

Sexual dimorphism in birds: why are there so many different forms of dimorphism?

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Variation in the extent of sexual dimorphism among bird species is traditionally attributed to differences in social mating system. However, there are many different forms of dimorphism among birds, and not all of them show an obvious correlation with social mating system. For example, recent work has shown that many highly polygamous species are, in fact, monomorphic, whereas many putatively monogamous species are dimorphic. In this paper we break up sexual dimorphism into subcomponents and then use comparative analyses to examine the pattern of covariation between these subcomponents and various aspects of sexual, social, and parental behaviour. Our first finding is that size dimorphism and plumage-colour dimorphism do not show the same pattern of covariation. Differences in size dimorphism are associated with variation in social mating system and sex differences in parental care, whereas differences in plumage-colour dimorphism are associated with variation in the frequency of extra-bond paternity. These results suggest that size dimorphism is associated with the sort of intrasexual competition described by traditional classifications of social mating system, whereas plumage-colour dimorphism is associated with cryptic female choice. However, when we break up plumage-colour dimorphism according to whether it is due to melanins, carotenoids or structural colours, we find that each category of plumage-colour dimorphism shows a different pattern of covariation. The correlation between overall plumage-colour dimorphism and the rate of extra-bond paternity is due to structural colours, whereas melanin-based dimorphism is associated with sex differences in parental care. The former result is particularly interesting given that new work suggests structural colours are associated with active sexual displays and the reflection of ultraviolet light.

Keywords: sexual dimorphism; size dimorphism; plumage dimorphism; mating system; parental care; extra-bond paternity; sexual selection

1. INTRODUCTION

In the European swift, *Apus apus*, the sexes are so similar that they appear almost identical, whereas in the mallard, *Anas platyrhynchos*, the sexes are so dissimilar that they were initially classified as different species (Andersson 1994, p. 3). Even more strikingly, sexual dimorphism can take a huge variety of forms: male and female corn buntings, *Miliaria calandra*, have nearly identical plumages but males are commonly 40% heavier than females; male and female superb fairy-wrens, *Malurus cyaneus*, are similar sizes but the iridescent blue plumage of the males is unlike anything found among females; and red-winged blackbirds, *Agelaius phoeniceus*, are a striking integration of both size and plumage dimorphism. Why is there so much variation among bird species in both the extent, and the form, of sexual dimorphism?

The traditional explanation for variation in the extent of sexual dimorphism is that it is a consequence of variation among species in social mating system and the pattern of parental care (from Darwin (1871) and Wallace (1889) onwards; reviewed in Butcher & Rohwer (1989) and Andersson (1994)). For example, polygamy leads to the

competitive sex being larger and more ornate than the choosy sex, whereas large differences between the sexes in parental care lead to the caring sex developing more cryptic plumage. Recently, however, two observations have challenged this traditional view. First, many extremely polygamous species in which one sex cares for the offspring alone are, in fact, largely monomorphic with respect to both size and plumage colour (Höglund 1989; Trail 1990; but see Oakes 1992). But even more strikingly, many apparently monogamous species that display classic biparental care are, in fact, highly dimorphic (Møller 1986; Harvey & Bradbury 1991). An exciting explanation for these iconoclastic observations is that the traditional classification of social mating system is not always a good index of sexual selection. This idea is based on the fact that molecular techniques for assigning true genetic parentage have revealed extra-bond fertilizations in approximately 65% of socially monogamous species studied (table 1: 8/19 non-passerine and 14/15 passerine species). For instance, Sheldon & Burke (1994) found that 17% of offspring from socially monogamous pairs of chaffinches, *Fringilla coelebs*, were fathered by males other than the putative father. If these copulations are distributed non-randomly, they should lead to sexual selection. Could the reason for chaffinches being so dimorphic be that females prefer 'showy' males when it comes to extra-pair sex?

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Table 1. *Species-specific data on subcomponents of dimorphism and social, sexual, and parental behaviours*

species	size dimorphism		plumage-colour dimorphism				social and sexual behaviour			sex-bias in parental care				references ⁿ
	FW ^a	SD ^b	O ^c	C ^d	M ^e	S ^f	MS ^g	EBO ^h	EBB ⁱ	I ^j	F ^k	P ^l	A ^m	
<i>Lagopus lagopus</i>	620.0	1	4	0	5	0	0	9.4	13.2	3	1	2	0	1
<i>Tetrao tetrix</i>	980.0	3	9	0	3	0	3	0.0	0.0	3	3	3	3	2
<i>Branta leucopsis</i>	1619.0	1	0	0	0	0	0	0.0	0.0	3	0	0	3	3
<i>Hymenolaimus malachorhynchus</i>	750.0	2	1	0	1	0	0	0.0	0.0	3	2	2	0	4
<i>Melanerpes formicivorus</i>	39.0	2	1	1	1	0	2	0.0	0.0	1	1	1	0	5
<i>Picoides borealis</i>	45.3	1	1	1	0	0	0	1.0	2.3	0	1	0	0	6
<i>Merops apiaster</i>	54.4	0	2	0	0	2	1	1.0	5.3	1	0	0	0	7
<i>Apus apus</i>	40.0	1	0	0	0	0	0	4.5	9.5	0	0	0	0	8
<i>Columba livia</i>	305.0	2	0	0	0	0	0	0.0	0.0	0	0	0	0	9
<i>Gallinula chloropus</i>	338.0	0	1	0	0	0	0	0.0	0.0	0	0	0	0	10
<i>G. mortierii</i>	1251.0	1	0	0	0	0	2	0.0	0.0	0	0	0	0	11
<i>Porphyrio porphyrio</i>	724.0	2	0	0	0	0	2	0.0	0.0	1	0	0	0	12
<i>Tringa macularius</i>	47.2	4	2	0	2	0	2	10.8	20.6	2	2	2	2	13
<i>Haematopus ostralegus</i>	516.0	0	0	0	0	0	0	1.5	3.9	1	0	0	0	14
<i>Charadrius morinellus</i>	117.0	2	3	0	3	0	2	4.6	9.1	2	2	2	2	15
<i>Catharacta longbergi</i>	1735.0	1	0	0	0	0	2	0.0	0.0	1	1	2	2	16
<i>Aethia pusilla</i>	118.0	1	0	0	0	0	0	0.0	0.0	0	0	0	0	17
<i>A. pygmaea</i>	79.4	0	0	0	0	0	0	11.0	11.1	0	0	0	0	17
<i>Coragyps astratus</i>	2172.0	1	0	0	0	0	0	0.0	0.0	0	0	0	0	18
<i>Buteo galapagoensis</i>	1357.0	5	0	0	0	0	1	0.0	0.0	2	2	0	0	19
<i>Falco columbarius</i>	212.0	3	4	0	4	0	0	0.0	0.0	2	2	2	1	20
<i>F. eleonorae</i>	388.0	1	0	0	0	0	0	0.0	0.0	2	2	2	1	21
<i>F. naumanni</i>	173.0	3	6	0	4	0	0	3.4	3.8	1	2	1	0	22
<i>F. tinnunculus</i>	193.0	2	6	0	4	0	1	1.9	2.7	2	2	3	0	23
<i>Phalacrocorax aristotelis</i>	1598.0	2	0	0	0	0	1	18.0	20.0	0	0	0	0	24
<i>Pygoscellis adeliae</i>	5400.0	1	0	0	0	0	0	3.0	2.2	0	0	0	0	17
<i>Eudiptula sclateri</i>	5434.0	2	0	0	0	0	0	3.9	7.7	0	0	0	0	17
<i>Fulmarus glacialis</i>	706.0	2	0	0	0	0	0	0.0	0.0	0	0	0	0	25
<i>Puffinus diomedea</i>	887.0	1	0	0	0	0	0	0.0	0.0	0	0	0	0	26
<i>P. tenuirostris</i>	528.0	1	0	0	0	0	0	11.0	10.8	0	0	0	0	27
<i>Oceanodroma leucorhoa</i>	44.9	0	0	0	0	0	0	0.0	0.0	0	0	0	0	28
<i>Malurus cyaneus</i>	9.0	2	8	0	3	8	2	76.0	95.0	3	2	3	0	29
<i>Lanius bucephalus</i>	33.0	0	4	0	4	0	0	10.0	17.0	2	1	1	1	30
<i>L. collurio</i>	31.7	1	4	0	4	0	1	5.2	16.6	3	2	3	0	31
<i>Corvus monedula</i>	243.0	1	0	0	0	0	1	0.0	0.0	3	1	1	1	32
<i>Sialia sialis</i>	31.9	1	4	0	0	4	0	8.4	24.0	3	1	2	0	33
<i>Erithacus rubecula</i>	19.9	0	1	0	1	0	0	4.0	12.5	3	1	3	0	34
<i>Luscinia svecica</i>	18.3	0	4	0	1	4	1	20.0	35.5	1	0	1	0	35
<i>Ficedula albicollis</i>	14.5	0	4	0	4	0	2	15.0	32.9	3	0	3	0	36
<i>F. hypoleuca</i>	13.0	0	4	0	4	0	2	4.0	15.0	3	0	3	0	37
	13.0	0	4	0	4	0	2	24.0	43.0	3	0	3	0	38
<i>Sturnus vulgaris</i>	76.0	1	3	0	0	4	1	9.7	28.6	3	1	2	0	39
	76.0	1	3	0	0	4	1	8.7	31.8	3	1	2	0	40
<i>Campylorhynchus griseus</i>	—	—	0	0	0	0	2	2.3	3.0	3	2	2	0	41
<i>C. nuchalis</i>	—	—	0	0	0	0	3	10.0	22.7	2	0	0	1	42
<i>Parus atricapillus</i>	11.4	0	0	0	0	0	1	17.0	37.5	2	0	2	0	43
<i>P. caeruleus</i>	11.4	1	1	0	1	0	1	11.0	31.0	3	0	3	1	44
	11.4	1	1	0	1	0	1	6.0	28.6	3	0	3	1	45
<i>P. major</i>	17.9	1	2	0	1	0	0	15.0	50.0	3	1	3	0	45
<i>Psaltriparus minimus</i>	5.4	0	1	0	1	0	2	0.0	0.0	1	0	0	0	46
<i>Delichon urbica</i>	19.7	0	0	0	0	0	0	14.5	32.0	0	0	1	0	47
	19.7	0	0	0	0	0	0	19.0	35.0	0	0	1	0	48
<i>Progne subis</i>	54.5	0	3	0	2	3	1	23.9	50.0	3	1	3	1	49
	54.5	0	3	0	2	3	1	18.8	24.4	3	1	3	1	50
<i>Hirundo rustica</i>	18.6	0	0	0	0	0	0	22.2	45.5	2	1	0	0	51
	18.6	0	0	0	0	0	0	30.0	56.0	2	1	0	0	52
<i>Tachycineta bicolor</i>	20.7	1	5	0	2	5	2	51.5	71.4	3	1	3	1	53
	20.7	1	5	0	2	5	2	68.5	84.0	3	1	3	1	54, 55

continued

Table 1 (continued)

species	size dimorphism		plumage-colour dimorphism				social and sexual behaviour			sex-bias in parental care				references ⁿ
	FW ^a	SD ^b	O ^c	C ^d	M ^e	S ^f	MS ^g	EBO ^h	EBB ⁱ	I ^j	F ^k	P ^l	A ^m	
<i>Zosterops lateralis</i>	13.0	0	0	0	0	0	0	0.0	0.0	0	0	0	0	56
<i>Acrocephalus arundinaceus</i>	28.4	1	0	0	0	0	2	3.1	5.4	3	0	2	0	57
<i>A. palaudicola</i>	10.8	1	0	0	0	0	2	36.0	50.0	3	3	3	3	58
<i>A. vaughani</i>	22.8	1	0	0	0	0	1	6.9	15.4	1	0	1	0	59
<i>Phylloscopus sibilatrix</i>	8.9	0	0	0	0	0	1	0.0	0.0	3	0	3	0	60
<i>P. trochilus</i>	9.1	0	0	0	0	0	1	0.0	0.0	3	0	3	1	60
<i>Passer domesticus</i>	28.5	0	4	0	3	0	2	14.0	26.1	1	0	0	0	61
<i>Prunella collaris</i>	36.1	1	2	0	2	0	2	0.0	0.0	3	1	3	0	62
<i>P. modularis</i>	21.1	0	2	0	2	0	2	1.0	2.2	3	1	3	0	63
<i>Taeniopygia guttata</i>	11.7	0	4	0	4	0	0	2.4	8.0	1	1	1	0	64
<i>Fringilla coelebs</i>	22.0	1	6	2	3	0	0	17.0	23.0	3	1	3	0	65
<i>Carpodacus mexicanus</i>	22.1	0	6	6	0	0	0	8.3	14.3	3	1	3	0	66
<i>Miliaria calandra</i>	39.6	4	0	0	0	0	2	0.0	0.0	3	2	3	2	67
<i>Emberiza citrinella</i>	27.4	1	5	3	3	0	0	37.0	69.0	2	2	2	1	68
<i>E. schoeniclus</i>	18.3	1	5	0	3	0	1	55.0	86.0	2	2	3	0	69
<i>Calcarius pictus</i>	24.3	2	3	0	2	0	2	0.0	0.0	3	0	2	0	70
<i>Passerculus sandwichensis</i>	16.4	1	0	0	0	0	2	25.0	57.1	3	1	3	1	71
<i>Dendroica petechia</i>	9.2	1	3	2	0	0	0	37.0	59.0	2	1	2	1	72
<i>Wilsonia citrina</i>	10.1	1	1	0	1	0	0	29.0	32.0	3	0	2	0	73
<i>Cardinalis cardinalis</i>	43.9	0	5	5	1	0	0	14.0	16.0	3	2	2	1	74
<i>Passerina cyanea</i>	14.4	0	10	0	5	10	0	35.0	48.0	3	2	3	2	75
<i>Agelaius phoeniceus</i>	41.5	5	9	2	4	9	3	23.7	41.0	3	3	3	1	76
	41.5	5	9	2	4	9	3	28.0	47.0	3	3	3	1	77
	41.5	5	9	2	4	9	3	35.0	55.0	3	3	3	1	78
	41.5	5	9	2	4	9	3	25.1	38.5	3	3	3	1	79

^aFemale body weight. ^bSize dimorphism. ^cOverall plumage-colour dimorphism. ^dPlumage-colour dimorphism due to carotenoids. ^ePlumage-colour dimorphism due to melanin. ^fPlumage-colour dimorphism due to structural colours. ^gSocial mating system. ^hExtra-bond paternity in terms of offspring. ⁱExtra-bond paternity in terms of broods. ^jIncubation. ^kBrood-provisioning. ^lPassive brood-defence. ^mActive brood-defence.

ⁿReferences for data on rates of extra-bond paternity. 1. Freeland *et al.* (1995); 2. Alatalo *et al.* (1996); 3. Larsson *et al.* (1995); 4. Triggs *et al.* (1991); 5. Dickinson *et al.* (1995); 6. Haig *et al.* (1994); 7. Jones *et al.* (1991); 8. J. Blakey, personal communication; 9. Lovell-Mansbridge (1995); 10. McRae & Burke (1996); 11. Gibbs *et al.* (1994); 12. Jamieson *et al.* (1994); 13. Oring *et al.* (1992); 14. Heg *et al.* (1993); 15. Owens *et al.* (1995); 16. Millar *et al.* (1994); 17. F. M. Hunter & I. R. Hartley, personal communication; 18. Decker *et al.* (1993); 19. Faaborg *et al.* (1995); 20. Warkentin *et al.* (1994); 21. Swatschek *et al.* (1993); 22. Negro *et al.* (1996); 23. Korpimäki *et al.* (1996); 24. Graves *et al.* (1992); 25. Hunter *et al.* (1992); 26. Swatschek *et al.* (1994); 27. Austad & Parkin (1996); 28. Mauck *et al.* 1995; 29. Mulder *et al.* 1994; 30. Yamagishi *et al.* 1992; 31. Fornasari *et al.* 1994; 32. I. Henderson, personal communication; 33. Meek *et al.* (1994); 34. J. Tobias & I. R. Hartley, personal communication; 35. Krokene *et al.* (1996); 36. B. C. Sheldon, personal communication; 37. Lifjeld *et al.* (1991); 38. Gelter & Tegelstrom (1992); 39. Pinxton *et al.* (1993); 40. Smith & von Schantz (1993); 41. Haydock *et al.* (1996); 42. Piper *et al.* (1995); 43. Otter *et al.* (1994); 44. Kempnaers *et al.* (1992); 45. Gullberg *et al.* (1992); 46. Bruce *et al.* (1996); 47. Riley *et al.* (1995); 48. Whittingham & Lifjeld (1995); 49. Morton *et al.* (1990); 50. Wagner *et al.* (1996); 51. Smith *et al.* (1991); 52. Primmer *et al.* (1995); 53. Lifjeld *et al.* (1993); 54. Dunn & Robertson (1993); 55. Dunn *et al.* (1994); 56. Robertson (1996); 57. Hasselquist *et al.* (1995); 58. Schuze-Hagen *et al.* (1993); 59. Brooke & Hartley (1995); 60. Gyllensten *et al.* (1990); 61. Wetton & Parkin (1991); 62. Hartley *et al.* (1995); 63. Burke *et al.* (1989); 64. Birkhead *et al.* (1990); 65. Sheldon & Burke (1994); 66. Hill *et al.* (1994); 67. Hartley *et al.* (1993); 68. Sundberg & Dixon (1996); 69. Dixon *et al.* (1994); 70. J. V. Briskie & R. Montgomerie, personal communication; 71. Wheelwright & Rising (1993); 72. Yezzerinac *et al.* (1995); 73. Stutchbury *et al.* (1994); 74. Richison *et al.* (1994); 75. Westneat (1990); 76. Westneat (1993); 77. Gibbs *et al.* (1990); 78. Grey (1996), personal communication; 79. Westneat (1995).

The idea that extra-bond paternity has a significant influence on sexual dimorphism recently gained support from a comparative study by Møller & Birkhead (1994). They demonstrated that the extent of extra-bond paternity in birds is correlated with the degree of sexual dimorphism in plumage brightness. In this paper we extend this work in three directions. First, we investigate dimorphism in terms of size, as well as in terms of plumage colour. Second, we examine previously neglected explanatory variables, such as the extent of sex bias in parental care. Finally, we break up plumage-colour dimorphism into

three subcomponents: dimorphism due to differences in melanin pigmentation; dimorphism due to carotenoid-derived pigmentation; and dimorphism due to structural colours. Our ultimate aim is to understand not only variation in the extent of dimorphism but also variation in the form of dimorphism.

2. DATA COLLECTION

We collated data on 73 bird species (83 populations; table 1). Our criterion for inclusion was whether we could

find data on the extent of extra-bond paternity, as shown by DNA fingerprint analysis. Using these data we tested for associations between variation in several components of sexual dimorphism and variation in indices of sexual, parental, and social behaviour. Initially, sexual dimorphism was simply split into size dimorphism and overall plumage-colour dimorphism. Subsequently, however, overall plumage-colour dimorphism was split into three subcomponents: dimorphism due to melanin-based pigmentation, dimorphism due to carotenoid-derived pigmentation, and dimorphism due to structural colours. Social and sexual behaviour were split into social mating system, frequency of extra-bond paternity in terms of young, and frequency of extra-bond paternity in terms of broods. Sex differences in parental behaviour were partitioned into incubation, brood provisioning, passive brood defence and active brood defence. Throughout, we recorded dimorphism *per se*, rather than scoring each sex separately and then comparing the scores. This was because measures of dimorphism simply required the observer to record the extent of difference between the sexes rather than make a subjective judgement of which sex is, for example, 'brighter' than the other. True plumage 'brightness' is the result of an interaction between (i) the reflectance spectrum of the plumage colour; (ii) the wavelength spectrum of the light environment(s); (iii) the spectral sensitivity of the natural observer; and (iv) the reflectance spectrum of the background(s) against which the plumage is seen (J. Marshall, personal communication; Owens & Bennett 1994). Nevertheless, measuring dimorphism *per se* does have the weakness that it cannot be used to test theories that predict, for example, that large female size is due to selection for increased fecundity whereas large male size is due to selection for increased competitiveness.

We used a six-point scale as an index of size dimorphism: 0, sexes of identical weight or the larger sex less than 5% heavier than the smaller sex; 1, the larger sex between 5% and 15% heavier than the smaller sex; 2, the larger sex between 15% and 25% heavier than the smaller sex; 3, the larger sex between 25% and 35% heavier than the smaller sex; 4, the larger sex between 35% and 45% heavier than the smaller sex; and 5, the larger sex between 45% and 55% heavier than the smaller sex. In species where the body weight of one or both sexes varied greatly through the season, we used weights from the beginning of the mating period wherever possible.

Overall sexual dimorphism in plumage colour was measured on a scale from zero (monomorphic) to ten (maximum dimorphism) (Owens & Bennett 1994). Total dimorphism scores were the sums of scores from five body regions (head; nape, back and rump; throat, chest and belly; tail; and wings), where each body region was scored separately: 0, no difference in colour, intensity or pattern between the sexes; 1, difference between the sexes only in shade or intensity of colour; and 2, difference in colour or pattern between the sexes. This scoring was done by three naive observers.

The extent of plumage-colour dimorphism due to melanins, carotenoids and structural colours, respectively, was estimated using a scale similar to that used for overall plumage dimorphism. For each subcomponent of plumage dimorphism, each species was scored for each of

the five body regions: 0, no difference in that body region; 1, no difference in the basis of the colour but a difference in the intensity of the colour (e.g. the same carotenoid-derived pigment is present in both sexes but at different hues); and 2, difference in the overall basis of the colour (e.g. structural colour present in one sex but not the other, or carotenoid-based colour in one sex but a mixture of carotenoids and melanins in the other). The scores from the five body zones were then summed to give an overall dimorphism score for each subcomponent of plumage dimorphism from zero (monomorphic) to ten (maximum dimorphism). We followed Voitkevich (1966) for initial diagnosis of the basis of plumage colours (see also Gray 1996). Namely, we predicted that bright yellows, oranges, reds and greens were due to carotenoid-based pigments; that blacks, browns, greys and dull reds were due to melanin-based pigments; and that iridescent blue, black, purple and green were due to structural colours. However, we checked these initial diagnoses by using a subspectrometer to quantify the reflectance spectrum of colours, which confirmed our initial predictions in all cases.

Our first index of social and sexual behaviours was the traditional classification of mating systems based on the social bonds that can be observed in the field (Møller 1986; Davies 1991). We assume that the potential for sexual selection increases with an increasing frequency of polygamy. Hence, we scored mating system on a four point scale: 0, polygamy not recorded or exceedingly rare (less than 1% of bonds of either sex); 1, occasional, facultative polygamy (between 1 and 5% of bonds of one or both sexes); 2, frequent facultative polygamy (more than 5% of bonds of one or both sexes, but not obligate); and 3, obligate polygamy in one or both sexes.

Our second two indices of social and sexual behaviours were the frequency of extra-bond paternity in terms of young, and the corresponding frequency of extra-bond paternity in terms of broods. We assume that the potential for sexual selection increases with an increase in the frequency of extra-bond fertilizations. We defined 'extra-bond paternity' as those fertilizations resulting from copulations outside the bonds considered by the traditional mating system classification. Hence, in monogamous species extra-bond fertilizations are any fertilization not by the single putative father, whereas in species displaying cooperative polyandry extra-bond fertilizations must be from outside the social group. The frequency of extra-bond fertilizations was measured at the population level. Where the extent of extra-bond paternity had been estimated in more than one population of the same species, we used the mean value of the population-specific rates. An obvious concern with the available data on the rate of extra-bond paternity is whether they really represent 'species-typical data'. The present data are, however, encouraging in this respect: among the eight species for which there are estimates of the rate of extra-bond paternity from more than one population (table 1), there is a significant positive correlation between the rate of extra-bond paternity found in one population and the rate found in the other (figure 1: $r=0.88$, $n=8$, $p<0.01$). (In the case of the red-winged blackbird, for which there are four estimates of the rate of extra-bond paternity, we chose the two most dissimilar

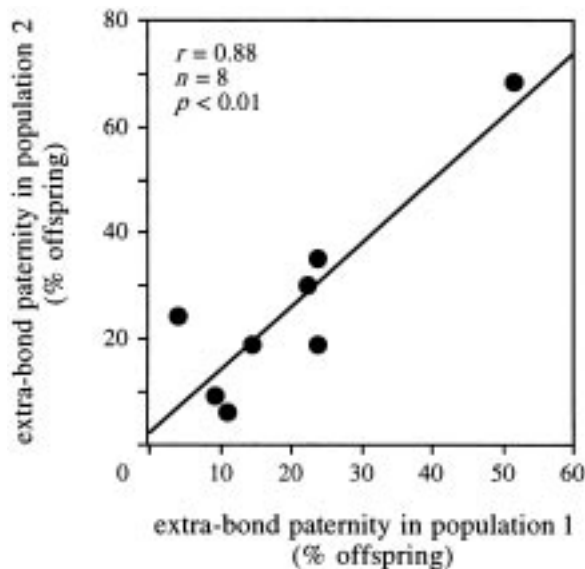


Figure 1. Correlation between the rates of extra-bond paternity found in different populations of the same species (see table 1 for species and data). Studies were randomly assigned to population 1 and population 2. r refers to linear correlation coefficient, n refers to sample size, and p refers to the associated two-tailed probability.

estimates.) Nevertheless, more data are required to test this assumption properly.

Parental care was divided into four components based on Cramp & Simmons's (1977) criteria: incubation behaviour; brood-provisioning behaviour; passive brood defence; and active brood defence. The extent of sex bias in the provision of the four forms of parental care were scored on a four point scale (see Owens & Bennett 1994, 1997): 0, both sexes usually contribute approximately equal amounts of care; 1, both sexes usually care but frequently, or always, one sex provides more care than does the other; 2, one sex usually cares alone but occasionally the other sex provides some care; and 3, only one sex cares.

In addition to the references cited in table 1 our data were from King *et al.* (1975), Cramp & Simmons (1977, 1980, 1983), the National Geographic Society (1983), Bennett (1986), Cramp (1985, 1988, 1992), Simpson & Day (1986), Marchant & Higgins (1991, 1994), Cramp & Perrins (1993, 1994a,b) Brunning (1993) and the series on the Birds of North America edited by Poole & Gill (Poole & Gill 1993).

3. STATISTICAL ANALYSES

Our analyses were divided into two groups: those looking at size and overall plumage-colour dimorphism, and those looking at the three subcomponents of plumage-colour dimorphism. When looking at size and overall plumage-colour dimorphism, our first step was to examine and analyse the raw data. We used two-tailed Kendall rank-order correlation coefficient tests (Siegel & Castellan 1988) to look for associations between each form of dimorphism and the various indices of social, sexual, and parental behaviour. However, because closely related species are not statistically independent (see

Harvey & Pagel 1991), we also performed a series of analyses based on the independent comparisons method (Felsenstein 1985), which identifies evolutionarily independent comparisons, or 'contrasts' (Pagel 1992), and can be easily implemented using the 'CAIC' software package (Purvis & Rambaut 1995). Because all our measures of dimorphism were ranked scales we used CAIC's BRUNCH algorithm to (i) identify the minimum set of nodes at which change needs to have occurred to account for the observed variation in the dependent variable, and (ii) calculate the amount of change that occurred at each of the nodes in this minimum set only. We assumed a phylogenetic topology based on Sibley & Ahlquist's (1990) 'tapestry phylogeny' above the family level and assumed multiple branching among genera within families, and among species within genera, with all branch lengths set to equal length. We then used two-tailed Kendall rank-order correlation coefficient tests to look for associations between changes in dimorphism and changes in behaviour. We checked these two-way analyses using the Kendall partial rank-order correlation coefficient (Siegel & Castellan 1988).

In our analyses of the three subcomponents of plumage dimorphism we again used CAIC's BRUNCH algorithm to identify a minimum set of evolutionarily independent changes in each subcomponent and calculate the associated changes in each behaviour at each of the nodes in this minimum set. Here, however, we used two-tailed Wilcoxon signed-rank tests (Siegel & Castellan 1988) to test the null hypothesis that, at nodes where the subcomponent of plumage dimorphism increased, it was equally likely that the index of behaviour would either increase or decrease. The null hypothesis would be rejected if the index of behaviour tended to either increase, or decrease, more often than expected by chance.

4. RESULTS

Our analyses of the raw data on size dimorphism and overall plumage-colour dimorphism suggest that these two variables show very different patterns of covariation with behaviour (figure 2). Variation in size dimorphism is significantly positively associated with variation in social mating system (figure 2a) and variation in the extent of sex bias in brood provisioning (figure 2b) and active brood defence ($\tau=0.15$, $n=71$, $p=0.05$), but was not significantly associated with variation in the frequency of extra-bond offspring (figure 2c), incubation behaviour ($\tau=0.01$, $n=71$, $p>0.90$) or passive brood defence ($\tau=0.02$, $n=71$, $p>0.75$). Conversely, variation in plumage-colour dimorphism is significantly positively associated with variation in the frequency of extra-bond paternity (figure 2f) and the extent of sex bias in brood provisioning (figure 2e), incubation ($\tau=0.37$, $n=73$, $p<0.001$) and passive brood defence ($\tau=0.46$, $n=73$, $p<0.001$), but not significantly associated with variation in social mating system (figure 2d) or variation in the extent of sex bias in active brood defence ($\tau=0.10$, $n=73$, $p>0.20$).

Our analyses using the independent comparisons method largely confirmed those based on the raw data. Changes in size dimorphism were significantly positively associated with changes in social mating system and changes in the extent of sex bias in brood provisioning

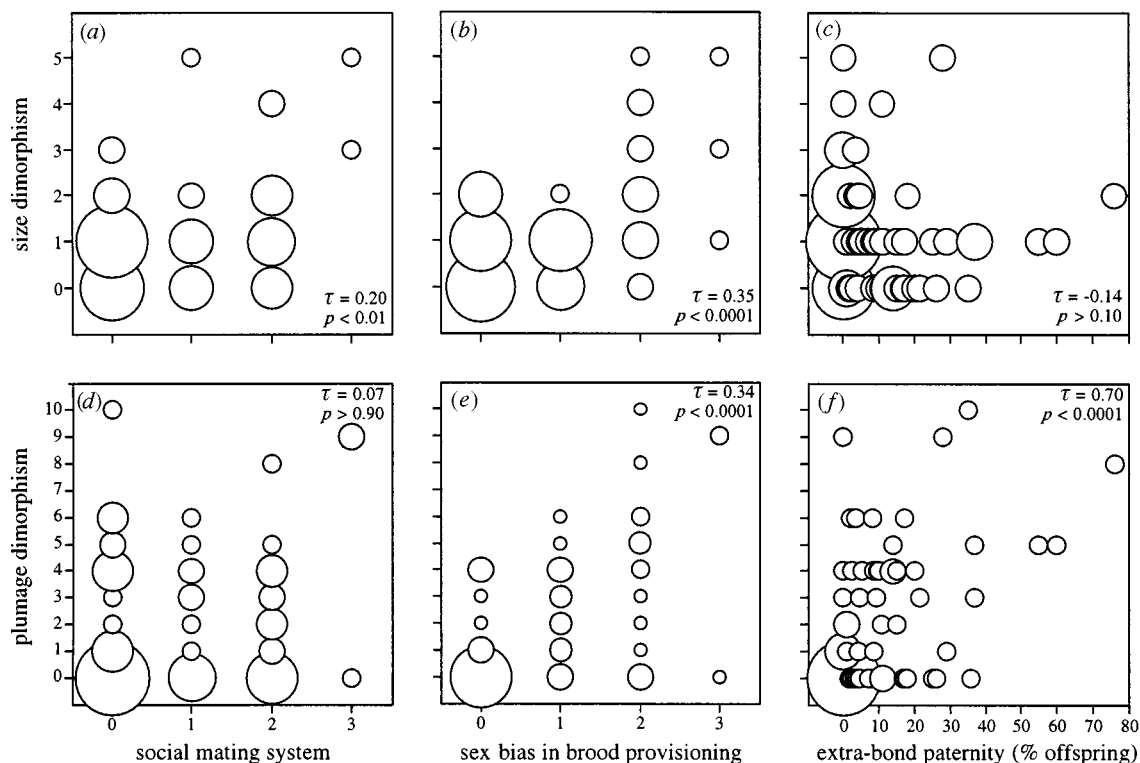


Figure 2. Associations between two measures of sexual dimorphism and three measures of social, sexual and parental behaviour, based on raw data. Area of dots is proportional to the number of overlapping data points, with the smallest dot size representing one data point in each case. Values of τ refer to Kendall rank-order correlation coefficient tests and p values are associated two-tailed probabilities. For analyses of size dimorphism and plumage dimorphism the sample sizes are 71 and 73, respectively. Variables are described in the text.

and active brood defence (table 2a). However, when we used a multivariate test the only one of these relationships that was significant was the relationship between size dimorphism and mating system (partial $\tau=0.33$, $n=26$, $p<0.05$). Changes in size dimorphism were not significantly associated with changes in female body size, the extent of sex bias in other components of parental care, or the extent of extra-bond paternity (table 2a). By contrast, changes in overall plumage-colour dimorphism were associated significant increases in the frequency of extra-bond young (table 2b). Changes in overall plumage colour dimorphism were, however, not correlated with changes in mating system, nor with changes in the extent of sex-bias in any component of parental care (table 2b), even when we controlled for the effects of variation in the rate of extra-bond offspring (partial $\tau<0.19$, $p>0.10$).

The results of our analyses of the three subcomponents of plumage dimorphism are shown in table 3. Increases in the extent of melanin-based dimorphism are associated with significant increases in the extent of sex bias in passive brood defence (table 3a), and increases in the extent of structurally based plumage dimorphism are associated with significant increases in the frequency of extra-bond young (table 3c). Changes in the extent of melanin-based dimorphism and structurally based dimorphism are not, however, associated with significant changes in any of the other independent variables and changes in the extent of carotenoid-based dimorphism are not associated with significant changes in any of the independent variables. However, the statistical power of these tests is weak and

accepted null hypotheses should therefore be treated with caution, particularly in the case of carotenoid-based dimorphism.

5. DISCUSSION

We found that sexual dimorphism in size and plumage colour are correlated with different aspects of reproductive and social behaviour in birds. Large size dimorphism is associated with high levels of social polygamy and big sex differences in the provision of parental care; striking plumage-colour dimorphism, on the other hand, is associated with high levels of extra-bond paternity.

Our finding that extensive size dimorphism is associated with social polygamy and large differences between the sexes in parental care agrees with the traditional explanation of size dimorphism based on intrasexual competition, and Webster's (1992) careful analysis of the New World blackbirds (Icterinae) but is contrary to the conclusions of Björklund (1990). In a detailed phylogenetic analysis within the finches (Fringillidae) and buntings (Emberizidae), Björklund found that size dimorphism was only correlated with mating system before the effects of body size were removed. Once he accounted for the fact that polygamous species were significantly larger than monogamous species this correlation was not statistically significant. However, given that our analyses differ from Björklund's in the taxonomic range of species examined, the manner in which size dimorphism and mating system were measured, and the method of

Table 2. Associations between two components of sexual dimorphism and various indices of social, sexual and parental behaviour, controlling for the effects of phylogeny

(Values of τ refer to two-tailed Kendall rank-order correlation coefficient tests of the null hypothesis that changes in dimorphism are not associated with changes in the independent variable. All tests are based on independent contrast scores resulting from CAIC analysis.)

independent variable	(a) size dimorphism ($n=26$)		(b) plumage-colour dimorphism ($n=19$)	
	τ	p value	τ	p value
female weight	-0.10	>0.25	—	—
mating system	0.37	<0.01	0.19	>0.25
frequency of extra-bond young	-0.09	>0.50	0.45	<0.01
frequency of extra-bond broods	-0.10	>0.25	0.40	<0.01
sex bias in incubation	-0.01	>0.90	-0.04	>0.75
sex bias in brood provisioning	0.30	<0.05	0.03	>0.75
sex bias in passive brood defence	0.05	>0.50	0.17	>0.25
sex bias in active brood defence	0.27	<0.05	0.22	>0.10

Table 3. Associations between three subcomponents of plumage-colour dimorphism and various indices of social, sexual and parental behaviour, controlling for the effects of phylogeny

($T+$ values refer to two-tailed Wilcoxon signed-rank tests of the null hypothesis that, at phylogenetic nodes where the subcomponent of dimorphism increases, the independent variable is equally likely to either increase or decrease. +ve/total refers to the ratio, at nodes where the measure of dimorphism increased, of increases in the independent variable compared with the total number of non-zero changes in the independent variable. All tests are based on independent contrast scores resulting from CAIC analysis.)

independent variable	(a) melanin-based dimorphism ($n=19$)			(b) carotenoid-based dimorphism ($n=6$)			(c) structural-colour dimorphism ($n=19$)		
	+ve/total	$T+$	p value	+ve/total	$T+$	p value	+ve/total	$T+$	p value
mating system	10/14	67.0	>0.20	2/4	3.0	>0.99	5/7	21.0	>0.10
frequency of extra-bond young	10/18	89.0	>0.70	3/6	12.0	>0.75	6/8	34.0	<0.05
frequency of extra-bond broods	10/17	87.0	>0.50	3/6	13.0	>0.50	7/8	33.0	<0.05
sex bias in incubation	6/12	47.5	>0.50	0/3	0.0	>0.10	5/6	14.0	>0.25
sex bias in brood provisioning	8/13	60.5	>0.25	3/3	6.0	>0.10	5/7	19.0	>0.25
sex bias in passive brood defence	9/13	71.0	<0.05	1/4	2.0	>0.25	5/8	22.0	>0.50
sex bias in active brood defence	7/13	47.0	>0.90	2/4	5.5	>0.75	3/6	14.0	>0.25

comparative analysis, it is difficult read much into the difference between our results until further analyses are complete.

Our finding that striking plumage-colour dimorphism is associated primarily associated with the frequency of extra-bond fertilizations, rather than social mating system, is contrary to the traditional view and agrees with the provocative conclusions of Møller & Birkhead (1994). However, our analyses of the raw data also suggest an association between plumage dimorphism and the extent of sex differences in parental care. Sex differences in parental care were not examined by Møller & Birkhead (1994). It is important, therefore, that our analyses using a modern comparative method indicate that the relationship between overall plumage-colour dimorphism and sex differences in parental care is an artefact of differing degrees of phylogenetic relatedness. Again, these findings are contrary to Björklund's (1990) analysis, who found that plumage dimorphism was associated with a high frequency of social polygyny. Because of multiple differences between the studies, it is difficult to identify the exact reason why our results differ from Björklund's. However, in this case we suspect the answer may lie in

the fact that, whereas we estimated plumage-colour dimorphism, Björklund used tail length as an index of plumage dimorphism.

The difference that we have observed between size dimorphism and overall plumage-colour dimorphism suggests that these two forms of dimorphism are the result of different selective pressures. Size dimorphism is usually attributed either to intrasexual competition or differences in parental care. Our results suggest that intrasexual competition may be the most important of these forces in the evolution of size dimorphism. Plumage dimorphism is commonly attributed to an interaction between sexual selection promoting showiness and natural selection promoting crypsis. Our results indicate that cryptic mate choice during extra-bond copulations may be an important component of sexual selection for showiness (see discussion in Møller & Birkhead 1994). Empirical evidence for such cryptic mate choice has now been published for several species (e.g. Møller 1988a, 1992, 1994; Smith 1988; Houtman 1992; Kempnaers *et al.* 1992, 1997; Sundberg & Dixon 1996; but see negative evidence in Hill *et al.* 1994). It seems likely, therefore, that extra-bond copulation behaviour could play an important

role in explaining the best-known paradox of plumage dimorphism among birds: why so many socially monogamous species display striking plumage dimorphism. However, another scenario is that variation among species in plumage-colour dimorphism is not the result of changes in the 'showiness' of the competitive sex but rather the result of changes in the level of crypsis exhibited by the sex that cares for the offspring. This scenario, originally favoured by Wallace (1889), has recently received support from a series of comparative analyses (Björklund 1991; Irwin 1994; Martin & Badyaev 1996; Bleiweiss 1997) and is consistent with our finding based on the raw data that overall plumage-colour dimorphism is correlated with sex differences in parental care. Also, a recent review on the role of hormones in controlling sexual dimorphism in birds (Owens & Short 1995) emphasized that, in many species, the showy male-type plumage is, in fact, the default plumage state that develops in the absence of any gonadal hormones. Plumage dimorphism is, therefore, often the result of the female actively suppressing the default showy plumage in order to become cryptic.

Our analyses of three subcomponents of plumage dimorphism—melanin-based dimorphism, carotenoid-based dimorphism, and structurally based dimorphism—suggest an even more complex pattern of differentiation. It appears that the association between overall plumage dimorphism and the frequency of extra-bond paternity is due mainly to structurally based colours such as iridescent blues, purples and blacks, whereas melanin-based dimorphism is associated with changes in the extent of sex bias in parental care. Although our present sample sizes are too small to extrapolate widely, we feel that the remarkable correlation between sexually dimorphic, structurally based colours and the rate of extra-bond paternity is particularly exciting in the light of recent suggestions that structurally based colours are both common in active sexual displays (Zahavi & Zahavi 1997; Hausmann 1997) and likely to reflect ultraviolet light (Andersson & Amundsen 1997; Bennett *et al.* 1997; Hausmann 1997).

6. CONCLUSIONS

Our results highlight the disparity between our deep understanding of the evolution of certain sexual ornaments, and our shallow understanding of why different species have different forms of ornament. For instance, there is good evidence that both the red bill of male zebra finches, *Taeniopygia guttata*, and the black throat patch of male house sparrows, *Passer domesticus*, are the result of sexual selection acting via female mate choice (e.g. Burley & Coopersmith 1987; Møller 1988*b*, 1992), but why do female zebra finches pay so much attention to bill colour while female house sparrows rely on bib size? Does the bill colour of a male zebra finch convey information that could never be transmitted through its plumage? More generally, is variation among species in the form of sexual ornaments due to differences in the type of information being relayed, differences in physiology or differences in the signalling environment? Or is variation in form due to chance?

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