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MATING SYSTEMS, SPERM COMPETITION, AND THE EVOLUTION OF SEXUAL DIMORPHISM IN BIRDS

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Abstract.—Comparative analyses suggest that a variety of factors influence the evolution of sexual dimorphism in birds. We analyzed the relative importance of social mating system and sperm competition to sexual differences in plumage and body size (mass and tail and wing length) of more than 1000 species of birds from throughout the world. In these analyses we controlled for phylogeny and a variety of ecological and life-history variables. We used testis size (corrected for total body mass) as an index of sperm competition in each species, because testis size is correlated with levels of extrapair paternity and is available for a large number of species. In contrast to recent studies, we found strong and consistent effects of social mating system on most forms of dimorphism. Social mating system strongly influenced dimorphism in plumage, body mass, and wing length and had some effect on dimorphism in tail length. Sexual dimorphism was relatively greater in species with polygynous or lekking than monogamous mating systems. This was true when we used both species and phylogenetically independent contrasts for analysis. Relative testis size was also related positively to dimorphism in tail and wing length, but in most analyses it was a poorer predictor of plumage dimorphism than social mating system. There was no association between relative testis size and mass dimorphism. Geographic region and life history were also associated with the four types of dimorphism, although their influence varied between the different types of dimorphism. Although there is much interest in the effects of sperm competition on sexual dimorphism, we suggest that traditional explanations based on social mating systems are better predictors of dimorphism in birds.

Key words.—Comparative analysis, extrapair mating, independent contrasts, life-history evolution, sexual selection.

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Evolutionary biologists have been trying to explain sexual differences in size and plumage of birds ever since Darwin (1871). Indeed, Krebs (1979) noted that this was one of the most difficult problems in evolutionary biology. Today sexual selection is generally accepted as one of the most important factors in the evolution of sexual dimorphism (Andersson 1994; reviewed by Savalli 1995; Badyaev and Hill 1999). Males that are relatively larger in size or brighter in plumage are assumed to gain more mates through a selective advantage in terms of male-male competition or female choice. This hypothesis was originally proposed by Darwin (1871) and has been supported by many intraspecific studies that show a mating advantage for larger or showier males (reviewed by Andersson 1994). Comparative studies also have found support for this hypothesis (Payne 1984; Webster 1992; Winquist and Lemon 1994), although the evidence in birds is controversial (e.g., Oakes 1992). In these analyses it has been assumed that variance in male mating success is correlated with the type of social mating system or number of mates per male. For example, the variance in male mating success is thought to be lower in monogamous than polygynous species because polygyny will result in some males monopolizing many mates, whereas most males in monogamous species will have just one mate.

Despite this support for the sexual selection hypothesis, there seem to be many exceptions. For example, many monogamous species are also dimorphic (Møller 1986; Burns 1998), which would not be predicted based on their apparently low variance in male mating success. Darwin (1871) recognized this problem and suggested that males with brighter plumage or larger body size will gain a reproductive advantage by mating with females that are more fecund. If the most fecund females arrive on the breeding grounds first and prefer to mate with the largest or brightest males, then those males will not be available as mates to later arriving and less fecund females (see also Kirkpatrick et al. 1990). Thus, the problem of low variance in number of mates per male is circumvented by large variance in the quality of females.

Another possible explanation for dimorphism in monogamous species is that male mating success is more variable than it appears. Recent genetic studies have shown that extrapair matings are common in some monogamous birds, and it has been suggested that females often seek copulations from extrapair males to improve the genetic quality of their offspring (e.g., Birkhead and Møller 1992). As a consequence, highly favored males in an apparently monogamous species will gain many of the fertilizations and increase the variance in actual mating success of males. Therefore, if sexual dimorphism is produced by female choice, it could evolve as a consequence of either direct or indirect selection. Direct selection occurs when females gain immediate reproductive or survival benefits (e.g., territorial resources) from choosing particular types of mates (the Darwinian hypothesis; see Kirkpatrick et al. 1990). In contrast, indirect selection occurs when females gain benefits through their offspring by improving their genetic quality and, as a consequence, the reproduction or survival of those offspring (e.g., good genes hypotheses).

In a comparative analysis of birds, Møller and Birkhead (1994) examined these direct and indirect hypotheses for sexual dimorphism in plumage coloration. They concluded that

TABLE 1. Geographic regions and mating systems of bird species examined in this study and by Owens and Hartley (1998) and Møller and Birkhead (1994).

	This study		Owens and Hartley (1998)		Møller and Birkhead (1994)	
	N species	% of sample	*N* species	% of sample	*N* species	% of sample
Geographic region						
North America	376	36	25	34	23	42
Eurasia	90	9	31	42	24	44
South and Central America	154	15	2	3	3	5
Africa	21	2	0	0	1	2
Australasian	372	36	8	11	4	7
Other (oceanic and Southeast Asia)	18	2	6	8	0	0
Social mating system[1]						
Polyandry	17	2	3	4	1	2
Monogamy	774	75	40	55	26	47
Monogamy/polygyny	33	3	11	15	15	27
Polygyny	46	4	5	7	5	9
Lek and promiscuous	55	5	1	1	1	2
Cooperative	106	10	13	18	7	13
Total species	1031		72		55	

[1] Our categories of social mating system differ from Owens and Hartley (1998) and Møller and Birkhead (1994); thus, we have reclassified some species in this table to fit our scheme.

sexual dimorphism was related to the population-wide level of extrapair mating and not to the type of social mating system (e.g., polygyny, lekking, monogamy). Because females rarely gain direct benefits (e.g., paternal care) from their extrapair mates, Møller and Birkhead argued that plumage dimorphism had evolved through indirect (i.e., good genes) rather than direct selection. Recently, Owens and Hartley (1998) also found that sexual dimorphism in plumage coloration was related to population levels of extrapair paternity and not to social mating system. They also examined sexual dimorphism in size (body mass) and found that it was related to social mating system, but not to levels of extrapair paternity. Thus, different mechanisms may have produced different types of sexual dimorphism. These studies provide interesting and plausible explanations for sexual dimorphism in monogamous species. However, there are several considerations that suggest further study is warranted. First, the studies of Møller and Birkhead (1994) and Owens and Hartley (1998) relied on estimates of extrapair mating from molecular studies that have been conducted on a relatively small subset of bird species in terms of both phylogeny and geographic distribution. For example, Owens and Hartley (1998) examined 73 species from 21% of all families (144 families in Monroe and Sibley 1993), and most (77%, 56/73) of these species were primarily north temperate in distribution. Second, recent reviews of the literature (Alatalo et al. 1998; Møller and Alatalo 1999) and theoretical models (Kirkpatrick 1996; Kirkpatrick and Barton 1997) suggest that indirect selection is probably weaker than direct selection on female mating preferences, and, thus, is unlikely to produce the extreme examples of sexual dimorphism seen in nature. This suggests that social mating systems might be more important to dimorphism than extrapair mating (sperm competition), assuming that indirect benefits are the main type of benefit from extrapair mating.

In this paper we analyze the relative importance of social mating system and sperm competition to sexual dimorphism of more than 1000 species of birds from throughout the world. We examine four types of dimorphism as these may evolve independently (e.g. Lowther 1975; Owens and Hartley 1998), including dimorphism in plumage, body mass, and tail and wing length. Our estimate of extrapair mating is based on testis mass (relative to total body mass), which is correlated with population levels of extrapair paternity in birds (Møller and Briskie 1995) and is a reliable indicator of the level of sperm competition in a wide variety of vertebrates and invertebrates (reviewed by Møller and Briskie 1995; Parker et al. 1997). Data on testis size are also available from a much larger and phylogenetically diverse sample of birds than has been studied to date with molecular parentage techniques.

METHODS

Sexual Dimorphism

We collected data on dimorphism in size (total body mass, tail and wing length) and plumage from both museum specimens and the literature (e.g., Ridgway 1901–1946; Cramp and Simmons 1977, 1980, 1983; Cramp 1985, 1988, 1992; Cramp and Perrins 1993, 1994a,b). Specimens were examined at collections in North America and Australia (see Acknowledgments). Published data on dimorphism vary in quality. For example, some references report data as ranges rather than means, in which case we used the midpoints of the ranges for each sex (e.g., Bannerman 1953). It is well known that dimorphism may vary geographically within the range of a species (e.g., Mayr 1942), thus, for each species we attempted to use data from the same location wherever possible. A summary of the data by geographic region and social mating system is presented in Table 1. The complete dataset is available from P.O. Dunn.

Size dimorphism

Morphometric data on body mass and tail and wing length were $\log_{10}$-transformed prior to analysis. Dimorphism in size was analyzed using the residuals from the regression of the male trait on the female trait, which avoids the statistical pitfalls of ratios (Sokal and Rohlf 1981, p.18; Ranta et al.

1994). The raw residuals were used in the analyses of species, whereas phylogenetically corrected values (see Martins and Garland 1991; Purvis and Rambaut 1995) were used for analyses of independent contrasts (see below).

Plumage dimorphism

Plumage dimorphism was scored on a scale from 0 (monomorphic) to 10 (maximum dimorphism) following Owens and Bennett (1994). For each species the difference in plumage between the sexes was scored over five regions of the body (head, nape-back-rump, throat-belly, tail, and wings) using three scores (0, no difference between the sexes; 1, difference in shade or intensity; 2, difference in color or pattern). Average dimorphism was obtained from scores of two persons, including at least one person unaware of our predictions. Several other studies of plumage dimorphism have estimated the brightness of each sex separately and then computed dimorphism by subtracting the female score from the male score (e.g., Møller and Birkhead 1994; Martin and Badyaev 1996). This method is valuable for studying the evolution of bright coloration, which can occur in both sexually monomorphic and dimorphic species (Amundsen 2000). However, it can sometimes lead to erroneous estimates of dimorphism, because differences among human scorers may lead to differences in dimorphism, even when none exist. To avoid this potential problem, we scored plumage dimorphism relative to the other sex of the same species, rather than in absolute terms of brightness or colorfulness. We scored plumage dimorphism of fully mature breeding adults and did not consider first-year plumages that are not as developed in some species.

Type of dimorphism

Darwin (1871, pp. 80–81) and others (e.g., Owens and Hartley 1998) have remarked on the different types of plumage dimorphism in birds. To quantify part of this variation, we classified the dimorphism of each species as either seasonal (dimorphism occurs in the breeding season) or year-round. The first category included groups such as the ducks (Anatidae), fairy-wrens (Maluridae), and some weavers (*Euplectes*) and wydahs (*Vidua*), in which the sexes are dimorphic during the breeding season, but the male plumage (eclipse) resembles the female plumage during at least a part of the nonbreeding season. These cases were identified from Bannerman (1953), Bellrose (1980), and Rowley and Russell (1997). This classification also allows one to examine the proximate control of plumage dimorphism, because plumage differences can be under genetic (as in year-round differences) or physiological control (as in seasonal or mostly year-round differences; see Owens and Short 1995).

Social Mating Systems

Species were assigned to one of six mating system categories: (1) polyandry; (2) monogamy ($<$ 5% polygyny); (3) mostly monogamy, but occasional polygyny (5–15% polygyny; see Ehrlich et al. 1988); (4) mostly polygyny ($>$ 15% polygyny; see Ehrlich et al. 1988); (5) cooperative breeding; and (6) lek or promiscuous. This last category includes species in which the male attracts mates to courts or arenas and contributes no resources other than sperm to the raising of young: lekking species, as well as lyrebirds, bowerbirds, and most birds of paradise. Assignments were made based on standard references (e.g., Ehrlich et al. 1988, 1994; Stiles and Skutch 1989; Readers' Digest 1990; Poole et al. 1992–1998; Higgins and Davies 1996) with preference given to the most current or detailed source where more than one was available. Mating systems of many species outside North America and Europe have not been studied sufficiently to discriminate between the monogamy and mostly monogamy categories, so in ambiguous cases we placed species in the monogamy category. Analyses that combined these two categories for all species provided qualitatively similar results and are not shown here. Sample sizes differ among analyses because the mating systems of some species were unknown.

Testis Mass

We used relative testis mass during the breeding season as an index of sperm competition in each species (Møller and Briskie 1995). Relative testis mass was estimated from the residuals of the regression of testis mass on total body mass of males. If male body mass was unavailable, we used total body mass as reported in the literature, which may contain both males and females. In our sample these two variables were highly correlated ($r^2 = 0.99$, $N = 542$, $P < 0.0001$), and our main results were unchanged when we restricted our analysis to species in which total mass was known for males. Both testis and total mass were $\log_{10}$-transformed prior to analysis, and, except where noted, all regressions controlled for phylogenetic effects (see below). Testis mass for each species was obtained using unpublished (e.g., Gamble 1966; McLaughlin 1993) and published compilations (Møller 1991; Møller and Briskie 1995; Stutchbury and Morton 1995) or data from tags of museum specimens, which consisted of testis length and width measurements. Testis mass was estimated from these measurements using the formula: testis mass (g) $= 2 \times 1.087\ \text{g}\cdot\text{cm}^{-3} \times 1.33\pi\ [a^2(\text{cm}^2)]b(\text{cm})$, where a and b are the shortest and longest radii of each testis (see Møller 1991; Møller and Briskie 1995). In cases where more than one estimate was available for the same species, we used the average of available estimates. Analyses with both the minimum and maximum estimates for each species gave similar results.

Average testis mass was calculated as the mean testis value from at least five breeding males, but typically 10 or more breeding males were used (e.g. Møller 1991; Møller and Briskie 1995). Breeding status was determined with a variety of methods in each study, but in our experience breeding season could be determined unambiguously with a visual inspection of testis size plotted against date. In some tropical species it was apparent that breeding occurred throughout the year or at variable times. In these cases only individuals with enlarged testes were used. Where possible, this was confirmed with independent data on the breeding season (e.g., presence of brood patch on specimens). Thus, it is possible that some nonbreeding individuals have been included in our analyses. However, using our own specimen data, there was a strong correlation between the mean and maximum testis masses (r^2

= 0.96, $P < 0.05$), which suggests that we did not underestimate mean testis mass because we included nonbreeders.

Potentially Confounding Variables

Recent studies have questioned the traditional view that sexual dimorphism is mainly the result of sexual selection on males and have shown that various ecological and life-history factors can also influence dimorphism in some groups of birds (e.g., Erwin 1994; Martin and Badyaev 1996; Burns 1998). Thus, we used multiple regression analysis to control for a number of factors that may influence sexual dimorphism, including nest height (Johnson 1991; Martin and Badyaev 1996), nest type, migratory behavior (Lowther 1975; Fitzpatrick 1994), and parental care (Owens and Hartley 1998). Following Martin and Badyaev (1996), nests were classified as ground nests if they were on the ground, shrub nests if generally above the ground but ≤3 m high, and tree level if higher than 3 m. Nest type was examined in two ways: (1) open (birds are exposed on the nest) or closed (cavity, burrow, or enclosed nests); and (2) cavity or noncavity. We coded migratory behavior as either migratory or resident. Species were considered migratory if they had largely nonoverlapping winter and summer ranges (≤ 50% overlap) and resident if there was little seasonal change in distribution (> 50% overlap in ranges; Lowther 1975). It has been suggested that male participation in incubation may limit the ability of males to engage in extrapair mating activity, and, thus, levels of extrapair paternity will be lower in species with male incubation (Ketterson and Nolan 1994). To control for this effect, we coded each species as female-only incubation or male and female incubation. Finally, we included geographic region for each species in our analysis because it is conceivable that the environment may influence dimorphism independent of phylogeny. These regions were North America (north of Mexico), Eurasia, Africa, South and Central America, Australasia (Australia, New Guinea, and New Zealand), and other (11 species from Southeast Asia and seven oceanic species; see Table 1 for distribution of data). In cases where a species overlapped two or more regions, we used the region from which we collected most of our testis or size dimorphism data (e.g., *Hirundo rustica* was considered Eurasian).

Comparative Methods

There is debate about the importance of using comparative methods to control for shared evolutionary history (Ricklefs 1996; Price 1997; Harvey and Rambaut 1998). However, differences between results using raw species data and phylogenetic methods may provide some biological insight (Price 1997). Thus, we have analyzed our data using both comparative methods that control for phylogeny (independent contrasts) and the raw species values. To produce data that were phylogenetically independent under a specific evolutionary model, we calculated standardized linear contrasts (Felsenstein 1985; Harvey and Pagel 1991) as implemented by the computer package Comparative Analysis of Independent Contrasts (CAIC) of Purvis and Rambaut (1995). The CAIC program produces linear contrasts that are standardized differences in traits at evolutionarily independent nodes in the phylogeny (Purvis and Rambaut 1995). Contrasts were standardized assuming that lengths of branches in the phylogeny were equal in length, which represents a punctuated model of evolution, or proportional to the number of taxa in each clade (Grafen 1989), which is similar to a gradual model of evolution. Owens and Hartley (1998) used equal branch lengths, whereas Møller and Birkhead (1994) used proportional branch lengths. In several cases these two assumptions produced different results in our study, so we present both types of analysis.

Our phylogeny was based on the molecular phylogeny of Sibley and Ahlquist (1990), which provides a branching pattern to the level of family, subfamily, or tribe, depending on the clade. When we had more than two species below the lowest level in Sibley and Ahlquist's phylogeny, we used recent phylogenetic analyses to complete the phylogeny to the species level (storks: Slikas 1997; waterfowl: Livezey 1996a,b; manakins: Prum 1990; bowerbirds: Kusmierski et al. 1997; fairy-wrens: Christidis and Schodde 1997; swallows: Sheldon and Winkler 1993; parids: Sheldon et al. 1992; Slikas et al. 1996; New World warblers: Bermingham et al. 1992; tanagers: Burns 1998; cardueline finches: Badyaev 1997; sparrows: Zink and Blackwell 1996; Icterids: Freeman and Zink 1995). In cases where there was no completely bifurcating phylogeny available, we formed polytomies (nodes with more than two descendant taxa), although we assumed that genera as described by Monroe and Sibley (1993) formed monophyletic groups. The CAIC package uses a predictor variable defined by the user to interpret polytomies (Purvis and Rambaut 1995). At polytomies, CAIC assumes that the true phylogeny is bifurcating and can be split in two based on the mean value of the predictor variable (see Purvis and Rambaut 1995). One group consists of taxa with values for the predictor variable that are above the mean and the other with values below the mean. Thus, it is assumed that the predictor variable can supply some phylogenetically useful information (Purvis and Rambaut 1995). In our bivariate analyses of dimorphism, the predictor variable was the independent variable (either testis size or social mating system), whereas in multivariate analyses we used testis size as the predictor variable because it was available for the largest number of species.

Tests of association between traits were performed by regressing the contrasts of one trait against the contrasts of another trait. All regressions were forced through the origin, because the mean value of independent contrasts is expected to be zero under the null hypothesis (Harvey and Pagel 1991). We used the CRUNCH procedure of CAIC to analyze both continuous and categorical variables. Categorical variables (geographic region, mating system, and nest height) were examined using dummy variables that were phylogenetically transformed (see Winquist and Lemon 1994; Martin 1995; Martin and Badyaev 1996). Independent contrasts for these categorical variables indicate the proportion of taxa in each category (Winquist and Lemon 1994). Multiple regression analysis was used to determine whether the proportions of taxa in different categories were associated with the dependent variable (dimorphism). The overall significance of categorical variables was tested by the cumulative change in sums of squares when $n - 1$ dummy variables were entered

TABLE 2. Sexual dimorphism among birds in relation to testis mass and social mating system. Probability values are given for regression analyses of species and independent contrasts (regressions forced through the origin using the CRUNCH procedure in CAIC; see Methods). Contrasts were calculated using phylogenies with both variable and equal branch lengths, corresponding to gradual and punctuated models of evolution, respectively. Bold indicates significant variables or ones included in the final stepwise regression model. Where two values are given for sample size, they are for testis mass and social mating system, respectively; otherwise they were the same for both. Plumage dimorphism was $\log_{10}$-transformed for the analysis of contrasts. Asterisks indicate results after one or two outliers were removed.

	Species		Independent contrasts			
			Bivariate		Multivariate	
Variables	Bivariate	Multivariate	Gradual	Punctuated	Gradual	Punctuated
Plumage dimorphism						
Testis mass (relative)	< **0.0001**	**0.01**	0.86*	0.21	**0.13**	**0.11**
Social mating system	< **0.0001**	< **0.0001**	**0.025**	**0.0014**	**0.008**	**0.009**
N	1011, 1010	621	462	462	343	343
Body mass dimorphism						
Testis mass (relative)	0.11	0.31	0.86*	0.79	0.22	0.62
Social mating system	< **0.0001**	< **0.0001**	< **0.0001**	< **0.0001**	< **0.0001**	< **0.0001**
N	517, 508	408	301	301	250	250
Tail length dimorphism						
Testis mass (relative)	**0.006**	**0.006**	**0.004**	**0.033***	**0.006**	**0.0001**
Social mating system	< **0.0001**	< **0.0001**	0.47	**0.002**	**0.007**	**0.038**
N	618, 614	463	326	326	271	271
Wing length dimorphism						
Testis mass (relative)	< **0.0001**	**0.0009**	**0.017**	**0.04**	**0.007**	**0.003**
Social mating system	< **0.0001**	< **0.0001**	< **0.0001**	< **0.0001**	< **0.0001**	< **0.0001**
N	719, 714	531	365	365	304	304

as a group into a regression model (Martin 1995). To determine which categories differed from one another, we calculated contrasts for each category and then used the Tukey-Kramer test for multiple comparisons, which holds the experiment-wide alpha level to 0.05 (SAS Institute 1995). Contrasts for each category were calculated by multiplying the standardized contrast for dimorphism by its corresponding contrast for the dummy variable throughout the phylogeny (note that here all *n* dummy variables were used). Our figures show the mean and SE for these products in each category.

We also performed several diagnostic analyses of our regression results, as suggested by Purvis and Rambaut (1995). For example, the method of independent contrasts implemented in CAIC is based on Felsenstein (1985) and assumes that continuous characters evolve in a random walk process. We tested this assumption by regressing the absolute values of standardized contrasts in plumage and size dimorphism against the estimated dimorphism values of ancestral taxa at corresponding nodes in the phylogeny (Purvis and Rambaut 1995). Although some of these regressions showed significantly positive slopes ($0.05 > P > 0.02$), the slopes (beta $<$ 0.05) and coefficients of determination ($r^2 < 0.025$) of these regressions were low, suggesting that different clades were equally likely to develop similar proportional changes in dimorphism. Plumage dimorphism was $\log_{10}$-transformed to provide a better fit to this random walk model (results were qualitatively similar with untransformed data). We also examined all regressions for the presence of outliers (residuals $\geq$ 3 SD from the mean; Kleinbaum and Kupper 1978) that might change the outcome. Regressions that were dependent on one or two outliers were considered weak, and, thus, we based our conclusions on the test results without outliers. For simplicity, we present our results without outliers; our main conclusions concerning testis size and mating system remain unaffected by their inclusion or removal.

We performed multivariate analyses to control for any potentially confounding relationships. However, complete data were not available for each species. For example, in the analysis of plumage dimorphism all 10 independent variables (listed in Table 3) were available for 621 of 1031 species. Thus, adding all variables to one regression model reduced our sample size to 343 contrasts (from a maximum of 462 in the bivariate analyses; see Table 2). Note that this change in sample size also changed the branches (and taxa) examined, and, thus, different results among models may be due to sample size or species differences. We attempted to address this problem by examining models with both the largest (bivariate) and smallest (multivariate models with all variables) sample sizes. Multivariate models with all variables were tested subsequently with stepwise regression to determine if any variables should be removed (*P* to enter and remove = 0.10). For any particular set of variables, we used Akaike's information criterion (AIC) to choose a final model that was simple yet had high predictive power (SAS Institute 1995).

RESULTS

Data on plumage dimorphism, testis size, and total body mass were obtained for 1031 species of birds, representing 20 of 23 orders (Bucerotiformes, Upupiformes, and Musophagiformes were not represented) and 91 of 144 families described by Monroe and Sibley (1993). Species from every continent were sampled, but most were from North America (36%), Australasia (36%), and South and Central America (15%). The geographic distribution of species in this study differed from that of species studied by Owens and Hartley (1998) and Møller and Birkhead (1994; see Table 1). Below, we begin by analyzing the effects of testis size and social mating system on each type of dimorphism. Then, we include all potentially confounding variables in multiple regression

TABLE 3. Multiple regression analysis of sexual dimorphism in plumage and body mass among birds. Probability values are given for the initial multiple regression analyses of species and independent contrasts with all 10 independent variables. Variables included in the final stepwise regression model are indicated in bold (individual *P*-values not shown). Plumage dimorphism was $\log_{10}$-transformed for the analysis of contrasts.

	Plumage dimorphism			Mass dimorphism		
Independent variable	Species *P*	Gradual *P*	Punctuated *P*	Species *P*	Gradual *P*	Punctuated *P*
Testis mass (relative)	**0.01**	**0.13**	**0.11**	0.31	0.22	0.62
Social mating system	< **0.0001**	**0.002**	**0.002**	< **0.0001**	< **0.0001**	< **0.0001**
Geographic region	**0.17**	< **0.0001**	**0.004**	0.49	< **0.0001**	**0.016**
Clutch size	**0.014**	0.22	0.95	**0.004**	0.63	0.38
Nest height	**0.002**	**0.019**	**0.035**	**0.044**	0.12	0.61
Total body mass	0.21	0.52	**0.032**	0.17	< **0.0001**	**0.068**
Migratory or nonmigratory	0.76	**0.002**	0.24	0.85	0.23	0.95
Female-only or female and male incubation	< **0.0001**	0.54	0.37	0.64	0.39	0.46
Cavity or noncavity nest	0.81	0.22	**0.022**	0.90	0.064	0.30
Closed or open nest	0.62	0.23	0.18	0.82	**0.017**	0.24
Multiple regression						
R^2	0.19	0.23	0.17	0.24	0.39	0.18
P	<0.0001	<0.0001	< 0.0001	< 0.0001	<0.0001	0.0003
N species used	621	621	621	408	408	408
N contrasts		343	343		250	250
Final stepwise model R^2	0.17	0.22	0.15	0.21	0.37	0.17

analyses. For brevity, we focus on the confounding variables that gave consistent results across several analyses.

Plumage Dimorphism

Social mating system and testis size

Plumage dimorphism was associated with social mating system when we analyzed more than 1000 species (Tables 2, 3). Overall, taxa were more dimorphic in plumage if they were polygynous or lek/promiscuous (Fig. 1A, B). In the analysis of species, plumage dimorphism was greatest in lek species, smaller in polygynous species, and smallest among all other types of mating system (Fig. 1A; Tukey-Kramer tests). When we analyzed independent contrasts, dimorphism differed primarily because of differences between monogamous and polygynous or lek species (Fig. 1B; Tukey-Kramer tests).

In contrast to social mating systems, plumage dimorphism was related less consistently to relative testis mass (Tables 2, 3). Although species with larger testes were more dimorphic (Fig. 2A, B), this relationship was less consistent when we analyzed independent contrasts (Table 2). The bivariate analysis of contrasts showed no relationship (Table 2), but in the final stepwise regression models testis mass was related positively to plumage dimorphism ($P = 0.08$ and 0.056 for gradual and punctuated models, respectively). This difference between bivariate and multivariate analyses was due to the use of different taxa in each type of analysis, as the bivariate relationship was significant ($P = 0.039$ for gradual model) when we restricted the analysis to those taxa used in the final stepwise regression. In summary, plumage dimorphism was related positively to testis size, although the relationship may depend on the taxa analyzed.

Geography, ecology, and life history

Plumage dimorphism was related also to nest height and geographic region (Table 3). Overall, taxa that nested at intermediate height (in shrubs) were more dimorphic than taxa that nested on the ground or in trees. When we analyzed the species data, there was little evidence that plumage dimorphism varied geographically (Fig. 3A), although geographic region was included as a predictor in the final stepwise model ($P = 0.10$; Table 3). However, when we examined independent contrasts, dimorphism in plumage was relatively greater in taxa from Eurasia, Africa, and other (Southeast Asia and oceanic) and smaller in taxa from North America (Tukey-Kramer tests, Fig. 3B). Some regression models also suggested that plumage dimorphism was greater in species that laid larger clutches, had female-only incubation (i.e., males did not incubate), and nested in open nests rather than in closed nests (Table 3). However, these results were not consistent across the three types of analyses (species and two types of contrasts). Plumage dimorphism also tended to be greater for species that were seasonally dichromatic (e.g., many ducks; mean ± SE = 4.9 ± 0.3, $n = 88$) than species that were dichromatic year-round (mean ± SE = 4.2 ± 0.2, $n = 321$; $t = 1.87$, $P = 0.06$).

Body Mass Dimorphism

Social mating system and testis size

Similar to plumage dimorphism, dimorphism in body mass was greater in polygynous and lek/promiscuous species than in monogamous taxa (Table 2, 3; Fig. 1C, D). This held for all three types of analyses (species and both types of contrasts; Tukey-Kramer tests). When we analyzed species, polyandrous species were less dimorphic in mass than all other mating systems, as might be expected based on the often greater total mass of females than males in these species. However, when we analyzed independent contrasts, polyandrous species were less dimorphic than polygynous taxa only under a punctuated model of evolution (Fig. 2D). In contrast to all other forms of dimorphism, dimorphism in

body mass was not related to relative testis mass in any analysis (Tables 2, 3; Fig. 2C, D).

Geography, ecology, and life history

Geographic region and total body mass were significant predictors of mass dimorphism when we analyzed independent contrasts, but not when we analyzed species (Table 3). Independent contrasts indicated that taxa were more dimorphic in mass in Eurasia and less dimorphic in North America (Tukey-Kramer tests, Fig. 3D). Dimorphism in body mass was also related positively to total body mass for both types of independent contrast, but not when we analyzed species (Table 3).

Dimorphism in Tail and Wing Length

Social mating system and testis size

Dimorphism in tail and wing length were associated with both levels of sperm competition (testis size) and social mating system in almost all analyses (Table 2, 4). Species were more dimorphic in tail and wing length if they had larger testes in all analyses (Fig. 2E–H). In fact, the relationship between dimorphism in tail length and testis mass was the most consistent of the four types of dimorphism we examined.

Similar to plumage and body mass dimorphism, dimorphism in tail and wing length were generally greater in lekking and polygynous species than species with other types of mating systems (Tukey-Kramer tests; Fig. 1E–H). Polyandrous species were less dimorphic in tail and wing length as a consequence of the relatively larger size of females than males in many of these species (Fig. 1E, G). As with dimorphism in body mass, the difference between polyandrous and other taxa disappeared when we examined independent contrasts (Tukey-Kramer tests; Fig. 1F, H). Here, dimorphism in wing and tail length varied primarily due to the difference between monogamous and lekking (tail length; Fig. 1F) or monogamous and both polygynous and lekking taxa (wing length; Fig. 1H; Tukey-Kramer tests).

Of the 24 tests examining the relationship between wing or tail length dimorphism and social mating system, only one was nonsignificant (Table 2). There was no association between tail dimorphism and social mating system ($P = 0.47$) when we conducted a bivariate analysis of independent contrasts using a gradual model of evolution; however, the relationship was significant ($P = 0.002$) when we used a punctuated model (Table 2). This difference was due mostly to the relatively greater tail dimorphism in lek/promiscuous species when we used a punctuated model (Tukey-Kramer tests; Fig. 1F). There were no outliers in these bivariate analyses that may have caused the inconsistency.

Geography, ecology, and life history

As with mass dimorphism, there were few consistent predictors of tail or wing length dimorphism among the other geographic and ecological variables (Table 3). For example, dimorphism in both tail and wing length were relatively greater in species with greater body mass and lower in species with male incubation, but these relationships were not always significant in the three types of analyses (Table 4). Also, wing dimorphism was greater for taxa that nested on the ground and lower for taxa nesting at intermediate height (shrub level). Although canopy nesting taxa tended to be less dimorphic in wing length than ground nesters, the difference was not significant (Tukey-Kramer test). In most analyses tail and wing dimorphism varied among geographic regions, but the patterns of dimorphism differed between analyses of species and contrasts (Fig. 3E, F), and the differences were only significant in the final stepwise regression models (Table 4).

DISCUSSION

Our analyses revealed that sexual dimorphism in size and plumage were related to traditional classifications of mating systems (i.e. ''social'' mating system) in more than 1000 bird species from nearly every taxonomic group and region of the world (Table 1). Our results also suggest that sperm competition, as estimated by relative testes size (Møller and Briskie 1995), has played an important role in the evolution of sexual dimorphism, although the effect was not as significant or as consistent as the effect of social mating system.

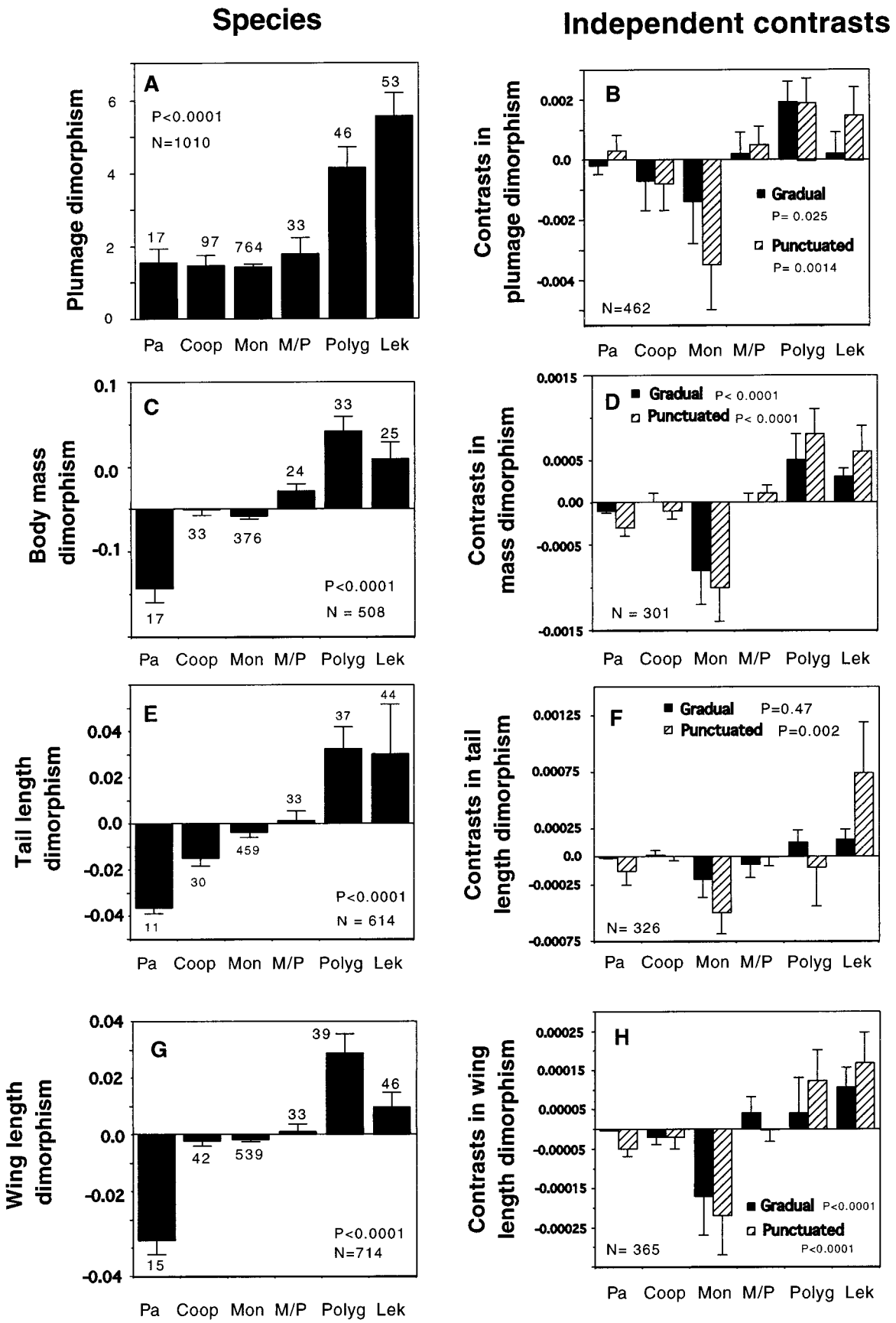
Of the four types of dimorphism examined in this study, testis size had the most consistent relationships with dimorphism in tail and wing length, a less consistent relationship with plumage dimorphism, and no relationship with dimorphism in body mass (Table 2). In contrast, social mating system was associated with all forms of dimorphism, except in one test of tail length dimorphism (Table 2). We also found evidence that geographic region, total body mass, clutch size, nest characteristics, and migratory status influenced dimorphism in birds, but their effects varied among the different types of dimorphism. Other studies have found similar patterns, but they have usually tested one or a few of these factors at a time, and often the datasets have been restricted to particular groups of birds or specific geographic regions (most notably the temperate zone). Our large-scale study suggests that some patterns may be restricted to particular taxa or types of dimorphism and may also be dependent on the evolutionary assumptions made in analyzing the data.

Dimorphism and Social Mating System

Dimorphism in plumage and body mass

Recent studies have concluded that sperm competition is more important to the evolution of sexual dimorphism in birds than variance in social mating success (Møller and Birkhead 1994; Owens and Hartley 1998). Plumage dimorphism was related positively to genetic estimates of extrapair paternity in studies by Møller and Birkhead (1994) and Owens and Hartley (1998), but not to traditional classifications of mating systems. Owens and Hartley (1998) also examined dimorphism in body mass and found that it was related to social mating system, but not to extrapair paternity. In contrast, we found significant relationships between sexual dimorphism in both plumage and body mass and social mating systems (Fig. 1B, D). Why do the results of these studies differ?

We suggest the main difference between these studies is


Species
Independent contrasts
A
P<0.0001
N=1010
Plumage dimorphism
17
97
764
33
46
53
B
Contrasts in plumage dimorphism
Gradual
P= 0.025
Punctuated
P= 0.0014
N=462
C
Body mass dimorphism
P<0.0001
N = 508
D
Contrasts in mass dimorphism
Gradual P< 0.0001
Punctuated P< 0.0001
N = 301
E
Tail length dimorphism
P<0.0001
N = 614
F
Contrasts in tail length dimorphism
Gradual P=0.47
Punctuated P=0.002
N= 326
G
Wing length dimorphism
P<0.0001
N=714
H
Contrasts in wing length dimorphism
Gradual P<0.0001
Punctuated P<0.0001
N= 365
Pa Coop Mon M/P Polyg Lek

differences in methods of scoring mating system or dimorphism. For example, when we reanalyzed the species data of Owens and Hartley (1998) using their dimorphism data, but our data and classification scheme for scoring mating system, we found that both size ($F_{5, 65} = 3.0$, $P = 0.018$) and plumage ($F_{5, 65} = 3.6$, $P = 0.006$) dimorphism were related to social mating system. We also found a significant effect of mating system on plumage dimorphism ($F_{5,49} = 6.75$, $P < 0.0001$) when we reanalyzed Møller and Birkhead's (1994) species data using our values for plumage dimorphism and mating system. Here polygynous species were more dimorphic than other species (Tukey-Kramer tests). This difference remained ($t = 3.2$, df = 52, $P = 0.002$) when we recoded species as either monogamous or polygynous, as originally done by Møller and Birkhead (1994). Thus, we suggest that the differences between these studies are smaller than they might appear at first. Studies of the effects of mating system on dimorphism in blackbirds also may have reached different conclusions because they differed in methodology (Webster 1992).

The effects of social mating system on dimorphism have been variable in other studies as well. For example, recent studies have reported conflicting results as to whether lekking species are more likely to be sexually dimorphic than nonlekking species (Hoglund 1989; Oakes 1992; Hoglund and Sillen-Tullberg 1994; Bleiweiss 1997). Hoglund (1989) found that lekking birds were not significantly more dimorphic in size or plumage than nonlekking birds, whereas Oakes (1992) found the opposite. The manner in which each author controlled for phylogeny may explain the differences in results (see also Hoglund and Alatalo 1995). Hoglund (1989) used Ridley's (1983) outgroup comparison method, whereas Oakes (1992) used independent contrasts, similar to this study. Independent contrasts use the magnitude of differences in dimorphism, whereas the outgroup method counts the number of associated evolutionary events and does not consider the magnitude. Thus, large contrasts in some groups could lead to an overall difference in dimorphism between lekking and nonlekking species (Hoglund and Alatalo 1995).

Dimorphism in wing and tail length

We also investigated dimorphism in wing and tail length and found that they were both related to social mating system (Fig. 1). Similarly, Bjorklund (1990) and Winquist and Lemon (1994) found that dimorphism in tail length was related to mating system. Bjorklund used an autocorrelation model to control for phylogeny in an analysis of 65 species of Fringillids, and Winquist and Lemon (1994) examined 754 species (not including Fringillids) using independent contrasts. Both studies compared tail dimorphism in relation to mating system, which was classified as monogamous or polygynous. In both studies, tail dimorphism was greater in polygynous than monogamous species. Our results were similar as the main effect of mating system on tail dimorphism was due to the difference between monogamous and lek/promiscuous taxa (other mating systems did not differ significantly; Fig. 1F). Similar to Winquist and Lemon (1994), we also found that the effect of social mating system on tail length dimorphism was relatively weak.

Dimorphism and Sperm Competition

Recent studies have argued that extrapair mating increases the intensity of sexual selection on male morphological traits and this results in sexual dimorphism. Using comparative analyses, Møller and Birkhead (1994) and Owens and Hartley (1998) both found that levels of extrapair paternity (i.e., sperm competition) were related to plumage dimorphism in birds. They both suggested that indirect fitness benefits to females of extrapair mate choice, rather than direct benefits, have resulted in the evolution of bright male plumage, because extrapair males never provide parental care or other material benefits to females. Our results are consistent with this hypothesis; we found that testis mass was correlated with dimorphism in tail and wing length and, less consistently, with dimorphism in plumage (Table 2). In contrast, we found no relationship between dimorphism in body mass and testis mass. This result also agrees with Owens and Hartley (1998). A new result for this study is the association between sperm competition and dimorphism in wing and tail length. Indeed, one of the strongest associations between sperm competition and dimorphism appeared to be with tail dimorphism. Overall, it appears that sperm competition may produce sexual dimorphism in monogamous species, and, as Owens and Hartley (1998) pointed out, sperm competition and variance in social mating success may have different targets of selection (e.g., dimorphism in body mass). Our study now suggests that they can also have the same target (e.g., plumage or wing length).

In general, relationships between dimorphism and sperm competition were less consistent or widespread than associations between dimorphism and social mating system (see Table 2, Figs. 1, 2). Testis mass was related to two forms of dimorphism (tail and wing length) in every test (species and independent contrasts), whereas social mating system was related to three forms of dimorphism in every test (plumage, body mass, and wing length; Table 2). In addition, it appeared that the magnitude of the effects was larger for social mating system (Fig. 1) than for testis mass (Fig. 2). Thus, traditional explanations for sexual dimorphism that are based on the number of social mates per individual appear to be better predictors of dimorphism than sperm competition. This conclusion is consistent with the relatively weak effects reported

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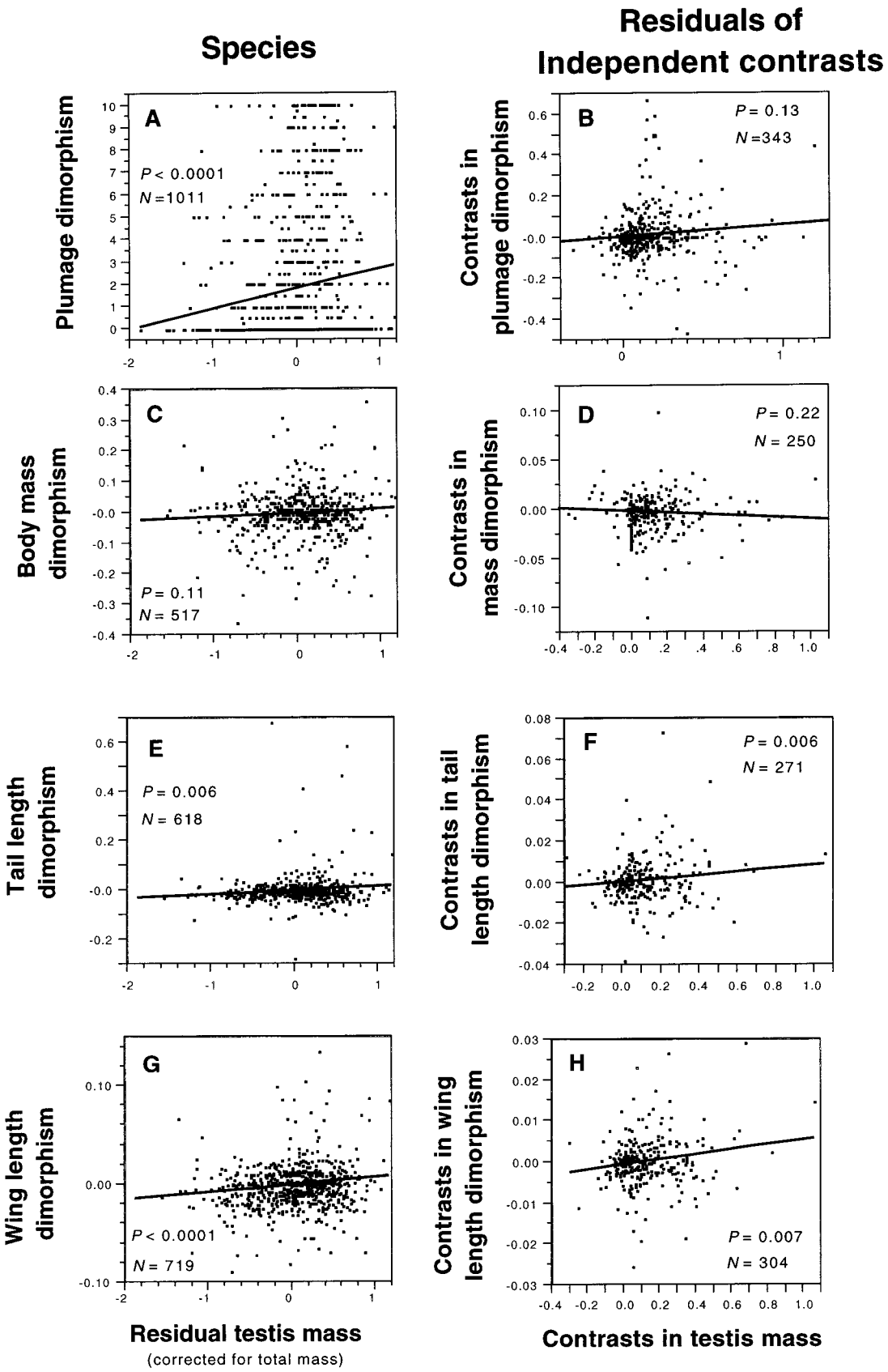
FIG. 1. Sexual dimorphism in birds in relation to social mating system. Mating systems are: polyandry (Pa); cooperative (Coop); monogamy (Mon); mostly monogamy, but occasional polygyny (M/P); mostly polygyny (Polyg); and lek/promiscuous (Lek). Panels on the left are based on bivariate analyses of species data, whereas panels on the right are phylogenetically independent contrasts from the bivariate analyses in Table 2. Phylogenetically independent contrasts were estimated assuming gradual and punctuated models of branch length evolution. The dummy variable for polyandry was used as the predictor variable in these CAIC runs. Means and 1 SE are shown for each mating system (see Methods for calculations).


Species
Residuals of Independent contrasts
Plumage dimorphism
A
P < 0.0001
N =1011
Contrasts in plumage dimorphism
B
P = 0.13
N =343
Body mass dimorphism
C
P = 0.11
N = 517
Contrasts in mass dimorphism
D
P = 0.22
N = 250
Tail length dimorphism
E
P = 0.006
N = 618
Contrasts in tail length dimorphism
F
P = 0.006
N = 271
Wing length dimorphism
G
P < 0.0001
N = 719
Contrasts in wing length dimorphism
H
P = 0.007
N = 304
Residual testis mass
(corrected for total mass)
Contrasts in testis mass

for indirect selection (good genes) in empirical studies (Møller and Alatalo 1999), as well as theoretical models that suggest indirect selection is unlikely to produce extreme levels of sexual dimorphism (Kirkpatrick 1996; Kirkpatrick and Barton 1997).

Dimorphism and Other Factors

The main focus of this paper was the effect of social and genetic mating systems on dimorphism; however, we found several other variables that were related to dimorphism (Tables 3, 4). In particular, most forms of dimorphism were affected by geographic region (Table 3), and plumage dimorphism was related to nest height in all analyses (Table 3). Total body mass was related to several forms of dimorphism, but not consistently across the three types of analyses. Below we provide a brief overview of these relationships and relate them to previous studies.

Geographic region

Using contrasts, there was an effect of geographic region on the four types of dimorphism, but this effect was not evident when we analyzed the raw species data (Fig. 3). In general, North American taxa were less dimorphic and Eurasian taxa were more dimorphic than taxa in other regions when we analyzed contrasts (Fig. 3), but this effect was weaker on tail and wing dimorphism than plumage and mass dimorphism (Tables 3, 4). Martin and Clobert (1996) found that European birds had higher mean clutch size and annual fecundity than North American species. Assuming that sexual dimorphism is greater in species with lower fecundity (Promislow et al. 1992; Badyaev 1997), one might expect there to be less dimorphism in Eurasian taxa due to their larger clutch size. We found the opposite pattern of dimorphism; however, we also found no consistent relationship between any type of dimorphism and clutch size, contrary to assumption. To our knowledge, other studies of dimorphism in birds have not examined differences in geographic regions using independent contrasts. This deserves additional study, because it seems likely that the ecology of a region may influence levels of sexual dimorphism, independently of phylogeny.

Nest height

Plumage dimorphism was greatest in taxa that nested at intermediate height (shrub level) rather than at ground or canopy level (Table 3). Martin and Badyaev (1996) found a similar association between plumage dimorphism and nest height. In an analysis of 106 species of warblers (Parulinae) and finches (Carduelinae), nest predation was greatest at intermediate nest height (shrub level) and dimorphism also tended to be greatest, mainly due to a decrease in female brightness, at intermediate nest height (Martin and Badyaev 1996). We did not examine the colorfulness of each sexes' plumage, so unlike Martin and Badyaev (1996) we cannot determine how the relationship with nest height arose. In contrast, wing dimorphism tended to be greater for ground nesters than shrub and canopy nesters. The significance of this is unknown. Nevertheless, these results suggest that ecological factors also influence sexual size dimorphism in birds.

Total body mass

Total body mass was related positively to dimorphism in plumage (punctuated model only), body mass, and tail length when we analyzed independent contrasts (Tables 3, 4). The positive relationship between body mass and dimorphism in mass (i.e., larger species are more dimorphic than smaller ones) has been found in many other studies (reviewed by Webster 1992). In fact, overall body mass may be a better correlate of dimorphism in mass than mating system. This has led some to suggest that sexual selection has little influence on some types of size dimorphism (e.g., Bjorklund 1990). We included body mass in our analyses to control for its potentially confounding effects, yet we still found relationships between mating systems (and testis size) and dimorphism in our multivariate analyses (Tables 3, 4). This suggests that the relationships between dimorphism and mating behavior (both social and genetic) found in this study are not artifacts of the relationship between overall size and dimorphism.

Dimorphism and Comparative Analyses

Our main conclusions about the effects of testes size and social mating system on dimorphism are strong and, in general, unaffected by whether we analyzed species or independent contrasts (Table 2). Analyses using independent contrasts and large phylogenies have greater statistical power (Harvey and Rambaut 1998), so our results are likely to be robust when compared to previous studies of avian dimorphism. Looking at just the main variables of interest, testis mass and social mating system, we conducted 48 bivariate and multivariate tests using both species and two types of independent contrasts (see Table 2). Of these, just three test results were not consistent between analyses of species and contrasts for a given type of dimorphism (see plumage and tail length dimorphism, Table 2). Overall, 8% of our test results using contrasts differed depending on the evolutionary model chosen (4/48 paired comparisons of gradual and punctuated results from bivariate and multivariate tests), and 43% of our test results differed between species and contrasts (34/80 paired comparisons of species and contrasts in Tables 3, 4). We think these differences are common enough to justify using multiple methods and, until further analysis is com-

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FIG. 2. Sexual dimorphism in birds in relation to relative testis mass. Relative testis mass controls for overall body mass. Panels on the left are based on bivariate analyses of species data (see Table 2), whereas panels on the right are the residuals from multiple regression analyses of phylogenetically independent contrasts (gradual branch lengths, see Tables 3, 4). Regression lines are shown for each panel; these were forced through the origin for the independent contrasts. Note that although CAIC always produces positive contrasts for the predictor variable (relative testis mass), the residuals of these contrasts can be negative or positive.

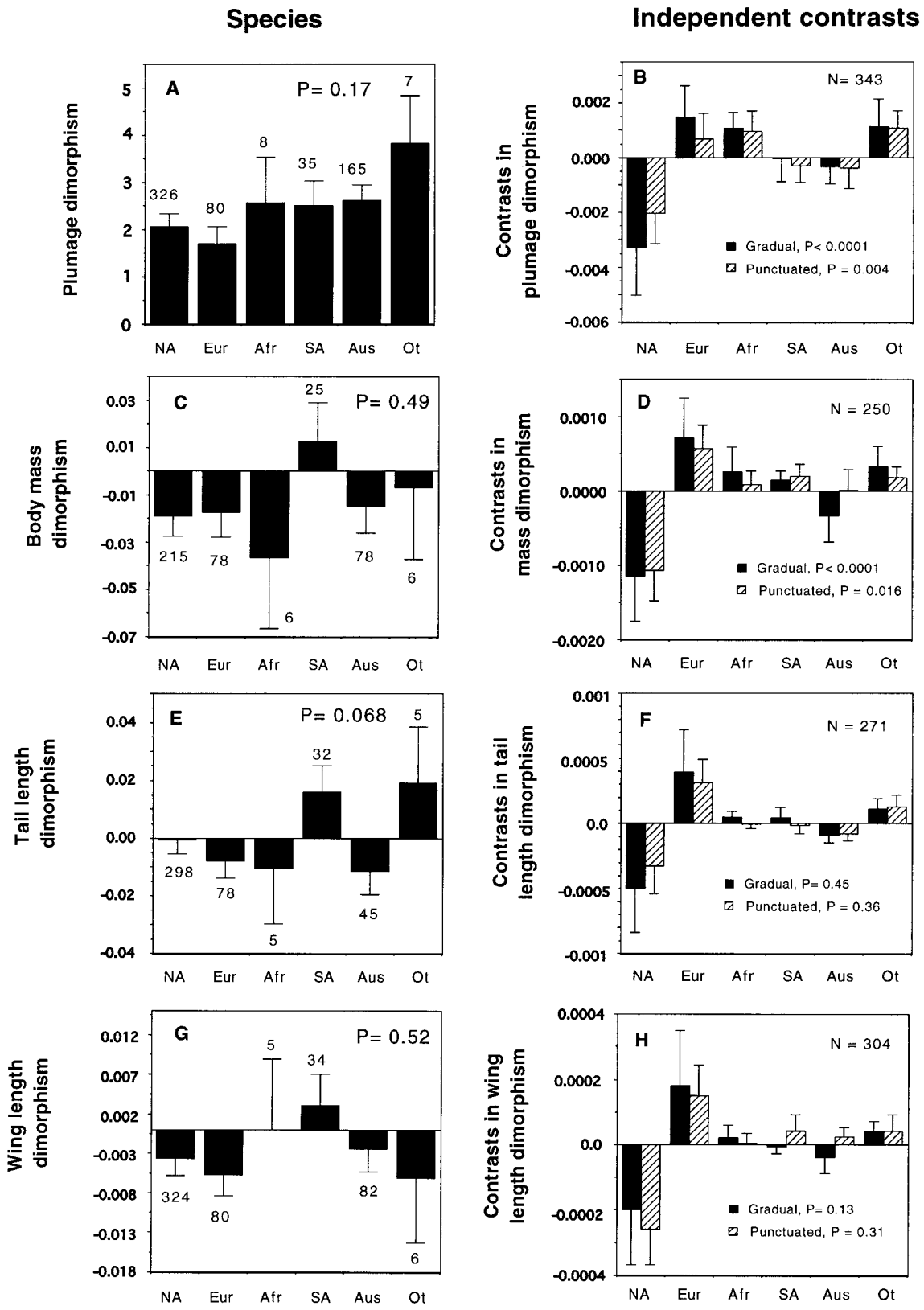

FIG. 3. Sexual dimorphism in birds in relation to geographic region. Regions are: North America (NA), Eurasia (Eur), Africa (Afr), South and Central America (SA), Australasia (Aus), and Other (Ot). Panels on the left are based on multivariate analyses of species data, whereas panels on the right are phylogenetically independent contrasts from the multivariate analyses (Tables 3, 4). Phylogenetically independent contrasts were made assuming gradual and punctuated models of branch length evolution. Relative testis mass was used as the predictor variable in these CAIC runs. Means and 1 SE are shown for each region (see Methods for calculations). Note that figures show results from regressions with all 10 independent variables (Tables 3, 4), not the final stepwise regressions, which had fewer variables.

TABLE 4. Multiple regression analysis of sexual dimorphism in tail and wing length among birds. Probability values are given for the initial multiple regression analyses of species and independent contrasts with all 10 independent variables. Variables included in the final stepwise regression model are indicated in bold (individual *P*-values not shown).

	Tail length dimorphism			Wing length dimorphism		
Independent variable	Species *P*	Gradual *P*	Punctuated *P*	Species *P*	Gradual *P*	Punctuated *P*
Testis mass (relative)	**0.006**	**0.006**	**0.001**	**0.0009**	**0.007**	**0.003**
Social mating system	< **0.0001**	**0.007**	**0.038**	< **0.0001**	<**0.0001**	< **0.0001**
Geographic region	**0.068**	**0.45**	**0.36**	0.52	**0.13**	**0.31**
Clutch size	**0.11**	0.94	0.78	0.085	0.37	0.79
Nest height	0.54	0.17	0.85	0.66	**0.041**	**0.09**
Total body mass	0.15	< **0.0001**	< **0.0001**	< **0.0001**	0.36	**0.72**
Migratory or nonmigratory	0.89	0.19	0.41	0.98	0.15	0.48
Female-only or female and male incubation	**0.002**	0.50	0.44	< **0.0001**	0.30	0.12
Cavity or noncavity test	0.95	**0.22**	**0.28**	0.60	0.78	0.85
Closed open nest	0.75	0.69	0.85	0.85	0.64	0.89
Multiple regression						
R^2	0.20	0.21	0.19	0.28	0.24	0.16
P	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
N species used	463	463	463	531	530	530
N contrasts		271	271		304	304
Final stepwise model R^2	0.18	0.20	0.19	0.27	0.24	0.15

pleted, to only accept results that are consistent under various evolutionary assumptions.

CONCLUSIONS

In this paper we reexamined the relationships between sexual dimorphism and both sperm competition (testis size) and social mating system. All forms of dimorphism were associated with social mating system; in most cases this was due to differences between monogamous and polygynous taxa. All forms of dimorphism except body mass were also associated with sperm competition, although generally to a lesser extent. Our results may have differed from previous studies at least partly because of differences in methodology, but we also had a wider sample in terms of both phylogeny and geographic distribution. Although there is currently much interest in sperm competition and extrapair mating, we suggest that traditional classifications of mating systems are better predictors of sexual dimorphism in birds.

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