Always together: an extremely long pair bond in rufous horneros

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Abstract

Prolonged pair bonds, commonly reported in long-lived non-passerines that reunite each breeding season, are often linked to enhanced reproductive performance through improved partner familiarity. However, such bonds are rarely described in year-round territorial birds, particularly those with low sexual conflict. Here, I report a rufous hornero (*Furnarius rufus*) pair that remained together for at least 10 years within the same urban territory. This surpasses known pair bond durations for passerines (2–7 years) and rivals the time the partners spent together in many non-passerines. Over time, I observed morphological and acoustic changes, with females showing more signs of senescence (feather deterioration) and partners tending to exhibit slower duet responses and reduced song synchronization. Conversely, duet-level vocal performance traits, such as minimum frequency, bandwidth, and frequency modulation, tended to improve. As a model of sexual cooperation and shared roles in reproduction and territoriality, rufous horneros likely represent other Neotropical ovenbirds (Furnariidae). Therefore, further research into the

adaptive trade-offs of prolonged pair bonds in rufous horneros could shed light on the evolution of perennial monogamy in birds.

Keywords Divorce, Furnariidae, *Furnarius rufus,* Monogamy, Pair bond, Prolonged pair bond

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Data availability: All data are provided in the manuscript or supplementary material. Some data on morphology, acoustics, and territoriality were previously utilized in studies by one the author and colleagues (Diniz et al., 2016, 2018, 2019, 2024; Amorim et al., 2023b) and are appropriately cited within the text. Duet recordings, associated data, and the analysis code are available in the supplementary material and will be permanently archived in Mendeley Data upon manuscript acceptance.

Declarations

Ethical approval: This study was conducted with approval from the Brazilian environmental agencies Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio, licenses 40806–1 and 95944–1) and Centro Nacional de Pesquisa para Conservação das Aves Silvestres (CEMAVE, license 3886).

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Social monogamy occurs in about 90% of bird species (Cockburn 2006), but the duration of pair bonds varies widely (Dubois and Cézilly 2002; Kvarnemo 2018). Many species exhibit sequential or serial monogamy, switching partners within or between seasons (Griffith 2019), while others only form new pairs after divorce or the death of a mate (Boucherie et al. 2018; Botero-Delgadillo et al. 2024). Rare cases include long-term, prolonged bonds (Nisbet and Dann 2009; Sánchez-Macouzet et al. 2014) or lifelong bonds (Black 2001; Griggio and Hoi 2011) (i.e., perennial monogamy). This variation is linked to life-history traits, with long-lived, slow-paced species more likely to maintain adaptive long-term pair bonds (Kvarnemo 2018; Botero-Delgadillo et al. 2024).

The longest pair bonds among socially monogamous birds are recorded in long-lived non-passerines, especially seabirds and waterfowl (Table 1). For instance, partners can remain together for over 12 years in eurasian oystercatchers (*Haematopus ostralegus*) (Van De Pol et al. 2006). Wandering albatrosses (*Diomedea exulans*) often maintain bonds for 20 years, with a record of 28 years (Jouventin et al. 2007; Sun et al. 2022). In contrast, passerines, with shorter lifespans (10 vs. >30 years for non-passerines) (Wasser and Sherman 2010; Silva-Jr et al. 2020), typically form shorter maximum bonds, such as 5 years in southern pied-babblers (*Turdoides bicolor*) (Wiley and Ridley 2018) and 7 years in sociable weavers (*Philetairus socius*) (D'Amelio et al. 2024) (Table 1).

Prolonged pair bonds can enhance reproductive performance in socially monogamous birds when the costs of staying with the same partner (e.g., genetic incompatibility, infertility) are low (Kwon and Kempenaers 2023), divorce costs (e.g., mate searching and bond formation) are high (Choudhury 1995; Culina et al. 2015). Additionally, partner familiarity can improve coordination in shared activities like nest building and offspring provisioning, ultimately advancing and prolonging the timing of breeding activities (Griggio and Hoi 2011; Gabriel and Black 2013; Sánchez-Macouzet et al. 2014; Culina et al. 2020). Although often linked with site fidelity, breeding experience, and age, mate retention or prolonged pair bond are frequently associated with higher reproductive success in many species (Black 2001; Griggio and Hoi 2011; Gabriel and Black 2013; Sánchez-Macouzet et al. 2014).

Evidence for adaptive prolonged pair bonds in passerines is mixed, partly due to their shorter lifespans, which may constrain the benefits of long-term pair bonds (Llambías et al. 2008; Botero-Delgadillo et al. 2024). Most documented cases involve short-lived passerines in the Northern temperate zone (Pampus et al. 2005; Culina et al. 2020) or long-lived migratory birds that reunite each breeding season but dissolve bonds afterward (Dubois and Cézilly 2002; Kloskowski 2022). In contrast, relatively little research exists on long-lived, year-round territorial passerines in the Southern Hemisphere (Llambías et al. 2008; Lv et al. 2016; D'Amelio et al. 2024). Antbirds (Thamnophilidae) and ovenbirds (Furnariidae) can live longer (Scholer et al. 2018; Bornschein et al. 2015; Silva-Jr et al. 2020) and face intense competition for territories in stable neighborhoods, where breeding positions are scarce (Freed 1987; Tobias et al. 2011; Diniz et al. 2019). These conditions likely enhance territory and pair fidelity while reducing sexual conflict (Massoni et al. 2012; Diniz et al. 2020), which are ideal for studying prolonged pair bonds and perennial monogamy (Griffith 2019).

The rufous hornero (*Furnarius rufus*) is a year-round territorial Neotropical passerine that breeds in austral spring and has a recorded maximum longevity of at least 8 years, accounting for one year to reach sexual maturity (Fraga 1980). Most pairs (59%) remain together for 2 or more years, with partner replacement likely due to death rather than divorce (Amorim et al. 2023b). Partners exhibit low sexual conflict, cooperating extensively in foraging, vigilance, duet singing, territorial defense, and reproduction (Massoni et al. 2012; Diniz et al. 2020, 2021; Amorim et al. 2023b), while rarely engaging in extra-pair copulations (Diniz and Biagolini-Jr. 2021) and showing a low extra-pair paternity rate (3% of the young; Diniz et al. 2019).

I recaptured a rufous hornero pair breeding 10 years after being banded and observed in the same territory (Table 1). This pair pertains to a long-term study population at Darcy Ribeiro campus in Brasilia, central Brazil (15°46'S; 47°52'W). The male and female were first captured and banded on 30 September and 9 October 2014, respectively (Diniz et al. 2016, 2019), and recaptured on 1 November 2024 (Supplementary Material Fig. S1) using a funnel fish-trap at the nest entrance (Braga et al. 2014). The territory was monitored biweekly from June to December 2015 (Diniz et al. 2018) but not systematically visited between January 2016 and October 2024. Given the lack of evidence for territory switching or reestablishment of pair bonds by replaced individuals (Fraga 1980; Amorim et al. 2023b), I confidently conclude this pair has remained together in the same territory for 10 years.

This rufous hornero pair has been subjected to several studies (Diniz et al. 2018, 2019, 2021; Amorim et al. 2023b). An 1 hour focal observation conducted on 11 December 2024 confirms that the pair inhabits and sing inside the same territorial boundary estimated in 2015 (Fig. 1 and Supplementary Material Fig. S2a) (Diniz et al. 2019). In 2024, the pair began building a nest on 12 October, a time when pairs in the population are often mid-incubation, including this same pair in 2014 and 2015 (Diniz et al. 2018, 2019). The nest was completed by 28 October, and on 1 November (Supplementary Material Fig. S2c), one partner was observed incubating eggs—later than the typical timing when most nests are in the late nestling stage or fledglings have already left (Diniz et al. 2018). For example, this pair was observed feeding three nestlings in October 2014 and November 2015 (Diniz et al. 2019). On 11 December 2024, the pair was seen feeding two unbanded post-fledglings (Supplementary Material Figs. S2b, S2d). Notably, the 2024 nest was built in a tree 17 meters from the nest site used in 2015 (Fig. 1).

The rufous hornero pair exhibited variation in morphology and duet acoustics over time. Morphological measurements (following Diniz et al. 2016) showed subtle changes: in 2024, the female had longer wings and tail but was lighter, while the male had shorter wings and tail. Both had larger bills in 2024 (Table 2). Additionally, the 2024 female had two missing toes on the left foot, worn feathers, and missing nape feathers (Supplementary Material Figs. S1a, S2b). I compared 7 duets from 2015 (following Diniz et al. 2024) and 8 from 2024 (see Supplementary Material for methods; Fig. 2). Duets from 2024 had higher frequency modulation index values (232.46 vs. 154.34; t-tests, adjusted $P = 0.03$) and tended toward lower minimum frequencies (2.9 vs. 3.04 kHz, adjusted $P = 0.07$) and wider bandwidths (1.01 vs. 0.73 kHz, adjusted $P = 0.07$) than those from 2015 (Supplementary Material Table S1). In 2024, response times to partner-initiated songs tended to be longer (female: 0.93 vs. 0.12 s, male: 0.66 vs. 0.19 s; ANOVA, adjusted $P = 0.11$), and song synchronization tended to be lower (78 vs. 90%) compared to 2015 (t-test, adjusted $P = 0.07$; Supplementary Material Tables S1, S2).

The rufous hornero pair exhibits the longest known pair bond duration among passerines, lasting at least 10 years (Fig. 1, Table 1). Rare partner replacement and territory vacancies (Diniz et al. 2020; Amorim et al. 2023b) make rufous horneros ideal for studying the benefits of extended pair bonds, including partner familiarity (Griffith 2019) and the costs of divorce (Choudhury 1995). Territory stability supports the idea that rufous horneros maintain well-defined territories, likely linked to their strong neighbor-stranger discrimination abilities (Amorim et al. 2022, 2023a). Therefore, high territorial

fidelity may be driven by the benefits of familiarity in territory defense and its association with prior reproductive success (Greenwood 1980; Sedgwick 2004).

Despite the potential benefits of prolonged pair bond, I found signs of senescence in this rufous hornero pair. The female appears to be in worse condition than the male, with deteriorate plumage and missing toes. In addition, egg-laying was delayed compared to the population average, potentially reducing reproductive success (Bonamour et al. 2025). These result aligns with the high physiological costs of territory defense for females than males (Mentesana and Adreani 2021), and likely high reproductive costs despite the similar and equitable parental investment (Massoni et al. 2012).

Some acoustic features of rufous hornero duets show signs of declining performance over time, though these results may be confounded by song variation due to breeding stage (Diniz et al. 2018). In 2024, both sexes tended to have longer response times to partner-initiated songs and lower song synchronization than in 2015, suggesting song senescence (Zipple et al. 2019). However, duets in 2024 exhibited higher frequency modulation, and tended to show lower frequency and wider bandwidth—traits often linked to better vocal performance and intrinsic quality in songbirds (Benedict and Najar 2019). Future studies could investigate whether these acoustic variations signal pair attributes like bond duration, age, or territory retention (Zipple et al. 2020).

In conclusion, I document a likely record pair bond duration for passerines, with an urban rufous hornero pair remaining together for 10 years—comparable to values in long-lived non-passerines (Table 1). This underscores the need for further research on the patterns and adaptive trade-offs of prolonged pair bonds in year-round territorial passerines to better understand the evolution of perennial monogamy in birds.

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Table 1 Maximum pair bond duration for some bird species, including passerines from the Southern Hemisphere and the rufous hornero, based on a non-systematic literature review. Systematic order and taxonomy following Billerman et al. (2022).

Species	Pair bond duration (in years)	Reference
Non-passerines		
laysan duck (*Anas laysanensis*)	9	Reynolds et al. (2009)
eurasian oystercatcher (*Haematopus ostralegus*)	12	Van De Pol et al. (2006)
thick-billed murre (*Uria lomvia*)	13	Gousy-Leblanc et al. (2023)
black-legged kittiwake (*Rissa tridactyla*)	7	Naves et al. (2007)
little penguin (*Eudyptula minor*)	13	Nisbet & Dann (2009)
blue-footed booby (*Sula nebouxii*)	9	Kim et al. (2007)
red-necked grebe (*Podiceps grisegena*)	5	Kloskowski (2022)
wandering albatross (*Diomedea exulans*)	28	Jouventin et al. (2007), Sun et al. (2022)
Passerines		
rufous hornero (*Furnarius rufus*)	10	This study
thorn-tailed rayadito (*Aphrastura spinicauda*)	6	Botero-Delgadillo et al. (2024)
hair-crested drongo (*Dicrurus hottentottus*)	6	Lv et al. (2016)
southern pied-babbler (*Turdoides bicolor*)	5	Wiley & Ridley (2018)
southern house wren (*Troglodytes musculus*)	2	Freed (1987)
buff-breasted wren (*Cantorchilus leucotis*)	4	Gill & Stutchbury (2006)
sociable weaver (*Philetairus socius*)	7	D'Amelio et al. (2024)

318 **Table 2** Morphological measurements of a rufous hornero pair caught at the same territory within the
319 Campus Darcy Ribeiro in Brasilia, central Brazil, on 30 September (male) and 9 October 2014 (female)
320 and then in 1 November 2024 (both sexes). Morphological terms and measurements after Diniz et
321 al.2016)

Measurement	Female		Male	
	2014	2024	2014	2024
Bill-depth (mm)	5.55	6.60	5.54	6.80
Bill-length (mm)	14.20	15.00	15.18	15.70
Bill-width (mm)	5.76	7.00	5.72	6.80
Mass (g)	53.00	50.50	53.05	54.00
Tail-length (mm)	65.14	66.00	71.20	69.70
Tarsal-length (mm)	33.01	33.30	35.65	36.30
Wing-length (mm)	88.54	90.50	96.60	94.40

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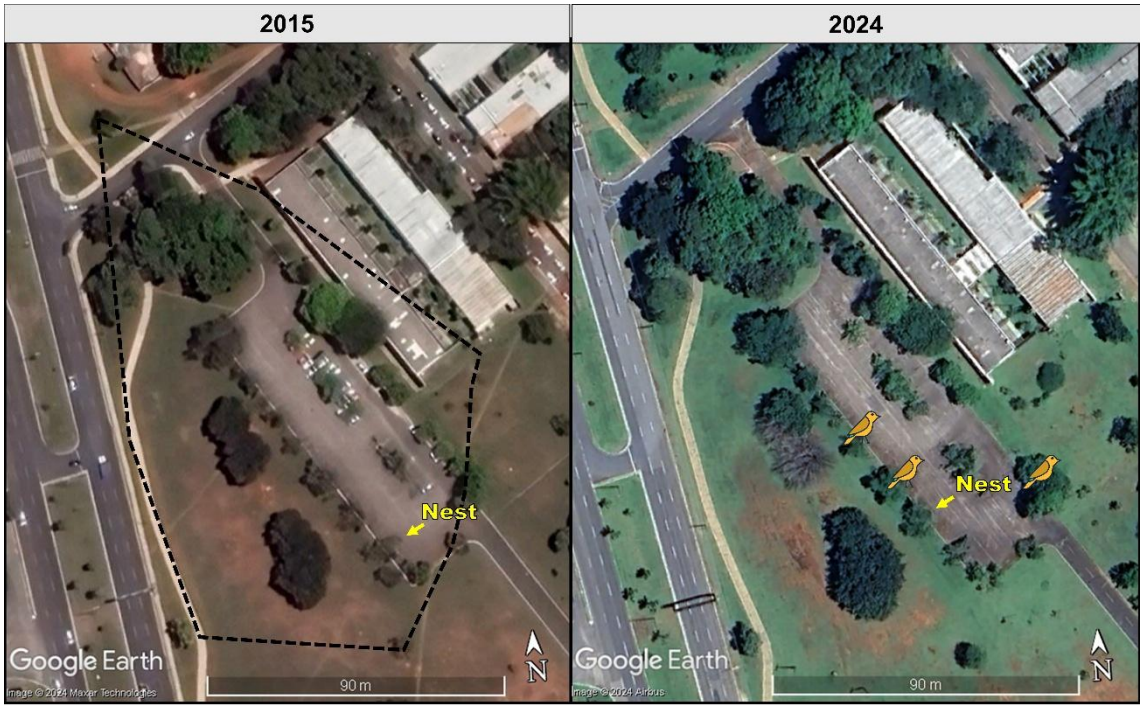
Figures Captions:

Fig. 1 Territory of the same rufous hornero pair recorded in 2015 and 2024. The nests (yellow arrows) from 2014 and 2024 were 17 m apart. The 2015 territory perimeter (dashed black polygon) was estimated from song posts and aggressive interactions during 14 one-hour focal sessions (Diniz et al. 2019). Bird icons indicate singing locations from a one-hour focal observation in 2024. Images: Google Earth (6 Nov 2015, 13 Feb 2024). Bird icons: Flaticon

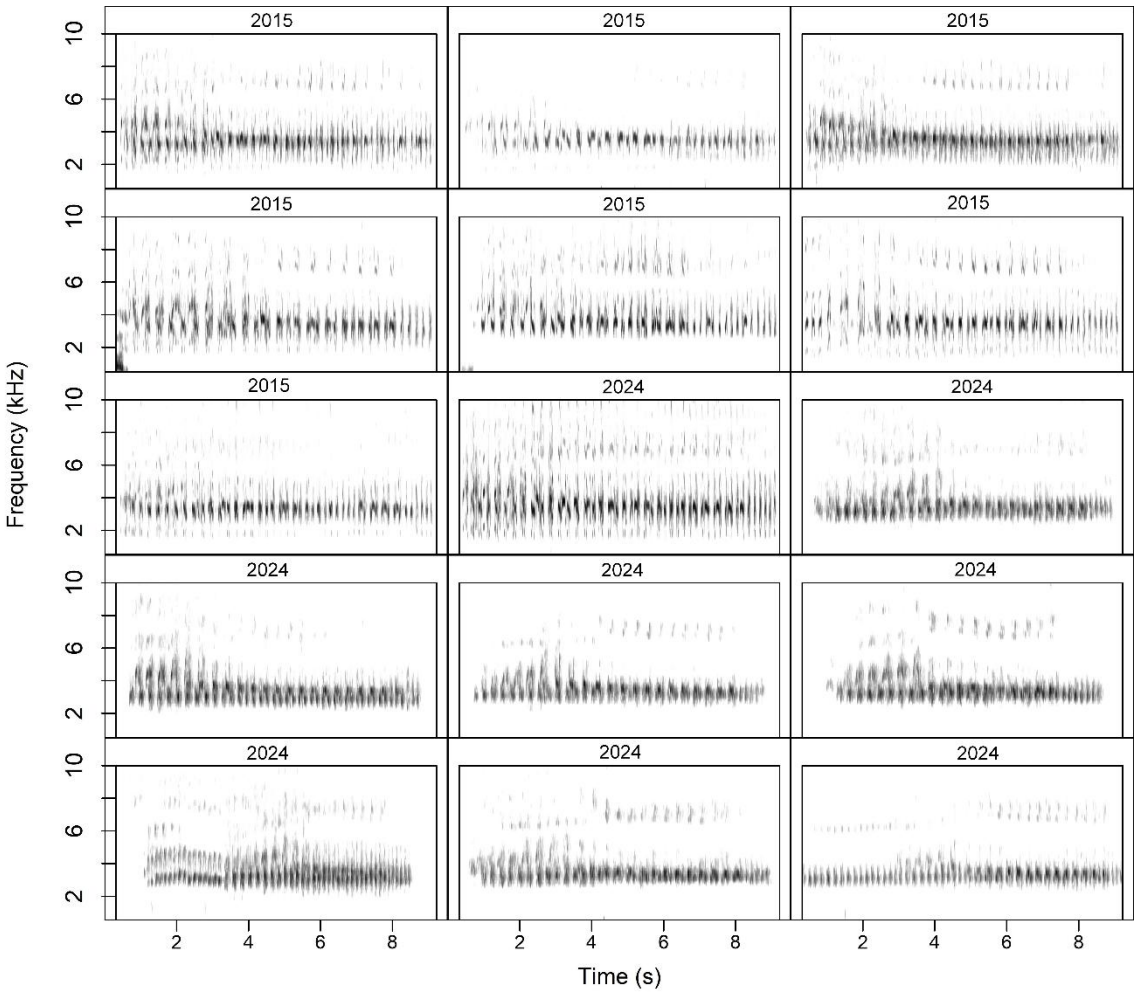
Fig. 2 Spectrograms of duets from the same rufous hornero pair recorded in 2015 and 2024. Created using the *catalog* function from the *warbleR* 1.1.32 package (frequency range: 0.5-10 kHz, window length: 256, overlap: 50)

Figures:

Figure 1



337 Figure 2



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