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TECHNIQUES FOR STUDYING THE BEHAVIORAL ECOLOGY OF FOREST-DWELLING TINAMOUS (TINAMIDAE)

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Resumen. – Técnicas para el estudio de la ecología del comportamiento de tinamúes de bosque (Tinamidae). – Por razones metodológicas, los tinamúes son uno de los ordenes de aves menos estudiados, a pesar de que son primitivos entre las aves actuales y muestran comportamientos poco comunes y fascinantes que son poco entendidos. Primero, todos los tinamúes presentan cuidado paternal exclusivo que no se encuentra siempre asociado con la poliandria ni con la reversión de los roles sexuales. Segundo, los tinamúes presentan una variedad de sistemas de apareamiento y se encuentran en diversos hábitat, así que estudios comparativos de su ecología reproductiva pueden ayudar a explicar como las variables ecológicas afectan las estrategias reproductivas. Tercero, estudios han sugerido que, en algunas especies, las hembras cooperan para completar nidadas para varios machos. Esta variedad de estrategias adaptativas y de hábitat crea obstáculos igualmente variados para el estudio de los tinamúes, especialmente en los bosques, donde se han realizado pocos estudios. En este artículo, describo y evalúo métodos para investigar la biología reproductiva y la influencia de las variables ecológicas en los sistemas de apareamiento de tinamúes de bosque, especialmente Tinamúes Grandes (*Tinamus major*), en una selva húmeda tropical de Costa Rica. Estas evaluaciones incluyen la observación, captura, manipulación, marcaje, determinación de sexos, telemetría, monitoreo de nidos y colecta de muestras de ADN, así como sugerencias para mejorar estas técnicas. Mi investigación demuestra que es posible e importante llevar a acabo estudios de la ecología del comportamiento en tinamúes.

Abstract. – For methodological reasons, tinamous are one of the least studied orders of birds, even though they are primitive among the extant birds, and display some rare and intriguing patterns of behavior that remain poorly understood. First, tinamous exhibit exclusive male parental care, although not always associated with sex role reversal or polyandry. Second, tinamous have varied mating systems and are found in diverse habitats, so comparative studies of their breeding biology can help explain how ecological variables affect mating strategies. Third, in some species, research suggests that females cooperatively assemble a clutch of eggs for different males. These varied adaptive strategies and habitats create equally diverse obstacles to tinamou research, especially in forests, where studies have been rare. Here I describe and evaluate methods for investigating the breeding biology and the influences of ecological variables on mating systems among forest-dwelling tinamous, primarily in Great Tinamous (*Tinamus major*) in a lowland Costa Rican forest. These evaluations include observation, capture, handling, marking, sexing, telemetry, nest monitoring and DNA sampling, along with suggestions for revised strategies. My research demonstrates that further behavioral ecological studies of forest tinamous are possible and important. *Accepted 1 January 2004*.

Key words: Tinamidae, male parental care, *Tinamus*, *Crypturellus*.

INTRODUCTION

The order Tinamiformes is primitive among the extant birds, comprised of 46 species confined to Central and South America (Davies 2002). The entire order remains one of the least studied groups of birds. Very little is known about tinamou behavior, and the few detailed ecological and behavioral studies that exist were published more than three decades ago (Schafer 1954, Lancaster 1964a, 1964b, 1964c, Bump & Bump 1969, Bohl 1970a, 1970b). In recent years, there have been a few tinamou publications on population status (e.g., Menegheti 1985), anatomy (e.g., Burger 1992), and captive observations (e.g., Moro *et al* 1994), but almost nothing on behavior with the exception of the anecdotal data found in bird guidebooks and handbooks (e.g., Sick 1993, Davies 2002). This almost complete lack of research is largely due to the difficulty of studying tinamous in the field and the lack of methods that can be used successfully to collect data.

There are three main reasons why the behavioral ecology of tinamous should be studied. First, tinamous exhibit exclusive male parental care. This type of care is rarely found in birds and only in tinamous is present in all species of the order (Handford & Mares 1985). Exclusive male parental care in birds is often associated with polyandry and sex role reversal (Clutton-Brock 1991); however, mating systems in tinamous vary among species.

Second, comparative studies of the varied tinamou mating systems are likely to help our understanding of how ecological factors help maintain adaptive mating strategies since tinamous are found in a wide diversity of habitats (Clutton-Brock 1991, Handford & Mares 1985). For example, monogamy has been reported as the mating system of Little Tinamous (*Crypturellus soui*; Skutch 1963), found in the forest edge and secondary growth forests, and Ornate Tinamous (*Nothoprocta ornata*; Pearson & Pearson 1955), found in grassy areas of high mountains. Serial and/or simultaneous polyandry with sex role reversal have been reported in a lowland forest species, the Variegated Tinamou (*C. variegatus*; Beebe 1925), and it may also be found in Ornate Tinamous (Pearson & Pearson 1955). The Elegant Crested-Tinamou (*Eudromia elegans*; Bohl 1970a, G. Gissing, J. Eadie & G. Ibarguchi unpubl.) also shows sex role reversal but associated with polygynandry. Polygynandry, where males and females mate with multiple partners, is the most common mating system among tinamous and is present in Highland (*Nothocercus bonapartei*; Schafer 1954), Slaty-breasted (*C. boucardi*; Lancaster 1964b) and Great (*Tinamus major*; P. Brennan unpubl.) tinamous, all found in humid tropical forests, as well as in Chilean Tinamous (*N. perdicaria*; Bohl 1970b) found in desert to semi-arid grasslands. The Brushland Tinamou (*N. cinerascens*; Lancaster 1964c), the Spotted Nothura (*Nothura maculosa*; Bump & Bump 1969), and the Red-winged Tinamou (*Rhyncothus rufescens*; Weeks 1973) are also polygynandrous and are found in different habitats.

The third reason why tinamous are behaviorally interesting, is that in polygynandrous species, males accumulate eggs from several females in at least two different ways: in some species females form stable groups and cooperate to lay the clutch for a male, sometimes even laying replacement clutches together (Schafer 1954, Lancaster 1964a, 1964b; Bohl 1970a, Weeks 1973; G. Gissing, J. Eadie & G. Ibarguchi unpubl.) while, in other species, multiple females lay eggs in a nest, but they do not form associations or travel together before or after being attracted by the male (Lancaster 1964c, Bump & Bump 1969, Bohl 1970b, P. Brennan unpubl.). The diversity of mating and social strategies shown by tinamous makes them a great model for understanding the ecological pressures that led to the evolution and maintenance of mating and social systems (Handford & Mares 1985, Vehrencamp 2000).

Most of the detailed behavioral studies in tinamous to date are from open habitat species where the birds are easier to observe. Prior to my work there have been only two long-term behavioral studies of tinamous in forest habitats (Schafer 1954, Lancaster 1964a, 1964b). I have conducted behavioral observations of four forest-dwelling tinamous: the Undulated Tinamou (*C. undulatus)* in the Colombian Amazon, the Little, Slaty-breasted and Great tinamous in a lowland tropical Costa Rican forest. Most of my research during the past five years has focused on Great Tinamous. Here I discuss the methods I have used, both successfully and unsuccessfully, and suggest how to use and improve these techniques further to answer behavioral and ecological questions.

METHODS

Observing and following

Despite the extensive distribution of the tinamous and the diversity of habitats they occupy, little is known about their behavior. With the forest tinamous this is partly attributable to their secretive habits and cryptic coloration, which makes them difficult to locate and observe. When spotted, they can react in different ways: they walk silently away and hide, freeze, alter their body profile so that they become harder to observe, and reluctantly fly away. These behaviors make continuous observation of tinamous very challenging. At La Selva Research Station in Costa Rica, Great Tinamous living close to the most trafficked paths are accustomed to people and allowed me to follow them. In paths less used by humans, however, Great Tinamous flew away almost immediately when spotted, and some made their presence known by flushing loudly as I walked within meters of them. Undulated Tinamous in the Amazon behaved in a similar way as the Great Tinamou.

The best way to find and follow tinamous, particularly the Slaty-breasted Tinamous, was by listening for their calls. While singing, tinamous reacted less to my presence and I could observe a bird if I did not make any sudden movements or loud noises. At most, however, I was able to follow an individual bird for 1.5 h, before it moved away too quickly for me to follow any longer. Although direct observations are difficult, I made some interesting observations on diet and mating behaviors. Direct observation was not sufficient to understand the breeding of the forest tinamous, so I captured birds and followed them using radiotelemetry.

Capture

I captured a total of 32 Great Tinamous and 14 Undulated Tinamous using two techniques. Fixed traps were placed in areas where the birds were likely to walk, either because they use the same paths or because they can be attracted with food or conspecific songs. Fixed traps have been used successfully on some tinamous, using food or water as bait (Bump & Bump 1969, Bohl 1970a, 1970b). I was able to catch Undulated Tinamous, but not Great Tinamous, using fixed baited traps. Baited traps were trip-traps of two types: a dome and a noose corral, both used by local hunters in the Amazon and in Costa Rica. Corn was used as bait, and the traps were set so that when the bird tried to get to the corn the dome would drop on top of it or the noose inside the corral would fasten about the leg and lift the bird from the ground. I also tried unsuccessfully to use noose carpets and mist nets to capture tinamous. Noose carpets (Schemnitiz 1994) were placed next to speakers to try to catch Slaty-breasted Tinamous because they are known to be attracted to playbacks (Lancaster 1964a), but the birds never approached close enough to step on the carpets. Mist nets placed at ground level were set up in areas where tinamous had been seen, but the birds simply bumped into them and walked around.

Mobile traps are a good alternative for species that do not reliably investigate playbacks or bait and whose movements are not predictable. Mobile traps were used to capture all Great Tinamous in my research. I used two methods: driving the bird toward mist nets, and a roosting site trap. The first method consisted of two people searching the forest, each carrying a mist net rolled around a pole, while a third person stayed with the bird after it was spotted. The mist nets were then deployed in a V-shape, and the bird was slowly induced to walk away from us and toward the net. Once the bird was less than 3 m from the net we would make it fly into it by approaching quickly. If the bird was rushed too soon, it would fly over the net, and if we waited too long, it would see the net and try to escape by running parallel to it. Approximately 60% of our catching attempts were successful when using this method.

To improve our chances of catching a specific bird, we developed a second method by taking advantage of our ability to find roosting Great Tinamous. Unlike most tinamou species, Great Tinamous roost in tree branches after calling from the ground at dusk (Skutch 1960). We located singing birds, listened until they flew up to their selected branches, and then waited for 2 or 3 h before attempting to catch them. Following a design used successfully in Venezuela (C. Vispo pers. com.), we built a bell shaped net with a hoop closure on the bottom and attached it to a long extensible pole to catch birds that were roosting less than 5 m high in the canopy. The bell was lowered over the roosting bird, and the hoop was closed quickly under the bird via a draw cord operated from the ground. To lower the risk that a tinamou would be depredated if released at night, we held birds overnight in small, dark, ventilated boxes. At first light the next morning the birds were released where they were caught. Approximately 80% of our trapping attempts were successful with this method, but we used it less often due to the difficulty of walking quietly off trail at night in the forest.

Marking

Some tinamou species such as Undulated and Slaty-breasted tinamous feign death upon capture, becoming completely limp if placed on their back, and run away when put back on their feet (pers. observ.). Great Tinamous, however, do not exhibit this behavior but rather struggle continuously when captured. Because the first Great Tinamou I caught died while being held (presumably due to stress), I placed all other captured birds inside a dark bag and minimized handling.

Birds were weighed and their legs released through the bag opening to mark the tarsi with standard color bands and permanent numbered aluminum bands. Unfortunately, color rings quickly became muddy and, in low light, it was too hard to identify the bird. I did not use wing tags because they may disrupt the bird's camouflage and increase depredation, cause abrasion of the wing and lead to infection, or get tangled in vegetation when the bird flies (Nietfield *et al.* 1994). Perhaps a small wing tag without conspicuous colors, attached firmly to some primary feathers, would avoid these difficulties and provide longer distance identification. Marking collars are sometimes used with Galliformes (e.g., Papeschi *et al.* 2003) and they may be adapted to some tinamou species, but care should be taken not to increase the conspicuousness to predators.

Sexing

Some species of tinamous are sexually dimorphic in their plumage. In most species, however, male and female plumages are virtually identical. Females tend to be larger than males, but there is extensive overlap which makes accurate sexing difficult. Male tinamous have a coiled white phallus which allows sexing by cloacal examination, although the penis is absent in the genera *Nothura, Rhyncotus* and *Nothoprocta* (Bump & Bump 1969). Females of at least some species have a phalloid organ as well (Sick 1993). If the bird is relaxed while being held, one can take time to sex accurately by hand, but blood should be collected to confirm the sex. A DNA probe specific for sexing tinamous has recently been developed and successfully used (de Kloet 2002).

Telemetry

Attachment of radios. Given the difficulty of directly observing tinamou behavior in the forest, I used telemetry as a tool for gathering behavioral data. Telemetry has been used successfully in many other avian species that are difficult to observe or follow (e.g., Priede 1992, Pope & Crawford 2001).

Before starting my fieldwork, I tried three radio attachment methods on captive Chilean Tinamous (*Nothoprocta perdicaria*) at the University of British Columbia with the collaboration of Kimberly Cheng. I used "figure 8" backpacks made out of Teflon ribbon (Tomkiewicz 1983, Tomkiewicz & Burger 1987, Anderka & Angehrn 1992), necklaces made out of 1/8-inch thick cable-ties covered with heat shrink tubing (placed so that my index finger could fit inside the necklace once tightened), and leg attachments made of a ¼-inch Velcro strap fitted snuggly above the tarsi. The Chilean Tinamous showed no reaction to backpacks and leg attachments but they immediately tried to remove necklaces, perhaps because they interfered with head and neck displays more common in tinamous from open habitats (Weeks 1973).

I used "figure 8" backpacks to radio tag nine Undulated Tinamous, with the radios centered on the back. In four birds, these tags stayed on until I recaptured the birds and removed them (4-10 weeks). Two birds removed their backpacks after a few days, thus in future attachments I added a chest strap to secure them. Three birds were depredated; one the same day it was captured, and two others 25 and 27 days after capture. I believe that the backpacks may have gotten tangled in the vegetation and prevented the birds from escaping.

I was worried about the entanglement risk so I did not use backpacks or leg attachments on Great Tinamous. I used necklaces, which were used successfully in Great Tinamous in Venezuela for up to 7 months (C. Vispo pers. com.). Unfortunately, the necklaces caused the death of five birds at my study site within 2-3 weeks when the fruits of *Virola sebifera* became available. Great Tinamous ate two or three of the large fruits at a time and the necklaces caused them to become lodged in their throats. Tinamous have small heads and slender necks, so bigger necklaces would constantly rub the back of their heads and could also be problematic. Concerned for the safety of the birds, I glued the remaining radios directly on the skin between the shoulder blades after trimming the feathers. The 24 radios I attached in this manner remained on the birds for an average of 3 weeks (range: 3 days to 6 weeks). Anderka & Angehrn (1992) discuss gluing methods in detail.

Types of radios. I first used homemade Cochran transmitters (Cochran & Lord 1963**)** donated by Charles Walcott of Cornell University to study Undulated Tinamous. Following these, I used transmitters from Telemetry Solutions (model TS-15), which at 7 g, were smaller and lighter than the Cochran radios at 20-25 g. They also had a mortality sensor, activated when there was no movement for 4 h, and could be recovered at the end of the season and refurbished with new batteries for a fraction of their initial cost.

Even though I had problems attaching radios to tinamous, I am convinced that telemetry is the best way to study ecological questions such as habitat use, territoriality, home range, mortality, and predation in adults and chicks, all of which are largely unknown in most tinamou species. Telemetry could also facilitate behavioral observations of individuals singing, roosting, feeding and providing parental care by allowing the same individuals to be located daily. Telemetry would be particularly useful for finding nests, although this would require tagging a large number of males over a long period during the breeding season, because only a small proportion, as in francolins (*Francolinus* spp.; Sande *et al.* 2000), may be nesting at any one time. A safe and permanent attachment system for Great Tinamous has yet to be demonstrated for my study site and would be needed to conduct long term telemetry studies. Different methods would likely be required for different species, even in the same habitat. Some attachments could be adapted from studies of Galliformes such as the flexible necklaces used in Mountain Quail (*Oreortyx pictus*) (Pope & Crawford 2001).

Locating nests

To understand the mating system of tinamous, it is necessary to locate and monitor nests in order to collect data on nest parentage, male attendance and female egg-laying behavior. Tinamous nest on the ground and most species do not build nests, which makes locating nests difficult. In over 2400 h of field work in Costa Rican forest, I found only five active Slaty-Breasted Tinamou nests and three active Little Tinamou nests. In the Colombian Amazon, I found only three depredated Undulated Tinamou nests in over 960 h of forest work.

Unlike most tinamou species, Great Tinamous always nest in tree buttresses, so I was successful at finding their nests by searching all buttresses of suitable trees. While time consuming due to low nest densities, the search criteria were greatly reduced. I found 45 active, 82 depredated, and 5 hatched nests in 2400 search hours spread over 3 years. To locate nests we divided a 4-km^2 area into five parcels. Each was searched during one day by two or three people, allowing the entire area to be searched weekly. On day 6, a new place would be chosen outside the 4-km^2 area and searched for nests. Searching was done by walking in the forest looking in every buttress of all accessible trees. Using telemetry, we found two active nests once the male sat to incubate. My failure to find more nests by using telemetry was probably due to the short-term attachment of my radios and to the fact that I only tagged eight males. Tagging more males for longer periods of time should greatly increase the success of locating nests. Other researchers collecting data for different projects in our field site found and reported five active Great Tinamou nests.

It is possible to use a trained dog to locate nests (Schafer 1954), but dogs were not allowed in any of my study sites, so I never tried this method.

Monitoring nests

Once the nests were found, I placed either a video camera or a motion-activated photographic camera in front of the nest. The video cameras I used (Panasonic PV-L601) were infrared motion activated and did not record depredation events by snakes, so I used the interval recording feature instead of the motion sensor. I recorded 5 or 10 s of every minute, so a day of monitoring was recorded in a single tape and required a single 12-V battery. Because the video cameras did not have nocturnal recording capabilities, several predation events on the eggs and on the incubating birds were not recorded. Commercially available monitoring systems provide 24-h nest surveillance and, although they are expensive, they have been used successfully (Staller 2001).

Sampling DNA

DNA analysis, widely used in behavioral ecological studies, can be obtained from any tissue, including blood, feathers, egg material and feces. Blood is most commonly used, but it requires that the animal be captured. I collected blood samples from the adults I captured by puncturing the tarsal vein, collecting blood in a capillary tube, and then storing it in lysis buffer solution.

Some of the most interesting questions about tinamous relate to their mating strategies: Is the male the father of all the chicks he is caring for? How many females lay eggs in one nest? Are those females related? These questions can only be answered through DNA analysis. To determine parentage of the clutches, I collected DNA from the incubating bird and the chicks in the clutch. I obtained DNA from feathers, which I collected from the male by hand, because Great Tinamous sit very tightly at their nests, particularly if they have been incubating for longer than 7 days (unpubl. data). Some birds were more nervous of my proximity, so I constructed a "feather puller" to grab the feathers while being a few feet away from the sitting bird. Most males left the nest after I collected the feathers but returned to sit after a few hours.

Collecting DNA from the chicks was problematic because 80% of Great Tinamou nests are depredated before hatching (Brennan unpubl.) and I could not use brood rings (Smith *et al.* in press) because my sample size would be greatly reduced if I waited for hatching to collect the DNA. Instead, I created an egg-exchange protocol to collect the real eggs and place artificial eggs at the nest. First I would collect the feathers from the incubating male, forcing him to leave the nest. I would then exchange the real eggs for artificial eggs, and incubate the real eggs in the laboratory (incubation: 99.5°F, +70% humidity). The male would return to the nest and incubate the artificial eggs. The precocial chicks hatched synchronously and I collected blood from their tarsal vein. I brought the chicks back to the sitting male less than 24 h after hatching, moved the male off the nest, and replaced the chicks in the nest with some broken eggshells. I placed a small barrier around the buttress so the chicks could not run off before the father came back. The male invariably came back within 2 h and brooded the chicks. To insure that the male would take the chicks, I played back chick peeping sounds to the male at the nest for a few hours on the day when the chicks were hatching.

To build the artificial eggs, I used blown chicken eggs (jumbo size) filled with a mix of plaster and foam matched for weight and color to those of the Great Tinamou. The eggs rolled in a similar way to a real egg because of the uneven distribution of foam and plaster. I decided against using resin eggs because snakes continued to depredate the artificial clutches, and I was concerned for their well-being. The plaster filled eggs, unlike resin, could be broken and expelled.

This egg-exchange scheme might work for other tinamous if realistic artificial eggs are made, and if males return after the disturbance. I exchanged resin eggs at a Little Tinamou nest while the male was feeding and he sat on them upon his return. Some tinamous may use a few feathers to line their nest, so one can wait until the male leaves the nest to collect feathers and exchange the eggs. Schafer (1954) noted that he could approach an incubating Highland Tinamou within 20 cm without causing it to react at all, and I noticed the same for both Little and Slaty-breasted tinamous.

CONCLUSION

Many aspects of the breeding biology and behavior of tinamous are known only from anecdotal or incomplete observations, and very few long term studies have been conducted in any tinamou species. Forest tinamous are especially difficult to study, but good quality data can be collected, particularly if telemetry is possible. I hope that the information contained in this paper proves useful to researchers and facilitate future investigations of this understudied and fascinating group.

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