Honey, I shrunk one of my gonads! Does 'feminization' of behaviour cause asymmetric testis development in coucals?

Wolfgang Goymann[1,2,3]

1) Department of Behavioural Neurobiology, Max Planck Institute for Biological Intelligence, 82319 Seewiesen, Germany

2) Ludwig Maximilians University Munich, Department Biology II, Großhaderner Str. 2, 82152 Martinsried, Germany

3) Coucal Project, PO Box 26, Chimala, Tanzania

Corresponding author: Wolfgang Goymann, email: wgoymann@bi.mpg.de

Abstract

In most birds, females develop only a single ovary. This asymmetry is usually explained as an adaptation to reduce weight for flight, or to prevent damage to hard-shelled eggs by a second egg in the other oviduct. By contrast, males retain paired testes with the left one typically being larger. Coucals break this pattern: as sex-role reversal intensifies across the genus, males show a progressive shift towards a dominant right testis, culminating in complete loss of the testis in the most sex-role reversed species. The prevailing explanation — that testis loss lowers testosterone to enable male-only care — has been rejected. I propose instead, that testicular asymmetry in coucals is a non-adaptive developmental by-product of estrogen-mediated feminization of the male brain. Estrogens normally drive the development of the left ovary. Transient estrogen production in males could prevent further development of the left gonad into a testis. In contrast, because of its innate testicular predisposition the right gonad can grow into a functional testis, once estrogen production stops. Hence, reduction of the left testis may be a developmental by-product of behavioural feminization in coucals and could be an excellent model for studies on sexual differentiation.

Key words: estradiol, testosterone, testis, ovary, gonad, aves, feminization, sex roles, sex-role reversal, DMRT-1, SOX9, FOXL2, aromatase, 17ß-HSD

Introduction: Testicular asymmetry in coucals: an evolutionary puzzle

Many organs in bilaterian animals, including vertebrates, come in pairs. This includes the reproductive organs, which are typically paired ovaries and testes. Birds, however, represent an exception to this rule. While male birds have two testes, females of most bird species develop only their left ovary; their right ovary regresses during embryonic development. Witschi (1935) suggested that retaining one ovary may reduce weight, thereby representing an adaptation to flight. An alternative hypothesis relates the absence of the second ovary to the fragility of hard-shelled eggs during the final stages of development. The ovum spends approximately one day in the oviduct acquiring its shell. During this stage, the ovum would be susceptible to physical damage if another shelled egg were in its vicinity (Guioli et al., 2014). This hypothesis is consistent with the finding that the few bird species with two ovaries (such as birds of prey and kiwis) still only have one oviduct, meaning that only one egg is present when the shell forms (Kinsky, 1971). The platypus, a non-flying

mammal that also lays hard-shelled eggs, also has only one functional ovary, further supporting this view (Grützner et al., 2008).

Unlike females, male birds generally have paired gonads, but there is typically some asymmetry, with the left testis being larger than the right testis (Calhim and Montgomerie, 2015). However, males of the coucal genus (Centropodinae) show a continuous reversal of this symmetry, resulting in the complete loss of the left testis in some species. The white-browed coucal (*Centropus superciliosus*), for instance, follows the general avian pattern of having a larger left testis (Friedmann, 1927). Other species, such as the blue-headed coucal (*C. monachus*), the Senegal coucal (*C. senegalensis*), the Madagascar coucal (*C. toulou*), the pheasant coucal (*C. phasianinus*), and the greater coucal (*C. sinensis*) exhibit the opposite pattern, with a smaller, vestigial left testis and a larger right testis (Fu et al., 2009; Maurer and Blomberg, 2009; Rand, 1933). The left testis is completely absent in lesser coucals (C. *bengalensis*) and African black coucals (*C. grillii*) (Bernstein, 1860; Chapin, 1939; Frey and Goymann, 2009). Hence, within the coucal genus there appears to be a tendency to reduce or lose the left testis.

Why the testosterone-reduction hypothesis fails

Coucals belong to the cuckoo family (Cuculidae) and are characterized by various degrees of slight to extreme reversed sexual size dimorphism. They probably show the greatest flexibility in sex roles of any altricial bird, ranging from joint territorial defence and biparental care to a complete reversal, with females becoming polyandrous and keeping harems of up to five males. In such instances, the males undertake all parenting duties, from incubation to tending and feeding the young (Andersson, 1995; Ligon, 1999; Safari and Goymann, 2021). Ligon (1997) suggested that the loss of one testicle is a physiological adaptation related to male-only care. Testes produce sperm and are the main endocrine glands that produce the sex steroid hormone testosterone. Since high levels of testosterone have been shown to suppress paternal care (reviewed by (Goymann and Flores Dávila, 2017), regressing one testis with a subsequent reduction in testosterone production may be an adaptation for male-only care in sex-role reversed coucal species (Ligon, 1997). While this adaptive explanation seems compelling at first, comparative hormone data refuse it: I compared testosterone concentrations in two species at the two opposite ends of the coucal mating system spectrum: the white-browed coucal and the African black coucal. White-browed coucals are the least sexually dimorphic species of coucal. Males sing to defend territories (Brumm and Goymann, 2017, 2018) and parental roles are balanced (Goymann et al., 2015; Goymann et al., 2016). Furthermore, males have two testes with the left one being larger than the right one (Friedmann, 1927), following the general avian pattern. In contrast, female African black coucals are 70% larger than males. Their sex roles are completely reversed, with females aggressively defending large territories that harbour up to five males and males providing the only care for eggs and young (Goymann et al., 2015; Goymann et al., 2004). However, despite retaining only their right testis (Frey and Goymann, 2009) testosterone concentrations of male black coucals are similar to those of white-browed coucals – if anything they tend to be slightly higher in black coucals than in white browed coucals (Goymann, 2023). Furthermore, the right testis of black coucals is enlarged, thereby apparently compensating for the loss of the left testis (Frey and Goymann, 2009). Similar evidence has been found in pheasant coucals (Maurer and Blomberg, 2009). Finally, circulating testosterone concentrations in both coucal species fall within the range typical of male birds with traditional sex roles. Therefore, the adaptive explanation that the loss of one testis reduces testosterone production, thereby fostering male-only care (Ligon, 1997), is not supported by these data.

Unilateral testis development as a developmental by-product of feminization

A developmental anomaly is also an unlikely explanation, given the continual reduction in size of the left testis from the regular bird pattern with a larger left testis in species such as the white-browed coucal to the complete loss of the left testis in lesser coucals or African black coucals. Ligon (1997) suggested that the loss of the right testis is developmentally unrelated to the asymmetry of female ovaries: females lose their right gonad (Guioli et al., 2014), whereas male coucals reduce or lose their left gonad. Hence, according to Ligon (1997), losing the right ovary, respectively the left testis are developmentally unrelated events triggered by different mechanisms. Having looked more closely at the processes of gonadal differentiation in birds, I propose the opposite hypothesis: the reduction in size and eventual complete loss of the left testis in coucals is a consequence of the ontogenetic processes of gonadal differentiation in birds. In this scenario, the reduction and eventual loss of the left testis represents a developmental side-effect of the behavioural feminization of coucal males. This feminization is most likely triggered by estrogenic action during embryonic development. Therefore, the reduction and eventual loss of the left testis therefore may be directly linked to the degree of sex-role reversal, with the white-browed coucal representing one of the least sex-role reversed species, and the African black coucal representing the most sex-role reversed species. Similar to the African black coucals, female lesser coucals appear to play a larger role in defending their territory, while only males incubate eggs and feed the young (Bernstein, 1860) J. Tsai & W. Goymann, unpublished data). For the species with a larger right than left testis, only the pheasant coucal has had its sex roles quantified: here, females and males cooperate in defending a territory, but males play a larger role in parental care (Maurer, 2008). Therefore, the extent to which the left testis is lost may be directly related to the extent to which sex roles are reversed.

Estrogens are a key hormone in the development of the single ovary in female birds, and they may play a role in the “feminization” of the brains of male coucals during ontogeny. Consequently, temporary estrogen production of estrogens in male coucals could explain the reversal of testicular asymmetry in partially sex-role reversed coucal species, as well as the complete atrophy of the left testis in species with complete sex-role reversal. Right testis dominance would therefore represent a non-adaptive side effect of the behavioural feminization of the male coucal brain and would be directly linked to the peculiarities of unilateral ovary development in birds. To explain how these phenomena might be developmentally connected, it is necessary to review important developmental processes during gonadal differentiation in birds.

Before turning to that molecular detail, it is worth considering why male birds would produce estrogens during development at all. Behavioural feminization of this kind is not without adaptive logic: sustained male-only care requires males to become less aggressive and less territorial, and more nurturing. Sex steroids are a plausible proximate route to such a shift in temperament. In ruffs (*Calidris pugnax*), for example, the distinct male mating tactics, ranging from aggressive, territory-holding Independents, via co-displaying Satellites to female-mimicking Faeders are underpinned by differential activity of sex-steroid-converting enzymes such as 17ß-HSD (Loveland et al., 2025). Therefore, a steroid-mediated mechanism could also operate in coucals. A temporary rise in estrogen production during male development offers a plausible route to behavioural feminization, with testicular asymmetry arising as an incidental by-product of this process rather than its intended outcome.

How does gonadal differentiation work in birds?

Gonadal differentiation in birds has been studied in detail in the domestic chicken (*Gallus gallus*; (Guioli et al., 2014). Female birds are the heterogametic sex, characterized by a ZW-allosome composition; males are homogametic and have ZZ-allosomes. The Z-linked transcription factor DMRT1 (Doublesex and Mab-3–related transcription factor 1) plays a key role in gonadal differentiation, with expression restricted to the gonads and the Müllerian ducts. Since males have two copies of the DMRT1 gene, DMRT1 expression is twice as high in males as in females. Double DMRT1 expression suppresses the production of forkhead box protein (FOXL2) (Ioannidis et al., 2021) and promotes the expression of anti-Müllerian hormone (AMH) and the SOX9 transcription factor. Together, AMH and SOX9 trigger the development of the two gonadal medullae into testes (Fig. 1). They also trigger the development of the Wolffian ducts via androgen production.

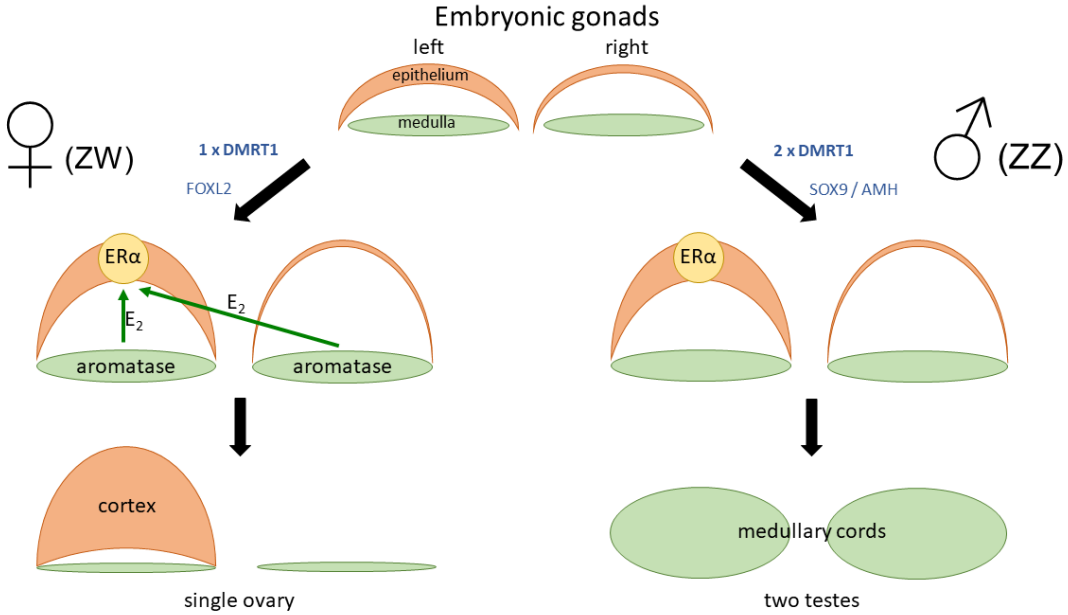


Fig. 1. Gonadal differentiation in birds (see text for details; abbreviations: AMH = anti-Müllerian hormone, DMRT1 = Doublesex and Mab-3–related transcription factor 1, E_2 = estradiol, FOXL2 = forkhead box protein, SOX9 = SOX9 transcription factor)

By contrast, females with their single Z chromosome produce half as much DMRT1 as males. This reduced concentration of DMRT1 is insufficient to suppress FOXL2 protein production. FOXL2 triggers the expression of aromatase (P450arom), which is a key enzyme in the conversion of precursor steroids to estradiol (see Fig. 2). Estradiol then blocks the male gonadal pathway and promotes the development of the left gonadal cortex into an ovary (Ioannidis et al., 2021) (Fig. 1). Estradiol turns out to be the key factor in female gonadal differentiation: injecting estradiol into chicken eggs can override the effects of DMRT1, thereby leading to the development of an ovary even in genetic males (Ioannidis et al., 2021). The reason genetic males have the potential to develop an ovary lies in the distribution of estrogen receptor alpha (ERα), which is expressed in the cortex of the left gonads in both sexes during early development. The cortex of the right gonad does not express Erα in either females or males (Bruggeman et al., 2002; Nakabayashi et al., 1998)(Fig. 1).

During normal female gonadal development, FOXL2 induces the medullae of both female embryonic gonads to express high levels of the two enzymes 17ß-hydroxysteroid dehydrogenase (17ß-HSD) and

aromatase (P450arom). The medullae thereby act as endocrine glands, converting precursor steroids such as androstenedione or testosterone into estradiol (for more details on the steroidogenic pathways see Fig. 2 and (Bruggeman et al., 2002). Estradiol then binds to the estrogen receptors within the left gonadal cortex, triggering its conversion into a functional ovary (Fig. 1). As the cortex of the right gonad does not express estrogen receptors, it cannot respond to estrogen signalling. Its development ceases, leaving it in a rudimental state.

In female chickens, gonadectomy or the loss of the left ovary due to disease masculinizes females (Groenendijk-Huijbers, 1967; Groenendijk-Huijbers, 1965). Specifically, loss of estradiol production after losing the ovary appears to reactivate the rudimentary right gonad, which subsequently develops into a testosterone-producing testis-like organ (Domm, 1931; Lambeth and Smith, 2012; Miller, 1939; Vaillant et al., 2003). Furthermore, inhibiting aromatase activity so that estradiol formation is blocked (for instance by injecting fadrozole) causes the right gonadal vestige to develop into a testicular structure. Fadrozole treatment leads to an upregulation of DMRT1, thereby increasing SOX9 levels and decreasing FOXL2 levels in both gonadal medullae. This invariably results in the differentiation of a testis on the right side of the female embryo. In contrast, the fate of the left gonad is less clear-cut (Ioannidis et al., 2021; Vaillant et al., 2003). Thus, the right gonad of birds appears to have an innate testicular predisposition (Major and Smith, 2016): when estrogen action is removed, the right gonad is freed from its developmental arrest and grows into a testis.

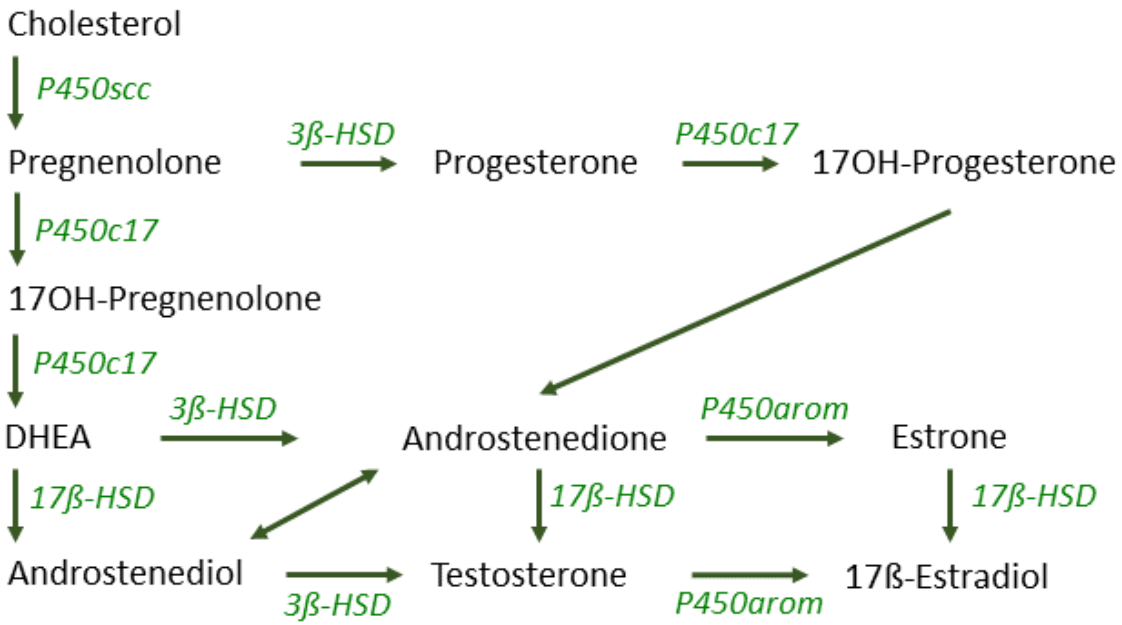


Fig. 2. Main enzymes involved in converting cholesterol in androgens and estrogens

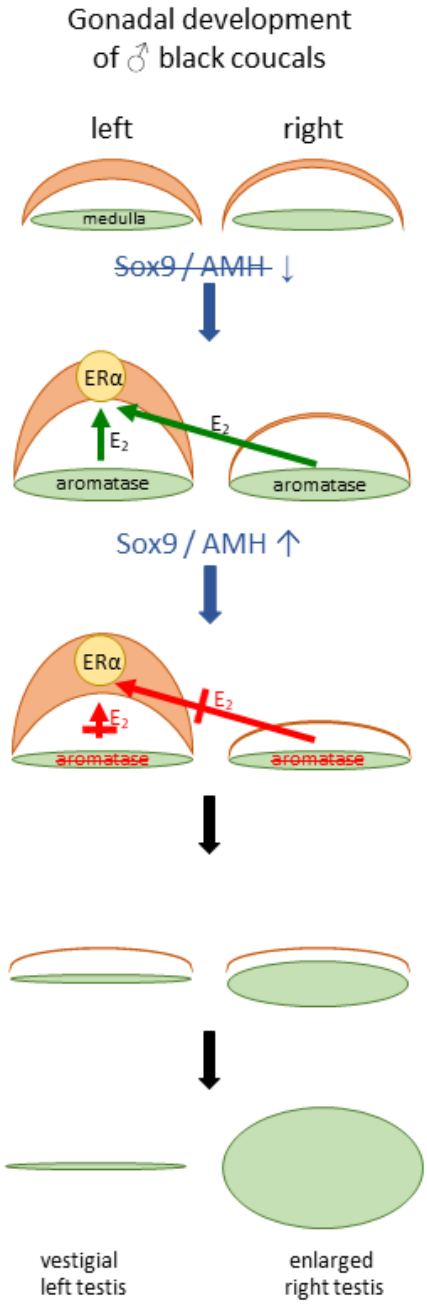
A unilateral right testis as a consequence of left-biased gonadal asymmetry in females?

These observations in chickens suggest a potential link between the pathways that lead to the development of a unilateral left ovary in females and the unusual testicular asymmetry found in male coucals. Therefore, the partial or complete loss of the left testis may not be independent of gonadal differentiation in females. Rather, the more prominent, or even unilateral, right testis may be a direct

result of the (feminizing) processes that normally guide the development of a single left ovary in female birds through estrogen action. Thus, the degree of prominence of the right testis may reflect the degree of feminization of male coucals and the respective reversal in sex roles.

Although the ontogenetic processes of testis development in coucals have not been studied, a possible scenario can be derived from what is known about chickens. Here, I outline how this could unfold at the molecular level, before considering what this could mean for species with partial versus complete reversal of testicular asymmetry. The first critical step could be a temporal differentiation in the expression patterns of AMH and estrogens in male coucals. As AMH expression inhibits aromatase expression and vice versa (Bruggeman et al., 2002), a delay or a reduction in the expression of AMH in the gonads of male embryos may free the estrogenic pathway by activating 17ß-HSD and aromatase expression (Nakabayashi et al., 1997). Subsequently, the medullae of both gonads may start synthesizing estradiol, which could play a role in feminizing the brain of male coucals. As the gonadal cortex of the left gonad expresses estrogen receptors in both sexes (Bruggeman et al., 2002; Nakabayashi et al., 1998), estradiol could stimulate the cortical development of the left gonad of males, thereby initiating ovary development. Subsequently, a delayed increase in AMH expression could inhibit further aromatase expression in the gonadal medullae. Estradiol production would stop, and AMH and SOX9 expression would inhibit any further cortical development of the left gonad, thereby stopping ovary development. The absence of estradiol releases the developmental arrest of the right gonadal medulla, allowing it to grow into a large testis (Fig. 3).

A necessary assumption of this scenario is, that – by the time AMH/SOX9 become active again – the medulla of the left gonad must have either partially or completely regressed. With a partial regression, the development of the left testis may be delayed, resulting in a smaller left testis, as seen in partially sex-role reversed greater, blue-headed, pheasant or Senegal coucals. In species with completely reversed sex roles, the left medulla may have regressed completely and lost its capacity to develop into a testis, thereby resulting in a unilateral right testis. This pattern is supported by evidence from chickens with ovarian disease, in which only the vestigial right gonad is plastic enough to develop into a functional testis, once estrogen production is blocked (Major and Smith, 2016).



216

217 Fig. 3. Hypothetical pathway leading to the development of the right testis and regression of the left
218 testis in sex-role reversed coucals (for abbreviations, see Fig. 1)

Why should male coucals produce estrogens during development?

Female African black coucals with reversed sex roles show behavioural traits that, in most other species, are typically male characteristics. At the beginning of the breeding season, these females sing and establish large territories, which they defend aggressively against competing females. One female's territory can encompass the home range of up to five males, each of whom receives a separate clutch from the territory holder (Goymann et al., 2015; Goymann et al., 2004). Territorial behaviour and aggression are reflected in female physiology. For instance, the testosterone concentrations of female black coucals are twice as high as those of female white-browed coucals, in which sex roles are not reversed (Goymann, 2023). Furthermore, female black coucals express high levels of androgen receptors in brain areas relevant to social and aggressive behaviour (Voigt and Goymann, 2007), thereby enabling testosterone to activate these areas effectively. Hence, male-like behavioural traits are associated with a masculinization of the gene expression and physiology of adult female African black coucals.

Similarly, male African black coucals show characteristics typically associated with females in most bird species. They are less aggressive, rarely sing, and do not defend territories. Instead, they are more selective when choosing mates and demonstrate a strong commitment to caring for eggs and young (Goymann et al., 2015; Goymann et al., 2016). Hence, males appear to be behaviourally feminized, which may be reflected in gene expression and physiology. Brain feminization could occur during ontogenetic development, with sex steroids such as estradiol likely triggering such processes. Estrogenic signalling is crucial in putting the avian gonads on a female developmental pathway. The conversion enzymes 17ß-HSD and aromatase are crucial to produce estradiol. These steroidogenic enzymes also play a significant role in the formation of alternative mating morphs, as observed in male ruffs (*Calidris pugnax*; (Giraldo-Deck et al., 2024; Loveland et al., 2021; Loveland et al., 2025). There are three types of male ruffs: Independents, who establish small display territories on leks; Satellites, who co-display with Independents at a lek; and Faeders, who are female mimics and engage in sneak copulations. The differential expression of sex steroids mediates the different behavioural tactics of these mating types. Independent males have higher levels of circulating testosterone. Satellites and Faeders have higher levels of circulating androstenedione. One of the key differences is the differential activity and effectiveness of the 17ß-HSD enzyme (Loveland et al., 2025). Hence, sex steroid conversion enzymes mediate behavioural differences in male mating morphs in ruffs, and it is reasonable to assume that sex steroids are also at work in mediating the behaviour of sex-role reversed male black coucals. The oddity of an asymmetric testis alongside estrogen-dependent processes involved in forming an asymmetric ovary in female birds strongly indicate that estrogens could be involved in feminizing male coucals, with the development of an asymmetric testis being a by-product of this temporary feminization process.

Predictions and how to test them

If testicular asymmetry in coucals is indeed a by-product of brain feminization during development rather than an independently selected trait, several testable predictions follow. Firstly, across the coucal phylogeny, the timing and extent of AMH, aromatase and DMRT1 expression in the embryo should correspond to the degree of testicular asymmetry in adults. Species with only partial reversal, such as the blue-headed, Senegal, greater or pheasant coucal, should show an intermediate shift in these expression profiles compared to the more symmetrical white-browed coucal at one end of the spectrum and the fully asymmetric lesser and African black coucals on the other. Secondly, the degree of behavioural and neural feminization should correlate with the degree of testicular asymmetry when mapped across species, not only at the two extremes for which data currently

exist; comparative data from species with partial reversal would be especially informative. Testing these predictions would require embryonic material, which is difficult to obtain because coucals are secretive and their nests are hard to find. However, since the last-laid eggs in a clutch rarely survive the first days after hatching due to sibling competition (Safari and Goymann, 2018), it would be ethically sound to remove these eggs, incubate them artificially to the required embryonic stage, and then investigate the developmental pathways of brain and gonadal differentiation. It would be much easier, though, if captive-bred coucals were used for such an endeavour.

Summary and conclusions

The reversal of testicular asymmetry in coucals, culminating in a unilateral right testis in the most sex-role-reversed species, may be a non-adaptive by-product of estrogen-induced brain feminization during embryonic development. Estrogen action may initially suppress the development of both gonadal medullae. Once this action stops, the left medulla may have already lost much of its potential to become a functional testis, whereas the medulla of the right gonad is freed from its developmental arrest and grows into a functional testis – much as happens in female chickens when aromatase inhibitors block estrogen action.

Seen this way, testicular asymmetry in coucals is not itself a target of selection. Rather, it is a pleiotropic by-product: selection has shaped behaviour and sex roles, and gonad morphology has simply followed along, carried by a shared hormonal pathway. This distinction matters beyond coucals. Developmental biology has repeatedly found that, once a regulatory circuit is in place, it can be redeployed for new purposes – and the morphological side effects of that redeployment can appear to be adaptive even when they are not. Coucals offer an unusually clear natural gradient for studying this kind of co-option, since the degree of both testicular asymmetry and behavioural sex-role reversal varies continuously across a single genus.

Testing this hypothesis will require embryonic expression data which do not yet exist for coucals. Coucals may therefore serve less as a self-contained curiosity and more as a natural experiment for a general question in developmental biology: when a conserved differentiation pathway is engaged for a new behavioural end, what happens to the morphological structures that pathway was originally built to produce?

Conflict of interest: I declare that I have no conflict of interest.

AI use: I have used Anthropic Claude (vs. Sonnet 5) to assist with structuring the manuscript and DeepL Write (vs. 26.5.1.20133) to assist with improving the language.

Acknowledgements: I thank the Max Planck Society for funding my research. For many years, I have contemplated the hypothesis that the asymmetry of coucal testes is related to brain feminisation. I have now decided to publish this idea in the hope that it will stimulate the interest of some developmental biologists in potential collaborations.

References

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. doi: 10.1006/bijl.1995.0010.

Bernstein HA, 1860. Über das Vorkommen eines einzigen Hodens bei *Centropus medius* Muell. und *Centropus affinis* Horsf. Archiv für Anatomie, Physiologie und Wissenschaftliche Medizin:161-168.

Bruggeman V, Van As P, Decuypere E, 2002. Developmental endocrinology of the reproductive axis in the chicken embryo. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology 131:839-846. doi: 10.1016/S1095-6433(02)00022-3.

Brumm H, Goymann W, 2017. On the natural history of duetting in White-browed Coucals: sex- and body-size-dependent differences in a collective vocal display. Journal of Ornithology 158:669-678. doi: 10.1007/s10336-016-1429-0.

Brumm H, Goymann W, 2018. The function of collective signalling in a cuckoo. Animal Behaviour 146:23-30. doi: 10.1016/j.anbehav.2018.10.008.

Calhim S, Montgomerie R, 2015. Testis asymmetry in birds: the influences of sexual and natural selection. Journal of Avian Biology 46:175-185. doi: 10.1111/jav.00503.

Chapin JP, 1939. The birds of the Belgian Congo. Bulletin of the American Museum of Natural History 75:1-632.

Domm LV, 1931. A demonstration of equivalent potencies of right and left testis-like gonads in ovarectomised fowl. Anatomical Records 49:211-249.

Frey R, Goymann W, 2009. A single functional testis and long deferent duct papillae: the peculiar male reproductive tract of the classically polyandrous, sex-role reversed Black Coucal (*Centropus grillii*). Journal of Ornithology 150:827-838.

Friedmann H, 1927. Testicular asymmetry and sex ratio in birds. Biological Bulletin 52:197-207.

Fu L-R, Liang W, Mo X-L, 2009. Anatomical and histological studies of the male reproductive system of *Centropus sinensis* in breeding season. Sichuan Journal of Zoology 28:717-719.

Giraldo-Deck LM, Loveland JL, Goymann W, Lank DB, Küpper C, 2024. A supergene affects androgen concentrations during early development in a bird with alternative reproductive morphs. Hormones and Behavior 166:105645. doi: 10.1016/j.yhbeh.2024.105645.

Goymann W, 2023. Androgen-armoured amazons: reversed sex roles in coucals are associated with testosterone in females but not males. Proceedings of the Royal Society B 290:20222401. doi: 10.1098/rspb.2022.2401.

Goymann W, Flores Dávila P, 2017. Acute peaks of testosterone suppress paternal care: evidence from individual hormonal reaction norms. Proceedings of the Royal Society B 284:20170632. doi: 10.1098/rspb.2017.0632.

Goymann W, Makomba M, Urasa F, Schwabl I, 2015. Social monogamy vs. polyandry: ecological factors associated with sex roles in two closely related birds within the same habitat. Journal of Evolutionary Biology 28:1335-1353. doi: 10.1111/jeb.12657.

Goymann W, Safari I, Muck C, Schwabl I, 2016. Sex roles, parental care and offspring growth in two contrasting coucal species. Royal Society Open Science 3:160463. doi: 10.1098/rsos.160463.

Goymann W, Wittenzellner A, Wingfield JC, 2004. Competing females and caring males. Polyandry and sex-role reversal in African black coucals, *Centropus grillii*. Ethology 110:807-823. doi: 10.1111/j.1439-0310.2004.01015.x.

Groenendijk-Huijbers M, 1967. Experimental studies concerning the compensatory growth of the rudimentary right ovary of sinistrally castrated chick embryos. Verhandlungen der Anatomischen Gesellschaft 62:321-325.

Groenendijk-Huijbers MM, 1965. The right ovary of the chick embryo after early sinistral castration. The Anatomical Record 153:93-105. doi: 10.1002/ar.1091530111.

Grützner F, Nixon B, Jones RC, 2008. Reproductive biology in egg-laying mammals. Sexual Development 2:115-127. doi: 10.1159/000143429.

Guioli S, Nandi S, Zhao D, Burgess-Shannon J, Lovell-Badge R, Clinton M, 2014. Gonadal asymmetry and sex determination in birds. Sexual Development 8:227-242.
Ioannidis J, Taylor G, Zhao D, Liu L, Idoko-Akoh A, Gong D, Lovell-Badge R, Guioli S, McGrew MJ, Clinton M, 2021. Primary sex determination in birds depends on DMRT1 dosage, but gonadal sex does not determine adult secondary sex characteristics. Proceedings of the National Academy of Sciences 118:e2020909118. doi: 10.1073/pnas.2020909118.
Kinsky FC, 1971. The consistent presence of paired ovaries in the Kiwi (Apteryx) with some discussion of this condition in other birds. Journal für Ornithologie 112:334-357. doi: 10.1007/BF01640692.
Lambeth LS, Smith CA, 2012. Disorders of sexual development in poultry. Sexual Development 6:96-103.
Ligon JD, 1997. A single functional testis as a unique proximate mechanism promoting sex-role reversal in coucals. Auk 114:800-801.
Ligon JD, 1999. The evolution of avian breeding systems. Oxford: Oxford University Press.
Loveland JL, Giraldo-Deck LM, Lank DB, Goymann W, Gahr M, Küpper C, 2021. Functional differences in the hypothalamic-pituitary-gonadal axis are associated with alternative reproductive tactics based on an inversion polymorphism. Hormones and Behavior 127:104877. doi: 10.1016/j.yhbeh.2020.104877.
Loveland JL, Zemella A, Jovanović VM, Möller G, Sager CP, Bastos B, Dyar KA, Fusani L, Gahr M, Giraldo-Deck LM, Goymann W, Lank DB, Tokarz J, Nowick K, Küpper C, 2025. A single gene orchestrates androgen variation underlying male mating morphs in ruffs. Science 387:406-412. doi: 10.1126/science.adp5936.
Major AT, Smith CA, 2016. Sex reversal in birds. Sexual Development 10:288-300.
Maurer G, 2008. Who cares? Males provide most parental care in a monogamous nesting cuckoo. Ethology 114:540-547. doi: 10.1111/j.1439-0310.2008.01498.x.
Maurer G, Blomberg S, 2009. Does testis size in cuckoos vary with paternal care? Auk 126:24-30. doi: 10.1525/auk.2009.07185.
Miller RA, 1939. Spermatogenesis in a sex-reversed female and in normal males of the domestic fowl, *Gallus domesticus*. Anatomical Records 70:155-190.
Nakabayashi O, Kikuchi H, Kikuchi T, Mizuno S, 1998. Differential expression of genes for aromatase and estrogen receptor during the gonadal development in chicken embryos. Journal of Molecular Endocrinology 20:193-202. doi: 10.1677/jme.0.0200193.
Nakabayashi O, Normura O, Kikuchi H, Kikuchi T, S. M, 1997. Estrogen synthesis and receptors during early gonadal development. In: Harvey S, Etches RJ, editors. Perspectives in Avian Endocrinology Bristol: Journal of Endocrinology. p. 27-36.
Rand AL, 1933. Testicular asymmetry in the Madagascar coucal. Auk 50:219-220.
Safari I, Goymann W, 2018. Certainty of paternity in two coucal species with divergent sex roles: the devil takes the hindmost. BMC Evolutionary Biology 18:110. doi: 10.1186/s12862-018-1225-y.
Safari I, Goymann W, 2021. The evolution of reversed sex roles and classical polyandry: Insights from coucals and other animals. Ethology 127:1-13. doi: 10.1111/eth.13095.
Vaillant S, Guémené D, Dorizzi M, Pieau C, Richard-Mercier N, Brillard JP, 2003. Degree of sex reversal as related to plasma steroid levels in genetic female chickens (*Gallus domesticus*) treated with fadrozole. Molecular Reproduction and Development 65:420-428. doi: 10.1002/mrd.10318.
Voigt C, Goymann W, 2007. Sex-role reversal is reflected in the brain of African black coucals (*Centropus grillii*). Developmental Neurobiology 67:1560-1573. doi: 10.1002/dneu.20528.
Witschi E, 1935. Origin of asymmetry in the reproductive system of birds. American Journal of Anatomy 56:119-141.