. Assume that there exists a distribution of four preferred directions, $\Phi_n (n=1,4)$, as illustrated in Figure 12-33 and described in the above hypothesis. Let θ be the angular location (in radians) of the correct direction, Φ_1, measured counterclockwise from south. $\Phi_n (n=1,4)$, measured clockwise from north, will therefore be given by

FIGURE 12-33

DISTRIBUTION OF PREFERRED DIRECTIONS, Φ_n (n=1,4), ACCORDING TO THE MIRROR IMAGE HYPOTHESIS (SEE TEXT FOR FULL EXPLANATION)



$$\begin{aligned} \Phi_1 &= \pi - \Theta \quad , \\ \Phi_2 &= 2\pi - \Theta \quad , \\ \Phi_3 &= \pi + \Theta \quad , \\ \Phi_4 &= \Theta \quad . \end{aligned} \tag{12-4}$$

Let α_i be defined as the midpoint of the i<u>th</u> $\frac{\pi}{12}$ or 15° sector measured (in radians) clockwise from north. Let $P(\alpha_i)$ be the proportion of the total activity contained in the i<u>th</u> sector,

$$P(\alpha_i) = \frac{A_i}{\sum_{i=1}^{24} A_i} \quad . \tag{12-5}$$

Now let β be defined as the minimum angular distance (in radians) that any given point, α, on the circumference of the circle is removed from the nearest preferred direction Φ_n. In order to make β compatible with the discreet circular data of a digitized orientation trace, we can define

$$\beta(i) = \min | \alpha_i - \Phi_n(n=1,4) | \quad . \tag{12-6}$$

Now a function must be defined that will be a measure of how well the digitized "footprint" data is concentrated around the four preferred directions, Φ_n. The most straightforward function is the mean distance, $\overline{\beta}$, that the total activity of the bird is removed from the preferred directions. This function may be designated as $F(\Theta)$ and defined as

$$F(\Theta) = \sum_{i=1}^{24} f_i(\Theta) \qquad (12\text{-}7)$$

where

$$f_i(\Theta) = \beta(i) \cdot P(\alpha_i) \quad \text{for} \quad \beta(i) \geq \frac{\pi}{24} \qquad (12\text{-}8a)$$

and

$$f_i(\Theta) = \left(\frac{\pi}{48} + \frac{12(\beta(i))^2}{\pi}\right) \cdot P(\alpha_i) \quad \text{for } \beta(i) < \frac{\pi}{24} . \qquad (12\text{-}8b)$$

Equation 12-8b defines the case where the nearest preferred direction, Φ_n, falls within the i<u>th</u> 15° sector. The means by which $F(\Theta)$ measures the concentration of activity about the four preferred directions is obvious. If the activity is highly concentrated about the preferred directions, large values of $P(\alpha_i)$ will correspond to small values of $\beta(i)$ so that the product $\beta(i) \cdot P(\alpha_i)$ will be small. If the acitivity is concentrated away from the preferred directions $P(\alpha_i)$ will be large when $\beta(i)$ is large and the product will be large. Thus, increasingly smaller values of $F(\Theta)$ indicate increasingly more concentration about the preferred directions. If the activity is perfectly concentrated about any or all of the preferred directions, all of the non-zero values of $P(\alpha_i)$ will correspond to zero values of $\beta(i)$ and $F(\Theta)$ will be zero. Nevertheless, for the test to be meaningful, another reference value of $F(\Theta)$ is needed. The uniform distribution may be defined as the null distribution and can serve as this reference value, $F_o(\Theta)$.

It can also be shown that the probability density function $P(\beta)$, for the uniform distribution, is given as illustrated in Figure 12-34. The area under the curve from $\beta=0$ to $\beta=\beta$ represents the probability, for the uniform distribution, that any randomly chosen point, α, lies closer than β to the nearest preferred direction. It can easily be seen that the area under the entire curve is always equal to unity. It is also obvious that the mean of this probability density function, $\overline{\beta}$, is identical to the desired value of $F_o(\Theta)$ since

$$F_o(\Theta) = \sum_{i=1}^{24} \beta(i)\cdot P(\alpha_i) = \frac{1}{24} \sum_{i=1}^{24} \beta(i) = \overline{\beta}(i) \quad . \quad (12\text{-}9)$$

The value of the mean of the probability density function for the uniform distribution is

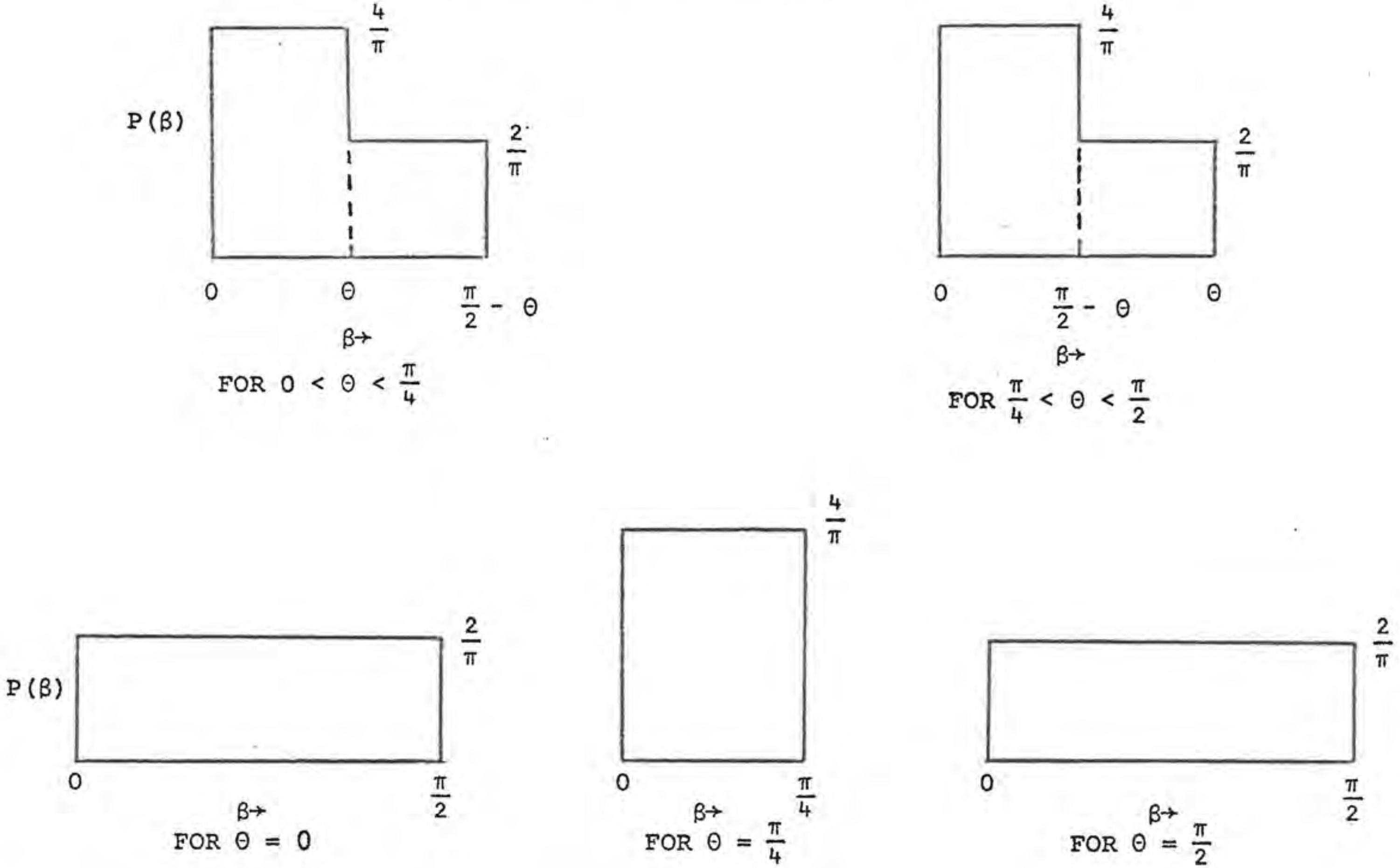
$$F_o(\Theta) = \left[\left(\frac{\pi}{2} - \Theta\right)^2 + \Theta^2\right] \cdot \frac{1}{\pi} \quad . \quad (12\text{-}10)$$

In addition, the standard deviation of the mean of the probability density function for the uniform distribution is

$$\sigma_o(\Theta) = \left\{\frac{\pi^2}{48} - \left[\frac{\Theta\cdot\left(\frac{\pi}{2} - \Theta\right)}{\frac{\pi}{2}}\right]^2\right\}^{\frac{1}{2}} \quad . \quad (12\text{-}11)$$

FIGURE 12-34

PROBABILITY DENSITY FUNCTION, $P(\beta)$, FOR THE UNIFORM DISTRIBUTION FOR VARIOUS VALUES OF Θ



FOR $0 < \Theta < \frac{\pi}{4}$

FOR $\frac{\pi}{4} < \Theta < \frac{\pi}{2}$

FOR $\Theta = 0$

FOR $\Theta = \frac{\pi}{4}$

FOR $\Theta = \frac{\pi}{2}$

Now a useful test statistic, $X(\Theta)$, can be defined which will provide an index of how well the digitized data on a single night's are concentrated about the preferred directions:

$$X(\Theta) = \frac{F(\Theta) - F_o(\Theta)}{\sigma_o(\Theta)} \qquad (12-12)$$

The operation of this statistic is obvious. If the data are distributed according to the null distribution, then $F(\Theta)=F_o(\Theta)$ and $X(\Theta)=0$. If the data are distributed with a high degree of concentration of activity around the preferred directions, $F(\Theta)<F_o(\Theta)$ and $X(\Theta)<0$. On the other hand, if the data are distributed with a high degree of concentration of activity away from the preferred directions, $F(\Theta)>F_o(\Theta)$ and $X(\Theta)>0$. The beauty of the test is that the mirror image hypothesis can directly be tested without ever having to consider the question of independence of jumps, or having to determine a value of the concentration about the mean, in fact, without ever having to be concerned with the mean direction of a distribution at all. Thus the operation of a mode finding algorithm and an approximate multimodal solution are of no concern.

The real power in the test, however, becomes evident when it is discovered that the probability density function shown in Figure 12-34 for the uniform distribution is identical to the probability density function for a certain two parameter family of distributions that have the property that the sum of the ordinates at points exactly π apart is constant. A few of the distributions that are included in the null hypothesis are shown in Figure 12-35.

Finally, this test can not only be used to indicate support (or lack of support) for the mirror image hypothesis, but can effectively be used to determine the probable correct direction (and thus the vagrant direction as well) of the sample of birds tested. To accomplish this, θ can be allowed to vary between 0° and 90° and the angle where the maximum negative value of $X(\theta)$ occurs can be determined. To obtain a more useful notation, the correct migratory direction, Ψ, can be defined as

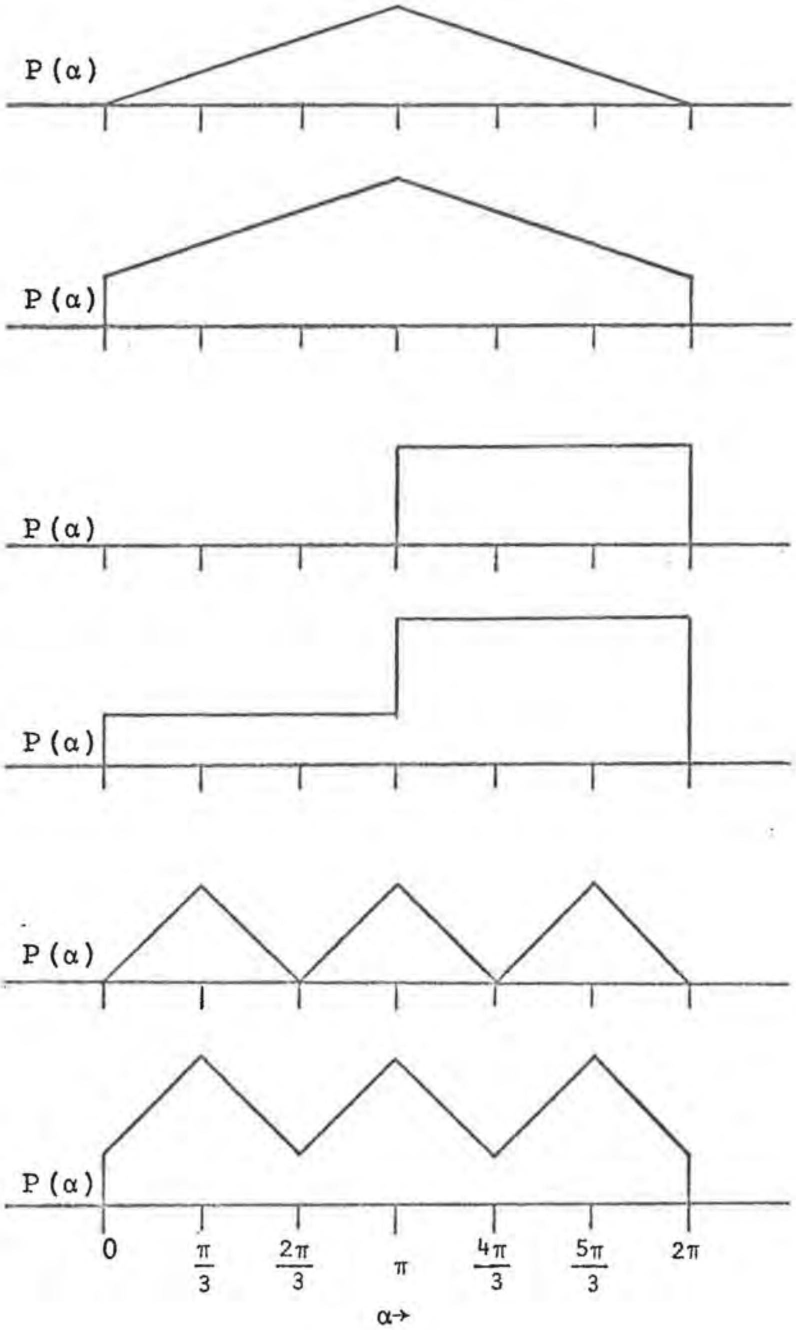
$$\Psi = 180^\circ - \theta \quad . \qquad (12\text{-}13)$$

This correct direction will, therefore, vary between 90° (E) and 180° (S).

Accordingly, therefore, this test was run on all 508 active Blackpoll Warbler traces allowing Ψ to vary by 10° intervals between $\Psi=90^\circ$ and $\Psi=180^\circ$. This mass of data was reduced by finding the mean value, $\overline{X}(\Psi)$, for each individual over all, N, of the nights it was tested as well as the standard deviation $SD(\Psi)$ of that mean. These data were, of course, obtained for each of the ten values of the potential correct direction. The value of the correct direction that produced the maximum negative value of $\overline{X}(\Psi)$ was then determined and this value of $\overline{X}(\Psi)$, along with the associated

FIGURE 12-35

SOME OF THE MEMBERS OF THE FAMILY OF DIAMETER CONSTANT DISTRIBUTIONS, P(α), FOR WHICH P(β) IS IDENTICAL TO P(β) FOR THE UNIFORM DISTRIBUTION



$SD(\Psi)$, was recorded. The significance of each of these maximum negative values of $\overline{X}(\Psi)$ was then determined by the t-test.

The results of this analysis are summarized in Table 12-13. First, 12 of of the 23 birds tested on several nights (52.2%) displayed maximum negative values of $\overline{X}(\Psi)$ that were highly significant ($P<.05$). Considering how rigorous the test is, this result supplies a strong indication that the entire sample of Blackpoll Warblers may actually show orientation behavior that is consistant with the mirror image hypothesis. Next, the number of individuals that attained their maximum negative value of $\overline{X}(\Psi)$ at each correct direction was determined. These data are presented in Table 12-14 along with the number of individuals for which this maximum negative $\overline{X}(\Psi)$ was highly significant ($P<.05$). It is immediately apparent that a very large proportion of the individuals attained their maximum negative $\overline{X}(\Psi)$ in the three adjacent correct directions 90°, 100° and 110°. In fact 17 out of the 24 birds have picked one of these three directions. The probability, P, that 17 or more out of 24 possible cases should accumulate entirely by chance in three or fewer adjacent cells out of a possible 10 cells can be determined by

$$P=8\cdot P(17|24,.3)+9\cdot P(17|24,.2)+10\cdot P(17|24,.1) \qquad (12\text{-}14)$$

where $P(x|n,p)$ is defined as the probability that n binomial trials, each with a probability p of success, should result

TABLE 12-13

MAXIMUM NEGATIVE MEAN VALUES OF THE TEST
STATISTIC $X(\Psi) = \frac{F(\Psi)-F_O(\Psi)}{\sigma_O(\Psi)}$ AND SIGNIFICANCE LEVELS
FOR CALIFORNIA CAPTURED BLACKPOLL WARBLERS

BIRD	SAMPLE SIZE N	CORRECT DIRECTION $\Psi(°)$	MAXIMUM NEGATIVE $\overline{X}(\Psi)$	STANDARD DEVIATION $SD(\Psi)$	"t" STATISTIC $t_{N-1}(\Psi)$	SIGNIFICANCE P
21	7	90	-0.047	0.315	-0.397	.352
22	1	110	-0.339	--	-	-
23	7	180	-0.017	0.126	-0.363	.365
24	28	90	-0.064	0.198	-1.710	.049
25	20	90	-0.175	0.519	-1.510	.074
26	23	130	-0.081	0.195	-1.993	.029
27	17	110	-0.107	0.245	-1.795	.046
28	20	140	-0.104	0.228	-2.030	.028
29	15	100	-0.130	0.193	-2.623	.010
30	9	110	-0.155	0.355	-1.312	.113
31	23	110	-0.180	0.306	-2.816	.005
32	31	100	-0.101	0.222	-2.541	.008
33	21	110	-0.104	0.415	-1.152	.131
34	31	110	-0.057	0.121	-2.636	.007
35	23	150	-0.057	0.363	-0.752	.230
36	29	90	-0.185	0.576	-1.731	.048
37	30	180	-0.084	0.464	-0.986	.166
38	29	120	-0.045	0.191	-1.261	.109
39	30	110	-0.034	0.409	-0.456	.326
40	30	90	-0.009	0.283	-0.178	.430
41	30	90	-0.191	0.498	-2.098	.022
42	24	110	-0.074	0.160	-2.259	.017
43	16	90	-0.181	0.309	-2.347	.017
44	14	160	-0.044	0.153	-1.074	.151

TABLE 12-14

DISTRIBUTION OF INDIVIDUAL CALIFORNIA CAPTURED BLACKPOLL WARBLERS OVER TEN POTENTIAL CORRECT DIRECTIONS AS DETERMINED BY THE TEST STATISTIC $\overline{X}(\Psi)$

POTENTIAL CORRECT DIRECTION Ψ	90°	100°	110°	120°	130°	140°	150°	160°	170°	180°	TOTAL
NUMBER OF INDIVIDUALS INDICATING THIS Ψ	(7)	2	8	1	1	1	1	1	0	(2)	24
NUMBER OF INDIVIDUALS FOR WHICH THIS CHOICE IS SIGNIFICANT $P<.05$	(4)	2	4/7	0	1	1	0	0	0	(0)	12/23

1) IF ALL DATA USED:

PROBABILITY OF DISTRIBUTION OCCURRING BY CHANCE = 0.0003

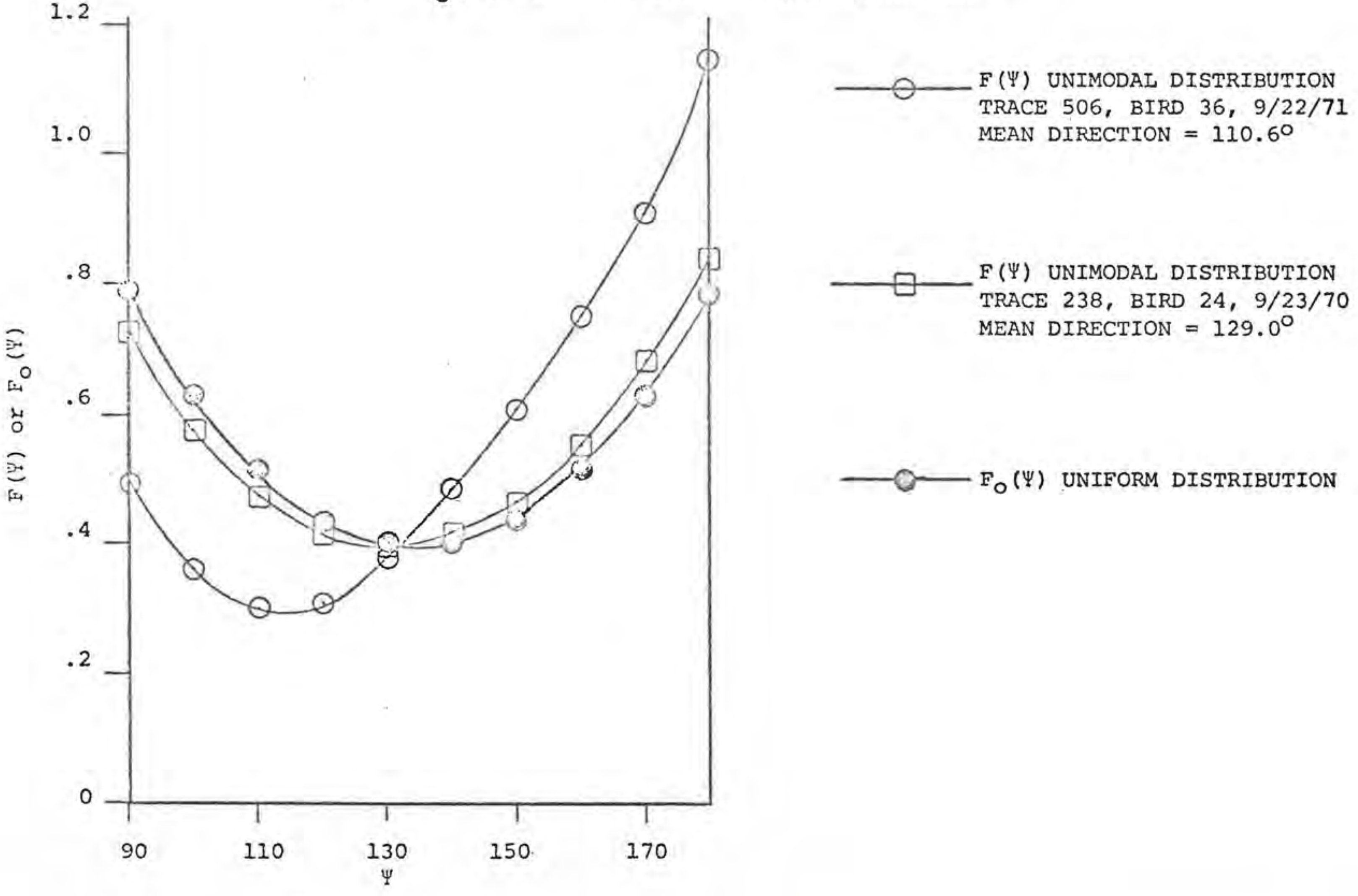
2) IF 90° AND 180° DATA ELIMINATED:

PROBABILITY OF DISTRIBUTION OCCURRING BY CHANCE = 0.00001 in x or more successes. Evaluation of P from probability tables is found to produce the result, P=.0003, indicating an extremely consistant choice of correct direction among these 24 birds.

The comparatively large number of individuals that exhibited their maximum negative $\overline{X}(\psi)$ at 90°, however, was the cause for much concern, especially since a mirror image Blackpoll Warbler cannot reach California by following a 270° direction from the breeding range. It was puzzling why 90° would be so favored when 100° was not. The fact that two individuals were apparently directed at 180° was also puzzling since 170° was avoided. It, therefore, appeared that some kind of spurious effect was occuring at these two locations where the four preferred directions decomposed into two opposite directions.

To get a feeling for how the function $X(\psi)$ was behaving, I compared the results of this test on individual traces with the raw data itself. A pattern soon emerged. It appeared that certain unimodal traces that displayed a mean direction between about 90° and 135° often showed their maximum negative value of $X(\psi)$ at ψ=90° rather than at a value of ψ closer to their actual mean direction. To understand why this occurred, the graphs of $F(\psi)$ for two such traces were examined along with $F_o(\psi)$ as a function of ψ. These data are presented in Figure 12-36. It is apparent that the curve of $F(\Psi)$ as a function of Ψ for these

FIGURE 12-36
COMPARISON OF F(Ψ) FOR TWO UNIMODAL DISTRIBUTIONS
WITH $F_o(\Psi)$ FOR THE UNIFORM DISTRIBUTION



unimodally directed traces is nearly identical to the curve of $F_o(\Psi)$, the uniform distribution. This is not surprising since it has already been shown that triangular distributions of period 2π or $\frac{2\pi}{3}$ are identical to the uniform distribution with respect to the function $F(\psi)$. All curves are concave upward with constantly increasing first derivatives as they move away from their minimum inflexion point. Therefore, if the inflexion point of the unimodal curve is displaced to the left of the inflexion point of the uniform curve, the slope of the unimodal curve will always be less, at any angle to the left of its inflexion point, than the slope of the uniform curve. As a result, the greatest negative difference between the two curves will alway occur at $\psi=90°$. Therefore, a unimodal trace that approximates a triangular distribution will tend to exhibit its maximum negative value of $X(\psi)$ at either 90° or 180° depending upon whether the mean direction of the trace is less than or greater than 135°. In this regard, it is significant that 7 individuals showed a correct direction at 90° while only 2 showed a correct direction at 180°. The interpretation of the results of this test on these 9 individuals, therefore, is that they do display an underlying "X" distribution in their total nocturnal activities, but that the correct direction of this "X" distribution is only known to lie somewhere between 90° and 135°.

The fact that certain unimodal data behaves similarly to the uniform distribution with respect to the function $F(\Psi)$ is not entirely undesirable. In effect, it makes the result that a given individual prefers a correct direction that is neither 90° nor 180° an even more powerful indication that the individual does display an underlying "X" distribution in its orientation behavior. Therefore, now consider those 15 individual birds that produced predicted Ψ values that were not 90° or 180°. Table 12-14 shows that 8 of these 15 birds display their maximum negative $\overline{X}(\Psi)$ in a single correct direction, $\Psi=110°$. The probability, P, that 8 or more out of 15 possible cases should accumulate, by chance, in a single cell out of a possible 8 cells can be computed as

$$P = 8 \cdot P(8|15,.125) \qquad (12-15)$$

and is found to be $P=0.00001$. The results of this test, therefore, supply very strong evidence that California captured Blackpoll Warblers do display orientation behavior that is consistant with the mirror image hypothesis proposed above. In addition, the birds strongly indicate the choice of a single correct (and mirror image) direction.

An accurate estimate of this correct direction, however, is difficult to obtain because of the effect of certain unimodal traces described above. Each unimodal trace that approximates a triangular distribution and displays a mean direction between 45° and 135° or between 225° and 315° will have the effect of slightly decreasing the value of $\overline{X}(\Psi)$ for values of Ψ that are less than the unimodal mean direction of that trace, while simultaneously increasing the value of $\overline{X}(\Psi)$ for values of Ψ that are greater than the mean direction of that trace. The net result of this effect, therefore, is a lowering of the observed correct direction for any individual that displays an "X" distribution in its nocturnal activity but that has produced a few approximately triangular unimodal traces. Thus, it can only be concluded that the correct direction of California captured Blackpoll Warblers lies somewhere between 110° and 135° and that the mirror image direction, therefore, lies, between 225° and 250°.

An alternative but completely analagous method of directly testing the mirror image hypothesis is available. This method involves the use of the distribution of mean nightly directions obtained, for each Blackpoll Warbler, by the Single Trace Analysis, rather than the use of the actual distributions of footprint activity. This method has the distinct advantage that spurious effects, caused by approximately triangular unimodal distributions of activity, are eliminated. The disadvantage of this method, however, is that the accuracy of the test is dependent upon the accuracy of the approximate multimodal analysis and mode finding algorithm. Nevertheless, this method can be used to determine an unambiguous estimate of the orientation of any

"X" distribution that exists in the distribution of mean nightly directions for each Blackpoll Warbler.

The distributions of mean nightly directions over all N nights that each Blackpoll Warbler was tested were presented in Figures 12-6b to 12-29b. Let the unimodal or primary mean direction obtained on each night for each Blackpoll Warbler be represented as $D_j (j=1,N)$. Then let ω_j be defined as the minimum angular distance that each D_j is removed from the nearest preferred direction $\Phi_n (n=1,4)$. These preferred directions are, of course, as defined in Figure 12-33, the mirror image hypothesis. Thus,

$$\omega_j = \min |D_j - \Phi_n (n=1,4)| \quad . \qquad (12-16)$$

The function ω_j is, therefore, analagous to the function β_i defined previously. Now let the distribution $P(\beta)$ for diameter constant distributions of mean directions (which includes the uniform distribution) serve as the null hypothesis. This distribution $P(\beta)$ is, of course, as shown in Figure 12-34.

Two different test statistics may now be defined to provide an index of how well the actual distribution of unimodal or primary mean nightly vectors, for each Blackpoll Warbler, is concentrated about the preferred directions of the mirror image hypothesis. The first statistic may be calculated as follows. Let $g_j(\theta)$ be defined as the area under the probability distribution $P(\beta)$ for the uniform distribution from $\beta=0$ to $\beta=\omega_j$. Thus

$$g_j(\Theta) = \int_0^{\omega_j} P(\beta;\Theta)d\beta \quad . \qquad (12\text{-}17)$$

This represents the probability, on the diameter constant (uniform) distribution, that the angular distance to the nearest preferred direction should be as small as the angular distance between the observed mean direction and the nearest preferred direction. Thus, a very small value of $g_j(\Theta)$ indicates that the observed mean direction is "significantly close" to the nearest preferred direction. The significance of this statistic can be determined since, for each Blackpoll Warbler, there exist several values of ω_j and thus $g_j(\Theta)$, one for each night the bird was tested. The question can therefore be stated: As a group, are the ω_j's obtained on several nights on the same bird "small"? The answer can be obtained by examining the product of the probabilities of these ω_j's, that is, by looking at $g_1(\Theta)\times g_2(\Theta)\times\ldots\times g_N(\Theta)$. Equivalently, $\sum \ln g_j(\Theta)$ can be examined. This is, in fact, Fisher's Method for combining independent tests. Thus, the test statistic $Z_1(\Theta)$ may be defined as

$$Z_1(\Theta) = -2\sum_{j=1}^{N} \ln g_j(\Theta) \qquad (12\text{-}18)$$

where N is the total number of active test nights. The better the mean directions are concentrated about the preferred direction, the greater will be the statistic $Z_1(\Theta)$. The statistical significance of $Z_1(\Theta)$ can, therefore, be directly obtained from Chi-square tables for 2N degrees of freedom.

The second test statistic is perfectly analagous to the test statistic $\overline{X}(\theta)$ previously used to determine how well the digitized footprint activity is concentrated about the preferred directions. Thus, $Z_2(\theta)$ may be defined as

$$Z_2(\theta) = \frac{1}{N} \sum_{j=1}^{N} \frac{\omega_j - F_o(\theta)}{\sigma_o(\theta)} \qquad (12\text{-}19)$$

where N is again the total number of active test nights and $F_o(\theta)$ and $\sigma_o(\theta)$ are respectively the mean and standard deviation of the probability distribution $P(\beta)$ for the diameter constant (uniform) distribution and are given by (12-10) and (12-11) above. The operation of the statistic $Z_2(\theta)$ is also straightforward; the better the unimodal or primary nightly mean directions are concentrated about the preferred directions, the greater will be the negative value of $Z_2(\theta)$. The statistical significance of $Z_2(\theta)$ can be determined by the t-test exactly as the statistical significance of $X(\theta)$ was obtained.

Each of the test statistics just defined can be used to obtain an estimate of the probable correct direction of the sample of Blackpoll Warblers by allowing θ to vary by 10° intervals between $\theta=0°$ and $\theta=90°$. Again this corresponds to letting $\Psi=180°-\theta$, the correct migratory direction, vary between $\Psi=90°$ (E) and $\Psi=180°$ (S).

The results of this analysis for both test statistics are summarized in Table 12-15. The maximum $Z_1(\Psi)$ was found

TABLE 12-15

MAXIMUM VALUES AND SIGNIFICANCE LEVELS FOR TWO TEST STATISTICS, $Z_1(\Psi)$ AND $Z_2(\Psi)$, FOR CALIFORNIA CAPTURED BLACKPOLL WARBLERS

(See text for full explanation)

		FIRST TEST STATISTIC				SECOND TEST STATISTIC		
BIRD	SAMPLE SIZE N	CORRECT DIRECTION Ψ(°)	MAXIMUM $Z_1(\Psi)$	SIGNIFICANCE P	CORRECT DIRECTION Ψ(°)	MAXIMUM NEGATIVE $Z_2(\Psi)$	"t" STATISTIC $t_{N-1}(\Psi)$	SIGNIFICANCE P
21	7	90	16.734	.271	140	-0.079	-0.134	.449
22	1	110	5.522	.063	110	-1.278	-	-
23	7	130	24.110	.045	130	-0.724	-18.266	<<.001
24	28	110	89.737	.003	120	-0.563	-1.766	.044
25	20	90	55.401	.054	100	-0.365	-1.678	.055
26	23	110	56.378	.141	120	-0.213	-0.880	.194
27	17	120	56.654	.009	120	-0.572	-2.951	.005
28	20	150	59.444	.025	110	-0.287	-1.416	.087
29	15	110	45.544	.035	110	-0.444	-11.507	<<.001
30	9	110	36.945	.005	110	-0.725	-3.145	.007
31	23	90	71.416	.010	90	-0.517	-1.332	.098
32	31	110	82.706	.041	100	-0.386	-19.788	<<.001
33	23	120	70.888	.011	120	-0.497	-5.121	<.001
34	31	110	89.524	.013	120	-0.445	-2.402	.012
35	23	150	62.642	.058	140	-0.364	-2.492	.010
36	29	110	77.092	.048	100	-0.245	-1.184	.123
37	30	150	68.167	.220	140	-0.088	-2.050	.025
38	29	130	84.127	.014	130	-0.251	-1.954	.030
39	30	140	87.037	.013	140	-0.435	-2.592	.007
40	30	120	66.854	.254	130	-0.091	-0.446	.330
41	30	120	72.488	.130	100	-0.254	-6.560	<.001
42	24	140	68.860	.026	140	-0.526	-2.427	.012
43	16	130	39.272	.177	140	-0.437	-2.389	.015
44	14	110	49.491	.008	130	-0.434	-1.255	.116
MEAN		119.2°			120.4°			

to be highly significant ($P<.05$) for 15 of the 24 birds tested (62.5%), while the maximum negative $Z_2(\Psi)$ was found to be highly significant ($P<.05$) for 15 of the 23 birds tested over several nights (65.2%). These results supply a very strong indication that the entire sample of Blackpoll Warblers may be oriented in a manner consistant with the mirror image hypothesis. The mean of the correct directions chosen by the 24 individual Blackpoll Warblers was found to be nearly identical for both of the test statistics, 119.2° and 120.4° respectively. It is also important to note that this direction, 120°, is very likely to be an excellent estimate of the correct transcontinental migratory direction flown by Blackpoll Warblers on their normal fall migration.

The actual distribution of the correct directions chosen by the sample of California captured Blackpoll Warblers is presented in Table 12-16 for both test statistics. In each case the distribution of correct directions chosen does not appear to be uniform over the ten potential correct directions but rather appears to be concentrated around the correct directions 110°-140°. For example, the use of the statistic $Z_1(\Psi)$ indicates that 16 out of the 24 birds prefer the three adjacent correct directions 110°, 120° and 130° while the use of $Z_2(\Psi)$ indicates that 15 out of the 24 birds prefer the three adjacent correct directions 120°, 130° and 140°. The probabilities of these concentrations given the model of equidistribution of correct directions can be

TABLE 12-16

DISTRIBUTION OF INDIVIDUAL CALIFORNIA CAPTURED
BLACKPOLL WARBLERS OVER TEN POTENTIAL CORRECT DIRECTIONS
AS DETERMINED BY THE TEST STATISTICS $Z_1(\Psi)$ AND $Z_2(\Psi)$
(See text for full explanation)

	POTENTIAL CORRECT DIRECTION Ψ	90°	100°	110°	120°	130°	140°	150°	160°	170°	180°	TOTAL
TEST I	$Z_1(\Psi)$											
	NUMBER OF INDIVIDUALS INDICATING THIS Ψ	3	0	9	4	3	2	3	0	0	0	24
	NUMBER OF INDIVIDUALS FOR WHICH THIS CHOICE IS SIGNIFICANT $P<.05$	1	0	7	2	2	2	1	0	0	0	15/24
	PROBABILITY OF THIS DISTRIBUTION OCCURRING BY CHANCE = 0.002											
TEST II	$Z_2(\Psi)$											
	NUMBER OF INDIVIDUALS INDICATING THIS Ψ	1	4	4	5	4	6	0	0	0	0	24
	NUMBER OF INDIVIDUALS FOR WHICH THIS CHOICE IS SIGNIFICANT $P<.05$	0	2	2/3	4	2	5	0	0	0	0	15/23
	PROBABILITY OF THIS DISTRIBUTION OCCURRING BY CHANCE = 0.008											

evaluated from probability tables according to the manner previously described in (12-14); they are found to be P=.002 and P=.008 respectively for the two tests. These results, therefore, supply very strong evidence that the sample of California captured Blackpoll Warblers is indeed oriented in a consistant manner compatible with the mirror image hypothesis.

In closing, it should be noted that all five methods of analysis of the nocturnal orientation of California captured Blackpoll Warblers produced results that are completely consistant with one another. The summation of activities method, on all tests of all individuals, produced a unimodal preferred direction of 67.3°, corresponding to a correct direction of 112.7°. The gap analysis of the distribution of directions produced by each of the 23 Northern California captured Blackpoll Warblers indicated the existence of a mirror image axis lying along the true N-S axis and a correct direction of 125.4°. The analysis of the avoided directions of each Blackpoll Warbler indicated the existence of an "X" distribution symmetric to both the N-S and E-W axes and a correct direction lying closer to east than to south. The analysis of the mean distance that the activity of each Blackpoll Warbler is removed from the preferred directions of the "X" distribution supported the existence of this distribution and indicated a correct direction lying between 110° and 135°. Finally, the analysis of the mean distance that the distribution of nightly mean directions of each Blackpoll Warbler is removed from the preferred directions of the "X" or mirror image distribution also supported the existence of this distribution and indicated a correct direction of 120°. Better agreement between these five methods of analysis could hardly be expected.

PART IV

SYNTHESIS

CHAPTER 13

180° REVERSE ORIENTATION - A DISCUSSION

The results presented in Chapter 12 have indicated that California captured immature Blackpoll Warblers generally display more activity in north or reverse directions than in south or forward directions. For example, the mean unimodal vector for the summation of activities of all tests on all 24 individual Blackpoll Warblers (Figure 12-30) was found to lie at 67.3°, the 180° reverse of the mirror image direction. As perhaps expected, this result was found to apply not only to the entire sample of Blackpoll Warblers considered as a whole, but also to most of the individuals comprising the sample. Thus, it was found that the mean unimodal or primary vector for the summation of activities for individual Blackpoll Warblers occurred in north or reverse directions for 18 of the 23 Northern California captured individuals (Figure 12-31). Although this result is, therefore, fairly consistant for most of the individuals tested, there is no overwhelming tendency for any of the birds to always choose the reverse directions. For example, if the results of single night's tests for all 24 birds are examined (Figures 12-6b to 12-29b), it is found that the 508 mean unimodal or primary directions divide fairly equally between directions lying in the north hemicircle and directions in the south hemicircle; 273 or 53.8% are in the north. In fact, of the 183 bimodal distributions produced by individual birds on single night's tests, only 92 or 50.3% displayed a primary mode lying in the north hemicircle. The orientation cage behavior of immature California captured Blackpoll Warblers may therefore be described as conflict orientation between the forward and reverse directions with a slight, but rather consistant, tendency among most individuals to show more activity in the reverse directions.

One may wonder why reverse directions appear at all in orientation cage experiments since it is obvious that freely migrating individuals must pick the forward direction for most flights in order to complete their long migrations in the observed amount of time. Nevertheless, the occurrence of reverse directionality is not unprecedented, either in orientation cage experiments or in freely migrating birds. Thus, Dolnik and Shumakov [1967] observed a high percentage of reverse orientation in two species of artifically displaced passerine migrants tested in Russia while Evans [1968] found that reverse orientation occurred in about 23% of the passerine migrants that he tested in Great Britain. Similarly, the occasional occurrence of extensive reverse migrations during the fall have been well documented by both radar and visual means [Hailman, 1961; Nisbet and Drury, 1968; Eriksson, 1970; Richardson, 1970, 1972]. These reverse migrations in freely migrating birds have generally been associated with reversed wind directions and abnormally high temperatures. Reverse orientations in experimental birds have generally been attributed to the stress of captivity.

The occurrence of reverse orientation in immature California captured Blackpoll Warblers may be attributed to yet another phenomenon. Recall that 22 of the 24 individuals tested were captured on Southeast Farallon Island, some 18 miles removed from the nearest point of the mainland. It is logical, therefore, to ask where these individuals were just prior to their arrival on the island. During the 15 weeks that I spent on the island in the falls of 1969, 1970 and 1971 it became apparent that all of the land birds present on any given day were not all present at the dawn of that day. Rather, arrivals of landbirds occurred throughout the day, although the vast majority did arrive within the first three hours of the morning. There seems to be no reason why a nocturnally migrating landbird, finding itself at dawn over the California mainland, would continue to fly out over the Pacific Ocean during the early morning hours. It is, therefore, logical to assume that dawn found all of the birds somewhere over the ocean. Since the island lies no more than 1 or 1-1/2 flying hours from the mainland along any south or west course, it would appear that at least some of the birds must have arrived from points beyond the island.

Direct observational data indicate that this is indeed the case. The actual arrival directions of many birds could be determined during the early morning hours from atop the hill next to the lighthouse. All observations that were made in this manner showed virtually all arrivals to be from the southwest quadrant, that is from beyond the island. Furthermore, many of the arriving birds did not stop on the island but continued on course toward the mainland. While this was especially true on days when the mainland was clearly visible, many birds maintained their heading and flew over the island toward the mainland on days when the mainland was totally obscured. In addition, some birds stopped atop the island only briefly before departing again toward the mainland. The vanishing directions of many of the birds seen flying over or leaving the island were recorded. These data are presented in Table 13-1 which shows that the mean vanishing direction for all birds observed in this manner was 36.1°, indicating that most, if not all, of these birds were following a reverse orientation back toward the mainland. Many of the birds recorded were warblers and, by a fortuitous occurrence, one Blackpoll Warbler was included in these data. It may be no mere coincidence that the vanishing direction of this individual was 70°.

The phenomenon just described is not unique to the Pacific Coast. Similar reverse diurnal migrations have been

TABLE 13-1

VANISHING DIRECTIONS OF FALL MIGRANTS DURING EARLY MORNING HOURS ON SOUTHEAST FARALLON ISLAND

SPECIES	NUMBER OF INDIVIDUALS INVOLVED	DATE	MAINLAND VISIBLE?	VANISHING DIRECTION
Water Pipit	3	Oct. 3,1969	Yes	40°
Audubon's Warbler	1	"	"	60°
Red-winged Blackbird	1	"	"	70°
Audubon's Warbler	2	"	"	30°
House Finch	1	"	"	30°
Pine Sisken	2	"	"	40°
Audubon's Warbler	1	Oct. 4,1969	Yes	10°
" "	3	"	"	30°
" "	1	"	"	60°
Brewer's Blackbird	6	"	"	40°
Audubon's Warbler	3	"	"	40°
" "	1	"	"	60°
Myrtle Warbler	1	"	"	60°
House Finch	1	"	"	30°
Audubon's Warbler	2	"	"	60°
" "	1	"	"	30°
" "	1	"	"	50°
Blackpoll Warbler	1	"	"	70°
Myrtle Warbler	1	"	"	80°
Red-winged Blackbird	2	"	"	40°
Audubon's Warbler	3	"	"	30°
" "	1	"	"	40°
" "	1	"	"	50°
" "	1	"	"	0°
Pine Sisken	2	"	"	80°
Audubon's Warbler	2	"	"	0°
" "	1	"	"	40°
Tanager (species)	1	"	"	50°
Audubon's Warbler	3	"	"	20°
Brewer's Blackbird	6	"	"	30°
Cooper's Hawk	1	"	"	10°
Audubon's Warbler	2	"	"	20°
Yellow Warbler	1	Sep.24,1970	No	10°
Yellow Warbler	1	Sep.28,1970	No	30°
Audubon's Warbler	1	Oct. 3,1970	No	40°
Water Pipit	3	"	"	30°
Audubon's Warbler	2	"	"	40°
" "	1	"	"	0°
" "	1	"	"	340°
Savannah Sparrow	4	"	"	10°
Audubon's Warbler	1	"	"	350°

TABLE 13-1 (CONT)

SPECIES	NUMBER OF INDIVIDUALS INVOLVED	DATE	MAINLAND VISIBLE?	VANISHING DIRECTION
		(cont)	(cont)	
Cedar Waxwing	1	Oct. 3,1970	No	30°
Audubon's Warbler	2	"	"	30°
Orange-crowned Warbler	1	"	"	60°
Myrtle Warbler	1	"	"	50°
Audubon's Warbler	1	"	"	350°
Yellow Warbler	1	Oct. 8,1970	Yes	40°
Black-throated Gray Warbler	1	"	"	40°
Audubon's Warbler	6	Oct. 4,1970	No	160°
" "	7	"	"	170°
" "	6	"	"	80°
" "	4	Oct. 5,1970	No	290°
" "	2	"	"	350°
" "	2	Oct. 7,1970	Barely	270°
" "	3	"	"	350°
" "	3	"	"	340°
" "	1	"	"	40°
Myrtle Warbler	2	Oct.12,1970	No	30°
" "	1	"	"	60°
" "	1	"	"	40°
Audubon's Warbler	2	"	"	0°
" "	1	"	"	30°
" "	2	Oct.25,1971	Barely	40°
" "	2	"	"	10°
" "	2	"	"	10°
Myrtle Warbler	2	"	"	70°
" "	2	"	"	80°
Audubon's Warbler	8	"	"	10°
Starling	16	"	"	40°
Cedar Waxwing	1	"	"	10°
MEAN OF ALL DEPARTURES				36.1°

recorded during the fall on Nantucket Island and Block Island, off the coast of New England, and elsewhere on the Atlantic Coast [Baird and Nisbet, 1960]. As would be expected, the direction of these movements was NW, again back toward the mainland. It may be reasonable, therefore, to hypothesize that when a nocturnally migrating landbird finds itself at dawn over unsuitable habitat such as an ocean, it reverses its orientation and returns along the same course that it flew. All Farallon captured Blackpoll Warblers could, therefore, be considered to have been in a reverse orientation mode when captured. It is not surprising that such individuals display some reverse orientation behavior when tested in nocturnal orientation cages. It is surprising, however, that this reverse orientation generally predominates (although not by much) throughout the period of time these birds are held in captivity. This may indicate that captivity itself provides a stress situation for the individual, similar, in effect, to that produced by arriving over unsuitable habitat at the end of a night's flight.

The experimental finding that the sample of California captured immature Blackpoll Warblers displays a consistant reverse direction in orientation cage experiments and that this reverse direction is 180° removed from the forward direction has interesting theoretical implications. The ability of individuals of a single species to consistantly choose a particular reverse direction indicates that there may be considerable adaptive value for that reverse direction. This adaptive value is straightforward if one considers the possibilities available to a landbird that finds itself at dawn over the ocean: it could continue on course to a virtually certain death; it could initiate a random search pattern; it could initiate a non-random search pattern such as flying in circles of ever increasing diameter; or it could follow a preprogrammed reverse direction back toward the mainland. The last will clearly be the most successful alternative. Whether such an alternative can be selected for will, of course, depend upon the frequency of encountering such a situation. In this regard, it seems likely that virtually all immature individuals of a species of landbird that regularly makes a long overwater crossing will encounter this situation the first time that they reach the coast. It seems unlikely that an immature landbird, having no prior experience with an ocean, will halt a nocturnal flight upon crossing a shoreline at night at an elevation of 1000+ feet. Rather, it probably will continue its flight until dawn, at which time it will be located some distance out over the ocean. Thus there will exist a strong selective pressure for some preprogrammed reverse orientation.

This same situation could also serve as the necessary stimulus to indicate to the young bird that it has indeed reached the coast and that it now must store the very large quantity of subcutaneous fat necessary for the impending overwater flight and, in some species, that it must initiate its next forward flight in a somewhat different direction. Recall that Nisbet [1970] has proposed that the transoceanic flight of the Blackpoll Warbler has a different orientation from the preceding transcontinental flight. Furthermore, this situation could be partially responsible for the high percentage of immature landbirds found along the immediate coast [Robbins et al. 1959; Drury and Keith, 1962; Nisbet et al., 1963; Murray, 1966a; Phillips et al., 1966]. Adults, having prior experience with transoceanic flight, might be expected to recognize the coast immediately upon reaching the shoreline, reverse their direction at that point, and alight at dawn some distance inland.

The implications of the experimental finding that the reverse direction, at least in California captured immature Blackpoll Warblers, is identically 180° removed from the forward direction may now be considered. First, this reverse direction will always be successful in returning the warbler to the mainland, provided that it has stored enough fat to complete the return flight. The distance of this return flight can, of course, never be greater than the distance of that night's forward flight. If a warbler were to choose any direction other than the 180° reverse direction, the distance of the return flight could either be shortened or lengthened depending upon the angle that the warbler's forward flight direction intersected the coast and the vagaries of the immediate coastline. If the bird's flight intersected the coast at 90°, of course, the 180° reverse direction would produce the shortest distance back to the mainland. Considering the variability in the preferred direction that is likely to exist in a population of warblers as well as the high local variations in the orientation of typical coastlines, the choice of any reverse direction other than 180° is likely to be risky business and, in the long run, may produce fewer successful returns than the 180° reverse direction.

It is also important to note that, in many species, the existence of a 180° reverse direction may not necessitate the inheritance of any additional information, but may simply represent an expression of the spring orientation which the bird may have already inherited. On the other hand, even if the 180° reverse direction does necessitate the inheritance of additional information, the bird need only inherit the angular relationship 180° and need not be concerned with the sense of that angle since $\phi+180°$ is an identical direction to $\Phi-180°$. Thus, the possibility of mirror image or left-right errors in the reverse direction is effectively eliminated.

Finally, the existence of a 180° reverse orientation may not be unique to landbird species that tend to find themselves over an ocean. Rather, 180° reverse orientation could be the response of any bird that finds itself, at the termination of a migratory flight, over unsuitable habitat, such as a forest adapted species over the desert. Nor must it even be limited to a response to adverse topography or habitat. It could also be triggered by adverse weather, thus accounting for the visual and radar observations of reverse migrations. Indeed, it could be a generalized response of a migrating bird to many kinds of adverse stress situations. Along these lines, it is difficult to imagine a more adverse situation for a migrating bird than being captured, held in captivity, effectively prevented from migrating and placed into an orientation cage. There is little wonder, therefore, that 180° reverse orientation is at least an occasional feature of the behavior of freshly captured migratory birds in orientation cages.

CHAPTER 14

MIRROR IMAGE MISORIENTATION - A DISCUSSION

The results of both the theoretical (Part II) and experimental (Part III) sections of this dissertation agree in indicating that left-right or mirror image errors are responsible for the fall occurrences of immature vagrant wood warblers in California. Such errors may not be an unlikely or unusual possibility in birds. In fact, as pointed out by Corballis and Beale [1971], mirror image or left-right confusion is a very common phenomenon in many diverse kinds of animals including pigeons. They suggest that such mirror image equivalence is a necessary result of the bilateral symmetry that is common to virtually all members of the animal kingdom and, furthermore, that any mirror image discrimination necessarily implies some bilateral asymmetry in the nervous system of an animal. They also claim that there is an "advantage for maintaining bilateral symmetry even in the face of asymmetrical experience". The advantage stems from the ability to symmetrically generalize pattern recognition (for predator, prey or prospective mate) as well as to symmetrically generalize prey capture or predator avoidance responses from asymmetric experiences. In summary they conclude that "in the natural environment there is more to be gained from mirror image equivalence than from mirror image discrimination".

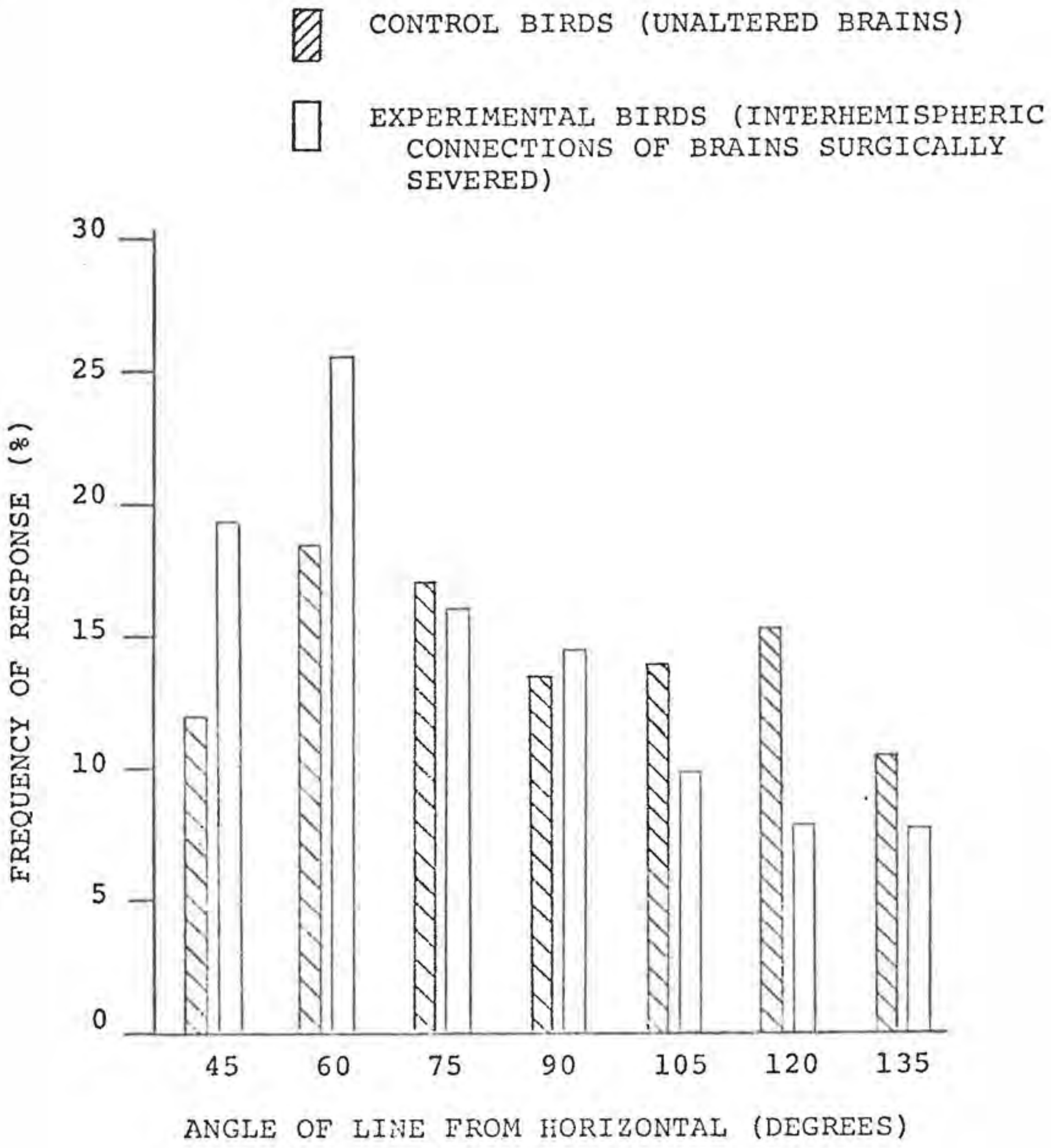
Corballis and Beale also point out that there are two basic tests that can indicate whether a given animal is capable of differentiating between left and right. The first test is called mirror image stimulus discrimination. In such a test an animal is asked to respond in two different ways that are not mirror images of each other when presented with two stimuli that are mirror images of each other. In other words, the experimenter demonstrates left and right and the animal is asked to name which is which. The second test may be even more rigorous and is generally more difficult for an animal to perform. It is called left-right response differentiation. In this test an animal is required to perform in two different ways that are mirror images of each other when presented with two stimuli that are not mirror images of each other. A simpler version of this test is to require an animal to make a consistant left or right response to a situation where no left or right information is provided. In these tests, the experimenter names left or right and the animal is asked to demonstrate each one.

Corballis and Beale present examples of the results of many mirror image stimulus discrimination tests that have been reported in the literature. They include Pavlov's result that it was impossible to condition a dog to salivate when touched on one side of its body and not to salivate when touched at the mirror image point on the other side, and Lashley's result that it was difficult, although not impossible, to teach a rat to discriminate between two visually presented mirror image patterns. Similar results have been reported for octopuses, goldfish, pigeons, cats, monkeys, chimpanzees, and children. A hypothesis presented to explain these results is that when a memory "trace" for a given stimulus pattern is being established during learning, a second "trace" is simultaneously being established for the mirror image of the pattern even though the mirror image of the pattern has not been presented.

A striking example that supplies evidence for such a hypothesis is taken from Corballis and Beale [1971] and is represented in Figure 14-1. Two groups of pigeons were trained to peck a key for a food reward when the key displayed a line at an angle of 60° to the horizontal but not to peck at a key that displayed no line. One group of birds had the interhemispheric connections in their brains surgically severed before they were trained. The second group (controls) had unaltered brains. Both groups of pigeons were then presented with keys that had lines ranging from 45° to 135° at 15° intervals. As shown in the histogram in Figure 14-1, both groups of birds tended to peck most frequently at the key with the "correct" 60° line. The control birds, however, also tended to peck frequently

FIGURE 14-1

RESULTS OF A VISUAL MIRROR IMAGE STIMULUS DISCRIMINATION TEST ON PIGEONS. SEE TEXT FOR FULL EXPLANATION. (AFTER CORBALLIS AND BEALE, 1971)



at the 120° or mirror image line. The experimental birds showed no tendency to peck preferentially at the mirror image line. These results suggest that when a memory "trace" for a given pattern is established in one hemisphere of an animal's brain, the mirror image of that "trace" may be established in the other hemisphere.

The histogram for the control pigeons presented in Figure 14-1 bears a striking resemblance to orientation cage data obtained on immature fall vagrant Blackpoll Warblers in California. In each case there appear to be two modes of activity, one having a peak centered on the "correct" orientation and the other having a peak centered on the mirror image of the "correct" orientation. By analogy, therefore, it may not be unreasonable to suggest that when the correct migratory direction is imprinted on the memory of an immature vagrant Blackpoll Warbler (by the process of learning the correct reference point to which to relate that direction), the mirror image duplication of that direction is simultaneously created. This is equivalent to suggesting that the correct migratory angle (declination from north) is imprinted on the memory of an immature vagrant Blackpoll Warbler with both the right (clockwise) and left (counterclockwise) sense.

The orientation cage experiment can then be viewed as a test of left-right response differentiation. The warbler is presented with a consistant visual stimulus pattern that contains either no left-right information (the location of celestial north) or, if the warbler perceives the rotation of the sky, only consistant left or consistant right information. The warbler is then asked to demonstrate either left or right but not both. The results of the orientation cage experiments presented in Part III of this dissertation supply evidence that the immature vagrant Blackpoll Warbler, when placed in an orientation cage, fails to consistantly differentiate between left and right, sometimes choosing right and sometimes choosing left. That the number of choices of left and right are virtually equal is indicated by the data shown in Table 14-1: the sample of vagrant Blackpoll Warblers is seen to choose right, the correct direction (NW or SE quadrants), 53.0% of the time. In view of the above model, these data indicate that the imprinting of the mirror image direction is virtually complete. Again, these results are analagous to the results of the mirror image stimulus discrimination test on the control pigeons shown in Figure 14-1: they chose the correct (entrained) direction 54.5% of the time.

At this time it is essential to point out a major dichotomy between the results of Parts II and III of this dissertation. Although the orientation cage results on immature vagrant Blackpoll Warblers captured in California suggest a high degree of mirror image or left-right equivalence, the timing of the arrival of these birds in

TABLE 14-1

DISTRIBUTION OF UNIMODAL OR PRIMARY MEAN DIRECTIONS DISPLAYED BY CALIFORNIA CAPTURED VAGRANT BLACKPOLL WARBLERS

	NUMBER OF	CORRECT DIRECTIONS			VAGRANT DIRECTIONS			% OF TESTS SHOWING CORRECT
BIRD	ACTIVE TESTS	NW	SE	TOTAL	NE	SW	TOTAL	DIRECTIONS
21	7	0	2	2	4	1	5	28.6
22	1	1	0	1	0	0	0	100.0
23	7	1	2	3	3	1	4	42.9
24	28	3	9	12	7	9	16	42.9
25	20	0	14	14	1	5	6	70.0
26	23	3	5	8	10	5	15	34.8
27	17	6	2	8	3	6	9	47.1
28	20	4	4	8	6	6	12	40.0
29	15	5	5	10	4	1	5	66.7
30	9	1	2	3	2	4	6	33.3
31	23	5	3	8	4	11	15	34.8
32	31	1	10	11	16	4	20	35.5
33	21	11	3	14	3	4	7	66.7
34	31	9	4	13	13	5	18	41.9
35	23	15	4	19	2	2	4	82.6
36	29	5	14	19	10	0	10	65.5
37	30	10	5	15	13	2	15	50.0
38	29	12	2	14	13	2	15	48.3
39	30	11	7	18	7	5	12	60.0
40	30	12	7	19	6	5	11	63.3
41	30	7	13	20	1	9	10	66.7
42	24	2	13	15	4	5	9	62.5
43	16	3	6	9	7	0	7	56.3
44	14	4	2	6	3	5	8	42.9
TOTAL	508	131	138	269	142	97	239	53.0

TOTAL IN NORTH HEMICIRCLE = 273
TOTAL IN SOUTH HEMICIRCLE = 235

California indicates a high degree of mirror image discrimination, that is, the warbler must have consistantly chosen left in order to arrive in California on time. Furthermore, if mirror image vagrant Blackpoll Warblers in the wild showed the high level of mirror image equivalence that they appear to demonstrate in orientation cages, then their flight path would be a zig-zag down the center of the continent. They would, therefore, be expected to occur more frequently in Texas than in California. The fact is, however, that Blackpoll Warblers are virtually unknown in Texas in the fall; none have been recorded there during the last eleven years even though observers regularly check coastal points such as Galveston and High Island [data from Audubon Field Notes and American Birds, Vol. 17-27]! This dichotomy indicates that the behavior of a bird in an orientation cage may not be truly representative of the behavior of that individual in the wild. It cannot be overemphasized that the results of an orientation cage experiment only represent the manner in which a bird directs its _Zugunruhe_; they do not necessarily represent the manner in which the bird directs its _actual migration_ since, very simply, the bird is not migrating in an orientation cage. There is only circumstantial evidence, summarized in Chapter 5, that the direction of Zugunruhe is, very often, similar to the migratory direction appropriate for the particular season.

In view of this fact, the above dichotomy may be resolved by the following argument which I present as a working hypothesis. Assume that the immature vagrant (or potentially vagrant) Blackpoll Warbler has imprinted the correct angular declination for its first fall migration with both the right and left sense. Now assume that the actual migration route flown by the bird is entirely determined by its initial choice of the sense (right or left) for its first actual nocturnal migratory flight. If, for example, the bird's choice for its first flight was left, the mirror image direction, then that direction is maintained on subsequent flights. This pattern of migration will cause the bird to arrive in coastal California on time, a result consistant with the data presented in Part II of this dissertation. This hypothesis, therefore, presupposes mirror image equivalence for the vagrant warbler's first nocturnal flight but mirror image discrimination for subsequent flights. Such a supposition is not unreasonable. Corballis and Beale [1971] have pointed out that the necessary asymmetry that makes possible the solution of mirror image problems might reside in a motor function rather than in a sensory or perceptual one. They refer to observations that mirror image confusion in children tends to occur less commonly in writing than in reading, perhaps indicating that handedness could provide the asymmetry necessary for mirror image discrimination. The situation with the vagrant warbler is analogous. The vagrant imprints the correct migratory direction and the mirror image of that direction by means of visual or perceptual stimuli and, for its first flight, may not be capable of distinguishing between the two directions. However, once the bird has completed its first migratory flight, the motor response involved could serve as an asymmetric cue for subsequent left-right determinations.

Now let us turn again to the behavior of the experimental bird captured in California. The results of Part III of this dissertation have shown the extremely important fact that the immature vagrant Blackpoll Warbler, when placed into the artificial environment of the orientation cage, is capable of demonstrating both the correct and mirror image directions, that is, both the right and left sense. This fact was previously interpreted as evidence that the warbler displays mirror image equivalence in its orientation behavior. However, it is important to note that, on a given night, such a warbler usually displays only a single choice of the sense, that is, chooses only a single direction or a single direction and its 180° reverse. Very rarely does such a bird display both a correct and a vagrant direction on a single night. When it is recalled that the captive experimental bird is held in an extremely high stress situation and effectively prevented from migrating, its orientation cage behavior may be interpreted as a stress induced alternation between two responses rather than as an indication of the inability of distinguishing between the two responses. Thus, the warbler orients its Zugunruhe first with one sense, then with the other sense. Such behavior is typical of the behavior of animals that are prevented from satisfying a particular urge, in this case, the urge to complete a migratory flight. In this regard, orientation cage behavior of a captive bird should perhaps be considered as indicative of all of the possible modes of migratory behavior available to that bird rather than as indicative of the particular mode chosen by that individual during the course of its actual migration. This consideration has extremely important consequences for researchers in this field and all hypotheses of migratory behavior based on interpretations of orientation cage behavior should be made with great caution.

One important question remains. Is the initial choice of the sense for the first actual migratory flight of an immature vagrant Blackpoll Warbler randomly determined or, is there some factor, perhaps environmental, that determines that choice? I propose that the wind direction is the environmental factor that determines that choice. As discussed in Part II, a growing amount of radar data shows that passerines normally fly more or less downwind. Richardson [1972], using the data from a radar study of fall migration and weather in eastern Canada, has concluded that different populations of passerines each have a "preferred" direction of flight and that each population normally migrates only when favorable weather (following winds) for their "preferred" direction occurs. Stated alternatively, winds aligned with the "preferred" direction are stimulatory for the initiation of migration while winds not aligned with the "preferred" direction are inhibitory. Under such a system, the mechanism for the initial choice of the sense of the direction of a potentially vagrant warbler is straightforward. Such a bird may be considered to have, at the onset of migration, two "preferred" directions, the correct direction and the mirror image direction. The initial choice is then determined by which of the two "preferred" directions the wind first aligns with when the bird's physiological readiness for migration and immediate fat accumulation have both first reached some critical threshold level. This "preferred" direction is then reinforced on subsequent flights.

At this point, it is logical to ask what happens to mirror image vagrant Blackpoll Warblers after they arrive on the Pacific Coast of California. They certainly do not turn and follow the coast south. If they did they would be expected to occur in large numbers at the southern tip of Baja California. However, DeSante [MS] did not observe a single Blackpoll Warbler in the Cape Region of Baja California between September 26, 1968 and January 2, 1969 even though daily censuses were conducted expressly for the purpose of locating vagrant birds. Parenthetically, these data also refute Austin's [1971] claim that Blackpoll Warblers regularly use the west coast as a migration route. What then do they do? Since all successful migrant Blackpoll Warblers, after arriving on the Atlantic Coast and accumulating a large quantity of subcutaneous fat, unhesitatingly set out on a long overwater flight [Nisbet, 1970], we can only assume that mirror image vagrant Blackpolls do the same. While successful migrant Blackpolls will reach the Lesser Antilles or the northern coast of South America after a flight of some 2000-2500 miles, the mirror image vagrant Blackpoll Warblers, flying SW from the Pacific Coast of California, are doomed to perish in the ocean. With such a virtually certain selection against mirror image vagrants, the question naturally arises, why hasn't mirror image misorientation been selectively eliminated from this species?

The answer is provided by the results of the experimental part of this dissertation, in particular by the fact that an individual California captured Blackpoll Warbler is capable of displaying both the correct and the mirror image directions when tested in an orientation cage under clear night skies. This result supplies conclusive evidence that the individual has not unambiguously inherited the wrong sense by which it relates its migratory direction to the reference point but rather that this sense is subject to some degree of mirror image or right-left confusion. This implies that any given individual Blackpoll Warbler that displays some degree of mirror image confusion regarding this sense is capable of initiating its migration in either the correct direction (in which case it can become a successful migrant and not be selected against) or in the mirror image direction (in which case it will become an unsuccessful vagrant and be selected against). As long as a few of such potentially vagrant individuals choose the correct direction, at least a small amount of mirror image misorientation can persist in the population for a comparatively long time.

If the choice of the sense of the first actual migratory flight is environmentally determined by the wind direction, as hypothesized above, then the rate of selection against mirror image confusion will be proportional to the fraction of the time that the wind lies in the mirror image direction (during the period when immature Blackpoll Warblers initiate their fall migration) divided by the fraction of the time that the wind lies in the correct direction (during this same time period). Similarly, the number of vagrant Blackpoll Warblers arriving in California during any given fall should be proportional to this same quotient calculated over the geographical area from which mirror image Blackpoll Warblers that reach California could originate. Variations from year to year in the average wind directions over central Canada would, therefore, produce the variations in the number of Blackpoll Warblers that arrive in California each year. Unfortunately, the detailed weather data necessary to support or refute this hypothesis are not presently available. However, an examination of gross wind directions over central Canada during the early fall, as obtained from daily weather maps, indicates that mirror image winds are more or less the exception; the prevailing winds lie between north and west. Thus, the rate of selection against mirror image confusion should be considerably less than 50%.

Another important consideration of the wind-triggered mirror image hypothesis is that the same wind directions that determined the initial migratory flight of the potentially vagrant warbler will also be stimulatory for the subsequent migratory flights of this same individual. This situation will cause vagrant warblers to arrive in California (or for that matter, correctly migrating warblers to arrive on the Atlantic Coast) in rather well defined waves that will be associated with favorable winds. For vagrant warblers, such winds will lie in the mirror image of the correct migratory direction. The existence of such waves was first suggested by Paxton [1965, 1967] and later confirmed, at least for Northern California vagrant arrivals, by Chandik et al. [1971], DeSante et al. [1972]

and DeSante and Remsen [1973]. This same correlation, well demonstrated by daily weather maps, prompted Bagg [1970, 1971] and Able [1972] to suggest that wind drift was the cause of westward vagrancy in wood warblers and other passerine migrants. The results of this dissertation, however, necessitate a somewhat different interpretation. Wind direction may now be considered as a stimulatory, perhaps necessary, factor for vagrancy but can not be considered as a sufficient causal factor by itself. The existence, in an individual bird, of some degree of mirror image confusion or, at least, the imprinting of the migratory direction with both the right and left sense is also a necessary factor. As such, mirror image misorientation must be considered to be an aberrant phenomenon in individual birds.

It is also important to note that the selection against mirror image misorientation will not be the same for all populations of warblers. Rather, it will depend upon the actual migratory direction of a given population. For example, mirror image vagrants of a population of warblers that migrates directly south will not be selected against since the mirror image of the correct direction is identically the correct direction. *Therefore, only when a given population of warblers evolves a migration direction that contains a strong E or W component, does it become*

<u>necessary for individuals of that population to distinguish between left and right</u>.

Mirror image misorientation, as here presented, is probably not unique to wood warblers. Instead, it may be a potential characteristic of all birds that make use of a distance-and-direction type of migration system. It is, therefore, likely that many of the fall vagrant occurrences of immatures of most species of eastern birds, particularly passerines, may be attributable to this phenomenon. All that is necessary to produce California occurrences of vagrants of any given eastern species is that the correct migration route of the more western populations of such species be southeastward. A glance at the range maps presented in Robbins et al. [1966] indicates that such a situation is typical of a great number of eastern species, particularly those whose breeding range extends northwestward north of the Great Plains or east of the northwestward curving base of the Rocky Mountains. Furthermore, it is generally believed that such northwestward extensions of the breeding range of eastern species may be relatively recent phenomena, certainly subsequent to the last major glaciation, only some 20,000 years ago. Thus, time may not have permitted (if it ever will) the complete selection for perfect right-left discrimination in these recently expanding populations. Wood warblers, in particular, may be experimenting with one of the most recently evolved avian migratory systems on the face of the earth. As such, there still may be some "bugs" in it, not the least of which is the inherent difficulty of telling left from right.

The above discussion is in agreement with DeBenedictis [1971] in interpreting the occurrences of vagrant warblers to be the result of a passive phenomenon -- the failure of some individuals of a population to be correctly oriented. Although there is no positive evidence to show that the number of vagrant warblers has increased in recent years, the extremely large number of records since 1962 tempts one to ask whether vagrant occurrences could also be the result of some recent active phenomenon. Along these lines, Able [1972] has asked the perhaps timely question, "...who knows what effect persistent pesticides (which accumulate in birds' brains) might have on their ability to orient properly?" The results of this dissertation point out one possible line in which to initiate an investigation to answer Able's question. In particular, one may ask the specific question, "Does the accumulation of persistent pesticides facilitate the interhemispheric transfer of memory traces in birds?" Further pursuit of such questions, however, is beyond the scope of this investigation.

Thus far we have considered only aspects of negative selection against mirror image misorientation. Are there any conditions under which positive selection for mirror image misorientation could occur? Certainly, all Pacific Coast vagrants of species in which all individuals normally make an overwater crossing will be selected against since all such birds will perish in the Pacific Ocean. However, there exist species in which some individuals do not normally make an overwater crossing but remain to winter in southeastern United States. We would expect that a few vagrant individuals of such species should remain to winter on the Pacific Coast of California. Data presented in Part I of this dissertation indicate that this is exactly the case. Each year, a few Black-and-white and Palm Warblers and an occasional individual of other species are found successfully wintering in California. Data are available to indicate that a successfully wintering vagrant warbler will return to winter at the exact same location in subsequent years. For example, one or more Palm Warblers were recorded at the exact same location in the Carmel Rivermouth, Monterey County, for four consecutive winters, 1962-63 through 1966-67. Unfortunately, none of these individuals were banded so some uncertainty exists as to whether they were indeed the same individuals each year. However, no uncertainty exists in the case of a Painted Redstart that was banded in Altadena, Los Angeles County, in the winter of 1941-42 and returned to the same location the next two winters, nor in the case of a Virginia's Warbler that was first found at Eagle Rock, Los Angeles County, in the winter of 1954-55, banded at the same spot in the winter of 1955-56 and found again in the winter of 1956-57. The possibility, therefore, does exist, at least in some species, that mirror image vagrants could be instrumental in establishing new winter ranges.

The simple survival of a few vagrant individuals in such areas, however, is not the only necessary requirement for the establishment of a new winter range. As pointed out by DeBenedictis [1971], the new wintering area must be ecologically similar to the normal winter range so that all of the arriving individuals will, in general, be well adapted to the environment. A possible additional requirement is that the new wintering area should not be already occupied by a potentially competing species. These requirements probably make the establishment of a new winter range by long distance vagrancy a rare event indeed. Nevertheless it is most interesting to note that both the Myrtle and Townsend's Warblers have Pacific Coast winter ranges that are isolated from their main wintering ranges further east and south. The location of these Pacific Coast wintering areas are consistant with a mirror image migration route although they are also consistant with a Pacific Coast migration route. It would, therefore, be most desirable to determine where Pacific Coast wintering individuals of each of these species breed. Pacific Coast wintering Myrtle Warblers are presently thought to breed in Alaska and northwestern Canada ("hooveri" race), in which case the establishment of the Pacific Coast wintering range by mirror image vagrancy is ruled out. However, Hubbard [1970] has recently supplied strong evidence to indicate that "hooveri" is not a valid race. The question, therefore, still remains open.

This entire investigation, up to this point, has been limited to considerations of mirror image misorientation in immature warblers, that is, in birds that presumably make their first fall migration according to a distance-and-direction migratory system. A brief discussion of the implication of vagrant occurrences of adult birds is perhaps appropos. As pointed out in Part I of this dissertation, a few adult warblers do occur as fall vagrants in California. Moreover, the occurrences of some of these adult birds (such as those on Southeast Farallon Island) cannot easily be attributed to the return of a previous year's immature vagrant. Thus, there must exist some mechanism to cause an adult bird, which presumably made a correct migration during its first autumn, to make an error on its second or subsequent fall migration and arrive on the Pacific Coast. Since we know virtually nothing of the actual cues or mechanism by which an adult bird homes, presumably by true bicoordinate navigation, to the exact same wintering location year after year, we are hard pressed to isolate a particular error which could be responsible for misorientation in such a bird.

There exists some circumstantial evidence to indicate that mirror image or left-right confusion may not be involved in adult misorientation. As previously discussed in this chapter, Corballis and Beale [1971] have demonstrated that pigeons display a high level of mirror image confusion, at least in regard to their behavior in visual mirror image stimulus discrimination tests. And yet pigeons are well known to be excellent navigators. This situation suggests one or both of the following possibilities: (1) visual mirror image or left-right discrimination is not necessary for successful bicoordinate navigation by visual cues, or (2) the cues used for bicoordinate navigation are not visual and, therefore, are not affected by visual mirror image or left-right confusion. Further discussion of this matter, however, is beyond the scope of this investigation and must await a more complete understanding of the mechanism of true bicoordinate navigation.

CHAPTER 15

SUMMARY AND CONCLUSIONS

1. The phenomenon of the fall occurrences of vagrant wood warblers in California may be characterized as follows: (a) It is a regularly occurring phenomenon that is widespread among virtually all species of migrant North American wood warblers. (b) Different species occur in California in widely varying abundances. (c) The number of occurrences of any given species or all species combined varies somewhat from year to year. (d) Most of the occurrences are concentrated along the immediate coast but occurrences are frequent in both northern and southern California. (e) Most of the individuals involved are immature birds on their first fall migration. (f) There is no positive indication that the phenomenon is of very recent origin.

2. Immature wood warblers are assumed to utilize a distance-and-direction migration system for their first fall migration. The various errors, inherent in such a system, that could be responsible for occurrences of vagrant warblers are found to fall into two types: disorientation, the inability of an individual to consistantly follow any direction, and misorientation, the inability of an oriented individual to follow the correct direction. Errors producing disorientation could arise by the failure of the

individual to (a) inherit any direction or (b) learn any environmental reference point to which to relate its inherited direction. Errors producing misorientation could arise by the failure of the individual to (a) inherit the correct direction or learn the correct stationary reference point -- simple misorientation or reference point misorientation, (b) exhibit the correct sign (forward or reverse, fall or spring) to its migratory direction -- 180° reverse misorientation or (c) relate the migratory direction to the reference point with the correct sense (right or left, clockwise or counterclockwise) -- mirror image misorientation.

3. A comparison of the actual average arrival dates in California with the predicted average arrival dates for vagrant individuals of all species of eastern warblers shows that they arrive exactly on time thus providing conclusive evidence that the vast majority of vagrant occurrences are due to misoriented rather than disoriented individuals.

4. An analysis of the relative species abundances, the locations of the occurrences within the state, both along a N-S and an E-W axis, and the relative timing of the occurrences within the state provides a strong and unanimous indication that mirror image misorientation, rather than either simple or 180° reverse misorientation, is the operative mechanism causing most vagrant individuals of all species of wood warblers to occur in California.

5. Twenty-four immature Blackpoll Warblers were captured in California during the fall migrations of 1969-1971. Twenty-three of these birds were captured in northern California, 22 of them on Southeast Farallon Island. A total of 521 "footprint" nocturnal orientation experiments were conducted on these individuals under clear, moonless California night skies.

6. The raw "footprint" orientation data was digitized by eye by comparing the amount of blackness in a given 15° sector of the trace with a logarithmic scale of 32 standard blackness values ranging from pure white (no marks) to the darkest 15° sector ever found on any trace. This scale of standard blackness values was constructed from 15° sectors cut out of actual traces. The amount of blackness on the standards was objectively determined by the use of a TV camera connected directly to a computer and programmed to perform as an optical densitometer. The reproducibility of this method of digitization was found to be extremely high; the Pearson product-moment coefficient of correlation for two independent digitizations of the same trace was found to average 0.97.

7. Both the body weights and the amounts of nocturnal activity displayed by captive Blackpoll Warblers indicated that there is nothing abnormal about the physiology that controls fat deposition and migratory readiness in vagrant individuals.

8. Visual inspection of the "footprint" data indicated that many of the traces produced by vagrant Blackpoll Warblers appeared to be bimodally directed. Since no statistical methods were available to handle such data, an approximate multimodal method of analysis was developed. This method consisted of (a) a mode finding algorithm designed to determine the number of "valid" modes on each trace and (b) an approximate solution to a multimodal mixture of circular distributions which produced, for each mode k present on each trace, estimates of the amount of activity, AT_k, the mean direction, Φ_k, and the concentration about the mean direction, r_k. If the trace was found to be unimodal, these parameters were determined by simple vector summation. This approximate multimodal analysis was tested on 225 combinations of bimodal mixtures of theoretical circular normal distributions having known parameters. It was always found to produce sufficiently accurate estimates of Φ_k and AT_k but occasionally produced spurious values of r_k.

9. The multimodal analysis indicated that multimodal behavior occurred in 186 out of 508 active tests. Of these, 183 were bimodal and only 3 were trimodal. The mean difference between the primary and secondary modes (measured clockwise) of the 183 bimodal traces was found to be $179.2 \pm 27.0°$ and was not significantly different from 180°. This indicates that bimodal orientation represents conflict

behavior between the choice of a given direction and its 180° opposite direction.

10. This 180° reverse orientation is considered to be a generalized adaptive response to adverse stress conditions such as arriving over unsuitable habitat at the termination of a migratory flight, encountering adverse weather or being captured and prevented from migrating. It is suggested that 180° reverse orientation may be common, not only to wood warblers, but to most nocturnal migrant passerines. Furthermore, it is suggested that some 180° reverse orientation will probably be characteristic of most orientation cage experiments on freshly captured nocturnal migrants, whether such birds are vagrant individuals or not.

11. The mean value of the concentration about the mean direction, r, for all 322 unimodal traces was found to be 0.554. This provides a strong (but not statistically testable) indication that vagrant Blackpoll Warblers are capable of directed behavior over the course of single night's orientation cage tests.

12. The distribution of nightly mean directions were analyzed for each of the 23 birds that were tested over several nights. Significantly directed behavior ($P<.05$), in one or more directions, was found in 43.5% of these birds, providing a strong indication that California captured vagrant Blackpoll Warblers are misoriented rather than disoriented individuals.

13. An analysis of the distribution of mean directions for the summation of activities of the 23 Northern California captured Blackpoll Warblers provided a strong indication (P=.058) that this sample of vagrant warblers, considered as a unit, displayed directed multimodal behavior. This indicates that all Northern California captured Blackpoll Warblers are indeed misoriented and, furthermore, that they are misoriented in a similar manner. Further analysis of this distribution indicated that this sample of birds preferred four directions, one in each quadrant. The SE direction was found to be 125° and represents a good approximation of the correct transcontinental migration route of the Blackpoll Warbler. The NW direction was found to be approximately the 180° reverse of the SE direction while the NE direction was found to be approximately the 180° reverse of the SW direction. The SW direction was then considered to be the mirror image of the correct direction. The mirror image axis was experimentally determined and found to lie at 0.9°, within 1° of true north. This supplies strong experimental evidence that mirror image misorientation is the operative mechanism causing immature Blackpoll Warblers to arrive in (at least Northern) California.

14. An analysis of the distribution of directions that are avoided by each of the 23 Blackpoll Warblers tested over several nights supported the above finding and supplied

evidence that each individual significantly avoids ($P<.05$) at least three of the four Cardinal directions, north and south being avoided more consistantly that east and west. The hypothesis was then stated that the orientation cage behavior of California captured Blackpoll Warblers can be described as the preference for a pair of diameters, symmetrically crossed with both the N-S and E-W axes, and represents oriented behavior in both the correct direction and the mirror image of the correct direction as well as in the 180° reverse direction of both of them.

15. This hypothesis was directly tested against the null hypothesis of a diameter constant distribution (which includes the uniform distribution). The test statistic used was the mean value, for each individual, of the mean distance over which its activity is removed from the nearest of the four preferred directions. The results of this test indicated that the activities of 12 of the 23 birds tested over several nights were significantly directed ($P<.05$) according to the crossed diameters or mirror image hypothesis. Moreover, the entire sample of 24 Blackpoll Warblers showed an extremely high preference ($P=.0003$) for a single orientation of the crossed diameters, that is, a single correct direction. This correct direction was experimentally found to lie between 110° and 135°, again in close agreement with the actual correct transcontinental migration route of the Blackpoll Warbler.

16. The mirror image hypothesis was directly tested against the null hypothesis of the diameter constant distribution by an alternative method which involved the use of the mean distance that the distribution of mean nightly vectors, for each Blackpoll Warbler, was removed from the preferred directions of the mirror image distribution. The results of this test indicated that the distribution of mean nightly directions was significantly directed ($P<.05$) according to the crossed diameters or mirror image hypothesis for at least 15 of the 24 birds. Again, the entire sample of Blackpoll Warblers was found to show an extremely high preference ($P<.008$) for a consistant orientation of the crossed diameters, that is, a single correct direction. Two different test statistics showed this correct direction to be approximately 120°, again in excellent agreement with the correct trancontinental route of the Blackpoll Warbler. These results, therefore, provide very strong evidence that California captured Blackpoll Warblers, when tested in "footprint" orientation cages, are capable of displaying both the correct direction and the mirror image of the correct direction.

17. A working hypothesis for mirror image misorientation is presented that is consistant with both the theoretical and experimental results of this investigation. Mirror image misorientation in individual immature warblers is considered to be caused by the imprinting of the

migratory direction with both the right (clockwise) and left (counterclockwise) sense, that is, in both the correct and mirror image orientations. The choice of the orientation (correct or mirror image) for the first actual migratory flight of the immature warbler is either determined randomly or, more likely, is environmentally triggered by the wind direction. In either case, the warbler displays mirror image equivalence regarding this initial choice. The orientation of this initial flight is reinforced so that the orientation of subsequent flights is determined by the orientation of the initial flight. The warbler, therefore, displays mirror image discrimination regarding these subsequent flights. When the warbler is captured, prevented from migrating and tested in an orientation cage over several nights, it displays a stress-induced alternation between the two orientations.

18. There are several ramifications of the wind triggered, mirror image misorientation hypothesis. (a) The selection against mirror image misorientation will be a function of the correct migratory direction of a population; negative selection will tend to increase as the component of the migratory direction that lies in the east or west direction increases. (b) The rate of selection against mirror image misorientation, for any given population, will be proportional to q, the fraction of the time that the wind lies in the mirror image direction divided by the fraction

of the time that the wind lies in the correct direction (during the period when immature warblers initiate their fall migration). (c) The number of mirror image vagrants that will occur each year will also be proportional to the value of q for that year. (d) The arrival of mirror image vagrant individuals will occur in rather well defined waves that will be associated with winds lying in the mirror image direction.

19. Mirror image misorientation is probably not unique to wood warblers but is likely to be a potential characteristic of all birds that utilize a distance-and-direction migration system. In addition, it could be responsible for the establishment of the isolated Pacific Coast winter ranges that are characteristic of several species of birds including both Myrtle and Townsend's Warblers.

PART V

REFERENCE MATTER

CHAPTER 16

BIBLIOGRAPHY

Aagaard, J.S., and A. Wolfson. 1962. Transistor equipment for continuous recordings of oriented migratory behavior in birds. IRE Trans. Bio-Med. Electron, 9:204-208.

Able, K.W. 1972. The changing seasons. American Birds, 26:25-30.

American Ornithologists' Union. 1957. Check-list of North American Birds. Fifth Edition. Lord Baltimore Press, Inc. Baltimore, Maryland.

Anderson, R., and P. Bauer. 1968. A Guide to Finding Birds in the St. Louis Area. Western Groves Nature Study Society. St. Louis, Mo.

Austin, G.T. 1971. On the occurrence of eastern wood warblers in western North America. Condor, 73:455-462.

Austin, O.L., Jr. 1961. Birds of the World. Golden Press, Inc. New York.

Bagg, A.M. 1970. The changing seasons. Audubon Field Notes, 24:4-13.

Bagg, A.M. 1971. The changing seasons. American Birds, 25:16-23.

Baird, J., A.M. Bagg, I.C.T. Nisbet, and C.S. Robbins. 1959. Operation recovery--report on mist-netting along the Atlantic coast in 1958. Bird Banding, 30:143-171.

Baird, J., and I.C.T. Nisbet. 1960. Northward fall migration on the Atlantic Coast and its relation to offshore drift. Auk, 77:119-149.

Batschelet, E. 1965. Statistical Methods for the Analysis of Problems in Animal Orientation and Certain Biological Rhythms. American Institute of Biological Sciences. Washington, D.C.

Batschelet, E. 1972. Recent statistical methods for orientation data. Animal Orientation and Navigation. NASA, SP-262:61-91.

Bellrose, F.C. 1958. The orientation of displaced waterfowl in migration. Wilson Bulletin, 70:20-40.

Bellrose, F.C. 1972. Possible steps in the evolutionary development of bird navigation. Animal Orientation and Navigation. NASA, SP-262:223-257.

Bent, A.C. 1953. Life Histories of North American Wood Warblers. U.S. Nat. Mus. Bull. 203. Washington, D.C.

Binford, L.C. 1971. Northern and Louisiana Waterthrushes in California. Calif. Birds, 2:77-92.

Bond, J. 1961. Birds of the West Indies. Houghton Mifflin Co. Boston, Mass.

Borror, D.T. 1948. Analysis of repeat records of banded White-throated Sparrows. Ecol. Monogr., 18:411-430.

Chandik, T., and A. Baldridge. 1968. Fall migration: middle Pacific coast region. Audubon Field Notes, 22:83-88.

Chandik, T., and A. Baldridge. 1969. Fall migration: middle Pacific Coast region. Audubon Field Notes, 23:99-106.

Chandik, T., D. DeSante, and E.A. Pugh. 1971. Fall migration: middle Pacific coast region. American Birds, 25:100-106.

Chapman, F.M. 1917. The Warblers of North America. D. Appleton and Co. New York.

Chase, T. Jr., and P. DeBenedictis. 1965. Fall migration: middle Pacific coast region. Audubon Field Notes, 19:71-76.

Clench, M.H. 1969. Additional observations of the fall migration of adult and immature Least Flycatchers. Bird Banding, 40:238-242.

Corballis, M.C., and I.L. Beale. 1971. On telling left from right. Scientific American, 224:3:96-104.

DeBenedictis, P. 1971. Wood warblers and vireos in California: the nature of the accidental. Calif. Birds, 2:111-128.

DeSante, D. (MS). The fall migration of birds at the southern tip of Baja California.

DeSante, D., R. LeValley, and R. Stallcup. 1972. Fall migration: middle Pacific coast region. American Birds, 26:112-118.

DeSante, D., and V. Remsen. 1973. Fall migration: middle Pacific coast region. American Birds, 27:110-119.

DeWolfe, B.B., G.C. West, and L.J. Peyton. 1973. The spring migration of Gambel's Sparrows through southern Yukon Territory. Condor, 75:43-59.

Dolnik, V.R., and M.E. Shumakov. 1967. Testing the navigational abilities of birds. Bionica, (1967):500-507 (in Russian).

Dorst, J. 1962. The Migration of Birds. Houghton Mifflin Co. Boston, Mass.

Drury, W.H., Jr., and J.A. Keith. 1962. Radar studies of songbird migration in coastal New England. Ibis, 104:449-489.

Eastwood, E. 1967. Radar Ornithology. Methuen. London.

Emlen, S.T. 1967a. Orientation of Zugunruhe in the Rose-breasted Grosbeak, Pheucticus ludovicianus. Condor, 69:203-205.

Emlen, S.T. 1967b. Migratory orientation in the Indigo Bunting, Passerina cyanea. Part I: Evidence for use of celestial cues. Auk, 84:309-342.

Emlen, S.T. 1967c. Migratory orientation in the Indigo Bunting, Passerina cyanea. Part II: Mechanism of celestial orientation. Auk, 84:463-489.

Emlen, S.T. 1969a. Bird migration: Influence of physiological state upon celestial orientation. Science, 165:716-718.

Emlen, S.T. 1969b. The development of migratory orientation in young Indigo Buntings. Living Bird, Eighth annual:113-126.

Emlen, S.T. 1970a. Celestial rotation: its importance in the development of migratory orientation. Science, 170(3963):1198-1201.

Emlen, S.T. 1970b. The influence of magnetic information on the orientation of the Indigo Bunting, Passerina cyanea. Anim. Behavior, 18(2):215-224.

Emlen, S.T. 1972. The ontogenetic development of orientation capabilities. Animal Orientation and Navigation. NASA, SP-262:191-210.

Emlen, S.T., and J.T. Emlen. 1966. A technique for recording migratory orientation of captive birds. Auk, 83:361-367.

Eriksson, K. 1970. Massive reverse migration of Redwings in spring 1959 in south Finland in relation to weather. Vogelwarte, 25:193-203.

Evans, P.R. 1968. Re-orientation of small passerine night migrants after displacement by the wind. British Birds, 61:281-303.

Farner, D.S., and L.R. Mewaldt. 1953. The recording of diurnal activity patterns in caged birds. Bird Banding, 24:55-65.

Fettis, H.E., and J.C. Caslin. 1969. Table of Modified Bessel Functions. Aerospace Research Laboratories.

Gauthreaux, S.A., Jr., and K.P. Able. 1970. Wind and direction of nocturnal songbird migration. Nature, 228(5270):476-477.

Griffin, D.R. 1969. The physiology and geophysics of bird navigation. Quat. Rev. Biol., 44:255-276.

Grinnell, J. 1922. The role of the "accidental". Auk, 39:373-380.

Grinnell, J., and A.H. Miller. 1944. The Distribution of the Birds of California. Pacific Coast Avifauna, No. 27. Berkeley, Calif.

Griscom, L., A. Sprunt, Jr., et al. 1957. The Warblers of North America. Devin-Adair Co. New York.

Gwinner, E.G. 1972. Endogenous timing factors in bird migration. Animal Orientation and Navigation. NASA, SP-262:321-338.

Hailman, J.P. 1961. An enigmatic northward migratory flight off North Carolina in September. Auk, 78:431-433.

Hamilton, W.J. 1962a. Bobolink migratory pathways and their experimental analysis under night skies. Auk, 79:208-233.

Hamilton, W.J. 1962b. Celestial orientation in juvenile waterfowl. Condor, 64:19-33.

Hubbard, J.P. 1969. The relationship and evoluation of the Dendroica coronata complex. Auk, 86:393-432.

Hubbard, J.P. 1970. Geographic variation in the Dendroica coronata complex. Wilson Bulletin, 82:355-369.

Keeton, W.T. 1971. Magnets interfere with pigeon homing. Proc. Nat. Acad. Sci., 68:102-106.

Keeton, W.T. 1972. Effect of magnets on pigeon homing. Animal Orientation and Navigation. NASA, SP-262:579-594.

Kramer, G. 1949. Über Richtungstendenzen bei der nächtlichen Zugunruhe gekäfigter Vögel. In Ornithologie als Biologische Wissenschaft. Heidelberg.

Leberman, R.C., and M.H. Clench. 1969. Bird banding at Powdermill, 1968. Powdermill Nat. Reserve Report, No. 23.

Lincoln, F.C. 1950. Migration of Birds. U.S. Dept Int., Fish and Wildlife Service, Circular 16. Washington, D.C.

Lowery, G.H. 1945. Trans-gulf migration of birds and the coastal hiatus. Wilson Bulletin, 57:92-121.

Lowery, G.H., Jr. 1960. Summary of seasonal occurrences of Louisiana birds. Louisiana Birds. Louisiana State University Press. Baton Rouge, La.

Lowery, G.H., Jr., and R.J. Newman. 1966. A continent wide view of bird migration on four nights in October. Auk, 83:547-586.

Mans, M. 1963. Fall migration: middle Pacific coast region. Audubon Field Notes, 17:61-66.

Matthews, G.V.T. 1968. Bird Navigation. Second Edition. Cambridge University Press. Cambridge.

Mayr, E. 1946. History of the North American bird fauna. Wilson Bulletin, 58:3-41.

McCaskie, G. 1966. Fall migration: southern Pacific coast region. Audubon Field Notes, 20:90-93.

McCaskie, G. 1967. Fall migration: southern Pacific coast region. Audubon Field Notes, 21:76-80.

McCaskie, G. 1968. Fall migration: southern Pacific coast region. Audubon Field Notes, 22:88-92.

McCaskie, G. 1969. Fall migration: southern Pacific coast region. Audubon Field Notes, 23:106-112.

McCaskie, G. 1970a. Fall migration: southern Pacific coast region. Audubon Field Notes, 24:96-100d.

McCaskie, G. 1970b. The American Redstart in California. California Birds, 1:41-46.

McCaskie, G. 1970c. The Blackpoll Warbler in California. Calif. Birds, 1:95-104.

McCaskie, G. 1972. Fall migration: southern Pacific coast region. American Birds, 26:118-124.

McCaskie, G., and P. DeBenedictis. 1966. Birds of Northern California: Annotated Field List. Golden Gate Audubon Society. Berkeley, Calif.

McCaskie, G., and E. Pugh. 1965. Fall migration: southern Pacific coast region. Audubon Field Notes, 19:76-82.

Mengel, Robert M. 1964. The probable history of species formation in some northern wood warblers (Parulidae). Living Bird, Third annual:9-43.

Merkel, F.W., and H.G. Fromme. 1958. Untersuchungen über das Orientierungsvermögen nächtlich ziehender Rotkehlchen (Erithacus rubecula). Naturwiss, 45:499-500.

Mewaldt, L.R., M.L. Morton, and I.L. Brown. 1964. Orientation of migratory restlessness in Zonotrichia. Condor, 66:377-417.

Mewaldt, L.R., and R.G. Rose. 1960. Orientation of migratory restlessness in the White-crowned Sparrow. Science, 131:105-106.

Moses, L.E., and D. DeSante. (MS). Statistical inference concerning a class of models for the directional behavior of vagrant migratory birds observed in orientation cages.

Murray, B.G., Jr. 1965. On the autumn migration of the Blackpoll Warbler. Wilson Bulletin, 77:122-133.

Murray, B.G., Jr. 1966a. Migration of age and sex classes of passerines on the Atlantic Coast in autumn. Auk, 83:352-360.

Murray, B.G., Jr. 1966b. Blackpoll Warbler migration in Michigan. The Jack-pine Warbler, 44:23-29.

Nisbet, I.C.T. 1962. South-east rarities at Fair Isle. British Birds, 55:74-86.

Nisbet, I.C.T. 1970. Autumn migration of the Blackpoll Warbler: evidence for long flight provided by regional survey. Bird Banding, 41:207-240.

Nisbet, I.C.T., and W.H. Drury, Jr. 1968. Short term effects of weather on bird migration: a field study using multivariate statistics. Animal Behavior, 16:496-530.

Nisbet, I.C.T., W.H. Drury, Jr., and J. Baird. 1963. Weight loss during migration. Bird Banding, 34:107-159.

Odum, E.P., C.E. Connell, and H.L. Stoddard. 1961. Flight energy and estimated flight range of some migratory birds. Auk, 78:515-527.

Paxton, R.O. 1965. The changing seasons: fall migration, 1964. Audubon Field Notes, 19:4-7.

Paxton, R.O. 1967. Oasis for migrants on outer Point Reyes, 1963-66. Point Reyes Bird Observatory Newsletter, 8:24-26.

Perdeck, A.C. 1958. Two types of orientation in migratory starlings Sturnus vulgaris L. and chaffinches Fringilla coelebs L., as revelaed by displacement experiments. Ardea, 46:1-37.

Perdeck, A.C. 1967. Orientation of Starlings after displacement to Spain. Ardea, 55:194-202.

Peters, J.L. 1968. Check-list of the Birds of the World. Museum of Comparative Zoology. Cambridge, Mass.

Phillips, A.R., M.A. Howe, and W.E. Lanyon. 1966. Identification of the flycatchers of eastern North America, with special emphasis on the genus Empidonax. Bird Banding, 37:153-171.

Pulich, W.M., and A.R. Phillips. 1953. A possible desert flight line of the American Redstart. Condor, 55:99-100.

Pyle, R.L. 1961. Birds of Southern California: Annotated Field List. Revised by A. Small. Los Angeles Audubon Society. Los Angeles, Calif.

Rabøl, J. 1969a. Reversed migration as the cause of westward vagrancy by four Phylloscopus warblers. British Birds, 62:89-92.

Rabøl, J. 1969b. Orientation of autumn migrating Garden Warblers (Sylvia borin) after displacement from western Denmark (Blävand) to eastern Sweden (Ottenby). A preliminary experiment. Dansk Orn. Forenings Tidsskr., 63:93-104.

Rabøl, J. 1970. Displacement and phaseshift experiments with night-migrating passerines. Ornis. Scand., 1:27-43.

Ralph, C.J. 1968. Migrants on the Farallon Islands, 1853-1967 (with special emphasis on warblers). Point Reyes Bird Observatory Newsletter, 9:2-7.

Ralph, C.J. 1971. An age differential of migrants in coastal California. Condor, 73:243-246.

Rao, J.S. 1969. Some contributions to the analysis of circular data. PhD dissertation. Indian Statistical Institute. Calcutta.

Richardson, W.J. 1970. Temporal variations in the volume of bird migration: a radar study in Canada. Proc. World Conf. on Bird Hazards to Aircrafts. Kingston, Ont. :325-334.

Richardson, W.J. 1971. Spring migration and weather in eastern Canada: a radar study. American Birds, 25:684-690.

Richardson, W.J. 1972. Autumn migration and weather in eastern Canada: a radar survey. American Birds, 26:10-17.

Robbins, C., D. Bridge, and R. Feller. 1959. Relative abundance of adult male redstarts at an inland and a coastal locality during fall migration. Maryland Birdlife, 15:23-25.

Robbins, C.S., B. Brunn, and H.S. Zim. 1966. Birds of North America: A Guide to Field Identification. Golden Press. New York.

Root, R.B. 1962. Comments on the status of some western specimens of the American Redstart. Condor, 64:76-77.

Rüppell, W. 1944. Versuche über Heimfinden ziehender Nebelkrähen nach Verfrachtung. J. Orn., 92:106-133.

Sauer, E.G.F. 1963. Migration habits of Golden Plovers. Proc. XIII Intern. Ornithol. Congr. 454-467.

Sauer, F., and E. Sauer. 1960. Star navigation of nocturnal migrating birds. Cold Springs Harbor Symp. Quant. Biol., 25:463-473.

Schmidt-Koenig, K. 1972. New experiments on the effect of clock shifts on homing in pigeons. Animal Orientation and Navigation. NASA, SP-262:275-282.

Schwartz, P. 1963. Orientation experiments with Northern Waterthrushes wintering in Venezuela. Proc. XIII Intern. Ornithol. Congr. 481-484.

Small, A. 1963. Fall migration: southern Pacific coast region. Audubon Field Notes, 17:66-71.

Southern, W.E. 1969. Orientation behavior of Ring-billed Gull chicks and fledglings. Condor, 71:418-425.

Southern, W.E. 1972. Influence of disturbances in the earth's magnetic field on Ring-billed Gull orientation. Condor, 74:102-105.

Stack, J.W., and R.L. Harned. 1944. Seventeen years of banding White-throated Sparrows and Slate-colored Juncoes at Michigan State College. Bird Banding, 15:1-14.

Stevensen, H.M. 1957. The relative magnitude of the trans-gulf and circum-gulf spring migrations. Wilson Bulletin, 69:39-77.

Stewart, R.M. 1972. The reliability of aging some fall migrants by skull pneumatization. Bird Banding, 43:9-14.

Stewart, R.M., L.R. Mewaldt, and S. Kaiser. (In press). Age ratios of coastal and inland fall migrant passerines in central California. Bird Banding.

Taylor, W.K. 1972. Analysis of Ovenbirds killed in central Florida. Bird Banding, 43:15-19.

Wagner, G. 1972. Topography and pigeon orientation. Animal Orientation and Navigation. NASA, SP-262:259-273.

Walcott, C. 1972. The navigation of homing pigeons: Do they use sun navigation? Animal Orientation and Navigation. NASA, SP-262:283-292.

Wallraff, H.G. 1967. The present status of our knowledge about pigeon homing. Proc. XIV Intern. Ornithol. Congr., Oxford. 331-358.

West, G.C., and L.J. Peyton. 1972. The spring migration of the Tree Sparrow through southern Yukon Territory. Bird Banding, 43:241-256.

Wiltschko, W. 1972. The influence of magnetic total intensity and inclination on directions preferred by migrating European Robins (Erithacus rubecula). Animal Orientation and Navigation. NASA, SP-262:569-578.

Wolff, W.J. 1970. Goal orientation vs. one-direction orientation in Teal, Anas c. crecca, during autumn migration. Ardea, 58:131-141.

Wolfson, A. 1954. Weight and fat deposition in relation to spring migration in transient White-throated Sparrows. Auk, 71:413-434.

CHAPTER 17

APPENDICES

APPENDIX I

DATA USED FOR THE CALCULATION OF PREDICTED AVERAGE ARRIVAL DATES FOR EASTERN WOOD WARBLERS

	AVERAGE ARRIVAL DATE	DISTANCE FROM CENTER OF BREEDING RANGE	
SPECIES	AT ISLAND BEACH, NEW JERSEY*	TO ISLAND BEACH (miles)	TO MORRO BAY, CALIF. (miles)
Black-and-white	Sep. 8	825	1815
Prothonotary			1848
Worm-eating			2046
Golden-winged			2046
Blue-winged			1914
Tennessee	Sep.23	1518	1815
Parula			1947
Magnolia	Sep.18	990	1947
Cape May	Sep.22	1023	1881
Black-throated Blue	Sep.18	528	2277
Black-throated Green	Sep.25	1254	1980
Cerulean			1815
Blackburnian	Sep.19**	1188***	2244
Yellow-throated			1848
Chestnut-sided	Sep. 7	627	2079
Bay-breasted	Sep.21	924	1947
Blackpoll	Sep. 25	1683	1848
Pine			1881
Prairie			2046
Palm	Oct. 5	990	2013
Ovenbird	Sep.13	792	1815
Northern Waterthrush	Sep. 8	1551	1749
Louisiana Waterthrush			1881
Kentucky			1881
Connecticut	Sep.20	1353	1782
Mourning	Sep. 6	858	2079
Hooded			2013
Canada	Sep. 1	759	2178
American Redstart	Sep. 9**	1188***	1749

* From Murray [1966a]

** Average arrival date at Baton Rouge, Louisiana. From Lowery [1960]

*** Distance to Baton Rouge, Louisiana

APPENDIX II

ENVIRONMENTAL DATA FOR ALL NIGHTS ON WHICH CALIFORNIA CAPTURED BLACKPOLL WARBLERS WERE TESTED

					WIND			CLARITY
DATE	NIGHT NUMBER	LOCATION	STARTING TIME OF TEST (PDT)	% CLOUD COVER	DIRECTION (°)	VELOCITY (knots)	TEMP. (°F)	OF NIGHT**
Sep. 9, 1969	36	Stanford	2250	0	170	1	65	
Sep.10	37	"	2205	0	360	1	67	
Sep.12	38	"	2205	0	-	0	65	
Sep.14	39	"	2055	0	270	1	61	
Sep.15	40	"	2315	0	315	1	49	
Sep.17	41	"	2205	30				
Sep.23	42	"	2005	0	250	0	62	
Oct. 5	45	S.E. Farallon	2100	0	345	10		
Oct. 6	46	"	2020	0	330	9		
Oct. 7	47	"	2000	20	330	7		
Oct. 8	48	"	2230	20	320	12		
Oct. 9	49	"	2050	0	330	12		
Oct. 9(10)	50	"	0540	50	290	10		
Oct.10	51	"	2035	0	340	15		
Oct.11	52	"	2145	0	330	12		
Oct.11(12)	53	"	0530	0	330	12		
Sep.21, 1970	103	S.E. Farallon	2114	0	320	9		4
Sep.22	104	"	2108	0	330	10		4
Sep.23	105	"	2103	0	330	10		4
Sep.24	106	"	2140	0	350	11		3
Sep.25	107	"	2200	0	90	4		3
Sep.26	108	"	2105	0	360	10		3
Sep.27	109	"	2032	0	320	10		3
Sep.30	110	"	2016	0	330	12		1
Oct. 1	111	"	2027	0	320	12		2
Oct. 5	112	"	2217	5	310	9		3
Oct. 6	116	"	2153	0	330	26		4
Oct. 6	117	"	2140	0	330	26		4
Oct. 7	120	"	2343	0	350	11		3
Oct. 8(9)	124	"	0033	0	330	6		2
Oct. 8(9)	125	"	0022	0	330	6		2
Oct. 9(10)	127	"	0434	55	335	8		3
Oct.16	134	Stanford	2020	60	135	4		2
Oct.17	135	"	1942	50	135	3		1
Oct.18	136	"	1948	2	-	0		3
Oct.19	137	"	2022	5	160	2		2
Oct.22	138	"	1938	10	225	3		3
Oct.23	139	"	2053	10	270	5		3
Oct.26	140	Point Loma	1842*	0	325	7		3
Oct.27	141	"	1904*	20	315	1		3
Oct.28	142	"	2052*	0	270	3		4

APPENDIX II (CONT)

DATE	NIGHT NUMBER	LOCATION	STARTING TIME OF TEST (PDT)	% CLOUD COVER	WIND DIRECTION (°)	WIND VELOCITY (knots)	TEMP. (°F)	CLARITY OF NIGHT**
Oct.29, 1970	143	Point Loma	2002*	35	315	2		3
Oct.31	144	"	1857*	2	360	6		3
Nov. 1	145	"	2215*	35	290	2		3
Nov. 3	146	"	1938*	0	130	5		2
Nov. 4	147	"	2102*	0	-	0		3
Nov. 7(8)	148	"	0100*	20	80	4		3
Nov. 8(9)	149	"	0145*	0	90	5		3
Nov. 9(10)	150	"	0315*	15	90	1		4
Nov. 10(11)	151	"	0430*	25	-	0		4
Sep.21, 1971	186	S.E. Farallon	2038	50	100	6	63	3
Sep.22	187	"	2037	0	360	7	56	2
Sep.22	188	"	2213	0	360	7	55	2
Sep.23	189	"	2037	0	320	8	57	2
Sep.25	191	"	2143	0	340	15	56	4
Sep.26	193	"	2241	0	335	9	56	4
Sep.27	195	"	2345	0	320	10	56	3
Sep.28(29)	197	"	0241	0	320	8	55	3
Sep.29(30)	199	"	0237	50	340	14	54	3
Sep.30(Oct. 1)	201	"	0328	0	290	5	52	4
Oct. 1(2)	202	"	0431	0	340	9	53	3
Oct.10	203	"	2021	5	335	19	55	3
Oct.11	205	"	2308	0	335	9	53	1
Oct.12	207	"	2020	2	340	10	55	2
Oct.13	209	"	2018	0	340	16	55	3
Oct.15	211	"	2019	5	330	21	49	3
Oct.16	213	"	2018	5	270	4	47	2
Oct.17	215	"	2017	5	340	9	47	3
Oct.18	217	"	2014	5	245	4	47	3
Oct.20	219	"	2010	0	340	17	52	4
Oct.21	221	"	2010	0	330	9	51	4
Oct.23	223	"	2042	2	330	17	50	4
Oct.24	225	"	2142	0	330	11	49	3
Nov. 5	228	Stanford	1850*	0	200	1	51	1
Nov. 6	229	"	1856*	0	255	4	50	3
Nov. 7	230	"	1838*	2	250	4	45	4
Nov.13	231	"	1905*	2	305	12	44	3
Nov.14	232	"	1846*	0	270	6	41	4
Nov.15	233	"	1853*	0	340	13	51	4
Nov.16	234	"	1851*	0	270	2	44	4
Nov.17	235	"	1849*	20	250	5	49	2
Nov.18	236	"	1855*	0	260	9	49	4

* PST

** 4 = Very clear. 3 = Clear. 2 = Somewhat hazy. 1 = Hazy

APPENDIX III

DIGITIZED RAW DATA FOR ALL ORIENTATION TESTS ON ALL CALIFORNIA CAPTURED BLACKPOLL WARBLERS

LEGEND: Computer printout of card input

CHARACTERS	DEFINITION
1 - 4	Trace number
5 - 7	Bird number
8	Test period number
9 - 11	Test night number
12 - 16	AC (end of trace)
17 - 21	AN (loc. of north)
22 - 23	V_1
24 - 25	V_2
26 - 27	V_3
⋮	⋮
66 - 67	V_{23}
68 - 69	V_{24}

APPENDIX III (CONT)

```
//DAVE JOB 'S632,223,1.0,9',DAVE
/*  SERVICE  LIST
 220 211 36254.2  0.0 6 7 91011 9 9 91010 7 7 4 3 7 6 4 3 3 4 6 4 5 5
 221 211 37254.6  0.0 1 1 0 0 1 2 1 0 0 1 1 1 1 2 1 3 5 5 5 2 1 1 1 1
 222 211 38254.2  0.01010101010 9 8 9 9 6 7 6 8 5 3 2 1 2 2 2 3 5 9 910
 223 211 39253.9  0.0131312121111121211111213131212111211111112121313
 224 211 40254.2127.1 1 1 2 2 4 4 5 3 2 4 5 6 910 9 9 7 6 3 2 2 2 3 2
 225 211 41254.2  0.0 1 2 1 1 3 5 5 6 8 9 9 7 4 5 4 2 1 2 1 1 1 2 2 2
 226 211 42255.1  0.0121313121314131711111110 9 8 9 8 910111212121313
 227 221 45255.7  0.0 3 4 5 6 8 9 7 5 3 3 3 2 2 3 4 6 7 4 6 9 9 9 7 6
 228 231 46255.1  0.0 6 2 0 0 0 0 1 2 1 1 1 1 0 0 1 2 2 2 7 8 7 4 2 4
 229 231 47254.8  0.01415131516131110111112111010 9 8 6 7 7 6 91113
 230 221 48255.0  0.0 3 2 1 1 1 2 1 1 0 0 0 1 1 3 3 3 3 2 1 0 0 1 1 1
 231 231 49255.1  0.0 6 5 7 7 8 6 6 7 8 9 6 6 7 6 5 3 6 6 5 5 6 6 6 5
 233 231 51253.8  0.0 5 5 5 6 6 7 7 9 8 7 6 5 4 2 2 3 2 2 1 1 1 0 3 5
 234 231 52256.0  0.0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
 232 232 50254.7  0.0121414161512 9 8 8 5 5 6 9 7 5 6 6 6 6 7 7 6 9 9
 235 233 53251.1  0.010 910 9 9 7 7 6 5 3 4 5 4 3 2 3 2 3 3 3 4 5 910
 236 241103255.7169.615161514141718202019171311 8 910 9 9111415141516
 237 241104254.9  0.0 4 7 9111314131414131310 9 6 6 5 5 4 4 4 3 3 3 3
 238 241105255.5  0.0 4 5 5 7 9 91010111010 9 6 8 5 5 4 5 4 2 1 0 0 0
 239 241106255.7168.8 4 6 7101415171819161310 6 4 1 2 1 1 3 2 3 3 4 5
 240 241107256.3 86.0 6 5 4 7 8 9 9 8 9 91010131211 9 8 7 7 6 8 9 8 7
 241 241108254.5  0.0 7 7 6 6 6 6 5 5 4 4 2 1 2 4 6 7 9 7 7 8 6 7 8 7
 242 241109255.2 98.0 7 7 8 9 7 7 6 4 2 2 2 1 3 2 2 2 2 2 5 6 7 7 8 8
 243 241110255.4  0.0 1 3 3 3 2 3 910131414131211 9 7 5 1 2 1 1 0 0 0
 244 241111255.6163.4141310 7 6 4 3 2 1 1 1 1 0 0 1 3 4 6 91012131414
 245 242112255.0  0.01817141516141413111010 9 8 7 9 810 9 9 912141617
 246 242117255.7 95.1121112 9 9 8 8 7 5 3 3 2 2 3 2 1 2 3 3 5 7 81010
 247 242120255.7164.3 5 5 7 7 8 7 7 5 2 4 5 3 2 4 4 3 3 5 8111211 9 6
 248 242125255.2  0.0 5 6 5 3 3 4 6 3 1 0 2 2 812131414121110 8 4 3 4
 249 242127255.5  0.0 1 1 1 1 0 0 3 7 6 6 5 4 8 9 8 9 9 7 5 4 1 0 0 0
 250 243134255.3 12.810 7 6 4 5 5 2 4 6 6 6 5 7 7 8 8 912131315171413
 251 243135255.2105.6 8 7 6 4 710 911121110 9 9 8 6 7 5 5 5 4 2 3 4 6
 252 243136255.2  0.0 5 5 2 6 6 7 2 3 5 4 3 6 6 8 9 810 9 8 7 6 6 6 5
 253 243137255.1165.8 6 7 5 3 4 5 7 6 6 5 4 5 4 6 6 6 6 7 9 8 7 5 5 5
 254 243138255.0 51.0 6 4 6 7 5 3 4 5 4 7 6 6 5 7 8 91010 8 8 6 8 6 6
 255 243139255.2  0.0 0 2 2 2 2 7 8 6 6 7 6 6 5 5 2 1 1 1 0 1 0 0 1 1
 256 244140255.1  0.010 7 5 5 8 7 8 6 6 9 910 8 6 3 3 4 4 0 0 0 0 2 8
 257 244141255.0175.0 8 4 2 0 1 0 4 3 0 0 0 0 0 0 1 1 4 6 6 810 9 8 8
 258 244142255.6100.3 1 1 2 3 2 1 2 1 4 5 3 4 7 8 9 9 8 6 2 5 5 6 5 2
 259 244143255.7  0.0 8 7 8 7 7 7 9 8 7 8 6 6 5 3 1 4 1 1 2 2 3 5 6 9
 260 244145256.3154.9 3 2 2 7 5 3 5 4 7 5 2 0 0 0 0 3 5 1 1 2 1 1 1 1
 261 244146255.5  0.0 6 9 7 8 7 7 7 6 4 2 3 0 1 1 0 1 0 0 1 2 2 4 4 5
 262 244147255.2 93.4 0 0 0 2 2 1 1 0 0 1 2 3 4 4 6 8 2 2 4 2 3 7 1 1
 263 244148255.6166.3 2 4 6101611 9 8 6 3 1 1 0 0 0 0 2 2 0 0 1 3 5 3
 264 251111254.6163.7151514131210 7 6 5 5 4 3 2 1 3 8 7 7 71011121314
 265 252112255.2  0.0 4 3 4 3 4 4 5 5 8 9 9 8 7 6 6 6 5 5 5 4 4 4 2 4
 266 252117255.0 95.4161310 8 6 4 3 4 5 6 8 9 8 7 5 4 2 4 5 5 5 71314
 267 252120254.7160.2 5 6 4 2 3 2 1 2 2 1 1 1 0 1 2 2 2 2 4 8 9 7 6 5
 268 252125254.8  0.0 4 2 2 2 2 3 2 2 1 5 812131310 8 6 7 6 8 8 5 4 4
 269 252127255.3  0.0 8 9 8 8 7 7 6 2 1 5 4 6 8 910 9 8 8 7 6 6 5 5 6
 270 253134255.1 12.8 1 5 2 2 4 4 7 8 6 5 5 4 5 4 1 2 1 1 0 0 1 1 1 1
 271 253135255.6105.6 7 0 0 0 1 2 3 2 1 0 0 0 0 0 0 0 0 0 0 0 0 0 2 6
 272 253136255.4  0.0 1 2 3 4 2 2 2 2 1 5 8 6 1 0 0 0 0 0 0 0 0 0 0 0
 273 253137255.6167.5 6 7 4 2 4 3 1 1 0 1 0 0 1 2 2 1 3 4 4 7 7 7 7 8
 274 253138254.9 90.5 0 0 0 0 0 0 0 0 0 0 1 5 5 4 61011121112 8 5 3 2
 275 253139255.2  0.0 0 0 0 0 0 0 1 1 5 9 4 1 1 1 0 0 0 0 0 0 0 0 0 0
 276 254140255.2  0.0 6 7 6 7 9 8 8 91010 9 9 8 6 3 3 3 2 5 6 910 9 6
 277 254141255.1177.9 5 6 3 1 1 5 7 3 0 0 0 0 1 3 2 0 0 0 0 0 0 3 2 1
```

APPENDIX III (CONT)

```
278 254142254.9 99.9 0 0 0 0 0 0 0 0 0 0 0 0 0 2 2 2 3 1 0 0 0 0 0 0
279 254143255.5  0.0 8 6 6 7 91010 7 91110 8 8 9 7 6 4 3 3 3 6 6 810
280 254144256.6 91.0 6 6 2 3 2 0 0 0 0 1 5 3 2 2 1 0 0 0 0 0 0 0 0 0
281 254145256.1156.0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 2 1
282 254146256.0  0.0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
283 254147255.8 93.8 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 3 2 0 0 0 0 0 0 0
284 254148255.8166.3 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 2 2 1
285 261112255.5  0.01310 9 8 910111010111213141515141413121112101213
286 261116255.7 90.0121516202223242424242323232222212019181614141312
287 261120255.3158.31515121211 9111010121416171920212324252524222018
288 261124255.2  0.0232122212020201918171615151514141518192123242423
289 261127255.7  0.0232120192020212020201916141312111012151719202223
290 262134254.9 12.8 4 3 2 2 1 0 1 0 0 0 0 0 0 0 1 1 2 4 3 4 4 3 4 4
291 262135255.7104.8151213121211101211121110 9 8 7 8 910 9 8 6 8 912
292 262136255.0  0.0 6 7 9 81012 8 8101110 8 9 7 9 8 6 6 6 7 7 8 8 6
293 262137255.1168.71513121010 7 7 8 9 91111162019201918181715171816
294 262138255.3 89.8 8 9 7 81016192021222423181615131210 9 7 5 3 5 8
295 262139255.0  0.0 0 3 9 5 1 0 0 0 0 2 3 2 5 810 6 6 6 7 7 6 2 2 1
296 263140255.1  0.02324252728272623211913 9 8 7 6 3 7 7 8 910131822
297 263141255.2175.3201613 9 8 8 9 9 7 3 5 6 6 812131112152022202120
298 263142255.7 99.1 6 910 9 8 6 3 3 7 6 7 8111516161312 8 7 7 8 9 6
299 263143255.5  0.0 5 9111115191820191612 9 9 6 3 3 2 3 2 1 0 0 1 3
300 263144255.4 90.0 6 2 2 2 3 6 7 7 7 81314 6 6131413121314 8 8 6 7
301 263145255.3155.612111312 7 4 5 6 6 6 7 911121317161617151115171 5
302 263146255.1  0.0 2 2 2 6 9111213121213131414141310 5 4 4 3 6 9 5
303 263147254.9 94.01511 9 8 5 6 5 5 5 4 4 7 610 910121111141518201 9
304 263148255.2166.1 6 5 6 8 810181922211817181510 7 5 4 2 1 3 5 6 7
305 263149255.1  0.0 5 5 2 2 3 4 2 2 4 6 4 6 4 5 5 6 5 5 8 8 910 9 7
306 263150254.8 80.8 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 2 0 0 0 0 0 1
307 264151255.7  0.0 0 0 1 1 1 0 0 0 0 0 0 0 0 0 1 2 1 1 1 0 0 0 0 0
310 271112255.7  0.0 9 5 4 3 2 1 1 1 2 2 5 9 9 7 8 8 6 3 2 4 5 8 9 9
311 271116255.7 91.2 9 91010 9 7 7 6 7 3 4 2 2 2 3 4 6 7 3 3 3 2 5 7
312 271120255.2157.2 7 5 5 9 8 6 6 7 8 8 8 7 8 8 6 5 6 7 7 4 4 3 3 4
313 271124255.3  0.0 9 8 7 8 6 5 5 8 9 8 7 6 6 6 9101010 91012131311
314 271127255.1  0.010 9 8 7 9101111 9 8 7 7 6 6 6 7 7 7 7 8 8 9 9 9
315 272134255.4 12.8 8 7 5 5 4 5 7 7 6 4 5 5 911121111131212121110 8
316 272135254.7105.3 2 5 2 3 6 3 2 3 3 2 0 0 0 1 1 1 2 2 2 1 0 1 2 4
317 272136255.0  0.0 4 6 5 7 8 9 8 2 5 4 5 7 6 8 9 7 6 5 5 3 2 2 4 2
318 272137255.1165.0 1 1 1 2 2 3 2 1 2 3 1 0 0 0 0 0 0 0 0 0 0 2 2 2
319 272138254.6 91.6 3 6 6 6 6 6 5 5 7 9 9 8 5 1 6 6 6 6 3 4 4 6 3 3
320 272139256.0  0.0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
321 273140255.3  0.0 3 1 0 1 1 1 3 7 6 4 2 5 2 1 1 1 1 2 5 6 6 2 1 2
322 273141255.1176.0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 2 2 1 1 1
323 273142255.6103.3 1 2 3 2 5 5 5 2 3 3 1 1 0 0 1 1 2 1 2 3 3 3 3 1
324 273143258.0  0.0 1 2 1 0 1 3 1 2 2 2 1 2 4 6 6 6 6 4 5 6 3 1 1 1
325 273144255.8 91.8 9 9 8 7 6 8 7 4 3 4 2 2 3 4 5 3 6 5 5 6 6 7 7 9
326 273145255.5156.7 2 1 1 1 0 0 1 1 1 1 1 1 1 2 5 9 91110 6 5 7 6 2
327 273146255.6  0.0 1 1 2 4 4 2 2 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1
328 281112255.3  0.01414 9 8 7 6 8 910131215161716161715141415131214
329 281116255.5 90.6151720191718171616171613121112111213131312141517
330 281120254.7156.0 6 5 7 8 8 7 8 9 8 5 5 7 7 9 910 911 9 6 5 5 4 4
331 281124255.8  0.0181919171614141311 11 9 9 7 6 8 7 7 7 91314151617
332 281127255.1  0.0 4 3 5 5 2 1 2 2 1 0 0 0 0 0 1 2 3 4 4 3 5 7 7 7
333 282134254.7 12.7 7 5 3 1 0 0 0 0 0 2 0 1 2 3 4 811111212151613 10
334 282135254.4106.0 7 2 0 1 2 2 1 2 3 3 3 2 3 6 5 5 4 5 6 7 5 2 2 3
335 282136255.0  0.0 0 0 0 2 6 6 3 3 7 6 4 2 2 0 0 0 0 0 0 0 0 0 1 0
336 282137255.1161.8 1 1 2 2 2 5 6 6 5 0 3 3 0 0 0 0 0 0 0 0 0 0 1 1
337 282138255.4 90.7 5 6 811 9 7 4 5 7 6 6 7 6 7 6 5 6 5 3 2 2 3 4 5
338 282139255.1  0.0 4 4 7 4 1 0 0 0 0 2 2 0 0 0 0 0 0 0 0 0 0 0 3 2
339 283140254.7  0.0 0 0 1 0 0 1 1 0 0 0 0 1 4 4 6 3 1 2 4 2 0 0 0 0
```

APPENDIX III (CONT)

```
340 283141256.0174.8 0 0 0 0 0 0 0 0 0 0 0 0 0 1 3 6 910 8 4 1 3 2 1
341 283142256.8101.8 0 0 0 0 0 0 0 0 0 0 1 2 1 4 5 6 7 6 3 1 1 0 0 0
342 283143257.6  0.0 1 3 611 9 6 8 4 3 2 1 0 0 0 0 0 0 0 0 0 0 0 1 1
343 283144255.5 93.1 3 0 0 0 0 0 0 0 0 3 2 1 0 0 0 0 0 2 1 0 2 6 7 3
344 283145255.9156.9 1 0 1 2 5 2 0 0 0 1 0 0 0 1 2 1 3 3 1 1 1 0 0 0
345 283146255.6  0.0 5 6 6 5 4 3 3 2 2 3 3 1 3 8 9 9 6 5 3 2 2 1 3 5
346 283147254.9 94.4 0 0 0 0 0 0 2 2 1 2 4 3 2 1 1 2 5 7 8 5 4 2 0 0
347 283148255.7166.5 5 911121211131415121313121110 9 9 9 8 6 5 6 8 8
348 291134255.4 12.81516181918171210 8 4 4 5 7 913141718191713111010
349 291135255.1105.0 6 5 2 1 1 1 2 1 3 5 6 3 7 912111113151413 9 6 7
350 291136255.2  0.0 8 2 2 6 9 8 910 9 8 6 6 6 6 5 5 7 91012 8 91412
351 291137255.4167.51110 911 9 9 8 7 5 5 7 7 9 8 8 6 6 6 7 7 9101113
352 291138255.2 91.4 2 2 5 4 5 6 7 9 6 8 7 5 4 4 3 2 2 2 2 2 2 2 3 4
353 291139255.7  0.0 5 7 910 8 6 7 9 9 8 7 6 7 7 6 5 3 0 0 0 0 2 2 1
354 292140255.3  0.0161716151619141110121113111213151414131515141615
355 292141255.9178.1 3 1 0 0 1 0 0 0 0 0 41110121211 9 7 2 2 6 6 4 3
356 292142254.1 98.1 3 9 6 6 2 2 4 7 8 8 9 910121412 9 8 6 8 7 6 2 1
357 292143254.4  0.0 5 913131716151411 9 7 7 8 7 6 6 6 6 5 7 8 7 6 5
358 292144255.2 91.3 1 1 2 3 4 4 6 7 6 711141517191410 5 1 1 0 0 0 0
359 292145255.7157.1 5 6 2 3 3 5 6 7 8 9 811 9 6 6 6 6 5 3 3 2 4 4 5
360 292146255.6  0.0 2 0 0 1 1 1 0 1 0 1 2 3 5 9101216181819201917 9
361 292147255.0 93.4 7 8 5 2 3 2 1 0 1 7 8 9 8 7 9 9 8 7 9 8 5 6 6 4
362 292148255.7166.4141413101015181719191715131210 8 6 3 1 2 2 2 712
363 301141255.8174.2121110 6 4 2 1 1 1 2 2 3 5 9 910 9 9 9 8 9101012
364 301142256.7100.4 4 5 8 3 9 7 7 7 8 9 9101113151312 9 8 8 8 8 5 3
365 301143256.0  0.01213121110 9101211121313131415151514131314131213
366 301144255.8 90.4 7 8 8 8 3 6 7 8 9 910121111131214131210 9 8 8 6
367 301145256.2154.51115171614111214 9 8 9 8 7 6 8121110 7 7 91010 9
368 301146255.8  0.0 6 7 5 6 5 6 6 5 6 9 9 7 91316171514131211 6 4 4
369 301147255.0 93.31310 9 8 7 8 6 5 3 5 6 4 3 1 1 3 4 7 810 9 91012
370 301148255.4167.1 8 6 5 6 5 4 3 5 3 0 1 1 1 0 0 0 2 3 4 5 6 6 8 8
371 301149255.1  0.0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 2 3 1 0 0 0
372 311187256.7  0.0 1 2 1 0 0 2 3 6 4 4 3 2 2 1 2 2 1 2 3 3 4 3 1 0
373 311189256.8 93.9 1 2 2 1 2 0 0 1 1 3 3 2 2 1 1 1 2 1 1 0 0 1 1 2
374 311191256.9156.6 0 0 1 3 5 4 3 5 6 5 6 7 5 2 0 1 0 0 0 0 0 0 0 0
375 311193256.7  0.0 0 0 0 0 0 0 0 2 2 1 1 0 0 0 0 1 2 6 6 7 7 6 4 2
376 311195256.3 87.0 0 0 0 0 0 0 0 0 1 0 2 2 2 3 3 3 2 2 1 1 0 1 0 0
377 311197256.6158.1 4 4 3 3 3 4 4 5 5 6 6 6 7 4 2 0 0 1 3 2 2 1 2 2
378 311199255.9  0.0 0 1 2 2 4 5 3 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0
379 311201256.0100.9 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 2 1 2 3
380 311202256.2161.1 2 2 3 4 3 3 4 3 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 2
381 312203256.8  0.0 91010 9101112111312111211131415171816151310 910
382 312205256.0  0.0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
383 312207256.6164.71010 9 8 3 8 9 9 910 9111010101111121212121211
384 312209256.7  0.0 8 7 8 8 7 9 9 910 9111011121416171715131210 9 6
385 312211255.3 68.11415151615131110 9 7 7 7 8 7 8 7 7 8 8 8 9 81012
386 312213255.0155.51210 911121414141414141313 12 9 8 9 8 8 7 9 8 910
387 312215256.0  0.0 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
388 312217255.1 85.91510 9 9 910 9 9 8 9 7 9 9 810101012111211131514
389 312219255.7157.0141415151617161515161513141310 7 5 5 4 6 8101113
390 312221255.8  0.010 910111112131213131415161718191918171615141412
391 312223256.5 93.31615181917131 0 9 7 7 9 9 8 910121010 9 9 9101012
392 312225256.3161.9 2 2 1 2 2 910131214131210 6 2 1 1 1 3 4 6 6 3 2
393 313228257.0165.6 6 7 8 9 91010 8101110 7 4 2 3 5 4 7 6 7 8 8 6 5
394 313229256.2101.811 9 910101010 8 6 2 2 6 8 8 7 7101212111111111111
395 313230256.2  0.0 8 9 9 91010111212121312131313131312111010 9 9 7
396 321186256.4  0.0 6 7 8 8 7 8 6 6 7 8 91010 9 910 9 7 6 7 7 7 6 6
397 322187256.3  0.0 4 3 4 6 6 5 5 3 5 7 8 7 5 4 8 9 6 3 3 3 4 2 2 1
398 322189256.5 93.9 6 6 5 3 2 1 1 2 2 4 7 5 3 7 4 2 4 3 4 3 3 2 2 4
399 322191256.9156.4 9 6 6 5 5 5 5 810 8 8 7 8 7 6 5101113121010 9 9
```

APPENDIX III (CONT)

```
400 322193256.5   0.0 9 91110111110 9 8 8 9 910111010 9 8 7 7 7 7 910
401 322195256.5 86.2 6 5 5 5 3 2 2 3 6 4 3 3 5 5 6 2 2 2 4 4 4 4 4 6
402 322197256.6158.9 9 9 8 4 5 5 4 2 3 3 2 3 5 5 6 912121314141310 9
403 322199256.4   0.0 1 1 1 1 1 2 2 4 7 8 7 4 3 2 2 3 3 1 2 1 0 0 0 0
404 322201255.5 97.311 9 8 7 3 9 91011111214151412131415161513121110
405 322202256.2159.8 5 2 1 1 1 1 1 1 1 0 0 1 1 1 1 2 3 3 4 4 2 4 3 6
406 323203256.7   0.0 6 7 9121419222322201511 7 6 4 2 2 2 3 2 3 6 5 7
407 322205256.5 83.2 7 9 8 7 6 7 8111419202124262725252422191310 8 6
408 323207256.3162.910 9 7 7 7 6 7 8 7 91110 91010101110111213141513
409 323209256.6   0.017132021212013161412 8 8 7 6 5 8 9 9101212131416
410 323211255.1 87.2 5 3 4 3 5 6 8 910111214161716161310 9 7 6 5 4 3
411 323213254.0156.1151314131213141515151517181920202121222323221917
412 323215256.3   0.0121417202224252422191712 9 7 6 4 7 7 6 4 3 6 710
413 323217254.7 84.8171718181921202223242526252423212219181716161516
414 323219255.7157.01614 9 6 3 2 1 2 0 0 1 3 71216192324252526272422
415 323221255.9   0.0162024262329292927252015 11 9 6 3 2 1 1 1 2 3 6 9
416 323223255.9 92.8 9 6 4 2 2 2 1 2 3 7 6 9141824252726241916141211
417 323225256.1160.4262524232110181715141 2 9101013151718202324252627
418 324228256.2164.811 8 910 9 9101110 9 911121111101110131212131413
419 324229256.3160.9 2 3 1 71114192'23232019171516141 1 9 6 4 3 4 4 3
420 324230255.5   0.016171614151617181714 9 4 2 2 4 3 5 4 1 1 2 71013
421 324231256.8159.0 5 7 3 7 5 3 7 6 5 6 5 3 2 2 1 2 2 3 4 5 5 3 2 1
422 324232257.0165.5 7 9 9 9 91110111211121111111010 910 9 8 7 7 7 6
423 324233257.0   0.0 6 5 4 6 6 7 813192324242320161513 10 9 8 6 4 5 5
424 324234257.1157.8 5 4 5 4 7 8 7 6 6 6 7 8 8 8 8 9 9 9 9 9 8 9 7 6
425 324235256.9 96.9 7 4 5 3 5 5 5 6 6 6 6 6 6 3 6 6 6 4 4 5 5 7 7 6
426 324236256.9   0.011 9 9 910 9 8 8 7 7 9 9 91011101010111011121111
427 331186256.5   0.0 4 5 5 5 6 5 4 3 4 1 1 4 5 6 1 1 1 2 6 7 8 8 8 8
428 332187256.6   0.0 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 2 0 0 2 5 4
429 332189256.5 96.2 0 1 0 1 0 0 0 1 0 0 0 0 0 1 2 3 2 2 4 3 1 1 0 0
430 332191257.0156.0 8 6 6 4 6 9 910 8 9 9 8 6 5 2 2 2 1 1 1 2 2 3 2
431 332193256.6   0.0 6 3 2 1 1 2 1 1 1 1 0 0 0 0 0 0 0 2 4 6 9 9 7 3
432 332195256.7 88.9 2 2 8 8 6 7 7 9 8 9 9 5 2 1 1 1 2 1 1 0 0 0 1 1
433 332197256.8161.1 7 6 6 6 5 6 8101112 9 6 3 3 4 3 3 2 2 2 4 6 5 6
434 332199256.2   0.0 0 2 1 2 2 2 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0
435 332201256.6103.9 5 4 4 4 3 7 8 9 91010 9 8 7 5 5 4 3 2 2 3 2 3 4
436 332202256.2154.2 7 8 5 4 3 3 7 7 9 6 511 8 3 2 1 0 2 3 5 3 4 7 8
437 333203256.6   0.0 3 1 0 0 0 0 1 2 2 1 0 0 0 0 1 2 1 2 1 2 1 1 1 2
438 333205256.5 87.4 6 7 8 9101113 7 8 9111212 8 7 6 3 4 1 0 2 2 3 4
439 333207256.3165.1 0 0 0 0 0 0 0 0 0 0 0 1 2 2 3 6 8 8 3 2 1 1 0 0
440 333209257.1   0.0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 3 5 7 9 8 6 4 2
441 333211255.2 87.7 9 6 8 7 3 5 3 2 1 1 0 0 1 0 1 0 1 2 4 4 3 4 5 8
442 333213255.4153.8 3 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 2 3 2 1
443 333215256.1   0.0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 3 1 2 1 1 2 3 2
444 333217256.0   0.0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
445 333219256.1158.0 1 1 0 0 0 0 1 3 2 0 0 0 0 0 0 0 0 1 2 2 1 0 0 0
446 333221255.1   0.0 0 0 0 1 2 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 2 1 0 0
447 333223255.8 89.0 1 1 2 2 2 1 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
448 333225256.2159.5 5 4 3 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 2 4
449 341186256.8   0.0 8101212141111101010 9 6 6 5 610 91112131210 9 8
450 342187256.5   0.011110 910 9 910 91010101010 9 7 6 7 7 8 910101111
451 342189256.4 93.5 9 81010 9 91010111214151715141211101010 910 910
452 342191256.6154.6111010111021101112141617161719202223201715141312
453 342193256.9   0.0151719171617151411101011111111121313141313121213
454 342195256.6 86.5131718171512111111101111121211111111111113151818
455 342197256.6159.7 9 8 7 7 91011121415151413131313131212111011 9 9
456 342199256.3   0.0111101313131 2 9 9 7 7 6 8 9 9 8 8 910111415151514
457 342201254.8101.5 9 9101112131211 9 8 6 7 4 4 3 2 4 5 5 4 5 5 5 7
458 342202255.9163.9 5 4 5 4 5 5 7 8 8 910121210 8 8 5 4 3 3 4 3 2 4
459 343203256.9   0.0191918171515141413141312141414161719191920212120
```

APPENDIX III (CONT)

```
460 343205256.6 82.2 6 5 5 3 4 6 6 6 7 6 8 9 7101010 9 7 6 2 3 2 0 1
461 343207256.6164.1 5 6 4 3 6 7 6 6 7 8 9 9131414111110 9 6 7 7 6 5
462 343209257.0  0.0141514161513121313111112131212111212111212121314
463 343211255.0 88.9161615131212121317181920202122232323222120191917
464 343213254.1154.5161718192020212119171616151718192020191818181717
465 343215255.8  0.0212020191818171612121010111110101112131415161718
466 343217255.1 86.3111110111110 9 9 9101010111314151613111211110 9 9
467 343219255.0157.91513111110 9 8 910111213141617182021222221201917
468 343221256.0  0.0171819212322212120171614131413121110121213141615
469 343223255.6 92.9201317151311121314141517201918192120201920212020
470 343225256.9161.7101517181920191918161311 6 5 5 5 3 4 3 6 5 6 5 7
471 344223252.8157.31313 9 9 9101011111010 9 9 910111214171614151513
472 344229255.9 92.91416171616171615141210 8 7 6 5 2 1 1 2 7 9111513
473 344230256.2  0.0 2 2 3 4 4 3 5 6 3 3 5 6 4 6 8 7 7 7 6 5 2 3 5 4
474 344231257.0161.3 0 1 1 0 0 0 1 3 3 3 5 7 7 8 6 4 1 0 0 1 1 0 0 0
475 344232257.1106.8 5 4 2 4 4 3 3 3 3 2 2 2 1 3 5 4 4 5 6 7 8 6 5 4
476 344233257.0  0.0 6 2 0 0 0 0 2 3 4 5 6 8111113141514121011 9 6 6
477 344234256.9158.2131312111111111010101213141516141118151514141313
478 344235257.0 98.6 61114121311 9 5 3 4 5 5 3 5 5 5 6 8 9 7 5 4 7 5
479 344236257.0  0.0 9 9 9 8 8 9 8 8 7 7 7 7 6 5 7 7 7 7 8 8 7 8 8 8
480 351186256.6  0.0 8 8 8 8 7 6 6 5 7 8 9 8 7 9 8 7 7 7 7 8 7 7 8 7
481 352187256.8  0.0 1 2 2 2 4 3 4 5 5 4 5 5 5 5 5 4 3 2 2 2 3 3 4 3
482 352189256.7 93.3141312121111111111121312131415161718161817161615
483 352191256.8156.1 5 2 1 2 2 3 4 3 4 3 3 6 9 8 7 6 5 5 3 3 2 1 3 4
484 352193256.7  0.0 6 6 4 3 3 4 4 6 6 6 8 6 5 4 3 3 3 5 6 8 7 7 6 6
485 352195256.3 85.1 1 2 3 4 3 2 3 5 3 1 0 1 1 3 2 1 2 1 2 1 0 1 3 3
486 352197256.3160.7 1 0 0 0 1 1 5 6 4 4 5 6 8 7 6 6 6 4 5 5 3 3 2 2
487 352199256.4  0.0 5 5 2 3 2 0 0 0 0 1 1 1 1 1 0 0 2 0 0 2 1 5 6 5
488 352201256.1 92.6 7 7 5 4 5 5 6 6 6 8 8 7 6 5 4 3 3 3 3 3 4 6 6 6
489 352202256.1156.6 1 0 3 2 3 4 5 5 5 4 5 5 5 3 5 3 5 3 3 2 4 4 3 2
490 353203257.1  0.01110 9 9111112121110 9 8 4 6 5 5 6 7101111121312
491 353205256.8 83.5202122232524232221191512111110 9 9 8 7 812141719
492 353207256.1164.2 910111213151821232423242322211917151413121110 9
493 353209256.5  0.0 7 4 2 1 1 1 1 1 3 3 4 7 91113172021222120191612
494 353211255.1 87.9 7 8 8 8 8 8 7 7 5 4 4 4 3 2 1 1 1 1 3 3 3 3 5 6
495 353213254.0157.1101214151619212223222221212020191716171615141310
496 353215256.0  0.01513 9 5 2 2 2 2 0 1 1 2 3 5 8111214171819201817
497 353217255.4 86.1141514131213121011111111111111121212111212131413
498 353219256.5158.6 0 0 0 0 0 0 2 2 4 3 4 7 6 5 3 2 1 1 0 0 0 1 1 0
499 353221255.8  0.0 2 3 1 1 1 0 1 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0
500 353223256.8 95.5 0 0 0 0 0 0 2 1 1 0 0 0 0 0 0 0 0 1 2 2 0 0 0 0
501 353225256.0160.8 0 0 0 0 0 0 0 0 1 1 1 1 1 1 0 0 0 0 0 1 2 3 1 1
502 354228256.6165.2 0 0 0 0 0 0 0 0 0 0 0 1 2 3 1 0 0 0 0 0 0 0 1 0
503 354229256.0  0.0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
504 354230256.0  0.0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
505 361186256.3  0.0 4 1 1 3 2 2 0 0 0 1 0 0 0 0 0 0 0 0 1 5 5 3 3 1
506 362187256.9  0.0 0 0 0 0 3 4 6 6 5 3 2 1 2 0 0 0 0 0 0 1 1 1 1 0
507 362189256.0  0.0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
508 362191257.0157.3 5 1 3 4 1 2 1 0 3 3 2 1 2 3 6 5 3 2 3 4 4 3 4 3
509 362193256.8  0.0 0 0 1 1 0 0 0 1 3 2 0 1 1 0 0 1 0 0 0 0 0 0 0 0
510 362195256.3 86.2 0 0 1 2 3 3 3 1 2 0 0 0 2 2 1 1 1 1 2 2 0 0 0 0
511 362197256.9163.7 1 0 0 0 0 0 0 0 0 0 0 1 1 0 1 0 1 0 1 3 4 3 0 2
512 362199256.5  0.0 0 0 0 1 2 2 1 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0
513 362201256.0 95.8 3 5 4 6 5 5 7 6 2 2 3 2 0 1 1 0 0 0 0 1 1 1 1 0
514 362202256.1156.0 0 1 0 0 0 0 0 0 0 0 0 0 0 2 1 1 1 0 0 0 0 0 0 0
515 363203257.1  0.0 2 2 2 2 5 6 6 5 7 5 4 3 2 2 2 1 1 0 0 0 0 1 2 4
516 363205256.4 82.9 3 2 2 2 1 0 0 0 0 1 2 2 4 4 6 9 7 5 6 6 4 2 3 3
517 363207256.5163.2 4 2 2 1 1 2 1 1 1 1 0 0 0 0 0 0 0 0 0 1 4 7 5 3
518 363209257.1  0.0 0 0 4 3 4 2 2 5 4 5 6 6 4 3 3 7 7 5 4 6 5 4 1 0
519 363211255.0 86.7 0 0 0 1 1 0 0 0 0 1 0 5 710 8 5 1 2 1 0 0 1 0 0
```

APPENDIX III (CONT)

```
520 363213255.3157.7 4 5 4 3 1 1 2 1 1 1 1 5 6 5 4 4 4 5 3 2 1 0 1 1
521 363215256.0  0.0 6 3 1 2 3 5 7 9 810 9 8 6 5 4 6 5 4 4 3 1 1 4 6
522 363217255.4 87.810 9 9 7 6 5 5 9 8 9 8 7 3 8 8 7 7 9 7 4 3 3 5 6
523 363219255.1157.110 9 7 6 6 6 6 3 2 3 3 1 2 1 1 1 2 4 5 2 2 3 8 8
524 363221255.9  0.0 0 0 0 0 0 1 3 1 1 0 0 0 0 0 0 0 0 1 1 1 1 1 1 0
525 363223256.0  0.0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
526 363225255.4159.9 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 3 3 2 0 0 0 0 0
527 364228256.3168.1 0 0 0 0 0 0 1 1 1 2 3 2 1 0 0 0 1 2 0 0 0 0 0 0
528 364229256.2102.7 0 0 0 0 0 0 0 0 0 0 1 1 3 0 0 0 0 0 0 0 1 0 0 0
529 364230255.8  0.0 0 0 0 0 2 5 2 3 2 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0
530 364231256.9156.5 3 2 0 0 0 2 3 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1
531 364232257.0106.2 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 2 1 0 0 0 0 0 0
532 364233257.0  0.0 1 1 1 1 3 2 1 3 4 6 9 6 3 2 1 1 1 2 3 3 2 2 0 1
533 364234256.9157.8 1 1 0 0 0 0 0 0 0 0 0 1 0 1 3 2 2 2 1 2 3 1 5 2
534 364235257.1 96.6 1 1 0 0 0 1 2 1 0 0 0 0 0 0 0 0 1 1 3 3 3 2 3 1
535 364236257.1  0.0 1 1 0 0 0 1 3 2 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0
536 371186256.5  0.0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 0
537 372187256.9  0.0 5 1 2 0 0 0 0 1 2 1 1 0 0 0 0 0 0 0 0 1 2 2 4 5
538 372189256.6 93.9 4 6 6 5 4 1 2 3 3 4 5 4 5 6 5 4 6 5 3 2 4 6 5 4
539 372191257.0156.5 0 0 0 0 0 0 0 0 1 2 1 2 4 4 3 1 0 0 0 0 0 1 0 0
540 372193256.8  0.0 6 5 8 9101111 5 6 5 5 4 3 3 3 2 3 2 2 2 3 2 1 5
541 372195256.5 90.2 0 0 0 0 0 1 0 3 2 0 0 0 0 1 3 2 2 0 0 0 0 0 0 0
542 372197256.6160.3 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 2 2 1 1 0
543 372199256.0  0.0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
544 372201256.1102.0 1 1 1 1 0 1 1 1 1 0 1 5 4 1 2 4 4 2 1 1 1 1 1 0
545 372202257.0160.9 2 4 3 3 3 1 0 1 0 0 0 0 0 0 0 0 0 1 1 2 2 1 1 1
546 373203256.9  0.0 2 3 4 3 1 2 0 0 0 0 0 0 0 1 2 0 0 0 0 0 0 0 0 0
547 373205256.8 85.6 3 3 4 6 6 3 4 4 5 6 1 1 1 2 2 1 1 1 5 6 4 5 6 6
548 373207256.5164.7 0 0 0 0 0 0 0 0 0 0 1 1 2 2 1 2 1 1 0 0 0 0 0 0
549 373209256.7  0.0 2 2 4 4 3 3 3 2 2 2 0 1 1 0 2 2 3 4 2 1 1 2 2 2
550 373211255.3 87.8 0 1 3 1 2 4 5 5 3 4 3 1 0 0 0 0 1 2 2 3 6 3 1 0
551 373213255.8154.5 6 5 5 6 7 4 4 3 2 4 5 6 7 8 9 8 6 6 4 2 2 3 4 4
552 373215256.1  0.0 0 0 0 0 0 0 0 1 2 2 1 1 0 0 0 0 0 0 0 0 1 1 2 1
553 373217255.5 92.4 6 6 6 4 4 6 7 8 9 8 9 9 9 8 5 7 6 4 3 3 3 3 3 5
554 373219256.3158.9 8 8 7 6 6 4 5 6 7 6 7101111 9 8 6 3 3 4 7 7 7 6
555 373221256.0  0.0 1 0 1 5 5 2 1 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 1 2
556 373223255.9 89.4 7 8 910 8 6 6 7 7 6 6 5 5 9 7 8 3 8 9 9 9 8 8 7
557 373225256.1159.2 4 2 0 0 1 0 0 0 0 0 0 0 1 0 1 3 4 4 5 5 4 3 4 3
558 374228254.9161.1 4 3 1 1 4 5 3 2 1 0 1 1 2 3 4 4 4 6 5 3 3 4 2 2
559 374229256.3102.0 7 6 5 4 2 1 2 1 3 4 5 2 3 2 2 2 1 3 6 4 3 3 5 3
560 374230255.6  0.0 3 4 3 0 0 0 0 0 0 0 0 0 0 0 1 2 2 3 4 3 3 3 5 4
561 374231256.9152.0 0 0 3 2 0 1 2 5 4 6 5 7 7 7 7 5 2 1 1 2 3 1 2 1
562 374232257.2104.5 6 6 5 2 2 3 4 3 1 0 6 8 8 7 7 8 8 5 6 8 7 3 4 3
563 374233257.0  0.0 4 3 2 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 0 1 1 3
564 374234257.1155.1 1 0 0 0 0 0 0 1 2 2 1 0 0 0 0 0 0 0 0 0 1 2 1 1
565 374235257.0 97.4 5 5 3 1 0 0 3 6 5 5 7 5 7 6 6 7 6 7 6 5 6 6 4 4
566 374236256.9  0.0 0 0 0 1 1 1 0 0 1 1 3 4 2 0 0 0 0 0 0 0 2 3 1 1
567 381186256.5  0.0 4 2 1 2 3 5 3 5 5 3 4 3 2 2 3 4 5 6 6 6 4 3 3 4
568 382187256.7  0.0 2 1 2 3 4 5 3 3 3 3 2 1 0 0 0 0 0 0 0 0 0 0 0 1
569 382189256.8 94.8 3 1 2 3 1 0 0 1 2 2 4 5 3 3 1 2 3 3 4 4 5 3 1 3
570 382191256.8155.2 9 7 4 6 6 4 5 4 6 8 6 5 6 8 8 7 8 7 8 910 9 8 9
571 382193256.8  0.0 91010 7 4 4 4 4 4 3 4 3 3 2 2 4 5 7 3 4 5 6 6 5
572 382195256.4 86.1 3 5 4 7 8 4 6 8 9 9 7 6 5 7 8 8 6 4 2 3 3 3 3 2
573 382197256.9153.3 8 6 5 5 3 5 4 3 2 2 710 8 8 7 6 5 8 9 7 7 6 5 7
574 382199256.2  0.0 3 1 1 0 0 0 0 0 0 0 0 0 0 0 0 1 2 3 4 5 6 6 4 3
575 382201255.2100.1 7 8 7 8 8 911121212111010 9 7 4 3 6 5 5 6 6 8 7
576 382202255.5164.7 2 2 4 4 5 5 6 7101010 9101010 8 7 5 3 2 3 5 4 3
577 383203256.1  0.0 910 7 7 8 8 7 7 7 7 6 7 7 6 5 6 7 810 8 9101211
578 383205256.7 83.9 2 1 3 3 4 5 5 2 3 6 5 3 0 0 0 0 0 0 0 0 0 0 0 1
579 383207256.4163.8 2 4 3 3 5 5 5 3 5 6 6 6 6 6 4 5 4 4 4 4 3 3 2 1
```

APPENDIX III (CONT)

```
580 383209256.8  0.0 2 1 0 0 0 0 0 0 0 0 0 1 0 0 1 2 4 6 6 7 7 5 3 1
581 383211255.1 86.8 5 3 7 910 9 8 5 5 6 4 5 3 3 1 2 3 1 1 2 2 2 4 4
582 383213255.0156.0 5 6 7 8 8 7 5 4 2 2 2 3 3 4 6 6 7 8 8 7 7 6 6 4
583 383215255.5  0.0 6 81214 9 6 4 5 4 3 4 3 5 7 6 6 6 6 3 1 1 2 3 5
584 383217255.1 88.6 9 910 910 9 91011 9 91010111011121110 7 7 810 8
585 383219255.6156.810 9 7 7 3 2 1 1 0 0 1 2 21010 61011 6 5 8 7 8 8
586 383221255.9  0.0 6 2 2 610141612 9 8 6 4 3 3 5 5 7 9 8 3 1 0 1 4
587 383223256.6 53.4 3 4 4 6 9 3 6 8121314 71010 7 8 7 8 4 1 1 1 1 1
588 383225255.9161.7 4 5 6 3 3 4 4 3 4 2 3 2 3 4 3 5 7 8 5 3 2 3 3 2
589 384228253.8156.4 0 0 0 0 0 0 0 0 0 0 0 2 6 6 5 4 4 5 6 4 5 6 6 2
590 384229256.0 92.810 9 7 6 9 7 7 8 9 7 8 7 6 6 5 1 1 2 3 4 4 4 3 6
591 384230255.4  0.0 6 1 0 0 0 0 0 0 0 0 1 0 2 4 6 6 5 5 5 6 4 3 4 9
592 384231256.9161.5 4 0 3 2 4 6 8 4 2 3 4 3 2 1 3 5 3 5 7 91114 8 6
593 384232257.0106.0 61414 7 1 0 0 0 0 0 0 0 0 0 3 3 1 0 0 2 2 6 7 4
594 384233256.9  0.0 7 4 3 1 0 2 5 6 6 7 6 3 3 3 2 5 4 6 5 6 4 4 5 8
595 384234256.9156.6 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 2 3 1 0 0 0 0 0
596 391188256.8  0.0 7 7 5 8 6 5 3 2 3 3 2 0 2 0 2 3 3 2 4 3 5 5 5 4
597 391189256.6 94.6 0 1 0 1 2 2 2 3 4 3 2 5 4 2 1 0 1 1 1 0 0 1 1 0
598 391191256.8155.8 0 0 0 1 0 0 0 0 1 2 5 5 4 4 4 3 1 0 0 0 0 0 0 0
599 391193256.9  0.0 2 4 2 0 0 2 3 1 0 0 0 0 1 1 1 2 4 4 2 3 2 1 2 1
600 391195256.5 86.8 1 2 2 2 3 4 2 1 1 2 1 1 1 0 0 0 0 0 1 0 0 0 0 0
601 391197256.3161.7 7 7 6 6 2 3 3 1 0 1 1 4 5 2 3 3 1 0 1 1 2 3 2 4
602 391199256.2  0.0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 2 1 0 0 0
603 391201256.1 96.5 0 2 5 2 1 1 1 3 2 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0
604 391202256.0156.3 0 0 2 2 1 0 0 1 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
605 392203256.6  0.0 1 3 5 3 5 6 6 7 7 9 9 6 3 2 2 2 2 1 1 1 2 1 1 2
606 392205256.9 82.7 4 2 3 4 4 3 5 3 3 4 5 6 8121010 9 5 3 2 5 6 7 5
607 392207256.5165.2 0 0 0 0 0 0 1 0 0 0 1 3 3 1 2 3 1 0 0 0 0 0 0 0
608 392209257.1  0.0 5 5 5 6 6 6 7 7 8 9 9 8 5 4 3 6 4 2 1 3 6 6 6 5
609 392211255.1 86.6 0 0 0 1 0 1 2 3 6 6 5 2 0 0 1 0 0 0 0 1 2 1 1 0
610 392213255.4158.0 3 3 4 5 5 5 5 5 4 1 2 3 2 2 5 7 7 5 6 5 4 3 4 4
611 392215256.0  0.0 0 2 3 3 1 2 911 6 1 0 0 0 0 0 0 2 3 5 2 1 0 0 0
612 392217255.1 87.0 8 8 8 8 7 3 4 4 4 5 3 2 3 4 5 7111310 8 6 3 5 5
613 392219255.8156.3 8 3 3 1 2 2 4 7 6 7 8 7 8 8 5 3 1 2 2 2 5 1 2 3
614 392221255.8  0.0 5 2 3 3 3 2 4 5 6 5 4 5 6 3 3 2 1 4 8 7 9 7 8 6
615 392223255.9 94.6 2 2 3 1 2 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 3 3
616 392225256.2161.0 3 1 0 0 0 1 1 2 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1
617 393228256.0165.2 0 0 0 0 1 2 1 0 0 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0
618 393229255.9102.8 7 7 4 2 3 3 4 5 7 7 8 9 9 3 2 1 2 2 2 3 6 3 6 5
619 393230256.0  0.0 4 4 3 4 3 8 8 7 5 5 4 2 2 2 4 3 4 3 5 8 8 5 7 8
620 393231256.9158.5 3 3 2 2 4 2 4 4 3 2 4 5 5 4 2 4 5 5 7 6 6 4 3 4
621 393232256.9105.0 3 2 6 5 1 0 1 0 0 0 0 0 0 1 1 0 1 2 3 1 2 2 3 6
622 393233256.9  0.0 0 0 0 1 2 2 1 1 2 1 2 4 2 2 2 2 2 2 1 2 1 1 1 0
623 393234257.1157.9 0 0 1 1 1 1 0 0 0 0 0 0 0 1 0 0 0 0 6 7 2 2 0 0
624 393235257.1 97.8 4 3 2 4 3 2 5 8 7 5 6 4 1 1 1 1 1 0 1 1 2 3 1 3
625 393236257.0  0.0 0 0 0 0 0 0 1 1 1 2 0 0 0 0 2 1 1 2 1 0 2 3 2 0
626 401187256.8  0.0 2 1 1 2 4 3 1 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 1
627 401189256.5 94.3201817161517181819202120181715161615161615161819
628 401191257.1155.9201715151517181920191918161716171718212223222120
629 401193257.1  0.0191817192122222323222120191919202121222222212019
630 401195256.5 90.0151618192021211917161616182022232322191715151413
631 401197256.4160.111 8 8 8 910101111121212121110 9 9 7 6 912111110
632 401199256.2  0.01310 9 911141618191816151411 8 9 910111113151716
633 401201255.7104.41716171820212019171411 9 7 7 8 911121012131314 14
634 401202256.4151.4252321191613 11 7 4 5 5 4 6 810121213141618212324
635 402203256.5  0.0191410 5 2 2 5 5 7 6 6 5 4 4 3 6 910111317212121
636 402205256.5 85.2 911151513131212111010 10 8 8 7 7 9111110 9 9 9 6
637 402207256.4164.5 0 0 0 1 1 4 7 6 916201817141 0 6 4 6 3 6 5 2 1 1
638 402209257.1  0.0181411 7 8 7 9 6 2 2 2 2 1 3 3 51014192123222120
639 402211255.1 87.1 0 1 5 810111114151513 8 4 4 3 2 0 1 0 0 0 0 0 0
```

APPENDIX III (CONT)

```
640 402213255.8157.6 6 7 6 7 7 8 9 7 6 6 7 8 9 9 910111011111 6 3 3
641 402215256.1   0.012131412101110 9 8 8 8 8 8 9 9101011101112111111
642 402217255.3 92.21010 9 8 9121010 9 8 6 6 6 7 6 8 9 8 8 7 8 7 6 6
643 402219256.5151.8 5 3 5 7 810 9 9 9 81212131314131417151210 7 6 5
644 402221256.2   0.015 5 2 5 6 7 7 6 6 6 6 5 5 6 710 912121114172016
645 402223255.5 89.312111110 9 7 8 910111114151413131212111010101111
646 402225255.7160.0111110 9101010 9 910101113121110 9 91010 9101111
647 403228255.6159.8 910101111 8 7 6 5 3 2 3 3 2 4 7 7 6 6 7 6 5 3 6
648 403229256.4 92.01517 7 2 0 0 0 0 0 0 0 0 0 1 3 4 6 71011101414 9
649 403230256.2   0.0 6 812 9 7 5 6 91211 9 6 6 4 7101314181311 9 5 4
650 403231256.9161.3 8101111 7 6 7 7 6 6 7 6 5 7 81312121214201614 8
651 403232256.9105.6 9 8 8 7 8 9 9 4 1 1 2 3 5 3 41110 2 2 4 4 5 6 8
652 403233256.9   0.0 1 1 1 0 1 2 7 7 912 8 6 6 6 7 6 7 8 8 8 7 6 4 1
653 403234256.8158.6 0 4 6 5 7 7 7 8 9 3 1 1 1 1 1 1 0 0 0 0 0 0 0 0
654 403235256.9 97.5 4 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 3 7 8 91210
655 403236256.9   0.0 4 3 3 3 4 4 5 7 8 6 6 7 7 5 5 4 5 6 7 6 5 7 6 4
656 411187256.8   0.0171716141110101111111211121312121616171617171616
657 411189256.7 96.2171615161617181715111010111111101215171617171516
658 411191257.0156.1 8 6 6 2 4 2 4 3 2 3 3 3 2 2 3 2 1 1 1 5 6 6 5 4
659 411193256.8   0.0 1 0 0 0 0 0 0 1 1 2 7 7 7 3 2 1 2 2 3 3 4 4 2 1
660 411195256.7 90.0 4 4 4 6 4 3 4 2 4 3 1 0 0 0 0 1 2 3 6 2 0 0 1 2
661 411197256.6158.5 7 6 8 6 5 6 6 6 6 6 7 8 5 6 5 6 5 3 2 1 2 5 6 7
662 411199256.6   0.0 6 9 9 6 2 5 3 5 6 7 9 713121513131210 5 3 2 4 4
663 411201255.5102.7 0 2 3 4 5 5 6 2 2 3 4 5 5 4 4 4 4 3 9 9 8 7 2 0
664 411202256.3153.8 810 8 7 7 6 4 5 710 8 2 3 4 1 1 4 5 4 2 2 3 4 5
665 412203256.7   0.0 4 7 6 5 2 4 4 91211 9 5 2 1 0 1 0 0 0 0 1 3 2 1
666 412205256.4 86.1 9 910 5 3 2 0 0 0 1 2 4 6 6 6 5 6 2 3 4 4 7 7 6
667 412207257.0163.911 6 8 9 8101110111110111312 6 5 6 9 8 7 8101315
668 412209257.0   0.0 1 4 2 2 2 2 2 2 4 8 8 9 8101316141110 7 4 6 5 3
669 412211255.2 89.9 4 4 7 8 7 7 9 7 3 2 2 0 1 2 2 2 5 710121110 7 6
670 412213255.8154.9 6 7 6 5 7 6 6 6 810101010 5 6 6 6 5 4 3 3 6 6 5
671 412215256.0   0.0 7 6 6 6101111121311 9 9 8 7 8 6 6 710 9 910 9 7
672 412217255.2 91.8 0 0 0 0 0 0 0 0 0 0 1 2 2 3 3 5 4 1 0 0 0 0 0 0
673 412219256.1153.4 5 5 4 4 4 3 3 3 2 1 1 2 3 4 2 1 0 0 0 0 1 1 2 3
674 412221256.0   0.0 2 2 0 1 2 6 6 6 9 7 6 6 5 3 3 4 3 1 1 0 0 0 0 0
675 412223255.4 88.3 0 1 1 0 1 0 0 1 2 3 3 4 3 2 2 2 3 5 5 2 2 2 1 0
676 412225255.9159.7 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 2 4 6 8 3
677 413228253.6152.9 4 5 6 8 3 1 1 2 1 3 4 6 5 7 4 7 6 4 8 7 4 2 3 4
678 413229256.3 91.7 6 7 6 6 710 7 4 4 3 4 4 5 5 6 9 9 6 5 4 3 2 3 4
679 413230255.9   0.0 0 0 1 2 2 810 7 2 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0
680 413231256.8161.8 0 0 0 0 0 1 2 7 4 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0
681 413232256.8106.4 1 1 1 2 5 6 1 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 0 1
682 413233256.9   0.0 0 0 1 0 0 0 0 0 0 0 1 1 2 1 1 1 2 1 0 1 1 0 0 0
683 413234256.9155.3 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 2 2 1 0
684 413235256.8 98.3 1 1 1 3 3 1 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0
685 413236256.7   0.0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 3 3 1 0 0 0 0 0 0 0
686 421187256.0   0.0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
687 421189256.0   0.0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
688 421191256.0   0.0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
689 421193256.7   0.0 0 0 1 1 2 1 1 0 0 0 0 1 1 2 2 2 3 2 2 3 1 0 0 0
690 421195256.7 85.8 6 7 5 6 5 5 5 5 4 3 1 1 0 0 0 0 4 5 5 2 1 1 1 4
691 421197256.9158.4 8 8 8 8 7 6 5 5 5 5 5 4 6 8 9 6 5 5 6 7 7 8 8 8
692 421199256.3   0.0 4 4 3 4 3 5 6 8 8 7 4 5 4 4 4 3 3 3 3 3 4 5 6 6
693 421201255.7102.0 6 5 4 6 5 4 4 5 4 3 4 3 3 4 3 4 4 5 5 6 5 5 5 6
694 421202256.3163.110 9 9 8 7 7 8 7 6 5 4 3 3 3 3 2 2 3 5 7 7 8 9 9
695 422203257.1   0.0181819202121222223222222212019191918171615151617
696 422205256.8 80.5 9 8 8 6 7 7 8 9101518202123232322201712121010 9
697 422207256.5164.3161412121110121211 8 7 6 7 5 4 4 6 9151718171817
698 422209256.8   0.0 6 7 81012131517191316141210 3 7 7 6 7 7 910 9 7
699 422211255.4 88.21310 8 5 4 3 3 5 8101314161819202120191716151412
```

APPENDIX III (CONT)

```
700 422213254.9155.8 6 5 4 3 2 2 1 2 2 1 1 1 3 4 6 7 5 7 91110 8 7 5
701 422215255.9   0.0 4 5 5 4 610 91010 9 9 9 9 8 7 7 9 8 6 5 3 3 3 2
702 422217255.6  85.9 2 2 3 1 4 4 3 2 4 3 3 3 3 4 5 5 4 3 3 2 1 2 1 1
703 422219254.8156.3 7 6 6 6 6 5 3 4 4 4 3 2 2 1 1 3 3 3 4 5 5 6 7 8
704 422221256.1   0.0 4 2 2 4 6 4 3 5 6 5 5 6 7 71010 8 8 7 6 4 4 4 3
705 422223256.6  93.0 6 3 2 4 3 3 3 2 1 1 2 3 4 6 6 6 7 8 9 9 8 7 6 5
706 422225256.0161.0 7 910 9 9 8 8 7 6 5 5 2 1 8 8 5 3 4 6 8 8 7 6 7
707 423228256.5165.4 2 1 0 0 0 0 0 0 0 0 0 0 0 0 1 2 3 2 3 4 3 2 2 0
708 423229256.4102.6 2 1 2 1 1 2 4 5 6 6 6 6 7 8 7 7 6 5 4 3 4 3 1 1
709 423230255.7   0.0 8 7 8 8 7 6 5 4 3 3 2 1 2 3 5 5 5 6 6 7 8 8 9 9
710 423231256.8158.3 7 7 8 8 8 7 7 6 7 6 5 5 4 5 6 6 7 7 6 6 6 6 5 5
711 423232257.1105.4 6 5 4 4 4 5 6 6 7 6 5 5 5 6 6 7 7 8101110 8 7 7
712 423233257.0   0.010 9 9 9 8 7 6 6 6 7 7 8 8 8 91110 9 9 8 8 8 7 9
713 431203255.9   0.0 91010 9101110 7 6 5 5 1 4 3 3 1 1 4 5 6 6 910 8
714 431205256.5  86.410 7 2 2 3 2 6 5 5 811101011 8 6 7 9 9 6 6 6 910
715 431207256.6164.4 1 1 0 0 0 0 0 0 0 0 3 2 4 4 3 2 1 0 0 0 2 5 5 1
716 431209256.5   0.0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 2 2 0 0
717 431211256.6  91.7 1 2 0 1 0 0 0 2 2 3 1 3 6 7 9 8 8 7 6 5 3 2 1 0
718 431213255.8159.3 1 1 2 0 2 1 0 0 1 0 0 0 0 0 0 0 1 2 1 1 2 4 2 0
719 431215256.2   0.0 1 0 1 3 4 5 6 7 8 9 8 7 6 5 4 3 2 2 1 1 0 1 0 0
720 431217255.2  93.0 0 0 0 0 0 0 1 1 1 1 2 1 0 1 0 0 0 0 0 0 0 0 0 0
721 431219256.3162.2 1 1 1 0 0 0 0 0 1 2 2 2 1 0 0 0 0 0 0 0 0 0 0 0
722 431221256.2   0.0 5 6 4 4 4 4 2 0 0 0 0 0 0 1 1 3 1 1 0 0 0 0 0 2
723 431223255.1  89.0 0 0 0 0 1 2 2 1 1 0 0 1 0 1 3 1 0 0 0 0 0 0 0 0
724 431225256.7159.3 3 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 2 4 9 8
725 432228253.1156.9 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 1 2 1 0 0 0
726 432229256.6  98.6 2 3 3 4 6 6 1 2 1 1 2 2 2 2 3 3 4 4 3 5 6 4 2 1
727 432230256.1   0.0 2 2 2 3 3 3 3 3 4 2 5 2 4 1 0 0 0 0 0 0 0 0 0 0
742 432231257.0160.7 2 3 3 4 5 4 5 6 7 9 910111112101213121211 9 8 6
728 441205256.6  79.9 8 6 6 6 4 4 5 5 6 5 6 7 7 6 5 5 4 4 4 5 5 6 6 8
729 441207256.0162.9 2 2 2 3 3 3 4 4 5 4 2 1 4 5 3 3 6 3 2 3 3 3 4 2
730 441209256.6   0.0 4 6 6 6 5 2 3 4 1 4 2 5 6 5 5 3 4 5 6 3 3 3 4 5
731 441211256.9  92.8 2 4 4 1 2 3 3 3 4 2 1 0 2 0 1 0 1 1 1 1 1 1 1 1
732 441213255.5156.0 4 2 3 4 3 4 7 5 3 5 4 3 3 4 3 2 3 3 3 2 3 2 2 3
733 441215256.3   0.0 1 1 1 2 1 1 1 1 1 1 1 2 0 1 1 1 1 1 1 1 1 2 5 2
734 441217255.2  92.8 1 1 1 0 1 1 1 1 1 1 1 0 1 1 1 3 2 2 3 2 1 1 0 1
735 441219256.3162.4 1 1 1 2 3 4 3 5 4 4 2 2 5 4 3 3 2 1 0 0 0 1 1 1
736 441221256.2   0.0 5 8 9 8 5 5 6 6 5 6 5 6 6 6 5 5 2 2 3 4 4 6 7 6
737 441223255.2  88.1 9 7 8 6 71010 910 9 7 5 4 3 4 5 3 3 5 4 7 91110
738 441225256.5160.0 6 7 6 3 8 9 8 6 3 5 8 7 8 6 4 4 7 7 6 7 3 7 5 9
739 442228253.4158.3 0 0 1 1 1 1 3 2 4 8 5 7 8 5 7 8 5 2 2 2 1 2 2 1
740 442229256.5  92.4 3 3 7 6 3 2 2 2 2 4 5 5 3 2 2 2 2 3 5 4 4 3 4 3
741 442230256.5   0.0 4 4 3 2 3 2 2 3 4 3 1 2 1 0 0 1 0 2 3 4 4 3 3 2
/*
```

```
RALPH JOB STATISTICS --      525 CARDS READ --        525 LINES PRINTED --
                             0.00 MINUTES CPU TIME    0.00 MINUTES WAIT TIME
```

APPENDIX IV

CONVERSION TABLE FOR PARAMETERS OF THEORETICAL CIRCULAR NORMAL DISTRIBUTIONS

PARAMETER OF CONCENTRATION κ	CONCENTRATION ABOUT THE MEAN ρ(or r)*	MODE INTENSITY I**	BESSEL FUNCTION OF PURELY IMAGINARY ARGUMENT OF ORDER ZERO $I_o(\kappa)$***
0.0	.00000	.04167	1.00000
0.1	.04994	.04601	1.00250
0.2	.09950	.05035	1.01003
0.3	.14834	.05501	1.02263
0.4	.19610	.05966	1.04040
0.5	.24250	.06452	1.06348
0.6	.28726	.06937	1.09205
0.7	.33018	.07431	1.12630
0.8	.37108	.07925	1.16651
0.9	.40984	.08419	1.21299
1.0	.44639	.08912	1.26607
1.1	.48070	.09397	1.32616
1.2	.51278	.09881	1.39373
1.3	.54267	.10350	1.46928
1.4	.57042	.10819	1.55340
1.5	.59613	.11271	1.64672
1.6	.61990	.11722	1.74998
1.7	.64183	.12153	1.86396
1.8	.66204	.12584	1.98956
1.9	.68065	.12994	2.12774
2.0	.69777	.13404	2.27959
2.1	.71355	.13794	2.44628
2.2	.72803	.14184	2.62914
2.3	.74138	.14556	2.82961
2.4	.75367	.14927	3.04926
2.5	.76500	.15280	3.28984
2.6	.77545	.15633	3.55327
2.7	.78511	.15971	3.84165
2.8	.79404	.16308	4.15730
2.9	.80231	.16631	4.50275
3.0	.80999	.16954	4.88079
3.1	.81711	.17264	5.29449
3.2	.82375	.17573	5.74721
3.3	.82993	.17870	6.24263
3.4	.83570	.18166	6.78481
3.5	.84110	.18453	7.37820
3.6	.84616	.18740	8.02768
3.7	.85091	.19016	8.73862

APPENDIX IV (CONT)

PARAMETER OF CONCENTRATION κ	CONCENTRATION ABOUT THE MEAN ρ (or r)*	MODE INTENSITY I**	BESSEL FUNCTION OF PURELY IMAGINARY ARGUMENT OF ORDER ZERO $I_o(\kappa)$***
3.8	.85537	.19292	9.51689
3.9	.85956	.19560	10.3690
4.0	.86352	.19828	11.3019
4.1	.86726	.20087	12.3236
4.2	.87079	.20346	13.4425
4.3	.87414	.20598	14.6680
4.4	.87732	.20850	16.0104
4.5	.88033	.21094	17.4812
4.6	.88320	.21338	19.0926
4.7	.88593	.21576	20.8585
4.8	.88853	.21814	22.7937
4.9	.89101	.22046	24.9148
5.0	.89338	.22278	27.2399
5.1	.89565	.22505	29.7889
5.2	.89782	.22732	32.5836
5.3	.89990	.22953	35.6481
5.4	.90190	.23174	39.0088
5.5	.90382	.23391	42.6946
5.6	.90566	.23607	46.7376
5.7	.90743	.23819	51.1725
5.8	.90913	.24031	56.0381
5.9	.91078	.24238	61.3766
6.0	.91236	.24445	67.2344
6.1	.91389	.24648	73.6628
6.2	.91536	.24851	80.7179
6.3	.91678	.25050	88.4616
6.4	.91816	.25249	96.9616
6.5	.91949	.25445	106.293
6.6	.92078	.25641	116.537
6.7	.92202	.25833	127.785
6.8	.92323	.26024	140.136
6.9	.92440	.26213	153.699
7.0	.92553	.26402	168.594
7.1	.92663	.26588	184.953
7.2	.92770	.26773	202.921
7.3	.92874	.26955	222.659
7.4	.92975	.27137	244.341
7.5	.93072	.27316	268.161
7.6	.93168	.27495	294.332
7.7	.93260	.27671	323.088

APPENDIX IV (CONT)

PARAMETER OF CONCENTRATION κ	CONCENTRATION ABOUT THE MEAN ρ (or r)*	MODE INTENSITY I**	BESSEL FUNCTION OF PURELY IMAGINARY ARGUMENT OF ORDER ZERO $I_o(\kappa)$***
7.8	.93350	.27847	354.685
7.9	.93438	.28021	389.406
8.0	.93524	.28195	427.564
8.1	.93607	.28366	469.501
8.2	.93688	.28537	515.593
8.3	.93767	.28706	566.255
8.4	.93844	.28874	621.944
8.5	.93919	.28990	683.162
8.6	.93993	.29106	750.461
8.7	.94064	.29320	824.450
8.8	.94134	.29533	905.797
8.9	.94202	.29695	995.240
9.0	.94269	.29856	1093.59
9.1	.94334	.30015	1201.73
9.2	.94398	.30173	1320.61
9.3	.94460	.30330	1451.45
9.4	.94521	.30487	1595.28
9.5	.94581	.30643	1753.48
9.6	.94639	.30798	1927.48
9.7	.94696	.30951	2118.86
9.8	.94752	.31103	2329.39
9.9	.94806	.31255	2560.96
10.0	.94860	.31406	2815.72

* From Table C, Batschelet [1965]

** Calculated from Table A, Batschelet [1965]

*** From Fettis and Caslin [1969]