



## Interspecific vocal discrimination in Neotropical wrens: responses to congeneric signals in sympatry and allopatry

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When animals defend resources using territorial signals, they must distinguish between competitors and noncompetitors. Conspecific animals routinely compete for resources and regularly engage in aggressive signalling exchanges. Heterospecific animals may also compete for resources, and therefore animals may direct their aggression towards heterospecific as well as conspecific rivals. In both cases, animals should benefit by discriminating between nonthreatening individuals versus threatening conspecific and heterospecific competitors. Experience may play an important role in competitor discrimination; animals living in sympatry with heterospecific competitors may gain experience with heterospecific rivals, but animals living in allopatry will not. We investigated whether experience influences species discrimination between two congeneric Neotropical wrens (rufous-and-white wrens, *Thryophilus rufalbus*, and banded wrens, *Thryophilus pleurostictus*) that live in sympatry in some parts of their range and in allopatry in other parts of their range. We simulated the presence of male conspecific, congeneric and control intruders in the territories of rufous-and-white wrens at sites where they are sympatric or allopatric with banded wrens. If species discrimination is influenced by experience, we predicted that wrens would always respond strongly to conspecific songs, but that in sympatry, they would respond more strongly to the congeneric competitor than to the control songs. Conversely, we predicted that, in allopatry, wrens would show similarly low responses to congener and control songs. In contrast to our predictions, we found that rufous-and-white wrens discriminated between conspecific and heterospecific animals, but that this response did not differ in sympatry or allopatry, suggesting that experience with heterospecific competitors does not influence interspecific discrimination in this species. By contrasting the responses of sympatric and allopatric populations, we can better understand the effect of experience on interspecific discrimination and gain insight into the evolution of species discrimination signals.

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Species discrimination is the identification and differentiation of conspecific animals from heterospecific animals (Bradbury & Vehrencamp, 2011). Misidentifying the species of a potential rival or a potential mate can have significant fitness consequences (Grether, 2011), and given the high cost of territorial displays, selection should promote species discrimination (Grether, Losin, Anderson, & Okamoto, 2009). Species discrimination may be innate, or shaped by experience (i.e. previous interactions with heterospecific rivals) or shaped by both genetics and experience. Experience with heterospecifics may allow animals to recognize competitors that they would not be able to identify in areas where

heterospecifics are absent. In spite of the large body of research on species discrimination (Grether, 2011), there is no consensus on the importance of experience for interspecific discrimination between closely related competitor species.

Animals are understood to construct species-specific templates, whether they are learned or innate, which they use to distinguish conspecifics from heterospecifics (Bradbury & Vehrencamp, 2011; Hauber & Sherman, 2001). Many studies suggest that animals have an innate species template, which they expand or modify through learning (Hauber, Russo, & Sherman, 2001; Sandoval, Méndez, & Mennill, 2013). Other studies have suggested that there is a learned component to species discrimination, with animals learning the characteristics of conspecifics through experience with parents or other individuals (Catchpole, 1978; Grant & Grant, 1997; Irwin & Price, 1999; Lynch & Baker, 1990; Matyjasik, 2004). Species discrimination may involve phenotype

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matching, where an individual learns the phenotype of parents or kin and then uses this template to discriminate between conspecifics and heterospecifics (Bradbury & Vehrencamp, 2011; Hauber & Sherman, 2001). This mechanism requires learning early in life but does not require prior experience with heterospecifics, since animals may respond appropriately to any species whose phenotype is different from their own (Kappeler, 2010). While phenotype matching is a potential mechanism for distinguishing conspecifics from heterospecifics, it does not allow for the differentiation of heterospecific competitors from heterospecific noncompetitors.

Most animals respond more intensely to the signals of conspecifics versus heterospecifics (e.g. frogs: Ryan & Rand, 1993; salamanders: Nishikawa, 1987; insects: Anderson & Grether, 2010; fish: Johnson & Peeke, 1972; birds: Baker, 1991). Conspecifics are expected to pose a greater threat because they compete for both resources and mates, whereas congeneric animals compete only for resources (Jankowski, Robinson, Levey, & Levey, 2010; Ord & Stamps, 2009). Although interspecific discrimination plays an important role in communication with conspecifics, it can also facilitate communication with heterospecifics, particularly when two or more species compete for access to similar resources such as foraging sites or nesting areas (Kodric-Brown & Brown, 1978; Ord & Stamps, 2009). Species that compete for resources on a regular basis should recognize each other as a potential threat. Red-cheeked salamanders, *Plethodon jordani*, for example, show similarly aggressive responses towards both conspecific and congeneric rivals (northern slimy salamanders, *Plethodon glutinosus*) in areas of high interspecific competition, but more aggressive responses towards conspecific than congeneric intruders in areas of low interspecific competition (Nishikawa, 1987). Likewise, mountain chickadees, *Poecile gambeli*, respond strongly to the songs of both conspecific and heterospecific rivals (black-capped chickadees, *Poecile atricapillus*), suggesting that both species' songs are equally threatening signals, whereas the socially dominant black-capped chickadees respond more strongly to conspecific songs (Grava, Grava, Didier, et al., 2012; Grava, Grava, & Otter, 2012). Species that never come into contact may not be able to discriminate between each other, as it may not be adaptive for species that have evolved in isolation to recognize one another (Grether et al., 2009).

Several studies have shown that birds have the ability to recognize closely related species as competitors, and this capacity appears to vary with experience. For example, blue-winged warblers, *Vermivora cyanoptera*, living in sympatry with golden-winged warblers, *Vermivora chrysoptera*, respond aggressively to both conspecific and congeneric songs, showing more aggression towards conspecific songs (Gill & Murray, 1972). In allopatry, however, blue-winged warblers only respond aggressively to conspecific songs (Gill & Murray, 1972). This result is consistent with the idea that animals learn to distinguish threatening from nonthreatening rivals when they live in sympatry. Conversely, white-eared ground-sparrows, *Melozone leucotis*, show stronger aggressive responses to conspecific songs versus congeneric Prevost's ground-sparrow, *Melozone biarcuatum*, songs regardless of whether they live in sympatry or in allopatry (Sandoval et al., 2013). This latter result is more consistent with the idea that conspecific discrimination does not require learning. By contrasting the behaviour of more animals in sympatry versus allopatry, we can gain insight into the importance of experience in species discrimination.

In this study, we investigated species discrimination in Neotropical wrens that live in zones of sympatry and allopatry in different parts of their ranges. Rufous-and-white wrens, *Thryophilus rufalbus*, and banded wrens, *Thryophilus pleurostictus*, are sister species (Mann et al., 2006) that nest primarily in bullhorn acacias, *Vachellia collinsii* (Joyce, 1993; Molles & Vehrencamp, 1999), and

occupy similar foraging niches (Ahumada, 2001; Molles & Vehrencamp, 1999). In zones of sympatry, banded and rufous-and-white wren territories do not overlap but may be abutting, with rufous-and-white wrens inhabiting mature evergreen forests and banded wrens favouring dry scrub forest. The two species are thought to engage in aggressive interactions where their territories meet (Battiston, Wilson, Graham, Kovach, & Mennill, 2015). We expect that rufous-and-white wrens living in sympatry with banded wrens have experience interacting with banded wrens, whereas the ones living in allopatry do not.

We tested the hypothesis that species discrimination in rufous-and-white wrens is influenced by experience by presenting conspecific and heterospecific songs to rufous-and-white wrens in an area of sympatry and allopatry with banded wrens. If species discrimination is influenced by experience, we predicted that rufous-and-white wrens living in allopatry with banded wrens would show a low response to both the congeneric and control songs, since neither represents a competitive threat, and that they would show a high response to conspecific songs. Conversely, we predicted that rufous-and-white wrens living in sympatry with banded wrens would show a stronger response to the congeneric songs than to the control songs, because they do represent a competitive threat, and that they would show the highest response to conspecific songs. Alternatively, if species discrimination does not require experience to distinguish competitive from noncompetitive heterospecific individuals, we predicted that wrens' responses would not differ between sympatry and allopatry.

## METHODS

### General Field Methods

We conducted a playback experiment at two sites within the Guanacaste Conservation Area in northwestern Costa Rica: Sector Santa Rosa ( $10^{\circ}40'N$ ,  $85^{\circ}30'W$ ) and Sector Rincón de la Vieja ( $10^{\circ}40'N$ ,  $85^{\circ}30'W$ ). Santa Rosa is a lowland dry-forest habitat where rufous-and-white wrens and banded wrens live in sympatry (hereafter, the 'sympatric population'), with the former species occupying the mature evergreen habitats (Mennill & Vehrencamp, 2005), and the latter species occupying adjacent, less mature habitats (Molles & Vehrencamp, 1999). Rincón de la Vieja is a mid-elevation rainforest habitat where the two species live in allopatry (hereafter, the 'allopatric population'). We have never encountered banded wrens at this second site. These two locations are approximately 45 km apart and separated by unsuitable habitat, and we therefore do not expect dispersal to occur between them; analysis of 13 years of banding returns from our laboratory suggests that rufous-and-white wrens disperse short distances from their natal territories. In the sympatric population, we studied only rufous-and-white wren pairs whose territory was within 200 m of a banded wren territory to increase the chance that they would have had previous competitive interactions with the congeneric species. For all of these territories, we could hear banded wrens singing nearby, and we assume that the resident rufous-and-white wrens could hear the congeners as well.

We conducted playback experiments from early April to early June 2013, during the end of the dry season and the beginning of the rainy season. This time of year coincides with the end of the nonbreeding season, when birds defend territories, and the early part of the breeding season, when birds build nests and lay their first clutches of the year (Topp & Mennill, 2008). Birds in both the sympatric and allopatric populations were in similar breeding stages of defending territories and building nests when the playback experiment was conducted. At this time of year, both rufous-and-white wrens and banded wrens are responsive to playback

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