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NATURAL HISTORY FIELD NOTE

Intra- and interspecific nest stacking in marsh-dwelling songbirds

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Abstract

Nest stacking is a rarely reported phenomenon in birds. Here, we place the behav-ior within the broader context of nest functions, describe new observations of nest stacking within and between Neotropical marsh-dwelling songbirds, and discuss the ecological significance of this behavior, including its role in interspecific facilitation.

Abstract in Spanish is available with online material.

KEYWORDS
ecology, Many-colored Rush Tyrant, marsh birds, nest, nest stacking, Peru, *Phleocryptes*, *Tachuris*, Wren-like Rushbird

1 | INTRODUCTION

Nest construction is a widespread phenomenon that has been documented across the tree of life in arthropods, fish, reptiles, mammals, and birds (Hansell & Hansell, 2005). A diversity of nest structures and nest-building behaviors exist, particularly among birds (Hansell, 2000). Nests primarily provide a protected location to lay eggs and/or raise offspring; however, bird nests are increasingly recognized as multi-purpose structures (Mainwaring et al., 2014). For example, nests can minimize predation risk (Lima, 2009; Prokop & Trnka, 2011), act as sexual and/or social signals (Moreno, 2012; Smith & Harper, 2003), reduce parasitism (Bush & Clayton, 2018; Scott-Baumann & Morgan, 2015), and modulate essential microclimates for developing young via controlling temperature and humidity (Englert Duursma et al., 2018; Heenan, 2013).

Nest site selection affects multiple functions of bird nests. In particular, competition for desirable nesting sites can lead to construction of nests within close proximity to one another and increased density of nests across the landscape can drive tradeoffs among nest functions (Berg et al., 2006; Clark & Robertson, 1979; Hogstad, 1995). For example, as nesting density increases, ectoparasites may spread more easily (Hoi et al., 1998; Kleindorfer & Dudaniec, 2009), intraspecific brood parasitism may go unnoticed (Brown, 1984; Emlen & Wrege, 1986), and predation risk may increase (Bellinato, 1995; Brown, 1996; Tinbergen et al., 1967). Nonetheless, nesting behaviors, such as colonial breeding, in which dozens to hundreds of individuals construct closely spaced nests (Siegel-Causey & Kharitonov, 1990; Wittenberger & Hunt, 1985), have evolved independently across many avian clades (Rolland et al., 1998; Siegel-Causey & Kharitonov, 1990). The prevalence of high-density nesting is likely due to several context-dependent benefits. Increased nesting density may confer antipredation defenses via dilution effects, mobbing, or mutual nest defense (Birkhead, 1977; Hogstad, 1995; Ims, 1990; Marzluff & Balda, 2010; Picman et al., 2002; Poiani, 1991). Increased intraspecific vigilance among densely nesting individuals may reduce interspecific brood parasitism (Brown & Lawes, 2007), and when food supplies vary spatially and/or temporally, dense nesting may facilitate foraging success (Horn, 1968). Thus, in certain contexts, the costs of densely distributed nests are balanced by the benefits.

One poorly understood and rarely described form of communal nesting behavior is nest stacking, which we define as the construction of nests directly on top of previously constructed (i.e., older) nests. Although seldom observed and rarely reported, with at least 4 examples from the primary literature, intra- and interspecific nest-stacking behaviors have been described from a variety of bird species worldwide. For example, Fierro-Calderón and Martin (2007) observed two female Violet-Chested Hummingbirds (*Sternoclyta cyanopectus*) in Venezuela constructing new nests on top of old nests. Verner and Engelsen (1970) noted Marsh Wrens (*Cistothorus palustris*) in the Pacific Northwest, USA, building stacked four-nest "apartments". A pair of Silver Gulls (*Chroicocephalus novaehollandiae*) were observed constructing a new nest on top of an unoccupied swan (*Cygnus* sp.) nest in Australia (Smith & O'Connor, 1955). In Argentina, Lara et al. (2011) documented an existing Many-colored Rush Tyrant (*Tachuris rubrigastra*) nest engulfed by a Wren-like Rushbird (*Phleocryptes melanops*) nest that was subsequently abandoned by the Rush Tyrant.

Here, we report additional observations of intra- and interspecific nest stacking between and among Many-colored Rush Tyrants and Wren-like Rushbirds in coastal Peru. We posit that interspecific nest stacking may represent an underappreciated biotic interaction and a form of interspecific facilitation (Bronstein, 2009) for two co-distributed, marsh-dwelling songbirds that have traditionally been perceived as competitors.

The Many-colored Rush Tyrant (family: Tachurididae) and Wren-like Rushbird (family: Furnariidae) are marsh passerines with largely overlapping ranges in freshwater and brackish marshes of southern and western South America (Figure 1). Both species eat mainly arthropods; however, they differ subtly in their prey size preferences and feeding behaviors, and broad geographic co-occurrence suggests resource partitioning. The Many-colored Rush Tyrant forages by gleaning from rushes, grasses, and the water's surface, occasionally sallying for smaller prey, while the Wren-like Rushbird mainly gleans larger arthropods from the surface of standing water and mud (Clock, 2020; Remsen et al., 2020). Both the Many-colored Rush Tyrant and Wren-like Rushbird build nests made of and protected among tall rushes and cattails (Favretto et al., 2017). The Many-colored Rush Tyrant typically builds a small, open cup nest, ranging from round to oblong and pointed, with a sharply tapered bottom (Amaro & Goyoneche, 2017; Figure 2a). The Wren-like Rushbird typically constructs a covered dome-shaped nest that is fully enclosed except for the side entrance (Figure 2b), using a mud-daubing technique to insulate and secure the inner nest chamber (Amaro & Goyoneche, 2017; Lara et al., 2011; Zyskowski & Prum, 1999). Multiple reports of both species' breeding phenologies (Figure 1) suggest that geographic subpopulations of the species tend to breed synchronously (Chiaradia et al., 2017; Garcia & Torres, 2017; Mason, 1985; Maurício et al., 2013).

On 14 July 2016 at Zona Reservada Humedales de Puerto Viejo (ZRHPV) south of Lima, Peru (12° 34′ 7.38" S; 76° 42′ 30.96" W), we observed a single Many-colored Rush Tyrant cup nest constructed directly on top of a Wren-like Rushbird closed dome nest, which was constructed above a second Wren-like Rushbird nest (Figure 2c). We observed the stacked nests among fragmented stands of bulrushes (*Schoenoplectus* sp.) housing approximately $n = 12$ standalone nests of each species in close proximity (~90-m^2 area). We matched nests to their corresponding species by comparing nesting materials,

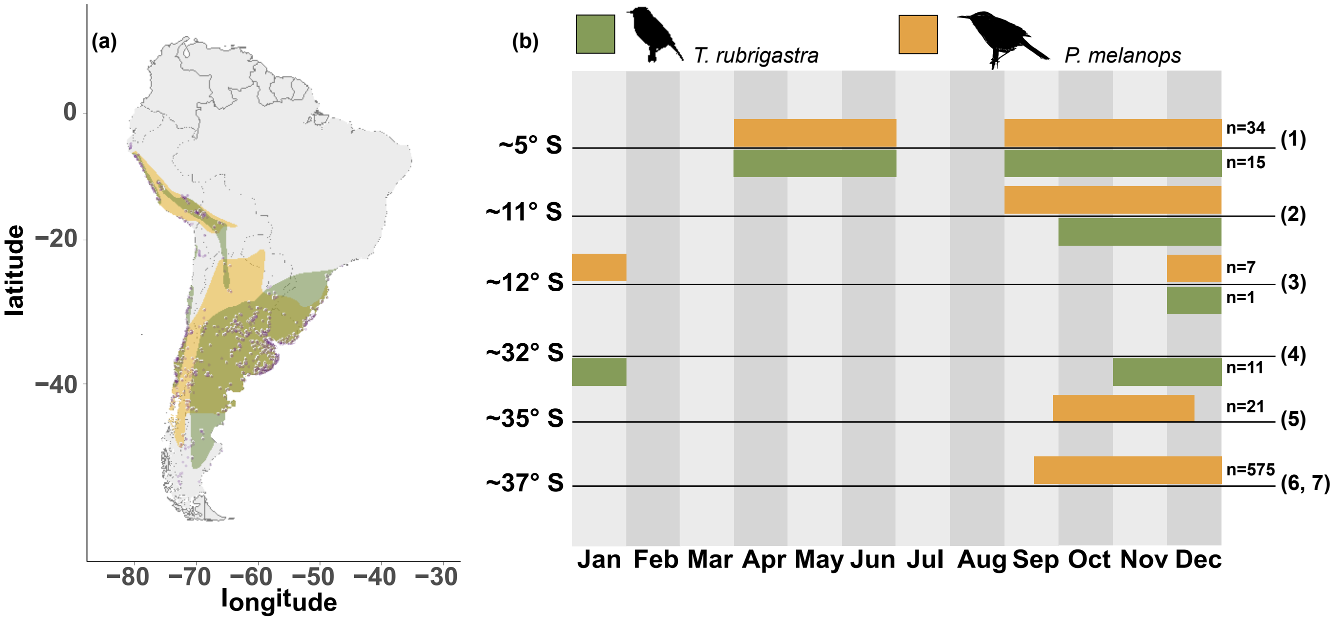

FIGURE 1 (a) Co-occurrence (purple points) and range overlap between the Many-colored Rush Tyrant (green bars) and Wren-like Rushbird (gold bars). Polygons were downloaded from BirdLife International (BirdLife international, 2021) and co-occurrence records from the Global Biodiversity Information Facility (GBIF, 2021a,2021b). (b) Breeding season chronogram of the Many-colored Rush Tyrant (green bars) and Wren-like Rushbird (gold bars). Approximate latitude is given at left; sample sizes, when available, are given at right with the prefix "*n*=". Data were compiled from (1) Garcia & Torres, 2017, (2) Quiñonez & Hernandez, 2017, (3) Amaro & Goyoneche, 2017, (4) Maurício et al., 2013, (5) Mason, 1985, (6) Chiaradia et al., 2017, and (7) Chiaradia et al., 2019. Specific observation start date from (5) was 29 October; observation start and end dates from (7) were 18 September and 23 November, respectively. When specific dates were not given, bars span finest temporal scale reported.

FIGURE 2 Many-colored Rush Tyrant and Wren-like Rushbird nests in *Schoenoplectus sp*. stands. (a) Many-colored Rush Tyrant nest showing open cup design and distinct tapered shape; (b) Wren-like Rushbird covered-dome nest showing entrance opening. (c) Conjoined stacked Many-colored Rush Tyrant and Wren-like Rushbird nest photograph taken on 14 July 2016 at Zona Reservada Humedales de Puerto Viejo, Peru. Three nests are present in the photograph: Two Wren-like Rushbird dome nests are built one on top of the other, with a third Many-colored Rush Tyrant cup nest fused onto the top. The Many-colored Rush Tyrant entrance is located on top of the nest; entrances to the two Wren-like Rushbird nests are located on each the left (bottom nest) and right (middle nest) sides. Photographs: Jessie L. Williamson.

structure (i.e., covered dome versus closed), and structural dimensions to published nest descriptions (Amaro & Goyoneche, 2017; Garcia & Torres, 2017; Lara et al., 2011). We identified Wren-like Rushbird nests as covered-dome nests constructed with masticated plant material secured with mud (Chiaradia et al., 2017), and Many-colored Rush Tyrant nests as smaller, rounded cup nests made of loosely woven marsh grasses and rushes. In addition to our observation of an interspecific stacked nest between a Many-colored Rush Tyrant and Wren-like Rushbird, we also observed two instances of intraspecific nest stacking of Wren-like Rushbird nests (i.e., rushbird nests stacked one atop another; Figure 2c).

It was not possible to confirm whether the occupation of nests was synchronous (i.e., took place during the same breeding season) or asynchronous (i.e., took place across multiple breeding seasons), as we observed no eggs or obvious breeding behavior, and because nests were mainly desiccated, consistent with records indicating that neither species nests in Peru in July (Figure 1; Garcia & Torres, 2017). Although both species have been recorded to breed synchronously across their range (Figure 1; Garcia & Torres, 2017), evidence from Lara et al. (2011), as well as our observation that the Many-colored Rush Tyrant cup nest (Figure 2c) was located above a previously used Wren-like Rushbird dome nest that appeared to be under construction, suggests that asynchronous nest occupation was more likely.

Although few observations exist, nest-stacking behaviors have been most frequently documented in marsh-nesting species (Lara et al., 2011; Verner & Engelsen, 1970). Lara et al. (2011) reported four instances from Chile of Many-colored Rush Tyrant nests built in close proximity (< ~78 cm) below Wren-like Rushbird nests, although these nests did not touch. The authors observed no aggressive interactions between individuals occupying adjacent nests; however, in one instance, they did note that a Wren-like Rushbird nest under construction had engulfed a Many-colored Rush Tyrant nest, resulting in abandonment by the Rush Tyrant (Lara et al., 2011).

Nest stacking may result from several non-mutually exclusive factors and is likely influenced by nest site availability, habitat quality, structural challenges, predation risk, and energetic demands. Marsh birds, generally rely on rushes, cattails, and grasses for nest-building materials, support structures, and foraging locations (Benvenuti et al., 2018; Chiaradia et al., 2017); thus, seasonality of marsh resources may dictate breeding windows and limit availability of nesting substrates and desirable nesting sites. It has been suggested that nest reuse in birds acts as an indirect signal of quality nesting sites that may reduce the energetic costs of new nest construction, potentially guiding nest site selection among some species (Cancellieri & Murphy, 2013; Cavitt et al., 1999; Styrsky, 2005). It is therefore possible that the analogous behavior of nest stacking evolved to maximize limited availability of high-quality nesting sites and/or to physically reinforce nests constructed with and/or on weak or flexible marsh substrates.

Additionally, it is well documented that birds select nesting sites to minimize predation risk (Lima, 2009). Thus, nest stacking, like nest reuse, could result from one species responding to environmental cues of another species' successful nesting site (i.e., lack of predator olfactory cues), which may indicate low predation risk and consequently may signal a high-demand location within a nesting area (Forsman et al., 2013; Tolvanen et al., 2018). If both species concurrently occupy stacked nests, anti-predator vigilance or mobbing behaviors could provide mutualistic benefit (Isenmann & Fradet, 1995). Behavioral responses to predators, such as mobbing, elicited from heterospecific calls are not uncommon in birds (Forsman & Mönkkönen, 2001; Magrath et al., 2015). Uninhabited stacked nests may act as decoys, and numerous abandoned and/or unoccupied nests may confuse or thwart predators (Watts, 1987). Taken together, evidence and theory suggest that the increased size of stacked nests could distract predators from occupied single nests in the vicinity (Biancucci & Martin, 2010).

Nests are energetically expensive for birds to build (Mainwaring & Hartley, 2013), providing an additional incentive for nest-stacking behavior. Nest reuse via construction of new nests on top of old nests may add structural support by reinforcing nest platforms (Fierro-Calderón & Martin, 2007; Smith & O'Connor, 1955), reducing overall energy expenditure during nest construction (Chiaradia et al., 2017; Jiménez-Franco et al., 2014). Nest stacking driven by energetic considerations may represent a commensally adaptive behavior to co-opt structural support and reduce energy expended on nest building; in this way, the presence of nests of one species could facilitate coexistence of the other.

Nest stacking may also represent an aberrant, possibly non-adaptive or maladaptive behavior. Stacked nests are undoubtedly larger, more conspicuous structures that may be more frequently depredated (Biancucci & Martin, 2010; Møller, 1990). Birds respond to environmental cues associated with increased nestling mortality (Beckmann & Martin, 2016). If stacked nests are more frequently targeted by predators, nesting individuals may develop low tolerance for conjoined nest construction and may abandon nesting efforts. Finally, high nest density and/or reuse of old materials may expose individuals to disease and/or parasites suggesting another reason the behavior may be avoided (Brown & Brown, 2004; Tomás et al., 2007). Future research should use manipulative field experiments to test whether stacked nests increase predation or parasitism risk.

The overall paucity of nest-stacking examples in the literature makes broad inference about the underlying causes of this behavior challenging. Of the few documented examples, half suggest energetic conservation and emphasize site selection through nest reuse (Fierro-Calderón & Martin, 2007, Smith & O'Connor, 1955), implying competition for optimal nesting locations. Our observations, and those of Lara et al. (2011), along with the broad pattern of species' geographic coexistence, suggest that Wren-like Rushbirds and Many-colored Rush Tyrants may have evolved this behavior due to its fitness benefits acting as a mechanism of mutualistic or commensal facilitation.

Studying rare intra- and interspecific behaviors, such as nest stacking, in species like the Many-colored Rush Tyrant and Wren-like Rushbird, provides a window into underappreciated interspecific biotic interactions that may increase competition and/or facilitate coexistence. We recommend that future research examines the frequency and geographic patterns of nest stacking in Many-colored Rush Tyrant and Wren-like Rushbird, particularly in the context of how these species partition resources in South American marshes. The fact that a northern hemisphere ecological analogue, the Marsh Wren, has been documented to build stacked nests (Verner & Engelsen, 1970) implies that some aspects of marsh habitats (e.g., patchy nesting habitat, flimsy substrates, or other factors) may facilitate evolution of this behavior. Broadening the scope, future global phylogenetic comparative analyses could deepen our understanding of the patterns and processes underlying nest stacking and related behaviors.

AUTHOR CONTRIBUTION

CRG and JLW conceptualized the study, made field observations, and wrote the paper. CRG made figures. CCW reviewed and edited the article.

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DATA AVAILABILITY STATEMENT

Original descriptions and photographs are presented as figures. Data sharing is not applicable to this article as no data were created or analyzed in this study.

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