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ORIGINAL PAPER

Why some rails have white tails: the evolution of white undertail plumage and anti-predator signaling

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Abstract Conspicuous plumage patches have evolved in birds as conspecific signals for mate attraction and assessment, intersexual competition or to signal alarm. Signals may alternatively be directed at potential predators to discourage pursuit. Rails (Family Rallidae) are ground-dwelling birds, many of which inhabit wetlands, while others occur in forests and grasslands. They are renown for their secretive nature and the tendency to flick their tails when observed. This behavior is more conspicuous in species with white undertail coverts that contrast sharply with darker body plumage. Using species comparisons and controlling for phylogeny, we investigated four hypotheses for the evolution of white undertail coverts in rails. We found little support for the hypothesis that white tails are sexually selected: white tails were not more common in species with polygamous as opposed to monogamous mating systems, species with sexual dimorphism, nor species that display their tails in courtship. Nor did our results support the hypothesis that white tail plumage evolved for intersexual competition during territorial interactions. Instead, we found that species that flock for at least part of the year and species found in open as opposed to concealing habitats were significantly more likely to have white undertail coverts. Rail species inhabiting concealing habitats are less commonly gregarious and more likely selected for crypsis. Using phylogenetically-controlled statistical inference we found that adaptation to open wetland habitats significantly precedes the evolution of white undertails, whereas gregariousness likely evolved later in some lineages. The inferred order of trait evolution suggests that this plumage characteristic could have been selected primarily for enhancement of an anti-predator signal rather than a social signal for conspecifics.

Keywords Character evolution · Concentrated changes test · Discrete · Omnibus test · Phylogeny · Plumage color · Pursuit deterrent · Rallidae · Signaling

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Introduction

Animals communicate using different sensory modalities for which they have a wide array of physiological and morphological adaptations (Bradbury and Vehrencamp 1998). Interspecific variation in plumage coloration among birds may function in both intraspecific and interspecific communication, evolving in response to factors such as sexual selection (Safran and McGraw 2004; Safran et al. 2005), foraging tactics (Mumme 2002), and variation in habitat (McNaught and Owens 2002; Endler and Thery 1996). Many studies of the color and morphology of plumage in birds have focused on their roles in sexual selection. However, recent research has begun to explore other plumage functions such as in signaling alarm to conspecifics or pursuit-deterrence to predators (Murphy 2006).

Conspicuous plumage color patches may be coupled with distinctive movements that reveal or enhance their display (Gomez and Thery 2007). Contrasting tail markings combined with behaviors such as flicking movements have been documented as pursuit deterrent signals in mammals (Bildstein 1983; FitzGibbon and Fanshawe 1988; Holley 1993; Caro et al. 1995; Caro 1995, 2005), lizards (Dial 1986; Hasson et al. 1989), and birds (Woodland et al. 1980; Murphy 2006). Pursuit deterrent signals are mutually beneficial, allowing both predator and prey to avoid unnecessary time and energy expenditure (Woodland et al. 1980). Recent studies have demonstrated that the predator receivers of such signals respond by changing their behavior (Clark 2005; Rundus et al. 2007).

Many rail species (Family Rallidae) are known to flick or jerk their tails up and down. Reviewing accounts in ‘Rails: a guide to the rails, crakes, gallinules and coots of the world’ (Taylor and van Perlo 1998) showed that undertail plumage coloration varies widely among rail species and that many species known to exhibit some sort of tail-flicking behavior do not have contrasting white undertail coverts. Why then did white tails evolve in some rails?

We developed four alternative hypotheses focusing on behavioral variation and signaling efficacy for the evolution of white undertails in rails.

1. White undertail coverts may have been favored by sexual selection in some species, and function in mate choice. Aragones et al. (1999) found evidence of sexual selection for conspicuous white wing and tail bands in red-necked nightjars (*Caprimulgus ruficollis*). Female great snipes (*Gallinago media*) show a preference for males with the whitest spots on their tails (Höglund et al. 1992).
2. White tails may have evolved to facilitate signaling in territorial interactions. Slagsvold and Lifjeld (1988) suggested that the conspicuous black-and-white plumage of pied flycatchers (*Ficedula hypoleuca)* might benefit territory owners by making them more conspicuous to intruding males, reducing territory-holding costs, if intruders usually retreat upon discovering that a territory is occupied. Some rails, such as the common moorhen *Gallinula chloropus* and American coot *Fulica americana*, direct at conspecifics elaborate displays and posturing at territorial boundaries (Taylor and van Perlo 1998; S. B. McRae, personal observation).
3. White undertail coloration might be used in intraspecific communication other than in agonistic contexts or sexual displays. For example, white tails might be used to warn conspecifics of danger (Alvarez et al. 1976; Stoner et al. 2003; Craig 1982) proposed that purple swamphens (*Porphyrio porphyrio*) use their white undertail coverts in submissive signals toward more dominant conspecifics. Moreover, white plumage coloration has been found to be associated with gregariousness in previous comparative studies of birds, possibly for social cohesion (Brooke 1998; Beauchamp and Heeb 2001).

4. Contrasting white tail feathers may serve to accentuate tail-flicking signals directed at predators. The pursuit deterrent function of tail-flicking behavior has been experimentally confirmed in three rail species (Woodland et al. 1980; Alvarez 1989,1993; Ryan et al. 1996; Randler 2007). In each case, the tail is elevated, exposing contrasting bright white coloration. Some evidence suggests that tail-flicking rate may reveal the relative health of the signaler (Alvarez et al. 2006).

White undertail coloration might further be adapted for conspicuous signaling where light levels are low (Galeotti et al. 2003). Many rails are crepuscular, while some also exhibit nocturnal activity. Hence, we further predicted that white tails may be favored in species exhibiting greater nocturnal or crepuscular activity.

We employed a comparative approach to test our hypotheses, using published data on over 130 species of rails and statistical methods allowing us to control for phylogeny.

Materials and methods

We collected data on ecological and behavioral traits of species in Family Rallidae from 'Rails: a guide to the rails, crakes, gallinules and coots of the world' (Taylor and van Perlo 1998). Plumage coloration and sexual dimorphism were also assessed from both the descriptions and illustrations in this book. The data were then categorized (Table 1) and coded into binary format, with "1" signifying the presence of a given trait and "0" denoting the absence of the trait.

In analyses controlling for common ancestry, we used a complete, morphologically based phylogenetic tree of the rails by Livezey (1998), as was done in a comparative analysis of chick ornamentation in the same Family (Krebs and Putland 2004). To resolve collapsed polytomies and simplify the extensively divided *Porphyrio porphyrio* "superspecies," only the species or subspecies for which the majority of behavioral data were available were included.

Incongruencies exist between the morphological phylogeny of the rails (Livezey 1998), based on 381 osteological characters, and a partial molecular phylogeny (Trewick 1997) constructed based on cytochrome *b* and 12S mitochondrial DNA sequences. Some deep forks in the molecular phylogeny have weak bootstrap support, including the placement of the *Porphyrio* genus. As the molecular tree was specifically constructed to investigate the evolution of flightlessness in endemic Polynesian rails, it only includes a small, non-representative segment ($N = 22$) of Family Rallidae. For these reasons, we were unable to achieve sufficient resolution using it. We also had difficulty in constructing a composite tree based on the two phylogenies, so we employed only the morphological tree of Livezey (1998).

Comparative methods incorporating phylogeny allow for a more rigorous investigation of the adaptive significance of traits by controlling for the confounding nature of shared ancestry on the environments and phenotypes of related species (Harvey and Pagel 1991). Recently, it has been argued that the use of such methods may be inappropriate if no phylogenetic effect exists, such as with rapidly evolving traits (reviewed in Rheindt et al. 2004). Plumage coloration and patterns are believed to evolve rapidly relative to other characters (reviewed in Omland and Lanyon 2000), perhaps with some variation under the control of a single mutation (Robbins et al. 1993; Theron et al. 2001; Driskell et al. 2002). As the application of phylogenetic correction is controversial in some cases, we initially tested our four alternative hypotheses for the evolution of contrasting undertail covert color

Table 1 Description of categories of variables used in the comparative analyses

Variable	Binary states	Description
Undertail-covert color	White	Solid white or white lateral coverts
	Not white	Barred or solid brown, reddish-brown, buff, gray or black
Plumage sexual year-round	Monomorphic	Sexes largely indistinguishable by plumage dimorphism
	Dimorphic	Sexually dimorphic non-breeding or breeding plumage
Mating system	Monogamous	Social organization described as largely monogamous in the wild or captivity, with few birds observed courting or copulating with more than one individual in breeding season; monogamy as supported by calling patterns or by observations of two adults accompanied by immature or chicks
	Polygamous	Sequential or simultaneous polyandry, polygyny, or polygynandry, observed at least at low frequency, in the wild or captivity
Use of tail in courtship or pair maintenance	Yes	Undertail coverts flicked, fanned, raised, fluffed, or otherwise displayed prominently (e.g., bowing) in or pair functions
	No	Courtship displays observed without note of undertail coverts employed by individuals
Use in agonistic behavior	Yes	Undertail coverts flicked, fanned, raised, fluffed, or otherwise displayed prominently (e.g., bowing, “mutual retreat”) during intraspecific territorial encounters
	No	Intraspecific territorial encounters observed without note of undertail coverts employed by individuals
Gregariousness	Flocking	Readily or consistently form large groups outside the breeding season, dense population with frequent interactions, or large aggregations of birds, such as breeding colonies or groups
	Not flocking	Maintain permanent territories year round; only observed singly, in pairs, or small family groups; usually solitary or territorial but occasionally form small foraging parties; communal feeding ground; overlapping home ranges or breeding areas
Habitat	Open	Open water, lakes, ponds, rivers, open marsh, bays, marshland, marshes, swamps, reedbeds, permanent or ephemeral wetlands, floodplains, lagoons, waters with fringing vegetation
	Not open	Forest, woodland, dense thickets, bush, marshland in forest, grassland, dry to moist grasslands, meadows, scrub, tussock grass, fern-bush, pastures, forest clearings, cultivation, savannah
Nocturnal activity	Yes	Any calling or other observed activities after dusk in captivity or the wild
	No	No nocturnal activities or calling noted

The plumage descriptions and both behavioral and ecological data were gathered from Taylor and van Perlo (1998) using simple contingency table analyses. We then examined the same hypotheses controlling for phylogeny.

We first coded Livezey's 1998 phylogenetic tree for 134 rail species in MacClade (Maddison 1990), and traced each binary character in our analyses onto the tree. In each analysis missing data were excluded. The number of species for which we had information on both undertail color and the independent variable under consideration ranged among tests from 34 to 132.

We conducted preliminary analyses using Maddison's Concentrated Changes Test (CCT; as implemented in Maddison and Maddison 2000). This test determines whether more gains ($0 > 1$) and fewer losses ($1 > 0$) of white undertail covert coloration are concentrated on branches with a particular state reconstruction in an independent variable than would be expected by chance (Maddison 1990). A significant P value may mean that the evolution of white undertail coverts is facilitated when an ecological or behavioral character is in a particular state. In the CCT, the ancestral state of both characters must first be reconstructed, e.g., using maximum parsimony. Both the DELTRAN and the ACCTRAN optimizations were explored to resolve equivocal reconstructions of both independent and dependent characters. In instances in which these algorithms left ambiguous branches unresolved, we examined the first and last most parsimonious reconstructions (MPR) produced by the "equivocal cycling" function in MacClade. We calculated P values using the "actual changes" simulation option for 10,000 replicates with either "0" or "1" reconstructed at the basal node of the tree (Maddison and Maddison 2000) for the in/dependent character.

We conducted our principal tests for correlated evolution between characters using the program *Discrete* (v. 1.0). *Discrete* uses a continuous time Markov model in a maximum likelihood framework, estimating parameters of trait evolution by summing the likelihood of each state at each node of the tree (Pagel 1994). Results therefore do not rely on ancestral state reconstruction, and so should not lead to biased results when traits evolve relatively rapidly (i.e. more than once on one tree). *Discrete* compares an independent model for character evolution with a dependent model in which two discrete characters of interest are correlated. In the omnibus test, the models are compared using a likelihood ratio statistic that approximates an asymptotic χ^2 distribution with four degrees of freedom (Pagel 1999). This method does not assume a priori one character to be independent and the other dependent. In contrast, *Discrete* provides the ability to predict the order of precedence of correlated characters by comparing, through contingency change hypothesis tests, models in which specific rates of directional transitions are restricted against the unrestricted model (Pagel 1994).

In the absence of information, branch lengths for all analyses were set to one, consistent with evolutionary changes being independent of time.

Results

In conducting the CCT, undertail color was considered the dependent variable. Non-white undertail coloration was reconstructed as the ancestral state based on the tail characteristics of more basal gruids (Livezey 1998). We removed missing data, so each CCT compared only species for which both the independent and dependent variable states were known. Maximum parsimony reconstruction showed white undertails evolving between seven and twelve times, depending on the species in the tree. We traced by maximum parsimony the independent variable under consideration, and determined how many times white undertails were gained and lost in lineages with the independent variable in the derived state.

The DELTRAN (which delays changes away from the root and increases independent gains) and ACCTRAN (which maximizes early gains and favors losses of the derived state; Swofford and Maddison 1987) reconstructions of equivocal tracings yielded similar P values.

Discrete provided a more powerful test of our hypotheses, as it does not rely on ancestral state reconstructions. Exactly the same variables were found to be significantly correlated using the CCT and the omnibus test function in *Discrete*. We present only the results of analyses using *Discrete* (Table 2). These results were generated by inclusion of Yang's (1994) gamma rate heterogeneity model that allows traits to evolve at different rates in different branches of the tree, where the distribution of rates is assumed to follow a gamma distribution with a mean of 1.0. The same results were obtained with and without the inclusion of Yang's model, which resulted in differences in the likelihood ratios of only 0–2% per test.

Sexual selection

We predicted that species with polygamous mating systems, which have higher degrees of mate competition, should have white undertails if this trait is sexually selected. We tested the possibility that white undertails are more likely in species in which at least a low frequency of polygamous associations have been observed, such as the common moorhen, which generally breeds monogamously but has also been known to exhibit polyandry and cooperative polygyny (McRae 1996). However, cross-species comparisons did not provide any evidence for a relationship between polygamous species and white tails (Table 2).

Species with intense intrasexual competition are more likely to compete with displays involving plumage (Darwin 1871; Andersson 1994). Some rails are known to display undertail coverts during territorial interactions and/or mate competition. Species we coded as engaging in these types of displays were those observed raising, spreading, or fluffing undertail coverts or adopting a posture that otherwise prominently reveals them. We tested whether rail species that use their tails in displays for courtship or pair maintenance were more likely to have light colored undertail coverts. This association proved to be non-significant at the $\alpha = 0.05$ level (Table 2).

We also tested whether sexual selection could be responsible for the evolution of white tails by examining the relationship between sexual dimorphism in plumage, as an estimator of high mate competition, and white undertail coverts. Most rails are monomorphic or only subtly sexually dimorphic in plumage. We coded a species as sexually dimorphic if distinct parts of male and female plumage differed in color at any time during the year or if plumage brightness differed between sexes to a greater extent than in American robins *Turdus migratorius*, a species we chose as a reference for monomorphism. For instance, the snoring rail (*Aramidopsis plateni*) was coded as sexually dimorphic since females have brighter orange hindnecks and less white at the throat. On the other hand, the chestnut rail (*Eulabeornis castaneoventris*) was considered monomorphic, since plumage between the sexes is alike, except for a slight olive-tinge to the upper parts in males in the olive morph. White tails and sexual dimorphism were moderately related only in cross-species comparisons (Table 2). This is an example of where the coincidence of characters is closely clustered on the phylogenetic tree, illustrating the need to control for shared ancestry in the analyses. These results taken together suggest a trend, but the lack of association between indicators of strong sexual selection and white undertails compels us to reject this hypothesis.

Table 2 Summary of significance levels for independent χ^2 tests (1 degree of freedom, species independent) and Markov model likelihood ratio tests (incorporating phylogeny) for correlated evolution of independent characters with white undertail coverts in rails

Hypothesis	Variables	Number of species	χ^2 test		Markov model			
			χ^2	*P*	Indep	Dep	LRT	*P*
Sexual selection	Mating system	74	0.14	0.71	−60.34	−59.72	1.26	$0.75 < P < 0.90$
	Use of tail in courtship or pair maintenance	34	3.31	0.081	−42.33	−39.85	4.98	$0.25 < P < 0.50$
	Sexual dimorphism	125	3.04	0.069	−105.64	−103.16	4.98	$0.25 < P < 0.50$
Agonistic behavior	Use of tail in behavior territorial	44	1.10	0.17	−52.72	−51.76	1.90	0.75
Other social signal	Gregariousness	85	22.01	<0.0001*	−72.74	−67.19	11.08	<0.05*
Tail-flicking	Habitat	132	19.74	<0.0001*	−127.24	−117.08	20.32	<0.001*
	Nocturnal activity	98	1.04	0.31	−97.89	−96.67	2.44	$0.50 < P < 0.75$

The likelihood ratio multiplied by two (LRT) between the independent model (Indep) and the dependent model (Dep) is compared to a χ^2 distribution with 4 degrees of freedom

Agonistic behavior

Species that use their tails in territorial displays should be more likely to have white undertail coverts if this plumage trait evolved to facilitate agonistic behavior. We coded as "1" species noted to flick, fan, fluff or adopt postures that show the undertail in well documented intraspecific threat displays. For example, opposing male soras (*Porzana carolina)* may perform "swanning" displays, in which birds bend down and spread the undertail coverts, at territory boundaries (Kaufmann 1983). We found no evidence for this association (Table 2).

Other conspecific communication

If light colored tails are used in other conspecific signals, such as an indication of social status or alarm, they should be found in gregarious species. Many species of birds are gregarious at least in the non-breeding season. Among rails, some species that are territorial in the breeding season aggregate in large feeding flocks when not breeding (e.g., common moorhens, American coots in the temperate winter), or congregate about pools in the dry season (e.g., gray-necked wood-rail *Aramides cajanea*, Friedmann and Smith 1950; Baillon's crake *Porzana pusilla*, water rail *Rallus aquaticus*, Taylor and van Perlo 1998), whereas others appear to remain remote year-round (e.g., Rouget's rail *Rougetius rougetii*, white-throated rail *Dryolimnas cuvieri*, flufftails *Sarothrura* spp. Taylor and van Perlo 1998). Rails described as gregarious or that flock at least during part of the year tended to have white tails. This result was upheld after controlling for phylogeny ($P < 0.05$; Table 2), providing support for this hypothesis.

Tail-flicking

In an investigation of plumage pattern differences among congeneric *Phylloscopus* warblers Marchetti (1993) found that species in darker environments may have evolved a greater number of conspicuous plumage patches to enhance the efficacy of territorial signals to conspecifics. Similarly, rail species found in concealing environments may have evolved bright tail plumage to enhance the efficacy of a different signal: tail-flicking as a pursuit deterrent to predators. We tested whether species in densely vegetated habitats, such as forest or grassland, are more likely to have vivid white undertails than those in more open habitats, such as open water or marshes that have patches of open water. Note that we consider grassland to be concealing from the perspective of rails because the height of grasses in natural habitats exceeds the height of most adult rails. Species-level comparisons of habitat and light tails revealed a highly significant association ($P < 0.0001$) but in the opposite direction from what we predicted: rails living in more open habitats were more likely to have white tails. This result was confirmed when controlling for phylogeny ($P < 0.001$; Table 2).

Some species of rail are known to show extensive nocturnal activity (e.g., gray-necked wood-rail Skutch 1994; yellow rail *Coturnicops noveboracensis* Robert and Laporte 1997). A related prediction is that species showing some sort of nocturnal or crepuscular activity should tend to have white undertail coverts to improve signal visibility. However, the 68 species described as calling or active in the evening or at night were no more likely to have white undertails (Table 2).

Although there is no evidence supporting a relationship between evening activity and white undertail coverts, there is a strong association between species occurring in open habitats and their bearing white tails, even after controlling for phylogeny.

Origins of white tails in rails

The two variable states that correlated most strongly the presence of white undertail coverts were ‘Flocking’ (Fig. 1) and ‘Open habitat’ (Fig. 2). Transitions to white undertails occur at significantly higher frequency in open as opposed to concealing habitats, and among lineages that flock than among lineages that do not form aggregations.

We set out to test the hypothesis that the tendency to flock precedes the origin of white tails in rails. The program *Discrete* enables us to determine statistically the order of precedence of traits via contingency change tests, without the need to assume ancestral states. We tested our hypothesis in *Discrete* by constraining q_{12} (the transition rate from ‘Not White’ to ‘White’ when the Gregariousness variable was in the state ‘Not flocking’) to be equal to q_{13} (the transition rate from ‘Not flocking’ to ‘Flocking’ when the undertail color variable was ‘Not white’) and asked whether the model fit is significantly worse than the full model where these two parameters are free to vary (Pagel 1994). There was a significant difference ($L(q_{12} = q_{13}) = -67.2$, LRT (1 df) = 11.0, $P = 0.001$); however, in the opposite direction from the hypothesis: the rate of transition to ‘White’ undertails in non-flocking lineages ($q_{12} = 0.05$) was higher than the rate of transition to ‘Flocking’ in non-white lineages ($q_{13} = 0.04$), suggesting that white undertail coverts tend to evolve before flocking (Pagel 1994). While this result was unexpected, it may be attributable to the low number of species in the state combination ‘Flocking, Not white’ (Fig. 3a).

It is perhaps of greater relevance to test specifically whether ‘White’ undertails originate most frequently overall in lineages that are gregarious. To do this, we constrain q_{12} (‘Not White’ to ‘White’ in lineages that are ‘Not flocking’) to be equal to q_{34} (the transition rate from ‘Not white’ to ‘White’ when the Gregariousness variable was ‘Flocking’), in the dependent model, and ask whether the fit is significantly worse than the full eight parameter model. There was a significant difference between these models ($L(q_{12} = q_{34}) = -67.5$, LRT (1 df) = 10.4, $P = 0.001$), indicating that the rate of transition to White tails was significantly higher among ‘Flocking’ ancestors ($q_{34} = 0.44$) as opposed to ‘Not flocking’ ($q_{12} = 0.05$) ancestors.

We similarly explored the possibility that the origins of white undertails were contingent on habitat by restricting the model with q_{12} (the transition rate from ‘Not white’ to ‘White’ in ‘Not open’ habitats) equal to q_{13} (the transition rate from “Not open’ to ‘Open’ when Undertail color was ‘Not white’), and comparing this to the unrestricted model (Pagel 1994). There was a strong significant difference between these models ($L(q_{12} = q_{13}) = -118.5$, LRT (1 df) = 17.4, $P \ll 0.001$). Thus, the transition to ‘Open’ habitats ($q_{13} = 0.13$) occurs at a significantly higher rate than the rate of transition to ‘White’ undertails ($q_{12} = 0.03$), implying that the colonization of open habitats generally precedes the evolution of white undertails (Fig. 3b). Again, though, this might be heavily influenced, this time in favor of our hypothesis, by the low number of instances of species in the combined state ‘Not open, White’.

To determine the effect of the habitat variable on the rate of transition to white tails, we set q_{12} equal to q_{34} (the transition rate from ‘Not white’ to ‘White’ in ‘Open’ habitats). Comparison with the unrestricted model again revealed a strong significant difference: the rate of transition to ‘White’ undertails was significantly greater in lineages occupying ‘Open’ habitats ($q_{34} = 0.07$) than those in ‘Not open’ habitats ($q_{12} = 0.03$; $L(q_{12} = q_{34}) = -119.2$, LRT (1 df) = 16.1, $P \ll 0.001$). This emphasizes that open habitats facilitate the evolution of white tails.

The variables ‘Open habitat’ and ‘Flocking’ were significantly correlated with one another ($r^2 = 0.27$). This is unsurprising since animals tend to aggregate when at risk,

Fig. 1 Phylogenetic reconstructions illustrating the correlated variables ‘Gregariousness’ and ‘Undertail color’. In **a** the state ‘Not flocking’ is traced as *white*, and ‘Flocking’ as *black*. In **b** ‘Not white’ undertails is traced as *white* and ‘White’ undertails is traced as *black*. Species with missing data are excluded. The tree topology is based on (Livezey 1998), and the DELTRAN optimization is shown for both characters. Note that ancestral trait reconstruction is not necessary for testing for correlated evolution using the maximum likelihood method in Discrete

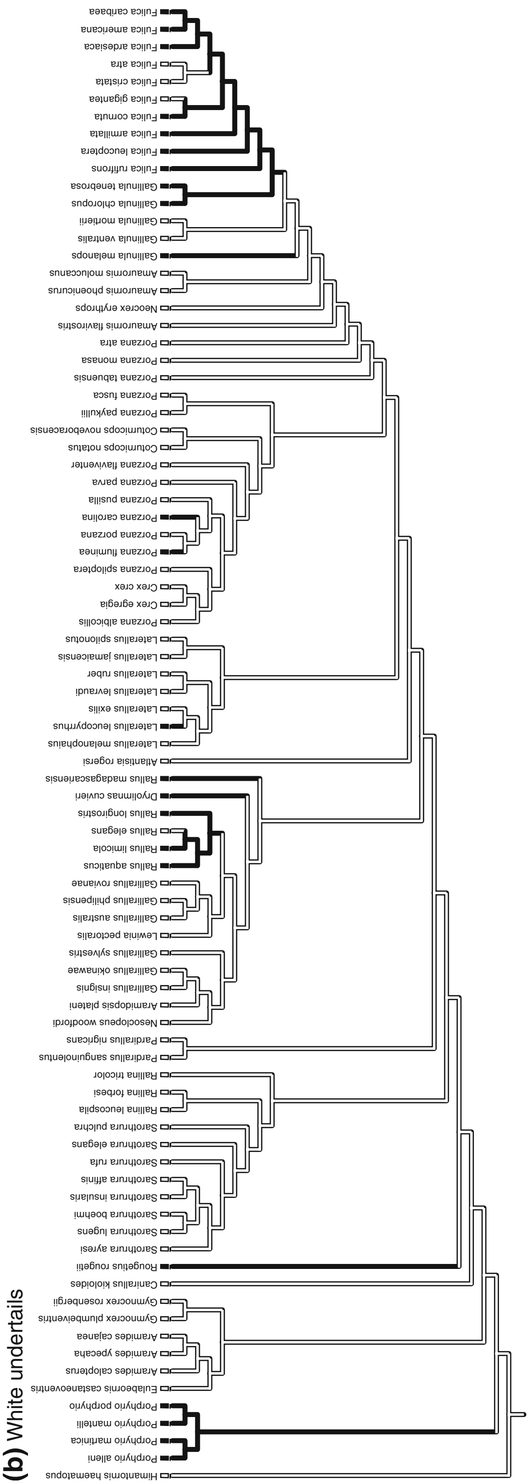

Fig. 1 continued

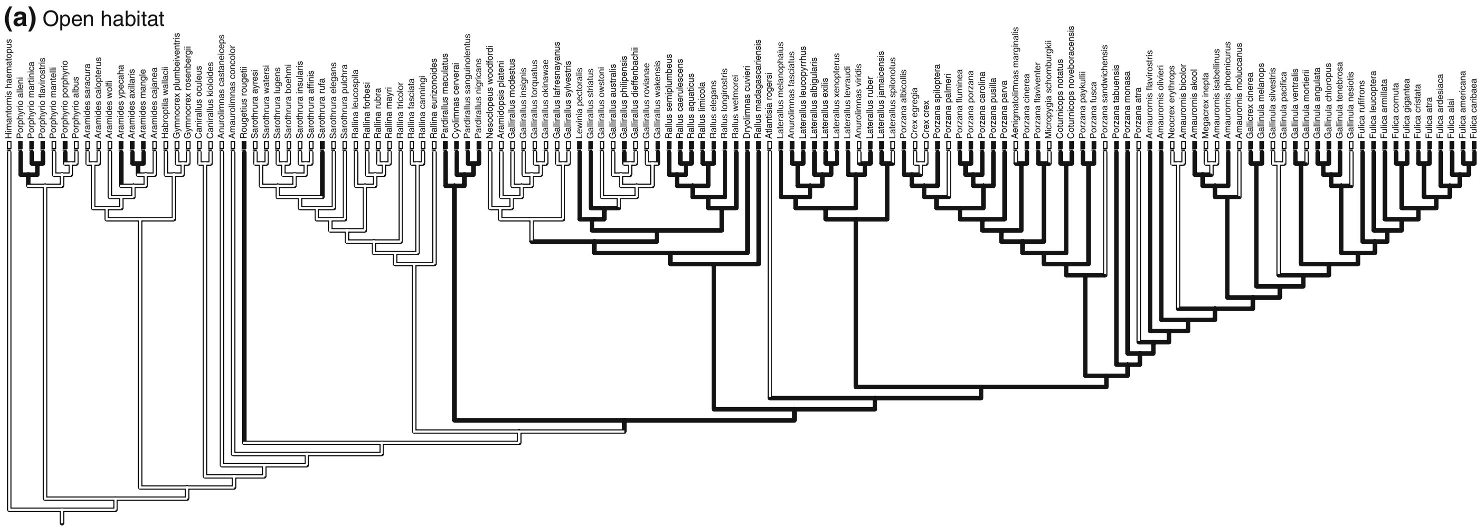

Fig. 2 Phylogenetic reconstructions illustrating the correlated variables ‘Habitat’ and ‘Undertail color’. In **a** the state ‘Not open’ is traced as *white* and ‘Open’ traced as *black*, and in **b** ‘Not white’ is traced as *white* and ‘White’ traced as *black*. Species with missing data are excluded. The tree topology is based on (Livezey 1998), and the DELTRAN optimization is shown for both characters. Ancestral trait reconstruction is not necessary for testing for correlated evolution using the maximum likelihood method in Discrete

Fig. 2 continued

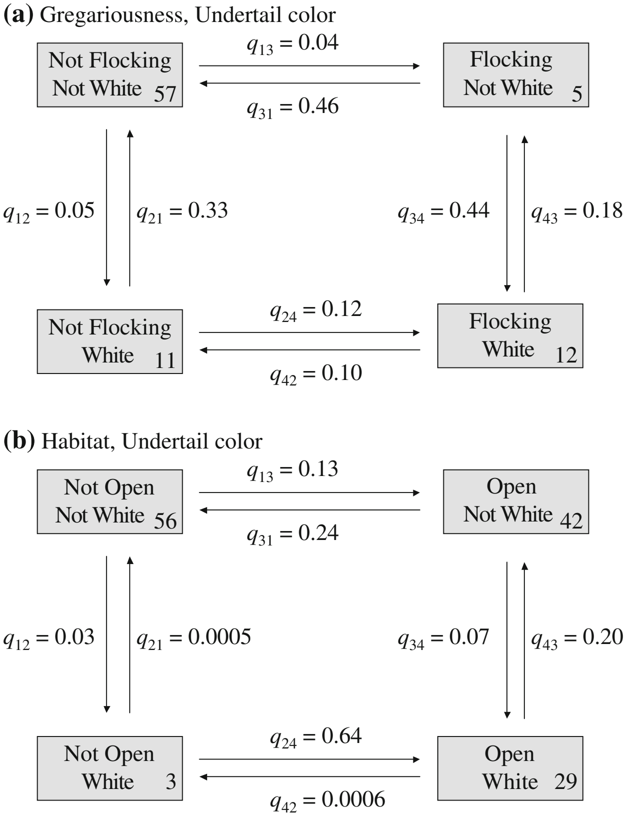

Fig. 3 Path diagram of transition rates (q_{12}, q_{23} etc.) calculated in *Discrete* between states of Undertail color (White, Not White) with **a** Gregariousness (Flocking, Not flocking), and **b** Habitat (Open, Not open). The corresponding numbers of species are shown in the lower right of the *boxes* indicating the trait combinations

which would occur more out in the open. The hypothesis that visually permissive habitats select for gains in white undertail coloration is more strongly supported by smaller *P* values in conjunction with a larger sample size. This in addition to evidence that white undertail coverts tend to evolve before gregariousness suggest that enhancement of the pursuit-deterrent function of tail-flicking, rather than a social signal to conspecifics, may be a major factor driving the evolution of conspicuous white undertail coverts in rails.

Discussion

Converse to our original prediction, species with white undertail coverts tended to be found in open habitats. More open or brighter habitats are in general more conducive to visual signals. Johnson and Lanyon (2000) found that nesting in marsh habitat favors the evolution of bright, contrasting plumage patches in male blackbirds. Here, visual signals are mediated by male-male competition over variable territory quality. In rails, however, the relationship between marsh habitats and the evolution of conspicuous white tails appears unlikely to be driven by sexual selection or agonistic interactions, as other indicators of each variable proved non-significant. Instead, the strong association between habitat and white tails may be indicative of two alternative anti-predator strategies among rails. First, species that spend time in the open may congregate and remain vigilant to deter predators through pursuit deterrent signals. By contrast, species that live in dense, concealing habitats may use crypsis as their main anti-predator strategy and may not be able to afford having a conspicuous white tail.

Conspicuous plumage signals are likely to be under strong selection by predators that hunt visually. For example, plumage brightness was the most important factor contributing to the vulnerability of prey species as highlighted in a recent study comparing characteristics of passerines preyed-upon by predatory birds (Huhta et al. 2003). Habitats are rarely uniform, making the dichotomous habitat variable the most difficult one to define. We attempted to be as specific as possible and assumed most natural terrestrial rail habitats have vegetation cover. Accordingly, the way that we defined rail habitats in our study, open habitats tend also to be more aquatic. White undertails might further enhance tail-flicking or other signals in open wetland and aquatic habitats by the illusion of larger size due to the feature's reflection on the water surface. Pursuit deterrence signals are intended for recipients that are far away (Smythe 1976). In habitats wrought with visual obstructions crypsis might be a more profitable strategy. Alternatively, audible signals may have evolved as in concealing habitats such as the drumroll-like sound uttered by Wallace's rail *Habroptila wallacei* when approached (Heinrich 2007). Notably, this is a species without white undertail coverts. Diversity in auditory signaling among rails awaits further investigation.

White undertail coverts were also associated with gregariousness, which suggests that it could have either evolved to facilitate intraspecific communication or enhance the pursuit deterrent function of tail-flicking. Predation has been proposed as a selective pressure that favors flocking. A large number of published studies have reported an inverse relationship between individual vigilance and group size (reviewed in Elgar 1989; Lima and Dill 1990; Quenette 1990). In the group vigilance hypothesis, animals may benefit from being in larger groups because the vigilance of flock-mates allows for an increased predator detection rate while requiring less individual time allocation to scanning (Pulliam 1973). Another explanation for the reduction in vigilance with increasing group size is the individual risk hypothesis: that an individual will be depredated is reduced in a group (Lazarus 1979; Lima 1995). High predation rates may select for both gregariousness and pursuit deterrent signaling among rails.

The use of omnibus tests in the program *Discrete* allowed us to test for correlated evolution of a suite of variables against our variable of interest, undertail color, without the need to reconstruct ancestral states. The CCT in MacClade, which does require ancestral state reconstruction identified exactly the same variables as correlated with the evolution of white tails. Since both of these tests are relatively conservative (Lorch and Eadie 1999; Pagel 1999), these results appear to be robust.

The contingent change hypothesis tests offered by the *Discrete* program (Pagel 1994) allowed us to obtain some insight into the relative precedence of evolution of correlated traits. While these tests appeared to be quite sensitive to the relative proportions of species with particular binary state combinations, they nonetheless allowed us to conclude that the colonization of open habitats, the stronger of the two correlates with white undertails, significantly precedes their evolution. By contrast, the results suggest white undertail evolution precedes gregariousness. Thus, white undertails could have evolved under threat of predation in conjunction with signals directed at predators as opposed to conspecifics.

Testing hypotheses concerning behavioral variation using the comparative method depends on good documentation of displays. The behavior of many rail species is still relatively poorly known. Since the absence of a particular trait is not explicitly stated in species accounts, it is possible that some missing data should have been listed as zeros instead. For this reason, we found it problematic to include tail-flicking in our analyses as a possible correlate of white tails.

Some of the relatively secretive rails in the genera *Rallus, Rallina, Crex, Porzana, Neocrex* and others have variously barred black and white undertails (Taylor and van Perlo 1998). In most, this is an extension of the plumage patterns on the belly and flanks, but in some, such as selected *Porzana* and *Rallus* species, it is distinct. When we began, we coded all of the variation in these patterned undertails in our database. However, procedural limitations of the phylogenetically-based statistical analyses forced us to collapse the data into a binary variable. It is possible that the barring, which varies among species in the thickness of stripes and in black or white emphasis, may represent a trade-off between the tail's use in signaling and the importance of maintaining a degree of crypsis. Empirical tests of the visibility of such patterns in different habitats, as well as a better understanding of visual predator pressure in these species, may help us to understand the adaptive significance of black and white stripes. Future comparative studies should attempt to address the issue of variable plumage patterns as well as color.

The majority of transitions in undertail color were from non-white to white, but there were a few notable reversions. In one case, we categorized the tail of *Rallus elegans* as not white, since it has black spots and bars on a predominantly white undertail. Reversions from white to not white in the *Fulica* clade warrant further consideration. Most extant members of this clade are endemic to South America, and the genus likely originated there and spread to the Old World (Olson 1973). According to our analysis, white undertail coverts evolved in the *Gallinula-Fulica* ancestor. Almost all extant members retain the trait, except for the two Old World species: the red-knobbed coot *F. cristata* of Africa with rare white tips to the undertail coverts and the Eurasian coot *F. atra* with fully black undertails matching their body plumage. It was probably the ancestor to the two Old World species that lost the white undertail trait, perhaps when it colonized new habitat that may have had greater expanses of water with fewer visual predators.

In addition to tail flicking, some species in the *Gallinula-Fulica* clade have similar behavioral displays. For example, common moorhens and American coots use elaborate displays and posturing at territorial boundaries with the actors, often less than two feet apart, turning slowly with back arched and tail splayed and erect, culminating in the birds being positioned tail-to-tail. These displays often avert conflict but sometimes escalate to a kick boxing battle (Taylor and van Perlo 1998; S. B. McRae, personal observation). That female Eurasian coots perform copulation solicitation displays, and both sexes use courtship displays involving tail-raising and expanding the undertail coverts (Taylor and van Perlo 1998), in spite of the loss of the white undertail, underscores the reduced importance of tail color in sexual signaling.

The loss of the white undertails in the giant coot *F. gigantea*, and its drastic reduction to two thin white stripes in the horned coot *F. cornuta* is perhaps more revealing of its function. These are the largest rail species, the giant coot being so heavy as to be nearly flightless. Their ranges are limited to barren, high-altitude lakes of the Andean altiplano, and both species are known for their large conspicuous nests (Taylor and van Perlo 1998). All of these factors indicate the likelihood of reduced predation pressure. The loss of white tails in these species seems to strengthen our argument for a predator-directed signaling function of tail color. The nominate subspecies of another species, the Andean coot *F.*

ardesiaca, with a wider range stretching into the foothills and lowlands, has white undertails. However, the subspecies *F. a. atrura* that occupies the northern part of the species range including a disjointed area spanning the Columbia-Ecuador border, has black streaking and freckling on the undertail coverts (Taylor and van Perlo 1998). No information exists on the behavior of this subspecies. A comparison of predator species and predation rates, habitat and behavioral differences of these Andean populations (including the giant and horned coots) would help disentangle the relative importance of each factor in the evolution of tail coloration and signaling.

Our results using both phylogenetically-based and independent statistical inference were congruent. Nevertheless, results of phylogenetic comparisons are dependent upon a well-resolved phylogenetic tree. A major discrepancy between the rail tree based on osteological characters (Livezey 1998) and the partial molecular phylogeny of Family Rallidae (Trewick 1997) is the placement of the *Porphyrio* genus. This clade is basal to most other rails in the osteological phylogeny but clusters with the more derived *Gallinula-Fulica* group in the partial molecular phylogeny. A complete molecular phylogeny is not currently available. As identified previously (Krebs and Putland 2004), a robust and complete molecular phylogeny of the rails is needed to reconstruct the evolutionary history of further behavioral and morphological characters. This will also help elucidate relationships among some of the less well-known species, many of which are island endemics with small population sizes including several species of grave conservation concern.

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