# Chic chicks: the evolution of chick ornamentation in rails

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Competition over access to food has led to the evolution of a variety of exaggerated visual and vocal displays in altricial nestling birds. Precocial chicks that are fed by their parents also vary widely in appearance ranging from those with inconspicuous coloration to those with brightly colored bills, fleshy parts, and plumes. These ornaments are lost by the end of the period of parental dependence, suggesting they function in competition over parental care. We use a comparative approach to evaluate which ecological or life-history variables may have favored the evolution of conspicuous ornamentation in precocial chicks. We compiled data on chick morphology, ecology, and social organization of species in the Family Rallidae, a group with highly variable downy chicks. Chick ornamentation in the form of brightly colored bills, fleshy patches, or plumes is observed in 36 of 97 species for which downy chicks are described. Phylogenetic reconstructions suggest that nonornamentation is the ancestral state. Chick ornamentation has evolved multiple times within the Rallidae and is significantly associated with large clutch sizes and polygamous mating systems. Chick ornamentation was also weakly associated with adult ornamentation and adult dimorphism. We argue that these results support the hypothesis that lineages with higher levels of sibling competition are more likely to evolve ornamented chicks. *Key words:* chick coloration, precocial chicks, Rallidae, sibling competition, signaling. *[Behav Ecol 15:946–951 (2004)]*

Bright coloration and bizarre ornamentation in birds are largely attributed to sexual selection via mate choice (Andersson, 1994). Mate choice can select for exaggerated traits when these traits signal the genetic quality, health, or attractiveness of a prospective mate (Kokko, 2001). Intriguingly, such apparently ornamental traits are also observed in the young of some species. Conspicuous traits such as bright bills, colored fleshy parts, and plumes are particularly pronounced in the downy young of some precocial species (Boyd and Alley, 1948).

Ornamentation in chicks clearly cannot have been favored by mate choice, and it is thought that visual and vocal displays have evolved in nestling birds as a result of competition over access to food (Mock and Parker, 1997). In passerines, altricial nestlings possess brightly colored gapes and engage in vigorous behavioral displays directed toward a feeding parent. Within a species, the variation in the begging displays typically reflects variation in chick hunger and influences parental food allocation (Kilner and Johnstone 1996). However, both ecological and social factors influence begging signals both across and within species. For example, gape and flange coloration differs between species nesting in darker and lighter environments (Kilner, 1999; Kilner and Davies, 1998). Begging intensity and the redness of the gape also increases in species with higher rates of extrapair paternity, presumably as a consequence of the higher levels of sibling competition within the nest (Briskie et al., 1994; Kilner, 1999).

Young in precocial birds that are fed by their parents also engage in vocal and postural begging displays. Intriguingly, conspicuous chick ornamentation is only common in precocial families, such as grebes and rails, in which parents physically feed chicks. In addition, chicks only remain ornamented during the period of intense parental care

(Baicich and Harrison, 1997; Taylor and van Perlo, 1998). For example, in common (*Fulica atra*) and American coots (*F. americana*), downy chicks sport brightly colored skin patches, bills, and plumes only for the first few weeks after hatching, gradually turning a uniform olive brown. This correlation with parental dependence suggests that chick coloration has evolved to signal either hunger or some aspect of chick quality to either parents or competing siblings.

Elaborate plumage has been shown influence parental food allocation in American coots (Lyon et al., 1994). Parents preferentially fed ornamented chicks, and these chicks subsequently had higher growth and survival. If exaggerated traits have evolved in chicks as a result of competition over food, species with higher levels of sibling competition within the brood should be more likely to have ornamented young. Alternatively, if conspicuous coloration in chicks functions to deter predators or increase visibility to parents, chick ornamentation should be more strongly correlated with ecological factors, such as predation rates or habitat type, rather than factors related to competition, such as clutch size.

Chick appearance varies widely among species in the Family Rallidae, making them an excellent group in which to evaluate factors favoring the evolution of conspicuous ornamentation in chicks. We examine the factors associated with the presence of chick ornamentation within this family both across species and controlling for phylogeny. Chick ornamentation is relatively common within rails, and the life history and ecology are well described for some species. We quantify a variety of social, ecological, and life-history variables for each species and examine their associations with chick ornamentation.

## METHODS

We compiled data on 14 morphological, behavioral, life-history, and ecological traits of species within the Family Rallidae (Table 1). Our data sources were primarily *Rails of the World* (Taylor and van Perlo, 1998), the *Handbook of Birds of the World* (Taylor, 1996), and several detailed studies from the

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**Table 1**

**Description of variables quantified for all species**

| Variable | Categories | Binary |
|---|---|---|
| Chick ornamentation | None, one ornamental trait, more than one trait | None, ornamental |
| Adult ornamentation | None, one ornamental trait | None, ornamental |
| Movements | Sedentary, nomadic, migratory | Sedentary, move |
| Territoriality | Nonterritorial, seasonally territorial, permanently territorial | Nonterritorial, territorial |
| Mating system | Monogamous, weakly polygamous, polygamous | Monogamous, polygamous |
| Habitat | Grassland, forest, marsh, swamp, aquatic | Grassland/forest, wetlands |
| Diet | Vegetation only, seeds only, insects only omnivorous | Vegetation/ seeds only, omnivorous |
| Adult dichromatism | Monochromatic, <25% different, >25% different, >50% different, completely dichromatism | Monochromatic, dichromatic |
| Adult dimorphism | Monomorphic, slightly dimorphic, dimorphic | Monomorphic, dimorphic |
| Clutch size | $1-2$, $3-5$, $\geq 6$ | $1-5$, $\geq 6$ |
| Hatching asynchrony | Synchronous, asynchronous | Synchronous, asynchronous |
| Parental care | Uniparental, biparental, cooperative | Biparental, cooperative |
| Egg mortality | Low, high | Low, high |
| Chick mortality | Low, high | Low, high |

Binary variables were created by dividing the categories into logical groups. However, for parental care and diet, no species were categorized as uniparental or as having a diet of insects alone; consequently, the binary variable does not include those categories.

literature (Craig and Jamieson, 1990; Garnett, 1978; Horsfall, 1984; Lyon, 1993; Lyon et al., 1994; McRae and Burke, 1996).

We constructed a composite phylogeny of the rails based on the data presented in Livezey (1998). Livezey's phylogeny is the most complete phylogeny currently available for rails and was constructed by using 381 osteological and 189 integumental characters (no chick characters were scored; for further details, see Livezey, 1998). However, this phylogeny does not incorporate any molecular data. Although Trewick (1997) has produced a molecular phylogeny of a subset of rail species ($n = 22$) based on mitochondrial genes (12S and cytochrome-b), it is difficult to combine the two phylogenies to produce an improved phylogeny of the family. One difficulty is that Trewick has included species on the basis on their geographic location, resulting in a small and irregular sample across the whole rail family. Second, as Trewick clearly states, the deep nodes of the rail phylogeny remain poorly resolved, making the correct placement of potentially contentious genera such as *Porphyrio* uncertain.

Livezey (1998) presented a strict consensus tree of the Rallidae (and Psophiidae, Aramidae, Gruidae, and Heliornithidae), together with finer scale majority consensus trees, for a number of genera and species complexes within the Rallidae. We combined these trees and additional information presented in the text of Livezey (1998) to produce a composite, purely bifurcating phylogeny as required for our analyses. Furthermore, where Livezey (1998) extensively divided a group based on slight geographical variations (e.g., the *Porphyrio porphyrio* complex), we have considered only the "superspecies" group (for a list of species groups, see Figure 1). This approach produced a total of 135 species and species groupings, a number close to the 146 species described by Taylor and van Perlo (1998).

**Analysis**

In most species of rails, downy chicks are black, often with a lighter bill. We considered a downy chick to be ornamented if it possessed one or more of the following traits: (1) a brightly colored bill (i.e., bright orange, red, or pink), (2) conspicuous coloration on the head or colored fleshy parts (i.e., red, orange, pink, purple, or blue), or (3) conspicuously colored filoplumes or modified down. Although brightly colored legs could potentially function as a signal, very few rail chicks had colored legs. Of the 97 species in which downy chicks are

described, 83 (86%) have black, grey, or brown legs; 11 (11%) have very weakly colored legs (e.g., *Porzana paykullii*: "legs and feet black, tinged reddish"; Taylor and van Perlo, 1998), which we would not class as ornamental; and two (2%) have pink legs, which appear ornamental (*Porzana carolina* and *P. porphyrio*; note that *Pardirallus nigricans* may also have bright legs, but is described from only one chick; see Naranjo, 1991). Because of the extremely small number of species with colored legs, we have not included leg color in our analysis. However, we note that both species with colored legs also possess other ornamental traits. In all cases, chick ornaments were only observed in downy chicks and were absent in immatures and juveniles.

All explanatory variables were classified by using species descriptions. Because most species vary slightly in attributes such as diet or habitat, we have used broad categories to define a variable (e.g., habitat) (for variable definitions, see Table 1). We classified clutch size by using the ranges in values reported for a species and calculating a median value. This allowed us to maximize the number of species with data and did not differ from estimates of clutch size based on mean values that were available for some species. We assessed the patterns of association between chick ornamentation and each of the categorical explanatory variables by using likelihood ratios (*G* tests).

To remove any confounding effects of phylogeny we used Maddison's concentrated changes tests (MacClade 4.0, Maddison and Maddison, 2000). We were not able to control for phylogenetic nonindependence by using independent contrasts (e.g., program CAIC) because all our variables are categorical and unordered (i.e., characters can shift from one state to the next in any order; Harvey and Pagel 1991). We therefore controlled for phylogenetic nonindependence by using Maddison's test. This test examines the association between changes in chick ornamentation and the variables of interest but requires that all equivocal branches for the dependent variable in the phylogeny are resolved and that all variables are reduced to a binary state (Table 1). We resolved equivocal branches by using the equivocal cycling option in MacClade. This produced 192 equally parsimonious reconstructions (most parsimonious reconstruction, MPR) for chick ornamentation. We conducted concentrated changes tests on the first and last MPRs, which represent the two most extreme reconstructions. The *p* values reported refer to the probability (based on 10,000 simulations) of obtaining the observed
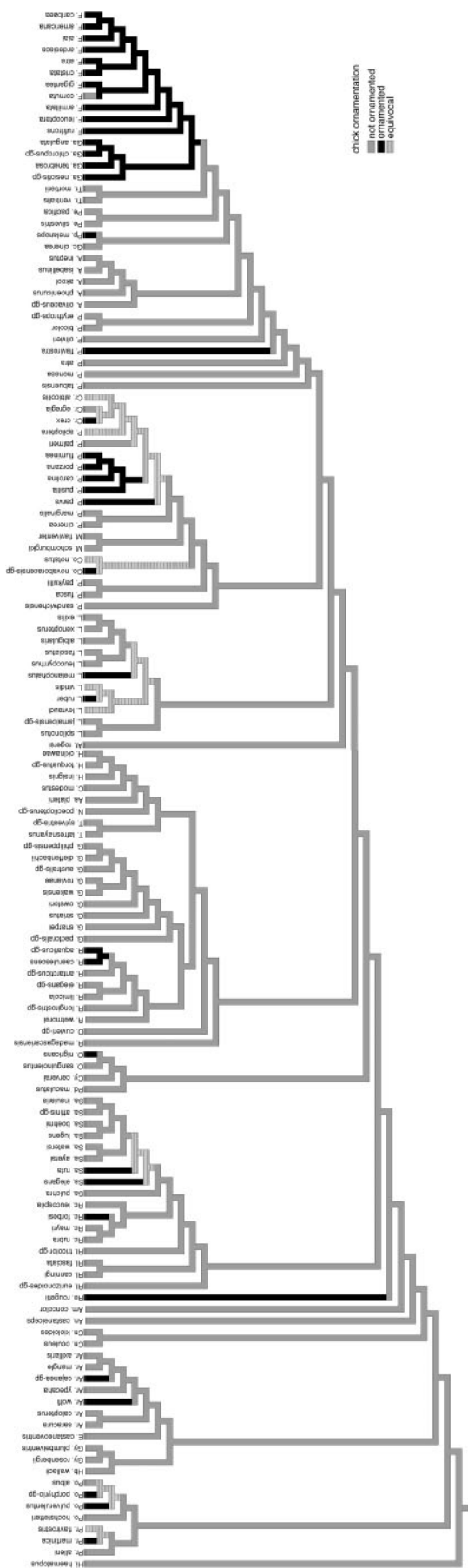
**Figure 1**
Phylogenetic reconstruction of chick ornamentation within the Rallidae using unordered parsimony (unordered refers to nonsequential categorical data). Ornamented branches are represented in black, nonornamented branches are in white, and equivocal branches are striped. Equivocal branches occur where there was insufficient data to resolve the evolution of the character in that branch. Boxes under the species name indicate data on ornamentation for that species. The Genera have been abbreviated in the following way (starting from the left of the tree): Hi indicates *Himantornis*; Pr., *Porphyrula*; Po, *Porphyrio*; Hb, *Habroptila*; Gy, *Gymnocrex*; E., *Eulabeornis*; Ar, *Aramides*; Cn, *Canirallus*; An., *Anurolimnas*; Am., *Amaurolimnas*; Ro, *Rougetius*; Rl., *Rallina*; Rc., Rallicula; Sa., Sarothrura; Pd., Pardirallus; Cy., Cyanolimnas; O., Ortygonax; R., Rallus; D., Dryolimnas; G., Gallirallus; T., Tricholimnas; N., Nesoclopeus; Aa., Aramidopsis; C., Cabalus; H., Habropteryx; At., *Atlantisia*; L., *Laterallus*; P., *Porzana*; Co., *Coturnicops*; M., *Micropygia*; Cr., *Crex*; A., *Amaurornis*; Gc., *Gallicrex*; Pp., *Porphyriops*; Pe., *Pareudiastes*; Tr., *Tribonyx*; Ga., *Gallinula*; and F., *Fulica*.

**Table 2**

**Patterns of association across species between chick ornamentation and explanatory variables**

| Variable | No. of Species | Likelihood ratio | df | p |
|---|---|---|---|---|
| Adult ornamentation | 95 | 11.02 | 2 | **.004**[a] |
| Range | 95 | 7.19 | 4 | .126 |
| Movements | 89 | 12.43 | 4 | **.014** |
| Territoriality | 76 | 18.73 | 4 | **.001**[a] |
| Mating system | 82 | 6.25 | 2 | **.044** |
| Habitat | 95 | 18.17 | 6 | **.006**[a] |
| Diet | 88 | 8.11 | 4 | .088 |
| Adult dichromatism | 94 | 5.70 | 6 | .457 |
| Adult dimorphism | 94 | 2.4 | 2 | .301 |
| Clutch size | 88 | 18.33 | 4 | **.001**[a] |
| Hatching asynchrony | 43 | 4.98 | 2 | .083 |
| Parental care | 63 | 4.19 | 2 | .123 |
| Egg mortality | 25 | 0.80 | 2 | .669 |
| Chick mortality | 21 | 4.79 | 2 | .091 |

All explanatory variables are categorical as defined in Table 1. The number of species with data is indicated for each comparison. The two highest categories were merged for mating system, adult dichromatism and adult dimorphism, to avoid low frequencies within a cell. Chick ornamentation is categorized as none, one trait, or multiple traits. Patterns of association were tested by using log-likelihood ratios (G statistics). Comparisons that are statistically significant ($p < .05$) are indicated in bold.

[a] Statistically significant after controlling for multiple tests.

number of gains and any number of losses in chick ornamentation at nodes in the phylogeny characterized by the distinguished state of the independent variable. For each character of interest, we defined distinguished states as the category with the highest frequency for ornamented chicks (Table 2).

Concentrated changes tests can be highly conservative if the tree structure is highly unbalanced (Lorch and Eadie, 1999). We assessed the symmetry of the tree by using the tree imbalance statistic $I$, which varies from zero (balanced) to one (unbalanced), using RadCon v1.1.5 software. The tree was relatively balanced, $I = 0.16$.

We applied a Bonferroni correction to all tests because our approach required using multiple univariate tests (Chandler, 1995).

## RESULTS

Species accounts were sufficiently detailed that we were able to evaluate chick ornamentation in 97 of 135 species of rails. Downy chicks are ornamented in 37.1% (36 of 97) of described species. For all ornamented chicks, just over one-half (20 of 36) have multiple ornaments.

### Species comparisons

Across species, ornamented chicks are more common in nomadic or migratory species, territorial species, and those living in aquatic habitats. Chicks are also more likely to be ornamented in species with large clutch sizes, polygamous mating systems, and adult ornamentation (Table 2). After correcting for multiple tests, only associations with adult ornamentation, territoriality, habitat, and clutch size remained statistically significant (Table 2).

### Comparative analyses

Nonornamentation of chicks was the ancestral state for all possible reconstructions of chick ornamentation on the rail

**Table 3**

**Summary of concentrated changes tests examining the association between chick ornamentation and potential explanatory variables while controlling for phylogeny**

| Variable | MPR #1 (20G/1L) | | | MPR #192 (14G/6L) | | |
|---|---|---|---|---|---|---|
| | Gains | Losses | p | Gains | Losses | p |
| Adult ornamentation | 8 | 1 | .06 | 6 | 2 | **.04** |
| Range | 19 | 1 | **.02** | 13 | 4 | .17 |
| Movements | 11 | 1 | **.05** | 7 | 2 | .11 |
| Social organisation | 20 | 0 | .24 | 14 | 5 | .39 |
| Mating system | 8 | 0 | **.0001**[a] | 5 | 1 | **.003**[a] |
| Habitat | 15 | 1 | .13 | 7 | 2 | .87 |
| Diet | 0 | 1 | .00 | 0 | 1 | .926 |
| Adult dichromatism | 16 | 1 | .88 | 13 | 5 | .45 |
| Adult dimorphism | 11 | 0 | **.04** | 7 | 2 | .09 |
| Clutch size | 11 | 0 | **.002**[a] | 6 | 2 | **.05** |
| Hatching asynchrony | 6 | 0 | .45 | 4 | 2 | .41 |
| Parental care | 7 | 0 | **.03** | 3 | 1 | .35 |
| Egg mortality | 6 | 1 | .67 | 5 | 2 | .36 |
| Chick mortality | 19 | 0 | .60 | 12 | 4 | .97 |

The binary categories used are defined in Table 1. The first and last most parsimonious reconstructions (MPRs) for chick ornamentation are presented. The $p$ values refer to the probability of having the stated number of gains and any number of losses in chick ornamentation in branches of the phylogeny characterized by distinguished state (see Methods) of the explanatory variable. The probabilities were determined by using 10,000 simulations in MacClade.4.0 (Maddison and Maddison, 2001). Comparisons that are statistically significant ($p < .05$) are indicated in bold.

[a] Statistically significant after controlling for multiple tests.

phylogeny (Figure 1). Our reconstructions suggest that chick ornamentation has evolved within the rails 14–20 times and been lost one to six times (Figure 1). Chick ornamentation is particularly concentrated within the coots and moorhens, illustrating the need to control for phylogeny in the analyses.

After controlling for phylogeny, chick ornamentation was significantly associated with polygamous mating systems and larger clutch sizes, although after controlling for multiple tests, the associations with clutch size was only significant in one MPR (Table 3). In addition, there were weak associations ($p < .10$ in both MPRs) with adult dimorphism and adult ornamentation (Table 3). Cooperative parental care, territoriality, and nomadic or migratory habits were associated with chick ornamentation in only one of the reconstructions of ornamentation (Table 3). None of these associations were statistically significant after controlling for multiple tests (Table 3).

## DISCUSSION

Reconstructions of chick ornamentation onto the phylogeny clearly show that nonornamented chicks are the ancestral state and that ornamented chicks have evolved multiple times within the Rallidae. Across species, several ecological and life-history variables were associated with chick ornamentation. However, after controlling for phylogeny, we found that chick ornamentation was most strongly associated with polygamous mating systems and large clutch sizes. This suggests that social rather than ecological factors have favored chick ornamentation in rails.

The role of chick ornamentation in precocial chicks is poorly understood. Chick coloration is unlikely to function as warning coloration in rails, because highly ornamented chicks, such as coot and moorhen chicks, are known to hide and conceal their heads when startled (Boyd and Alley, 1948; Garnett, 1978). Nor is it likely chick ornaments have evolved

to facilitate the localization of chicks by parents in visually occluded habitats, because brightly colored chicks were more common in open aquatic habitats before controlling for phylogeny and brightly colored legs were only observed in two of 36 ornamented species. In any case, after controlling for phylogeny, there were no statistically significant associations among habitat types or mortality rates and the presence of chick ornaments.

One reason rail chicks might be most strongly ornamented during the period of parental dependency is to signal their competitive ability. The competitive ability of chicks is likely to be very important in precocial species that are fed by their parents because food is primarily distributed by scramble competition. For example, in common moorhens (*Gallinula chloropus*), the chick closest to the parent is most likely to be fed, and larger chicks are quickest at moving into this position (Leonard et al., 1988). There is currently no evidence that bright chicks have higher competitive ability than do duller chicks. Common moorhen chicks fed a high-carotenoid diet had greater immune response and pecking rates than those fed a control diet, suggesting a potential link between chick brightness and behavior (Fenoglio et al., 2002b). The extent to which ornaments and chick color vary within broods is completely unknown. However, American coot parents allocated more food to fully ornamented chicks within a brood, suggesting that parents may be sensitive to the relative ornamentation of chicks (Lyon et al., 1994).

In rails, feeding parents show active discrimination between young, suggesting that chick ornamentation might signal some aspect of chick quality to parents. For example, parent coots and moorhens sometimes pick up and shake particular chicks as they beg for food (tousling; Garnett, 1978; Horsfall, 1984; Leonard et al., 1988) and, at least in common coots, divide the brood and feed only certain chicks (Horsfall, 1984). Parental control over the distribution of food is likely to reduce sibling competition (Leonard et al., 1988). Chick coloration could signal nestling hunger and allow parents to better discriminate which chick to feed. Several investigators have noted that the color of bare skin patches varies temporally, a trait that could signal hunger in much the same manner as does the flushing of gapes in altricial species (Garnett, 1978; Lyon et al., 1994). Flushing of bare patches apparently also occurs in grebes, the other precocial group with ornamented chicks that are fed by their parents (Baicich and Harrison, 1997).

To date, parental feeding preferences have been linked to the level of chick ornamentation in only one species. Lyon et al. (1994) experimentally trimmed filoplumes of American coot chicks and found that parents preferentially fed the chicks in the brood with intact plumes. Chicks with experimentally shortened plumes had reduced growth and survival in comparison to orange plumed chicks in the brood. Interestingly, begging in this species involves displaying the head to parents, underlining the importance of chick ornamentation in signaling to parents (Boyd and Alley, 1948; Lyon et al., 1994).

Alternatively, the correlation between adult and chick ornamentation could arise simply as the nonselected by-product of selection on adult phenotypes. We observed an association between chick and adult ornamentation across species, but this pattern was not statistically significant once we controlled for phylogeny. In adult rails, ornamental traits probably function in dominance interactions. For example, frontal shields in common moorhens are larger in heavier, more socially dominant individuals (Petrie, 1984, 1988). Frontal shields and bills are also more intensely colored in larger and fatter moorhens, suggesting these traits signal body condition (Fenoglio et al., 2002a). Adult coloration in

moorhens only develops in sexually mature individuals and peaks seasonally when territorial interactions are frequent (Gullion, 1951; Petrie, 1988; Shirley et al., 2003). Consistent with these patterns, the coloration and development of pronounced shields and bills in both sexes of American coots and in common moorhens are regulated by testosterone titers (Eens et al., 2000; Gullion, 1951).

If chick ornaments are also regulated by testosterone, a correlation between testosterone levels in females and their eggs could produce a similar appearance in adults and chicks, especially in the period after hatching. Testosterone is transmitted maternally to young via egg yolk (Schwabl, 1993) and reflects variation in maternal testosterone titres (Groothuis and Schwabl, 2002; Reed and Vleck, 2001). However, we think that it is unlikely that chick ornaments are the unselected by-product of adult ornamentation, for two reasons. First, if chick ornaments develop simply as a by-product of adult ornamentation, the correlation between ornaments in adults and chicks should be high. This was not the case in our database; any association between adult ornamentation and chick ornamentation in our analyses was weak and not significant after controlling for multiple tests. Only 59% of all ornamented adults produced ornamented chicks, and 26% of species with unornamented adults produced ornamented chicks. Second, the traits exhibited by chicks differ from adult ornaments. For example, in the common coot, downy chicks have a red shield, filoplumes around the head, and bare patches of red and blue colored skin on the head, whereas adults have a white shield and bill. Thus, even if ornaments in chicks in some species were originally unselected, other factors must have led to the maintenance and elaboration of these traits in some species and not in others.

The present study suggests that chick ornamentation has evolved in species with higher levels of sibling competition. Sibling competition is predicted to increase in intensity as brood size increases and per capita food availability decreases (Mock and Parker, 1998). Thus, chick ornamentation should be more common in species with larger clutch sizes, as we observed. Although the effect of clutch size was only statistically significant in one of the reconstructions of chick ornamentation, this is at least partly owing to the loss of power resulting from dichotomizing variables for comparative analysis. Clutch size was strongly associated in one reconstruction and across species. An improved phylogeny or additional species would help to clarify the importance of clutch size.

The factor, however, likely to have the most direct influence on sibling competition is the level of relatedness within the brood (Mock and Parker, 1998). As levels of relatedness within the brood decrease, selfishness within the brood and, hence sibling competition, is predicted to intensify. This has been demonstrated in altricial nestlings, in which begging rates increase as relatedness within the brood decreases due to extrapair young (Briskie et al., 1994). We propose that the strong association between polygamous mating systems and chick ornamentation exists because of the underlying changes to within-brood relatedness. Mating systems are poorly described in many species of rails, but polyandry, joint nesting of females, and creching of young are common (Taylor, 1996). In addition, even within many of the putatively monogamous species, there is some level of polygamy (for an example, see McRae and Burke, 1996). Within-brood relatedness is therefore likely to be reduced by the multiple mating, joint nesting, and social systems observed in rails. We suspect that the weak association between adult size dimorphism and chick ornamentation observed in our analyses partly reflects the underlying association between size dimorphism and mating system across birds (Dunn et al. 2001).

Complex mating systems, however, are not the only factor that will lead to reductions in within-brood relatedness. In monogamous systems within-brood relatedness is also reduced in species with high rates of extrapair paternity or intraspecific brood parasitism. Unfortunately, direct measures of within-brood relatedness are almost nonexistent in rails, as detailed studies of their breeding biology and genetics are generally lacking (but, for an example, see McRae, 1996). Intrabrood relatedness is unlikely to be reduced by extrapair paternity, because extrapair paternity has not been reported in this group (Arnold and Owens, 2002). However, the extreme lack of paternity studies in rails must be noted! In contrast, intraspecific brood parasitism is a relatively common female tactic in rails and has been described in 10% (nine of 94) of the relatively well-studied species. Intraspecific brood parasitism is especially common among coots and moorhens (nine of 19 species), a mainly monogamous group characterized by highly ornamented chicks. For example, American coots and common moorhens are primarily socially monogamous but are observed to have high levels of intraspecific brood parasitism (Lyon, 1993, 2003, McRae, 1996).

Although there was insufficient detail across species to include a measure of within-brood relatedness in the database, we suspect this variable would strongly predict the distribution of ornamentation across the family. Further understanding of the function of ornamentation in rail chicks requires examining variation within a single species. A cosmopolitan species complex such as *P. porphyrio* would be ideal for this purpose because the geographic variation in mating system and clutch size in this group will alter the intensity of sibling competition, and potentially the benefits of chick ornamentation.

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