The Condor 97:415–426

REPRODUCTIVE BIOLOGY AND VOCALIZATIONS OF THE HORNED GUAN *OREOPHASIS DERBIANUS* IN MEXICO[1]

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Abstract. Reproductive biology and vocalizations of the Horned Guan (*Oreophasis derbianus*) were studied in the El Triunfo Biosphere Reserve in Chiapas, Mexico. The nest and eggs are described here for the first time. The Horned Guan apparently has a polygynous mating system. Males make at least five different kinds of vocalizations. Females produce seven or eight different types of calls, which are guttural compared with those of males. One female took 2.81 (±0.40) incubation recesses daily during 16 days of observation, and individual recesses averaged 32.9 (±13.1) min. Incubation sessions averaged 191 min ± 44.6. The incubation period was estimated to be 35–36.5 days. Likely predators of Horned Guan eggs are described. Suggestions for the conservation of this species and its habitat are presented.

Key words: Oreophasis derbianus; *vocalizations; mating system; Cracidae; cloud forest; Chiapas.*

Resumen. Se estudió la biología reproductiva y vocalizaciones del Pavón (*Oreophasis derbianus*) en la reserva de la biósfera El Triunfo, Chiapas. El nido y los huevos son descritos por primera vez. Las observaciones de campo sugieren que el sistema social de esta especie está basado en la poliginia. Los machos emiten cinco diferentes tipos de vocalizaciones y las hembras de siete a ocho, las cuales a diferencia de los machos, son todas guturales. Durante la incubación una hembra realizó 2.81 (±0.40) recesos diarios durante 16 días de observación y en promedio cada receso fue de 32.9 (±13.1) min. Las sesiones de incubación promediaron 191.13 ± 44.60 min. El período de incubación se estimó de 35–36.5 días. Se mencionan a los probables depredadores. Finalmente, se mencionan algunas estrategias para la conservación de la especie.

Palabras clave: Oreophasis derbianus; *vocalizaciones; sistema social; crácidos; bosque mesófilo de montaña; Chiapas.*

INTRODUCTION

The few previous studies of the Horned Guan (*Oreophasis derbianus*) focused on description, taxonomy, and distribution (Salvin and Godman 1902, Ridgway and Friedmann 1946, Friedmann et al. 1950, Vaurie 1968, Delacour and Amadon 1973, Blake 1977). Studies which treat more of its biology are those by Wagner (1953), Andrle (1967), Parker et al. (1976), Alvarez del Toro (1976) and González-García (1984, 1986, 1988a, 1988b, 1994). Data on reproduction and vocalizations are scarce and the nest and eggs of the Horned Guan have remained unknown. Because this species is in danger of extinction due to habitat destruction and hunting pressure (Collar et al. 1992), knowledge of its nest, eggs, and behavior is of critical importance.

This species occurs only in Guatemala and Mexico. In the latter, it is limited to the highlands of the Sierra Madre in Chiapas and possibly eastern Oaxaca (Estudillo 1979, Binford 1989, Collar et al. 1992). The habitat of this species, montane broadleaf or cloud forest, has a restricted distribution in Mexico (Rzedowski 1978, Leopold 1950, Pennington and Sarukhán 1968) and is disappearing at an increasing rate as these forests are felled for agriculture, animal husbandry, lumber and coffee plantations (Veblen 1976, Collar et al. 1992).

In this paper, I present observations on the breeding biology and vocalizations of the Horned Guan, and also discuss aspects of its conservation.

STUDY AREA AND METHODS

The El Triunfo Biosphere Reserve (Diario Oficial de la Federación, 13 March, 1990) consists of five core areas and a buffer zone which together

[1] Received 1 June 1994. Accepted 19 January 1995.

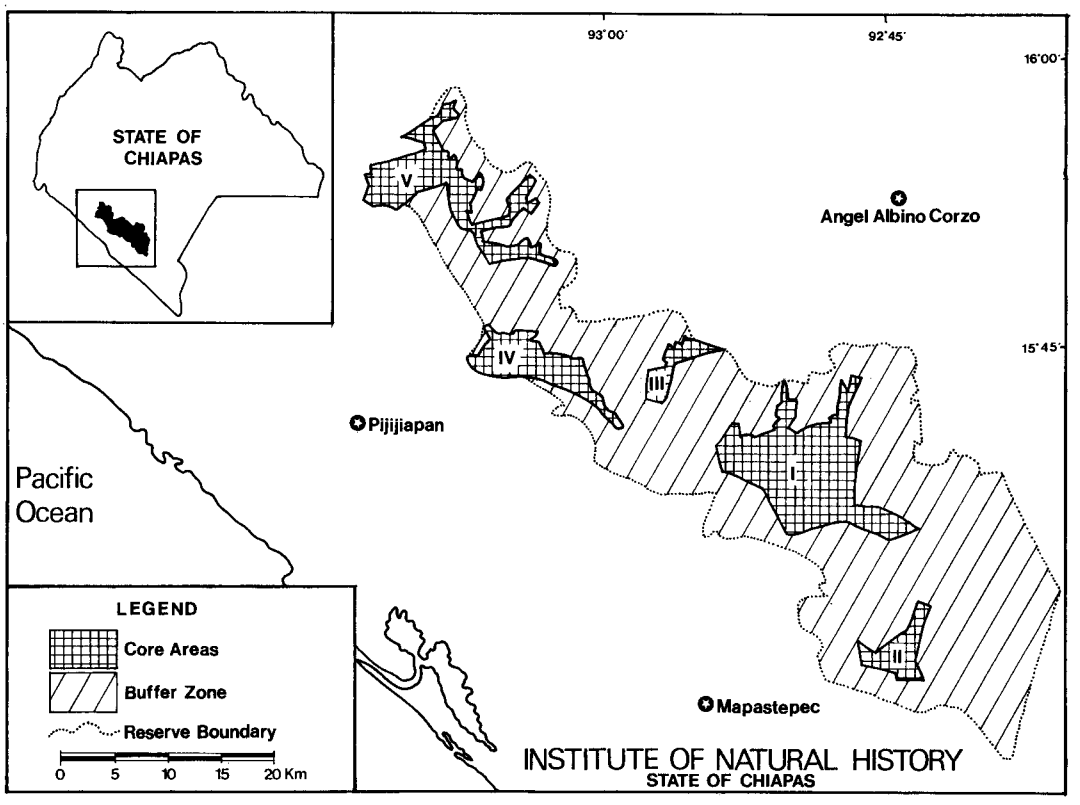

FIGURE 1. The El Triunfo Biosphere Reserve, Chiapas, Mexico. The study site is located in core area I.

have an area of 119,000 ha (Fig. 1). The Reserve includes parts of the municipalities of Acacoyagua, Angel Albino Corzo, La Concordia, Mapastepec, Villa Corzo, Pijijiapan and Siltepec. The study site is located in core area I, which has an area of 11,594 ha and elevations between 700 and 2,500 m. It contains five main vegetation types: tropical evergreen forest, pine-sweetgum forest, coniferous forest, and lower and upper cloud forests. The study area is in the upper cloud forest at an elevation of 1,850 to 2,100 m. This forest is dense, with broad-leaved evergreen trees 20 to 30 m in height and some individuals even taller.

The dominant tree species in the cloud forest are: *Matudaea trinervia, Quercus oocarpa, Hedyosmum mexicanum, Ocotea* spp., *Conostegia volcanalis, Amphitecna montana, Symplococarpon flavifolium, Calyptranthes* sp., *Glossostipula concinna, Eugenia malensis* and *Zunila cucullata* (Williams 1991, Ramírez and González-García, unpubl. data). The following tree species are also common: *Dendropanax pallidus, D. pulifolius, Drymis granadensis* var. *mexicana, Podocarpus matudae, Ulmus mexicanum, Ternstroemia lineata, Oreopanax sanderianus, O. capitatus, O. xalapensis, Nectandra* sp. *Ocotea chiapensis, O. matudai, O. uxpanapana, Phoebe siltepecana, P. bourgeviana, Clethra lanata, C. matudae, C. pachecoana.* Shrubs and herbs are represented by *Cavendishia* sp., *Centropogon* spp., *Miconia glaberrima, Senecio* sp., *Clusia mexicana, Rondeletia piramidalis, Malviscus arboreus, Gentlea tacanensis, Fuchsia speniculata, Ardisia* spp., and *Chamaedorea* spp. Ferns are abundant, including tree ferns (*Cyathea fulva*) which reach heights of up to 15 m. Bromeliads (e.g., *Tillandsia ponderosa, T. vicentina, Vriesea breedloveana* and orchids (e.g., *Epidendrum difforme, Maxilaria praestans, Odontoglossum cordatum*) are also abundant (González-García 1984, Ramírez and González-García, unpubl. data).

Data collected by the author in 1983 indicate that the maximum daily temperature averages 15°C and the minimum daily temperature averages 5°C, but temperatures down to −2°C have

been recorded. There is a relatively dry season from March to May, although rain can be abundant throughout the year. Average annual precipitation exceeds 3.3 m. Strong winds, originating in the Gulf of Mexico and Pacific Ocean, are common in autumn and winter. Mist is common throughout the year. Frost occurs from January to March.

This study was carried out over a period of eight months (February to May 1982 and February to May 1983) and supplemented in 1984. Daily observations ranged from 30 min to 11.5 hr. Total observation time during the study was 842 hr.

At the beginning of February 1982, I made a walking survey of core area I, taking advantage of established trails, to determine sites from which the Horned Guan could be observed and recorded. Once the first individuals were located, efforts were focused on following the birds to record their behavior continuously. Two blinds were built to observe a nest and a dust bath. Detailed observations were made of morphological and plumage characteristics in order to distinguish individuals. To determine the age of young individuals, particular attention was paid to the size and development of the horn for comparison with data published by Alvarez del Toro (1976) and González-García (1986, 1988a). Nests were located by following the incubating females.

The polygynous mating system was determined by using characteristics which differed among the individuals. One male was identified by the presence of an incomplete feather in the center of his tail. Females were distinguished from the male by their calls and from each other by the following characteristics: Female 1, discontinuous white band on the tail; Female 2, discontinuous white band on the tail (probably same individual as Female 1); Female 3, left side of the lower mandible without feathers; Female 4, no distinguishing marks.

Two female Horned Guans were observed at their nests during incubation, and time budgets on various activities were recorded. The constancy of incubation, i.e., the percentage of the day that a bird spends on the eggs, was calculated following Skutch (1976). One nest was monitored for 24 days, including watches of over 8 hr on each of 16 days; the other for 10 days (watches over 8 hr on four days). The first nest was watched on average from 07:30 (06:30 on four days) to 17:40 hr (after 18:00 hr on 10 days).

Percent times spent in each area and during each recess were compared with a Kruskal-Wallis test (Zar 1984). A simple linear regression was used to test for significant differences in total daily recess time during 16 complete days of observation (Sokal and Rohlf 1979, Zar 1984).

Birds were observed using 10 × 40 binoculars. Vocalizations were recorded with a Uher 4000 tape recorder and parabolic reflector (recordings are deposited in the author's sound library). A chronometer was used to measure the length and timing of vocalizations as well as the time spent by the females during incubation sessions and recesses.

RESULTS

These observations are based mainly on the behaviors of one male (referred to hereafter as "the male") and three or four females which were found in the same area in 1982, although data are included on some of the 23 additional individuals (12 solitary adult males, four "pairs," and three young individuals) observed in other trails of the reserve.

Sexual dimorphism. Without the aid of vocalizations and behavior, the sexes cannot be reliably separated under field conditions. However, in the hand the lengths of horn, wing, tail and tarsus of males average longer than those of females (Vaurie, 1968). On the majority of occasions when it was possible to compare adult males and females directly, the difference in horn size was slight. In only two pairs (out of the seven or eight observed) was this difference easily noted; in one pair the horn of one male was estimated to be approximately 6 cm long (well-developed adult), while that of the female was approximately 3–4 cm. This difference in horn size may also represent individual or age variation rather than sexual dimorphism.

Breeding season and mating system. The breeding season began in early February and continued until the beginning of June. This period was initiated by "mooing" of the males (described below under Vocalizations). According to my observations in 1982, the Horned Guan exhibits serial polygyny, the male pairing with different females in succession (see Table 1).

The male and the first female (first pair) were observed on three different days during the middle of February. The second pair was seen on four different days about the middle of March. It is important to note that this second pair fe-

TABLE 1. Observations on one male and four female Horned Guans during courtship in 1982 in the El Triunfo Biosphere Reserve, Chiapas, Mexico.

Date 1982	Females 1	2	3	4	Male I	Remarks
5 Feb.					X	Solitary male.
6 Feb.					X	Solitary male.
9 Feb.	X				X	First pair.
14 Feb.	X				X	First pair; copulation.
17 Feb.	X				X	First pair; copulation.
20 Feb.					X	Solitary male.
26 Feb.					X	Solitary male.
9 Mar.					X	Solitary male in dust bath.
10 Mar.					X	Solitary male.
11–12 Mar.					X	One Horned Guan (♂ or ♀) encountered each day by male.
14 Mar.		X			X	Second pair; probably Female 1 in courtship again.
17 Mar.		X			X	Second pair.
18 Mar.		X			X	Second pair.
20 Mar.		X			X	Second pair.
21 Mar.			X		X	Third pair.
23 Mar.					X	Solitary male.
25 Mar.			X		X	Third pair.
26 Mar.			X		X	Third pair.
27 Mar.			X		X	Third pair.
28 Mar.			X		X	Third pair.
29 Mar.			X		X	Third pair.
30 Mar.			X		X	Third pair; copulation.
31 Mar.			X		X	Third pair; double copulation.
1 Apr.					X	Solitary male.
2 Apr.			X		X	Third pair.
4 Apr.			X			Third solitary female.
5 Apr.				X	X	Fourth pair.
6 Apr.			X			Female 3 on the nest.
7 Apr.			X		X	Female 3 on the nest. Solitary male.
8 Apr.			X	X	X	Female 3 on the nest. Fourth pair; Female 4 in the dust bath.
9 Apr.			X	X		Two females in dust bath (3 and 4).
10 Apr.			X		X	Female 3 on the nest. Solitary male.
11–14 Apr.			X			Female 3 on the nest.
15 Apr.			X	X	X	Female 3 on the nest. Fourth pair.
16 Apr.			X			Female 3 on the nest.
17 Apr.			X		X	Female 3 on the nest. Solitary male.
18 Apr.			X			Female 3 on the nest.
19 Apr.			X			Female 3 on the nest.
20 Apr.			X	X	X	Female 3 on the nest. Fourth pair.
21 Apr.			X			Female 3 on the nest. Eggs collected and substituted.
22 Apr.			X			Female 3 on the nest.
23 Apr.			X			Female 3 on the nest.
24 Apr.			X			Female 3 on the nest.
25 Apr.			X			Female 3 on the nest.
26 Apr.			X			Female 3 on the nest.
27 Apr.–1 May			X			Female 3 on the nest.
2 May			X			Substituted eggs of female 3 missing.
10 May						Two chicks hatched in captivity.

TABLE 2. Behavioral contexts for different types of vocalizations of the Horned Guan during the breeding season.

Context	Female calls	Male calls
Aggressive	*au,au,au . . . . . raauuu*	
	áh-woo-ah	
	bill clacking	
Alarm	*gra, gra, gra, . . . gra*	bill clacking
		áh-woo-ah
Nesting	*gat, gat* (like a sneeze)	
Courting	*guurk, guurk, guurk*	*hum; hum,hummm; hum,hummm; hum,hummmmm.*
	guauuu, guauuu, guauuu	*áh-woo-ah*
	garr, garr, garr, garr	brief "teeth grinding"; *trrr* with Spanish
	guaak, guaak, guaak	sound r).
Mating	*gra, gra, gra, gra*	
	garr, garr, garr,	*áh-woo-ah*
	guurk, guurk, guurk	
	guauuu, guauuu, guauuu	
	gra, gra, gra . . . gra	
Dust bathing	*gat,gat*	
	guurk, guurk, guurk	*hum; hum,hummm; hum,hummm; hum,hummmmm.*
Territoriality	*au,au,au . . . . . raauuu*	*hum; hum,hummm; hum,hummm; hum,hummmmm.*
	áh-woo-ah	bill clacking
	bill clacking	*áh-woo-ah*
Comfort activities	*gat, gat*	*gat, gat; trrr*
Flying	*gra, gra, gra, gra*	*áh-woo-ah*
Courtship feeding	*guurrk, guurk, guurk*	*hum; hum,hummm; hum,hummm; hum,hummmmm.*
	guauuu, guauuu, guauuu	*áh-woo-ah*
		trrrr

male was probably the first female observed in February, yet it was courting with the same male almost one month later. This probably means either that it courted but did not mate in February, or that it mated but its first nesting was unsuccessful. The third pair was observed in courtship on nine almost full days, from 21 March until 2 April; they copulated once on 30 March and twice on 31 March, and its nest was found six days later and monitored during the following 24 days. The fourth female was observed in courtship with the male three days after he was last seen courting Female 3 (Table 1).

Territoriality. The male established its courtship territory along a stream and its tributary. This territory had an estimated length of 500–600 m. It included at least two small valleys, but the exact width could not be determined owing to the difficulty of following the male in the forest.

Defense of courtship territory by males was observed on two occasions (in the same site, see Table 1) on 11 and 12 March. The defending male threatened the intruder by beating its wings, spreading its tail and stretching its neck forward, but there was no physical contact. No vocalizations were made by either participant. It was not possible to determine the sex of the intruding bird, as it quickly retreated in silence on both occasions.

Territorial behavior was observed in more detail between two females on 9 April (Table 1). Female 3 (which was nesting) encountered Female 4 (which was courting with the male) at a dust bathing site. Female 3 took up a position similar to that used by alarmed males (neck stretched, head pointing downward, see Andrle 1967 and Delacour and Amadon 1973) and approached Female 4, several times uttering strong and deep guttural calls (Table 2). Female 4 opened its beak, but made no sound. Although the two were quite close, they made no physical contact. This encounter lasted 15 min. Then both females walked away, Female 3 to its nest and Female 4 started off in the same direction but was then lost.

Vocalizations. One of the most important differences between the sexes is their vocalizations (Table 2). Males make at least five different kinds of vocalizations. The first is a very deep, slow and soft "mooing," similar to that of the Great Curassow (*Crax rubra*) (Andrle 1967, Parker et

al. 1976), but still more similar to that of the Northern Helmeted Curassow (*Crax pauxi*) (Delacour and Amadon 1973; pers. observ.). This call is characterized by seven notes, a single brief *hum* followed by six paired *hums* (the second in each pair more prolonged, especially in the final pair) (Table 2). This call, which can be described as *hum*; *hum, hummm*; *hum, hummm*; *hum, hummmmm,* is repeated an average of 3.28 ± 0.66 times per min (n = 1,302, range: 2.0–4.75). Each call has an average duration of 7.18 sec (n = 1,850). The time between the end of one call and the start of the next varies depending on the bird's activity. During continuous calling, the average intercall length is 14.58 ± 14.95 sec (n = 103, range: 5–141). A male can emit this type of call for more than an hour.

Males make this call either standing or squatting crosswise on a branch. When in a squatting position the neck takes an "S" shape, the wings are held slightly drooped, and the tail is either held straight out or resting on the branch. In a standing position, the neck is partially stretched, the wings held tight over the sides, and the tail may either hang straight down or be held at "resting position" (45° down with respect to the horizontal body axis). During the call the throat and the upper part of the breast expand and contract with each note, expanding to the maximum in the last note. The throat does not attain the shape of a wattle as asserted by Wagner (1953), but it is intensely red, at least during the breeding season.

The second type of call made by the male is stronger and consists of mandible clacking. The sounds are somewhat similar to those made by the Keel-billed Toucan (*Ramphastos sulfuratus*). Generally, after clacking the beak, the male emits a third call which sounds like a hoarse áh-woo-ah. These calls are accompanied by clacking of the beak and apparent restlessness exhibited by walking among the branches. Then it suddenly stretches its neck forward and downward (in a motion similar to regurgitation), opens its bill widely, and emits the explosive, deep and hoarse third call. The male's *áh-woo-ah* is stronger than the similar call made by females.

The fourth call is a brief *trrr,* like that produced by grinding the teeth strongly, or running a pencil along the teeth of a comb, but deeper. The fifth is *gat gat,* resembling a human sneeze.

Females produce seven or eight different calls. All are guttural compared with those of males. Most are made in response to the calls of males, with others made during territorial defense (Table 2).

The first call can be interpreted as a *guurk, guurk, guurk, . . .* or *guauuu, guauuu, guauuu,* each note repeated 35 to 40 times per minute (n = 10). These vocalizations are produced when the female is approaching a courting male. The call has an echoing quality and may be an invitation to the male to copulate. The *áh-woo-ah* call is similar to the male's call, but shorter and deeper. Mandible-clacking is given in a similar context to that of the males, but is more guttural. There is another call similar to the grunt of a pig or the alarm call of the Neotropic Cormorant (*Phalacrocorax brasilianus*). A further call emitted while flying sounds like a hoarse *gra, gra, gra, gra* (Table 2).

One call used to defend territory sounds like *au, au, au, . . . raaaauuuu.* Calls are louder than those of males (Table 2).

Courting behavior. The first courting calls are given at the beginning of February and the last at the end of May. Courtship display is not elaborate. The encounter between the male and female usually occurs in fruiting trees. On meeting for the first time, the two rub necks, during which both are silent. The male then makes short flights from tree to tree, "mooing" continuously, sometimes for more than an hour. The female may perch for up to an hour without responding, sometimes eating fruits or preening. A little later it responds by flying toward the male. The male then moves to another tree and continues mooing. During some of its flights the male emits its *áh-woo-ah* call (Table 2).

The male and the female spend little time together. When the birds are near each other, the male perches higher than the female. As courtship progresses they spend more time together. They may be in the same tree, but apart from each other, or in adjacent trees. As part of the courtship the male descends to the ground and calls to the female to offer it green leaves or to lead it to the dust bathing site.

The male was observed courting three or four females and was observed from three to nine days with each female (Table 1). This was best documented with Females 3 and 4.

The data suggest that one female (number 1 and 2 in Table 1) participated in two courtships about one month apart, perhaps due to loss of her first clutch. This suggests that each female

may be able to start courtship again if the breeding season is not too far advanced.

Copulation. The six copulations observed took place on thick (larger than 8 cm diameter) horizontal branches of fruiting trees. The female invites the male to copulate by guttural calling (*gra, gra, gra*; *garr, garr, garr*; *guurk, guurk, guurk*), followed by an echo-like call (*guauuu, guauuu, guauuu*) (Table 2).

The first copulation observed was on 14 February 1982 at 17:00 hr and took place in a *Nectandra sinuata* tree. The second copulation was on 17 February 1982 at 11:00 hr in a *Dendropanax populifolius* tree. The third occurred on 30 March 1982 at 10:45 hr in a *Conostegia volcanalis* tree. The fourth and fifth copulations, involving the same pair, both took place on 31 March 1982 at 09:35 and 11:50 hr in a *Conostegia volcanalis* tree. An additional copulation was observed on 30 April 1983 (Rafael Solís, pers. comm.). Based on the five copulations I observed, the general pattern is as follows. The female responds to the call of the male, which is in the upper branches of the tree, by moving to branches beneath it and remaining perched there. The male approaches the female in two or three jumps, showing aggression in its movements and emitting an *áh-woo-ah* with each jump (except on the first copulation of 31 March). Once together, the male mounts the female and grasps the upper part of its neck with its bill, while opening its wings slightly to maintain balance. The female lifts its tail and the cloacas come together. Copulation lasts only a few seconds. The male dismounts and walks slowly among the branches, sometimes eating fruit, and then flies to another tree. The female remains on the same branch for some minutes and then flies after the male.

After copulation, the male continues its courtship calls and every few seconds scratches its perch with its feet while beating its wings and tail synchronously against its body and nearby plants. This display, which may be an invitation to nest, was observed for the first time when the male was on a diagonal tree trunk which was covered with bromeliads, orchids and leaf litter. The female stayed near the male and emitted *guurk, guurk, guurk* calls. On other occasions, the male could only be heard performing these movements but not seen.

Feeding behavior during courtship. As with other members of the Cracidae, the male Horned Guan feeds the female several times per day during courtship. The quick head movements characteristic of other Cracids (Flieg and Dooley 1972) were not observed during courtship feeding or under conditions of stress. The only movement observed was a slow turning of the head to one side when the male was feeding the female. This occurs on branches and sometimes on the ground. On branches, it takes one of three forms. (1) The male swallows fruit and moos to the female. The female approaches the male and eats the food which the latter regurgitates. (2) After eating many fruits or green leaves in a tree, the male flies toward the female and upon arriving makes the *áh-woo-ah* call and regurgitates (fruits are regurgitated one at a time). (3) When the two birds are together in the same fruit tree the male picks fruit from branches and passes them directly into the female's mouth.

The male also fed the female green leaves and grit several times in the dust bath. One time the male gave the female 8 to 10 fruits of *Nectandra sinuata* (30 × 20 mm each) and 20 to 25 fruits from either *Dendropanax populifolius* (8 × 9 mm) or *Conostegia vulcanicola* (8 × 7 mm).

Nest and eggs. The first nest was found on 6 April 1982 at an elevation of 2,070 m on the trail to Palo Gordo, northwest of the El Triunfo field station. It was 24.1 m above the ground in a *Matudaea trinervia* tree. The second nest was found on 21 April 1983 on the same trail and at the same elevation in a *Clethra lanata* tree at a height of 16.7 m.

As nesting sites, these two trees shared several characteristics. They were both tall (28 and 18 m respectively), relatively isolated and near a ravine with a slight slope and a flowing stream. Their few branches provided ideal sites for the accumulation of leaf litter and the establishment of bromeliads, orchids and vines.

Each nest consisted of a shallow depression, apparently produced by the weight of the bird, in a heap of leaves, bromeliads, orchids, and vines. Unlike other Cracids, no material foreign to the site, such as green leaves, small branches or sticks, were found in the nest. However, some dry bromeliad and orchid leaves, as well as feathers from the back and breast of the female, were found. The first nest measured 30 × 32 cm and the second 33 × 36 cm. Both were oval and small in relation to the size of the adults.

As do most Cracids, the Horned Guan produces a clutch of two white eggs with slightly

TABLE 3. Time spent (in minutes) and frequency of visits to each area (number and percentage) by a Horned Guan female during recesses from incubation (see text).

	Number of recesses = 46											
	First				Second				Third			
Foraging areas	Mean (min)	SD	*n*	% (times)	Mean (min)	SD	*n*	% (times)	Mean (min)	SD	*n*	% (times)
A (NE)	33.0	12.3	8	50.0	36.8	13.7	14	87.5	34.0	16.4	7	50.0
B (SE)	39.3	10.9	6	37.5	26.0	—	1	6.25	32.5	3.54	2	14.28
C (SW)	27.0	2.83	2	12.5	13.0	—	1	6.25	21.2	4.60	5	35.71

rough texture and subelliptical shape. The first two eggs measured 84.6 mm × 58.9 mm and 83.7 mm × 57.7 mm. The eggs of the second clutch measured 85.0 mm × 57.0 mm and 82.0 mm × 60.0 mm.

Incubation period. The incubation period in the first nest, occupied by female 3, was estimated as 35–36.5 days. Between 31 March and the discovery of the nest on 6 April, the female was either absent or by herself in the area. It was observed only on 2 and 4 April (Table 1). On the morning of 4 April, it took a dust bath and stayed for 4:45 hr in or around the dust bath site, where it ate green leaves and fruits; after that it walked away and disappeared in the trees where the nest was later found. This period is too long to be an incubation recess and thus she was not incubating that morning. The bird was followed to her nest on 6 April, when it appeared to be incubating. It incubated its own eggs until 21 April, on which date they were replaced with Crested Guan eggs (see beyond). The Horned Guan eggs hatched in captivity on 10 May. If it laid the first egg on the afternoon of 4 April, the maximum duration of the incubation period would be 36.5 days. If it started on 6 April, the minimum duration of the incubation period is 35 days.

Incubation sessions and recesses. In 24 days, I observed 38 incubation sessions and 60 recesses on the first nest. In 16 days of continuous observation, total daily incubation time averaged 191.13 ± 44.60 min per day (range 123–299; n = 38; total minutes 7,263), whereas total daily recesses averaged only 93.76 ± 30.6 min per day (range 30–146; n = 16; total minutes 1,483). The calculated constancy of incubation was 84.9%.

The female left the nest an average of 2.81 ± 0.40 times per day (n = 16) for an average of 32.9 ± 13.1 min per recess (range 13–74; n = 46). The first recess occurred in the morning between 07:50 and 11:39 hr and averaged 32.8 ± 11.26 min (range 15–53; n = 19). These excursions were made exclusively to feed. The second recess was between 11:22 and 15:05 hr, averaged 34.16 ± 13.1 min (range 13–74; n = 24), and was divided between feeding and dust bathing. The last recess, when it took place, was between 14:37 and 18:09 hr, averaged 28.1 ± 12.54 min (range 11–64; n = 17) and was spent feeding.

There is no difference in daily recess time as incubation advances ($r = -0.46$, $n = 16$, $P > 0.05$, $Y = 118.71 - 2.19X$, $t = -0.14$, $P = 0.050$). During 22 days of observation, this female bathed 16 times, including two days in which it bathed twice in the same day. The male did not approach the nest during incubation.

The directions of flight and areas visited by the female are indicated by directional abbreviations NE, SE and SW in Table 3. The female had a significantly greater preference for area NE (Kruskal-Wallis; H = 9.0; $P < 0.025$; df = 2; n = 46), which she visited primarily during the midday excursions.

Behavior at the nest. There was a single, 14 cm diameter horizontal branch, without any leaves, on which the female landed prior to moving onto the nest. On three occasions the female added dry orchid and bromeliad leaves in the nest during incubation.

During incubation the female behaved as follows. (1) Gular fluttering was done with the beak slightly open and the neck retracted or stretched. This movement was observed five times toward the end of the incubation period, once lasting up to one hour. (2) When there were strange noises, the female assumed an alert position with its neck completely stretched out and looked in the direction of the noise, cocking its head in order to do so. (3) It stretched its neck and opened its beak wide in what looked like a yawn (n = 4). (4) It preened, generally beginning with its wings and following with its breast, back, rump and tail; to preen its belly, scratch its face, or stretch,

the female always stood up or briefly left the nest. (5) On three occasions, it sunned with one or both wings stretched out. (6) Infrequently, it caught small flying insects.

The behavior of the female on the second nest, found on 21 April 1983, was similar to that of the female observed on the first nest. I observed the second female for nine days; the nest was observed continuously for over 8 hr on each of three days. The female left the nest 3.23 ± 0.6 (n = 3) times each day. Recesses averaged 36.47 ± 24.67 min (range 16–132; n = 21). An average of 199.1 ± 72.9 min (range 100–360; n = 11) was spent on the nest between recesses. The calculated constancy of incubation was 84.5%.

Captive preservation. The nests and eggs described above are the first reported for the Horned Guan. Because of the critical situation for this species with respect to survival and conservation, it was decided to substitute the eggs of both clutches with unfertilized eggs of Crested Guan (*Penelope purpurascens*). This allowed the continued observation of the incubating females and the beginning of a captive breeding program. The eggs in the second nest were switched during an absence of the female. Observations on this nest were terminated at this point.

In both cases, the eggs were transported to Mexico City and incubated by a female Wild Turkey (*Meleagris gallopavo*). The eggs from the first nest hatched on 10 May 1982 and those of the second on 24 May 1983. The latter weighed 94.1 and 96.7 g, respectively. This part of the program was successful; the four birds are still in captivity. From this stock, at least 15–20 young have been born.

The eggs that were substituted for those of the Horned Guan on 21 April 1982 disappeared 11 days later, either during a recess or possibly when the female was driven from the nest. When observations of this nest began on 2 May, the female was absent. Later it returned, but instead of settling on the nest, it began to scratch and disturb it with its feet. It repeatedly entered and left the nest, giving the impression that it was reluctant to leave it. Then the female moved to a branch above the nest, where it remained for an hour. I climbed to the nest and found it completely modified and without any trace of egg remains. Below the tree I found a small fragment of eggshell, suggesting that the eggs were taken from the nest. The fate of the eggs which were placed in the second nest is unknown.

Predators. Little is known about the predators of the Horned Guan. Wagner (1953) suggested that the Tayra (*Eira barbara*) is the main predator. In the El Triunfo Reserve, other mammals which may prey upon adults, young and eggs of the Horned Guan include Kinkajou (*Potos flavus*), Coati (*Nasua narica*), Ring-tail (*Bassariscus sumichrasti*), Gray Fox (*Urocyon cinereoargenteus*), Jaguar (*Panthera onca*), Cougar (*Puma concolor*), Margay (*Leopardus wiedii*), Ocelot (*Leopardus pardalis*) and Jaguarundi (*Herpailurus jagouaroundi*). My observations suggest that the Emerald Toucanet (*Aulacorhynchus prasinus*) and the Fulvous Owl (*Strix fulvescens*) may be predators of the eggs and the chicks, respectively. The former was observed taking a pair of large white eggs from a nest of a Horned Guan. On one occasion (16 March 1982, 14:20 hr) my field assistant and I heard a strong flapping sound in the forest subcanopy, and we could only see a Horned Guan's tail as it flew by. At the same time, feathers were scattered in the air. We observed an Emerald Toucanet at the nest, where it picked up an egg and flew away with it. The other egg was evidently broken in the nest because two toucans returned and each took a piece of shell. I believe the Horned Guan was chased from its nest. Finally, we also observed a Fulvous Owl trying to catch a young Highland Guan (*Penelopina nigra*).

DISCUSSION

Salvin (1860) asserted that in the Horned Guan "the female differs in no way except in being rather smaller in size and in having the crest on the head rather shorter and more tapering." Vaurie (1968) stated that the horns of males average 5 mm longer. In the field, this difference is usually not discernable; vocalizations and behavior are the most reliable means of separating the sexes.

Based on data from Horned Guans reared in captivity (Alvarez del Toro 1976, González-García 1986, 1988a), I estimate that the female attending the first nest was adult (two or three years old, horn size 6 cm approximately) and the female of the second nest was 12 to 14 months old (horn size 3–4 cm). I have seen females with small horns being courted by males with long horns but have never seen males with short horns courting. This suggests that females reach sexual maturity earlier than males and probably begin reproducing in their first year, as Wagner (1953) suggested.

Cracids are thought to be monogamous, with the exceptions of the Highland Guan (Delacour and Amadon 1973) and Yellow-knobbed Curassow (*Crax daubentoni*) (Schaefer 1953; Strahl and Silva 1989; Buchholz 1989, 1991). Based on my observations, the Horned Guan is also polygynous.

Sick (1970) suggested that males of the genus *Crax* may have a high natural mortality rate, which results in an excess of females and occasional polygyny. Delacour and Amadon (1973) suggested that this tendency toward polygyny results in the males being more successfully hunted because their frequent vocalizations make them easy to locate. These theories may also apply to the Horned Guan.

For the Horned Guan, two conditions may influence the establishment of a polygynous mating system: the lack of participation by the male in incubation and care of the young; and the reliance on fruits and green leaves that are concentrated, abundant and easily accessible. The first condition gives the male time to court other females, provided the females are continuously or asynchronously receptive. When food resources are concentrated, abundant and easily accessible, males may be able to control female access to them, allowing polygyny (Emlen and Oring 1977, Beehler 1983, Wheelwright 1983). In my study site, some fruit species eaten by the Horned Guan are known to be spatially clumped (*Conostegia volcanalis, Ocotea uxpanapana, Symplococarpon flavifolium*) (Ramírez and González-García, unpubl. data).

Courtship displays are among the simplest within the Cracidae, lacking the elaborateness of some species of the genera *Crax* and *Penelope*. The male's scratching movements interspersed with synchronous beating of the wings and tail may function as an invitation to the female to a potential nest site. Courtship feeding, with the male feeding the female, is common in the Horned Guan, and probably in the majority of Cracid males, as I have also observed it in Highland Guans and other Cracids in captivity.

"Quick nervous" movements of the head, characteristic of 26 species in nine genera of Cracids (Flieg and Dooley 1972), may be associated with courtship feeding (Stokes and Williams 1971) or with defense against flies and parasitic insects (Sick 1970, Flieg and Dooley 1972). Quick head movements were not observed in the Horned Guan either during courtship or under conditions of stress. However, the male did engage in a slow ritualized turning of the head to one side (by about 45°) when feeding the female with fruits and leaf fragments. This movement, may well be homologous to the "head flicking" of other Cracids (Flieg and Dooley 1972), and if so, the courtship theory is supported.

Contrary to Wagner (1953) and unconfirmed reports in Andrle (1967), this species nests high in trees (24.1 and 16.7 m) and may be the only Cracid to do so. The nest is small, relative to the size of the bird, and rudimentary.

The incubation period for the Horned Guan estimated at 35–36.5 days, is most comparable to that of some species of the genus *Crax*, which have periods of 30 to 36 days (Delacour and Amadon 1973, Skutch 1976).

The vocalizations emitted by the male have been reported by Andrle (1967) and Parker et al. (1976) but without indication of what function they might serve. The behavioral contexts of different calls and bill clacking are given in Table 2. The fourth vocalization (*trrr*) which had not been reported before, is emitted, during courtship and comfort activities, but only rarely. In addition, Wagner (1953) reported another call made by the male which sounds like "*tschia, tschia, tschia.*" This may be homologous to the *gat, gat* of the female.

CONSERVATION

The Horned Guan has been classified as rare by various researchers (Sclater and Salvin 1859; Salvin and Godman 1902; Wagner 1953; Andrle 1967, 1969; Alvarez del Toro 1976, 1980; Parker et al. 1976; Delacour 1977; Leopold 1977; Collar et al. 1992). At most, only 23 individuals were seen during my study. The world population has diminished as a consequence of habitat destruction, immoderate hunting and, recently, by the capture of live birds. As such, the species should be considered endangered.

Considering its low reproductive capacity (two eggs per year) the species cannot endure the pressures of hunting and habitat destruction without a significant decrease in population size and perhaps extinction. Effective and practical measures, such as habitat protection and the development of a captive breeding program, must be taken to protect the species. Captive breeding should be coordinated between interested institutions and individuals and be initiated either by obtaining more birds and eggs from the wild

or by using the birds currently in captivity (15–20 produced by the four from El Triunfo, as well as a few in Mexican zoos and other private collections). This captive population can play a significant conservation role as a genetic reservoir from which new populations can be founded (Magin et al. 1994).

Conservation of the cloud forest in the El Triunfo Biosphere Reserve is necessary for several reasons. This is a habitat of very limited distribution in Mexico (Pennington and Sarukhán 1968, Rzedowski 1978). Full protection would guarantee the survival of species that are currently threatened with extinction in Mexico, such as Horned Guan, Highland Guan, Maroon-chested Ground-Dove (*Claravis mondetoura*), Resplendent Quetzal (*Pharomachrus mocinno*), Azure-rumped Tanager (*Tangara cabanisi*), Jaguar, Cougar, Tapir (*Tapirus bairdii*) and various amphibians and reptiles, and would help minimize population declines for many other species (Terborgh 1974, Smith 1976, Myers 1979, Collar et al. 1992, Olney et al. 1994). Humans in general and Mexicans in particular are obligated to protect this biological legacy and to conduct programs that assure that populations of these species will not just exist, but prosper (Ramos 1981). More research in the El Triunfo Biosphere Reserve is needed to understand the biology of the flora and fauna. Research could also identify possible scientific, economic and tourist uses that are compatible with the ecosystem, but this work must be accomplished before this valuable ecosystem disappears.

ACKNOWLEDGMENTS

I am particularly grateful to the former Instituto Nacional de Investigaciones sobre Recursos Bióticos (INIREB). I thank Mario A. Ramos and Jesús Estudillo, who provided valuable advice on my research. My field work would have been impossible without the unfailing assistance of the Solís-Gálvez family, especially Rafael Solís Gálvez and Ismael Gálvez Gálvez. Ismael Calzada helped collect plants. I thank them for their assistance and encouragement. I also thank the Instituto de Historia Natural of the state of Chiapas and the Secretaría de Desarrollo Urbano y Ecología which allowed me to work and live in the reserve. Finca Prusia helped with logistic support on several trips to the reserve. Sonia Gallina, Alberto González, Victor Rico-Gray, Salvador Mandujano, Carlos Martínez del Río, Bianca Delfosse, Patricia Escalante, Héctor Gómez de Silva, Robert T. Andrle, L. C. Binford and two anonymous reviewers provided helpful comments on earlier versions of this manuscript. This research was supported by Consejo Nacional de Ciencia y Tecnología (Conacyt), Brehm Funds, and Wildlife Conservation International.

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