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Behavior, Reproduction, and Development in Little Tinamou (*Crypturellus soui*)

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ABSTRACT.—Two captive pairs of Little Tinamou (*Crypturellus soui*) were studied to describe reproduction, development, and associated behaviors of this extremely cryptic forest dwelling species. Pairs were strongly territorial. Precopulatory courtship behaviors were performed by the female. Male tinamous showed strong nest attendance during incubation and sat without leaving the nest from day 14 until the eggs hatched. Nest abandonment and false abandonment occurred due to environmental stress, flushing by humans, eggs being laid in a poor location, and if clutch size was too large. Renewed reproductive efforts began shortly following loss

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of a previous clutch, with calling activity and inter-clutch duration being a minimum of 3 and 5 days, respectively. *Received 12 May 2015. Accepted 9 July 2015.*

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Forty-six species of tinamous (Family Tinamidae) are divided into two subfamilies: Nothurinae (*Rhynchotus*, *Nothoprocta*, *Nothura*, *Taoniscus*, *Eudromia,* and *Tinamotis*) and Tinaminae (*Tinamus* and *Crypturellus*; Bertelli and Porzecanski 2004). The Nothurinae are found in South America and tend to occur in more open and xeric habitats. In contrast, the Tinaminae are found principally within mesic tropical forests in Mexico, Central America, and South America (Cabot 1992; Davies 2002; DMB, pers. obs.).

Despite their abundance, the Tinaminae are more poorly known than are the Nothurinae (cf. Cabot 1992, Davies 2002). This paucity of information is primarily due to the secretive habits of these cryptic forest species (Brennan 2004, Brooks et al. 2004). In the field, most tinamous are detected by sound with few are detected by sight (DMB, unpubl. data).

The Little Tinamou (*Crypturellus soui*) is widespread, with a disjunct distribution from southern Mexico through the Amazon basin to northern Bolivia, and with an allopatric population in eastern coastal Brazil (NatureServe 2007). Despite the species broad distribution and abundance, there are many gaps in what we know about the natural history of *C. soui*, (cf. Cabot 1992, Davies 2002).

Most of what is known of *C. soui* is anecdotal in nature (e.g., Skutch 1963, Brooks et al. 2004, Schelsky 2004), and only available in local treatises and field guides (e.g., Wetmore 1965, Haverschmidt 1968, ffrench 1976), and compilations (e.g., Cabot 1992, Davies 2002, Baur et al. 2014). To date, the publication of Skutch (1963) is the only article dedicated solely to *C. soui*, involving anecdotal natural history, limited observations of two different incubating males, and a description of the chicks.

Habituated individuals held in captive or semi-captive settings permit fine-scale observations of reproduction and behavior (e.g., Brooks 2010), behavior and taxonomy (e.g., Brooks 2014), and social interactions (e.g., Hobson et al. 2014) not possible in natural settings (e.g., Holbrook and Smith 2000), This is especially true of courtship and reproduction, which is represented by large information gaps for many species of tinamou (Cabot 1992, Davies 2002).

Herein I describe novel observations of the behavior, reproduction and development for *C. soui* that have not been possible to observe in natural settings. Using experimental manipulation, direct observations, and recordings of captive *C. soui* I addressed the following objectives: 1) determine whether *C. soui* is territorial, 2) determine whether females perform a courtship display, 3) describe nesting parameters and conditions of nest abandonment, 4) describe parental protection of chicks, and 5) describe chick development.

METHODS

Observations were made of two separate captive pairs (1 pair = 1 male and 1 female) housed outdoors in the subtropical climate of Houston, Harris County, Texas. Both pairs were obtained on loan from the Dallas World Aquarium (DWA; Dallas County, Texas). These birds were descended from stock imported from Chiriqui Province, Panama and designated *C. soui modestus*. Pair 1 (male = M1, female = F1) was obtained on 20 June 2010 at approximately one year of age. Pair 2 male (M2) was obtained on 29 September 2011 and the female (F2) on 15 October 2011, both at approximately six months of age. Although they were banded for identification, the sexes are dimorphic and easily distinguishable with the female more reddish and slightly larger than the brownish-grey males (Cabot 1992).

The aviary housing Pair 1 was 3.0 m wide × 4.0 m long × 3.0–2.5 m high with a sloped roof. The aviary housing Pair 2 was 2.7 m wide × 10 m long × 2.7–2.0 m high with a sloped roof. Additional details of housing and feeding are described in Brooks (2010). With the exception of brief manipulation experiments, the birds were housed in their respective aviaries from their arrival dates until all were returned to DWA on 24 September 2012.

Pair 1 and 2 were observed for approximately 300 and 140 total hrs, respectively, during daytime and crepuscular (dawn and dusk) periods. Territoriality experiments involved switching birds into an aviary that was the territory for one bird, and novel for the other. Each manipulation trial was only performed once. Courtship was described from recordings made using a BlackBerry Torch 9810 telephone camera (BlackBerry Ltd.,

Waterloo, Ontario, Canada). Nests were measured using a metric ruler, and a nest was considered abandoned if the male did not return to his nest after an event. Chick observations were made daily, and a metric ruler was used for measuring flight distance. Data for parental behavior and chick development were obtained anecdotally with chicks that M1 hatched ($n = 2$), as well as chicks artificially hatched ($n = 5$) and successfully reared ($n = 2$). The female of Pair 2 laid fertile eggs in a shallow depression nest of leaf mulch, but M2 made no attempts to incubate and the eggs never hatched. A Brinsea© incubator (Mini Advance EX model; Brinsea Products Inc., Titusville, FL, USA) and brooder (EcoGlow 20 model; Brinsea Products Inc., Titusville, FL, USA) were used to artificially incubate eggs and brood chicks that males did not incubate and raise. Artificially reared chicks were fed commercial Purina© gamebird starter-grower mash (Nestlé Purina Petcare Co., Wilkes-Barre, PA, USA). Sex was determined by extracting DNA from breast feathers of chicks, with sex testing performed by Avian Biotech (Avian Genetics Inc., Tallahassee, FL, USA).

RESULTS

Territoriality.—Both sexes were territorial to novel mates. M1 aggressively attacked F2 when she was moved to his aviary. F2 aggressively attacked M1 when he was moved to her aviary, pecking his head, back, and wings. M2 hid after experiencing aggression from F1 when he was moved to her aviary.

Female Courtship Display.—Precopulatory courtship behaviors were performed by the female (F1). This behavior involved walking slowly in circles (0.3–0.5 m in diameter), pointing the tail up, and keeping the anterior portion of the body stationary while the posterior portion slowly pendulated from side to side (http://hmns.org/tinamou_display). The female presented herself to the male by squatting on the ground, and copulation consisted of the male mounting the reclining female with the entire sequence lasting 3–4 sec ($n = 2$).

Nesting Behavior.—Nest sites were used repeatedly, comprising a slight depression in the ground and measuring 10–11 cm in diameter. The nests ($n = 4$) were lined with leaf mulch. Male tinamous showed strong nest attendance during incubation, and sat continuously on the clutch without interlude from day 14 until hatching ($n = 3$ clutches incubated through hatching). Nest abandonment and false abandonment (described below) occurred in cases of environmental extremes (e.g., floods and high temperatures), flushing by humans, or the egg laid in an unprotected location. A rainstorm resulted in M1 leaving a nest when the ground flooded during morning, but returned in the afternoon after the inundation subsided ($n = 1$). When flushed from his nest, M1 often returned ($n = 7$), but abandoned on one occasion. One clutch laid in a poor location with no cover was abandoned by M1 after the first day of incubation.

One clutch had three eggs. Although M1 attempted to incubate the clutch of three, one of the eggs was not completely covered during incubation, and the clutch was abandoned as temperatures peaked at >38 °C for five consecutive days. The three eggs were candled to determine viability. The first egg, which was slightly larger than other two, was fertile and still viable. The embryo in the second egg appeared to have died after four days of development, and the status of the third egg was not determined. The tinamous often showed signs of reproductive effort soon after termination of a clutch. F1 initiated calling activity as soon as three days after a chick hatched ($n = 2$). The duration from one clutch terminating to the first egg laid of the next clutch was as short as five days (mean = 9.8, range = 5–15, $n = 9$ inter-clutch durations).

Parental Defense Behavior.—Parental defense behavior was apparent when the chicks were in potentially harmful situations. F1 mildly attacked 3–4-day old chicks with a brief charge and soft peck ($n = 2$ occurrences observed; http://hmns.org/tinamou_aggression). M1 thwarted her attack by standing between F1 and the chick, and squatting down with ruffled feathers in a defense posture ($n = 2$ observations). When a 4-day old chick was briefly removed from the enclosure, both parents ruffled all feathers, with open wings and chest down while charging the door of the enclosure separating them from the chick ($n = 1$).

Chick Development.—Observations of chick development are presented in Table 1. For some observations, data from the artificially hatched and parent-reared chick was pooled.

DISCUSSION

Territoriality.—Introductions of a new individual resulted in significant aggression from the resident individual in its territory, illustrating that pairs maintain actively defended territories.

TABLE 1. Development in Little Tinamou (*Crypturellus soui*) chicks.

Age[1]	Observation	*n*
Hatching	Under ideal conditions chicks hatched between 60 and 90 min from the time of the first egg pip until totally out of the egg	5 hatchings
1	Chicks began actively pecking the ground	3 chicks
2	M1 pointed out many small mealworms DMB offered, which chick then consumed	2 chicks
5	Wing feathers began erupting	2 chicks
7	Chicks produced mono-syllabic attenuated whistles, similar to an extended high-pitched "peep"	10 observations
14	Chicks still had a downy ventrum	2 chicks
15	Chicks able to fly ~25 cm above ground for a distance of ~2–3 m when frightened	2 chicks
16	Chicks able to fly ~0.5 m straight up from a resting position	2 chicks
16	Outer breast feathers present	2 chicks
19	Chicks able to fly ~2 m straight up when alarmed	2 chicks
19	Flank feathers began coming in	2 chicks
25	Chicks capable of full flight	2 chicks
25	Chicks almost fully feathered except for the mid-sagittal feather tract just beginning to come in on head and a bare mid-sagittal line along ventrum. The ventral surface and tail are a rich rufous color similar to an adult female; however, both were determined to be males (gender determined with DNA tests, see Methods).	2 chicks
27	Feathers began to develop along the mid-sagittal feather tract of the ventrum	2 chicks
40	Ventrum completely buff-feathered similar to an adult female, even though they were males	2 chicks
45	Chicks produced a series of 8–10 slightly ascending serial notes when they were stressed and pacing	2 chicks
6 months	Began producing contact calls	2 observations
1 year	F2 began to lay eggs	1 female

[1] Days old unless otherwise indicated.

Repeated observations of tinamous calling from the same sites over seasons and years in the Peruvian Amazon (DMB, unpubl. data) suggests strong site fidelity to a defended territory (Baur et al. 2014). Male tinamous in Venezuela have fairly small home ranges (20 × 50 m, Schäfer 1954), which are probably more easily defended than larger areas.

Female Courtship Display.—Although female *C. soui* initiated courtship displays towards males, this is not always the case in birds where the male is the primary caretaker of offspring. For example, male Ostriches (*Struthio camelus*) and Rheas (*Rhea americana*) initiate courtship despite also incubating and rearing the chicks (Davies 2002). In contrast, female *Turnix* buttonquail like female *C. soui* initiate courtship and have no role in incubating and rearing chicks (Debus 1996). Considering that male ratites are larger than females (Davies 2002), and the converse holds for *Turnix* buttonquail (Debus 1996) and *C. soui*, it is possible that the constraint predicting which sex initiates courtship is body size, with the larger sex initiating courtship.

Nesting Behavior.—Single events of an egg being laid in a poor location, and flushing by a human (DMB) were the two primary causes of nest abandonment. Skutch (1963) found that a male *C. soui* did not leave the nest when it was touched by him, and Brennan (2004) indicated male Greater Tinamou (*Tinamus major*) do not abandon the nest if handled.

Additionally, the only clutch of three eggs in this study was abandoned due to either too many eggs for the male to cover, high ambient temperature, or a combination of these two factors. Although clutches of two eggs are typical, three egg clutches have been reported but are not the norm (Cabot 1992). The observation of the male having difficulty covering all three eggs suggests a proximate cause for the average clutch size being constrained to two eggs.

Parental Behavior.—The observation of a female mildly attacking 3–4 day old chicks (n = 2) in this study reinforces the suggestion that the male raises the chicks alone without help from the female (Cabot 1992). An apparently novel aggressive display was observed involving the

parents ruffling all feathers, wings open and chest down while charging the threatening stimulus.

Chick Development.—A number of observations on chick development regarding vocalizations, plumage, and flight are presented that are previously unreported. Chicks were active from day 1, and during the first week they learned how to feed, their wing feathers began erupting, and they produced various vocalizations. By day 25, the chicks were fully capable of flight bursts and were nearly fully feathered. Young males initially had plumage coloration more similar to the brightly colored females. Contact calls were produced by six months of age, and egg laying began at one year of age.

Conclusion.—Our understanding of the life history details for many forest bird species are represented by large gaps because they cannot be observed with any detail due to their shy and cryptic nature. This problem was addressed for *C. soui* by studying captive birds. While detailed research is sorely needed for other cryptic forest species, studies of captive individuals can be valuable in the interim to link fine-scale behavior to broader species ecology.

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