

Ecological segregation and vocal interactions in two sympatric *Laterallus* crakes

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Abstract Ecological segregation and interspecific territoriality can reduce exploitative competition in morphologically and ecologically very similar species allowing their coexistence. We studied habitat use and features, ecomorphology and homo- and heterospecific playback responses in the similar and sympatric Red-and-white Crake (*Laterallus leucopyrrhus*) and Rufous-sided Crake (*Laterallus melanophaius*) on the coast of the Río de la Plata, Argentina. We carried out playback sessions with stimuli of both crakes in four habitat types potentially used by them across the four seasons (coastal humid scrub, bulrush, floodable grassland and exotic yellow iris). Crakes were segregated year-round by habitat, with minor overlap: Red-and-white Crakes used bulrush, while Rufous-sided Crakes used coastal humid scrub. Patterns of habitat use were the same when using homo- or heterospecific playback stimuli, and both species responded similarly to homo- and heterospecific playback trials in their selected habitats. Crakes were morphologically distinct and some of their differences can be related to habitat features and resource exploitation: Red-and-white Crakes had longer tarsi and “blunt” bills and inhabited the deeper and denser bulrush, while Rufous-sided Crakes had shorter tarsi and “dagger” bills and inhabited the shallower and more open coastal

humid scrub. Habitat use resulting in spatial segregation in these crakes seems to be more related to specific abilities to exploit different habitats than to interspecific competition or interspecific territoriality. Habitat adaptation would be more relevant within large patches of homogeneous and simple habitats selected by each Crake, while interspecific territoriality would gain importance at habitat boundaries with heterogeneous or intermediate conditions.

Keywords Habitat use · Playback · Interspecific territoriality · Ecomorphology · Rallidae · Neotropics

Zusammenfassung

Ökologische Trennung und vokale Interaktionen zweier sympatrischer Rallen (*Laterallus*)

Ökologische Trennung und interspezifisches Territorialverhalten können ausbeuterische Konkurrenz bei morphologisch und ökologisch sehr ähnlichen Arten verringern und damit deren Koexistenz ermöglichen. Wir untersuchten die Habitat-Besonderheiten und dessen Nutzung, die Ökomorphologie und die homo- und hetero-spezifischen Playback-Antworten bei den sehr ähnlichen und sympatrischen Arten Weißbrustralle (*Laterallus leucopyrrhus*) und Rothalsralle (*L. melanophaius*) am Río de la Plata, Argentinien. Dafür führten wir Playback-Sitzungen mit vokalen Stimuli beider Rallenarten und in denjenigen vier Habitat-Typen durch, die von den beiden Arten über die vier Jahreszeiten genutzt werden (feuchte Küsten-Macchia, Binsen und Schilf, regelmäßig überflutetes Grasland und Wasserschwertlilien). Die Rallen blieben rund ums Jahr mit nur kleinen Ausnahmen durch die Habitate voneinander getrennt: die Weißbrustralle nutzten Binsen und Schilf, die Rothalsralle die feuchte

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Küsten-Macchia. Die Art und Weise der Habitat-Nutzung blieb gleich, egal ob homo- oder heterospezifische Playback-Reize gegeben wurden, und beide Arten antworteten auf ähnliche Weise auf homo- und heterospezifische Playbacks in ihren jeweiligen Habitaten. Die Rallen sind morphologisch klar unterschiedlich, wobei einige Unterschiede auf die unterschiedlichen Habitat-Eigenschaften und Ressourcen-Nutzung zurückgeführt werden können: die Weißbrustrallen haben längere Tarsi und stumpfe Schnäbel und leben im tieferen und dichteren Schilfdickicht, wohingegen die Rothsrallen kürzere Tarsi und schärfere Schnäbel haben und die flachere und offenere Küsten-Macchia bewohnen. Ihre Habitat-Nutzung und die sich daraus ergebende räumliche Trennung scheinen bei beiden Rallen-Arten mehr von den jeweiligen Fähigkeiten abzuhängen, unterschiedliche Habitate zu nutzen als von interspezifischer Konkurrenz oder Territorialität. Eine Anpassung an ein Habitat wäre eher bei großen, zusammenhängenden Habitaten relevant, die sich jeweils eine Rallen-Art aussuchen würde, wohingegen interspezifisches Territorialverhalten dann eine Bedeutung hätte, wenn die Habitatgrenzen sehr heterogen wären oder es ausgeprägte Übergänge zwischen den Habitaten gäbe.

Introduction

The geographic and local distributions of animals are neither purely random nor completely deterministic. Animal life is ecologically structured, and species are frequently found in only one or a few habitat types (Rosenzweig 1981; Cody 1985). The question of habitat specificity bears on that of species coexistence. Ecologically very similar species that exploit similar resources may compete for them (Miller 1967). Exploitative competition can be reduced by differences in morphology and behavior, and spatiotemporal segregation of competing species (Grether et al. 2013). Spatial segregation between two possibly competing sympatric species can be achieved in two basic ways. Passively, by using different habitats or microhabitats that each species is especially prepared to exploit, or actively, by interspecific territoriality independently of their exploitative abilities. The relationship between specific morphological features and resource exploitation is well known in birds (James 1982; Winkler and Leisler 1985). For example, tarsal length in relation to water depth and bill shape in relation to foraging strategies have been implied as important features influencing habitat use and compartmentalization in rails (Johnson and Dinsmore 1986; Flores and Eddleman 1995). Interspecific territoriality has been demonstrated in a wide array of bird taxa (Prescott 1987; Leisler 1988; Martin et al. 1996;

Martin and Martin 2001). Although it has been frequently interpreted as the product of resource competition (Cody 1973; Robinson and Terborgh 1995; Grether et al. 2013), interspecific territoriality could also be the result of misdirected intraspecific aggression, especially if signals used in territorial defense are similar between species (Murray 1971, 1976). For whichever reason, interspecific territoriality can act as a spacing mechanism between species. The Red-and-white Crake (*Laterallus leucopyrrhus*) and the Rufous-sided Crake (*Laterallus melanophaius*) are cursorial birds of wet habitats. They are similar in plumage, morphology and vocalizations and coexist on the coast of the Río de la Plata, Argentina (Hartert and Venturi 1909; Arballo and Cravino 1987; Areta and Depino 2012). Their phylogenetic position is not known with certainty, but molecular, morphological and vocal data suggest that they are not sister species (Storer 1981; Livezey 1998; Areta and Depino 2012; Garcia-R et al. 2014). In both species, the sexes are alike and strongly bonded pairs defend small year-round territories [ca. 20 × 25 m (Maurício and Dias 1996)]. All *Laterallus* crakes signal their territories by giving loud duets known as “trills.” Vocal signaling plays a crucial role in long-distance species communication, since visual cues are difficult to use in crakes’ dense habitats. Trills of Red-and-white and Rufous-sided Crakes are very similar and have been confused in the literature (e.g., Taylor and Van Perlo 1998); however, trills of Red-and-white Crakes are less strident, slightly lower-pitched, and more gurgled than those of Rufous-sided Crakes (Areta and Depino 2012).

The range of the Red-and-white Crake is embedded within that of the much more widespread Rufous-sided Crake (Ripley 1977). Habitat use of these Crakes has been poorly described in the literature (Ripley 1977; Taylor and Van Perlo 1998) although some evidence suggests that they are sympatric but rarely or never syntopic. Red-and-white Crake has been reported mostly from *Scirpus giganteus* bulrushes in the Río de la Plata coast (central-east Argentina), where it presumably avoids adjacent *Schoenoplectus californicus* reedbeds (locally known as “juncales”) which would be used mostly by Rufous-sided Crakes (Pereyra 1938; Pagano et al. 2012; J. I. A. and E. A. D., personal observation). General habitat descriptions of other *Laterallus* species suggest syntopy between different species (e.g., Erickson and Mumford 1976; Storer 1981), while more detailed studies show that species coexisting at a local scale are segregated in different habitats (e.g., Stiles and Levey 1988).

Accurate knowledge on habitat use, ecomorphological traits and species recognition signals are indispensable for understanding the coexistence and interactions of similar species (Peiman and Robinson 2010; Pigot and Tobias

2012). Interspecific territoriality is more likely to exist between syntopic species that have similar plumage and vocalizations than in species that are segregated by habitat and differ in visual and vocal signals (Losin et al. 2016). Thus, Red-and-white and Rufous-sided Crakes are excellent candidates to assess patterns of habitat use, and to evaluate interspecific interactions and morphological features related to habitat use and resource exploitation.

This study aims to understand the processes that permit the coexistence of the morphologically and vocally similar Red-and-white and Rufous-sided Crakes. To this end, we performed systematic playback sampling in different habitats to test two patterns of spatial segregation in crakes (habitat segregation and habitat compartmentalization), and obtained morphological data to assess ecomorphological (habitat adaptation) and behavioral mechanisms (interspecific territoriality) that may cause these patterns.

Methods

Hypotheses and predictions

We evaluated the existence of two possible patterns of spatial segregation in Crakes (habitat segregation and habitat compartmentalization). If Red-and-white and Rufous-sided Crakes are segregated by habitat each would occur preferentially in a habitat or suite of habitats seldom or never used by the other species. On the other hand, compartmentalization predicts that both species will share the same habitat or suite of habitats, eventually using different microhabitats within a general habitat type. The distinction between habitat types and microhabitats within a habitat depends critically on how different the habitats taken into consideration are. We studied four clearly defined, adjoining and very different habitats, making this distinction very easy (see “Study area”).

We tested predictions derived from ecomorphological and behavioral hypotheses that may explain the patterns of spatial segregation previously evaluated. The habitat adaptation hypothesis predicts that ecomorphological features of each species will match specific features of their own different habitats, if segregated by habitat, or of their microhabitats, if sharing a habitat. Specifically, we predict that species walking on deeper waters should exhibit longer tarsi than those living in more shallow waters, and species feeding on muddier substrates should exhibit more slender bills to probe on the ground than those living in more densely vegetated habitats with little access to the soil. The interspecific territoriality hypothesis predicts strong behavioral responses to heterospecific playback of territorial vocalizations. These strong positive responses could be symmetrical, if both species respond indiscriminately to

homo- and heterospecific playback, or asymmetrical, if homospecific playback elicits significantly more responses than heterospecific playback.

Study area

We studied crakes in four localities on the coast of the Río de la Plata, Buenos Aires province, Argentina: the Reserva Natural Punta Lara (RNPL; 34.8°S 58.2°W), Isla Santiago (IS; 34.83°S 57.93°W), La Balandra (LB; 34.93°S 57.72°W) and Atalaya (A; 35.01°S 57.53°W). We selected a priori four homogeneous and adjacent habitat types potentially used by crakes based on extensive previous experience in the study area, literature data, and similarity to other habitat types used by crakes in general (Ripley 1977; Storer 1981; Klimaitis and Moschione 1987; Taylor and van Perlo 1998). Three habitat types were native and one exotic. Native habitat types were coastal humid scrub, characterized by the dominance of *Schoenoplectus californicus* and *Ludwigia bonariensis* on sandy and muddy shores influenced by the river’s tidal regime; bulrush, monospecific *Scirpus giganteus* stands with sparse individuals of *Erythrina crista-galli*; and floodable grassland, a temporarily flooded grassland of *Stipa* sp., *Paspalum* sp. and *Bromus* sp. The exotic habitat type was yellow iris, consisting of monospecific stands of invasive *Iris pseudacorus*. All habitat types generally replace each other in succession from the shore of the Río de la Plata towards inland, beginning with coastal humid scrub, through bulrush and yellow iris to floodable grassland. Occasionally, all four habitat types might enter in contact with each other. For further details on these habitat types see Herrera and Torres Robles (2012).

Field sampling design

Habitat use and playback design

Since crakes are elusive and difficult to detect, we assessed habitat use through systematic playback surveys. For playback use we recorded vocalizations with a Sennheiser ME-62 mounted on a Telinga Universal parabola, and a Marantz PMD-661 digital audio recorder with sampling set at 24 bit and 48 kHz. All our recordings are archived at the Macaulay Library of Natural Sounds (Cornell Lab of Ornithology, Ithaca, NY) (for more details on the recordings, see “Appendix 1”). To avoid pseudoreplication (Kroodsma 1986) we used as playback stimuli two packages of recordings, one with duet trills of 12 different Red-and-white Crake pairs and another with duet trills of 12 different Rufous-sided Crake pairs recorded in our study area. Playback stimuli were 1-min sound files (pulse-code modulation uncompressed), each including four duet trills.

Digital files were played back using a 1-W portable speaker set at 81- to 85-dB sound pressure level at 1 m from the speaker (measured with Radio Shack 33-099; C-weighting; fast response) to match the natural amplitude of duet trills of both species.

We sampled during every season from 25 August 2011 to 25 February 2013, from sunrise to noon, in comparable days of good climatic conditions and when wind speed was <20 km/h to maximize the playback-response detection probability (see Conway 2011). Sampling was conducted by two trained observers capable of discriminating crakes by sight and ear (one of us and a trained field assistant). We established twelve 25 m-radius points systematically and similarly spaced on each habitat type depending on habitat availability in our study sites: coastal humid scrub (four points at IS, four at LB and four at A), bulrush (ten points at RNPL and two at LB), floodable grassland (12 points at RNPL) and yellow iris (12 points at RNPL). Sampling points were spaced at least 150 m from their borders (i.e., points were separated by a distance approximately equivalent to that of eight territories). Each of the 12 playback stimuli per species was randomly assigned to a sampling point in each habitat type, resulting in one recording of Red-and-white Crake and one recording of Rufous-sided Crake being assigned to each point. Each pair of stimuli was used twice in the corresponding point (once in fall and once in winter), and twice in a different randomly assigned point (once in spring and once in summer). At each point we waited for 1 min before playback and then played the chosen 1-min stimulus twice consecutively. Detections of crakes by sight or voice after 5 min since the beginning of the playback within each 25-m-radius point were noted (i.e., we took note of the presence/absence of each crake species, regardless of the number of individuals responding, within the 2-min playback period and in a 3-min post-playback period). This playback protocol was repeated at each point with recordings of both crake species on independent and non-consecutive days (with at least 4 days between consecutive trials) in every season (spring, summer, fall and winter). To summarize, each of 12 points at each of the four habitats was sampled twice each season, once with playback of each crake species, ensuring the same search effort for each species of crake in all habitats and in all seasons. We carried out 384 playback sessions (192 with Red-and-white Crake stimuli and 192 with Rufous-sided Crake stimuli) in 48 points (12 points per habitat), comprising 96 samples per season and 32 h of total effort.

Habitat features

To evaluate whether presence/absence of crakes in each habitat was related to habitat features, we measured water

depth (to the nearest 1 cm) and vegetation height on the highest plant present (to the nearest 5 cm) at the center of each 25-m-radius point during each playback trial.

Morphology

To determine whether crakes differed in morphology in relation to habitat use and habitat features, we measured exposed culmen, culmen at nares, bill depth and width at the anterior edge of the nostril, tarsus length (to the nearest 0.01 mm using a dial caliper), wing chord and tail length (to the nearest 0.5 mm using a metallic ruler) from museum specimens of Red-and-white Crake ($n = 22$) and Rufous-sided Crake ($n = 40$) held at the Instituto Miguel Lillo (IML; Tucumán, Argentina), the Museo Argentino de Ciencias Naturales (MACN; Buenos Aires, Argentina) and the Museo de Ciencias Naturales de La Plata (MLP; La Plata, Argentina) (see “Appendix 2”).

Statistical analyses

Habitat use and playback responses

Since our design depended critically on playback responses we analyzed the performance of the stimuli used. To be a valid tool to evaluate habitat use, each of the 12 recordings of each recording package should elicit equivalent responses; if not, our results could have been biased by preferential responses to some of them. We used χ^2 -tests of goodness-of-fit to compare the distribution of responses generated by each playback package against a uniform distribution. We performed four separate tests comparing intra- vs. interspecific detections generated by each playback package, in each of the main habitats where crakes were found (coastal humid scrub and bulrush). Both 12-recording playback packages elicited uniform playback responses in intra- and interspecific playback trials, and in bulrush and in coastal humid scrub (χ^2 -tests of goodness-of-fit, P -values >0.05), indicating that overall individual recordings in each playback package did not differ in their capabilities of eliciting responses from both species. Hence, our stimuli dataset and associated detections were adequate to evaluate habitat use by both crake species.

We used Wilcoxon matched-pairs tests to evaluate whether crake responses to playback were species specific or not. Since we did not expect stronger hetero- than homospecific responses, we used one-tailed tests. We performed two tests, one for each species in the habitat where each was predominantly found (coastal humid scrub for Rufous-sided Crake and bulrush for Red-and-white Crake). In each test we compared the accumulated number of detections in response to homo- vs. heterospecific playback, by pairing detections within each sampling point.

Habitat use and habitat features

We compared the total number of detections of Rufous-sided and Red-and-white Crakes in coastal humid scrub and bulrush using χ^2 -tests. We carried out two contingency tables, one with number of detections of each species in each habitat using homospecific playback and a second one with number of detections of each species in each habitat using heterospecific playback.

Points with and without crakes did not differ in water depth and vegetation height within each season in coastal humid scrub and in bulrush (Mann–Whitney U -tests: all P -values >0.05), thus we used all samples to characterize the four habitat types. We evaluated differences in water depth and vegetation height between seasons in the four habitat types with Kruskal–Wallis tests.

We performed a multiple correspondence analysis to associate data points with detections and no detections of crakes to the four habitat types sampled and their features. We subdivided the full sampled range of values for vegetation height and water depth in all four habitats into three equal-sized categories: low, medium and high. For vegetation height categories were: low (0.05–1.03 m), medium (1.03–2.01 m) and high (2.01–3 m). For water depth the categories were: low (0–0.13 m), medium (0.13–0.27) and high (0.27–0.40).

Morphology

We compared morphological measurements of museum specimens of Red-and-white and Rufous-sided Crakes. Since specimens were taken at different localities in Argentina and our goal was to relate morphology to habitat features, we needed to assure that morphology did not vary geographically. We used Mann–Whitney U -tests (α -level = 0.05) to compare specimens from populations of Rufous-sided Crake that were allopatric to and sympatric with Red-and-white Crake, and to assess sexual dimorphism in both species. We found no differences between allopatric and sympatric populations, and no sexual dimorphism in either species, allowing us to merge morphological data from all specimens for each species. Interspecific differences were analyzed with two-tailed t -tests, after checking for normality (Shapiro–Wilk's tests; P -values >0.05).

Results

Habitat use and playback responses

We obtained 97 detections of Red-and-white and Rufous-sided Crakes in response to playback: 52 in coastal humid

scrub (53.6 % of detections) and 44 in bulrush (45.4 % of detections), with a single record from yellow iris (1 % of detections), and no record from floodable grassland (Fig. 1; Table 1). Red-and-white Crake was detected 52 times, 40 in bulrush, 11 in coastal humid scrub and once in yellow iris, whereas Rufous-sided Crake was detected 45 times, 41 in coastal humid scrub and 4 in bulrush (Fig. 1; Table 1).

Crakes were clearly segregated by habitat (Figs. 1, 2). Detections of Red-and-white Crake were higher than expected by chance in bulrush, and detections of Rufous-sided Crake were higher than expected by chance in coastal humid scrub when using either homo- or heterospecific playback in both cases (χ^2 -test; P -values <0.001). The pattern of habitat use of each crake uncovered was so robust, that it was uncovered when using homo- or heterospecific playback stimuli (Fig. 1). In the multiple correspondence analysis, sampling points with crake detections were also clearly associated with coastal humid scrub and bulrush (Fig. 2). While Red-and-white Crake was associated with bulrush and intermediate values of vegetation height and water depth, Rufous-sided Crake was associated with coastal humid scrub and high vegetation height (Fig. 2). Yellow iris and floodable grassland were associated with sampling points with no crake detections, extreme water depth values (high and low) and low vegetation height (Fig. 2).

Crakes responded strongly to heterospecific territorial vocalizations. Homo- and heterospecific playback trials elicited similar number of responses by each crake in their preferred habitats: Red-and-white Crake answered similarly to playback of Red-and-white Crake and Rufous-sided Crake in bulrush with a marginal lack of statistical significance [Wilcoxon matched-pairs test; P (one-tailed) = 0.059] and Rufous-sided Crake answered identically to playback of Rufous-sided Crake and Red-and-white Crake in coastal humid scrub [Wilcoxon matched-pairs test; P (one-tailed) = 0.5].

Habitat use and habitat features

Vegetation height and water depth differed significantly among seasons and habitats (Kruskal–Wallis tests; vegetation height, $H = 288$; $P < 0.001$; water depth, $H = 216.17$; $P < 0.001$; Supplemental Material Table S1, S2). Seasonality in vegetation height was moderate in habitats used by crakes driven by lower values of vegetation height in spring: coastal humid scrub showed significant differences only between spring and summer ($P < 0.002$) and bulrush showed significant differences only between spring and fall ($P = 0.05$) (Fig. 3). Habitats without crakes did not show concordant vegetation changes among seasons: seasonality was marked in yellow iris with obviously lower vegetation height in fall/winter vs. spring/summer (P -values <0.001),

Fig. 1 Habitat use of Red-and-white Crake (*Laterallus leucopyrrhus*) and Rufous-sided Crake (*Laterallus melanophaius*) in four habitat types sampled through playback on the Río de la Plata coast. Habitat illustrations are based on vegetation height and water depth during spring

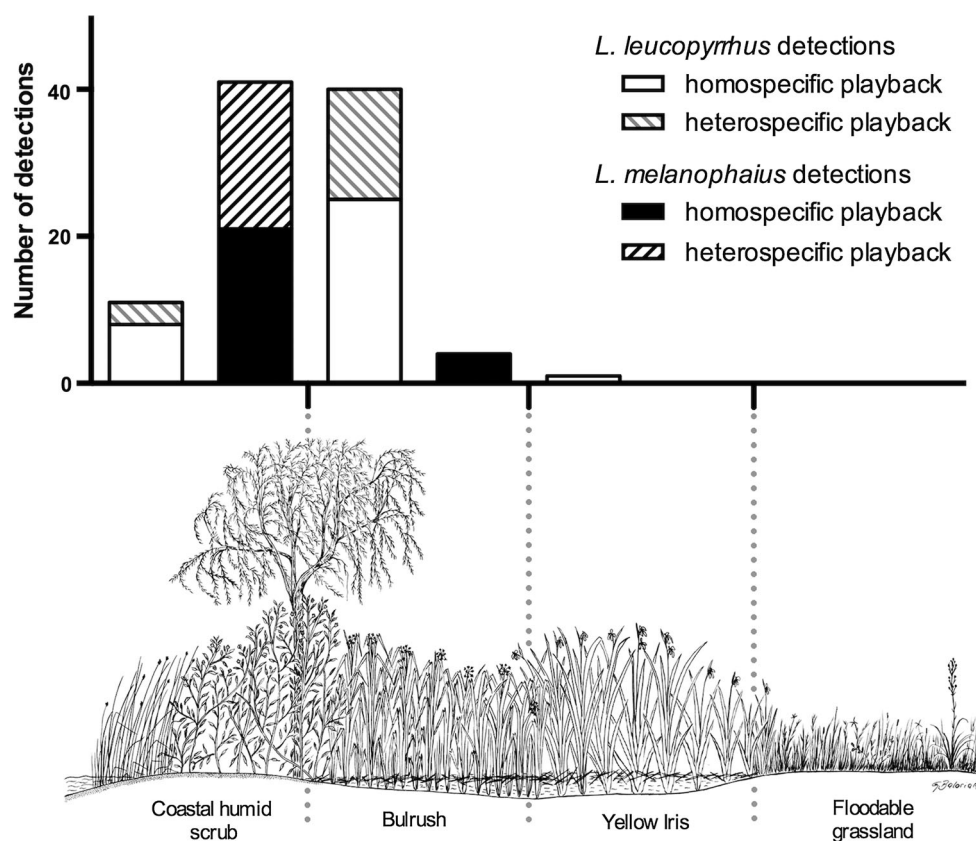


Table 1 Detections of Red-and-white Crake (*Laterallus leucopyrrhus*) and Rufous-sided Crake (*Laterallus melanophaius*) according to habitat type, playback stimulus and season

Habitat	Red-and-white Crake detections		Rufous-sided Crake detections		Total
	Red-and-white Crake playback	Rufous-sided Crake playback	Red-and-white Crake playback	Rufous-sided Crake playback	
Coastal humid scrub	8 (4) [0, 4, 3, 1]	3 (2) [0, 1, 1, 1]	20 (10) [1, 4, 6, 9]	21 (10) [1, 6, 9, 5]	52 (12) [2, 15, 19, 16]
Bulrush	25 (10) [5, 10, 5, 5]	15 (10) [3, 7, 1, 4]	0	4 (3) [0, 3, 0, 1]	44 (12) [8, 20, 6, 10]
Yellow iris	1 (1) [0, 1, 0, 0]	0	0	0	1 (1) [0, 1, 0, 0]
Floodable grassland	0	0	0	0	0
Total	34 (15) [5, 15, 8, 6]	18 (12) [3, 8, 2, 5]	20 (10) [1, 4, 6, 9]	25 (13) [1, 9, 9, 6]	97 (25) [10, 36, 25, 26]

Values are number of detections; number of points where detections occurred are shown in *parentheses* and number of detections per season (spring, summer, fall, and winter respectively) are shown in *brackets*

and there was no seasonality in floodable grassland (P -values >0.05) (Fig. 3). Low vegetation height in fall/winter in yellow iris and year-round low vegetation height in floodable grassland (average height <0.6 m in both habitats) did not differ (P -values >0.05), but were significantly different in comparison to all other seasons and habitats (P -values <0.001) (Fig. 3).

There was no seasonality in water depth in habitats used by crakes (P -values >0.05), but coastal humid scrub showed consistently lower average values than bulrush across seasons (P -values <0.05) (Fig. 3). Habitats without crakes had no water during fall and exhibited different

seasonal changes in water depth: yellow iris showed extreme differences with high values in spring/winter vs. low values in fall/summer (P -values <0.001), while in floodable grassland the dry fall (with no water) differed from winter/summer (P -values ≤ 0.01) (Fig. 3).

Morphology

Red-and-white and Rufous-sided Crakes were clearly separated in morphospace, differing significantly in exposed culmen, culmen at nares, bill width, tarsus length and tail length, but were indistinguishable in wing chord

Fig. 2 Multiple correspondence analysis depicting association of sampling points with and without Red-and-white Crake (*L. leucopyrrhus*) and Rufous-sided Crake (*L. melanophaius*) to habitat type and habitat features

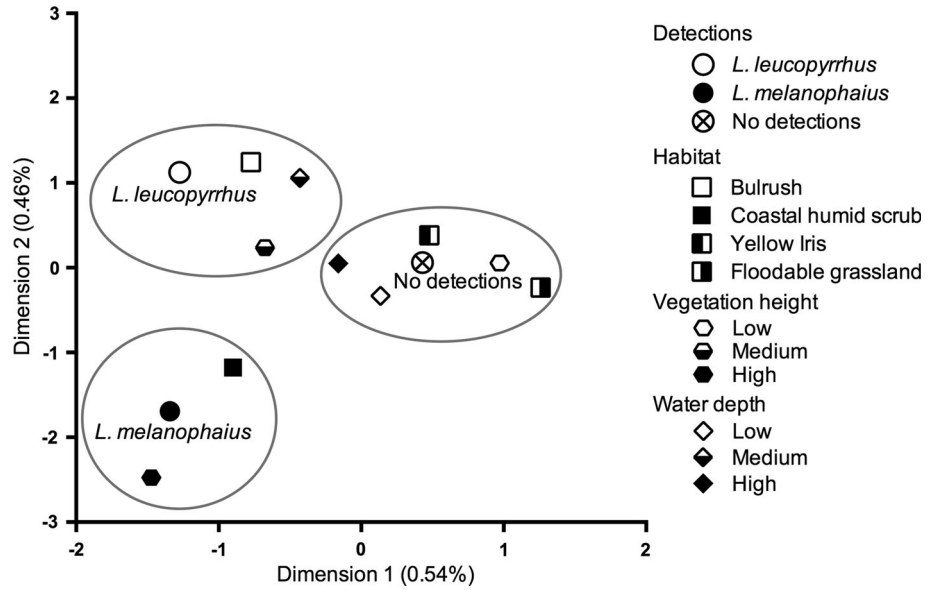
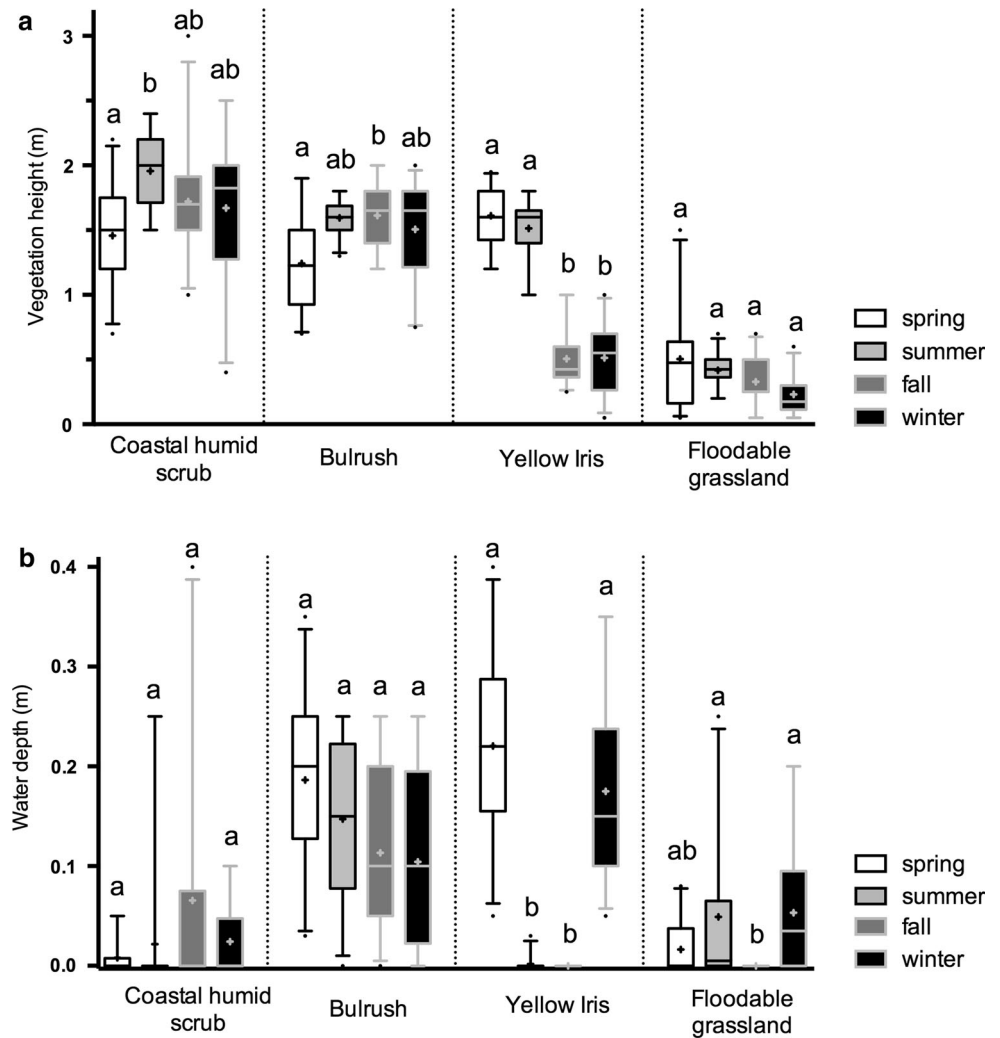


Fig. 3 Seasonality in vegetation height (m) and water depth (m) in the four habitats sampled (coastal humid scrub, bulrush, yellow iris and floodable grassland) characterized at playback points of Red-and-white Crake (*L. leucopyrrhus*) and Rufous-sided Crake (*L. melanophaius*). The number of samples (*n*) was 24 for each habitat per season. The *plus* symbol indicates mean values; *horizontal bars* denote 5th, 25th, 50th, 75th, and 95th percentiles; *points* are outliers. See Supplemental Material Table S2 for data. *Different lowercase letters* indicate meaningful statistical differences between seasons within each habitat



and bill depth (Fig. 4; Table 2). The lighter Red-and-white Crake had shorter but wider bills, and longer tarsi and tail than the heavier Rufous-sided Crake (Fig. 4; Table 2).

Discussion

In this study we have shown that:

1. Red-and-white and Rufous-sided Crakes are sympatric but not syntopic on the coast of the Río de la Plata.
2. Both species responded similarly to homo- and heterospecific playback trials in their preferred habitats suggesting interspecific territoriality.
3. Both species exhibit different morphologies potentially related to features of their preferred habitats.

Patterns of habitat use

Crakes were segregated by habitat, with minor overlap, supporting the existence of the habitat segregation pattern while rejecting the habitat compartmentalization pattern. Plant composition and habitat structure differed between bulrush selected by Red-and-white Crakes and coastal humid scrub selected by Rufous-sided Crakes, suggesting that both features influence habitat selection in these Crakes. Interestingly, our single record of Red-and-white Crake in yellow iris occurred in spring, the season when vegetation height and water depth between bulrush and yellow iris were statistically equal.

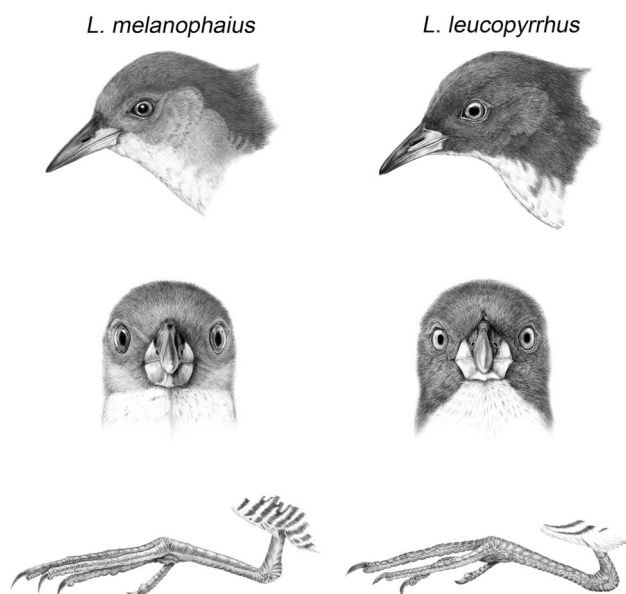


Fig. 4 Illustrations of lateral (*above*) and frontal (*middle*) views of heads and tarsi (*below*) of Rufous-sided Crake (*L. melanophaius*) and Red-and-white Crake (*L. leucopyrrhus*). Note the “dagger” bill and shorter tarsus of Rufous-sided Crake vs. the “blunt” bill and longer tarsus of Red-and-white Crake

Seasonal shifts in habitat use in *Laterallus* could be linked to the extent of change in water depth and vegetation height. Red-and-white and Rufous-sided Crakes used the same, different habitats year-round, which had no water depth seasonality and moderate vegetation height changes. Low values in these variables in some seasons explained the lack of crakes in the other two habitats sampled. Similarly, the sympatric Grey-breasted Crake (*Laterallus exilis*) and White-throated Crake (*Laterallus albigularis*) were generally segregated by habitat year-round in Costa Rica (with the latter using wetter sites). However, habitat use changed between the dry and the wet season in these species, which was somehow related to water availability and vegetation height (Stiles and Levey 1988). Our study contributes evidence supporting that structural features, such as vegetation height and water depth, and plant composition are critical variables influencing habitat use in marsh-walking rails (Rundle and Fredrickson 1981; Anderson and Ohmart 1985; Johnson and Dinsmore 1986; Darrah and Kremetz 2011; Conway and Sulzman 2007).

Habitat adaptation and interspecific territoriality

Morphological differences between Red-and-white and Rufous-sided Crakes indicate that each species exhibits different potential adaptations to features of their specific habitats, supporting the habitat adaptation hypothesis. First, longer tarsi length could provide improved wading in deeper waters. Despite their lower weight, Red-and-white Crakes had longer tarsi and inhabited bulrush with deeper waters than coastal humid scrub, which is inhabited by Rufous-sided Crakes. Second, the longer and thinner “dagger” bill of Rufous-sided Crakes seems especially suited to exploit the higher availability of sandy and muddy substrates for probing in search of food in shallower coastal humid scrub; the shorter and wider “blunt” bill of Red-and-white Crakes might be more suitable for searching for food amongst the numerous abrasive plant axils in the deeper and very dense bulrush. Overall, the data suggest that *Laterallus* crakes possess remarkable differences in bill shapes related to distinct feeding habits that might influence patterns of habitat use (Storer 1981; E. A. D. and J. I. A., in preparation).

The strong mutual responses to playback of territorial vocalizations in Red-and-white and Rufous-sided Crakes support the interspecific territoriality hypothesis. It has been predicted that heavier birds should be dominant over smaller ones, and heterospecific playback should result in stronger responses by the dominant species in comparison to the subordinate (Robinson and Terborgh 1995; Martin et al. 1996). The symmetric responses to homo- and heterospecific playback as evaluated by the number of detections suggest that no crake is dominant over the other despite their weight differences. However, since our

Table 2 Morphological measurements of Red-and-white Crake (*L. leucopyrrhus*) and Rufous-sided Crake (*L. melanophaius*)

Species	Exposed culmen $P < 0.001^{***}$ $d = -2.13$	Culmen at nares $P < 0.001^{***}$ $d = -2$	Bill depth $P = 0.24$ $d = 0.33$	Bill width $P < 0.001^{***}$ $d = 2.13$	Tarsus length $P < 0.001^{***}$ $d = 1.9$	Wing chord $P = 0.44$ $d = -0.23$	Tail length $P < 0.001^{***}$ $d = 2.82$	Weight ^a
Red-and-white Crake	16.0 ± 0.75 [14.8–17.3] (19)	9.2 ± 0.45 [8.4–10.0] (22)	5.8 ± 0.29 [5.4–6.5] (20)	4.0 ± 0.26 [3.6–4.6] (22)	31.0 ± 1.24 [28.5–33.3] (22)	80.2 ± 2.06 [75.5–84.0] (22)	50.0 ± 3.57 [40.0–53.5] (20)	45.5 (15)
Rufous-sided Crake	17.5 ± 0.65 [15.6–18.8] (33)	10.1 ± 0.45 [9.0–11.2] (37)	5.7 ± 0.32 [5.1–6.4] (31)	3.4 ± 0.30 [2.6–3.9] (34)	28.7 ± 1.18 [26.6–31.9] (36)	80.7 ± 2.23 [76.0–86.5] (36)	41.6 ± 2.23 [34.5–45.5] (39)	52.1 (11)

Measurement values (mm) are mean, SD, range (in *brackets*), *n* (in *parentheses*), *P*-values of *t*-test comparisons between species for each variable, Cohen's index of effect size (*d*)

*** $P < 0.001$

^a From Dunning (2007)

playback assays were not target oriented but habitat oriented and responses were not quantified, examination of detailed behavioral responses to playback are necessary before concluding that these two species respond identically in intensity to homo- and heterospecific playback.

Interspecific territoriality might be frequent in *Lateralus* crakes, since White-throated and Grey-breasted Crakes have also been considered so based on few playback trials (Stiles and Levey 1988). Trills of several *Laterallus* species are similar albeit diagnostic, suggesting that trills and heterospecific responses to them could be phylogenetically conserved traits. If this is the case, heterospecific responses might not be necessarily related to interspecific competition (Mikami and Kawata 2004; Grether et al. 2013), but rather represent phylogenetically inherited responses to a common vocal template. Additionally, acoustic adaptation might limit variation in acoustic features of trills constraining their evolution (Ręk and Kwiatkoska 2016).

Habitat adaptation and interspecific territoriality seem to be responsible for habitat segregation in Red-and-white and Rufous-sided Crakes. But what is their relative importance in explaining the patterns of habitat use? Since these Crakes seldom share habitats, interspecific encounters must not occur as often as intraspecific ones, and habitat use based on adaptive morphological features seems to be the main force explaining habitat segregation. We suggest that the adaptive process would be more relevant within large patches of homogeneous and simple habitats selected by each crake, while the interspecific territoriality process would gain importance at habitat boundaries with heterogeneous or intermediate conditions, where territories would be established by virtue of both inter- and intraspecific behavioral interactions. Phylogenetically controlled playback experiments of allopatric and sympatric species pairs in *Laterallus* should provide more rewarding answers on the importance of habitat adaptation and interspecific territoriality in constraining habitat use and limiting distributional boundaries

in Neotropical crakes (Peiman and Robinson 2010; Janowski et al. 2010).

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Appendix 1

Catalogue numbers of recordings of duet trills of Red-and-White-Crake (*Laterallus leucopyrrhus*; $n = 12$) and Rufous-sided Crake (*Laterallus melanophaius*; $n = 12$) used to prepare playback stimuli (see "Methods" for details). All recordings archived at the Macaulay Library of Natural Sounds (<http://www.maculaylibrary.org>).

Red-and-white-Crake: 166715, 166716, 166718, 166719, 166726, 166730, 166732, 166736, 218282, 220425, 220427, 220428.

Rufous-sided Crake: 166727, 166728, 166731, 166735, 166735, 166737, 166738, 171001, 171728, 179205, 220356, 220357.

Appendix 2

Museum specimens of Red-and-white-Crake (*L. leucopyrrhus*; $n = 22$) and Rufous-sided Crake (*L. melanophaius*; $n = 40$) examined and measured for this study. Specimens are held at the IML, the MACN and the MLP.

Red-and-white Crake: IML: 2602, 2605, 2611, 9513, 9606, 12233. MACN: 2503a, 3706a, 4568a, 5415a, 8405, 8812, 9162, 9563, 9631, 9631, 9631, 9631, 35204, 40112, 40245, 43351. MLP: 5891, 5992, 13706, 13707.

Rufous-sided Crake: IML: 2606, 2607, 2608, 2610, 2612, 6967, 6968, 8860, 9398, 10413, 10414, 12853, 13502, 13995, 14997, 15143, 15194, 15195. MACN: 2052a, 2053a, 2633, 7436, 7436, 9291, 9631, 39217, 42141, 42142, 42143, 48383, 56104, 56345, 57561, 58795, 59378. MLP: 2990, 6845, 13710, 13985, 14124.

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