

Short Communications

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Description of Male Vocalizations of the Turquoise Cotinga (*Cotinga ridgwayi*)

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ABSTRACT.—We describe the first recordings of a male vocalization of the Turquoise Cotinga (*Cotinga ridgwayi*) along with reviewing the sound production in the genus *Cotinga*. Vocalizations were heard in the Coto Brus region of southwestern Costa Rica from late 2003 until early 2005. The vocalization described is different from previous calls known for the species and genus. The vocalization is a pure tone, produced at a high frequency. These vocalizations were observed in a variety of contexts, although more often during alarm or advertisement situations. Received 18 September 2006. Accepted 14 December 2006.

The genus *Cotinga* is a monophyletic lineage comprising seven species (Snow 1982, Prum et al. 2000). It is part of one of the least-studied neotropical bird families in which little is known about the ecology and behavior of the majority of species. The *Cotinga* are considered almost voiceless (Snow et al. 2004) but adult males produce mechanical rattling noises during flight (Snow 1982). Until recently, vocalizations had been described only for the Spangled Cotinga (*Cotinga cayana*) (Chaves 2001). Its vocalization is described as a soft, medium-pitched “*hoo*” repeated 2–3 times at irregular intervals, produced while displaying. These displays did not include mechanical sounds emitted during male flights. The other known vocalizations have been produced by females of the genus (Snow et al. 2004). Skutch (1969) observed a female Turquoise Cotinga (*Cotinga ridgwayi*) emitting a clear, monosyllabic “*ic, ic, ic*” alarm-call after its nest was attacked by a tou-

canet and while searching for the fledgling. The only known male vocalization of the Turquoise Cotinga was heard by F. G. Stiles (pers. comm.) while manipulating a mist-netted bird. The bird emitted a surprisingly loud, mule-like raucous “*caaaoo*.” Here we describe another vocalization uttered by males of the Turquoise Cotinga while adding information on the context of the call production of a Vulnerable and endemic species (Birdlife International 2000). We also provide a general discussion on the sound production of this little known but widespread genus (*Cotinga*).

METHODS

Our observations were from late November 2003 until mid-January 2005. Most observations were made opportunistically while conducting bird-watching tours and every time a cotinga was observed (or heard), we compiled the data. Most of our observations were recorded at Las Cruces Biological Station (LCBS) in southwestern Costa Rica (8° 47' N, 82° 57' W), but included observations from Las Alturas Biological Station (8° 57' N, 82° 50' W) and other nearby sites. The area surrounding LCBS is a botanical garden that includes a mixture of secondary growth with some emerging canopy trees (Borgella et al. 2001). Turquoise Cotingas varied widely in occurrence during the observation period, ranging from zero individuals for up to 2 months to 2–4 individuals on a daily basis for as long as 30 days. These visits were consistent with high fruit abundance of *Ficus* spp., *Erythroxylum* sp., and species of wild avocados (Lauraceae). Turquoise Cotingas frequently perch on dead exposed branches of trees above canopy level (Stiles and Skutch 1989). Fourteen of 17 observed vocalizations were emitted while cotingas perched high above the ground although, on three occasions, the birds were observed vocalizing below the canopy while feeding as low as 4 m above the ground.

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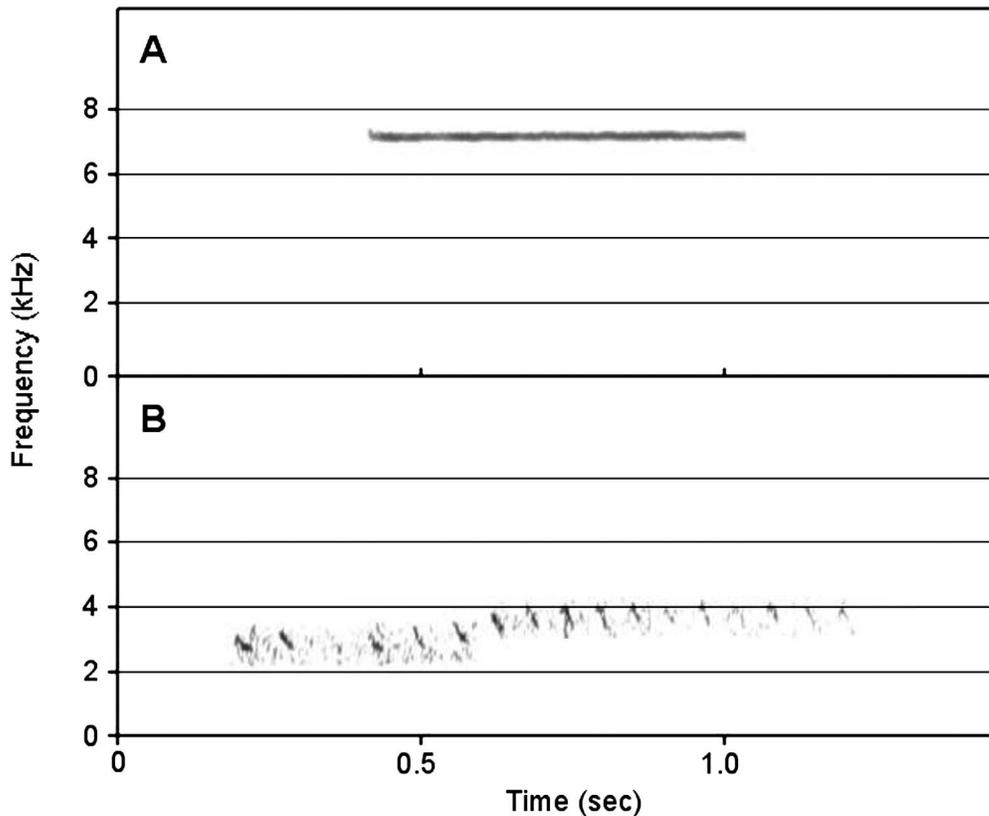


FIG. 1. Vocalization (A) and mechanical sound (B) (produced during flight) of adult male Turquoise Cotingas, Estación Biológica Las Cruces, Puntarenas, Costa Rica.

We were able to make recordings along with our observations of the Turquoise Cotingas. Vocalizations were recorded with a Marantz PMD-222 tape recorder and a Sennheizer MKH-70 microphone. Tapes were deposited at Laboratorio de Bioacústica, Universidad de Costa Rica. Sounds were digitized with Raven 1.2.1 (Charif et al. 2004) at 44100 Hz (16 bit). We used this software to measure and analyze the sonograms following these settings: transform length = 512 points, frequency resolution = 86.1 Hz, time resolution = 1.18 msec, and window = hamming.

OBSERVATIONS

We observed males uttering vocalizations during 15 occasions at LCBS and two occasions at Las Alturas. Some individuals were observed opening their bills wide while emitting the vocalization. The vocalization is a pure tone, resembling a metallic high pitch,

with almost no frequency modulation (Fig. 1A). Two songs were recorded on 21 July 2004, although we were not able to detect whether they were emitted by the same male or by two individuals. Both vocalizations are similar and the variables measured confirm their resemblance: high frequency = 7.33 and 7.30 kHz, respectively; low frequency = 7.06 and 7.02 kHz; frequency range = 0.27 and 0.28 kHz; song length = 0.59 and 0.62 sec; maximum frequency = 7.17 and 7.14 kHz; maximum power = 97 and 82.7 decibels. The different distances from the birds to the microphone (4 and 25 m) largely explains the difference in maximum power. The first vocalization occurred when a male flew directly towards another, which was perched and feeding. When the approaching male was close to the perched male, it vocalized and proceeded to move within the same tree. The second vocalization was recorded while one male was

feeding, but we were not able to see the individual at the moment it vocalized.

We also heard but did not record this same type of vocalization on 15 occasions. During two observations, adult males vocalized after interacting with individuals of the same or other species. One occurred when an immature male flew towards an adult perched male, landing within 2 m. The adult vocalized once as soon as the immature male landed. Another non-recorded vocalization was produced when a male, perched at the top of a ~25 m tall tree, was approached by two flying Brown-hooded Parrots (*Pionopsitta haematotis*), which landed within a meter. The cotinga vocalized when the parrots landed, but afterwards the bird remained in the tree for at least 10 min without vocalizing. Other observations occurred—seemingly—without interactions with other birds. On two consecutive occasions, we heard an individual emit a series of three vocalizations every 20–30 sec. Another individual produced one vocalization three times about every 2 min. Males were observed emitting the same vocalization in three other occasions, but no apparent interactions were noticed with other individuals from the same or other species. Several interactions (e.g., harassments, fly-overs) were observed between males, females, and both genders without vocalizations being emitted. All vocalizations observed were produced by adult males; we observed females or young males on eight occasions but they did not vocalize.

The other sounds known for male Turquoise Cotingas are mechanical “rattles,” produced during flight (Fig. 1B). Each time a male flies, it produces a stuttering or tittering sound, even when making short sallies (>1 m) (CS, pers. obs.). These sounds are a series of short pulses, which start at low frequencies and increase in frequency and bandwidth until leveling off at the fourth or fifth pulse. The length of each pulse is variable and the number of pulses depends on the length of the distance traveled by the bird. We speculate these sounds are produced by the modified 9th and 10th primaries. These feathers are thinner than the rest of the primaries, and slightly bent at the tip, with P 9 measuring about half the width of P 10 (P 9 = 2.3 mm, P 10 = 4.45 mm, measured at 10 mm from the tip, $n = 1$, UCR # 1481). The mechanics of sound pro-

duction with wing feathers have not been studied for Turquoise Cotinga or any other species in the genus to our knowledge.

DISCUSSION

Our observations indicate that male Turquoise Cotinga not only produce vocal sounds, but they also produce them fairly regularly. The vocalization was only seen produced by adult males, despite several months of observations, and not by females or young males. The predominance of male vocalization in the Cotingidae is a common phenomenon, a trait often considered to be sexually selected (Andersson 1994). This is consistent with the high extent of sexual dimorphism present in most members of the family, including the genus *Cotinga*. Kroodsma (2004) recently suggested that some members of the Cotingidae can learn their songs. Young Three-wattled Bellbirds (*Procnias tricarunculatus*) take 6–7 years to perfect their dialects and it can be expected that other members in the family can take several years to perform their adult vocalizations. This might explain why no young male Turquoise Cotingas were observed vocalizing.

The vocalization seems to serve as an advertisement or as an alarm, as it was produced during encounters with individuals approaching the calling male. Other vocalizations heard occurred during events where we did not record interactions between members of the same or other species. It is possible the vocalization occurs in another context rather than advertisement-alarm. Our observations span more than a year suggesting cotingas do not emit calls only during the breeding season as Turquoise Cotingas are known to breed during March (Stiles and Skutch 1989).

The function of mechanical sounds produced with the wings remains untested but probably is related to sexual displays and mate attraction (Snow 1982). We suggest this because: (1) modified feathers are only found in males of this highly dimorphic genus, (2) modifications of feathers are known to occur in species that produce mechanical sounds (which are mainly used during courtship) (Stettenheim 1976, Prum 1998), and (3) a sister clade, Pipridae (Prum and Lanyon 1989) also exhibits sexual dimorphism, and males produce mechanical sounds with modified

feathers during courtship (Snow 2004). Our observations indicate that male Turquoise Cotingas produce at least three different sounds used in different contexts. The available information shows the importance of vocalizations in a genus that until recently was considered almost voiceless (Snow et al. 2004). More detailed observations should show whether Spangled and Turquoise cotingas are the only species of *Cotinga* that vocalize.

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Nesting Behavior and Nestling Care of the Pavonine Quetzal (*Pharomachrus pavoninus*)

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ABSTRACT.—I describe the nesting behavior of the Pavonine Quetzal (*Pharomachrus pavoninus*) at Los Amigos in the southeastern Peruvian Amazon. I found a single nest cavity 4.2 m above ground in a dead snag in *terra firme* forest. The cavity contained

two pale blue eggs each with a few small brown-buff speckles, of which one hatched. I observed incubation between 18 February and 2 March 2004. Based on an average of 0.7 observation hrs/day, the male appeared to incubate during most of the day from at least 0950 hrs until sunset (near 1745 hrs) when the pair would switch before nightfall. The female appeared to incubate at night and during the early morning. Fifty-six percent of 32 food deliveries observed between 6 and 26 March were tree frogs and 44% were fruits. The

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nestling fledged on 26 March, 20 days after the first observed food provisioning. The nestling period is estimated to be 21–24 days. The plumage development of the nestling, vocalizations, and other observations are discussed and compared with the Resplendent Quetzal (*Pharomachrus mocinno*). Received 2 October 2006. Accepted 28 December 2006.

The Pavonine Quetzal (*Pharomachrus pavoninus*) is widespread in the Amazon, but little is known about its natural history. One probable nest of this species was reported 9 m above ground in a large tree during February in Brazil (Oriki and Willis 1983, in Johnsgard 2000). There is an unreferenced mention in Collar (2001) of a full grown nestling seen in a hollow 5 m above ground in a dead tree on 19 July 2000 along the Río Susucari, Loreto, Peru (Josep del Hoyo, pers. comm.). The diets of other trogons are known to include a mixture of animals and fruit, but *Pharomachrus* quetzals are thought to be almost entirely frugivorous (Remsen et al. 1993, Collar 2001), specializing on Lauraceous fruits and serving as important seed dispersers (Avila et al. 1996). Remsen et al. (1993) examined nine Pavonine Quetzal stomachs and found eight to contain only fruit and one to contain fruit and arthropods. The Resplendent Quetzal (*P. mocinno*) is known to feed its nestlings fruit, arthropods, and vertebrates (Skutch 1944, Wheelwright 1983, Avila et al. 1996).

Here I report observations of a Pavonine Quetzal nest, including descriptions of the nest cavity, eggs, incubation behavior, and food provisioning during February and March 2004 in southeast Peru. I also discuss the plumage development of the nestling, vocalizations, and other observations and compare the nesting behavior and food-provisioning to that of the better known Resplendent Quetzal.

METHODS

I discovered the Pavonine Quetzal nest near the Centro de Investigación y Capacitación Río Los Amigos (CICRA), Depto. Madre de Dios, Peru. CICRA is at an elevation of 250 m above sea level, along the north bank of the Río Madre de Dios near the mouth of the Río Los Amigos (12° 34' S, 70° 05' W). The lowland tropical forests and climate of CICRA are similar to that of other, better known field stations

in the region within Manu and Tambopata National parks. More information on climate, geology, vegetation, and trails at CICRA is available at www.amazonconservation.org/home and in Pitman (2006).

I monitored the quetzal nest most days during the rainy season between discovery on 18 February and fledging of the single nestling on 26 March 2004. I spent ≥ 6.3 hrs observing the nest during incubation over 9 days between 18 February and 2 March (mean = 0.7 hrs/day) and ≥ 40.3 hrs when adults provisioned food to the nest over 14 days between 6 and 26 March (mean = 2.9 hrs/day). I constructed a blind 12 m uphill from the nest tree using a small tent to observe adults switch incubation duties at the nest at sunset (1413–1800 hrs on 21 Feb, 1655–1750 hrs on 23 Feb, 1711–1756 hrs on 24 Feb) and, to minimize disturbance. I examined the nest and eggs directly on 22 February using a ladder to access, photograph, and measure the nest and eggs, spending less than 20 min near the nest to minimize disturbance.

I sat quietly in the open to observe food provisioning because of limited visibility inside the tent. Adults arrived with food and approached to within 2 m of the nest cavity, but appeared wary of entering while I was nearby. I identified delivered food items as fruit or animal, described them in my notes, and left the nest site for 20–40 min to allow the adult to feed the young. I accessed the nest again on 15 March by ladder to count nestlings and to collect regurgitated seeds. I also collected regurgitated seeds from the nest cavity on 27 March after the nestling fledged. Seeds were identified by Fernando Cornejo Valverde (Botanical Research Institute of Texas). I identified frogs using photographs accompanying Cocroft et al. (2001).

RESULTS

The nest cavity was in a large dead tree trunk on a hillside in *terra firme* forest at an elevation of 205 m above sea level (12° 33' S, 70° 07' W). The tree snag was 7–8 m tall, rotting with multiple cavities, small buttresses at the base, and a circumference at breast height of 0.85 m. The nest was in a cavity on the western and uphill side of the snag 4.2 m above ground. The nest entrance was circular with a large wedge-shaped opening descend-



FIG 1. Nest entrance of the Pavonine Quetzel (note ruler [mm] for scale).

ing from the bottom of the entrance (Fig. 1). The circular portion was 9 cm high by 11 cm wide and the wedge-shaped opening below was 7 cm wide and descended 6 cm downwards. The cavity was 16 cm wide and 21 cm deep from the base of the entrance. The cavity appeared shallow, but both adults fit inside without a single feather visible from outside. I observed no lining in the nest, but the bottom contained soft bits of rotten wood.

The nest contained two eggs on 22 February, each pale blue with a few small brown-buff speckles and warm to the touch. The first egg was 31.5 mm long \times 27.6 mm wide and weighed 8.5 g. The second egg was 32.4 mm long \times 28.1 mm wide and 13.5 g. The second egg failed to hatch and was rotten when I examined the nest on 15 March. I removed it from the nest and prepared it as a specimen for the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos in Lima, Peru.

I observed the male incubating during the daytime (0950–1015 hrs, 22 Feb; 1210 hrs, 27 Feb; 1241–1304 hrs, 20 Feb; 1300 hrs, 18 Feb; 1413–1744 hrs, 21 Feb; 1530 hrs, 19 Feb; 1655–1717 hrs, 23 Feb) between 18 February and 2 March from at least 0950 hrs until

sunset near 1745 hrs when the pair would switch. The female appeared to incubate at night and during the early morning (0650 hrs, 2 Mar). Incubation appeared to last \geq 14–17 days, but is not known because I likely discovered the nest after eggs had already been laid.

I observed the adults deliver 32 food items to the nest between 6 and 26 March. The male (25 of 32 food deliveries) seemed to provision the nestling more often than the female, especially near time of fledging. I observed the male deliver food on 16 occasions and the female deliver food once from 22 to 26 March. On 25 March, I observed the male bring food to the nestling 10 times while the female delivered no food. Frog deliveries tended to be alternated with fruit deliveries and the type of fruit (based on color and size) seemed to be alternated between fruit deliveries so that no single food item was repeatedly delivered in three consecutive observed deliveries.

Tree frogs were the most-frequently delivered food item and no insects, lizards or other animal prey were observed delivered to the nest. Eighteen (56%, $n = 32$) of the food deliveries observed were tree frogs and the remaining 14 (44%, $n = 32$) were fruits. Between 6 and 15 March, 66% (10 of 15 food items) of food brought to the nest were frogs. After 21 March, the percentage of fruit brought to the nest increased to 53% (9 of 17 food items), but frogs were still delivered through the nestling's last full day at the nest. Fruits brought to the nest varied in color (black, green, red) and in size, but were difficult to identify by sight. All tree frogs appeared to belong to the genera *Hyla* and *Phyllomedusa*.

Seeds ($n = 31$) regurgitated by the nestling were collected from within and directly below the nest. These were predominantly (52%, $n = 16$) Lauraceae seeds of various sizes, but also included six *Euterpe precatoria* (Arecaceae) seeds, four *Iryanthera* sp. (Myristicaceae) seeds, one unidentified seed, and one seed of each of *Pouteria* sp. (Sapotaceae), *Guatteria* sp. (Annonaceae), and *Unonopsis* sp. (Annonaceae). A seed capsule fragment of *Tetragastris* sp. (Buceraceae) also was found on the ground beneath the nest.

I observed the single nestling on 15 March at 10–13 days of age (Fig. 2), sitting in the



FIG. 2. Dorsal view of nestling Pavinine Quetzel (on 0.5 cm grid paper), 15 March 2004.

nest with its head propped against the cavity wall and its beak pointing up towards the cavity entrance. The nestling was weighed (103 g) and described: bill black with pale tip; legs and feet gray with flesh colored pads; eyes dark; plumage lacking from most of head and belly below sternum, skin gray; breast covered in soft tawny feathers tipped buff to give a somewhat mottled appearance; short black feathers surrounded the cloaca; downy undertail coverts tawny; pin feathers protruded from skin on crown and back; scapulars blackish, edged rufous to golden green; lesser coverts blackish tipped brown, greater coverts blackish tipped buff, remiges blackish with buff margins; upper tail coverts dusky; remiges blackish, new and short, with outer remiges possibly emerging with white tips.

The nestling fledged on 26 March, 21 days after the first observed food provisioning. The nestling period is estimated to be between 21 and 24 days. The nestling spent ≥ 5 hrs peering out of the entrance on 25 March, at times leaning out to look in the direction of the male, and other times calling softly. I heard the nestling give a soft “ow,” and at other times I heard the male call “Eeeoow tuk”

and the female give a soft “Wa op-op-op-op” chuckle (possibly in alarm).

The nestling peered out of the entrance while the male was not nearby and appeared undisturbed by my activities or other researchers on a nearby trail. On three occasions I observed it lift its wings within the entrance and preen once. On five occasions the male sallied to the nest and returned to a nearby perch without delivering the food item in its beak to the nestling. At times the male called, possibly urging the nestling to follow. Upon my arrival at 0747 hrs on 26 March, I found the nestling peering from the entrance with the male perched 2 m distant holding a small green fruit in its beak. At 0755 hrs the male sallied to the entrance and returned to the perch with the fruit still in its beak. Soon after, the nestling flew ~ 30 m to the south, immediately followed by the male. I observed the male again 50 m to the south of the nest with nothing in its beak, but it soon regurgitated a small green fruit. I spotted the fledgling awkwardly land on a branch about 14 m above ground in the forest midstory after what presumably was a short second flight. The male quickly flew and perched on a nearby branch underneath

the fledgling. Both birds then moved south out of view.

At fledging, most of the fledgling's head was covered by short gray plumage, with a few pin feathers still coming in on the forehead. The skin around its eyes, lores, and throat appeared bare. Its back and upper breast plumage was green, bordered by mottled tawny plumage on the remainder of the breast and belly. The wings were blackish with buff spots on the coverts and buff margins on the remiges. The short retrices were black, with a short whitish tip visible on the right outer retrix.

The adult female had a dark gray bill (not red as sometimes illustrated). Overall the female's plumage was: head brownish gray (rather than green as sometimes illustrated), bordered by a band of emerald around the upper breast, neck and back; mid-breast brownish gray like the head, contrasting with ruby lower belly; undersides of retrices black with thin white bands on lower half of outer web, one white band on inner web, and thin white terminal band.

DISCUSSION

This paper reports the first measurements of the nest cavity and description of eggs, nestling, and food provisioning for the Pavonine Quetzal. The timing of breeding at this nest in southeastern Peru (Feb–Mar) was different from Loreto (mid-Jul, Collar 2001). January, February, and March at CICRA are on average the three wettest months of the year (CICRA 2004), whereas July is relatively dry in Loreto (Marengo 1998). Data from additional nests across the range of this species are necessary to investigate how rainfall or seasonality may influence timing of breeding, but it is interesting these two nests were found during such different seasons (dry vs. wet).

The nest, clutch, egg color, nestling plumage, and nestling posture of the Pavonine Quetzal appear similar to that of Resplendent Quetzals (Skutch 1944, Johnsgard 2000). The male Pavonine Quetzal's plumage became quite worn by the time the nestling fledged, as occurs in Resplendent Quetzals (Skutch 1944). Frogs, rather than other animals, accounted for 56% of food deliveries to the Pavonine Quetzal nestling, more than delivered to Resplendent Quetzal nests in Mexico (25.9% arthropods, 4.9% reptiles, 0.6% amphibians;

Avila et al. 1996) and Costa Rica (61.7% arthropods, 4.1% snails, 4.6% reptiles, no amphibians; Wheelwright 1983). No frogs were recorded among food items delivered to a Golden-headed Quetzal (*Pharomachrus auriceps*) nest in Ecuador (R. G. Lohnes, pers. comm.).

The Pavonine Quetzal nestling was provisioned with a higher percentage of fruit (33%) during the first 10 days of observation than Resplendent Quetzal nestlings in Mexico (24%; Avila et al. 1996) and Costa Rica (21%; Wheelwright 1983). The Pavonine Quetzal nestling was provisioned with 53% fruits after the first 10 days of development, lower than Resplendent Quetzal nestlings in Mexico (72%; Avila et al. 1996), but higher than nestlings in Costa Rica (34%; Wheelwright 1983). These differences could reflect different food availabilities or diet requirements between quetzal populations or may be due to small sample sizes (one nest here and in Avila et al. 1996, 11 nests in Wheelwright 1983). Lauraceae seeds represented 52% of the seeds recovered from the Pavonine Quetzal nest and comprised 50% of the total fruit items in the diet of the Resplendent Quetzal in Mexico (Avila et al. 1996). The observed nestling period of 21–24 days for this nest was similar to that of Resplendent Quetzals (21–23 days in Costa Rica, Skutch 1944, Wheelwright 1983; 27 days in Mexico, Avila et al. 1996). Conclusions from this and other studies of quetzal nests based on small samples are difficult, and further research could reveal more variation over multiple nests, years, and locations in timing of breeding, incubation patterns, and food items provisioned.

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Mating Behavior of Reed Buntings (*Emberiza schoeniclus*) in Captivity

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ABSTRACT.—We studied sexual pair behavior and cuckoldry of nine female and five male Reed Buntings (*Emberiza schoeniclus*) in a large outdoor aviary. Three males established small territories and paired with females. We observed 23 copulation attempts with identified partners during a period of approximately 6 weeks, 10 between social mates, 12 between unpaired females and paired males (extrapair for males), and one between a paired female and a paired male which was not the social mate (extrapair for both). Both males and females initiated copulation attempts which, in most cases, were preceded by precopulatory displays. No forced copulations were observed and females appeared to have an active role in mating behavior. Received 2 October 2006. Accepted 15 December 2006.

Paternity analyses have revealed the majority of socially monogamous birds are genetically promiscuous (e.g., Birkhead and Møller 1992, Westneat and Stewart 2003). Surprisingly little is known about the actual mating behavior in contrast to a flood of genetic data. Detailed knowledge of events that lead to copulations is crucial for deciding whether extrapair behavior is male or female-driven, or both (Westneat and Stewart 2003). Observations of extrapair copulations in the field are scarce and studies of birds in captivity may yield more data on this behavior. The rate of extrapair paternity (EPP) in the Reed Bunting (*Emberiza schoeniclus*) is one of the highest reported in socially monogamous birds (Westneat and Stewart 2003). It ranges from 30 to 55% of the young (Dixon 1993, Buchanan 2001, Kleven and Lifjeld 2005, Bouwman et al. 2006; EN, unpubl. data). However, observations of extrapair copulations (EPCs) in this species are rare (Bouwman et al. 2006); to our knowledge there are no published data on which partner initiates copulations. Marthin-

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sen et al. (2005) observed intrusions of extra-pair males into female territories. That suggests that males intend to initiate EPCs, but it is not known how the female reacts to these intrusions and whether she intrudes into extra-pair male territories (Kleven et al. 2006). The objective of our study is to provide detailed descriptions of copulatory behavior in the Reed Bunting with social mates as well as with extra-pair partners. We investigated this behavior in a large outdoor aviary where males and females had access to different mating partners.

METHODS

Fourteen Reed Buntings (9 females, 5 males) were studied in captivity from mid-June to late July 2005 at the Konrad Lorenz Institute in Vienna, Austria. They had been caught one and one-half year before observations started. The color-ringed birds were kept together with 10 Bearded Tits (*Panurus biarmicus*) in an outdoor aviary. The aviary was 78.8 m² in area and consisted of 14 interconnected rectangular compartments (3 × 1.88 m). The maximal height was 3.20 m. Each compartment contained pots with sedges and dead reed stems, willow (*Salix* spp.) branches, and bamboo (*Phyllostachys aurea*). Pine (*Pinus* spp.) twigs were attached to the walls because they have been demonstrated to be used as nest sites by captive Reed Buntings (Giebing 1995). All nests except one were built in small wicker baskets, 5 cm in diameter, mounted with wire on reed stems or pine twigs at a height of 0.5–1.8 m. Sufficient nesting material (dog and horse hair, dried grass) was placed in each compartment. We provided *ad libitum* mealworms, ant pupae, crickets, and soft food with various seeds, insects, and mussels. Territory sizes ranged from one to six compartments and each territory had at least one feeding place. The entire aviary was divided between territorial males and there were no neutral or common feeding grounds. Three of the five males were paired.

Pairs or individuals were observed for 1–3 hrs (all pairs in 40 hrs total) between 0800 and 1800 hrs CET. Either the male's social mate or a female in the territorial neighborhood was fertile during observation. We ascertained social pairs by mate guarding and the male's participation in incubation or feed-

ing of young. We recorded the distance between pair members every 2 min similar to Marthinsen et al. (2005) to investigate mate guarding. The male followed his mate in close proximity, more or less constantly, in this period. We defined the time a male spent within 3 m of the mate as time spent mate guarding. Mate guarding was clearly distinguishable from periods without mate guarding when males showed little interest in their mates. Unpaired females were not mate-guarded or relegated to one territory. We scored copulations of these females with paired males as EPCs for males. We classified copulation attempts as male or female initiated when we were able to observe precopulatory behavior. We scored copulation attempts as female initiated if the female approached the male first or showed a soliciting display. All other cases were classified as male initiated.

OBSERVATIONS

Males sang and defended their established territories and, after pair formation, females started building nests. Twenty-five of 28 broods failed due to predation. We could not ascertain the type of predators responsible but the most likely candidates were mice (*Mus musculus*, *Apodemus* spp.), snakes (Colubridae), and weasels (*Mustela* spp.). We assume they gained access to nests through small gaps and holes in the aviary. Only 11 chicks fledged from the three successful nests from May to July.

Three of the five males in the aviary mate guarded their females 36 to 100% of the observed time (8 observation sessions). The earliest mate guarding observed was 7 days before egg-laying. Mate guarding did not occur after the day the second egg of the clutch was laid.

Copulation attempts ($n = 25$) occurred between day 4 of the pre-egg-laying phase and day 2 after the first egg. All but one occurred on the ground. We observed 17 successful and eight failed copulation attempts (Table 1) within 9–11 different pairs. Only three of these pairs were social pairs (10 copulation attempts). Six females and 3–5 males were involved in all attempts; in two cases male identity could not be ascertained. Within pairs, unsuccessful attempts failed because females rejected males. EPCs of paired males with un-

TABLE 1. Copulation attempts of captive Reed Buntings (within-pair [WP], extrapair [EP], with unidentified males [?]).

	Failed	Successful	Initiation by male	Initiation by female	Initiation unknown
WP	2	8	1	3	6
EP paired males - unpaired females	3	9	3	4	5
EP paired males - paired females	1				1
? Unidentified males - unpaired females	2		1	1	

paired females failed because females rejected males ($n = 2$) or the attempt was interrupted by the social female ($n = 1$). We observed one unsuccessful EPC attempt between a paired male and a paired female, which were not social partners. It failed, because an unidentified male interfered. The two additional unsuccessful copulation attempts with unpaired females and unidentified males failed because females rejected the attempts.

We were able to observe the behavior preceding copulations in only 13 of 25 mating attempts. Copulations occurred on two of these 13 occasions without any preceding displays. In all other cases precopulatory behavior consisted of more or less complex interactions between males and females. Our observations showed that both males and females initiated copulation attempts (Table 1). Males showed a complex precopulatory courtship display (the 'fluffed-run' [Andrew 1957]) in 77% (10/13) of the cases. The fluffed run occurred in open spaces on the ground when males made a series of swift runs towards or in a circle around the female with a more or less vertical, sometimes erect body, bent legs, ruffled feathers on rump and head, the bill occasionally lowered, trailed wings, and a spread and drooped tail. Before mounting, males approached females from behind and hovered over them, standing with flapping wings, looking down, and then attempted to copulate. The bodies of the females during copulation were horizontal, the tails erect, so that cloacae could come in contact. The males flew some distance (0.5–1.5 m) after copulating for approximately 3–4 sec. Males started the fluffed run either before females were approaching them (4/10) or when females were already nearby (6/10). Females approached singing males three times. On two of these occasions, males ceased singing and started the fluffed run; in one case the male continued

to sing at low volume during the fluffed run. These were the only observations where male song preceded a mating attempt. Males performing a fluffed run were attacked by neighboring males at least three times. In one copulation attempt a female displayed a fluffed run in reaction to the mate's fluffed run.

We found high plasticity in female behavior connected to copulations. Both paired and unpaired females approached displaying or non-displaying males (8/13) to initiate copulations (Table 1). On two occasions, females rejected copulation attempts by a bill forward gesture towards the males, which already hovered over them. In one case the rejected male was the social partner. One unpaired female gave the female soliciting display (Andrew 1957) twice when a male was nearby. In this display, the female crouched with her body in a horizontal posture and the bill, head, and tail were raised while she rapidly quivered her raised wings. We did not observe a female performing this soliciting display in reaction to the male's courtship run.

We observed male post-copulatory behavior on one occasion when a male became prostrate on the ground with the bill pointing upwards. When the male gave this display, the female mounted, and the male disengaged himself by walking forward.

DISCUSSION

Mating was often initiated with displays described by Andrew (1957). Copulations occurred on only two occasions without any preceding displays. Precopulatory interactions were a complex behavioral chain consisting of male and female displays to demonstrate the inclination to copulate. Reed Bunting males, in contrast to three other Emberizinae species (Andrew 1957), often displayed with an erect head. In this position their black badge, which extends from their submoustachial white

stripe to the upper breast, was clearly visible. Badge color was correlated with fertilization success in a Dutch population (Bouwman et al. 2006). The fluffed run could have developed to present the male's plumage features provided that females choose between males. One male sang during his fluffed run on one occasion, indicating that song might also be an indicator of male quality as shown by Bouwman et al. (2006).

We observed a male post-copulatory behavior which had only been reported once for the Reed Bunting (Andrew 1957), but which is common in the Yellow-breasted Bunting (*Emberiza aureola*). This was the prone-display ('head-up-lie-flat') (Masatomi and Kobayashi 1982) which resembles the female's soliciting display. The female reaction to the male prone-display was mounting in the Reed Bunting as well as in the Yellow-breasted Bunting. Male post-copulatory and reversed sexual displays have been described for other Emberizinae species (Andrew 1957) and are known in passerine and non-passerine species (e.g., Lorenz 1941, Nero 1982). The function of this display is enigmatic in the Reed Bunting as it is in other species. It possibly may have a role in pair bond maintenance or signaling a successful copulation (Johnson et al. 2000).

Males spent a considerable amount of time mate guarding and ceased guarding after the second egg was laid as reported by Marthinsen et al. (2005). The frequency of copulation attempts was probably influenced by the specific situations in the aviary. Thirteen of 25 copulation attempts were extrapair for males and we observed only one paired female copulating with an extrapair male. Our results are probably not directly applicable to field conditions due to the female biased sex ratio and good mate guarding conditions in the aviary. However, our observations reveal that females actively engage in sexual behavior and we are not convinced that females behave completely different in the field. No copulation appeared to be forced by the male. In both within-pair and extrapair copulation attempts, females could show their willingness for copulation by approaching the male and were able to reject copulations. It seems doubtful that females have a passive role in cuckoldry as proposed by Marthinsen et al. (2005). We expect that

female Reed Buntings are able to selectively accept and reject EPCs in the field.

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