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Phenotypic variation and fluctuating asymmetry in sexually dimorphic feather ornaments in relation to sex and mating system

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Secondary sexual characters have been hypothesized to demonstrate increased phenotypic variation between and within individuals as compared to ordinary morphological traits. We tested whether this was the case by studying phenotypic variation, expressed as the coefficient of variation (CV), and developmental instability, measured as fluctuating asymmetry (FA), in ornamental and non-ornamental traits of 70 bird species with feather ornamentation while controlling for similarity among species due to common descent. Secondary sexual characters differed from ordinary morphological traits by showing large phenotypic CV and FA. This difference can be explained by the different mode of selection operating on each kind of trait: a history of intense directional (ornaments) and stabilizing selection (non-ornaments). Phenotypic variation is reduced in the sex with more intense sexual selection (males), but does not differ among species with different mating systems. The strength of stabilizing selection arising from natural selection is associated with decreased CV (wing CV is smaller than tarsus or tail CVs). We found evidence of FA being reduced in ornamental feathers strongly affected by aerodynamics (tail feathers) compared to other ornaments, but only in females. In conclusion, CV and FA were not related, suggesting that phenotypic plasticity and developmental instability are independent components of phenotypic variation.

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ADDITIONAL KEY WORDS:---developmental stability – feathers – fluctuating asymmetry – ornaments – phenotypic variation.

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INTRODUCTION

One of Darwin's most important contributions to evolutionary biology was the realization that phenotypic variation among individuals was essential for the operation of sexual (and natural) selection (Darwin, 1871). To Darwin it seemed obvious that secondary sexual characters were highly variable, allowing discrimination by potential mates (and/or rivals) based on such exaggerated characters.

A number of different theories have been put forward to explain the evolution and the maintenance of costly ornamentation, and these include the Fisherian mechanism of arbitrary traits, the handicap mechanism, the sensory exploitation mechanism and several others (Andersson, 1994). Pure Fisherian traits should be arbitrary with respect to condition while the handicap mechanism would predict condition-dependent expression with huge variation in trait size and only individuals in prime condition developing the most exaggerated secondary sexual characters (Andersson, 1994).

Ornamental feathers in birds are secondary sexual characters that are assumed to have arisen and be maintained by sexual selection. Numerous studies have demonstrated that secondary sexual characters are currently subject to a directional mate preference with males with more exaggerated traits enjoying a mating advantage (review in Andersson, 1994). An interesting but overlooked observation is that a number of studies of birds has demonstrated a selective advantage for males with the most extreme degree of ornamentation (Andersson, 1982a; Møller, 1988; Barnard, 1990; Petrie, Halliday & Sanders, 1991; Evans, 1991; Andersson, 1992), while others have been unable to demonstrate such an advantage (Gibson & Bradbury, 1987; McDonald, 1989; Pruett-Jones & Pruett-Jones, 1990; Zuk, Thornhill & Ligon, 1990; Wittzell, 1991a; Rintamäki, Alatalo, Höglund & Lundberg, pers. comm.). This heterogeneity has been hypothesized to arise from some ornaments not being the current target of mate choice, these traits being subject to a strong influence of natural stabilizing selection, with a resultant decrease in phenotypic variation (Møller, 1993). Given that secondary sexual characters are costly to produce and maintain, sexual selection must still be operating to some degree on traits with no strong sexual selective advantage; otherwise they would disappear due to costs of natural selection, although the speed of disappearance would depend on the strength of natural selection.

Population genetics theory suggests that underlying genetic variation in traits closely related to fitness should be rapidly diminished under intense directional selection (Falconer, 1989). The reason is that any alleles affecting the expression of secondary sexual characters should go to fixation and thus show very low genetic variability (Borgia, 1979; Taylor & Williams, 1982). Hence, we should expect lower genetic variation in sexually selected than in ordinary morphological traits. However, there is little evidence of lack of genetic variation in traits subject to strong directional selection (Hedrick, 1988), including secondary sexual characters which tend to have not less genetic variation than ordinary morphological traits (Pomiankowski & Møller, 1995). This high genetic variability of secondary sexual characters can be explained by a greater than linear directional selection because this selects for greater phenotypic variation (Pomiankowski & Møller, 1995). Long-term directional selection would produce an increase in both the number of genes and the average effect of each locus on the trait. Traits subject to long-term stabilizing selection would demonstrate the opposite effect, restricting the effect of environmental and genetic factors on the expression of the genotype (Pomiankowski & Møller, 1995). Thus a large number of pathways will contribute to the development of secondary sexual characters (i.e. secondary sex traits show condition-dependence) and genetic variability in all of these different pathways will independently contribute to the expression of the sex trait (Rowe & Houle, 1996).

Empirical tests have demonstrated that phenotypic variation in sexually selected traits, measured as the coefficient of variation (CV), is higher than in non-sexual characters, including feather ornaments of birds (Alatalo, Höglund & Lundberg, 1988; Møller & Pomiankowski, 1993a; Pomiankowski & Møller, 1995). Furthermore, the phenotypic coefficient of variation is strongly positively correlated with the additive genetic and the residual coefficient of variation for secondary sexual characters (Pomiankowski & Møller, 1995). Hence, traits with a high degree of phenotypic variation also have a high degree of genetic variation. Empirical studies of phenotypic variation in secondary sexual characters and ordinary morphological traits, elucidating the relative strength of sexual and natural selection, could thus contribute considerably to an understanding of the factors involved. For example, Evans & Barnard (1995) have shown that fully grown feather ornaments were almost twice as variable in monogamous species as in polygynous ones, suggesting that this variability arose as a consequence of the greater relative strength of sexual selection in polygynous species, which would tend to reduce the underlying genetic variation (Falconer, 1989).

Developmental instability represents the second kind of phenotypic variability that is hypothesized to be influenced by the mode of selection. Fluctuating asymmetry (FA) reflects small, random deviations from symmetry in otherwise bilaterally symmetrical characters (Ludwig, 1932; Van Valen, 1962; Palmer & Strobeck, 1986; Leary & Allendorf, 1989; Parsons, 1990; Møller & Swaddle, 1997). These minor deviations from perfect symmetry are thought to represent a direct measure of the ability of individuals to control development (Zakharov, 1992; Møller & Swaddle, 1997). The causes of FA are both genetic (e.g. mutation, inbreeding, hybridization) and environmental (e.g. food deficiency, parasites, audiogenic stress, pesticides) (Parsons, 1990; Møller & Pomiankowski, 1993b; Møller & Swaddle, 1997).

FA in secondary sexual characters has been found to be considerably larger than that of ordinary morphological characters of the same individuals (Møller, 1990, 1992a, 1992b; Møller & Höglund, 1991; Møller & Pomiankowski, 1993a), suggesting that ornaments are more susceptible to disruption of developmental homeostasis than ordinary morphological traits (Møller & Pomiankowski, 1993b). This difference in asymmetry can be explained by stabilizing selection favouring individuals with trait values close to the mean due to the action of modifiers that limit expression of extreme trait values (Prout, 1962; Milkman, 1970). Strong directional selection for larger size favours new mutants that code for higher trait values which generally are associated with increased FA (Clarke & McKenzie, 1987; Møller & Swaddle, 1997). Furthermore, directional selection acts against modifiers that control the expression of extreme phenotypic values (Møller & Pomiankowski, 1993b), thereby relaxing the level of developmental control. Finally, a trait that is larger than the optimum under natural selection is likely to impose greater stress during development (Møller & Swaddle, 1997).

Individual FA in secondary characters and other morphological traits may reflect the ability to cope with stress, a quality feature that may be of importance during mate choice and male-male competition. A large number of observational and experimental studies has provided evidence that females choose their partners based on asymmetry of secondary sexual characters and ordinary morphological traits (review in Møller & Thornhill, 1998). The level of asymmetry of a secondary sexual character may reveal direct benefits in terms of foraging (Møller, 1991; Møller & Swaddle, 1997) or indirect benefits in terms of superior developmental control (Watson & Thornhill, 1994; Møller & Swaddle, 1997). The degree to which the level of asymmetry depends on the strength of natural selection and how the asymmetry differs among mating systems and hence in relation to the intensity of sexual selection still remain to be elucidated.

The aims of this paper were to test the following: (1) whether secondary sexual characters in general demonstrate greater phenotypic variation and FA than ordinary morphological traits. (2) If sexual selection is more intense in the sex with secondary sexual characters, we should also expect phenotypic variation in females to be larger than in males. (3) If the intensity of sexual selection is weaker in monogamous than in polygynous mating systems, we should expect phenotypic variation to be greater in monogamous species. (4) If natural selection is more intense in wings than in tails or tarsi, we should expect smaller phenotypic variation in wings. (5) If natural selection is more intense in feather ornaments directly involved in aerodynamic performance (tails), we should expect phenotypic variation of this kind of ornaments to be smaller than in head or body feather ornaments.

We will elucidate the degree to which the level of asymmetry depends on the strength of natural and sexual selection. The relationship between phenotypic variation and FA will also be assessed. These predictions were tested using a large data set (70 species) on phenotypic variation and asymmetry in birds with sexually size dimorphic feather ornamentation.

METHODS

Phylogenetic information and definition of feather ornaments

We identified 70 different evolutionary events of exaggerated feather ornaments in birds using available phylogenetic information. We did not consider sexually size monomorphic traits because there is only limited evidence for these being associated with sexual selection (review in Andersson, 1994). We admit that more studies have to be performed before we can dismiss mutual sexual selection as an important factor in the evolution of exaggerated sexual size monomorphism. For the time being we assume that extravagant sexually size dimorphic traits are associated with sexual selection, as demonstrated by numerous observational and experimental studies (see Andersson, 1994). Sexually size dimorphic traits were considered to qualify as a secondary sexual character if there was a sex difference in their size of at least 5%. Thus sexual size monomorphism, as well as feather colours or naked skin patches were not the subject of the present study. If we suspected that a species might be sexually size dimorphic, we investigated this by measuring ten males and ten females of the species in question. A total of 82 such cases resulted in 12 being considered to be sexually size monomorphic and the remaining 70 being size dimorphic. A few species could not be included in our data set due to a shortage of specimens in the museum collections visited. The degree of dimorphism of ornaments (((male size—female size)/(female size)) × 100) among species with partial sex limitation of ornament expression ranged from 5.0 to 450.9%, with a mean value of 68.4% (SE=13.4, n=49 species). Species with a feather character only being expressed in males (n=19) were all included in the study. In three species (*Pteridophora alberti, Pavo cristatus*, and *Pipra cornuta*), only males were available.

We used the phylogeny of Sibley & Ahlquist (1990), based on DNA-DNA hybridization, to identify different evolutionary events of extravagant feather ornamentation. For the family Hirundinidae, we use the phylogeny of Sheldon & Winkler (1993). Our analyses did not depend on the use of a particular phylogeny since identification of independent events based on the classification by Howard & Moore (1991) yielded exactly the same 70 evolutionary events.

Feather ornamentation has evolved a large number of times. If no other information was available, we assumed that there was only a single evolutionary event in each family. If ornaments appeared in subfamilies or tribes that were phylogenetically separated, these were considered to be different evolutionary events. However, if for example an extravagant tail had evolved in one species and an extravagant head plume had evolved in another species of the same family, we assumed that they represented two different evolutionary events, since these traits were obviously developmentally and morphologically independent. If more than a single ornamented species occurred within a taxon, we exclusively used abundance as the criterion for choice of a species due to more museum specimens being available for abundant species.

Closely related species will tend to share many characters through common descent rather than independent evolution (Harvey & Pagel, 1991; Harvey & Purvis, 1991). For example, the appearance of ornamental feathers in species of two related avian families could have evolved due to shared characteristics that both families have inherited from a common ancestor. Thus, different events of ornamentation are not completely statistically independent. This problem was resolved using the programme CAIC (Comparative Analyses by Independent Contrasts; Purvis & Rambaut, 1995) which calculates independent standardised linear contrasts that can be used to analyse the relationship between two or more variables while controlling for similarity due to common ancestry. We used a model of punctuated evolution in the analyses, although a model of gradual evolution provided qualitatively similar results.

Data collection and calculations

For each species we measured ten adults of each sex in the following museum collections: Alexander Koenig Museum, Bonn, Germany, British Museum (Natural

History), Tring, U. K., Doñana Biological Station, Seville, Spain, Natural History Museum, Stockholm, Sweden, and Zoological Museum, Copenhagen, Denmark, although it was impossible to obtain this number of specimens in some cases. The mean number of specimens per species and sex was 9.9 ± 0.4 SD, with a minimum value of 7. Specimens were chosen in the order in which they appeared in the collections, which prevents any involuntary bias in sampling. We only included adult specimens in breeding plumage and good feather condition. Individuals with broken or worn feathers were excluded. We were especially careful excluding specimens in moult by checking for the presence of feather quills. All specimens of each species belonged to the same subspecies and, when possible, to the same population. In *Hydrophasianus chirurgus* females were more ornamented than males apparently due to the polyandrous mating system.

We measured the length of the left and the right character of the ornament (with a ruler to the nearest mm; usually elongated tail feathers or crests, but sometimes elongated feathers in wings and other feather tracts), flattened wing (with a ruler to the nearest mm), tail (with a ruler to the nearest mm), and tarsus (with a digital calliper to the nearest 0.1 mm) according to Svensson (1984). Tail length was only used as a character in species where tail feathers were not the secondary sexual character. The size of characters was defined as the mean of the left and the right character. Variability of traits was estimated as the coefficient of variation (CV).

Absolute fluctuating asymmetry (FA) was estimated as the unsigned numerical difference between right and left trait value. For each combination of species, sex, and type of trait we tested if the morphological characters demonstrated directional asymmetry or anti-asymmetry as determined from measures of signed right-minus-left character values deviating from normal distributions with a mean value of zero. After sequential Bonferroni-adjustment (435 tests; Rice, 1989), none of the tests for deviation from a mean value of zero (one sample *t*-tests) or for normality (Kolmogorov–Smirnov tests) was statistically significant.

We assessed the repeatabilities of our measurements in four species with different kinds of ornaments and different body sizes by measuring the same individuals on two different days without knowledge of the results obtained on the first day. Repeatabilities (Becker, 1984) were for Anas platyrhynchos 0.993 (right wing), 0.996 (left wing), 0.996 (right tail), 0.995 (left tail), 0.990 (right tarsus), 0.989 (left tarsus); for Hirundo rustica 0.993 (right wing), 0.998 (left wing), 0.999 (right tail), 0.999 (left tail), 0.985 (right tarsus), 0.988 (left tarsus); for Sturnus unicolor 0.996 (right wing), 0.995 (left wing), 0.987 (right tail), 0.986 (left tail), 0.992 (right tarsus), 0.991 (left tarsus), 0.989 (right ornament), 0.990 (left ornament); and for Vanellus vanellus 0.996 (right wing), 0.994 (left wing), 0.988 (right tail), 0.988 (left tail), 0.987 (right tarsus), 0.989 (left tarsus), 0.998 (right ornament), 0.998 (left ornament). In all 28 cases $F \ge 131.3$ and P < 0.0001. For Hirundo rustica and Sturnus unicolor df = 29,30; for Anas *platyrhynchos* df = 27.28; for *Vanellus vanellus* df = 30,31 (wings, left tail feathers, and left tarsi), df = 31,32 (righ tail feathers and right tarsi), or df = 27,28 (crest feathers). Repeatabilities were large, suggesting that our measurements were sufficiently precise to allow quantitative analyses, without any indication that small species had larger measurement errors than large species.

For each species and trait we conducted two-way ANOVAs (sides \times individuals) to determine whether between-sides variation was significantly larger than measurement errors (Palmer & Strobeck, 1986). The interaction variance was highly significant

in all 14 tests ($F \ge 2.08$, P < 0.01; for Hirundo rustica and Sturnus unicolor df = 29,60; for Anas platyrhynchos df = 27,56; for Vanellus vanellus df = 29,60 (wings), df = 30,62 (tail feathers and tarsi), or df = 24,50 (crest feathers)). Another way of assessing the relative importance of measurement error associated with asymmetry estimates was to compute replicate right-minus-left values for each individual and trait, using the first set of measurements for one value and the second set for the other. We analysed these values with one-way ANOVAs (individuals as treatment levels) to partition total variability into within- and among-individuals components (Yezerinac, Lougheed & Handford, 1992; Dufour & Weatherhead, 1996). Estimates of these components were then used to compute repeatabilities of right-minus-left values. Repeatabilities (Becker, 1984) were for Anas platyrhynchos 0.94 (wing), 0.99 (tail), 0.94 (tarsus); for Hirundo rustica 0.73 (wing), 0.91 (tail), 0.91 (tarsus); for Sturnus unicolor 0.89 (wing), 0.92 (tail), 0.91 (tarsus), 0.75 (ornament); and for Vanellus vanellus 0.82 (wing), 0.91 (tail), 0.75 (tarsus), 0.99 (ornament). The observed among-individual variability was greater than expected, given the magnitude of within-individual variability, since in all 14 cases $F \ge 6.3$ and P < 0.001. That is to say, measurement error was small compared to individual variability. For Hirundo rustica and Sturnus unicolor df=29,30; for Anas platyrhynchos df = 27,28; for Vanellus vanellus df = 29,30 (wings), df = 30,31 (tail feathers and tarsi), or df = 24,25 (ornaments).

We tested if absolute FA depended on trait size by regressing the mean standardized (mean =0, SD = 1) asymmetry on mean standardised trait length. All eight regressions (4 traits \times 2 sexes) were highly significant ($F \ge 44.62$, $31 \le df \le 69$, P < 0.0001), implying that size correction is necessary. We used as an estimate of relative FA residuals from the regression of arctg((absolute FA + 0.001)^{0.4}) on (trait length - 5)^{0.3}. Transformations were necessary to obtain normally distributed data (Swaddle, Witter & Cuthill, 1994).

Species were classified according to information in the literature as (1) socially monogamous if a male and a female associated for reproduction, (2) polygynous if at least 5% of the males in one population was associated with more than a single female for reproduction, (3) polyandrous if at least 5% of the females was associated with more than a single male for reproduction, and (4) lekking if males aggregated at communal display grounds where females arrived to make their mate choice. Category (1) was considered monogamy and categories (2)–(4) polygamy throughout the analyses.

According to some authors (Barnard, 1991) museum samples can seriously underestimate the degree of within-population variation in sexual characters, but according to others (Swaddle, Witter & Cuthill, 1995) museum studies based on pooled samples may overestimate within-population variation in all kind of traits. Hence, we have compared estimates of coefficient of variation and absolute fluctuating asymmetry of ornaments obtained from our measurements in museums with estimates for the same species from the field. The species considered (only males) and the sources for the field studies are as follow: *Anas acuta* (Sorenson & Derrickson, 1994), *Euplectes jacksoni* (Andersson, 1992), *Euplectes macrourus* (Savalli, 1994), *Euplectes progne* (Andersson, 1982b), *Hirundo rustica* (Møller, de Lope & Saino, 1995), *Nectarinia johnstoni* (Evans & Barnard, 1995), Otis tarda (Carranza & Hidalgo, 1993), Pavo cristatus (Petrie et al., 1991), *Phasianus colchicus* (Wittzell, 1991b), *Tetrao tetrix* (Rintamäki et al., 1997), *Trochilus polytmus* (Evans, Martins & Haley, 1994), Vidua paradisaea (Oakes & Barnard, 1994), and Vidua regia (Barnard, 1990). All ornaments are elongated tails except for the moustache in Otis tarda. Coefficients of variation have been corrected for bias due to sample size (Sokal & Rohlf, 1995). We did not find any significant difference in CV between museum and field samples (paired *t*-test, t=1.13, df=12, NS). This result implies that museum estimates are comparable to those from the field. Regarding absolute FA, we have not found enough field data, but for four species (*Hirundo rustica* (Møller, 1994), *Nectarinia johnstoni* (Evans & Hatchwell, 1993), *Tetrao tetrix* (Rintamäki *et al.*, 1997), and *Trochilus polytmus* (Evans *et al.*, 1994)), differences between museum and field samples were not significant either (Wilcoxon signed ranks test, z=-1.46, n=4, NS).

A complete list of species and mean (SE) size, phenotypic coefficient of variation (CV) and absolute FA (SE) for the different characters is provided in the Appendix.

We tested the predictions while controlling for phylogeny. We made repeated measures analyses of variance with character and sex as repeated measures factors when testing differences between sexes or among traits, because in these cases we were doing comparisons within species that represented different evolutionary events of ornamentation. We did not consider non-ornamental tail as a category for the factor character because species with ornamental tail feathers could not have been included, thereby excessively reducing sample sizes. Since sex was a repeated measures factor, we could not include in the analyses of variance species with ornaments only present in males. However, statistical methods that treat species values as statistically independent points are not valid when we are doing crossspecies comparisons (Harvey & Pagel, 1991; Harvey & Purvis, 1991). Thus, differences between monogamous and polygamous species, or between tail and head ornaments, were calculated using the statistical software CAIC to control for similarity due to common descent (Purvis & Rambaut, 1995). We had information for only 60 of the 70 species in our data set to build a dichotomous phylogenetic tree (Fig. 1). When we had to choose among several species, first we chose the species yielding the maximum number of independent contrasts and, otherwise, simply by alphabetic order. Every branch in the phylogeny was considered to have the same length. A positive contrast in the dependent variable at a node means that this variable is varying in the same direction as the predictor variable (mating system or kind of ornament). Under the null hypothesis that evolution in the continuous variable has not been linked to the evolution of the categorical trait, we should expect half the contrasts in the dependent variable to be positive and half negative, and the mean value of the contrasts to be zero. We have tested this null hypothesis using one sample t-tests on the mean contrasts for each combination of sex and kind of trait. The relationship between two continuous variables (phenotypic variation and fluctuating asymmetry) can be assessed by regressing the independent contrasts of the two variables through the origin. The expected value of the slope equals the true relationship between the variables in the absence of phylogenetic effects (Pagel, 1993). We have tested if these slopes differed significantly from zero.

CVs were log₁₀-transformed before analysis in order to obtain normal distributions. Statistical tests were performed according to Sokal & Rohlf (1995). CAIC procedures were performed according to Purvis & Rambaut (1995) using the 'Brunch' algorithm when one variable is categorical and the 'Crunch' algorithm when none of the variables is categorical. For multiple statistical testing we used sequential Bonferroniadjustment (Rice, 1989), with comparison-wise error rate at 5%. All tests were two-tailed.



Figure 1. Phylogenetic relationships among 60 ornamented bird species included in this study based on Sibley & Ahlquist (1990) and Sheldon & Winkler (1993). Open branches indicate socially monogamous taxa. Solid branches polygynous, polyandrous, or lekking taxa. Equivocal branches are striped.

RESULTS

Phenotypic variation

We tested for differences in phenotypic variation between sexes or traits by means of repeated measures analysis of variance, with CV as the dependent variable, and sex and kind of trait (ornamental feathers, wing feathers, and tarsi) as factors. We

Source of		Phenoty	pic variance			Relative	asymmetry	
variation	df	MS	F	Р	df	MS	F	Р
Sex	1	0.110	4.69	0.036	1	0.003	0.41	0.53
Error	46	0.023			35	0.007		
Trait	2	7.113	244.64	< 0.0001	2	0.988	53.34	< 0.0001
Error	92	0.029			70	0.019		
Sex \times Trait	2	0.020	1.19	0.31	2	0.012	2.02	0.14
Error	92	0.016			70	0.006		



Figure 2. Phenotypic coefficients of variation (CV)(SE) in male (\blacksquare) and female (\square) birds for the size of morphological characters (ornamental feathers, tail feathers, tarsi, and wing feathers). Sample size (number of species) is indicated. *P*-values from paired *t*-tests comparing \log_{10} -transformed CVs between sexes are indicated unless larger than 0.05 (none of them is significant after sequential Bonferroni-adjustment). All CV comparisons among traits (paired *t*-tests) are significant in both sexes.

found a significant difference in CV between sexes and among traits (Table 1). In general, the phenotypic coefficient of variation was larger in females than in males (Fig. 2), although separate analyses for each trait revealed that the difference did not reach significance after sequential Bonferroni-adjustment (Rice, 1989) for any trait (paired *t*-tests; wings: t = -2.33, df=66, P = 0.023; ornaments: t = -1.76, df= 48, NS; tarsi: t = -1.55, df=63, NS; tails: t = 0.11, df=28, NS). For both sexes CV was larger in ornaments than in ordinary morphological traits, and among ordinary morphological traits, it was larger in tail feathers than in the other two traits, and larger in tarsi than in wings (Fig. 2). All 12 paired *t*-tests comparing CVs among traits in both sexes were statistically significant ($t \ge 2.07$, $20 \le df \le 69$, $P \ge 0.045$), even after sequential Boneferroni-adjustment. The relationship between phenotypic

TABLE 1. Phenotypic variance $(\log_{10}$ -transformed coefficient of variation (CVs)) and relative fluctuating asymmetry (FA) in relation to sex and kind of trait (ornament, wing, tarsus) in two factor repeated measures analyses of variance with sex and trait as repeated measures.



Figure 3. Mean (SE) independent standardized linear contrasts for phenotypic coefficient of variation (CV) in relation to mating system and kind of ornament. Males (\blacksquare); females (\square). Sample sizes (number of independent contrasts) are indicated. *P*-values from one sample *t*-tests (population mean=0) are indicated unless larger than 0.05 (none of them is significant after sequential Bonferroni-adjustment). A, relationship between \log_{10} -transformed CV and mating system. A positive contrast means that CV tends to be larger in polygamous species and a negative contrast that CV tends to be larger in monogamous species. B, relationship between \log_{10} -transformed CV and kind of ornament. A positive value means that CV tends to be larger in species with tail feather ornaments and a negative value that CV tends to be larger in species with head feather ornaments.

coefficient of variation and mating system using independent standardized linear contrasts was not significant for any trait (Fig. 3A).

All the ornamental feathers included in this study could be classified in two types depending on whether they are aerodynamically very important (tail and a few wing ornaments) or supposedly without adverse aerodynamic impact on their bearers (head and body feathers). Moreover, tail feather ornaments are much longer, relative to body size, than head and body ornaments. Natural selection forces, which must be countering the elaboration of these sexually selected ornaments, are thus predictably different and could have differential effects on the morphological variability shown by the two types of species. In one group we included species with the following feather ornaments: central and external tail feathers, tail coverts, and wing feathers. In the other we included species with the following feather. We did not find significant differences in CV between the two groups of species for any trait or sex after sequential Bonferroni-adjustment (7 tests) (Fig. 3B).



Figure 4. Relative FA (SE) in male (\blacksquare) and female (\square) birds for the length of morphological characters (ornamental feathers, tail feathers, tarsi, and wing feathers). Sample size (number of species) is indicated. All FA comparisons (paired *t*-tests) among sexes are non-significant. All FA comparisons (paired *t*-tests) among traits in both sexes are significant except the tarsus-wing comparison in females.

Fluctuating asymmetry

We tested for differences in FA between sexes and traits using a repeated measures two factor ANOVA with relative FA as the dependent variable, and sex and kind of trait (ornamental feathers, wing feathers, and tarsi) as factors. There was no significant difference in relative FA between sexes, but FA was significantly different among traits (Table 1). For both sexes relative FA was larger in ornaments than in ordinary morphological traits, and among ordinary morphological traits, it was larger in tarsi than in the other two traits (with the exception of tarsus FA not being significantly different from wing FA in females; paired *t*-test, t=1.86, df=63, P=0.068), and larger in wings than in tail feathers (Fig. 4). The remaining 11 paired *t*-tests for relative FA among traits in both sexes were statistically significant ($t \ge 2.47$, $13 \le df \le 63$, $P \le 0.016$) after sequential Bonferroni-adjustment (Rice, 1989). Using contrasts we found that the relationship between relative FA and mating system did not reach significance for any test after sequential Bonferroni-adjustment (8 tests) (Fig. 5A).

Since natural selection forces are predictably different depending on the kind of ornament (aerodynamically important or not), they could have differential effects on the relative asymmetry shown by the two types of species. Female feather ornaments showed larger fluctuating asymmetry when they were head feathers (mean contrast = -0.087 (SE = 0.015), df = 11, t = -5.66, P < 0.001), but there were no significant differences for the other female traits or for any male trait (Fig. 5B).

Relationship between phenotypic variation and fluctuating asymmetry

We have also examined if CV and FA covaried for each combination of trait and sex. We have regressed through the origin the independent contrasts of the two variables and tested if the slopes differed significantly from zero. None of the 8 slopes differed significantly from zero after sequential Bonferroni-adjustment (Rice, 1989) $(2.87 \ge t \ge -1.15, 59 \ge n \ge 26, P \ge 0.0068)$.



Figure 5. Mean (SE) independent standardised linear contrasts for relative FA in relation to sex and mating system. Males (\blacksquare); females (\square) Sample sizes (number of independent contrasts) are indicated. *P*-values from one sample *t*-tests (population mean = 0) are indicated unless larger than 0.05 (only female ornament test in (B) is significant after sequential Bonferroni-adjustment). A, relationship between relative FA and mating system. A positive contrast means that FA tends to be larger in polygamous species and a negative contrast that FA tends to be larger in monogamous species. B, relationship between relative FA and kind of ornament. A positive value means that FA tends to be larger in species with tail feather ornaments and a negative value that FA tends to be larger in species with head feather ornaments.

We have repeated the analyses separately for species with the two kinds of ornaments, i.e. ornamental feathers directly involved in flight (tail, wings) and ornamental feathers not directly involved in flight (head and body feathers). None of the slopes in any of the two types of species separately was significantly different from zero after sequential Bonferroni-adjustment (in all 15 tests: $2.55 \ge t \ge -2.51$, $34 \ge n \ge 9$, $P \ge 0.019$).

DISCUSSION

We found that the phenotypic coefficient of variation is larger in secondary sexual characters than in ordinary morphological ones (Fig. 2). This finding has previously been reported in other studies (Alatalo *et al.*, 1988; Møller & Pomiankowski, 1993a; Pomiankowski & Møller, 1995), although these previous results were not based on statistically independent observations. Furthermore, these differences in CV are

present not only in males, as other studies have shown, but also in females. This difference in phenotypic variability among traits is supposedly due to different selection regimes, with directional selection mainly affecting ornaments and stabilizing selection mainly other traits (Pomiankowski & Møller, 1995). For ordinary morphological traits we found for both sexes that phenotypic variation in length of tail feathers is larger than in tarsi and wings, even when tails are not exaggerated by sexual selection. Fitzpatrick (1997) has previously reported that tails, including ornamental tails, are more variable than tarsi and wings. We have shown for both sexes that phenotypic variation of ornamental feathers is larger than that of non-ornamental tails. Differences in phenotypic variability among non-ornamental traits are likely to be due to differences in the strength of natural selection, with the strongest stabilizing selection affecting wing feathers (Thomas, 1993).

How does the strength of directional selection affect levels of phenotypic variation? We have based our reasoning on the supposition (widely accepted) that the intensity of sexual selection is stronger in more polygynous mating systems, and in males as compared to females (review in Andersson, 1994). Sexual selection will obviously affect ornamental traits, but ordinary morphological traits might also be affected because the entire phenotype of males of an ornamented species may change to reduce the costs of the ornament, or because sexual selection results in a reduction in genetic and hence phenotypic variance due to alleles going to fixation (Andersson, 1994; Balmford, Jones & Thomas, 1994; Møller, 1996). It seems reasonable to think that phenotypic variation of non-ornamental traits is affected by both natural and sexual selection. We have found that phenotypic variation was generally larger in females than in males (Table 1, Fig. 2), suggesting that intense sexual selection will reduce variability in males. This finding is consistent with quantitative genetics theory which posits that strong directional selection reduces underlying genetic and phenotypic variation (Falconer, 1989). However, the difference in CV between monogamous and polygamous species was not significant (Fig. 3). Previously, Evans & Barnard (1995) found that CV in socially monogamous species was larger than in polygynous ones, although this conclusion was not controlled for similarity among species due to common ancestry. One possibility would be that differences in the strength of directional selection between mating systems are not so strong as previously thought since sexual selection may also operate relatively intensely under monogamy (Andersson, 1986; Grafen, 1990; Kirkpatrick, Price & Arnold, 1990; Møller & Birkhead, 1994). Another possibility would be that the relationship between intensity of sexual selection and phenotypic variation is not so clear-cut and might be obscured by other factors, e.g. the intensity of natural selection. Anyway, this result should be interpreted with caution because it is based on a relatively low number of independent contrasts (Fig. 3A).

Ornamental feathers included in this study have been classified in aerodynamically very important (tail and a few wing ornaments) and without strong aerodynamic impact on their bearers (head and body feathers). There is no reason to think that the strength of sexual selection will be different for the two types of ornaments although natural selection forces are predictably strongest in feather ornaments directly involved in aerodynamic performance. This could have differential effects on the morphological variability shown by the two types of species. Although we should expect phenotypic variation of tail and wing ornaments to be smaller than in head or body feather ornaments, this effect was not confirmed by our comparative analyses. Perhaps effects of natural selection through aerodynamics have relatively little influence on phenotypic variance, because particular categories of ornaments are associated with particular ecologies, and this association will tend to reduce the cost of extravagant ornamentation.

Fluctuating asymmetry in ornamental feathers was larger than in ordinary morphological traits (Fig. 4), which corroborates the results of previous studies on birds (Møller, 1990, 1992b; Møller & Höglund, 1991; Møller & Pomiankowski, 1993a). These differences among traits cannot be caused by allometry since our conclusions are based on relative asymmetries. This finding is consistent with the hypothesis that directional selection reduces developmental control, while stabilizing selection has the opposite effect. Since FA of tail feathers is smaller than FA of wing feathers (Fig. 4), and wing feathers are the trait supposedly subject to intense stabilizing selection (Thomas, 1993), we cannot conclude that the strongest natural selection produces the lowest levels of FA, as was the case for phenotypic variation. Females may choose their partners based on asymmetry of secondary sexual characters and ordinary morphological traits (review in Møller & Thornhill 1998), and females may more easily perceive symmetric tails than symmetric wings, since tail feathers are closer to each other. Therefore, sexual selection pressures for symmetric tails might be more intense than for other ordinary morphological traits.

We did not find a significant difference in asymmetry between sexes (Table 1). Sexual selection is supposedly stronger in males but this difference did not result in differences in asymmetry. Moreover, sexual selection for symmetric mates would also predict the lowest levels of FA in males. Very little is know about female selection by males, and in the few species of birds studied, results are contradictory: in some species, males seem to choose their partners according to sexual signals (Hill, 1993; Jones & Hunter, 1993; Amundsen, Forsgren & Hansen, 1997) and in others that is not the case (Muma & Weatherhead, 1989; Potti, 1993; Cuervo, de Lope & Møller, 1996). We should consider the possibility that, in the same way females may be choosing symmetric males, males might be selecting symmetric females. This could reduce the difference in FA between sexes.

Comparing FA between the two groups of species classified according to the relative aerodynamic importance of their ornaments (tail versus other ornaments), we found that FA of tail ornaments was smaller than FA of other ornaments in females, but not in males (Fig. 5B). We could imagine that the most intense natural selection would reduce FA of ornaments, but mainly in the sex with less intense sexual selection (females).

The patterns of phenotypic variation and fluctuating asymmetry between sexes, mating systems and categories of traits are sometimes similar, but in other cases results are quite different. Phenotypic variation and FA for each trait and sex were generally unrelated to each other. This finding is consistent with the results of quantitative genetics studies showing that phenotypic plasticity and developmental instability of a trait are under separate genetic control (*Drosophila melanogaster* (Scheiner, Caplan & Lyman, 1991); *Daphnia magna* (Yampolsky & Scheiner, 1994); *Iris pumila* (Tarasjev, 1996)).

In conclusion, directional sexual selection is associated with increased CV and FA. Phenotypic variation is reduced in the sex with more intense sexual selection (males), but does not differ among species with different mating systems. The strength of stabilizing natural selection is associated with reduced CV. Feather ornaments that are strongly affected by aerodynamics had lower asymmetry than aerodynamically less

important ornaments, but only in females. CV and FA were generally unrelated, implying that phenotypic plasticity and developmental instability are unrelated features of phenotypic variation.

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Mean (SE) size (mm), coefficient of variation (CV)(%), and absolute fluctuating asymmetry (FA)(SE)(mm) of morphological characters in ornamented bird species. Mating system (M = monogamy, P = polygyny, P = polyandry, L = lekking; references in parentheses) and type of feather ornament are indicated. m =

male, f=female.										
Species	Sex	u	Wing Mean (SE) CV	FA (SE)	Tail Mean (SE) CV	FA (SE)	Tarsus Mean (SE) CV	FA (SE)	Ornamen Mean (SE) CV	t FA (SE)
Podiceps cristatus	Е	10	188.50 (1.44) 2.42	1.00 (0.26)	1	1	63.84 (0.87) 4.30	0.50 (0.15)	39.95 (1.27) 10.07	1.30 (0.26)
M (6, 18) - ears	Ļ	10	183.85 (1.73) 2.97	0.70(0.30)	1	1	62.34 (0.86) 4.38	0.97(0.31)	36.30(1.32)11.46	1.00(0.42)
Anas falcata	E	10	250.20 (1.63) 2.06	1.40(0.37)	65.55 (1.68) 8.09	0.10 (0.10)	37.75 (0.46) 3.82	0.24(0.05)	182.45 (3.28) 5.69	8.10(2.48)
\mathbf{M} (18, 19) - wing feathers	f	10	231.05 (1.23) 1.68	1.30(0.30)	68.60(1.11)5.11	0.00(0.00)	36.43 (0.37) 3.18	0.28 (0.07)	100.70 (3.50) 10.98	1.40(0.34)
Anas platythynchos	ш	10	269.00 (4.19) 4.93	0.80(0.33)	82.50(1.01)3.89	0.40(0.16)	43.90 (0.53) 3.85	0.15(0.06)	64.20 (2.38) 11.70	1.80 (0.57)
M (6, 8) - central tail feathers	ب	10	249.50 (2.84) 3.60	1.80(0.68)	79.40 (1.10) 4.38	0.20(0.13)	41.65 (0.61) 4.61	0.21 (0.07)		
Aythya fuligula	н	10	203.25 (1.55) 2.41	1.10(0.35)	53.25 (0.83) 4.95	0.10 (0.10)	33.86 (0.27) 2.50	0.24(0.06)	62.30(2.83)14.34	1
M (6, 19) - crest	Ļ	10	194.50 (1.34) 2.18	1.20(0.39)	49.80(0.57)3.64	0.00 (0.00)	33.49 (0.16) 1.52	0.17(0.04)	24.10(2.76)36.20	1
Clangula hyemalis	E	10	227.75 (2.39) 3.32	0.70(0.34)	. 1		34.42 (0.41) 3.76	0.19(0.06)	201.45 (7.99) 12.54	6.10(3.53)
M(6, 19) - central tail feathers	f	10	209.10 (2.37) 3.58	0.80(0.29)	66.45(2.05)9.76	0.10 (0.10)	33.06 (0.31) 2.95	0.21(0.04)	. 1	I
Tetrao tetrix	ш	10	254.85 (1.55) 1.93	3.10(0.62)	.		47.86 (0.59) 3.93	0.98(0.22)	173.50 (3.87) 7.05	2.20(0.49)
L (6, 24) - external tail feathers	f	10	223.70 (2.79) 3.95	1.80(0.49)	I	I	44.22 (0.51) 3.65	0.92(0.25)	105.20 (2.51) 7.56	1.40(0.52)
Lophortyx californica	ш	10	113.78 (0.89) 2.48	1.35(0.29)	83.90 (0.88) 3.32	0.80(0.29)	29.96 (0.38) 4.01	0.23 (0.05)	32.70 (0.72) 6.96	
M(8, 22) - head plumes	f	10	111.23 (0.78) 2.21	0.95(0.19)	80.80 (1.66) 6.51	0.70(0.29)	28.56 (0.20) 2.16	0.13(0.03)	19.90 (0.80) 12.69	ļ
Rollulus rouloul	E	10	140.30 (1.53) 3.44	0.80(0.33)	62.70 (1.63) 8.21	0.80(0.29)	43.41 (0.25) 1.84	0.56(0.12)	37.50 (1.72) 14.51	I
M (18, 22) - crest	ų.	10	139.95 (0.92) 2.07	0.50(0.22)	63.00 (1.43) 7.18	0.40(0.16)	43.09 (0.39) 2.84	0.45(0.16)	1	1
Gallus gallus	E	10	232.30 (3.24) 4.41	1.20(0.29)	I	l	69.23 (1.03) 4.69	1	105.30 (3.66) 10.99	1.80(0.44)
$P(1\overline{8}, 21)$ - neck feathers	f	10	198.50 (1.84) 2.93	1.00(0.47)	149.45(2.01)4.25	1.10(0.31)	59.42 (0.64) 3.38	0.73 (0.20)	54.35(1.41)8.23	2.10(0.48)
Phastanus colchicus	ш	10	245.60 (2.64) 3.39	2.20(0.84)	I	1	70.39 (1.40) 6.28	0.40(0.06)	458.90 (13.82) 9.52	4.80(1.64)
P (6, 21) - central tail feathers	ليس	10	220.65 (1.95) 2.79	3.30(0.76)	I	ł	61.70 (0.62) 3.19	0.43(0.10)	277.65 (8.31) 9.46	2.90(0.89)
Pavo cristatus	ш	10	456.75 (3.42) 2.37	5.80(1.74)	509.33 (12.30) 7.25	4.22(1.65)	135.16 (2.83) 6.62	1.19 (0.33)	529.45 (46.68) 9.65	23.29 (6.82)
L (21, 24) - tail coverts	÷	1	. 1		. 1		. 1	1	1	, I
Otis tarda	Ξ	10	603.50 (7.66) 4.02	9.40(4.73)	242.65(3.43)4.47	4.50(0.85)	156.18 (3.59) 7.27	2.30(0.68)	128.90 (6.31) 15.47	8.20 (1.98)
L (6, 24) - moustache	Ļ	10	470.30 (4.62) 3.11	4.80 (0.85)	210.65 (2.38) 3.58	4.10 (0.72)	116.98 (1.69) 4.57	3.12(0.80)	23.40(2.27)30.68	2.80 (1.47)
Hydrophasianus chirurgus	B	10	197.35 (4.61) 7.39	0.90(0.28)	I	I	51.58 (1.32) 8.11	1.22(0.76)	240.30 (13.31) 17.52	3.00(0.89)
$P_{0}(1)$ - central tail feathers	نمنا	10	221.55 (4.50) 6.42	1.89(0.48)			55.90 (0.98) 5.53	0.52(0.13)	287.65 (13.25) 14.57	2.88(0.81)
Vanellus vanellus	E	10	224.60 (1.56) 2.20	1.20(0.59)	98.45 (1.56) 5.00	0.30(0.21)	50.73 (0.39) 2.45	0.31 (0.07)	78.45 (2.67) 10.76	3.70(1.28)
M (6, 20) - crest	t.	10	222.10 (2.14) 3.05	1.00(0.33)	97.90(1.21)3.90	0.20 (0.20)	49.89 (0.45) 2.87	0.25(0.06)	52.60(3.79)22.80	1.80 (0.65)

PHENOTYPIC VARIANCE AND ASYMMETRY IN ORNAMENTS

continued

Species	Sex	и	Wing Mean (SF) CV	FA (SE)	Tail Mean (SE) CV	FA (SF)	Tarsus Mean (SF) CV	FA (SE)	Ornamen Mean (SF) CV	t FA (SF)
			· ~ (ma) man			(max)				(mm) +++
Philomachus huonax	Ε	01	186 10 /1 33/ 9 96	111 (0.31)	69 70 /0 89) 3 71 (0.16)	51 33 (0 36) 9 95	0.73 (0.14)	30 45 /1 34) 10 75	1 30 (0 45)
I. (6. 94) - neck tuff	<i>ب</i>	9	153.10 (1.03) 2.13	1.00 (0.26)	58 10 (1 22) 6 66 (00 00 000	41 60 (0 42) 3 18	0.56 (0.11)		-
Synhaptes baradoxus	. 8	01	237.65 (6.29) 8.37	1.10(0.35)	=	-	=	-	167.90 (6.87) 12.93	9.20 (3.47)
M (6. 23) - central tail feathers	<i>د</i>	0	225.70 (2.28) 3.19	1.60 (0.52)	;	I		1	126.55 (3.30) 8.24	1.90 (0.67)
Treron abicauda	н	10	172.05 (1.68) 3.08	0.90 (0.35)	Ι		25.70 (0.33) 4.04	0.21 (0.05)	181.50 (2.39) 4.16	4.20 (1.19)
M (1, 15) - central tail feathers	ليسو	01	167.90 (1.31) 2.48	0.40(0.22)	1.000		24.55(0.31)3.98	0.15(0.03)	150.55 (4.08) 8.57	2.50(0.65)
Psittacula longicauda	Е	10	178.68 (0.90) 1.59	1.05 (0.32)	Ι	I	17.48 (0.11) 1.92	0.56(0.10)	242.88 (3.30) 4.30	6.55 (3.27)
M (11) - central tail feathers	÷	01	169.25 (1.62) 3.03	1.20(0.32)	ļ		17.75 (0.17) 2.94	0.43(0.16)	180.40 (7.65) 13.41	2.00(0.64)
Scotornis climacurus	ш	10	142.30 (1.21) 2.69	0.60(0.16)	I	I	16.87 (0.17) 3.13	0.49(0.12)	218.45 (7.58) 10.97	4.10(1.30)
M (4) - central tail feathers	f	10	143.45 (1.42) 3.13	0.70(0.21)	I	I	16.74(0.19)3.53	0.65(0.22)	172.35(5.10)9.35	2.70(1.40)
Macrodipteryx longipennis	Е	10	179.45 (1.28) 2.25	0.70(0.21)	I	i	19.64(0.18)2.91	0.03(0.01)	450.30(12.17)8.55	6.40(1.50)
P (4) - wing feathers	Ļ	10	168.55 (0.97) 1.82	0.90(0.28)	97.80 (1.23) 3.97 (0.20 (0.20)	19.42 (0.21) 3.40	0.21 (0.05)		, ,
Hydropsalis brasiliana	ш	10	176.45 (3.26) 5.84	1.22(0.32)	, I	·	18.52 (0.29) 4.97	0.32(0.08)	285.55 (15.71) 17.40	8.70 (2.72)
M (32) - external tail feathers	f	10	171.30 (1.93) 3.57	1.20(0.20)	Ι	I	18.86(0.31)4.93	0.28(0.12)	148.55 (4.57) 9.72	1.63(0.50)
Phaethomis superciliosus	ш	10	59.55(0.41)2.18	0.78(0.22)			, ,	×	71.40(0.73)3.23	0.67(0.44)
L(24, 32) - central tail feathers	Ļ	10	60.20(1.02)5.37	0.33(0.21)	Ι	I	I	I	68.65(1.01)4.66	0.60(0.40)
Lophornis omata	ш	10	39.90 (0.32) 2.56	0.20(0.13)	24.95 (0.40) 5.04 (0.10(0.10)	ļ	ł	20.93(0.64)9.74	0.35(0.13)
P (16) - throat plumes	Ļ	10	37.80(0.29)2.43	0.00(0.00)	21.40 (0.22) 3.27 (0.00 (0.00)				
Trochilus polytmus	Е	10	66.60(0.60)2.83	0.40(0.22)	. 1	i i	$6.09\ (0.08)\ 4.27$	0.17 (0.04)	169.50 (3.85) 7.18	3.00(0.79)
P(36) - 2nd external tail feathers	Ļ	10	57.44 (0.56) 2.93	0.67 (0.29)	į	Ι	5.66(0.08)4.27	0.18(0.04)	39.75(1.30)10.38	0.56(0.24)
Topaza pella	Е	10	85.00(0.66)2.47	0.80(0.20)	į	Ι	10.11 (0.05) 1.54		21.91(0.43)6.16	0.64(0.38)
I. (24, 32) - breast feathers	Ļ	10	75.75(0.49)2.05	0.70(0.21)	45.10 (0.36) 2.50 (0.20(0.13)	$6.89\ (0.11)\ 5.13$	0.24 (0.04)		I
Oxypogon guerinii	В	10	73.35 (0.47) 2.01	0.70(0.15)	54.85 (0.57) 3.27 (0.11 (0.11)	7.25 (0.07) 3.03	0.20(0.05)	$19.35\ (0.61)\ 9.96$	0.50(0.15)
I. (10, 17) - crest	÷	10	66.15 (0.48) 2.31	0.50 (0.17)	45.89 (0.96) 6.28 ((0.18)	7.26 (0.17) 7.44	0.15(0.06)	.	
Aglaiocercus kingi	Ш	10	70.25 (0.44) 1.96	$0.30 \ (0.15)$	1		6.18 (0.04) 2.27	0.01 (0.01)	127.95 (3.64) 9.00	1.50(0.50)
P (10, 17) - external tail feathers	f	10	58.00(0.59)3.23	0.60(0.16)		ļ	6.31 (0.08) 3.79	0.04 (0.02)	41.25(1.07)8.17	0.30(0.15)
Pharomachrus mocinno	Ε	10	210.30 (1.73) 2.60	2.80(0.55)	í	1	21.17 (0.55) 8.19	0.18(0.06)	752.45 (29.94) 12.58	49.30(18.21)
M (28, 37) - tail coverts	Ļ	10	218.20 (2.24) 3.25	1.80(0.44)	ı		20.81 (0.14) 2.08	0.03(0.01)	177.80(4.42)7.86	2.40(0.81)
Tanysiptera galatea	E	01	108.60 (0.83) 2.41	1.20(0.25)			18.00 (0.08) 1.39	0.04 (0.01)	242.55 (4.70) 6.13	21.70 (8.17)
M (12) - central tail feathers	Ļ	10	107.95 (1.53) 4.48	0.70(0.21)		;	17.84 (0.09) 1.67	0.04 (0.01)	204.00(10.20)15.82	4.20(1.60)
Coracias abyssinicus	ш	10	161.90 (0.88) 1.73	0.60(0.27)	123.80 (1.24) 3.16 (0.20(0.20)	22.55(0.32)4.45	0.10(0.04)	238.75 (5.73) 7.59	4.10(1.32)
M(4, 12) - external tail feathers	Ļ	10	159.60 (1.80) 3.57	1.00(0.26)	124.95 (1.91) 4.84 0	0.10 (0.10)	22.27 (0.39) 5.52	0.05(0.02)	226.85 (5.02) 6.99	4.70 (1.43)
										continued

APPENDIX --- continued

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J. J. CUERVO AND A. P. MØLLER

continued	
APPENDIX-	

Species	Sex	u	Wing Mean (SE) CV	FA (SE)	Mean (SE) CV	FA (SE)	Tarsus Mean (SE) CV	FA (SE)	Ornamer Mean (SE) CV	ıt FA (SE)
Dinopium javanense M (1, 38) - crest	е ч	10	133.15 (2.10) 4.99 129.65 (1.45) 3.54	$1.00 (0.29) \\ 0.70 (0.15)$	95.95 (1.85) 6.08 95.60 (1.40) 4.64	1.00 (0.44) 1.11 (0.51)	23.45 (0.25) 3.37 22.20 (0.30) 4.33	0.56 (0.15) 0.30 (0.10)	$\begin{array}{c} 23.80 \\ 21.60 \\ (0.42) \\ 5.53 \\ 21.60 \\ (0.95) \\ 13.84 \end{array}$	
Pithys albifrons	н	10	72.55 (0.57) 2.46	0.70(0.26)	39.00 (1.00) 8.11	0.40(0.16)	22.14 (0.30) 4.34	0.18 (0.08)	20.80 (1.05) 15.93	0.89 (0.20)
M (16, 32) - crest	Ļ	10	70.15 (0.65) 2.93	0.50(0.17)	37.25(0.69)5.84	0.10 (0.10)	22.04 (0.18) 2.51	0.24(0.05)	17.45 (0.68) 12.30	1.30(0.55)
Rupicola peruviana	m	10	191.25 (1.13) 1.87	1.50(0.40)	125.55 (1.05) 2.65	0.50(0.22)	39.07 (0.54) 4.33	0.29(0.06)	30.45(0.67)6.94	1.50(0.40)
L (24, 34) - crest	Ļ	10	181.40 (1.79) 3.12	1.40(0.31)	121.22 (0.74) 1.83	0.67 (0.24)	36.99 (0.67) 5.72	0.25(0.05)	20.05 (0.81) 12.74	1.30(0.34)
Pipra comuta	ш	10	66.55 (0.43) 2.02	0.50(0.28)	43.45(0.40)2.89	0.10 (0.10)	18.00 (0.11) 1.93	0.19(0.04)	15.40(0.32)6.64	0.40(0.19)
L (24, 32) - crest	f	1	1	1	.)		. 1	1	.	1
Chiroxiphia linearis	ш	10	71.15 (0.41) 1.82	0.50(0.17)	ł	Ţ	$18.39\ (0.38)\ 6.60$	I	141.75 (4.06) 9.06	3.70(0.96)
L (24, 28) - central tail feathers	Ļ	10	70.15 (0.60) 2.69	0.70(0.21)	$34.30\ (0.53)\ 4.92$	0.20(0.13)	18.23 (0.18) 3.17	0.33 (0.11)	54.30 (1.93) 11.25	1.60(0.81)
Tyrannus sabana	Е	10	111.35 (1.39) 3.96	0.70(0.26)	. 1		17.80 (0.19) 3.40	0.24(0.08)	239.25 (10.46) 13.83	6.50(3.20)
M(17, 32) - external tail feathers	Ļ	10	105.40 (0.92) 2.76	1.40(0.27)	Ι	I	17.51 (0.16) 2.83	0.17 (0.06)	178.00 (7.33) 13.02	3.20(1.25)
Anairetes reguloides	E	8	52.06(0.63)3.42	0.13(0.13)	50.63 (2.29) 12.80	0.00(0.00)	20.09 (0.24) 3.42	0.24(0.04)	17.88 (0.85) 13.52	1.20(0.49)
M (10) - crest	Ļ	7	49.93 (0.56) 2.97	0.17(0.18)	47.79 (0.53) 2.95	0.43(0.30)	19.61 (0.47) 6.29	0.21(0.07)	15.86(0.81)13.56	1.20(0.72)
Menura novaehollandiae	E	10	293.35 (2.46) 2.65	1.50(0.48)	1		110.85 (1.21) 3.46	1.10 (0.35)	612.45 (23.56) 12.16	13.70 (5.35)
L (25, 31) - central tail feathers	f	œ	272.19 (6.38) 6.63	2.88(0.72)	I		104.87 (2.47) 6.67	0.56(0.21)	482.81 (9.86) 5.78	19.25 (27.71)
Eremophila alpestris	E	10	109.40 (0.73) 2.12	0.60(0.22)	70.70 (1.10) 4.91	0.20(0.13)	22.24 (0.28) 4.03	0.26(0.06)	9.53(0.20)6.62	0.74 (0.24)
M (6, 8) - head plumes	f,	10	102.45 (1.14) 3.51	0.50 (0.17)	61.55 (0.94) 4.82	0.10 (0.10)	21.42 (0.33) 4.82	0.23 (0.04)	7.69 (0.25) 10.40	0.88(0.20)
Hirundo rustica	u	10	127.50 (1.29) 3.19	0.40(0.16)	1	I	11.56 (0.11) 3.03	0.15(0.04)	111.85(2.27)6.43	1.90(0.64)
M(6, 35) - external tail feathers	Ļ	10	125.90 (0.89) 2.25	0.40(0.16)	I	I	11.35 (0.14) 3.88	0.12(0.04)	91.55 (2.26) 7.81	1.10(0.35)
Hirundo semirufa	ш	10	118.25 (1.21) 3.23	0.30(0.15)	I	I	14.20 (0.17) 3.70	0.13 (0.05)	114.50 (4.24) 11.72	4.40(1.83)
M (4, 35) - external tail feathers	f	10	117.15 (1.11) 3.00	0.50(0.17)	Ι	ł	14.19 (0.19) 4.13	0.19 (0.06)	102.15 (2.93) 9.06	2.30(0.84)
Psalidoprocne obscura	ш	10	97.35 (0.76) 2.46	0.50(0.22)	-	ł	9.41 (0.18) 5.95	0.05 (0.04)	97.85 (3.51) 11.35	1.50(0.34)
M(4, 35) - external tail feathers	دسا	6	88.28 (0.83) 2.81	0.56(0.24)	ł	ł	9.25 (0.25) 8.23	0.22 (0.09)	68.67 (2.96) 12.92	
Dryoscopus sabini	ш	10	84.40 (0.98) 3.67	0.40(0.16)	69.70 (0.66) 3.01	0.20 (0.13)	24.78 (0.40) 5.04 (0.18 (0.04)	34.20(0.49)4.53	I
	Ļ	10	80.60 (0.73) 2.86	0.40(0.22)	69.05 (1.05) 4.82	0.30(0.15)	24.05 (0.14) 1.82 (0.16 (0.06)	32.00(0.70)6.91	1
Philogonys caudatus	u	10	97.10 (0.61) 1.97	0.00(0.00)	I	I	18.67 (0.19) 3.25	0.20 (0.05)	133.10 (2.77) 6.59	0.40(0.22)
M (28, 37) - central tail feathers	Ļ	2	94.71 (0.71) 1.97	0.29(0.18)	l	I	18.64 (0.32) 1.69	0.19 (0.06)	116.07 (2.11) 4.82	0.50(0.22)
Phainopepla nitens	ш	10	93.75 (0.80) 2.71	0.50(0.22)	96.85(0.96)3.15	0.30 (0.15)	18.06 (0.23) 4.02	0.18 (0.04)	25.50 (0.37) 4.62	
M (8) - crest	f	10	91.85 (1.36) 4.70	0.78 (0.15)	91.70 (1.69) 5.84	0.44 (0.18)	18.32 (0.27) 4.69	0.26 (0.06)	20.80(0.49)7.45	I
Copsychus malabaricus	Е	10	96.50 (0.85) 2.79	0.60(0.16)	ł	I	25.68 (0.22) 2.72	0.26 (0.05)	171.60 (6.23) 11.48	3.00(0.68)
M (l) - central tail feathers	с.	10	92.00 (1.38) 4.76	0.20(0.13)	•	I	25.19 (0.28) 3.52	0.15 (0.04)	134.00 (2.99) 7.05	0.80(0.39)
i						I				continued

Species	Sex	u	Wing Mean (SE) CV	FA (SE)	Tail Mean (SE) CV	FA (SE)	Tarsus Mean (SE) CV	FA (SE)	Ornamer Mean (SE) CV	tt FA (SE)
Panurus hiarmicus	e a	0	60.00 (0.48) 2.52	0.20 (0.13)	83.50 (1.42) 5.36	0.60 (0.22)	20.42 (0.21) 3.32	0.27 (0.06)	12.05 (0.25) 6.69	0.30 (0.15)
M (6) - moustache	نب	10	58.15 (0.26) 1.41	0.10 (0.10)	77.25 (0.88) 3.61	0.90(0.35)	20.15 (0.17) 2.59	0.25 (0.06)	9.40 (0.19) 6.54	0.80 (0.13)
Orthotomus sutorius	ш	10	50.03(0.57)3.57	0.45(0.09)		.	19.10 (0.06) 0.98	0.18(0.04)	78.05 (4.55) 18.43	2.20(0.74)
M (1) - central tail feathers	f	10	46.68(0.49)3.30	0.35(0.13)	I	I	19.65(0.13)2.09	0.21 (0.02)	$38.30\ (1.00)\ 8.28$	0.20(0.11)
Malurus splendens	В	10	51.40(0.26)1.58	0.89(0.20)	60.25 (0.55) 2.88	0.63 (0.26)	22.06 (0.17) 2.50	0.16 (0.07)	8.45(0.16)5.88	0.60(0.25)
M (31) - moustache	f	10	50.20(0.62)3.91	0.60(0.22)	58.17 (0.76) 3.89	0.38(0.26)	21.73 (0.26) 3.74	0.16(0.05)		.
Terpsphone viridis	H	10	84.65 (1.13) 4.21	1.30(0.26)			16.91 (0.29) 5.40	0.14(0.05)	272.55 (13.20) 15.32	6.30 (1.78)
M (26) - central tail feathers	Ļ	10	77.30 (0.72) 2.93	0.80(0.25)	Ι	I	16.06 (0.21) 4.07	0.13(0.03)	85.95 (3.08) 11.32	1.30(0.52)
Nectarinia johnstoni	Ε	10	79.45 (1.13) 4.49	0.30(0.15)		I	16.74 (0.19) 3.67		155.70 (6.80) 13.81	4.00 (0.78)
M (9) - central tail feathers	ني.	10	71.55 (1.20) 5.30	0.50(0.17)	50.80 (1.18) 7.37	0.22(0.08)	17.80 (0.52) 9.22	0.23(0.24)	I	
Anthochaera carunculata	ш	10	154.95 (1.92) 3.93	0.50(0.22)	I	ļ	34.48 (0.28) 2.59	0.29 (0.07)	159.95 (3.85) 7.61	0.90(0.31)
M (25) - central tail feathers	f	10	144.95(2.84)3.65	0.50(0.27)	I	I	33.37(0.35)3.32	0.31 (0.08)	147.00 (2.27) 4.87	1.20(0.53)
Prosthemadera novaeseelandiae	ш	10	151.95 (2.05) 4.26	0.90(0.28)	121.35 (2.02) 5.27	0.90(0.23)	38.61 (0.34) 2.78	0.79 (0.15)	$33.45\ (0.93)\ 8.81$	0.50(0.17)
M (30) - neck feathers	f	10	140.85(2.26)5.08	1.10(0.46)	115.65 (1.98) 5.40	1.10(0.46)	36.22 (0.81) 7.11	0.34 (0.07)	30.65(1.05)10.85	0.70(0.26)
Melophus lathami	Е	10	84.70 (0.51) 1.89	0.70(0.26)	70.88 (1.19) 5.30	0.25 (0.13)	20.64 (0.20) 2.98	0.20(0.06)	$24.50\ (0.48)\ 6.24$	I
M(1) - crest	بب	10	77.93 (0.68) 2.78	0.75(0.24)	66.75 (1.01) 4.77	0.60(0.22)	20.35 (0.18) 2.72	0.24 (0.08)	16.00(0.40)7.93	i
Cardinalis cardinalis	ш	10	95,48 (1.00) 3.32	0.35(0.13)	102.08 (1.73) 5.36	0.25(0.08)	24.56 (0.25) 3.20	0.09 (0.03)	$30.10 \ (0.66) \ 6.95$	I
M (8, 29) - crest	f	10	91.65 (0.76) 2.62	0.70 (0.17)	96.25(1.09)3.59	0.40(0.26)	$24.50\ (0.21)\ 2.65$	0.16(0.02)	28.80 (0.60) 6.56	I
Quiscalus mexicanus	ш	10	199.45 (2.67) 4.24	0.50(0.17)	1		51.22 (0.65) 4.03	0.17 (0.04)	199.60(6.48)10.26	2.00(0.60)
P (8, 29) - central tail feathers	ر	10	160.40 (2.07) 4.08	1.00(0.30)	a ta	ţ	41.94 (0.59) 4.46	0.18(0.03)	149.95(4.62)9.73	0.70(0.42)
Erythrura prasina	Ш	10	58.73 (0.22) 1.18	0.45(0.12)	I	I	14.56 (0.08) 1.67	0.17 (0.03)	59.63(1.38)7.33	1.05(0.23)
M (5, 14) - central tail feathers	<i>ب</i>	10	59.53 (0.31) 1.63	0.55(0.17)	į	I	14.67 (0.11) 2.41	$0.11 \ (0.03)$	41.38(1.14)8.69	0.75(0.31)
Vidua macroura	Е	10	73.40 (0.77) 3.32	1.10(0.26)	ļ	I	16.65 (0.20) 3.87	0.24(0.07)	215.45(5.03)7.39	1.70(0.58)
L (24) - central tail feathers	Ļ	10	69.68 (1.05) 4.78	0.85(0.24)	53.60 (0.73) 4.32	0.20(0.08)	16.31 (0.16) 3.13	0.20 (0.07)	I	1
Euplectes jacksoni	ш	10	92.10 (0.76) 2.62	0.40(0.22)	į		28.27 (0.22) 2.46	0.20(0.06)	208.40(2.11)3.20	2.40(0.95)
L (24) - central tail feathers	ب	10	84.10(0.69)2.61	1.40(0.40)	50.00(0.99)6.25	0.80(0.33)	28.85(0.19)2.06	0.65(0.12)	ŧ	
Aplonis metallica	Ħ	01	110.60 (0.41) 1.18	0.60(0.22)	l		22.39(0.21)2.99	0.29(0.09)	99.00(1.54)4.91	1.20(0.33)
M (2, 3) - central tail feathers	Ļ	10	106.15 (1.06) 3.15	0.78(0.15)			22.44 (0.25) 3.50	0.13(0.04)	94.05(1.81)6.10	1.50(0.58)
Stumus unicolor	ш	01	130.90 (0.45) 1.09	0.89(0.20)	65.20 (0.81) 3.91	0.40(0.16)	29.79 (0.22) 2.34	0.30(0.06)	32.60 (1.22) 11.79	1.80(0.53)
M (6) - throat feathers	·	10	127.20 (0.79) 1.95	0.60(0.22)	61.75 (0.75) 3.84	0.30(0.21)	29.42(0.31)3.31	0.27 (0.08)	22.70 (0.94) 13.14	$0.80 \ (0.25)$
										continued

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Species	Sex	u	Wing Mean (SE) CV	FA (SE)	Tail Mean (SE) CV	FA (SE)	Tarsus Mean (SE) CV	FA (SE)	Ornamen Mean (SE) CV	t FA (SE)
Dicrurus paradisaeus M (1) - external tail feathers	f m	10	161.80 (2.06) 4.02 156.05 (1.86) 3.76	1.20 (0.33)		1	$26.70 \ (0.37) \ 4.36$ $95 \ 94 \ (0.47) \ 5 \ 74$	0.27 (0.05) 0.18 (0.05)	356.25 (15.82) 14.04 329 50 (9.08) 8 90	3.90 (1.39) 6 20 (1.31)
Amblyomis subalaris	- u	2 2	122.25 (0.74) 1.92	0.70 (0.21)	90.70 (0.80) 2.80	0.40 (0.16)	34.40 (0.43) 3.93	0.37 (0.07)	37.50 (0.82) 6.91	-
L (13, 24) - crest	Ļ	10	122.75 (1.19) 3.06	0.90(0.28)	88.85(0.84)2.99	0.50(0.22)	34.98(0.40)3.64	0.32(0.07)	.	1
Pteridophora alberti	E	6	123.89 (1.29) 3.11	0.63(0.26)	87.56 (1.06) 3.63	0.44 (0.24)	31.85 (0.27) 2.51	0.67 (0.18)	435.11 (15.26) 10.52	4.44(1.59)
L (13, 24) - eye feather	ц,	I			1	1	1		I	1
Ptiloris magnificus	Е	10	186.45 (0.96) 1.62	1.30(0.37)	106.05 (1.03) 3.08	0.11 (0.11)	41.48 (0.37) 2.80	0.37 (0.10)	179.30(4.42)7.80	3.20(0.90)
L $(13, \overline{24})$ - flank plumes	f	10	156.30 (1.86) 3.77	0.80(0.29)	102.35 (1.15) 3.54	0.70(0.21)	37.26 (0.58) 4.92	0.45(0.11)	72.90 (2.13) 9.22	3.00(1.08)
Semioptera wallacei	E	10	153.65 (0.79) 1.62	0.90 (0.31)	87.55 (1.46) 5.28	0.50 (0.17)	42.38 (0.30) 2.23	0.58(0.15)	158.90(2.46)4.90	4.00(0.91)
L (7, 24) - wing feathers	f	10	143.45 (1.96) 4.32	0.70(0.30)	88.25 (1.18) 4.22	0.70(0.30)	40.69 (0.33) 2.58	0.72 (0.17)		I
Lophorina superba	Е	10	130.60 (0.80) 1.93	1.00(0.30)	90.30 (0.53) 1.87	0.22(0.15)	32.67 (0.27) 2.65	0.45(0.13)	122.60(1.90)4.91	1.40(0.31)
L (13, 24) - cape	f	10	115.80 (1.03) 2.80	0.60(0.22)	82.30 (1.05) 4.03	0.40(0.16)	29.87 (0.32) 3.36	0.33(0.08)		I
Diphyllodes magnificus	Ħ	10	113.75 (0.85) 2.35	0.40(0.15)	43.50 (0.68) 4.91	0.40(0.22)	32.15 (0.14) 1.40	0.19(0.04)	41.00 (1.00) 7.71	2.20 (0.92)
L (13, 24) - neck tuft	f	10	107.70 (0.54) 1.58	0.40(0.16)	62.80 (1.28) 6.43	0.40(0.16)	30.15 (0.23) 2.40	0.46(0.09)		
Paradisaea rubra	н	10	168.80 (1.00) 1.88	1.60(0.54)	I	I	43.44 (0.37) 2.54	0.33 (0.17)	517.00 (4.84) 2.96	14.00(7.63)
L (7, 24) - central tail feathers	ب	10	152.60 (1.55) 2.28	2.00(0.63)	119.00 (1.00) 1.88	2.00(2.00)	40.95 (0.80) 4.37	1.10(0.40)	I	1
Parotia lawesii	Ħ	10	156.85 (1.95) 3.93	0.90(0.18)	I		47.76 (0.85) 5.63	1	24.00(0.47)6.13	1.00(0.21)
L (7, 24) - breast shield	Ļ	10	148.75 (1.77) 3.75	0.90(0.31)	99.90 (0.92) 2.91	0.60(0.22)	49.69 (0.76) 4.86	0.28(0.06)		
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APPENDIX-continued

PHENOTYPIC VARIANCE AND ASYMMETRY IN ORNAMENTS

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