DOES TESTIS SIZE IN CUCKOOS VARY WITH PATERNAL CARE?

GOLO MAURER[1,3] AND SIMON BLOMBERG[2,4]

[1]*School of Botany and Zoology, Australian National University, Canberra, ACT, 0200, Australia; and*
[2]*Centre for Resources and Environmental Studies, Australian National University, Canberra, ACT, 0200, Australia*

ABSTRACT.—Male birds confront a tradeoff between increasing the number of offspring they sire and providing parental care. This behavioral tradeoff may be manifested as variation in testis size: larger testes, producing more sperm and testosterone, are advantageous for sperm and mating competition, thus ensuring paternity, yet high levels of plasma testosterone also inhibit parental care. There is good evidence that relative testis size is greater in species in which males compete more intensely to fertilize females, but it remains unclear whether, in turn, smaller testes prevail in species with greater levels of paternal care. Cuckoos provide an opportunity to test for an effect of paternal care on testis size because of the diversity of breeding systems in this family: parasitic species lack parental care altogether, whereas some coucals (Centropodinae) show exclusively or predominantly male care. In addition, coucals have a reduced left testis, which Ligon (1997) suggested may promote male care. We tested the idea that species with more paternal care have smaller testes in a phylogenetic analysis of 18 parasitic and 15 nonparasitic species and, specifically, quantified the reduction of the mass of the left testis in the Pheasant Coucal (*Centropus phasianinus*). Contrary to expectation, nesting cuckoos had larger testes than parasitic species and coucals compensated the reduction of the left testis by an increase of the right. These findings suggest that plasma testosterone is regulated independently of testis size and paternal care is not associated with testis size in cuckoos. *Received 7 November 2007, accepted 25 July 2008.*

Key words: coucals, cuckoos, parental care, sperm competition, testis asymmetry, testosterone.

La taille des testicules chez les coucous varie-t-elle en fonction des soins parentaux?

RÉSUMÉ.—Les oiseaux mâles doivent faire un compromis entre augmenter le nombre de rejetons engendrés et fournir des soins parentaux. Ce compromis comportemental peut se manifester par une variation de la taille des testicules : les gros testicules, produisant plus de sperme et de testostérone, sont avantageux pour la compétition spermatique et la compétition pour l'accouplement, ce qui assure la paternité, mais des niveaux élevés de testostérone dans le plasma inhibent aussi les soins parentaux. Certains faits appuient l'hypothèse que la taille relative des testicules est supérieure chez les espèces dont les mâles rivalisent davantage afin de fertiliser les femelles. En contrepartie, il demeure incertain si des testicules plus petits prédominent chez les espèces présentant des soins parentaux plus élaborés. Les coucous fournissent une opportunité pour tester l'effet des soins parentaux sur la taille des testicules en raison de la diversité des systèmes de reproduction dans cette famille : les espèces parasites ne fournissent pas de soins parentaux, alors que certains coucals (Centropodinae) font preuve de soins par les mâles exclusivement ou de façon prédominante. De plus, les coucals ont un testicule gauche réduit pouvant promouvoir les soins par le mâle selon Ligon (1997). Nous avons testé l'hypothèse que les espèces allouant plus de soins parentaux ont des testicules plus petits, à l'aide d'une analyse phylogénétique sur 18 espèces parasites et 15 espèces non-parasites et, plus spécifiquement, nous avons quantifié la réduction de la masse du testicule gauche chez *Centropus phasianinus*. Contrairement à ce qui était attendu, les coucous nicheurs avaient de plus gros testicules que les espèces parasites et les coucals ont compensé la réduction de la taille du testicule gauche en augmentant celle du droit. Ces résultats suggèrent que la testostérone plasmatique est régulée indépendamment de la taille des testicules et que les soins parentaux ne sont pas associés à la taille des testicules chez les coucous.

SEXUAL COMPETITION AND parental care pose conflicting selection pressures on male birds and, thus, shape the behavior of individual males as well as a species' reproductive strategy (Magrath and Komdeur 2003). Morphologically, this conflict may become apparent in a species' testis size. On one hand, larger testes provide an advantage in sexual competition because they can produce more sperm (Lake 1984, Kirby and Froman 2000). In particular, males of species with high levels of paternal care may

have evolved large testes to secure paternity and ensure that their efforts benefit their own offspring. On the other hand, larger testes also produce more testosterone (Lake 1984, Garamszegi et al. 2005), which, in turn, can inhibit paternal care (Wingfield 1990, Wingfield and Silverin 2002), and large testes may, therefore, be selected against in species with extensive paternal care. Attempts to determine the role of paternal care in the evolution of testis size have met with mixed success. Two large comparative studies investigating the factors associated with testis size in birds (Møller 1991, Pitcher et al. 2005) demonstrated that species with higher levels of sperm competition have larger testes. However, only Pitcher et al. (2005) found a relationship between testis size and paternal care. They showed that species with male provisioning had smaller testes than species in which males do not feed young, but this pattern was not repeated in species with male incubation. In a different approach to examining the relation between paternal care and testis size, we focus here on a comparison of closely related species with extreme differences in paternal investment and diverse mating systems.

Cuckoos show some of the greatest variation in breeding biology and male parental investment of all bird families and also exhibit substantial variability in mating systems (Payne 2005). The cuckoo family is, therefore, ideal for investigating the association between paternal care and testis size and how this may interact with the mating system. Female-only care is unknown in cuckoos, but male care varies from none in obligate brood-parasites to male-only care in the sex-role-reversed African Black Coucal (*Centropus grillii*; Goymann et al. 2004). Furthermore, intermediate levels of male care occur in the cooperatively breeding anis (Crotophaginae; Vehrencamp et al. 1986, Macedo 1992) and nesting cuckoos such as the Greater Roadrunner (*Geococcyx californianus*; Calder 1967). If male care in birds indeed favored the evolution of small testes, the testes of nesting cuckoos should be smaller than those of the brood parasites. Coucals (Centropodinae) play a crucial role in such a comparison, because male coucals invest heavily in care and show an unusually reduced left testis.

Extensive male parental care in coucals is intriguing, given that predominantly male care for eggs and offspring is rare in birds and found mostly in species with reversed sex roles (female rather than male competition and male choice), which constitute <5% of the world's bird species (Lack 1968, Clutton-Brock 1991). These species are virtually all from families with precocial young, such as waders (Scolopacidae) or button-quails (Turnicidae), in which parental care consists of little more than incubation. The evolution of sex-role reversal has been considered impossible for bird species with altricial chicks, because males would have to care for both eggs and nestlings (Clutton-Brock 1991, Andersson 1994), but coucals demonstrate that this can occur (Andersson 1995). In the polyandrous African Black Coucal, only males incubate and care for the altricial, nidicolous young, while females compete for males and territories (Goymann et al. 2004). Similarly, in the monogamous Pheasant Coucal (*C. phasianinus*), males incubate alone and provide ~80% of nestling feedings (Taplin and Beurteaux 1992, Maurer 2008).

Ligon (1997) argued that male care of eggs and offspring in African Black Coucals may be promoted by the "unique proximate mechanism" of a reduced left testis. Parental care in birds is usually controlled by two hormones: prolactin, which stimulates parental behavior, and testosterone, which suppresses it (Wingfield et al. 1990, Wingfield and Silverin 2002). In most species, the males counteract the suppressive effect of testosterone on parental care by rapidly reducing plasma testosterone levels just before they start caring for their offspring (Fivizzani and Oring 1986, Ketterson and Nolan 1994; but see Peters et al. 2002). Consistent with this general pattern, male African Black Coucals lower their testosterone levels during the nestling stage (Goymann and Wingfield 2004). However, the exceptionally high investment in paternal care in coucals may have led to the evolution of a diminished left testis as an additional mechanism to reduce testosterone levels more permanently. Coucals are unique among birds in having both high levels of male care and a reduced left testis. Even the direction of the testis asymmetry is unusual, given that most species have either a larger left testis or similar-sized testes (Ludwig 1932, Stresemann 1934). This pattern suggests that coucals have actually reduced the size of the ancestrally larger of the two testes (Ligon 1997).

Here, we used a phylogenetic approach to examine variation in testis size in relation to body mass in cuckoos. Specifically, we tested two hypotheses. (1) The reduction of the left testis in coucals led to a smaller total testis mass in coucals compared with other cuckoos. This is the critical assumption behind Ligon's (1997) suggestion that a diminished left testis in coucals facilitates male care. To address this question, we quantify the reduction of the left testis in the Pheasant Coucal—to our knowledge, the only coucal species for which quantitative data on testis size in the breeding and non-breeding seasons are available. (2) Nesting cuckoos have smaller testes than brood-parasitic species to facilitate paternal care. To test this idea, we compared the testis mass of 18 parasitic and 15 nesting cuckoo species (including five species of coucal).

Methods

Data.—We extracted collectors' measurements of body weight and testis length and width for 21 Pheasant Coucal specimens collected in Australia (19) and Papua New Guinea (2). Ten specimens were taken during the breeding season and 11 during the non-breeding season. We collated the same data for 4 coucal species (8 specimens) and 28 other cuckoo species (252 specimens), collected on all continents except Europe, from published data (Goymann and Wingfield 2004), databases, and specimen labels and original field-data sheets in museum collections. All specimens used for the phylogenetic analysis were collected during the species' respective breeding seasons as described in del Hoyo et al. (1997) and Higgins (1999). For the comparison of the left and right testes in Pheasant Coucals, we used adult birds collected in the breeding and nonbreeding seasons. We cannot rule out collection bias in our data. In particular, individuals with big testes and high testosterone levels may be over-represented in collections if they behave more conspicuously and were collected preferentially. However, this bias should be similar for all species. Information on the species used, sample sizes, and breeding system are presented in the phylogenetic tree (Fig. 1). This tree is an adaptation of the molecular phylogeny of Sorenson and Payne (2005) for the subset of cuckoo species in our analysis.
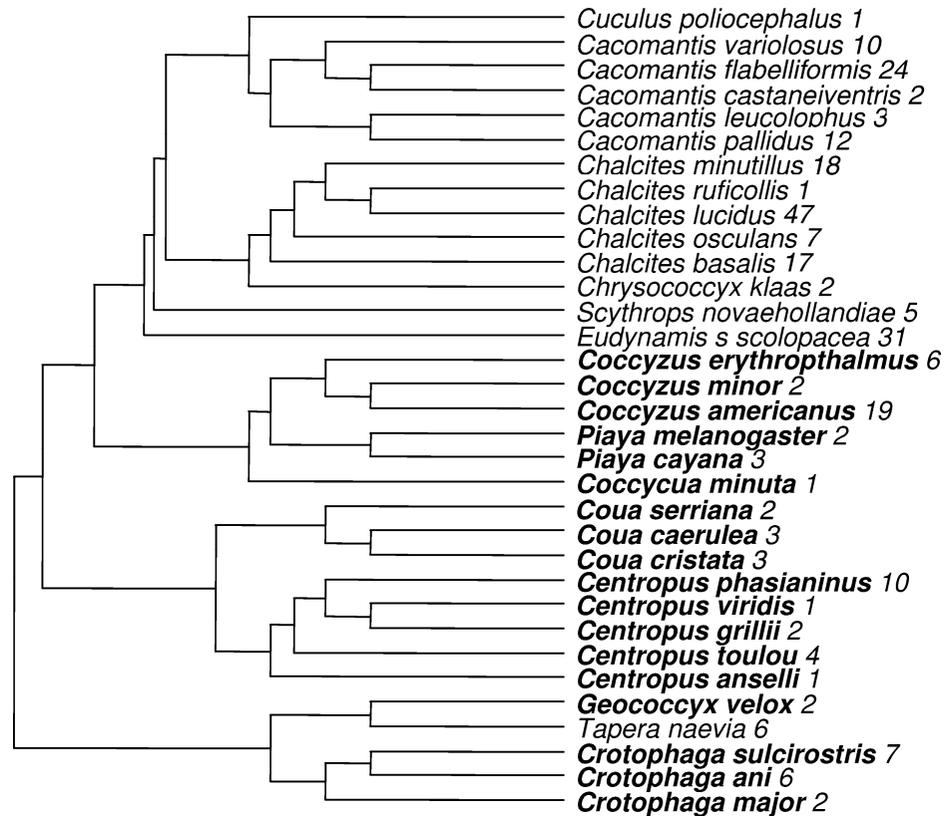
Fig. 1. Species used in the phylogenetic regression of log(testes mass) vs. log(body mass) in cuckoos. The tree shows the relationships of the 33 species in our data set following Sorenson and Payne's (2005) molecular phylogeny. Species with parental care (18) are indicated in bold. The number after each species name indicates sample size.

Phylogenetic and statistical analyses.—In most birds, the testes are shaped like broad beans (Lake 1984); therefore, we calculated volume as an ellipsoid using the formula (testis $[cm^3] = 4/3 * \pi * a^2 [cm^2] * b [cm]$), where a is the smallest and b is the largest radius of each testis (after Møller 1991, Pitcher et al. 2005). We then multiplied the volume by Møller's (1991) estimate for the density of testis tissue in birds (1.087 g/cm^3) to obtain total mass, because no data are available for the specific density of testis tissue in cuckoos and most other birds.

We compared the volume (cm^3) of the right and left testes of 10 breeding and 11 nonbreeding Pheasant Coucals, in relation to the individual's body mass (g), to account for the slight variation in size among males. The left and right testes within the same breeding and nonbreeding birds were compared in a paired-samples *t*-test. For the comparisons between the left and right testes of breeding and nonbreeding Pheasant Coucals, we used an independent-samples *t*-test. Tests were two-tailed.

To compare the testis mass of cuckoos, we calculated mean total testis mass and body mass for all 33 species in our analysis. We log-transformed means to satisfy the assumption of equal variances. Next, we fitted a generalized least-squares model in the R statistics package (Paradis et al. 2004, R Development Core Team 2006) to those means using Grafen's (1989) phylogenetic regression approach and the tree in Figure 1. A phylogenetic regression is a valid analysis only for data that contain a phylogenetic

signal, defined as the tendency of related species to resemble each other, given the phylogentic tree (Blomberg et al. 2003). We confirmed that our subset of the cuckoo family contained such a signal by assessing Grafen's ρ parameter (Grafen 1989, Blomberg et al. 2003). It was significantly different from zero ($P < 0.01$) and one ($P < 0.01$). Grafen's (1989) ρ value of 0.3013 shows that the signal in our tree was smaller than that implied by the full original tree, with standard Grafen branch lengths (i.e., ρ = 1; Sorenson and Payne 2005). We then estimated the parameters for the regression of testis size on body mass. To determine whether mean testis size of a particular species or group of species differed significantly from that of other cuckoos, we constructed indicator variables for species or groups, respectively. If the effect of the indicator variable was not significant at the 5% level, we concluded that the mean testis size of this species or group of species did not differ from the remainder of the data set.

Results

Breeding Pheasant Coucals have a small left and a large right testis.— Breeding male Pheasant Coucals had a significantly larger right than left testis ($t = 2.35$, df = 9, $P = 0.04$, $n = 10$), whereas there was no testis asymmetry among nonbreeding males ($t = 0.88$, df = 10, $P = 0.4$, $n = 11$; Fig. 2). We did not detect a significant difference in size of the left testis between breeding and nonbreeding
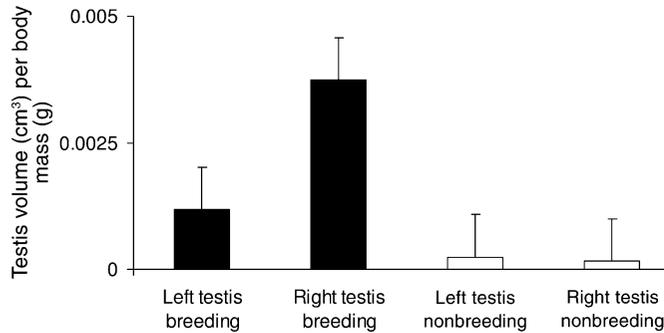
FIG. 2. Testis size standardized by dividing testis volume (cm³) by the individual's body mass (g) in breeding (black) and nonbreeding (white) Pheasant Coucals. Error bars indicate 95% confidence intervals of the mean.

males ($t = 1.23$, df = 19, $P = 0.2$, $n = 10$ and 11), but the right testis of breeding males was significantly larger ($t = 3.56$, df = 19, $P < 0.01$, $n = 10$ and 11).

Relationship of testis size to body mass in cuckoos.—Testis mass in cuckoos increased with body mass at a rate not significantly different from 0.66 (Fig. 3), the rate at which organs generally scale
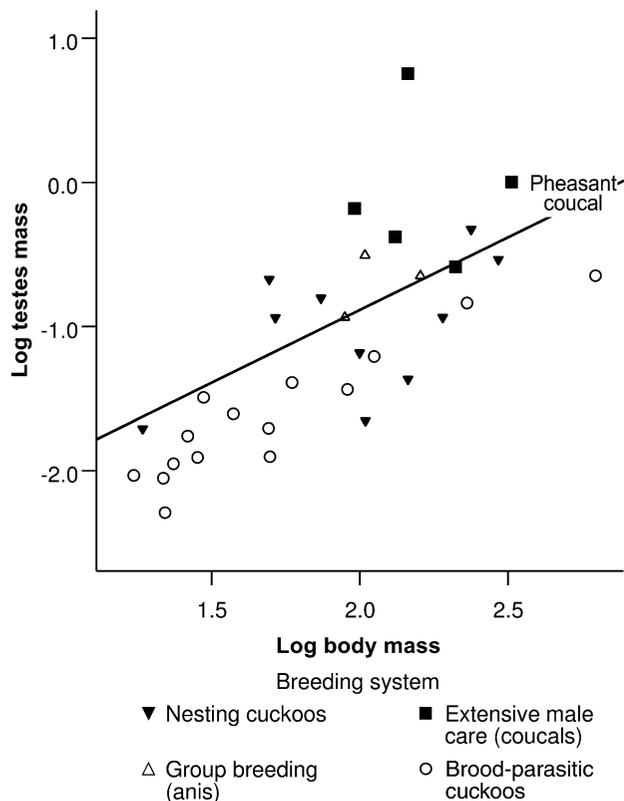

FIG. 3. Phylogenetic regression of log(testes mass) on log(body mass) for 18 species of brood-parasitic cuckoo (circles) and 15 nesting species: various genera (black triangle), anis (white triangle), and coucals (square). The datum for the Pheasant Coucal is labeled. The line represents the phylogenetic regression model across all species.

with body mass (Calder 1984). The phylogenetic regression for the entire data set was log(testes mass) = −2.9022 + 1.0085 * log(body mass) ($t = 4.21$, df = 33, $P < 0.001$; SE of the intercept = 0.521, SE of the slope = 0.24).

The intercept of the regression line is smaller than that of –1.56 calculated by Pitcher et al. (2005) for a set of 1,010 bird species. This suggests that cuckoos may have smaller testes than most other birds.

Paternal care and testis size.—Contrary to expectation, cuckoo species with some degree of paternal care had relatively larger testes than obligate brood-parasitic species (effect of species with parental care on the slope of the regression = 0.498 ± 0.202 [SE], $t = 2.5$, df = 33, $P = 0.02$). The testis size of *Centropus* spp. exceeds that of other cuckoos (effect of coucal species on the slope of the regression = 0.718 ± 0.28, $t = 2.6$, df = 33, $P = 0.01$). When tested individually, neither the African Black Coucal nor the Pheasant Coucal had smaller testes than expected for a cuckoo their size (effect of Black Coucal on the slope of the regression = 0.022 ± 0.38, $t = 0.57$, df = 33, $P = 0.96$; effect of Pheasant Coucal on the slope of the regression = −0.07 ± 0.41, $t = −0.16$, df = 33, $P = 0.87$). The datum for the largest total testis mass was from a single specimen of Philippine Coucal, *Centropus viridis*. As a group, anis tended to have larger testes than other cuckoo species (effect of anis on the slope of the regression = 0.63 ± 0.36, $t = 1.8$, df = 33, $P = 0.09$), but this effect was likely driven by the Smooth-billed Ani (*Crotophaga ani*) with its large testis mass.

DISCUSSION

Contrary to expectation, cuckoos with male parental care did not have smaller testes than brood-parasitic species that lack male care altogether. In fact, as a group, nonparasitic cuckoos had larger total testis mass than parasitic species. Remarkably, this result was also repeated for the coucals, which have very high levels of male care and a reduced left testis. The coucals' enlarged right testes more than compensated for their reduced left testes. Overall, these results suggest that greater paternal care is not associated with the evolution of smaller testes in cuckoos and that the extreme reversed testis asymmetry of coucals is not an adaptation for paternal care. Rather, variation in total testis mass in cuckoos may be related to mating competition.

Differences in mating systems are the most reliable correlate of testis size variation in birds (Møller 1991, Pitcher et al. 2005) and may explain why nesting cuckoos have larger testes than parasitic species. In general, species living in groups or colonies have larger testes than those living in pairs at lower densities, presumably because grouping increases opportunities for sperm competition. Unfortunately, the social or genetic mating systems are known only for very few of the brood-parasitic (Marchetti et al. 1998, Martínez et al. 1998, Langmore et al. 2007) and nesting cuckoo species (Vehrencamp et al. 1986, Goymann et al. 2004, Payne 2005, Maurer 2007a). These scant data, however, suggest that nesting cuckoos occur in greater densities than the parasitic species, which is in line with the idea that larger testes prevail in species that live in greater densities. Brood parasites may occur in lower densities than nesting cuckoos because their territories must be big enough to hold several breeding pairs of the

host species to ensure that a nest is available for each egg in the female cuckoo's clutch. Parasitic Horsfield's Bronze-Cuckoos (*Chalcites basalis*; 22 g), for instance, control 10-ha territories, whereas Pheasant Coucal territories are only about 2–3× bigger (18–28 ha), though male coucals (300 g) are >14× the size of Bronze-Cuckoos (Langmore et al. 2007, Maurer 2007a). Also in accordance with this pattern, we found that the group-breeding anis tended to have larger testes than the other cuckoos in our analysis.

Testes that produce more sperm are advantageous both for gaining extrapair fertilizations and for ensuring intrapair paternity (Møller 1991, Birkhead and Møller 1992, Møller and Briskie 1995, Pitcher et al. 2005). The latter may be of particular importance for the coucals, which invest heavily in paternal care (Taplin and Beurteaux 1992, Goymann et al. 2004, Maurer 2008) and, therefore, need to secure paternity. Similarly, Briskie (1993) found comparatively large testes in males of polygynandrous species with paternal care, which may use frequent copulations to ensure that their paternal investment is directed mostly at their own offspring. Ironically, male-only incubation in coucals starting with the first or second egg could reduce the ability of males to guard their mate while the remaining two or three eggs of the clutch are fertilized (Higgins 1999, Goymann et al. 2004, Maurer 2008). Sperm competition and accordingly enlarged testes may, therefore, be important factors in coucal mating systems, though copulation frequency in coucals appears to be very low (Maurer 2007b).

The small testes of parasitic cuckoos are intriguing, especially given that testis size in cuckoos already seems to be at the lower end of bird testis size (Pitcher et al. 2005). Any interpretation of this finding is hampered by lack of data on mating systems and testis sizes of many brood parasites. Monogamy, polygamy, and promiscuity all occur in parasitic cuckoos (Marchetti et al. 1998, Martínez et al. 1998, Langmore et al. 2007), but more information is needed to determine whether polygamous species have larger testes than those with other mating systems. In particular, the present study's emphasis on Southern Hemisphere migrants may have influenced its results, and future comparisons should strive to include Northern Hemisphere and resident tropical species if data become available.

Our results do not support Ligon's (1997) hypothesis that the reduced left testis of coucals facilitates paternal care; we found no evidence for the postulated decrease in total testis size. Neither our subsample of the genus as a whole, nor Pheasant or African Black coucals, had smaller testes than expected for cuckoos their size, though the coucal species used in our analysis all have reduced left testes (Rand 1933, Goymann and Wingfield 2004, G. Maurer unpubl. data). This result is remarkable because the reduction of the left testis is substantial. In breeding male Pheasant Coucals, the right testis was enlarged whereas the left testis remains at nonbreeding size and probably produces little if any testosterone or sperm (Lake 1984). The decreased plasma testosterone level required to facilitate the extraordinary levels of paternal care in coucals is, therefore, more likely achieved using the same quick testosterone reductions found in other bird species with paternal care rather than through reduction in testis size (Fivizzani and Oring 1986, Hegner and Wingfield 1987, Ketterson et al. 1992). Such quick adjustments have been documented in the polyandrous African Black Coucal but are yet to be measured in

a monogamous coucal species (Goymann and Wingfield 2004). The current mechanism of testosterone regulation in coucals does not preclude that in the ancestor of coucals a reduced left testis evolved as a means to decrease total testis size and testosterone levels, which may have facilitated paternal care. After male care was established, an enlarged right testis may have evolved in response to further selective pressures such as male–male competition for territories.

Both the extent and direction of the testis asymmetry in coucals are unusual, and the functional significance of this remains enigmatic. In most bird species, the smaller (right) testis accounts for 40–45% of total testis mass (Møller 1994, Birkhead et al. 1998), whereas the left testis of breeding male Pheasant Coucals accounts for only 27.8% of total testis mass (G. Maurer unpubl. data). To date, there is no conclusive explanation for either the typical or the reversed pattern of testis asymmetry in birds (Birkhead et al. 1998). However, it has been proposed that male birds evolved a larger left testis together with a preference to mount from the left side to facilitate sperm transfer into the female's only functional oviduct, which also sits on the left (Petersen et al. 2001, Delehanty et al. 2005). If this is true, female coucals should have a functional right, rather than left, ovary, and males with their reversed testis asymmetry should preferentially mount from the right. To our knowledge, neither the female reproductive anatomy nor the mounting preference of any coucal has been described, but copulations from either side have been observed in Pheasant Coucals (Maurer 2007b).

Cuckoos with paternal care have larger testes than parasitic species when phylogeny and body size are controlled. Even coucals, despite their reduced left testis, have a greater net testis mass than other cuckoo species. We conclude from these results that (1) the extensive paternal care in coucals is not associated with a reduction in testis mass and (2) liberation from parental care is not linked to larger testes in parasitic cuckoos. This suggests that similar selection pressures apply to the evolution of testis size in brood-parasitic cuckoos and nesting bird species. In particular, the effect of sperm competition on testis size in cuckoos probably exceeds that of paternal care. The data on parental care in cuckoos need to be augmented by information on their mating systems to allow a better understanding of how male birds resolve the trade-off between provisioning and procuring offspring.

Literature Cited

Andersson, M. 1994. Sexual Selection. Princeton University Press, Princeton, New Jersey.

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.

Birkhead, T. R., F. Fletcher, and E. J. Pellatt. 1998. Testes asymmetry, condition and sexual selection in birds: An experimental test. Proceedings of the Royal Society of London, Series B 265:1185–1189.

Birkhead, T. R., and A. P. Møller. 1992. Sperm Competition in Birds: Evolutionary Causes and Consequences. Academic Press, London.

Blomberg, S. P., T. Garland, Jr., and A. R. Ives. 2003. Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. Evolution 57:717–745.

Briskie, J. V. 1993. Anatomical adaptations to sperm competition in Smith's Longspurs and other polygynandrous passerines. Auk 110:875–888.

Calder, W. A. 1967. Breeding behavior of the roadrunner, *Geococcyx californianus*. Auk 84:597–598.

Calder, W. A. I. 1984. Size, Function and Life History. Harvard University Press, Cambridge, Massachusetts.

Clutton-Brock, T. H. 1991. The Evolution of Parental Care. Princeton University Press, Princeton, New Jersey.

del Hoyo, J., A. Elliott, and J. Sargatal, Eds. 1997. Handbook of the Birds of the World, vol. 4: Sandgrouse to Cuckoos. Lynx Edicions, Barcelona, Spain.

Delehanty, D. J., and P. Paasché O'Hearn. 2005. Behavioral and morphological asymmetries in chukar *Alectoris chukar* copulation. Journal of Avian Biology 36:276–279.

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.

Garamszegi, L. Z., M. Eens, S. Hurtrez-Boussès, and A. P. Møller. 2005. Testosterone, testes size, and mating success in birds: A comparative study. Hormones and Behavior 47:389–409.

Goymann, W., and J. C. Wingfield. 2004. Competing females and caring males. Sex steroids in African Black Coucals, *Centropus grillii*. Animal Behaviour 68:733–740.

Goymann, W., A. Wittenzellner, and J. C. Wingfield. 2004. Competing females and caring males. Polyandry and sex-role reversal in African Black Coucals, *Centropus grillii*. Ethology 110:807–823.

Grafen, A. 1989. The phylogenetic regression. Philosophical Transactions of the Royal Society of London, Series B 326:119–157.

Hegner, R. E., and J. C. Wingfield. 1987. Effects of experimental manipulation of testosterone levels on parental investment and breeding success in male House Sparrows. Auk 104:462–469.

Higgins, P. J., Ed. 1999. Handbook of Australian, New Zealand and Antarctic Birds. Oxford University Press, Oxford, United Kingdom.

Ketterson, E. D., and V. Nolan, Jr. 1994. Male parental behavior in birds. Annual Review of Ecology and Systematics 25:601–628.

Ketterson, E. D., V. Nolan, Jr., L. Wolf, and C. Ziegenfus. 1992. Testosterone and avian life histories: Effects of experimentally elevated testosterone and behavior correlates of fitness in the Dark-eyed Junco (*Junco hyemalis*). American Naturalist 140:980–999.

Kirby, J. D., and D. P. Froman. 2000. Reproduction in male birds. Pages 597–616 *in* Sturkie's Avian Physiology (G. C. Whittow, Ed.). Academic Press, New York.

Lack, D. 1968. Ecological Adaptations for Breeding in Birds. Methuen, London.

Lake, P. E. 1984. Male Genital Organs. Academic Press, London.

Langmore, N. E., G. J. Adcock, and R. M. Kilner. 2007. The spatial organization and mating system of Horsfield's Bronze-Cuckoos *Chalcites basalis*. Animal Behaviour 74:403–412.

Ligon, J. D. 1997. A single functional testis as a unique proximate mechanism promoting sex-role reversal in coucals. Auk 114:800–801.

Ludwig, W. 1932. Das Rechts-Links-Problem im Tierreich und beim Menschen. Springer Verlag, Berlin.

Macedo, R. H. 1992. Reproductive patterns and social organization of the communal Guira Cuckoo (*Guira guira*) in central Brazil. Auk 109:786–799.

Magrath, M. J. L., and J. Komdeur. 2003. Is male care compromised by additional mating opportunity? Trends in Ecology and Evolution 18:424–430.

Marchetti, K., H. Nakamura, and H. L. Gibbs. 1998. Host-race formation in the Common Cuckoo. Science 282:471–472.

Martínez, J. G., J. J. Soler, M. Soler, and T. Burke. 1998. Spatial patterns of egg laying and multiple parasitism in a brood parasite: A non-territorial system in the Great Spotted Cuckoo (*Clamator glandarius*). Oecologia 117:286–294.

Maurer, G. 2007a. Ecology and evolution of sex-roles in the Pheasant Coucal *Centropus phasianinus*. Ph.D. dissertation, Australian National University, Canberra.

Maurer, G. 2007b. Love is in the air: Arboreal copulations in the Pheasant Coucal *Centropus phasianinus*. Northern Territory Naturalist 19:48–50.

Maurer, G. 2008. Who cares? Males provide most parental care in a monogamous nesting cuckoo. Ethology 114:540–547.

Møller, A. P. 1991. Sperm competition, sperm depletion, paternal care, and relative testis size in birds. American Naturalist 137:882–906.

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.

Møller, A. P., and J. V. Briskie. 1995. Extra-pair paternity, sperm competition and the evolution of testis size in birds. Behavioral Ecology and Sociobiology 36:357–365.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: Analyses of phylogenetics and evolution in R language. Bioinformatics 20:289–290.

Payne, R. B. 2005. The Cuckoos. Oxford University Press, Oxford, United Kingdom.

Peters, A., A. Cockburn, and R. Cunningham. 2002. Testosterone treatment suppresses paternal care in Superb Fairy-wrens, *Malurus cyaneus*, despite their concurrent investment in courtship. Behavioral Ecology and Sociobiology 51:538–548.

Petersen, A. D., M. P. Lombardo, and H. W. Power. 2001. Left-sided directional bias of cloacal contacts during Tree Swallow copulations. Animal Behaviour 62:739–741.

Pitcher, T. E., P. O. Dunn, and L. A. Whittingham. 2005. Sperm competition and the evolution of testes size in birds. Journal of Evolutionary Biology 18:557–567.

R Development Core Team. 2006. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

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

Sorenson, M. D., and R. B. Payne. 2005. Molecular systematics: Cuckoo phylogeny inferred from mitochondrial DNA sequences. Pages 68–94 *in* The Cuckoos (R. B. Payne). Oxford University Press, Oxford, United Kingdom.

Stresemann, E. 1934. Aves. Page 899 *in* Handbuch der Zoologie, vol. 7, part 2 (W. Kükenthal and T. Krumbach, Eds.). Walter de Gruyter, Berlin.

Taplin, A., and Y. Beurteaux. 1992. Aspects of the breeding biology of the Pheasant Coucal *Centropus phasianinus*. Emu 92:141–146.

Vehrencamp, S. L., B. S. Bowen, and R. R. Koford. 1986. Breeding roles and pairing patterns within communal groups of Groove-billed Anis. Animal Behaviour 34:347–366.

Wingfield, J. C. 1990. Interrelationships of androgens, aggression and mating systems. Pages 187–205 *in* Endocrinology of Birds: Molecular to Behavioral (M. Wada, S. S. Ishii, and C. G. Scanes, Eds.). Japan Scientific Societies Press, Tokyo, and Springer-Verlag, Berlin.

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.

Wingfield, J. C., and B. Silverin. 2002. Ecophysiological studies of hormone–behavior relations in birds. Pages 587–647 *in* Hormones, Brain and Behavior, vol. 2 (D. W. Paff, A. P. Arnold, A. M. Etgen, S. E. Fahrbach, and R. T. Rubin, Eds.). Academic Press, Amsterdam.

Associate Editor: J. V. Briskie