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Courtship behavior of a secretive forest tinamou, *Tinamus major* (Great Tinamou)

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ABSTRACT

The mating systems of many rainforest birds remain poorly understood, especially those that elude observation in dense forest understories. Here we documented mating behaviors in a pair of *Tinamus major* (Great Tinamou), a secretive species with a wide distribution across the lowland Central and South American tropics. Despite anecdotal preconceptions that males court females, we observed predominant courtship displays from the putative female tinamou. In this mating ritual recorded in the birds' natural habitat, only the putative female vocalized in the form of clucking and soft-rolling songs, and courted the putative male with a suite of courtship displays, such as neck-elongation, tail-raising, crouching, and feather-fluffing. In contrast, the putative male watched while standing still, approached, tail-raised, walked away, and mounted the putative female a few times. The clucking song of the putative female had not been described previously but we repeatedly observed this song type immediately before the soft-rolling songs during the courtship interaction. Clucking was of lower frequency and around 10 times shorter than the soft-rolling songs. The clucking and soft-rolling songs sung by the putative female were of lower frequency than the common morning territorial songs recorded in the vicinity. This behavioral auditory analysis of the secretive mating ritual of a rainforest tinamou reveals a previously underappreciated female role in their courtship displays.

Keywords: courtship display, courtship song, mating behavior, mating system, Paleognath, *Tinamus major*

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LAY SUMMARY

- In the dense understory of the Panamanian rainforests, we witnessed the secretive courtship ritual of *Tinamus major* (Great Tinamou).
- In this species, only males incubate the eggs, so females might contribute more courtship efforts to secure male parental duties. However, the courtship ritual of this species has rarely been observed.
- We recorded female-biased courtship in a pair of *T. major* and characterized previously undescribed vocalizations and female courtship displays such as feather-ruffling, tail-raising, neck-stretching, wing-drooping, and crouching. This female-biased courtship is distinct from other paleognaths, such as ostriches and rheas, which exhibit male-biased courtship.
- This observation sheds light on the evolution of the mating system and courtship behaviors in the origin of avian radiation.

Comportamiento de cortejo de un sigiloso tinamú del bosque, Tinamus major

RESUMEN

Los sistemas de apareamiento de muchas aves de la selva tropical siguen siendo poco conocidos, especialmente los que eluden la observación en los sotobosques densos. Aquí documentamos los comportamientos de apareamiento de una pareja de Tinamus major (Tinamidae), una especie reservada con una amplia distribución en las tierras bajas de los trópicos de América Central y del Sur. A pesar de las preconcepciones anecdóticas de que los machos cortejan a las hembras, observamos muestras predominantes de cortejo por parte de la hembra tinamú. En este ritual de apareamiento grabado en el hábitat natural de las aves, sólo la hembra vocalizó en forma de cacareos y cantos suaves, y cortejó al macho con una serie de exhibiciones de cortejo, tales como alargamiento del cuello, levantamiento de la cola, agacharse y aleteo de plumas. En cambio, el macho observó mientras permanecía quieto, se acercó, levantó la cola, se alejó y montó a la hembra unas cuantas veces. El canto de cacareo de la supuesta hembra no se había descrito anteriormente, pero observamos repetidamente este tipo de canto inmediatamente antes de los cantos de balanceo suave durante la interacción de cortejo. El cacareo era de menor frecuencia y unas diez veces más corto que los cantos de balanceo suave. Los cacareos y los cantos de balanceo suave entonados por la supuesta hembra eran de menor frecuencia que los cantos territoriales matutinos comunes registrados en las inmediaciones. Este análisis del comportamiento

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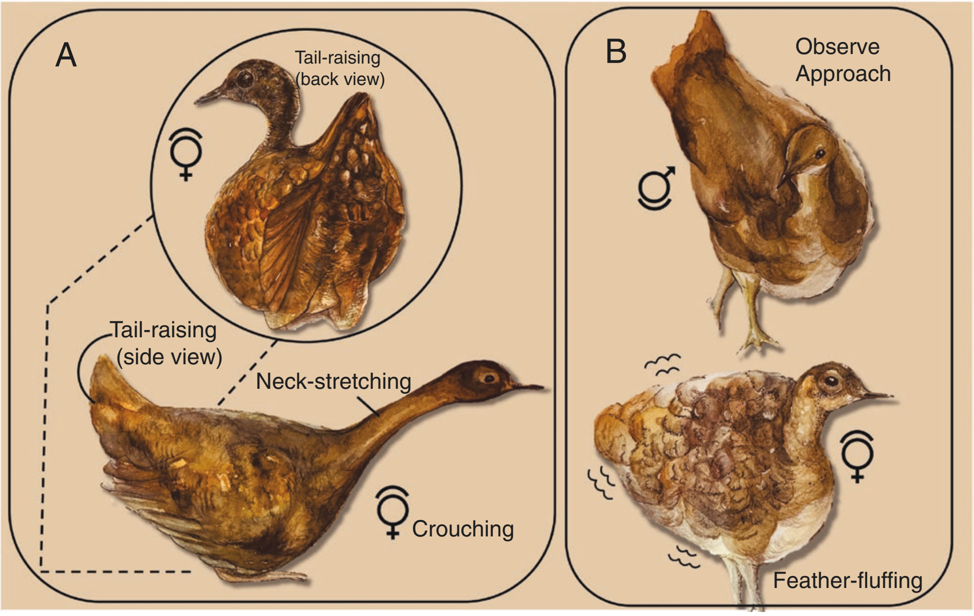
auditivo del misterioso ritual de apareamiento de los cetrinos de la selva tropical revela el hasta ahora infravalorado sesgo femenino en las exhibiciones de cortejo de las aves.

Palabras claves: cortejo, canto de cortejo, comportamiento de apareamiento, sistema de apareamiento, Paleognath, Tinamus major

Graphical Abstract



INTRODUCTION

Paleognaths are the basal lineage of birds, and are crucial for understanding dinosaur–bird evolution (Del Hoyo et al. 2013). In contrast to most birds where both sexes incubate eggs and provision young, many paleognaths demonstrate extensive male or male-only parental care (Davies 2002, Del Hoyo et al. 2013). Higher male post-mating reproductive investment predicts higher relative premating efforts in females.

However, detailed behavioral descriptions of paleognath breeding behavior remain scarce as most observations have been limited to captive individuals. For paleognaths living in closed forests, mating behavior remains elusive. There is limited understanding of the life history of these rainforest tinamous (Tinamidae), the most species-rich family of paleognaths (Brennan 2004; Schelsky 2004). The grassland tinamous, such as *Nothoprocta*, demonstrate simple courtship displays where a male displays and is chased by a vocalizing female (Pearson and Pearson 1955). The courtship rituals of the rainforest tinamous are considered more complex, yet remain poorly understood, especially as to whether there is a disparity in courtship efforts, and if so, which sex predominates in courtship efforts (Beebe 1925, Pearson and Pearson 1955, Bonilla-Sanchez 2008, Del Hoyo et al. 2013).

Tinamus major (Great Tinamou) is one of the most widely distributed tinamou species in Neotropical rainforests (Davies 2002, Li et al. 2023). The mating ritual of this species has only been described in captivity (Bonilla-Sanchez 2008), where mating behavior resembled the mating interaction of a congener, *T. tao* (Grey Tinamou) (Solano-Ugalde et al. 2018), except that in *T. major* the male, as opposed to the female, was the courting sex. However, mating rituals in the wild may differ in complexity. In wild *T. tao*, the females exhibited courtship bias with a suite of displays such as tail-raising, neck-stretching, and crouching (Solano-Ugalde et al. 2018). Female courtship is expected when the male exclusively incubates and cares for the young. It remains an open question whether wild *T. major* exhibits female courtship dominance, as seen in its congener *T. tao*, or aligns with previous observations of captive individuals.

Careful observation and analysis of a tinamou mating ritual in the wild would allow us to understand this elusive rainforest paleognath. Here we provide a detailed description and analysis of a recorded mating interaction in a pair of *T. major* in Gamboa, Panamá. With this first description of the wild *T. major* courtship ritual, we asked whether there is a disparity in courtship efforts between sexes; and if so, which sex is dominant in acoustic and behavioral efforts? We discovered previously undescribed courtship behaviors and vocalizations and examined how these new acoustic and behavioral displays differ from the known ones. This observation sheds light on the intricate courtship dynamics of tinamous, offering new insights into their elusive behaviors in the dense forest understory.

METHODS

Location

At 10:42 AM, on November 6, 2023, in Gamboa, Panama (9°7’2.28”N, 79°41’43.44”W), S.W. incidentally recorded (audio and video) the interaction of 2 *T. major* individuals for 11 min and 12 s with an iPhone 12 Pro (iOS version 17.2.1) before an accidental interruption (see Video Abstract). The distance between the single observer (S.W.) and the 2 tinamous was ~15 m. Both tinamous were observed and tracked for the entire interval. No other tinamous were in sight.

TABLE 1. Ethogram of the mating ritual of *Tinamus major*. The example snapshots in Figure 1 in which the behavior occurred are listed in the fifth column.

Putative sex	Category	Behavior	Description	Figure	Time occurred
Putative female	Vocal	Soft-rolling song	Soft-rolling song with syllables around 0.7s long, maximum amplitude ~490 db, and low frequency ~1,153 Hz	2, 5	Continuous
(yellow)	Vocal	Clucking	Short soft clucking-like notes, each lasting around 0.7 s, with maximum amplitude ~316 db, and low frequency ~1051 Hz	2, 5	Continuous
	Posture	Tail-raising	Raising the tail and flaring light undertail coverts while standing	1, 4A, S1	00:28; 01:13; 02:41–03:06; 03:26; 03:57; 08:24
	Posture	Neck-stretching	Elongating the neck horizontally	1, 4A, S1	02:33–02:41; 03:39; 08:53; 10:48
	Posture	Crouching	Lowering the body to the ground, like an egg-laying position	1, 4A, S1	3:36–3:53; 04:01; 04:18; 10:32
	Posture	Wing-drooping	Lowering and spreading the primary feathers	1, S1	01:44–02:41
	Movement	Feather-fluffing	Fluffing up whole-body feathers, then gentling flapping the wings	1, 4B, S2	03:24–03:31
	Movement	Following	Moving toward the other bird, while the other was moving away	1	06:49–06:58
Putative male	Movement	Approach	Moving toward the other bird, while the other was not moving away	1	2:33
(turquoise)	Movement	Flank-inspecting	Within 0.5 m, facing other bird's flank	1, S1	3:24; 4:24; 10:48
	Movement	Mouth-opening	Leaning toward the other bird while opening its mouth	1	1:44
	Movement	Mount attempt	Jumping over and briefly touching the other bird's back with feet	1, S3	3:57; 04:29
	Movement	Standing atop	Standing on the back of the other bird	1, S3	7:14

We analyzed each frame of the behavioral interaction to describe the courtship ritual. Because the birds were unmarked and sexual dimorphism in *T. major* is subtle, we could not visually determine the sex of the 2 individuals. Instead, we traced each individual throughout the recording, and classified putative sexes based on their distinctive positions during mounting: in Tinamidae, in which the male stands on top of the female during mating (Beebe 1925, Bonilla-Sanchez 2008, Solano-Ugalde et al. 2018).

Mating Behavior and Songs

To characterize the behavioral interaction during the mating ritual, we constructed an ethogram that highlights clips in the recording in which each behavioral variable occurred (Table 1).

To characterize song variations during the mating ritual, we extracted auditory recordings during 0:42–2:32 (Figure 1) of the video recording when the tinamous were close to the recorder so that the sound quality was sufficient for song analysis. The audio file was then analyzed by a single observer (Y.G.) using the song analysis software, Raven Pro version 1.6 (Charif et al. 2010). A waveform and a spectrogram were generated (Figure 2). The window size and the color (turbo) of the spectrogram analysis were optimized to ensure a sharp contrast, making it easier to visualize the syllables. Each syllable then was manually selected. We used a cursor to measure 2 spectrogram-based variables, minimum and maximum frequency, for each syllable. We also noted the beginning and end times of each syllable in order to calculate its duration. Lastly, we recorded the waveform-based time at which the amplitude peaked. To capture the variations in the timing of peak amplitude within each syllable, we derived a song variable called Relative Peak Position to identify the time at which the peak amplitude occurred relative to the total duration of each syllable as (peak time–start time)/(end time–start time) (Figure 3).

To test whether there was a difference in the quantitative features of the 2 song types sung by the putative female, we applied linear mixed effect models using the *lmer* function in the *lme4* package (Bates et al. 2015) in R 4.3.1 (R Core Team 2023). In each model, the response variables were quantitative measures of songs (e.g., minimum frequency), the fixed effect was song types (clucking versus soft-rolling), and the random effect was song bouts (Figure 3). We compared the full models to the corresponding null models with the same response variable and random effect, but no fixed effect.

We further compared the putative female song syllables to regular songs of *T. major* recorded during the morning chorus in the vicinity. We downloaded the nearest (3.3 km away) recording XC363937 (9.1332°N–79.7195°W) from the incidental observation from Xeno-Canto (www.xeno-canto.org). This recording was recorded at 6:04 AM on April 7, 2017, and lasted for 95.117 s containing 58 syllables. We compared the quantitative features among the 3 song types with principal component analysis. To test for specific variation among the 3 song types, we used linear mixed effect models with quantitative syllable measurements (e.g., minimum frequency) as response variables, song types as fixed effects, and song bouts from different individuals as random effects.

FIGURE 1. Mating ritual of *Tinamus major*. Sequential snapshots during the 11 min and 12 s of mating interactions with the time point of each frame labeled in the corner grey rectangle. In each frame, the putative female is labeled with a yellow female symbol; the putative male is labeled with a turquoise male symbol.

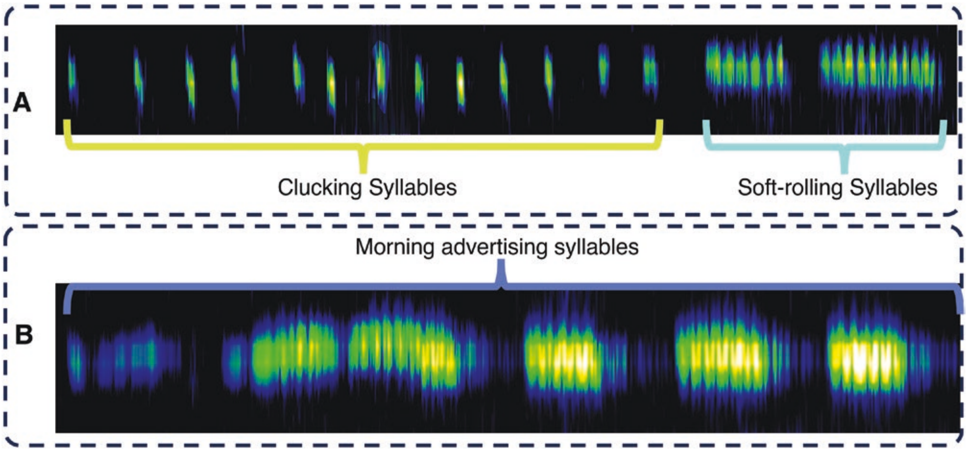


FIGURE 2. Spectrograms of clucking (underlined by yellow bracket), soft-rolling songs (underlined turquoise bracket), and regular songs (dark blue bracket). (**A**) An example of a spectrogram from a song recording during the incidental observation of *Tinamus major* mating ritual highlighting clucking and soft-rolling songs by the putative female. (**B**) An example of a spectrogram of regular morning advertising songs.

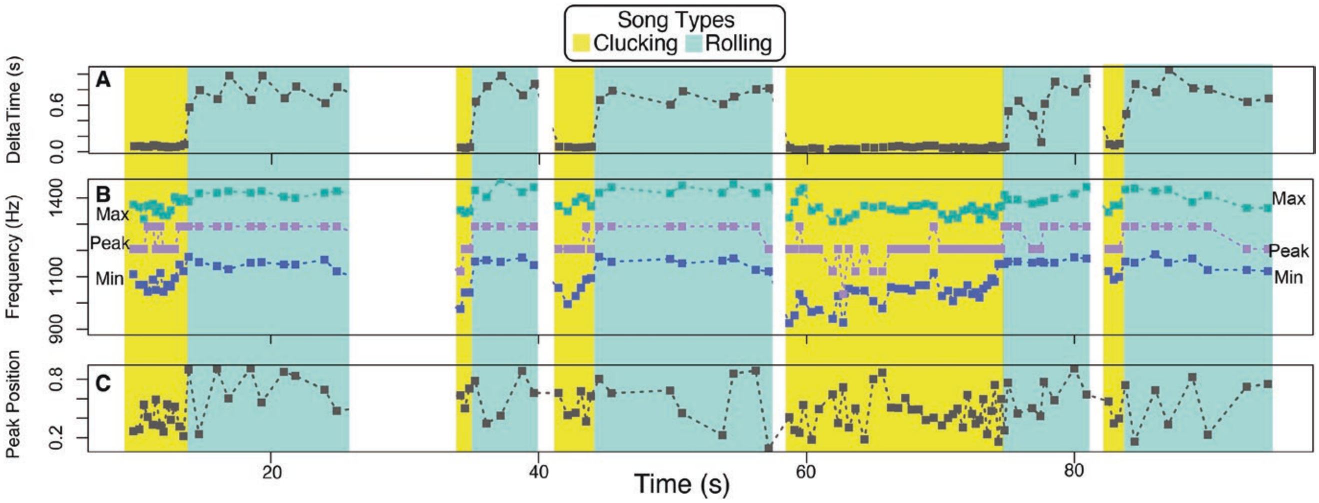


FIGURE 3. Quantitative features of putative female vocalization during mating ritual. There was significantly lower delta time (**A**), frequency (**B**), and relative peak position (**C**) of clucking (left, yellowshaded intervals) versus soft-rolling songs (right, turquoise shaded intervals). All the songs in 110 s are quantified here. Relative peak position is the time at which the peak frequency occurred relative to the total duration of each syllable, (peak time − start time)/(end time − start time).

RESULTS

The putative female tinamou demonstrated several behavioral characteristics that had been previously described in other tinamou species, such as tail-raising (Table 1, Figures 1 and 4A), neck-stretching (Figures 1 and 4A), crouching (Figures 1 and 4A), wing-drooping (Figures 1 and 4A), following (Figure 1), and soft-rolling songs (Table 1, Figures 2 and 5). The putative male demonstrated approaching, flank-inspecting, mount attempts, and standing atop. We did not observe copulation in this recording. We discovered 2 previously undescribed mating behaviors performed by the putative female: feather-fluffing (Table 1, Figure 4B) and clucking (Table 1, Figures 2, 3, and 5).

Only the putative female vocalized during the mating interaction with 2 types of song, clucking and soft-rolling songs (Figure 2). Clucking was hen-like repeated short notes that always preceded soft-rolling syllables (Table 1). There was a significant difference between clucking and soft-rolling songs. The clucking songs showed lower delta time, minimum and maximum frequency, and relative peak position ($P < 0.001$; Figures 3 and 5). The soft-rolling syllables were intermediate (Figure 5A) between morning advertising syllables and clucking syllables in several audio measurements: delta time (Figure 5B) and high frequency (Figure 5C). The soft-rolling songs were similar to morning advertising songs in delta time (Figure 5B) and low frequency (Figure 5C,D). Soft-rolling songs are intermediate between clucking and morning advertising songs, but more like the latter (Figure 5A). Soft-rolling songs have the amplitude peaks shifted toward the end of each syllable, away from the middle as in clucking or advertising songs (Figure 5E).

DISCUSSION

We offer one of the first detailed descriptions of the *T. major* mating ritual in the birds' natural habitat. The behavioral interaction was similar to the mating ritual observed in wild *T. tao* (Solano-Ugalde et al. 2018), for which the putative female

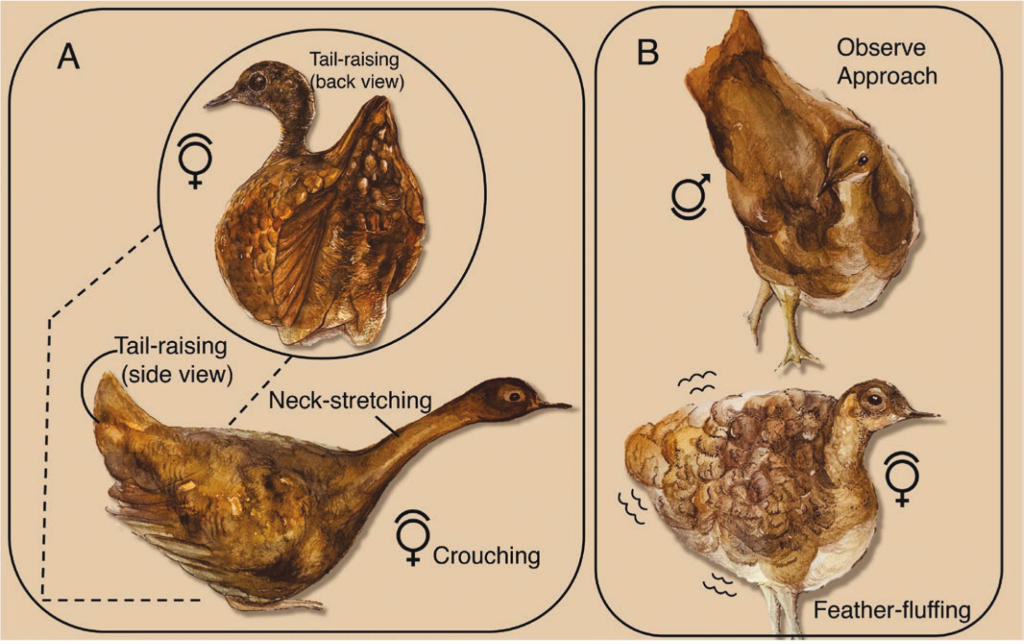


FIGURE 4. Illustrations of the courtship displays of *Tinamus major* as reconstructed from our video recording. (**A**) The putative female crouched with her neck stretched horizontally and tail-raised revealing tail coverts. (**B**) The putative female demonstrated feather-fluffing, puffing up the whole-body feather while fluffing her wings, in front of the putative male. Illustrations by Silu Wang.

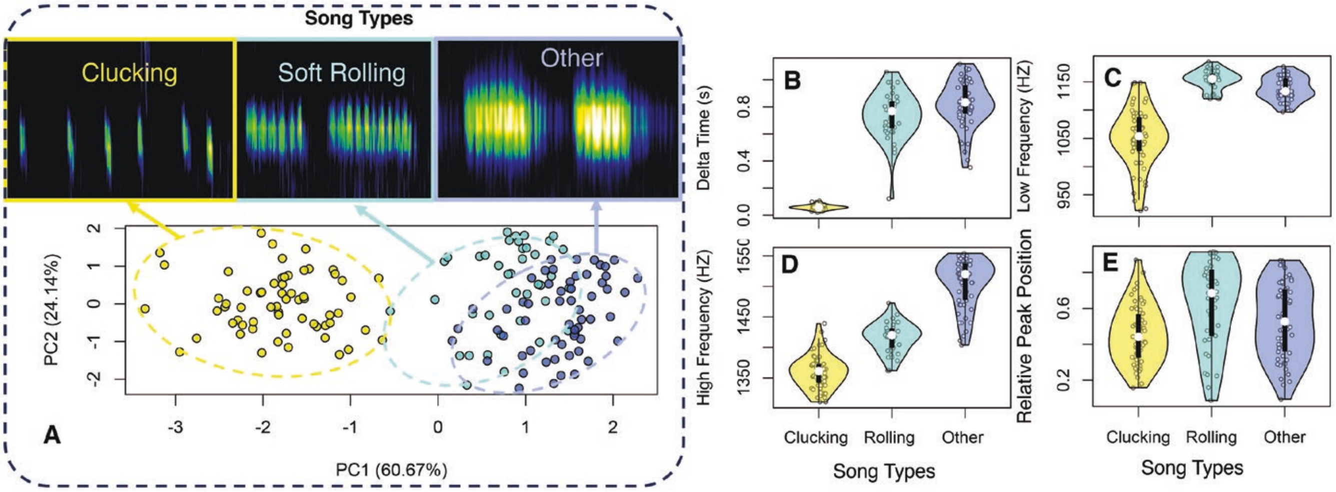


FIGURE 5. Acoustic comparison among song types. The clucking and soft-rolling songs from the putative female are different from the morning advertising songs (labeled as "other") recorded in the vicinity (3 km apart). (**A**) Principal component analysis of song variables among the 3 song types. (**B–E**) Violin plots of song variables among song types. (**E**) Relative peak position is the time at which the peak frequency occurred relative to the total duration of each syllable (peak time − start time)/(end time − start time).

demonstrated neck-stretching and crouching, while the putative male stood on the back of the putative female. Contrary to the previous mating description of captive *T. major* (Bonilla-Sanchez 2008), we observed female bias in both vocal and behavioral courtship efforts. The putative female repeatedly displayed (Table 1, Figures 1 and 4; Supplementary Material Figures 1 and 2) and vocalized (Figures 2, 3, and 5) during the mating interaction while the putative male watched. In particular, similar to *T. tao* females, the *T. major* female performed soft-rolling songs (Figures 2 and 3), neck-stretching (Figures 1 and 4A; Supplementary Material Figure 1), crouching (Figures 1 and 4A; Supplementary Material Figure 1), wing-drooping (Figure 1, Supplementary Material Figure 1), and tail-raising (Figures 1 and 4A; Supplementary Material Figure 1). The putative male did not show any display-like behavior (Figure 1, Supplementary Material Figure 1), was mostly watching while standing still (Figure 1, Supplementary Material Figure 1), approached (Supplementary Material Figure Figure 2), did flank-inspecting (Figure 1, Supplementary Material Figure 1), mounting attempts (Figure 1, Supplementary Material Figure 3), and standing atop (Table 1, Figure 1, Supplementary Material Figures 3). Female tail-raising was also observed in *Crypturellus variegatus* (Beebe 1925).

We also observed a previously undescribed behavior in the putative female, feather-fluffing (Table 1, Figure 4B, Supplementary Material Figure 2). Both feather-fluffing

(Figure 4B) and neck-stretching (Figure 4A) enlarge the apparent female body size. This form of display thus exaggerates the female-biased sexual size dimorphism in *T. major* (Davies 2002), which could be selected by sex-specific niche-partitioning and/or sexual selection. Female body size enlargement could be attractive to males, as immediately after the feather-fluffing (Figure 4A), the putative male approached (Supplementary Material Figure 2) and then performed his first mounting attempt (Supplementary Material Figure 3), despite the previous prolonged hesitation (Figure 1, Supplementary Material Figure 1). This suggests that male preference for larger females may contribute to female-biased size dimorphism. As female body size is largely correlated with the egg weight in birds (Dyke and Kaiser 2010), female body size can be a fertility signal to the males. Feather-fluffing therefore exploits this male preference by inciting male attraction. More observations in *T. major* and other tinamou species are needed to leverage phylogenetic methods for understanding the variation of courtship display in different sexual and ecological contexts.

The putative female was the sole singer throughout the mating ritual with a complex suite of display-like behaviors (Table 1, Figures 1 and 4, Supplementary Material Figures 1 and 2). The clucking and soft-rolling songs during mating were distinct from the morning advertising songs with lower frequency and shorter duration (Figure 5). The morning advertising songs are more commonly heard and distinctive from other sympatric tinamou species (Bertelli and Tubaro 2002). To our knowledge, this is the first observation of the clucking syllables in the tinamou mating ritual. This type of syllable occurred quite frequently (~34 times min^{-1}) and occurred immediately before the soft-rolling songs (Figures 3 and 5). Clucking is much shorter, with lower frequency than soft-rolling songs (Figures 3 and 5) during sexual displays (Figure 3, Supplementary Material Figures 1 and 2), which might prime the motivation state of sexual interactions. The soft-rolling songs resemble the regular advertising songs (Figures 3 and 5), but exhibited lower frequency. The intervals among clucking were uneven, and the counts of clucking before soft-rolling songs were variable (Figures 2 and 3).

The clucking, soft-rolling, and advertising songs that we compared (Figures 2, 3, and 5) might represent female versus male song dimorphism of *T. major*. However, *T. major* females might also sing the morning advertising song type. Although there is limited understanding of song sexual dimorphism in *T. major*, it has been postulated in various species from its closely related genus, *Crypturellus* (Boesman et al. 2018). In *C. brevirostris*, *C. cinereus*, and *C. soui*, the primary versus secondary songs are thought to be sung by territorial males versus paired females during mating duets. Similar to our observation, the primary songs, or morning advertising songs, were of higher frequency, more species-specific, and more frequently heard than the secondary songs (Boesman et al. 2018), or clucking and soft-rolling songs in this study. However, no video recording was paired with the putative duetting song analysis by Boesman et al. (2018), thus ethotypic sexing was impossible. Multimodal observations have been scarce because of the secretive behavior of the rainforest tinamous, which constrains our ability to document the song dimorphism of rainforest tinamous.

Consistent with the prediction of female bias in premating efforts based on greater male post-mating reproductive investment, we observed female bias in courtship. In contrast to the preconception that males court the females in *Tinamus* (Del Hoyo et al. 2013), here we found that the putative female predominantly courted with a complex suite of displays, while the putative male seemed passive (Figure 1, Supplementary Material Figures 1–3). Notably, the *Tinamus* male-display preconception was mostly based on anecdotal reports (Davies, 2002), which could have miscategorized the sexes. Because mating behavior is poorly understood in rainforest tinamous (Brennan 2004; Schelsky 2004) and there is a lack of obvious sexual dimorphism, we should be cautious with sexing or even putative sexing based on ethotypic assignment. Our observation of female-only courtship aligns with the rare field observations of mating rituals in *T. tao* (Solano-Ugalde et al. 2018) and *C. variegatus* (Beebe 1925). Future studies could track sexed individuals in courtship interactions with GPS tags, but there are enormous technical challenges for studying intricate behavior in the dense forest understory.

Female premating efforts could be favored by selection when male post-mating reproductive investment overweighs total female reproductive investment (Andersson and Iwasa 1996). The *T. major* mating system in which males are the primary parental-caregiving sex could select for female courtship and male choosiness, aligning with the reversed sexual size dimorphism in this taxon. Variation in post-zygotic investment among paleognaths may have resulted in a gradient of female bias in courtship interactions. Consistent with this logic, ostriches have biparental care and male-biased courtship (Bolwig 1973). However, this relation does not apply universally for paleognath, as rheas have male parental care and still carry out male-biased courtship displays (Raikow 1969). Future phylogenetic studies of paleognath sex-partitioning in pre- and post-mating efforts could shed light on mating system evolution at the origins of avian radiation.

Supplementary material

Supplementary material is available at *Ornithology* online.

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Ethics statement

We followed the ethical guidelines of IACUC of the State University of New York at Buffalo and the Smithsonian Tropical Research Institute. Research in Panama was permitted under MiAmbiente ARB-076-2023.

Conflict of interest statement

The authors declare no competing interests.

Author contributions

J.F. arranged fieldwork logistics; J.F., J.M., and S.W. conducted fieldwork supported by funding acquired by S.W.; S.W. recorded the video which was analyzed by Y.G. under the supervision of S.W.; S.W. wrote the first draft, which was edited by J.F., Y.G., and J.M.; J.M. conducted translation of the manuscript into Spanish.

Data availability

Analyses reported in this article can be reproduced using the raw video and data provided by Guo et al. (2024).

LITERATURE CITED

Andersson, M., and Y. Iwasa (1996). Sexual selection. *Trends in Ecology & Evolution* 11:53–58.

Bates, D., M. Mächler, B. Bolker, and S. Walker (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.

Beebe, W. (1925). The Variegated Tinamou (*Crypturus variegatus variegatus*) (Gmelin). *Zoologica* 6:195–227.

Bertelli, S., and P. L. Tubaro (2002). Body mass and habitat correlates of song structure in a primitive group of birds: Song structure in tinamous. *Biological Journal of the Linnean Society* 77:423–430.

Boesman, P., O. Claessens, T. V. V. Costa, V. Pelletier, J. Ingels, and A. Renaudier (2018). Songs of Rusty Tinamou *Crypturellus brevirostris* and duetting in *Crypturellus* species. *Bulletin of the British Ornithologists' Club* 138:69.

Bolwig, N. (1973). Agonistic and sexual behavior of the African Ostrich (*Struthio camelus*). *The Condor* 75:100–105.

Bonilla-Sanchez, S. (2008). Descripción del cortejo, apareamiento y puesta de huevos en Tinamus major (Tinamiformes, Tinamidae) bajo condiciones de cautiverio en el ZooAve. *Zeledonia* 12: 22–26.

Brennan, P. L. R. (2004). Techniques for studying the behavioral ecology of forest-dwelling tinamous (Tinamidae). *Ornitologia Neotropical* 15:329–337.

Charif, R., A. Waack, and L. Strickman (2010). *Raven Pro 1.4 User's Manual*. Cornell Lab of Ornithology, Ithaca, NY, USA.

Davies, S. (2002). *Ratites and Tinamous*. Oxford University Press, New York, NY, USA.

Del Hoyo, J., A. Elliot, J. Sargatal, and J. Cabot (Editors) (2013). *Handbook of the Birds of the World*. Lynx Edicions, Barcelona, Spain.

Dyke, G. J., and G. W. Kaiser (2010). Cracking a developmental constraint: Egg size and bird evolution. In *Proceedings of the VII International Meeting of the Society of Avian Paleontology and Evolution* (W. E. Boles and T. H. Worthy, Editors). Records of the Australian Museum, Sydney, Australia. pp. 207–216.

Guo, Y., J. J. Falk, J. L. Medina-Madrid, and S. Wang (2024). Data from: Courtship behavior of a secretive forest tinamou, *Tinamus major* (Great Tinamou). *Ornithology* 142:ukae062. https://doi.org/10.5061/dryad.79cnp5j5p [Dataset].

Li, Q., D. Chen, and S. Wang (2023). Character displacement of egg colors during tinamou speciation. *Evolution* 77:1874–1881.

Pearson, A. K., and O. P. Pearson (1955). Natural history and breeding behavior of the tinamou, *Nothoprocta ornata*. *The Auk* 72:113–127.

R Core Team (2023). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Raikow, R. (1969). Sexual and agonistic behaviour of the Common Rhea. *The Wilson Bulletin* 81:196–206.

Schelsky, W. (2004). Research and conservation of forest-dependent tinamou species in Amazonia, Peru. *Ornitología Neotropical*. 15:33.

Solano-Ugalde, A., L. Ordóñez-Delgado, C. Vits, and J. F. Freile (2018). Breeding biology of Gray Tinamou (*Tinamus tao*) in southeastern Ecuador. *The Wilson Journal of Ornithology* 130:427–436.