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Testosterone, testes size, and mating success in birds: a comparative study

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Abstract

Reproductive behaviors of vertebrates are often underpinned by temporal patterns of hormone secretion. We investigated interspecific patterns of circulating testosterone in male birds to test the hypothesis that testosterone plays a crucial role in sexual selection as determined by degree of polygyny and extra-pair paternity. We predicted that the evolution of increased levels of polygyny and extra-pair paternity would have resulted in the evolution of increased levels of testosterone to allow males more efficiently to compete for mates. This hypothesis was tested in comparative analyses of 116 species of birds using Generalized Least Squares Models. We assessed the importance of latitudinal distribution, because this can confound the relationship between testosterone and mating success. There were weak positive phylogenetic correlations between measures of testosterone and estimates of mating success at the social level, but this association appeared to be confounded by latitudinal distribution, a significant correlate of testosterone titers. However, we found a significantly positive relationship between peak and residual peak testosterone (which is the peak testosterone level that is controlled for the baseline level) and extra-pair paternity independent of latitude. These results suggest that selection pressures arising from social and sexual mating differently affected testosterone levels with the former being mediated by factors associated with latitudinal distribution. An analysis of residual testes size revealed a positive association between peak and residual testosterone and testes size relative to body size. In a path analysis, we show that relative testis size primarily evolved in association with intense sperm competition and thus high sperm production, and these mechanisms had a secondary impact on blood testosterone levels at a phylogenetic scale. Our results suggest that sperm competition has played an important role in the evolution of reproductive mechanisms in birds.
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Introduction

The evolution of reproductive mechanisms is determined by natural and sexual selection to optimize reproductive success under given environmental conditions. Given that reproductive mechanisms presumably are so closely associated with reproductive success and fitness, it seems likely that sexual selection plays an important role in the evolution of such mechanisms. Two components of male mating success have repeatedly been found to influence the intensity of sexual selection: social mating success (i.e., the number of females acquired) and sexual mating success (i.e., sperm competition) (reviews in Andersson, 1994; Birkhead and Møller, 1998).

Circulating levels of testosterone during the breeding cycle seems to play crucial roles in avian reproduction. Manipulating testosterone levels affects male mating success measured as the proportion of polygynous males (Silverin, 1980; Watson and Parr, 1981; Wingfield, 1984a) and extra-pair paternity (Raouf et al., 1997). These results suggest that polygynous males with higher testosterone levels are able to win in sexual competition over access to

females, or females prefer to mate with such males. Similarly, males with relatively high testosterone levels may efficiently defend their mates against potential extra-pair males, but also obtain more extra-pair copulations with neighboring females because females prefer to copulate with such males. Testosterone may also influence male mating success by enabling males to enlarge their territories and home ranges resulting in encounters with more females (e.g., Ball and Wingfield, 1987; Beletsky et al., 1990b; Ketterson and Nolan, 1999; Moss et al., 1994; Silverin, 1980; Veiga et al., 2001, but see also Chandler et al., 1997).

Testosterone enhances male reproductive display such as the production of song or other sexual signals (reviews in Ball et al., 2002; Folstad and Karter, 1992; Owens and Short, 1995; Roberts et al., 2004). This effect is important because these sexual traits are associated with high male mating success (Andersson, 1994), including paternity (review in Westneat and Stewart, 2003). Therefore, high levels of circulating testosterone may have partly evolved as a physiological basis for high levels of sexual display in polygynous species and species with high levels of extra-pair paternity.

Testosterone is associated with a second mechanism of sperm competition through its effects on the intensity of mate guarding, as shown by experimental and observational studies (Hegner and Wingfield, 1986; Moore, 1984; Saino and Møller, 1995, but see also Chandler et al., 1997). Temporary male removal studies showed an increased frequency of extra-pair copulations in the absence of the male mate (review in Birkhead, 1998). The evidence for mate guarding being associated with reduced extra-pair paternity from male removal experiments has only been partly supportive (Currie et al., 1999; MacDougall-Shackleton et al., 1996; Riley et al., 1995; Westneat, 1994).

Sperm production is dependent on secretion of different hormones (Johnson, 1986; Wingfield and Farner, 1993). Completion of meiosis of spermatocytes and production of haploid spermatozoa occurs directed by such reproductive hormones, including testosterone. Sperm production plays a crucial role in sperm competition because males win at sperm competition through insemination of a larger number of sperm (Parker, 1970). Consistent with this prediction, comparative studies of birds and mammals have shown that males of species with more intense sperm competition, as demonstrated by a higher frequency of extra-pair paternity, consistently have larger sperm reserves and a larger amount of sperm producing tissue, as reflected by the relative size of the testes (Birkhead et al., 1993; Møller, 1989; Møller and Briskie, 1995). Hence, testosterone-mediated sperm production may affect the outcome sperm competition.

Given that circulating levels of testosterone in male birds are associated with mating success, the expression of secondary sexual characters, mate guarding, and sexual

competition at the intraspecific level, testosterone may have played an important role in the evolution of reproductive strategies. Therefore, variation in patterns of circulating levels of testosterone among species should be associated with the intensity of sexual selection. In accordance with this hypothesis, Wingfield et al. (1990) reported that highly polygynous bird species with little male parental care had a small ratio of peak to baseline testosterone, while monogamous species of birds tended to have a large ratio. In addition, Hirschenhauser et al. (2003) in a phylogenetic analysis demonstrated that male androgen level is responsive to social environmental factors, such as mating system and paternal incubation. Here, we hypothesize that in addition to polygyny, sperm competition as reflected by extra-pair paternity has an important contribution in shaping the evolution of patterns of circulating levels of testosterone.

The aims of the present paper were to investigate interspecific patterns of covariation between testosterone and reproduction, by determining the relationship between testosterone and male mating success using polygyny and extra-pair paternity as estimates of the intensity of sexual selection. Furthermore, we have tested the prediction that levels of circulating testosterone are associated with relative testes size. We predicted that males of species that have evolved high levels of circulating testosterone also have evolved more intense mate guarding and aggression directed towards male intruders during the fertile period of their mate than males of species with low levels of testosterone. Thus, species with high levels of extra-pair paternity or polygyny should have evolved high levels of testosterone as a means of protecting their paternity. Since high levels of circulating testosterone may serve as a physiological basis for high levels of sexual display in polygynous species and species with high levels of extra-pair paternity, it should also result in an association between testosterone and polygyny and extra-pair paternity, respectively, at the interspecific level. Therefore, we predicted that males of species with high levels of testosterone should have evolved relatively large testes size.

Latitudinal distribution may be a potentially confounding variable that could affect the relationship between testosterone and reproductive behavior. Birds breeding in northern latitudes generally have elevated plasma testosterone levels throughout the breeding season with a peak at the onset of the breeding season, probably because of the shorter breeding season and the socially unstable situation with which they have to cope (Levin and Wingfield, 1992; Moore et al., 2002; Wingfield et al., 1997). A recent study demonstrated a latitudinal trend in extra-pair paternity caused by more synchronous breeding away from the equator (Spottiswoode and Møller, 2004). Females are better able to assess potential extra-pair partners when males are simultaneously in breeding condition (e.g., Thusius et al., 2001). Hence, to control for the potential effect of latitudinal distribution on both testosterone levels

and extra-pair paternity, we included this variable in our analysis.

Methods

Data set

Information on testosterone, frequency of polygyny and extra-pair paternity was obtained from an extensive search of the literature for a total of 116 species (Table 1).

Circulating levels of testosterone were used as reported in the original sources and expressed as ng/ml. We used two estimates of circulating testosterone: (1) peak levels for males were estimated as the maximum mean values of the natural level during the breeding cycle (level C sensu Wingfield et al., 1990), while (2) the non-breeding baseline level for males was the mean low level outside the reproductive cycle (level A sensu Wingfield et al., 1990). Wingfield et al. (1990) and Hirschenhauser et al. (2003) used baseline levels of testosterone during reproduction in their analyses (level B), but we were unable to extract repeatable estimates of breeding baseline levels from the literature when using the procedures described in their papers. The non-significant repeatability of a trait implies that its intraspecific variation is as high as the interspecific variation, thus comparisons of mean values among species do not make biological sense. The increase of testosterone from non-breeding baseline levels to breeding baseline levels caused by environmental cues is similar in all species (Wingfield et al., 1990), which may result in breeding baseline levels not exhibiting consistent variation among species. Consequently, we avoided using breeding baseline levels of testosterone during reproduction in our analyses. Our baseline estimates outside the reproductive cycle were strongly positively correlated with the non-breeding baseline values from Wingfield et al. (1990) ($r = 0.623$, $N = 20$, $P = 0.003$). Thus, the two sets of estimates provide similar kinds of information (hereafter we refer to non-breeding baseline levels as baseline levels). Estimates of circulating levels of testosterone may vary for biological reasons, but also for other reasons. For example, studies differ in the intensity of sampling, and some studies are made in captivity while others are field studies. Furthermore, Wingfield et al. (1990) suggested that differences in procedures among laboratories may increase the noise in the data. All such heterogeneity will tend to cause noise, but not bias in the data set, and any statistical relations reported here are thus bound to be conservative. We have directly assessed the reliability of the estimates of both peak and baseline testosterone concentrations from different studies by calculating the repeatability (Falconer and Mackay, 1996) from one-way analyses of variance based on all species with more than a single estimate available (peak testosterone concentration: $F = 13.30$, $df = 22,46$, $P < 0.001$, $R = 0.80$; baseline testosterone concentration: $F = 3.92$, $df = 18,33$, $P < 0.001$,

$R = 0.50$). Repeatability of peak testosterone level was in particular very high. The lower repeatability for baseline testosterone level, as compared to peak testosterone level, suggests that any conclusions based on analyses of this variable may be biased because of the quality of the data as compared to analyses of peak testosterone. However, the significant repeatabilities indicate that variation within species is small compared to variation among species, and that measures of circulating testosterone levels are species-specific attributes that can justifiably be represented by a single estimate. Thus, estimates were sufficiently reliable to provide the basis for comparative analyses. The level of circulating peak testosterone was on average 3.11 ng/ml (SE = 0.23), range 0.33–13.30, $N = 107$ species. The level of circulating baseline testosterone was on average 0.41 ng/ml (SE = 0.04), range 0.01–2.40, $N = 99$. Thus, baseline level was on average 13.2% of peak level.

A phylogenetic analysis demonstrated a positive relationship between $\log_{10}$-transformed peak and baseline testosterone level in males ($r = 0.291$, $P = 0.005$, $N = 90$, see Comparative methods for explanation). The slope of the phylogenetic regression (0.212) was significantly less than unity ($t = 13.52$, $df = 88$, $P < 0.001$). Thus, peak levels increased less than expected from isometry. The third measure of circulating level of testosterone was residuals from this phylogenetically corrected regression of peak testosterone level on $\log_{10}$-transformed baseline level (see Comparative methods). This measure is subsequently termed residual peak testosterone. We avoided using the ratio of peak to baseline testosterone as done by Wingfield et al. (1990). Ratios are difficult to interpret because a given value may arise from a small numerator, a large denominator, or a combination of the two. Moreover, general statistics handbooks warn against the use of ratios due to their problematic statistical properties (Sokal and Rohlf, 1995, pp. 17–19). These problems include the fact that they are not accurate, and that they are often not normally distributed. Values for a given variable relative to another variable can more appropriately be expressed as residuals from a regression of the first variable on the second variable. Although our database probably contains the most wide-ranging interspecific data set on circulating levels of testosterone ever published, we cannot totally exclude the possibility that a few published data were not included. (Unpublished data were available for 11 additional species, and when we included these species in our analysis the results and conclusions were very similar to those reported here.) Our preliminary calculations indicated that to detect an explanatory effect by an independent variable of 10% of the variance in a dependent variable at 80% power, a sample size of 73 is needed. Hence, a test of our predictions using information for more than a hundred species was not likely to suffer from insufficient statistical power. Throughout the paper, we assumed that available information on testosterone provided us with an unbiased and representative database. All results with baseline testosterone levels were

Table 1
Testosterone levels, mating success, testis size, and latitudinal distribution in birds

Species	Polygyny (%)	Mating system	Peak testosterone (ng/ml)	Baseline testosterone (ng/ml)	Extra-pair paternity (%)	Testes mass (g)	Body mass (g)	Mean latitudinal distribution	References
Struthio camelus	0	M	3.63	1.35		115.35	100000	2.1	T: Degen et al. (1994)
Dromaius novaehollandiae	0	M	6.05	0.07		126.77	34 994.5	27.5	T: Malecki et al. (1998)
Apteryx australis	0	M	2.30	0.18			1999.9	41.3	T: Cockrem and Potter (1990)
Coturnix japonica		L	7.85	0.20		3.00	129.1	47.9	P: Del Hoyo et al. (1994); T: Follett and Maung (1978), Ottinger (1983)
Tetrao tetrix		L	1.15	0.29	0	3.10	1199.5	54.0	P: Del Hoyo et al. (1994); T: Alatalo et al. (1996b); EPP: Alatalo et al. (1996a)
Tetrao urogallus		L	1.00	0.20		3.00	3801.9	54.0	P: Del Hoyo et al. (1994); T: Hissa et al. (1983)
Lagopus lagopus	7	P	1.91	0.17	9.40	1.5	699.8	55.2	P: Hannon et al. (1998); T: Stokkan and Sharp (1980), Hannon and Wingfield (1990); EPP: Freeland et al. (1995)
Phasianus colchicus		L	2.40	0.20	6.00	8.20	1318.3	50.0	P: Del Hoyo et al. (1994); T: Sakai and Ishii (1986); EPP: Grahn (1992)
Gallus gallus		L	7.83	0.84		27.99	2301.4	22.3	P: Del Hoyo et al. (1994); T: Furr and Thomas (1970)
Perdix perdix	0	M	1.80	0.28		0.57	399.9	47.9	T: Sharp et al. (1986), Fraissinetet al. (1987), Beani et al. (1988), Lupo et al. (1990)
Meleagris gallopavo		L	5.60	0.60		27.99	15 995.6	41.4	P: Del Hoyo et al. (1994); T: Lisano and Kennamer (1977)
Colinus virginianus	20	P	2.68	0.13			179.9	38.6	P: Brennan (1999); T: Vleck and Dobrott (1993)
Anser indicus	0	M	3.21	0.19			2630.3	48.7	T: Dittami (1981), Dittami and Reyer (1984)
Tadorna ferruginea	0	M	3.65	0.32			1321.3	43.9	T: Veselovsky (1990)
Aix sponsa	0	M	0.71	0.03			680.8	41.8	T: Heep et al. (1991)
Anas platyrhynchos	0	M	3.44	0.25	3.00	9.60	1140.3	43.9	T: Balthazart and Hendrick (1976), Jallageas et al. (1978), Paulke and Haase (1978), Donham (1979), Wingfield and Farner (1980a), Balthazart (1983), Stunden et al. (1998); EPP: Evarts and Williams (1987)
Picoides borealis	0	M	2.06	0.16	1.25			33.6	T: Khan et al. (2001); EPP: Haig et al. (1994)
Ceryle rudis	0	M		0.50		1.00	76.9	12.0	T: Reyer et al. (1986)
Psittacula krameri	0	M	0.93			0.44	127.9	12.1	T: Krishnaprasadam et al. (1988)
Columba livia	0	M	1.24	0.59	1.00	2.02	304.8	30.5	T: Haase et al. (1976); EPP: Johnson (1992)
Streptopelia risoria	0	M	0.70	0.20		0.70	113.0	23.1	T: Feder et al. (1977)
Streptopelia decaocto	0	M	2.09	0.27		0.82	144.9	48.7	T: Péczely and Pethes (1979)
Chlamydotis undulata		L	9.06	1.20			1798.9	46.5	P: Del Hoyo et al. (1996); T: Saintjalme et al. (1996)
Gallirallus philippensis	0	M	0.62	0.08				15.7	T: Wiley and Goldizen (2003)
Chionis minor	0	M	1.67	0.12		1.05	505.8	50.3	T: Burger and Millar (1980)
Tringa macularia	0	M	6.10	0.15	9.90	0.56	40.3	20.7	T: Rissman and Wingfield (1984), Fivizzani and Oring (1986); EPP: Oring et al. (1992)
Calidris pusilla	0	M	2.99	0.14		0.49	28.0	32.9	T: Gratto-Trevor et al. (1990)

Table 1 (*continued*)

Species	Polygyny (%)	Mating system	Peak testosterone (ng/ml)	Baseline testosterone (ng/ml)	Extra-pair paternity (%)	Testes mass (g)	Body mass (g)	Mean latitudinal distribution	References
Calidris mauri	0	M	1.59	0.18	6.56	0.49	26.0	38.4	T: O'Reilly and Wingfield (1995)
Phalaropus tricolor	0	M	4.91	0.42	0	0.77	51.8	20.7	T: Fivizzani et al. (1990), Oring et al. (1988), Oring and Fivizzani (1991); EPP: Delehanty et al. (1998)
Phalaropus lobatus	0	M	5.46	0.04		0.45	35.0	20.7	T: Gratto-Trevor et al. (1990)
Phalaropus fulicarius	0	M	6.00	0.45	8.57	1.63	46.0	20.7	T: Fivizzani et al. (1990); EPP: Dale et al. (1999)
Larus occidentalis	0	M	0.41	0.30	0.00	2.03	1129.8	40.9	T: Wingfield and Farner (1980a,b), Wingfield et al. (1980); EPP: Gilbert et al. (1998)
Larus ridibundus	0	M	4.66	0.20		0.42	274.8	23.1	T: Groothuis and Meeuwissen (1992)
Parabuteo unicinctus	0	M	0.52	0.02			724.4	8.8	T: Mays et al. (1991)
Falco tinnunculus	0	M	2.55	0.50	1.88	0.72	191.9	29.3	T: Meijer and Schwabl (1989); EPP: Korpimäki et al. (1996)
Sula capensis	0	M	0.85	0.26			2648.5	15.7	T: Hall (1986)
Phalacrocorax capensis	0	M	0.42	0.19		23.01	1258.9	15.7	T: Berry et al. (1979)
Threskiornis melanocephalus	0	M	2.80					41.8	T: Wingfield et al. (2000)
Eudocimus albus	0	M	1.05	0.36				23.0	T: Heath et al. (2003)
Ciconia ciconia	0	M	2.40	0.60			3396.3	30.5	T: Hall et al. (1987)
Aptenodytes patagonicus	0	M	7.26	0.03			15 995.6	50.0	T: Chèrel et al. (1994), Mauget et al. (1994), Jouventin and Mauget (1996)
Aptenodytes forsteri	0	M	13.30	2.40		40.00	33 962.5	59.0	T: Groscolas et al. (1986, 1988)
Eudyptes chrysolophus	0	M	3.20	0.75			3581.0	55.0	T: Williams (1992)
Pygoscelis papua	0	M	2.97	0.10		19.59	6194.4	59.0	T: Mauget et al. (1995)
Pygoscelis adeliae	0	M	9.62	0.11	9.09	19.59	5000.4	55.0	T: Groscolas et al. (1986); EPP: Pilastro et al. (2001)
Spheniscus humboldtii	0	M	3.32	0.16			5000.4	29.2	T: Otsuka et al. (1998); EPP: Schwartz et al. (1999)
Spheniscus magellanicus	0	M	2.75	0.55		8.36	4466.8	23.7	T: Fowler et al. (1994)
Diomedea exulans	0	M	5.12	1.04		59.43	8590.1	25.0	T: Hector et al. (1986a)
Diomedea chrysostoma	0	M	1.96	0.07			3664.4	50.0	T: Hector et al. (1986b)
Diomedea melanophris	0	M	2.03	0.08			3749.7	22.0	T: Hector et al. (1986b)
Manacus vitellus		L		1.10		0.14	19.3	4.9	P: Snow (1976); T: Wikelski et al. (1999)
Gymnopithys leucaspis	0	M		1.10		0.08	31.1	12.1	T: Wikelski et al. (1999)
Hylophylax naevioides	0	M	1.60	0.30		0.10	17.0	4.9	T: Wikelski et al. (1999)
Ptilonorhynchus violaceus		L	5.70			0.11	173.0	27.5	P: Gilliard (1969); T: Borgia and Wingfield (1991)
Malurus cyaneus	0	M	3.30	0.11	66.99	0.48	9.8	27.5	T: Peters et al. (2001); EPP: Dunn and Cockburn (1999)
Malurus leucopterus	0	M	4.10			0.33	9.3	27.5	T: Astheimer and Buttemer (1999)
Malurus lamberti	0	M	5.11			0.25	7.8	27.5	T: Astheimer and Buttemer (1999)
Lichenostomus penicillatus	0	M	1.50			0.15	21.0	27.5	T: Astheimer and Buttemer (1999)
Phylidonyris albifrons	0	M	2.00			0.25	18.3	27.5	T: Astheimer and Buttemer (1999)
Epthianura tricolor	0	M	1.30			0.08	10.0	27.5	T: Astheimer and Buttemer (1999)
Manorina melanophrys	0	M		0.57	4.20	0.19	30.0	27.5	T: Poiani and Fletcher (1994); EPP: Põldmaa et al. (1995)
Manorina flavigula	0	M	0.50			0.38	57.9	27.5	T: Astheimer and Buttemer (1999)

Table 1 (*continued*)

Species	Polygyny (%)	Mating system	Peak testosterone (ng/ml)	Baseline testosterone (ng/ml)	Extra-pair paternity (%)	Testes mass (g)	Body mass (g)	Mean latitudinal distribution	References
Pomatostomus superciliosa	0	M	2.10			0.18	42.0	27.5	T: Astheimer and Buttemer (1999)
Pomatostomus ruficeps	0	M	1.30			0.18	50.2	27.5	T: Astheimer and Buttemer (1999)
Acanthagenys rufogularis	0	M	0.90			0.45	50.0	27.5	T: Astheimer and Buttemer (1999)
Lanius collurio	0	M	2.40	0.50	5.26	0.24	28.2	30.5	T: Fornasari et al. (1991); EPP: Fornasari et al. (1994)
Lanius collaris	0	M	1.50	0.50		0.21	38.0	4.3	T: Dittami and Knauer (1986)
Laniarius funebris	0	M	2.94	0.27				2.1	T: Schwabl and Sonnenschein (1992)
Pachycephalus rufiventris	0	M	4.00			0.10	20.0	22.3	T: Astheimer and Buttemer (1999)
Aphelocoma coerulescens	0	M	1.56	0.19	0.00	1.81	80.2	27.9	T: Schoech and Lipar (1998), Schoech et al. (1991); EPP: Quinn et al. (1999)
Corvus frugilegus	0	M	3.40	0.20		17.66	534.6	50.0	T: Lincoln et al. (1980)
Gymnorhina tibicen	0	M	1.51	0.14		2.14	313.3	20.2	T: Schmidt et al. (1991)
Turdus merula	0	M	2.56	0.04	17.77	1.24	105.9	47.8	T: Schwabl et al. (1980); EPP: Creighton (2000)
Turdus grayi	0	M		1.90	37.84	0.78	73.8	12.4	T: Wikelski et al. (1999); EPP: Stutchbury et al. (1998)
Ficedula hypoleuca	16	P	2.20	0.10	7.98	0.04	11.6	41.6	P: Lundberg and Alatalo (1992) T: Silverin (1993, 1998), Silverin and Wingfield (1982); EPP: Brün et al. (1996); Ellegren et al. (1995); Gelter and Tegelström (1992); Lifjeld et al. (1991); Rätti et al. (1995)
Saxicola torquata	0	M	1.84	0.50		0.30	16.0	45.8	T: Dittami and Gwinner (1985, 1990), Gwinner et al. (1994)
Lamprotornis chalybaeus	0	M	1.24			0.48	92.9	4.3	T: Dittami (1987), Dittami and Gwinner (1990)
Lamprotornis purpuropterus	0	M	0.91	0.50		0.11	60.0	2.1	T: Dittami (1987), Dittami and Gwinner (1990)
Sturnus vulgaris	29	P	2.78	0.30	9.09	0.45	84.7	30.5	P: Pinxten et al. (1989); T: Hilton (1968), Temple (1974), Dawson (1983), Ball and Wingfield (1987); EPP: Pinxten et al. (1993); Smith and von Schantz (1993)
Mimus polyglottos	0	M	2.30	0.70	8.00		50.7	45.0	T: Logan and Wingfield (1990, 1995); EPP: Derrickson and Breitwisch (1992)
Toxostoma curvirostre	0	M	3.19	0.11		1.14	79.4	34.1	T: Vleck (1993)
Campylorhynchus brunneicephalus	0	M	1.03	0.13		0.09	38.9	34.1	T: Vleck (1993)
Thryothorus nigricapillus	0	M		0.50			21.9	4.6	T: Wikelski et al. (1999)
Cyphorhinus phaeocephalus	0	M		0.40		0.06	24.6	4.6	T: Wikelski et al. (1999)
Parus montanus	0	M	1.33	0.30	0.96	0.11	10.2	54.4	T: Silverin et al. (1986), EPP: Orell et al. (1997)
Parus major	0	M	1.05	0.17	8.69	0.13	19.0	42.8	T: Röhss and Silverin (1983), Rost (1990), Silverin (1990); EPP: Blakey (1994); Gullberg et al. (1992); Krokene et al. (1998); Lubjuhn et al. (1999); Strohbach et al. (1998); Verboven and Mateman (1997)

Table 1 (*continued*)

Species	Polygyny (%)	Mating system	Peak testosterone (ng/ml)	Baseline testosterone (ng/ml)	Extra-pair paternity (%)	Testes mass (g)	Body mass (g)	Mean latitudinal distribution	References
Parus caeruleus	17	P	2.32		12.88	0.08	11.1	54.7	T: Foerster et al. (2002); EPP: Gullberg et al. (1992), Kempenaers et al. (1997); Krokene et al. (1998); Leech et al. (2001)
Hirundo rustica	0	M	1.90	0.90	28.78	0.55	19.0	20.7	T: Saino and Moller (1995); EPP: Moller and Tegelström (1997); Saino et al. (1997)
Cettia diphone	75	P	2.97				14.1	47.9	T: Wingfield et al. (1995)
Acrocephalus scirpaceus	0	M		1.10		0.15	12.0	30.5	T: Dittami et al. (1991)
Passer domesticus	10	P	5.65	0.41	9.83	0.42	28.0	48.7	P: Veiga (1992); T: Hegner and Wingfield (1986), Wingfield and Wada (1989); EPP: Wetton and Parkin (1991), Wetton et al. (1995), Cordero et al. (1999), Griffith et al. (1999)
Passer motitensis	0	M	1.09	0.18				5.9	T: Dittami (1986), Dittami and Gwinner (1990)
Plocepasser mahali	0	M	0.33	0.02		0.31	44.0	6.8	T: Wingfield et al. (1991), Levin and Wingfield (1992)
Ploceus baglafecht	0	M	0.80	0.20		0.30	31.5	2.1	T: Dittami (1986), Dittami and Gwinner (1990)
Ploceus philippinus	0	M	1.55	0.36		0.69	25.0	22.3	T: Narasimhacharya et al. (1988)
Taeniopygia guttata	0	M	3.48	0.01	2.40	0.05	12.0	2.2	T: Arnold (1975), Pröve (1978), Astheimer and Buttemer (1999); EPP: Birkhead et al. (1990)
Lonchura striata	0	M	1.54	0.10		0.07	11.3	22.6	T: Seiler et al. (1992)
Loxia leucoptera			2.35	0.71				50.3	T: Deviche and Sharp (2001)
Serinus canaria	0	M	3.20	0.45	0.00	0.23	13.0	40.4	T: Nottebohm et al. (1987); EPP: Voigt et al. (1997)
Carduelis flammea	0	M	4.50	1.33	4.55	0.39	12.0	50.3	T: Hunt et al. (1995); EPP: Angst (1998)
Calcarius lapponicus	17	P	8.91	0.45	12	0.54	27.3	55.8	P: Cramp and Perrins (1994); T: Astheimer et al. (1995), Hunt et al. (1995, 1997)
Plectrophenax nivalis	0	M	4.20	0.17		1.00	33.0	55.8	T: Romero et al. (1998)
Melospiza melodia	0	M	7.87	0.12	8.80	0.38	21.0	55.7	T: Wingfield (1984b, 1994), Wingfield and Hahn (1994), Smith et al. (1997); EPP: Smith (1991)
Zonotrichia capensis	0	M	1.70					22.3	T: Moore et al. (2002)
Zonotrichia leucophrys	7	P	2.99	0.30	36.00	0.42	29.4	58.5	P: Chilton et al. (1995); T: Wingfield and Farner (1978a,b, 1980a), Wingfield and Moore (1987), Morton et al. (1990), Hunt et al. (1995), Brenowitz et al. (1998); EPP: Sherman and Morton (1988)
Zonotrichia albicollis	0	M	2.79	0.40	12.80	0.43	27.0	58.8	T: Wiley et al. (1993); EPP: Tuttle (1993)
Junco hyemalis	0	M	6.75	1.12	28.34	0.29	21.0	57.2	T: Ketterson and Nolan (1994), Chandler et al. (1997), Raouf et al. (1997); EPP: Ketterson et al. (1998)
Spizella arborea	0	M	0.57	0.05		0.29	20.2	58.8	T: Hunt et al. (1995)
Pooecetes gramineus	0	M	4.40	0.70		0.60	27.0	54.8	T: Wingfield and Farner (1980b)
Amphispiza bilineata	0	M	4.65	0.20		0.25	13.5	40.7	T: Vleck (1993)
Pipilo erythrophthalmus	0	M	5.72	0.20		0.18	39.3	38.0	T: Brenowitz et al. (1991), Smith (1996)
Thraupis episcopus	0	M		0.30		0.32	35.0	4.8	T: Wikelski et al. (1999)

Table 1 (continued)

Species	Polygyny (%)	Mating system	Peak testosterone (ng/ml)	Baseline testosterone (ng/ml)	Extra-pair paternity (%)	Testes mass (g)	Body mass (g)	Mean latitudinal distribution	References
Xanthocephalus xanthocephalus	96	PP	5.70	0.90		0.97	79.6	54.8	P: Orians (1980); T: Beletsky et al. (1990b)
Agelaius phoeniceus	90	P	3.77	0.41	28.27	0.54	63.5	51.3	P: Yasukawa and Searcy (1995); T: Kerlan and Jaffe (1974), Beletsky et al. (1989, 1990a, 1992), Cristol and Johnsen (1994), Johnsen (1998); EPP: Gray (1996); Weatherhead and Boag (1995); Westneat (1993)
Sturnella neglecta	53	P	4.00	1.00		1.51	85.9	55.8	P: Lanyon (1994); T: Wingfield and Farner (1993)
Molothrus ater	0	M	1.92	0.33		0.88	44.0	54.8	T: Dufty and Wingfield (1986a,b), Dufty (1989)

Polygyny: % polygynous males; mating system: M: monogamous, P: polygamous, L: lek; extra-pair paternity: % of offspring being extra-pair offspring; References: P: polygyny, T: testosterone, EPP: extra-pair paternity.

non-significant ($P > 0.05$). Therefore, due to space limitations, we present results for peak and residual peak testosterone levels only (non-significant results are available from the authors upon request).

We estimated two components of variance in male mating success at different stages of the reproductive cycle: polygyny as a measure of social mating success and extra-pair paternity as a measure of fertilization success. These two components estimate different aspects of male mating success. While the index of polygyny estimates the relative number of social mates, the index of extra-pair paternity estimates the proportion of offspring sired by the social mate in its own nest(s) (Møller, 1998). Polygyny was scored on a continuous scale from 0 to 1, where 1 represents 100% of males being polygynous. We used estimates of the frequency of polygyny from different sources that are given in Table 1. The meaning of polygyny may be obscure in lekking species, and we avoided estimating polygyny for these birds, as no quantitative information was available for variance in matings among males at the display ground. The distribution of polygyny was strongly left skewed due to the large number of species that were strictly socially monogamous. Our chosen phylogenetic approach based on generalized least squares models (see Comparative methods) may be sensitive to the non-normal distribution of data (R. Freckleton unpublished data), and thus we used the ranks of polygyny in our phylogenetic models. To avoid loss of information due to the exclusion of lek species, we applied an alternative measure to reflect mating bias at the social level. Species were classified as being either (i) monogamous, in which no evidence of polygyny was reported; (ii) regularly polygynous, in which more than 5% of males attract more than one female (in our database, there was no species with irregular polygyny defined as less than 5% of males attracting more than one female); and (iii) lek species. This estimate for mating success at the social level is a traditional and reliable

classification of mating systems (Davies, 1991; Møller, 1986, 1991). However, it is difficult to handle three-state categories in relation to continuous variables in a phylogenetic context (see Purvis and Rambaut, 1995), especially when confounding variables are also considered (see below). Therefore, we tested our predictions regarding mating system categories by using statistical approaches on the raw species data. Finding no evidence for polygyny in a species may arise for biological reasons in strictly monogamous species, or it may be due to the absence of observers. Given that polygyny is probably common in birds (Møller, 1986), we suspected that differences in research effort in different species may cause bias in the polygyny data. We estimated research effort by using the number of studies published since 1972 on each species as cited in the ISI Web of Science (http://isi1.newisiknowledge.com), and related it to polygyny. We found that in species for which polygyny was not reported, the mean number of papers published was significantly smaller than in species for which polygyny data were available (respective means $\pm$ SE: 112.2 ± 25.6 vs. 355.2 ± 83.8; t test on $\log_{10}$-transformed data: $t = -4.125$, $df = 113$, $P < 0.001$; correlation between polygyny and research effort: Kendall $\tau = 0.236$, $P = 0.003$, $N = 106$). Therefore, we assessed the importance of research effort in the subsequent analyses of polygyny and mating system.

The frequency of extra-pair paternity was assessed as the percentage of offspring sired by males other than the attending (or the first) male, as determined from studies of paternity using allozymes (corrected for detection probability) and mini- and microsatellite studies. Extra-pair paternity strictly only applies to species with a pair bond between males and females. However, a male may lose paternity to another male if a female copulates with more than one male, and if the sperm of the second male fertilize some or all of the eggs, independent of whether the male has formed a pair bond with the female. Hence, from an

evolutionary perspective, selection will act similarly via sperm competition in a monogamous and a lekking species. Therefore, we define extra-pair paternity in this extended way and included lekking species if paternity data were available. If more than a single estimate of extra-pair paternity was available for a species, we used the mean value for all studies weighted by sample size. Repeatability of extra-pair paternity estimates among studies has previously been estimated to be 0.68 and highly significant (Petrie et al., 1998). Extra-pair paternity is in fact an estimate of the loss of mating success due to some offspring being sired by other males. However, this is not different from the estimate of polygyny, which is also an indirect measure of the loss of mating success due to some males remaining without mates. However, both polygyny and extra-pair paternity are *also* measures of variance in male mating success. Species with a high frequency of extra-pair paternity have a high standardized variance in male siring success in their own broods, but also in other broods (review in Møller, 1998). There is empirical evidence that males that gain paternity in other nests tend to have higher paternity in their own nest (Burley et al., 1996; Gibbs et al., 1990; Saino et al., 1997; Weatherhead and Boag, 1995; Yezerinac and Weatherhead, 1997). Testosterone levels did not differ significantly between species with and without information on extra-pair paternity indicating that our restricted sample for species with information on extra-pair paternity is not biased (all $Ps > 0.132$).

Sperm production estimates are uncommon in any organism, but we used an indirect estimate that has been shown to correlate with sperm production and sperm reserves (e.g., Møller, 1988a,b, 1989). This was the mean mass of the two testes during the peak breeding cycle, measured in grams. These data together with body mass data derive from Møller (1991), or were obtained from postmortem observation of dead birds carried out by a taxidermist (J. Erritzøe). Testes mass was measured on a balance to the nearest milligram blindly with respect to the hypotheses under test. Testes size showed significantly greater variation among than within species, verifying that the estimates are reliable for comparative analyses (Møller, 1991). Testes size scales allometrically with body mass, and thus to control for such allometric effects, we used residuals from a phylogenetically corrected regression of $\log_{10}$-transformed testes mass on $\log_{10}$-transformed body mass (see Comparative methods). This measure is subsequently termed residual testes size.

The potentially confounding effect of latitudinal distribution was assessed. We used a continuous variable that was obtained from distribution maps published in standard ornithological handbooks (e.g., Cramp and Perrins, 1985–1994; Marchant and Higgins, 1991–2001; Poole et al., 1993–2002; Ridgely and Tudor, 1989–1994), supplemented where necessary with regional field guides. Mean latitude was taken as the midpoint of the northernmost and southernmost limits of each species' geographical breeding and

wintering range, which has previously been shown to be a biologically meaningful measure (Gaston and Blackburn, 1996).

The entire data set is presented in Table 1. Since we did not have information for all variables, sample sizes differ slightly among analyses.

Comparative methods

We analyzed the predictions posed in the Introduction using statistical tests controlling for similarity in variables of interest due to common ancestry, using Generalized Least Squares (GLS) Models (Pagel, 1997, 1999). We used the computer program CONTINUOUS for the analyses (Pagel, 1997). The GLS approach controls for similarity due to common descent and allows investigation of correlated evolution between pairs of characters, estimates ancestral states, examines random-walk versus directional change models, assesses the tempo and mode of trait evolution and also estimates the importance of phylogenetic corrections. The GLS model characterizes evolutionary changes along each branch of a phylogenetic tree through the variance components of traits (Martins and Hansen, 1997; Pagel, 1997, 1999). Hypotheses are tested with likelihood ratio statistics. We present the phylogenetically corrected correlation coefficient between traits and the associated P values as given by corresponding log-likelihood ratio statistics relying on the most appropriate evolutionary model that had been adjusted for the mode of trait evolution. The following variables were $\log_{10}$-transformed to normalize variables: testes mass, body mass, research effort, testosterone levels. Extra-pair paternity was square root-arcsine-transformed and we used the ranks of polygyny. Some variables were clearly dependent on others due to allometric effects (e.g., peak testosterone on baseline testosterone, or testes size on body size). These effects were controlled by calculating residuals from the regression of the $\log_{10}$-transformed dependent variable on $\log_{10}$-transformed independent variable, using CONTINUOUS. Based on this equation, residuals were calculated on the raw species data (see also Purvis and Rambaut, 1995). Since the phylogenetic method does not allow insight on the phylogenetically transformed data, for illustrative purposes, we present figures based on the raw species data.

We constructed a composite phylogenetic hypothesis mainly based on information in Sibley and Ahlquist (1990) derived from extensive studies of DNA–DNA hybridization. This phylogeny for higher taxa was supplemented with information from Randi et al. (1991), Nunn et al. (1996), Zink and Blackwell (1996), Patten and Fugate (1998), Searcy et al. (1999), and Kimball et al. (1999) to resolve relationships in taxa with many species. We applied branch lengths from the tapestry tree of Sibley and Ahlquist (1990) for higher taxonomic levels. Within families, the distance between genera was set to 3.4 $\Delta T_{50}H$ units, and between species within genera to 1.1 $\Delta T_{50}H$ units (see also Bennett

and Owens, 2002; Sibley and Ahlquist, 1990). The composite phylogeny is available from the authors upon request.

Results

Patterns of circulating testosterone in relation to latitudinal distribution

Circulating level of peak testosterone was positively and significantly correlated with mean latitudinal distribution, while there was a similar tendency for residual peak testosterone (Fig. 1, peak testosterone: $r = 0.235$, $P = 0.014$, $N = 107$; residual peak testosterone: phylogenetic
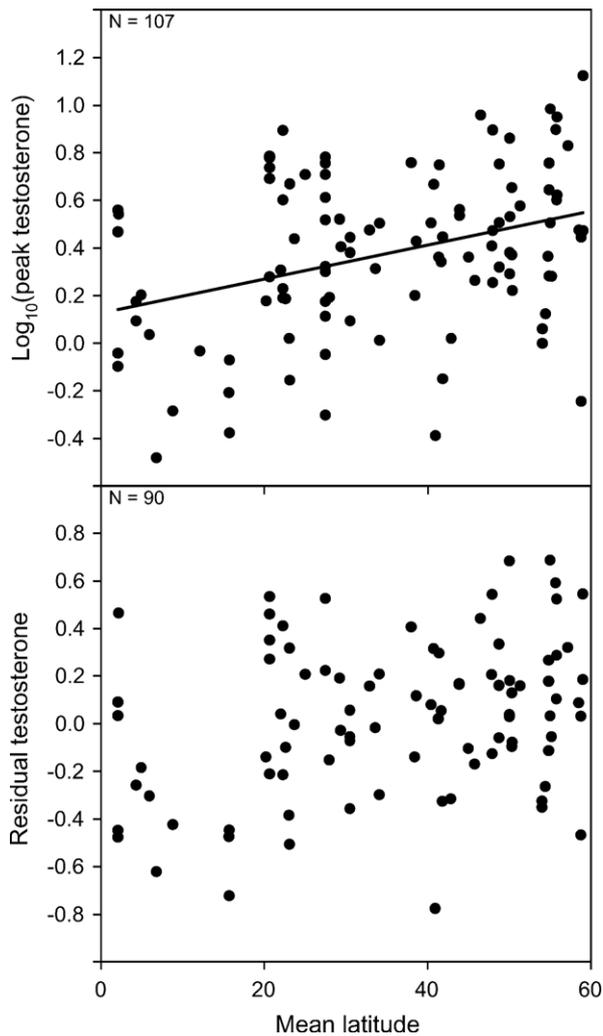

Fig. 1. Circulating level of testosterone in male birds in relation to latitudinal distribution: (top panel) peak testosterone level, (bottom panel) and residual testosterone (residuals from the phylogenetically corrected regression of $\log_{10}$-transformed peak testosterone on $\log_{10}$-transformed basal testosterone level). Values are transformed species-specific values, while lines are regression lines given if the corresponding phylogenetic relationship is significant (see text).

correlation: 0.179, $P = 0.088$, $N = 90$). Hence, we controlled for latitudinal distribution in the following analyses.

Testosterone, male mating success, and extra-pair paternity

An analysis of polygyny and testosterone using a phylogenetic approach revealed a tendency for higher levels of peak and residual peak testosterone in more polygynous taxa (peak testosterone: $r = 0.153$, $P = 0.128$, $N = 98$; residual peak testosterone: $r = 0.172$, $P = 0.116$, $N = 82$). When we included latitudinal distribution and research effort, these relationships remained non-significant (partial phylogenetic correlations with polygyny: peak testosterone, $r = 0.159$, $P = 0.097$; residual peak testosterone, $r = 0.147$, $P = 0.163$).

We tested for similar associations with mating system categories by applying statistics to the raw species data (previous evolutionary modeling revealed minor roles for phylogenetic effects for the relationships between different testosterone levels and social mating success). Peak testosterone titers varied consistently within monogamous, polygynous and lek species, as indicated by the corresponding ANOVA (Fig. 2; peak testosterone: $F = 3.839$, $df = 2,105$, $P = 0.025$; residual peak testosterone: $F = 1.768$, $df = 2,88$, $P = 0.177$). However, when we controlled for the confounding variables, research effort and latitudinal distribution as covariates, the relationship between peak testosterone and mating system disappeared (peak testosterone: overall model, $F = 4.798$, $df = 4,105$, $P = 0.001$, effect for mating system, $F = 0.843$, $df = 2,105$, $P = 0.433$; effect for latitude, $F = 6.886$, $df = 1,105$, $P = 0.010$; residual peak testosterone: overall model, $F = 3.024$, $df = 4,88$, $P = 0.022$, effect for mating system, $F = 0.155$, $df = 2,88$, $P = 0.857$; effect for latitude, $F = 4.786$, $df = 1,88$, $P = 0.032$). This result is probably due to the effect of latitudinal distribution on both testosterone and mating system, because mating system also showed a strong relationship with latitudinal distribution [$F = 8.104$, $df = 2,114$, $P < 0.001$; means (SE) monogamous: 30.29 (1.67); polygynous: 49.45 (4.66); lek: 38.71 (5.38)].

An analysis based on Generalized Least Square Models demonstrated a positive relationship between extra-pair paternity and peak testosterone level (Fig. 3; $r = 0.363$, $P = 0.028$, $N = 34$), with similar results for residual peak testosterone (Fig. 3; $r = 0.333$, $P = 0.048$, $N = 33$). The frequency of extra-pair paternity was not significantly related to the frequency of polygyny or to mating system (polygyny: phylogenetic correlation: 0.267, $P = 0.113$, $N = 34$; mating system: $F = 1.743$, $df = 2,35$, $P = 0.191$). When we assessed the effect of latitudinal distribution, we found that this variable could not confound the relationship between extra-pair paternity and testosterone levels (partial phylogenetic correlations with extra-pair paternity: peak testosterone, $r = 0.340$, $P = 0.026$; residual peak testosterone, $r = 0.350$, $P = 0.024$).
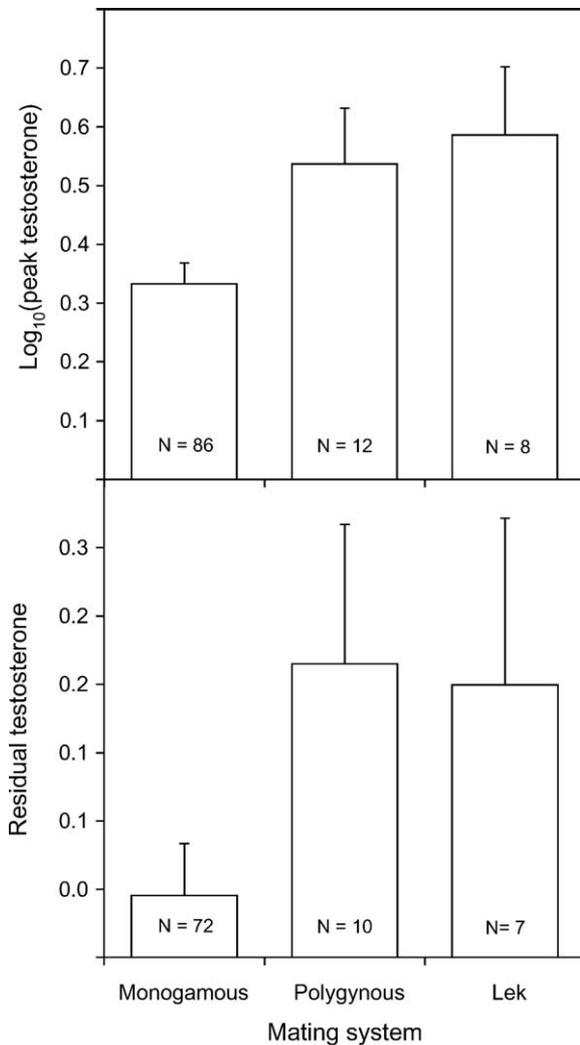
Fig. 2. Circulating level of testosterone in male birds in relation mating system: (top panel) peak testosterone level, and (bottom panel) residual testosterone (residuals from the phylogenetically corrected regression of $\log_{10}$-transformed peak testosterone on $\log_{10}$-transformed basal testosterone level). Means ($\pm$SE) are given.

Testosterone and reproductive physiology

There was a positive and significant phylogenetic relationship between testes mass and body mass (phylogenetic correlation: 0.767, $P < 0.001$, $N = 91$). Residual testes mass from the phylogenetic regression was significantly positively related to residual peak testosterone level (Fig. 4; peak testosterone: $r = 0.181$, $P = 0.096$, $N = 83$; residual peak testosterone: $r = 0.248$, $P = 0.037$, $N = 69$).

Since testes produce both sperm and testosterone, we estimated the partial phylogenetic correlation coefficients between testosterone levels, residual testes mass and extra-pair paternity. Since males win over competitors in sperm competition by production and insemination of more sperm (see Introduction), we used the proportion of extra-pair offspring as an estimate of relative production of sperm. In our data, there was a significant positive phylogenetic association between relative testes size and extra-pair

paternity ($r = 0.378$, $P = 0.022$, $N = 34$). We entered relative testes size, extra-pair paternity and relative peak testosterone level in a single model and assessed the significance of their concerted evolution. This model showed significant effects for the coevolution of the three traits ($P = 0.014$, $N = 31$). We obtained partial correlations based on the pairwise phylogenetic correlations of this model. In this sample, only the correlations between extra-pair paternity and residual testes mass reached significance (testes mass and extra-pair paternity: $r = 0.361$, $P = 0.024$; testes mass and residual peak testosterone: $r = 0.186$, $P = 0.284$; extra-pair paternity and residual peak testosterone: $r = 0.230$, $P = 0.176$). Based on the pairwise correlations among residual peak testosterone, relative testis size and extra-pair paternity given by the corresponding phylogenetic
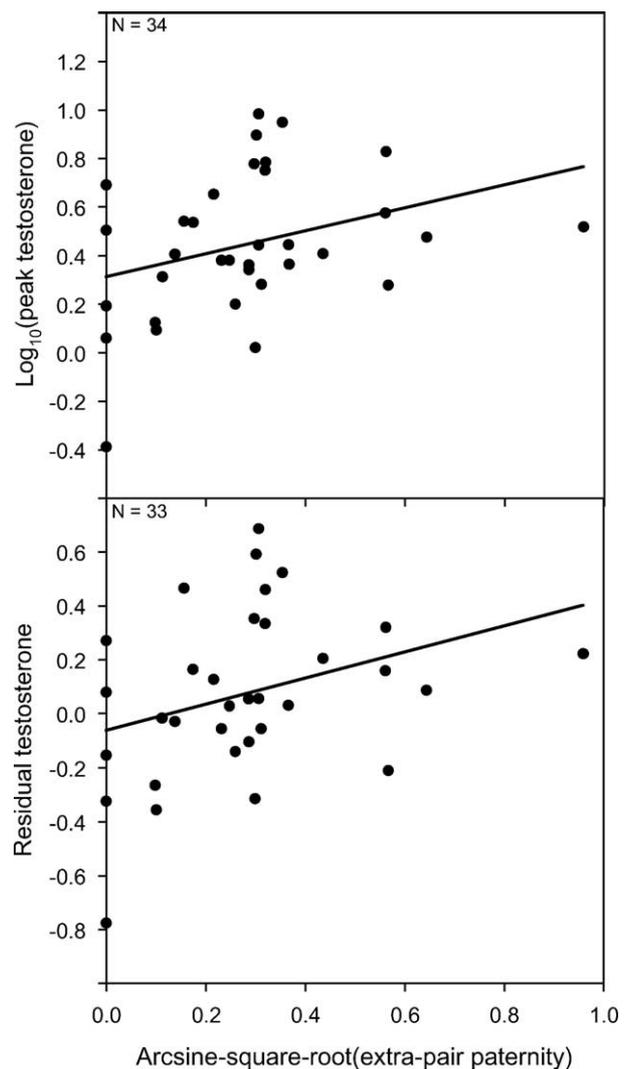

Fig. 3. Circulating levels of peak testosterone level in male birds in relation to extra-pair paternity based on statistically transformed raw species data: (top panel) peak testosterone level, and (bottom panel) residual testosterone (residuals from the phylogenetically corrected regression of $\log_{10}$-transformed peak testosterone on $\log_{10}$-transformed basal testosterone level). Lines are regression lines given if the corresponding phylogenetic relationship is significant (see text).
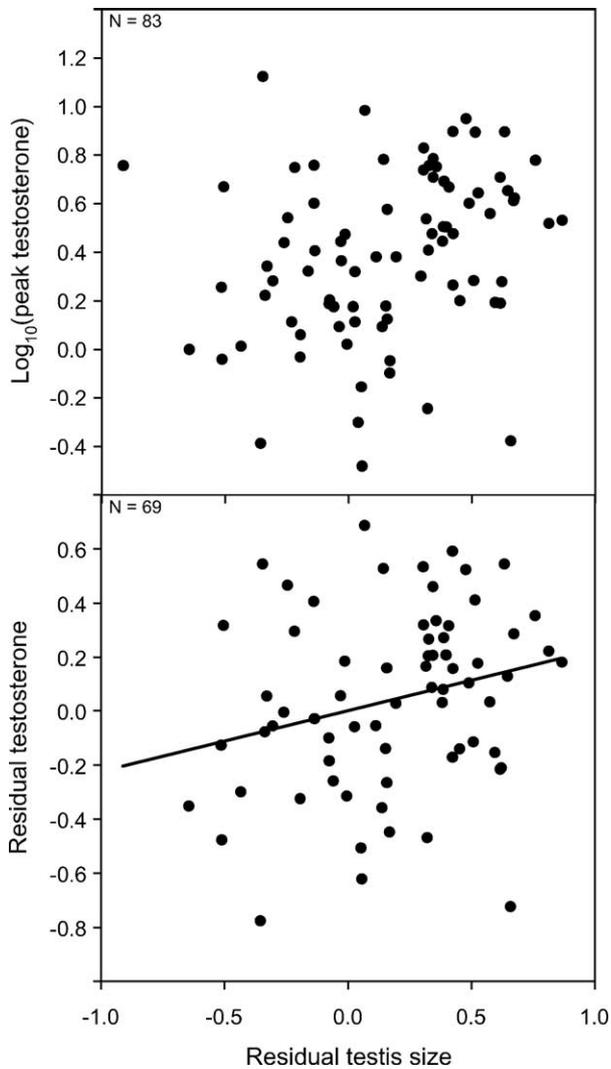
Fig. 4. Circulating levels of testosterone in male birds in relation to relative testes mass during the breeding season: (top panel) peak testosterone level, and (bottom panel) residual testosterone (residuals from the phylogenetically corrected regression of $\log_{10}$-transformed peak testosterone on $\log_{10}$-transformed basal testosterone level). Relative testes mass was residuals from a phylogenetically corrected regression of $\log_{10}$-transformed testes mass on $\log_{10}$-transformed body mass. Values for testosterone are transformed species-specific values. The line is the regression line.

model, we applied path analysis to identify the statistical model that explained most variance in the relationship among these three variables (Li, 1975; Wright, 1968). This was done by creating three different models to provide likely scenarios for causal relationships: (1) arising from the same selection pressures, extra-pair paternity and residual peak testosterone level mutually influence each other and both affect the evolution of relative testis size; (2) relatively larger testes evolve to allow intense sperm competition and production as reflected by extra-pair paternity that has a secondary impact on testosterone production; and (3) testis size primarily has an evolutionary effect on testosterone production that subsequently favors higher rates of extra-pair paternity. The three different path diagrams linking the three factors are

presented in Fig. 5. Based on the greatest explanatory power, the model which assumes a primary relationship between relative testis size and extra-pair paternity and a secondary consequence on testosterone production is the most likely (this model explained 28.4% of the variance compared to 20.7% and 19.4% of the variance explained by the two alternative models).

Discussion

Covariation and latitudinal variation in estimates of circulating testosterone

Circulating levels of peak and baseline testosterone were positively correlated across species of birds, when calculations were based on phylogenetically independent data. The regression line had a slope that was significantly smaller than one (the regression coefficient was 0.212, which implies that peak testosterone increased considerably less than baseline testosterone). Thus, species with high baseline levels of circulating testosterone have relatively low peak levels. This finding is reminiscent of a result reported by Wingfield et al. (1990), who showed that species of birds with a polygynous mating system tended to have high peak and baseline levels of testosterone, while monogamous species tended to have high peak, but low baseline levels. The pattern found here has implications for reproduction and costs of relatively high testosterone titers. The fact that males of all species do not have equally high testosterone levels, although such high levels can enhance mating success (see review in Introduction), and that peak testosterone level increases less than baseline level, suggests that there are important costs associated with high levels. One such hypothesized cost is the immuno-suppressive effects of testosterone (Folstad and Karter, 1992). Although the evidence in favor of this hypothesis is far from conclusive (Roberts et al., 2004), and that other costs of relatively high testosterone levels are possible (risk of injury: Beletsky et al., 1995; effects on sperm production: Folstad and Skarstein, 1997; Hillgarth et al., 1997), this is at least one viable explanation.

Higher peak and residual peak testosterone titers have been found in species living farther away from the equator (Fig. 1, for residual peak testosterone, see the analyses with mating system in the main text). This finding is in accordance with interspecific studies across a selection of passerine species that suggested that birds breeding in temperate zones have elevated plasma testosterone levels during the breeding season compared to birds of the tropics (e.g., Levin and Wingfield, 1992; Moore et al., 2002; Wingfield et al., 1997). Here, by relying on a comparative study of more than one hundred species, we demonstrated a positive relationship between testosterone and latitudinal distribution, as predicted by Wingfield et al. (1992). Tropical species living in stable, saturated environments tend to breed
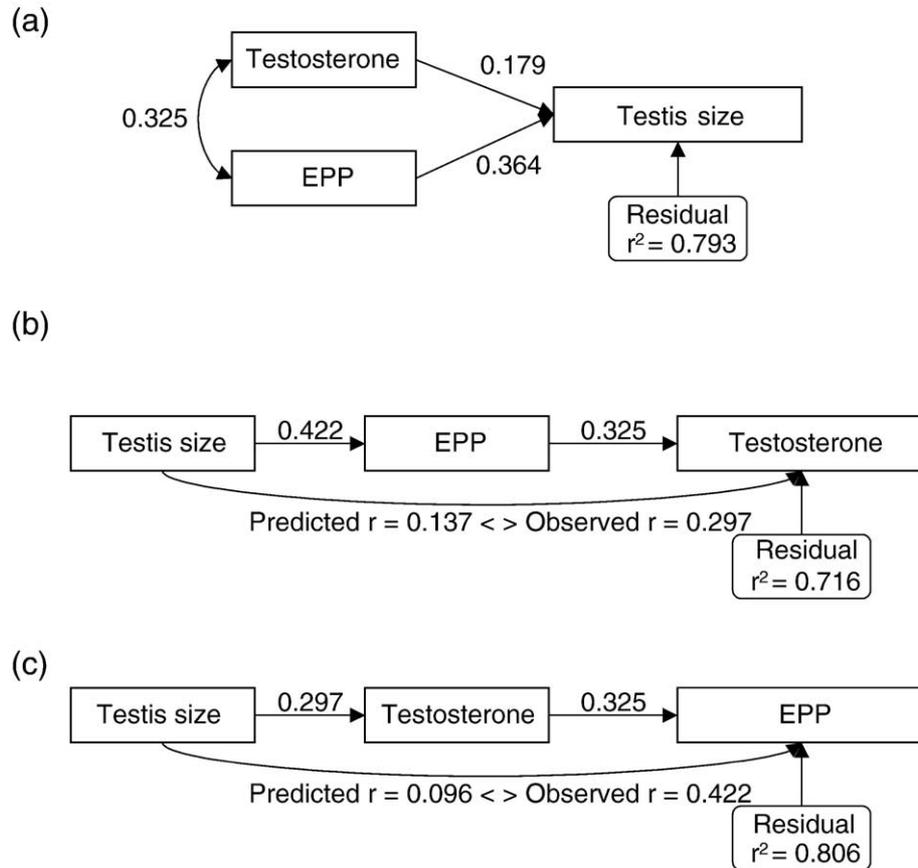
Fig. 5. Path analysis of relative peak testosterone levels, extra-pair paternity, and relative testis size. Values are path coefficients calculated from the pairwise phylogenetic correlation among the three traits (EPP: extra-pair paternity). The three models correspond to the causal mechanisms in which (a) extra-pair paternity and residual peak testosterone level mutually influence each other and both affect the evolution of relative testis size; (b) testis size evolves first to allow intense sperm competition and production as reflected by extra-pair paternity that has a secondary impact on testosterone production; and (c) testis size primarily has an evolutionary effect on testosterone production that subsequently favors higher rates of extra-pair paternity. Correlation coefficients between indirectly related traits as predicted by different evolutionary models (Predicted r) are compared with observed phylogenetic correlations (Observed r). Residual variance is the amount of variance that is not explained by the model, the explained variance can be computed as $1 - r^2$.

less synchronously throughout the year and also usually experience less extra-pair paternity than do generally synchronous temperate or high-latitude species (Stutchbury and Morton, 2001). Species breeding in northern latitudes frequently have shorter breeding seasons than species breeding at lower latitude and corresponding shorter periods of elevated testosterone (Wingfield et al., 1997). Testosterone peaks of greater magnitude in northern latitude species may be associated with socially unstable situations during territory establishment (Hunt et al., 1995). These elevations in plasma testosterone levels above baseline breeding levels occur during the breeding season when the testes are recrudesced and are consistent across species breeding in the high arctic (Hunt et al., 1995). While it is not clearly understood why equatorial birds have low plasma testosterone levels, this trend is consistent across a variety of new and old world equatorial species (see Introduction in Moore et al., 2002). The hypothesis that circulating testosterone levels vary latitudinally draws heavily on life-history differences between tropical and temperate regions (Lack, 1968), which have been generally accepted explanation for the phenom-

enon. However, there may be other important ecological factors that vary from the equator towards the poles, suggesting that the interspecific relationship between testosterone and latitudinal distribution needs to be carefully examined in order to distinguish causality from correlation. We infer that latitudinal distribution is not the direct measure of the quality that drives differences in testosterone levels. For example, the duration of the breeding season, difference between mean summer and winter temperature or breeding asynchrony that covary with latitudinal distribution may be more important determinants of testosterone levels than distribution per se. However, the identification of these potential causal mechanisms is well beyond the focus of the present paper. Clearly, the interspecific association between testosterone titers and latitudinal distribution needs further investigations, and our findings from this aspect should be interpreted with caution. On the other hand, our results do indicate that the apparent relationship between testosterone and mating success may be confounded by latitudinal distribution or other factors that are associated with it (see discussion below).

Testosterone and male mating success

Testosterone has been implicated in the evolution of polygyny (Wingfield et al., 1990). High testosterone levels during the breeding season should increase the mating success of males by increasing display rates. Experimental administration of testosterone in males of socially monogamous bird species has resulted in a shift in the mating system towards polygyny (Wingfield, 1984a), although that is not always the case (Ketterson and Nolan, 1992; Saino and Møller, 1995). Wingfield et al. (1990) and Hirschenhauser et al. (2003) reported that the peak testosterone to baseline testosterone ratio, termed androgen responsiveness, was lower in polygynous than in monogamous species of birds. We found a similar but non-significant tendency for a positive association between circulating levels of peak and residual peak testosterone and degree of polygyny across birds. When we tested for differences among mating systems, we found significant differences in peak testosterone levels between monogamous, polygynous and lek species (Fig. 4). However, this relationship appeared to be confounded by latitudinal distribution, a factor that has been neglected in previous interspecific appraisals. Both testosterone level and apparent mating system exhibit strong latitudinal variation. The factors that cause testosterone titers and mating strategies to vary with latitude remain to be identified. However, our results imply that such factors as "third variables" can mediate the evolutionary relationship between polygyny and testosterone levels, indicating that perhaps there is no causal relationship between them.

Hormones elicit responses only in the presence of appropriate hormone receptors (Nelson, 2000). Hence, the relationship between testosterone and behavior could be mediated without changing the circulating concentration of testosterone, by changing the concentration of testosterone receptors or the affinity of binding to receptors. By using circulating levels of hormones, it may be difficult to detect relationships between mating patterns and testosterone due to such receptor-mediated mechanisms potentially varying among species. However, we assume that testosterone titers in the blood are subject to selection because of their high repeatability, and are biologically relevant given their correlations with latitude, extra-pair paternity and relative testes size. Therefore, our negative findings with social mating success may indicate that testosterone truly played only a minor role in the evolution of polygyny through paternal care and male–male competition. On the other hand, Wingfield et al. (1990) suggested that the reproductive physiology in monogamous and polygynous species may be different in terms of temporal distribution of peak testosterone levels during the breeding season. Hence, the timing of peak circulating testosterone may have profound effects on mating patterns, as polygynous species seem to have consistently high levels of testosterone during an extended period of the breeding season (Beletsky et al., 1995;

Wingfield et al., 1990). Our data do not allow investigation of this possibility.

Testosterone was also hypothesized to be involved in sperm competition because high levels of extra-pair paternity will select for males that are able to defend their fertile females against the approach of other males, or because females prefer to mate with extra-pair males with relatively high testosterone levels (see Introduction). This prediction was confirmed since peak and residual peak testosterone levels were higher in species with frequent extra-pair paternity (Fig. 3). Indeed, this association was independent of latitudinal distribution. Extra-pair paternity explained 13.2% of the variance in peak testosterone level and 11.1% of the variance in residual testosterone level, while polygyny explained 2.3% of peak testosterone level and 3.0% of residual testosterone level. These findings suggest that sperm competition has been an important, but overlooked selective force increasing levels of circulating testosterone.

Comparative analyses are based on correlations and they thus usually cannot be used to infer causation. That is also the case in the present study. Therefore, the reported findings may fit two possible directions of causality between the variables of interest. First, sexual selection arising from extra-pair paternity may affect testosterone levels on an evolutionary time scale. Second, high levels of testosterone may allow the evolution of high levels of extra-pair paternity. For example, females preferring to copulate with extra-pair males with relatively high testosterone levels may select for relatively high testosterone levels. On the other hand, testosterone may promote evolutionary changes in the level of sexual selection by allowing males to defend their territories or their females from extra-pair copulations. Our results are in line with both causal mechanisms, which suggest that the evolution of reproductive behaviors associated with extra-pair paternity depends upon the evolution of steroid hormone secretion.

Testosterone and male reproductive physiology

Testes produce both testosterone and sperm. At the interspecific level, evolution of large testes will result in evolution of large amounts of testosterone producing tissue and large amounts of sperm producing tissue. Extensive theoretical and empirical studies of sperm competition have indicated that sperm competition selects for increased investment in sperm producing tissue because this increases the probability of fertilization (Møller, 1988a,b, 1989; Parker, 1970; review in Møller and Briskie, 1995). Since sperm production is strongly positively correlated with testes mass (Møller, 1989), we can predict that species with intense sperm competition will tend to have relatively large testes (Brown and Brown, 2003; Dunn et al., 2001; Harcourt et al., 1981; Short, 1979). Indeed, our data also provided significant support for this

prediction. However, the hypothesis that relative testes mass is an indicator of both sperm production and testosterone production has never previously been tested. We found that relative testes mass tended to positively correlate with peak testosterone level (Fig. 4), explaining 3.3% of the variance. Residual testosterone explained 5.8% of the variance in relative testes mass, a pattern that was significant. Since the publication of the seminal paper by Parker (1970), testes size has been used as a measure of the intensity of sperm competition through increased sperm production. However, our results imply that relative testes mass can reflect the importance of testosterone production as well. A phylogenetic model including peak testosterone, extra-pair paternity (a measure of the intensity of selection arising from sperm competition) and relative testes mass did in fact provide evidence for coevolution of these reproductive characters. Hence, relative testes size can reflect the intensity of both testosterone production and sperm production. We proposed three evolutionary scenarios determining the relationship between testosterone, extra-pair paternity and relative testes mass (Fig. 5). Based on the detailed partial correlation analyses with residual testosterone levels, we found a stronger phylogenetic relationship between extra-pair paternity and relative testes mass than between residual testes mass and testosterone, or between testosterone and extra-pair paternity. Moreover, our path analysis supported that sperm production as reflected by extra-pair paternity seems to have been a stronger selective agent for the evolution of large testes than testosterone. We hypothesize that the explanation that predicts a closer evolutionary link between extra-pair paternity and testes size than between testosterone levels and testes size is more likely. Hence relative testes mass may primarily have evolved to allow intense sperm competition, with the latter favoring increased testosterone production. Hence larger testes may have evolved primarily to produce more sperm, as more sperm allow males to compete for fertilization of eggs. Secondly, higher levels of testosterone have evolved to allow males to defend their females against threats of extra-pair copulations. However, based on the small sample size in this analysis, we suggest that this mechanism needs further study as more data become available.

Acknowledgments

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