ing the annual reproductive cycle of Starlings (*Sturnus vulgaris*). General and Comparative Endocrinology 22:470–479.

WITMER, M. C. 1996. Consequences of an alien shrub on the plumage coloration and ecology of Cedar Waxwings. Auk 113:735–743.

WOLFENBARGER, L. L. 1996. Fitness effects associated with red coloration of male Northern Cardinals (*Cardinalis cardinalis*). Ph.D. dissertation, Cornell University, Ithaca, New York.

Received 27 January 1997, accepted 21 April 1997.
Associate Editor: J. S. Marks

The Auk 114(4):800–801, 1997

A Single Functional Testis as a Unique Proximate Mechanism Promoting Sex-role Reversal in Coucals

J. DAVID LIGON[1]
Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131 USA

Sex-role reversal, where the male provides most or all of the care of eggs and young, occurs in a small fraction of the world's approximately 9,700 living species of birds. Although it is best known in a few temperate-zone shorebirds, sex-role reversal also occurs in ratites, tinamous, and buttonquail, all of which produce precocial young (Ligon 1993). Sex-role reversal also occurs in at least one group of altricial birds, the coucals, genus *Centropus* (Vernon 1971, Irwin, 1988, Ligon 1993, Andersson 1995). Coucals are a distinctive group of nonparasitic cuckoos that occurs over much of the Old World tropics.

The puzzling mating system known as classical polyandry is associated with sex-role reversal. Consequently, the proximate factors that promote this phenomenon should be of interest to students of avian mating systems. Testosterone has a negative effect on parental care in male birds (Wingfield et al. 1990), which leads to the question: What physiological or endocrinological alterations have taken place to bring about sex-role reversal? In two sex-role reversed North American shorebirds, high levels of testosterone are present in preincubating males (Rissman and Wingfield 1984, Fivizzani and Oring 1986, Fivizzani et al. 1986, Oring et al. 1988), but as the male begins to incubate testosterone levels rapidly drop by up to 25-fold (Fivizzani and Oring 1986). The fact that males of these species exhibit normal levels of circulating testosterone prior to incubation led Fivizzani and Oring (1986) to suggest that the internal factors responsible for the preincubation sex-role reversal must be the specificity of neural receptors rather than changes in the gonadal hormonal state typical of each sex.

In coucals, as in precocial species with sex-role reversal, the male assumes a role generally considered to be more typical of female birds; i.e. in addition to being smaller, males construct the nest and carry out most or all incubation and care of the chicks (e.g. Vernon 1971, Irwin 1988). A morphological trait possibly related to this sex-role reversal is great asymmetry in size and development of the testes. In at least some species of coucals, the left testis is "atrophied" or "rudimentary," or even absent altogether, whereas the right testis is of normal size (Rand 1933, 1937; Chapin 1939). Based on a sample of 43 male specimens of the Madagascar Coucal (*Centropus toulou*), Rand (1933) reported that, ". . . the right testis was always larger than the left, which was atrophied, never being firm and oval, and never showing any enlargement in the breeding season, even when the right was at its maximum size." In addition to the Madagascar Coucal, absence or severe reduction in size of the left testis also has been reported in three African species of coucals (Rand 1937, Chapin 1939), including the classically polyandrous Black Coucal (*C. grillii*; Vernon 1971, Irwin 1988).

To obtain additional information on this apparently unique testicular condition, I examined two pickled specimens of males of the Madagascar Coucal in the collections of the Field Museum of Natural History. These birds were collected in October 1989, which is early in the breeding season. Each male had a large right testis (ca. 12.1 × 8.5 mm and 13.7 × 7.8 mm), whereas the left testis was noted by the collector as degenerate in one specimen and was not discernible to me in the other.

Loss of the left testis, rather than the right, is, in itself, peculiar, because in birds the left testis usually is the larger of the two (Lake 1981, Møller 1994; but see Kimball et al. 1997). Although the reasons for this directional asymmetry are not well understood, at the end of embryonic growth the left testis has more

[1] E-mail: jdligon@unm.edu

primordial germ cells than the right (Witschi 1935, Venzke 1954). Moreover, in the great majority of avian species the right ovary is vestigial. Thus, the single functional testis of male coucals apparently is unrelated developmentally to the fact that female birds also typically possess only one functional gonad. That is, the evolved loss of a functional left testis in male coucals probably is not homologous to the loss of a functional right ovary in females of a majority of avian species.

In male birds, testosterone inhibits parental care (Wingfield et al. 1990), and proximate control of incubation in sex-role reversed male shorebirds is based on a dramatic drop in testosterone and on increased production of pituitary hormones, especially prolactin (Rissman and Wingfield 1984). One might suspect that the loss of one functional testis, as in coucals, has the effect of reducing the level of circulating testosterone relative to the hormones important in nest building, incubation, etc. Thus, the absence of a functional left testis may be causally related to the evolved sex-role reversal in coucals. If so, then "feminization" of male coucals by such a proximate mechanism appears to be unique among birds.

Acknowledgments.—I thank Scott M. Lanyon, Thomas S. Schulenberg, and David E. Willard, of the Field Museum of Natural History for their help, and for allowing me to examine specimens in their care; J. C. Hagelin for help in dissection of specimens; and R. T. Kimball and S. H. Ligon for comments on the manuscript.

Literature Cited

ANDERSSON, M. 1995. Evolution of reversed sex roles, sexual size dimorphism, and mating system in coucals (Centropodidae, Aves). Biological Journal of the Linnean Society 54:173–181.

CHAPIN, J. P. 1939. The birds of the Belgian Congo. Part II. Bulletin of the American Museum of Natural History 75:1–632.

FIVIZZANI, A. J., AND L. W. ORING. 1986. Plasma steroid hormones in relation to behavioral sex role reversal in the Spotted Sandpiper, *Actitis macularia*. Biology of Reproduction 35:1195–1201.

FIVIZZANI, A. J., M. A. COLWELL, AND L. W. ORING. 1986. Plasma steroid hormone levels in free-living Wilson's phalaropes, *Phalaropus tricolor*. General and Comparative Endocrinology 62:137–144.

IRWIN, M. P. S. 1988. Order Culculiformes. Pages 58–104 *in* The birds of Africa, vol. III (C. H. Fry, S. Keith, and E. K. Urban, Eds.). Academic Press, San Diego, California.

KIMBALL, R. T., J. D. LIGON, AND M. MEROLA-ZWARTJES. 1997. Testicular asymmetry and secondary sexual characters in Red Junglefowl. Auk 114: 221–228.

LAKE, P. E. 1981. Male genital organs. Pages 1–61 *in* Form and function in birds (A. S. King and J. McLelland, Eds.). Academic Press, London.

LIGON, J. D. 1993. The role of phylogenetic history in the evolution of contemporary avian mating and parental care systems. Current Ornithology 10:1–46.

MØLLER A. P. 1994. Directional selection on directional asymmetry: Testes size and secondary sexual characters in birds. Proceedings of the Royal Society of London Series B 258:147–151.

ORING, L. W., A. J. FIVIZZANI, M. A. COLWELL, AND M. E. EL HALAWANI. 1988. Hormonal changes associated with natural and manipulated incubation in the sex-role reversed Wilson's Phalarope. General and Comparative Endocrinology 72:247–256.

RAND, A. L. 1933. Testicular asymmetry in the Madagascar Coucal. Auk 50:219–220 .

RAND, A. L. 1937. The distribution and habits of Madagascar birds. Bulletin of the American Museum of Natural History 72:143–499.

RISSMAN, E. F., AND J. C. WINGFIELD. 1984. Hormonal correlates of polyandry in the Spotted Sandpiper, *Actitis macularia*. General and Comparative Endocrinology 56:401–405.

VENZKE, W. G. 1954. The morphogenesis of the indifferent gonad of chicken embryos. American Journal of Veterinary Research 15:300–308.

VERNON, C. J. 1971. Notes on the biology of the Black Coucal. Ostrich 42:242–258.

WINGFIELD, J. C., R. E. HEGNER, A. M. DUFTY, JR., AND G. F. BALL. 1990. The "challenge hypothesis": Theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. American Naturalist 136:829–846.

WITSCHI, E. 1935. Origin of asymmetry in the reproductive system of birds. American Journal of Anatomy 56:119–141.

Received 27 January 1997, accepted 3 June 1997.
Associate Editor: E. Greene