The evolution of sexual dimorphism in parasitic cuckoos: sexual selection or coevolution?

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Sexual dimorphism is ubiquitous in animals and can result from selection pressure on one or both sexes. Sexual selection has become the predominant explanation for the evolution of sexual dimorphism, with strong selection on size-related mating success in males being the most common situation. The cuckoos (family Cuculidae) provide an exceptional case in which both sexes of many species are freed from the burden of parental care but where coevolution between parasitic cuckoos and their hosts also results in intense selection. Here, we show that size and plumage differences between the sexes in parasitic cuckoos are more likely the result of coevolution than sexual selection. While both sexes changed in size as brood parasitism evolved, we find no evidence for selection on males to become larger. Rather, our analysis indicates stronger selection on parasitic females to become smaller, resulting in a shift from dimorphism with larger females in cuckoos with parental care to dimorphism with larger males in parasitic species. In addition, the evolution of brood parasitism was associated with more cryptic plumage in both sexes, but especially in females, a result that contrasts with the strong plumage dimorphism seen in some other parasitic birds. Examination of the three independent origins of brood parasitism suggests that different parasitic cuckoo lineages followed divergent evolutionary pathways to successful brood parasitism. These results argue for the powerful role of parasite–host coevolution in shaping cuckoo life histories in general and sexual dimorphism in particular.

Keywords: brood parasitism; comparative analysis; evolutionary pathways; plumage dimorphism; size dimorphism

1. INTRODUCTION

Many species exhibit differences in size and coloration between the sexes (Fairbairn 1997; Colwell 2000; Bennett & Owens 2002). The evolutionary and ecological significance of intersexual differences has attracted attention since Darwin (1859), who coined the term sexual selection to explain the evolution of traits that increase mating success but seemed maladaptive in terms of survival. Since then, sexual selection has typically been invoked to explain the often striking differences between the sexes (Andersson 1994).

Particularly, when freed from the burden of parental care, higher potential reproductive rates in males (Trivers 1972) may lead to intense male–male competition for access to females and the elaboration of secondary sexual characters as well as size dimorphism (Trivers 1972; Andersson 1994; Thomas *et al.* 2006).

While differences between the sexes have traditionally been explained by sexual selection, they may also result from natural selection favouring sex differences associated with other aspects of a species' ecology, such as effective resource partitioning (Darwin 1871; Shine 1989; Radford & du Plessis 2003). Because sexual and natural selection may interact in complex ways in both sexes, testing their relative importance is often difficult (Andersson 1994; Krüger 2005). What is needed is a

well-defined taxonomic group for which predictions from both sexual and natural selection hypotheses can be derived, and the ability to analyse results for each sex separately because sexual dimorphism can result from a change in males, a change in females or both (Krüger 2005). While a comparative approach is always plagued by confounding variables and the problem of identifying causation, modern approaches enable the most likely evolutionary pathways to be reconstructed.

The cuckoos (family Cuculidae) provide just such an opportunity. First, the 141 species in this family show remarkable variation in breeding system, from parental care to obligate brood parasitism (Payne 2005). Second, a comprehensive and well-resolved molecular phylogeny was recently completed (Sorenson & Payne 2005). Third, brood parasitism has evolved independently three times in cuckoos, more than in any other avian family (Sorenson & Payne 2002: in New World cuckoos (three parasitic species), Old World crested cuckoos of the genus *Clamator* (four parasitic species) and the Old World Cuculinae (52 parasitic species in 11 genera, all derived from a common ancestor)). This offers a rare opportunity to analyse how variation in breeding strategy influences sexual dimorphism. Particularly interesting from the perspective of life-history evolution, both sexes are freed from the burden of parental care in parasitic cuckoos (Krüger 2007), which rely on other species as hosts to incubate their eggs and feed their young. The often severe fitness costs to the host species have set the stage for well-documented evolutionary arms races (Davies & Brooke 1989a,b; Rothstein 1990; Moksnes *et al.* 1991;

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Davies 2000; Stokke *et al.* 2002). Therefore, two competing hypotheses might explain the evolution of sexual dimorphism in parasitic cuckoos.

The *sexual selection hypothesis* emphasizes that males are freed from parental care in parasitic cuckoos and therefore number of matings should be the principal determinant of their fitness. While parasitic females are also freed from parental care, their potential reproductive rate is still much lower when compared with males. Under this hypothesis, two predictions can be made:

- (i) Size dimorphism is driven by male–male competition with larger males at a competitive advantage (Lack 1968; Bennett & Owens 2002), resulting in male-biased size dimorphism in parasitic cuckoos. Changes in size dimorphism should occur after the evolution of brood parasitism and due to changes in male size.
- (ii) Plumage dimorphism is driven by male–male competition and female choice and hence parasitic cuckoos should evolve more extravagant male plumage as a signal of quality. Changes in plumage dimorphism should occur after the evolution of brood parasitism and due to changes in male plumage.

The *coevolution hypothesis* emphasizes that female fitness in parasitic cuckoos crucially depends on circumventing host defences to ensure successful egg laying and survival of parasitic young in the nests of host species that are often much smaller than the cuckoo. Under this hypothesis, two predictions can be made:

- (i) Given the strong allometry between body size and egg size in birds generally (Rahn *et al.* 1975), size dimorphism is driven by selection on females to reduce their body size in order to lay a small egg that more closely matches the host egg in size and development time (Payne 1974; Krüger & Davies 2004). This hypothesis also predicts that male-biased size dimorphism should evolve after the evolution of brood parasitism, but in contrast to the sexual selection hypothesis, this should be due to changes in female size.
- (ii) Plumage dimorphism is driven by selection on females of parasitic species to become more cryptic, which would facilitate egg laying by helping them escape detection and avoid defensive behaviours of hosts. As in the sexual selection hypothesis, changes in plumage dimorphism should evolve after the evolution of brood parasitism but should be due to changes in female plumage.

Both hypotheses predict the evolution of male-biased size and plumage dimorphisms in parasitic cuckoos. The key difference is that the sexual selection hypothesis predicts that these patterns are due to changes in males, while the coevolution hypothesis predicts changes in females. Here, we use a modern comparative approach to test whether the evolution of sexual dimorphism in cuckoos is associated with the evolution of brood parasitism and which of the two alternative hypotheses better explains differences between the sexes in parasitic cuckoos.

2. MATERIAL AND METHODS

(a) Data collection

Data were collected for all 141 cuckoo species recognized by Payne (2005). In addition, we treated the two subspecies of *Centropus sinensis*, *Clamator jacobinus* and *Eudynamis scolopacea* separately because *Centropus sinensis andamanensis* is often recognized as a distinct species (Payne 1997) and the two subspecies of the latter two species have different parasitism strategies (Krüger & Davies 2002, 2004). The total sample size in our analyses was therefore 144 (see electronic supplementary material, Appendix A for the raw data).

We scored breeding strategy as 0 (parental care) and 1 (obligate brood parasite). Sexual plumage dimorphism was scored using the plates in del Hoyo *et al.* (1997): 0, no difference; 1, slight difference (eye colour or eye ring); 2, some difference (less than 25% of the plumage); 3, marked difference (more than 25% of the plumage but not the whole plumage); 4, completely different plumage (following Krüger & Davies 2002).

To further analyse plumage differences between the sexes, four traits for each sex (crest presence; head, upperpart and underpart plumage) were scored as 0, cryptic (no crest; plumage colours grey, beige, brown or rufous) or 1, showy (crest present; red, yellow, black, white or all shiny colours), again using the plates in del Hoyo *et al.* (1997). If a conspicuous skin patch or eye ring was present on an otherwise cryptically coloured head, it was scored as showy. In addition, we looked at a fifth measure, barring on the breast and/or belly. Barring has been identified as a trait specifically increasing crypsis (Ferguson-Lees & Christie 2001), thus enabling us to test the coevolution hypothesis more rigorously. It was scored as 0 if absent and as 1 if present. In order to assess interobserver and intersource reliability of our plumage variables, a subset of 40 species was scored by O.K. and N.D. and the same species were also scored using plates from a different source (Payne 2005). All variables showed correlations above 0.9 for both interobserver and intersource repeatability, giving us confidence that the plumage scoring was objective. A principal component analysis was used to combine these five measurements into one variable for each sex, with zero mean and unit variance. The principal component for male plumage accounted for 36.7% of the variance, had an eigenvalue of 1.834 and the coefficients for the five plumage traits were as follows: head crest, 0.152; head plumage, 0.465; back plumage, 0.454; breast plumage, 0.209; and barring, -0.236 . The principal component for female plumage accounted for 39.7% of the variance, had an eigenvalue of 1.985 and the coefficients for the five plumage traits were as follows: head crest, 0.170; head plumage, 0.431; back plumage, 0.383; breast plumage, 0.165; and barring, -0.339 .

Since we used colour plates to assess plumage, we were not able to assess UV wavelengths. As UV reflectance is often a sexually selected signal, we would expect it to be higher in those species with showy plumage, which might change our results quantitatively but probably not qualitatively. In addition, it is known that plumage can interact with habitat types, so we used the habitat categories in Krüger & Davies (2002) to test for such an effect. Neither male nor female plumage principal component contrasts were significantly correlated with contrasts in habitat preference ($r = -0.026$, d.f. = 143, $p > 0.5$ and $r = 0.031$, d.f. = 143, $p > 0.5$, respectively). This suggests that our plumage principal component scores are not greatly confounded by habitat.

Sexual size dimorphism was calculated as male wing length over female wing length, and this ratio was cubed (following Ferguson-Lees & Christie 2001). For species with multiple populations sampled, we used the one with the largest sample size. There are no data for separate sexes in the now extinct snail-eating coua *Coua delalandei*, so we excluded it from this analysis. Ratios do not have the same statistical properties as the original data and their use may lead to erroneous conclusions. In the present case, a ratio should be used only if the regression of the female trait against the male trait is linear and passes through the origin. We tested this and found a linear relationship with a reduced major axis slope (1.016) not statistically different from one ($t=1.318$, d.f. = 97, $p>0.2$). Hence, using wing-length ratios is statistically justified.

(b) Statistical analysis

Phylogenetic comparative analyses implemented in DISCRETE (Pagel 1994) used the phylogeny of Sorenson & Payne (2005) with maximum likelihood estimates of branch lengths (see electronic supplementary material Appendix B for details). DISCRETE uses binary variables only, so variables had to be made dichotomous. For size dimorphism, we used a threshold of 1.0 and all species with larger females were coded as 0 and those with larger males were coded as 1. Results did not change qualitatively if we used the mean size dimorphism (0.991) as a threshold. When analysing each sex separately, we categorized a male or female as large (1) if the wing length was above the sex-specific mean and as small (0) if the wing length was below the sex-specific mean. All species showing any plumage dimorphism were scored as 1, while all monomorphic species were scored as 0. The principal components scores of male and female plumage were dichotomized into cryptic (0) if the score was negative and showy (1) if it was positive.

The maximum likelihood approach implemented in DISCRETE estimates the parameters of trait evolution by summing the likelihood over all possible states at each node of a phylogeny. Instead of estimating ancestral states as is done in maximum parsimony approaches, DISCRETE estimates the probabilities of each character state at each node. This more flexible approach is considered superior to maximum parsimony (Pagel 1994) because it takes into account branch lengths and, by estimating rates of trait evolution along all branches, effectively controls for phylogenetic inertia. Although brood parasitism evolved only three times independently in the cuckoo family, by using a maximum likelihood approach, all nodes across the phylogeny contribute to the analysis, yielding enough analytical power to test for correlated evolution. In order to examine whether similar changes occurred in all the three origins of brood parasitism, we tabulated changes in size and plumage dimorphism for each case.

DISCRETE tests the null hypothesis that brood parasitism and size or plumage traits evolved independently along the phylogeny against the alternative hypothesis that the two traits show correlated evolution. This is done through a likelihood ratio test. Evidence for correlated evolution is found when the model of the two traits showing correlated evolution fits the data (values for extant species) significantly better than the null hypothesis. For trait combinations with few changes along the phylogeny, 100 simulations were done to determine the most likely degrees of freedom for the test of correlated evolution (Pagel 1994). DISCRETE also enables an analysis of evolutionary pathways between character states.

This is depicted in a flow diagram. With two binary traits, eight transitions are possible and DISCRETE tests which ones are statistically significant by setting them one by one to zero. If a transition parameter is significant, setting it to zero will significantly reduce the likelihood of the dependent model. This establishes the most likely sequence of evolutionary changes and thereby allows tentative inferences about cause and effect, enhancing the explanatory power of comparative analyses (van Noordwijk 2002). We did not restrict our analyses only to those parameters predicted to change under the different hypotheses, but tested each one in order to find all evolutionary pathways and establish the most likely one.

Because the phylogeny contained many species and branch lengths varied substantially, the scaling parameter κ was used in all analyses. This scaling parameter shortens longer branches relative to shorter ones, thus making it easier to find the global maximum likelihood (Pagel 1994). To find the most likely ancestral state, the proportion for each state at the root of the tree was calculated using the local option as described in Pagel (1999).

Because DISCRETE requires dichotomous variables to reconstruct evolutionary pathways, much of the information in continuous variables is lost. Hence, as another test for correlated evolution of continuous traits, independent contrasts and ancestral values were computed using comparative analysis by independent contrasts (CAIC; Purvis & Rambaut 1995). We used the CRUNCH algorithm so that categorical variables such as breeding strategy were assumed to reflect a continuous spectrum, following Purvis *et al.* (2000). Contrasts were analysed using non-parametric Spearman's rank correlation and reduced major axis regression (McArdle 1988) because data were often non-normally distributed.

3. RESULTS

(a) Data distribution

In most cuckoo species with parental care, females are larger than males (71.1%), whereas in most parasitic species, males are larger than females (83.6%, figure 1). With regard to plumage, most parental species are monomorphic (95.2%), whereas 41.0% of parasitic species are dimorphic (figure 1).

(b) Evolution of size dimorphism

The evolution of sexual size dimorphism was correlated with the evolution of breeding strategy in cuckoos (LR = 20.681, d.f. = 4, $p<0.001$). Ancestral states were most likely parental care (0.999 probability, LR = 22.4, d.f. = 1, $p<0.001$) and females being larger than males, but not significantly so (0.618 probability, LR = 0.961, d.f. = 1, $p>0.5$). The most likely evolutionary pathway (figure 2a) is that male-biased size dimorphism preceded the evolution of brood parasitism rather than being a consequence of it. Changes in both directions between female- and male-biased size dimorphism were reconstructed for both parental and parasitic cuckoos (figure 2a). There was no significant evolutionary pathway directly from parental care with female-biased size dimorphism to parasitism with female-biased size dimorphism (figure 2a). Looking at the three independent origins of brood parasitism (table 1), there was a change from female- to male-biased size dimorphism both in the *Clamator* cuckoos and the Old World parasitic cuckoos,

Figure 1. Frequency distribution for (a) sexual size dimorphism and (b) sexual plumage dimorphism for species with (i) parental care and (ii) brood parasitic species. The x -axis for size dimorphism shows the cubed ratio of male over female wing length and the x -axis for plumage dimorphism refers to the five categories of plumage dimorphism from 0, no difference in plumage to 4, completely different plumage.

Table 1. Changes in size and plumage related variables for each of the three independent origins of brood parasitism in the cuckoos.

evolutionary origin of brood parasitism	size dimorphism	plumage dimorphism	male plumage	female plumage
New World parasitic cuckoos	more male biased	decrease	from showy to cryptic	from showy to cryptic
<i>Clamator</i> cuckoos	female to male biased	no change	more showy	more showy
Old World parasitic cuckoos (Cuculinae)	female to male biased	increase	from showy to cryptic	from showy to cryptic

while male-biased size dimorphism increased in the New World parasitic cuckoos.

To test whether the evolution of sexual dimorphism in parasitic cuckoos was due to changes in males or females, we examined each sex separately. Using DISCRETE, we found no evidence of correlated evolution between breeding strategy and either male wing length (LR = 6.692, d.f. = 4, $p > 0.1$) or female wing length (LR = 3.061, d.f. = 4, $p > 0.5$). Treating wing length as a continuous variable in an independent contrasts analysis in CAIC, however, we found that both male and female wing length contrasts were significantly negatively correlated with contrasts in breeding strategy ($r_s = -0.281$, $n = 142$, $p = 0.001$ and $r_s = -0.282$, $n = 142$, $p = 0.001$, respectively), indicating the evolution of smaller size in parasitic species. The reduced major axis slope for log female on log male wing length contrasts was 1.109,

significantly higher than 1 ($t = 4.399$, d.f. = 99, $p < 0.001$), indicating greater selection pressure on female size than on male size (cf. Fairbairn 2005). There was also a significant difference in the slopes of log female on log male wing length contrasts between parental and parasitic species (ANCOVA, $F_{1,129} = 27.688$, $p < 0.001$). The reduced major axis was 1.210 for parental species and 0.934 for parasitic species, so female size increased more than male size in parental species while it increased less than male size in parasitic species.

(c) Evolution of plumage dimorphism

The evolution of sexual plumage dimorphism and breeding strategy was weakly correlated across the phylogeny (LR = 8.816, d.f. = 3, $p < 0.05$). Plumage monomorphism was most likely the ancestral state (0.996 probability, LR = 11.1, d.f. = 1, $p < 0.001$). The

Figure 2. Flow diagram of the most likely evolutionary pathways between breeding strategy and (a) sexual size dimorphism and (b) sexual plumage dimorphism. In each, the likely ancestral state is shaded in light grey, whereas the most recently derived state in brood parasitic cuckoos is the boldly lined box. Solid arrows represent significant evolutionary pathways ($p < 0.05$) and dashed arrows represent trends ($p < 0.1$). If a pair of arrows is significant, a comparison of the transition rates is indicated by the labelling. If no labelling is applied, both transition rates are similar.

most likely evolutionary scenario (figure 2b) suggests a two-step process: first, species with parental care and plumage monomorphism evolved brood parasitism, followed by the evolution of plumage dimorphism. Looking at the three independent origins of brood parasitism (table 1), no consistent pattern is evident. Plumage dimorphism decreased in the New World parasitic cuckoos, it remained unchanged in the *Clamator* cuckoos while it increased in the large clade of Old World parasitic cuckoos.

Considering each sex separately, there was evidence for a statistical association between male plumage, as categorized by the principal component of five plumage traits and breeding strategy ($\text{LR} = 11.812$, d.f. = 4, $p < 0.02$). The ancestral state for male plumage was more likely to be showy, but not significantly so (0.578

Figure 3. Flow diagram of the most likely evolutionary pathways between breeding strategy and (a) male (b) female plumage. The ancestral state is the box shaded in light grey, the boldly lined box shows the most recently derived state in parasitic cuckoos.

probability, $\text{LR} = 0.626$, d.f. = 1, $p > 0.5$). There were no significant pathways linking any parental care state with any parasitic state (figure 3a), so it is not clear whether changes in male plumage evolved before or after the evolution of brood parasitism. The three independent origins of brood parasitism also do not show consistent changes. While there was a change from showy males to cryptic males in both New and Old World parasitic cuckoos, the *Clamator* cuckoo males became more showy.

There was stronger evidence for correlated evolution between female plumage and breeding strategy ($\text{LR} = 15.106$, d.f. = 4, $p < 0.01$). The ancestral state for female plumage was most likely showy (0.962 probability, $\text{LR} = 6.464$, d.f. = 1, $p < 0.02$). The significant evolutionary changes include female crypsis evolving before brood parasitism and also after brood parasitism (figure 3b), hence cryptic female plumage might be both a precursor and a consequence of the evolution of brood parasitism. The three independent origins of brood parasitism again do not provide a consistent pattern, but suggest different evolutionary

Figure 4. Distribution of plumage scores (first principal component for (a) males and (b) females). Histograms are shown separately for species with (i) parental care and (ii) brood parasitic species.

pathways. While there was a change from showy females to cryptic females in both New and Old World parasitic cuckoos, the *Clamator* cuckoo females became more showy in their plumage.

Inspection of principal component scores for both sexes suggests that both males and females are more cryptic in parasitic species (figure 4). Thus, there is no general support for the sexual selection hypothesis. Instead, plumage dimorphism in parasitic cuckoos evolved primarily due to changes in female plumage rather than in male plumage. However, males of some parasitic species, such as the shining cuckoos in the genus *Chrysococcyx*, have very showy plumage.

Barring on the breast and/or belly in birds of prey has been interpreted as a break-up pattern that increases crypsis. If barring increases crypsis in cuckoos, it should be particularly prominent in parasitic species. Therefore, we tested this directly. While 80 out of 84 parental species have no barring in either sex, among 60 parasitic species barring occurs in males of 31 species and in females of 35 species. In four parasitic species, the female is barred but the male is not. Analysing the sexes separately, we found good evidence for correlated evolution between barring in females and breeding strategy ($\text{LR}=12.816$, $\text{d.f.}=4$, $p<0.01$), but only a trend in males ($\text{LR}=7.962$, $\text{d.f.}=4$, $p<0.1$). The most likely ancestral state for females was absence of barring (0.953 probability, $\text{LR}=6.020$,

Figure 5. Flow diagram of the most likely evolutionary pathways between breeding strategy and plumage barring in females. The ancestral state is the box shaded in light grey, the boldly lined box shows the most recently derived state in parasitic cuckoo females.

$\text{d.f.}=1$, $p<0.02$) and the most likely evolutionary pathway (figure 5) has barring evolving after the evolution of brood parasitism.

4. DISCUSSION

The evolution of sexual dimorphism in cuckoos is more likely explained by the coevolution hypothesis rather than the sexual selection hypothesis. Instead of selection on males to become larger, we found that both sexes became slightly smaller with the evolution of brood parasitism. While Owens & Hartley (1998) pointed out that size and plumage dimorphism are not necessarily explained by the same factors, we found support for the coevolution hypothesis explaining not only size dimorphism but also plumage dimorphism. There was no evidence for male plumage becoming more showy in parasitic cuckoos, but female plumage became more cryptic with the evolution of brood parasitism.

Evolutionary pathway analyses suggested that the transition from size dimorphism with larger females to dimorphism with larger males most likely occurred before the evolution of brood parasitism (figure 2a). This suggests that smaller female size was a pre-adaptation for brood parasitism. Plumage dimorphism, however, most likely evolved after parasitism (figure 2b). This suggests that more cryptic female plumage, perhaps functioning to reduce detection by hosts before egg laying evolved in the context of host–parasite coevolution. Separate pathway analyses of female plumage suggested that more cryptic female plumage evolved both before parasitism and after it (figure 3), while barring (a major component of crypsis) most likely evolved after parasitism (figure 5).

Examining the three independent origins of brood parasitism in cuckoos suggests that the different parasitic lineages have followed different pathways to successful brood parasitism. Common to all three origins of brood parasitism is a decrease in egg size, with small egg size most likely being an adaptation for successful parasitism of relatively small hosts (Payne 1974; Krüger & Davies 2002, 2004). This might help to explain male-biased size dimorphism in parasitic lineages as decreased female size enabled them to lay smaller eggs with shorter developmental periods. With regard to plumage, it seems that while more cryptic females have evolved in both the New and Old World parasitic cuckoos, the *Clamator* cuckoos have followed a different path, evolving more showy plumage. This is likely to reflect their different laying tactics: while Old World Cuculinae cuckoos tend to rely on secretive behaviour to reduce detection by hosts, *Clamator* cuckoos often adopt conspicuous displays to lure hosts away from their nests (Davies 2000).

Our analyses reveal the importance of selection pressures acting on females but also suggest that male cuckoos in parasitic lineages have undergone rather similar changes. Males decreased slightly in size with the evolution of brood parasitism and their plumage also became more cryptic, changes that are opposite in direction to predictions of the sexual selection hypothesis. Elaborate sexually selected plumage and display traits exist in the brood-parasitic whydahs (Barnard 1990), so the scarcity of such traits in male brood-parasitic cuckoos is especially intriguing and suggests a limited role for sexual selection in this group. Recent evidence of the genetic mating system in avian brood parasites has documented surprisingly low levels of polygyny, and in some cases patterns consistent with monogamy (Marchetti *et al.* 1998; Martinez *et al.* 1998; Alderson *et al.* 1999; Hauber & Dearborn 2003; Woolfenden *et al.* 2003).

One note of caution is necessary. There is substantial variation both within parental and parasitic lineages in all traits considered. For example, our analyses indicate significant evolutionary changes in both size and plumage dimorphism within both parental and parasitic lineages (figure 2), clearly suggesting that changes in dimorphism can occur independently of changes in breeding strategy.

Previous comparative studies that have examined sexual dimorphism in birds (Webster 1992; Møller & Birkhead 1994; Owens & Hartley 1998; Thomas *et al.* 2006) have all emphasized the importance of mating system, levels of parental care, and opportunities for extra-pair copulations. All of these studies, however, have specifically tested explanations within the sexual selection domain (see Székely *et al.* (2000) for an example looking at both sexual and natural selection) and have not examined patterns of morphological evolution for each sex separately. Hence, our results have two important implications. First, coevolution can have a profound influence on traits that traditionally have been explained by sexual selection, both in hosts (Soler *et al.* 1999; Garamszegi & Aviles 2005) and parasites. Second, selection on females can be important in generating sexual dimorphism (see Irwin 1994 for another example).

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