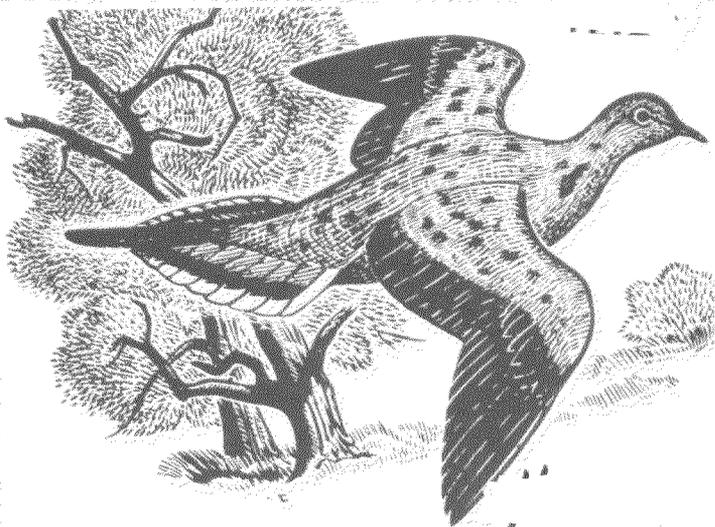


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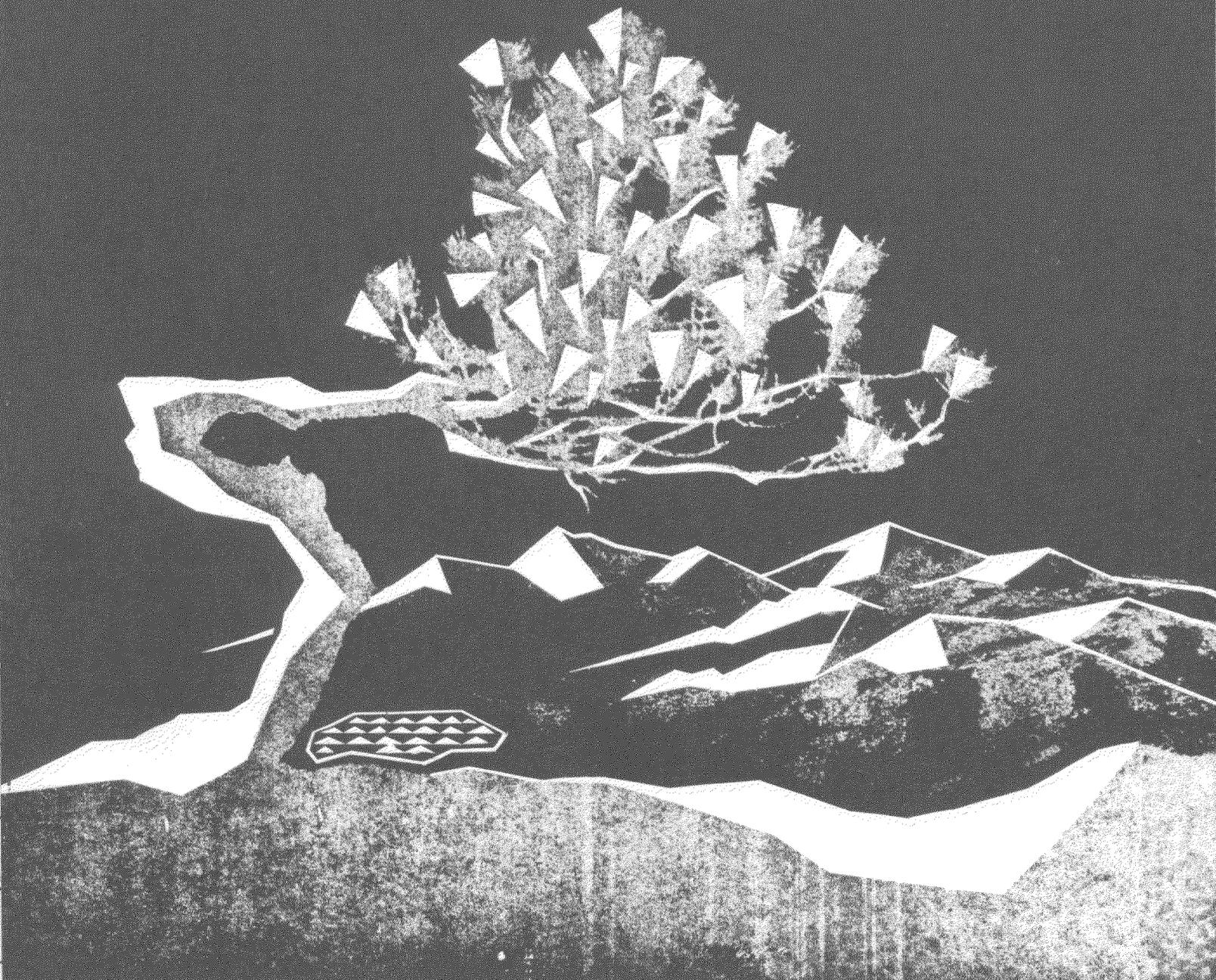
A LITERATURE REVIEW  
ON MOURNING DOVE SONG  
AS RELATED TO THE COO-COUNT CENSUS

by  
Charles P. Stone



STATE OF COLORADO

DEPARTMENT OF GAME, FISH, AND PARKS  
GAME RESEARCH DIVISION  
AND  
COOPERATIVE WILDLIFE RESEARCH UNIT



# A Literature Review on Mourning Dove Song as Related to the Coo-Count Census

by

Charles P. Stone

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Game, Fish and Parks Commission

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## Introduction

Materials presented in this review of literature are concerned with the influents and meaning of mourning dove (Zenaidura macroura ) cooing. A general review of the concepts and functions of bird territory and song is presented as background material requisite to understanding dove song. Emphasis is placed on the internal and external influents of cooing, the meaning of the mourning dove perch-coo, and the problems associated with

the coo-count as a population index. Individual treatment of the influents of cooing does not imply that they act independently of one another, but rather that studies to date have largely considered influents separately. Some of the ideas presented are speculative, and hopefully will stimulate further research. Some of the problems discussed should be solved by research now in progress.

# A Literature Review on Mourning Dove Song as Related to the Coo-Count Census

## Coo-Count Census Method

The coo-count census method for mourning doves was founded upon the basic studies of H. Elliot McClure (1939:323-328). Edward Wellein, Waterfowl Flyway Biologist, Fish and Wildlife Service, and Leonard E. Foote, Field Representative, Wildlife Management Institute, discussed the possibilities of the method, and in 1950, research to refine the method was undertaken by Foote, H. S. Peters, Research Biologist, Fish and Wildlife Service, D. J. Nelson, Georgia State Game and Fish Department, and A. J. Duvall and C. S. Robbins, Bureau of Sport Fisheries and Wildlife. These studies resulted in confirming the practicability of certain procedures in the coo-count method, including distance between stops, length of stops, time of day, and duration of count (Foote and Peters 1952:1).

Coordinated research was begun in 1951 after statistical analysis of previous work, and culminated in papers by McGowan (1952, 1953), Kerley (1952), Duvall and Robbins (1952), Peters (1952), and Wagner (1952). It was thus determined that the dove population was most homogeneously distrib-

uted 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" (Peters 1952:2). The early morning calling level was found to be nearly four times that of the average evening intensity, and day-to-day variation in morning calling was less than in evening calling (Southeastern Association of Game and Fish Commissioners 1957:12-13). Dove calling was found to reach a peak at sunrise, and decrease for the next 1.5 hours, so counts were rigidly standardized for comparative purposes as to starting times. Data from Athens, Georgia counts indicated that wind affected the audibility of calling and the intensity of calling itself; accordingly, counts were not made when wind velocity exceeded 8 to 12 miles per hour (McGowan, 1952:4). In 1953, Peters conducted time-interval tests of call-counts and found the three-minute listening period to be the most efficient (Southeastern Association of Game and Fish Commissioners 1957:13,90).

# Concepts of Territory

## Definitions of Territory

Oliver Goldsmith first proposed the word "territory" for a bird's defended area in 1774 (Lack 1946:137). Previous references to territory may have been as ancient as 3 B.C. (Lack 1946:135), but not until 1868 was the theory of territory formally promulgated. A German ornithologist named Bernard Altum stated the essentials of modern territory theory, but his ideas were not known outside of Germany (Nice, 1943:162). In 1920, H. Eliot Howard presented the first clear, readily available description of the territory concept in his classic work, "Territory in Bird Life."

Howard did not define the word "territory," but stated that two dispositions of territorial birds are to be intolerant of others and to remain about a particular spot (Howard 1920:6). Mayr (1935:31) defined territory as "an area occupied by one male of a species which it defends against intrusions of other males of the same species and in which it makes itself conspicuous." Mayr's definition fits Howard's concept. Tinbergen (1939:69) defined territory as "an area that is defended by a fighting bird against individuals of the same species and sex shortly before and during the formation of a sexual bond." The difficulty with Tinbergen's definition is that many species defend the territory after pair formation. Nice (1941:441) preferred the short, widely used, but confusing definition of Noble: "a territory is any defended area." This definition does not state by what or against what the area is defended.

## Classifications of Territory

Nice (1941:457) listed several types of breeding territories, but emphasized that the types are not rigid and that some species do not fit well into any of the types. She discussed four types of breeding territories: Mating, nesting, and feeding ground for young; mating and nesting but not feeding ground; mating station only; and nesting station, restricted to narrow surroundings of the nest. Dice (1955:247) listed colonial, mating and feeding, and moving territories in addition to those already mentioned. In addition to breeding territories, many species defend food supply, roosts, or other essentials. When all types of territory are considered, it is probable that there are few non-territorial species.

## Protective Functions of Territory

In conjunction with his theory of food conservation, Howard (1920:208) considered that territorialism could prevent overcrowding of a species. Gibb (1961:440) believed that territory size was at least partially dictated by normal resources of the

environment, although presumably a product of natural selection also. Nice (1943:167) said that territory does limit the population, but when food is "superabundant" territorial lines often break down. Lack (1946:142) believed that Howard's views on overcrowding require large numbers of birds to be ejected from territories in favorable years. In this way, the average territory would remain the same size, and the population size would be controlled. Lack considered the average territory size to be near the territorial limit. In other words, further decrease in territory size below the average value is unlikely (p. 143). In contrast, Huxley and Erickson, in Dice (1955:256), considered the territories of coots and wren tits to be compressible to a certain minimum area. Tinbergen (1939:70) drew similar conclusions from his studies of male snow buntings. He noticed that pugnacity of the males increased with a decrease in territory size, and hypothesized that "aggressiveness may increase until that level is reached where it is strong enough to conquer all newcomers." He conducted experiments with blackbirds in captivity and found that on an area smaller than the minimum territory size despotism developed, one male killing all of the others. He concluded that territory has the function of preventing overcrowding, but not in the absolute sense. Presumably he meant that, under favorable conditions, average territory size could decrease. Nice (1943:167) probably correctly concluded that the chief function of territory is not prevention of species increase.

Howard (1920:246) suggested that territory has the function of preserving adequate food for the young. An adjacent food supply permits more trips per day to the young. A greater amount of food is brought to the nestlings and healthier, larger young result. In arguing against a nutritional function for territory, Lack (1946:140) stated that European robins and other territorial species make no serious attempt to eject food competitors of other species, and Mayr (1935:35) stressed the fact that territorial defense is not strongest at the time of feeding the young. Tinbergen (1939:72) stated that territory is necessary to provide a certain amount of food, but that some, or even most, of it may be taken outside of the territory, especially if the young are large and able to be alone for long periods.

Based on her studies with song sparrows, Nice (1943:167) concluded that one of the chief functions of territory is to prevent interference in family affairs. She cited an example of territorial breakdown and the ensuing difficulties in "The Watcher at the Nest" (Nice 1939:20-27). Howard (1920:247)

also considered the prevention of interference as one of the functions of territory.

Another function of territory may be to help maintain the pair-bond. Association with a familiar area makes a male nearly undefeatable on the area, and the protective instinct toward the young is associated with an area (Nice 1943:169). Territory may also function in the perpetuation of monogamy. When both sexes fight intruders monogamy is especially promoted (Tinbergen 1939:67). Darling, in Orians (1961:330), postulated that the main value of territory is social stimulation. The act of defense was thought to provide the stimulation necessary to bring birds into reproductive condition. The territorial system also decreases energy expenditure; an individual need fight only his immediate neighbors (Dice 1955:259), and after becoming familiar with them, few encounters may be necessary. In general, territory may be said to protect things indispensable for reproduction against sexual competitors (Tinbergen 1939:67).

#### Attraction Function of Territory

In addition to the protective functions of territory, there is an attraction function. Females of the species are drawn to an area by display, song, or sound of the male. The territorial system saves both time and energy in this respect. There is no random searching for mates; male and female have a common ground to keep them together. Other males can readily avoid occupied areas, and females may be able to distinguish mated and unmated males by frequency and intensity of display or sound production. Lack (1946:144) considered territory to be of primary importance in pair formation and perhaps in maintenance of the pair-bond. The chief argument for this view seems to be that song and territorial defense wane with and after the arrival of the female of many species. Nice (1943:173) listed some European and American species in which song is known to decrease upon arrival of the female. Odum and Kuensler (1955:134) measured territory and home-

range sizes of kingbirds, chipping sparrows, and blue grosbeaks as the nesting season progressed. They found that the maximum territory (extreme points defended, connected by straight lines) was greater in the nest-building and incubation stages than in the brooding stage. This seems to point to a decrease in territorialism as the breeding season progresses.

Arguments against mate attraction as the primary function of territorialism suggest that territorial defense does not readily diminish after arrival of the female. Aggressiveness is manifested whenever territory is threatened throughout the breeding season, and song decreases due to anxiety for the female (Nice 1943:174). Increased parental and protective duties and an increasing population may account for the reduction in territory size. Adjustment of adjacent territory holders to boundaries may permit a decrease in defensive activities (Lack 1946:38). Nice (1941:454) and Lack (1946:38) both stated that unmated males are less aggressive than mated males. Song in itself may not be a good index of territorial aggressiveness; decreased singing seems more related to the presence of a female than to aggressiveness in many cases.

Thorpe (1961:94) stated that if the main function of song is to repel rivals rather than attract females, some relaxations of characteristics for specific distinctiveness will occur. Thus, we would expect species with monotonous, unvarying songs to possess territories chiefly for mate attraction. Tinbergen (1939:80) separated attractive from protective territories by song frequency after arrival of the female. In species showing marked inhibition of song on arrival of the female, the attractive function is predominant; in species that sing during the entire year with only a slight increase in song frequency during the premating period, the protective function is more important. Advertising song and territory probably fulfill both of these functions to some degree in most species.

# Concepts of Song

## Definitions of Song

In daily life, the word "song" is applied to sounds that are beautiful and not too short (Tinbergen 1939:74). Neither criterion is particularly helpful in defining bird song. Nicholson, in Van Tyne and Berger (1959:136), gave perhaps the most quoted definition of song as "a sustained, more or less interrupted repetition of one or more notes conforming recognizably to a constant specific type, and used by the male as an expression of independent sovereignty." As Nice (1943:144) pointed out, the inclusion of the word "sometimes" in the last clause makes the definition satisfactory; otherwise, it is restricted to that type of song advertising position to a prospective mate and warning sexual rivals.

Tinbergen (1939:74) stated that the most important character of song in most song birds is its loudness and far-reaching capacity. He restricted his definition to "advertising song," and considered advertising song to consist of loud songs given by one sex, especially at the beginning of the reproductive period. His definition included sounds not produced by the syrinx, and sounds produced by non-oscines. Craig (Van Tyne and Berger, 1959:136) stressed the formality connected with song. He believed that if formality is lacking in the song, it is manifested in the accompanying behavior.

Thorpe (1961:15) considered differences between song and call notes: song is a series of notes, generally of more than one type, uttered in succession and so related as to form a recognizable sequence or pattern in time. Thus the song as a whole displays the features of accent, increased duration, increased rhythmical complexity, . . . not discernible to anything like the same extent in call notes.

Thorpe held that song is primarily under the control of the sex hormones, is concerned with the reproductive cycle, often serves as a substitute for physical combat, and is concerned with maintenance of the pair-bond and the mutual adjustment of the sexual cycle of a pair. By contrast, call notes are concerned with coordination of behavior of other members of the species in maintenance activities such as feeding, flocking, migration, and predator response. Despite these seemingly clear distinctions, call notes often serve the functions of song, especially in non-oscines (Thorpe, 1961:16).

It is evident from the preceding that a definition of the word "song" necessitates mention of the functions served by song. Tinbergen (1939:74) considered only the type of song which has the function of advertising the presence of a sexually active bird on territory. Thorpe (1961:16-17) considered utterances by non-song birds as call

notes, but included doves in the "song bird" category. He mentioned that many non-oscines have extraordinary vocal powers, and that separating oscines and non-oscines does not help much in defining the word "song." But he continued to restrict song to "song birds" despite the difficulties. In this review, song is considered to be any sound which serves to defend the territory against intruders or to attract females for mating purposes, whether the sound is produced by the syrinx or not, and whether the species is an oscine or not.

## Classifications of Song

Van Tyne and Berger (1959:137-142) classified song as primary or secondary, chiefly on the criterion of loudness. Secondary song is "low and inward, often being so faint as to be inaudible at a few yards range," whereas primary song is generally louder.

There are three types of primary song - advertising song, signal song, and emotional song. Advertising or territorial song is a "loud sound given by a bird of one of the two sexes, especially at the beginning of the reproductive period, that serves to attract a sex partner, to warn off a bird of the same sex, or both" (Tinbergen 1939:80). Advertising song is most often heard in the spring and is in reality a form of substitute fighting (Lack 1946:17). Signal song coordinates activities of a mated pair, and may sound the same as territorial song, but the function differs. Emotional song "encompasses a variety of songs that cannot be associated directly with securing a mate and defense of territory" (Van Tyne and Berger 1959:138). Tinbergen (1939:79) and Lack (1946:21) discussed cases in which birds uttered songs of great intensity after a narrow escape or when alarmed. It is possible that emotional song is a substitute activity, triggered when the usual reaction is blocked or exhausted.

The four types of secondary song are not well understood. Whispering song is a quiet primary song. Subsong is a quiet song differing from primary song. Rehearsed song is incomplete primary song, seemingly a form of practice for old and young birds. Female song is any song sung by a female (Van Tyne and Berger 1959:139). Both subsong and rehearsed song appear to function in the development of primary song, and Lanyon (1960:331) presented a diagram of the hypothesized sequential development of primary song which will be discussed later in the review. Whispering song is not yet understood (Lanyon 1960:330), and may occur in the autumn as well as the spring (Lack 1946:21). Female song has been induced in the female canary by injecting male sex hormone by many workers (Lanyon 1960:332). Lack (1946:146)

implied that unnaturally high level of male sex hormone in a wild female may produce the same result.

#### Functions of Song

The chief functions of song are the following: to proclaim territory and warn against intrusion; to identify the sex of the sound-producer, thus attracting the opposite sex; to maintain an emotional relationship between the sound-producer and the sex partner; to release excess energy; and to express emotion (Pettingill 1958:245).

By warning against intrusion, energy which would have been used in fighting is conserved. Song also conserves energy on the part of the non-singing sex partner in that no random searching for a mate is needed. In addition, the non-singing sex partner may be able to distinguish mated from unmated birds by frequency and intensity of sound production. Sexual rivals conserve energy by avoiding occupied areas. Individual variation in song may allow identification of old established

rivals or previous mates (Marler 1960:359). Conservation of time may be a more important function of song than conservation of energy. The competition for suitable breeding places and the short breeding season make time an important element in a bird's life.

The maintenance of the sexual bond is undoubtedly an important function of song in some species. The use of song as an energy release or emotional outlet when the usual response is blocked or exhausted was discussed by Tinbergen (1939:79) and Lack (1946:21). Huxley in Nice (1943:148) said that song is an outlet for nervous energy. A bird sings in all moments of excitement or exultation, non-sexual as well as sexual. Tinbergen (1939:78) thought that autumn song (which appears to have no function) is correlated with recrudescence of the testes in the fall. He believed that warm weather stimulates testis growth for a short period, but that development is usually not completed. The factors stimulating or inhibiting song will be discussed in connection with mourning dove song.

# Mourning Dove Territory

## Establishment and Defense of Territory

Mackey (1954:47,88) believed that male doves secure territories before mating. Webb (1949:29) stated that it is not known whether choosing of a nest site precedes or follows the establishment of a nesting territory. He observed defense of the nest site before and after nest construction. Jackson and Baskett (1964:301) noted that unmated male doves were aggressive near their cooing perches, but showed little evidence of well defined territories. One unmated male cooed from perches in a 15 to 20 acre area, and several males often used different parts of a given area simultaneously. In contrast, mated males defended well defined territories (p. 306).

Varying degrees of aggressiveness during the nesting cycle have been noted in several studies. Webb (1949:29) observed defense of the nest site at all times during the cycle except for a short time between broods. He stated that defense of the territory against small birds was most vigorous in the late brooding stage (p. 27). Mackey (1954:47,88) believed that territorialism increased between broods. Swank (1955:500) stated that doves defend territories less vigorously once the nest is established. He based his opinion on the fact that several doves were found nesting in the same tree, and also on observations of "foreign" doves landing within a few feet of a nest without being disturbed. He found that nests in the same tree were all in different stages of the cycle, and reasoned that this was the result of strong territorial behavior until nest building. Baskett (1964), however, found multiple nestings in the same tree, wherein nests were in similar stages, and Jackson and Baskett (1964:302) stated that mated males showed strong territorial tendencies throughout the nesting cycle. Intruding doves were pursued when seen by the territorial male, even when flying through the territory. Doves were aggressive toward several other species, especially in the early stages of the nesting cycle.

## Size and Type of Territory

As stated previously, unmated males seem to defend cooing perches over a rather large area. Mated males have been reported to defend both nest sites and surrounding areas. Perhaps differences in territorialism of mated and unmated doves, and different degrees of aggressiveness in various stages of the nesting cycle, are responsible for some of the conflicting observations of dove territory.

Nice (1962) stated that dove territory probably involves nesting-area defense, but did not recall seeing anything that might be construed as defense of the nesting territory in her studies. Barber as

quoted in Frankel (1961:128) also stated that doves defend the nest site. Several other authors have observed that doves defend larger areas. Observations by Swank (1955:500) indicated that doves may fly 20 to 30 feet to attack other doves, presumably in defense of territory. Mackey (1954:47) found that doves defend an area within an average 50-foot radius of the nest, although territory sizes are "extremely variable." He described a territorial conflict between an incubating dove and an intruder 15 feet from the nest (p. 48), and stated that territorial size may be limited by the farthest distance that male doves can see the nest or nest tree (p. 52). He found that when dove populations were dense the area of defense was sometimes limited to one tree (p. 47). Mackey believed that territorial boundaries were limited by natural boundaries such as street intersections and buildings. Calhoun (1948:141) presented maps of minimal dove territory sizes. Some of the territories were well over 200 feet in length, while others were approximately 50 feet in length. Lund, as quoted in Jackson and Baskett (1964:303), stated that prenesting territories of doves are 100 to 300 yards in diameter, but are decreased to a few feet in diameter after the nest is built. Jackson and Baskett (1964:302) determined the boundaries of seven territories of mated doves, and all were 70 to 100 yards in diameter. The authors stated that there was little competition from other doves in the area and that the mapped territories may have been relatively large for this reason.

## Colonial Nesting and Territorialism

The problem of determining the territorial habits of doves is complicated by their tendency to nest in colonies in some areas. It is well known that territorialism often breaks down under enforced crowding (Lack 1946:41), but in the wild, crowding is presumably not forced unless there is a shortage of available nesting sites. Strongly territorial birds might be expected to move to a new and perhaps unfavorable area rather than nesting in the same tree with another of their species, but in some cases doves do not seem to be strongly territorial. Even in areas where other seemingly suitable nesting sites are available, doves have their "patron trees," or trees that are preferred year after year. McClure (1944:561-562) noted that patron trees contained up to seven active nests at one time, and averaged 2.1 to 3.5 nests in different areas and different years. He concluded that dove territory demands are "elastic" enough to permit crowding.

Fichter (1959:443) thought that better breeding areas attract more doves and allow more success per se. He stated that proximity of neighboring

territory holders is in itself a corollary of kind of habitat, and that the degree of proximity (density) may be a function of habitat condition. It has been suggested elsewhere (Selander and Nicholson 1962:90) that the chief adaptive significance of colonialism is in efficient exploitation of environmental resources by a population. Social stimulation, or the "Darling effect," may also be significant in colonial species. Studies such as those of Swank (1955) and McClure (1942) suggest that high nesting success and productivity often result from colonialism (Hopkins and Odum 1953:140). Despite the advantages of colonialism, the adaptability of doves to non-colonial conditions may be responsible for their present wide distribution. Bent (1932:408-409) believed that the extinction of the passenger pigeon was a result of dependency on colonial nesting. The effects of colonialism on the territorialism of doves is undetermined at present.

#### Territorial Behavior of Related Species

The territorial habits of the rockdove (Columba livia) have been well studied, and observations are relevant to the study of mourning dove territory. Whitman (1919:13) stated that the disposition to drive other doves off becomes strong with nest building, and stronger with laying and after the hatch. He stated that, in pigeons, the disposition to resist enemies is manifested as soon as a place for a nest is found (p. 89), and that the mood recurs with each reproductive cycle. Levi (1957:37) recorded domestic pigeon pairs chasing intruders with an intensity inversely proportional to the distance from the nest. Lorenz, as quoted in Nice (1941:468), also mentioned differences in fighting intensity in relation to a "certain center" of the territory; perhaps this may help to explain some of the observations on the territorialism of mourning doves. Ritchey (Castoro and Guhl 1958:57) noted definite territories among caged rock doves, and suggested possible correlations between

the percentage of encounters won and area of territory defended.

Johnston (1960:15-17) described the territorial behavior of Inca doves (Scardafella inca). He noted that non-breeding birds were ignored by breeding birds, and that territories varied in size and shape, "presumably in relationship to the spatial configurations of important elements in the immediate environment." Some doves were found to behave spatially in an unpredictable manner, and Johnston thought that the operation of "psychological factors" might be important. He noted that territorial behavior occurred in low intensity two or three weeks after early courtship behavior, or from one to three weeks before egg laying. His description of the driving habit or herding of the female by the male is interesting in view of the as yet unexplained chase flights of mourning doves: "The usual form of driving is one in which the male appears to attempt to occupy the spot the female is on; invariably the female moves a short distance away. When the female moves one to six feet, the male follows, and three or four to a dozen such moves may be made before the male ceases to "push" the female onward . . . In other columbids . . . it seems that a mated male "drives" when another male is near the former's mate. This is true in the Inca dove. Driving always occurs if a male encroaches either on a pair sitting or foraging together or on a temporarily unaccompanied female; driving is in fact the only expression of aggression by the territorial male under these circumstances. Straightforward aggression against the intruder sometimes follows an instance of driving, but territorial aggression may actually be terminated by the territory holder in order to drive his mate from the arena."

Recent observations by Jackson and Baskett (1964:305) suggest that two males and a female are involved in the three-bird chases of mourning doves. It has not been determined which birds chase which.

# Mourning Dove Song

## Types and Functions of Song

In addition to warning or alarm calls and copulation, begging, and different conversational notes (Nice 1921:58; 1931:148), mourning doves utter three songs on the breeding grounds. All serve to attract or stimulate the female, and at least two serve to inform other doves that a territorial dove is near.

The territorial "perch-coo" is a series of three or four notes "on one pitch, preceded by an introductory note which begins below the sustained pitch, glides up above it, and then down to it" (Craig 1911:401). According to McClure (1939:323-324), "In giving the call the male arches his 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 very faint version (Frankel and Baskett 1961:374). According to Mackey (1954:73), females coo only upon relieving males at the nest. The perch-coo functions to identify a territorial male and to attract and court the female, although perhaps the attraction function is more important since perch cooing decreases soon after pair-bond formation. The use of the perch-coo as a signal song has not been mentioned in the literature. After describing the perch-coo, alarm note, and nest call, Mackey (1954:72) stated, "All of these three types of coos may be issued at varying levels of intensity." The perch-coo is presumably the only song recorded on coo-counts.

Another song produced by mourning doves is the "nest call." Craig (1911:402-403) wrote: "The male mourning dove, not content with one exquisite lay, sounds also a nest-call which is very different in expression and in its way as perfect as the song. This call is much shorter than the song, and much fainter, so that the field observer may fail even to hear it. Its typical form is of three notes, a low, a high, and a low, thus somewhat resembling the first bar of the song, but differing in that the three notes do not glide into one another, there being a clear break from each note to the next."

According to Frankel and Baskett (1961:374), females often sing the nest call, and an individual male dove delivers the nest call almost as loudly, and certainly as often, as the perch-coo in captivity, although under different conditions (Frankel 1961:38). Jackson and Baskett (1964:296) stated that the volume, length, and inflection of the nest call are variable. They found that the posture assumed when giving the nest call also is variable. The nest call is given most frequently when selecting the nest site or building nests (p. 297). The nest call functions to attract the female to the prospective nest site, to call either mate to relieve the other at the nest, and to renew the nest

cycle (Whitman, 1919:23). When the nest call is repeated many times, it serves as an indicator of the pair-bond (Frankel 1961:97), but frequently there is no purpose for the nest call (Whitman 1919:61). Mated doves have been observed giving nest calls after territorial conflicts, and unmated males gave nest calls occasionally when courting (Jackson and Baskett 1964:297).

The bow-coo was recently described by Jackson and Baskett (1964:298-299) and by definition is considered a song in this review. It is often given without bowing, and sounds like the perch-coo. It is uttered directly at another bird from an erect position with the head held forward. The bow-coo was observed in association with charging while defending territory against other males and while courting females. In one case, a male charged and gave the bow-coo when trying to drive a female away from another male. Jackson and Baskett concluded that the bow-coo and charge are low-intensity expressions of dominance (p. 302).

## Nature of Dove Song

Although the functions of dove territorial song seem to be chiefly attraction of the mate and repulsion of sexual rivals, it does not follow that doves sing to fulfill these functions. Until it is proven that birds exhibit consciousness in their singing behavior, it seems preferable to assume that they do not.

The question, "Why do doves sing?" is basic to judging the feasibility of the audio census technique. If doves do not sing for the specific purpose of attracting mates or repulsing rivals, the factors that prompt or influence singing must be ascertained. In the following discussion, an attempt is made to identify the type of behavior represented by territorial song through review of studies concerned with the ontogeny of song. An attempt is also made to determine the factors that influence, and perhaps "trigger," territorial song through review of studies concerned with the environment of dove song. Finally, the chief influents of cooing are summarized, and a proposed explanation of dove singing behavior is presented.

## Ontogeny of Song

In all birds that have been studied to date, there is a sequential development of territorial song (Lanyon 1960:330). In general, definitive primary song is preceded by subsong and rehearsed song in that order. Studies of Kaspar Hauser birds (young birds that have been isolated from other birds in varying degrees) have demonstrated that higher passerines are able to develop rough primary song patterns that are similar in duration and quality to definitive primary song developed by

wild birds. Development of the definitive pattern requires that young birds learn from experienced birds of their species and, in some cases, from experienced birds of other species (Lanyon 1960:344).

In lower passerines and non-passerines, the development of primary song seems to be different. It has been suggested that, although the same sequential pattern is required for development of definitive song, young birds do not need to listen to experienced birds (Lanyon 1960:333). Although the suggestion that birds might hear and learn the song of the parent through the egg has not been disproved, Lanyon (1960:333) hypothesized that learning is not important in forming definitive primary song in lower passerines, and probably in non-passerines. Craig, in Nice (1931:149), stated that ring doves reared in isolation developed the notes characteristic of the species, and Nice (1931:149) suggested that the perch-coo of mourning doves develops without learning from experienced birds.

In the light of present evidence, it seems correct to assume that the perch-coo is instinctive or innate behavior. Singing fulfills the criteria listed by Lack (1946:183-184) for instinctive behavior, but even if some components of song are learned, there is apparently a receptive or critical period in which learned and innate components are fixed in the central nervous system (Lanyon 1960:344). Emlen (1955:120) used the term "behavior pattern" for the organized combination of innate and learned behavior, and the term "instinct" for strictly innate behavior. Thus, song in higher passerines would be considered a behavior pattern, and song in non-passerines (such as doves) and lower passerines would be considered instinctive. Determination of the factors affecting and "triggering" the instinctive behavior requires examination of the environment of song.

#### Internal Environment of Dove Song

The internal environment of song is ultimately concerned with the hormonal and nervous systems. Lack of knowledge as to how these systems really affect singing behavior necessitates examination of more tangible influents such as stage in the nesting cycle, presence or absence of the pair-bond, molting, and age.

Physiological stage in nesting cycle -- Few workers have studied and contrasted the cooing behavior of doves while courting, building nests, laying, incubating, and brooding. Great differences in cooing among any of the stages could affect the results of coo-count comparisons. Coo-counts taken at different times in the breeding season could sample different proportions of doves in each physiological stage, and synchronization of the nesting cycles of many doves could result in atypically high or low counts.

Mackey (1954:79) reported that the frequency of

cooing varied from "practically no coos when the male had young nestlings in the nest to 323 coos when the male was in an interval between nestings." He recorded the cooing of a male while brooding an eight day old chick, and noted that the cock cooed 14 times in 10 minutes, although about half of the coos were nest calls (p. 73-74). During incubation and early brooding, males were noted on their cooing perches almost as regularly as between broods, but they spent more time preening and less time cooing (p. 88). Mackey believed that nesting activities exert a profound influence on cooing behavior.

Webb (1949:12) made the following observations in regard to cooing and stage in the nesting cycle: "The author has observed a marked male dove arrive from the roost, alight near its nesting site, and leave for its early morning feeding without uttering an audible coo, while other doves nearby were cooing every few minutes. In most observed cases, the male was noted to coo for longer periods during the mornings when the mate was incubating eggs than on mornings when the mate was brooding nestlings. Possibly the presence of nestlings stimulated the male bird to spend more time feeding and less time cooing near the nest site."

Craig (1911:405-407) found that the nest call increased in frequency during nest construction, but found his penned doves to be comparatively quiet during incubation and brooding. Every evening throughout incubation the male sat in his roost some distance from the nest and serenaded his mate with song or nest call, repeating one or the other every few minutes. When the young were fledged, "song and nest call are redoubled . . . Thus is inaugurated another brood cycle."

Frankel and Baskett (1961:377) worked with penned doves, but found no significant differences in cooing frequency at different stages of the nesting cycle. They divided the breeding cycle into four statuses: courtship-nest building, egg laying, incubation, and brooding. Of 30 t-tests between statuses, they found that only seven were significant, and that these were quite evenly spread among statuses. They stated: "Even though there may be differences in its [the male's] cooing frequency in different stages of the nesting cycle, these differences are small and overshadowed by its [the male's] ebullient performance when unmated" (p. 382). Frankel (1961:124) reported on the same study, and noted that his findings conflicted with other literature on the effect of breeding status on cooing. He believed that the difference in cooing frequency at different stages of the breeding cycle was not manifested by his penned doves for the following reasons: he worked with small numbers of doves, the males did not have to seek a new female, there was no need to build a new nest, there was no opportunity to establish a sexual territory, and the males were not separated from the females (p. 134). He stated, "Since cooing

is a seasonal phenomenon directly related to the initiation of the nesting cycle . . . there is no reason to believe that once cooing begins in the spring, that the nesting cycle does not continue to influence cooing in all its manifestations, including starting time."

Jackson and Baskett (1964:295) observed wild, marked, male doves on 65 mornings. They found that the male's position in the nesting cycle had little effect on the rate of perch cooing. Their observations were confined to birds in successful nesting cycles. In contrast, Blankenship (Department of the Interior 1963:53) found great differences in daily calling activity in different stages of the nesting cycle. Mated males gave 0.81 calls per minute when between nestings, 0.45 calls per minute when building nests and laying eggs, 0.10 calls per minute when incubating, and 0.05 calls per minute when brooding. Blankenship's findings are tentative at present, but are supported by more extensive data gathered by Irby (1964) and also by similar, but less marked, differences in Jackson and Baskett's data (Baskett 1964).

General and specific observations of singing in relation to the stage in the nesting cycle of other species are of interest. Buxton (1950:8,14) found that European redstarts stop singing with nest building, start again with incubation, and stop when the chicks hatch. Lack (1946:24) noted that European robin song increased when the young left the nest. Nice (1943:118-119) observed that male song sparrows sing most upon taking up a territory, stop singing when mates arrive, and start singing again during nest building and incubation. Singing is reduced when young are being fed, and song decreases with each brood.

Michener and Michener (1935:136) noted that the song of male mockingbirds diminished with nest building and remained at low levels until the young were large enough to allow leisure time. Frank (1947:315) found that spring drumming of ruffed grouse ceased with the appearance of broods. Bohl (1956:84) stimulated wild chukar partridges with recorded calls and noted that adults with broods did not answer, although 50 to 60 percent of the total birds did answer.

Sherman (1924:86) stated that many species, including doves, show a period of song and rewooing before the second and third nestings. Thorpe (1961:54) thought that the intensity of song is typical for a given individual at a given stage in the reproductive cycle.

Pair-bond and absence of female.--Of the literature reviewed, five studies considered the effect of the female dove upon cooing of the male. In the first, Mackey (1954:40) observed two wild males, one of which he presumed mated. He found that both cooed considerably and regularly in the early morning and late afternoon. He believed that unmated males may coo to attract females, and mated males may coo to stimulate their mates.

Intensive studies on the effects of pairing on dove song began with studies of penned birds in Missouri. On the basis of cooing records from two daily 2.5-hour study periods from April 12 to September 5, 1960, Frankel and Baskett (1961:383) concluded: "The major influence upon the cooing frequency of a male dove is whether it is mated. If the male is mated and nesting, it coos very little . . . Tenfold increases in frequency of perch coos resulted when females were removed from their mates. When the females were returned, cooing dropped to the previous levels, if pair bonds were restored. . . If our results can be extended to the field, then any precise interpretation of call-count data requires information on the ratio of mated to unmated male doves."

Jackson and Baskett (1964:295) studied the calling behavior of wild mated and unmated doves in Missouri. They found that unmated males cooed more than 13 times as often per three-minute period as did mated males. There was no overlap between the two groups in the mean number of coos per three-minute period. Their study was limited to a two-hour period beginning one-half hour before sunrise. Goforth and Baskett (1964) found that females similarly inhibited the song of penned males. They also found that the presence of eggs or young in the nest inhibited song even in the absence of females (p. 6-7).

Blankenship (Department of the Interior 1963:54) found that unmated male doves called at a rate of 1.99 calls per minute, whereas mated males called at an average rate of 0.47 calls per minute. Again, his results were tentative.

The effect of pair-bond formation upon song has been noted for many species. Nice (1943:173-174) listed several European species in which song ceases upon arrival of the female, but noted that we have few American examples, chiefly from lack of study. She noted (p. 118-119) that when the mates of male song sparrows arrive, the males become almost completely silent unless the arrival of a new neighbor renews territorial activity. Lack (1946:14,19) noted that unmated European cock robins generally sing better than mated robins in the spring. Song was found to decline after arrival of the female. Kendeigh (1944:86) stated that male house wrens reduce singing after mating. Howard (1920:131-133) stated: "The partial or complete suspension of the song after pairing has taken place is the most interesting, as it is the most noticeable, feature. . . Not that it is by any means universal . . . but it is sufficiently widespread to demand explanation. . . In fact, in greater or less degree, a change is noticeable in the song of many resident and migratory species . . . a deterioration so marked that we learn by experience to regard it as a certain indication of the arrival of a mate."

Thorpe (1961:44-45) stated that it is very unusual for a mated male to sing more frequently

than an unmated male bird. He noted that unmated pied flycatchers sang later in the day as the season progressed, and that newly mated males behaved like unmated males, singing loudly until the female appeared. Buxton (1950:16) stated that when Montagu removed the female from a mated male redstart, the male came into full song. Tinbergen (1939:25-26) stated that even temporary absence of a female snow bunting sets the male singing.

Quaintance (1938:97-99) noted that prior to actual nesting, permanently mated male brown towhees did not sing, while unmated males did. He released what he believed to be a female into the territory of an unmated male, and reported repression of song for four days. On the fifth day, the female had apparently left, and the male resumed singing. When the female returned the next day, the male ceased singing.

Michener and Michener (1935:136) found that the song of male mockingbirds decreased and almost ceased upon arrival of mates. Unmated males sang until late in the season and then left their territories. If a mated male lost his mate, song increased suddenly and continued for several days. If no new mate appeared, the male stopped singing and left his territory (p. 136).

Stoddard (1946:98-99) noted that the number of whistling bobwhite quail coincided with the known surplus males in a population. Whistling cocks were numerous in areas where nests were never found, and no calls were heard in many areas where nests were most numerous. He noted that penned quail started calling if the hens died or were removed. Elder (1956:639) and Bennitt (1951:12) also believed that the bulk of bobwhite calling was done by the unmated cocks.

Age -- No studies have considered the effect of age on the cooing of mourning doves, and few studies have considered the effect of age on the singing of any bird. Swank (Department of the Interior 1961:89) stated that early-nesting doves may be those entering their second nesting season. If this is true, age ratios may have some effect on the seasonal cooing pattern. Other studies suggest that older birds tend to begin breeding earlier than younger birds. Howard (1920:38) quoted a study in which older birds were found to arrive earlier than young birds on the breeding grounds, and stated that old and young birds seem to mate with equal ease, despite the imperfect song of the latter (p. 166). Kendeigh (1941:15) found that older and more experienced house wrens constituted a greater proportion of earlier arrivals on the breeding grounds than younger birds. He observed (p. 44-45) that over 80 percent of the non-breeders were first-year birds.

Whitman (1919:28) quoted a study of Fulton in which it was implied that young pigeons have stronger voices than old pigeons. Fulton advised against placing an old cock and young hen in the

same pen with a "lively young cock with a strong voice, for if this is the case, the young hen will frequently leave her eggs to reach and pair with the young bird, even though he be already mated." Considering the first-year mortality of mourning doves, it seems likely that migrational and flocking patterns of different age groups are more important influents than any differences in voice between old and young birds.

Molt -- According to Jenkins (Department of the Interior 1961:22), doves have one complete molt per year, beginning in mid-May and ending in early October. The very length of the molt period suggests that molting is a gradual process in doves, and that suspension of other energy-consuming activities (including song) in order to channel great amounts of energy into the molting process is not necessary.

Hormones -- Much of the instinctive behavior of birds is influenced through the effects of sex hormones on the nervous system (Welty 1962:143). The crowing of a rooster, combativeness, and copulation pattern all disappear in capons; but if a capon is injected with androgens, sexual behavior returns. In addition to the sex hormone produced by the testes, three hormones produced by the pituitary gland are important influents of song: A hormone similar to the follicle-stimulating hormone of the female is produced under the influence of light and stimulates testes growth; the luteinizing hormone stimulates the growth and activity of the interstitial cells in both the ovary and testes; and prolactin depresses the production of the hormone inducing testes growth and the luteinizing hormones. It also initiates broodiness (Welty 1962:136-137). The possible effect of prolactin on dove song is especially interesting since, "The abrupt loss of interest in sexual matters often shown by birds once incubation has begun may be attributed to this antigonadal action of prolactin" (Hohn 1961:94). Prolactin has an antigonadal effect in fowl and pigeons of both sexes, and is the hormone that stimulates growth and secretion of the crop sac in pigeons. It is possible that differing prolactin levels are partly responsible for any differing song intensities in different stages of the nesting cycle. It has been postulated that prolactin levels may be responsible for the behavior of bird parasites and for species differences in the role of the sexes in incubation (Hohn 1961:94-95).

A thyroid hormone may also be an influent of song. Similar peaks in song and thyroid activity have been found in the spring and fall for European robins and yellowhammers (Welty 1962:200-201). Thyroidectomy resulted in gonadal disfunction in pigeons (Levi 1957:275) and in starlings and domestic fowl (Hohn 1961:99). Heavy doses of thyroid hormone produce molt in pigeons (Levi 1957:275), and song ceases during the molting period of many species.

Nervous system. --Many of the variations in cooing behavior of individual doves seem traceable to the endocrine and nervous systems. Frankel (1961:90-91) noted that each of his penned doves had a fairly unique time for awakening song. He also stated that two of his paired males perch-cooed when relieving their mates at the nest, and one did not (p. 121-122). Such differences might be expected to have their bases in the endocrine and nervous systems.

The use of song as an energy release or emotional outlet when the usual responses are blocked or exhausted also points to the nervous system as the basis for bird song. Frankel (1961:43) found that many extraneous disturbances influenced the time of first and last coos of the day. Jackson and Baskett (1964:297) reported that mated male doves sometimes gave nest calls after territorial conflicts or for no apparent reason. Lack (1946:161) reported that the song of other species, or even the noise of a saw, could induce song.

Circadian or daily rhythms, and perhaps other rhythms, seem governed by the nervous system. Thorpe (1961:54-55) stated: "song-intensity is typical for a given individual in a given stage of its reproductive cycle and fluctuates endogenously at short intervals. It is no doubt this endogenous fluctuation which gives rise to the periodical waves or bursts of song every few minutes or half-hour within the daily song-period. The internal factors which control these short period rhythms are as yet not all understood. There is no evidence that they can be primarily hormonal and one has to assume provisionally that they are neurogenic."

#### External Environment of Dove Song

Light and seasonal song patterns. --There is considerable evidence that an increase in daily photoperiod stimulates testes growth via the eyes and an encephalo-hypophysial receptor (Farner 1955:219-220). Many birds exhibit a seasonal song pattern associated with testes development and seasonal production of testosterone (Thorpe 1961:41), and the mourning dove probably is no exception. One explanation of the seasonal periodicity of song is that a change in photoperiod acts on the testes through the pituitary to raise the level of sex hormone in the body. The increased hormone level is thought to allow the release of song. Thus, doves sing in response to stimuli that were present previously, but ineffective in stimulating song before the sex hormone lowered the threshold of release. There seems to be a pre-season increase in singing as the sex hormone level rises, a level period when the sex hormone is stable, and a declining period in which the sex hormone declines. In view of the importance of the stable period in the coo-count census, examination of seasonal calling patterns in different areas seems important. At present, coo-count routes are completed

between May 20 and June 10 on a nationwide basis, "a period during which dove calling activity is relatively stable, as indicated by intensive studies in eastern United States" (Wight 1962:1).

Studies of seasonal song patterns. --The South-eastern Association of Game and Fish Commissioners (1957:12) stated that the plateau or stable period of calling at Athens (Georgia), Knoxville (Tennessee), Columbus (Ohio), and Madison (Wisconsin) extended from about mid-May until mid-June. They noted that "usually" the plateau period was preceded by a sharp peak in late April or early May. One variation mentioned was a two-week delay in the plateau period in one area, resulting from unfavorable weather conditions. A variation in the onset of the plateau period from the first to the third week of May also was noted in the same area. They apparently did not consider the variations large enough nor frequent enough to be significant. They made no statistical analyses on the uniformity or variability of the plateau period in the four areas mentioned, and the longest study encompassed four breeding seasons. The other studies included one to two cooing seasons. A further analysis of studies made in the four areas and in other areas of the country follows:

McGowan (1952:5) found that morning calling activity remained at a low level in March and early April of 1951, increased abruptly in late April, and reached a plateau between May 10 and June 15. After the plateau there was a gradual decline. In 1952, however, there was no pre-season peak, and the plateau was reached later in May. Although the two seasons differed in timing, there was no significant difference in the average calling populations in the two years. The number of coos per dove increased from 3.8 in March and April to 6.2 in May and June. Stations showing high activity in April and May remained "best" in June and July (McGowan 1953:439-440).

Kerley (1952:12) noted that in early summer doves coo for long continual periods, but that in late summer they call for short periods and remain quiet for long periods. He stated that there were some mornings in August during which no doves called, but on the following mornings calling activity was sometimes intense. Late-season calling was thought to be more sporadic than early-season calling. Kerley's graph of seasonal calling activity (Fig. 1, n.p.) shows that a plateau was reached in early May and continued to late July.

Duvall and Robbins (1952:17, Fig. 1, n.p.) noted that more doves were heard than seen toward the beginning of the nesting season, but, toward the end of the nesting season, more were seen than heard. Their graph (Fig. 1, n.p.) shows that this was so because doves became more conspicuous, and because calling was reduced as the nesting season progressed. Although they did not graph calling activity in their three routes separately, analysis of Table 11 (p.30) shows that calling

plateaus in the Piedmont Province were reached in the last half of May and extended through the month of June. Calling on the Coastal Plain Province route reached a plateau in mid to late June, and decreased rapidly in early July. Duvall and Robbins stated (p. 29) that the plateau period in their study was "in the month of June" on the basis of all three routes graphed together. Also, on the basis of three routes, calling declined sharply after the late June - early July peaks (Fig. 1, n.p.; Fig. 3, n.p.). The decline, however, was largely caused by a decrease in the number of doves heard on Route two (p. 30).

Wagner (1952:47) found that calling in south-central Wisconsin increased to a peak in late April and early May, and dropped to a rough plateau in late May and early June. Two of his three routes showed a second peak in late July, and the third showed a tendency to peak again in July.

Peters (1952:38) heard more calls per dove in August than in June in three periods - before sunrise, the first hour after sunrise, and the second hour after sunrise. He heard more calling doves in June than in August in the same three periods, however. In 1951, four routes in Ohio showed upward trends in numbers of calling doves from May to June, one route remained nearly level, and two showed downward trends (Fig. 2, n.p.). In 1950, two routes showed progressively downward trends in numbers of calling doves from June to August; two remained nearly level from June to early August and then decreased; two increased until late July and dropped suddenly; one peaked in mid-July, dropped suddenly and leveled off; and another climbed progressively from June until early August (Fig. 1, n.p.). An examination of Peter's data suggests that doves on all of his routes were not in the plateau stage of calling from May 20 to June 10.

Dahlgren (1955:25) found that calling reached a peak in the first week of June in Utah, remained at plateau level until the end of July, and rapidly declined in August. He stated that the plateau period was shorter than that reported by other writers because doves arrived later and began to nest later in his area (p. 29). He found that spring migration continued through most of June (p. 32). Only three coos were heard after the 18th of August (p. 40).

McClure (1939:326) stated that cooing in Iowa was nearly constant from April to August, with a slight rise in May. He stated that in June and July birds cooed 6.8 percent more than in April and May or August and September. Webb (1949:22) stated that cooing proceeds at a decreasing rate throughout the nesting season in Ohio.

Lowe (1956:429) found a cooing plateau in May and June, and a slow decline in June and July, followed by a rapid decline in calling in Georgia. Peak calling occurred in early and late May. He believed that the seasonal curves for early-

morning counts were similar in the north and southeast (p. 432).

Frankel and Baskett (1961:375) studied individual, penned doves. They found that each of the male doves reached a cooing peak in a different month and they observed no peak season plateau (p. 378-379). The unmated males seemed to exhibit steady high plateaus which lasted as long as the males remained unmated, or until the season decline. They suggested that as the proportion of unmated to mated males shifts in favor of mated males, the cooing of wild populations may decrease, even though the number of males actually present has not changed. Frankel (1961:133) hypothesized that the frequency of cooing reaches a peak before nesting, and is low at any other time because the two main functions of the perch-coo (winning a mate and defense of territory) are fulfilled and unfulfilled, respectively.

Blankenship (Department of the Interior 1963: 53) observed a rapid buildup in calling activity in early spring and a decrease subsequently. He found that there were several peaks of calling in Arizona, but generally the peaks were lower as the season progressed. Early peaks were attributed to both transient and resident doves, and the dove population did not become stabilized until mid-May. His findings and conclusions are tentative at present.

Seasonal song patterns and the coo-count census. -- An analysis of the seasonal song patterns discussed in the previous section suggests that the concept of a "plateau" is valid only in the sense that there are no long-term increases or decreases in numbers of calling doves. There are sometimes large fluctuations in the number of doves heard during the plateau period. Variations in the number of doves heard during the period May 20 - June 10 are also large at times (McGowan 1952:Fig. 2; Duvall and Robbins 1952: Table 11; Peters, 1952; Figs. 2 and 3; Wagner 1952: Fig. 1; and Lowe 1956: Fig. 1). The causes of the fluctuations in numbers of doves heard over a short period on the same route are probably complex. The term "plateau" has perhaps obscured the importance of investigating variations in the number of calling doves, however. "Plateau" implies a uniform number of calling doves and, in many instances, this is not the case.

The dates of plateau periods may be different in different areas. It seems likely that areas showing nesting peaks in July (Swank 1952), June and August (Sprunt 1957), and late July and August (Boldt and Hendrickson 1952), would manifest different calling patterns. The wide range of latitude, altitude, climate, and the correspondingly variable phenology and migration patterns encompassed by dove breeding range, suggest that the national coo-count dates are oversimplified. Mackey (1954:64) thought that singing male censuses of mourning doves might well be undertaken

as early as April in Ohio. Hanson and Kossack (1963:46-47) believed that roadside censuses made in early spring are of limited value in predicting nesting populations because doves are quite sensitive to temperature. It is possible that weather sometimes seriously affects spring coo-counts by delaying or stimulating migration and nesting. Blankenship (1964) stated: "Running the routes between May 20 and June 10 could possibly be incorrect for the northern part of the country. We are trying to find out what the proper time in Arizona would be, be it the current period in use or some other period." He believed that, "We need to decide specifically what we are going to measure and what the population fluctuations mean before we settle on the proper census period."

Light and daily song patterns - Many studies of the relation of light intensity to awakening song have been completed. Aldo Leopold made hundreds of observations of 20 species of birds and confirmed the fact that cloudiness delays the time of awakening songs. He also found that bright moonlit nights were associated with earlier singing by robins (Welty 1962:203). A revealing graph from Leopold's observations on mourning doves (Welty 1962:202) showed that awakening song was earlier as day length increased, and that on rainy and cloudy days, dove song began later than on clear days. Welty (1962:202) suggested that, "Light intensity is the chief trigger which sets off awakening song in birds."

Frankel (1961:92) found no reliable measure of light intensity that coincided with the initial cooing of penned doves. He believed that there is a certain light threshold necessary to stimulate a coo, but did not observe any consistent change in awakening song with cloudiness. He believed that the initiation of cooing was governed by the stage in the nesting cycle as well as by light intensity. Many of the influents that impinge upon doves influence cooing, and this will be discussed in a later section of the review.

Studies of daily song patterns - Several studies have related the calling of doves to sunrise. The Southeastern Association of Game and Fish Commissioners (1957:13) stated that calling reaches a peak at sunrise and diminishes gradually for the next 1.5 hours. In view of studies reviewed below, this statement seems an oversimplification.

Duvall and Robbins (1952:25) found that more doves were calling 0.5 to 0.75 of an hour before sunrise than during any other observation period. In several areas the number of doves cooing in the first hour after sunrise was high, but in one case the small number of samples, together with unfavorable habitats visited before sunrise, "seemed to be the factors contributing to a low count in the pre-sunrise period."

Peters (1952:36) heard more doves and more calls per dove in the first hour after sunrise than in the period before sunrise or the second hour

after sunrise. His pre-sunrise period was only half as long as his two post-sunrise periods, however.

Kerley (1952:11, Fig. 11, n.p.) plotted the number of calling doves heard over a three month period against time in relation to sunrise. He found that more calling doves were heard at sunrise in June, but that in April and August more doves were heard approximately 30 minutes after sunrise. Peters (Southeastern Association of Game and Fish Commissioners 1957:13,90) found that two factors contributed to decreased calling activity during the latter part of the national two-hour census period: "fewer doves were calling at a less persistent rate." He found that a higher mean percentage of doves was heard during the half-hour before sunrise than in the subsequent three half-hour periods. McGowan (1952:5) also found that fewer doves called in the second hour of the coo-count route, and stated that fewer doves were heard at the end of the route than at the beginning, even if the population at the end of the route was equal to that at the beginning. Lowe (1956:431) found calling activity to be less intense and more irregular on the last few stations on a call-count route.

Cohen et al. (1960:210) stated that a sign test showed that doves coo more during the first half hour following sunrise than during the second half hour after sunrise. However, the average number of calls per bird for the two time periods was not significantly different on the basis of a "t" test. There was no significant difference between the number of calls in the first and second quarter hours after sunrise.

Mackey (1954:75) found that cooing intensity "rose sharply at 30 minutes before sunrise to a peak that was maintained until sunrise." Cooing was found to diminish from sunrise until 30 minutes after sunrise, when it dropped abruptly and became erratic. Dahlgren (1955:30) found that cooing decreased from an average of 3.6 to 1.8 birds per station during the hours of 5:00 to 7:00 a.m.

Frankel and Baskett (1961:379-380) stated that the cooing of penned, mated, male doves began approximately one hour before sunrise, increased in frequency until 30 minutes before sunrise, and leveled off until 15 minutes before sunrise. After this, cooing decreased sharply and remained fairly level for an hour and 45 minutes. The cooing of unmated males showed no sharp peak, but a high frequency was attained about 30 minutes before sunrise, after which cooing slowly declined. These investigators suggested that the cooing of mated males, which concentrate their calling near sunrise, "is superimposed upon the cooing of the unmated males which coo at a high level throughout the morning period." Jackson and Baskett (1964:296) obtained similar results with wild doves, but found that cooing by wild mated males

peaked later than with penned mated males. Different proportions of mated and unmated males in wild populations may be responsible for the above differences in daily cooing patterns.

Studies of the singing patterns of bobwhite quail and pheasant have produced data similar to dove patterns. Kozicky (1952:433) found that the effect of time in relation to sunrise on the pheasant crowing count is statistically significant. Crowing showed a definite decline from 35 minutes before sunrise to 10 minutes after sunrise. Bennitt (1951:15) used the first hour after sunrise to record bobwhite whistling because "most calling is done then." He found no great decrease of whistling during that hour. Elder (1956:643-644) noted that bobwhite call-indices for the first hour after sunrise were greater than indices for the second hour after sunrise, but found frequent exceptions.

Weather and dove song: -Several workers have studied the relationships of temperature, humidity, barometric pressure, and cloud cover to dove cooing activity. Statistical analyses were not made in all cases, and analyses involving the interaction of two or more influents were seldom made. It is assumed that the studies all refer to the mourning dove perch-coo rather than the nest call. Some effects of weather on the singing of other birds are mentioned for comparison.

McClure (1939:325) stated that cooing activity was not greatly affected by temperature except at the extremes. He found that doves did not coo much below 0° Centigrade or above 25° Centigrade. Duvall and Robbins (1952:29) noted that cold temperatures had little effect on cooing, and stated that the reduction in calling frequency in July and August is probably caused by breeding-season decline rather than temperature. Mackey (1954:82-83) stated that lower temperatures favor high cooing intensity. He noted little persistent cooing when temperatures were in excess of 70° Fahrenheit, and observed that May sunrise temperatures in excess of about 60° Fahrenheit were associated with reduced cooing. Davey (Department of the Interior 1961:50) noted little effect of temperature on cooing except at temperatures below 45° Fahrenheit. McGowan (1953:439) found that the first pronounced increase in calling during the season was associated with an approximate 20° rise in morning temperature. Wimmer (Department of the Interior 1961:38) found that calls were reduced when the temperature exceeded 85° Fahrenheit. Frankel and Baskett (1961:381), working with penned doves, found that four of seven significant linear correlations between cooing frequency and separate elements of weather involved temperature, but three were positive and one was negative. Moreover, six other possible correlations between temperature and cooing activity were not significant. They stated: "Possibly cooing behavior is governed by environmental extremes, between which the small daily changes have little effect."

Mackey (1954:86) found no correlation between relative humidity and cooing activity. Wimmer (Department of the Interior 1961:38) found a similarity between the season trend of relative humidity and the number of calling doves. Frankel and Baskett (1961:382) also found no significant correlation between humidity and cooing activity, but Frankel (1961:73) stated that relative humidity and barometric pressure must be interrelated and serve as an explanation of the "deathly quiet" before storms among birds.

Mackey (1954:84) and Frankel and Baskett (1961:382) found no significant correlations between cooing and barometric pressure.

McClure (1939:325) stated that light winds decreased audibility and cooing activity somewhat, medium winds lowered activity more, and strong winds stopped cooing activity completely. Duvall and Robbins (1952:29) suggested that calling activity and audibility (p. 31) are both reduced by wind. McGowan (1952:5; 1953:440) stated that wind reduced cooing and decreased the audibility radii of cooing doves. Mackey (1954:84-85) found no cooing decreases by winds less than 10 to 12 miles per hour. He stated that low cooing intensities with winds of 10 to 12 miles per hour were largely the result of poor hearing conditions. Frankel (1961:74), in studies of penned doves, noted that doves did not coo less with increasing winds, but moved their cooing sites to the ground. He found no significant correlation between wind and cooing activity (Frankel and Baskett 1961:382).

Leopold's observations on the effect of cloud cover on cooing were mentioned previously. Mackey (1954:86) could establish no definite correlation between nebulosity and cooing intensity, but believed that a 100-percent overcast did not lower cooing intensity. He found a delay in initiation of cooing for as much as 15 minutes on heavily overcast mornings, however. Webb (1949:71) stated that doves may coo for longer periods when the morning is cloudy than when it is clear. Davey (Department of the Interior 1961:50) noted that cloud cover seemed to influence cooing only if rain threatened. Peters (Southeastern Association of Game and Fish Commissioners 1957:13) found no significant difference in the mean number of doves heard on clear and cloudy days. Frankel and Baskett (1961:382) also found no significant difference in the mean number of doves heard on clear and cloudy days. Frankel (1961:91-92) observed that initial daily cooing is possibly governed by stage in the nesting cycle as well as by light. Heavy rains are known to have a depressing effect on cooing (Mackey 1954:87); Southeastern Association of Game and Fish Commissioners 1957:13), perhaps as a result of lowered light intensity.

Despite the number of studies on the effects of weather on cooing, further study could be enlightening. Many investigators considered weather

effects over a long period when relationships between weather and cooing could be obscured by spring migration patterns, temperature extremes, and the effects of pair-bonds and breeding status on cooing. During the short period in which coo-counts are made, other influents are more stable and variation in weather may sometimes be an important influent. Some of the observed fluctuations in numbers of calling doves during the census period may possibly be explained by more critical analyses of weather during the census period.

Weather and the song of other birds - The effects of weather upon bird song in general, and upon other species in particular, is of interest. According to Welty (1962:199), both cool weather and very hot weather are song depressants in most species. He cites several examples of the effects of wind and temperature on the number of songs of different species. Thorpe (1961:53) noted that most birds sing less in mid-day because of the increase in wind and heat. He stated that increased humidity may stimulate singing. Erickson (1948:582) stated that high temperature shortens the daily song period in the South. Petraborg et al. (1953:294) stated that cloudy, misty mornings, rain, and thunder curbed or stopped the drumming of ruffed grouse. Winds did not affect the intensity of grouse drumming, but reduced radii of audibility. Bennitt (1951:19-21) found that bobwhite quail call-indices were not significantly affected by cloudiness or winds up to 10 miles per hour. Fewer bobwhites called as the temperature rose, but there were no demonstrable relationships between relative humidity and call indices. Elder (1956:650) stated that wind and temperature had no significant effects on bobwhite calling. Kozicky (1952:432) found no significant difference in pheasant crowing means under complete and partial cloud cover. Crow counts were influenced by wind, however. There was a decrease of 15 crows per station when the wind rose from 8 to 10 miles per hour. He found no significant differences in crowing means above and below 40° Fahrenheit. Kimball (1949:112) also found that wind affected crowing counts. He recommended that no crow-count censuses be taken when wind velocity exceeded 8 miles per hour. Nice (1943:112) noted that the awakening song of the song sparrow is stimulated by mild temperatures, and is closely correlated with light. She mentioned studies in which some birds were found to sing more frequently at high humidities, and less frequently with high winds (p. 112-113).

Population density and dove song - If the appearance or sound of another bird stimulates a given bird to sing, different singing patterns at different population densities would be expected. At high population levels, more audio and visual contacts would stimulate birds to sing more than at low population levels. Thus, coo-counts in low and high populations would not be comparable; a

cooing dove would be an index to different numbers of breeding doves at low and high densities. The following studies suggest that the effects of density on cooing are still undetermined.

Duvall and Robbins (1952:33) thought that individual doves call more frequently when other doves are calling, and that the number of calls per dove decreases when fewer doves are calling. They concluded that there might be a correlation between the number of doves calling and the number of times each dove calls in a given period. "This seeming correlation continues to prevail after the late June-early July peaks, even though the number of calling birds declines sharply."

The Southeastern Association of Game and Fish Commissioners (1957:14,140) compared average total calls and numbers of doves calling on all eastern routes in 1954. They found that the calling activity increased faster than the number of doves calling, producing a curvilinear relationship. They also noted that fewer doves were seen than heard in low populations, but more doves were seen than heard in high populations (p. 16, 95). Doves in low-population areas were less readily seen, were cooing disproportionately less than doves in high-population areas, or both.

Mackey (1954:88) noted that loafing and preening doves began calling upon hearing neighboring doves. He suggested that the calling behavior of urban and rural doves might differ, since a given urban dove has a greater number of audio contacts than a rural dove. McClure (1939:325) stated that large numbers of doves stimulated other doves to coo.

Frankel (1961:64-65) calculated linear coefficients of correlation for 60 days of cooing between doves in any two of his pens. The only significant correlation indicated that cooing in one pen inhibited cooing in an adjacent pen in one case. He noted that his study disagreed with other studies on the effects of density (p. 124), and suggested that outside cooing or cooing in adjacent pens determined when cooing took place, but did not increase the total coo-count (p. 64-65). He believed that density-dependent calling could occur in any three-minute period, but that it would not affect the total calls in a 2.5-hour period.

Cohen et al. (1960:208,210) stated that dove calling may depend somewhat upon previous calling activity. They found that calling in one three-minute interval was not often independent of calling in the following three-minute interval. Thus, adjacent doves might stimulate a dove to sing, and his own singing might provide continual stimulation. They also found that a decrease in the number of calling birds was accompanied by a significant decrease in the average number of calls per dove. They did not, however, believe that their data warranted the assumption that some birds induced others to call. Rather, they believed that time of year or some factor associated with time of year

could be responsible for decreased calling. Perhaps some or all of the stimulating effect attributed to density in wild populations can be explained by unmated males which call at high rates, and are thus likely to be heard. Unmated males would be heard more often singing at higher rates than mated males, simulating an increase in calling at higher densities.

Population density and the song of other birds. -- The effect of intra-specific contacts upon song in other species is relevant. Again, the effects of density upon song appear questionable. Johnston (1960:16) described the effect of density on Inca dove song: "A simple human imitation of the call will cause males from two or three nearby territories to respond in like manner. . . . If one Inca dove intrudes into another's territory, the 'song' increases in frequency."

Bennitt (1951:13) noted that the few mated bobwhite quail that sing usually do so when stimulated by other calls. Elder (1956:645) also stated that one whistling bobwhite may physiologically stimulate another to call.

Thompson and Lemke (n.d.:4) concluded that the number of ruffed grouse drums per bird remains constant, "irrespective of high and low populations and irrespective of whether drumming is at a seasonal peak or not." They heard "larger than theoretical numbers of crowings [of pheasants] at the higher intensities of crowing," and suggested a stimulatory effect of crowing as the number of cocks increases. Ruffing (Mackey 1954:88) stated that the crowing of one cock pheasant does not stimulate other cocks to crow.

Habitat type, migrational homing, and song. -- Quantitative comparisons of calling populations in different areas require knowledge of similarities and differences in calling patterns in the different areas (Cohen et al. 1960:203). Since "song is the expedient used by inconspicuous birds to compensate for the drawbacks of being inconspicuous" (Nicholson in Nice 1941:460), it seems possible that doves living in open areas may sing less frequently than doves living in areas of denser cover. Birds of open areas are more readily located by a few calls and by sight, both by prospective mates and territorial rivals. Enemies are also able to locate open-area birds easily, and silence means safeness (Quaintance 1938:101).

In order to postulate the existence of differentially calling dove populations, it becomes necessary to examine the accuracy of migrational homing. If doves are faithful to a given breeding area, development of different song patterns is possible on genetic or traditional bases. Studies of homing have generally shown that adult males are very faithful to a breeding area (Harris 1961:65; Tomlinson et al. 1960:264). Chambers et al. (1962:158) have suggested that the high rate of homing may be partly attributable to wintering of some of the males near the areas. Female doves

were found to be very accurate homers in one study (Tomlinson et al. 1960:264), and moderately accurate in another (Harris 1961:63). Nestling birds seemed to exhibit inaccurate homing tendencies to a 160 acre study area, but many may have returned to the general area (Harris 1961:65). Hanson and Kossack (1962:14) thought that nestlings probably return to nest in the general area of their birthplace, and Wight (Hanson and Kossack 1963:14) found that some nestlings of breeding adults returned to within a mile of the point of banding in the following year. If homing is accurate, inheritance of different song patterns through inbreeding would be possible, especially if there are advantages to different patterns in different areas. The studies of Downing (1959:118) suggest that doves prefer to nest in the same general habitat (ground or trees) in which they were raised.

Studies of the effects of habitat on song. -- Little work has been completed on the cooing differences of doves in different habitat types. Coo-count samples for 1953 and 1954 were analyzed on the basis of life zones, biotic provinces, soil provinces, and soil associations. Significant differences were found in subgroups for each major classification and within one of the two soil provinces tested. Low interclass correlation suggested that variation within each subgroup in the major classification was large (Southeastern Association of Game and Fish Commissioners 1957:17,97).

Cohen et al. (1960:204,212) conducted studies at stations in the Carolinian Life Zone in Indiana and the Prairie Life Zone in Illinois. They counted calls for 60 minutes after local sunrise, chiefly in July. Differences in the mean number of calls per bird in the two zones were not statistically significant.

Stair (n.d.:3) noted extreme variability of coo-count surveys in Arizona, "due to the varied types of vegetation throughout the state." He noted that the nature of the habitat around some routes changed radically from year to year with resultant increases or decreases in calling by as much as 108 and 100 percent. Part of the change was probably caused by natural population fluctuation. Hanson and Kossack (1963:110) found natural changes in breeding populations as high as 94.9 percent from year to year.

Latitude. -- Although the effect of latitude on the calling behavior of doves has not been analyzed, there is a possibility that southern doves call less frequently than northern doves at comparable population densities. McGowan (1953:443) thought that it would be logical to expect a pronounced pre-season peak in calling in the North "where there would be little previous nesting activity (and hence no prior establishment of nest sites or territories)." Erickson (1948:581) suggested that species that occupy the same territories in summer and winter "know pretty well where they fit"

at the beginning of the reproductive season and that there is not the contesting for space that migratory species exhibit. Since most doves do not occupy similar summer and winter territories, competition would be less intense in the South only if some doves established territories earlier in southern states than in northern states. Non-migratory components of dove populations may do this. Erickson (1948:581) suggested that the long nesting season in the South may be a factor causing reduced singing. Temperature may work with latitude in that "the morning chorus is definitely shorter than farther north in cooler temperatures."

#### A Proposed Explanation of Dove Song

Attempts to explain any facet of bird behavior are ultimately based on the largely unknown workings of the nervous system. The Lorenz-Tinbergen theory of bird behavior has such a basis, and the following is an attempt to explain song in the terminology of that theory.

Within each animal there are a number of "fixed action patterns" that embrace sensory, motor, and integrating elements, all in one rigidly organized packet. Each pattern somehow generates its own nervous tension or "specific action potential" in the central nervous system, and this tension builds up as long as the specific action pattern is quiescent. Every specific action pattern remains blocked until its correlated "releasing mechanism" within the central nervous system receives a "specific sign stimulus" or "releaser" from the external environment. The discharge of a specific action pattern is the "consummatory act," and this relieves the tension or specific action potential (Welty 1962:161-162). In addition to the releaser, there are a number of "motiva-

tional factors" that do not evoke the consummatory act, but lower (or raise) the threshold governing release (Emlen 1955:121). If the releaser does not appear, the action potential builds up and the threshold for the stimuli required to release a given action is lowered (Welty 1962:165). Sometimes the threshold is lowered to such an extent that the action pattern is released without stimulus in "vacuum activity." In other instances, the nervous tension may overflow into other "inappropriate" channels and activate the discharge of irrelevant "displacement activities." Under certain conditions, low intensity or incipient instinctive responses will be exhibited. These result from low internal tension or low specific action potentials and are called "intension movements." These serve as indicators of the "mood" of a bird or of its specific internal readiness for certain activities (Welty 1962:165-166).

In mourning doves the fixed action pattern in this case is the perch-coo. The perch-coo generated its own specific action potential or tension in the central nervous system, but cooing is prevented from being released by a releasing mechanism in the central nervous system. The releaser for the first song in the morning (awakening song) is probably light intensity. After the awakening song, however, many factors in the internal and external environment of the bird influence song, and the bird probably responds to this environmental complex of "Gestalt" rather than a simple releaser. Hormone levels, sight of the female bird, sight of the nest, eggs, or young (Goforth and Baskett 1964: 6-7), pair-bonds, audio and visual contacts with other birds of the species, and weather conditions may raise or lower the threshold governing release of the perch-coo.

# Sex Ratios of Dove Populations and the Coo-Count

Since it has been well established that unmated male doves call more than mated males (Frankel and Baskett 1961:382; Jackson and Baskett 1964: 295; Blankenship (Department of the Interior 1963: 54), a proportionately larger number of them may be expected in coo-count totals. It thus becomes necessary to determine whether the ratios of mated to unmated males remain similar from year to year (Wight 1961:378). If sex ratios do exhibit great changes, the differential calling behavior of male doves would seem to make the coo-count liable to serious error unless sex ratios are determined annually. Since the problem of differential calling by male doves looms large in present dove management, an examination of what is known about dove sex ratios, and factors that may influence their stability, seems advisable.

## Primary and Secondary Sex Ratios

Hanson and Kossack (1963:64-66) examined the early literature on the physiological influents of sex in doves. Early laboratory breeding tests showed that eggs with small energy content, small yolk size, and high water content were correlated with maleness. Eggs of large yolk size, low water content, and greater energy content were correlated with femaleness. In ring doves, the eggs producing an excess of males were produced in the winter, and those producing an excess of females were produced in the summer. Hanson and Kossack found no seasonal difference in the sex ratios of nestling mourning doves, but noted that Wight (p. 65) did find a difference in sex ratios early and late in the nesting season. They also stated that the sex ratios of immature doves shot by hunters showed a seasonal differential, although they emphasized that the origin of the birds was unknown. They stated (p. 64-65): "This apparent seasonal difference of sex ratios in mourning doves could relate both to seasonal environmental conditions (mainly temperature) and to physiological conditions associated with the increasing reproductive experience of the adults. The latter may be of greater importance in influencing sex ratio in populations of immature doves than in those of many other species because of the fact that the dove is notably multi-brooded. Late-hatched doves

would be, on the average, from females that had previously produced at least two clutches of eggs."

If there are seasonal differences in the primary and secondary sex ratios of wild populations, a large number of nesting failures early or late in the season would affect sex ratios of immatures and probably subsequent coo-counts.

## Tertiary Sex Ratios

After fledging, male and female doves may be subject to differential mortality before the next breeding season. Any such differential mortality may accentuate or moderate any disproportionate secondary sex ratios. Nice (1937:39) stated that the males of migratory species often winter farther north than the females, and Hanson and Kossack (1963:67) suggested that sexual differences in basal metabolism may explain such tendencies in doves. The studies of several investigators suggest that male doves do winter farther to the north than females (Leopold 1943:153-154; Quay 1951:65-66; Hanson and Kossack 1963:67; and Chambers et al. 1962:157-158). Because male and female doves have different migrational and wintering habits, they may be subject to differing mortality rates. According to Jackson and Baskett (1964:305): "It is conceivable that yearly changes in call counts may represent changes in the ratio of mated males to unmated males rather than actual changes in breeding densities. . . Further studies are needed to determine the annual variation in the ratio of mated to unmated males in the breeding population."

In a recent paper, Wight (1964:280) suggested that where sex ratios of the adult population approach equality, changes in matedness ratios will not affect the results of coo-counts significantly. He determined matedness ratios through adult sex ratios derived from mortality and production data and concluded: "using the limited data available, it would appear that the expected matedness ratio of the dove population over much of the range will be such that the bias due to differing calling ratios among mated and unmated males does not greatly alter the capability of the dove coo-call census to measure annual trends in the mourning dove breeding population."

# Relationships of Cooing to Breeding Populations

Coo-counts are generally thought to be indices to breeding populations of doves (Wight 1962:4). Critcher and Overton (1960:106-107) believed that coo-counts measure some function of breeding intensity as well as breeding density. They thought that coo-counts might reflect some general condition conducive to nesting activity, and thus provide more than just an index of the abundance of breeding doves. Two obvious measures of breeding are the actual number of birds present and the nesting activity on an area. In the following discussion, these will be examined in relation to cooing activity.

## Relation of Cooing to Nesting Activity

Lowe (1956:429-430) stated that the peak of nesting in his Georgia study coincided with the plateau of the coo-count. McGowan (1953:443) also found that the plateau in Georgia coincided with the peak in nesting. He defined the peak in nesting as the period when the largest number of pairs is engaged in some phase of nesting.

Caldwell (Department of the Interior 1961:48) found that the maximum number of calling birds was not correlated with the peak of nesting in Michigan. He found that the calling peak occurred 54 days later than the peak of nesting. Jackson (1963:50) listened to the number of doves cooing in 28 randomly selected, three-minute intervals. He determined the mean number of doves cooing during these intervals for each of five days in June, and compared the mean number of doves heard for each day with the number of active nests on a "large lawn" surrounding his listening point. He found no consistent relationship between the two sets of data. Blankenship (Department of the Interior 1963:53) found that calling activity was inversely related to nesting activity when dove populations stabilized. As calling decreased, more nests were likely to be found; and as calling increased, fewer active nests were located on the study area.

## Relation of Cooing to Breeding Populations

Kerley (1952:10-12) censused a 283-acre tract (radius 1,980 feet) around a coo-count station in Tennessee. He heard an average of two doves at the station in June and found eight calling doves in his complete census of the 283 acres. In July, he heard an average of 1.5 doves at the station and found six calling doves within the 283-acre area. He apparently censused the area for breeding doves chiefly by spot-mapping territorial males, since he "sometimes found it necessary to remain in the same spot for an hour waiting for . . . spells of sporadic calling."

Hopkins and Odum (1953:135) censused a 100-acre tract around a coo-count station in Georgia. The average number of doves heard calling was 2.6, and the range was one to four birds on 17 trips in May and June. The census of the 100-acre area revealed four pairs nesting "within easy hearing distance." One cooing dove represented an average of 1.53 breeding pairs. These authors also used the spot-mapping method to estimate breeding doves.

McGowan (1953:442,444) found that the correlation between coo-counts and breeding doves was better when the population of 100 acres plus a 50-acre buffer (1443 feet radius) was censused, than when the breeding density of only 100 acres was censused. He found an average of 1.6 breeding pairs on the 150-acre area for each dove heard on the coo-counts. Analyses of his data showed that a cooing dove represented from 1.36 to 4.00 breeding pairs during the height of the breeding season at different stations on the route (p. 439).

Lowe (1956:429) censused seven study areas of 150 acres each in Georgia, located around coo-count stations and chosen to represent low, average, and high populations of doves. Breeding pairs on the areas were spot-mapped. Doves heard on coo-counts represented an average of 1.72 pairs during the plateau. A calling dove represented a low of 0.76 pairs on one area and a high of 2.39 pairs on another area (p. 432). Lowe stated that stations 16 and 20 on the route (with 0.76 and 1.50 pairs per calling dove) would be expected to exhibit inconsistent calling since they were reached when calling activity was low (p. 431).

Webb (1949:11) recorded doves heard in five-minute periods from 6:30 a.m. to 8:30 a.m. in May. He found that a calling dove represented a minimum of 1.88 pairs, a maximum of 7.50 pairs, and an average of 4.20 pairs.

There seems to be a general relationship between cooing and breeding birds. Attempts to determine specific relationships between calling doves and breeding pairs are fraught with difficulties. The individual who determines the relationship has hearing and attentive abilities peculiar to himself, and attempts by others to apply his figures are inaccurate. In addition, the acreage to be searched for breeding doves is variable since radii of audibility are variable (Kerley 1952:10; Hopkins and Odum 1953:135; McGowan 1953:442; Department of the Interior, 1961:50, 67); and Blankenship (Department of the Interior 1963:55). Another difficulty is that in wild populations the number of breeding doves is perhaps never completely known (Frankel 1961:16). The general method of determining breeding birds has been to

locate singing or territorial males. All birds may not be mated at the time of the census, and all breeding birds may not be singing or on territory at the time of the census. According to Tester (1961:8) spot-mapping is most accurate for birds that mate, nest, and feed in their territories. He

reviewed studies that recommended from three to five censuses to estimate accurately the population on a given area. The number of censuses required to provide an accurate estimate of the population is subject to a number of variables such as weather conditions and time of day and season.

## Relationships of Song to Production of Young and Fall Populations

Coo-counts are "currently thought of as indicators of fall population levels, and are being administratively treated in this capacity, even though the relationships have not been established" (Cricher and Overton 1960:106-107). According to the same authors, total production of young is not necessarily in direct proportion to the level of the breeding population. "This has been reported true for quail, deer, and other species, and in this respect, dove populations seem to be no exception." Hanson and Kossack (1963:118) formed similar conclusions from their Illinois studies. They found that the lowest calculated dove mortality rate occurred in the year following that in which the breeding population reached its lowest point. Calculations from a study by Lowe (1956:430-432) show that a cooing dove in spring represented from 1.5 to 15.2 young produced. Spring coo-counts

may not be indicative of fall or huntable populations in many cases, and determining hunting season regulations on the basis of potential production may not be wise. Peters (1952:42) warned against forecasting total production by counts made in May and June when half of the breeding season still remains. Wight (1961:388) remarked that administrative procedure demands that counts be made of breeders and not production. He stated that "establishing the regulations before any measurement of the major segment of the population has been produced would appear to be a highly questionable procedure." As Cricher and Overton (1960:109-109) intimated, we need to decide what aspect of the dove population would be most valuable to measure, prior to establishing an index to it.

## The Use of Singing Males as Indices

The use of singing males as population indices has been discussed by several authors. According to Gibb (1961:415): "It is sometimes sufficient to count only the number of males heard calling in spring, or the number of occupied nests; and provided that it is not then assumed that every male has a mate or only one mate, or that there is a pair of birds to each nest found and that every bird is paired and has a nest, such short cuts are useful and justified."

Kendeigh (1944:85-86) stated that there is a potential degree of error when counting only singing male wrens, since the percentage of males that do not find mates in any one breeding period is high. For the season as a whole, however, most wrens obtained mates. Kendeigh counted all singers as potential breeding pairs. Perhaps this will be possible with doves if unmated males eventually mate.

Kimball (1949:117) stated that the crowing frequencies of ring-necked pheasants may or may not be directly proportional to pheasant populations. He believed that at least two factors could be operating against a direct proportion: Crowing of each cock might stimulate other cocks to crow, and some cocks might not crow at all. In the first case, a crowing count of 50 might represent something less than twice the population represented

by a crowing count of 25. In the second case, an increase in population would produce something less than a proportional increase in crowing.

Call-counts provide "the only population index for doves currently available on a national and international scale" (Wight 1962:4). Whether coo-counts are accurate and adequate indices to breeding populations or fall populations seems a moot point at present. Difficulties in obtaining more precise relationships between coo-counts and breeding and nesting doves and fall populations may be the result of the problems discussed in a previous section. It is also possible that cooing is not strongly indicative of breeding density or intensity of fall populations. On the other hand, coo-counts alone may not be adequate or accurate indices to dove populations. According to Critcher and Overton (1960:107): "In light of the presently available data, it may well be that knowledge of the general welfare of the dove population at the time of breeding, or even during the previous hunting season, is sufficient to intelligently manage and protect the resource."

As suggested previously, there are inherent administrative problems in dove management, and a better index has not yet been developed. Future research is the key to determining the adequacy of the coo-count.

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