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Photo: Alex Levitskiy



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Broad-billed Tody (*Todus subulatus*) response to playback of vocalizations and non-vocal sounds

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Abstract In order to test the hypothesis that the Broad-billed Tody (*Todus subulatus*) is territorial during the non-breeding season, we assessed the species' response to playback of three sounds (song, chatter call, and non-vocal wing-rattle) in January 2020 at twenty sites across two plots of native scrub forest in Punta Cana, La Altagracia Province, Dominican Republic. Todies responded more frequently to song (73%) than to chatter call (42%) or wing-rattle (25%). The response to song was more rapid, and todies approached closer to song than to chatter call or wing-rattle playback. Todies responded silently to broadcasting song (51%) less frequently than to wing-rattle (67%) or chatter call (76%). Todies that approached song playback silently appeared later than birds that responded with a wing-rattle or song. Regardless of their behavior, all came very close to the speaker. Although not all tests were statistically significant, they all showed a more rapid and intense response to song. We conclude that in January most of the habitat is defended aggressively and that Broad-billed Todies in Punta Cana have partitioned all suitable habitat into territories.

Keywords Broad-billed Tody, Dominican Republic, Hispaniola, playback experiments, Punta Cana, song, territoriality, *Todus subulatus*, wing-rattle

Resumen Respuesta de *Todus subulatus* a la reproducción de vocalizaciones y sonidos no vocales • Con el objetivo de probar la hipótesis de que *Todus subulatus* es territorial durante la temporada no reproductiva, evaluamos la respuesta de la especie a la reproducción de tres sonidos (canto, parloteo y vibración no vocal de las alas) en enero de 2020 en veinte sitios de dos parcelas de bosque de matorral nativo en Punta Cana, provincia La Altagracia, República Dominicana. Los individuos de esta especie respondieron con más frecuencia al canto (73%) que al parloteo (42%) o a la vibración de las alas (25%). La respuesta al canto fue más rápida y los individuos se acercaron más cuando se reprodujo el canto que el parloteo o la vibración de las alas. Fue menos frecuente que no hubiera respuesta a la emisión del canto (51%) que a la vibración de las alas (67%) o al parloteo (76%). Los individuos que se acercaron sin responder a la reproducción del canto aparecieron más tarde que los que respondieron con una vibración de las alas o un canto. Independientemente de su comportamiento, todos se acercaron mucho al altavoz. Aunque no todas las pruebas fueron estadísticamente significativas, todas mostraron una respuesta más rápida e intensa al canto. Concluimos que en enero la mayor parte del hábitat se defiende de manera agresiva y que *Todus subulatus* en Punta Cana han dividido todo el hábitat adecuado en territorios.

Palabras clave canto, experimentos de reproducción de canto, La Española, Punta Cana, República Dominicana, territorialidad, *Todus subulatus*, vibración de alas

Résumé Réaction du Todier à bec large (*Todus subulatus*) à la repasse de vocalisations et de sons non vocaux • Afin de tester l'hypothèse selon laquelle le Todier à bec large (*Todus subulatus*) est territorial en dehors de la saison de reproduction, nous avons évalué la réaction de l'espèce à l'écoute de trois sons (chants, cris de contact et bruits d'ailes non vocaux) en janvier 2020 sur vingt sites répartis sur deux parcelles de broussailles indigènes à Punta Cana, dans la province de La Altagracia, en République dominicaine. Les Todiers réagissaient plus souvent aux chants (73 %) qu'aux cris (42 %) ou aux bruits d'ailes (25 %). Lors de la diffusion de chants, les Todiers réagissaient plus rapidement et se rapprochaient davantage que lors de la diffusion de cris ou de bruits d'ailes. Ils réagissaient silencieusement moins souvent à la diffusion de chants (51 %) qu'à celle de bruits d'ailes (67 %) ou de cris d'appel (76 %). Les Todiers qui s'approchaient silencieusement du haut-parleur diffusant un chant apparaissaient plus tardivement que les oiseaux qui réagissaient par des bruits d'ailes ou un chant. Quel que soit leur comportement, ils se sont tous approchés très près du haut-parleur. Bien que tous les tests n'aient pas été statistiquement significatifs, la réaction de tous les Todiers au chant était plus rapide et plus intense. Nous concluons qu'en janvier, la plupart des habitats sont défendus

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de manière dynamique et que les Todiers à bec large de Punta Cana ont divisé tous les habitats appropriés en territoires.

Mots clés bruit d'ailes, chant, expériences de repasse, Hispaniola, Punta Cana, République dominicaine, territorialité, Todier à bec large, *Todus subulatus*

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The Broad-billed Tody (Todus subulatus) is the largest (8.43 \pm 0.39 g, *n* = 23; AAD unpubl. data) of the five tody species endemic to the Greater Antilles, and one of two species endemic to Hispaniola. Although the species is abundant, only two detailed studies of Broad-billed Todies have been published. Latta and Wunderle (1996) studied foraging behavior of the Hispaniolan todies, especially in areas where they are sympatric, and Kepler's (1977) monograph focused on the Puerto Rican Tody (Todus mexicanus), though she also provides details on the general behavior of all tody species. Todies are insectivorous and spend most of their time foraging. No sexual dimorphism has been described. Pairs remain together year-round, excavate nests in embankments from September until the onset of breeding, and breed from March through July (Kepler 1977, Keith et al. 2003, Latta et al. 2006). It can therefore be assumed that they would defend their territory year-round, or at least from September onwards, although this has not been confirmed. The Broadbilled Todies in Punta Cana seem to remain in the same territories over multiple years, as demonstrated by a few color-banded individuals that were reobserved in two successive Januarys at the exact same locations (AAD pers. obs.).

Todies are most vocal from February to May (Kepler 1977). The main vocalization of the Broad-billed Tody is a monotonous whistled call, "terp-terp," that can be heard year-round. Here, we will refer to this as their "song" following Xeno-canto (2020) and Cornell's Macaulay Library (2020), and consistent with Pérez Mena and Mora (2011) who described a similar vocalization of the Cuban Tody (Todus multicolor) as song. Kepler (1977) further reported a "trilly, chattering vocalization" that she heard a few times during aggressive encounters (which we will refer to as the "chatter call"), as well as various guttural sounds. Todies have a limited repertoire that in all species includes wing-rattling: a sound produced by air passing rapidly through the slightly attenuated outer wing primaries (Kepler 1977). Todies wing-rattle year-round, mostly during aggressive encounters and almost only when the birds are in flight (Kepler 1977, authors pers. obs.). Flying birds can modulate wing-rattling volume, with sounds ranging from silent to intense, and predominantly wing-rattle during close interactions. During our visits in January, wing-rattling was often used by a bird approaching an observer. Although wing-rattling is also used for courtship and nest defense, in January it is normally associated with territory defense (Kepler 1977).

Playback is a technique frequently used in bird studies to determine how individuals respond to specific sounds. For example, playback has been used to investigate whether birds distinguish between individuals by position (Brooks and Falls 1975), by performance (Dhondt and Lambrechts 1992), by geographical location (Pegan *et al.* 2015), and to determine the function of a particular vocalization (Xia *et al.* 2019). Because very little research has been published on the territoriality and vocalizations of Broad-billed Todies during the non-breeding season, we used playback of song, chatter call, and wing-rattle to test the hypothesis that in January (the non-breeding season), Broad-billed Tody pairs defend a territory. We also assessed whether different vocalizations have different functions by evaluating the variability in responses to the two vocal sounds (song, chatter call) and one non-vocal sound (wing-rattle). We expected that birds would show stronger responses to song, a long-distance vocalization, than to wing-rattle and chatter call, which are used during close aggressive interactions. Additionally, we anticipated that birds that approached song playback would predominantly use the wing rattle.

Methods

Study Plots

During January 2020, the dry, non-breeding season, we studied Broad-billed Todies in Punta Cana, La Altagracia Province, Dominican Republic (18°32'N, 68°24'W). The study site was predominantly covered with dry scrub forest or degraded dry scrub forest with some ornamental plants. We conducted playback experiments in two different plots: one near the Fundación Grupo Puntacana building and the water treatment ponds (referred to as the "Lodge"; Fig. 1), and the other about 500 m west, around the abandoned nature casitas of the former Punta Cana Beach Resort & Club (referred to as the "Casitas"; Fig. 1). The Lodge plot covered an area of ~6.5 ha and was bordered by wastewater treatment ponds to the west, the Fundación Grupo Puntacana building to the east, and trails to the north and south. We selected ten different sites at least 100 m apart from each other. Based on observations in January 2019 using playback at a site in Punta Cana with color-banded Broad-billed Todies, AAD was able to determine that playback at locations more than 100 m apart never attracted the same individual (unpubl. data). Most sites were along trails lined with trees, ornamental plants, and bushes



Fig. 1. The location of the sample plots, Lodge (red) and Casitas (orange), used for Broad-billed Tody playback experiments in Punta Cana, La Altagracia Province, Dominican Republic, January 2020. FPC marks the location of the Fundación Grupo Puntacana building and Ecological Reserve indicates the location of the Indigenous Eyes Ecological Reserve. Map credit: Aly Ollivierre.

on both sides. In the Casitas plot, which was ~8 ha and surrounded by native forest vegetation, we also selected ten sites. Eight sites were ~250 m apart and adjacent to an 8-m wide concrete road. Two other sites were ~100 m apart and near trails lined with trees, ornamental plants, and bushes. We selected the sites such that they were far enough apart so that the same individual tody would not encounter playbacks at multiple sites, and so that the observers could spread out to record tody behavior. We tagged sites on the first day of observation with orange flagging tape and recorded latitude-longitude to ensure that trials were completed at the same location throughout the entire study. All flagging tape tags were removed after the study concluded.

Playback Procedure

We broadcast playback using various speakers (UE Roll [Ultimate Ears, Irvine, CA, USA], Soundbox Color [DOSS, Montclair, CA, USA], and JBL Clip 3 [Harman International Industries, Los Angeles, CA, USA]) connected via Bluetooth to distinct smartphones (iPhone 8, iPhone X [Apple, Cupertino, CA, USA], or Samsung Galaxy S9 [Samsung, Seoul, South Korea]). For each trial, we placed the speaker in a tree or shrub ~1 m above the ground and three observers stood ~7 m away from the speaker. Each 9-min observation session consisted of 2 min of silent observation, followed by 3 min of observations during playback, then 4 min of post-playback observations. We used recordings from the Merlin Bird ID app (Cornell Lab of Ornithology, Ithaca, NY, USA). The song used was Macaulay Library catalogue number ML134950931 (recorded 7 January 2019, Punta Cana Ecological Foundation). The chatter call used was Macaulay Library catalogue number ML179944821 (recorded on 9 January 2019, Punta Cana Ecological Reserve), and the wing-rattle used was Macaulay Library catalogue number ML179942931 (recorded on 9 January 2019, Punta Cana Ecological Reserve). All sounds were recorded by Jay McGowan (Cornell Lab of Ornithology) and are available on the Macaulay Library (2020) database.

In order to have a balanced playback design whereby we played all sounds equally at each site and in both the morning (0800–1030) and afternoon (1600–1830), we used a schedule spread over 3 days (Table 1). On all 3 study days, each of the two plots was visited both in the morning and in the afternoon by a three-person observer group. In the morning, the observers played one of the three sounds at all 10 sample sites, and in the afternoon, the observers played a second sound at all 10 sample sites. In total, it took three days to carry out all playback experiments in which we played each sound (song, chatter call, and wing rattle) at all of the 10 sites in each plot, once in the morning and once in the afternoon. We conducted this 3-day playback design twice, once on 10, 11, and 12 January 2020, and again on 14, 16, and 17 January 2020.

We played the audio file assigned for the corresponding day and location (Table 1) on loop for 3 min from the Merlin Bird ID app. We approximated the volume levels to natural levels. For the UE Roll and SoundBox Color, we estimated natural levels to be 50% maximum volume for the song and 75% maximum volume for the chatter call and wing-rattle. For the JBL Clip 3, we estimated natural levels to be 70% maximum volume for the song, and 90% maximum volume for the chatter call and wing-rattle. **Table 1.** Study design of Broad-billed Tody sound broadcasting among study plots and times of day in Punta Cana, La Altagracia Province, Dominican Republic. The 3-day protocol was conducted twice in January 2020.

Study Plot	Time of Day	Sound			
Day 1					
Ĺodge	morning	call			
Casitas	morning	call			
Lodge	afternoon	rattle			
Casitas	afternoon	rattle			
Day 2					
Lodge	morning	song			
Casitas	morning	song			
Lodge	afternoon	call			
Casitas	afternoon	call			
Day 3					
Lodge	morning	rattle			
Casitas	morning	rattle			
Lodge	afternoon	song			
Casitas	afternoon song				

During each playback experiment, we recorded the weather conditions, tody response time after the start of playback, any behavioral responses (e.g., flight, movements), audio response elicited (song, chatter call, wing-rattle, or silent), number of individuals present, closest approach distance to the speaker for todies that responded (estimated by the observers), and if possible, whether any birds had color bands from a study conducted the previous year. We also recorded any tody observations during the pre-playback period.

Data Analysis

In order to minimize bias and determine if responses to the three sounds differed, we excluded all observations in which we detected a tody vocalizing within 50 m of the playback site during the 2-min pre-playback observation period. We compared response frequencies using a χ^2 test, or a Fisher-exact test where appropriate, using Statistix 10.0 (Analytical Software, Tallahassee, FL, USA). To compare continuous variables (approach distance, latency in response time), we used an ANOVA followed by a Tukey HSD *a posteriori* test if significant.

Results

We attempted to conduct 240 broadcast trials, 180 (75%) of which were successful (i.e., no todies were detected prior to broadcast). We detected todies responding to broadcasts in 86 (47.8%) of the successful trials (Tables 2 and 3).

Effect of Location and Time of Day on the Response Rate to Different Playback Sounds

Response rate to song (72.6%) did not vary between locations (χ^2 = 0.59, df = 1, p = 0.44) or time of day (χ^2 = 1.90, df = 1,

p = 0.17). Response rate to wing-rattle playback (25.4%) did not vary between locations ($\chi^2 = 3.01$, df = 1, p = 0.08), but it was significantly higher in the morning (37.5%) than in the afternoon (11.1%) ($\chi^2 = 5.38$, df = 1, p = 0.02). Response rate to playback of chatter call (42%) did not vary between locations ($\chi^2 = 0.33$, df = 1, p = 0.56) or time of day ($\chi^2 = 0.00$, p = 0.99) (Table 2).

Response rates differed significantly with the sound type broadcast ($\chi^2 = 27.62$, df = 2, p < 0.00001). The response rate to song was significantly higher than to wing-rattle ($\chi^2 = 26.89$, df = 1, p < 0.00001) and to chatter call ($\chi^2 = 10.71$, df = 1, p < 0.001), while the difference between wing-rattle and chatter call was marginally significant ($\chi^2 = 4.06$, df = 1, p = 0.044). Though in the morning the response rate to playback of wing-rattle and chatter call did not differ ($\chi^2 = 0.30$, p = 0.59), in the afternoon, the response rate to wing-rattle was significantly lower than to the chatter call (two-tailed Fisher-exact test: p = 0.012).

Variation in Response Type to Different Playback Sounds

Regardless of the sound broadcast for playback, the most frequent response was a silent approach (61%), during which todies approached the speaker silently, often flying around and approaching the loudspeaker very closely (Table 3). The least frequent response was singing (7%), while wing-rattle as a re-

sponse occurred in 32% of the cases.

Latency and Approach Distance

The closest approach distance differed significantly between the sounds broadcast ($F_{2,101} = 4.46$, p = 0.014) (Table 3). A posteriori tests indicated that todies came closer to the speaker when song was played than when chatter call was played (Table 3). Approach distance to wing-rattle playback was intermediate. Differences in response time were not statistically significant ($F_{2,96} = 1.75$, p = 0.18) (Table 3).

Approach distance did not differ with the response behavior, but time to approach was significantly longer for birds that approached silently than for birds that sang or produced a wing-rattle when approaching (F = 17.30; df = 2, 48; p = 0.00001) (Table 4). We did not perform the same analysis for the other sounds broadcast because sample sizes were too small.

Discussion

The most common response to all playback types was a silent approach. Song playback attracted todies more frequently than other playback sounds, and birds responding to song came closer to the speaker than in response to other sounds. On the other hand, birds did not usually respond to song playback with song

Sound played	Song				Wing Ra	attle	Chatter Call			
	n	Response	% Response	n	Response	% Response	n	Response	% Response	
Location										
Casitas	39	27	69.2%	34	10	29.4%	30	15	50.0%	
Lodge	23	18	78.3%	25	5	20.0%	29	11	37.9%	
Time of Day										
Morning	35	23	65.7%	32	12	37.5%	34	15	44.1%	
Afternoon	27	22	81.5%	27	3	11.1%	25	11	44.0%	
Total	62	45	72.6%	59	15	25.4%	59	26	44.1%	

Table 2. Broad-billed Tody response to playback of three sounds by location and time of day (before noon, after noon) in Punta Cana, La Altagracia Province, Dominican Republic, January 2020.

Table 3. Type of response, distance approached, and time to response of Broad-billed Todies responding to playback of different sounds in Punta Cana, La Altagracia Province, Dominican Republic, January 2020. Groups that differ significantly in distance approached are indicated by a different letter as calculated by the Tukey HSD *a posteriori* test. The detection of a single chatter call in response to a wing-rattle playback is not listed in this table so that n = 85.

Type of Response				Closest Distance Approached (m)				Time to Response (s)			
Sound Played	n	Wing Rattle	Song	Silent	n	Mean	SE	Group	n	Latency	SE
Call	26	5 (19%)	2 (8%)	19 (74%)	34	9.7	1.36	A			
Wing rattle	15	5°(33%)	0 (0%)	10 (67%)	18	6.3	1.87	AB	32	176	19.3
Song	45	18 (40%)	4 (9%)	23 (51%)	52	4.5	1.10	В	15	163	28.3
Total	86	27 (32%)	6 (7%)	52 (61%)							

^a Wing-rattle in response to wing-rattle includes one chatter call response.

Table 4. Mean time (s) to response (Latency) and closest approach distance (m) per response behavior in Punta Cana, La Altagracia Province, Dominican Republic, January 2020. Group indicates the groups identified by a Tukey HSD *a posteriori* test.

Response	n	Latency ± SE	Group	Approach Distance ± SE
Silent	24	199.5 ± 15.71	А	5.58 ± 0.70
Song	4	78.75 ± 38.49	В	3.75 ± 1.71
Wing-rattle	23	71.43 ± 16.05	В	3.52 ± 0.71

but more often with wing-rattle. Songs are thought to be longrange signals, while wing-rattles are used in close aggressive encounters (Kepler 1977). This could explain the relative lack of response to playback of wing-rattle. We agree with Kepler (1977) that wing-rattle is an aggressive, short distance sound as todies used it in flight when approaching song playback, but only rarely when responding to wing-rattle itself. Our observation that response to wing-rattle was much lower in the afternoon might suggest that todies are more aggressive in the morning, although this needs to be explored further.

Although Kepler (1977) does not give a name to what she describes as a "monotonous whistled call," we believe that calling this vocalization "song" is correct (see also Pérez Mena and Mora 2011). Song has essentially two functions: mate attraction and territory defense (Kroodsma and Byers 1991). Our observation that todies responded frequently to song playback in the non-breeding season, often approaching with an aggressive wing-rattle (Table 3), suggests that song is used in the non-breeding season to claim or defend a territory.

Another interesting observation is the high proportion of Broad-billed Todies that approached the speaker silently. In some cases, these birds stayed close and silent until the playback was stopped, after which some started to sing. These birds might have been neighbors or unpaired individuals that approached to investigate the foreign bird in the area. A study using color-banded birds would be needed to elucidate this hypothesis. Finally, the high response rate to song across both study plots suggests that in January, most of the habitat was occupied by todies that were either defensive of territories or curious about new or unknown intruders. Unfortunately, we were unable to conduct surveys for reliable occupancy or density estimates.

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Title Page Illustration

Vivian Lee and Jordan Chan observing the response to Broadbilled Tody playback in Punta Cana, Dominican Republic. Photograph taken by Alex Levitskiy in January 2020.

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