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Commentary

It isn't always sexy when both are bright and shiny: considering alternatives to sexual selection in elaborate monomorphic species

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Since the dawn of abstract thinking, humans have wondered about the seemingly unnecessary elaborate ornamentations of birds. Gaudy colours, cumbersome tails, complex vocalizations and bizarre displays are found in bird species from all corners of the globe. Darwin (1871) provided an elegant explanation for the existence of these non-utilitarian traits: they increase mating success, and although they may impair survival, the costs of producing and bearing elaborate ornaments can be repaid in the currency of additional offspring. Darwin's model still serves as the foundation for our concept of sexual selection but great strides have been made in our understanding of sexual selection processes since his time (e.g. Zahavi 1975, 1977, Lande 1980, Hamilton & Zuk 1982, Kirkpatrick 1982, Grafen 1990, Andersson 1994). The great majority of work to date has focused on species in which males alone are elaborately ornamented. Far less has been published on the function of ornaments that are expressed in both sexes (Kraaijeveld *et al.* 2007), a condition sometimes termed 'elaborate monomorphism.' As such, the question remains whether the strong generalizations that we make regarding male ornamentation also apply to species in which both sexes are ornamented.

The relationship between female and male ornamentation can take several forms. In some species (for example, some fringillids and parulid warblers), females express relatively subdued vestiges of male ornaments. The presence of male-like characters in females of such species is consistent with the genetic correlation hypothesis (Lande 1980), which posits that females

express non-adaptive traits as a by-product of sexual selection on male ornaments. Females bear the genes that give rise to the expression of ornaments in males, but because the costs to females of ornament expression are typically not repaid with increased fecundity, natural selection favours reduced expression of costly ornaments (Kokko & Johnstone 2002, LeBas *et al.* 2003, Chenoweth *et al.* 2006). In support of this hypothesis, some studies have detected sexual selection only on male traits but have failed to find a relationship between female ornamentation and reproductive success, performance, or a measure of female condition or quality (e.g. Muma & Weatherhead 1989, Cuervo *et al.* 1996, Wolf *et al.* 2004).

However, in some species (for example, many parrots, motmots and relatives, and tropical songbirds), elaborately ornamented females and males are indistinguishable, or nearly so. The female 'version' of ornamentation in these species seems more elaborate than would be expected if these traits were only expressed as non-adaptive genetic by-products of sexual selection on males, or if they were shaped solely by natural selection. Indeed, compelling evidence from many species, including some that are sexually dimorphic, suggests that elaborate female traits may also function as signals, although female ornamentation may or may not stem from the same selective processes that lead to elaborate male ornamentation (Amundsen 2000, Lebas 2006, Clutton-Brock 2007, 2009, Kraaijeveld *et al.* 2007, Dey *et al.* 2012). Some studies have supported the role of mutual sexual selection in maintaining ornamentation in both sexes by showing that males prefer more ornamented females (e.g. Amundsen *et al.* 1997, Griggio *et al.* 2005) or that more ornamented females are in better condition (Velando *et al.* 2001, Jawor *et al.* 2004, Siefferman & Hill 2005, Dakin 2011). Similarly, some studies have found that female–female competition for sexual or non-sexual resources can lead to the evolution of elaboration in females, wherein female ornaments convey information about fighting ability or dominance (e.g. Murphy *et al.* 2009a,b, Midamegbe *et al.* 2011, Cain & Ketterson 2012). In contrast, other studies have failed to find evidence of signal value associated with female ornamentation in elaborate monomorphic species (Murphy & Pham 2012). As we learn more about the potential costs and benefits of mate choice and competitive interactions, a richer understanding of how selection can favour sex-based signalling strategies in females is emerging. Such a perspective was rarely considered even 15 years ago (Amundsen 2000).

Among many elaborate monomorphic species, members of a mated pair tend to be similarly ornamented, a phenomenon called assortative pairing (e.g. Møller 1993, Andersson *et al.* 1998, Regosin & Pruett-Jones 2001, Daunt *et al.* 2003, Masello & Quillfeldt 2003, Massaro *et al.* 2003, Boland *et al.* 2004, Kraaijeveld

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et al. 2004, Safran & McGraw 2004). Mutual mate choice, wherein females prefer to mate with the most elaborate males while males simultaneously choose the most elaborate females, is one of the most common mechanisms giving rise to assortative pairing. Indeed, assortative pairing is among the most accessible measures that researchers use to test the mutual sexual selection hypothesis, and is often one of the first measures made.

In this issue of *Ibis*, van Rooij and Griffith (2012) test whether elaborately monomorphic Long-tailed Finches *Poephila acuticauda* mate assortatively with respect to ornamental traits. Both males and females of these Australian estrildids have long tails, a conspicuous throat patch and colourful bills during the breeding season. The species is an ideal candidate to test whether male and female homologous ornamental traits are favoured by mutual mate choice, as it has many of the life-history traits that typically favour mate choice in both sexes: they are socially monogamous and pairs remain together across multiple breeding seasons, and both sexes incubate, feed the offspring and defend the nest. Given the gaudy nature of the male and female ornaments in this species, the authors expected that the ornaments of both sexes are sexually selected signals. However, against expectations, van Rooij and Griffith find no evidence for assortative pairing in their study population. None of the ornamental traits they measured was correlated within mated pairs. Likewise, the birds did not pair assortatively with respect to tarsus length or size-adjusted mass, which might be expected if those more general measures of body size were correlated with unmeasured targets of mate choice or success at competing for mates.

It is possible that Long-tailed Finches do not mate assortatively with respect to those ornaments because, although the ornaments are expressed in both sexes, they have a signalling function in only one sex and are expressed in the other sex as a non-adaptive by-product of a genetic correlation. If that were the case, indicator models of sexual selection still predict the ornaments should be related to individual condition and ultimately to reproductive success in one of the sexes, and Fisherian models of sexual selection similarly predict that ornaments should be related to reproductive success. Therefore, van Rooij and Griffith tested these possibilities. However, in neither sex were the ornamental traits related to the number of fledglings per nest. Additionally, individual condition, as measured by body size and size-corrected mass, did not relate to ornamental expression in either sex.

Why, then, do such gaudy ornaments exist? van Rooij and Griffith offer several plausible explanations. For example, because Long-tailed Finches are long-lived, it is possible that these ornaments are maintained by mutual sexual selection, yet assortative pairing was difficult to

detect. For example, in some pairs the ornaments may have been similar between mates upon initial pairing, but diverged since that time. Likewise, some pairs may have formed under conditions in which mate choice was highly constrained, such as following the death of a former mate, which could lead to a breakdown of the correlation between males and females. The authors tested this by restricting their analysis to newly formed pairs (those that had bred with different individuals in previous nesting attempts) in an attempt to evaluate pairs that were formed by choosing from a common pool of potential mates (Murphy 2008). This is a strong approach, although it is possible that the pool during the time of the formation of any given new pair was relatively small and that mate choice therefore remained constrained. However, van Rooij and Griffith also compared the morphology of birds that had successfully paired with birds thought to be unpaired. Because they found no difference between these groups, they reasoned that the pool of potential mates available to birds that were choosing initial or replacement mates was essentially like the pool of mated birds in terms of ornaments, and thus was unlikely to be limiting. The authors also considered the possibility that mutual sexual selection may have been weak or that the focus of selection was variable between years, as has been observed in some other studies (Andersson *et al.* 1998, Griffith *et al.* 2003, Chaine & Lyon 2008, Parker *et al.* 2011), and they therefore analysed data from each of 3 years separately. None of these analyses revealed compelling relationships, suggesting that even if assortative mating does occasionally occur, mutual sexual selection on the ornaments is unlikely to be strong. Given these results, van Rooij and Griffith suggest that the traits simply may not honestly signal individual condition or quality at all. Fisherian sexual selection acting in both sexes could also lead to elaborate monomorphism without giving rise to correlations between ornamentation and condition in either sex. However, such a process should lead to mutual mate choice and therefore assortative pairing. Again, this hypothesis was not supported because the Long-tailed Finches were not paired assortatively.

'Negative' results in ecological and evolutionary studies can get a bad rap, as editors and reviewers tend to be harsh on studies that do not support the tested hypotheses. There are very good reasons for a high level of caution on the part of editors. Studies that report statistically non-significant results are not particularly helpful when the lack of support for hypotheses may be due to poor study design. If a study is unable either to reject or to support a hypothesis because of flaws in logic or design, editors and reviewers are wise to encourage the authors to find a better way to test their ideas. Likewise, weak or negative results often stem from small sample sizes and the consequent high statistical uncertainty that they yield. In the case of the

Long-tailed Finches, however, van Rooij and Griffith report tests on a dataset that seems large enough to allow confident rejection of functional hypotheses. In cases such as this, in which we can have confidence that a lack of trend is likely to represent a real lack of a relationship, negative results can be extremely valuable because they reveal limitations in our understanding of how the world works (or at least in our tendency to generalize broadly from a small number of studies) and thereby inspire new, perhaps iconoclastic, hypotheses. Indeed, stepping back to examine the frequency of studies that confidently do and do not provide support for major hypotheses can potentially lead to important insights into mechanisms and theory (e.g. Prum 2010, Hill 2011).

If the hypothesis that the ornamental traits of Long-tailed Finches are maintained by mutual mate choice can be confidently rejected, what then *can* account for elaborate monomorphic traits in this species? As van Rooij and Griffith suggest, it is possible that the ornamental traits carried a signalling function in one or both sexes in the past but that the signalling role of the traits they measured is now redundant with other traits, or alternatively, the function of the traits may vary geographically and thus be important in some areas but not others. In essence, the costs and benefits associated with expressing and/or attending to ornamentation may change over time or space, in which case a single study may not detect trends that are important in other contexts. Similarly, it seems possible that genetic variation for the trait may have been exhausted in one or both sexes, thus rendering the traits meaningless and relaxing selection on receivers to attend to them. Another possibility is that the traits in one sex may signal an unmeasured aspect of viability that is not correlated with body size or number of fledglings per nest, and may be expressed non-adaptively in the other sex. Because indicator models of sexual selection suggest that ornaments should be correlated with traits that influence viability (e.g. Grafen 1990, Getty 2006), measures of physiological condition such as immunocompetence, oxidative stress, or other cellular and biochemical processes (i.e. measures of condition that are probably more closely linked to survival) may be better targets of investigation than body size (Hill 2011). This is important because indicator models do not necessarily predict a strong correlation between ornaments and reproductive output during a given nesting attempt. 'Good' genes for viability should promote survival and thereby influence lifetime reproductive success through an increase in number of mating opportunities rather than through an increase in fecundity within nesting attempts. Good viability genes therefore may have little correlation with the success of a single reproductive attempt. Thus, if Long-tailed Finches of one sex choose mates based on ornaments that signal viability, and if the traits are

expressed in the other sex as a correlated by-product, then van Rooij and Griffith may have simply missed the effect in their study.

It is important to keep in mind that even when assortative pairing is detected, its interpretation is not straightforward. One issue is that mechanisms other than mutual sexual selection can lead to assortative pairing. For example, if individuals pair assortatively by age-class (which is often mediated by availability of similar-aged mates) and ornaments become more exaggerated with age in both sexes, older pairs will tend to be highly ornamented while younger pairs will be less ornamented. In such a scenario, assortative pairing exists but does not arise via mutual mate choice for ornaments. On the other hand, the lack of assortative pairing is also difficult to interpret, as its absence does not necessarily indicate a lack of selection acting on the ornament. For example, both sexes could use ornaments as socially selected status signals to mediate competition (within and between sexes) for access to non-sexual resources such as food or territory. As this type of signal does not necessarily increase mating success (and therefore is not considered a form of sexual selection) it is unlikely to lead to assortative pairing.

Studies like that of van Rooij and Griffith remind us that ornamental traits may have nothing to do with mate choice or sexual selection in general. Ornaments may be used as 'badges of status' in intra- or intersexual competition over non-sexual resources (Rohwer 1975), they may function as predator deterrent signals (Hasson 1991, Murphy 2006), or they may have utilitarian functions (Mumme 2002). Thus, lack of support for sexual selection hypotheses such as seen in the study of van Rooij and Griffith should encourage ornithologists and behavioural ecologists explicitly to consider alternatives to sexual selection when studying ornamentation. Sexual selection will remain pervasive and important in light of alternative hypotheses, but we may come to realize that it may not be omnipresent, especially in species in which females are elaborately ornamented.

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