

A rallid ballad: Communal signaling is correlated with year-round territoriality in the most duet-rich family of birds (Gruiformes: Rallidae)

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ABSTRACT

Duetting, in which 2 or more individuals call in coordinated unison, is common in birds, yet most research investigating the function of avian duets has focused only on oscine passerines. However, we have discovered that duetting occurs in 61 species (59%) in the family Rallidae (rails), one of the highest known rates in any bird clade, and that rail duets are also significantly associated with year-round territoriality and habitat type. We applied a comparative approach to study the occurrence of duetting relative to socio-ecological traits and call properties in 103 rail species, with the prediction that duetting rails produce low-frequency calls that spread well over short distances in densely vegetated habitats. Using a model correcting for phylogenetic signal, we found that duetting is the ancestral state in Rallidae, and that duetting rails show a trending effect for being sedentary and nonmigratory. Contrary to our predictions, there was no significant correlation between rail duetting and social bond length, breeding system, breeding latitude from the equator, or sexual dimorphism, as year-round territoriality and forest or heterogeneous habitats were the strongest predictors of duets. Despite the prevalence of duetting in Rallidae, few studies have tested duet functions such as territory defense in this family, and our comparative phylogenetic study lays the groundwork for future research, as little remains known about the behavioral ecology and vocal interactions of many rails.

Keywords: ancestral state, call properties, duetting, habitat, rails, year-round territoriality

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Lay Summary

- Many birds duet, but most research into avian duetting has focused on songbirds.
- Rails include a high percentage of duetting species but are not well-studied.
- Using a published phylogeny, call recordings, and life history traits, we compared 103 rail species and measured their call properties to determine what behaviors and environments are associated with duetting in rails.
- Duetting is most common in rails that defend territories year-round, but it is not strongly associated with other life history traits or call properties.
- Future studies of rails will increase our understanding of duet evolution in birds.

La balada de los rálidos: La señalización comunal se correlaciona con la territorialidad durante todo el año en la familia de aves más rica en duetos (Gruiformes: Rallidae)

RESUMEN

Hacer un dueto, en el que 2 o más individuos realizan llamadas coordinadas al unísono, es común en las aves, pero la mayoría de los trabajos que investigan la función de los duetos de aves se han centrado solo en los passeriformes oscinos. Sin embargo, hemos descubierto que el dueto ocurre en 61 especies (59%) en la familia Rallidae (rálidos), una de las tasas más altas conocidas en cualquier clado de aves, y que los duetos de los rálidos también están significativamente asociados con la territorialidad durante todo el año y el tipo de hábitat. Aplicamos un enfoque comparativo para estudiar la aparición de duetos en relación con rasgos socio-ecológicos y las propiedades de las llamadas en 103 especies de rálidos, con la predicción de que los duetos producen llamadas de baja frecuencia que se propagan bien a distancias cortas en hábitats con vegetación densa. Usando un modelo que corrige la señal filogenética, encontramos que el dueto es el estado ancestral en Rallidae, y que los rálidos con duetos muestran un efecto de tendencia por ser sedentarios y no migratorios. Contrariamente a nuestras predicciones, no hubo una correlación significativa entre los rálidos realizando duetos y la longitud del vínculo social, el sistema de reproducción, la latitud de reproducción desde el ecuador o el dimorfismo sexual, ya que la territorialidad

durante todo el año y los bosques o los hábitats heterogéneos fueron los predictores más fuertes de los duetos. A pesar de la prevalencia de los duetos en Rallidae, pocos estudios han evaluado las funciones del dueto, como por ejemplo la defensa del territorio en esta familia, y nuestro estudio filogenético comparativo sienta las bases para futuras investigaciones, ya que se sabe poco sobre la ecología del comportamiento y las interacciones vocales de muchos rálidos.

Palabras clave: duetos, estado ancestral, hábitat, propiedades de la llamada, rálidos, territorialidad durante todo el año

INTRODUCTION

Studies of animal communication have revealed an enormous diversity of species that utilize collective acoustic signaling, in which multiple individuals combine their sound production into duets and choruses that are greater signals than the sums of their parts (Langmore 1998, Hall 2009, Logue and Krupp 2016). Collective acoustic behavior is widespread in social animals, including insects, anurans, and mammals (Pika *et al.* 2018), and it is especially common in birds (Logue and Hall 2014). Avian duets are among the most coordinated of these communal signals, as they may involve tight temporal precision, may be initiated by one or both partners, and often show sex-specific vocal contributions (Dahlin and Benedict 2014). Duets can be further classified as (1) antiphonal or alternating, in which partners take turns with nonoverlapping calls that follow each other in tight precision; (2) asynchronous, in which partners show partial temporal overlap of their calls in a duet; or (3) synchronous, in which partners show complete temporal overlap of their calls in a duet (Hall 2009, Logue and Krupp 2016, Pika *et al.* 2018). Most duets are performed by male–female mated pairs, and choruses are made by >2 members of a social group toward conspecifics of other social groups (Logue and Krupp 2016). Temporally coordinated vocal displays that can be considered duets are additionally used as a courtship signal by male dyads in manakins (*Chiroxiphia*) (Hall 2009) and potentially other species, while coordinated vocalizations of three birds, known as “triets”, have recently been discovered in both polygynous and polyandrous groups of Sarus Cranes (*Antigone antigone*) as well (Roy *et al.* 2022).

A variety of hypotheses have been proposed for duetting in birds (Hall 2004), which fall into both social and ecological categories. The best-supported social function is year-round joint territory defense, as duets are more threatening than solo calls because they signal the presence of 2 birds at once, but some species also use duets for maintaining contact between pair-mates, as well as mate guarding (Hall 2009, Mikula *et al.* 2020). Moreover, duets are often structurally identical to solo calls, and both types of calls transmit at similar distances (Sandoval *et al.* 2015). Many duetting birds across diverse clades are socially monogamous with stable long-term pair bonds, which are expected to facilitate the evolution of cooperative multifunctional signaling by mated individuals (Benedict 2008, Dahlin and Benedict 2014). As migration reduces partnership duration time, it is unsurprising that many duetting songbird species are sedentary (Logue and Hall 2014, Mitchell *et al.* 2019), though both migration and duetting can be gained and lost repeatedly over evolutionary time. Phylogenetic analyses have found that duetting is conserved across closely related taxa, as seen in oscine families such as wrens (Troglodytidae, Keenan *et al.* 2020) and New World sparrows (Passerellidae, Cicero *et al.* 2020), and duets may be preceded by natural histories favoring the evolution of female vocalizations, as in New World blackbirds (Icteridae, Odom *et al.* 2015).

Duetting bird species have historically been reported most often in the tropics, with fewer duetting species reported from temperate regions (Hall 2009). The perceived correlation between tropical breeding and duets may be a result of the negative relationship between migration and breeding latitude in birds (Logue and Hall 2014), and the unequal geographic distribution of avian duetting may be biased toward the southern hemisphere and equatorial regions, because year-round territoriality and long-term social bonds are common there (Slater and Mann 2004). Much less understood is the influence of habitat type on the evolution of duetting (Hall 2009), but several studies in passerines suggest that duets can be used for short-range communication by breeding partners in dense vegetation, which scatters sound especially at higher frequencies, and where visual communication is limited due to the lack of a line of sight (Mays *et al.* 2006, Sandoval *et al.* 2015, Graham *et al.* 2016). Indeed, one of the first hypotheses of avian duet function was that mated pairs duet to maintain contact in dense forests, even though this early analysis did not quantify habitat density relative to the presence of duetting (Thorpe 1972).

The vast majority of duetting studies have been conducted on passeriform birds (Austin *et al.* 2021), especially oscines, in which female song is an ancestral trait (Odom *et al.* 2014). Duets are common in many avian clades beyond songbirds (Malacarne *et al.* 1991, Hall 2009). Yet only a few nonpasserine clades, such as parrots (Psittaciformes), owls (Strigidae), and barbets (Capitonidae), have been subjects of detailed observational and comparative research (Bradbury and Balsby 2016, Yee *et al.* 2018, Soma and Brumm 2020). In one particularly understudied family of birds, Rallidae, including rails, crakes, coots, and gallinules, the frequency of duetting is twice as that of all other avian taxa, which warrants further investigation into duetting and it correlates in this clade. Unlike both passerines, in which 18% of species duet, and nonpasserines overall, in which 20% of species duet (Tobias *et al.* 2016), at least 49 rail species are known to duet, and rail duets range from asynchronous to synchronous to antiphonal, although some species exhibit multiple duet types, or males and females call at slightly different rates in their duets (Huxley and Wilkinson 1979, Winkler *et al.* 2020). However, behavioral evidence of rail duets has been mostly observational and anecdotal to date (Taylor 1998), and only a handful of experimental studies have verified that duets are used for territorial defense, pair contact, and pair bond commitment in Rallidae (e.g., Huxley and Wilkinson 1979, Depino and Areta 2020, Jedlikowski *et al.* 2021). Moreover, duetting has been correlated with cooperative breeding in birds, and Rallidae includes genera such as *Fulica* (coots), *Gallinula* (moorhens), and *Porphyrio* (swampheens), in which multiple species exhibit polygamy and conspecific brood parasitism, and care for young in social groups of more than just the 2 parents, but do not appear to duet (Taylor 1998).

We analyzed whether patterns of duet occurrence in Rallidae are similar to those of better-studied taxa such as oscines, as these patterns in rails can shed light on conditions

that are conducive to the evolution of communal signals in general. Our hypothesis was that rail duets have been shaped by the same social and ecological pressures as have duets in other avian groups. Thus, we predicted that duetting rails are more likely to exhibit long-term social bonds and year-round territoriality, be sedentary or only partial migrants, breed cooperatively, and be concentrated in tropical latitudes. As duetting occurs in many non-passerine species in which males and females are similar in body mass (Malacarne *et al.* 1991), we predicted that duetting rails should also be size-monomorphic compared to nonduetting rails. Finally, we investigated whether duetting rails inhabit more densely vegetated habitats and show call properties conducive to optimal transmission in these habitats: specifically, that they produce longer calls at lower frequencies and narrower frequency ranges than nonduetting species.

METHODS

Species Selection

For our comparative analyses, we used a recent total-evidence maximum likelihood phylogeny of the family Rallidae (Garcia-R and Matzke 2021) based on morphology (271 integumentary, myological, and osteological characters), mitochondrial DNA (3 gene fragments totaling 2,900 continuous base pairs [bp]), and nuclear DNA (10 gene fragments totaling 20,828 aligned nucleotides). We chose this tree over the most recent published phylogeny of Rallidae (Kirchman *et al.* 2021), because Garcia-R and Matzke's (2021) phylogeny has much greater taxon coverage (158 vs. 65 species) and has an almost identical topology except for the placement of the Nkulengu Rail (*Himantornis haematopus*). We pruned the phylogeny down to a subset of 103 species that met the following criteria: (1) at least 2 call recordings were available online from the Macaulay Library (<http://macaulaylibrary.org/>) or Xeno-Canto (<http://xenocanto.org/>), (2) duetting and life history trait data were available, (3) body mass and sexual size dimorphism information were available, and (4) habitat information and range maps were available. We did not use recordings that were rated fewer than 3 stars in the Macaulay Library or as "C" grade or below on Xeno-Canto, due to their excess background noise or faintness of their vocalizations. We maintained the taxonomy of the original phylogenetic tree (Winkler *et al.* 2020, Garcia-R and Matzke 2021) except for *Laterallus*, in which we included 3 species (*L. fasciatus*, *L. viridis*, and *L. spilopterus*) previously assigned to *Anurolimnas* and *Porzana*, but otherwise left this in-flux genus intact (Stervander *et al.* 2019); *Amaurornis*, in which we returned *A. marginalis* to *Aenigmatolimnas*; and *Gallirallus*, in which we returned *A. wallacii* to *Habroptila*, assigned *A. calayanensis* to the newly-proposed *Aptenorallus*, and put the remaining species in *Hypotaenidia* except for *G. australis* (Kirchman *et al.* 2021). We visualized the phylogeny in FigTree 1.4.2 (<https://github.com/rambaut/figtree>) to re-root the tree using *Himantornis haematopus* as the outgroup, matching Garcia-R and Matzke's (2021) phylogeny.

As in previous studies (Logue and Krupp 2016, Tobias *et al.* 2016), we defined duets as synchronized and coordinated vocalizations of 2 individual birds within a pair, and choruses as synchronized and coordinated vocalizations of 3 or more individuals within a social unit. We pooled duetting and chorusing rail species together because these vocalizations show

identical behaviors of closely matched timing, initiation, and answering (Hall 2009, Logue and Krupp 2016), and because a handful of rail species, such as the Black Crake (*Zapornia flavirostra*) and the Henderson Crake (*Z. atra*), also exhibit coordinated calling of entire family groups (Jones *et al.* 1995, Parker and Parker 2019), akin to duets by mated pairs. In agreement with Huxley and Wilkinson (1979), we considered duets of mated pairs (and choruses of social units) to be distinct from simultaneous calling of birds on different territories that may by chance vocalize at the same time. We scored rails as duetting (coded as 1) if there was at least 1 published source that described duets in the species (Taylor 1998, Winkler *et al.* 2020), or 2 different recordists (from the Macaulay Library or Xeno-Canto or personal correspondence) who described duets in the species. We scored rail species with detailed descriptions of male and female vocalizations, but no mention of duets or choruses, as nonduetting (coded as 0), and we scored rail species with poorly known calls in general as unknown (coded as NA). Sources used to score duets and all predictor variables are provided in the electronic Supplementary Materials (Supplementary Material Table S1).

Predictor Variables

We downloaded sound files of the calls of our selected species from the Macaulay Library and Xeno-Canto, and we digitized all recordings in .wav format at a rate of 44.1 kHz in Audacity 2.2.2 (Audacity Team 2018). In total, we obtained calls from 364 individuals (mean per species = 3.5) representing 103 (~65%) of the 159 known species of rails. We visualized spectrograms in Raven Pro 1.5.1 (Center for Conservation Bioacoustics 2014, Cornell Laboratory of Ornithology, Ithaca, New York) using the following parameters: a Hann window type with a DFT size of 512 samples, 70% overlap (resulting in a hop size of 3.5 ms), and frequency grid spacing of 86.1 Hz. We measured 8 acoustic variables from each individual rail vocalization (Figure 1): delta time (call length), low (i.e., minimum) frequency, high (i.e., maximum) frequency, peak (i.e., highest call amplitude) frequency, frequency bandwidth, 5% frequency (i.e., the frequency where the summed energy exceeds 5% of the total energy in the selection), 95% frequency (i.e., the frequency where the summed energy exceeds 95% of the total energy in the selection), and bandwidth 90% (i.e., the difference between the 95% frequency and 5% frequency measurements of the selection). We chose these acoustic variables as they include common measurements used in prior phylogenetic studies of call structure in birds, and because 3 variables (5% frequency, 95% frequency, and bandwidth 90%) can be estimated using the by-eye method but account for subjectivity biases and deal well with overlapping noise (Mason and Burns 2015, Billings 2018). All acoustic variables were measured automatically from spectrograms in Raven Pro when we manually drew boundary boxes around the entirety of each vocalization. We measured fundamental frequency, or the first harmonic, of the selected rail calls (Figure 1), and for greater precision we averaged measurements across multiple calls (up to 5) per recording and multiple recordings (up to 6) per species (Supplementary Material Table S1).

We obtained behavioral life history traits used as predictor variables from a published monograph on the family Rallidae (Taylor 1998), a comprehensive comparative

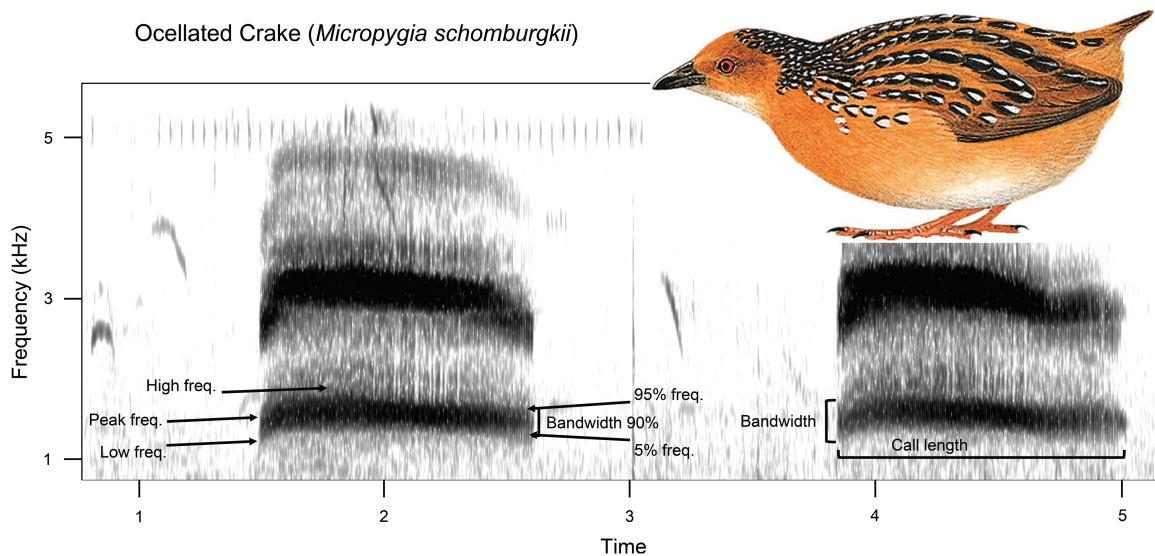


FIGURE 1. Spectrogram made in Raven Pro 1.5.1 illustrating how specific acoustic variables were quantified, with Ocellated Crane (ML 101342) as an example. We included call length, low frequency, high frequency, peak frequency, frequency bandwidth, 5% frequency, 95% frequency, and bandwidth 90% measurements, shown here for calls of *Micropygia schomburgkii*. Illustration by Norman Arlott from Birds of the World (Winkler *et al.* 2020), used with permission (© Lynx Edicions).

study of avian cooperative breeding (Cockburn 2006), and Birds of the World (Winkler *et al.* 2020). These discrete predictor variables included territoriality (scored as territorial either seasonally or year-round), social bond length (scored as short-term or long-term pair bonds), parental care type (scored as biparental care or cooperative breeding), and migration (scored as sedentary, partial or latitudinal migrant or nomadic, or long-distance migrant), which have been used in previous studies of duetting in birds (Benedict 2008, Logue and Hall 2014). Depending on the predictor variable, we scored life history traits as either binary (0 or 1) or multistate (0, 1, or 2), and we searched the published literature to fill in missing data for each species in the dataset (Supplementary Material Table S1). To calculate sexual size dimorphism, we used male and female wing length (in mm, $n = 38$ species), or alternatively male and female body mass (in g, $n = 65$ species), obtained from Taylor (1998) and Dunning (2008). From these data, we estimated a continuous measure of sexual size dimorphism as either $\log(\text{male wing length}) - \log(\text{female wing length})$, or $\log(\text{male body mass}) - \log(\text{female body mass})$. Positive values of both calculations indicate species in which males are larger than females, and therefore exhibit male-biased sexual size dimorphism (Mikula *et al.* 2021).

We grouped each species into one of 8 biogeographical realms described by Olson *et al.* (2001) and Cockburn (2006), with only Oceania and Antarctica excluded due to a lack of rail species in the phylogeny that are both extant and native to these realms. We considered species “Widespread” if their worldwide breeding ranges spanned 2 or more biogeographical realms. We classified habitat type for each species into one of 3 categories—open, heterogeneous, and forest (0, 1, or 2)—according to the satellite data categorization of land cover types created by Crouch and Mason-Gamer (2019). We used range maps of our focal rails from Birds of the World (Winkler *et al.* 2020) to identify the northern- and southern-most breeding latitudes for each species in Google Earth Pro (<https://www.google.com/earth/>), and we averaged these geographic coordinates to obtain the central breeding latitude

(Supplementary Material Table S1), which is a robust method for latitudinal comparisons in birds (Logue and Hall 2014, Mitchell *et al.* 2019).

Phylogenetic Comparative Analyses

All analyses were conducted in R (R Core Team 2020). To reconstruct the evolutionary history of duetting in rails, we used the threshold model to find ancestral states (Revell 2014). This model assumes the representation of discrete traits over evolutionary time using a continuous “liability” variable, with liabilities below a fixed threshold representing 1 state (duetting) and liabilities above the threshold representing the other state (nonduetting). We therefore removed the 14 rail species scored as unknown from the ancestral state analysis, and we treated liabilities of the remaining 89 rail species as prior probabilities that evolved by Brownian motion, using Bayesian Markov Chain Monte Carlo (MCMC) algorithms to sample liabilities at all nodes in the tree. The resulting proportion of MCMC generations with the liability above the threshold at each node is the likelihood that the character state of duetting was present at that node. We ran an MCMC of 50 million generations for $n = 205$ tips and internal nodes, with a 20% burn-in time to account for slowly stabilizing variables, subsampling every 100 generations, and an alpha (α) prior value = 0.05, following Mitchell *et al.* (2019). After the MCMCs finished, we visually inspected the resulting traces for convergence, and we calculated both the effective sample size (ESS) and Geweke’s diagnostic, to ensure that the former value was maximized for all variables, and the latter value was nonsignificant to indicate sufficient MCMC stabilization (Revell 2014). We performed the ancestral state reconstruction in the R package *phytools* (Revell 2012) and used the R package *coda* to run the MCMC diagnostic tools (Plummer *et al.* 2006), while we created threshold trees and latitude diagrams in *phytools* and the *ggplot2* package (Wickham 2011), respectively. The ancestral state reconstruction for duets was robust with all 177 (100%) estimates based on

an ESS > 200, and 140 of 177 (79%) Geweke's diagnostic Z scores (Supplementary Material Figure S1) supported stable MCMCs, with the MCMC trace showing stable convergence over 50 million generations.

After natural-log-transforming all 8 acoustic variables to meet the normality assumption for regressions (Freckleton 2009), we next ran a principal component analysis (PCA), as well as a phylogenetic principal component analysis (PPCA), to reduce dimensionality and visualize potential patterns of grouping among the acoustic variables based on shared ancestry (Revell 2009). We ran regular and phylogenetic multivariate analyses of variance (MANOVAs) in the R package GEIGER (Harmon *et al.* 2008) on both the uncorrected PC scores and the phylogenetically corrected PC scores, to test for multivariate differences in acoustic values between species. We followed the MANOVAs with univariate analyses of variance (ANOVAs) to evaluate which PCs varied significantly by habitat type or in duetting vs. nonduetting rails (Garland *et al.* 1993). Finally, we conducted post-hoc pairwise t -tests to identify significant differences in acoustic variables between habitat types.

To compare the occurrence of rail duetting with categorical socio-ecological variables (life history traits and biogeographical realms) and with continuous socio-ecological variables (sexual size dimorphism and central breeding latitude), we had to account for phylogenetic non-independence, as trait values are more likely to be similar in closely related species than in more distant relatives (Felsenstein 1985). Thus, we analyzed trait evolution in the R packages *caper* and *phylolm* (Ho and Ané 2014, Orme 2018). As duetting is a binary dependent variable, we measured its phylogenetic signal by calculating the D statistic of trait lability (Fritz and Purvis 2010), which equals one when a binary trait is randomly distributed across the tips of a phylogeny and equals zero when the distribution approximates that expected under Brownian motion (Cicero *et al.* 2020). Next, we performed multivariate phylogenetic logistic regressions, which model the evolution of binary traits through Brownian motion (Ives and Garland 2010), to examine correlations among duets and the socio-ecological variables. We checked for multicollinearity using variance inflation factors (VIF) in the *car* package in R and removed biogeographical realm due to its VIF indicating significant correlations with other explanatory variables. To meet the sufficiently large sample sizes for trait value groups, we also omitted the 14 rail species that lacked information about duetting, grouped the 5 forest-dwelling species with heterogeneous habitat species, and classified species as sedentary or migratory for the trait of migration. We also converted central breeding latitude to its absolute value to test the hypothesis that distance from equatorial regions affects the presence of duetting. For each model, we maximized penalized likelihood of the logistic regression in the *logistic_MPLE* function with Firth's correction as the penalty (Ho and Ané 2014), ran each model for 1,000 bootstrap replicates, and selected the best model in a stepwise approach using Akaike's Information Criterion (AIC) and likelihood ratio tests (LRT). The logistic regressions additionally calculated a phylogenetic correlation parameter α that determined the magnitude of phylogenetic signal from the data: as α increases with the speed of transition rates due to species divergence, high values of this parameter indicate low levels of phylogenetic signal (Ives and Garland 2010).

RESULTS

Of the 103 rail species in our comparative analyses, we found evidence of duetting in 61 species (59%). Duetting in rails is taxonomically widespread, as our ancestral state reconstruction of 89 species estimated duetting frequencies of 14% in the genus *Porphyrio*; 25% in *Gallinula*; 63% in *Zapornia*; 89% in *Laterallus*; and 100% in *Amaurornis*, *Aramides*, *Hypotaenidia*, *Mustelirallus*, *Pardirallus*, *Porzana*, *Rallina*, *Rallus*, and 10 monotypic genera (Figure 2). Only the genera *Coturnicops*, *Fulica*, and *Lewinia*, and the monotypic genera *Crex*, *Gallicrex*, and *Porphyriops* showed no duetting. Our ancestral state reconstruction indicated that the last common ancestor of Rallidae was likely a duetting species (likelihood = 0.88) but duetting was lost in multiple rail lineages over time. There is little evidence at the basal node of the coot and moorhen clade (*Fulica* and *Gallinula*, respectively) to indicate a duetting ancestor (likelihood = 0.19), nor did the most recent common ancestor of swamphens (*Porphyrio*) likely duet (likelihood = 0.15). On the other hand, duetting appears to have been regained recently in a few species within these clades, such as the Gough Moorhen (*Gallinula comeri*), Tasmanian Nativehen (*Tribonyx mortierii*), and South Island Takahe (*Porphyrio hochstetteri*). We found a strong phylogenetic signal for duetting ($D = 0.18$), suggesting that this trait is highly phylogenetically conserved.

The PCA and PPCA of the eight acoustic variables each resulted in three axes totaling 98% of the vocal variation (Table 1). PPC1 corresponded to call frequency and had trait loadings in the same negative direction, as rail species with higher scores produce higher minimum, maximum, peak, 5%, and 95% frequencies. PPC2 corresponded to delta time and had a strong positive loading, in which species that produce longer calls showed higher scores. Lastly, PPC3 corresponded to call bandwidth and had strong positive loadings for bandwidth and 90% bandwidth, indicating that species with higher scores produce calls of wider frequency ranges. There was a slight effect of habitat on acoustic variables given by the PCs ($F_{2,100} = 1.98$, $P = 0.07$) and the PPCs ($F_{2,100} = 1.99$, $P = 0.067$), as well as a significant effect of duetting on the acoustic variables from the PCs ($F_{1,87} = 8.81$, $P < 0.001$) and the PPCs ($F_{1,87} = 8.92$, $P < 0.001$). Pairwise post-hoc t -tests revealed that rails in open habitats vocalize over lower frequencies ($F = 3.88$, $P = 0.14$) and narrower bandwidths ($F = 2.70$, $P = 0.24$) than rails in heterogeneous habitats or forests, whereas forest-dwelling rails produce shorter calls ($F = 2.28$, $P = 0.32$) than rails in open or heterogeneous habitats (Figure 3A). Duetting rails vocalize at higher frequencies ($F = 2.56$, $P = 0.53$) and wider bandwidths ($F = 5.30$, $P = 0.36$), with slightly shorter calls overall ($F = 0.18$, $P = 0.86$), than nonduetting rails (Figure 3B). Nevertheless, these differences disappeared after accounting for common ancestry in both the phylogenetic MANOVA of PC scores (habitat: $P = 0.39$, duets: $P = 0.16$) and the pMANOVA of phylogenetically corrected PC scores (habitat: $P = 0.38$, duets: $P = 0.14$).

The distribution of duetting rail species across socio-ecological trait values is shown in Figure 4. The alpha value obtained from our phylogenetic logistic regression model (Ives and Garland 2010) indicated that there was strong phylogenetic signal for duetting in Rallidae ($\alpha = 0.051$), consistent with the D statistic. After we corrected for phylogenetic signal, there appeared no significant association between sexual size dimorphism (likelihood ratio test [LRT] $\chi^2 = 0.16$,

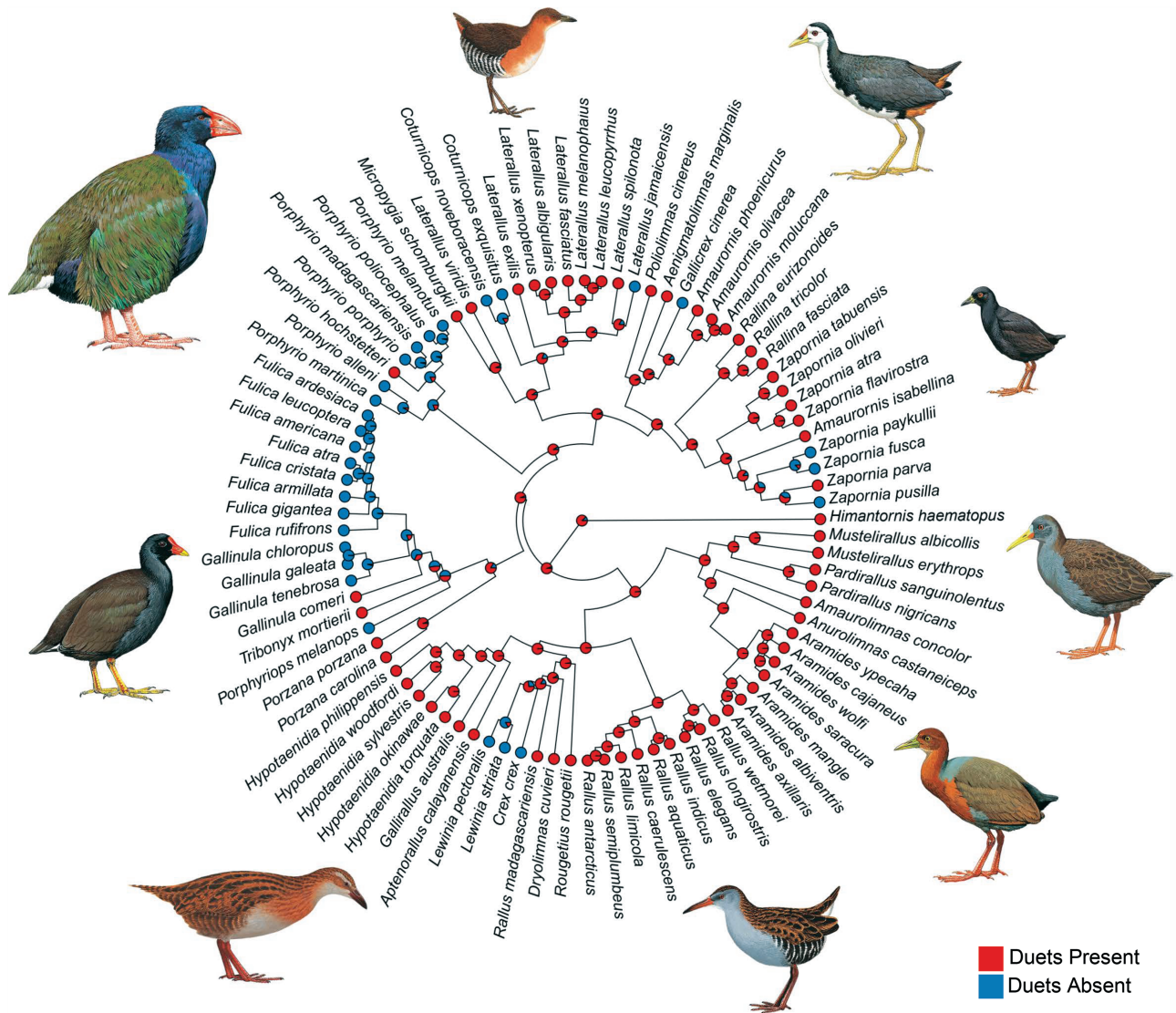


FIGURE 2. Ancestral state reconstruction for 89 rail species, indicating that their common ancestor was likely a duetting species. Circles at tree branch tips and nodes represent posterior estimates from the threshold model. Artwork of representative duetting rails (images not to scale) was drawn by Hilary Burn and Norman Arlott from Birds of the World (Winkler et al. 2020), used with permission (© Lynx Edicions).

TABLE 1. Phylogenetic principal component analysis loadings for the first 3 axes using 8 acoustic variables measured in this study. The first, second and third axes account for 55.18%, 34.43%, and 8.38% of the total variation, respectively. The loadings of the first PPCA axis have been switched from negative to positive values for ease of interpretation.

Acoustic variable	PC1	PC2	PC3
Call length	0.23	0.97	-0.04
Minimum frequency	0.92	-0.17	-0.32
Maximum frequency	0.97	-0.13	0.15
Peak frequency	0.98	-0.16	0.01
Bandwidth	0.72	-0.05	0.61
Bandwidth 90%	0.62	0.10	0.72
5% frequency	0.95	-0.19	-0.20
95% frequency	0.98	-0.12	0.11

df = 1, $P = 0.69$), central breeding latitude distance from the equator (LRT $\chi^2 = 0.26$, df = 1, $P = 0.61$), breeding system (LRT $\chi^2 = -0.28$, df = 1, $P = 1$), or social bond length (LRT

$\chi^2 = 0.72$, df = 1, $P = 0.40$) and the presence of duetting (Table 2). Including migration in the model caused a significant improvement in its fit (LRT $\chi^2 = 7.68$, df = 1, $P = 0.006$), with a marginally non-significant coefficient showing that duetting is more likely in species that are migratory as opposed to sedentary (Table 2). However, habitat type was significantly correlated with duetting (LRT $\chi^2 = 5.42$, df = 1, $P = 0.02$), as species native to forests or heterogeneous habitats are more likely to duet than species native to open habitats. Territoriality was also significantly associated with duetting (LRT $\chi^2 = 14.08$, df = 1, $P < 0.001$), with species exhibiting year-round territoriality more likely to duet than species exhibiting seasonal territoriality (Table 2).

DISCUSSION

Our comparative analyses revealed that duetting is highly prevalent in rails and has likely evolved in association with year-round territoriality. Within Rallidae, 59% of 103

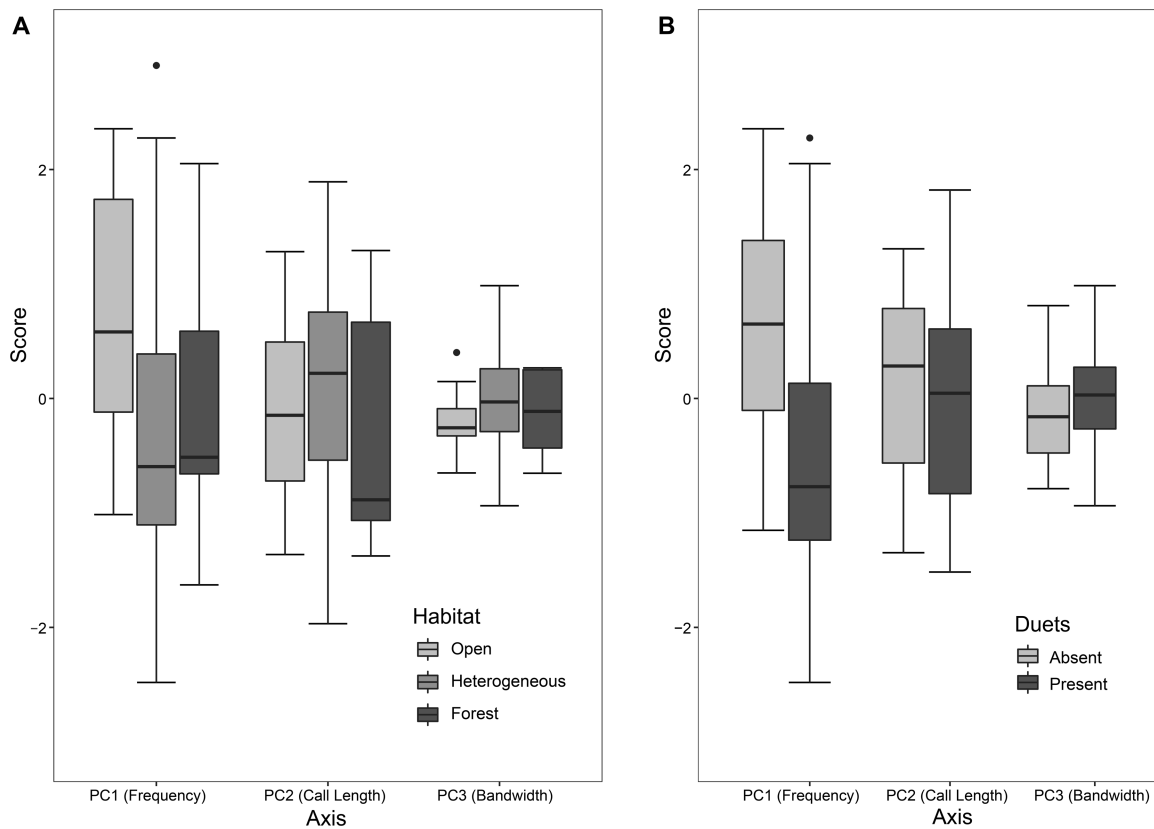


FIGURE 3. Box plots of associations between rail species acoustic variables collapsed to three principal component axes (main weighting variable in parentheses) and **(A)** habitat type or **(B)** duetting behavior (boxes represent interquartile ranges with medians as a solid bold horizontal line, with whiskers encompassing data within 1.5x to interquartile range and outliers shown by solid points).

measured species duet, which is almost 4x the percentage estimated for all birds (~16%, Tobias *et al.* 2016) and oscine passerines (15.6%, Logue and Hall 2014), and almost 5x the percentage in non-passerine barbets (12.5%, Soma and Brumm 2020). Duets occur in all major clades of rails (Garcia-R and Matzke 2021), with the highest concentration of duetting species found in the genera *Amaurornis*, *Aramides*, *Hypotaenidia*, *Laterallus*, and *Rallus*. Our ancestral state reconstruction revealed that the most recent common ancestor of all rails was likely a duetting species, and that duetting has been lost at least 12 times within the family, with a handful of species in otherwise nonduetting lineages regaining this behavior (Figure 2). This ancient origin is well-explained by the widespread occurrence of duetting in other gruiform clades, as duets are used by all 15 crane species (Gruidae), all 3 trumpeter species (Psophiidae), the Limpkin (*Aramus guarauna*), the Sungrebe (*Heliornis fulica*), and at least 3 flufftail and forest-rail species (Scolopacidae), though the latter family includes many species poorly known to science in which duetting may yet be discovered (Tobias *et al.* 2016). Future research may determine whether the common ancestor of Gruiformes was itself a duetting species.

Duetting is generally a labile avian trait and can evolve rapidly, with up to 17 independent origins known in North American Passeriformes (Benedict 2008) and 6–9 independent origins known in Capitonidae (Hall 2009, Soma and Brumm 2020). The robust phylogenetic signal that we discovered for rail duets emphasizes some extent of the conservation of the presence or absence of this trait over evolutionary time within Rallidae. Notably, we found that duetting was lost in the

lineage leading to coots (*Fulica*) and moorhens (*Gallinula*), as well as the separate lineage of swampheens (*Porphyrio*). These genera form the bulk of cooperative breeding rails (Cockburn 2006), but we found no significant relationship between breeding system and duetting (Figure 4E). The loss of female song (which is associated with duetting in passerines) has been suggested to occur following the evolution of colonial breeding in New World blackbirds (Price 2009), though this does not explain why certain group-breeding avian clades have maintained duetting, but others have not (Mikula *et al.* 2020, Soma and Brumm 2020). There was also no relationship between duetting and sexual size dimorphism in rails, irrespective of whether males or females are greater in body mass. In birds generally, sex-specific contributions to duets within pairs may arise from the emergence of sexual size dimorphism and selection for lower-frequency vocalizations in the larger sex (Hall 2004, Mikula *et al.* 2021), but the timing and types of male and female duet components in rails remain currently unexplored.

Our discovery that duetting is associated with year-round territoriality in rails was marked but unsurprising, given that previous research has found these traits to be tightly linked across birds (Dahlin and Benedict 2014, Hall 2009). For example, in a study of 12 passerine families, Benedict (2008) discovered that 50% of the duetting species defended their territories over entire years, as opposed to 11% of the nonduetting species, and a similar pattern was seen in a broad sampling of Aves, in which 51 of 58 duetting species defended territories throughout the year (Dahlin and Benedict 2014). Almost all rails are territorial either seasonally or year-round,

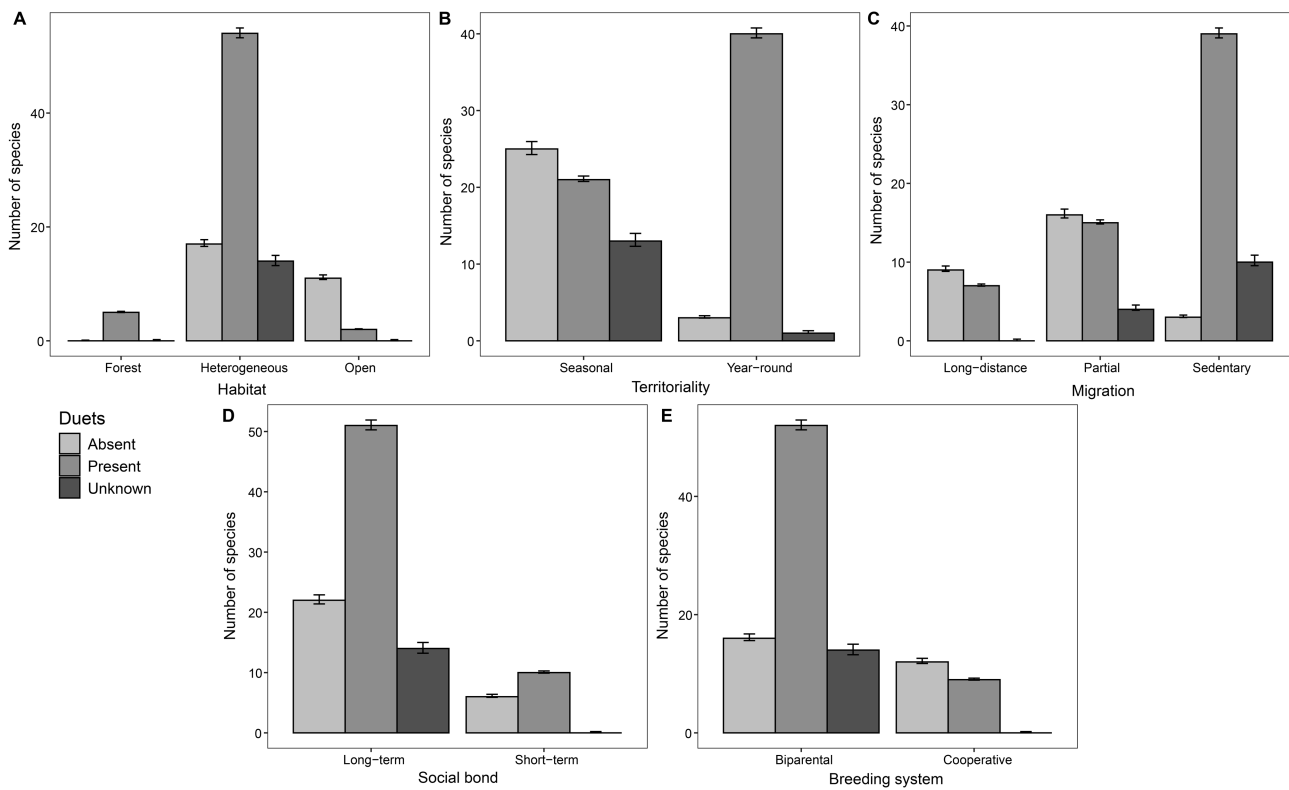


FIGURE 4. Number of rail species (mean \pm 95% CIs) for each socio-ecological trait and the respective trait values. These bar charts are not corrected for phylogeny, but a phylogenetic generalized linear model found habitat (**A**, modified grouping combining forest with heterogeneous) and territoriality (**B**) to be significantly associated with duetting. Migration (**C**, grouped as sedentary or migratory) had a marginally non-significant effect on duetting presence. Social bond (**D**) and breeding system (**E**) were not significantly associated with duetting.

TABLE 2. Phylogenetic logistic regression coefficient estimates for the association between socio-ecological traits and duetting in rails. Terms that were kept in the final model are highlighted in bold, and values for other terms come from the step before their removal.

Coefficient	Estimate	SE	Lower boot CI	Upper boot CI	<i>z</i>	<i>P</i>
Intercept	-1.32	1.20	-3.35	1.10	-1.11	0.27
Habitat: Heterogeneous	2.17	0.98	0.24	4.26	2.21	0.03
Social bond: Long-term	0.42	0.87	-0.78	1.48	0.48	0.63
Territoriality: Year-round	3.19	0.92	1.27	4.95	3.46	<0.001
Migration: Migratory	-1.03	0.68	-2.81	0.26	-1.52	0.13
Breeding system: Cooperative	-0.11	0.76	-1.73	1.43	-0.14	0.89
Latitudinal distance from equator	-0.02	0.01	-0.04	0.004	-1.61	0.11
Sexual size dimorphism	1.32	2.31	0.93	2.06	0.57	0.57

with many species defending winter feeding territories as well as summer breeding territories (Taylor 1998), and we found that most year-round territorial rails duet, whereas most seasonally territorial rails do not (Figure 4B). In contrast to the strong positive correlation between long-term social bonds and duetting that is typical in birds (Mikula *et al.* 2020), we found no strong relationship between pair bond length and duetting in rails (Figure 4D). Most rails exhibit high mate fidelity and long-term social bonds that are stable year-round, while only a handful show low mate fidelity and seasonal or unstable social bonds, but the proportions of duetting and nonduetting rail species are almost identical regardless of pair bond length (Taylor 1998). Although year-round territoriality and long-term social bonds are often found together in birds, territoriality may be a precursor to the evolution of duetting,

while long-term social bonds may evolve after duetting is already in place, due to increased selection for joint resource defense (Mikula *et al.* 2020).

Evolution of latitudinal migration in passerines has been significantly correlated with loss of female song and duetting behavior, as migration reduces the time available for breeding partnerships and the benefits of duetting (Benedict 2008, Price 2009, Logue and Hall 2014, Mitchell *et al.* 2019). Yet we uncovered only a slight correlation between migration and duetting in rails (Figure 4C). Long-distance, partial, and altitudinal migrants together make up a minority of species in Rallidae, and rails' typically poor flight performance and tendency toward flightlessness on islands could account for the sedentariness observed in most species in this family (Taylor 1998, Kirchman 2012). Sedentary and geographically isolated

insects, birds, and mammals have been thought to produce simpler calls than their wider-ranging or migratory relatives, which may free males and females to vocalize separately on islands; this “duet splitting” has been proposed to account for a loss of duetting in insular gibbons (Geissmann 2002). In rails, however, flightless species have repeatedly evolved within volant clades and yet have retained the duetting behavior shared by their flying relatives (Kirchman 2012, van de Crommenacker *et al.* 2019). Only in the coots, gallinules, and swamphens have duetting, flightless, and island-endemic rails evolved within nonduetting flying clades (Figure 2), so the possibility of duet splitting appears dubious for Rallidae but cannot be ruled out entirely. We also did not find a significant relationship between duetting and central breeding latitude distance from the equator. Rails, thus, stand in contrast to many systematic comparisons of songbirds that have observed duetting mostly in tropical species, probably due to the noncausal negative relationship between migration and latitude in which equatorial species are more sedentary (Hall 2004, 2009, Logue and Hall 2014, Mitchell *et al.* 2019). This relationship can be explained by a stable climate and readily available resources in the tropics, which lead to reduced mortality and increased longevity in avian populations (Slater and Mann 2004). Moreover, tropical birds may exhibit sex role convergence and reduced extra-pair paternity because of their year-round territoriality, long-term social bonds, and coordinated duets (Slater and Mann 2004, Riehl 2020).

Early research into avian duets suggested that these coordinated signals may be used instead of visual communication by paired individuals in densely vegetated habitats where vision is heavily obscured (Hall 2009). Duetting in non-passerines is not exclusive to species inhabiting closed habitats such as forests (Short and Horne 1983, Malacarne *et al.* 1991), but duets have been proposed to function over short ranges for songbird pairs in dense vegetation (Mays *et al.* 2006, Sandoval *et al.* 2015, Graham *et al.* 2016). We discovered that rail duetting is significantly associated with forest and heterogeneous habitats as opposed to open habitats (grasslands and open-water wetlands) (Figure 4A). A previous study of three European rails found that the grassland-dwelling Corn Crake (*Crex crex*) calls using wide bandwidths that transmit broadly, while two rails native to heterogeneous habitats—the Water Rail (*Rallus aquaticus*) and the Spotted Crake (*Porzana porzana*)—call with narrow bandwidths that degrade less over smaller ranges (Ręk and Kwiatkowska 2016). However, these authors did not address duetting, even though the Water Rail and Spotted Crake both duet, whereas the Corn Crake does not. Rails are predominantly ground-dwelling and may be under similar selective pressures as forest-dwelling terrestrial mammals, which make high-frequency calls that are easily detected with sensitive hearing but may thwart eavesdropping by predators (Charlton *et al.* 2019). In addition, if duetting rails are communicating over short distances, these birds may utilize high frequencies because their proximity should minimize call degradation. Rails like coots and swamphens in open habitats such as ponds could also be under selection for producing lower-than-average call frequency as a signal of body size (Cardoso 2012), as these species should be more visible while vocalizing than rails that inhabit densely vegetated forests or habitats with less dense vegetation.

Our results add to the growing body of comparative research documenting the presence and evolutionary history of duetting in diverse avian taxa (Logue and Hall 2014,

Mitchell *et al.* 2019, Soma and Brumm 2020, Mikula *et al.* 2020). Compared to the large number of studies focused on oscine passerines, rails have rarely been subject to manipulative experiments to test duet functions, despite the ubiquity of duetting in the family Rallidae. Only the Water Rail, the White-throated Rail (*Dryolimnas cuvieri*), and 4 South American *Laterallus* crakes have been examined with call-playback experiments that found duetting used for territory defense and pair-contact maintenance; all other proposed functions of rail duets have been based on anecdotal or opportunistic field observations (Huxley and Wilkinson 1979, Depino and Areta 2020, Winkler *et al.* 2020, Jedlikowski *et al.* 2021). Overall, only 7 rail species have been the focus of more than 6 publications that documented their vocal behavior in detail (Williams 2021). Our discovery that Rallidae includes entire genera of either duetting or nonduetting rails is timely, given that previously understudied rail species have recently been found to duet when they were not known to beforehand (Schroeder and McRae 2019, Bodrati and Lammertink 2020, Depino *et al.* 2021). Anecdotal evidence suggests that rails may engage in heterospecific calling bouts or individual vocalizations that resemble duets, if not simultaneous duets between pair members (Skinner 1979, N. Pieplow, personal communication). Advances in brain imagery have even enabled investigations into the neuronal and hormonal coordination of duetting, and neural scanning of rails could shed light on potentially distinct call ontogeny compared to song learners like passerines (Brenowitz 1997, Logue and Krupp 2016). As rail calls are innate rather than learned, they may be less plastic than songbird vocalizations in adaptability to local habitats, a prediction which remains to be tested (Hardt and Benedict 2020).

In conclusion, this study presents a detailed framework for future studies of duetting in rails, an avian family that exhibits duets in 58% of 103 sampled species. Our findings indicated a strong phylogenetic signal for duetting, supported an origin of duets in the common ancestor of Rallidae, and uncovered a significant relationship between rail duetting and year-round territoriality. Furthermore, we found evidence that duetting rails tend to be sedentary species from forests and heterogeneous habitats. Whether duets are shaped by selection for close-range communication in such cluttered environments should be further explored in avian lineages with duetting species. Considering that detailed descriptions of vocal behavior are lacking for many rails, we expect that this diverse group of innately calling non-passerines will provide fertile ground for future studies into the origin, ontogeny, and maintenance of duets and choruses.

Supplementary material

Supplementary material is available at *Ornithology* online.

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Ethics statement

Animal care is not relevant to this study, as we did not work with live birds.

Conflict of interest statement

The authors declare that we have no competing interests.

Author contributions

D.L.G. conceived of the study idea and collected data; D.L.G., B.M.S., and A.P.C. wrote or substantially edited the paper; D.L.G. designed and developed methods; D.L.G. and B.M.S. analyzed the data; and A.P.C. contributed resources, software, and advice.

Data availability

Comparative analyses reported in this article can be reproduced using the data files and R code provided by Goldberg et al. (2022).

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