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A new species of *Tinamus* (Aves: Tinamiformes) from the western Amazon, Brazil

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Abstract

We describe *Tinamus resonans* **sp. nov.**, a new species of tinamou from the montane forests of the Serra do Divisor, western Amazonia, Brazil. The species is distinguished by a unique combination of plumage pattern, vocal repertoire, and ecological characteristics, including a conspicuous dark slate facial mask, vivid rufous-cinnamon underparts, and a uniform brownish-gray back. Its vocalizations are remarkable, consisting of long and powerful songs that echo strikingly across the steep montane slopes, producing a characteristic resonant effect. The species was documented exclusively at higher elevations within a transitional zone between submontane and stunted forests, where the understory is densely structured by root mats. A preliminary population estimate, based on field detections and spatial extrapolation, suggests approximately 2,106 individuals restricted to the Serra do Divisor massif. Although no immediate anthropogenic pressures were observed within its range, the species may be highly vulnerable to climate change and to proposed infrastructure projects that threaten the integrity of this federally protected region. The discovery of *T. resonans* highlights the biological uniqueness of the Serra do Divisor, reinforces its status as a center of montane endemism, and underscores the critical importance of maintaining its long-term conservation.

Key words: amazon rainforest, endemic species, extinction, Tinamidae, Serra do Divisor National Park, Acre

Introduction

The genus *Tinamus* Hermann, 1783 was recently redefined by Bertelli *et al.* (2025), who restored its priority for the clade historically referred to as *Crypturellus* Brabourne & Chubb, 1914. Following their treatment, we here consider all species phylogenetically allied with *Tinamus soui* Hermann, 1783 as belonging to *Tinamus*. This genus comprises the small forest tinamous and is the most diverse within Tinamidae, with 21 recognized species (Gill *et al.* 2023). Despite its diversity, *Tinamus* remains one of the least-studied avian groups in the Neotropics, largely due to its cryptic habits and the inaccessibility of the dense forest habitats it occupies (Brennan 2004; Schelsky 2004).

The western Amazon harbors the greatest diversity of *Tinamus* species co-occurring within the same region. However, few studies have addressed the taxonomy of tinamous in this area, leaving several important questions unresolved. These include the taxonomic status and distributional limits of *T. undulatus undulatus* Temminck, 1815, *T. u. yapura* (Spix, 1825), and *T. u. adspersus* Temminck, 1815 (Piacentini *et al.* 2015); the diagnoses and potential overlap between *T. soui soui* Hermann, 1783, *T. s. inconspicuus* (Carriker, 1935), *T. s. harterti* (Brabourne & Chubb, 1914), and *T. s. nigriceps* (Chapman, 1923) (Winkler *et al.* 2020); the distributional boundaries and appropriate

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species delimitation between *T. brevirostris* Pelzeln, 1863 and *T. bartletti* (Sclater & Salvin, 1873) (Hellmayr & Conover 1948); as well as many others. Notably, Olmos *et al.* (2013) suggested the existence of an undescribed species in the interfluve between the Juruá and Madeira rivers allied to *T. bartletti*. However, this taxon may in fact correspond to the form originally described as *Crypturus bartletti caroli* by Brabourne & Chubb (1914) from Humaitá on the left bank of the Rio Madeira.

Amid the vast lowland forests of western Amazonia, rising from elevations of 150 to 180 meters, lies the Serra do Divisor, an isolated mountain complex located on the border between Brazil and Peru, with peaks reaching up to 800 meters (Vriesendorp *et al.* 2006a). This is a remote and poorly known region, where the few surveyed localities have been accessible mainly by helicopter (Gonzalez & Acuy 2017). The mountain formations are covered by sandy, highly drained, nutrient-poor soils, and receive moisture from the surrounding lowlands, which condenses along their steep slopes. These conditions create rare habitats for the region, including dense submontane forests at the base of the elevations, which gradually give way with increasing altitude to drier, stunted forests near the mountain summits (Vriesendorp *et al.* 2006b). This unique mountain environment harbors a distinctive avifauna, including endemics such as *Thamnophilus divisorius* Whitney, Oren & Brumfield, 2004.



FIGURE 1. Photos of an individual of the new *Tinamus* described in the present study at Morro Queimado, Serra do Divisor National Park, Mâncio Lima, Acre, Brazil, by Luis A. Morais.

On 3 October 2021, FIG recorded a distinctive vocalization in the understory of the Serra do Divisor mountain complex (XC1034606), Acre, Brazil. The song resembled those of *Tinamus*, yet no species could be confidently identified at the time, and no visual confirmation was obtained. Comparisons with all *Tinamus* vocalizations known from the region, alongside consultations with ornithologists experienced in Amazonian avifauna, failed to produce a conclusive match. The song appeared unlike any known tinamou vocalization, raising the hypothesis that it might represent an undescribed form. The same vocal signature was subsequently heard by RAAP on 18 November 2021, 23 September 2023, 10 October 2023, and 16 October 2024, and by LAM on 2 and 4 November 2024, all at the

same locality. Nonetheless, visual confirmation remained unattained, as efforts were hampered by dense vegetation, steep terrain, and, most notably, by an unusual acoustic phenomenon: the bird's vocalization exhibited pronounced diffusion within the forest understory, often misleading the observer's perception of the sound's distance and direction. However, on 6 November 2024, LAM succeeded in attracting two individuals using a digitally synthesized playback from earlier recordings, obtaining excellent views and photographs of one bird (Fig. 1), which revealed an equally distinctive and previously undocumented plumage pattern. After obtaining the requisite permits and licenses from the governmental agencies, we were able to collect some specimens of the observed species.

In this context, we recognize and formally describe this taxon as a new species of *Tinamus*, supported by a consistent set of diagnostic characters, including unique vocalizations, distinctive plumage, and specific ecological traits.

Methods

We examined skins of Tinamidae deposited in the ornithological collections of the Museu Nacional/Universidade Federal do Rio de Janeiro, Rio de Janeiro (MN); Museu Paraense Emílio Goeldi, Belém (MPEG); Departamento de Zoologia da Universidade Federal de Minas Gerais, Belo Horizonte (DZUFMG); and Instituto Nacional de Pesquisas da Amazônia, Manaus (INPA). We also relied, in the search for available names, on analyses and photographs previously taken by MAR of type specimens housed in fifteen of the most renowned scientific collections worldwide, including: the Colección Ornitologica Phelps, Caracas; the American Museum of Natural History, New York; the Smithsonian Institution, Washington DC; the Museum of Comparative Zoology, Harvard; the Museum of Zoology (Louisiana State University), Baton Rouge; the Field Museum of Natural History, Chicago; the Carnegie Museum, Pittsburgh; the Academy of Natural Sciences, Philadelphia; Natural History Museum, Tring, Muséum National d'Histoire Naturelle, Paris; the Museum für Naturkunde, Berlin; Naturhistorisches Museum, Vienna; the Naturalis Biodiversity Center, Leiden; and the Muséum d'Histoire Naturelle de Neuchâtel. A list of examined specimens is given in Appendix 1.

A field expedition was conducted from 7 to 20 July 2025 by LAM and MAC at the Serra do Divisor National Park, during which a preliminary survey of vocalizing individuals was conducted across the study area. Given that good-quality recordings were unavailable at the time, playback sounds were artificially designed by LAM in *Adobe Audition* v.25 by generating pure tones and manually trimming, timing, and modulating their pitch to reproduce the resonant voice of the species, based on spectrograms of recordings obtained by FIG. Then, additional sound recordings were obtained and deposited at macaulaylibrary.org (ML), and three specimens of the undescribed form were collected (under permit SISBIO-97489-1). These specimens are deposited in the ornithological collections of the Museu Nacional/Universidade Federal do Rio de Janeiro (MN), Museu de História Natural do Ceará Prof. Dias da Rocha/Universidade Estadual do Ceará (MHNCE) and Genetic Resources Collection of the Instituto Nacional de Pesquisas da Amazônia (CRG/INPA). Ecological information was obtained directly in the field and through necropsy of the collected specimens.

To obtain a preliminary estimate of the minimum population size of the new taxon in the Serra do Divisor region, we employed a simplified spatial analysis using QGIS. Circular buffers were generated around each confirmed observation point, with radio corresponding to the mean pairwise distance among all known occurrences. This procedure allowed an approximation of the average area potentially occupied by each individual. The total buffered area was divided by the number of recorded individuals to yield an estimated density coefficient (expressed in hectares per individual), which was subsequently applied to the extent of potential habitat. Potential habitat was modeled based on elevation data obtained from the Shuttle Radar Topography Mission (SRTM GL1, 30 m resolution) for the Serra do Divisor mountain complex in Brazil and Peru. The elevational range used in the model corresponded to the altitude range recorded at confirmed observation sites. From this filtered range, a polygon was constructed representing contiguous areas of potentially suitable topography for the species.

Results

During the field expedition to Serra do Divisor National Park, five recognized species of *Tinamus* were detected:

T. bartletti, T. cinereus (Gmelin, 1789), T. soui, T. strigulosus Temminck, 1815, and T. variegatus (Gmelin, 1789). All these species were recorded in lowland forests and along the lower montane slopes. In contrast, the only representative of the genus encountered in the higher elevations of the mountains, above 250 m a.s.l., were the specimens representative of the taxon here assumed as an undescribed species, exhibiting an unique combination of plumage coloration and vocal structure, which we formally name as:

Tinamus resonans sp. nov.

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Proposed Portuguese name: Sururina-da-serra Proposed English name: Slaty-masked Tinamou

Type locality: Serra do Divisor, left bank of the Rio Moa, Mâncio Lima, Acre, Brazil (7°25'46.8"S / 73°40'08.7"W, 415 m a.s.l.).

Holotype: MN 53848 (Fig. 2), skin and an open wing, adult female, collected and prepared by Luis A. Morais and Marco A. Crozariol on 14 July 2025. Alcohol specimen (carcass) MHNCE 1289. Tissue sample MNT (MN) 5020, MHNCE 1289 and INPA A 34051.

Description of holotype: Lores, crown, nape, and entire posterior portion of the neck dark slate-gray; cheeks, throat, anterior and lateral regions of the neck, and the upper chest vivid cinnamon-rufous, shifting to a slightly more ochraceous tone in the upper cheek area (Fig. 2A); when the bird adopts a calling posture, the throat assumes a noticeably whitish-cream hue (as can be seen in the individual photographed in Fig. 1D); dark slate-gray postocular stripe extending from behind the eye across the auriculars, partially enclosed by the cinnamon-rufous cheeks and a distinct superciliary stripe of the same cinnamon-ochre coloration; this superciliary stripe is subtly interrupted by the slate coloration at the rear edge of the auriculars but continues into the post-auricular region, creating a masked facial impression (Fig. 2B); the slate-gray of the hindneck descends from the crown as a broad stripe that contrasts abruptly with the rufous tones of the neck and throat and then blends posteriorly into the mantle; entire upperparts, including the mantle, scapulars, upper back, and dorsal surface of the wings, uniformly taupe brownishgray, lacking any transverse barring (Fig. 2C); remiges slightly darker dorsally (Fig. 2E) and light gray ventrally with a silvery sheen; underwing coverts pure white (Fig. 2F); abdomen sepia, with a well-defined whitish-cream area along the central posterior ventral line, extending from the level between the thighs to the cloacal opening, and also visible along the inner surfaces of the thighs; flanks with a darker shade of sepia, tending toward brown, and the feathers bear narrow whitish-cream margins, producing a subtly scaled pattern (Fig. 2D); undertail coverts with a central dark-brown triangular marking on each feather with contrasting whitish-cream edges; iris dark-brown; tarsi and toes dull olive-lead-gray; bill straight, dark-grey with a slate gloss, and with a slight dorsal curvature of the maxilla between the nostrils and the tip; proximal base of maxilla with a small ivory-white spot; mandible bicolored, proximal edges near the commissure dark-grey, similar to the maxilla, and entire ventral surface sharply contrasting ivory-white. Weight 342g, total length 296 mm, wingspan 517 mm, wing chord 149 mm, culmen length 28.8 mm, height of bill at nostrils 5.7 mm, tarsus length 49.1 mm, and tail length 40 mm. The ovary measured 12.1 × 7.7 mm, with the two largest follicles measuring 3.9 mm and 3.5 mm.

Paratypes: 1) MN 53847, skin (shmoo) and an open wing, adult female, Serra do Divisor, left bank of the Rio Moa, Mâncio Lima, Acre, Brazil (7°24'58.2"S / 73°40'06.8"W, 351 m a.s.l.), collected by Luis A. Morais and Marco A. Crozariol on 11 July 2025. Weight 362g, total length 310 mm. The ovary measured 19.8 × 8.7 mm, with the largest follicle measuring 7.7 mm. Alcohol specimen (carcass with complete skull preserved) MHNCE 1282. Tissue sample MNT (MN) 5019, MHNCE 1282 and INPA A 34049. 2) MN 53849, skin, adult female, Serra do Divisor, left bank of the Rio Moa, Mâncio Lima, Acre, Brazil (7°26'32.6"S / 73°40'14.5"W, 435 m a.s.l.), collected by Luis A. Morais and Marco A. Crozariol on 12 July 2025. Weight 360g, total length 320 mm, wingspan 508 mm, wing chord 153 mm, culmen length 29.7 mm, height of bill at nostrils 6.5 mm, tarsus length 51.1 mm, and tail length 42.4 mm. The ovary measured 16 × 11.5 mm, with the largest follicle measuring 6.8 mm. Alcohol specimen (carcass) MHNCE 1285. Tissue sample MNT (MN) 5021, MHNCE 1285 and INPA A 34050.

Diagnosis: This species differs from all other Tinamidae by presenting, at least in females (the three individuals whose sex could be determined were female), a distinctive dark slate-colored crown, which extends into a prominent stripe down the hindneck and into the post-ocular region, forming a conspicuous facial mask (Fig. 1 and 2). The

ferruginous coloration of the breast places it near the *T. variegatus/brevirostris* group, from which it is readily distinguished by its uniform brownish-gray dorsum lacking any barring, a condition otherwise shared only with *T. soui*. It can be further separated from *T. soui* by its ferruginous breast, neck, and cheeks and the presence of white on the lower belly. Its vocalization is unique and therefore diagnostic among the vocalizations attributed to other Tinamidae. As described below, it is distinguished by its overall structure and note modulation.

Variation: No significant variation in plumage was observed among the type series or the photographed and observed individuals. Only minor differences in body size were noted. Notably, the bifurcated pattern of the post-auricular mask was consistently present in all specimens.



FIGURE 2. Holotype of *Tinamus resonans* **sp. nov.** (MN 53848). Ventral view (A), lateral view (B), dorsal view (C), flanks (D), dorsal surface of the wing (E), ventral surface of the wing (F).

Etymology: From Latin, resonans is the present participle of the verb resonare ("to resound," "to echo"), used here in its adjectival sense meaning "resounding" or "echoing." The verb is composed of the prefix re- ("again" or "back") and the root sonare ("to sound"), which derives from the noun sonus ("sound"). The name refers to the striking echoing effect of the species' song, which reverberates across the steep montane slopes of its habitat as a result of strong acoustic diffusion. The common name "sururina" is an onomatopoeic term used by local riverine people to refer to ground-dwelling tinamous with modulated songs and is commonly applied to several species in the region, including Tinamus soui and T. variegatus. The addition of "-da-serra" ("from the mountains") highlights the distinct identity and montane habitat of this species, setting it apart from other sympatric taxa.

Song: We collected and analyzed a total of 52 audio recordings of *T. resonans*, which revealed three distinct vocal patterns, hereafter referred to as Pattern A, Pattern B, and Pattern C.

- **Pattern A** (25 recordings) is the most acoustically complex vocalization and was the only type spontaneously emitted without playback. In all encounters, it was consistently the first song pattern performed following playback stimulation. Pattern A can be divided into two distinct sections: prelude and climax (Fig. 3A). The prelude consists of five to seven pure-toned, flute-like notes with a smooth tonal quality, resembling *T. cinereus*. Each note lasts between 2.3 and 3 seconds, with duration gradually increasing throughout the sequence. Conversely, the intervals between

notes progressively shorten, beginning at approximately 2.5 seconds and decreasing to just under 1 second between the last two notes. Spectrogram analysis shows that these notes exhibit an asymmetrical "U"-shaped frequency contour. They begin around 1530 Hz, descend to approximately 1480 Hz, and rise again to about 1560 Hz. Each successive note starts at a slightly higher frequency, with the final note reaching up to 1660 Hz, representing an upward tonal shift of roughly two semitones from the first. The climax follows immediately after the final prelude note and typically comprises four repeated cycles. Each cycle includes three or four short, descending whistles followed by a longer whistle that begins at the same pitch as the final short note. After approximately 0.5 seconds, this long note abruptly rises about one tone and acquires a pronounced modulated (tremolo-like) quality, resembling the climax phrase of *T. soui*. With each repetition, the pitch of the climax increases slightly, reaching up to 1960 Hz in the final iterations. The vocalization ends with four to six short, descending chirps that extend the rhythmic cadence of the climax and mark the end of the call. Across the full sequence, the total tonal rise may span up to five whole tones and can last more than 45 seconds. Examples: ML641279042; ML641278816; ML641278817; ML641278818.

- **Pattern B** (22 recordings) resembles an excited response and was generally heard after a few minutes of interaction with playback, typically following several renditions of Pattern A. It consists of a sequence of 5 to 17 short, tremulous notes, beginning with notes approximately 2.5 seconds long, which gradually shorten to about 1 second toward the end of the sequence. The notes accelerate progressively throughout the sequence (Fig. 3B), with initial intervals of about 3 seconds decreasing to less than 0.5 seconds toward the end. The notes also gradually ascend in pitch, ranging from approximately 1400 Hz to 1900 Hz, occupying the same frequency band as Pattern A. This vocalization closely resembles the excited song of *T. soui* from southeastern Brazil's Atlantic Forest (LAM pers. obs.). Unlike Pattern A, which is highly stereotyped, Pattern B exhibits substantial structural variability. Examples: ML641278867; ML641278868; ML641279131; ML641279132.
- **Pattern C** (5 recordings) is a short, single-note call heard only in contexts involving multiple simultaneously vocalizing individuals, suggesting a possible social or responsive function. This call has a slightly tremulous tonal quality and lasts approximately 1.5 seconds (Fig. 3C). It begins near 1500 Hz and descends slightly in frequency by approximately one semitone. Examples: ML641278898; ML641278899.

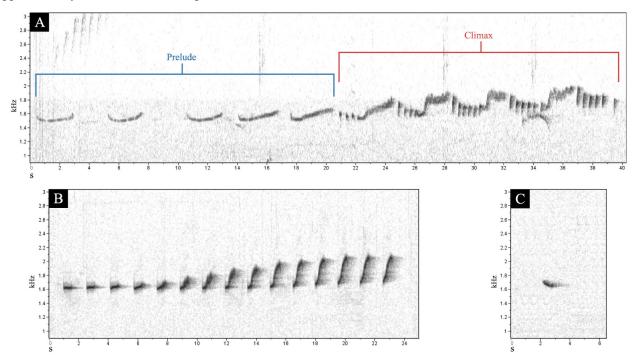


FIGURE 3. Spectrograms of the vocal patterns recorded from *Tinamus resonans* **sp. nov.** Song pattern A (A), song pattern B (B), song pattern C (C). Time and frequency scales are standardized across spectrograms.

At least one individual was observed performing all three vocal types, ruling out the hypothesis of vocal sexual dimorphism. One individual produced a structurally typical Pattern B, but with atypical tonal modulation and abrupt shifts in pitch within and between notes, resulting in a yodel-like effect (ML641277867). This irregularity is likely related to syringeal muscle control and has been previously observed in individuals of other *Tinamus* species (LAM pers. obs.), though its physiological basis remains, to some degree, uncertain.

Distribution and habitat: Tinamus resonans was detected at eight sites across the mountainous region of the Serra do Divisor, occurring on both banks of the Moa River, but predominantly along its left bank, within the Serra da Jaquirana (Fig. 4). All records are restricted to the municipality of Mâncio Lima, Acre, Brazil (see Discussion). The species was observed exclusively on the steep forest floor within a narrow transitional zone between 310 and 435 m a.s.l., representing a gradient between submontane and stunted forest. This habitat is characterized by an exceptionally dense and widespread mat of fine roots and leaf litter, forming a continuous network over nutrient-poor, quartzitic sandstone soil (Mendonça et al. 2020, 2023), through which the tinamou moves and forages. At all surveyed sites, the species was found in sympatry with *Thamnophilus divisorius*, which in Brazil was previously known only from its type locality, Morro Queimado.

Population size estimate: Over the course of ten independent encounters at eight sites, we confidently identified at least 15 distinct individuals. The mean distance between recorded individuals was 673 meters. Circular buffers with this radius were generated and clipped to the available elevational habitat (310–435 m a.s.l.), resulting in a total area of 450.81 hectares occupied by the 15 individuals. This corresponds to an estimated population density of approximately one individual per 30 ha. Considering the total extent of suitable habitat within the defined elevational range (63,302 ha), we estimate a preliminary population size of approximately 2,106 individuals in the Serra do Divisor mountain complex (Fig. 4).

Behavior: Tinamus resonans was recorded vocalizing spontaneously during the late afternoon and dusk, between 17:40 and 18:30 local time. Its song is loud and carries over long distances, but undergoes marked acoustic diffusion along the steep slopes of the Serra, which alters the temporal structure of the song due to echo. On one occasion, a vocalizing individual was detected from the camp at 23:00 h, at an estimated distance of approximately 900 m from the nearest slope. The species consistently responded to playback within its estimated home range, approaching the observer within a few minutes in all trials. When confronted directly, individuals showed no avoidance behavior and appeared remarkably tame, seemingly failing to recognize humans as potential predators. In addition, individuals were observed crossing open areas of understory slowly and without signs of vigilance, a behavior contrasting with the typically wary responses of other tinamous. Between vocal responses, birds were also observed foraging on the forest floor, probing and overturning leaf litter with the bill in search of food items.

Conservation: The Serra do Divisor is protected as national parks in both Brazil and Peru, forming a continuous conservation corridor of nearly two million hectares (Koga et al. 2022; Vriesendorp et al. 2006b). On the Brazilian side, the Serra do Divisor National Park (SDNP) was established in 1989, covers 843,012 ha and overlaps two Indigenous Lands as per the Decreto Federal n° 97.839, of June, 16th 1989 (available from: ttp://www.planalto. gov.br/ccivil 03/decreto/antigos/d97839.htm and https://uc.socioambiental.org/pt-br/arp/598, both accessed 15 September 2025). Although approximately 400 people live in the northern sector, where the park's mountainous terrain lies and where T. resonans is found, anthropogenic disturbances remain minimal, with less than 1% of primary forest altered since the park's creation (Koga et al. 2022). These alterations are concentrated mainly in the foothills of the Serra do Divisor, particularly along the banks of the Moa River. In areas where T. resonans has been recorded, there are no signs of human disturbance, and access trails had to be opened by us during field surveys. The only site within the range where human presence occurs is at Morro Queimado, which hosts the Mirante Trail leading to its summit, a popular viewpoint for sunrise and sunset. The summit clearing formed naturally in 1995, following a small fire triggered by a lightning strike (Whitney et al. 2004). This trail appears to have no measurable impact on the local avifauna: it is narrow, experiences low annual visitation, is the sole site where tourists can reliably observe Thamnophilus divisorius, and is also where T. resonans was first documented, confirming its occurrence even at this location. Aside from this localized visitation, other human activities in the montane zone are scarce, particularly hunting. We conducted interviews with local residents, which indicated that they do not ascend the mountains for this purpose, preferring to hunt larger-bodied animals inhabiting the lowlands, as also reported by Lemos et al. (2018). These authors further noted that the second most preferred vertebrate for hunting is the Whitethroated Tinamou Pezus guttatus (Pelzeln, 1863), targeted primarily at night while roosting a few meters above ground, a behavior distinct from that of *Tinamus* species, likely including *T. resonans*. The most immediate threat

to the conservation of T. resonans, and to the biodiversity of the SDNP as a whole, is a proposal to downgrade the park's legal status from National Park to Environmental Protection Area (Área de Proteção Ambiental), enabling the construction of a highway crossing the park as part of the planned extension of BR-364, linking the Brazilian municipality of Cruzeiro do Sul to Pucallpa, in Peru (Brazil 2019). This anti-ecological proposal also includes mineral exploitation in the mountainous area of the Serra do Divisor, the only known habitat for *T. resonans*, placing the species at direct risk. Furthermore, there is an additional proposal for a transcontinental railway connecting the Atlantic to the Pacific, also crossing the SDNP (Farrell & Silva-Macher 2017). The implementation of these projects, driven primarily by economic interests, would trigger well-documented negative environmental and social impacts associated with road building in the Amazon, including displacement of Indigenous peoples and loss of Indigenous languages (Krokoszyński et al. 2007, Farrell & Silva-Macher 2017, Short 2018, Rojas et al. 2021, Koga et al. 2022, Ruaro & Laurance 2022, Frisbie et al. 2025), significantly undermining conservation efforts in one of the planet's most pristine and biodiverse regions. Moreover, species restricted to specific microhabitats within narrow elevational ranges, such as T. resonans and Thamnophilus divisorius, are particularly vulnerable to climate change. Even minor shifts in temperature or precipitation can cause significant changes in vegetation structure and resource availability, thereby increasing extinction risk for highly specialized, range-restricted taxa (Neate-Clegg & Tingley 2023). Furthermore, due to the extremely shallow soils in the area where T. resonans occurs (Mendonça et al. 2020, 2023), the habitat is prone to landslides in years of intense rainfall, as has already been documented in the SDNP (Silva et al. 2022), another factor that should be considered in the context of climate change. Currently, *Thamnophilus divisorius* is classified as Least Concern (BirdLife International 2018), however, with the proposed downgrading of the SDNP, mining and the construction of roads, both species would certainly face elevated extinction risk.

Discussion

The species described here clearly belongs to the genus *Tinamus* Hermann, 1783, as recently redefined by Bertelli *et al.* (2025), which is now used for all species formerly classified within *Crypturellus*. This assignment is supported by its size, the typical body shape of small forest tinamous, and the presence of transverse plantar and tarsometatarsal scutes arranged in a single row of large scales, one of the key morphological diagnostic characters of the genus (Bertelli *et al.* 2025). The phylogenetic relationships of the new species to other members of *Tinamus* remain unknown, but certain morphological traits, such as the coloration of the underparts and the straight bill, suggest an affinity with the *T. variegatus/brevirostris/bartletti* group. The vocalization is most closely related to that of *T. variegatus*, as it includes elements composed of both smooth and frequency-modulated notes. This issue warrants further investigation in future studies.

All three individuals collected and sexed were females. Therefore, the appearance of the male remains unconfirmed, considering the possibility that other visually observed and photographed individuals may also have been females. However, pronounced sexual dimorphism in plumage is rare or poorly documented within the genus *Tinamus*, with only a few species, such as *T. strigulosus*, showing clear differences between sexes. The absence of males in the type series may be attributed to the behavioral ecology of *Tinamus* species, in which females tend to be the dominant sex and are primarily responsible for territorial defense (Magalhães, 1994; Sick, 1997). Consequently, females are more likely to approach playback, potentially resulting in a sampling bias favoring the collection of females.

The sites where *T. resonans* were observed suggest that the species may be ecologically associated with habitats similar to those occupied by *Thamnophilus divisorius*. The authors of that description hypothesized that *Thamnophilus divisorius* would likely occur in other physiognomically similar ridges throughout the Serra do Divisor (Whitney *et al.* 2004), a prediction that has since been confirmed. The species is now known to occur along the entire Serra do Divisor range (Gonzalez & Acuy 2017), including an isolated western massif, separated by a c.80-km-wide expanse of lowland forest from the main Serra do Divisor mountains, known as Ojo de Contaya in Peru (Vriesendorp *et al.* 2006b) (Fig. 4). Spatial occupancy and density patterns in Tinamidae are poorly known, with home range estimates varying widely among species and methods, from 0.1 to 118 ha (Garitano-Zavala). Our estimated density for *T. resonans*, one individual per 30 ha, likely reflects its occurrence as the only tinamou inhabiting the steep montane habitats of the Serra do Divisor. However, this data should be considered preliminary, and more robust approaches

are needed to clarify the species' spatial dynamics.

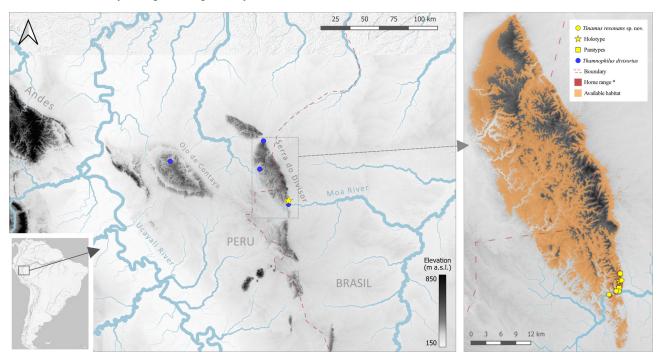


FIGURE 4. Elevation map of western Amazonia showing the distribution of rivers and mountain ranges. The yellow symbols indicate localities where *Tinamus resonans* **sp. nov.** was recorded. Blue dots represent current known occurrences of *Thamnophilus divisorius*, according to Gonzalez & Acuy (2017). The dashed red line represents the border between Peru and Brazil.

If *T. resonans* shares similar ecological requirements, a comparable distribution pattern may be revealed as additional areas are surveyed. However, several factors must be considered when comparing the ecological traits of the two species. Tinamous represent a much older avian lineage than antbirds, with most known speciation events predating those of the Thamnophilidae (Prum *et al.* 2015, Almeida *et al.* 2022). Furthermore, *Tinamus* species are strictly terrestrial, foraging, nesting, and roosting on the forest floor, and exhibit limited flight capability (Winkler *et al.* 2020). Consequently, their dispersal dynamics are markedly different and likely more restricted. Their ground-dwelling lifestyle may also impose stricter requirements regarding soil characteristics and understory composition. One of these adaptations may involve an adjustment in the breeding period of *T. resonans*. During fieldwork, we observed that most lowland bird species were undergoing molt, and many species in general were silent, suggesting they were outside the breeding season, whereas the three collected females exhibited enlarged ovaries. July is the driest month in the region (INMET 2025), which may be an important factor for *T. resonans* nesting, considering that it likely nests on the ground in a steep, shallow-soil environment. No reproductive information is currently known for *Thamnophilus divisorius* for comparison.

The mountains of the Serra do Divisor represent the easternmost known extensions of the Andes, belonging to the same tectonic cycle, and are the only place in Brazil where this mountain range is present (Silveira *et al.* 2008, Mendonça *et al.* 2023). However, in general, the SDNP remains poorly studied with regard to its biodiversity (Gonzales & Acuy 2017, Lemos *et al.* 2018, Koga *et al.* 2022), including birds (Whitney *et al.* 2004, Guilherme 2016). Even less is known about the higher elevations of the Serra do Divisor, which harbor several Andean elements in both fauna and flora (Vriesendorp *et al.* 2006, Silveira *et al.* 2008), making it a priority area for research and, especially, for conservation. The range may host a resident population of the Oilbird *Steatornis caripensis*, recorded both in the northern (Vriesendorp *et al.* 2006) and in the southern portion of the Serra do Divisor (De Luca 2025). It also harbors the main population of *Thamnophilus divisorius* and the only known population of *T. resonans*. During our fieldwork, we also recorded *Myiornis albiventris* (ML641276036; ML641276466), which represents the first record of this species for Brazil (Pacheco *et al.* 2021). Its song was detected at several sites on both banks of the Moa River, always in the higher elevations of the mountains, and often in the same area with *T. resonans* and *Thamnophilus divisorius*. Thus, the mountains of the Serra do Divisor represent a unique biogeographic history within the Amazonian context.

The SDNP is the only National Park in the state of Acre and the fourth largest in Brazil. It currently faces serious threats of being downgraded to an Environmental Protection Area to facilitate the construction of roads, railways, and mining activities (Farrell & Silva-Macher 2017, Brazil 2019, Koga *et al.* 2022, Ruaro & Laurance 2022, Frisbie *et al.* 2025). Such a downgrade must be strongly opposed, given its importance and unique characteristics. The discovery of *T. resonans*, in addition to strengthening this case, provides further justification for conservation while also representing a potential source of income for local communities. Ecotourism, particularly birdwatching, is undoubtedly one of the main income-generating activities in the northern portion of the SDNP. As the only place in the world with easy access to observe *Thamnophilus divisorius*, it will now also offer opportunities to see *T. resonans* occurring side by side. The awareness that local communities have developed regarding the value of conserving their environment and its species as a source of income has undoubtedly contributed to maintaining the pristine condition of the SDNP.

Nevertheless, many challenges remain. Not only do we lack a complete inventory of the species inhabiting the mountainous portion of the SDNP, but we also know even less about their ecology. In particular, detailed studies on the natural history and ecology of *T. resonans* are urgently needed. Understanding its environmental requirements, population dynamics, and sensitivity to habitat changes will be essential for guiding conservation strategies and ensuring the species' long-term persistence.

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References

- Almeida, F.C., Porzecanski, A.L., Cracraft, J.L. & Bertelli, S. (2022) The evolution of tinamous (Palaeognathae: Tinamidae) in light of molecular and combined analyses. *Zoological Journal of the Linnean Society*, 195, 106–124. https://doi.org/10.1093/zoolinnean/zlab080
- Bertelli, S., Almeida, F.C. & Giannini, N.P. (2025) A new phylogeny and classification of the tinamous, volant palaeognathous birds from the Neotropics. *Cladistics*, 41, 239–263. https://doi.org/10.1111/cla.12605
- BirdLife International (2018) *Thamnophilus divisorius*. *The IUCN Red List of Threatened Species*. Available from: https://doi.org/10.2305/IUCN.UK.2018-2.RLTS.T22733324A132181336.en (accessed 4 November 2025)
- Brabourne, L. & Chubb, C. (1914) A key to the species of the genus *Crypturus*, with descriptions of some new forms. *Annals and Magazine of Natural History*, Series 8, 14 (82), 319–322. https://doi.org/10.1080/00222931408693579
- Brennan, P.L.R. (2004) Techniques for studying the behavioral ecology of forest-dwelling tinamous (Tinamidae). *Ornitología Neotropical*, 15, 329–337.
- Carriker, M.A. (1935) Descriptions of new birds from Bolivia, with notes on other little-known species. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 87, 313–341.
- Chapman, F.M. (1923) Descriptions of proposed new birds from Venezuela, Colombia, Ecuador, Peru, and Chile. *American Museum Novitates*, 96, 1–12.
- Daly, D.C. & Silveira, M. (2008) Primeiro catálogo da flora do Acre, Brasil. EDUFAC, Rio Branco, 555 pp.
- De Luca, A.C. (2025) WA6954484, Steatornis caripensis Humboldt, 1817. Wiki Aves. Available from: http://www.wikiaves.

- com/6954484 (accessed 15 September 2025)
- Farrell, K.N. & Silva-Macher, J.C. (2017) Exploring futures for Amazonia's Sierra del Divisor: An environmental valuation triadics approach to analyzing ecological economic decision choices in the context of major shifts in boundary conditions. *Ecological Economics*, 141, 166–179.
 - https://doi.org/10.1016/j.ecolecon.2017.04.015
- Frisbie, A., Spera, S.A. & Salisbury, D.S. (2025) Transboundary road-building in the southwestern Amazon. *Journal of Latin American Geography*, 24, 18–52.
 - https://doi.org/10.1353/lag.2025.a962800
- Garitano-Zavala, A., Chura, Z., Cotín, J., Ferrer, X. & Nadal, J. (2013) Home range extension and overlap of the Ornate Tinamou (*Nothoprocta ornata*) in an Andean agro-ecosystem. *The Wilson Journal of Ornithology*, 125 (3), 491–501. https://doi.org/10.1676/12-151.1
- Gill, F., Donsker, D. & Rasmussen, P. (2023) *IOC World Bird List. Version 13.1*. Available from: https://www.worldbirdnames.org/ (accessed 15 September 2025)
- Gmelin, J.F. (1789) Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, Cum Characteribus, Differentiis, Synonymis, Locis. Vol. 1. Pt. 2. Impensis Georg, Leipzig, 768 pp.
- Gonzalez, O. & Acuy, M. (2017) A new location in Peru for the poorly-known Acre Antshrike *Thamnophilus divisorius* endemic of Serra do Divisor. *Revista Brasileira de Ornitologia*, 25, 137–139. https://doi.org/10.1007/BF03544390
- Gray, G.R. (1840) *A list of the genera of birds: with their synonyms and an indication of the typical species of each genus*. R. and J.E. Taylor, London, vii + ii + 80 pp. https://doi.org/10.5962/bhl.title.13777
- Guilherme, E. (2016) Aves do Acre. EDUFAC, Rio Branco, 900 pp.
- Hellmayr, C.E. & Conover, B. (1942) Catalog of birds of the Americas and the adjacent islands. Publications of the Field Museum of Natural History, Zoological Series, 13, 1–636.
- Hermann, J. (1783) Tabula affinitatum Animalium. Imprensis J.G. Treuttel, Strassburg, XVI + 371 pp.
- Illiger, J.K.W. (1811) Prodromus systematis mammalium et avium. C. Salfeld, Berlin, XIV + 301 pp. https://doi.org/10.5962/bhl.title.106965
- Koga, D.M., Brown, I.F., Fearnside, P.M. & Silva, S.S. (2022) Serra do Divisor National Park: a protected area under threat in the south-western Brazilian Amazon. *Environmental Conservation*, 49, 74–82. https://doi.org/10.1017/S0376892922000091
- Krokoszyński, Ł., Stoińska-Kairska, I. & Martyniak, A. (2007) *Indigenas aislados en la Sierra del Divisor*. UAM-AIDESEP, Iquitos-Lima-Poznań, 167 pp.
- Latham, J. (1790) Index ornithologicus, sive systema ornithologiæ; complectens avium divisionem in classes, ordines, genera, species, ipsumque varietates: adjectis synonyms, locis, descriptionibus. Vols. 1 & 2. Leigh and Sotheby, London, 16 + 919 pp.
 - https://doi.org/10.5962/bhl.title.131313
- Lemos, L.P., Bizri, H.R.E., Amaral, J.V., Santos, A.S., Koga, D.M. & Silva, F.E. (2018) Caça de vertebrados no Parque Nacional da Serra do Divisor, Acre. *Diversidade Brasileira*, 8, 69–88. https://doi.org/10.37002/biodiversidadebrasileira.v8i1.795
- Magalhães, J.C.R. (1994) Sobre alguns tinamídeos florestais brasileiros. *Boletim do Centro de Estudos Ornitológicos*, 10, 16–26.
- Mendonça, B.A.F., Schaefer, C.E.G.R., Fernandes-Filho, E.I., Simas, F.M.B. & Amaral, E.F. (2020) Genesis and micropedology of soils at Serra do Divisor and Moa river floodplain, northwestern Acre, Brazilian Amazonia. *Revista Brasileira de Ciências do Solo*, 44, e0200038.
 - https://doi.org/10.36783/18069657rbcs20200038
- Neate-Clegg, M.H.C. & Tingley, M.W. (2023) Building a mechanistic understanding of climate-driven elevational shifts in birds. *PLOS Climate*, 2, e0000174.
 - https://doi.org/10.1371/journal.pclm.0000174
- Olmos, F., Silveira, L.F. & Benedicto, G. (2013) A contribution to the ornithology of Rondônia, southwest of the Brazilian Amazon. *Revista Brasileira de Ornitologia*, 19, 31–44.
- Pacheco, J.F., Silveira, L.F., Aleixo, A., Agne, E.C., Bencke, G.A., Bravo, G.A., Brito, G.R.R., Cohn-Haft, M., Maurício, G.N., Naka, L.N., Olmos, F., Posso, S.R., Lees, A.C., Figueiredo, L.F.A., Carrano, E., Guedes, R.C., Cesari, E., Franz, I., Schunck, F. & Piacentini, V.Q. (2021) Annotated checklist of the birds of Brazil by the Brazilian Ornithological Records Committee—second edition. *Ornithology Research*, 29, 94–105. https://doi.org/10.1007/s43388-021-00058-x
- Pelzeln, A. (1863) Ueber vier von Natterer in Brasilien gesammelte, noch unbeschriebene Vogelarten. Verhandllungen der kaiserlich-kongiglichen zoologish-botanischen Gesellschaft in Wien, 13, 1125–1130.
- Piacentini, V.Q., Aleixo, A., Agne, C.E., Maurício, G.N., Pacheco, J.F., Bravo, G.A., Brito, G.R.R., Naka, L.N., Olmos, F., Posso, S., Silveira, L.F., Betini, G.S., Carrano, E., Franz, I., Lees, A.C., Lima, L.M., Pioli, D., Schunck, F., do Amaral, F.R., Bencke, G.A., Cohn-Haft, M., Figueiredo, L.F.A., Straube, F.C. & Cesari, E. (2015) Annotated checklist of the birds of Brazil by the Brazilian Ornithological Records Committee. Revista Brasileira de Ornitologia, 23, 91–298.

- https://doi.org/10.1007/BF03544294
- Prum, R.O., Berv, J.S., Dornburg, A., Field, D.J., Townsend, J.P., Moriaty-Lemon, E. & Lemmon, A.R. (2015) A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature*, 526, 569–573. https://doi.org/10.1038/nature15697
- Rojas, E., Zutta, B.R., Velazco, Y.K., Montoya-Zumaeta, J.G. & Salvà-Catarineu, M. (2021) Deforestation risk in the Peruvian Amazon basin. *Environmental Conservation*, 48, 310–319. https://doi.org/10.1017/S0376892921000291
- Ruaro, R. & Laurance, W.F. (2022) Pending bill could devastate Brazil's Serra do Divisor National Park. *Nature Ecology & Evolution*, 6, 120–121.
- https://doi.org/10.1038/s41559-021-01632-8
- Schelsky, W.M. (2004) Research and conservation of forest-dependent tinamou species in Amazonia Peru. *Ornitología Neotropical*, 15, 317–321.
- Short, C. (2018) The creation of the Sierra del Divisor National Park: the conservation of foreign investment in Peru, or how a national park neglects to fully protect natural resources or indigenous communities. *University of Miami Inter-American Law Review*, 49, 167–210. Available from: https://repository.law.miami.edu/umialr/vol49/iss1/8 (accessed 15 September 2025)
- Sick, H. (1997) Ornitologia brasileira. Editora Nova Fronteira, Rio de Janeiro, 912 pp.
- da Silva, S.S., Nascimento, E.S., de Almeida, M.R.N., Koga, D.M., de Melo, A.W.F., de Araújo, E.A., Brown, I.F., do Amaral, E.F., da Costa, J.G. & Souza, C.G. (2022) Natural mass movements in Serra do Divisor in the far west of the Western Amazon [Movimentos naturais de massa na Serra do Divisor no extremo oeste da Amazônia Ocidental]. *Research, Society and Development*, 11, e38711124724.
 - https://doi.org/10.33448/rsd-v11i1.24724
- Spix, J.B. (1825) Avium species novae, quas Brasiliam anus MDCCCXVII-MDCCCXX. Tom. 2. Impensis, Munich, 62 pp. https://doi.org/10.5962/bhl.title.63182
- Temminck, C.J. (1815) Histoire naturelle générale des pigeons et des gallinacés. Tome 3. J. C. Sepp & Fils, Amsterdam, 757 pp.
 - https://doi.org/10.5962/bhl.title.64844
- Vriesendorp, C., Schulenberg, T.S., Alverson, W.S., Moskovits, D.K. & Moscoso, J.-I.R. (Eds.) (2006) Perú: Sierra del Divisor. *Rapid Biological Inventories Report Vol. 17*. The Field Museum, Chicago, Illinois, pp. 1–200. [https://www.biodiversitylibrary.org/bibliography/96840]
- Whitney, B.M., Oren, D.C. & Brumfield, R.T. (2004) A new species of *Thamnophilus antshrike* (Aves: Thamnophilidae) from the Serra do Divisor, Acre, Brazil. *The Auk*, 121, 1031–1039. https://doi.org/10.1642/0004-8038(2004)121[1031:ANSOTA]2.0.CO;2
- Winkler, D.W., Billerman, S.M. & Lovette, I.J. (2020) Tinamous (Tinamidae). *In*: Billerman, S.M., Keeney, B.K., Rodewald, P.G. & Schulenberg, T.S. (Eds.), *Birds of the World*. Cornell Lab of Ornithology, Ithaca, New York, pp. 1–30. https://doi.org/10.2173/bow.tinami1.01

APPENDIX 1. Specimens examined.

Departamento de Zoologia da Universidade Federal de Minas Gerais: DZ 0356; 0357; 0358; 0359; 0360; 0361; 0363; 0364; 0365; 0367; 0369; 3885; 3886; 3887; 3921; 4217; 5058; 5059; 5060; 5061; 5062; 5063; 5064; 5065; 5400; 5978; 7369.

Museu Paraense Emílio Goeldi: MPEG 1703; 1704; 1705; 2857; 3202; 3329; 3393; 3440; 4506; 9650; 9651; 9653; 10017; 12560; 12561; 12562; 13008; 13766; 13768; 13769; 15906; 16280; 17967; 17968; 17969; 18211; 18798; 19143; 19691; 19692; 19790; 19791; 19792; 19793; 19794; 19795; 20605; 20903; 22621; 28225; 28354; 28439; 28494; 28495; 28496; 28497; 28498; 28507; 28508; 29939; 29940; 31614; 31615; 31616; 31991; 32689; 32690; 34903; 37476; 37660; 40650; 42240; 42241; 42242; 42243; 45618; 45619; 45620; 48028; 48477; 48478; 48479; 49201; 50711; 52537; 52538; 56038; 58395; 58396; 59305; 63242; 63243; 63244; 63672; 63854; 64035; 64957; 65102; 65726; 66162; 66163; 66164; 66165; 66395; 66396; 66598; 66599.

Museu Nacional/Universidade Federal do Rio de Janeiro: MN 4525; 4526; 4527; 4528; 4529; 4530; 4531; 4532; 4533; 4534; 4535; 4536; 4537; 4538; 20123; 23261; 23277; 23278; 23279; 24562; 24633; 25491; 25970; 26090; 26092; 26802; 26803; 26804; 26805; 26806; 26807; 27585; 32346; 32595; 32596; 32597; 32598; 32599; 32600; 32601; 32602; 32603; 32604; 32605; 32612; 33766; 33767; 33768; 35641; 36277; 38205; 39579; 39580; 37110; 4365; 4366; 4367; 4368; 4369; 4370; 4371; 4372; 20121; 20125; 20665; 20666; 25154; 26800; 26801; 32350; 38036; 38040; 39251; 39369; 39534; 39582; 53873.

Instituto Nacional de Pesquisas da Amazônia: INPA 561; 564; 5104; 2106; 6766; 6915; 6914; 6913; 3405; 2479; 8651; 565; 4334; 6916.

American Museum of Natural History: AMNH 6740; 45833; 108692; 115608; 123204; 178384; 245912; 388917; 468975; 469003; 469020; 469083; 469096; 469114; 254824; 272144; 469026.

The Academy of Natural Sciences of Drexel University: ANSP 119473.

Carnegie Museum of Natural History: CMNH 9206; 72997.

Collecion Ornitologica Phelps: COP 33207; 33288; 71972.

Field Museum of Natural History: FMNH 10368; 19702; 22971; 43208; 120805.

Museum of Comparative Zoology: MCZ 5002; 70055; 146457; 420855; 80123; 173012.

Muséum d'Histoire Naturelle de Neuchâtel: MHNN 921020.

The Natural History Museum: BMNH 1802; 926950; 1902313; 18926945; 18926951; 18926969; 18954123; 19133123; 189269128; 1892116152; 9023131862; 959111.

Naturalis Biodiversity Center: RMNH.AVES 87005; 87006.

Smithsonian Institute National Museum of Natural History: USNM 158434; 167715; 372312; 461692; 477516; 35005.

Museum of Natural History Vienna: NMW 20512; 20513.

Museum für Naturkunde: ZMB 11920; 19173.