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THE RELATIONSHIP OF CALLING BEHAVIOR TO MOURNING DOVE POPULATIONS AND PRODUCTION IN SOUTHERN ARIZONA

by

Harold Dewey Irby

A Dissertation Submitted to the Faculty of the

DEPARTMENT OF WILDLIFE MANAGEMENT

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In the Graduate College

THE UNIVERSITY OF ARIZONA

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THE UNIVERSITY OF ARIZONA

GRADUATE COLLEGE

I hereby recommend that this dissertation prepared under my direction by Harold Dewey Irby entitled THE RELATIONSHIP OF CALLING BEHAVIOR TO MOURNING DOVE POPULATIONS AND PRODUCTION IN SOUTHERN ARIZONA be accepted as fulfilling the dissertation requirement of the degree of DOCTOR OF PHILOSOPHY

Dissertation Director — Date: JULY 28, 1964

After inspection of the dissertation, the following members of the Final Examination Committee concur in its approval and recommend its acceptance:*

Aug. 19, 1964

Aug. 3, 1964

Aug 3 1964

*This approval and acceptance is contingent on the candidate's adequate performance and defense of this dissertation at the final oral examination. The inclusion of this sheet bound into the library copy of the dissertation is evidence of satisfactory performance at the final examination.

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TABLE OF CONTENTS

TABLE OF CONTENTS--Continued

LIST OF ILLUSTRATIONS

LIST OF ILLUSTRATIONS--Continued

LIST OF TABLES

ABSTRACT OF DISSERTATION

THE RELATIONSHIP OF CALLING BEHAVIOR TO MOURNING DOVE POPULATIONS AND PRODUCTION IN SOUTHERN ARIZONA

by

Harold Dewey Irby

An intensive study of the relationship of calling behavior to mourning dove (Zenaidura macroura) populations and production was made on a 20-acre area on the University of Arizona's Campbell Avenue Farm, Tucson, Arizona in 1962 and 1963. Production studies and visual and coo-count censuses were made, including measurement of the tendency of birds to induce others to call, sex ratios in the dove population, and position of the individual in the court-mate-nest-brood cycle. Doves were trapped and color-marked to facilitate the studies. Also, a standard 20-mile coo-count route north of Tucson was censused on a weekly basis to measure the changes in calling activities of a breeding population through the complete breeding season.

Observations of individual male doves showed that the primary factor affecting the rate of perch-cooing was whether or not they were mated. Unmated males called much more frequently and for longer morning periods than did mated males. The rate of cooing of mated

males was affected by their position in the nesting cycle. They called only infrequently while searching for a nest-site and while building nests. Calling increased during the laying and incubation phases and then decreased while the males were brooding the nestlings. Mated males called most during the periods between nesting attempts.

Male doves, whether unmated or mated, cooed at highest rates during the interval 30-15 minutes prior to sunrise. Thereafter cooing decreased, unmated males gradually and mated males sharply.

I found that sight or auditory contacts with other nearby doves have a positive effect on the frequency of cooing of an individual mated male. However, unmated males cooed at a high rate regardless of whether or not other males were cooing nearby or were in sight. Weather factors were found to influence cooing only under extreme conditions. Dove production could not be predicted on the basis of cooing records, for cooing variability was too great to relate cooing to production.

The seasonal cooing pattern showed an early season peak resulting from the cooing activities of resident and migrating males. Following this peak there was a steady decline to a mid May low which was associated with the nest establishment activities of the recently arrived migrating segment of the local breeding population. Thereafter the cooing pattern was an undulating series of highs and lows as the breeding population progressed through successive nesting attempts.

Other aspects of breeding behavior studied included territoriality, pair-bond formation and duration, flapping-gliding flights, and other dove calls.

Included in this report is a discussion of the coo-count census, the method now used to measure or evaluate the annual mourning dove population fluctuations.

CHAPTER I

INTRODUCTION

One of the fundamental requirements of successful game management is the measurement or evaluation of annual population fluctuations. This essential population appraisal should be based on a knowledge of population distribution, breeding stock, productivity, and removal. Unfortunately, in many cases, it is difficult if not impossible to gather sufficient information on all of these population factors. In these instances appraisals are based upon population indexes or trends derived from sight, sound or sign enumerations. The assumption is made that the same proportion of the total population will be tabulated when the same technique is used each year under similar conditions with the same species. Such is the case with the numerous and widely distributed mourning dove (Zenaidura macroura).

The mourning dove is a migratory bird, and thus is under the regulatory authority of the United States Fish and Wildlife Service, Bureau of Sport Fisheries and Wildlife. The Bureau, in cooperation with State and independent observers, conducts the annual survey of the mourning dove breeding populations during the period May 20 to June 10. This survey censuses the number of doves heard cooing at each of 20 stops (listening stations), one mile apart, along established routes. The censuses are standardized to begin one-half hour before local sunrise and continue to one and one-half hours after sunrise, and the listening period at each stop is three minutes.

The coo-count census method was founded upon the research of H. Elliot McClure (McClure, 1939). In 1950 a group of biologists, working in close cooperation with one another began research to refine the auditory index method. Individuals and organizations involved in this effort included Edward Wellein, Flyway Biologist for the U. S. Fish and Wildlife Service; Leonard E. Foote, Field Representative for the Wildlife Management Institute; D. J. Nelson, Federal Aid Project Leader, Georgia State Game and Fish Commission; and A. J. Duvall, H. S. Peters, and C. S. Robbins, Branch of Wildlife Research, U. S. Fish and Wildlife Service. These studies determined the practicability of certain procedures in the coo-count method, including distance between stops, the length of these stops, and the time of day and duration of the count (Foote and Peters, 1952).

Coordinated research was started in 1951 following statistical analysis of the 1950 data, and culminated in papers by McGowan (1952, 1953), Kerley (1952), Duvall and Robbins (1952), Peters (1952), and Wagner (1952). As a result of these studies it was determined that the dove population was more homogeneously distributed in the spring, and that ". . . calling activity in different parts of the range was relatively uniform, usually with a pre-plateau peak in late April and early May which was followed by approximately a month of near-level calling activity."

The early morning calling level was found to be nearly four times that of the average evening intensity during the plateau period, and day-to-day variation in morning calling was less than in evening calling. Also, dove calling was found to reach a peak at sunrise and decrease for the next one and one-half hours, so counts were rigidly standardized as to starting time for comparative purposes (Southeastern Assn., 1957). Data from Athens, Georgia counts indicated that wind affected the audibility of calling and the intensity of calling itself, and the counts were not made when wind velocity exceeded 8 to 12 MPH (McGowan, 1952). In 1953 Peters conducted time-interval tests of call-counts and found the three-minute listening period to be most efficient (Southeastern Assn., 1957).

The above studies, plus the statistical reliability of the data, suggested that an economical census index could be developed for the mourning dove. Thus the coo-count census was first adopted to measure the breeding populations in the United States in 1953. Subsequently the route coverage was expanded to include parts of Canada, and in 1963 approximately 800 coo-count routes were run.

The Problem

Despite the large amount of research that was conducted in order to establish the coo-count census technique, it was not until later that more intensive research on the biology of cooing revealed that bias may exist that affects the results of the dove coo-count census. Mackey (1954) found that mating activities seemed to be closely correlated with cooing intensity. His limited observations showed that cooing nearly ceased during the middle of the brooding period and increased to a new peak prior to the next nesting attempt. He also found that the cooing of one male may stimulate others to coo, thus resulting in a higher cooing intensity in a dense population than in a widely scattered population.

Cohen, Peters, and Foote (1960) critically analyzed dove song as a population index and found that:

> Apparently the calling behavior of some birds in 3-minute intervals can be considered to be random while for other birds it cannot . . . . the mourning dove calling pattern may be a physiologic-behavior mechanism related to the court-mate-nest-brood cycle . . . . The calling pattern of an individual mourning dove apparently depends upon the time of season (Southeastern Assn., 1957), time of morning, weather and probably upon sex ratio in the surrounding dove population and relative position of the individual in the court-mate-nest-brood cycle. Effects of the latter three factors have not been evaluated. Research on these phases using individually marked members of a breeding group should be undertaken to compare calling behavior with reproductive functions.

Frankel and Baskett (1961), using penned doves, demonstrated that unmated males cooed at a much higher rate than did mated males.

This finding was substantiated by a field study (Jackson and Baskett, 1964). Thus a serious bias may result if the ratio of mated to unmated males in the breeding population changes materially from year to year. Both of these studies found only small differences in the cooing frequency in different stages of the nesting cycle.

As indicated by the above studies, the current method of mourning dove population appraisal, based upon McClure's (1939) thoughts that cooing activity during the breeding season "was very constant," and that there was a "direct relationship between the number of Mourning Doves present in an area and the number cooing," may have serious bias. This was recognized when the National Mourning Dove Research and Management Program listed the improvement of population appraisal techniques as a high priority research need (Kiel, 1961).

The western race of the mourning dove (Zenaidura macroura marginella) has been the subject of only a relatively small amount of research. Additional studies of the behavioral characteristics of this important segment of the continental dove population was needed to allow management techniques to be representative of the entire continental dove population.

Objectives

This study, in view of the hiatus existing in the knowledge of mourning dove calling behavior, had several objectives as follows:

1. To evaluate calling in relation to the presence or absence of the pair-bond, physiological stage in the nesting cycle, climatic factors, and individual differences in dove cooing.

2. To compare calling frequency, intensity and timing with a known nesting population density as a means of measuring the relation between calling doves and reproductive functions.

3. To develop techniques for obtaining annual production indexes.

4. To obtain information on other aspects of breeding behavior.

CHAPTER II

PROCEDURES

<u>Study Areas</u>

The primary study was conducted during the spring and summer of 1962 and 1963 on the University of Arizona's Campbell Avenue Farm at the northern edge of Tucson, Arizona. To facilitate the collection of observational data the study area was divided into two segments.

<u>Paddock Area:</u> This area of approximately 15 acres had been divided into four paddocks for portions of the dairy herd (Fig. 1). The northeastern corner housed the Cooperative Wildlife Research Unit's javelina pens and storage facilities. The vegetation was largely composed of islands and peninsulas of mesquite (*Prosopis juliflora*) with scattered catclaw (*Acacia greggi*). Except for the small fenced portion surrounding the javelina pens, the area was almost devoid of shrubs, forbs and grasses due to the grazing and browsing of the large number of cows, which usually totalled in excess of 100 animals.

The extreme condition of overgrazing helped me keep track of individual doves for long periods of time. However, the interference by the cows was at times a detriment to portions of the study.

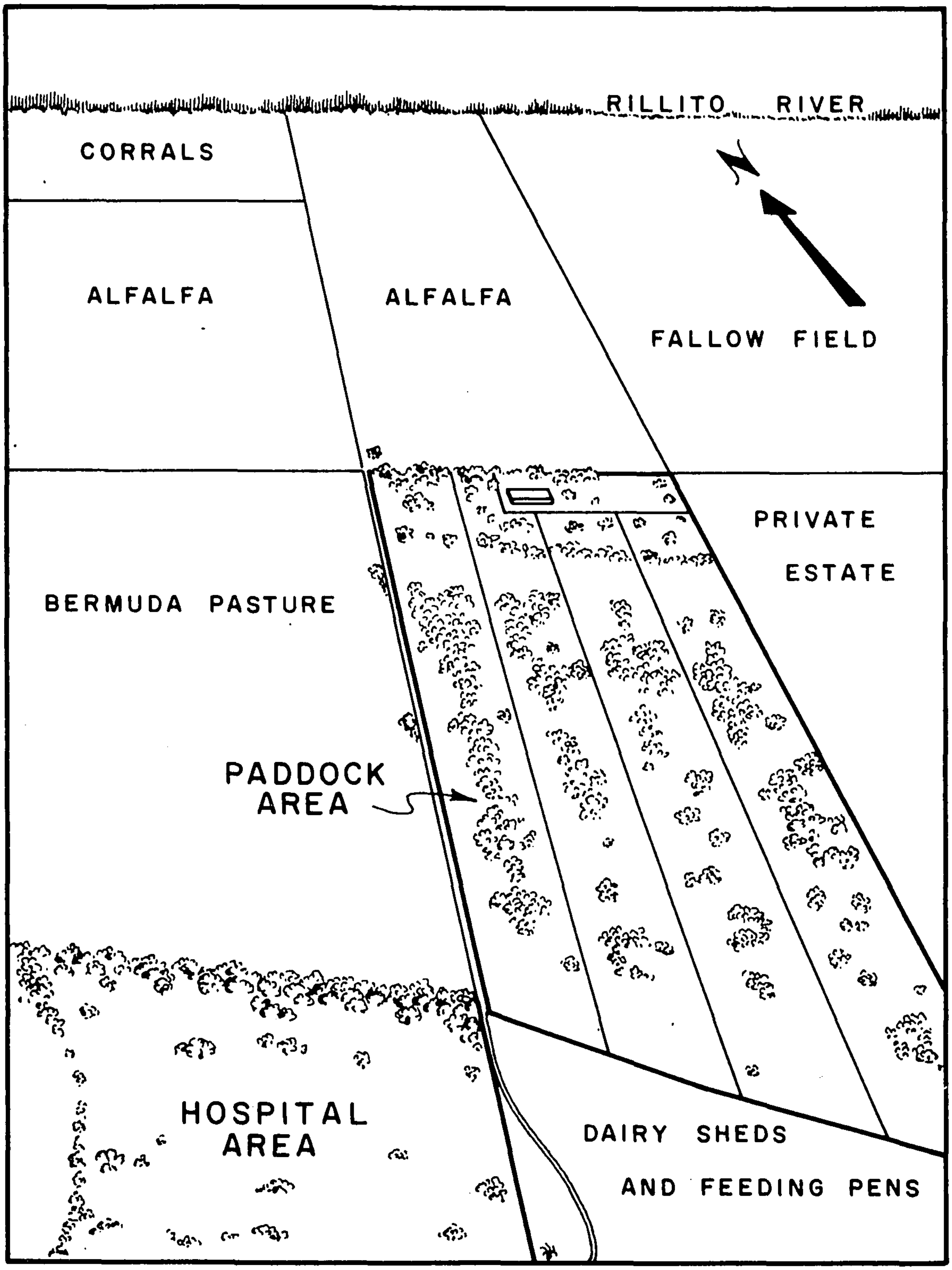

Figure 1. Perspective drawing of the study areas.

<u>Hospital Area</u>: This small area of approximately five acres lies diagonally across a farm lane from the southwestern corner of the paddock area. It is an unused, unimproved plot which was added to the study when it became apparent that the paddock area would not yield completely natural life history data.

The northern border was a continuous band of mesquite with a scattering of catclaw. The remainder was largely open with scattered mesquite trees and cactus (*Opuntia* spp.). The ground cover consisted of clumps of bush muhly (*Muhlenbergia porteri*) and annual forbs and grasses.

<u>Coo-count Route</u>: A standard coo-count route was set up north of Tucson to gain information on dove calling patterns throughout the complete breeding season (Fig. 2). This route was run at weekly intervals from onset to cessation of calling in 1962, 1963, and also through June of 1964. It traversed a desert shrub area whose primary non-riparian trees were foothill palo verde (*Cercidium microphyllum*), sahuaro (*Cereus giganteus*), and ironwood (*Olynea tesota*). The primary riparian trees of the "dry" arroyos and washes were blue palo verde (*Cercidium floridum*), mesquite (*Prosopis juliflora*), and catclaw (*Acacia greggi*).

Capturing

All dove trapping was restricted to the primary study area and all birds were released at the site of capture. Trapping began the last

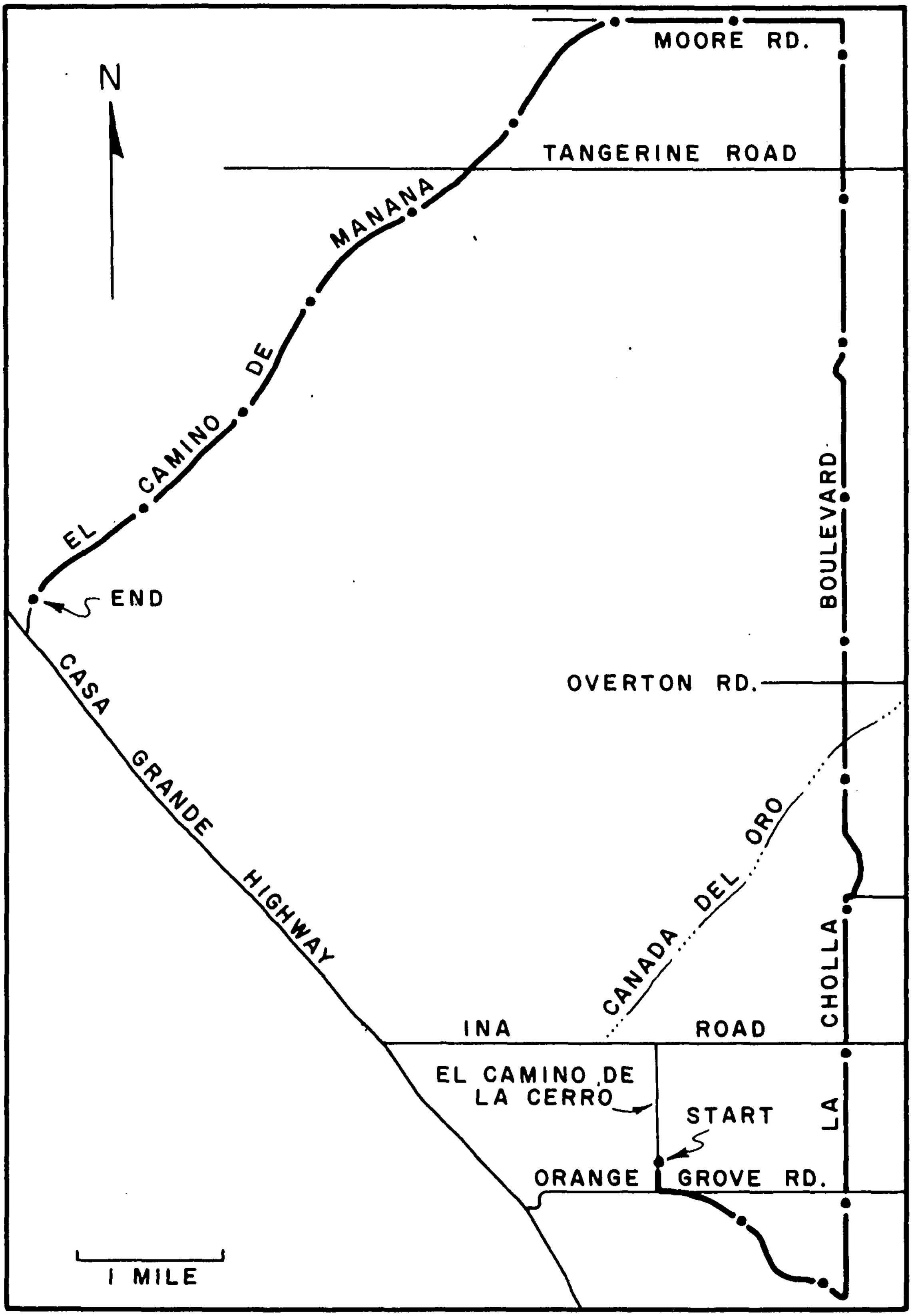

Figure 2. Coo-count route north of Tucson, Arizona.

week in December, 1961 and continued almost daily through August, 1963. These efforts had as their objectives the marking of individual doves and sampling of the population to study sex and age characteristics. A total of 2,666 doves was captured during this study as shown in Table 1. Three methods used to capture mourning doves were:

Ground Trapping: Most doves captured were trapped with modified Stoddard quail traps (Stoddard, 1931) placed in an arc in the vicinity of the javelina pens. In an effort to prevent doves from escaping, second traps were wired to the backs of the original traps to serve as holding pens. When the doves had entered the second compartment they would have to find their way back through two funnels before they could escape. Palm fronds were placed on the rear compartments to provide shade for the doves. Observations indicated that this modification had a double bonus: congestion and harassment were alleviated at the entrance funnel which allowed more doves to enter, and less birds were able to escape once they had entered the rear compartment.

One male dove was caught below his nest-tree with a string-triggered drop trap. This male was seen feeding while gathering nest material. The following morning before daylight the baited trap was placed beneath the nest-tree and the male readily entered the trap a short time later. This did not disturb the pair as they continued nest building.

Table 1. Number, age, and sex of doves captured during this study.

Date		Adults Male	Female	Total	Immatures	Total All Ages
1961	Dec.	3	3	6	3	9
1962	Jan.	33	27	60		60
	Feb.	55	43	98		98
	Mar.	54	53	107	8	115
	Apr.	23	20	43	49	92
	May	20	13	33	172	205
	June	11	14	25	174	199
	July	10	6	16	212	228
	Aug.	13	12	25	105	130
	Sept.	7	9	16	88	104
	Oct.	3	3	6	8	14
	Nov.	5	5	10	5	15
	Dec.	19	10	29	19	48
1963	Jan.	34	27	61		61
	Feb.	17	19	36		36
	Mar.	18	11	29	20	49
	Apr.	46	32	78	117	195
	May	52	47	99	178	277
	June	45	19	64	220	284
	July	17	13	30	172	202
	Aug.	20	13	33	212	245
Totals		505	399	904	1762	2666

Nest Trapping: Nine doves (seven males, two females) were trapped on their nests with the nest-trap developed by Swank (1952). This method, although it successfully caught doves, was discarded for several reasons: (1) in a number of cases the pair abandoned the nest after one member had been trapped, (2) the set traps attracted the curiosity of the dairy cows, resulting in either an upset trap or in such harassment that the doves refused to return to the nest, (3) many nests were so placed that it was impossible to properly install the traps, and (4) in one instance a loggerhead shrike (Lanius ludovicianus) was seen entering the trap and quickly carrying off the two nestlings before I could reach the scene.

Noosing: Some incubating or brooding doves would allow me to approach quite closely before they flushed from the nest. A noosing stick was made by attaching a string noose to the end of a short fishing pole. In experiments off the study area noosed doves were not injured in the few seconds that were necessary to bring them to hand. Moreover, they were disturbed so little that they did not abandon their nests. This method was used to capture only one dove on the study area. However, five roadrunners (Geococcyx californianus) were noosed on the study area and released in other areas.

Marking

To work with known individuals, it was necessary to color-mark a number of doves. In this study two methods of color-marking individual doves were used. The first, and most permanent, involved attaching a colored plastic back-tag on the dove (Fig. 3). This type of marker was developed by Blank and Ash (1956). To assist in identifying back-tagged doves when viewed from the front, their breasts were colored with aniline dyes. Four adult males were back-tagged. The second method was to color-mark the birds with various aniline dyes obtained from the National Aniline Division of the Allied Chemical Corporation, 235 Montgomery Street, San Francisco 4, California. The colors used in this study, and listed in descending order of permanence and visibility at a distance, were fast crimson, wool orange, fast light yellow, alizarine violet, and alkali fast green.

After it became apparent that nest-trapping doves was not desirable, I decided to use a "blanket" method of color-marking most adult doves captured in ground traps in hopes that some of them would nest on the study area--and a number of them did. In order to gain the maximum number of marked individuals from the limited number of available colors, it was necessary to use various combinations. By either clipping off the tip of the tail or leaving it entire, or by banding on either the right or left leg it was possible to use the same marking pattern on four different birds. This technique did not make it possible to accurately identify the bird in flight or when only seen for a short time. It was satisfactory when the bird was seen for a longer period of time as was the case during most of this study. Observations were

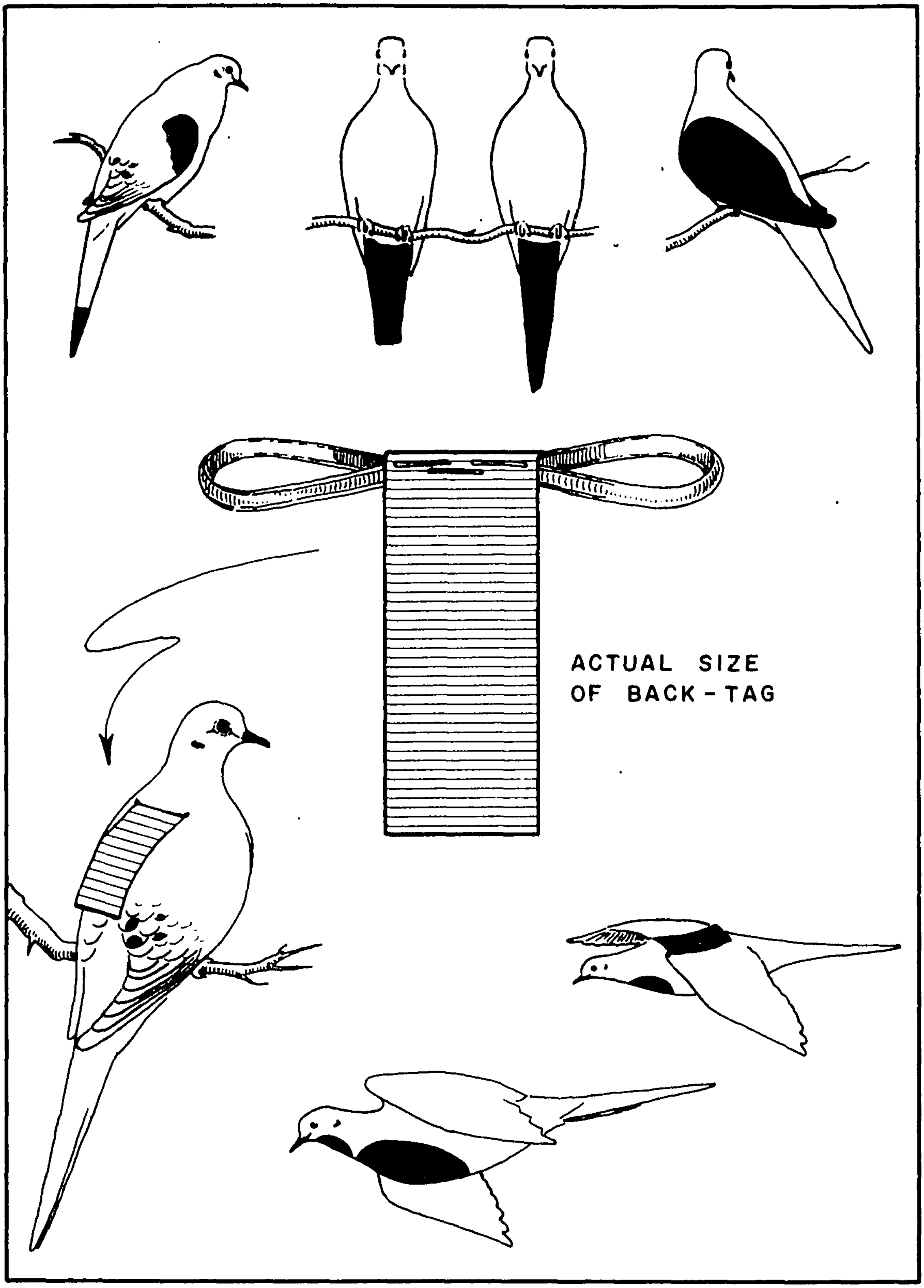

Figure 3. Methods used to mark individual doves.

aided by the fact that no similarly marked doves nested on the study area. Also, many of the area nesters were retrapped and could be more conspicuously marked. A total of 250 adult males and 73 adult females was color-marked during this study.

Later in the nesting season the early-hatched immatures became potential breeders and were also color-marked. All males (determined by presence of cloacal papillae) were tail-clipped and their breast feathers dyed red. The females (determined by presence of oviduct opening) were tail-clipped and their breast feathers dyed orange. A total of 43 immature males and 39 immature females was color-marked during this study.

Observations

Observations were made of both individually marked birds and unmarked birds. All observations of cooing behavior were made on or near the study areas. They began one-half hour before local sunrise and continued for two hours to comply with the period used for the mourning dove coo-count. Cooing was recorded by one-minute periods within the two-hour interval. Observations of other breeding behavior were made during the same period and at other intervals throughout the day.

To record the cooing behavior of individual doves, I used either a portable blind or a vehicle. The doves on the study areas, conditioned by daily farm traffic, were unafraid by nearby vehicles and the sound of motors. Thus it was possible to move about without disturbing the birds. Also, both study areas were bordered on two sides by farm roads. In no case did the vehicle disturb a dove under observation.

To record the cooing behavior of the males of a breeding area, I used a portable blind. The blind was so placed that it was possible to separate out those males which were calling from outside the area. It would have been desirable to accurately record the total number of doves calling during the two-hour interval, or even during three-minute periods within this interval. However, this was not possible due to the large numbers frequently calling at the same time, and their movements around the area. Thus area-calling data were recorded by one-minute periods, a period during which the number of birds calling could be more accurately assessed. The number of coos heard per minute were also recorded. Observational methods are discussed in greater detail in the appropriate sections of this report.

Analysis

The data collected during this study were subjected to various analytical methods which are discussed in the appropriate sections. In general, the standard statistical methods relied upon were from Snedecor (1956), and Steel and Torrie (1960). Among the methods applied were: Standard Deviation, Standard Error, and Variance to express absolute variation, upon which determinations of significance were based; and Coefficient of Variability to compare relative variation.

CHAPTER III

RESULTS

Factors Affecting Perch-Cooing

McClure (1939) described the perch coo as "five to seven notes; one note, then a higher one, and finally three to five lower notes held at greater length." He also stated that when giving the perch-coo the male arches the neck, puffs out the throat, stiffens the body, and bobs the tail at each note. The perch-coo is uttered chiefly by male doves, although the female sometimes sings a faint version (Frankel and Baskett, 1961). In this report perch-cooing is also referred to as cooing and as calling; all refer to the dove song described above unless otherwise specified.

Data used for the analysis of factors affecting perch-cooing were obtained from 270 mornings of observation. Twenty-five marked mated males, seven marked unmated males, and numerous unmarked males were studied. Five marked males were studied while both unmated and mated (Table 2). Jackson and Baskett (1964), as an arbitrary measure to improve the quality of data, excluded observations of less than 30 minutes duration. Data collected during this study were analyzed both by all observations and by those of greater than 30 minutes duration. The differences were not significant (Fig. 4). Therefore,

Table 2. Number of marked males observed in the various breeding phases.

Marked Male	Unmated	Unmated-Active Courtship	Nest-Site Selection	Nest Building	Laying	Incubation	Brooding	Between Nests-Successful	Between Nests-Disrupted	Mated-Off Territory
M2	X									
M9	X	X								
M10	X									
M14	X									
M20	X									
M22	X	X	X	X		X	X	X		X
M23										X
M24										X
M32	X		X	X	X	X	X	X	X	X
M40				X	X				X	
M52	X									
M63				X				X		
M87	X	X		X	X	X	X	X		X
M93				X		X	X	X		
M110				X	X	X	X	X	X	
M112				X	X	X	X	X		X
M127										X
M133				X		X	X		X	
M139				X	X	X		X	X	
M143	X							X		
M146			X	X	X	X	X			
M152	X									
M155				X		X	X	X	X	
M157				X						
M158	X		X	X		X	X	X		X
M160			X	X	X	X			X	
M163				X	X					X
M164										X
M170			X	X	X	X	X	X		
M175										X
M178										X
M206								X		
Totals 32	12	3	6	17	10	13	11	13	7	12

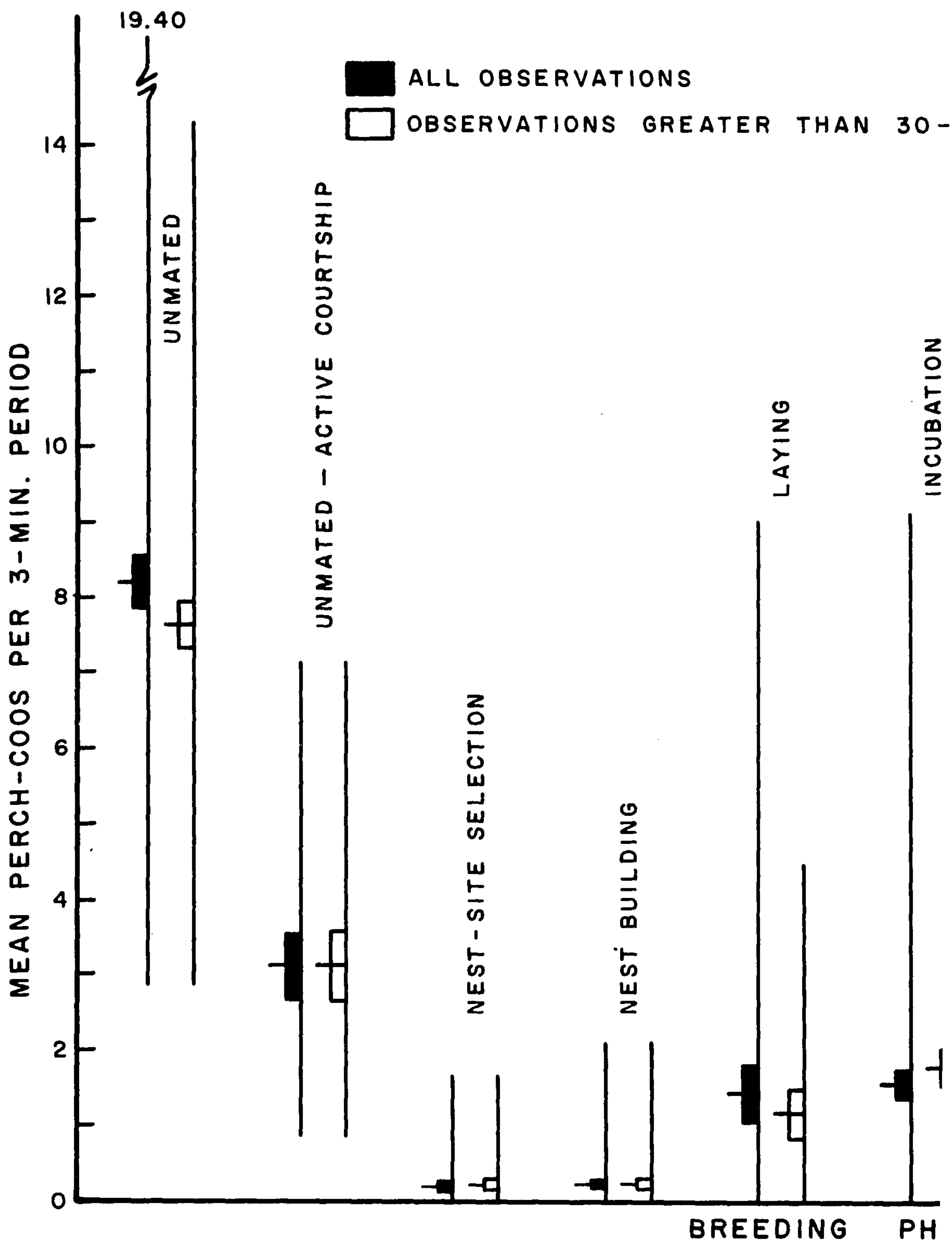

Figure 4. Comparison of cooing data from all observations with
lines - ranges; horizontal lines means; rectangles

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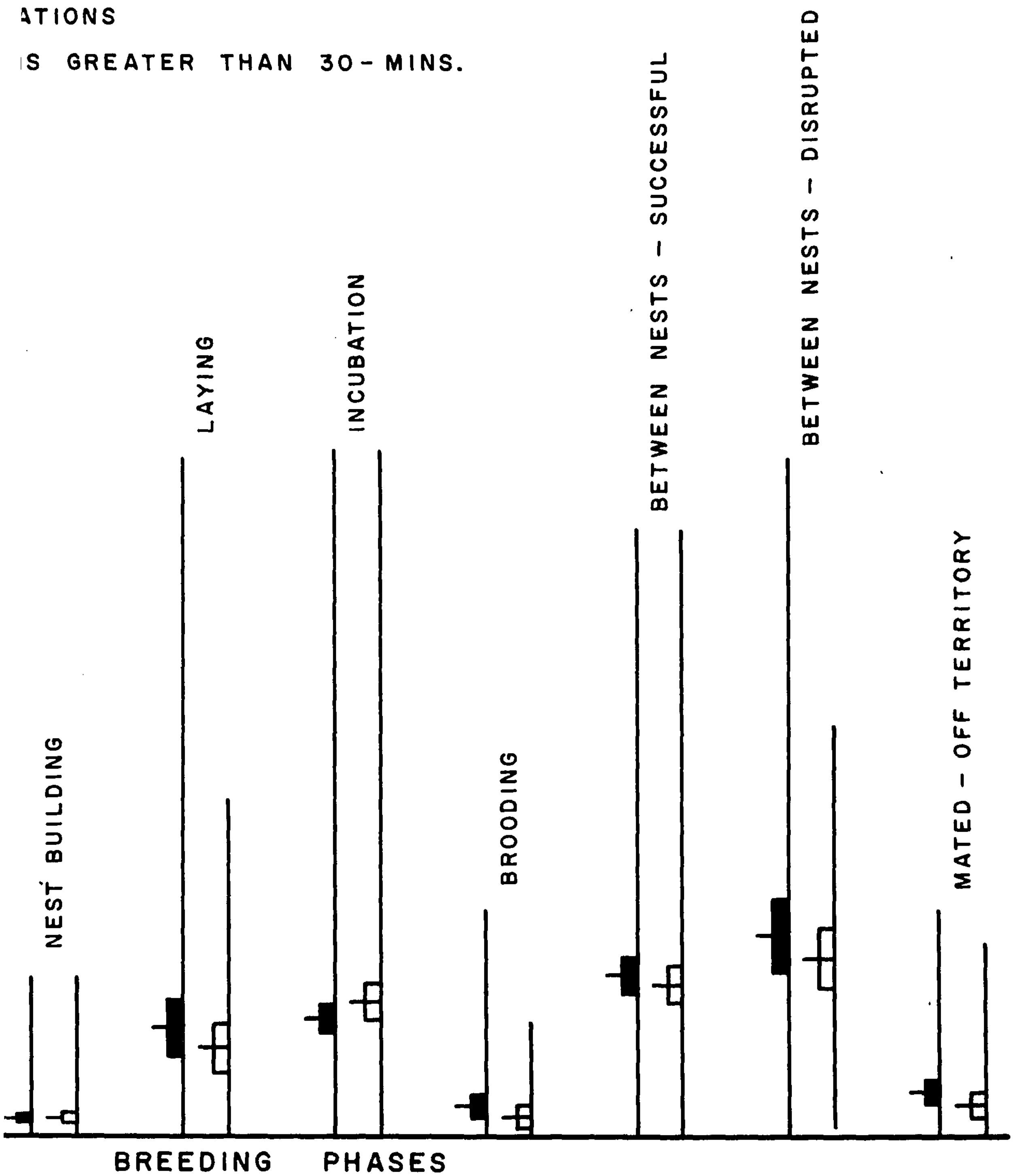
S GREATER THAN 30- MINS.



rom all observations with observations greater than 0 minutes. Vertical lines = means; rectangles = one standard error on either side of means.

data analysis was based upon information from all observations to take advantage of the larger sample size.

Pairing: By color-marking males as early as February, it was possible to collect information from near the onset of breeding activity until its cessation in September. Also, the total of 493 observations of approximately 488 hours was a much larger sample than had been obtained on any previous study of wild mourning doves.

Several investigators (Frankel and Baskett, 1961; Stone, 1963; and Jackson and Baskett, 1964) reported on the great effect of pairing on the rate of mourning dove perch-cooing. The results of this study confirm their findings that pairing is the most important factor affecting the rate and duration of perch-cooing.

Jackson and Baskett (1964) stated that unmated males cooed more than 13 times as often per three-minute period as did mated males. I found the differences to be large, but not of such magnitude (Fig. 5). Also, repeated observations of unmated males revealed that their calling rate decreased abruptly when they were actively courting a female, even though no pair-bond was formed. The mean rate for unmated males was 8.19 calls per three-minute period, but dropped to 3.11 calls when the male was attentive to a female. Later, when the female left, the male resumed calling at the higher rate. The mean rate for mated males was 1.21 calls per three-minute period. Mean calling rates were derived by dividing the total calls a male

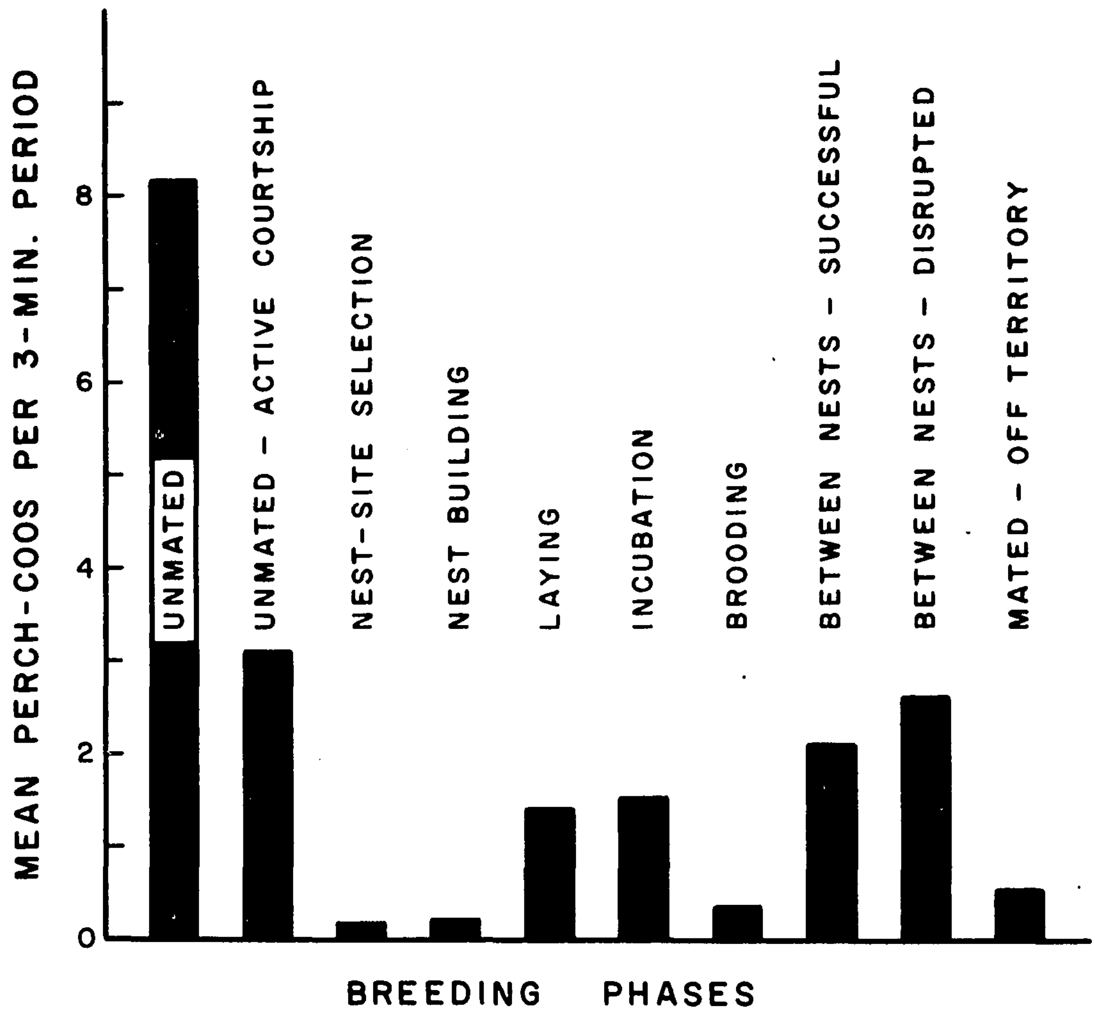


Figure 5. Comparison of rate of cooing of unmated males with that of mated males in various phases of the nesting cycle.

uttered in one morning by the number of three-minute periods during which he was observed that morning. Then the values for each morning were totalled and this mean of means calculated.

Accounts of prolonged observations of several marked males further illustrates the effects of unsuccessful courtship and also pairing on cooing. Male M9 was first seen on February 12, 1963 and last observed on April 5. His cooing rate was 7.45 coos per three-minute period during the 20 mornings when he was alone. But during the 12 mornings when he was actively courting females his cooing rate decreased to 3.36 coos per three-minute period (Fig. 6). This male, although he was attentive to several different females and copulated repeatedly with one over a period of two weeks, evidently did not form a firm pair-bond with any of them.

Male M32 was first observed on March 11, 1963. During nine mornings of observation through April 5 his cooing rate was 8.34 coos per three-minute period. During this interval he was never seen courting a female. On April 7 he was observed searching for a nest-site with a female. While searching for a nest-site and building his nest his cooing rate dropped to only 0.62 coos per three-minute period (Fig. 7). This male was observed regularly through five nesting attempts and his cooing rate never approached the earlier intensity.

Male M22 was nest trapped on March 1, 1963. After his capture he was never seen brooding the nestlings. His mate regularly

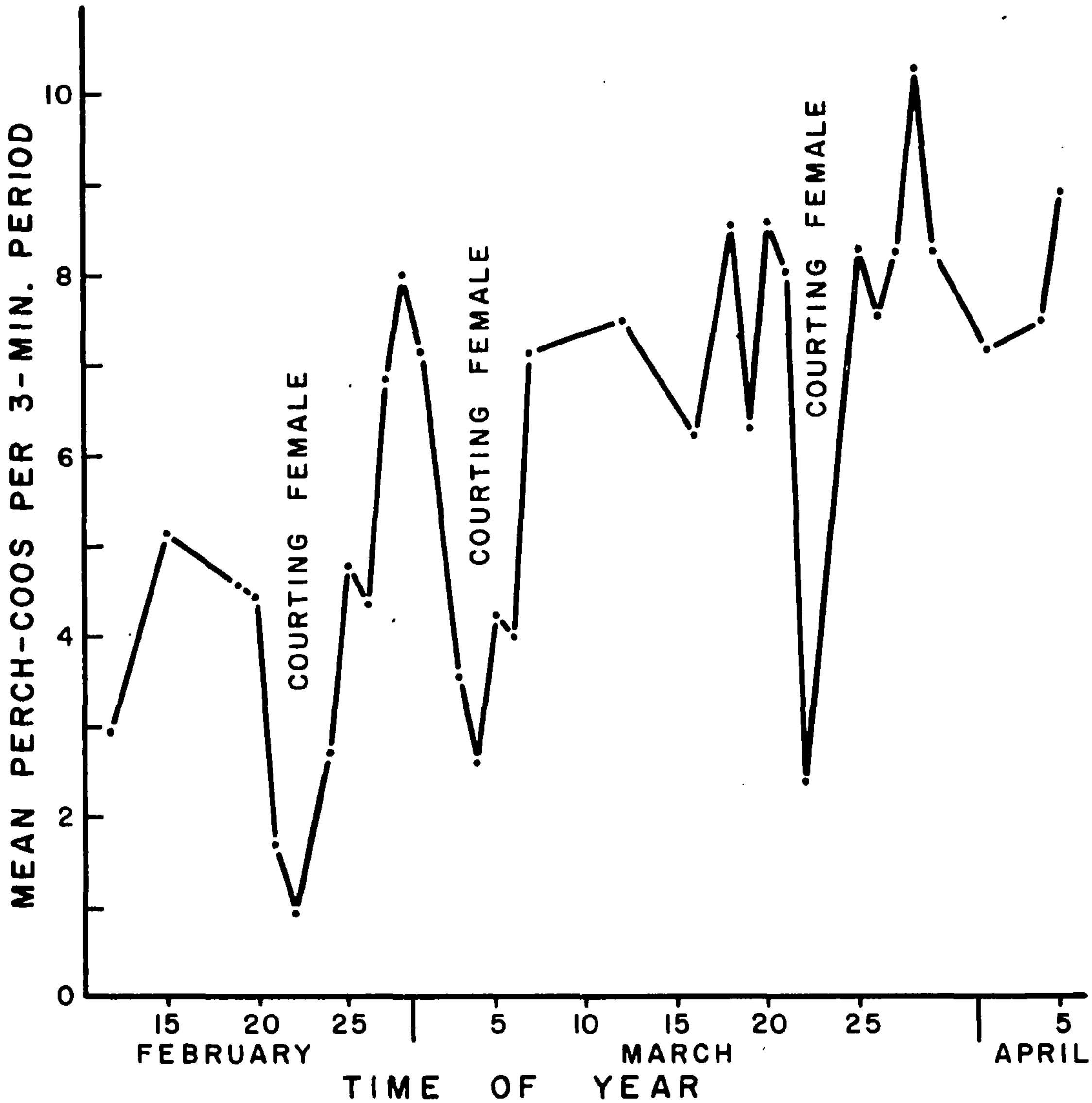


Figure 6. Effect of unsuccessful active courtship on the cooing rate of unmated male M9.

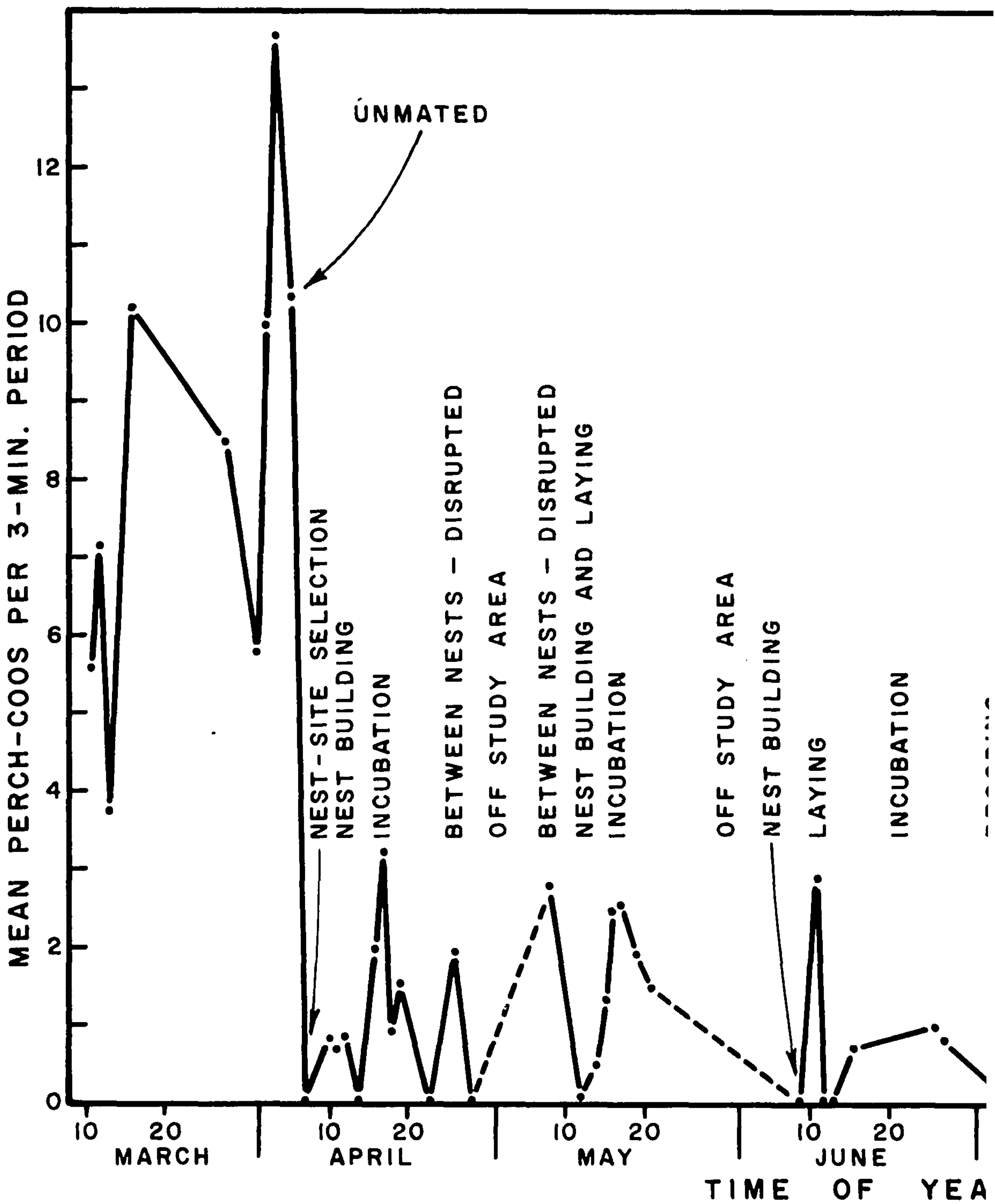
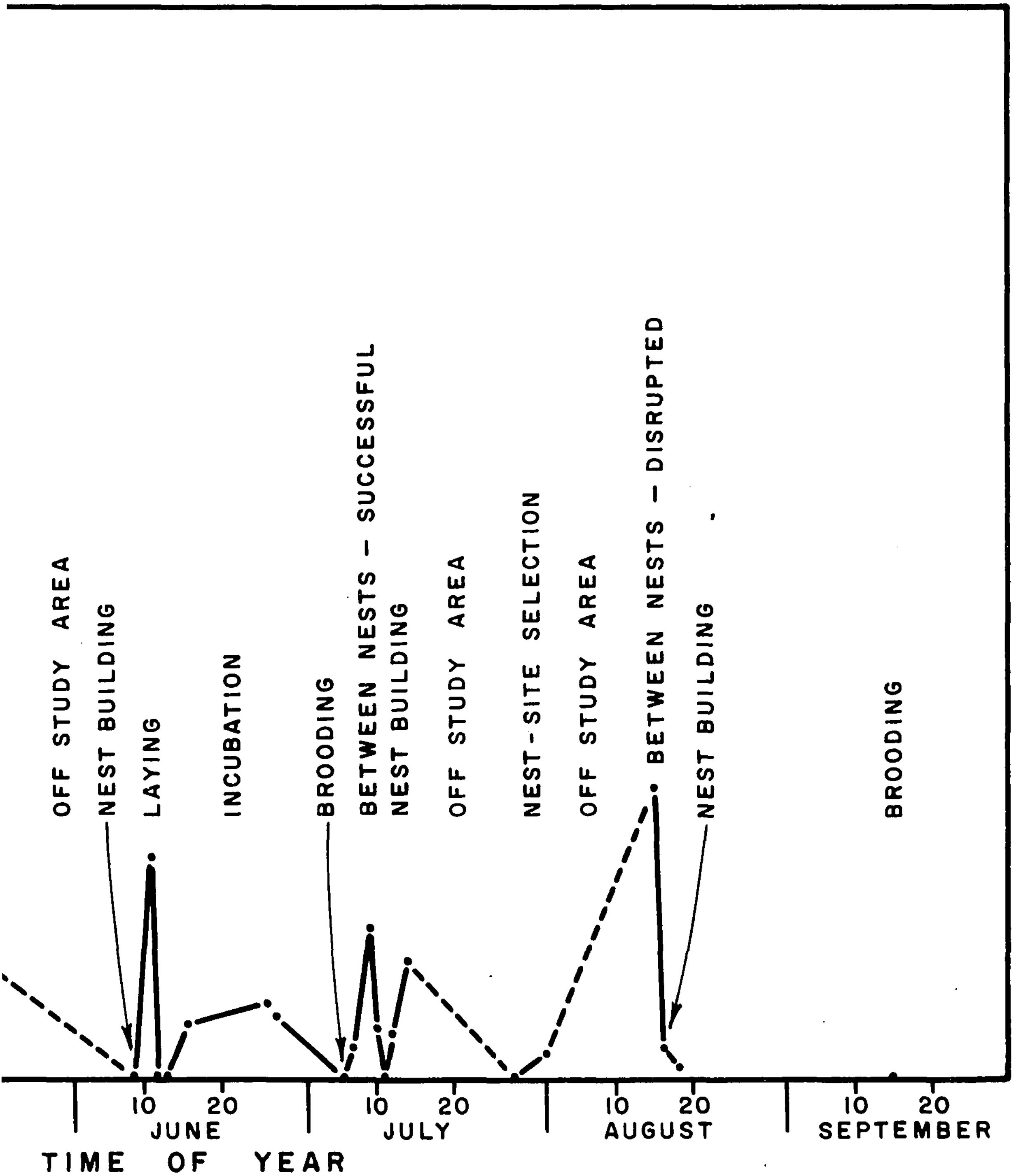


Figure 7. Effect of pairing and position in the nesting cycle on the c



ne nesting cycle on the cooing rate of male M32 brooded the young during the nights, and the young fledged a few days later. The female disappeared after the young fledged and was never seen again. However, the male returned to feed the young near the nest. He then abruptly began calling at a consistently high rate. For almost a month he was seen and heard, but never in the company of a female. On three mornings when records were kept, his cooing rate was 6.41 coos per three-minute period. On April 3 he was observed searching for a nest-site with a different female only 150 feet from his first nest. During five mornings of observations, while searching for a nest-site and building the nest, he did not utter a single coo (Fig. 8). The male's cooing rate remained low through incubation and brooding. His cooing increased to 2.29 coos per three-minute period after his young left the nest. This male was then driven from his territory by a nearby nest-building male. He left the study area and did not return until more than a month later. On June 24 he returned alone and his cooing rate was 7.37 coos per three-minute period. Two days later he began unsuccessfully courting another female, and his cooing rate dropped to 1.29 coos per three-minute period during four mornings of observation. His cooing rate then sharply increased to 5.76 coos per three-minute period for an interval of 17 days during which he was never seen in company with a female. Then, three days later on July 22, he was observed building a nest with yet another female approximately 250 feet from his original nest site. On this morning his cooing

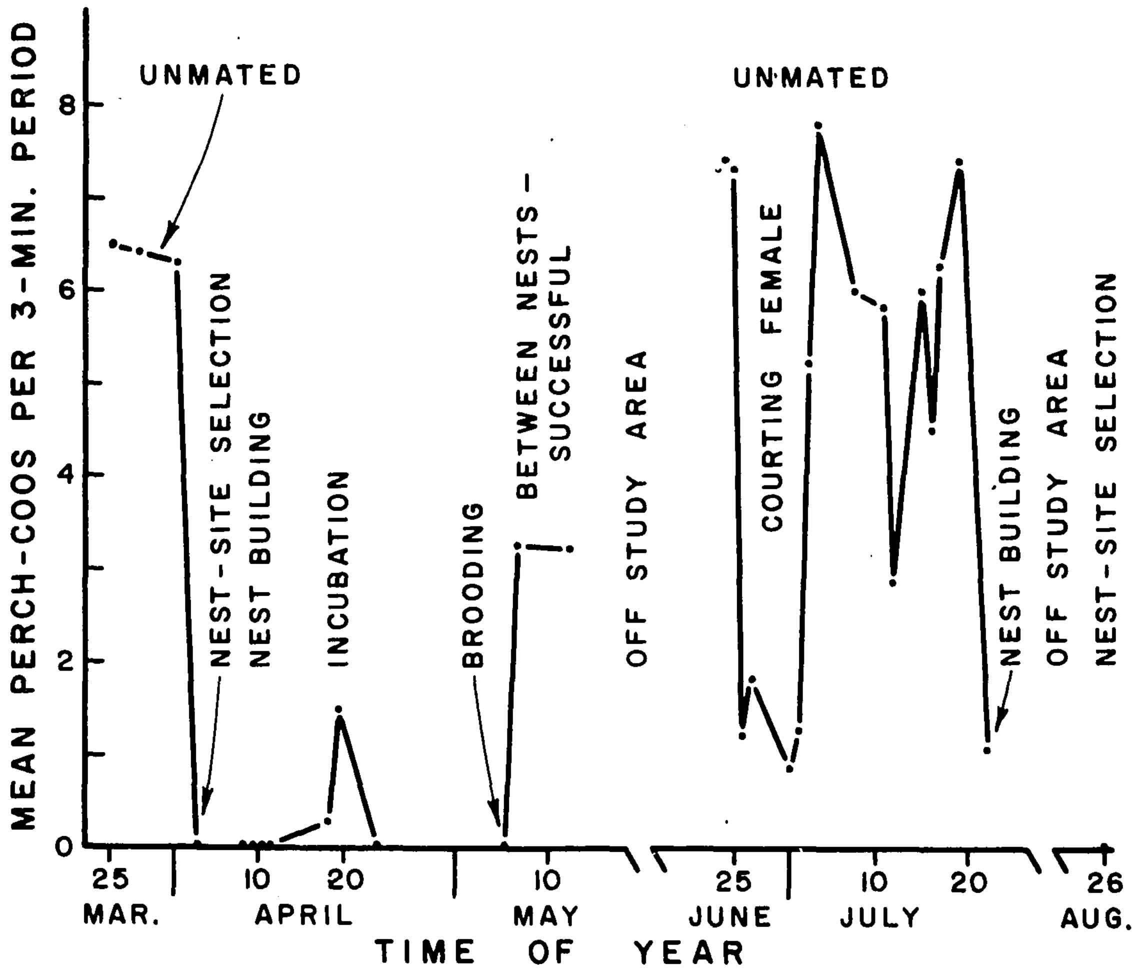


Figure 8. Effect of pairing and position in the nesting cycle on the cooing rate of male M22.

rate was 1.09 coos per three-minute period. This nesting attempt was broken up during incubation and the pair left the study area. On August 26, the pair returned and started searching for another nest-site. The male did not utter a single coo during the one morning of observation. The pair left the study area and were never seen again.

Position in the Nesting Cycle: A number of investigators have reported on the possible effects of position in the nesting cycle on cooing. Frankel and Baskett (1961), Stone (1963), and Jackson and Baskett (1964) found numerical differences in cooing rates during various phases of the nesting cycle. However, the differences were not statistically significant. Jackson and Baskett (1964) reported:

> The male's position in the nesting cycle had little effect on the rate of perch-cooing. Although there were some numerical differences in the mean rate of cooing among mated males in different phases of the cycles (Fig. 1), none were statistically significant at the 5 percent level. These data were based on observations of birds in successful nesting cycles. Data on birds prior to the first nesting and birds with disrupted cycles were not obtained. Cooing behavior of birds at these times might have been different.

Frankel and Baskett (1961) divided the nesting cycles of their penned doves into courtship and nest building, egg laying, incubation, and brooding. Jackson and Baskett (1964) divided the cycle of wild birds into building and laying, incubating, brooding, and between nestings. I divided the nesting cycle of wild doves into seven phases as follows: nest-site selection, nest building, laying, incubation, brooding, between nestings when the last nest was successful, and between nestings when the last nest was disrupted. This was done because of the relatively large sample data available with which to test the differences in cooing in the greater division of the nesting cycle. Those wishing to make direct cooing-rate comparisons with Jackson and Baskett (1964) may simply average the first three, and the last two phases above.

The present study, based upon 360 observations of 25 color-marked mated males and numerous unmarked mated males, found differences in the mean rate of cooing in different nesting phases to be statistically significant at the 5 percent level when subjected to an analysis of variance. Twenty-one t-tests were then made to determine exactly where the differences lay. Eight tests were not significant at the 5 percent level, two were significant, and 11 tests were highly significant. The t-tests are summarized in Table 3.

The mean cooing rates listed for the various nesting phases are based upon the cooing activities of the males around their nests. The listed rates do not take into account the portions of the two-hour morning period when the males were elsewhere, which were substantial during some phases of the nesting cycle, especially during incubation and brooding. While away from their nesting areas the males called little or not at all. Thus the listed rates represent maximum rather than average cooing rates for the complete two-hour morning period.

Table 3. Significance of differences in cooing rates between various phases of the nesting cycle by t-tests.

Nesting Phases	Nest-Site Selection	Nest Building	Laying	Incubation	Brooding	Between Nests-Successful	Between Nests-Disrupted
Nest-Site Selection	*						
Nest Building	NS	*					
Laying	HS	HS	*				
Incubation	HS	HS	NS	*			
Brooding	NS	NS	S	HS	*		
Between Nests-Successful	HS	HS	NS	NS	HS	*	
Between Nests-Disrupted	HS	HS	NS	S	HS	NS	*

NS - Not Significant
S - Significant (.05 Level)
HS - Highly Significant (.01 Level)

Nest-Site Selection: Perch-cooing by males decreased abruptly when the pair began selecting a nest-site. This was true whether the pair-bond was only recently formed or the pair had already made one or more nesting attempts. The only difference was that the selection of the initial nest-site usually spanned a longer interval of time, thus the first nesting had a longer period during which the male's cooing rate approached zero. Three of four pairs observed selecting their initial nest-site took more than a week before they began building the nest. The other pair took four days. In contrast, doves selecting later nest-sites usually began building on the first to third day after starting the search for a new nest-site. The mean cooing rate of six marked males and 14 unmarked males during 34 observations of nest-site selection was 0.19 coos per three-minute period. The perch-coo was largely substituted with the softer and shorter nest call which will be discussed in a later section.

Nest Building: When the pair actively started building a nest, the male's perch-cooing rate increased only very slightly. The mean cooing rate of 17 marked males and about 24 unmarked males during 100 observations of nest building was 0.21 coos per three-minute period. As with nest-site selection, the construction of the first nest proceeded at a more leisurely pace than did subsequent nest constructions. Thus the period of little perch-cooing was lengthened further in the first nesting attempt when compared with later nestings.

Egg Laying: Twenty-six observations of 10 marked males and four unmarked males were made while their mates were laying eggs. The males' perch-cooing rate increased sharply to 1.41 coos per three-minute period. This cooing increase was probably a result of the males having been released from the chores of nest construction. Although the males now spent less time around the nest than when they were constructing it, more of their energy was expended in cooing. The females laid their two eggs on successive or alternate days; therefore the egg laying phase was usually the shortest part of the nesting cycle.

Incubation: Incubation began immediately after the laying of the second egg. If it was laid in the morning the male incubated first; if it was laid in the evening the female remained to incubate that night. Data for the incubation period were obtained during 93 observations of 13 marked males and six unmarked males. During incubation the mean cooing rate increased further to 1.53 coos per three-minute period. Although this increase was not significantly different from the preceding short egg laying phase, it was significantly different from the nest-site selection and nest building phases. This increased rate of cooing persisted for the full 14 or 15 days of incubation. However, the listed cooing rate does not include portions of the two-hour morning period when the males were feeding and watering off their nesting areas.

On many mornings of observations during incubation phases, males failed to show up in their territories until after the end of the regular two-hour observational period. Some males regularly arrived near their nests before sunrise, spent various lengths of time cooing and preening, and then left. Occasionally these males returned again before the end of the observational period. Other males did not show up near their nests until late in the period and spent the remainder of the time either quietly preening or occasionally cooing. Their cooing activities appeared to depend upon the activities of other nearby males; this is discussed in a later section of this report.

Some males, during the incubation phase of their first nesting attempt in March and April, cooed at a higher rate than they did in subsequent nesting attempts. This increased calling rate was probably affected by the nearby presence of a number of highly active unmated males. Although males incubating early in the year cooed at higher rates than they did later in the nesting season, the differences were not significant at the 5 percent level when subjected to an analysis of variance.

Brooding: When the eggs hatched and brooding began the males curtailed their cooing activities. Now most of their morning and evening activities were channeled into food gathering, both for their own body maintenance and the development of their young. The mean cooing rate was 0.37 coos per three-minute period, based upon 24 observations of 11 marked males and three unmarked males. This decreased cooing rate was highly significant when compared with the preceding incubation phase. Not only were the males calling at a much lower rate, they also spent less time around their nests. Many morning periods were spent fruitlessly waiting for a brooding male to show up. This resulted in the smallest sample size of all the phases, despite the long brooding period (10 to 14 days) and the many nests under observation. Males cooed during only eight of the 24 observations, and mostly during late brooding when the males were reopening courtship in preparation for the next nesting attempt. Thus brooding may be classed, along with nest-site selection and nest building, as a very quiet phase of the mourning dove nesting cycle.

Between Nests: The between nests phase of the nesting cycle was the interval between the end of one nesting attempt and the start of nest-site selection for the next. The length of this interval varied from zero days to 18 days. Although there were a few exceptions, it was generally true that when a nest was disrupted the pair would not start a new nest until a week or more later. However, if the nest was successful the pair normally initiated the next nest almost immediately. Separate records were kept of the cooing behavior of males who had just successfully or unsuccessfully completed a nesting attempt.

Fifty-nine observations were made of 13 marked males and one unmarked male whose last nest had been successful. The mean cooing rate was 2.11 coos per three-minute period. This represents a highly significant increase over the cooing rate of brooding males. Not only were the males cooing at an increased rate, they were now spending much more time around their nesting areas. Thus the listed cooing rate more nearly approaches an average rather than maximum rate. The males, now freed from their daytime brooding duties, could spend more early morning time cooing and then do their feeding later in the day. The effect of being relieved of the rigors of an active nest were pronounced on the cooing activities of Male M170. This male was observed during two consecutive successful nestings. While searching for a nest-site, nest building, laying, incubating, and brooding, his mean cooing rate was only 0.17 coos per three-minute period. But during the interval between the two nests, a period of eight days, his mean cooing rate increased to 4.33 coos per three-minute period.

Twenty-four observations were made of seven marked males and one unmarked male whose last nest had been disrupted. The mean cooing rate was 2.64 coos per three-minute period. If the nest was disrupted during the incubation phase, the cooing rate increased significantly. But if the nest was disrupted during the brooding phase, the increased cooing rate was highly significant. Although the cooing rates after successful and disrupted nests were numerically different, these differences were not found to be significant. Normally, the pair of doves whose nest was disrupted reacted in one of two ways. They either stayed in the vicinity of the disrupted nest for a period of a week or more before starting to renest; or they abruptly left the area, only to return in a week or more and start searching for a new nest-site.

Effect of Time of Day on Cooing: A number of field investigations (Duvall and Robbins, 1952; McGowan, 1952, 1953; Peters, 1952; Mackey, 1954) studied the effects of time of day on the cooing behavior of doves. More recently, two investigations (Frankel and Baskett, 1961; Jackson and Baskett, 1964) delineated the differences between the daily cooing behavior of both unmated and mated males. All studies generally agree that morning cooing is at a peak at or before sunrise.

To measure the effect of time of day on the cooing activities of doves during this study the data were analyzed in the following manner. The two-hour morning period was divided into eight 15-minute periods. Thus two periods occurred prior to sunrise and six periods after sunrise. Then all observations within each of the 15-minute periods were totalled, and the number of coos divided by the number of three-minute observations. This resulted in eight mean cooing rates for unmated males, and eight for each phase of the nesting cycle for mated males. For mated males, the average cooing rate for each 15-minute period was the mean of the means of all nesting phases.

These data are presented in Figure 9. The results agree closely with the findings of Frankel and Baskett (1961) that dove cooing peaks about 30-15 minutes prior to sunrise and then decreases, the unmated males gradually and mated males sharply. Unmated males

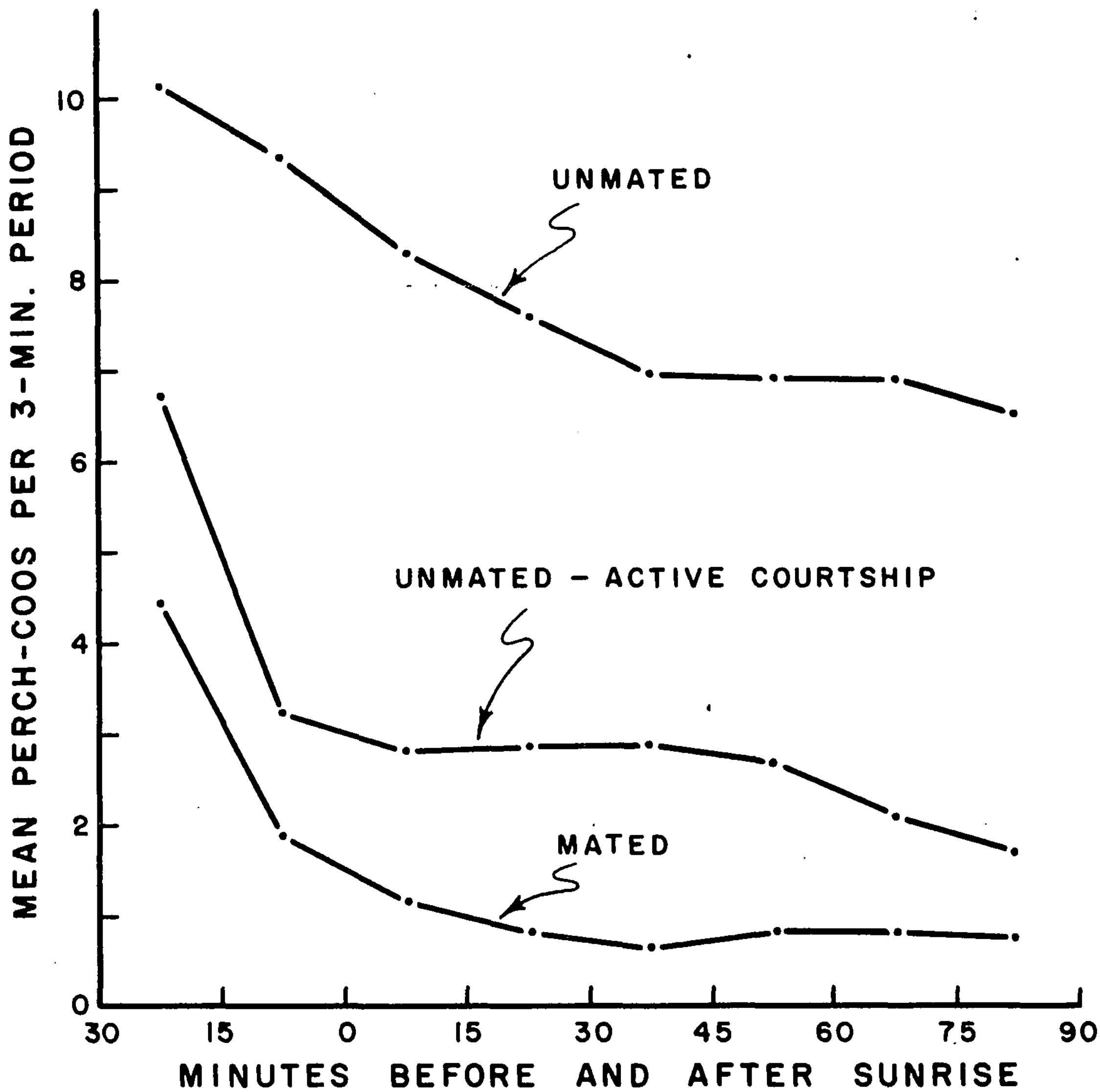


Figure 9. Comparison of cooing patterns of mated and unmated males.

cooed at a mean rate of 10.18 coos per three-minutes during the first 15-minute period and then gradually decreased to 6.47 coos per three-minutes during the final 15-minute period. Mated males cooed at a mean rate of 4.44 coos per three-minutes during the first 15-minute period. The cooing rate decreased sharply to 1.95 coos per three-minutes during the next 15-minute period and then gradually decreased until they were calling at a rate of only 0.75 coos per three-minutes during the final 15-minute period.

Figure 10 shows the effect of time of day on the cooing rates of males in various phases of the nesting cycle. The differences in cooing rates between nesting phases are more pronounced after sunrise. As discussed in the previous section, the mean rate of cooing of males in the incubation phase included data from early nests (March and April) and is greater than cooing rates computed from later nesting attempts. Thus the cooing rates of males incubating after April would be slightly less than is shown in Figure 10, with the decrease occurring during the first 90 minutes of the two-hour period.

Effect of Other Calling Males: Mackey (1954) stated: "Whether or not the cooing of one male dove can stimulate other males to coo is a question that can not be decisively answered. Interpretations of this type of behavior vary with the ability and personal beliefs of the observer." He went on to say that during his study it appeared that the cooing of one male dove frequently stimulated another male to coo.

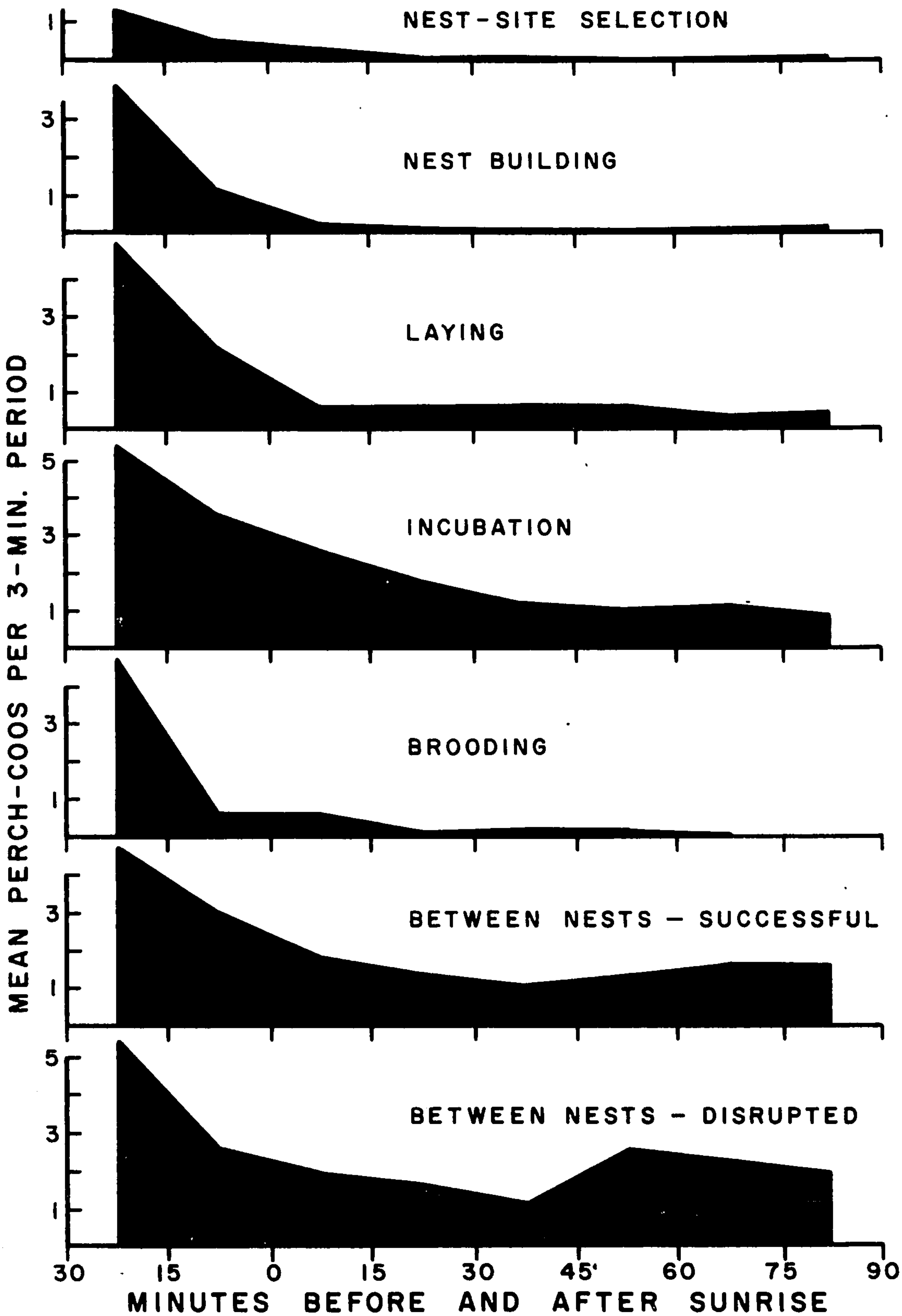


Figure 10. **Effect of time of day on the rate of cooing of males in various phases of the nesting cycle.**

Other dove investigations (McClure, 1939; Duvall and Robbins, 1952; Southeastern Assn., 1957; Cohen, Peters, and Foote, 1960) agreed that the calling of one dove might stimulate other nearby doves to call. Thus at high population levels, more audio and visual contacts would stimulate birds to call more than at low population levels.

My study, based upon numerous observations of individuals and groups of doves, shows that the calling rate of an individual mated dove is affected by sight or auditory contacts with other doves. But unmated doves usually called throughout the two-hour morning period unless they were actively courting a female or were feeding. This cooing behavior persisted regardless of whether or not other males were cooing nearby or were in sight. The study by Jackson and Baskett (1964) based upon a "moderate-density" dove population found a mean cooing rate of 8.40 coos per three-minute period for unmated males. The present study, based upon a more dense population of doves, found the mean cooing rate of unmated males to be 8.19 coos per three-minute period. Although the dove density--and thus the number of visual and auditory contacts--was different in the two studies, the cooing rates of unmated males were not materially different. Also, the most persistently calling male recorded during my study was a marked unmated male whose mean cooing rate over a period of four days was 14.75 coos per three-minute period. This performance was in early July when cooing by other males was much less than earlier in the year.

Any stimulating effect by other calling males on the cooing behavior of a solitary unmated male would be hard to measure because of its already exuberant cooing activity.

In contrast, the cooing activity of mated males was generally affected by sight and auditory contacts with other nearby doves. Again comparing the findings of the study reported on by Jackson and Baskett (1964) and the present study, the mean cooing rate of mated males in the "moderate-density" population was only 0.63 coos per three-minute period. In the present study of a more dense population, the mean cooing rate was 1.21 coos per three-minute period, an increase of almost 100 percent. An analysis of the calling behavior of doves in the paddock area and the hospital area gives further insight into the effect of density on calling intensity. Both areas had approximately 15 pairs of breeding doves in 1963. The hospital area, consisting of five acres, thus had a density of three pairs per acre, and there were 65 nesting attempts. The paddock area of 15 acres had a breeding density of one pair per acre, and there were 68 nesting attempts. A comparison of calling records accumulated during 27 weekly two-hour periods on each area shows that an average of 616 calls per two-hour period was heard on the more densely populated hospital area and only 417 calls per two-hour period on the paddock area.

A comparison of the cooing rates of individual males on the two areas also substantiates my belief that cooing is increased with more sight and auditory contacts with other doves. The average cooing rate of males in the hospital area was approximately twice that of paddock area males during nest-site selection, nest building, and brooding. The hospital area males also called more during incubation but the difference was not as pronounced. Males on the two areas called at approximately the same rates during laying and between nests phases. Carrying this comparison further, individual males actively nesting on the hospital area cooed at an average rate of 0.74 coos per three-minute period. This average does not include the between nests phase. Multiplying the 0.74 rate by the estimated maximum of 15 nesting males gives a total of 444 coos per morning period. The actual average number of coos heard per morning period during the peak of nesting in May and June was 405 coos, a close agreement. In comparison, individual males actively nesting on the paddock area cooed at a lower average rate of 0.56 coos per three-minute period. Multiplying the 0.56 rate by the estimated 15 nesting males gives a total of 336 coos per morning period. The actual average number of coos heard per morning period during May and June was 333 coos, a very close agreement.

Observations of one marked male serve as an illustration of the effect of other nearby doves on the cooing behavior of an individual dove. This dove, male M133, nested within 50 feet of two other active dove nests in the hospital area. His nest area was under observation for nine mornings during one incubation phase. On five mornings there was other dove activity nearby, and this male cooed at an average rate of 2.85 coos per three-minute period. He remained around his nest for an average of 67 minutes per two-hour period, chasing off other doves that lit nearby or passed overhead. On the four mornings when there was little or no other nearby dove activity, he only cooed at an average rate of 1.13 coos per three-minute period. He also stayed around the area less on quiet mornings, an average of only 29 minutes per two-hour period.

Effects of Weather Conditions: A number of investigators have studied the relationships of temperature, humidity, wind, barometric pressure, rainfall, and cloud cover to cooing activity (McClure, 1939; Webb, 1949; Duvall and Robbins, 1952; McGowan, 1953; Mackey, 1954; Southeastern Assn., 1957; Frankel and Baskett, 1961; Stone, 1963). In many cases statistical analyses were not made, nor were the interaction of two or more influents considered. In general, these investigators agreed that extreme weather conditions, especially temperature, wind, and rainfall, may result in a decrease or cessation of cooing activity. But small daily changes had little effect or none at all.

The present study considered only temperature, wind, rainfall, moonlight, and cloud conditions. Temperatures were recorded at the beginning and at half hour intervals during each morning of observation. Wind velocity and cloud coverage were recorded at the start and end of each observation, with changes noted as they occurred.

Rainfall was recorded as light or moderate as it occurred.

Temperature fluctuations normal for the Tucson area did not measurably influence dove cooing activity. Males cooed at high rates during two-hour morning periods when the temperatures ranged from a low of 24°F to a high of 88°F. During the cooing season (mid January to mid September) the daily temperature on the study areas ranged from a minimum of 15°F to a maximum of 110°F. The greatest cooing activity on the study areas occurred in March and April, when night-time temperatures frequently dipped below freezing; and again in July and August, when daytime temperatures frequently exceeded 100°F. However, the higher cooing activity was a result of more unmated and transient males in March and April, and the addition of cooing by early-hatched immature males in July and August. Prolonged observations of marked males through wide temperature ranges gave no evidence that temperature had any measurable influence on cooing in the two-hour early morning period. The effect of high temperatures on cooing after the early morning period was not considered in this study, but incidental observations indicated that such temperatures may depress cooing and other activities. However, morning and evening cooing was highly erratic even in moderate temperatures.

McClure (1939) reported that light winds decreased audibility and cooing activity somewhat, medium winds lowered activity more, and strong winds stopped cooing activity altogether. Most other authors agree; however, Mackey (1954) found no cooing decreases because of winds of less than 10 to 12 MPH. Also, Frankel and Baskett (1961) found no significant correlation between wind and cooing activity of penned doves. The present study agrees closely with Mackey's findings. Winds never exceeded Beaufort 3 (8-12 MPH) during observations of individual males. Thus the effect of stronger winds on cooing was not ascertained during this study. However, any increase in wind velocity certainly decreases the audibility radii and therefore adversely affects any attempt to count cooing doves. I found no direct evidence that wind had any influence upon the cooing of an individual dove. As with temperature, the influence, if any, of wind was completely overshadowed by the effects of pairing, position in the nesting cycle, and dove density.

The Southeastern Assn. (1957) reported that light rains have a depressant effect upon cooing, and that dove calling practically ceases during heavy rains. Mackey (1954) stated that light rain did not inhibit cooing but that heavy rain caused dove cooing to cease. The present study, conducted in an arid region, adds little to the knowledge of the effects of rainfall on dove cooing activities. The few light showers that fell during the early morning observation periods had no effect upon cooing. All cooing doves, whether exposed or not, continued to coo during the showers. Even in February, with low temperatures, doves continued to coo during light rainfall. As with wind, rainfall could decrease the audibility radii without actually affecting the calling doves themselves.

Most dove investigations mentioned above found no significant correlation between cloud cover and cooing activity. However, some evidence was found that overcast mornings delayed initiation of cooing for as much as 15 minutes (Mackey, 1954), and Webb (1949) stated that doves may coo for longer periods when the morning is cloudy than when it is clear. The present study investigated the effect of cloud cover on both individual and groups of doves. No evidence was found that cloudiness had any influence on cooing intensity. But heavy cloud cover did at times delay the initiation of dove cooing, especially early in the breeding season. Thirty-two observations of one marked unmated male were made in February, March, and early April. On clear mornings this male consistently arrived in his display territory and began cooing at least one-half hour before sunrise. On mornings when cloud cover was 90-100 percent he arrived and began cooing 9-12 minutes later. On mornings when the sky was neither clear nor overcast, this male arrived from his roosting area and began cooing only a few minutes later than on clear mornings. These observations agree with Welty's (1962) suggestion that ". . . light is the chief trigger which sets off awakening song in birds." However, later in the breeding season, awakening song was usually well in advance of one-half hour before sunrise. Thus any cooing delay caused by overcast conditions would have little influence on cooing during the standard two-hour morning period.

The effect of bright moonlit nights on dove calling has not been reported on. Welty (1962) reported that such nights were associated with earlier singing of robins. Data from the present study reveal that bright moonlight may influence doves to start cooing a little earlier than normal. Again, however, such influence is negligible when considering dove calling during the standard two-hour morning period. On the one morning when bright moonlight occurred with complete cloud coverage, the two influents canceled each other out with the result that dove cooing started as if neither influent was operating.

Mated Males Off Territory: Jackson and Baskett (1964) reported that ". . . mated males often did not remain within their territories the full 2 hours, and when they were outside their territories they did not coo." This is the only study that has reported on the differences in cooing behavior of mated males on and off their nesting territories.

During the present study 12 marked mated males, and one unmarked mated male, were observed away from their nesting territories a total of 36 times during the two-hour morning periods. Their average cooing rate was 0.57 coos per three-minute period. Incidental observations of a much larger number of male doves feeding, watering, and loafing away from any possible nesting territory suggest that this cooing average is higher than actually exists in the local dove population. Chance alone, or simply redoubled efforts on the part of the observer to pursue the more active males off their nesting territories, could have resulted in the seemingly high cooing rate. Six of the 13 males observed did coo when they were off their nesting territories. Thus the fact remains that some males do call off their territories, although at a lesser rate.

To a great extent, cooing by mated males off their territories was influenced by the nearby presence of other doves. Whenever mated males were feeding alone they never cooed, but if their feeding activities brought them in contact with other doves they frequently uttered a few perch-coos and then resumed feeding. Also around watering places many males cooed a few times. This happened all too frequently to be the behavior of unmated males only. On the study areas and along the coo-count route many doves were seen alighting on power lines, cooing several times, and then flying off out of sight. These instances were also too numerous to represent unmated males only.

One marked mated male was observed off his territory seven times during the early morning periods. This male never uttered a sound although he was frequently near other cooing males. Even during numerous afternoon observations he was absolutely quiet. No doubt a number of other mated males exhibited this quiet behavior away from their familiar nesting territories.

As reported by Jackson and Baskett (1964), the territory and nest-site may be changed as the pair enters a new nesting cycle. Such behavior was frequently observed during the present study. Several males habitually returned to their former territories to feed their recently fledged young or, later, to simply coo and preen. This occurred even though their former and present territories were separated by two or more active dove territories. Such actions were considered to be off territory cooing. Other marked males were often observed cooing within one foot of an adjacent active dove nest when the rightful male was not around. These actions were not considered to be off territory.

Probability of Hearing a Cooing Dove

The previous sections dealt primarily with male dove cooing rates, valuable statistics for evaluating various internal and external influences on cooing intensity. However, as the present system of censusing mourning doves depends primarily on the number of doves cooing, it is most important to know the mean probability that mated and unmated males will coo during any one three-minute listening period.

Despite the numerous investigations that have studied the cooing behavior of doves, only the study reported on by Jackson and Baskett (1964) analyzed the mean probability values. They stated that ". . . the chances of an unmated male's cooing once during any 3-minute period are about four times those of a mated male's cooing if the position of the mated male in the cycle is not considered." They reported that the mean probability for unmated males was 0.93 and for mated males only 0.23. The values were derived by dividing the number of three-minute periods in which each dove cooed by the number of periods during which it was observed.

Data from the present study were analyzed in a similar manner. However, the much larger sample data enabled me to also derive probability estimates for each of the eight 15-minute periods of the morning observation period (Table 4). It is readily apparent from the values listed in this table that the probability of hearing a male dove coo is highly variable. This variability is a result of the time of day; whether the male is mated or unmated; and, if the male is mated, its position in the nesting cycle. The data on mated males were subjected to several analyses of variance with the following results: (1) probability differences between nesting phases were significant, with the differences found primarily in the last hour where they were highly significant, and (2) the greater probability of hearing a mated male coo during the first hour was significantly different from the second hour.

Cooing and Production Relationships

I studied the possibility of using dove cooing behavior as an index to production. In 1962 weekly coo-counts were made on the

Table 4. **Estimates of mean probability of a male dove cooing during any three-minute period within successive 15-minute portions of the standard morning census period.**

15-Minute Periods of Two-Hour Census Period	Unmated	Mated - On Territory: Nest-Site Selection	Nest Building	Laying	Incubation	Brooding	Between Nests-Successful	Between Nests-Disrupted	Average
1	0.98	0.26	0.65	0.92	0.74	0.91	0.89	0.91	0.75
2	0.98	0.11	0.24	0.52	0.65	0.29	0.58	0.60	0.43
3	0.94	0.09	0.06	0.22	0.54	0.12	0.47	0.45	0.28
4	0.92	0.02	0.06	0.17	0.36	0.05	0.47	0.36	0.21
5	0.92	0.05	0.03	0.23	0.34	0.07	0.30	0.21	0.18
6	0.95	0.04	0.03	0.25	0.31	0.09	0.36	0.50	0.23
7	0.91	0.04	0.03	0.16	0.32	0.04	0.41	0.50	0.21
8	0.89	0.03	0.04	0.15	0.26	0.00	0.35	0.45	0.19
Average	0.94	0.08	0.14	0.33	0.44	0.20	0.48	0.50	0.31
First hour	0.96	0.12	0.25	0.46	0.57	0.35	0.60	0.58	0.42
Second hour	0.92	0.04	0.03	0.20	0.31	0.05	0.36	0.42	0.20

paddock area throughout most of the breeding season, but coo-counts were made on the hospital area only during the latter part of the season. In 1963 weekly coo-counts were made on each area throughout the complete breeding season, February through early September. The areas were thoroughly checked for dove nests on the same days that coo-counts were made. Records were kept on the fate of each dove nest.

A graphical analysis of these records is given in Figures 11 and 12, and reveals an interesting relationship in light of the cooing behavior of mated males discussed in previous sections of this report. The initial peak of cooing occurred in March. This peak represented the cooing of winter residents and transient males, a fact verified by sight and trapping records. Later, another cooing peak was reached in late April as the migrating segment of the local breeding population returned. The conclusion that this peak represented returning breeders was substantiated by sight and trapping records and the fact that the sharp increase in nesting efforts which followed was the result of an abrupt increase in breeding pairs. These early season cooing peaks have not been reported in previous dove investigations and the reason is now obvious. By the time the migrating dove populations had reached their more northern latitude breeding areas there were relatively few unmated males, and the pairs were in advanced breeding condition and began nesting with little courtship activity.

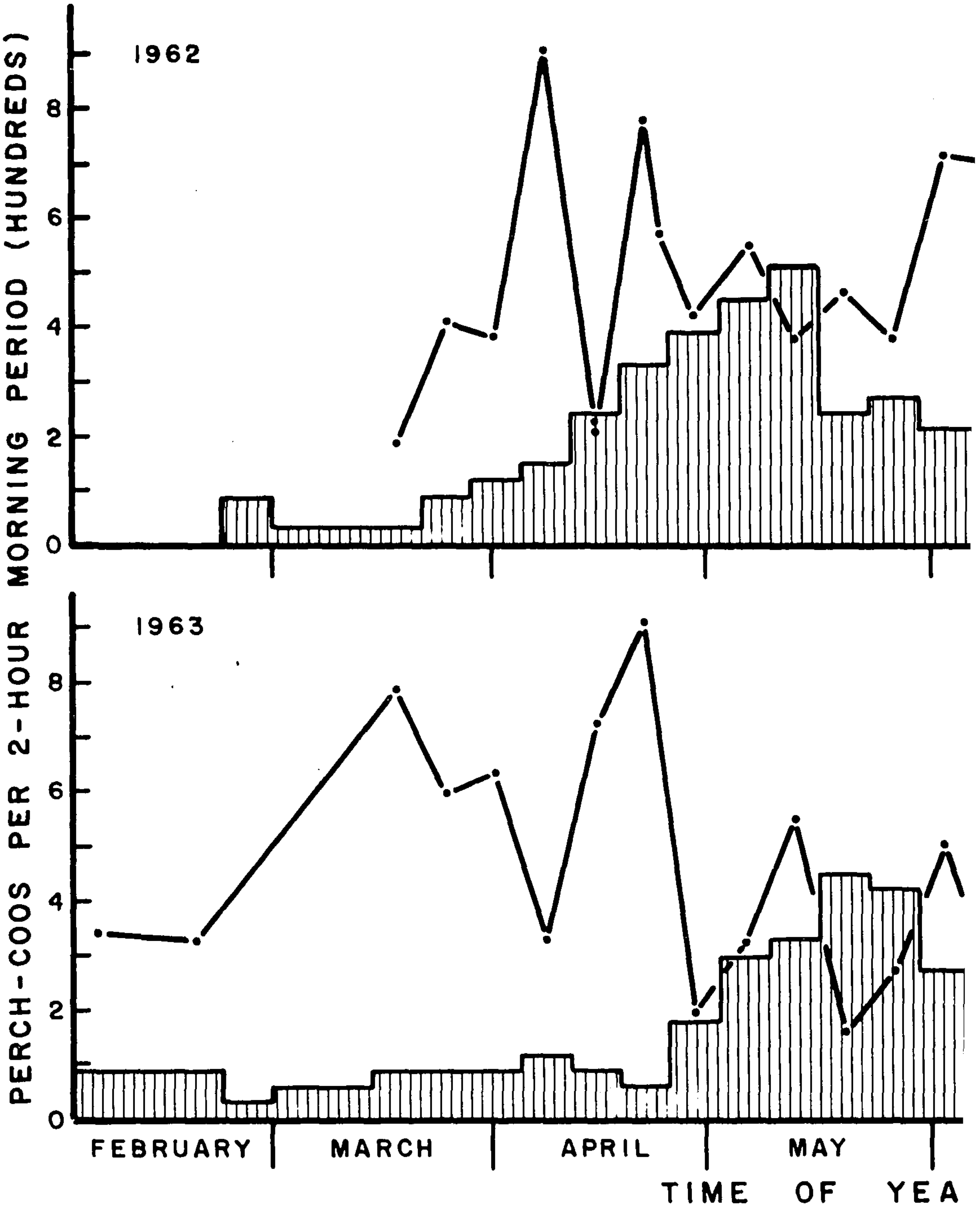
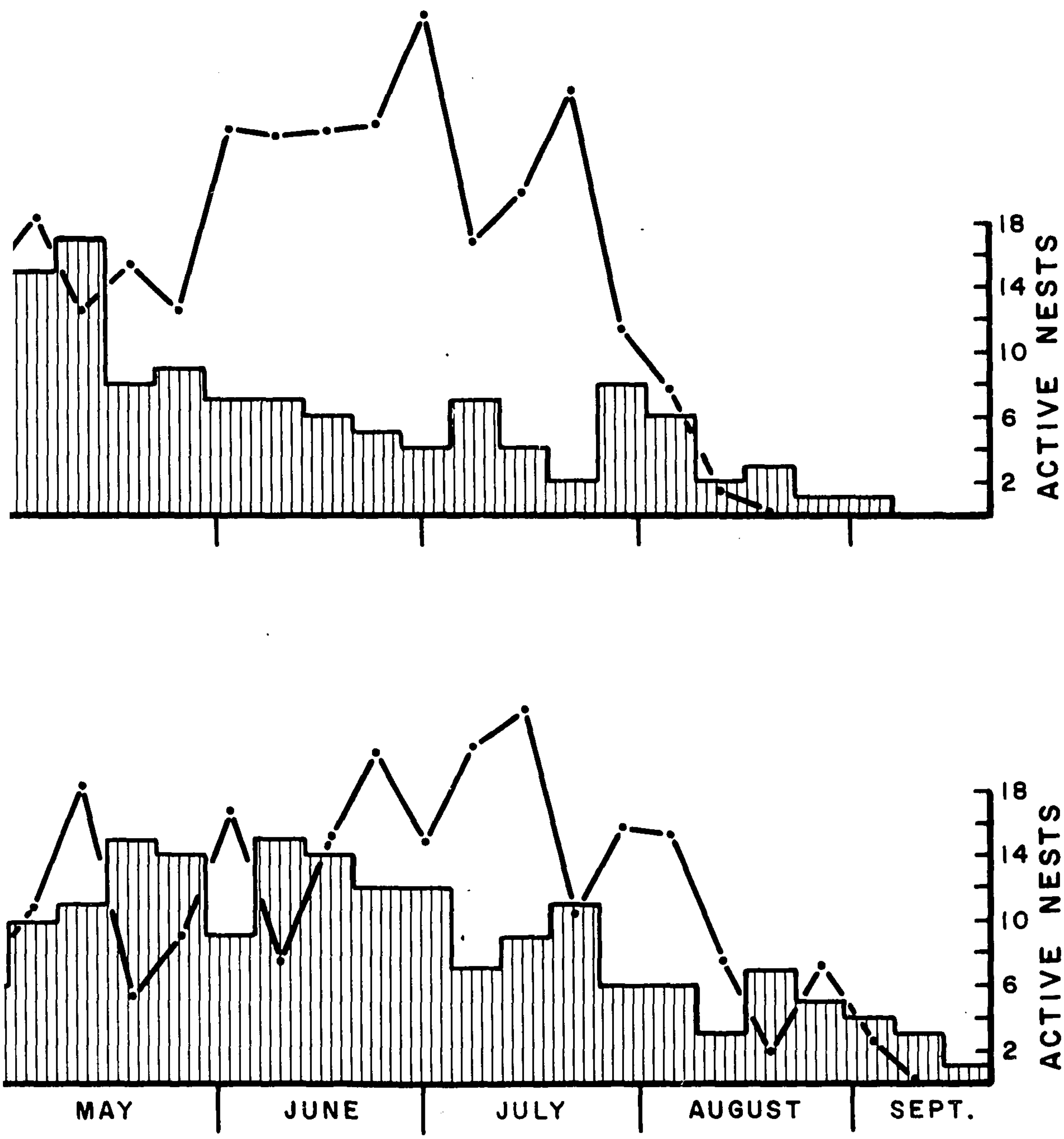


Figure 11. Relationship between cooing and number of active nc



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umber of active nests on the paddock area in 1962 and 1963.

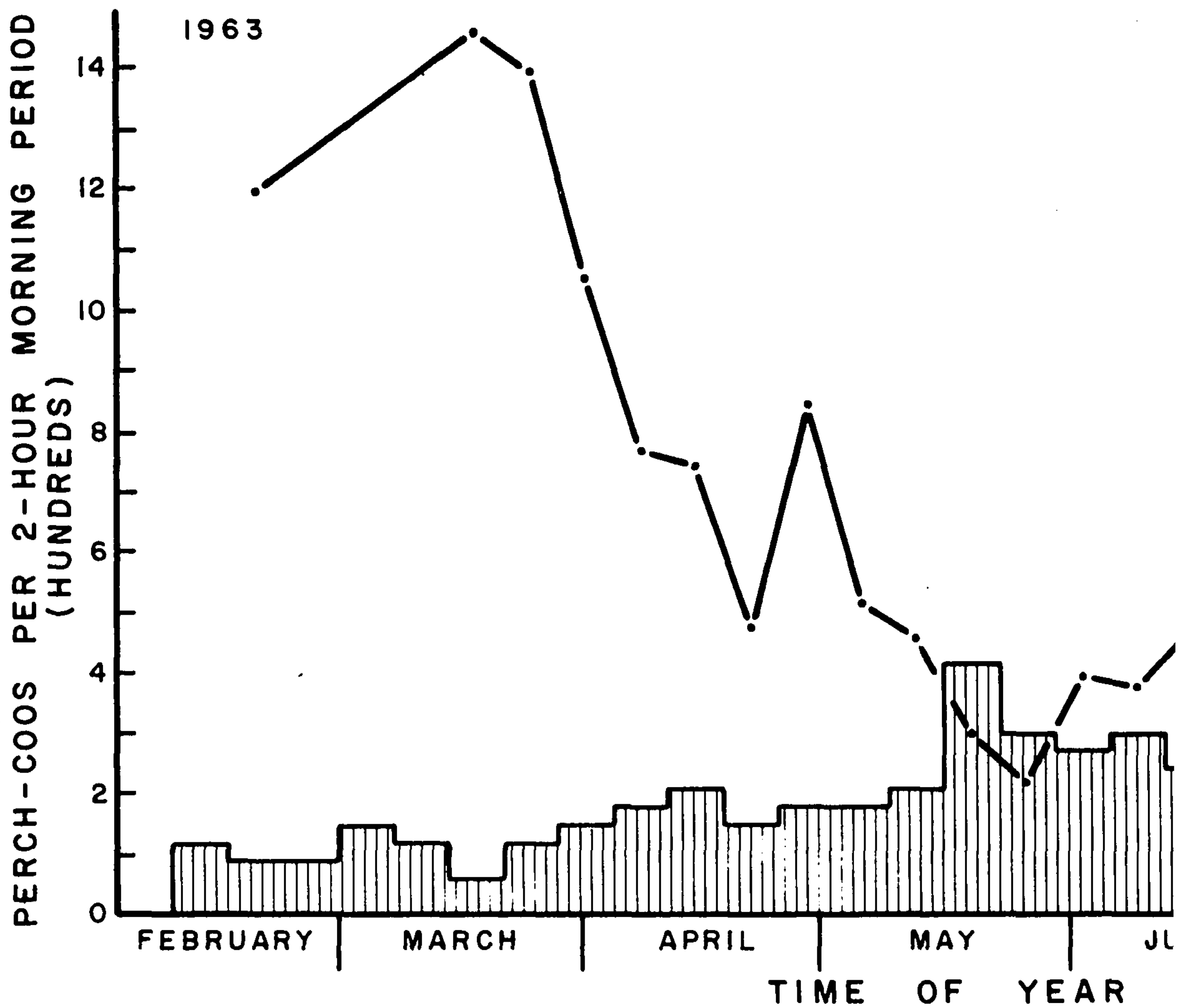
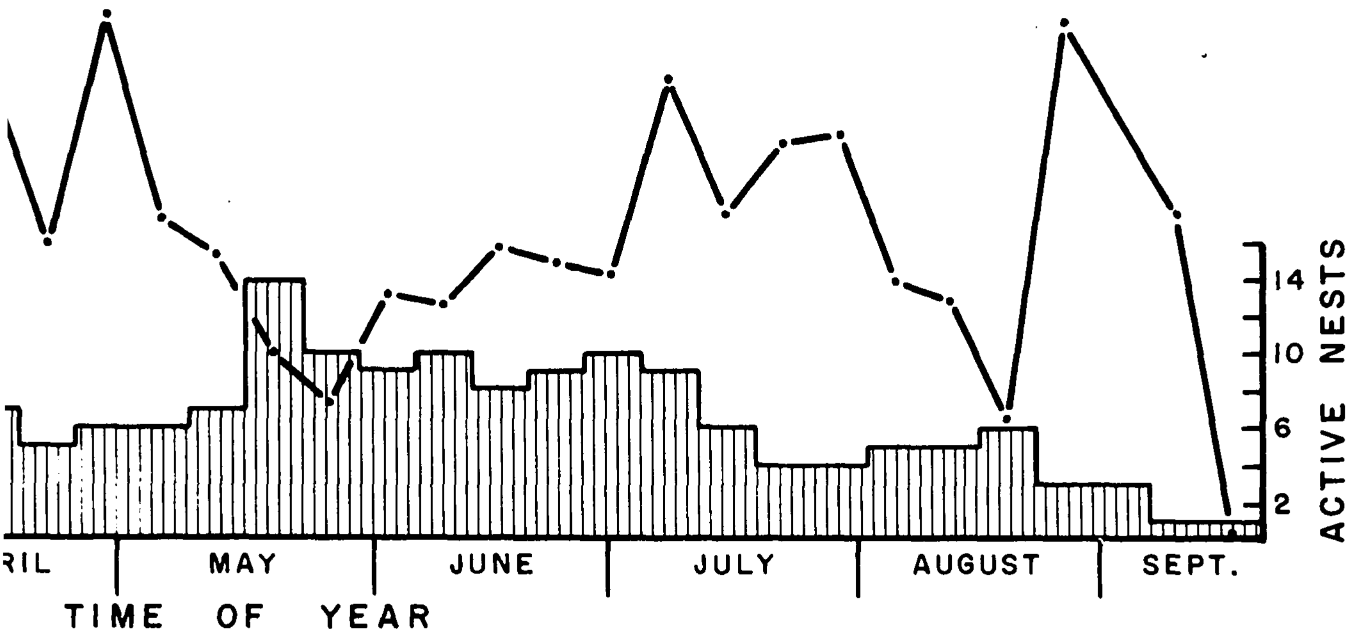


Figure 12. Relationship between cooing and number of active nests



ing and number of active nests on the hospital area in 1963.

In the present study, when all of the local breeders began nesting in May, cooing activity remained relatively low. Fluctuations in cooing occurred as the males progressed through the various phases of the nesting cycle. Cooing activity was generally lowest when a number of pairs were building nests. Then, as these nests entered the incubation phase or were disrupted, cooing increased. Of course, predictable cooing fluctuations could occur only if nesting was synchronized (many pairs starting and completing nesting cycles together), a condition which did not occur due to the continuing disruption of various numbers of nests. Nevertheless, the paddock area data for 1963 yields some information concerning the progression of the nesting season. Starting with the low in calling on April 8 (Fig. 11), the cooing pattern shows a succession of lows at three-week intervals, with peaks in between. It has been discussed in previous sections that male doves coo only infrequently while searching for a nest-site and nest-building. Nest records further showed that many of the pairs were actually starting nests at or near the time of the lows in cooing. The time required to successfully complete the first nest and start the second was usually 38-41 days, as shown by nesting records of marked pairs. Thus alternate lows in cooing represented the start of successive successful nests. Most nest disruptions occurred during incubation. Following disruption, the pair usually delayed starting their next nest for at least one to two weeks. Therefore this time sequence would account, along with the hushed brooding males, for the lows in cooing at three-week intervals.

Later nesting cycles usually spanned an interval of only 31-36 days. This fact, coupled with decreasing nest synchronization and the onset of cooing by early-hatched immature males, made it impossible to appraise late season dove nesting by cooing data only. However, the cooing data plus nesting records of marked pairs indicates that doves can successfully complete four nesting cycles between the first of May and mid September.

The data from the hospital area in 1963 (Fig. 12) does not show the pronounced and rhythmic peaks and lows in cooing during May and June. Cooing activity remained relatively low, and active nests high, throughout the two months. The lack of pronounced peaks was probably a reflection of the fact that during the period there were no great changes in the number of active nests. Nest disruptions occurred throughout the nesting cycle, rather than primarily during incubation as was the case in the paddock area. Nest destructions during the brooding phases were caused by house cats, roadrunners, and young boys. The net result was that on most days in May and June the breeding doves were more or less equally divided as to their nesting phases--some were searching for nest-sites and building nests, some were incubating, some were brooding, and some were between nests. Thus the relatively stable cooing activity was a reflection of the complete lack of nesting synchronization. Beginning in early July, as was the case in the paddock area, early-hatched immature males began cooing, resulting in a distorted cooing-nesting relationship.

The dove breeding activities in the paddock area in 1962 were greatly disturbed and altered by human activities (Fig. 11). Resident doves began nesting in late February, and nesting increased rapidly in late April and early May as migrating local breeders returned. Then in mid May, personnel of the Dairy Science Department began a partial brush clearing program on the area. Approximately half of the active dove nests were disrupted by this operation. The brush clearing so altered the nesting habitat that about half of the breeding pairs were unable to find suitable nest-sites. The disposed doves did not leave the area immediately. They remained for varying periods of time, harassing the actively nesting doves. The result was that cooing activity increased sharply in late May and remained high. The number of active nests remained low throughout this period.

Although I deplored the alteration of the nesting habitat, the situation afforded an excellent opportunity to test the relationship of cooing to actual production. The deterioration of nesting habitat in 1962 resulted in only 36 immature doves being produced on the paddock area from 82 nests attempted, yet the average number of calls heard per morning period in May and June was 541. In 1963, 65 immature doves were produced from 68 nests attempted and calling during May and June decreased to only 333 calls per morning period. This inverse relationship between cooing and production would be expected, as a greater percentage of the breeding pairs were forced by habitat changes to spend more time in the between nests phase of the nesting cycle in 1962.

The data collected over a two-year period on the study area indicate that cooing does not necessarily reveal dove production. Dove cooing variability--affected by breeding status of the males, position in the nesting cycle, dove-density, and nesting synchronization--is so great that it would be impractical or impossible to relate cooing to production. However, cooing data does show that a once-a-year dove coo-count gives more information than just the number of males cooing. By calculating the percentage of coos heard during only the first hour of the morning two-hour period, information is gained on the relative number of males that have an active nest. The discussion of the probability of hearing male doves call in the previous section shows that those actively nesting coo very little during the second hour. Thus, if a large percentage (80 plus) of cooing occurs during the first hour, most doves have active nests and the calling males represent only a small portion of the breeding males actually present. The highest first hour calling percentages indicate that many doves are searching for nest-sites or building nests. This is usually indicative of the first nesting attempts of the recent arrivals to the breeding areas. If, on the other hand, only 50-80 percent of the total coos occur during the first hour, the probability is great that a number of males are between nesting attempts. Thus a larger portion of the males actually present would be recorded. Figure 13 shows the relationship between calling activity and number of active nests. In a fixed breeding population calling activity fluctuates inversely to the number of active nests present.

Seasonal Cooing Pattern

The mourning dove research which served as a basis for the present national dove census was conducted primarily in northern and eastern United States. In the west and southwest, very little research has been conducted on the pattern and biology of dove cooing. Thus the national dove census is based on research data that excludes a large portion of the area that it is supposed to sample. A standard 20-mile coo-count route was established north of Tucson, Arizona with its objective being to determine the seasonal cooing pattern of doves in this region. This route was run at weekly, or near weekly, intervals throughout the cooing seasons of 1962 and 1963 and until July in 1964.

The seasonal cooing data presented in Figure 14 show that the pattern was generally similar from year to year, but with some differences in phenology and early and late-season population levels. Doves began cooing in late February in 1962. In 1963 and 1964 cooing began six weeks earlier, in mid January, probably associated with the more mild early winters. In each year there was a quick increase in cooing

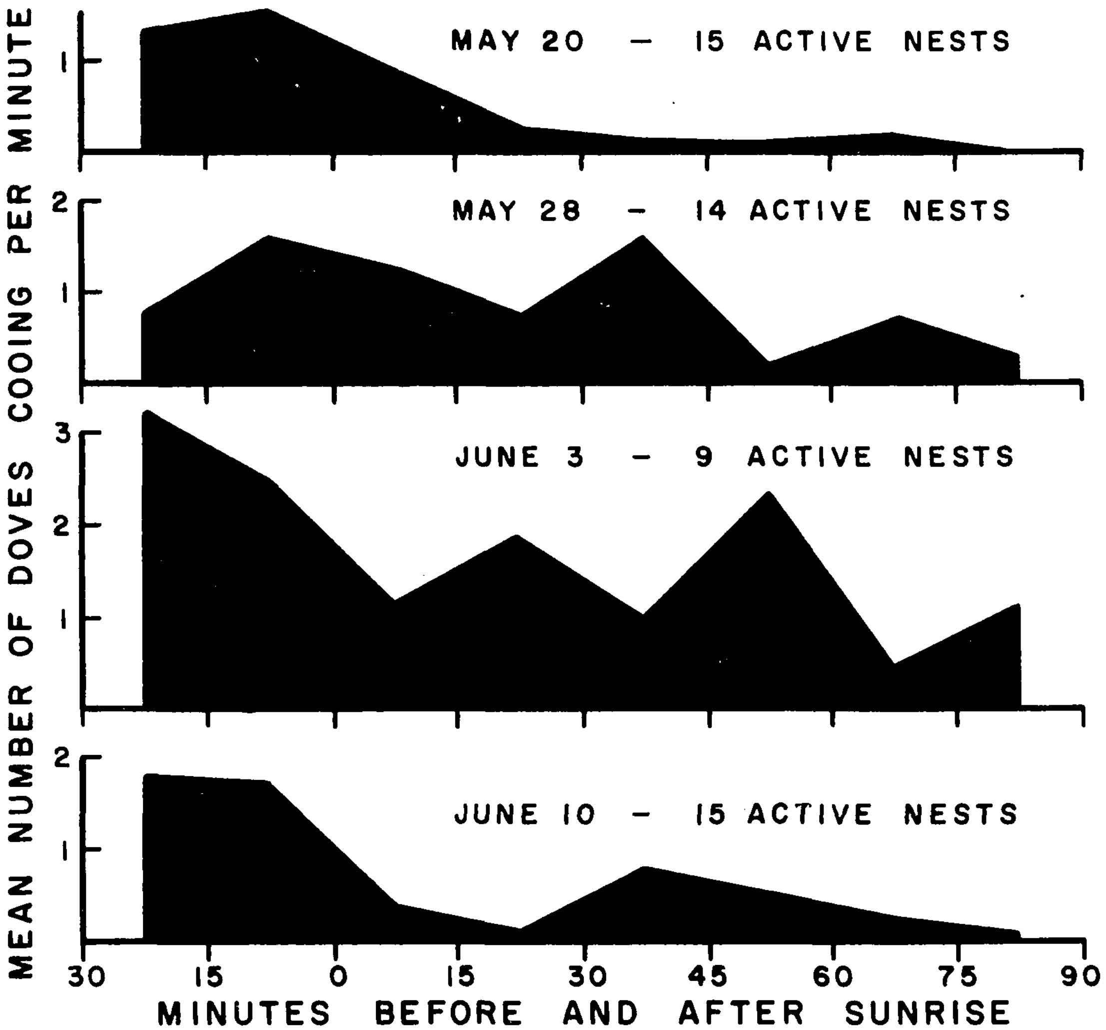


Figure 13. Relationship between number of doves cooing and active nests on the paddock area during the national coo-count period of 1963.

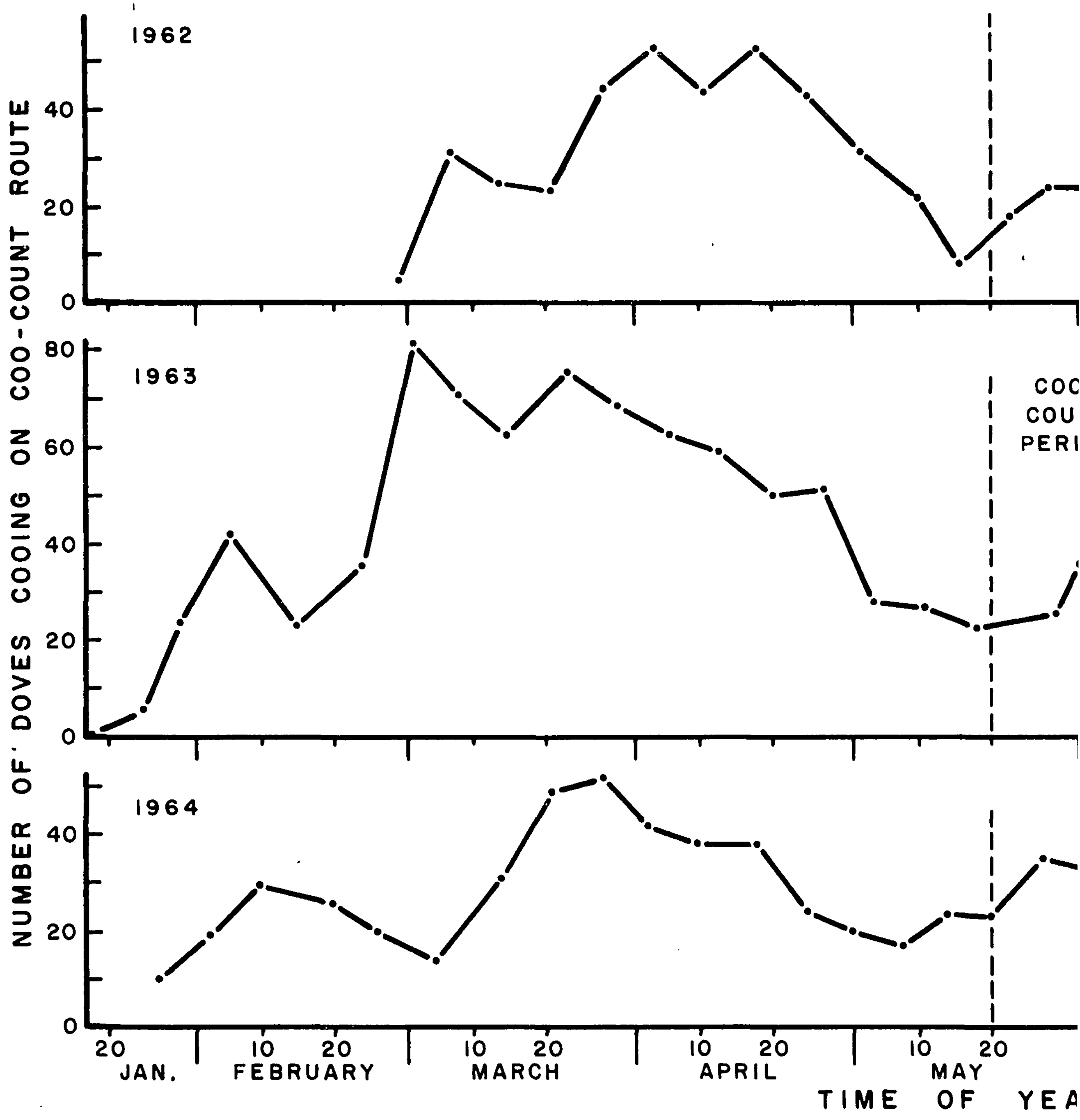
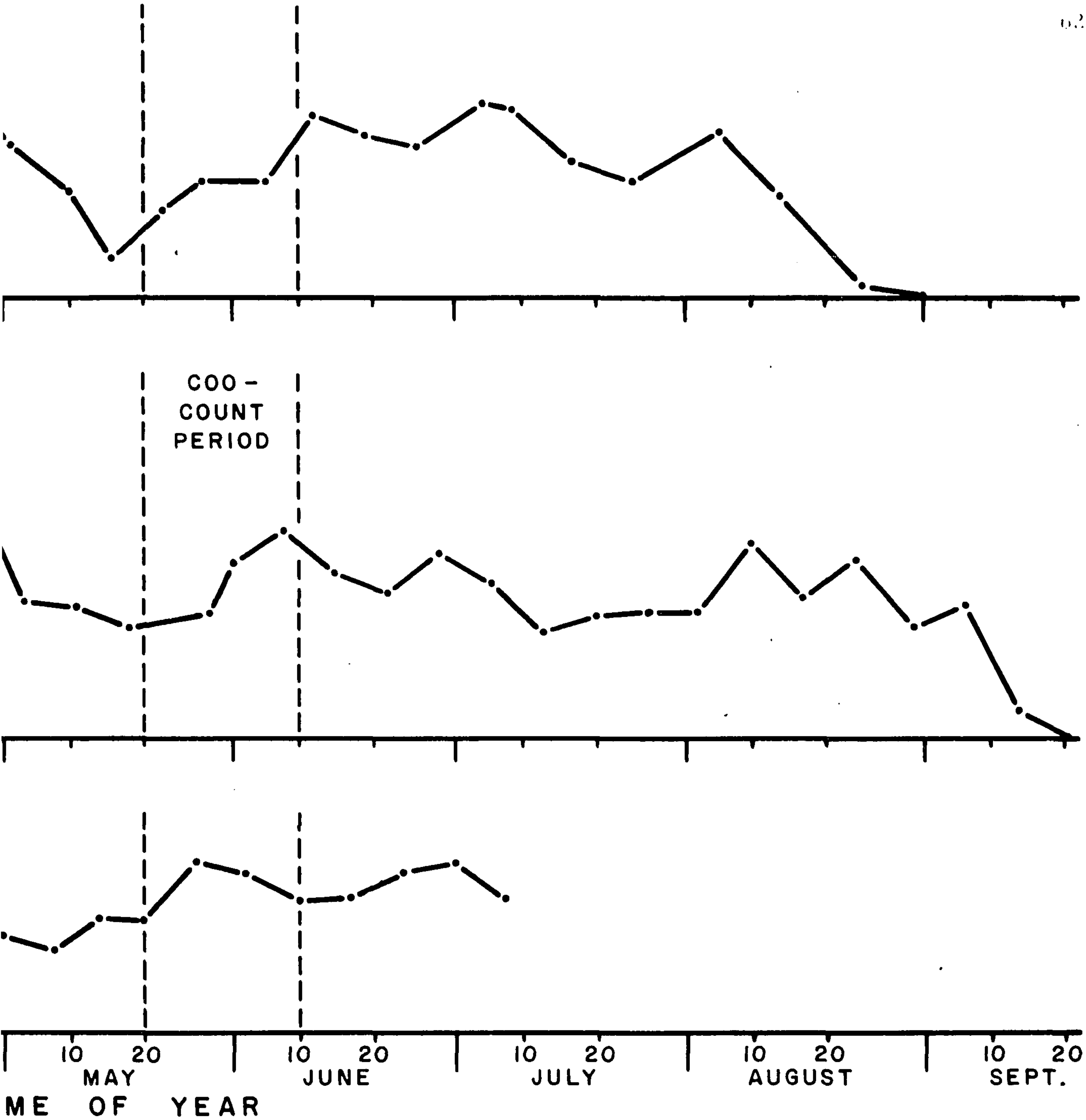


Figure 14. Seasonal cooing pattern along the coo-count route in 1962, 1963, an



in 1952, 1953, and 1954.

as the resident males became sexually active. Then, also in each year, there was a decrease in cooing males as these early breeders entered their first nesting cycles. A sharp increase in cooing males occurred in March and April as migrating transients passed through and the migrational segment of the local breeding population returned. That many of the males cooing in March and early April were indeed transients was substantiated by sight observations and by trapping and marking. On several occasions along the route doves were seen plummeting earthward with wings folded, alighting in trees and on power lines, and then cooing. The high flying actions of those doves indicated that they were making more than just a local flight. Also, of 123 adult doves trapped and color marked in March and April on the study area, only 17 were seen or retrapped later than April.

In each year, during the latter half of April, the number of cooing doves decreased as the transients continued northward and the returning local breeders began their first nesting cycle. Cooing intensity continued to decrease until about mid May, the time when most males were mated and had an active nest. The mid May low in 1962 was very pronounced, evidently signaling synchronization of nest building activities. Each year, following the mid May low, cooing increased and then followed an undulating pattern as the breeding doves progressed through the various phases of successive nesting cycles.

The time of the national dove coo-count census, May 20 to June 10, is set off by dotted lines in Figure 14. It is evident that the number of cooing males may vary greatly within this time period. There was no evidence that the fluctuations in the number of cooing males during this period was caused by either a change in the ratio of mated males to unmated males or weather differences. I am certain that the differences were primarily a result of the mated males' progression through the nesting cycle. It is apparent that a single census along this route could be biased by cooing variability affected by position in the nesting cycle rather than being a true index to the number of breeding males. Thus yearly population fluctuations would have to be great before they could be accurately detected. For example, censuses conducted on May 20 in both 1963 and 1964 would indicate that the breeding populations were unchanged. Censuses conducted on May 27 would show a substantial population increase in 1964. However, censuses made late in the period would indicate a substantial decrease in 1964. Thus single censuses could indicate an unchanged, an increased, or a decreased breeding population along this route in 1964. A comparison based upon the averages of all censuses conducted in the coo-count period shows that the breeding population was slightly less in 1964.

The May 20-June 10 so-called dove cooing "plateau" is in reality a "plateau" only in comparison with the sharp peaks and lows found earlier in the season. Information gained during this study indicated that a slightly later period, June 1 to June 21, would show less variability, for the influence of the mid May low in cooing would be lessened. However, the Dove Regulations Committee must meet no later than late June in order to provide for the required publication of hunting regulations, and census statistics must be summarized for consideration by this Committee. Thus a census period later than is presently used would be administratively impractical. A dove census during this region's peak cooing period of March and April would be inaccurate in that a number of the same doves would be counted twice, once here and then again after they arrive in more northern states to nest.

Flapping-Gliding Flight

A number of investigators have described or discussed the flapping-gliding flight of male doves (Barrows, 1912; Taylor, 1941; Webb, 1949; Lund, 1952; Edminster, 1954; Mackey, 1954; and Jackson and Baskett, 1964). Jackson and Baskett (1964) described the flight as follows:

> In performing the flapping-gliding flight, the male leaves his cooing perch with a vigorous and noisy flapping of wings. The wing beats are exaggerated and the tips of the wings touch beneath the body. The bird may rise to a height of a hundred feet or more. He then extends his wings and carries them motionless on a plane somewhat below that of the body and begins a long spiraling glide. He may make a complete circle before alighting at the original or a different perch. Often he makes a series of flaps and glides before alighting.

All investigators agree on the description of the flapping-gliding flight. However, there is disagreement as to its function. Jackson and Baskett (1964) noted that the flight frequency for unmated males was 83 times as great as that for mated males, suggesting that its function is to attract a female. Also, Lund (1952) and Mackey (1954) reported that lone or unmated males made this display more frequently than paired males. However, Barrows (1912), Taylor (1941), Webb (1949), and Edminster (1954) reported or implied that the flights functioned as a territorial display, for they noted that males often performed the flight in the presence of their mates during pair formation.

During the present study records were kept on all flapping-gliding flights. The sample was large and encompassed the complete breeding season. The data (Fig. 15) indicate that the primary function of the flight is to locate and attract a female. Also, to a lesser extent, it functions as a territorial display, especially early in the breeding season.

Unmated males were observed making as many as 27 flights during a two-hour morning period, but the average was approximately 13 flights. In contrast, mated males averaged less than one flight per two-hour period. Mated males were more prone to make these flights early in the nesting season. One incubating male, during his first nesting attempt, made 13 flights in one two-hour period; another made 10

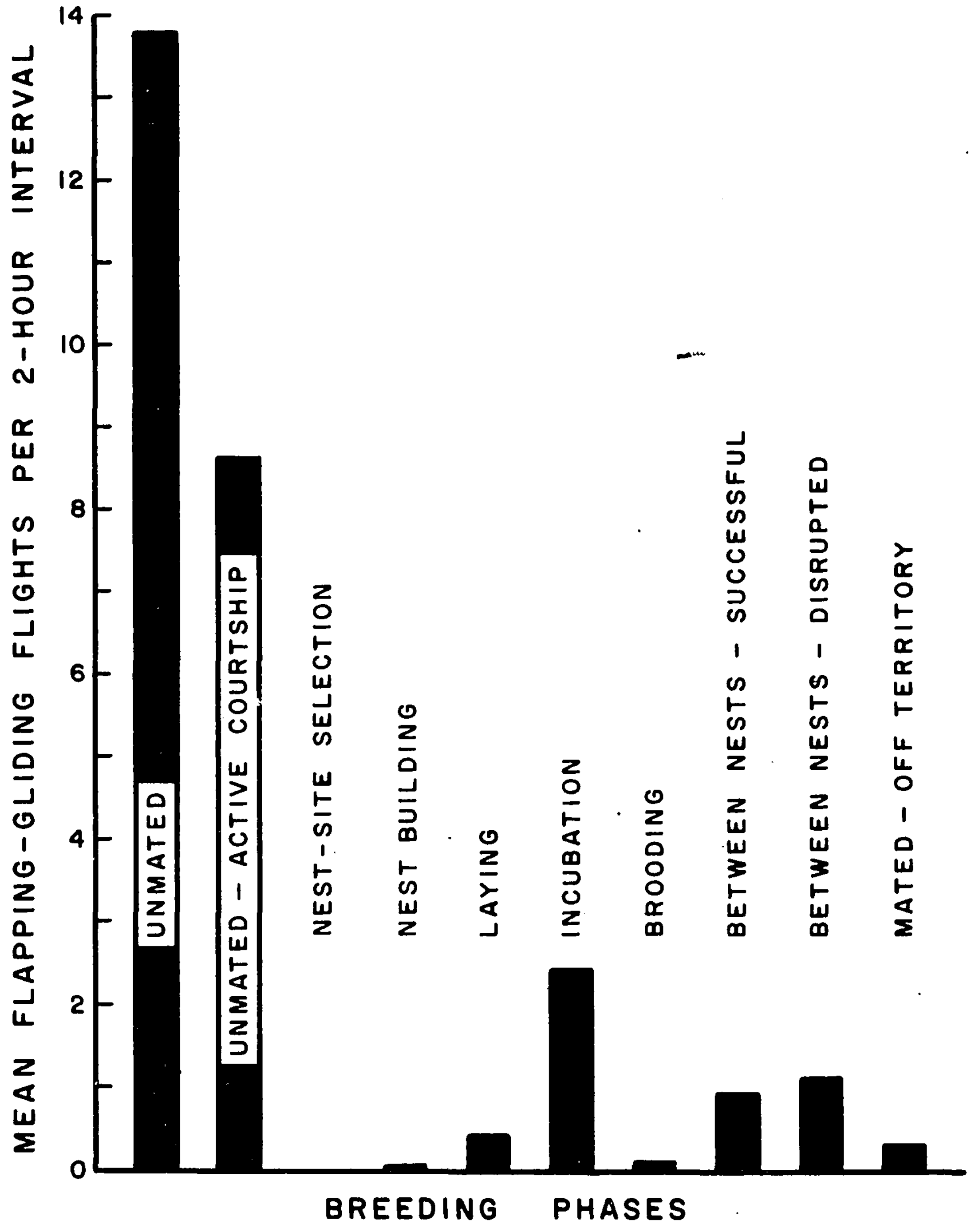


Figure 15. Frequency of flapping-gliding flights in relation to breeding status and position in the nesting cycle.

flights. These same two males rarely made flights later in the nesting season. The early season records account for most of the seemingly disproportionate incubation average shown in Figure 15.

Territorial Behavior

Most observers generally agree that mourning doves exhibit territoriality. However, they do not agree on all aspects of territorial behavior. The differences in degree of territoriality reported by the various observers may simply have been a result of the variability in dove density, breeding status (unmated versus mated), and differences in aggressiveness among individual doves. I found great differences to exist in the territorial behavior of individual mourning doves, both male and female.

Unmated Males: Jackson and Baskett (1964) found that unmated males were aggressive near their cooing perches, but that there was little evidence of well-defined territories. They reported that the cooing perches of one male were scattered over a large area (15-20 acres), and often several males used different parts of a given area simultaneously.

Prolonged observations of marked unmated males during the present study confirm those findings. Unmated males were aggressive, but not necessarily only within a defined territory. Frequently a male was observed driving off all doves alighting near his cooing perch or flying over his perch, then abruptly flying off as far as one-fourth mile and repeating his aggressive actions. In February and March, 1963 six marked unmated males were consistently observed calling and performing flapping-gliding flights in the study areas. These males occasionally used different parts of a one- or two-acre area simultaneously. All of these males appeared to have favorite perches, to which they returned again and again. However, these same perches were frequently used by other calling males when the dominant male was elsewhere. Unmated males occasionally called from trees containing active dove nests.

Of the six males observed over a long period of time, only two eventually nested on the study areas. The others drifted off short distances to nest after they became mated. These four males were seen a number of times throughout the nesting season in a residential area one-fourth mile from the study areas. And only one of the two males who remained on the study areas nested in the same area where he usually called prior to becoming mated. Thus it appears that unmated males, actively in quest of a mate, display over a much larger area than a truly defended territory. The area used by an unmated male might best be termed a moving display territory, with only the area immediately around the male being defended with aggressive behavior.

Mated Males: The territorial actions of mated males were extremely variable during the present study. Observations of the differences in aggressiveness of more than 25 mated male doves appear to clarify the somewhat contradictory reports of dove territoriality. Reports based upon only small samples, studied in areas of different nesting densities, could easily arrive at different conclusions concerning territorial behavior.

Male doves generally defended an area around their nests. The size of the defended area appeared to be dictated by both the individual aggressiveness of the male and the proximity of other dove nests. Some males would not allow the intrusion of other doves within approximately 50 feet of their nests. Other males, however, were indifferent to all bird activity away from the nest tree.

The more aggressive males defended their territories in the manner described by Jackson and Baskett (1964). If a male saw an intruder alight within his territory, he immediately flew toward the interloper, extending his legs forward when nearing the target. The intruding bird usually flew off as the resident male approached. If the intruder stood firm, the defending male usually lit beside it and immediately began striking with sharp blows of the wing. The majority of these encounters were short-lived, as the intruder would quickly retreat and fly off. Occasionally, however, the intruder chose to do battle. The two birds would rush and strike each other with wings and bodies, rarely pecking. Most battles lasted less than one minute, but a few continued for as long as 15 or 20 minutes. The victor, the resident male in all but one case, would then pursue the ejected bird out of the territory.

In only one observed instance was a resident male displaced by another male dove. This male was brooding large nestlings when another pair of doves began building a nest only 30 feet away. No antagonism was noted until the nestlings fledged two days later. One nestling flew out of the nest and lit under the tree in which the intruding pair were building their nest. The nest building male immediately flew down and began pecking and striking the young bird. The male parent was considerably agitated but would not go to its young. He patrolled an arc on the ground some 15 feet away. When he tried to approach closer, the other male quickly repulsed him with wing blows. The male parent continued to patrol the ground, alternately feeding and cooing, for about 30 minutes. The intruding male returned to his nest construction, but would quickly respond with active belligerence when the male parent tried to come near its injured young, or if the young dove tried to move. A short while later the young dove died from the severe pecking it received on its head and body, and the male parent returned to his nest tree. The resident male's territory was now only about half its original size. Six days later a long hard battle took place between the two males. This battle resulted in the complete displacement of the original resident. He moved completely off the study area.

Reports in the literature describing the sizes of dove territories vary greatly. These large differences (two square feet to more than 100 yards in diameter) were probably only symptomatic expressions of nesting densities. Observations during the present study show that territory size can vary greatly even within a small nesting area. The preferred nesting sites on the 20-acre study area were the small islands and peninsulas of mature mesquite trees. In these areas doves frequently nested in adjacent trees with no great show of aggressiveness other than cooing. Mapping of these territories was impossible, for males of adjacent pairs many times used common cooing and preening perches. These preferred perches were not used by more than one male at any one time, but as many as three nesting males would use the same perch in the course of one morning. When more than one of these males was present at the same time, the dominant male would use the favored perch and the others would retreat closer to their nests or fly away. Thus territories in the more preferred nesting areas were highly elastic, ebbing and flowing with the presence and absence of other nearby males. Several times, in the absence of the resident male, other nearby mated males were observed cooing within one foot of another active nest. In the more open portions of the study area dove nesting territories were larger and less elastic, but in no instance was a defended territory greater than 100 feet in diameter.

Most published reports agree that mourning dove territorial drive is greatest during the early phases of the nesting cycle, and appears to lessen during the later phases. Results of this study agree with those reports, but found that individual differences in male aggressiveness and aggressive opportunities frequently altered the degree of territorial drive. In most instances, males actively building a nest were most aggressive. Many times, the initiation of a new nest entailed carving out a territory from portions of existing adjacent dove territories. Only the more aggressive males could accomplish this task if they were actively challenged by nearby nesting males. The apparent lessening of territorial drive in incubating and brooding males, coupled with their decreased early morning presence around the nest, made it possible for new nesting territories to be established with a minimum of intraspecific strife. Nest-building males usually defended a territory the size and shape of the area in which they gathered nest material. When incubation began, male doves generally became more tolerant of other nearby dove activity unless the sanctity of the nest tree was violated. During the later nesting phases, most males responded to other nearby dove activity merely by uttering a few perch-coos. Rarely was physical aggressiveness shown. Similar progressive shrinkage of dove territory size was reported by Lund (1952) and Edminster (1954).

There were great differences in aggressiveness among individual doves. In two instances the females were more aggressive than the males. These females were observed several times leaving their nests to chase off other doves that lit in the nest trees. Their mates were never seen to do this even though strange doves occasionally lit in the nest trees while the males were incubating and brooding. One male showed no aggressiveness when another male invaded his territory to harass his mate. This male, perched only 20 feet away, watched unconcerned as his mate repulsed and drove off the strange male. At the other end of the aggressiveness range were a few males who were intolerant of any other nearby dove activity. These males were aggressive even when feeding among other doves away from their territories. However, most male doves exhibited behavioral characteristics midway between the two extremes of aggressiveness.

During the course of this study, no males were found roosting within their nesting territories. All males nesting on the study area, and the surrounding areas as well, roosted in a group of eucalyptus (Eucalyptus spp.) and cottonwood (Populus spp.) trees located approximately 200 yards south of the study area. At dusk, male doves funneled into these trees with little show of strife. Incidental observations away from the study area indicated that other dense groves of trees also served as communal dove roosts. At daylight the doves left the roost trees to return to their nesting territories or to feeding areas.

According to Jackson and Baskett (1964), dove territory can be classified by Nice's (1941) system as a Type B or mating-and-nesting territory since nesting and copulation take place within the territory. I found that under colonial, or semi-colonial, nesting conditions mating does not necessarily take place within the nesting territory. Copulations frequently occurred away from the territory. Thus, under these conditions, dove territories were simply nesting territories.

Pair Formation

As discussed previously, pairing has an important effect upon the cooing behavior of male doves. Thus it is important to have knowledge of the timing, permanence, and other aspects of the biology of pair formation. Jackson and Baskett (1964) reviewed and discussed certain observations of courtship behavior. Little information has been published concerning when and how firm pair bonds are formed among wild birds. And these reports were inconclusive in that, for the most part, they represented short observations of unmarked doves. The majority of published evidence points toward some degree of monogamy in dove mating behavior and that some doves remain paired for two or more years (Mackey, 1954).

Internal examination of 20 male and 18 female doves collected on January 2, 1963 showed no gonadal development. Five days later an examination of a male and female found an increase in the size of the gonads. Shortly thereafter male doves began cooing on the study area, and the first dove eggs were found on February 5.

I began observing color-marked unmated males on February 12, and found that wild doves exhibited great differences in mating behavior. These individual differences were so pronounced that it would be premature to state that a pair bond had been formed until the pair actually started nest construction. Male M9 was observed cooing and performing flapping-gliding flights from the northwest corner of the paddock area from February 12 to February 19. The following morning he made a flapping-gliding flight at an approaching dove. This dove, a female, followed the male into a large mesquite tree. They began billing immediately and copulated two minutes later. The male then hopped into a nearby old dove nest and began uttering faint nest calls. The female approached him and then flew off out of sight to the south. The male left the nest, made a series of large looping flights over the area in which the female disappeared, and then returned alone to his display area to resume cooing. The same female returned approximately one hour later. The male immediately flew to the old nest, but the female then flew out of sight to the north. The male resumed cooing from various nearby perches. The female returned 70 minutes later and joined the male on a fence post. They preened each other and then flew off together four minutes later. The next morning similar behavior was noted. The male arrived in his display area alone. Fifty minutes later the same female joined him; they copulated and then both went into the old nest. The following morning the male again flew into his display area alone and immediately began cooing. Twenty minutes later he made a flapping-gliding flight at an approaching dove. This dove, the same female, followed the male down to the mesquite tree. They billed and preened, copulated twice in eight minutes, and then the male went into the old nest. Another male dove lit on a wire 50 feet away and began cooing. The female flew up to the wire and lit beside the strange male. Male M9 left the nest, made a flapping-gliding flight, and returned to a tree 70 feet from the other two doves. He then flew at the strange male and chased it off in an aerial battle. During this melee the female disappeared. Male M9 then went into the old nest and began uttering nest calls. The female returned 15 minutes later and both went into the old nest to bill and preen. These doves stayed in the area for 45 minutes, copulated again, and then flew off to the west out of sight. The next morning the male arrived in his display area alone and began cooing. Fifteen minutes later the same female flew into the area and began billing with the male. He tried to mount her but she jumped away. They then began searching for a nest-site with the male calling the female to prospective sites with faint nest calls. This activity continued for approximately 90 minutes. I then left the area so as not to disturb them. The following morning, for the first time, the male arrived in his display area accompanied by the female.

Almost immediately they began searching for a nest-site and continued this activity for two hours. The next morning the male cooed and made flapping-gliding flights, but the female did not appear. The following morning the same female appeared in the area 12 minutes after the male. They stayed quietly on adjacent fence posts for about 15 minutes and then the female flew off alone. During the next few mornings the female was present for only short periods of time, and each time she flew off alone. On March 6, the same marked female only visited the male's display area for a few minutes before she flew off alone. About an hour later a new female (unmarked) was with male M9. They billed and the female squatted, but when the male mounted her, the female flew off a short distance. Both then flew off together out of sight. During the next 15 days male M9 was less regular in the use of his customary display area, and was never seen with a female for more than several minutes at a time. On March 22, the male was observed cooing in his display area. He made a flapping-gliding flight at an approaching dove. This dove, a banded female, followed the male down to the ground. Then both flew into a nearby tree where the male went into a recently abandoned dove nest. The female followed him into the nest and they began billing and preening. The male then flew into another unused dove nest 100 feet away, and the female followed him. The two then flew from tree to tree as if searching for a nest-site. Some 45 minutes later the female flew south out of sight, and the male followed a few minutes later. During the following two weeks male M9 regularly cooed and made flapping-gliding flights from his display area, but was never seen with a female. After April 5 he was never seen in his display area. He evidently became mated at last and was nesting somewhere in the vicinity of the study area. I saw him on the evening of April 26 for the last time, quietly feeding in a fallow field some 300 yards from his favorite display area. This male was consistently observed over a period of 53 days. He was seen copulating with one female, attempting copulation with three, and nest site hunting with at least four different females. However, before a firm pair bond was formed, he evidently courted yet another female. Although the courtship activities of male M9 were surely atypical, they illustrate the difficulty in judging matedness based only upon short observations of unmarked birds.

Observations of other doves gave further evidence that males may court more than one female before a firm pair bond is formed. As reported in the previous section, six marked unmated males were observed over a long period of time in February and March, 1963. These males made flapping-gliding flights at most of the doves that flew over their cooing perches. Occasionally a female dove, met in mid-air by one of these unmated males, would follow the male down to the ground or to a tree in his display area. If the two lit on the ground the male usually charged at the female and performed bow coos. These two courtship displays were reviewed and discussed by Jackson and Baskett (1964). In charging, the male makes a stiff-legged short leap or series of rapid leaps at another dove, in this case a female. After charging the other dove, the male usually performs one or more rapid bows with his head and body. He then abruptly rises to an erect position, head forward and tail touching the ground, and gives a loud coo. The charge and bow coo are not always performed together. Either display may be given singly, in series, or in combination with the other. If they lit in a tree the male usually immediately elevated his tail and began nest calling and quivering his wing-tips. In all observed instances the females only stayed with the males for short periods before flying off alone or followed by the unmated males. In most instances the males returned to their display areas alone only a short while later. These brief encounters were evidently unsuccessful courtships; the females appeared to be disinterested in the males or their display areas, or both. Apparently unmated males tried to induce females to mate with them and nest in a portion of the display area. If they were unsuccessful for a long period of time, the males enlarged their areas of activity, even following the females to their preferred areas to form a pair bond and to nest. Observations indicated that this is what occurred with five of the six marked males.

At the other extreme, at least three pair bonds were formed with little or no courtship activity. The males apparently formed pair bonds with the first females that entered their display areas. All three pairs quickly copulated, and then entered quiescent periods which lasted from one to three weeks before they began building nests in the immediate vicinity of where they were first observed.

Resident doves began forming pair-bonds shortly after gonadal development in early January, and the successfully paired birds began nesting in February. Most of the migrational segment of the local breeding population returned in late April, following the transient doves which passed through in March and early April. Judged on the basis of lack of courtship activity and the small number of obviously unmated males, most of the returning breeders had formed pair bonds either on their wintering areas or enroute to their local breeding areas. A number of these returning migrants quickly and quietly began constructing their first nests.

In most observations of marked birds the male remained paired with the same female for the length of one breeding season. In at least four instances, however, pair bonds were disrupted following nest-trapping and marking of the males. The cause of these pair disruptions was probably the trapping itself rather than the marking of the males, for each male was later observed with a new mate. Two pair bonds were broken by the death of the females at night on their nests, and at least two other incubating females disappeared overnight. If there was a disproportionate loss of nesting females, as appeared to be in the case, there should have been a surplus of unmated males throughout the breeding season. But there was no evidence that a surplus of males existed for any period of time during the height of the breeding season--May through July. All marked males deprived of their first mates through human disturbance or predator loss were able to acquire new mates and continue nesting. Thus it appeared that there was an equal loss of other males through unknown causes, or that a number of males left the area and became non-breeders for the remainder of the season. I believe that the surviving members of broken pairs were about equally divided as to sex, enabling new pair bonds to be formed.

Several instances of mated males exhibiting brief lapses of fidelity were observed. Male M87 copulated three times with an immature female while his mate was incubating less than 200 feet away. This female tried to interest him further by following closely while he fed, but he then ignored her and shortly relieved his mate at their nest. Male M112 was seen with an immature female while his mate was also incubating about 300 feet away. He squatted beneath a bush, quivered his wing-tips, and uttered nest calls. The female was two feet away and then approached him. Both flew out of sight together, but the male remained mated with his original female for the remainder of the nesting season. Several other marked mated males were observed charging, bow cooing, and attempting copulation with females other than their mates. Each of these males flew off out of sight with the females, so it was not known whether or not copulation took place. Nevertheless each male continued nesting with his original mate.

The Nest Call and Other Short Calls

Other than the perch-coo, the most frequent call uttered by doves is the nest call. Craig (1911) stated that the nest call was much shorter and more faint than the perch-coo. Jackson and Baskett (1964) reported that the volume, length, and inflection of the nest call was variable.

I found that not only were the auditory characteristics of the two calls different, their rhythm was also distinctive. Perch-coos were usually uttered at rhythmic 15-20 second intervals, rarely more than four per minute; whereas nest calls were generally given in staccato fashion, as many as 13 per minute. These distinctive features were helpful in separating the two calls when a large number of doves were calling at the same time.

The frequency of nest calling, unlike perch-cooing, appears to be little affected by external influents. The data (Fig. 16) indicate that nest calling frequency is affected primarily by the readiness of the dove to initiate a nesting cycle. Solitary unmated males occasionally interspersed a series of nest calls with their perch-cooing, but nest

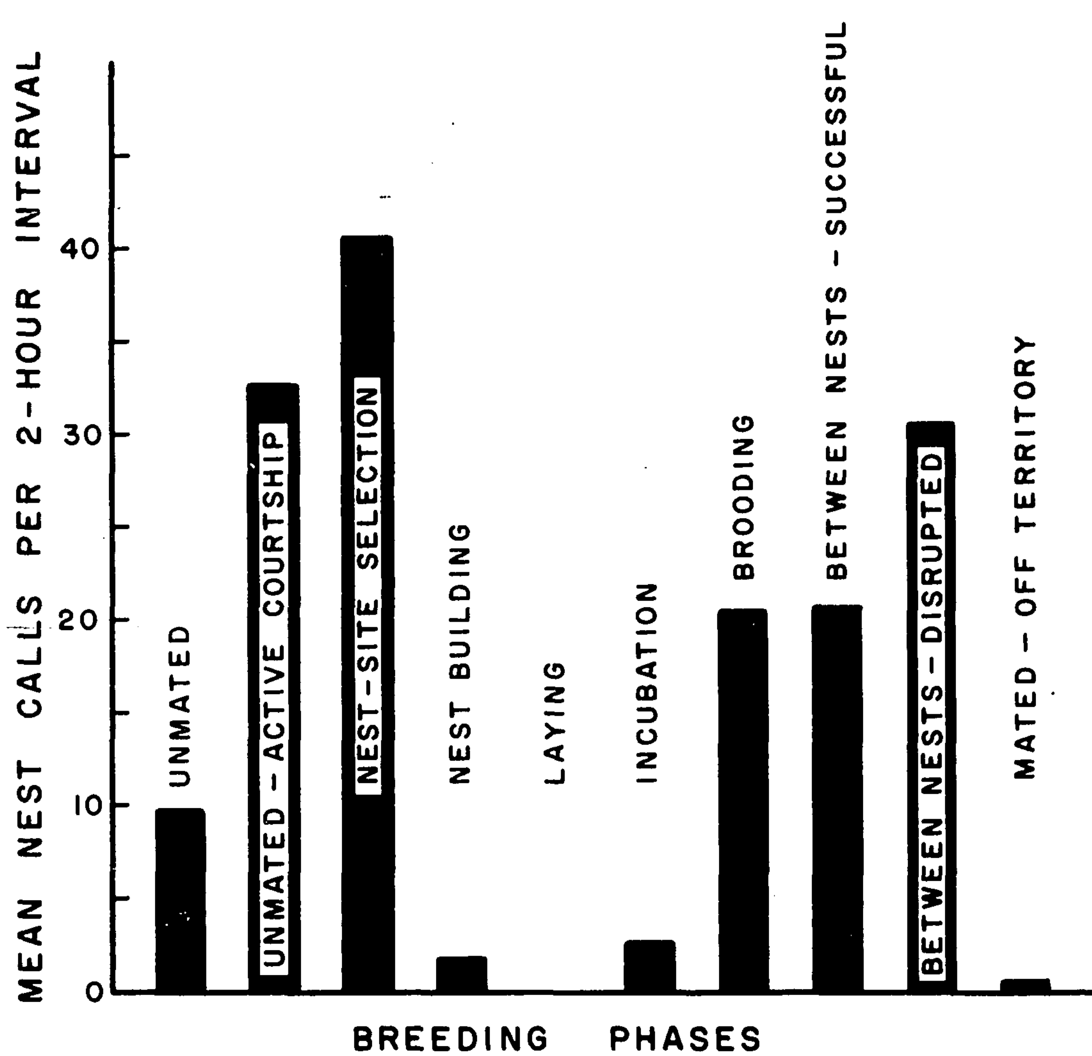


Figure 16. **Frequency of nest calls in relation to breeding status and position in the nesting cycle.**

calling increased threefold when they were actively courting a female, even though no pair bond was formed. The frequency of nest calling was greatest, and perch-cooing the least, during the period in which the pair was searching for a nest-site. In searching for a nest-site, the male precedes the female. He hops from branch to branch and flies from tree to tree searching for a potential nesting site. The nest call functions to call the female to the male at the prospective nest site. The female occasionally gives the nest call to the male. When nest construction begins, nest calling abruptly decreases, usually being given only at the start of each day's construction activity. Nest calls were never heard during the egg-laying phase and only infrequently during the incubation period. Late in the brooding phase nest calling increased sharply and continued through the period between nestings even though the pair was not actively searching for a site for their next nesting attempt. However, nest calling rates were higher in those pairs that initiated a new nesting cycle with little delay.

One mated male, away from his nesting territory and after he chased off another male, was heard uttering a call which sounded like a nest call. Occasionally similar short calls were heard from other mated males after disputes that occurred on evening feeding areas. Apparently those short calls, although sounding like nest calls, had an entirely different function. Doves also uttered short warning calls when humans, house cats, and roadrunners approached. Warning calls connoted danger by the abrupt, alarmed manner in which they were uttered. It appears that doves may utter a number of very faint, short calls and that hearing them depends upon the nearness and hearing acuity of the observer. Although I heard no calls directly associated with the exchange of nesting duties there well could have been a faint sound signal between mates. Many times a dove on a nest would fly off before its mate appeared near the nest. The arriving mate, approaching from behind dense cover, possibly uttered faint recognition calls that I failed to hear.

CHAPTER IV

DISCUSSION AND CONCLUSIONS

Cooing Behavior and the Coo-Count Census

Results of this study of the cooing behavior of marked wild mourning doves confirm, in the main, most of the important cooing characteristics reported by previous investigators. The results which differ from previous reports are probably a reflection of sampling size and the fact that this study encompassed two complete breeding seasons, from onset of sexual activity in January to its cessation in September. Also, the variability in nesting densities on the two adjacent study areas, the wide temperature range during the cooing season, and the relative ease of making prolonged observations made it possible to record dove behavior under a broad range of environmental conditions.

In the most complete previous study of the cooing behavior of wild doves Jackson and Baskett (1964) concluded that:

> (1) Unmated males utter the perch coo much more frequently than mated males. Unmated males cooed during 93 percent of the 3-minute periods in which they were observed, while mated males cooed in only 23 percent. (2) Unmated males maintain a high rate of cooing for a longer period each morning than do mated males. (3) The position of a mated male in a successful nesting cycle has relatively little effect on the rate of cooing.

My observations confirm their findings that unmated male doves coo much more frequently and for longer periods in the morning. Data from the present study show that unmated males cooed during 94 percent of the three-minute periods; whereas mated males cooed in only 31 percent. Thus unmated males cooed with approximately the same frequency regardless of the apparent differences in dove densities between the Missouri study and this Arizona study. However, mated males in Arizona, in a more dense nesting population, cooed more frequently than their counterparts in Missouri. Information presented in this report indicates that nesting density does affect the rate of cooing of mated males.

Jackson and Baskett's (1964) conclusion that position in the nesting cycle had little effect on the rate of cooing was based on a sample size about one-fourth as large as the present study. I found that position in the nesting cycle does have a significant effect on the rate at which mated males coo. Our disagreement on this point is probably primarily affected by differences in sample size and to a lesser extent by differences in nesting densities. That position in the nesting cycle affects dove cooing is surely implied in the seasonal cooing patterns depicted in reports by McGowan (1952), Kerley (1952), Duvall and Robbins (1952), Wagner (1952), and the Ohio Department of Natural Resources (1963).

The fact that unmated males coo at least three times more frequently than mated males could indeed, as stated by Jackson and Baskett (1964), have great significance in interpreting dove coo-count figures. However, whether or not this is actually the case remains problematical. I found no evidence on the study areas that the number of unmated males, at least during late May and June, was such that they could materially affect coo-count figures. The mean number of coos per male per three-minute period in late May and June along the coo-count route was 6.0. On the study areas the mean number of coos per mated male per three-minute period in which they cooed was 3.9. Thus it appears that the higher cooing rate found on the coo-count route could represent an unknown number of unmated males. A number of factors other than the number of unmated males could account for the difference between the 3.9 and 6.0 cooing rates. The calculated 3.9 mated male cooing rate is based on observations throughout the two-hour morning period, but with added weight given to observations during the second hour simply because mated males were in their territories more, but calling less, later in the morning. Thus the 3.9 cooing rate is lower than actually exists among mated males. When equal weight was given to all portions of the morning period the mean cooing rate of mated males was calculated to be 4.6. The 4.6 to 6.0 spread between calculated and observed cooing rates seems less significant when one considers that the 4.6 rate gives equal weight to all portions of the two-hour census period, but the 6.0 rate gives unequal weight to the first hour peak cooing period simply because many more doves were heard then. The calculated average cooing rate for mated males during the first hour only is 5.0; for males incubating and between nests, 5.4; for incubating males only, 5.9. Also, along a coo-count route nearby cooing doves and other singing birds could completely mask out distant doves that only coo once or twice, thus causing cooing rates to be abnormally high. I believe that unmated males, at least in this area, exert no significant influence on coo-counts conducted in late May or June.

Position in the nesting cycle is the dominant factor affecting the variability in the number of doves heard along a coo-count route, at least in late May and June. The probability that a mated male will coo during any one three-minute period is low in the nest-site selection and nest building phases of the nesting cycle, increases during incubation, decreases during the brooding phase, and then again increases until the male starts actively searching for a new nest-site. Thus coo-counts made during the three week period of May 20 to June 10 could sample the population when many pairs are either in quiet or vocal phases of the nesting cycle. Significantly different portions of the same breeding population could be recorded. Yearly comparative estimates of breeding population fluctuations on a small area could be erroneous if in one year the coo-count was made when many of the males were in a quiet phase and the following year when most males were in a vocal phase of the nesting cycle. Of course, when the comparative data are gathered from many coo-count routes over a large area and then averaged, chances are great that the effect of position in the nesting cycle would be insignificant. However, this assumption remains unproven.

The present system of conducting the coo-count census could be improved in several ways. Data collected during this study suggest that coo-counts should not be conducted in this area until about June 1 to lessen the influence of the mid May low in cooing. Replicate coo-counts made in other areas could determine the most favorable times to conduct counts. Most variation in cooing rates occurs during the second hour of the morning period; therefore restricting the coo-count route to only the first 10 miles should decrease the standard deviation. However, any shortening of the routes would also decrease the mean number of doves heard and thus possibly offset the decrease in standard deviation, with the result that the coefficient of variability could remain the same or even increase. May 20-June 10 data from the Tucson coo-count route reveal that the standard deviation decreased from 7.73 to 5.46 when only the first hour was considered; but the coefficient of variability remained the same, 27 percent, as a result of the decrease in the mean number of doves heard. If the first half of the route would be censused one morning and the second half early the following morning the coefficient of variability would be only 13 percent. This refinement would of course entail more expense, time and effort, and may be unnecessary at the present time.

Cooing and Production Relationships

Observations of the amount of cooing associated with known numbers of active nests and production of young doves reveal that it is impossible, or at least impractical, to estimate production from the amount of cooing heard. Male dove cooing is affected by a number of variables--breeding status (unmated or mated), position in the nesting cycle, dove density, and nesting synchronization--which would make necessary continuing intensive studies in all dove breeding areas in order to relate production to cooing.

Cooing does indicate how the nesting season is progressing. If cooing activity remains relatively stable, at least in late May and June, nesting is not synchronized and nest disruptions are irregular. When sharp peaks and lows in cooing occur, nesting is more synchronized.

Behavioral Characteristics Associated with Pairing

Among the numerous behavioral differences noted between unmated and mated doves, the most pronounced was the much lower rate of cooing by mated males. This is in agreement with the findings of Frankel and Baskett (1961) and Jackson and Baskett (1964). Also, unmated males made flapping-gliding flights much more frequently than did mated males. However, performance of these flights was not always indicative of unmatedness, especially early in the breeding season. Mated males made these flights often enough to inject error into any attempt to use flights as an index to the ratio of mated males to unmated males.

Unmated males were aggressive, but not necessarily only within a defined territory. They ranged over a wide area, a moving display territory, with only the area immediately around the male being defended with aggressive behavior. It appeared that during pair formation the female selected the area in which the nest would be built, for only one of six males observed prior to becoming mated eventually nested in the same area where he usually cooed. The other five moved elsewhere to nest, and in one instance the female was observed leading the male into the area where they soon nested. Mated males maintained loose nesting territories, generally of small size. With as many as 29 active nests on the 20-acre study area it was impossible to map territories. Defended areas surrounding nests constantly changed, indicating that under semi-colonial conditions territoriality breaks down.

CHAPTER V

SUMMARY

1. The primary factor affecting the rate of perch-cooing of wild male doves was whether or not they were mated. Unmated males called at a mean rate of 8.19 coos per three-minute period, while mated males called at a mean rate of only 1.21. Also, unmated males called during 94 percent of the three-minute periods in which they were observed; mated males called in only 31 percent of the three-minute periods.

2. When a male dove becomes mated and starts on the nesting cycle, its cooing rate is affected by its position in the cycle. Male doves coo at a low rate during nest-site selection and nest building. During the egg laying and incubation phases cooing increases sharply, then decreases again to a low rate during the brooding phase. Mated males coo at their highest rates during the interval between nestings, until they begin searching for a new nest-site. Of 21 t-tests made to determine significance of the cooing rate differences associated with position in the nesting cycle, eight were not significant, two were significant (.05 level), and 11 were highly significant (.01 level).

3. Male doves, whether unmated or mated, cooed at highest rates during the interval 30 to 15 minutes prior to sunrise. Thereafter

cooing decreased, unmated males gradually and mated males sharply. Among mated males, position in the nesting cycle had its greatest effect on cooing rates during the last hour of the two-hour morning period.

4. Sight or auditory contacts with other nearby doves have a positive effect on the cooing of an individual mated dove--mated males in a dense population coo more than males in a less dense breeding population. However, unmated males cooed at a high rate regardless of whether or not other males were cooing nearby or were in sight.

5. Weather generally influences dove cooing only under extreme conditions. The following weather conditions had no detectable influence on cooing: temperatures ranging from 24°F to 88°F, light showers and winds from 0-12 MPH. Overcast conditions appeared to delay initiation of cooing about 9-12 minutes. Bright moonlight may influence doves to start cooing a little earlier than normal. Adverse wind or rainfall conditions decrease the audibility radii, and thus are of extreme importance in the dove coo-count census.

6. Some mated males coo when they are away from their nesting territories, although at a lesser rate. Whether or not a mated male will coo away from his territory appears to depend on its individual aggressiveness and its opportunities to exhibit aggressiveness.

7. Dove production can not be predicted on the basis of cooing records. Cooing variability--affected by breeding status of the males (unmated or mated), position in the nesting cycle, dove density, and

nesting synchronization--is so great that it would be impossible, or at least impractical, to relate cooing to production. Replicate coo-counts on small areas may, however, provide information on the progression of the nesting season.

8. In the Tucson area, the seasonal cooing pattern shows an early season peak resulting from the cooing activities of resident and migrating males. Following this peak there is a steady decline to the mid May low. This low is associated with the nest-site selection and nest building activities of the recently arrived migrating segment of the local breeding population, and may be a major or minor reduction, depending upon nesting synchronization. Thereafter the cooing pattern is an undulating series of highs and lows as the breeding population progresses through successive nesting attempts.

9. Unmated males performed flapping-gliding flights much more frequently than mated males. However, performance of these flights alone is not indicative of unmatedness. The flapping-gliding flight primarily functions in locating and attracting a female. To a lesser extent it apparently is a territorial display, especially early in the breeding season.

10. Unmated males do not maintain well-defined territories. They coo and perform flapping-gliding flights over a large area, a moving display territory, with only the area immediately around the male being defended with aggressive behavior. Mated males nesting in

semi-colonial conditions maintain loose nesting territories, generally of small size. Defended areas surrounding nests constantly changed, indicating that under semi-colonial nesting conditions territoriality is weak.

11. Behavior associated with pair formation is highly variable. Some pair bonds were formed with little courtship behavior, while some males diligently courted several females before forming firm pair bonds.

12. A male dove generally remains paired with the same female at least through one nesting season. In the few instances where the female was killed or disappeared the male was able to find a new mate and continue nesting. No evidence was found during this study that a preponderance of male doves existed in the breeding population.

13. Several instances of mated males exhibiting brief lapses of fidelity were observed, but in each case the male remained mated to his original female.

14. In addition to the perch-coo, male doves utter several faint, short calls. The nest call functions to call the female to the male at the prospective nest-site. Other short calls are given when danger approaches and often after disputes. There may be faint recognition calls associated with the exchange of nesting duties. Females only rarely uttered a faint version of the perch-coo, but they commonly gave the nest call and the warning call.

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