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LIFE HISTORY OF THE BOUCARD TINAMOU IN BRITISH HONDURAS Part II: BREEDING BIOLOGY

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In a previous paper (1964) I discussed the nonbreeding biology of the Boucard Tinamou (*Crypturellus boucardi*). In this paper I shall describe the behavior associated with the breeding cycle. In presenting the material, I have divided the breeding cycle into chronological phases. The breeding cycle begins with calling. Territoriality, mating, and nesting follow in order.

TERRITORIALITY AND MOVEMENTS

Territoriality begins shortly after the commencement of the calling period of the males in late January and February. Calling duels and boundary encounters are then common occurrences, for individuals are attracted to the calls of adjacent males early in the season. Soon, however, they become familiar with one another's call; and later in the season the number and duration of meetings between neighboring males decrease.

The male Boucard Tinamou confines most of his activities to a restricted area, which meets the requisites of territory, that is, it is an area in which an individual shows aggressiveness toward other members of its own species. He advertizes his presence in this area and defends it against other males. Territoriality in this species, however, is not a highly developed behavior pattern when compared with that of many passerines. The male alone is concerned with defending the territory, and his aggressive behavior is directed toward other males. Females that are accompanying a male continue to forage, showing no reaction if another male is encountered. This is a reversal of the condition found in the Ornate Tinamou (*Nothoprocta ornata*), in which the female is the aggressive sex in territorial defense (Pearson and Pearson, 1955:120).

RELATION OF HOME RANGE AND TERRITORY

The size of the home range is surprisingly large. Males that remained mostly within the study area moved about in tracts of 28 to 47 acres (figs. 1-3). Not all of a tract could be considered territorial, since a male normally ranged over a wider area than he defended. No male could traverse and defend in a single day the entire area covered during a season. The home ranges were much too large for defense. For this reason, boundaries were poorly defined and the regions of overlap were often extensive. One area of overlap between two males is shown in figure 1.

Some tinamous (for example, male 23, fig. 4a) moved about extensively in a large area without any pronounced concentration of activity in a smaller tract within the home range. Others (males 22, 25, and 35) confined much of their activity to a smaller portion of their range (fig. 4b). In yet another group of males (2 and 20) the territory and home range fluctuated in size and location, largely in accordance with the presence or absence of adjacent males, and perhaps also with the acquisition of females. For instance, male 20 moved about in the area of the bulldozer trail until April 2 (fig. 5). From April 3 until his disappearance on April 15, male 20 and the females mated with him remained, for the most part, in an area east of compass line N3.

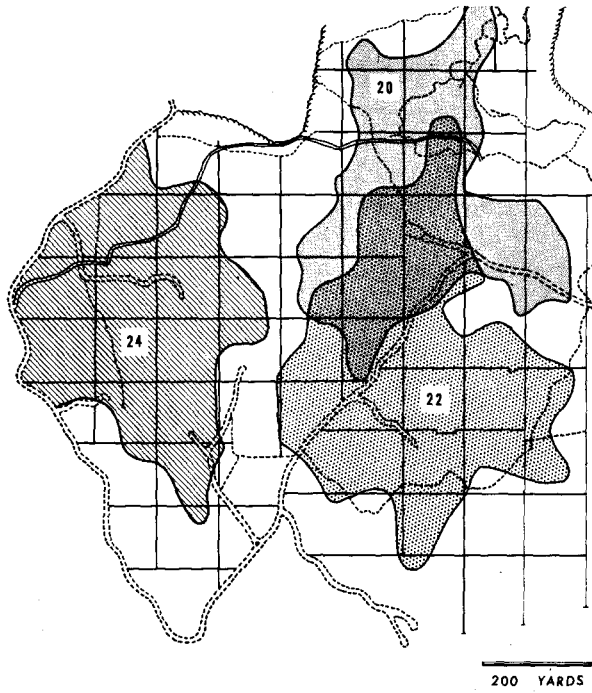


Fig. 1. Home ranges of three males (20, 22, and 24) in the study area in 1958. Note the extensive area of overlap between males 20 and 22. Overlap zones between other males with adjacent ranges were also extensive.

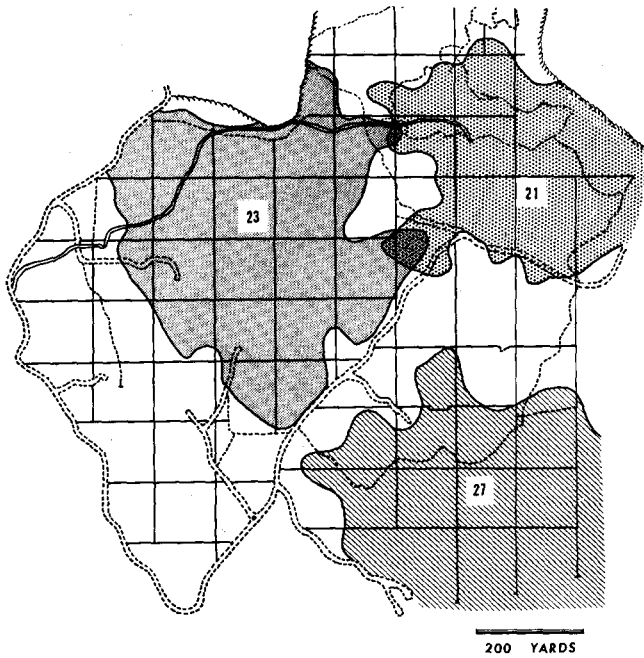


Fig. 2. Home ranges of three males (21, 23, and 27) in the study area in 1958.

FUNCTIONS OF TERRITORY

The establishment and defense of a territory by the male serve to provide an area for courtship, mating, and feeding. Courtship and mating appear to be the primary functions of territory. It seems unlikely that food supply dictates the claim for such a large area. Observations throughout the period of study disclosed an abundant food supply on the ground, a food supply that could support a number of males and their broods in any given territory. Additional evidence that strongly suggests the improbability that food supply is a factor controlling the size of territory and home range is the fact that between May 6 and 23, 1957, the young of male 1 were seen only in an area slightly larger than one-half acre. In the same period a pair of immature Little Tinamous (*Crypturellus soui*) foraged over the same ground.

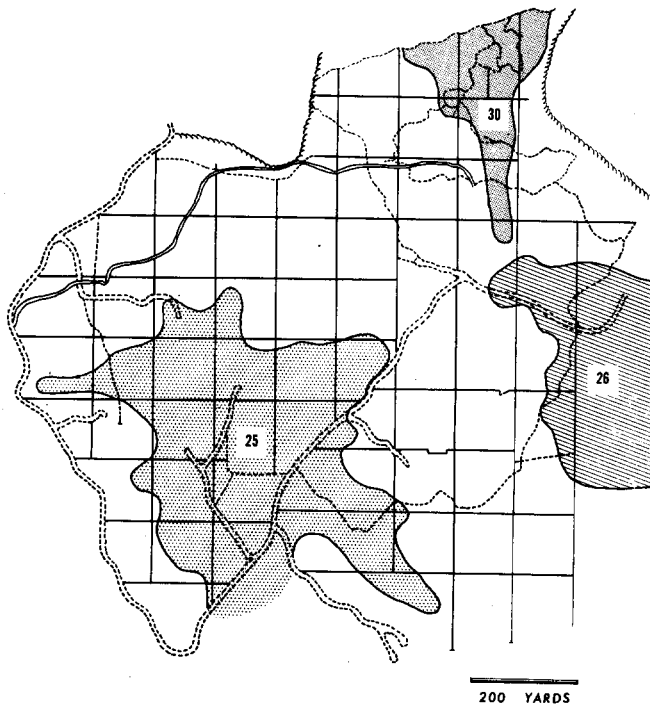


Fig. 3. Home ranges of three males (25, 26, and 30) in the study area in 1958.

Evidence indicates that the territory does not determine the location of the nest site in this species. The single nest studied was at the periphery of the male's range (fig. 12). Another male with at least one chick suddenly appeared in an area in which he had not been found prior to nesting. Since the pair bond is not a strong one in this species, I suggest that a large range and territory serve the primary function of providing a considerable area to ensure successful courtship and mating without interference from other males.

Population density probably plays a role in determining to some extent the size of the home range. After April 2 male 20 established itself, as already mentioned, in an area in which no other males had been observed up to that time. Had a male already been located in that area, male 20 could not have extended its territory. The same was true for male 2.

DEFENSE OF TERRITORY

Defense of the territory takes on two forms. It may involve a calling duel between two males at an indefinite boundary, or even within the territory of one male. Or, if a male has penetrated some distance into another male's territory, the latter may attack and chase the intruding bird. When one male attacks another, the head and neck are outstretched horizontally. No sounds are heard from either bird. The attacks witnessed lasted from two to four seconds and covered a distance of five to ten yards.

Several factors are involved in determining the types of territorial behavior exhibited at any one time. Among these the extent of encroachment by one male on another

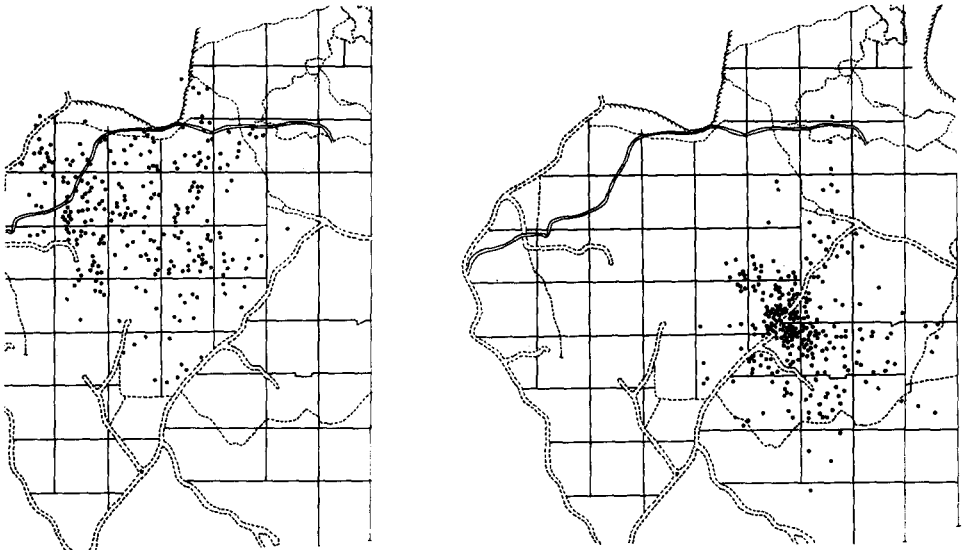


Fig. 4. Left, *a*, points of record of male 23 in 1958. This male did not confine its activities to a small portion of its home range. Right, *b*, points of record of male 22 in 1958, showing the concentration of activity of this male.

male's territory is undoubtedly the most important. It was impossible to determine the exact point at which a calling duel gave way to more aggressive attack behavior, but no boundary disputes other than calling duels were observed in the poorly defined overlap zones. The farther one male penetrated into an adjacent tinamou's territory, the more likely he was to meet with attack from the defending male. The few manifestations of aggressive behavior noted all occurred deep within one male's territory. Furthermore, all observed attacks occurred when one male was mated or was attending young, or when two males were decoyed by an imitated female call.

Frequently there was no encounter, even when a male had encroached on another male's territory, for the trespassing male left the area when the calls of another male indicated the approach of the defending bird. Two males calling near one another often remained out of sight of each other but continued calling for a period of time before moving apart. One male, calling in an open area, ran into a tangle of vines upon the approach of another male and continued calling until the male moved away. Calling males frequently converged to within sight of each other without showing any aggressiveness. However, the approach of two males to within 10 to 20 feet of one another

usually resulted in an attack. On the few occasions when attack behavior was observed, the two birds were at close range before the chase commenced. Here again, however, the distance that two males tended to maintain varied with the locality of the encounter and the stage of the breeding cycle.

That the degree of aggressiveness varies with the stage of the sexual cycle is indicated by the fact that males tended to approach each other more closely at the boundary of their territories at the beginning of the season. By the time a male had mated with several females, he seemed able to recognize the calls of adjoining males and tended to move about in the periphery of his range less frequently. In determining call recognition of one male by another, I noted that in an overlap zone where two males were

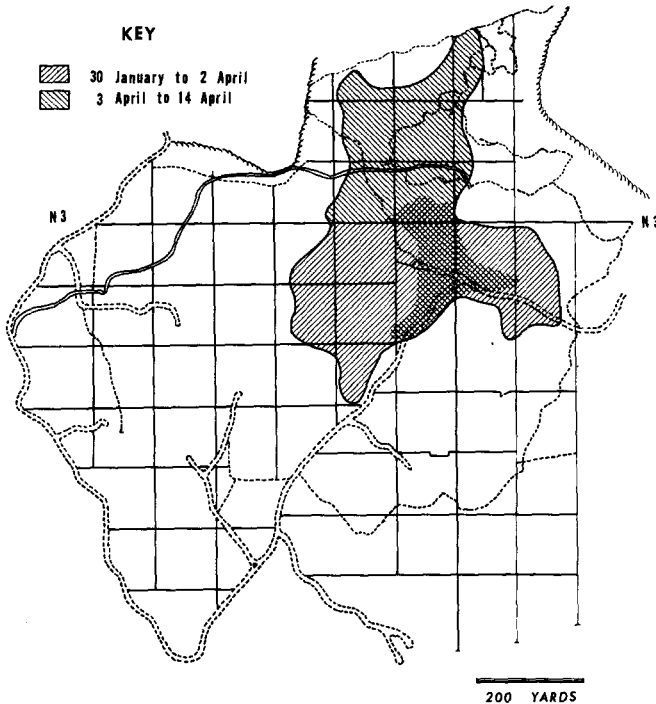


Fig. 5. Fluctuation of the territory and home range of male 20 in 1958.

sometimes found, imitated calls of one male given periodically brought fewer and shorter responses from the other male as the season progressed.

Still another factor to consider in assessing the mechanisms that control the degree of aggressive behavior displayed by one male toward another is the level of some other motivation. There is considerable variation in the distance maintained between two males and the duration of calling when they come together. There are times when this variation is inconsistent with the location of the encounter, that is, whether the encounter is at the boundary or within one male's territory. It may be that some other motivation, such as hunger, is stronger at the time than the attack drive. Complete behavior patterns of two different drives cannot be manifested concomitantly. A male whose feeding drive is strong will often tolerate the presence of another male in its territory. In the Ornate Tinamou the female, which is the aggressive member in courtship and territorial defense, sometimes tolerates a bird other than the mate in its feeding area

(Pearson and Pearson, 1955:120). This may be an example of one drive that is normally activated by the presence of another bird on its feeding area (territorial defense) being inhibited by a more strongly activated feeding drive.

Once incubation begins, aggressive behavior toward other males completely disappears. This is a necessary adaptation, since only the male attends the nest. Leaving the eggs to chase off nearby males may not significantly prolong the incubation period, but the exposure of the nest to predation would be augmented.

During the entire period of incubation the male is silent. With the cessation of calls and of territorial behavior to advertise his presence, other males frequently enter the area of the incubating male, probably seeking mates. Male 1 showed no reaction, while incubating, to the activity of other males, no matter how close the intruders moved toward the nest. Nor did the nesting bird display any interest in mounted specimens placed ten feet from the nest, or in imitated calls within ten yards of the nest.

Tinamous that trespassed on the incubating male's territory did not acquire and defend any part of it as their own except in overlap areas. This happened in the case of male 25. In March, when male 22 had mated with several females, male 25 occasionally ventured into the periphery of male 22's territory but retreated when male 22 approached. After several weeks of silence, during which male 22 was presumably nesting, the calls of the latter bird were again recorded regularly from the area of its previous territory. During male 22's silence male 25 had mated with several females and now moved about in an area from which it was formerly turned back by male 22. Male 22 did not approach to defend this area as it had previously done.

Although a male did not often enter the home range of an adjoining male except in the overlap zones, it invariably penetrated a male's adjoining territory when the latter, after courting several females for a number of days, stopped calling. For example,

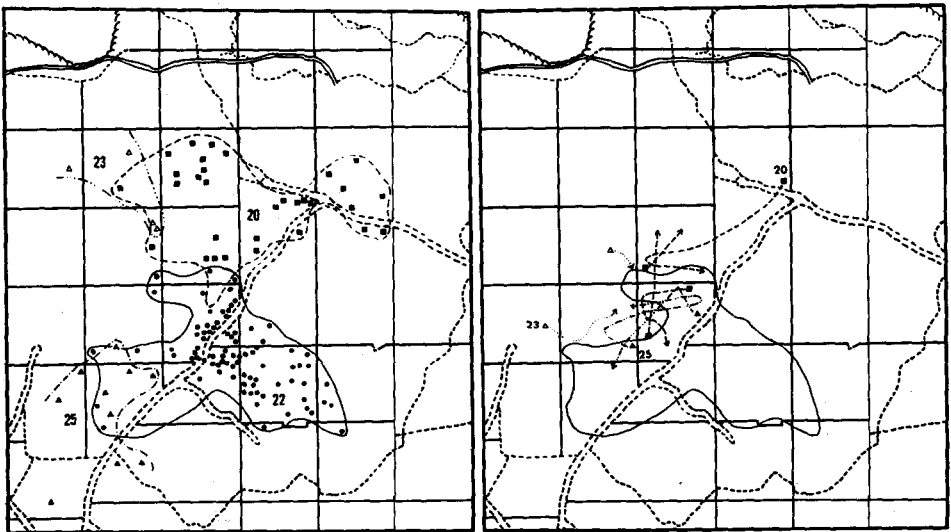


Fig. 6. Reaction of adjacent males to the silence of a mated male. Left, *a*, the points of record and range of four males between March 13 and 19. Only male 22 was mated. The range of the latter during this period is represented by the solid line surrounding the points of record. Right, *b*, the movements of three males on March 20 into the range of male 22, which was silent most of the day.

male 22 was the first tinamou in the study area to acquire females. Between March 13 and 19 he engaged in several calling duels and turned back two males (20 and 25) that entered his territory (fig. 6a). Male 22 and the females did not call a great deal on March 20. Except for several whining calls in the early morning and a calling period from 5:10 to 6:04 p.m., he was silent. His silence brought a reaction from three adjacent males (20, 23, and 25) that moved into his territory and remained the entire day (fig. 6b). In mid-May male 25 mated with several females. On May 23, the calls of this male were subdued and infrequent. On the following day, male 25 was not heard at all. An adjoining male (23) entered male 25's territory during the morning and afternoon of May 24, calling extensively, one day after male 25 stopped calling.

To test the reaction of a male to members of its own species, dummies were placed near a calling male. These dummies, prepared by P. A. Daigre at Louisiana State University, were museum study skins mounted to resemble living birds. A string was attached to the base of the dummy and passed to a blind five to ten yards away. The calling male was then decoyed to the scene by an imitation of its call. The results from the trials varied and were not sufficiently numerous to permit many generalizations. Marginal males, that is, males that were decoyed to a dummy in a zone of overlap, usually did not approach as closely as males in whose territory the dummy was placed. The reactions of males 22 and 35 under the latter circumstance were different. Male 35 advanced toward the mount several times, once within eight feet, but did nothing more than eye it intently. When the effigy was moved, when male and female mounts were presented together, and when a mount was arranged in a "rump-up" posture, male 35 merely "froze" its position or walked slowly away.

Male 22 exhibited an entirely different reaction to a dummy male placed in the center of its territory. It walked hurriedly toward the imitated call coming from the blind and passed within two feet of the mount without noticing it. When the mount was moved, the male turned and attacked. The dummy was facing away from the attacking male. Male 22 pecked several times at the scapulars, mounted the dummy, administered several blows to the head and neck with its bill, and slid off. It then walked quickly out of sight in the opposite direction from which it had appeared. The attack lasted approximately four seconds from the time male 22 turned on the dummy until he dismounted. Two females accompanied male 22. One of them followed male 22 from the scene after the attack. The other moved close to the dummy (six feet) and watched it for several minutes before moving off. To a decoy in another location nearer the periphery of its range this same male reacted differently only one hour later. He approached the dummy no closer than 20 feet. When the decoy was moved he ran behind a tree, where he continued to call. The difference in male 22's reaction in the two situations described is explicable on the basis of the location of the encounters, one occurring in the center of the territory and the other near a zone of overlap between the ranges of two males.

The dummy trials indicated the importance of movement and the attitude of the intruder. The trials discussed above, and others not specifically mentioned, revealed that the decoy often goes unnoticed, even at close range, until moved. The attitude of the intruder is important also. No attack by one male upon another was observed until the trespassing tinamou turned away from the defending bird either before or immediately after the defending male began to approach. Male 26 on one occasion started a head-on attack on a mount, but stopped about six feet away, turned, and walked hastily out of sight.

After the eggs hatched and the male led the young from the nest (male 1), antago-

nistic behavior toward other males again became apparent. The object of defense was probably the young. One example occurred with an encounter between male 20 and male 21. After several weeks of silence male 20 reappeared in an area in which no other male had been found except male 21. Male 20 had not previously moved about in this area. Male 21, which was foraging with two females at the time of the incident, immediately moved toward male 20 when the latter began calling. In the tangle of underbrush from which male 20 called a single chick was seen. As male 21 advanced within sight, the male with the chick attacked. Male 21 took to the air and flew about 30 feet. Moving in the direction of the flight, male 20 attacked again three minutes later. Once more male 21 flew in the same direction, and once more male 20 moved toward the point where the male had come down. One minute later came a third attack followed by a final flight.

MOVEMENTS IN RELATION TO SEASON

It is not known how the Boucard Tinamou moves about prior to the breeding season, whether singly or in small groups. A solitary existence is probably maintained except for accidental meetings while foraging. With one exception, records in January and February of males that had not commenced calling included only individual birds. There is no relation between the extent of movement and advancement of the breeding season prior to the time incubation begins. A male that walks about over a large area one day may move but little the following day.

MOVEMENTS IN RELATION TO TIME OF DAY

In the breeding season the males are most active in the early morning and late afternoon, not only in calling but also in movements. As a rule a male covers a more extensive area during the morning calling period. Most of the more extensive recorded movements of several males in the study area are shown in figures 7 to 9. Not uncommonly a male covered a five-to-ten-acre area in from two to four hours in the morning, moving 400 to 600 yards. Sometimes the bird traversed 15 or more acres. Male 23 on



Fig. 7. Left, *a*, sample movements of male 22; right, *b*, sample movements of male 23.

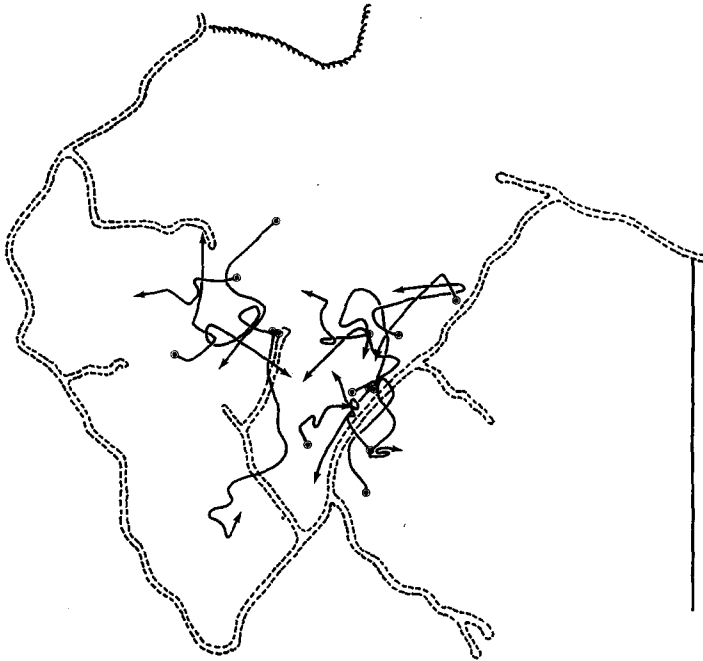


Fig. 8. Sample movements of male 25.

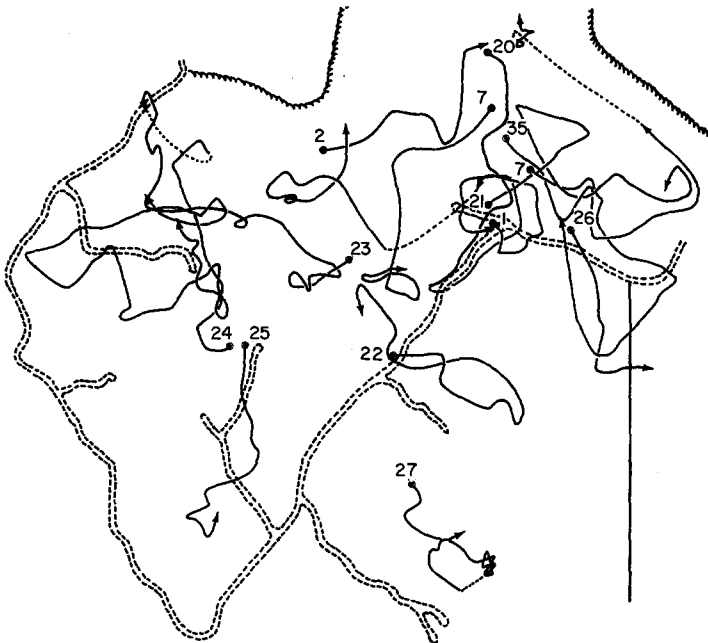


Fig. 9. Longest recorded movements of various males in the study area.

one occasion covered almost a mile in a single day, traveling approximately 910 yards in the morning in less than three hours and about 570 yards from midday to late afternoon. A minimum of 145 yards was traversed during a two-and-one-half hour period of silence late in the morning (fig. 9). For other males (20, 22, 24, and 35) I recorded movements almost equally as great.

The calls of adjacent males most likely provide the incentive for extensive movements in many cases. Yet considerable ground is sometimes traveled when no neighboring tinamou is calling or when the calls of other males are only distantly heard. When a male is calling, it is usually on the move. I have, however, observed males sitting on a log or knoll from which they called for a considerable length of time (up to 25 minutes). But the Boucard Tinamou does not have special calling sites, such as those described for other species of the genus *Crypturellus* (Beebe, 1925; Sutton, 1951). Having acquired one or more females, a male *boucardi* often called from the same area for several evenings. Seldom, however, was he observed calling from a particular spot on any two days.

It is clear (figs. 7-9) that the movements of males do not follow any prescribed route. Their erratic wanderings over a large area are to some extent governed by the calls of other males. The movements, along with calling, serve a three-fold function: territorial defense, attraction of mates, and feeding.

Usually the movements drop off at midday. The male then forages in a small area, calls seldom or may cease calling, preens, and sleeps. I watched one male feed in a 30-foot square area for more than one hour. It moved back and forth over the same ground many times and never advanced more than one yard at a time in a single direction. In the afternoon when calling commences the males move again, the extent of their movement depending to some degree on whether they are mated, in which event they tend to move less.

At dusk the male ceases calling. I have no evidence that special sites are selected for roosting. The end of the day may find a male in any part of the territory. Only when a male has mated is there a tendency to roost in the same small area of the territory for several successive days to a week or more. Thus early in the morning a male is found where he ceased calling the previous evening, for there is no nocturnal activity.

MATING

Mating follows the manifestations of calling and territoriality. These three "phases" of the breeding cycle become contemporaneous in the period just before egg laying and incubation. The male moves about within a large home range advertising his readiness to mate by means of lengthy calling periods. A female is eventually attracted to the call of a male and will approach him with whining notes. I did not witness any aggressiveness toward a female either by the male or another female. The male assumes the initiative in courtship as in territoriality. A peculiar feature of the reproductive habits of this species is that the male mates not with one female but with two to four females. Once mated, the male does not stop calling or cease to defend its territory but continues to advertise his presence to other males and females in the vicinity up to the time of incubation.

In 1957 the first female was discovered on March 21. She was not calling at the time. The first calling female was recorded on April 8 with male 5. In 1958 a female accompanying male 22 was heard on March 10. This male was the first to mate in the study area during the season.

Points of record and movements of calling males in 1958 indicate that almost the

entire study area was traversed during the breeding season. A number of females were, of course, also in this area. Their movements prior to mating probably consisted of random wanderings. Whether they moved singly or in groups of two or more I could not positively determine, but circumstantial evidence indicated that they were solitary. On several occasions a single female was observed that was not known to be mated to any male. Females, whenever seen together, were individuals known to be mated to a particular male. Lastly, observations revealed that a male acquired one female at a time. For example, male 20 was mated with two females but acquired them on different days; the first female was acquired on March 27, the second joined the male on March 31. Male 22 first mated on March 10 and became polygynous on March 15. Two females with male 25 were first noted on May 17. A third female joined the harem on May 22, followed by still another female on the succeeding day. In 1957, male 7 acquired his three females on May 8, 9, and 11.

After a male had mated with several females he continued to call but tended to move about in a smaller area. The male and his females were found together in the early morning, and both sexes (sometimes only the male) called frequently. The male then began to forage, and the females followed. Similar follow-feeding behavior has been noted for *Nothoprocta ornata* (Pearson and Pearson, 1955:117). In the latter species the role of the sexes is reversed, the males following the females. During follow-feeding in *boucardi* the distance maintained between the individuals of a mated group varied greatly. When decoying, a male appeared three to fifteen minutes before the one or more females in his entourage. When not decoying, the males and females were probably closer together as they foraged. But to the calls of another male nearby, real or imitated, a mated male often responded with direct and quickened movements, and the females were left behind. Several times a single female and male were observed foraging silently during the middle part of the day only five to fifteen feet apart. No male that was mated with more than one female, however, was ever observed with the females during the middle part of the day. Although the females usually kept closer to each other than to the male, they by no means remained in a flock at all times. Females were often noted following one another at distances of 20 to 30 feet. Several times two females mated to the same male were observed foraging silently at points as much as 100 yards apart. Furthermore, when the females of a harem began to call in the late afternoon they were frequently separated by distances of 50 to 100 yards. Yet, the females mated to a certain male tended to remain in the same small area and were seldom separated by greater distances.

After a period of calling in the morning the male usually became silent. The females called much less, and it was more difficult to keep them under surveillance. By the time the male ceased calling in the morning the females were usually far behind. Thus, as a rule, a male and his mates remained apart most of the day.

In the late afternoon the male commenced calling from one general area (fig. 10). The females then began walking toward their mate. The male, moving very little, remained in one small area until the females returned. Sometimes, when the females had not yet joined him after a long calling period of more than one hour, he advanced a short distance (10 to 30 yards) toward them. In no instance, however, did the male seek out the females. The females mated with male 22 remained in one area for most of the day. This male always began calling for the females sometime between 2:26 and 4:18 p.m., except on one day when he waited until 5:10 p.m. In the case of every male in the study area that was mated with females, calling continued until all females joined the male. The male and females either remained at the meeting site, or they moved a short distance, in which case communication between the sexes usually con-

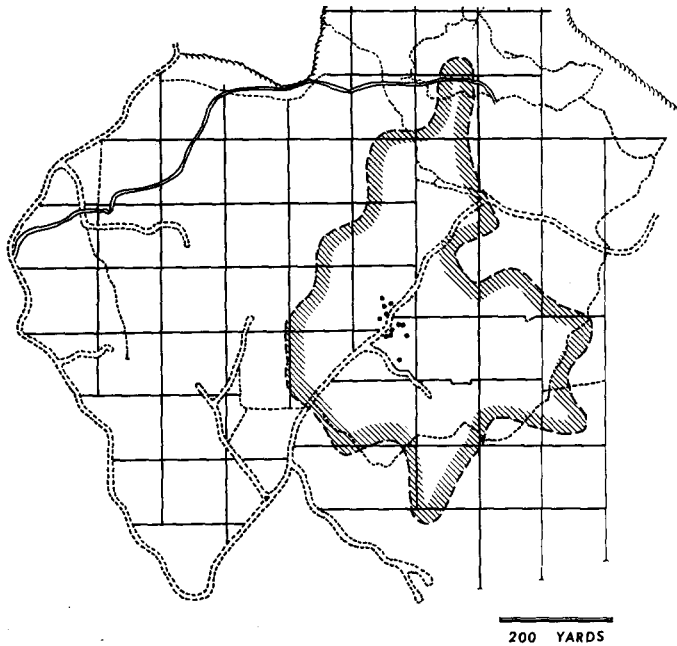


Fig. 10. Calling-up points of male 22. The entire home range of male 22 is shown in outline. Within a small area of this home range are shown the points from which male 22 called to his females on different afternoons.

tinued. Only now did the male and females move in a compact group, and one or more females occasionally preceded the male. The group never moved very far, seldom more than 100 yards.

Courtship took place at this time of day. The actual behavior patterns associated with pairing and maintenance of the bond were witnessed in the case of males 20 and 25. Most of the time reunions of male and female in the late evening were not observable because of the density of the vegetation. After a female came within sight of the calling male, he ran 10 to 20 feet toward her with quick, short steps and with his neck outstretched, sometimes below the horizontal of the body. Feathers of the lower back and the upper tail coverts were erected. Wings were held down and slightly open. This behavior was often preceded and followed by "gurgle" calls and soft whining notes. The movement was sometimes away from, instead of toward, the female. Thus, male 25 ran along beside one female and then a moment later moved directly away, still performing his courtship maneuvers. On another afternoon this same male displayed successively to two females, pausing only long enough to change the direction of his attention. The females were never observed to reciprocate with any visible behavior pattern. Following this display the male resumed his foraging and preening. No coition was observed following this ritual.

A function of courtship is the establishment of a psychological state in which both sexes are receptive to coition. I never was able to observe actual coition, probably because my observations of mated groups in the afternoon were so infrequent and of such short duration. Since courtship displays were noted only in the afternoon, coition probably occurred at this time. In a mated pair of Elegant Tinamous (*Eudromia*

elegans) raised in captivity the male mounted the female every afternoon according to Pereyra (1935:76).

Whether or not a single mated female will lay is not known. Perhaps two types of social bonds are necessary for successful reproduction: the usual intersexual bond, and a social bond between two or more females. The fact already indicated, that the males in the study area paired with females on different days, suggests that prior to mating the females do not move about together.

Four different males were known to have remained mated with one or more females for periods ranging from 8 to 15 successive days during the two seasons of observation. Females were occasionally found in the company of a male for one to four days. They then left the male, indicating that a pair bond was not sufficiently strong to result in successful nesting. Male 24 was seen with one or two females on four occasions for one to three successive days. Despite close observation no females were found with this male at other times. Two females foraged with male 21 on the morning of May 17, but no female was seen in his company at any other time. Male 35 had females for four days; then they moved elsewhere.

After the period of mating, male and females "disappear"—that is, they are neither seen nor heard. I assume that this development marks the beginning of the nesting phase. Soon, an adjoining male acquires females. The females of the original male, after laying at one nest, move on to another male, and this pattern continues throughout the breeding season. Females probably tend to mate with a small number of males with adjoining ranges during the breeding season. The females that moved among four males (23, 24, 25, and 27) were probably different individuals from the ones that moved among four others (20, 21, 22, and 35). Evidence supporting this hypothesis is the fact that of the eight "regular" males in the study area, no more than two were in the company of females at any one time, and these were always males in widely separated regions of the study area. Only one male of each of the two groups just mentioned was accompanied by a female on any one day. Furthermore, one of the females that moved among the latter group had a call with a characteristic low pitch. Another possessed an unusually high-pitched call. No females were recorded at any time with males 26 and 30. And only three males in the study area proper are believed to have nested between March and the end of May, 1958, although several peripheral males may have done so.

On one occasion I actually witnessed the transfer of females from one male to another. Male 22 had moved about with two females for six days in mid-March and then dropped out of sight on March 21. On March 26 an adjacent male (20) obtained one female, and several days later mated with a second female. I believe that these two females were the same ones that had previously mated with male 22, for they were the females with the distinctive call notes previously mentioned. Male 22, after having been silent and probably nesting since March 21, reappeared on April 9. The two females accompanying male 20 on the morning of April 9 left male 20 and moved toward male 22 shortly after the latter began to call in the vicinity. Between April 11 and 18 the females that had been mated with male 20 were recorded with male 22. Male 20, in the meantime, moved to the extreme eastern portion of the study area. No females were found with him. Thus the pair bond apparently was not sufficiently strong, even after an entire week, to prevent the females from leaving one male and returning to another male with which they had previously mated. A renewed period of calling was noted in a number of males. And the data on male 22 indicate that in some cases a male nesting twice in the same season remates with the same females.

DISTRACTION DISPLAY

Distraction display is a behavior pattern found in many terrestrial birds, serving to draw attention away from either the eggs or the young. Distraction display in tinamous has been recorded in *Crypturellus tataupa* (Hudson, 1920:220) and *Eudromia elegans* (Wetmore, 1926:31) when driven from the nest or accompanying young. In both cases the parent, presumably the male, fluttered away on its breast.

I observed what may be a form of distraction display in *boucardi* several times, but it is not a well-developed behavior pattern and is not an entirely convincing performance. When this behavior was noted the birds (males 22 and 35) were neither incubating nor with young, but male 22 had mated with females, and male 35 was in the company of two females. Male 22 was not with the females at the time of the distraction-like display, but they may have been near. On the first occasion the bird had been foraging and stood still when I approached to within 25 feet. It then flew about three or four feet from the ground and came down against some vegetation with wings fluttering. The procedure was immediately repeated. The same male performed in a like manner three days later with four such displays. Distraction-like behavior in male 35 occurred in the presence of two females. As the females ran off, the male lifted itself about three or four feet off the ground, flapping its wings loudly on both ascent and descent. After coming to the ground, the male walked quickly away. The beating wings in both males sounded much like that of a wounded bird flapping its outstretched wings against the ground.

MOVEMENTS OF MALE 35

The movements and calls of male 35 exhibited a different pattern than was manifested in other males and presented several interesting aspects of behavior in the breeding season. The call of this bird was unusually high-pitched and was the most easily recognized call in the study area.

In the late afternoon of March 3, 1958, three calls several minutes apart in the vicinity of three calling males marked the first appearance of male 35. During the period of observation that followed, male 35 moved with two mated males before finally manifesting the typical behavior shown by a male in breeding condition. One of the three males (20) calling in the area of male 35 when it was first discovered was one with which male 35 later associated.

The latter was not recorded again until March 19, when it was found in the vicinity of male 22. It remained there until March 22, calling only a few times each day, and then moved east of the bulldozer trail. For seven days beginning on March 23, male 35 called more frequently. The calling periods, however, were short compared with those of other males at this time. No attempt to defend a territory was noted. When under observation the male did not visibly react to the notes of other males calling within 30 yards. This phase of male 35's movements is shown in figure 11A. The next phase began on April 3, when male 35 began moving with male 20 and the two females mated with the latter (fig. 11B). On April 10 male 35 went over to male 22 along with the females and remained with them until male 22 and the females dropped out of sight on April 18 (fig. 11C). Male 35 could not be located again for three days. The final phase began on April 21. Male 35 had returned to the eastern portion of the study area. Male 20 was no longer conspicuous in this area; he had not been calling for some time and was presumably nesting. Male 35 now began to call more frequently, to react to the calls of other males, and to confine most of his movements to the eastern part of the study area (fig. 11D). A female was observed with him on April 25 and was joined on the following day by a second female. The two females remained with male 35 for three

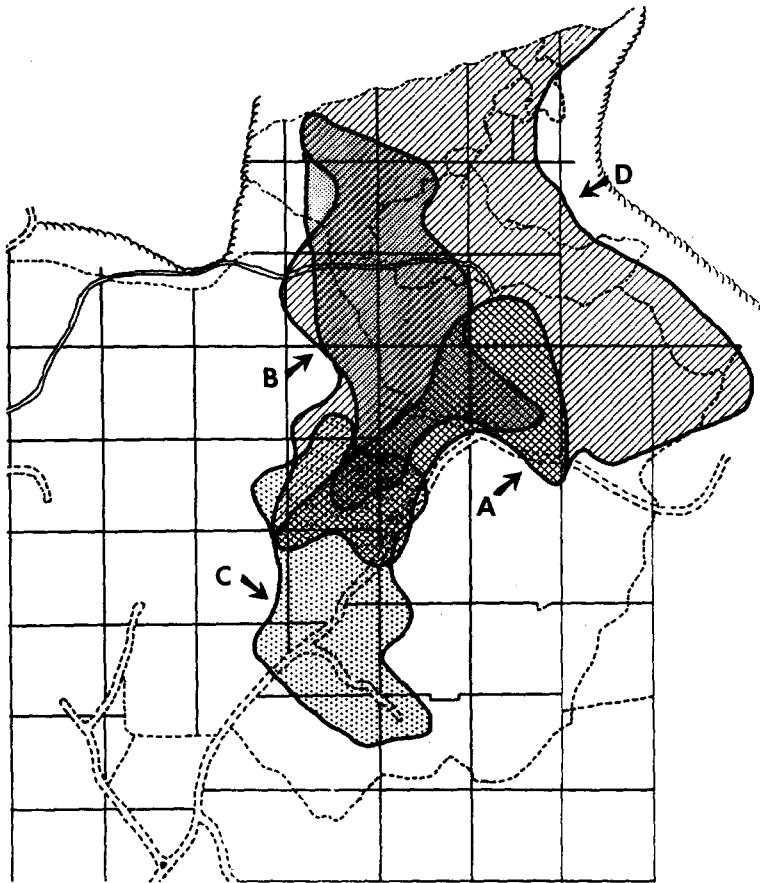


Fig. 11. Home range of male 35, showing the fluctuation of the range at different periods of the breeding season. Male 35 was not in breeding condition in March (A). He moved with male 20 (B) and later with male 22 (C). Finally he moved about by himself and called frequently, indicating a readiness to mate (D).

days. He continued calling after the females disappeared and moved about in the same region until he was collected on May 23. His calling periods reached a peak during the middle of May.

The observations of male 35 present several interesting aspects. In the Boucard Tinamou wing spotting is characteristic of the plumage of immature and subadult males. The presence of this feature in male 35 indicated a probable age of one year or less. This may explain why the typical behavior of the breeding male, exemplified in lengthy calling periods, territoriality, and mating, did not manifest themselves in male 35 until the latter part of April. The behavior of male 35 also revealed that a male not yet in breeding condition may occasionally associate with other males and females that have mated. No courtship display or coition was observed between male 35 and the females mated with males 20 and 22. No antagonistic behavior was observed between male 35 and the males that he accompanied.

SEX RATIO

The sex ratio of adult birds that exhibit polygamous behavior usually favors one sex or the other. But the gathering of data to determine sex ratio is often difficult. And the data, once collected, are frequently inadequate to provide a correct interpretation. One of the difficulties arises from nonrandom collecting. One sex may be so much more conspicuous in plumage, calls, or habits, that a greater disparity often occurs in the number of skins of one sex in collections than actually exists in nature. Under such conditions the conclusions reached concerning the sex ratio may be an inaccurate interpretation of field data. Likewise, the use of calls as an index to sex ratio is useful only if an area is thoroughly worked for a period of time and the habits and calls of both sexes are well known.

Initial field observations in British Honduras indicated many more males than females. After one month in the field, I would have concluded that females were rare, for during that time only one was seen and none was heard. The more subdued, whining calls of the female remained undiscovered until six weeks of field work had elapsed. When collecting, I found that males of this species decoyed readily. From February 28 to April 5, 1957, 11 individuals were collected, all males in breeding condition. After the behavior and calls of the females were discovered, attention was directed to their collection with the result that by the end of May, 17 males and 15 females had been obtained.

My determination of the sex ratio in this species represents an approximation on the basis of daily observations within the 183-acre study area during two breeding seasons. The method employed involved establishing the identity of males, using call variation as the criterion (Lancaster, 1964). The study area contained an estimated 50 per cent or more of the ranges of eight males (1958), while two others were regular visitors to a smaller portion of the study area estimated to include less than one-half of their entire home range. A number of other males, which were frequently heard calling, entered the study area only occasionally. More difficult was the attempt to ascertain the number of females. They did not have a fixed range except during the time they were paired with a male. Their calls were heard less frequently and did not carry for distances as great as the calls of males. The largest number of females recorded was six on April 15 and 17 and five on a number of days in April. Other females may have been present. As mentioned earlier, no more than two males in the study area were known to be accompanied by females at any one time. The ratio on the basis of the males and females regularly observed in the study area appears to be eight males to approximately six females. And since the females are more difficult to keep track of, there may have been several more than the six observed. The sex ratio among adult birds is probably very close to 1:1.

MATING PATTERNS IN TINAMOUS

The type of mating or pair bond in the Tinamidae varies considerably. Some species are monogamous, others polygamous. Promiscuity exists. In the Boucard Tinamou the males are polygamous, mating with several (up to four) females at one time. Both males and females may mate a number of times during the lengthy breeding season, although this study has shown that some males probably do not succeed in nesting even once. In the wild state evidence that a female mates with, and lays eggs for, more than one male during a single breeding season is reported in the literature for the Variegated Tinamou, *Crypturellus variegatus* (Beebe, 1925:201), the Ornate Tinamou (Pearson and Pearson, 1955:125), the Highland Tinamou, *Nothocercus bonapartei* (Schäfer, 1954:231), and now the Boucard Tinamou.

Among tinamous in general the plumages of male and female are similar; or if not, the male is the duller and usually smaller sex. The female is usually mentioned as the aggressive sex in courtship and territorial defense. This is in keeping with the rule that among ground-nesting birds the more colorful sex is usually the one that manifests territorial defense and initiates courtship behavior. These roles are reversed, however, in the Boucard Tinamou. For the male, although smaller and lacking the conspicuous barring found on the wings and rump of the female, defends a territory, calls to attract the females, and initiates the courtship activity. Only the male incubates the eggs and performs what parental care is necessary.

The Boucard Tinamou achieves a maximum of efficiency in reproduction in two ways: polygyny and multiple matings. Polygyny, whereby several females mate with one male and deposit their eggs in a single nest, permits a shortened egg-laying period. In slightly more than two days, three females, laying at the rate of one egg every 24 hours, can lay a clutch of nine eggs. Polygyny followed by successive matings by both sexes, in which the females lay eggs for a number of males and each male incubates several clutches in one breeding season, assures the maximum utilization of breeding potential. With these two patterns of breeding behavior, *boucardi* can bring off many more young than if both sexes participated in incubation, or if the females laid for only one male during the nesting season.

The color of the eggs of tinamous can hardly be considered an adaptation for protection from predators. Their glossy sheen and pastel shades show up vividly on the forest floor. They may be less conspicuous to animals that are unable to distinguish color; yet the relatively large size of the eggs and the glossiness of their shells still make them easy to see. It is difficult to imagine that selection might have favored such highly-colored eggs, since they serve only to attract predators in a habitat where egg destruction is high. On the other hand, the eggs, although readily visible on the forest floor, are exposed for only relatively short periods of time. The reproductive behavior mentioned previously, in which several females lay in a single nest, shortens the egg-laying period and thus permits a minimum period of exposure of the eggs at the time of laying. Furthermore, the attentive periods are lengthy, and the inattentive periods are relatively few in number and of short duration. Finally, when leaving the nest, the male manifests egg-concealment behavior, although the results are admittedly not very convincing. All of these behavior traits may serve to lessen selection pressure on egg coloration.

EGG LAYING AND INCUBATION

NEST SITE AND EGG LAYING

This phase of the breeding cycle begins with the commencement of egg laying since this species does not construct a nest. Despite a careful and methodical search for nests, only one was discovered. The nests were sought by dividing each two-and-one-half acre block into four or five strips with string. Two or three persons then searched the ground between two string lines. Most of the study area was searched in this manner, and many of the blocks were covered two and three times.

The base of a large tree between two buttresses marked the site of male 1's nest. Outside the study area several other nest sites were encountered containing the remains of egg shells. These observations, and the reports of natives, indicate that the eggs are usually laid between the buttresses of trees and less frequently at the base of a fallen tree or in an entanglement of vines that reach the forest floor. The eggs simply rest upon a mat of leaves, but as incubation progresses, a distinct depression is formed.

In the case of males 20, 22, and 25, nesting was foretold by reduced calling and more extensive movements one or two days before the male and females disappeared. These movements may serve the purpose of nest-site selection, although this was never determined. The male probably leads the females to a general area for nesting. I was not able to determine whether the actual site is selected by the male or the female. No mention of nest-site selection in the Tinamidae is recorded in the literature, except

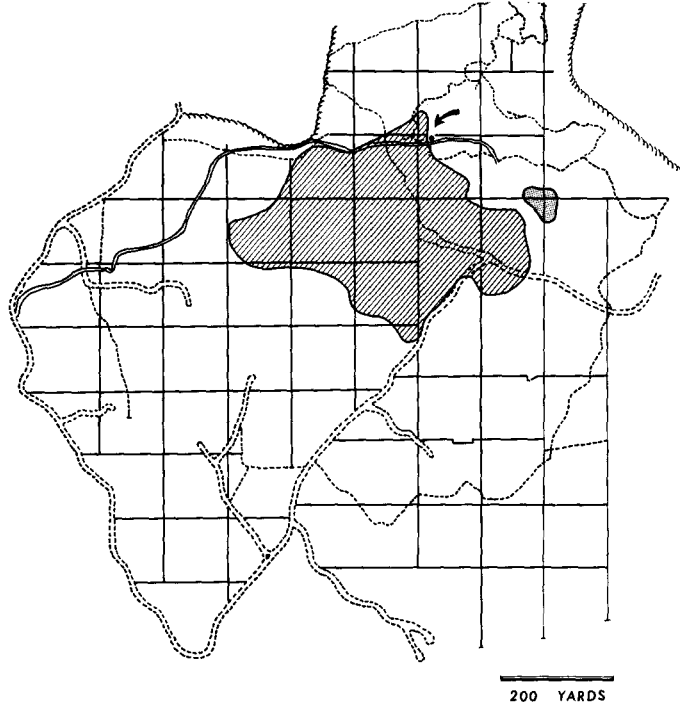


Fig. 12. Home range and nest site of male 1 in 1957. The home range indicated here is the area in which male 1 was recorded until the nest was discovered on April 16. The nest site is shown by the dot and arrow. The region in which the young were recorded between May 6 and 23 is indicated by the small, shaded area.

by Beebe (1925:204), who mentions it only as an hypothesis, stating that the male Variegated Tinamou must be the sex that selects the nest site.

The females ceased calling and "disappeared" before the male in all cases (males 1, 20, 22, and 25), and I suspect that their silence indicated readiness to lay. However, a calling female with a shelled egg in the oviduct was collected in the company of a male on April 11, 1957. Two females in similar breeding condition were moving and calling with a male when taken on May 22, 1957.

From April 2 to 12, 1957, the recorded movements of male 1 occurred a considerable distance from the nest site later selected (fig. 12). This and other observations suggest that a male does not nest in the territory or in the portion of his range occupied from the time mating has taken place until the nest site has been selected. As evidence in support of this hypothesis, other males (20, 22, and 25) made extensive movements after having been mated for some time. These movements occurred just before the male and his females "disappeared" and often extended into areas in which the male

had not previously been observed. Second, a careful search of the territory and former range of males that had ceased calling failed to locate nests or yield any indication of the presence of the birds. Last, male 20 was seen in May, 1958, with a chick not more than two or three days old in an area not included in his previously recorded range.

When the nest site of male 1 was discovered, egg laying was still in progress. It continued until April 18. The increase in clutch size was recorded as follows:

- Four eggs, 11:45 a.m., April 16 (nest discovered)
- Six eggs, 5:45 a.m., April 17
- Eight eggs, 4:08 p.m. April 17
- Nine eggs, 4:23 p.m., April 17 (laying of 9th egg)
- Ten eggs, 5:35 p.m., April 18 (laying of 10th egg)

In most birds at least 24 hours are required for the development of the ovum from the time of ovulation to a shelled egg ready for laying. Five eggs were added to the nest of male 1 in less than 29 hours, indicating that at least three females must have been laying for this one male. The ten eggs ranged in size from 43.3 to 49.0 mm. in length, and from 37.1 to 42.5 mm. in width, averaging 46.4 by 39.9 mm. Neither the variation in size nor the intensity of coloration of the eggs fell into categories that might indicate which were the product of the same female.

Egg laying in many birds is restricted to a certain time of day. Among tinamous several females of the Great Tinamou (*Tinamus major*) raised in captivity laid eggs "during the first hours of afternoon" [translation] (Taibel, 1938:375). Whether or not this is true of *boucardi* can only be conjectured. The laying of two eggs (numbers 9 and 10) was observed from the blind. Both were laid in the late afternoon. By 4:08 p.m. on the 17th two more eggs had been added to the nest since early morning, one of which was warm and had undoubtedly been recently laid. A female approached the nest at 4:17 p.m., sat at 4:18 after pushing a few leaves aside, and five minutes later, having deposited an additional egg in the nest, walked quietly away. The final egg was laid at 5:35 p.m. the following day. A female was observed near the blind at 5:11 but did not approach the nest until 5:29. She pushed several leaves aside, squatted for two minutes, and walked away.

On April 17, male 1 called in the vicinity of the nest only in the afternoon (4:31 to 5:48). His first period of attentiveness began at 5:54 p.m. on the 17th and ended at 8:02 the following morning. No calls issued from the bird on the 18th until he returned to the nest late in the afternoon. He was beside the nest when the last egg was laid. Male 1 then called five times between 5:22 and 5:33 p.m., his last recorded calls either on or off the nest until May 3, 15 days later.

Other males (2, 7, and 13), reacting to the silence of male 1, moved into the nesting area of the latter and called frequently in the period of incubation. After April 18 no females were seen in the immediate vicinity of the nest, although two were seen singly at separate locations and called several times within 150 yards of the nest on April 19 and 20. Three females that later mated with male 7 were probably the same individuals that laid for male 1.

INCUBATION

Incubation is the period between the laying of the last egg and the hatching of the last young of an entire brood (Nice, 1954:173). In the nest observed, this period lasted 16 days. During this time male 1 left the nest to feed at least nine times and probably also on the afternoon of April 21, the third day of incubation. This was the only afternoon when observations of the nest were not maintained. Assuming that

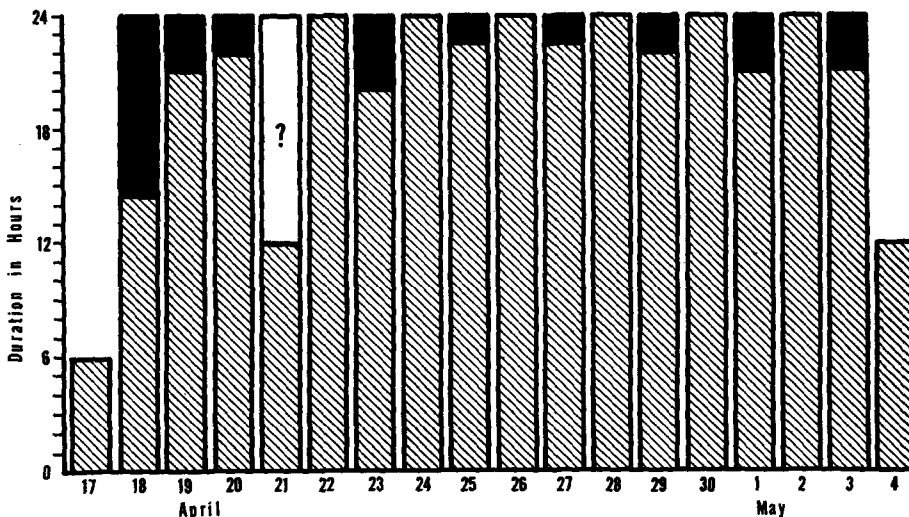


Fig. 13. Periods of attentiveness at the nest of male 1. The nest was under observation during the entire period of incubation, except on the afternoon of April 21. The lightly shaded area of each bar represents the attentive period, while inattentiveness is shown by the darkly shaded portions of the bar. Note that the male recessed only once every other day after April 21.

male 1 recessed on this day, he was absent for varying periods in the first four days, and thereafter moved off the nest only once every other day. Thus the attentive periods were long ones, ranging from 14 hours and 8 minutes to 46 hours and 43 minutes (fig. 13), and averaging 30 hours and 30 minutes. In the course of these long periods of sitting, the male rose to shift the eggs and his position a number of times each day (5 to 10). Usually he faced away from the tree. He dozed for short intervals but was repeatedly alerted by a gust of wind, a falling branch or leaf, and a number of animals that moved close to the nest. The latter included a swarm of army ants that advanced over the sitting male, a skink, two unidentified snakes, scolding ant-tanagers (*Habia gutturalis*), foraging doves (*Leptotila plumbeiceps*), tree squirrels (*Sciurus yucatanensis*), flying squirrels (*Glaucomys volans*), pacas (*Cuniculus paca*), and a band of coatis (*Nasua narica*). To some sounds, such as those caused by gusts of wind through the canopy and falling leaves and branches, the male became habituated as incubation advanced, and these stimuli, after several days, evoked progressively weaker responses from the sitting bird.

The greatest disturbance to the incubating male was caused by a Little Tinamou. This encounter indicated, I believe, the degree to which sounds are relied upon, and the precedence of sound over sight as a factor in species recognition in closely related tinamous. A female Little Tinamou came within sight of the nesting bird (male 1) in response to an imitated call, noticed the incubating male, and in the ensuing seven minutes alternated several steps toward the nest with short periods of stationary observation. When I then imitated another *soui* call, the female immediately took several steps in the direction of my blind but then turned and attacked the sitting male. The male remained on the nest and assumed a defense posture with wings partially open, head and neck drawn back, and bill open. The two birds exchanged several blows on the back and shoulder. The Little Tinamou then turned and walked away.

While the periods of attentiveness lasted for many hours, the inattentive periods were correspondingly short, ranging from 1 hour and 19 minutes to 3 hours and 56 minutes, except for the first inattentive period, which lasted 9 hours and 36 minutes (fig. 13). Except for the one long inattentive period on the 18th, all recesses occurred during the afternoon, beginning from 1:23 to 3:02.

Hunger is probably the motivating factor that brings the male off the nest after long periods of incubation. The departure to feed was preceded by pecking motions at twigs and leaves within reach of the bill. Sometimes the leaves were merely pecked at; at other times the male picked up leaves and immediately dropped them. Frequently leaves picked up by the sitting bird were pulled or dropped next to the body.

Male 1, upon rising after a long period of attentiveness, exhibited a behavior pattern that I have termed "leaf-tossing." After pulling, dropping, or occasionally pushing several leaves onto the eggs, the male picked up one leaf at a time (or more rarely, a twig) and with a sideways motion of the head tossed it toward the nest. The time involved in this activity during each recess ranged from one to eight minutes. The number of tosses increased in the first three days to a maximum of 100 and then became fewer as the incubation period progressed until, with the final inattentive period, only 11 leaf-losing movements were accomplished. The distance from the nest at which the activity was performed varied from beside the nest itself to a distance of five feet. Here, also, a correlation was noted with the day of incubation; leaf-tossing occurred at greater distances earlier in incubation. After a number of leaf-tosses, the male walked several steps away and repeated the process. Invariably, he returned to the nest and pulled several leaves on top of the eggs with his bill. Then, after walking several steps from the nest, he began tossing leaves once more.

The function served by leaf-tossing is probably egg concealment, but it is a behavior pattern that has not evolved to a high degree of efficiency. Seldom were as many as half of the eggs covered with leaves. A tossed leaf rarely traveled more than 12 to 18 inches; yet much of the time spent in this activity was at a distance of two or more feet from the nest. Not infrequently, the leaf was tossed away from the nest instead of toward it. And occasionally the leaf pecked at was not picked up; yet the male completed the motions of the behavior pattern.

After the leaf-tossing ceremony, male 1 moved away from the nest. Only once did he begin to feed before passing out of sight. He always left the nest in one general direction, and always returned from that same direction. Several observations on different days at points away from the nest indicated that the male may have had a general feeding route, but the bird was not following a trail of any sort. How far afield his foraging took him during the inattentive periods was never determined, for his call was never heard.

HATCHING AND NEST ABANDONMENT

Hatching began on the afternoon of May 3, 15 days after the start of incubation. When the male left the nest on his last recess, three eggs that had been laid on different days were pipped, and cracks were noted in two others. Continuous *perp* sounds issued from within the shells. The first chick emerged at 4:19 p.m. The male had returned by this time but remained six feet away from the nest for 15 minutes before approaching closer. At the nest he moved several leaves and an egg shell before sitting. Until dusk, several soft whining notes (recognition calls) were rendered every minute by the incubating male.

On the following day there was no activity until 6:24 a.m. when one chick moved

out from underneath the parent. From that time on, the young were active, moving under the male's body, then out again. Most of the activity of the chicks involved preening, pecking, and wing exercise. As many as seven chicks were seen at one time. The hatching of the last egg probably occurred about 8:00 a.m., since a chick emerging from beneath the male at 8:18 had wet and matted-appearing plumage. Thus, the entire clutch hatched in 15 to 16 hours.

The male left the nest with the young at 12:02 p.m., May 4, less than 20 hours after the first egg had hatched. He called the young off the nest with a whining call. This call was similar to that given after the first egg hatched but it was considerably more forceful. The departure from the nest might have taken place earlier had it not been for two disturbances. After the male had moved several yards away from the nest at 7:29 a.m., a foraging Gray-headed Dove (*Leptotila plumbeiceps*) that paused five feet from the chicks caused the male to return. At 9:53 a.m. the male again moved off the nest. At this time I moved out of the blind and toward the nest. The young crouched facing the tree while the male ran a short distance away. Almost all the broken shells were still in the nest. After 30 minutes the male returned and finally led the young off the nest at 12:02 p.m.

POST-NESTING PERIOD

Male 1 was silent during the post-nesting period except for whining recognition calls that were heard infrequently for three days following nest abandonment. If a prolonged silent period is an indication that a male is incubating, as it was in the case of male 1, and as I believe it is in all males, then at least three of the eight males (20, 22, and 25) nested between January and June, 1958. Male 22 was silent for two intervals of time, a 17-day period (March 23 through April 8) and a 25-day period (April 21 through May 15). Male 20 was silent for 34 days (April 13 through May 16). Male 25 began its silent period on May 27. Other males (21, 24, 26, and 27) were silent for varying periods of time, but I suspect that at least some of these males simply transferred their activities to a portion of their range far removed from the study area. Male 7 in 1957 was silent from April 23 through May 5 (13 days). The fact that males 7, 20, and 22 resumed calling after a relatively long noncalling period indicates that this species may nest several times in a single season. Male 22 probably did nest twice, since it mated twice, and after moving about with several females for a week or more began a prolonged period of silence in each case. Male 22 underwent a third calling period in the last half of May, but the calls were less vigorous and not as frequent, and the movements were more restricted.

Except in the case of male 20, close observation of each male after it had reappeared failed to reveal the presence of young, either with the calling male, or in the vicinity of the male. A single chick, at most two or three days old, was seen with male 20 on May 17. Recognition calls were heard on this date and on the 19th, but male 20 was not heard or seen again until May 23. The primary call was heard on the latter date, and the male now called for extensive periods until the end of May.

It is likely that in all of these cases either the eggs or young were lost through predation or that the male abandoned the chicks soon after leaving the nest.

Male 1 did not follow up incubation with another calling period, as in the males mentioned previously (7, 20, and 22). He remained apart from the young much of the time, although he probably stayed in the same general area. Male 1 and the chicks were not found on the day following nest departure (May 5) but were relocated on May 6. After May 14, only one chick was observed. From May 6 until May 23,

the young were recorded in an area less than one acre in size and about 170 yards from the former nest (fig. 12). The parent moved about in a somewhat larger area but was seen only twice with the young. The young are, therefore, probably on their own after several days.

The spot in which the young *boucardi* were most often seen was one in which the canopy was fairly open and where the forest floor contained some herbaceous plants, mostly grasses. Between May 7 and 17 a pair of chicks of the Little Tinamou were seen foraging here, several times associating with the immature *boucardi*. The area of the chicks' range was one frequently traversed by male 7 after May 6.

The chicks of *boucardi* either "froze" their positions as I approached, or walked away. Vigorous flight motions on May 13 lifted one chick several inches off the ground. No sounds were heard from the young after May 11.

By May 11 the distinct markings characteristic of the day-old chick had faded somewhat. Reddish-brown was apparent in the upper parts by the 13th but was lighter than in the adult plumage. The chicks were now about three times larger than at day 1. Barring was obvious on the wings and rump of both chicks, although it was more distinct on one chick. The browns on the head of the downy chicks had faded and were giving way to gray at ten days (May 13), and the presence of the two differently colored types of feathers gave the head and neck a ragged and mottled appearance. The wing coverts and scapulars were a dark blue-gray.

At 15 days the remaining chick was about three-fourths as large as the adult. Except for the head and neck, the entire plumage now resembled that of an adult. The crown and occiput were solid blue-gray as in the adult, but the nape and upper neck still possessed part of the brown downy plumage. The dark line through the eye was present but now was poorly defined. The face was mottled, still largely buff, but with gray feathers appearing.

At 20 days the remaining chick had acquired a fully adult plumage, except for a few scattered buffy feathers on the face and upper neck and a line of buffy feathers surrounding the dorsal margin of the eye.

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SUMMARY

A study of the Boucard Tinamou (*Crypturellus boucardi*) was carried on in British Honduras in 1957 and 1958. The breeding cycle begins with calling in late January and February. Under certain conditions the males manifest aggressive behavior toward other males. Calling duels between adjacent males occurred in the boundary zone between their territories, whereas attack behavior was noted only when one male was well within the territory of another male. Males roamed about in a much larger area than they defended. The size of the territory was not determined, but the home range varied from 28 to 47 acres. The home range and territory changed in size and location in two of the males that were studied. The degree of overlap of home ranges was extensive. Within its territory and home range the male moved extensively, sometimes covering nearly a mile in a single day. These movements were purely random during foraging but often became directed when an adjacent male began calling nearby.

The Boucard Tinamou is polygynous, the male mating with two to four females. The females lay a clutch for one male and then move on to mate with another male.

The male incubates. The females mate successively with a number of males during the breeding season. The male may nest several times in one breeding season. The male and the females that are mated with him roost together at night but usually separate sometime in the morning in the course of feeding. The females remain apart from the male most of the day but are attracted to his calls in the afternoon. Courtship behavior was noted at this time.

No nest is constructed in this species. The eggs are usually laid between buttresses at the base of a tree. The single nest studied contained 10 eggs. The commencement of incubation brought with it the cessation of calling. Incubation lasted 16 days. During this time the male recessed more often during the early stages but never more than once a day. The attentive periods were long, reaching a maximum of almost 47 hours. Upon leaving the nest to forage the male partly concealed the eggs by tossing leaves upon them. The inattentive periods did not exceed four hours after the first recess.

All the purplish-pink, highly glazed eggs hatched within 16 hours of each other, and the precocial chicks left the nest less than 20 hours after the first egg hatched. The young led an independent existence early in life and were seldom seen in the company of the parent.

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