Historical mating systems and the origin of sexual ornament

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Abstract

Ornamental traits are commonly interpreted as products of runaway sexual selection or costly signals of male quality, but many ornamental traits appear to be functionally redundant, and, especially in birds, multiple ornaments coexist without clear links to condition or survival. This new proposal explains the evolution of ornament through sexual selection. based on looking for historic circumstances under which such traits might once have been functional. If mating systems are seen on a spectrum between polygyny and monogamy then in an intermediate state, when are both systems are viable, females may benefit from identifying males likely to provide parental care rather than pursue additional mates. Selection may then favour traits that function as signals of fidelity. If mating subsequently resolves into pure polygyny or monogamy these signals may persist through a coupling between female preference and male ornament, as predicted by standard models of sexual selection. Repeated transitions between mating strategies will cause ornament traits to accumulate. Traits may also be vulnerable to deceptive mimicry by males pursuing alternative mating strategies, leading to an evolutionary arms race that selects traits that are costly or difficult to imitate. This helps to explain the extravagance and diversity of plumage and behaviour observed in species such as Birds-of-paradise.

Keywords: *sexual selection, parental investment, mating systems, ornament evolution, Birds-of-paradise*

1. The problem of ornament

The evolution of elaborate sexual ornaments presents a challenge for evolutionary explanation because such traits may reduce survival through their cost and increased visibility to predators. Nevertheless, conspicuous ornaments are widespread among animals, particularly among males in species where mate choice is primarily exercised by females. Among birds ornament is associated with, but is not exclusive to, polygynous mating systems. (Marcondes and Douvas 2024). In the most extreme forms of polygyny, males contribute little or no parental care. Where females choose a mate at a lek they obtain little more from mating than sperm. Kirkpatrick and Ryan (1991) described this situation as the "paradox of the lek". Why should females show strong preferences for elaborate male displays when direct benefits from males are minimal, and their male descendants will be burdened with what seem to be maladapted traits?

My suggestion is that sexual ornaments originate not as indicators of genetic quality but as signals allowing females to identify males likely to provide parental care during periods when populations transition between monogamous and polygynous mating systems. When the transition is complete the signal, even though it is now redundant, is preserved by female sexual preferences. If a species makes many transitions between monogamy and polygyny it will amass multiple ornaments.

To illustrate this idea, consider ornamental plumage in birds. It has evolved independently at least seventy times across avian lineages, (Cuervo and Møller, 1999). and often appears in combinations that seem redundant or functionally unnecessary. Standard theory is divided between ornament signaling good genes and other non-adaptive explanations, (Kirkpatrick, 1987). The good genes school argues that ornament should evolve to favour ecologically adapted males, so ornament is correlated to condition or has evolved condition-dependent expression through being a handicap, as Zahavi suggested. The nonadaptive school holds that preferences usually evolve in maladaptive ways through Fisherian runaway processes in which genetic correlations between male traits and female preferences allow the exaggeration of arbitrary traits. Experiments suggest that multiple ornaments are best understood as Fisherian signals that no longer convey information about male quality. For instance, Møller and Pomiankowski, (1993) examined relationships between mating systems and occurrences of feather ornaments and concluded that multiple ornaments in birds are Fisher traits and unreliable indicators of genetic qualities other than attractiveness. As Prum (2010) put it: 'traits are neither honest nor dishonest, and indicate nothing other than mating availability through their potential to correspond to mating preferences.'

If no good reason for ornament is evident today we should consider the possibility that it might have originated in response to historical selective pressures that are no longer present. I suggest that present-day sexual traits reflect historical ecological conditions and to understand ornament we might have to reconstruct the environment in which it was meaningful. Ornaments as seen today can seem maladaptive only because the environment in which they represented good genes no longer exists. Unless they are preserved by female preference they would be vestigial.

One way this could happen is if sexual ornaments originated as signals of paternal commitment in populations in which both monogamy and polygyny are viable mating strategies. In most species female reproductive success depends strongly on male parental care, while in others males pursue multiple mating opportunities and contribute little to offspring rearing. When ecological conditions place populations near the boundary between monogamous and polygynous systems, females may benefit from identifying males likely to provide parental care rather than pursue additional mates. Under these circumstances traits associated with paternal investment could become targets of female choice. Once female preference for such traits is established, standard models of sexual selection predict that ornaments and preferences for them may become coupled and persist even if the ecological conditions that originally favoured them change.

2. Persistence of ornament through sexual selection

The Lande-Kirkpatrick null model of intersexual selection is a standard model of sexual selection that can explains how burdensome male traits can be stable even when they provide little or no direct benefit to either males or females. It requires a statistical coupling between a heritable male trait and a heritable female preference for that trait. Once established the coupling will last for as long as it does not affect female fecundity. This is because a female that deviates from the prevailing preference will produce sons that are less attractive to other females and daughters that share her atypical preference and thus encounter fewer acceptable mates. A reduction in the male trait that lowered its cost and risk of exposure to predators might lead to a marginal change in female fecundity through improving mate availability, but this is outweighed by the reduction being unattractive to females. Once the trait and the preference for it are coupled the most sexually advantageous trait value any male can possess is the one that matches the mean female preference, (Kirkpatrick and Ryan, 1991). Except that they might drift along a line of equilibria, traits, and the preferences for them, will only move from one point of equilibrium to another if they directly affect the survival or fecundity of females. The null model explains their stability and nothing more. None of this explains why any ornament, or female preference for it, might have arisen in the first place, or why it might be subject of runaway growth. A new idea is needed.

Crossing between mating strategies is an obvious candidate for a transitory event where an ornamental signal might evolve. What the null model explains is why traits that once indicated paternal commitment could remain after mating systems shifted to one or other end of the monogamy-polygyny spectrum. Since their function would be redundant after that shift any subsequent transitions between mating strategies would require a fresh signal of fidelity, thus ornaments could accumulate over evolutionary time whenever the species shifted on the mating system spectrum.

3. The monogamy–polygyny interface

Marcondes and Douvas, (2024) studied how mating systems evolved by mapping them on to a phylogenetic tree of birds allowing them to identify ancestral behaviour and thus estimate when transitions have occurred. Mating systems can be seen arrayed on a spectrum, which they divided into three broad categories: monogamy, resource-defence polygamy, (here simply refered to as polygyny) and lek polygamy. Of 6620 species in their survey 91% were socially monogamous, 2.8% were resource defence polygamous, and 6.2% were lekking. They found that polygamy is easily lost, with transitions from polygamy to monogamy having the highest rate. Their results suggest that resource-defence polygamy is an evolutionarily unstable state tending to either be lost or to drive its lineage to extinction. Lekking is more stable. Most transitions to lekking have been directly from monogamy, although they point out that the passage through a polygamous stage in the evolution from monogamy to lekking could be so brief that it is undetectable using their methods.

Many species have at some time changed their mating system and thus passed through intermediate states in which both monogamy and polygyny can yield reproductive success. In such situations female reproductive output may depend critically on whether a mate provides parental care. In that case selection would favour mechanisms allowing females to distinguish males likely to invest in parental care from their polygynous rivals. Male traits that reliably correlate with paternal investment could therefore evolve through female choice. These traits need not initially be elaborate; even modest morphological or behavioural signals might be sufficient if they allowed females to identify males that contribute to parental care.

For a signal of fidelity to evolve, the trait must initially correlate with male behaviour through physiological linkage or behavioural association. Signals that influence female mate choice are susceptible to exploitation. A male pursuing additional mates might benefit from displaying a trait associated with paternal investment if doing so increased its mating success. Signals such as nest building, or courtship feeding are ways to indicate a good mate within an environment in which monogamy is a dominant strategy, but if parental care is no longer essential for viable offspring then their honesty becomes harder to enforce. Traits that initially functioned as simple indicators of fidelity could escalate in cost and complexity if selection favours signals that are more reliable. For that reason a physiological change might be more reliable than a change in behaviour as its development costs make it harder to mimic. A trait that is continuously displayed, such as a difference in plumage or a repeated song, has the advantage of being easily learned. If the male appears at the nest then offspring can be imprinted with the mark of a suitable mate.

Once such signals appear, assortative mating will occur if females preferentially choose males displaying the signal and males expressing the signal tend to provide parental care. Now suppose the mating system later settles on polygyny or monogamy as a dominant strategy. A dominant strategy is one that it is the best course of action whatever other players choose to do, in which case traits that signal parental care are no longer needed. The traits will, however, persist if they are coupled to female preference even when the link to male behaviour is decoupled. Once a signal is no longer maintained by selection it becomes vestigial and its original function is unlikely to be restored. This process provides a potential explanation for the accumulation of multiple ornaments. If mating systems fluctuate through time, repeated episodes of signalling and counter-signalling could favour the addition of new display traits while earlier ones are retained through preference–trait coupling. The result may be complex display repertoires composed of traits that originated under different historical conditions.

The idea that polygyny is unstable supports the idea of an erratic journey from an assumed monogamous ancestral state. Ornament will accumulate for as long as the environment does not permanently favour either monogamy or polygyny. If, after a long journey, a stable end state such as lekking is reached males may be burdened with plumage that is meaningless but which persists because of female preference for it.

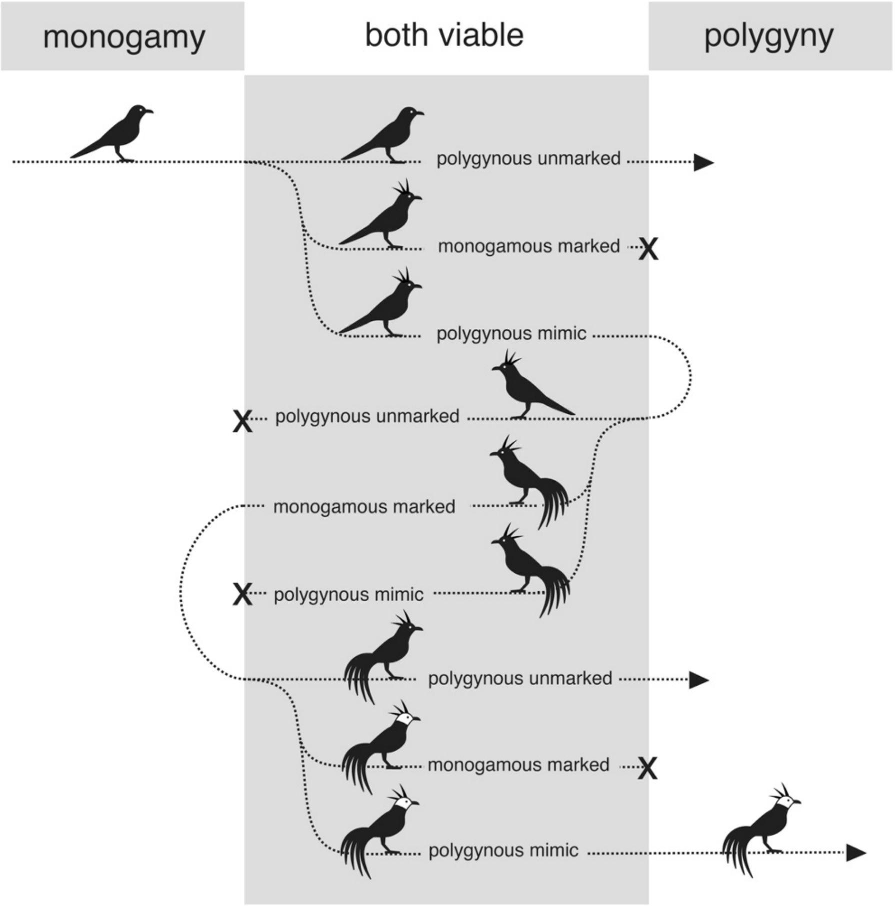

Fig. 1 Cartoon schematic of ornament accumulation. In the top line a bird changes from monogamy to polygyny, but when both mating strategies are equally viable some monogamous males acquire marks of fidelity leading to associative mating indicated by the diverging paths. This ornamental line divides further if it is mimicked by polygynous rivals. One or other of these lines is extinguished (shown by x), depending upon whether monogamy or polygyny is eventually dominant. At each crossing the bird acquires a new ornament.

This accumulation of ornaments is shown in the cartoon representation in Figure (1). It illustrates an extreme case of a species alternately switching completely between monogamy and polygyny. Depending on the direction of travel, ornament that signifies fidelity, or a deceptive copy of it, survives preserved by female preferences. These ornaments come and go every time the species crosses the ambiguous zone.

This process of accumulation and elaboration is one possible explanation of the extreme ornament in species such as Birds-of-paradise. Sexual selection theory predicts that extravagant ornaments can arise from sexual conflict and deception. Many cases are known in which elaborate sexual signals have evolved via antagonistic coevolution whereby one sex uses deceptive mimicry to manipulate the opposite sex into mating, (for instance as described in Dalziell et al., 2021). I suggest that extreme ornamental plumage in birds has a similar origin. It is the result of an evolutionary arms race that selects signals that are costly or difficult to imitate.

4. Experimental support for ornament as a sign of fidelity

Cuervo J.J., Møller A.P. (1999) made pairwise comparison of species to identify factors associated with extravagant feather ornaments. They found no correlation with variables such as migration, nesting habits, sociality, or foraging mode. No correlation with male parental care, which they classified as present or absent, was found. The most significant factor in the acquisition of feather ornaments was with social mating systems belonging to a higher degree of polygyny. Their findings were consistent with the Fisher mechanism of sexual selection, meaning that traits do not currently signal male condition.

All this is consistent with the idea of ornament being the result of a change of mating system rather then the mating system itself requiring ornament. At first glance the lack of a correlation with parental care appears to contradict the idea that ornaments might signal paternal investment, but becomes explicable if the association was temporary. Likewise the idea that ornament does not currently signify condition is explicable if its function was historic.

Birds-of-paradise provide a striking example of extreme ornamental diversity that comply with this model. The 42 species show a mixture of monogamous, polygynous mating systems, with about one third using leks, (Diamond, 1986). Lekking can be seen as the stable end point of transition from monogamy with the plumage as a fossil record of now redundant signals of parental care accumulated in the unstable polygynous zone. Birds-of-paradise belong to the Corvoidea superfamily, whose members are predominantly socially monogamous with biparental care yet their mating strategies. Their change from an ancestral monogamous state is traced in Marcondes and Douvas, (2024).

While this hypothesis does not exclude other explanations for ornament evolution, it highlights the possibility that historical ecological conditions may leave lasting signatures in present-day sexual traits. It implies that ornament will likely arise in birds descended from ancestors with monogamous mating systems that cross into polygyny for a period. The ornament will persist whether or not polygyny is the stable outcome. It follows that there will be no more than an partial association with polygyny, and explains why there are monogamous ornamented species. The hypothesis is therefore consistent with the finding of Marcondes and Douvas's phylogenetic analysis of bird species showing that ornamental radiations are associated with lineages that historically experienced shifts in mating strategies.

5. Testable predictions

The hypothesis leads to some other predictions that could, in principle, be confirmed experimentally.

(i) Mating-system transitions are assumed to be transitory historic events this are difficult or impossible to study. It might, however, be possible to observe it in species where alternative mating strategies coexist. Macrondes and Douvas noted a small number of species with intraspecific variation in social mating systems, which in this hypothesis would be species in the act of transition. In that case traits associated with male parental investment may still function as signals influencing female mate choice rather than being redundant. Behavioural and experimental studies could then examine whether particular ornaments correlate with paternal care or mating strategy.

(ii) If the creation of ornaments arising through assortative mating associated with signalling leads to speciation it suggests that the differences between those species might be relatively superficial. If so then the possibility hybrids will remain despite substantial differences in appearance. High rates of hybridization reported in birds-of-paradise, (Martin, 2015, Diamond, 1986), are consistent with this possibility, although additional comparative work would be needed to evaluate the pattern more broadly.

(iii) Ornaments associated with deceptive or competitive signalling should display greater variance, and possibly more strongly skewed distributions, than traits primarily shaped by natural selection. According to the hypothesis here some of the ornament in lekking or polygynous species is the result of mimicry as shown in Figure 1. If this is so that ought to leave a statistical signature. This is because the distribution of ornamental trait sizes will differ depending upon whether the trait is a target or is being mimicked, as demonstrated by Dixit, et al., (2021). Under ordinary natural selection, morphological traits typically show approximately Gaussian variation because they reflect the additive effects of many small genetic and developmental factors. However, when a trait functions as a signal that must approximate a perceptual threshold or target value, selection may act on the perceived scale rather than directly on the physical one. Since perception is proportional to the logarithm of a stimulus intensity rather than its scalar value the target that the mimic must match is positioned on a logarithmic scale. Selection would then favour an approximately lognormal distribution of trait size. Overshooting the target signal may impose a smaller perceptual error than undershooting it favouring exaggerated traits. Therefore in polygynous species, where the mimic has prevailed traits size distributions are likely to be right-skewed, literally, long tailed, compared to a monogamous species with a more Gaussian distribution.

This prediction is consistent with studies showing that sexually selected ornaments can show higher coefficients of variation than ordinary morphological traits. For example, Alatalo and Höglund's survey of avian ornaments, (1998), found that body size characters typically had coefficients of variation of between 2–6%, whereas sexually selected tail ornaments went from about 6% to more than 20%. Although these data were unable establish the form of the underlying distributions, they suggest that sexually selected traits can exhibit unusually high variance. There are other reasons why ornament intensity distributions might be right-skewed, so to interpret it as a trace of mimicry would not be decisive without a careful experiment designed to exclude them. Better tests of this prediction would require large datasets of ornament measurements within populations correlated with mating systems and alternative reproductive strategies.

6. Conclusion

The difficult issue in understanding the origin of extreme ornament is finding its function. This problem dissolves if present-day sexual traits reflect historical conditions that are no longer observable. It follows from this that much ornamental plumage currently has no function. If correct, this mechanism could help explain both the persistence of apparently arbitrary ornaments and the accumulation of multiple display traits in some lineages. More speculatively, it allows us to look at extreme ornament, such as seen in Birds-of-paradise, as the result of a runaway process of mimicry in which the similarity between a mimic and a model confers a selective benefit onto the mimic.

The correlation between coloured plumage and polygynous mating systems such as lekking makes it appear that ornament might be in some way necessary for it to work. Of course correlation does not definitely entail cause, but it seems plausible if our understanding of social mating systems is largely based on an *atemporal* ecological framework. Marcondes and Douvas's reconstruction of the evolution of social mating systems themselves is therefore very illuminating. They demonstrate that transitions from an ancestral monogamous state have occurred and that the changes are in some way connected to ornament. This suggests that it is the transition itself that is the cause of physiological changes especially if there are mechanisms, such as female sexual selection, that can preserve traits when the need for them is gone. The theory of evolution allows us to see creatures in an adaptive equilibrium with an environment that changes more slowly than they do. In contrast to this atemporal approach ornament might be a fossil example of an adaption to a relatively brief event.

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9. References

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