Behavior of Boucard's Tinamou, Crypturellus Boucardi, in the Breeding Season.

Douglas Allan Lancaster

Louisiana State University and Agricultural & Mechanical College

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Louisiana State University, Ph.D., 1960
Zoology

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BEHAVIOR OF BOUCARD'S TINAMOU, CRYPTOCELLUS BOUCARDI, IN THE BREEDING SEASON

A Dissertation

Submitted to the Graduate Faculty of the Louisiana State University and Agricultural and Mechanical College in partial fulfillment of the requirements for the degree of Doctor of Philosophy in The Department of Zoology

by
Douglas Allan Lancaster
B.A., Carleton College, 1950
August, 1960
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ABSTRACT

The study of Boucard's Tinamou, Crypturellus boucardi, in British Honduras sought to increase the understanding of the natural history of a distinct, but little known family, the Tinamidae.

The habitat of this tinamou, and other closely related species in British Honduras, is discussed. C. boucardi and Tinamus major both exhibit a wider tolerance of habitats than is usually attributed to them.

Certain aspects of nonbreeding behavior of Boucard's Tinamou were studied in some detail. Its feeding habits were noted and the type of food examined. A number of plants were identified as food for this species. Insects, especially ants, were commonly eaten by boucardi, and its food occasionally included small vertebrates, such as toads and lizards. Observations of interspecific associations were rare and were believed to be strictly fortuitous.

Alarm reactions noted in Boucard's Tinamou were similar to those described for other members of this family, and included "freezing" its position, running or moving stealthily away, or flying. The latter was rarely witnessed. Flight habits of the Tinamidae are compared. Like other members of the family Boucard's Tinamou is a poor flier, taking to the air only when pursued or alarmed by shot. Its flight is short, loud, and direct. The suggestion is made that the strongly developed breast musculature appears to be an adaptation for escape from predators.

The breeding cycle is treated in chronological order, consisting of four phases: calling, territoriality, mating, and nesting. The various
types of calls are described. The calls of females were easily distinguished from those of the males. The variability of the calls of different males plus the frequency of calls were noted. Calling periods of any given male varied from day to day. Factors that might influence the extent of the calling periods are discussed, such as the presence of other males, the presence of females, the advancing season, and weather factors. With respect to time of day calling was most frequent in the early morning and late afternoon, but some calling was noted in all study-area males during the middle part of the day.

Territoriality by Boucard's Tinamou was expressed either by calling duels or actual attack, depending upon the location of the encounter between two males. The males moved about in a much larger area than was defended. This home range varied in size between 28 and 47 acres. The movements were studied in some detail. They proved to be random and, in many cases, extensive.

The type of mating is polygyny. The males were mated with several females at the same time. Upon the completion of a clutch the females left to find another mate, while the male incubated. Evidence showed that males nested several times during the breeding season. Courtship behavior was noted in several instances.

One nest was found and studied in detail. There was no nest construction. Ten purplish-pink eggs were laid on a mat of leaves at the base of a tree. The number and duration of the attentive periods were recorded. Incubation lasted 16 days. The parent led the chicks off the nest in less than 20 hours after hatching began.

Mating types in birds are briefly reviewed. Polyandry, as currently applied to tinamous and other species, is rejected. It is noted that the
standard definition of polyandry, in which a female is mated with more than one male at the same time, does not apply to any bird about which the breeding biology is known. True polyandry is suspected, however, for Monias benschi.
INTRODUCTION

In the spring of 1955 the Museum of Zoology at Louisiana State University sent an expedition to British Honduras to collect birds and mammals and to obtain materials for a habitat exhibit. As a member of the field party I became more and more aware of the plaintive, whistled calls of the tinamous, or "partridges," as the natives called them. Yet I did not see more than three or four of these birds during the entire trip, and collected but a single specimen. The natives in British Honduras could not enlighten me on any aspect of these birds other than their general appearance and their culinary virtues (tinamous are game birds throughout Middle America). Following the first trip to British Honduras these birds continued to hold my fascination. One of the most interesting features of tinamous is their unusual breeding behavior, referred to as polyandry. Yet, except in the case of Crypturellus variegatus, the term had never been applied to any tinamou on the basis of a study in the bird's natural habitat.

Tinamous have successfully eluded scientific investigation, largely because of their secretive behavior. A perusal of the literature indicated that only three of the approximately forty-five species have been seriously studied in the field. These studies were carried on by Beebe in British Guiana, 1925 (Crypturellus variegatus), Pearson and Pearson in Peru, 1955 (Nothoprocta ornata), and Schäfer in Venezuela, 1954 (Nothocercus bonapartei). A fourth species, Tinamotis pentlandii, has recently been investigated by Koford (MS, fide personal communication).
In view of the fact that so little was known of the family Tinamidae, I began a study of Boucard's Tinamou, *Crypturellus boucardi*, occurring in British Honduras.

The study was carried out over a period of eight months during the springs of 1957 and 1958. The locale of the study was Gallon Jug, British Honduras, a permanent lumbering establishment operated by the Belize Estate and Produce Company, Limited (Figure 1). The camp is situated approximately 125 meters above sea level in the tropical forest of the northwestern part of the colony, about seven miles east of the Peten region of Guatemala at 17° 33' N, 89° 02' W.

It was realized at the outset that special difficulties had to be overcome with respect to the study of this species. Most ground-nesting birds are secretive in their habits. The tinamous that inhabit the tropical forests of Middle America seem to excel in this trait. Data concerning these birds are so difficult to obtain that virtually all information presented here on *C. boucardi* was previously unknown. The literature contains almost nothing about the natural history of this species. Occasional accounts have noted its abundance, habitat, breeding condition of collected specimens, and taxonomic notes. Leopold (1959:120-122) summarizes the existing knowledge of this species.

Using calls as an index, I selected a site where tinamous seemed to be common. Here, one mile north of Gallon Jug, I set up a study area of approximately 140 acres, which was expanded in 1958 to about 183 acres (Figure 2). The compass-line trails were set up running north-south and east-west. These trails were approximately 330 feet apart as determined by pacing and were cut with the aid of one or two native boys and their machetes. The trails were kept clean and open so that movement throughout
the study area could be accomplished quickly, and so that a tinamou crossing one of the compass lines could be seen up to a distance of several hundred feet.

Although *Crypturellus boucardi* was the primary object of the study, data on several other species of tinamous were also recorded. Much of this information is not recorded in the literature and is, therefore, discussed here in conjunction with *C. boucardi*.

In presenting the material that follows I have divided the breeding cycle into chronological phases and have discussed each phase as manifested by *C. boucardi* with the advancing season. Some of the behavior, plus data concerning the geographical range and habitat, are not directly related to the breeding biology and constitute the first two sections of the dissertation. Calling, territoriality and movements, mating, and nesting follow in order.
Figure 1. Locale of the study in British Honduras.
Figure 2. The study area and its vegetation. The solid north-south and east-west lines represent compass-line trails. Randomly cut trails are indicated by a single dotted line. The double dotted lines are bulldozer trails. A creek bed (double solid lines) runs for some distance on a general north-south course. The vegetation subtypes are represented by stippling for Huamil and shading for Drypetes-erosimum. The unshaded portion is Aspidosperma-Ampelocera.
RANGE AND HABITAT

Range

_Crypturellus boucardi_ is one of the four species of the family Tinamidae whose range extends north of Panama and is the only member of that family that does not occur in South America. The other three species are _Tinamus major_, _Crypturellus cinnamomeus_, and _Crypturellus soui_.

Collecting localities recorded in the literature (Figure 3) indicate that the range of _C. boucardi_ extends along the Caribbean slope of Central America from southern Mexico (southern Veracruz, Tabasco, northern Oaxaca, northern Chiapas, southern Campeche, southern Quintana Roo) south through Guatemala, British Honduras, Honduras, Nicaragua, to northern Costa Rica, reaching the western slope in northern Costa Rica and southern Nicaragua. The range shown in the figure is based solely on published collecting records and therefore represents the minimum distribution of the species.

Blake (1955:16) denies that _C. boucardi_ occurs only in Middle America; for he would make it conspecific with _Crypturellus columbiarmus_, which occurs in a disjunct range in northern Colombia. If this is so, it is curious that neither of these forms is found in the tropical forests on the Caribbean slopes of Panama and southern Costa Rica. In my opinion, the lumping of _C. boucardi_ and _C. columbiarmus_ into a single species should be deferred until a more careful search for specimens has been made in the geographical hiatus between their present known ranges and until a study of the life history of _C. columbiarmus_ has been carried out.

Altitudinally _C. boucardi_ ranges from sea level to 5000 feet and
Figure 3. Geographical range of *Crypturellus boucardi* based on locality records cited in the literature.
perhaps higher, but its altitudinal range is variable locally. Wetmore (1943:230) found that in southern Veracruz C. boucardi is confined to elevations above 1000 feet. In the region of the Cockscomb Mountains in British Honduras the species ranges from sea level to about 1200 feet (Russell, personal communication). In the region of this study I have found C. boucardi to be common in some areas, but uncommon in similar habitats one mile away. Human interference through logging operations and milpa cutting may be the primary factor that results in this situation.

Habitat

The habitat of the four species of tinamous in Middle America falls into two main categories: high forest with a closed canopy and open understory; low woods, or bushy areas, with dense undergrowth. Tinamus major inhabits the high forest with an open understory (Aldrich and Bole, 1937:29; Leopold, 1959:113; Lowery and Dalquest, 1951:543). C. boucardi is likewise found in the high tropical forests (Leopold, 1959:122, Lowery and Dalquest, 1951:544), although Paynter (1957:249) found it to be most common in Chiapas in the low, dense transitional association between the higher pine forests and tropical evergreen forests. This association, called the monte, contains a low canopy (5 to 10 meters) and consists of dense stands of small slender hardwoods. However, the undergrowth is "relatively scant." Throughout its range in Middle America C. soul inhabits young forests, forest margins, and low bushy second growth (Aldrich and Bole, 1937:23; Griscom, 1932:98; Leopold, 1959:123; Peters, 1929:402). C. cinnamomeus is not as restricted in its habitat selection as the other tinamous and is found in the higher, more humid forests (Leopold, 1959:117; Lowery and Dalquest, 1951:545), as well as scrubby woods and dense,
low thickets (Sutton, 1951a:67; 1951b:173; Sutton and Pettingill, 1942:6).

My experience indicates that the tinamous in British Honduras are commonly found in the situations described above for each species, but that ecologically there is a decided overlap in habitat preference. The three species of Crypturellus were twice heard calling together at Gallon Jug within 100 yards of each other in low woods with a moderate undergrowth. In 1957 T. major, C. soui, and C. boucardi were commonly seen in the Huamil Association in the study area, although T. major and C. boucardi were never found in the very dense second growth of a grown-over plantation, or milpa, where C. soui is most common. Nor was C. soui ever found in the high forest with little undergrowth inhabited by T. major and C. boucardi. Leopold states that T. major and C. boucardi are abundant in the selva, the high, wet, virgin forest. Although both species can be found in such a habitat, they are not restricted to it. In fact C. boucardi in Chiapas (Paynter, 1957:249) and British Honduras is most abundant in the lower and less humid second growth forests.

C. boucardi is equally at home in all the associations of the study area. Not far from the study area boucardi was fairly common in an area that was a plantation not long ago. The cover was only 15 to 20 feet high, yet the ground cover was no more dense than in much of the medium second growth in the study area. Dickey and van Rossem (1938:60) found that C. cinnamomeus was common in a variety of associations in El Salvador, and that the one "requisite seems to be a low, protective growth." The density of the undergrowth seems to be the main factor, also, in determining the local ranges of the tinamous in British Honduras.

Where closely related species occur sympatrically they are usually adapted to different niches. Significant competition between the species
is thereby avoided. Ecologically C. soul is isolated, for the most part, from the other tinamous by its preference for a habitat with dense undergrowth. Here, small size is an adaptation for ease of movement in an environment that is physically impractical, or even impossible, for species of larger size such as T. major and C. boucardi. The latter two species are not isolated from one another by any observable habitat differences. Both occur together at Gallon Jug. If adaptations exist that tend to prevent competition between these species it is not clear what they might be. Only a few stomach contents of T. major were inspected, but they indicate that the primary foods of both tinamous are the same plant species, although several items in the crop of one T. major were larger than any food item found in C. boucardi.

Study Area Habitat

Analysis of the vegetation within the study area was accomplished by running 13 two-meter wide transects. Each transect extended between two compass lines, a distance of approximately 110 yards. Attention was limited to those species which appeared to be conspicuous by their abundance or physiognomy and thus indicative of a particular association or subassociation. The species or plants collected and identified are listed in appendix A.

The forest at Gallon Jug is called a Semi-evergreen Seasonal Forest by Beard (1944:138). This forest is characterized by two tree stories. A few scattered individuals extend above the canopy, which is largely closed. Lianes are abundant. Epiphytes are not as much so, but a few species are conspicuous. A distinct shrub layer prevails, and herbaceous ground cover is scarce. Whereas the canopy dries quickly from continued
exposure to the sun during the drought, the understory manifests a different microclimate and retains some moisture at all times. For this reason the deciduous trees of the canopy change their leaves during the dry season, although trees of the understory and saplings of species that are considered to be deciduous do not lose their foliage. Even during the dry season the floor of the Gallon Jug forest is damp until at least mid-morning, and the moisture falling from the trees reminds one of a light rainfall.

The Gallon Jug forest is a part of the Sabal-Give and Take Association of Standley and Record (1936:22), so named for the two most conspicuous palms, *Sabal mayarum* (Bayleaf or Botan Palm) and *Cryosophila argentea* (Give-and-Take Palm). The latter is by far the most common of the two trees. I encountered no fewer than 10, and as many as 42, individuals of *Cryosophila argentea* in every transect. It is a low palm forming a part of the understory; about half of the individuals recorded were saplings only four to seven feet high. The Botan Palm, *Sabal mayarum*, though not nearly as abundant, is a large palm and forms an important part of the canopy. Within the study area several subtypes or subassociations can be readily determined (Figure 2).

Huamil. This subtype includes an area that had been cut over in recent years, probably for planting corn and plantain. Because it is still in its early successional stages, it is an area that is changing rapidly and is somewhat difficult to define. The vegetation is dense. Except for a few large trees the canopy rarely exceeds 10-12 meters. Common in this succession are several species of trees which are uncommon or rare elsewhere in the study area. Among them are the low, spreading palm, *Desmoncus sp.* (Basket-Tie-Tie), *Dracaena americana* (Wild Casava), *Cecropia*
peltata (Trumpet), Coccoloba schiedeana (Wild Grape), Belotia campbellii (Moho), and Cameraria belizensis (White Poison Wood). Lianes and epiphytes are uncommon and there is no well-developed shrub layer.

Aspidosperma-Ampelocera. The Huamil gradually intergrades into this forest type. The canopy is higher (about 15-17 meters) and the forest floor is more open and easier to traverse. Two conspicuous tree species are Aspidosperma megalocarpon (Red My Lady) and Ampelocera Hottlel (Female Bullhoof). Others considered as common or frequent are Xylopia frutescens (Polewood), Pouteria durlandii (Mamey Cerilla), Pouteria campechiana, Vitex gaumeri, Vochysia hondurensis (Yemeri), Trichilia minutiflora, Protium copal (Copal), Pseudolmedia spuria (Wild Cherry), and Caesalpinea gaumeri (Warree Wood). Lianes are common. The only liana collected was a legume, Machaerium marginatum. The most conspicuous epiphytes belong to the genera Aechmea and Tillandsia. Piper spp., Rinorea guatemalensis (Wild Coffee) and Ouratea peckii constitute a well-marked shrub layer.

Drypetes-Brosmim. Several large hills are located within the study area. The vegetation on these hills is somewhat different than the Aspidosperma forest. The Drypetes-Brosimum forest possesses the highest canopy of the three subtypes (approximately 20-25 meters). The undergrowth is not dense and one can see for a considerable distance. Practically no Bactris or Desmoncus are encountered here. Of the palms which are present Sabal mavarum and Cryosophila argentea are the most common, as they are in the other subtypes. Other Palmaeae, however, are characteristic of this subtype. The small palm, Chamaedorea concolor, is common and Euterpe oleracea, though infrequent, is not encountered elsewhere. Other species characteristic of the Breadnut forest are Pimenta officinalis (Spice),
Brosimum alicastrum (Breadnut), Drypetes Brownii (Male Bullhoof). Aspidosperma and Ampelocera are not common and most of the individuals encountered are saplings. Rinorea guatemalensis and several species of the genus Piper comprise most of the shrub layer. Forchhammeria trifoliata is also a fairly conspicuous shrub. Lianes and epiphytes are fairly common.

Achras zapota is present in all forest types. Its presence in the Huamili is due to the fact that when some area of forest is cleared for planting, sapodilla and mahogany trees are left standing.

In the study area there is a low area where the stream bed fans out and its margins become indefinable. Here is the only location of Roya- tonea oleracea, the huge Cabbage Palm which characterizes low, damp sites. Other large trees found here are Acacia acantlenis (John Crow Wood), Ampelocera Hottei (Female Bullhoof), Swietenia macrophylla (Mahogany), Calophyllum brasiliense (Santa Maria), Spondias radkoferi (Hogplum), and Matayba oppositifolia (Boy Job). In the order of abundance Rinorea guatemalensis (Wild Coffee), Psychotria sp. and Piper spp. form a marked shrub layer. The forest here is quite open.

Precipitation and Temperature

The breeding cycle of C. boucardi coincides with the dry season in British Honduras, which extends from January through May. During this five-month period the average monthly rainfall over the ten-year interval ending in 1957 was less than 2.2 inches. Even with a long rainy season Gallon Jug receives only a mean annual rainfall of 59.57 inches. The amount of rainfall during January and May fluctuates considerably from year to year. During the ten-year period ending in 1957 January experienced an average
Figure 4. Precipitation at Gallon Jug, British Honduras, for the ten year period, 1948 through 1957. The bar graph represents the average monthly rainfall in inches. The line graph indicates the average number of days of rain per month.
monthly rainfall ranging from 0.37 inches to 6.95 inches, while the average monthly rainfall for May varied from 0.16 inches to 3.74 inches. February, March, and April all averaged less than two inches per month during this period. The first months following the dry season (June and July) are the wettest ones, averaging ten inches (Figure 4).

Temperature data had not previously been recorded at the camp since, unlike rainfall, it has little effect upon the lumbering operations. During 1957 temperatures were recorded three times daily in April and May. Similar temperature readings were made in 1958 from the end of January through May. During the period of study daily temperature fluctuations averaged 13 degrees. The average temperatures (Fahrenheit) for March and April were 77 and 80 degrees, respectively. During the spring of 1958 the average monthly temperatures were: March, 77 degrees; April, 80 degrees; May, 80 degrees. These temperatures were based on readings taken at 0600, 1200, and 1800, and were made in the study area. The noonday readings were not the highest temperatures. When hourly temperatures were recorded, the peak was attained between 1300 and 1430 and was often three to four degrees higher than temperatures at 1200. Occasionally the difference was as much as six degrees.
GENERAL BEHAVIOR

Nonreproductive Social Relations

Like most tinamous, C. boucardi is solitary in its habits. Aside from members of their own species Boucard's Tinamou does not regularly associate with any other species. Only four records of association between two species of tinamous were noted: a male foraging with T. major; a female seen with T. major; four C. boucardi with T. major; and a C. boucardi in company with two C. soui. Judging from the behavior of Boucard's Tinamou, these associations during the breeding season are strictly fortuitous.

Accidental meetings occur between C. boucardi and other terrestrial birds during foraging, but such encounters do not lead to any social behavior. Leptotila plumbeiceps and Formicarius analis cross paths occasionally with C. boucardi, but each species continues on its own way. Ant swarms sometimes bring tinamous together with a number of species with which they do not otherwise associate.

Intraspecifically, most tinamous are solitary, although several tinamous are gregarious at certain times of the year. There is no evidence that any of the tinamous in Central America are gregarious, although C. soui in Venezuela reportedly roosts in groups of three to five (Schäfer, 1954:220). There are several examples, however, of apparent gregarious behavior in South American tinamous. Tinamotis pentlandii is frequently seen in groups of three to eight (Morrison, 1939:461). Pearson and Pearson (1955:117) report that this species commonly associates in trios.
According to Osgood and Conover (1922:24) "large numbers" of the tinamou Tinamus tao may be seen together feeding under certain trees bearing fruit. Small coveys of Nothoprocta ornata, which apparently are family groups, have been noted by Pearson and Pearson (1955:117). The most gregarious of all tinamous is the pampas-inhabiting species, Eudromia elegans. During the nonbreeding season they roam about in groups that include as many as 100 adults (Wetmore, 1926:32).

Feeding Habits

The foraging movements of C. boucardi are reminiscent of the movements of domestic fowl. The bird moves erratically on the forest floor with jerky motions of head and body. The head is generally held low, but periodically the bird stands erect to survey its surroundings. A male that is calling and moving a great deal may feed hastily, only picking up a seed every ten feet or so. On the other hand, males and females sometimes forage for several hours at midday in an area of 15 to 20 square yards. Mated females, moving toward the male in the late afternoon, sometimes forage very slowly; they even turn about at times and walk a few yards in the opposite direction. On one particular occasion the over-all progress of three foraging females responding to the calls of a male was only 40 yards in one hour. C. boucardi frequently tosses leaves and twigs to one side with the bill when looking for food, but does not use its feet to scratch for it.

Like all tinamous, C. boucardi is primarily vegetarian and feeds upon fruit and seeds that have fallen to the ground. An examination of the crop and gizzard of ten C. boucardi plus observations of foraging birds show that fruits or seeds of the following plants (plus seeds of seven
unidentified plants) comprise much of the food of this species in the
Gallon Jug area during the breeding season.

- Acacia acantlensis
- Acacia gentilei
- Aspidosperma megalocarpon
- Brosimum alicastrum
- Cryosophila argentea
- Dracaena americana
- Drupetes Brownii
- Forchhammeria trifoliata
- Manilkara zapotilla
- Maytensis sp.
- Pouteria durandii
- Protium copal
- Pseudolmedia spuria
- Rinorea guatemalensis
- Sabal mayarum
- Spondias sp.
- Swietenia macrophylla
- Trophis racemos

Protium copal was found in all but two of the examined specimens.
Pseudolmedia spuria and Brosimum alicastrum were also dominant foods. Two
plants, Swietenia macrophylla and Aspidosperma megalocarpon, present
special difficulties to the birds since their large winged seeds can not
be swallowed until the wings are broken off. The wing of Swietenia macro-
phylla projects from one end of the seed; the bird removes it by picking
up the wingless part and knocking the seed against the ground. The winged
portion in Aspidosperma megalocarpon is disciform and completely encloses
the centrally located seed. In this case the seed itself is grasped, with
the wing projecting from either side of the bill. The combined effect of
knocking the winged seed against the ground plus vigorous head-shaking
removes enough of the winged portion so that the seed can be swallowed.

C. boucardi does not feed exclusively on vegetable matter. Parasol
ants (Atta) were found in the crop of several birds and individuals were
observed feeding on these ants. An incubating male consumed many army
ants (*Eciton burchelli* or *Labidus praedator*) that passed over the nest. A female fed for five minutes on a column of termites making its way along the forest floor beneath the layer of fallen leaves. One bird was seen taking a lepidopteran larva, and remains of Coleoptera were found in another. Occasionally the prey is larger, as indicated by the female that chased, but did not catch, a lizard; and by a male that killed a tree frog. In the latter case the bird was decoyed into sight with the frog in its bill, shaking its head vigorously and beating its prey against the ground. It dropped the frog and ran off when I was spotted. One of a pair of foraging Little Tinamous, *C. soui*, killed a small frog in the same manner as did the *C. boucardi* male and then swallowed it.

**Alarm Behavior**

When alarmed *C. boucardi* will react in one of three ways: 1) The bird may "freeze," becoming motionless in an erect or crouched posture and almost imperceptible against a forest floor covered with a layer of leaves that blend with the browns and greys of the plumage. This behavior occurs most often when the bird is disturbed suddenly. 2) The common escape mechanism is a stealthy movement away from the source of disturbance; or, if the intruder is moving in the bird's direction and is within sight, the bird may dash quickly away on a zigzag course keeping behind as much vegetation as is available. 3) Rarely, *C. boucardi* may take to the air in a sudden roar of wings that is startling even when the bird is under surveillance. This latter type of behavior may be preceded either by "freezing" or running, and is resorted to only when the bird is closely approached or is pursued.

In crouching the bird either adopts what appears to be a normal sitting
posture with the body parallel to, and touching, the ground; or it assumes an attitude that when first observed might be mistaken for courtship behavior. The body is angled at about 30 to 40 degrees from the horizontal with the breast nearly touching the ground and the rump raised. The head and neck are drawn back. The tail is not fanned out, but from the rear a boldly patterned crissum is exposed. This "rump-up" posture was observed three times in two males (30 and 35). The males did not seem to be greatly alarmed. After I had watched male 30 in this posture for several minutes, it walked slowly away when I started toward it. Male 35 actually dozed, closing its eyes repeatedly while in this posture. After six minutes, during which I remained motionless, the male resumed an erect posture, preened for one-half minute, and walked slowly away. Twice when the posture was assumed the tail was pointed toward the observer, but it was turned away on one occasion. The "rump-up" posture as a reaction to alarm has been recorded in the adult and young of Crypturellus tataupa (Seth-Smith, 1904b:289-290) and I have observed it in T. major. The chief difference in the posture among the three species is that the rectrices and tail coverts in T. major and C. tataupa are erected and spread in fanlike fashion, while in C. boucardi these feathers are not fanned, and are held on the same axis as the body. C. tataupa sometimes adopts this same posture when sitting on the nest, probably upon the approach of danger (Hudson, 1920:220; Seth-Smith, 1904b:286).

Two C. boucardi foraging together reacted differently from one another on one occasion when alarmed. A male and female moving side by side came into view about 20 feet from my point of observation. The male immediately spotted me and hastily ran 30 to 40 feet off into the underbrush. The female, which had not yet noticed the object of disturbance,
crouched and remained motionless for three minutes. As soon as the male commenced calling the female rose and began moving in the direction of the male. Then the female spotted the observer and quickly ran out of sight.

The three behavior mechanisms in response to danger are typical, with modifications, of all tinamous whose reactions to alarm have been observed. *G. soul* prefers to remain motionless and is much less prone to fly when approached than *T. major*. Moore (1859:63) states that the big tinamous (*T. major*) attempt to hide by "diving their heads amongst the brambles." I failed to notice this trait. A similar type of behavior was reported for *Crypturellus noctivagus* (Osgood and Conover, 1922:27), which "stood watching the intruder for a moment and then ducked their heads under the nearest vine and, keeping as near a crouching position as possible, glided away." Of this same species Smith (in Friedmann and Smith, 1950:426) noted that when disturbed it usually ran rapidly away with outspread wings. Crouching with spread wings was observed when *G. cinnamomeus* was alarmed (Sutton and Pettingill, 1942:7). *Nothura maculosa* may feign death when captured (Hudson, 1920:226).

The "freezing" behavior of *T. major* is sometimes modified. When the observer becomes motionless as soon as the bird is spotted, a jerky mechanical bobbing of the head takes place, in addition to short, quick steps, each of which progresses the tinamou one-half inch at most. If the observer remains quiet and stationary the tinamou walks slowly away after 10 to 15 minutes. It seems likely that this exaggerated head and neck movement is a means for "better assessing the disturbance" as pointed out by Pearson and Pearson (1955:115), who noted head bobbing in *Nothoprocta ornata*. For this motion occurred only when the observer surprised
the tinamou and immediately "froze" his position.

The reaction of immature birds to alarm is almost always to crouch with the tail toward the object of disturbance; but they may move stealthily away if the danger is not imminent.

**Flight**

Tinamous are poor flyers. They usually try to escape on the ground and take to the air only when hard pressed. During the 14 months spent in the field I saw only five individuals of *C. boucardi* leave the ground. Two were birds at which I had shot. One was flushed by a fox, another by a male *C. boucardi*. And a female flushed when I attempted to follow it. Thus few data were obtained regarding flight in this species. Although Boucard's Tinamou is a poor flier, its flight is direct and strong, but of short duration. It has been likened to the flight of quail. Tinamous rise with a series of rapid and loud wingbeats and then glide to the ground some distance away. Continuous wingbeats characterize the flight of *Rhynchosaurus rufescens* (Hudson, 1920:221), but a short period of rapid wingbeats followed by a glide is typical of most tinamous including *C. boucardi* and *T. major*. Several species (* budromia elegans* and *Notura maculosa*) may alternate several periods of wingbeats and gliding in a single flight (Friedmann, 1927:143; Wetmore, 1926:30–31), although Wagner (1949:244) did not notice any gliding in either of these species.

Flight covers varying distances depending on the species. I was able to follow only one flight of *C. boucardi* at Gallon Jug, and its distance was 30 to 40 yards. In an unspecified number of instances, Wagner (1949:243) found that in *T. major* the greatest distance covered by a single flight was not more than 26 yards, while Leopold (1959:113) estimates their
flights at 50 to 100 yards. The average distance of nine recorded flights of *T. major* in British Honduras was approximately 48 yards, about twice the distance recorded by Wagner. The longest flight was about 100 yards.

Two flights of *C. soui* were about 17 yards and over 65 yards. Hudson (1920:222) states that *Rhynchotus rufescens* is capable of flights over three-quarters of a mile (1500 yards).

Very little is mentioned in the literature as to the height at which tinamous fly. I recorded two *C. boucardi* at heights estimated at six and seven meters. Wetmore (1926:30,38) states that *Eudromia elegans* rises three to six meters and that *Nothura maculosa* rises two to five meters.

Of the Mexican tinamous Wagner (1949:243) states that "Seldom do they rise higher than one meter above the ground." Twenty records of the height attained by three species of tinamous in British Honduras indicate a minimum of about three meters and a maximum of twelve to thirteen meters.

The thirteen records dealing with *T. major* show the extremes mentioned above and average out to seven meters.

According to various accounts in the literature, the flight of tinamous is direct and, in many cases, not well controlled. The poorly developed rectrices are inadequate for any degree of maneuverability, and several instances are on record of tinamous colliding with objects. On two of the five flights observed, *C. boucardi* caused considerable disturbance as it came to earth through the underbrush, apparently unable to maneuver for a descent into a spot clear of vegetation. Beebe (1925:200) saw *C. variegatus* fly against a tree. Hudson (1920:225) cites examples of three tinamous flying into a fence and of another bird flying against the wall of a house. Wetmore (1926:34), however, speaking of the same species (*N. maculosa*), states that the flight is well controlled.
I did not witness any comparable uncontrolled flights. *Tinamus major* in several cases turned nearly 180 degrees in flight. A captured *C. soui*, when released, rose quickly to about six meters, gradually turned in flight about 140 degrees and disappeared from sight. Except in *C. boucardi* all landings of tinamous observed were silent indicating the birds were able to steer clear of any undergrowth that might have been present.

Hudson relates an experience, not his own, of a tinamou (*N. maculosa*) that was flushed by a horse and, climbing to a considerable height, was unable to make any headway against a strong wind and finally crashed to the earth. A somewhat similar vertical flight occurred at Gallon Jug when a *C. soui* flushed and flew straight up to an estimated height of 19 meters, hovered for several seconds, then descended with weaker wing action back into the underbrush, having made practically no forward progress. There was only a gentle breeze at the time of the incident.

Escape is certainly the primary, if not the only, function of flight in most tinamous; however, *Nothoprocta ornata* may also fly "to cross streams, to reach feeding grounds, or at times for no obvious reasons." (Pearson and Pearson, 1955:115). Hudson, in stating that *Rhynchotus rufescens* is capable of flights of over three-quarters of a mile does not mention the conditions under which such flights are made.

*Tinamus major* is more prone to fly than the species of *Crypturellus*. The fact that the larger birds are heavily hunted in preference to the other tinamous may be, at least in part, an explanation for this inclination to fly when alarmed. Russell (personal communication) noted that in the uninhabited regions of the Cockscomb Mountains *T. major* was considerably tamer and flushed less often than at Gallon Jug.
Upon first consideration the flight and anatomy of tinamous seem to present a paradox. The sternum is relatively long, and a keel of considerable size affords attachment for very large pectoral muscles, muscles which seemingly could carry the tinamou on a powerful and long flight. Wagner (1949:240-243) compared the relative size of the pectoral muscles of several birds and noted that in proportion to total body weight the weight of the breast musculature of tinamous (\textit{T. major, C. cinnamomeus}) is the same as that of hummingbirds, which possess a pectoral muscle to body size ratio far above the average for flying birds. Wagner also noted the small heart capacity and the small diameter of the blood vessels. In hummingbirds the weight of the heart, like the weight of the pectoral musculature, is greater in proportion to the body weight than in other birds. And, though tinamous possess a comparable breast musculature in proportion to body weight, the weight of the heart is extremely low when compared with that of the body. The poorly developed circulatory system may be directly responsible for the incapability of sustained flight in tinamous by indirectly causing fatigue soon after the bird takes to the air.

It may seem incongruous that the evolutionary process has endowed the tinamou with strikingly large pectoral muscles used solely for flight, yet has not selected for a circulatory system capable of supplying these active muscles for more than a short time. The best explanation is that, in terrestrial birds of such secretive habits and with a plumage blending so perfectly with the immediate environment, flight is seldom necessary as a means of escape. Tinamous, however, possess some enemies from which flight is the only escape once the bird is detected. The adaptive significance of such disproportionately large pectoral muscles is
that it provides sudden and strong flight for escaping from such a predator.
CALLING PHASE OF THE BREEDING CYCLE

Description of the Calls

The notes of tinamous are familiar sounds in the forests of Middle and South America. Calls of these birds thus far described in the literature seem to indicate that a certain whistle-like quality is common to members of the Tinamidae. The whistle may be either low in pitch or high. Some of the calls are monotonic. Others ascend or descend the scale for short distances. In several species the quality is ventriloquistic. One of the calls of Nothura maculosa is described by Hudson (1920:224) as seeming "to swell mysteriously on the air, for the listener cannot tell whence it proceeds." The notes of Crypturellus boucardi possess a similar property.

Crypturellus boucardi

The call of C. boucardi is distinctly different from the calls of other Middle American tinamous. It is characterized by a faraway, pigeon-like quality that makes its source hard to locate. At a distance its direction is more difficult to determine than that of any other tinamou call in British Honduras. On numerous occasions when I decoyed calling birds, I found that they were closer and in a different direction from that expected.

Davis (MS) describes the phrasing as "Uh-wuh" or "Ah-wuh." Although at a distance the call sounds like the two-note call described by Davis, I could clearly discern three notes when the bird was within 20 to 30
yards. I phoneticized these as "Ah-oo-wah." Shortly after the call begins it slurs down about one-quarter to one-half note, then slurs upward to the starting pitch. In all the males studied the second and third notes were slurred together, but a momentary break existed between the first and second notes. Unless one is fairly close to the calling male, this break or pause is not detected in some individuals. The call lacks the waver or tremor characteristic of some tinamou notes and is much lower in pitch. The duration of the call is about two seconds, sometimes closer to three seconds.

Two factors with regard to calling facilitate a behavioral study of this species in the wild. One is the relatively long periods of calling of the males. The other is the distinctiveness—that is, the individuality—of the call of each separate male and indicated in Figures 5 and 6. The calls of any given male, on the other hand, are remarkably constant and rarely manifest any detectable variability.

This variability between individuals can best be illustrated by describing the differences in the notes of the males in the study area. Differences in pitch were the most easily detected variations. They extended over a range of slightly more than one full note (F to G#); most of them fell within a one-half note range (F# to G). Yet any two males whose calls exhibited a difference of only one-quarter note in pitch were easily distinguished with a pitch instrument. Males 21, 23, 26, 29, 30, and 33 possessed calls beginning invariably on F#; males 20, 22, 24, and 31 always began on G.

Although the starting notes of several males were on the same pitch, the pitch of the other notes varied sufficiently to make identification of the specific individuals possible (Figure 5). In some males the
Figure 5. Diagramatic representations of the calls of several *O. boucardi* males, showing variability.
Figure 6. Reproductions of sonagrams of calls of five *G. boucardi* males.
last note was on a slightly different pitch from the first note. Such was the case in male 28, in which the call terminated on a slightly higher note. In still another male the last note was almost one full note above the first note of the call. In males 26 and 33 the second or middle note dropped almost imperceptibly in pitch. In another male the middle note dropped almost one full note and the call terminated below the starting pitch.

But even when the calls of two or more males were on the same pitch they could often be differentiated by other characteristics. For example, the call notes of males 20, 22, and 25 had essentially the same pitch; yet each of these males could be separated from the others on the basis of its call. In male 20 the last note was invariably longer and louder than the rest of the call. The call faded in volume instead of abruptly terminating as in the other two males. In male 25 the first note was the longest—twice as long as the last note, which was cut off sharply. The first and last notes of male 22's call were equal in length of time and thereby this bird could be distinguished from either male 20 or male 25.

Variability within a male's call was noted only in the case of three individuals. This variability, however, seldom changed the call to such a degree that it was not recognizable as belonging to a particular male. Such variations occurred very seldom. In the case of two males it was associated with intensity of calling. When they called loudly the last note sometimes terminated with a drop in pitch.

I was not able to detect any variation in the calls of tinamous in British Honduras that could be attributed to sex, except in the case of *C. boucardi*. The female of this species possesses a call that can briefly be characterized as more subdued, highly variable, and having a typical
whining, nasal quality; in contrast to the more mellow, less variable, and more throaty note of the male. The call often covers a greater range of notes than the male's call and has a slightly higher pitch. The latter sometimes is more apparent than actual, however, because of the whining quality of the female's call. Her whistle carries for a distance up to several hundred feet, and is usually heard only when a male is close at hand. Its variability is illustrated in Figure 7. All these calls were diagramed one afternoon from three females mated with male 22. Such variations as those exemplified made it difficult to determine exactly how many birds were calling when the females were together and their calls were similar in pitch, especially since one female often called several times in succession with only momentary pauses between calls.

On occasions the female rendered a call that was similar to the male's. This variation was usually heard when the females began to call in the afternoon in response to their mate or prospective mate. If a female was both some distance away from the male and separated from the other females, her calls followed the pattern of the male's call but were usually slightly longer and often more wavering. The calls had a less nasal quality than the typical female whistle. The number of these calls apparently depended on the proximity of the females to the male and also on the number of females together at the time. As the females approached closer to the male, they commenced the whining and more subdued call, which was the call previously described and the one most often heard. The malelike calls were more numerous when the females approached the male from separate points. Females seldom rendered this call when they approached the male together. A solitary female sometimes called in this
Figure 7. Diagrammatic representations of the calls of three *C. boucardi* females showing the degree of variability.
manner until its mate was within sight. In addition to these two calls, barely audible "app" notes were heard when a female laid an egg.

While the female possesses a male-like call, the male also has a call that, in quality, is much like that of the female. It is a call that retains the pattern of the male's primary call, but takes on a whining quality. This call was heard in two situations: after the male had successfully attracted one or more females; and after the young had appeared. The soft, subdued, whining whistles issued from both sexes when the females were in the company of the male. The calls have been heard several times in the morning (males 5 and 22) when the male foraged out of sight of the females, but more often in the afternoon (males 20, 22, 25) when the male was calling to the females that were not near. These whining calls of the male were not commonly uttered and were usually interspersed irregularly with the primary call, although on one occasion male 25 called in this fashion every 20 seconds for 13 minutes.

Once incubation had begun male 1 made no sound either on or off the nest until the first egg hatched. Then he emitted very soft notes, 10 to 15 seconds apart, that were hardly detectable 30 feet away. These notes were monotone, whining whistles lasting one-half to one second. As the male prepared to leave the nest with the young, these recognition calls became louder, more prolonged, and similar in pattern to the primary call except that the last note usually rose above the pitch of the starting note. This was the only call heard from the male as long as the brood remained with him.

Morrison (1939:461) characterizes one of the calls of Tinamotis pentlandii as "a sort of laughing gurgle"; the description is very applicable to one of the calls rendered by G. boucardi males. The latter
consisted of three ascending staccato notes (usually two notes in the case of male 22) and lasted less than one second. The notes had a throaty and gurgling quality and were not audible unless the male was within 50 feet of the observer. The gurgle calls were heard most often just after a female had joined its mate in the evening. On several occasions the calls were repeated in rapid succession with faster and faster tempo until for short periods of up to 20 seconds they sounded like a single continuous gurgle (males 20 and 27). The gurgle call was also heard on a number of different occasions after a male had been decoyed into sight.

An alarm call consisting of short, high-pitched, staccato notes was heard only once—when male 21 was flushed by an attacking male (20). A similar call was heard from Tinamus major many times as it ran from me or took wing. Alarm calls have been noted in other tinamous as well. Notoprocta cinerascens frequently gives "a loud clucking call" when flushed (Wetmore, 1926:39). Under similar conditions Notoprocta ornata "explodes into the air with a loud and startling series of screeches" (Pearson and Pearson, 1955:115). When running Nothura maculosa emits a "sweet melancholy whistle" (Friedmann, 1927:143). When taking wing Eudromia elegans sometimes gives a low whistled call (Wetmore, 1926:31). Tinamotis pentlandii utters "a shrill and loud whistle upon rising" (Bridges, 1847:28). Beebe (1925:197), however, noted only silence from Crypturellus variegatus as it flushed.

Tinamus major

The call of this species is more melancholy than other Central American tinamous. It consists of a series of wavering couplets (usually
three) preceded by several whistled notes (Figure 8). The sound carries for a considerable distance, and the direction of the caller is sometimes difficult to determine. Davis (MS) described this call as "... a series of three closely joined couplets; a single one of which may be recognized by its similarity to a tremulous, dragging whistling of a couplet phrased as 'How-now' at such a speed that the three are completed in five seconds." Almost invariably the call is preceded by a series of whistled notes, most commonly four. The call of T. major encompasses a small range of pitch. The first note of each couplet and the antecedent notes are given on the same pitch. The second note of each couplet terminates one-quarter to one-half note lower. The notes of the couplets are wavering whistles whereas the preceding notes are not usually tremulous.

Considerable variation occurred in the call of this species in British Honduras. Between any two individuals the only obvious variation was that of pitch. The variations within any one bird were largely quantitative; mostly they concerned either the number of the couplets executed, the number of notes that preceded the couplets, or both. Rarely, a call began with the couplets, with the preceding single notes omitted. As many as 13 couplets have been recorded in a single calling. The number of notes that preceded the couplets ranged from one to eight. If the call consisted of more than three couplets, the pause between the third and fourth couplets was often longer than the pause between the first and second, and between the second and third couplets. The remaining pauses were of variable length.

The time required to complete the call depended in part upon the number of notes rendered. Nevertheless, even when the calls of two
individuals contained the same number of notes, it sometimes took twice as long for one bird to complete its call. An individual bird's call was noticeably hurried on occasions, with practically no pause between the three couplets, and required as little as three seconds to complete. Infrequently, the notes of one or more couplets were slurred together into a single note.

_Crypturellus soui_

The principal call of _C. soui_ was fairly high-pitched and consisted of several notes slurred together in a single whistle (Figure 9A). The call rose one-half note above the starting pitch and then usually dropped about one full note, one-half note lower than the starting pitch. The last part of the call was tremulous, the tremor beginning at, or just before, the peak pitch of the call. The most common variation was the termination of the call on the same pitch as the opening note. Calls without any noticeable tremor at all were sometimes heard.

One of the calls of this species is a "tremulous whistle consisting of steadily ascending notes of diminishing length" (Blake, 1953:2). Not only are the last notes of the call shorter in length but the interval between successive notes is often of shorter and shorter duration.

The decrease in time lapse between successive notes as the call progresses is a common feature of a number of calls of tinamous in addition to _C. soui_. Thus _Nothura maculosa_ gave "a single note repeated with increasing rapidity until it terminated in a trill" (Wetmore, 1926:34). Hudson (1920:220) describes a somewhat similar call for _Crypturellus tatua_ in which a single note is repeated with greater and greater rapidity until it runs into a trill. _Nothura darwini_ gives a series of
Figure 8. Diagram of the call of *Tinamus major*.

Figure 9. *Crypturellus soulii*. A. Diagram of two calls. B. Four recorded patterns of duetting. The first non-tremulous note is given by one bird; a second bird renders the tremulous portion of the duet.
short whistled notes which are more rapid at the conclusion of the call.
Mitchell (1957:15) described the call of what she believed was Crypturellus obsoletus as "a clear, rising series of whistles," each succeeding note of shorter duration than the note preceding it.

The number of notes recorded in the series call in British Honduras varied from three to nine. But by far the greater number of calls recorded contained five, six, or seven notes. The first note of the ascending series was usually nontremulous, the second was rarely so, and the remaining notes exhibited increasing tremor. Not infrequently the first several notes of this series call showed no rise in pitch, and as many as four notes have been recorded on the same pitch before any rise was evident. Likewise, the final two, and sometimes three, notes were sometimes delivered on the same pitch. Only once was a bird actually seen while it rendered the series call. It was a female that approached the blind and remained close at hand for some time. The duration of the call depends, of course, on the number of notes in the ascending series, but usually lasted from five to eight seconds.

The significance of the series call is unknown. A calling bird sometimes failed to execute the series call during a given calling period; but when given, the series call always preceded the principal call, never followed it. I believe the repertoire of both sexes includes the series call, as it does the main call; although, as stated earlier, only on one occasion was a bird under observation while calling in this manner. The main call is by far the most commonly heard call. An analysis of 621 calls of C. soui revealed that 77, or 12 percent, were series calls; the remainder were principal calls.

A high-pitched, subdued, monotone whistle that was barely audible
more than 30 or 40 feet away was given frequently by both sexes of a mated pair as they foraged together. Other calls were rarely heard. Davis (MS) describes one call of *C. soui* as "a song of three or four shorter whistles given as a series." I heard a call matching this description three times on one occasion but only a few other times. Each consisted of three tremulous notes on the same pitch and lasted about two seconds. A call heard on only one occasion was a single nontremulous note rising in pitch and lasting one second. Fourteen such calls were given five seconds apart.

The literature contains no mention of duetting among any of the tinitamous, but I have seen supposedly mated pairs of *C. soui* in the act of duetting. At other times, whenever I heard duetting, the two birds seemed to be close together. The calls were similar to the principal call. The ascending note was given by one bird, the tremulous, descending note by the other. The two calls usually overlapped (Figure 9B).

**Seasonal Pattern of Calling**

The breeding season for *C. boucardi* begins shortly after the start of the calendar year, and may be divided into several chronologically overlapping phases: advertising phase, territoriality, mating, and nesting.

The first indication of the breeding season is the calling of males in late January and February. The breeding season was already underway in 1957 when field work began. In 1958 the first calls of *C. boucardi* were heard on January 20 (field work began January 18), but none were heard in the study area during the first six days of observation, until, on January 27, a male (20) called nine times during midday. Other males in the study area were first recorded as follows: male 22, January 31;
male 21, February 1; males 23 and 24, February 26; males 25 and 26, February 28; male 27, March 1; male 35, March 3; male 28, March 4. Thus, after their initial state of winter quiescence, one male after another began calling. Though sporadic at first the calling periods of each male became more numerous and longer in duration. A period of five weeks passed before all the males in the study area came into breeding condition.

The peak months of calling are probably April and May, and a gradual decline after the commencement of the rainy season in June is likely. But since no field study was undertaken in the fall of the year, no data are available regarding the calls of C. boucardi or the other tinamous in British Honduras during this period.

The seasonal pattern of calling varies among tinamous, and apparently is a manifestation of the breeding condition. Few calls of T. major were recorded in the study area or elsewhere until March 17 (1958). On this date the number of calls were notably more numerous. In 1957 a marked increase in the number of calls of this tinamou occurred after the first of March. Calls of several species have been recorded at all months of the year. Among these are Crypturellus variegatus in British Guiana, where Beebe (1925:201) discovered nests in all but three months of the year (November, January, February); Crypturellus obsoletus in Brazil (Lüderwaldt, 1909; Holt, 1928:278); Crypturellus tataupa (Hudson, 1920:220), Rhynchotus rufescens (Hudson, 1920:222), and Nothura maculosa (Wetmore, 1926:34 and Hudson, 1920:224) in Argentina. In all these species, however, calling probably reaches a peak during the breeding season, although no mention is made of this with regard to C. tataupa and C. variegatus. Other species are silent during the period of gonadal quiescence. Shore-Bally (1925:19) reported that in an aviary in England
Nothoprocta cinerascens first called at the end of May. *Eudromia elegans* in Argentina begins calling in September (Hudson, 1920:229). In Venezuela *Crypturellus noctivagus* is quiet until the dry season ends in April, and calls through the month of August (Friedmann and Smith, 1950:425).

**Daily Pattern of Calling**

In *C. boucardi* the daily pattern of calling is similar to that found in many tinamous. The calling periods are more extensive during the morning and evening than at other periods of the day (Figure 10). The pattern differs considerably, however, from that found in the other species in British Honduras. *C. boucardi* is heard more often during the middle part of the day than the other species. Calling drops off sharply around 1800, whereas the other species reach their peak of calling at this time or later. No *C. boucardi* have been heard after 1826. Calling is somewhat heavier during the early morning in *C. boucardi*, while in the other species more calls are rendered in the evening.

For *C. boucardi* the pattern of individual calling is more erratic than the daily and seasonal pattern presented by the species as a whole. The individual males of this species call for much longer periods during the day than do individuals of the other tinamous in British Honduras. It is this characteristic, more than any other, which facilitated certain aspects of this study.

The general pattern for each individual (Figures 16 to 20) indicated a period of calling in the early morning and later afternoon and evening, somewhat more pronounced in the morning.

From February 22, 1958, until the end of May, not a single day of
Figure 10. Daily pattern of calling of *Crypturellus boucardi*, based on 63 full field days in 1958.

Figure 11. Daily pattern of calling of *Crypturellus soui* in the study area, based on 52 full field days in 1957.
silence was noted in the study area with regard to this species. Even so, a given male, after calling most of one day, may call for a short period on the following day. For example, male 20 on April 11 called for about four hours during the morning, but did not call at all the following morning. Male 21 on March 17, 18, and 19 called from one-half to one hour on the 17th and 19th, but called for a total period of five to six hours on the 18th. Male 22 on the same days one month later called for periods of approximately five hours, two minutes, and three hours, respectively.

On days when several males are silent, or are heard for only a matter of minutes, other males occupying adjacent areas may call for many hours. Thus, male 21 on April 16 was heard for only a few minutes around 0630, while male 26 called from 0550 to 1745, with only short punctuating periods of silence. This inconsistency in day to day calling is apparent in the graphs in Figures 16 to 20, which show the daily pattern of calling of five C. boucardi males. These bar graphs do not represent all calling by the five males during the entire breeding season, for there were days during which their calls were not recorded. Nor were these males under observation during the entire day in many cases, as indicated by the dots, which signify my departure from the area of the male while he was still calling.

There was no apparent correlation with regard to the duration of calling among any two males on a given day, except between males that were establishing adjacent territories during the earlier part of the breeding season. At the latter time the calls of one male initiated a vocal response from another male within easy hearing range. The two or more males then exchanged calls. It is probable that males soon learned the calls
of nearby males, for later in the season a given male did not respond as readily to the call of a member of the same sex occupying an adjacent territory. The same was true during decoying. It became increasingly more difficult to decoy a given male within sight after several successful attempts.

Females call much less frequently than do the males. Almost all of the subdued calls of females that were recorded came from mated individuals.

Night calling by tinamous has been reported by several authors. Aldrich and Bole (1937:29) reported that *T. major* is "occasionally heard at night." Sutton and Pettingill (1942:6) stated that the call of *C. cinnamomeus* was heard at all hours during the full moon period of April in Tamaulipas, Mexico. The call of *C. variegatus* can be heard at intervals throughout moonlight nights, according to Beebe (1925:197). I frequently heard *T. major* and *C. soui* when in the field at night, although the time spent in the field after dark was not sufficient to determine the extent of calling by tinamous during the night. I never heard Boucard's Tinamou after dark. Lowery and Dalquest (1951:544) reported that this species rarely calls at night.

The calls of *T. major* and *C. soui* were heard at all hours of the day. Friedmann and Smith (1955:475) reported that *C. soui* in Venezuela "would pass unnoticed" except for the calls of the early morning and evening. This is not the case in British Honduras. Here *C. soui* called during every hour of the day, although the majority of calls were heard in the early morning and evening. The most extensive calling periods of the Little Tinamou were from 0530 to 0630 and from 1800 to 1830. Calls of a pair of *C. soui* were recorded in the study area during a period of 52 field days (February 20 to May 25, 1957). The results are shown in
Figure 11. This graph shows the relative frequency of calling periods for every half hour of the day from 0530 to 1800. These frequencies are expressed as percentages. I usually left the study area at approximately 1800, so that the graph does not include one of the heaviest periods of calling, but it does show that the calls of this species were not confined to the early morning and evening. If, however, data had been collected on the calls of all C. soui, rather than those confined to the study area, the graphic representation would have been similar to, and more accentuated than, the graph in Figure 10 for C. boucardi.

In Tinamus major a similar pattern exists, i.e., individuals may be heard at any hour of the day, but calling occurs most often in the early morning and in the evening. The two graphs (Figures 12 and 13) for T. major are quite different. Figure 12 covers over twice the time period of Figure 13 but represents only the individuals heard within the study area. As in Figure 11 the heaviest calling periods are not shown. Figure 13, however, records the calls of all individuals heard, but covers only a 25-day period. Nonetheless, the pattern is a typical one with a notably heavier calling period during the evening than during the early morning. A similar pattern is recorded by Lowery and Dalquest (1951:544) in Veracruz although Austin (1929:369) noted that T. major called more frequently in the early morning. Not only were more individuals heard during the evening at Gallon Jug, but individuals rendered more calls at this time. The evening calling period was during an hour between 1730 and 1830, with most individuals heard five minutes on either side of 1800. The morning calling period extended from 0500 to 0630 with sporadic calling until evening.

Where mentioned in the literature, the daily pattern of calling is
Figure 12. Daily pattern of calling of *Tinamus major* in the study area, based on 59 full field days in 1957.

Figure 13. Daily pattern of calling of *Tinamus major*, based on 25 full field days in 1958.
much the same for all the Tinamidae. Most species, when studied for some
length of time, are heard calling during all daylight hours, though a
large preponderance of calls occurs in the early morning and late after-
noon or evening. Beebe (1925:199) recorded the call of *C. variegatus* at
all hours of the day, but states that nine-tenths of the calls occurred
between 0530 to 0630 and 1700 to 1900. If calls are more frequent at one
time or another it is usually the evening. *C. noctivagus* (Friedmann and
Smith, 1950:425) and *Rynchotus rufescens* (Hudson, 1920:222) call mostly
at sunset as does *Eudromia elegans* (Hudson, 1920:229). The call of
*Crypturellus soui* was heard only about sunset by Riker and Chapman in
Brazil (1891:163). In Tamaulipas, Mexico, *C. cinnamomeus* was heard almost
constantly during the month of April by Sutton and Pettingill (1942:6).

Rate of Calling

The number of calls that a single bird delivers varies greatly from
day to day (Figure 14). *C. boucardi*, though calling more frequently than
the other tinamous found in British Honduras, is not as likely to gain as
much attention because of its lower-pitched, more mellow call.

To determine the rate of calling the calls of different males were
periodically recorded for varying time intervals. Forty-one such samples
of 25 minutes duration or more were taken for 14 males to ascertain the
variation, if any, in the rate of calling under various conditions
(Appendix B).

The average rate of calling of all samples ranged from one call every
25 seconds to one call every 62 seconds. Where adequate sampling was
accomplished the results indicate that each male has a rather extensive
range of interval between calls (Figure 15). There is, however, some
<table>
<thead>
<tr>
<th>Male</th>
<th>Date</th>
<th>No. of Calls</th>
<th>Hour of Day (in hundreds)</th>
</tr>
</thead>
<tbody>
<tr>
<td>7</td>
<td>20 May 1957</td>
<td>856</td>
<td>6 7 8 9 10 11 12 13 14 15 16 17 18</td>
</tr>
<tr>
<td>7</td>
<td>23 May 1957</td>
<td>57</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>24 May 1957</td>
<td>233</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>30 April 1958</td>
<td>379</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>3 May 1957</td>
<td>435</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>23 April 1958</td>
<td>337</td>
<td></td>
</tr>
<tr>
<td>20</td>
<td>4 April 1958</td>
<td>380</td>
<td></td>
</tr>
<tr>
<td>20</td>
<td>29 April 1958</td>
<td>650</td>
<td></td>
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<tr>
<td>35</td>
<td>23 April 1958</td>
<td>337</td>
<td></td>
</tr>
<tr>
<td>35</td>
<td>29 April 1958</td>
<td>650</td>
<td></td>
</tr>
<tr>
<td>23</td>
<td>30 April 1958</td>
<td>379</td>
<td></td>
</tr>
</tbody>
</table>

Figure 14. Frequency of calls per day. These bar graphs are samples indicating the variation of calling frequency of several males. The top bar of each sample represents the duration of observation of the male. The solid bar below indicates the calling time. Note the difference in the number of calls in the three samples of male 7.
<table>
<thead>
<tr>
<th>Male</th>
<th>Number of Samples</th>
<th>Total Time of Samples</th>
<th>Range of Time Between Calls (in seconds)</th>
</tr>
</thead>
<tbody>
<tr>
<td>25</td>
<td>3</td>
<td>9 hrs. 6 min.</td>
<td>25 30 35 40 45 50 55 60</td>
</tr>
<tr>
<td>35</td>
<td>4</td>
<td>11 hrs. 31 min.</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>4</td>
<td>15 hrs. 43 min.</td>
<td></td>
</tr>
<tr>
<td>20</td>
<td>6</td>
<td>10 hrs. 51 min.</td>
<td></td>
</tr>
<tr>
<td>22</td>
<td>7</td>
<td>10 hrs. 4 min.</td>
<td></td>
</tr>
</tbody>
</table>

Figure 15. Time interval in seconds between calls of various males.
evidence of variation between the rate of calling in several males. In no male was a correlation noted between the average rate of calls during a given period and the time of day, or with the progressing season. A mated male called consistently no more or less than one that had not succeeded in attracting females. Nor did two males exchanging calls in close proximity to one another show a consistent increase or decrease in the number of calls. In all males studied, the first call, or first several calls, of the afternoon calling period was usually followed by a rather long pause (up to two minutes), longer than the usual interval between succeeding calls.

The four samples for male 7 were recorded in a six-day period. No females were with male 7. Yet the call rate varied from a call every 39 seconds to one every 58 seconds. Male 7 called three to five times per minute for a 20 minute period at mid-morning on May 20. Male 20 was sampled during March and April. In close proximity with other males, the rate of calling varied between 37 and 51 seconds. When it was not exchanging calls with other males a somewhat similar variation was manifest with intervals of 28 and 44 seconds.

The only samples recorded before March 13 were of male 22 on February 26 and 28. These calls were rendered at average intervals of 62 and 53 seconds respectively, and might be indicative of the call rate common at the beginning of the breeding season. Two weeks later, however, this same male exchanged calls with another bird for over an hour at an average rate of one call every 56 seconds. The first calls recorded in the study area in 1958 were from male 20 at midday on January 27 and were about 30 seconds apart. Males 25 and 27, even in May, averaged 46, 47, 55, and 60 seconds between calls.
Males 25 and 35 revealed less variation in the rate of calling than the other males mentioned. There was no overlap in the rate of calling of these two males, though male 25 called less frequently during a given period than male 35.

*T. major* was the least continuous caller of the three species of tinamous in the study area. Even during the early morning or evening a single individual rarely called more than eight or ten times. During the middle part of the day single calls were usually heard and were frequently answered by another individual. There were instances, however, when calling was more extensive.

In *C. soui* as many as 71 calls were recorded between 0520 and 0550 on one morning enroute from camp to the study area. The calls came from an estimated eight to twelve birds. In the evening of the same day I heard 64 calls between 1817 and 1828 while returning to camp. Though the majority of the calls were heard at these times, some calling, as mentioned earlier, occurred in the middle part of the day. One individual in the study area called 23 times between 0627 and 1617. When an individual of this species called in the early morning or evening the number of calls usually ranged between five and ten.

Weather Factors and Calling

I once thought that perhaps weather conditions might in some way be the cause of the sporadic day-to-day calling of male *C. boucardi*. It has been shown, however, that on no day were all males silent. And regardless of weather factors one male might call most of the day while an adjacent male could be heard for only a few minutes. Neither cloud cover nor temperature seemed to affect daily calling. Beebe (1925:197) has
stated that *C. variegatus* can occasionally be heard at noon on cloudy days. In British Honduras as much calling was recorded on cloudy days as on sunny ones. There was no correlation between cloud cover and length of calling periods. One of the heaviest calling periods, early morning, is more often cloudy than not, while the other heavy calling period, late afternoon, is usually sunny.

There is an average difference of approximately 15 degrees Fahrenheit between 0600 and midday temperatures from March through May. It might be suggested that increased temperatures inversely affect the vocalization of tinamous. But often the males call through the heat of the day, though frequently the calling ceases around 0900, long before the temperature below the canopy has risen to the midday level. Furthermore, the afternoon calling period commonly begins between 1500 and 1600, when the temperature has fallen a few degrees, at most, from the peak which it obtains between 1300 and 1430.

I have never heard a tinamou call during a rain. Precipitation will halt the calls of a male *C. boucardi*. I have been close to calling males on some occasions when it began to rain, and within two minutes the males ceased calling.
Figure 16. Daily pattern of calling of male 20.
Figure 17. Daily pattern of calling of male 22.
Figure 18. Daily pattern of calling of male 23.
Figure 19. Daily pattern of calling of male 25.
Figure 20. Daily pattern of calling of male 35.
The second phase of the breeding cycle, 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 of Boucard's Tinamou confines most of his activities to a certain area, which meets the requisites of territory (i.e., an area in which an individual shows aggressiveness toward other members of its own species). He advertises his presence in this area and defends it against other males. Territoriality in the species, however, is not as highly developed as in many other birds, especially 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 another tinamou, Notopropstra ornata (Pearson and Pearson, 1955), in which the female is the aggressive sex in territorial defense.

Two factors regarding calls facilitated the investigation of movements and territory of G. boucardi: the frequency of calls and the intra-specific variation in the calls of different males.

The impracticality of trapping and marking a bird as nervous and
wary as a tinamou became apparent when I captured and marked a Little Tinamou (*C. soui*). When released the bird flew out of the study area and was never seen again. Following a tinamou visually, as anyone who has attempted it knows, is all but impossible. Even if it were a simple matter, it is unlikely that the tinamou's movements would be normal if it were aware of the observer.

The method I employed was to anticipate the direction of the tinamou's movement by ascertaining its location from calls at the time, and then to place myself in front of the bird. Partially hidden from view, I was able to watch the tinamou approach and pass by. This method did not always succeed. The tinamou sometimes changed its course. Most of the time, however, the bird passed close enough to be viewed at least momentarily and to permit me to plot its movements accurately.

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 (Figures 27 to 30). Not all of this area can 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. Even the male's territory was much too large for adequate defense. For this reason, boundaries were poorly defined and the region of overlap was often extensive. One overlap area between two males is shown in Figure 28; the extent of overlap zones of all males in the study area is shown in Figure 21.

Some tinamous (for example, male 23, Figure 37) 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 movements to a smaller portion of their range (Figures
36, 39, and 42). 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 bull-dozer trail until April 2 (Figure 22). 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. Another example of change in the home range and territory is shown in Figure 23 for male 2 in 1957.

The size of home ranges and territories of tinamous has been reported for only five other species, but reveals a wide variation from the small 1192 square yards (one-quarter of one acre) of the Little Tinamou (C. squi andrej) in Venezuela (Schäfer, 1954:220) to the 49 acre area of Tinamou tao larense, also in Venezuela (Schäfer, loc. cit.).

The establishment and defense of a territory by the male C. boucardi served to provide an area for courtship, mating, and feeding. Courtship and mating appeared to be the primary functions of territory. It seems unlikely that food supply dictates the establishment of 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, which strongly suggests the improbability that food supply is a factor controlling the size of territory, is the fact that between the 6th and 23rd of May, 1957, the young of male 1 were seen only in an area slightly larger than one-half acre. During the same period a pair of immature C. soui foraged over the same ground.

It is interesting that the large hill in the center of the study
Figure 21. The extent of overlap zones in the home ranges of nine males in the study area. The only part of the area not traversed by any male at any time during the study is noted by the smaller, shaded area.
Figure 22. Fluctuation of the territory and home range of male 20.
Figure 23. Fluctuation of the territory and home range of male 2.
area just south and west of the bull-dozer trail was largely avoided by all males whose territories adjoined the hill, even though the food supply there was excellent (Figure 21).

Evidence indicates that the nest site does not determine the disposition of territory in this species. The single nest studied was located on the periphery of the male's range. 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 for courtship and foraging without interference from other males.

Population density probably plays an important role in determining 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. It would be interesting to learn the extent to which the home range or territory of any tinamou varies in different sections of its geographical range. *C. soui* in Venezuela has an unusually small home range (20 by 50 meters) according to Schäfer (1954:220). Observations of a pair of *C. soui* in the study area indicated a much larger range for this species in British Honduras.

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 tinamou attacks another the head and neck are outstretched
horizontally. No sounds are heard from either bird. The chase lasts from two to four seconds and covers a distance of five to ten yards.

Several factors are probably involved in determining the types of territorial behavior exhibited at any one time. Among these the encroachment by one male on another male's territory is probably the most important. It was impossible to determine the exact point at which a calling duel gave way to a 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 was he 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. This lends support to the hypothesis that it is not the area per se that is defended, but some object or factor within a given area.

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 often resulted in an attack by one individual or the other. 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 apart that two males tended to main-
tain varied with the locality of the encounter and the stage of the
breeding cycle.

The degree of aggressiveness varies with the stage of the sexual
cycle. This 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 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 state of some other instinct. 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 individual distance and with the location of the
encounter, i.e., whether 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 feed-
ing drive is strong will often tolerate the presence of another male
in its territory. In Notoprocta ornata the female, which is the ag-
gressive member in courtship and territorial defense, sometimes
tolerates another bird in its feeding area other than its mate (Pearson and Pearson, 1955:120). This may be an example of one drive (territorial defense), which is normally activated by the presence of another bird on its feeding area, 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 would not necessarily 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 and his territory, 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 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 territory except in overlap areas. The latter happened in the case of male 25. During several weeks 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. Now, however, male 25 had mated with several females and 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 territory of an adjoining male, it invariably did so when an adjoining male, after courting several females for a number of days, stopped calling. For example, 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. Male 22 and the females did not call a great deal during the day on March 20; except for several whining calls in the early morning and a calling period from 1710 to 1804, he was silent. His silence brought a reaction from three adjacent males (20, 23, and 25), which moved into his territory and remained the entire day (Figures 24 and 25). 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, calling extensively (Figure 26).

To test the reaction of a male to members of its own species, dummies were placed near a calling male. These dummies 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, but several conclusions can be reached. Although experiments were not undertaken to present the males with dummies in which the plumage had been altered with adornments or in coloration, the normal plumage of the mounted specimens did not affect the male's reaction. Marginal males, i.e., males that were decoyed to a dummy in a zone of overlap, usually did not approach as closely as
Figure 24. Points of record and range of four males between March 13 and 19. Only male 22 was mated during this period.
Figure 25. Reaction of adjacent males to the silence of a mated male, showing the movements of three males on March 20 when male 22 was silent most of the day. The males (20, 23, and 25) moved into the territory previously occupied by male 22.
Figure 26. Reaction of male 23 to the silence of an adjacent, mated male. Territory and points of record of male 25 (circles) are shown for the period of May 16 through May 23. Male 25 was mated with several females during this period. This male was silent on May 24, but was noted with the females at three points where he had not been previously observed. The reaction of male 23 (squares) to male 25's silence on May 24 is indicated by his movements (dotted line) into the territory of male 25.
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 made to move, 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 dummy without noticing it. When the mount 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 at the head and neck, and slid off on the other side, walking quickly out of sight. 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, and when the decoy was moved, ran behind a tree, where he continued to call.

The difference in male 22's reaction in the two situations can be explained on the basis that one encounter occurred in the center of the territory and the other near a zone of overlap. But why male 22 and male 35 reacted differently is not clear. It is true that male 22 had mated
with several females, and that male 35 was an unmated bird. Yet, aggressive behavior by males that were not mated had been observed.

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 most striking example was the behavior of male 22 discussed above. But similar unperceptiveness was evident in other males as well. 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 dummy, 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 antagonistic behavior toward other males again became manifest. The object of defense was 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, but there were probably others. 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.

Casal (1940:377) raised Rhyynchotus rufescens in captivity and noted that a male, which had successfully incubated, defended its chicks against an attack by an incubating male.

**Movements in Relation to Season**

It is not known how Boucard's 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**

During 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 male *C. boncardi* cover 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 43 to 48. Not uncommonly a male covered a five-to-ten-acre area in two to four hours in the morning, moving 400 to 600 yards. Sometimes the bird traversed 15 or more acres. Male 23 on 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 (Figure 46). Other males (20, 22, 24, 35) have walked distances almost equally as great.

The calls of adjacent males undoubtedly 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 observed males sitting on a log or knoll from which they called for a considerable length of time (up to 25 minutes), but Boucard's Tinamou does not have special calling sites, such as those described for other species of the genus Crypturellus.

Several species of tinamous reportedly call from particular sites day after day. Beebe (1925:199) could identify a certain male (Crypturellus variegatus) because it "called so regularly from exactly the same spot each evening and morning." C. cinnamomeus likewise calls from the same spot day after day according to Sutton (1951b:173-174). At Gallon Jug this tendency was noticed only in C. soui and, even in this species, was not constant over long periods of time.

Having acquired one or more females a male C. 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 at a glance (Figures 43 to 47) 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 if at all, 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 in the afternoon.

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 for several successive days to
a week or more. The evidence indicating lack of special roosting sites
and an absence of nocturnal activity for C. boucardi is the fact that
for any particular male the calling usually ceases on successive
evenings in different parts of the territory (except after pairing),
and the fact that in early morning a male is found where he ceased
calling the previous evening.
Figure 27. Home range of male 7, 1957.
Figure 28. Home ranges of three males (20, 22, and 24) in the study area, 1958. Note the extensive area of overlap between males 20 and 22. Overlap zones between other males with adjacent ranges were also extensive.
Figure 29. Home ranges of three males (21, 23, and 27) in the study area, 1958.
Figure 30. Home ranges of three males (25, 26, and 30) in the study area, 1958.
Figure 31. Points of record of male 1, 1957.
Figure 32. Points of record of male 2, 1957.
Figure 33. Points of record of male 7, 1957.
Figure 34. Points of record of male 20, 1958.
Figure 35. Points of record of male 21, 1958.
Figure 36. Points of record of male 22, 1958.
Figure 37. Points of record of male 23, 1958.
Figure 38. Points of record of male 24, 1958.
Figure 39. Points of record of male 25, 1958.
Figure 40. Points of record of male 26, 1958.
Figure 41. Points of record of male 27, 1958.
Figure 42. Points of record of male 35, 1958.
Figure 43. Sample movements of male 1, 1957.
Figure 44. Sample movements of male 20, 1958.
Figure 45. Sample movements of male 22, 1958.
Figure 46. Sample movements of male 23, 1958.
MOVEMENTS

MALE 25

Figure 47. Sample movements of male 25, 1958.
Figure 48. Longest recorded movements of various males in the study area, 1957 and 1958.
MATING PHASE OF THE BREEDING CYCLE

Mating follows the manifestations of calling and territoriality. These three "phases" of the breeding cycle became contemporaneous in the period just before nesting begins. The male moves about within a large home range advertising his readiness to mate with lengthy calling periods. A female will eventually be attracted to the call of a male and will approach him with whining notes. I never witnessed 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.

In 1957 the first female was discovered on March 21. She was not calling at the time. The first calling bird 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 (1958) indicate that almost the entire study area was traversed by calling males during the breeding season. A number of females were undoubtedly 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 mated to a particular male. Lastly, observations revealed that a male acquired one female at a time (Figure 49). For example, male 20 was mated with two females, but acquired them on different days; the first on March 27, the second 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 its 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) except that the role of the sexes in that species is reversed. During follow-feeding 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, real or imitated, a mated male 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
Figure 49. Mating periods of study-area males, 1958. Each horizontal bar represents one female. The length of the bar identifies the number of days that a female was observed in the company of a particular male. It was not possible to keep all males in the study area under close surveillance, so that in some cases the observed associations of males and females are undoubtedly incomplete. Males 20, 22, 25, and 35 were the most closely watched of all the males, and the period of mating of these males is probably complete, or nearly so.
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 more than 100 yards.

After a period of calling in the morning the male usually became silent. The females called much less, and it became 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 (Figure 50), and the females 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. In the case of male 22 the females remained in one area for most of the day. This bird always began calling for the females sometime between 1426 and 1618, except on one day when he waited until 1710. 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 continued. Only now did the male and females move in a compact group, and one or more females sometimes preceded the male. The group never moved very far,
Figure 50. Calling-up points of male 22 during mating. The map shows that a male tends to call up his mates from the same area on successive afternoons. The entire observed home range of male 22 is shown in outline. Within a small area of his home range are shown the points from which he called to the females on different afternoons.
however, seldom more than 100 yards.

Courtship usually 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, mincing steps and with his neck outstretched, sometimes below the horizontal of the body. The feathers of his lower back and the upper tail coverts were fluffed up. His 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. For example, male 25 ran along side of 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 transfer 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 copulation, probably because my observations of mated groups in the afternoon were so infrequent and of such short duration. This was the time when males called to the females after having been separated from them for most of the day. Since courtship displays were noted only in the afternoon, coition must have 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).

The male and the females spent the night together and then usually separated sometime during the morning while follow-feeding. The females acquired a knowledge of the call of their mate, and always joined him in the late afternoon in spite of the calls of other males in the vicinity. In one instance male 25 was closer to the females than was male 22 to which the females were mated. The females moved directly toward the call of male 22, bypassing male 25.

The length of time during which the sexes are together before the onset of incubation may be dependent upon the number of days required to pair with several females. Whether or not a male will nest with a single female is not known. 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 days during the two seasons of observation.

Females were occasionally found in the company of a male for one to four days (Figure 49). This indicates that a pair bond was lacking, or at least 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 (Figure 49). 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 were not seen in his company at any other time. Male 35 had females for only four days; then the females moved elsewhere.

After the period of mating, when both sexes are together for a
number of days, male and females "disappear"—that is, are neither seen nor heard. I assume that this development marks the beginning of the nesting phase. Soon, an adjoining male acquires females. Presumably, the females, after laying for one male, move on to another, 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 ten "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, after having been silent and probably nesting since March 21, reappeared on April 9. At this time an adjoining male (20) had been mated with two females for a week. The males moved about in the same general area on April 9 and 10. The two females accompanying male 20 on the morning of April 9 moved toward male 22 shortly after the latter bird began to call in the vicinity. No females, however, were recorded with either of the males in the afternoon of
April 9 and 10. On the following day and until April 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 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 at least a
male nesting twice in the same season remates with the same females.

Injury feigning is a behavior pattern found in terrestrial birds,
serving to draw attention away from either the eggs or the young. Injury
feigning in tinamous has been recorded in _C. 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 injury feigning in _C. boucardi_ several times, but it is
not a well-developed behavior pattern and is not an entirely convincing
performance. When injury feigning 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 the distraction display was observed. On
the first occasion the bird had been foraging and stood still when I
approached to within 25 feet. It then flew a yard or so about three or
four feet from the ground and came down against some vegetation with
wings fluttering. The process was immediately repeated. On each flight
the bird moved approximately a yard farther away. It performed in a like
manner three days later with four such displays. Injury feigning 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, and walked quickly away after coming to the ground. The sound of the beating wings was much like the flapping of a wounded bird on the ground.

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 (Figure 51). 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 bull-dozer trail. For seven days beginning with March 23, male 35 began calling 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 (Figure 51, A). The next phase began on April 3, when male 35 began moving with male 20 and the two females mated with the latter (Figure 51, B). On April 10 male 35 went over to
Figure 51. 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).
male 22 along with the females and remained with them until male 22 and the females dropped out of sight on April 18 (Figure 51, C). 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 (Figure 51, D). 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 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 have several interesting aspects. Wing spotting is characteristic of the plumage of immature and subadult males. The presence of this feature in male 35 indicates a probable age of one year or less. It also indicates that the breeding season is a long one, for 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. Whether or not any courtship display and coition took place between male 35 and the females mated with males 20 and 22 was never determined. No antagonistic behavior was observed between male 35 and the males that he accompanied.
**Sex Ratio**

The tertiary sex ratio of birds that exhibit polygamous behavior usually favors one sex or the other. 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; and the conclusions reached concerning the sex ratio may be an inaccurate interpretation of field data.

The unusual mating habits of Boucard's Tinamou imply an unbalanced tertiary sex ratio. My determination of the sex ratio in this species represents an approximation on the basis of daily observations within the 183-acre tract.

Using calls as a criterion is useful only if an area is thoroughly worked and the habits and calls of both sexes 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 were heard. The more subdued whining calls of the female remained undiscovered until six weeks of field work had elapsed. Recording the number of males by using their calls as an index to sex ratio and population density can likewise be misleading, unless a particular area is observed closely for a period of time; for individual males range over a wide area and may be silent on a given day though they call for hours on preceding and succeeding days. Furthermore, the breeding season is prolonged, and the number of calling males increases with gonadal development. Males were discovered in the study area from January 27 to March 3, and several males were discovered in the periphery of the study area as late as May. The question in this case, however, is whether these late-appearing birds
represented males approaching a breeding condition or simply males that had extended their ranges.

Random collecting is often an inaccurate index to sex ratios (Mayr, 1939:160-161). My own experience with C. boucardi bears this out. 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 collected.

The study area contained an estimated 50 percent, or more of the ranges of seven males (1958), while three 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 much less frequently heard 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 occasions in April. Other females may have been present. The ratio on the basis of the regular males and females in the study area appears to be 10 males to 6 females, or 1.7:1.0.

The sex ratio of other tinamous reportedly varies, but is probably not as uneven as the 4:1 (males to females) ratio mentioned by Beebe (1925:202) for C. variegatus and based upon the number of collected specimens. Koford reported a 2:1 sex ratio favoring the females in Tinamotia pentlandii, a polygynous species (Koford fide Leopold, 1959:}
Pearson and Pearson (1955:114) noted a normal 1:1 ratio in *Nothoprocta ornata*, a monogamous species. The sex ratio in *C. soui* likewise "approximates 1:1, deduced from very many individual identifications" (Schäfer, 1954:220). In Mexico Leopold (1959:115, 120) found an approximately even ratio of males and females in *Tinamus major* and *C. cinnamomeus*. Schäfer (1954:225) also discovered an even ratio in *Nothocercus bonapartei*, although this species is polygynous.

**Mating Patterns**

The mating type or pair bond formation in the Tinamidae varies considerably. Females in captivity mating successively with several males have been demonstrated in several species of tinamous, but it is well known that in captive birds the breeding behavior sometimes varies from the condition existing in nature. In the wild state evidence that a female mates with, and lays eggs for, more than one male during the breeding season is reported for three species: *C. boucardi*, *C. variegatus* (Beebe, 1925:201-202), and *Nothoprocta ornata* (Pearson and Pearson, 1955:125). The study of *C. boucardi* in British Honduras has shown that the male, too, may nest several times during the season, but that some males probably do not succeed in nesting even once. Beebe (loc. cit.) believed that a male *C. variegatus* nested three times in succession. His evidence shows that monogamy is the rule for this species. Monogamy also occurs in *C. noctivagus* (Schäfer, 1954:220) and *Nothoprocta ornata* (Pearson and Pearson, loc. cit.); while *C. boucardi*, *Nothocercus bonapartei* (Schäfer, 1954:231), *Eudromia elegans* (Pereyra, 1935:74), and *Tinamotis pentlandii* (Koford, *fide* Skutch, 1957:86) are polygynous. Both monogamy and polygyny possibly occur in *Tinamus tao* (Schäfer, 1954:221).
Present evidence indicates that the males are the sole caretakers of the eggs and young. Only in C. boucardi is it known that the male is the aggressive sex in courtship and territorial defense, a role usually occupied by the females in this family. Among tinamous in general the plumages of male and female are similar; or if not, the male is the duller and usually smaller sex. 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. The situation in C. boucardi is reversed, for the male is smaller and lacks the conspicuous barring found on the wings and rump of the female. Yet the male defends a territory, calls to attract the females, and initiates the courtship activity.

This summary of mating in tinamous includes evidence on only 8 of the 45 species and therefore emphasizes the lack of knowledge regarding the breeding behavior of most of the members in this family. Yet from the few data available, considerable variation is apparent in the breeding biology. This suggests that the Tinamidae were an early evolutionary offshoot with a long period of divergent trends in breeding behavior.

In ground nesting birds polygamous mating is often found in all the species of entire families and is most frequent among forest dwelling species. Efficiency of breeding behavior is at a maximum in polygamy where the separation of parental duties is complete with one sex assuming the active role in courtship and the other in incubation and care of the young. In the Phasianidae and some Tetraonidae the duties of the male involve only courtship, while the female attends the nest. In the Tinamidae the sexes are reversed with respect to parental duties.

C. boucardi achieves a maximum of efficiency in reproduction in two
ways. Polygyny permits a shortened egg-laying period. The nonadaptive-
ness of egg coloration is countered by a minimum period of exposure at
the time of egg-laying. In slightly more than two days, three females,
laying at the rate of one every 24 hours, can lay a clutch of nine eggs.
Polygyny followed by successive matings in which the females lay eggs for
a number of males assures the maximum utilization of breeding potential.
With these two mechanisms of breeding behavior C. 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 C. boucardi 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 attractions. It is difficult to imagine that selection might
have favored such highly-colored eggs, since they only serve to attract
predators in a habitat where egg destruction is high. Willis (MS), in
a study of ant-tanagers at Gallon Jug, British Honduras, recorded a
low percentage of nest successes, and suggested that the light colored
eggs and relatively conspicuous nest site are adaptations that attract
predators. In this way, if the bird happened to build a nest along a
predator "route" the eggs would be quickly destroyed, thus conserving
energy and time that might have been otherwise wasted.

Although this hypothesis perhaps has merit concerning ant-tanagers
and probably some other tropical bird species, it is not a logical
explanation to account for the conspicuousness of tinamou eggs. In the
first place Boucard's Tinamou does not build a nest of any sort that
might attract predators. The time of egg-laying is short, the entire clutch being completed within several days. The eggs are obviously in greater danger from a host of mammal species and many more snakes than are those of tree nesting birds. Observations of mammals, such as coatis and peccaries, and snakes indicate a random movement of these predators. Except for the coloration of the eggs many of the adaptations of this species seem to be to prevent detection. Evidently the selection for a protectively colored egg is not a necessary adaptation in *C. boucardi*.

I have made no mention of polyandry as a type of mating in tinamous, for I question the reality of this phenomenon as usually defined. An evaluation of the terminology regarding mating types in birds is pertinent here, since the nature of mating behavior in tinamous is varied. Generally speaking, the type of pairing in all birds falls into two main categories. The majority of birds are monogamous, possessing but one mate at a time. Some, however, manifest polygamous behavior, in which an individual of one sex is mated at the same time with two or more individuals of the opposite sex. Even rarer among birds than polygamy is the lack of any type of bond that holds the sexes together for any length of time beyond the consummatory act of copulation. This type of behavior is called promiscuity, which Pettingill (1956:252) defines as "copulation without relation."

Davis (1955:266) states that pairing is "the formation of a psychological bond between male and female" and that pairing, copulation, and even courtship may be considered mating. All authors distinguish pairing from the actual sex relation, or copulation. I define a pair bond as any positive social relation between male and female, during the breeding
season, that lasts longer than the time involved in copulation. Its function is to assure the success of coition and nesting and, in most cases, rearing of the young as well. In the case of polygamy, pairing involves several individuals of one sex forming a bond with the same individual of the opposite sex.

The two requirements of polygamous behavior are: 1) more than one mate; and 2) the possession of these mates at the same time. The distinction between polygamy and promiscuity is not always a clearly defined one. Polygamy exists in some gallinaceous birds and others which establish leks, communal courting grounds on which a number of males display to females and defend a small territory against adjacent males. Lack (1940:275), however, states that in such birds the term "promiscuity" should be applied, since no pairing bond is formed. In these birds the males maintain a territory only for copulation. Though the males copulate with several females, they do not assist in the selection of a nest site or in building the nest. Nor do they partake in incubation or caring for the young. Nevertheless, it seems that a pair bond is established if copulation with one male is repetitive, i.e., if a female returns by choice to the same male more than once. In polygamous birds this is more likely to occur in species in which the males do not perform their courtship behavior in a communal area with other males, such as occurs in some species of the family Pipridae. Here a male maintains a special courting area removed from other males, and which serves to attract the females.

Polygyny is a type of polygamous behavior in which the male has two or more females at the same time. It has been demonstrated in a number of families. Typically the male is larger with a more colorful plumage.
The female performs most, or all, of the duties involving the nest, eggs, and young. As already noted, polygyny is the type of pairing found in *G. boucardi*, although in this species the typical morphological and behavioral role of the sexes is reversed.

In polyandry the role of the sexes is reversed with respect to parental duties, with the male assuming them all. Tinamous have long been considered polyandrous. Practically no general treatment of birds, or of their breeding biology, fails to mention this unusual type of mating in tinamous. Polyandry was first described in birds by Seth-Smith (1904:104-106) on the basis of individuals of *Crypturellus tataupa* maintained in captivity, and also on specimens of *Budromia elegans* raised by Dulaurier. The criterion he set forth as indicative of polyandry is "the fact of the female pairing successively with two males." This definition has since served as a basis for the description of a number of so-called polyandrous birds, in which the normal role of the sexes is reversed regarding parental duties, and in which the female mates with more than one male during the breeding season. This definition, currently in use in ornithological literature, contradicts the standard one of polyandry in which the female possesses more than one mate at the same time (*Webster's New International Dictionary*, 1958). The latter definition appears to me to be the correct one. It has never been applied to any bird except *Monias benschi* of Madagascar. In species to which the term "polyandrous" is currently applied (including some of the Tinamidae) the female mates with a single male at any one time, and maintains that bond until the clutch has been laid. The female then seeks another male while her former mate undertakes parental duties alone.

The type of mating in numerous species is unknown, but our present
knowledge indicates that only in Monias benschi of Madagascar is there a possibility of true polyandry, i.e., the possession by a female of more than one mate at the same time. Rand (1936:365-367) observed on different occasions two to four males in company with a single female during the breeding season. A female accompanied by two males was "nearly ready to lay."

When defined as successive matings by a female during the breeding season, polyandry is difficult to distinguish from the breeding behavior of some birds that are not regarded as polyandrous. House Wrens, Catbirds, Bluebirds, and some Song Sparrows change mates for the second brood (Van Tyne and Berger, 1959:313), so that each sex has more than one mate during the breeding season. Yet the females of these passeriform species are not considered polyandrous. Among the tinamous both sexes of Crypturellus variegatus may likewise mate several times during the breeding season (Beebe, 1925:201-202). The mating in this species involves a single pair of birds at a time, but is generally regarded as polyandry. The distinction between the matings of the above mentioned songbirds and the tinamou is not the type of pairing with regard to the number of individuals participating but the duration of the pair bond in relation to the breeding cycle. In the House Wren and other songbirds the pair bond is maintained throughout the breeding cycle with both sexes participating in nesting duties. In the Variegated Tinamou (C. variegatus), on the other hand, the bond is evidently broken after the single-egg clutch has been laid, and only the male incubates.

In a truly polyandrous condition, if it actually exists, egg-laying might follow several patterns. The female might alternate the laying of eggs among several nests. Rarely, however, does this occur in nature.
I have witnessed two Prothonotary Warbler nests placed side by side into which a single female was alternately laying eggs. Alternate egg-laying leaves the eggs exposed for twice the normal length of time before the clutch is completed. In terrestrial birds this greatly increases the chances for predation. On this basis alone the adaptiveness of alternate egg-laying to survival in many habitats would be very low. Polyandry is more feasible in a species that lays a one-egg clutch, as in Monias benschi; or when a clutch of several eggs is completed for one nest at a time, as evidently occurs in the Red-legged Partridge, Alectoris rufa. This species is monogamous. Goodwin (1953), on the basis of his study of this species in a large aviary, believes that "it is probably normal for two clutches to be laid and for the male to incubate the first." If true polyandry existed in which the female laid one clutch at a time, what would be the benefit of mating with several males at the same time? What behavioral mechanism would determine what male incubates each clutch of eggs? The selection for a polyandrous condition in ground nesting birds, such as tinamous, does not appear to be an advantageous one.
NESTING PHASE

The Nest and Egg Laying

The final phase of the breeding cycle, nesting, 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 blocks were covered two and three times.

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. Since there is no nest construction the first female that is ready to lay is most likely the selector of the actual nest site. No mention of nest-site selection in the Tinamidae is recorded in the literature, except by Beebe for Cryp
turellus variegatus (1925:204), who mentions it only as a hypothesis, claiming that the male must be the sex that selects the nest.

The females ceased calling and "disappeared" before the male in all cases (males 1, 20, 22, 25), and I suspect that their silence indicated readiness to lay. However, a calling female with a shelled egg in the oviduct was found in the company of a male on April 11, 1957, and was collected. And two females in a 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 (Figure 52). The male was not heard between the 12th and the 16th, and his location remained unknown. The nest was found on April 16. Observations that followed were carried out from a blind situated 28 feet from the nest. A path was cleared to the blind so that it was possible to approach quietly, unseen by the incubating male.

The nest was discovered between two buttresses at the base of a Bull-hoof tree (Drypetes Brownii) opposite the creek bed. No nesting material had been utilized; no depression made. The four purplish-pink, highly glazed eggs were simply resting on a mat of leaves. After the first period of attentiveness, however, a distinct depression had been formed. A native boy at Gallon Jug collected a male beside a nest of broken eggs. The nest was on a hill and was also between the buttresses of a large tree. Similar nest sites were found in the case of T. major, one of which was in the study area. Natives in the Gallon Jug area, who had come across nests of the "partridges," as tinamous are called, described them as much like the nests referred to above.

The location of the nest of male 1 was on the periphery of his range (Figure 52). 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, 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
Figure 52. Home range and nest site of male 1. 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.
observed. Secondly, a careful search of the territory and former range of males that had ceased calling failed to locate nests or yield any indication of their presence. Lastly, male 20 appeared 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, 1145 hours, April 16 (nest discovered)
- Six eggs, 0545 hours, April 17
- Eight eggs, 1608 hours, April 17
- Nine eggs, 1623 hours, April 17 (laying of ninth egg)
- Ten eggs, 1735 hours, April 18 (laying of tenth egg)

In avian reproduction approximately 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 mm. to 49.0 mm. in length, and from 37.1 mm. to 42.5 mm. in width, averaging 46.4 mm. 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 species *T. major* raised in captivity laid eggs "during the first hours of afternoon" (Taibel, 1938:375). Whether or not this is true of *C. boucardi* can only be conjectured. The laying of two eggs (9 and 10) was observed from the blind. Both were laid in the late afternoon. By 1608 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 1617, sat at 1618 after pushing a few leaves aside, and five minutes later, having deposited an additional egg to the nest, walked quietly away without looking back. The final egg was laid at 1735 the following day. A female was observed near the blind at 1711, but did not approach the nest until 1729. She pushed several leaves aside, squatted for two minutes, and also walked away without looking at the nest.

On April 17 male 1 called in the vicinity of the nest only in the afternoon (1631 to 1748). His first period of attentiveness began at 1754 on the 17th and ended at 0802 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. Six minutes before the female approached the nest, male 1 advanced into sight. He did not move toward the nest but walked across the creek bed. When the female approached, he retraced his steps back toward the nest and remained standing about eight feet away while the clutch was completed. Male 1 called five times (1722 to 1733), his last recorded calls, either on or off the nest, until May 3, 15 days later.

Other males (2, 7, and 13) moved into the nesting area of male 1 and called frequently during 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 during the next two days. 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 after-
noon of April 21, the third day of incubation. This was the only after-
noon when observations of the nest were not maintained. Assuming that
male 1 recessed on this day, he was absent for varying periods 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 8
minutes to 46 hours 43 minutes (Figure 53), and averaging 30 hours 30
minutes. During 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 vucatanensis),
lying 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; i.e., the above stimuli, after
several days, evoked progressively weaker responses from the sitting
bird.

The greatest disturbance to the incubating male was caused by another
bird. An encounter with C. soui 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
Figure 53. Periods of attentiveness at the nest, 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.
Little Tinamou (*C. soui*) came within sight of the nest 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. The *C. soui* female moved to within three feet of the male. After the bird had watched the sitting male from this distance for several minutes, I imitated a *C. soui* call. The female immediately took several steps in the direction of the blind, but then turned and attacked the sitting male, which 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 moved off three feet and started to attack again, but this time she stopped just short of the male, turned, and walked away. The attack of the Little Tinamou on the nesting Boucard's Tinamou in response to an imitated call of its own species indicated an auditory basis of species recognition of greater importance than a visual one. This observation and the results with the dummy specimens stress the importance of vocalization in terrestrial nesting birds that seldom fly and that inhabit forested regions.

While the periods of attentiveness lasted for many hours, the inattentive periods were correspondingly short, ranging from 1 hour 19 minutes to 3 hours 56 minutes, except for the first inattentive period, which lasted 9 hours 36 minutes (Figure 53). Again, except for the one long inattentive period, all recesses occurred during the afternoon, beginning from 1323 to 1502.

Hunger is apparently 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, 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 during 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-tossing movements were accomplished (Figure 54). 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. Then, after walking several steps from the nest, he began tossing leaves once more.

The function served by leaf-tossing is nest 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 seldom 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
Figure 54. Leaf-tossing. Each point represents the number of leaf-tosses by male 1 at the beginning of each inattentive period.
the male completed the motions of the behavior pattern.

I interpret the behavior of leaf-tossing as a displacement activity, one that might have arisen as (1) the result of conflict between two unrelated drives, feeding and incubation, and (2) one that has resulted in a functional and adaptive effect, that of nest concealment. This behavior pattern does not seem to manifest one drive. Instead, aspects of the pattern are recognizable as parts of both the feeding drive and the incubation drive. The pecking at leaves and picking them up clearly resemble feeding activity, while the tossing of leaves represents the incubation drive and the motivation directed toward the nest and its contents. Leaf-tossing, as already mentioned, occurred most frequently during the earlier stages of incubation; it appeared to be correlated inversely with the duration of the attentive periods, which were much shorter during the first four days of incubation. Since the male left every day during the first part of the incubation period, the feeding drive at the time of recess was not as strongly activated as it was later in the period, and an increasing number of leaf-tosses in the early stages was a manifestation of the initially augmenting drive to incubate. The increasing incubation drive was soon apparent with the longer periods of attentiveness; but when the feeding drive finally superceded the incubation drive after 45 hours of sitting, the attention directed toward the eggs became less with each inattentive period as the male hastened to leave the nest and commence feeding. Thus the number of leaf-tosses during the latter part of this phase of the breeding cycle now was reduced with each inattentive period.

The evolution of nest concealment may very well have arisen as a displacement activity, first expressing itself as ambivalent behavior, and
then giving rise to a behavior pattern of adaptive significance. Concealing the eggs during periods of inattentiveness has been recorded in two other tinamous, Crypturellus tatuupa (Seth-Smith, 1904b:237) and Nothoprocta ornata (Pearson and Pearson, 1955:121). The manner in which the eggs were covered was not mentioned.

After his leaf-tossing behavior 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 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 in the afternoon of May 3, 15 days after the start of incubation. When the male left the nest on its 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 1619. The male had returned but remained six feet from the nest for 15 minutes before approaching. At the nest he moved several leaves and an egg shell aside 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 0624 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 around 0800, since a chick emerging from beneath the male at 0818 had a wet and matted-appearing plumage. Thus, the entire clutch hatched in 15 to 16 hours.

The male left the nest with the young at 1202, less than 20 hours after the first egg had hatched. He called the young off the nest with a whining sound, similar to that heard after the first egg hatched but considerably more forceful. The departure might have taken place earlier had it not been for two disturbances. After the male had moved several yards away from the nest at 0729, a foraging Leptotila that paused five feet from the chicks caused him to return. At 0953 the male again moved off the nest. At this time I moved out of the blind and toward the nest. As the male ran off, the young crouched facing the tree. Almost all the broken shells were still in the nest. After 30 minutes the male returned.

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 ten males (20, 22, 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 peripheral males (21, 24, 26, 27) were absent for varying periods
of time, but these might have simply transferred their activities to a
portion of the 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 noncalling period indicates that
a Boucard's Tinamou may nest several times during a single season. Male
22 probably did nest twice, since it mated twice and, after a period of
a week or more, began a prolonged period of silence in each case. Male
22 underwent a third calling period during the last half of May, but
the calls were less vigorous and not as frequent, and the movements more
restricted.

Except in the case of male 20 close observation of each male after
it again 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. Recogni-
tion 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 seems 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. Few observations are recorded in the literature on the
bond between chicks and adults following nest abandonment. Only in
Endromia elegans do the adults reportedly "move about with the chicks
until they are quite large" (Pereyra, 1935:74). In some cases the young
begin an independent existence very soon after leaving the nest. Seth-
Smith (1913:48; 1916:298) raised several species in captivity, noting
that in Nothura maculosa the parent bird showed no interest toward the
young, and that the young of *Rhynchotus rufescens* were independent after several days. Of the latter species Hudson (1920:222) also noted that they lead an independent life "when still very small." Shore-Baily (1925:19; 1929:252) likewise recorded that the young of two species (*Crypturellus cinereus* and *Nothoprocta perdicaria*) raised in a large aviary commenced a solitary existence early in life. In Mexico the young of *Tinamus major*, according to Leopold (1959:115), separated from the company of the adults by the time they are full grown, "for in winter the birds are found singly, never in coveys or organized flocks."

Though male 1 did not follow incubation with another calling period, as in the males mentioned previously (7, 20, 22), he remained apart from the young much of the time, although probably in the same general area. Male 1 and the chicks were not relocated until May 6, two days after he had led them away from the nest. At this time only two chicks were seen, which was the maximum number observed on any day following May 6. After May 14, only one chick was still present. From May 6 until May 23, the young were observed in an area less than one acre in size about 170 yards from the former nest (Figure 52). The parent probably moved about in a slightly 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 *C. bouardi* young 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 *C. soni* chicks were seen foraging here, several times associating with the immature *C. bouardi*. The area of the chicks' range was one frequently traversed by male 7 after May 6.
The two *boucardi* chicks 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, though more distinct on one. 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 *C. boucardi* 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 though poorly defined. The face was mottled, still largely buff, but with gray feathers appearing.

At twenty days the 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 half of the eye.
SUMMARY

During the springs of 1957 and 1958 a behavioral study of Boucard's Tinamou, Crypturellus boucardi, was undertaken at Gallon Jug, British Honduras, in a 183-acre study area in which compass lines were cut to facilitate movement of the observer and the plotting of the birds under consideration.

The habitat of C. boucardi in British Honduras varied from a low second-growth forest to tall stands of second-growth timber, indicating a wider tolerance of habitat than usually recorded for this species. A greater density of undergrowth may be a possible limiting factor in determining habitat selection locally.

In food habits, C. boucardi, like all tinamous, is primarily a vegetarian but was noted feeding upon various insects, mostly ants. Even toads and lizards may occasionally be preyed upon. Seventeen plant species representing 16 genera were identified among the seeds taken as food. No evidence was found that Boucard's Tinamou is gregarious. Observations of other species of tinamous in company with C. boucardi were rare enough to suggest that such associations occur only accidentally.

When reacting to alarm C. boucardi "freezes" its position, runs or moves stealthily away, or flies. The last response was rarely witnessed. Like all members of this family, Boucard's Tinamou is a poor flier, takes wing only when pursued or when suddenly alarmed. Its flight is short, loud, and direct. The strongly developed breast musculature
appears to be an adaptation for escape from predators.

Individual males were distinguishable by their calls. The individual peculiarities of the calls of any given male plus the large number of calls were the most important factors in facilitating the collection of data in this study. The breeding condition was first manifested when the males began to call in late January and February. The calling periods of males were variable and could not be correlated with mating, weather factors, or in many cases, with the calling of other males. Calling periods were most extensive in the early morning and late afternoon, but all study-area males called occasionally during the middle part of the day. The females called less frequently and their calls were easily distinguished from those of the males.

Boucard's Tinamou is territorial; under certain conditions it manifests 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 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. Evidence indicated that population density and the acquisition of females may have been factors involved in the fluctuation noted. 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.
Boucard's Tinamou is polygynous, the male mating with two to four females at the same time. 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 during this period. The male and the females that are mated with him roost together at night but usually separate sometime in the morning during 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. Polyandry is the type of mating commonly attributed to tinamous. The standard definition of this term does not agree with the one currently in use in ornithological literature. True polyandry—the possession by a female of more than one mate at the same time—does not exist among the Tinamidae that have been investigated.

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 partially concealed the eggs by tossing leaves upon them. The inattentive periods did not exceed four hours after the first day. 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.
APPENDIX A

PLANTS COLLECTED AT GALLON JUG

Gramineae
Axonopus voioptyllus
Cenchrus brownei
Leersia hexandra
Leptochloa virgata
Oplismenus hirtellus
Panicum bartletti

Cyperaceae
Scleria bracteata

Palmaceae
Bactris major
Bactris mexicana
Chamaedorea (concolor)*
Cryosophila argentea
Desmoncus (ferox)
Euterpe (oleracea)
Orbignya cohune
Roystonea oleracea
Sabal mavarum

Liliaceae
Dracaena americana

Zingiberaceae
Costus apicatus
Renealmia aromatica

Piperaceae
Piper nitidulifolium
Piper (pseudoaspirifolia)
Piper (psilorhachis)
Piper yucatanense

Ulmaceae
Ampelocera Hotllei
Trema floridana

* Parentheses indicate insufficient plant material for positive identification.
Moraceae
  Brosimum alicastrum
  Castilla elastica
  Cecropia peltata
  Ficus involuta
  Ficus Popenoi
  Ficus radula
  Pseudolmedia spuria
  Trophis racemosa

Polygonaceae
  Coccoloba schiedeana

Annonaceae
  Sapranthus microcarpus
  Xylopia frutescens

Lauraceae
  Nectandra globosa
  Phoebe helicterifolia

Capparidaceae
  Forchhammeria trifoliata

Rosaceae
  Hirtella (americana)

Leguminosae
  Acacia (acantlensis)
  Acacia gentlei
  Acacia glomerosa
  Caesalpinia zanmier
  Caesalpinia recordii
  Dialium guianense
  Gliricidia sepium
  Lonchocarpus (amarus)
  Lonchocarpus Castilloy
  Machaerium marginatum
  Ormosia coerctata
  Pithecolobium arboreum
  Pithecolobium belizense
  Pithecolobium erythrocarpum
  Pithecolobium tenellum
  Pterocarpus hayesii
  Schizolobium parahvum
  Vatairea lundelli

Vochysiaceae
  Vochysia hondurensis

Rutaceae
  Zanthoxylum sp.
Simaroubaceae
   Simaruba glauca

Burseraceae
   Bursera simaruba
   Protium copal

Meliaceae
   Cedrela mexicana
   Guarea guara
   Swietenia macrophylla
   Trichilia minutiflora

Euphorbiaceae
   Croton reflexifolius
   Drypetes Brownei
   Drypetes lateriflora

Anacardiaceae
   Astronium (graveolens)
   Metopium Brownei
   Mosquitoxylum jamaicense
   Spondias radilkoferi

Celastraceae
   Maytenus sp.

Sapindaceae
   Cupania belizensis
   Cupania guatemalensis
   Cupania (schippi)
   Matayba oppositifolia

Rhamnaceae
   Krugiodendron ferreum

Tiliaceae
   Belotia campbellii
   (Luchea semmannii)

Bombaceae
   Ceiba pentandra
   (Hampea trilobata)
   Ochroma limonensis

Ochnaceae
   Ouratea neckii

Guittiferae
   Calophyllum brasiliense

Violaceae
   Rinorea guatemalensis
Rhizophoraceae
Cassipourea podantha

Combretaceae
Hucida buceras
Terminalia amazonia

Myrtaceae
Eugenia yucatanensis
Pimenta officinalis
Paidium sp.

Melastomaceae
Clidemia deppeana
Miconia impetiolaris

Theophrastaceae
(Jacquinia aurantiaca)

Sapotaceae
Chrysophyllum mexicanum
Manilkara chicle
Pouteria campechiana
Pouteria durlandii
Pouteria mammosa
Pouteria meyeri
Sideroxylon gaumeri

Apocynaceae
Aspidosperma megalocarpon
Camareria belizensis
Plumerions ahouai
Stemmadenia Donnell-Smithii

Boraginaceae
(Cordia alba)

Verbenaceae
Vitex gaumeri

Bignoniaceae
Tabebuia pentaphylla
Tabebuia (chrysantha)

Rubiaceae
Bouvardia sp.
Guettarda (combsii)
Psychotria sp.
Psychotria (uliginosa)
Sickingia (salvadorensis)

Compositae
Eupatorium niettieri
APPENDIX B

NUMBER OF CALLS OF INDIVIDUAL MALES

<table>
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<th>Male Number</th>
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<th>Duration of Calling Period (in Minutes)</th>
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* Asterisk indicates bird was observed for the entire day.
NUMBER OF CALLS OF INDIVIDUAL MALES (con't)

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TAIBEL, A. M.

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WAGNER, H. O.

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EXAMINATION AND THESIS REPORT

Candidate: Douglas Allan Lancaster
Major Field: Zoology
Title of Thesis: Behavior of Boucard's Tinamou, Crypturellus boucardi, in the Breeding Season

Approved:

[Signatures]

EXAMINING COMMITTEE:

[Signatures]

Date of Examination:

23 July 1960