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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.

Keywords: Birds; Extra-pair paternity; Latitudinal distribution; Polygyny; Sexual selection; Sperm competition; Sperm production; Testosterone

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

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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