

SOCIAL ORGANIZATION OF PENNED MOURNING DOVES

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THE purpose of this study was to examine the social hierarchy of penned Mourning Doves (*Zenaidura macroura*) and to determine some of its functions. Special attention was given to the relationships among social status, territories, and reproductive behavior.

Seasonally Mourning Doves exhibit marked social behavior. They form assemblages in late summer, fall, and winter. Occasionally they concentrate nests in densities suggestive of colonial nesting. Social hierarchies within these concentrations may influence mate selection as well as other reproductive behavior.

Other columbiform birds are known to have social hierarchies, but not of the rigid straight-line type described for the domestic chicken (*Gallus domesticus*) by Schelderup-Ebbe (1922). Masure and Allee (1934), working with pigeons (*Columba livia*), described a system of ranking that they termed "peck dominance." This type of dominance is the result of win-or-lose relationships where first one bird retreats and then the other. The one retreating fewer times is said to show "peck dominance." Relative ranking of any two individuals is expressed as the ratio of wins to losses. "Peck dominance" or something quite similar to it has been described for sexually segregated flocks of Ringed Turtle Doves (*Streptopelia risoria*) by Bennett (1939) and for pigeons by Ritchey (1951).

It is often more difficult to assign definite ranks to the individuals in this type of social structure than in the straight-line hierarchy, known as "peck right." In "peck dominance," situations sometimes occur where bird "A" dominates "B" and "B" dominates a third bird, "C," which at the same time dominates "A." Such triangular patterns usually develop among birds of midrange social status rather than those near the top or bottom (Allee, 1938). Assignment of rank is also made difficult by reversals. A bird that has been losing most of the conflicts with another bird may suddenly start winning more than he loses.

Most workers agree that the social rank of an individual has profound effects on its existence. As Armstrong (1942: 173) put it, "To have a reasonably secure . . . position in society a bird must not be very low in the scale of social precedence." An important advantage of high rank may be mating priority. Top-ranking individuals may leave more progeny, and those progeny may have a better chance of success. For example Noble (1939) stated "It would seem that roosters high in the social order

would have greater opportunity for mating." Individuals of low rank are frequently denied access to food and mates (Collias, 1944).

There is also evidence that low-ranking birds may sometimes be prevented or delayed in establishing territories (Collias, 1944; Collias and Taber, 1948). Earlier, Allen (1934) held that the most virile and strongest males are most successful in territorial defense. He also implied that reproductive development each spring may be greatly influenced by the results of an individual's conflicts with other birds.

MATERIALS AND METHODS

This study began in February 1963 and ended in May of 1966. All birds used were wild-trapped.

FACILITIES

Nine small pens, measuring $8 \times 6 \times 6$ feet, were built from 2- \times 2-inch wood framing and 1-inch mesh poultry netting. The ground served as a floor. The single large pen was 45×80 feet, with roof height ranging from 7 to 10 feet, and was built of wooden posts and 1-inch poultry netting.

The large pen and some small pens contained nest sites similar to those described by Calhoun (1948), consisting of a cone-shaped piece of tarpaper in a wire loop. Pine needles were provided for nesting material. Water and poultry scratch were constantly available to the birds.

OBSERVATIONS

Doves were housed in the small pens during fall and winter. In early spring three pairs were placed in the large pen, and breeding behavior, territoriality, and social structure were followed there. Most observations were made from a 15-foot tower.

During the breeding season daily observations began at $\frac{1}{2}$ hour before sunrise and continued for at least 2 hours. On days when courtship or territorial behavior was evident during the morning period, an additional period was added in the evening. This evening period started 1 hour before sunset and continued until the birds went to roost. During fall and winter there were two daily observation periods, each lasting 1 hour; one started at sunrise and the other 2 or 3 hours before sunset.

In recording incidents of territorial defense the following types of interactions were recognized: (1) Chasing—the determined advance of one bird toward another, on foot or in flight. (2) Pecking—rapid thrusting of the bill toward another bird in close proximity. The thrust may or may not have resulted in actual contact. (3) Threat posturing—any position of obvious threat, usually charging as described by Jackson and Baskett (1964). (4) Striking—any aggressive contact (other than pecking), usually a blow with the wing.

In determining the social position of the birds the same four types of interactions were noted. In addition, avoidance reactions were used as indicators of submission. Avoidance was recognized when a bird moved from the path of an approaching bird that was not exhibiting obvious aggressive behavior, as when the avoided bird was simply moving to or from the feeding or watering station. Interactions were totalled numerically without weighting; that is, a peck was considered equal to striking, a chase, or a threat posture.

The two methods of analyzing the data we used to determine social positions were essentially the same as used by Shoemaker (1939). In the first, each bird was ranked

according to the number of birds dominated. This in turn was determined by winning a majority of confrontations with each other bird in question during a given period. When the results of this analysis were not clear, the second analysis was employed; a "dominance" score of one unit was tallied for a bird each time it "won" an interaction with another bird. A "submissiveness" score of one unit was tallied for each bird whenever it was submissive to another. A fraction representing the ratio of these two numbers for each bird was compared with ratios for all the other birds in the group to obtain a measure of rank.

These methods of analysis made the rankings fall in a straight-line hierarchy. The straight-line pattern is very useful for comparative purposes, and quite accurate over time spans of a few days. However reversals are common in Mourning Dove hierarchy, and over longer periods, such as a few weeks, the straight-line pattern may fail.

MARKING AND REPLACEMENT

We marked the birds with back tags of the type developed by Blank and Ash (1956) and modified by Jackson (1963). This tag is a 1- × 3-inch strip of colored vinyl plastic, secured to the bird by loops of sewing elastic passed over the wings and brought up close to the body.

The primary group consisted of six birds: three males each marked with a green, blue, or red tag; and three females each marked with a black, white, or brown tag.

The green-tagged male and the blue-tagged male were the same individuals throughout the study. Three different males wore the red tag. The original red-tagged male was the low-ranking male. The replacements for this position were made with the lowest-ranking birds of the reserve males held in the small pens.

All the females were replaced twice. The birds were not paired at either of these replacement times. Each time the females were replaced, three reserve females were placed together and their relative ranks determined before they were tagged and became part of the study group.

RESULTS AND DISCUSSION

The results of this study are organized and presented in the sequence of an annual cycle of behavior, although data were gathered over 4 years.

WINTER BISEXUAL HIERARCHIES

When pairs broke up in September the birds within the large pen formed a single unit that resembled a flock. All six birds occupied the same general area of the pen, and when disturbed all moved together as a group. Most of the data on winter hierarchies were collected in 1964, but the hierarchy was also followed through the winters of 1963 and 1965.

In each year all six of the birds formed a simple hierarchy. Sex did not seem to determine social positions. Table 1 shows a typical hierarchy pattern for the six birds during early October 1964.

Changes in rank occurred occasionally in the winter hierarchy. Middle rankings were not so stable as the top and bottom rankings. Table 2 shows a reversal of rank by White and Brown from the arrangement shown in Table 1.

TABLE 1
HIERARCHY FOR SIX DOVES IN SMALL PEN 4-10 OCTOBER 1964

Interactions between individuals		
Birds interacting	Ratio of wins for period	Social rankings for period
Green/brown	77/0	1. Green (M)
Green/blue	21/0	2. Blue (M)
Green/red	41/0	3. Brown (F)
Green/white	20/0	4. White (F)
Green/black	2/0	5. Red (M)
Blue/brown	21/0	6. Black (F)
Blue/red	12/0	
Brown/white	9/0	
Brown/black	17/0	
White/red	16/0	
White/black	2/0	
Red/black	4/0	

Frequent changes in social position identified the winter hierarchy pattern as the "peck-dominance" social structure described by Masure and Allee (1934). In addition to these reversals, birds often won individual encounters with higher-ranking birds to which they remained subordinate.

Definite resting sites were used by birds in the small pen. Other birds usually did not challenge the holder of a site.

TABLE 2
HIERARCHY FOR SIX DOVES IN SMALL PEN 16-22 OCTOBER 1964

Interactions between individuals		
Birds interacting	Ratio of wins for period	Social rankings for period
Green/red	48/0	1. Green (M)
Green/brown	16/0	2. Blue (M)
Green/blue	30/0	3. White (F) ¹
Green/white	11/0	4. Brown (F)
Green/black	1/0	5. Red (M)
Blue/white	9/0	6. Black (F)
Blue/brown	37/0	
Blue/red	6/0	
Blue/black	4/0	
White/red	13/0	
White/brown	32/6	
White/black	9/0	
Brown/black	17/0	
Brown/red	8/0	
Red/black	6/0	

¹ Notice that white and brown reversed rank after mid-October (compare with Table 1).

TABLE 3
INTERACTIONS BETWEEN INDIVIDUALS OBSERVED 16-19 FEBRUARY 1964

Birds interacting	Ratio of wins for period ¹
Green/brown	3/0
Green/white	1/4
Green/blue	4/2
Green/black	2/0
Green/red	1/1
Blue/brown	1/1
Blue/white	3/2
Blue/black	2/2
Blue/red	3/2
White/brown	3/2
Brown/black	2/0
Red/white	2/0
Black/white	3/0
Black/red	2/0

¹ Notice the lack of a definite social order during the spring period of restlessness.

SHIFT TO UNISEXUAL SOCIAL ORDERS

By the middle of February 1964, restlessness was evident in the group of birds. This restlessness lasted 3 days, and was characterized by the lack of a recognizable hierarchy and increased activity. Table 3 shows the interactions that were considered to be win-loss conflicts. A similar period of restlessness was observed in February 1966.

On 18 February a difference in location of the resting sites was apparent. Figure 1a, top, shows the sites on 10 February, and Figure 1b, bottom, shows the new sites. By 20 February the hierarchy was no longer bisexual. No interactions between sexes occurred, and a definite pattern of dominance existed in each unisexual group. Unisexual hierarchies were also established after the period of restlessness in 1966. Table 4 shows the hierarchies for the unisexual groups; among birds of each sex the relative social positions remained the same.

The only contact between the two sexes occurred at the feeding station and these were few because the females usually visited the station somewhat later than the males. No assertions of dominance were observed between sexes when both were at the station.

PREBREEDING SOCIAL BEHAVIOR

The six birds were moved from the small pen to the large pen on 1 March 1964. In reporting observations from the large pen we have used letters to designate the birds. Female "A" and Male "A" were the dominant birds, the "B" birds were next in rank, and the "C" birds were low-ranking. Such designations are appropriate because no shifts in rank occurred during the reproductive season.

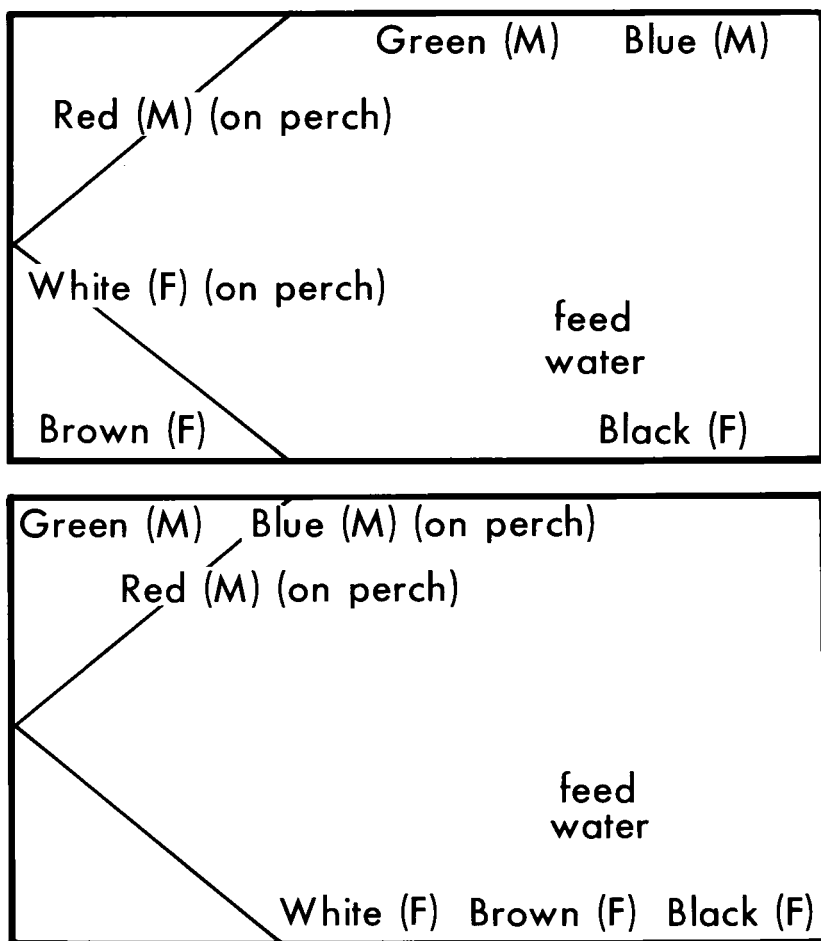


Figure 1. Resting sites of individual birds before and after unisexual hierarchy establishment (small pen). Top, resting sites for 2-10 February 1964; Bottom, resting sites for 18-24 February 1964.

The designations for the individual birds are as follows: Green, Male A; blue, Male B; red, Male C; brown, Female A; white, Female B; and black, Female C.

Defense of resting areas.—After 2 days in the large pen, the birds established resting areas. The female areas were on the ground along the east end of the pen. The male sites were on high perches within a distance of 15 feet along the midportion of the south side of the pen (Figure 2). Female A defended an area about 6 × 6 feet, twice as large as those Females B and C defended.

TABLE 4
HIERARCHY FOR EACH OF THE UNISEXUAL GROUPS 20-24 FEBRUARY 1964

Interactions between individuals		
Birds interacting	Ratio of wins for period	Social rankings for period
Females		
Brown/white	19/2	1. Brown (3) ¹
Brown/black	6/0	2. White (4)
White/black	9/1	3. Black (6)
Males		
Green/blue	22/1	1. Green (1)
Green/red	16/0	2. Blue (2)
Blue/red	12/2	3. Red (5)

¹ Former ranks, in bisexual hierarchy, shown in parentheses.

The dominant male perch-cooed for the first time on 13 March 1964. The two subordinate males started cooing 3 mornings later. On 18 March the frequency of cooing increased. On this day (18 March) the dominant male began regular use of two perches for cooing instead of one.

Mate selection.—The 1964 data best illustrate the events leading to pairing and competition among males; the patterns in other years were generally similar. On 7 April 1964 all three males entered the dominant female's territory. Male B arrived first, at 07:50. Male A lit 2 feet from her territory and walked into it at 08:15. Male C flew into her territory at 08:19. All three males walked around Female A and wandered in and out of her territory, and sometimes entered territories of the other females. Female A was busy pecking at the grass and ground. At one time Female C attempted to enter Female A's territory, but was repelled by a rushing attack from Female A. Female A then returned to her apparently indifferent attitude. There was one encounter between males during the time they were in Female A's territory on this morning. At 08:29 Male C walked up close behind Female A whereupon Male B turned and threat postured toward him. Male C immediately walked out of the territory, but returned less than a minute later. The males all left at 08:41 and flew to a feeding station.

On this same day (7 April) several other cases of area defense were noted between the females, including one encounter in which Female A and Female B exchanged several wing blows. All birds were relatively inactive on 8 April, a rainy day.

Choice of mate and territory establishment as related to dominance.—On each of the next four mornings (9, 10, 11, 12 April) the activity pattern was similar to that of 7 April, with no apparent order of entry by males

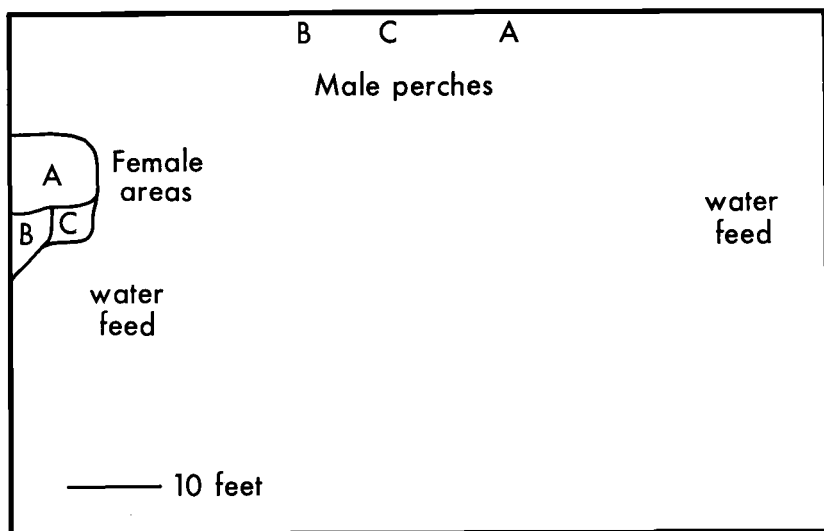


Figure 2. Resting areas and perches of the six birds in the large pen 3 March-3 April 1964.

into Female A's territory. All males flew away together each morning, after being in Female A's territory for an hour or so. On 13 April at 07:03, Male A flew from his perch and entered Female A's territory; he began occasional cooing and walking around her. At 07:09, Male C flew from his perch and lit close to Female A's territory and walked into it. Female A immediately attacked Male C by rushing and pecking at him. As she began this, Male A turned toward Male C and began threat-posturing toward him. Male C quickly flew from the territory. Female A and Male A both preened for 3 minutes, then Male A again started walking around Female A, cooing occasionally. At 07:20, Male B flew down to the edge of Female A's territory. As soon as he touched the ground Female A and Male A turned toward him and threat-postured. Male B immediately flew back to his regular perch. Neither Male B nor C attempted to enter Female A's territory again during any observation period. Male A stayed in Female A's territory until 08:34, but was much less active than on previous visits. Most of his time he spent sitting about 8 or 10 inches away from Female A, facing her. The next morning (14 April) Male A visited Female A's territory briefly, then flew back to his perch and resumed cooing.

When Male B attempted to return to his own resting perch from the feeding station (at 07:16), Male A met him in the air, chased him back to the area of the feeding station, and returned immediately to his resting

perch. Male A cooed very frequently (8 or 9 coos per 3-minute period) until 08:40 that morning. The observation time was extended to 10:00, during which time six additional conflicts occurred between Male A and the other two males, all of them aerial, and all as the other males tried to fly to perches near Male A's resting perches.

On 15 April Male A was cooing more frequently (11 or 12 coos per 3-minute period). The two subordinate males stayed away from the defended region. At 07:10 Female A flew to Male A's secondary perch. Male A flew over to share the perch with her. Female A never returned to her territory, but remained constantly with Male A.

Mating behavior in the lower-ranking birds.—On 16 April 1964 both females B and C expanded their territories to include most of the area that Female A had been defending. This same day Males B and C entered the territory of Female B and walked about, cooing occasionally, as they had done previously in the territory of Female A.

On 17 April Male C was not allowed to enter Female B's territory. At 06:41 Males B and C lit within 3 feet of Female B's territory and walked toward her together. Female B threat-postured toward Male C as he approached, and he flew away. Male B courted Female B with bowing and cooing for 22 minutes. Jackson (1963) described this bow-coo behavior in detail. Later the two birds flew to the other end of the pen and lit on the same perch.

Male B and Female B were together most of the time from this day on, but they did not appear to have an established territory. They could be found at most times of the day perched along the side of the pen opposite the territory of the dominant pair.

The day after Female B left her territory with Male B, 18 April, Male C entered Female C's territory; he only stayed 8 minutes. Four other times within the next 2 weeks Male C was seen in Female C's territory for brief periods. These two birds apparently did not establish a pair-bond. Female C continued to stay in her small area except for trips to feed and water at the station near her area. Male C took up a perch position near the ground in the least used corner of the pen and rarely was seen away from his perch except for his visits to the food and water station.

The lowest-ranked birds did not become firmly paired in any of the three breeding seasons. The difficulties of the lower-ranking birds in becoming paired and establishing nests could have been due to the space limitations of the pen. This might not be entirely artificial. In many parts of the species' breeding range nesting habitat is a small part of the total range, thus the low-ranking birds may suffer from space limitations in the wild as well as in pens.

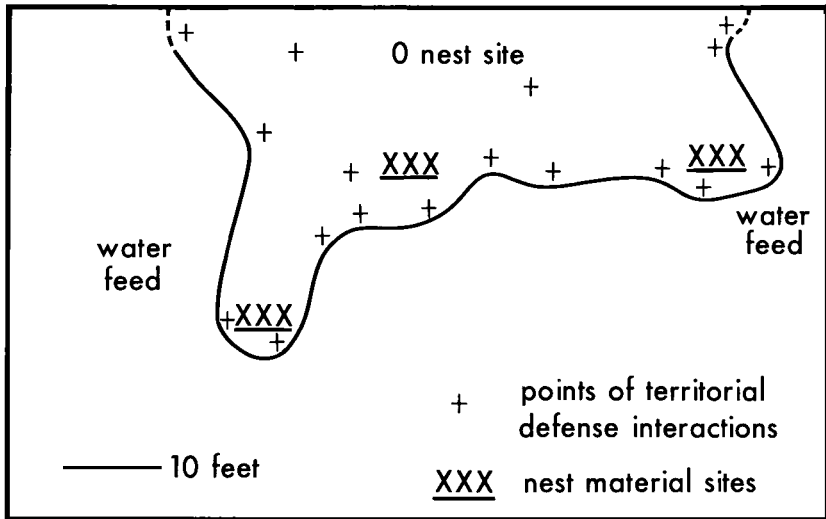


Figure 3. First breeding territory of the dominant pair for 1964.

Supplemental experiments on dominance and mate selection.—Four supplemental experiments were carried out in the small pens during the summer of 1965 to gain information on the relationship of dominance to priority of mating. In each experiment two males were isolated in one pen and two females in another. After the dominant bird of each sex was determined, the four birds were placed together. Nest material and two nest cones were provided in these pens.

In all four cases, the two dominant birds became paired with each other within 10 days. In only one case did the two lower-ranked birds show courtship behavior; this occurred on the 21st day after they were placed together. Three of the four pairs of dominant birds established nests and laid eggs. In each of these experiments the two males and two females were together for 30 days.

IMPORTANCE OF NEST MATERIAL

Size and shape of territory.—The initial breeding territory defended by Male A (April 1964) included three nest cones and all three of the nest material sites. This included a large portion of the pen as shown in Figure 3. This nest material was pine needles, which doves often use in the wild; natural grass cover on the pen floor was also available for nest material. We suspected that the shape of Male A's territory was influenced by the location of choice nest material. To test this, we moved two of the nest material sites after dark on 18 April. Male A responded

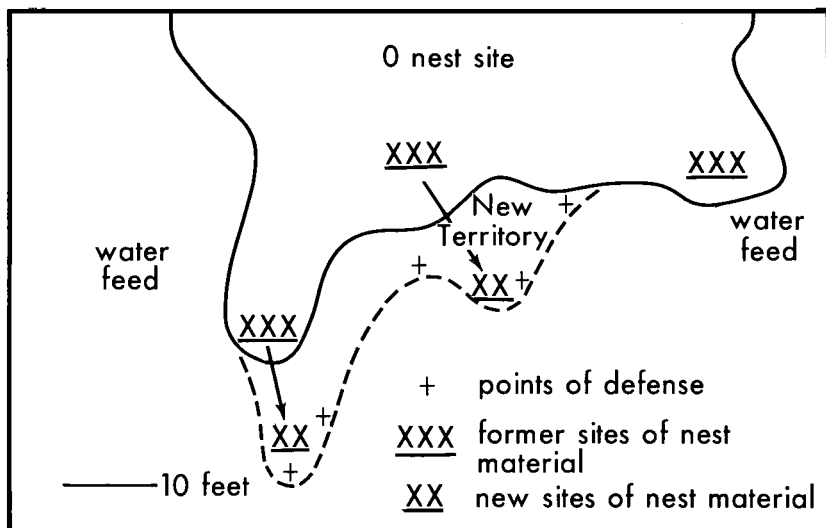


Figure 4. New territory claimed from 18–20 April 1964, which includes repositioned sites of nest material.

by increasing the size of his territory, so it again included all of the nest material (Figure 4).

On 20 April Pair A began nestbuilding, and they completed the nest on 23 April. On 24 April, we moved one of the nest material sites again. During the next 2 days the defended area, as shown by confrontations with other males, was enlarged to include it.

During the summer of 1965 we relocated nest material in two other experiments. In both all of the choice nest material (pine needles) was included in the established territory. In the first experiment two nest material sites were moved during the last day of nestbuilding, and the territorial limit was expanded to include them. In the other a single pile of pine needles that had been within 4 feet of the nest site was moved on the 6th day of incubation, and the male made no effort to expand the territory to include it.

Nesting influenced by availability of nest material.—Once in 1963 and once in 1964 the presence of all the choice nest material within the dominant male's territory prevented nesting by the next-ranked pair. In 1963 the second-ranked birds paired on the day the dominant pair started nestbuilding and went through extensive courtship behavior each morning until the 3rd day of incubation by the dominant pair. On this day the subordinate pair flew to a nest cone; the female got into the cone, nest-cooed repeatedly, and fluttered her wings. The male got into the cone

with her and the two stayed there for 26 minutes. The next morning both flew to the cone at 06:50. The female settled into the cone and 2 minutes later the male flew off to get the first piece of nest material. Having reduced the size of his territory, Male A did not defend the nest material.

In 1964 the single pile of choice nest material was located within 1 foot of the post that supported the dominant pair's nest. The second-ranking birds became paired and were with each other constantly, but made no attempt to establish a nest through the dominant pair's 7th day of incubation. At noon on the 7th day, we moved the nest material 25 feet away from the post. The next morning the second-ranked pair had started nestbuilding when observation started at 07:05.

To test further the effect of availability of acceptable nesting material on nest site selection and nest establishment, we placed two pairs of doves in two separate small pens on 4 June 1964. The pens contained nest cones but no nest material other than grass. Both these pairs began courtship after a few days, but neither pair had shown signs of nest establishment at the end of 21 days. On the 22nd day nest material was placed in the pens. One of the pairs (both birds) spent an hour in the nest cone the same afternoon and were nestbuilding the next morning. The other pair started nestbuilding the 3rd day after being supplied with nest material.

On 8 June 1965 a pair was placed in a small pen equipped with a nest cone but no nest material other than the grass on the floor of the pen, and no nest material was ever supplied them. They established a nest in the bare cone after being in the pen for 37 days and laid two eggs, but never tried to incubate them.

Availability of suitable nest materials might well be necessary to culminate courtship. While the pen floors were always grassed, they had no pine straw or loose twigs. Evidently grasses did not suffice for nesting material, or provide the stimulus to release such advanced courtship behavior as nest establishment. Lehrman (1958) and Lehrman et al. (1961) found that presence of nest materials stimulated gonadal activity and readiness to incubate in Ringed Turtle Doves. Marshal and Disney (1957) found that green grass of a particular type was necessary to stimulate nest construction and advanced breeding behavior in the Red-billed Quelea (*Quelea quelea*).

In this study nest sites were established very near the piles of nest materials. Dominant pairs were reluctant to give up control of the nest material during nestbuilding and for a few days thereafter. Two to five days after incubation began territory size was reduced and nest material was no longer defended unless it was very close to the nest site.

TABLE 5
REPRODUCTIVE EFFORTS OF PAIRS AT THE THREE SOCIAL RANKS

	Pairs								
	1963			1964			1965		
	A	B	C	A	B	C	A	B	C
Started nestbuilding	3	1	0	4	4	0	3	2	0
Nestbuilding completed	3	1	0	4	3	0	3	2	0
Cycles in which only one egg was laid	0	0	0	1	1	0	0	1	0
Incubation attempted	3	1	0	4	1	0	3	2	0
Successful incubation (hatching)	2	0	0	3	1	0	3	1	0
One young fledged	1	0	0	0	1	0	0	0	0
Two young fledged	1	0	0	3	0	0	2	1	0

REGULAR TERRITORIAL FLUCTUATIONS

By the 3rd day of incubation the territory of the dominant pair was reduced to a small area around the nest in 9 of 10 instances. In only one case did a male still show defense behavior some distance from the nest on the 5th day of incubation. This male left the nest twice during his incubation shift to chase birds flying through the territory. After territory size was reduced the exact boundaries could not be determined. Lund (1952) and Swank (1955) recognized that territorial defense by free-flying Mourning Doves was curtailed after the nesting cycle was underway.

Pairs reexpanded the boundary of the territory at the start of each new nesting cycle, but the new boundary was not identical to that for the previous nesting attempt, which agrees with findings of Jackson and Baskett (1964) for wild Mourning Doves.

In no instance were territories established that included either of the food and water stations. When stations were moved into a defended territory the exact site of food and water was not defended.

The territory of the dominant pair usually covered about a fourth to a third of the space in the pen. Territories of wild doves are reported to be larger than this entire pen. Many workers mention that territories shrink with crowding (Huxley, 1934; Edminster, 1954; Mackey, 1954; and others).

REPRODUCTIVE PERFORMANCE RELATED TO RANK

In the large pen the dominant pair had no difficulty in initiating and completing a nesting cycle (Table 5). The second-ranked pair usually was able to establish a nest and lay eggs, but incubation was not always successful. Once the eggs hatched, the second-ranked pair was successful

in brooding the young. The lowest-ranking pair was never able to complete the courtship phase of the reproductive cycle. The second-ranked pair occasionally exhibited territorial defense behavior, but not consistently enough to allow determination of precise territorial boundaries.

Evidently high rank has several benefits to the individual. Among these are priority in mate selection and the ability to establish an early nest. The ease with which the dominant male (or dominant pair) can establish a territory without competition from other birds contributes to the success of the first nesting cycle, and the early start allows a longer season for reproduction.

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SUMMARY

Social organization of groups of six penned Mourning Doves (3 males and 3 females) was studied over a 4-year period with special attention to relationships between social status and reproductive behavior. Winter hierarchy was found to be of the "peck dominance" variety. Both males and females were included in the winter hierarchy and sex had no apparent influence on social ranking. Before onset of the breeding season the hierarchy split into two separate social orders, one for each sex.

All males were attracted to the dominant females at the onset of the mating season. Dominant males always became paired with dominant females. This dominant pair was always the first pair to be formed and the first to establish a territory and choose a nest site. The dominant pair was always the most successful in its reproductive efforts.

Choice nest material was defended rigorously and was a factor in determining territorial boundaries in early phases of the nesting cycle. Food and water sites were not defended. Territory size was reduced markedly early in the incubation phase of the cycle. When suitable nesting material was lacking reproductive cycles did not progress beyond courtship. Cycles of subordinate pairs were arrested when all suitable material was defended by the dominant male. Lowest-ranking pairs did not establish nests.

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