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Why are female birds ornamented?

Trond Amundsen

Sexual selection is now widely accepted as the main evolutionary explanation of extravagant male ornaments. By contrast, ornaments occurring in females have received little attention and often have been considered as nonadaptive, correlated effects of selection on males. However, recent comparative evidence suggests that female ornaments have evolved quite independently of male showiness. Also, new theoretical models predict that both male mate choice and female contest competition will occur under certain circumstances. This is supported by recent experimental studies. Thus, selection acting on females might be a widespread cause of female ornaments.

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Recently, sexual selection theory[1] has proved extremely successful in explaining extravagant male traits, such as colourful plumage and elaborate vocal and visual displays[2]. However, few attempts have been made to address whether sexual selection also acts to produce similar traits in females. This lack of interest has theoretical, as well as empirical, roots. Theoretically, it has been acknowledged that male reproductive success often is limited by access to females; thus, sexual competition selects for secondary sexual characters in males. When sexual selection acts on males, traditionally it has been assumed that it does not act on females. Empirically, the view that sexual selection is mainly about males has been corroborated by observations that females are often much less showy than males. There is no reason to challenge these theoretical and empirical statements as broad generalizations.

However, the fact that sexual selection acts on males does not preclude selection on females. Indeed, female showiness is far from uncommon. Having established a relatively detailed understanding of male visual extravaganza, it is now time to ask why females of many species are also beautifully decorated. For instance, among birds, conspicuous crests or beaks often occur in both sexes (e.g. auks and cormorants) and showy female colours are found in a variety of taxa (e.g. toucans, parrots, hummingbirds and tanagers). Likewise, many ungulate mammals have horns or antlers in both sexes, and many fish display identical colours in the two sexes (e.g. butterflyfishes) or showy colours specific to females (e.g. many wrasses). Among invertebrates, there are several taxa where females, not only males, display ornamental structures or colours. As stated by Johnstone and colleagues, 'nature abounds with biparental care species in which both sexes are ostentatiously plumed or brightly colored'[3].

Recently, studies focusing on female traits have enhanced our understanding of mate choice and sexual selection[4–6]. In spite of decorative female traits being taxonomically widespread, it is only since the late 1970s that evolutionary biologists have started to approach questions related to female ornamentation from a functional perspective[7]. During the past decade, theoretical[3,8] and empirical[9–13] research have provided intriguing results indicating that female showiness might be related to male mate choice and female competition. Clarifying the role of these two processes, and their selective consequences on female appearance, is essential for a complete and realistic understanding of animal mating dynamics.

**Box 1. Darwin and Wallace on female ornamentation**

Darwin[1] was well aware that females of many animal species are ornamented conspicuously. He explained female ornaments in species with 'sex role reversal' by sexual selection:

> 'There are… exceptional cases in which the males, instead of having been selected, have been the selectors. We recognise such cases by the females having been rendered more highly ornamented than the males …'[1].

However, when females were either equally or less ornamented than males of the same species, Darwin's explanation was 'the laws of inheritance':

> 'The laws of inheritance, irrespectively of selection, appear to have determined whether the characters acquired by the males for the sake of ornament … have been transmitted to the male alone or to both sexes…'[1].

Hence, Darwin's general view can be seen as a precursor to the genetic correlation idea. He seems to have dismissed the idea of mutual sexual selection in animals, although he thought that both sexes are choosy among humans. Overall, Darwin did not explain the presence or absence of female ornaments in terms of selection. He opposed Wallace's idea that female drabness, as seen in many species, was a selective response to predation.
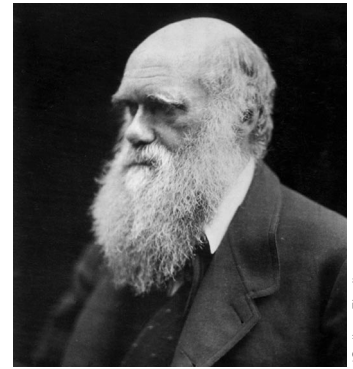
(Online: Fig. I)

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(Online: Fig. II)

Wallace[16,49] was generally sceptical to the idea of sexual selection, and explained gaudy male ornaments as an artefact of anatomy and physiology:

> 'Colour may be looked upon as a necessary result of the highly complex chemical constitution of animal tissues and fluids'[16].

Hence, he needed no selective explanation for female conspicuousness. However, he suggested that female drabness was a result of 'selection for protection' in species that were vulnerable to predation at the nest:

> '…whenever the male is gay and conspicuous and the nest is open so as to expose the sitting bird to view, the female is of dull or obscure colours'[49].

Wallace's idea of selection for crypsis in females has been accepted widely and, today, is still considered one of the main reasons for sexual dimorphism.

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The aim of this article is to review the latest advances in the study of female visual showiness, primarily with a focus on birds. For simplicity, I term any conspicuous and decorative female character an 'ornament'. The review is mainly limited to species with conventional sex roles, because female ornaments in sex-role reversed species are no more puzzling than male ornaments among conventional species. I focus on birds simply because most empirical studies have been made on members of this taxon. However, the processes potentially favouring female ornamentation are general and probably apply in several other taxa.

Genetic correlation or selection on females?

Since Darwin[1] (Box 1), influential theoreticians have explained female ornaments mainly as a genetically correlated result of sexual selection on males[14]. This correlated response hypothesis (Box 2) has been adopted to explain not only female ornaments that are rudimentary versions of male ornaments, but also cases where females and males are equally ornamented. Hence, with the exception of sex-role reversed species[1,15], female showiness frequently has been considered nonfunctional. However, female crypsis has been explained by selection on females for protection[16] (Box 1), a view that recently has been corroborated by comparative evidence[17].

Female ornaments in birds generally share the basic features of male ornaments in the same species, strongly indicating a common genetic basis. Given that most of the genome is shared between males and females, an underlying genetic correlation between the sexes is inevitable, regardless of whether the trait is expressed in both sexes. The expression of secondary sexual characters appears to be, at least partly, under hormonal control[18]. Hence, the question is not whether female ornaments are genetically correlated to those of the males, but whether selection

is acting on female trait expression, either to diminish (selection for crypsis) or to maintain and possibly enforce (sexual selection; Box 2) female showiness. Exaggerated sexual characters are generally thought to be costly to develop and maintain; thus, a selective advantage is needed to explain their existence. This applies to females as well as males. The fact that there is an underlying genetic correlation does not preclude selection on females; indeed, it might instead act as a 'preadaptation' for functional female ornamentation. Potentially, female ornaments might be selected through a signalling function in female contest competition[19] or in attraction of male mates[3,9].

Comparative evidence: female ornaments unconstrained?

During the 1990s, the view that female trait expression is mainly due to a genetic correlation with males has been challenged. Exploring the distribution of monomorphism and dimorphism across all passerine species, Price and Birch[20] showed that evolutionary transitions between dimorphism and monomorphism had occurred at least 150 times. They concluded that genetic correlations seemed not to pose any severe constraint on transitions between the two stages, provided there are appropriate selection pressures. Quantifying the degree of showiness in both sexes, recent phylogenetic studies of New World blackbirds (Icterinae)[10], tanagers (Thraupidae)[12] and dabbling ducks (Anatini)[21] have revealed that evolutionary changes in plumage have, in fact, been far more common among females than males. Changes in female plumage have led more frequently to increased, rather than decreased, showiness (Box 3). A study of intraspecific variation in dichromatism between geographically isolated populations came to the same conclusion[22]. Therefore, current comparative knowledge strongly indicates that selection

has acted on females for increased showiness. However, it does not reveal whether this selection pressure arises from male mate choice, female contest competition or natural selection favouring a conspicuous female appearance.

Patterns of conspicuousness and dimorphism among lekking birds and their closest relatives are also inconsistent with the idea that genetic correlation is the main cause of female showiness[23]. Overall, the comparative studies indicate that changes from dimorphism to monomorphism have been three to five times more frequent than changes from monomorphism to dimorphism[21], and that most of these changes have resulted in relatively monomorphic showiness. If trait expression was mainly owing to genetic correlations, evolutionary transitions where both sexes increased in showiness should be common. This seems not to be the case[12], implying that genetic correlations probably play a minor role in explaining evolutionary changes in female plumage.

Female contest competition

When resources essential to female fitness are scarce, female competition is expected[19,24]. Female competition can occur over sexual (mates) or nonsexual resources (e.g. food)[19]. Competition for access to mates is expected when variation in male quality is high or when there is a shortage of available males[24]. These conditions typically apply when sex roles are reversed[24], and there is compelling evidence that female ornamentation acts as a 'badge of status' in mating competition among sex-role reversed pipefish (*Syngnathus typhle*)[15] and dotterels (*Charadrius morinellus*)[25]. However, variation in quality, or limited availability, of males could also promote female competition in species with conventional sex roles. Female–female aggression might constrain a male's ability to attract multiple partners[5,26], but the possibility that female competition selects for signals informative of competitive ability (badges of status), just as in males, has received little attention. Recently, Langmore[5] reviewed evidence that female vocalizations are used frequently in intrasexual, and sometimes in intersexual, communication, but so far no study has tested whether females with more elaborate songs are superior in sexual competition.

Almost 20 years ago, West-Eberhard[19] argued that monomorphic showy plumage was associated with aggressive social displays (over territories or other resources) by both sexes. Her argument was supported by examples from several taxa including toucans, parrots and hummingbirds. West-Eberhard's suggestions resulted in surprisingly little empirical research in the following years. However, among published studies, most seem to support her view. In hummingbirds, females vary dramatically in conspicuousness both between and within species. Across species, female showiness is associated with defence by visual display of nectar-rich individual feeding territories during the nonbreeding season. In some species, immature nonbreeding females are more colourful than adults and defend feeding territories[27]. These findings support a nonsexual competitive function of female ornamentation. Among New World blackbirds (Icterinae), nonsexual female competition has been suggested to explain interspecific variation in female ornamentation[28].

Trail[29] contrasted monomorphic showy capuchinbirds (*Perissocephalus tricolor*) and dimorphic Guianan cock-of-the-rocks (*Rupicola rupicola*), and reported that only the capuchinbirds showed frequent female–female aggression, including courtship disruption. Courtship disruptions, and other aggressive means by which females determine access to mates, have been described in a variety of taxa[24]. Trail[29] argued that female aggression was generally absent among dimorphic lekkers, and that showy monomorphism among lekking species was a result of intense sexual competition in both sexes.

Studies addressing the competitive consequences of intraspecific variation in female colour are scarce, but some evidence now exists for pinyon jays (*Gymnorhinus cyanocephalus*)[30], red-winged blackbirds (*Agelaius phoeniceus*)[31] and crested auklets (*Aethia cristatella*)[13]. In captive pinyon jays, female head coloration has been shown to reflect dominance in competition for access to mates[30]. By contrast, Muma and Weatherhead exposed female red-winged blackbirds to same-sex mounts with colourful and dull epaulets and found no difference in aggressive response[31]. This does not support a competitive function of female showiness. However, the finding that female epaulet colour in red-winged blackbirds reflects condition is consistent with a status-signalling function[32]. Interestingly, females of Cuban populations are ornamented similarly to males and participate in year-round territorial defence against male and female intruders, whereas the duller North American females do not defend territories[33]. Based on a large set of observational data, Jones and Hunter[13] reported that crested auklet females with naturally large crests were superior in intrasexual agonistic interactions at the mating arenas. However, the finding is not completely conclusive because it was not confirmed when crest size was manipulated on taxidermic mounts and aggressive responses from live females were recorded.

Box 2. Female ornamentation: artefact or selection?

Female conspicuousness ('ornamentation') can be explained in two different ways: by selection on the females (either sexual or natural) or as an artefact of selection on males ('genetic correlation'):

Genetic correlation: conspicuous female traits have evolved as a genetically correlated response to selection on males[14] (sexual or natural). Because most of the genome is shared by the two sexes, females will inherit the genetic basis for ornamentation. The correlation can only be broken if consistent and strong selection acts to inhibit female trait expression. Such selection for sexual dimorphism is a slow process and, during intermediate evolutionary stages, females can therefore be expected to carry more or less 'rudimentary' or 'vestigial' versions of male traits. Not only might genetic correlations explain female 'ornaments'; even male choosiness might be a correlated effect of selection for choosiness in females[50].

Direct selection: selection (sexual or natural) directly favours conspicuous female traits, which might be important in relation to:

- Male mate choice: under certain circumstances, males are selective in their choice of breeding partners and females compete for the attention of the males. Sexual selection might then act on females in favour of elab orate secondary sexual traits, in exactly the same way as selection operates on males of many species.
- Female contest competition: If females compete for limited resources, selection can act in favour of conspic uous badges of status in competitive interactions. West-Eberhard[19] has termed this process 'social selection'. When the limited resource is male partners, female competition might lead to sexual selection for female ornamentation.

Genetic correlations and direct (sexual) selection are not mutually exclusive phenomena. Instead, vestigial trait expression resulting from genetic correlation might provide the starting point for further trait exaggeration through sexual selection. Moreover, if a genetic correlation exists, a male choosing a showy female partner might benefit from producing not only attractive daughters but also ornamented sons.
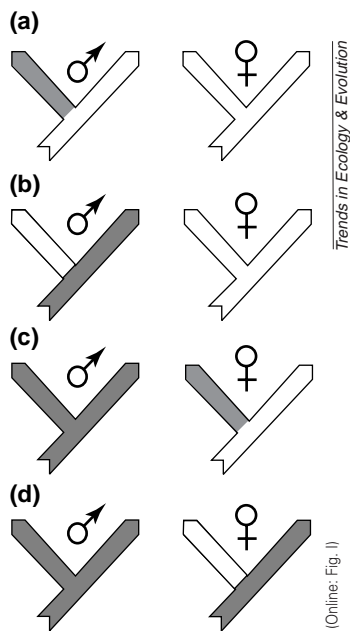
Box 3. Female ornaments: the comparative approach

(a)

(b)

(c)

(d)

(Online: Fig. I)

Simplified illustrations of four evolutionary scenarios resulting from selection on males (a, b) or females (c, d). Male and female phylogenies are the same and are separated only to emphasize sexual differences in character states (conspicuous, shaded bars; drab, open bars). Both represent two-species phylogenies with known ancestral states. (a) Sexual selection on males has produced male conspicuousness; (b) predation-generated natural selection on males has produced male crypsis; (c) sexual selection on females has produced female conspicuousness; and (d) predation-generated natural selection on females has produced female crypsis.

Two recent comparative studies have estimated the numbers of evolutionary transitions affecting male and female coloration in tanagers[12] and icterids[10], based on cytochrome *b* phylogenies.

Change in:	Tanagers[a]	Icterids[b]
Male, not female	**8**	**2**
Increase (Fig. Ia)	1	–
Decrease (Fig. Ib)	7	–
Female, not male	**16**	**10**
Increase (Fig. Ic)	13	–
Decrease (Fig. Id)	3	–
Male and female	**12**	**2**
Increase	3	–
Decrease	9	–

[a]Data taken from Table 1 in Ref. 12.
[b]Data taken from Table 2 in Ref. 10.

(Online: Table I)

The table reports the average number of transitions affecting one or both sexes. Numbers of transitions similar to the kinds described in the figure are mentioned specifically. In both taxa, dimorphism with drab females and showy males were found to be the ancestral state. Plumage changes were more frequent in females than males, and female changes were largely independent of male changes. In tanagers, most female changes were in the direction of a more showy plumage.

Together these studies show that female competition is important and there is suggestive evidence that female showiness plays a role. However, this field is still surprisingly unexplored empirically and any general conclusion would be premature.

Concealment of sex

Burley[34] has argued that members of species living in social groups during breeding can avoid sexual competition by concealing their sex. The benefit was hypothesized to be strongest for males because of their usually more intense intrasexual competition, selecting for male resemblance of females (drab monomorphism)[34], in particular among subordinates[35]. However, it is also possible that females of some species might avoid competition or male harassment by behaving as 'pseudomales'[29], selecting for conspicuous monomorphism. Burley's work on pigeons[34], and recent experiments on long-tailed finch (*Poephila acuticauda*)[35],

have demonstrated convincingly that males of some monomorphic species are unable to distinguish unfamiliar males from females based on visual appearance, but currently we have no evidence to tell if this is an effect or the cause of monomorphism. In case of the latter, the selection pressure would have been on the males not the females.

Mutual mate preferences

Theoreticians have long realized that mate choice can occur in both sexes, even in species with conventional sex roles[2,36]. Accordingly, male choice has received considerable attention in studies of fish, amphibia and invertebrates, mainly in relation to female fecundity. By contrast, male choice has been little studied in birds[2]. This taxonomic difference might be because female birds vary much less in fecundity than do females of taxa with indeterminate growth. However, few studies before 1990, in any taxa, have examined male choice for female ornamentation. In fact, many researchers have taken monomorphic showiness in fish and birds to indicate absence of sexual selection, instead of looking for mutual mate choice in such species. The view of mate choice traditionally communicated through empirical avian research has been that of eager males and coy females, or, in other words, of choosy females and indiscriminate males. However, there is no reason to expect that, if one sex is choosy, the other sex should be completely indiscriminate and accept all mating offers. Instead, various combinations of choosiness in the two sexes are possible, depending on the costs and benefits to each sex of being choosy[3,8]. When both sexes are choosy, mutual sexual selection might produce ornamental traits not only in the less choosy sex (normally males) but also in the choosier one (normally females).

Using verbal modelling based on Trivers' parental investment theory, Burley[37] had already suggested in 1977 that, when both sexes provide parental care, mutual choosiness should be expected. She argued that the sex investing more should be the more choosy, and that low quality individuals should be less discriminating than those of high quality[37]. Recent work emphasizes that it is not parental investment *per se* that matters, but rather the fact that parental care leads to a 'time-out' of sexual competition and, thus, influences the potential reproductive rate (PRR) of the sexes[38]. Together with the adult sex ratio, 'time-out' is the main factor determining the ratio of fertilizable females to sexually active males [the 'operational sex ratio' (OSR)][38]. The OSR largely determines which should be the competitive sex[39], but the extent to which it also applies to sex differences in choosiness is less straightforward.

As pointed out by Parker[36], costs and benefits of choice might change in concert, making effects on choosiness nontrivial. The PRR and the OSR affect the costs of rejecting a potential mating partner. The sex with the higher PRR will suffer the greater reduction in reproductive success from rejection, and, therefore, should be less choosy. Johnstone and co-workers[3] have argued that such costs of choice are the main determinants of choosiness. Concerning the benefits of choice, Owens and Thompson[8] have pointed out that the caring sex would vary both phenotypically and genetically, and hence be more variable overall. When mating rate and quality variation is similar for the two sexes, as in many monogamous birds with biparental care, both sexes should exhibit active choice[3,8]. In conclusion, choosiness should often be expected in both sexes, either at similar levels or with one sex (most often the female) being choosier than the other. Individuals of high

Table 1. Studies testing whether male birds prefer more ornamented females

Species	Ornamental trait	Field or aviary	Type of study	Response variable	N[a]	Result[b]	Refs
Crested auklet (*Aethia cristatella*)	Crest length	Field	Manipulative	Approach and display	333[c]	+	9, 13
Feral pigeon (*Columba livia*)	Colour morph	Aviary	Nonmanipulative[d]	Association and display	58	+	37
Lesser kestrel (*Falco naumanni*)	Rump and tail colour	Field	Nonmanipulative	Laying date	163	0	51
Barn swallow (*Hirundo rustica*)	Tail length	Field	Nonmanipulative	Mating date[e]	343	+	43
		Field	Manipulative	Laying date	46	0	44
Bluethroat (*Luscinia svecica*)	Throat colour	Aviary	Nonmanipulative	Association and display	20	+	11
Red-winged blackbird	Epaulet and	Aviary	Nonmanipulative	Association and display	18	0	31
(*Agelaius phoeniceus*)	chin colour	Field	Nonmanipulative	Laying date	87	+/0[f]	31
Blue tit (*Parus caeruleus*)	UV head colour	Aviary	Manipulative[g]	Association	6	+	52
House finch	Plumage colour	Aviary	Manipulative	Association	13	+	53
(*Carpodacus mexicanus*)		Field	Nonmanipulative	Laying date	169	0	53
Zebra finch (*Taeniopygia guttata*)	Beak colour	Aviary	Nonmanipulative	Association	36+28[h]	+/−[i]	41
Pinyon jay	Head colour	Aviary	Nonmanipulative	Courtship[j]	20[k]	0	30
(*Gymnorhinus cyanocephalus*)							

[a]For aviary studies, *N* refers to the number of trials conducted (each involving two to four females of varying ornamentation). For field studies, *N* normally refers to the number of females involved.
[b]+ indicates a significant preference; 0 indicates no statistically significant discrimination; − indicates negative preference.
[c]*N* refers to the total number of individuals approaching mounts with long or short crests (only a minority displayed).
[d]Complex design with various colour morphs as choosers and stimuli.
[e]Mating date not defined operationally; apparently different from laying date (as judged from Table 1).
[f]Significant positive relationship for epaulet colour, but not for chin colour.
[g]Preference for males with and without ultraviolet (UV) reflection, manipulated by means of UV-blocking filters.
[h]*N* refers to trials using two different stimulus set-ups. In each case, response males were re-used; thus, N overestimates the number of respondents.
[i]Male preference for intermediate (orange) over extreme (red or yellow) phenotypes.
[j]Includes displays and attempted feeding.
[k]26 trials, but only 20 male respondents (some males used two or more times).

Table 2. Studies testing for a relationship between ornamentation and quality in female birds

Species	Ornamental trait	Quality measure	Number of broods	Result	Refs
Lesser kestrel (*Falco naumanni*)	Rump colour	Nestlings fledged	142	0	51
	Tail colour	Nestlings fledged	122	0	51
Barn swallow (*Hirundo rustica*)	Tail length	Total fledged	343+212[a]	+	43
		Frequency of 2nd clutches	343	+	43
		Nestlings fledged	46	0	44
		Feeds per nestling	36	0	44
		Female proportion of feeds	36	0	44
Bluethroat (*Luscinia svecica*)	Throat colour	Body mass	54	+	11
		Tarsus length	56	+	11
		Feeds per nestling	13+14[b]	0	45
		Fledgling mass	32	0	45
		Feeding rate	28	0	46
		Feeding rate, male removed[c]	27	0	46
		Compensation for male care[c]	28	0	46
Pied flycatcher (*Ficedula hypoleuca*)	Forehead patch	Trypanosome infection	57	+	47
Northern cardinal (*Cardinalis cardinalis*)	Underwing colour	Feeding rate	17	0	42
		Feeds per nestling	17	+	42
		Female proportion of feeds	17	+	42
	Body colour	Feeding rate	17	0	42
		Female proportion of feeds	17	0	42
Red-winged blackbird (*Agelaius phoeniceus*)	Epaulet colour	Condition[d]	58	+	32
House finch (*Carpodacus mexicanus*)	Plumage colour	Condition	124	0	53
		Nestlings fledged	63	0	53
		Annual survival rate	176	0	53

[a]First and second clutches, respectively.
[b]Nestlings aged 7 and 8 days, respectively.
[c]Male removed temporarily.
[d]Coloration related to last year's condition.

quality should be choosier than those of poor quality, especially early in the breeding season[8,37].

With extensive biparental care in most species, birds are obvious candidates for mutual mate choice. The theoretical prediction that males should, sometimes, show mate preferences is now receiving empirical support. Monaghan and co-workers[40] supplied female zebra finches (*Taeniopygia guttata*) with food that enhanced their fecundity, and found that males preferred such females despite them being indistinguishable from control females to a human observer.

Do male birds, like females, discriminate between potential mates on the basis of ornamental traits? The answer seems to be yes, at least sometimes. The strongest evidence comes from experiments with crested auklets[9,13]. These small auks live in dense colonies and display at communal arenas located centrally in the colony. Manipulating crest size of male and female mounts, Jones and Hunter found that large-crested individuals of both sexes received more sexual interest and displays (from opposite-sex individuals) than those with small crests (Table 1). So far, this is the only study testing male preferences for female ornamentation in a bird species where both sexes are equally ornamented.

Mainly two kinds of study have been undertaken on species where females carry a less developed version of the male ornament (Table 1): controlled aviary mate choice trials and field studies recording indirect measures of mate choice (most typically the date of egg laying). The latter have not produced much evidence in favour of male ornament preferences (Table 1). However, male choice is probably of minor importance in determining the date of laying; such studies are therefore likely to have low power in detecting male preferences. Controlled mate choice experiments in aviaries have proved somewhat more promising (Table 1). In bluethroats (*Luscinia svecica*), a species where female plumage is highly variable and sometimes almost identical to that of a typical male, males associated more with, and performed more sexual displays towards, colourful than drab females[11]. Similar results have been found in house finches (*Carpodacus mexicanus*), but not in red-winged blackbirds and pinyon jays (Table 1). In zebra finches, males appear to have different beak colour preferences from females, being attracted most strongly to orange instead of red beaks[41].

Signalling content of female ornaments

Female ornaments, like those of males, might reflect phenotypic or genetic qualities. Among the few studies addressing this issue, most have focused on phenotypic qualities (Table 2). In northern cardinals (*Cardinalis cardinalis*), colourful females fed the nestlings more often than did drab ones[42]; the first evidence for the 'good parent process' of sexual selection in females. However, similar studies of barn swallows (*Hirundo rustica*)[43,44] and bluethroats[45,46] have been unable to find such effects. Several studies have analysed relationships between female ornamentation and fledging success (Table 2), but this parameter is strongly confounded by male care and is probably not very informative of female quality. More suggestive is the finding that female epaulet colour in red-winged blackbirds was influenced by condition in the previous year[32]. The condition-dependence of female ornaments is almost unstudied.

When it comes to genetic qualities, even less data exist. In pied flycatchers (*Ficedula hypoleuca*), females with a white forehead patch had fewer parasites than those lacking this trait[47]. This might suggest that female ornamentation reflects heritable parasite resistance, but alternative explanations cannot be ruled out. During the 1990s, several studies have demonstrated heritable variation for ornamental viability indicators in male birds, sometimes related to immunological capacity. Similar studies of females are needed; clarifying the relationship between individual quality and ornamentation is crucial to understanding female ornament evolution.

Priorities for future research

What do we know and what remains in the study of decorative female traits? Recent comparative studies provide strong evidence that female ornamentation is not severely constrained by selection on males. Thus, female visual showiness must be explained primarily with reference to selective processes affecting females directly. There is some suggestive evidence that female ornaments have a function both in female contest competition and in mate attraction. These two functions are not mutually exclusive[13]. Instead of assuming that female showiness is a result of either a genetic correlation or one specific selection pressure on females, researchers should consider how various selection pressures and genetic constraints together shape female appearance. It should be taken into account that, sometimes, mate and/or species recognition[48], predator avoidance and other forms of natural selection might select for conspicuousness; likewise, social selection might sometimes select for crypsis.

Most studies so far have been minor parts of larger projects related to sexual selection on males and have included relatively limited samples. There is now a need for larger research programmes specifically designed to explore the functions of female showiness. Such programmes should take advantage of recent methodological advances from studies of males, including molecular techniques. Studies of relatively monomorphic species might have the highest potential for producing positive results, but research should include the continuum of female ornament expression, from complete male-likeness to only vestigial ornamentation. It should also be investigated why female ornaments in birds are mostly similar to those of males. This poses no problem in the case of Fisherian sexual selection, but would perhaps not be expected from indicator models where essential qualities, and hence optimal signal design, might differ between the sexes. Is it possible that the presence of female ornaments is a result of selection, but that their exact form is constrained by a genetic correlation?

What ecological and social conditions favour the evolution of female showiness? Theoreticians and comparative empiricists need to combine their efforts in further clarifying this issue. Comparative work should analyse the relationship between showiness and social and ecological characteristics, such as parental care, mating system, territoriality, social structure, migratory behaviour, habitat and predation.

Current knowledge from certain avian model systems now allows researchers to ask quite specific questions related to female ornaments, for instance, on relationships between ornamentation and individual quality. At the same time, it should be acknowledged that female visual showiness is almost unexplored in most taxa apart from birds. Future studies of nonavian species have great potential to provide exciting insights into the evolution of female ornamentation.

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