

1 **Author version of an article published in Journal of Evolutionary Biology in 2015:**

2 *Goymann et al. Journal of Evolutionary Biology 28 (2015). DOI: 10.1111/jeb.12657*

3

4 **Social monogamy versus polyandry: ecological factors associated with sex-roles in two closely**
5 **related birds within the same habitat**

6 Wolfgang Goymann^{1,2}, Musa Makomba², Felister Urasa³ and Ingrid Schwabl^{1,2}

7 1) Max-Planck-Institut für Ornithologie, Abteilung für Verhaltensneurobiologie, Eberhard-Gwinner-
8 Str. 6a, D-82319 Seewiesen, Germany

9 2) Coucal Project, P.O. Box 26, Chimala, Tanzania

10 3) University of Dar es Salaam, Department of Zoology, P.O. Box 35091, Dar es Salaam, Tanzania

11

12 **Running title:** Ecological factors associated with sex-roles

13

14 **Corresponding author**

15 Wolfgang Goymann

16 Max-Planck-Institut für Ornithologie

17 Abteilung für Verhaltensneurobiologie

18 Eberhard-Gwinner-Str. 6a

19 D-82319 Seewiesen, Germany

20 Email: goymann@orn.mpg.de

21 Tel. +49 8157 932 301

22 Fax: +49 8157 923 260

23

24 **Abstract**

25 Why mainly males compete and females take a larger share in parental care remains an exciting
26 question in evolutionary biology. Role-reversed species are of particular interest, because such
27 'exceptions' help to test the rule. Using mating systems theory as a framework, we compared the
28 reproductive ecology of the two most contrasting coucals with regard to sexual dimorphism and
29 parental care: the black coucal with male-only care and the bi-parental white-browed coucal. Both
30 species occur in the same lush habitat and face similar ecological conditions, but drastically differ in
31 mating system and sexual dimorphism. Black coucals were migratory and occurred at high breeding
32 densities. With females being obligatory polyandrous and almost twice as heavy as males, black
33 coucals belong to the most extreme vertebrates with reversed sexual dimorphism. Higher variance in
34 reproductive success in fiercely competing females suggests that sexual selection is stronger in females
35 than males. In contrast, resident white-browed coucals bred at low densities and invariably in pairs.
36 They were almost monomorphic and the variance in reproductive success was similar between the
37 sexes. Black coucals were more likely to lose nests than white-browed coucals, probably facilitating
38 female emancipation of parental care in black coucals. We propose that a combination of high food
39 abundance, high population density, high degree of nest loss, and male bias in the adult sex ratio are
40 ecological conditions that facilitate role reversal and polyandry in coucals and terrestrial vertebrates
41 in general.

42

43 **Key words:** sex-role reversal, mating system, coucal, sexual selection, sex ratio, migration, predation,
44 parental care, variance in reproductive success

45

46

47 **Introduction**

48 In his theory on sexual selection Darwin (1871) explained the evolution of male weapons that are used
49 in combat and ornaments that are attractive to females. More recent work suggests that sexually
50 selected ornaments are common also in females (Andersson, 1994, Berglund et al., 1996, Kraaijeveld
51 et al., 2007, Clutton-Brock, 2009), whereas sexually selected weapons are rare in females (Berglund et
52 al., 1996, Berglund, 2013). These observations support the view that males more often compete
53 directly and intensely amongst each other for mating opportunities than females. There is also a
54 common sex-bias in parental care patterns, with female vertebrates typically providing more parental
55 care than males (reviewed by Kokko & Jennions, 2008, Reynolds et al., 2002). The main exception are
56 fish, in which the trade-off between competition over mates and parental care is often absent or
57 reduced (Jennions & Kokko, 2010, Kvarnemo, 2010). In birds, with about 90% bi-parental care and 9%
58 female-only care, the female bias is weaker than in reptiles, mammals (Reynolds et al., 2002), and
59 invertebrates (Tallamy, 2000, Trumbo, 2012). But even in birds, females usually have a larger share in
60 nest-building and incubation (Schwagmeyer et al., 1999) whereas males often are the more
61 competitive sex.

62 Why males predominantly compete directly and females take a larger share in parental care
63 remains an exciting and unsolved question in evolutionary biology (e.g. Kokko & Jennions, 2012). Role-
64 reversed species, in which females compete and males take a larger share in parental effort are
65 therefore of particular interest for evolutionary biology, because such 'exceptions' help to test the rule
66 (Andersson, 1994). Sex-roles are reversed in less than 1% of bird species with females being the more
67 competitive sex and polyandrous, and males providing exclusive parental care (Ridley, 1978, Reynolds
68 et al., 2002, Cockburn, 2006). This mating system – termed social or classical polyandry (Emlen & Oring,
69 1977, Andersson, 1994) – typically occurs in bird species that lay small clutches and are precocial, with
70 prolonged periods of embryonic development and young that gather their own food after hatching. In
71 such species, selection for bi-parental care may have been reduced and this has been suggested to
72 facilitate the evolution of classical polyandry (Emlen & Oring, 1977, Clutton-Brock, 1991, Ligon, 1993,

73 1999). Such facilitators reflect the evolutionary or phylogenetic history of a taxon which has been
74 identified as a possible key factor in determining sex-roles (Ligon, 1993, 1999). For example, the
75 prolonged period of embryo development inside the body of female mammals may explain why direct
76 paternal care is so rare in mammals compared to birds. Quite to the contrary, in many fish males can
77 fan and protect many eggs simultaneously, and such egg-caring males are attractive for females.
78 Hence, males can increase their mating success while caring for young (i.e. there is no conflict between
79 mating and parental care), explaining why parental care is typically male-biased in fish (Reynolds et al.,
80 2002, see also Andersson, 2005, Kvarnemo, 2010).

81 Here, we investigated which factors are currently associated with a reversal in sex roles and
82 polyandry in coucals (*Centropodinae*), a bird taxon belonging to the cuckoos and in which the ancestral
83 condition is social monogamy and bi-parental care. The black coucal (*Centropus grillii*) is the only
84 migratory coucal species (del Hoyo et al., 1997) and the only known obligate classically polyandrous
85 bird species with altricial young. Hence, in contrast to all other classical polyandrous species – in which
86 clutch sizes are fixed and young are precocial – coucal fathers are tending clutches that are quite
87 variable in size and feed altricial nestlings (Vernon, 1971, Goymann et al., 2004, Goymann et al., 2005,
88 Muck et al., 2009). With females being considerably larger than males (Goymann et al., 2004) and
89 highly competitive (Goymann et al., 2008, Geberzahn et al., 2009, Geberzahn et al., 2010) the black
90 coucal is one of the most unusual vertebrates with a `reversed` sexual size-dimorphism (Andersson,
91 1995) paralleled only by some species of jacana (Jenni & Collier, 1972, Butchart, 2000, Emlen & Wrege,
92 2004). Andersson (1995) suggested male incubation to be a necessary primer for classical polyandry in
93 black coucals and provided evidence that females of socially monogamous coucal species have
94 intervals of 2-3 or even more days between laying two eggs, indicating they may be having difficulties
95 gathering sufficient resources to rapidly finish a clutch. Thus, they could benefit from male assistance
96 during incubation. Also, coucals do not develop a vascularized brood patch (W. Goymann, pers. obs.),
97 suggesting that successful incubation does not require a change in the vascularization of the skin, thus
98 making it easy for males to contribute to incubation without developing morphological specializations

99 typical for females. As a migrant, the black coucal can exploit grassland habitats with seasonally
100 superabundant food resources. This may enable females to quickly gather resources to lay a number
101 of successive clutches for different males within a short period of time, and males to raise a brood
102 without help from a partner (Andersson, 1995, 2005). However, in some regions, such as the Usangu
103 plains of Tanzania, the migratory black coucal co-occurs with year-round resident coucal species, such
104 as the white-browed coucal (*C. superciliosus*, Baker & Baker, 2003). The white-browed coucal is similar
105 in size to the black coucal and relies on similar food sources (mainly large insects such as grasshoppers
106 or mantids, as well as frogs; (Goymann et al., 2005 and W. Goymann, unpublished data). According to
107 Irwin (1985) the two species may represent sister clades (but see Sorenson & Payne, 2005). Despite
108 these ecological similarities, the white-browed coucal appears to be the least sexually dimorphic of all
109 27 described coucal species (Andersson, 1995) and, being socially monogamous and bi-parental, also
110 the one with the most similar sex-roles (van Someren, 1956, Rowan, 1983). So far, detailed field studies
111 of this species have been missing, though.

112 To find out which factors potentially drive the differences in mating systems we compared the
113 reproductive ecology of individually marked black and white-browed coucals, the two most contrasting
114 coucal species with regard to sexual size dimorphism and mating system, in their shared habitat in
115 south-western Tanzania. We are aware of the conceptual criticism of two-species comparisons
116 (Garland & Adolph, 1994), but the opportunity to test specific hypotheses in the taxon's two most
117 extreme representatives under similar ecological conditions in their shared habitat in our view
118 represents a unique opportunity to advance our understanding regarding the ecology and evolution
119 of sex-role reversal. Two-species comparisons remain to be useful, in particular when addressing
120 specific hypotheses (Garland & Adolph, 1994) and for formulating new hypotheses that should then
121 be discussed in a broader context (Cooper, 1999).

122 Hence, the aim of this study was a comprehensive comparison of the two coucal species with
123 regard to critical factors that have been hypothesized to play a role in the determination of mating
124 systems and sex-roles, to then relate these factors to the broader context of sex role reversal in birds

125 and other terrestrial vertebrates. Specifically, we (1) measured the degree of sexual dimorphism and
126 morphology of the two coucal species, (2) quantified species densities, territory sizes, length of the
127 breeding seasons, and the adult sex-ratios of the breeding populations. Further, we (3) described and
128 compared nesting behavior, clutch size, and nestling sex ratios. Finally, we (4) measured nest predation
129 rate, nesting intervals, reproductive rate and variance in reproductive output. Our predictions with
130 regard to this comprehensive comparison were as follows (summarized in Table 1):

131

132 *Species differences in sexual dimorphism and morphology*

133 We expected a larger reversed sexual size dimorphism in polyandrous black coucals than in socially
134 monogamous white browed coucals, because competition among females and efficiency of laying
135 large numbers of eggs may favor large body size in female black coucals, and foraging energetics may
136 favor smaller body size in male black coucals (Andersson, 1995). We have previously published data
137 on body size dimorphism in black coucals (Goymann et al., 2004), but body size parameters of white-
138 browed coucals have been available only for a few individuals (summarized in Eritzoe et al., 2012),
139 preventing definitive conclusions. Further, considering that migration has been hypothesized a key
140 factor in the reversal of sex roles in the black coucal (Andersson, 1995), we expected morphological
141 adaptations for migration in black coucals, but not in white-browed coucals. Specifically, we
142 investigated differences in wing load and tail length and expected a lower wing load and a shorter tail
143 that reduces drag in black coucals than in white-browed coucals.

144 In a previous study we have shown that there is a high degree of sperm competition in black
145 coucals, with the highest rate of paternity loss recorded in any classically polyandrous bird species
146 (Muck et al., 2009). Birkhead et al. (1993) showed that the size of the cloacal protuberance in song
147 birds is an excellent indicator of sperm competition and copulation frequency. Black coucals have a
148 pronounced cloacal protuberance in which the enlarged papillae of the deferent ducts serve as sperm
149 storage organs (Frey & Goymann, 2009), a situation very similar to songbirds (Birkhead et al., 1993).
150 Currently, genetic paternity data for white-browed coucals are not available, but because they live in

151 pairs and at lower densities (see results) we expected a lower degree of sperm competition in this
152 species compared to black coucals, where females regularly copulate with several different males
153 (Muck et al., 2009). We thus investigated the size of the cloacal protuberance as an indirect indicator
154 of the degree of sperm competition and predicted that the cloacal protuberances of male white-
155 browed coucals should be smaller than those of black coucals.

156 Andersson (2004) proposed that “scramble competition among females for limited uniparental
157 care by males favors reduced female gamete size” (p. 31) in classical polyandrous species, suggesting
158 that sexual selection drives the reduction in female gamete size. In addition, ecological selection may
159 favor small eggs in classical polyandrous species, helping females to maximize the number of clutches
160 (Slotow, 1996, Liker et al., 2001). Accordingly, we predicted that black coucals lay smaller eggs than
161 white-browed coucals.

162

163 *Species densities and territory sizes*

164 In a comparative study Owens (2002) found that species with male-only care nest at lower densities
165 than species with female-only care: at low densities males would gain little from deserting a clutch
166 because they would be unlikely to find another female in reproductive condition. Females, on the other
167 hand, may have a larger benefit from desertion because they can mate with any male. In contrast to
168 Owens (2002), Goymann et al. (2004) suggested that high nesting densities are a necessary condition
169 for polyandry and male-only care in coucals, because high nesting densities enable single females to
170 monopolize and control more than one male simultaneously. In addition, we propose that the breeding
171 density of the migratory black coucal is not limited by the carrying capacity of the breeding habitat
172 during the harsh non-breeding season. In contrast, all other coucals species – including the white-
173 browed coucal – are resident (del Hoyo et al., 1997) and hence their breeding density may be limited
174 by the carrying capacity of the habitat during the food-limited dry season. Thus, according to Owens
175 (2002) black coucals should nest at lower densities than white-browed coucals, whereas Goymann et
176 al. (2004) predict higher nesting densities in black coucals.

177 Because the two coucal species rely on the same food sources to raise their young we expect
178 territories of pairs of white-browed coucals and male black coucals to be similar in size. In contrast,
179 territories of female black coucals should be larger, because they typically need to accommodate
180 several males per female.

181

182 *Length of the breeding season, nesting behavior, clutch size, nestling number, and nestling sex ratios*

183 Resident white-browed coucals have already established territories before breeding. We thus
184 expected them to start breeding earlier than black coucals which first need to establish territories and
185 find mates after arriving on the breeding grounds. A shorter breeding season may increase selection
186 pressure towards male-only incubation if the rate of nest failure is high (for details see section on nest
187 predation).

188 Previous observations of nesting behavior of white-browed coucals have been rather
189 anecdotal (van Someren, 1956, Rowan, 1983). We thus aimed at providing a detailed description of
190 clutch size and nestling numbers of white-browed coucals, and compare them with those of black
191 coucals in the same habitat. In a habitat with superabundant food we expected the bi-parental white-
192 browed coucals to lay larger clutches and raise more nestlings per clutch than black coucals with male-
193 only care.

194 A male bias in the adult sex ratio has recently been identified as a potential key factor for
195 female competition and male parental care (Kokko and Jennions, 2008). If such a bias would already
196 exist at the nestling level we would predict a male biased nestling sex ratio in black coucals but not in
197 white-browed coucals.

198

199 *Nest predation, nesting intervals, reproductive rates and variance in reproductive success*

200 Frequent nest failure has been suggested as a factor facilitating female emancipation of parental care
201 in jacanas (Jenni, 1974, Butchart, 2000) and black coucals (Goymann et al., 2004). Both partners would
202 benefit from male-only incubation, because this frees females to gather resources for a quick

203 replacement clutch in case the first attempt fails. Indeed, in a previous study Goymann et al. (2005)
204 observed a high rate of nest failures particularly during the incubation stage in black coucals. If nest
205 failure plays a role in sex-role reversal we would expect higher nest-failure rates in black compared to
206 white-browed coucals.

207 Mating system theory predicts that in sex-role reversed polyandrous species the nesting
208 interval should be shorter in females than in males, and that females should have a higher reproductive
209 rate and a higher variance in reproductive output than males (Emlen & Oring, 1977, Clutton-Brock &
210 Vincent, 1991, Andersson, 1994, Shuster & Wade, 2003). We thus predicted a shorter nesting interval,
211 a higher reproductive rate, and a higher variance in reproductive output in female than male black
212 coucals, whereas we did not expect such differences between the sexes in white-browed coucals.

213 Because the two coucal species co-occur in the same habitat and rely on the same food sources
214 during breeding we could also test Andersson's (1995) idea that superabundant food resources may
215 lead to classical polyandry in coucals. If superabundant food resources were a major driver of classical
216 polyandry in coucals, we would expect to observe classical polyandry – at least occasionally – also in
217 white-browed coucals.

218 Finally, we use the comprehensive comparison of the two coucal species to discuss whether
219 potential factors that may drive classical polyandry in coucals can be generalized and facilitate sex-role
220 reversal and polyandry also in other terrestrial vertebrate species, a topic that has been highly
221 controversial (e.g. Erckmann, 1983, Reynolds & Szekely, 1997, Ligon, 1999).

222

223 **Methods**

224 We studied a population of black and white-browed coucals, each in partially flooded grassland of the
225 Usangu wetland (8°41'S 34°5'E; 1000m above sea level) in Mbeya region, Tanzania, during the breeding
226 seasons of 2005 (Jan. 23 – May 27), 2006 (Jan. 15 – Apr. 25), 2008 (Feb. 10 – March 13), 2010
227 (Feb. 20 – April 25), 2011 (Feb. 18 – June 6), 2012 (Dec. 18 – June 18), 2013 (Jan. 25 – June 29), and
228 2014 (Jan. 15 – June 29). The habitat belongs to the flooded grasslands and savannahs biome (Olsen

229 et al., 2001), which is characterized by wet and dry seasons that typically occur on a relatively regular
230 and predictable annual basis (Goymann & Helm, 2015). It mainly consists of long-term uncultivated
231 rice fields and adjacent grasslands, both with natural grassland vegetation dominated by rhizomateous
232 grasses (*Echinochloa spp.*), wild and domestic rice (*Oryza spp.*), herbaceous *Cassia*, and *Acacia* shrubs.
233 Daily rainfall data were obtained from the weather station of the Kapunga rice farm within the study
234 area. Major rains typically occur in the period between December and May, and turn the dry and
235 desert-like area into a lush and green wetland that serves as a breeding habitat for hundreds of bird
236 species (Baker & Baker, 2003).

237 Coucals were caught with mist nets, measured and ringed with numbered aluminium rings and
238 colored plastic rings for individual identification. In addition, most birds were equipped with a Holohil
239 BD-2 radio-transmitter (<2g; Holohil Systems Ltd., Carp, Ontario, Canada) using a Rappole harness
240 (Rappole & Tipton, 1991) made out of soft rubber (1 mm diameter). The GPS positions of the capture
241 sites were noted.

242 We took the following measurements: body mass (to the nearest 1 g), bill-, wing- and tail-
243 length (to the nearest 1 mm), length of the right tarsus (to the nearest 0.1 mm), and the length of the
244 claw (to 1 mm) on the 4th toe of the right leg. This claw is elongated compared to the claws of the other
245 three toes and used by coucals to grasp vegetation upon perching. The claws of black coucals are
246 particularly long, which is probably an adaptation to perch on bundles of grasses. Further, as an
247 estimate for sperm competition and sperm storage (Birkhead et al., 1993), we measured the height
248 and diameter of the elevation of the cloaca relative to the surrounding pubic region (to the nearest
249 1 mm), from which we calculated the volume of the elevation of the cloaca, assuming a cylindrical
250 shape ($vol = \pi * r^2 * h$). Although the term is typically only used for songbirds, we use the term cloacal
251 protuberance for the elevation of the cloaca. An index of wing load was calculated using the ratio of
252 body mass versus wing length squared (in g/cm^2), which seems a justified proxy given that the shape
253 of the wings of black and white-browed coucals is similar (see also Andersson, 1995). In the field, birds
254 were sexed using body mass in black coucals (no overlap between the sexes), and tail-length (little

255 overlap between the sexes) and behavioral observations (e.g. copulations) in white-browed coucals.
256 To confirm the field data, a small blood sample was taken from each bird for genetic sexing (Fridolfsson
257 & Ellegren, 1999) in the laboratory, which unambiguously confirmed the morphological or behavioral
258 sexing in the field. The morphological measurements include data from some female black coucals
259 caught during 2004 and 2007 for a different study.

260 Daily observation of birds and the GPS positions of the capture sites were used to obtain rough
261 population density estimates for both species. For each year (and in 2006 and 2011 for two study sites)
262 we counted the number of known individuals. From our daily field observations of marked and
263 unmarked birds we estimated the approximate proportion of marked birds. For black coucals, we
264 caught and marked about 60 % of individuals during each season (except in 2014, where we caught
265 and marked a larger proportion, estimated as 80 %). For white-browed coucals we caught and marked
266 a larger proportion, conservatively estimated as 80 % of all individuals in the respective study area
267 during each season (except in 2008, where we had caught only 40 %). These estimates are conservative
268 with respect to the expected differences in densities (higher in black than in white-browed coucals),
269 because in most years we probably caught less than 60 % of black coucals and more than 80 % of white-
270 browed coucals, thus underestimating the density of black and overestimating the density of white-
271 browed coucals. Using the adjusted numbers we calculated density, estimated as the number of birds
272 per km² of the study area.

273 A Global Positioning System (GPS) position of each radio-tagged bird was noted at least every
274 2 – 3 days. Additionally, we recorded the positions of marked individuals perching at or close to
275 landmarks with known GPS positions (e.g. certain bushes, perches or trees). On average we obtained
276 24.9 ± 15.9 (mean \pm std; range 6-75) locations for each individual. We calculated territory or home
277 range sizes for each bird as individual utilization distribution areas (bivariate normal kernels; Worton,
278 1989). Because female black coucals and pairs of white-browed coucals defended an area we classified
279 such areas as territories. Male black coucals did not defend areas and hence we classified the areas
280 they used as home ranges. We used the 60% isopleths as an estimate of territory or home range

281 boundaries, using a Mollweide projection. Territory and home range sizes were calculated in R version
282 3.1.2 (The R Foundation for Statistical Computing, 2014) with the packages `ade4`, `adehabitat`, `sp`,
283 and `rgdal` (Calenge, 2006, Thioulouse et al., 1997, Bivand et al., 2013). These 60% kernels were used
284 to statistically compare territory/home range sizes between the species and sexes (see below).

285 Nests were located by (a) following white-browed coucals, carrying long grasses in their beaks,
286 which is a very obvious sign of nest-building. This behavior does not occur in black coucals, because
287 only female black coucals build the nest and use only local grasses gathered directly at the nesting site.
288 Nests were further located by (b) finding incubating birds that had been equipped with radio-
289 transmitters, (c) by following male black coucals or white-browed coucals carrying leaves (used as inner
290 lining for the nest), or finally (d) in the nestling phase, by following birds carrying food in their beaks.
291 To avoid affecting the vegetation close to the nest we never approached the nest directly but instead
292 passed by the nest at a distance of about half a meter and reached into the nest from that distance.
293 Upon finding nests we counted the number of eggs or nestlings. The length and diameter of eggs were
294 measured to the nearest 0.1 mm using calipers. Egg volume was calculated according to Goymann et
295 al. (2005) following Hoyt (1979): $0.51 * \text{length} * \text{width}^2$. The period of incubation was defined as the
296 number of days between 1st egg laid until 1st chick hatched. Once at least one chick had hatched, nests
297 were checked every other day, and the nestlings measured until they left the nest. When the nestlings
298 were about 5-7 days old we took a small blood sample for genetic sexing.

299 The length of the breeding season was estimated as the period between the first-laid egg from
300 the first nest in the season to the first-laid egg of the last nest in each season (in case the nests were
301 found in the nestling stage the date of the first-laid egg was calculated assuming 15 days of incubation
302 in black coucals and 16 days of incubation in white-browed coucals and adding one additional day for
303 each egg of the respective clutch). These estimates could be reliably done for the breeding seasons
304 from 2011-2014, during which we were present in the field for a sufficiently long period. A similar
305 period was covered during 2005, but this was the first year we had included white-browed coucals and
306 thus we lacked the experience to reliably locate the first nests for this species. All procedures were

307 approved by the respective governmental authorities of Tanzania, i.e. the Tanzania Wildlife Research
308 Institute (TAWIRI) and the Tanzanian Commission for Science and Technology (COSTECH).

309 **Statistical analysis**

310 Statistical analyses were conducted using R version 3.1.2 (The R Foundation for Statistical Computing,
311 2014) and a Bayesian statistical approach. Nest predation rates were calculated using the R package
312 BayesianFirstAid (Bååth, 2014) and compared between species using the region of practical
313 equivalence (ROPE; Kruschke, 2013), which can be considered as a measure of the likelihood that two
314 distributions are similar to each other. For all other calculations we used the packages ‘arm’ (Gelman
315 et al., 2014) and ‘lme4’ (Bates et al., 2014). Linear models and linear mixed models were calculated
316 using the maximum likelihood (ML) method. Posterior means and their 95 % credible intervals were
317 calculated using the function sim (running 10,000 simulations).

318 All biometric measures of individuals were compared between species and sexes using linear
319 models (function lm). Densities of black and white-browed coucals were compared using linear mixed
320 models (function lmer) with year as a factorial random intercept. To compare territory sizes between
321 species and sexes we used linear mixed models with the individual as random intercept using linear
322 mixed models (functions lmer and glmer). Adding random slopes did not improve the model fit, as
323 indicated by AIC or DIC values.

324 For the comparison of egg volumes we used two approaches. First, we compared the volumes
325 of all available egg measurements between the species using a mixed model with maternal ID as
326 random intercept (after making sure that including a random slope did not improve model fit). Second,
327 by using a subset of all data for which female body mass was also known, we compared the egg
328 volumes between the two species including body mass of the mother as a fixed effect nested within
329 species, and controlling for maternal ID as a random intercept. Again, including a random slope did not
330 improve the model fit.

331 Clutch size was analyzed with a linear mixed model with number of eggs as the dependent
332 variable, Julian date and species as fixed effects, and ID of the mother as a random factor. Total number
333 of nestlings and fledglings were analyzed similarly.

334 The nestling sex ratio was analyzed with a binomial mixed model (using the function `glmer`
335 implemented in the R package `arm`) with the number of female and male nestlings as the dependent
336 variable, species and Julian date as fixed effects, and the ID of the mother as a random factor.

337 The interval between subsequent clutches within a season was compared between individual
338 female and male black coucals and pairs of white-browed coucals, respectively, using linear mixed
339 models with individual ID (or pair) as random factor and fate of the previous nest (egg predation,
340 nestling predation and successfully fledged) as fixed effect.

341 Annual reproductive rate (i.e. the number of eggs, nestlings and fledglings produced per
342 individual per year) was analyzed using linear models. We ran separate models for the number of eggs,
343 number of nestlings and number of successfully fledged young as respective dependent variable for
344 individual female and male black coucals and pairs of white-browed coucals as the dependent
345 variables. The variance in reproductive success and its' 95% confidence interval was determined using
346 the methods described in Sokal and Rohlf (1995, pp. 51, 155).

347 Model residuals were examined using graphical methods (i.e. qq plots of residuals and random
348 effects, fitted values versus residuals) for homogeneity of variance, violation of normality assumptions
349 or other departures from model assumptions and model fit. For inferences from the models we
350 obtained Bayesian parameter estimates and their 95 % credible intervals, using an uninformed prior
351 distribution. The Bayesian approach is the only method that allows the drawing of exact inferences
352 while avoiding the difficulties of determining the degrees of freedom in mixed model analyses (Bolker
353 et al., 2009). Unlike null-hypothesis testing, Bayesian methods do not provide p-values. Instead,
354 biologically meaningful differences between groups can be assessed by comparing the ranges of the
355 95 % credible intervals between groups. The 95 % credible interval provides an estimate for the mean
356 with a probability of 0.95. If the credible interval of one group does not overlap with the mean estimate

357 of another group, the groups can be assumed to differ from each other. If not indicated otherwise,
358 data are presented as individual data points in combination with posterior means and their respective
359 95 % credible intervals (reported in squared brackets). We also provide measures of the goodness-of-
360 fit of the models (i.e. how much of the variance they explain) by reporting R^2 -values for linear models
361 or the respective marginal and conditional R^2 -values for mixed models (Nakagawa & Schielzeth, 2013).
362

363 **Results**

364 *Species differences in mating system, adult sex ratios, sexual dimorphism and morphology*

365 The large majority of female black coucals formed polyandrous groups with at least 2 males (Table 2).
366 Monogamous pairings were the exception and females without a partner were never seen. In contrast,
367 males that were caught and radio-tagged within the territory of a female early in the breeding season
368 sometimes moved and settled elsewhere (N = 12), suggesting that males may investigate several
369 female territories before settling with a female. However, males being permanently without a partner
370 were also never seen. In combination, these data suggest that the sex-ratio of the local breeding
371 population was strongly male-biased.

372 In contrast, white-browed coucals typically stayed together in socially monogamous pairs for
373 one entire season (Table 2). Exceptions include two cases, where one partner died during the breeding
374 season and one female that abandoned her partner, presumably to nest with another male. Four times
375 during the whole study, we observed a male white-browed coucals regularly singing on a territory, but
376 without a female partner. Single females and polyandrous groups of white-browed coucals did not
377 occur. These data suggest that the sex-ratio of the local breeding population was more or less equal
378 or only slightly male-biased.

379 Body mass differed between the sexes and the two species (GLM: $F_{3,314} = 444.1$, adjusted
380 $R^2 = 0.81$). The 95 % credible intervals indicated that females of both coucal species were heavier than
381 their respective males (Fig. 1a). With a sexual dimorphism index (male/female) of 0.59 the sexual
382 dimorphism was much stronger in black coucals than in white-browed coucals (0.89). Female black
383 coucals were heavier than female and male white-browed coucals. In turn, both female and male
384 white-browed coucals were heavier than male black coucals (Fig. 1a).

385 The length of the claw of the 4th toe differed between species and the sexes (GLM:
386 $F_{3,311} = 125.3$, adjusted $R^2 = 0.54$). Female black coucals had longer claws than males and the claws of
387 male black coucals were longer than those of female and male white-browed coucals (Fig. 1b). The

388 strong difference in claw length indicates that black coucals are adapted to perching on bundles of
389 grasses (which they grasp using the elongated claw), a behavior that is indeed very common in black
390 coucals but that we rarely observed in white-browed coucals.

391 The index of wing load (body mass/wing length²) was lowest in male black coucals and lower
392 in black coucals than in both sexes of white-browed coucals (GLM: $F_{3,308} = 193.6$; $R^2 = 0.65$; Fig. 1c).
393 Also the lengths of the tails differed (GLM: $F_{3,300} = 350.7$; $R^2 = 0.776$), with female white-browed coucals
394 having longer tails than conspecific males and white-browed coucals having longer tails than female
395 and male black coucals (Fig. 1d). Within black coucals, female tails were longer than those of males
396 (Fig. 1d).

397 We measured the volume of the cloacal protuberance as an estimate of the degree of sperm
398 competition in the two species. The volume differed between the species and the sexes (GLM:
399 $F_{4,311} = 93.37$, adjusted $R^2 = 0.540$) with a slight influence of Julian date ($\beta = 0.052$ [0.030 – 0.075],
400 $F_{1,311} = 28.92$). In both species, males expressed larger cloacal protuberances than females. But
401 regardless of sex, the protuberances of black coucals were more elevated than those of white-browed
402 coucals (Fig. 2a). Within males, black coucals had larger cloacal protuberances than white-browed
403 coucals ($F_{1,137} = 147.27$), a difference that would be even more extreme if we would have scaled it to
404 body size. The size of the cloacal protuberance in males also changed with breeding stage
405 ($F_{3,137} = 12.34$): cloacal protuberances were smallest before the onset of breeding, and largest during
406 the mating and incubation stages (overall GLM: $F_{4,137} = 46.07$, adjusted $R^2 = 0.56$; Fig. 2b), highlighting
407 their potential role in sperm competition (for a summary of further body size measures and exact
408 sample sizes see Table 2).

409 White-browed coucals typically laid larger eggs than black coucals (GLMM: $F = 60.13$,
410 marginal $R^2_{\text{glmm}} = 0.34$, conditional $R^2_{\text{glmm}} = 0.78$, Fig. 3a). When considering only eggs from females with
411 known body mass, egg volume still differed between black and white-browed coucals ($F = 15.55$) and
412 was positively related to female body mass ($F = 9.11$). Thus, female white-browed coucals laid larger

413 eggs than female black coucals of similar size (GLMM: marginal $R^2_{\text{glmm}} = 0.33$, conditional $R^2_{\text{glmm}} = 0.73$;
414 Fig. 3b), but in both species, larger females laid larger eggs (Fig. 3b).

415

416 *Species densities, territory sizes, and adult sex ratios*

417 During the breeding season, black coucals occurred at higher densities (11.6 [6.5 – 15.9] birds per km²)
418 than white-browed coucals (5.5 [0.8 – 10.1] birds per km²; GLMM with year as random factor:
419 $F = 4.673$; marginal $R^2 = 0.17$, conditional $R^2 = 0.32$).

420 Territory sizes differed between the species and the sexes (GLMM: $F = 17.991$, marginal
421 $R^2_{\text{glmm}} = 0.16$, conditional $R^2_{\text{glmm}} = 0.16$). The territories of female black coucals were almost three times
422 larger than the home ranges of conspecific males, and about twice as large as the territories of white-
423 browed coucals. The home ranges of male black coucals were slightly smaller than the territories of
424 female and male white-browed coucals, which were similar in size (Fig. 4).

425 Of a total of 142 color-banded female black coucals only one individual was seen during two
426 consecutive field seasons, and of a total of 98 color-banded male black coucals only two males were
427 sighted at different locations during two consecutive seasons. All other color-banded individuals were
428 seen only during one field season. In white-browed coucals, of a total of 31 color-banded females one
429 individual was relocated for 3 seasons, and two females for 2 consecutive seasons, all of them with
430 their respective color-banded male partner and in the same area. Of 53 color-banded males, one was
431 relocated during 4 seasons, five males during 3 seasons, and two during 2 seasons, all of them in the
432 same area. All other color-banded white-browed coucals were present only during one season.

433

434 *Length of the breeding season, nesting behavior, clutch size, nestling number, and nestling sex ratios*

435 In both species, the breeding season was closely associated with the rainy season. For the years 2011-
436 2014 we estimated the total length of the breeding season to be 84 ± 36 days (mean \pm 95 % confidence
437 interval) in black coucals and 112 ± 21 days in white-browed coucals. The difference mainly stems from

438 the fact that the resident white-browed coucals typically started breeding earlier (Julian day 17 ± 26)
439 than the migratory black coucals (Julian day 48 ± 26), which were still establishing territories and “pair”
440 bonds at the time when pairs of white-browed coucals already built their first nests (Fig. 3).

441 Because male black coucals had been observed to carry leaves into their nests it has been
442 assumed that male black coucals build the dome-shaped nest (Goymann et al., 2005, Goymann et al.,
443 2004). However, the leaves are only used for the inner lining of the nest cup and new leaves are
444 frequently added during incubation. More recently, we have observed during several occasions that
445 females very secretively build the nest structure, using living grasses with which they form the dome.
446 Conversely, both female and male white-browed coucals contribute to building the nest dome using
447 grasses that they cut in areas at some distance from the nest. Black coucals almost invariably placed
448 their nests in patches of dense grass ($N = 214$) and rarely in thorny shrubs ($N = 5$), whereas white-
449 browed coucals typically built their nests in thorny acacias or shrubs ($N = 93$) and less often in reeds,
450 thorn-less shrubs or grasses ($N = 44$).

451 The mean numbers of eggs per clutch, number of nestlings and number of nestlings that left
452 the nest (coucals are still unable to fly for about 1-2 weeks after leaving the nest) was similar in both
453 species and none of these variables varied with Julian date (Table 4). Also the mean estimates for the
454 periods of incubation between the two species were similar (Table 4). In black coucals, only males
455 incubated, whereas in white-browed coucals both sexes incubated the eggs. The nestling periods (i.e.
456 the time between hatching and the last day a nestling was found in the nest) was 1-2 days shorter in
457 black than in white-browed coucals (Table 4). Within each species, there was no sex difference, i.e.
458 female and male nestlings stayed in the nest for similar periods of time.

459 We counted a total of 214 female and 194 male black coucal nestlings ($N = 121$ nests) and 133
460 female and 125 male white-browed coucal nestlings ($N = 82$ nests). Thus, the nestling sex ratio did not
461 differ from equality in both black (GLMM: $z = -1.145$, $\beta = -0.116$ [$-0.312 - 0.073$]) and white-browed
462 coucals (GLMM: $z = 0.221$, $\beta = -0.077$ [$-0.328 - 0.168$]; $R^2_{\text{glmm}} < 0.0001$, conditional $R^2_{\text{glmm}} < 0.0001$).

463 Hence, the estimated mean proportion of males was 47.1 % [42.3 – 51.8%] in black and 51.0% [43.2 –
464 58.5%] in white-browed coucals.

465 Overall, black coucals left the nest at a lower body mass than white-browed coucals. In both
466 species, females left the nest at a higher body mass than their respective conspecific males (Table 5).
467 Female black coucals left the nest at the lowest body mass relative to their adult mass. Thus, body
468 mass when leaving the nest corresponded to 45.7 % of adult body mass in female black coucals,
469 whereas males fledged at 66.9 % of adult body mass. White-browed coucals fledged at 61.2 %
470 (females) and 65.8 % (males) of adult body mass.

471

472 *Nest predation, nesting intervals, reproductive rates and variance in reproductive success*

473 Nest predators of coucals included various species of snakes, monitor lizards (*Varanus niloticus*),
474 rodents, mongoose (mainly marsh mongoose, *Atilax paludinosus* and slender mongoose, *Herpestes*
475 *sanguinea*), feral and wild cats, various raptors and coppery-tailed coucals (*Centropus cupreicaudus*).
476 Because the majority of white-browed coucal nests were built in acacias or other thorny shrubs they
477 probably offered a better protection against predators than the unprotected nests of black coucals
478 that were built into grasses (see section on nest building above). Indeed, nests of black coucals were
479 more likely to be depredated than nests of white-browed coucals: From a total of 178 black coucal
480 nests 87 were depredated (posterior mean proportion: 0.49 [0.40 – 0.56]), whereas in white-browed
481 coucals only 33 out of 105 nests were depredated (posterior mean proportion: 0.32 [0.23 – 0.40]). The
482 credible intervals of nest predation rates did not overlap each other's posterior mean proportion and
483 the *region of practical equivalence* (ROPE) was 0.018, suggesting that there was only a 1.8% likelihood
484 that overall nest predation rate was similar in black and white-browed coucals. Most of the difference
485 in nest predation rates seems to come from egg-predation during the incubation stage. From the total
486 of 178 black coucal nests 56 were depredated during incubation (posterior mean proportion =
487 0.32 [0.25 – 0.39]), whereas in white-browed coucals only 18 out of 105 nests were depredated during

488 incubation (posterior mean proportion = 0.18 [0.11 – 0.25]). The credible intervals of egg-predation
489 rates did not overlap each other's posterior mean proportion and ROPE was 0.042. Thus, with a
490 likelihood of only 4.2% the rate of egg predation was similar in black and white-browed coucals. The
491 results likely underestimate the true egg predation rate in black coucals, because black coucals are
492 much more secretive in nest-building and incubation than white-browed coucals. Hence, nests of black
493 coucals were much harder to find during these phases than nests of white-browed coucals, in which
494 both parents conspicuously contribute to nest-building. Further, because white-browed coucals
495 typically build their nests in acacias or thorny shrubs they are much easier to locate for a human
496 observer than those of black coucals that are hidden in dense vegetation.

497 Nest depredation during the nestling stage was more similar, with 31 of the remaining 122
498 nests in black coucals (posterior mean proportion 0.26 [0.18 – 0.33]) and 15 of the remaining 87 nests
499 in white-browed coucals (posterior mean proportion 0.18 [0.10 – 0.26] being depredated. In this case,
500 the ROPE value was 0.289. Thus, the likelihood of similar nest predation rates during the nestling stage
501 between the species was 28.9%.

502 For 91 female and 28 male black coucals, and for 54 pairs of white-browed coucals we could
503 determine the interval between the date of the first egg of one clutch and the date of the first egg of
504 the next clutch. These inter-clutch intervals were smaller for individual female black coucals than for
505 conspecific males or for pairs of white-browed coucals (GLMM: $F = 46.615$; Fig. 6). In both species, the
506 inter-clutch interval was longer when the nest was successful than when the nest was depredated
507 during incubation or in the nestling stage (GLMM: $F = 32.819$; marginal $R^2_{\text{glmm}} = 0.51$, conditional
508 $R^2_{\text{glmm}} = 0.59$; Fig. 6). This predation effect was reduced in female black coucals compared to males and
509 pairs of white-browed coucals (Fig. 6). For female black coucals these results represent a conservative
510 estimate, because we were less likely to detect all nests of individual female black coucals than those
511 of conspecific males or pairs of white-browed coucals. Unlike males female black coucals spend little
512 time on the nest (only during laying) and if not all of the partners of a female were radio-tagged, we

513 could not reliably find all nests of the respective female. Hence, the true inter-clutch intervals of female
514 black coucals were probably even shorter than those reported here.

515 Reproductive rates differed between female black coucals and conspecific males and pairs of
516 white-browed coucals. On average, female black coucals laid 3.8 [3.2-4.4] clutches (range 1-8), black
517 coucals incubated 1.5 [1.1-2.0] clutches (range 1-4), and pairs of white-browed coucals had 2.1 [1.6-
518 2.5] clutches (range 1-5). Overall, individual female black coucals laid more eggs than individual male
519 black coucals incubated, or pairs of white-browed coucals laid and incubated per season (Fig. 7a; GLM:
520 $F_{2,89} = 18.485$, adjusted $R^2 = 0.28$). Interestingly, there was a negative relationship between female
521 body size and number of eggs laid in black coucals, with smaller females laying more eggs than larger
522 females (model slope with tarsus length: -2.22 [-4.30; -0.15]; slope with body mass -0.25 [-0.45;-0.05]).
523 In white-browed coucals there was no such relationship between the number of eggs laid and female
524 body size (slope with tarsus length: -0.38 [-1.89; 1.13]; slope with body mass 0.05 [-0.11; 0.22]).

525 A similar bias was found for the number of nestlings: individual female black coucals produced
526 more nestlings than individual male black coucals cared for, or individual pairs of white-browed coucals
527 cared for per season (Fig. 7b; GLM: $F_{2,91} = 7.889$, adjusted $R^2 = 0.13$). Also the number of young that
528 successfully left the nest differed. Individual female black coucals produced more young that left the
529 nest than individual male black coucals or individual pairs of white-browed coucals (Fig. 7c; GLM:
530 $F_{2,90} = 2.538$, adjusted $R^2 = 0.03$). There was no relationship between female body size and number of
531 nestlings or young that successfully left the nest. For female black coucals all these results represent
532 conservative estimates, because we were less likely to detect all nests of each individual female black
533 coucal (see explanation for clutch intervals above).

534 The variance in reproductive output and success (number of nest, eggs, nestlings, and young
535 that successfully left the nest) was higher for female black coucals than for male black coucals, as
536 indicated by the confidence intervals that did not overlap with the variance of the other sex (Table 6).

537 In white-browed coucals the variance in reproductive output was similar between females and males
538 (Table 6).

539

540 **Discussion**

541 Our detailed comparison of the two most extreme coucal species with regard to sexual dimorphism
542 and sex roles revealed that classical polyandry in black coucals probably results from a combination of
543 the evolutionary history of coucals facilitating a male role in incubation, and special ecological
544 conditions that favor male-only care and potentially a male bias in the adult sex ratio. Thus, our study
545 provides empirical support for recent theory regarding the reversal of sex roles (Kokko & Jennions,
546 2008).

547

548 *Species differences in mating system, adult sex ratios, sexual dimorphism and morphology*

549 Because the large majority of female black coucals formed a social group with at least two males, the
550 adult sex-ratio of the breeding population seemed to be strongly male-biased. Alternatively, the adult
551 sex ratio may have been less male-biased, but because females fiercely compete for territories high
552 quality females may have excluded less potent competitors. Such competitive exclusion may
553 occasionally happen, but we doubt that it can be a major cause for the male-biased breeding sex ratio:
554 in some years seemingly suitable habitat was not occupied by female black coucals, while all the
555 occupied habitats were filled by polyandrous groups. Given a sufficient pool of females without
556 territories and assuming that males would benefit from pairing with a yet unpaired female, such
557 suitable areas should have been taken by females not yet owning a territory. Thus, we consider it very
558 likely that the adult sex ratio of black coucals was strongly male-biased.

559 In contrast, white-browed coucals invariably formed socially monogamous pairs and the
560 occasional occurrence of solitary males suggests only a slight male-bias in the adult sex ratio, as it is
561 common in most birds (Donald, 2007). Recent theory suggests that a bias in the adult sex ratio should

562 lead to stronger competition for matings in the less common sex and higher parental care in the more
563 common sex (Kokko & Jennions, 2008, 2012, Andersson, 2005, Thomas et al., 2007). Our comparison
564 of black and white-browed coucals supports these predictions. But what may have been the reasons
565 for such a stronger bias in the adult sex ratio in black coucals compared to white browed coucals? The
566 nestling (and fledgling) sex ratios were unbiased, but given that female black coucals leave the nest
567 with only 45 % of their adult body mass, whereas males leave with 66 % of their adult body mass,
568 females may face higher mortality after having left the nest (see Benito and González-Solís (2007) for
569 comparative evidence in other species). Further, female black coucals had a higher wing load than
570 males. Thus, females may be less efficient in escaping aerial predators and the annual migration from
571 and to the breeding grounds may be more risky and energetically costly for them, all of which could
572 potentially result in higher mortality in females than males (see Tarboton (1992) for a similar argument
573 in African jacanas, *Actophilornis africana*, and evidence for high female mortality in American jacanas,
574 *Jacana spinosa*; Jenni and Collier (1972)). We currently study the survival of juveniles after leaving the
575 nest to investigate sex-specific mortality in juvenile coucals.

576 Sexual dimorphism and morphological data confirmed our predictions: female black coucals
577 were almost twice as heavy as males, suggesting that the dimorphism is at least as extreme as that of
578 sex-role reversed jacanas, which were previously considered as the bird taxon with the largest reversed
579 sexual dimorphism (Jenni & Collier, 1972, Butchart, 2000, Emlen & Wrege, 2004). The large cloacal
580 protuberances of male black coucals indicate strong sperm competition (Birkhead et al., 1993),
581 corroborating our earlier study that demonstrated that black coucals experience the highest loss of
582 genetic paternity of all classical polyandrous species investigated so far – with 37% of all nests
583 containing young sired by a different male (Muck et al., 2009). Compared to white-browed coucals
584 female black coucals laid small eggs, offering evidence for Andersson's (2004) proposal that sexual
585 selection in females may favor reduced female gamete size, and for ecological selection that may favor
586 small eggs in classical polyandrous species helping females to maximize the number of clutches they
587 can lay (Slotow, 1996, Liker et al., 2001). Hence, the reversed sexual size dimorphism, small egg

588 volumes, the observation that females routinely form polyandrous groups with at least 2 males, and
589 the higher variance in female reproductive success compared to males indicate that black coucals have
590 evolved strong morphological, physiological and behavioral adaptations for sex-role reversal and
591 polyandry. Thus, the current study substantiates evidence of earlier work (e.g. fierce territory
592 boundary conflicts among females, Goymann et al., 2004, 2008, Geberzahn et al., 2009, 2010) that
593 female black coucals are under stronger sexual selection than males, as expected from theory
594 (Andersson, 1994, Queller, 1997, Kokko & Jennions, 2008).

595 In contrast, male white-browed coucals were only slightly smaller than females, the egg
596 volumes were large compared to those of black coucals, and white-browed coucals invariably formed
597 socially monogamous pairs. Further, according to Birkhead et al. (1993) the smaller size of the cloacal
598 protuberances of male white-browed coucals indicated a low level of sperm competition. While this
599 rather indirect evidence requires confirmation from genetic paternity studies (currently pursued by
600 our lab), it suggests that mating with multiple partners may be more likely in black than in white-
601 browed coucals. The absence of multiple matings by females has been suggested as a potentially
602 important factor favoring male-only care (Kokko & Jennions, 2008, 2012). However, given the high
603 sperm competition and the high loss of genetic paternity in black coucals (Muck et al., 2009), and the
604 likely lower levels of sperm competition in white-browed coucals, we consider it rather unlikely that
605 high mate fidelity led to male-only care in black coucals. In combination with the observation that 7
606 out of 8 investigated bird species with male-only care (reviewed by Muck et al., 2009) have similar or
607 higher rates of paternity loss than bi-parental species, there is currently little evidence that absence of
608 multiple matings by females would have been a critical factor in the evolution of male-only care in
609 classical polyandrous birds.

610 A low wing load and short tails that reduce drag may represent adaptations for migration
611 (Andersson, 1995). Hence, the low wing load and the short tails of black coucals compared to white-
612 browed coucals likely represent an adaptation to their migratory life style, which is unique among
613 coucals. Wing load is particularly low and tails are particularly short in male black coucals, and both of

614 these factors may improve the foraging energetics in this species, in which only males frequently fly
615 back and forth between the nest and foraging patches to feed the young (Goymann et al., 2004).

616 Black coucals use the elongated claw of their 4th toe to grasp onto bundles of grasses enabling
617 them to perch high in dense grassland, even when there are no shrubs in the area. In contrast, white-
618 browed coucals with their substantially shorter claws are less able to do so and prefer to perch on
619 thorny shrubs, bushes, or reed grasses with thicker stems. Thus, black coucals may be better suited to
620 inhabit shrub-less grasslands. In line with this conjecture, white-browed coucals typically occur only in
621 areas with at least some thorny shrubs, reeds or bushes for perching. However, given that both species
622 mainly feed on the ground and efficiently move through heavily entangled grasses, we currently do
623 not have any indication that white-browed coucals would be less efficient in exploiting the abundant
624 food resources during breeding compared to black coucals.

625

626 *Species densities and, territory sizes*

627 Breeding density was higher in black coucals than white-browed coucals supporting the predictions of
628 Goymann et al. (2004) that high nesting densities facilitate monopolization and control of several
629 males by one female territory owner. The Usangu basin is a highly seasonal habitat with lush vegetation
630 only during the rainy season between December and May, which is also when most bird species breed.
631 Outside the rainy season the area is dry and desert-like and offers only limited food. With some
632 exceptions black coucals are absent between June and December (W. Goymann and M. Makomba,
633 pers. obs.). They arrive in large numbers, when food abundance increases and leave once resources
634 start to decline. Because of this migration their nesting density only depends on the food supply of the
635 breeding habitat during the lush season. In contrast, the carrying capacity of the same habitat for
636 white-browed coucals is likely to be limited by the harsher conditions during the dry season.
637 Furthermore, white-browed coucals rarely exploit areas without any acacias or thorny bushes that

638 they use for perching and nesting, thus limiting their choice of suitable territories compared to black
639 coucals.

640 As predicted, the sizes of territories from female black coucals were larger than those of
641 conspecific males and those of white-browed coucals, reflecting the need of female black coucals to
642 defend areas large enough to host several males. Unlike expected, though, the territories of white-
643 browed coucals were slightly larger than those of male black coucals. Potentially, this may be related
644 to the overall lower breeding density of white-browed coucals, relieving them from the pressure to
645 confine themselves to a more restricted area. This may be particularly so, because there was no
646 indication that territories of black coucals would be richer in food supply than those of white-browed
647 coucals.

648

649 *Length of the breeding season, nesting behavior, clutch size, nestling number and sex ratios*

650 Both species of coucals breed during the rainy season, but as predicted white-browed coucals regularly
651 started to breed earlier, thus experiencing a longer breeding season than black coucals. Being year-
652 round residents, white-browed coucals occurred at lower densities, but unlike black coucals they do
653 not have to establish new breeding territories or find new mates prior to each breeding season.
654 Territory establishment and obtaining new mates in black coucals can take several weeks, resulting in
655 a delayed onset of breeding compared to white-browed coucals.

656 To ours surprise, clutch size, incubation and nestling periods were similar in both species. So
657 was the number of nestlings and fledged young per successful nest. Thus, despite the fact that in black
658 coucals only one parent is responsible for incubation and parental care, clutch size was not reduced in
659 black coucals compared to white-browed coucals, suggesting that limited clutch size and incubation
660 capacity was probably not a causal part in the evolution of classical polyandry in coucals (unlike the
661 situation in *Charadriiformes*, see e.g. discussion by Erckmann (1983)).

662 The higher rate of nest failure in black compared to white-browed coucals supports earlier
663 suggestions that frequent nest failure facilitates female emancipation from parental care (Jenni, 1974,
664 Butchart, 2000, Goymann et al., 2004). The preferred use of thorny shrubs as nesting sites by white-
665 browed coucals was probably the main reason for the differences in nest predation rates between the
666 two species. Both coucal species are not capable of actively defending their nests against the most
667 frequent nest predators (snakes, monitor lizards, cats, mongooses and raptors). But the thorns of
668 acacias or other shrubs may more effectively limit predation attempts on nests of white-browed
669 coucals. In contrast, the grass nests of black coucals provide little protection and rely on camouflage
670 only. But because their nests can be placed anywhere black coucals may benefit from a larger selection
671 of potential nesting sites.

672 As expected from mating systems theory (e.g. Emlen & Oring, 1977, Shuster & Wade, 2003)
673 the reproductive potential was highest in female black coucals: due to polyandry and male-only care,
674 individual female black coucals on average produced more offspring than individual males could care
675 for. Female black coucals were limited in their reproductive rate mainly by the availability of mates.
676 This was demonstrated by the fact that the inter-clutch interval of female black coucals was shorter
677 than the inter-clutch interval of males and that of pairs of white-browed coucals, but increased with
678 the nesting success of their partners. If a partner of a female black coucal lost his nest, a female could
679 provide him with a new clutch within a few days.

680 Also the variance in reproductive output was higher for female black coucals than for males,
681 supporting the morphological evidence that females are under stronger sexual selection than males.
682 In contrast, the variance in reproductive output was similar in both sexes of white-browed coucals.
683 According to theory (e.g. Queller, 1997, Kokko & Jennions, 2008, 2012) the sex with the greater
684 variance in mating success pays a greater cost if increasing parental care and should rather invest in
685 further matings. Typically, variance in mating success is higher in males, but here we provided evidence
686 that this is reversed in black coucals. Accordingly, female black coucals invest into mating rather than

687 parenting. This nicely illustrates that exceptional mating systems, such as the one realized by black
688 coucals, help to test the rule.

689

690 *Superabundant food resources as a factor for female emancipation and male-only care*

691 Our data partially support Andersson (1995, 2005) who suggested that male contribution to incubation
692 and superabundant food resources that allow a single parent to successfully raise a brood were
693 necessary preconditions for the evolution of classical polyandry in black coucals. Similar preconditions
694 are met in other bird species with a classical polyandrous mating system (e.g. Maxson and Oring (1980),
695 i.e. classical polyandry is always associated with large food supplies allowing one parent to raise the
696 offspring and the idea that limited food supply would favor such a mating system (Graul et al., 1977)
697 has been refuted previously (see e.g. Erckmann, 1983). However, white-browed coucals live in the
698 same habitat, feed on the same prey, and have similar clutch sizes, but they are obligatory socially
699 monogamous. Hence, superabundant food resources alone are unlikely to be a key-trigger for classical
700 polyandry in black coucals.

701

702 **Factors relevant for the evolution of sex-role reversal and classical polyandry in coucals and** 703 **terrestrial vertebrates**

704 The results of this study offer partial empirical support and extend the framework for the evolution of
705 classical polyandry in black coucals offered by Andersson (1995) and recent theoretical considerations
706 by Kokko and Jennions (2008). Classical polyandry in black coucals probably results from a combination
707 of the evolutionary history of coucals, a taxon in which males have been typically involved in
708 incubation, and special ecological conditions that favor competition between females and male-only
709 care (summarized in Fig. 8). The black coucal seems to be the only coucal that migrates, thus enabling
710 it to invade areas with temporarily high food resources and breed at high densities. High breeding
711 densities may enable one partner to monopolize several mates more easily. Because high nest

712 predation may select for females that can rapidly produce replacement clutches and for males that
713 fully take over incubation, females may find themselves in a better position to monopolize several
714 males rather than vice versa. If the clutch incubated by the first male is successful, the female is free
715 to search for additional mates. In such situations females that are larger than males may have an
716 advantage, because they can lay more eggs than females that are similar in size than males. Further,
717 large females may be better at competing with other females. But the advantage of large body size
718 may come at a cost in form of higher female mortality after leaving the nest because females leave the
719 nest at a much lower body mass relative to their adult size than males. Also, during migration their
720 larger size in combination with a higher wing load may be more energetically costly and more risky
721 because of a potentially lower maneuverability. This could easily lead to a strong male-biased adult
722 sex ratio enforcing mate competition in females and male-only care (Fig. 8). These selective forces
723 towards male incubation and large female body size may eventually have led to the complete and
724 invariable sex-role reversal that has been confirmed in all black coucal populations observed so far
725 (Vernon, 1971, Goymann et al., 2004, Christian & Davies, 2008). The morphological, physiological and
726 behavioral adaptations for female competition and male-only care (Frey & Goymann, 2009, Geberzahn
727 et al., 2009, Geberzahn et al., 2010, Goymann et al., 2005, 2008, Goymann & Wingfield, 2004) are
728 lacking in white-browed coucals and other socially monogamous coucal species. Possibly, the risk of
729 nest predation could be used to predict more subtle differences in sex-roles in competition and
730 parental care in other coucal species (e.g. Maurer, 2008, Maurer et al., 2008, 2011), of which white-
731 browed and black coucals represent the two extremes. Such comparative investigations would help to
732 further elucidate potential evolutionary pathways from social monogamy to classical polyandry.
733 Unfortunately, little is known yet about the breeding biology and nesting success of most other coucal
734 species, so that a comparative analysis is currently not possible.

735 In his comparative study on the evolution of classical polyandry in shorebirds Erckmann (1983)
736 concluded that “a high rate of nesting failure (...) increases the availability of males for emancipated
737 females, and can favor the evolution of polyandry” (p. 163). Similarly, Maxson and Oring (1980)

738 suggested that classical polyandry in spotted sandpipers is a result of “high food availability and
739 relatively high nest loss” (p. 258). For classical polyandrous jacanas, similar suggestions have been put
740 forward (Jenni, 1974, Osborne, 1982, Tarboton, 1992, Tarboton, 1995) and a recent study in
741 polyandrous frogs also suggests that high nest loss favors polyandry (Byrne & Keogh, 2009). Thus, there
742 seems to be a common theme in that high food availability and high nest loss are ecological conditions
743 that facilitate the evolution of sex-role reversal and polyandry, at least in terrestrial vertebrates (see
744 also green areas in Fig. 8). If these ecological conditions are encountered by a species in which males
745 already contribute to incubation and in which the adult sex ratio may already be slightly male-biased,
746 a classical polyandrous mating system could easily evolve (see also Andersson's (2005) conceptual
747 model for similar conclusions). The mating system could become fixed if selection on larger female
748 than male body size (for efficient egg-laying and competition with other females) also increases female
749 mortality, thus enhancing the male bias in the adult sex ratio. Of course, not all taxa that fulfill these
750 conditions have evolved sex-role reversal and polyandry. Evolutionary processes are complex and
751 probabilistic, rather than simple and deterministic, and as a consequence there is more than one path
752 in the adaptive landscape that organisms can “choose” to take. This complexity limits our ability to
753 exactly predict evolutionary processes (requested by some researchers, e.g. by Murray, 2001) as
754 opposed to the many laws in physics and chemistry that allow exact inference.

755 In summary, this comparison of two extreme coucal species has highlighted ecological and
756 morphological differences likely to be important in maintaining their current differences in sex roles.
757 Ours and other results suggest that sex-role reversal in terrestrial vertebrates occurs mainly in taxa
758 that combine a phylogenetic background of male contributions to parental care with ecological
759 conditions of abundant food and high nest loss.

760

761 **Acknowledgements**

762 We thank Christina Muck, Beate Apfelbeck, Emmanuel Ayoub, Raimund Barth, Makubi R. Joseph, Poyo
763 Makomba, Monika Trappschuh, and Andrea Wittenzellner for assistance in the field, and Liz and Neil
764 Baker and Susanna Joos for logistical support. Anja Lohrentz assisted with genetic sexing and Mihai
765 Valcu gave helpful advice with regard to calculating and mapping territories. Malte Andersson,
766 Michaela Hau, Willi Jensen, Ignas Safari Mng'anya, Hubert Schwabl, Wolfgang Wickler, and two
767 anonymous referees commented and helped to improve previous versions of the manuscript. We
768 thank the Tanzania Wildlife Research Institute (TAWIRI), the Tanzanian Commission for Science and
769 Technology (COSTECH) for permissions to work in Tanzania, and the Kapunga Rice Irrigation Project for
770 support and allowing us to work on their property. This project was funded by DFG grant Go985/2 to
771 WG, who received further support from Manfred Gahr and the Max-Planck-Gesellschaft. The authors
772 declare that they do not have a conflict of interest.

773 **References**

- 774 Andersson, M. 1994. *Sexual selection*, 1st ed. Princeton University Press, Princeton.
- 775 Andersson, M. 1995. Evolution of reversed sex roles, sexual size dimorphism, and mating system in
776 coucals (Centropodidae, Aves). *Biol. J. Linn. Soc.* **54**: 173-181.
- 777 Andersson, M. 2004. Social polyandry, parental investment, sexual selection, and evolution of reduced
778 female gamete size. *Evolution* **58**: 24-34.
- 779 Andersson, M. 2005. Evolution of classical polyandry: Three steps to female emancipation. *Ethology*
780 **111**: 1-23.
- 781 Bååth, R. (2014) Bayesian First Aid: A package that implements Bayesian alternatives to the classical
782 *.test functions in R. In: *Proceedings of UseR! 2014 - the International R User Conference*.
- 783 Baker, N. & Baker, E. 2003. *Important bird areas in Tanzania. A first inventory*. Wildlife Conservation
784 Society of Tanzania, Dar es Salaam.
- 785 Bates, D., Mächler, M., Bolker, B. & Walker, S. (2014) Fitting linear mixed-effects models using lme4.
786 pp. Cornell University Library, arXiv:1406.5823.
- 787 Benito, M. M. & González-Solís, J. 2007. Sex ratio, sex-specific chick mortality and sexual size
788 dimorphism in birds. *J. Evol. Biol.* **20**: 1522-1530.
- 789 Berglund, A. 2013. Why are sexually selected weapons almost absent in females? *Curr. Zool.* **59**: 564-
790 568.
- 791 Berglund, A., Bisaza, A. & Pilastro, A. 1996. Armaments and ornaments: an evolutionary explanation of
792 traits of dual utility. *Biol. J. Linn. Soc.* **58**: 385-399.
- 793 Birkhead, T. R., Briskie, J. V. & Møller, A. P. 1993. Male sperm reserves and copulation frequency in
794 birds. *Behav. Ecol. Sociobiol.* **32**: 85-93.
- 795 Bivand, R. S., Pebesma, E. & Gómez-Rubio, V. (2013) *Applied Spatial Data Analysis with R*. Springer,
796 New York, Heidelberg.
- 797 Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. & White, J.-S. S.
798 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends*
799 *Ecol. Evol.* **24**: 127-135.
- 800 Butchart, S. H. M. 2000. Population structure and breeding system of the sex-role reversed,
801 polyandrous bronze winged jacana, *Metopidius indicus*. *Ibis* **142**: 93-102.
- 802 Byrne, P. G. & Keogh, J. S. 2009. Extreme sequential polyandry insures against nest failure in a frog.
803 *Proc. Royal Soc. B* **276**: 115-120.
- 804 Calenge, C. 2006. The package "adehabitat" for the R software: A tool for the analysis of space and
805 habitat use by animals. *Ecol. Modell.* **197**: 516-519.
- 806 Christian, M. B. & Davies, G. B. P. 2008. African black coucal nests in KwaZulu-Natal. *Bird Numbers* **14**:
807 13-17.
- 808 Clutton-Brock, T. 2009. Sexual selection in females. *Anim. Behav.* **77**: 3-11.
- 809 Clutton-Brock, T. H. 1991. *The evolution of parental care*. Princeton University Press, Princeton.
- 810 Clutton-Brock, T. H. & Vincent, A. C. J. 1991. Sexual selection and the potential reproductive rates of
811 males and females. *Nature* **351**: 58-60.
- 812 Cockburn, A. 2006. Prevalence of different modes of parental care in birds. *Proc. Royal Soc. B* **273**:
813 1375-1383.

- 814 Cooper, W. E., Jr. 1999. Supplementation of phylogenetically correct data by two-species
815 comparison: support for correlated evolution of foraging mode and prey chemical
816 discrimination in lizards extended by first intrageneric evidence. *Oikos* **87**: 97-104.
- 817 Darwin, C. 1871. *The descent of man, and selection in relation to sex*. W. W. Norton & Company, New
818 York.
- 819 del Hoyo, J., Elliot, A. & Sargatal, J. 1997. *Handbook of the birds of the world. Volume 4. Sandgrouse to*
820 *cuckoos*. Lynx Editions, Barcelona.
- 821 Donald, P. F. 2007. Adult sex ratios in wild bird populations. *Ibis* **149**: 671-692.
- 822 Emlen, S. T. & Oring, L. W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*
823 **197**: 215-223.
- 824 Emlen, S. T. & Wrege, P. H. 2004. Size dimorphism, intrasexual competition, and sexual selection in
825 wattled jacana (*Jacana jacana*), a sex-role reversed shorebird in Panama. *Auk* **121**: 391-403.
- 826 Erckmann, W. J. (1983) The evolution of polyandry in shorebirds: an evaluation of hypotheses. In: *Social*
827 *behavior of female vertebrates*, (Wasser, S. K., ed.). pp. 113-168. Academic Press, New York.
- 828 Eritzoe, J., Mann, C. F., Brammer, F. P. & Fuller, R. A. 2012. *Cuckoos of the World*. Christopher Helm,
829 London.
- 830 Frey, R. & Goymann, W. 2009. A single functional testis and long deferent duct papillae: the peculiar
831 male reproductive tract of the classically polyandrous, sex-role reversed Black Coucal
832 (*Centropus grillii*). *J. Ornithol.* **150**: 827-838.
- 833 Fridolfsson, A. K. & Ellegren, H. 1999. A simple and universal method for molecular sexing of non-ratite
834 birds. *J. Avian Biol.* **30**: 116-121.
- 835 Garland, T. & Adolph, S. C. 1994. Why not to do two-species comparative studies: limitations on
836 inferring adaptation. *Physiol. Zool.* **67**: 797-828.
- 837 Geberzahn, N., Goymann, W., Muck, C. & ten Cate, C. 2009. Females alter their song when challenged
838 in a sex-role reversed bird species. *Behav. Ecol. Sociobiol.* **64**: 193-204.
- 839 Geberzahn, N., Goymann, W. & ten Cate, C. 2010. Threat signaling in female song—evidence from
840 playbacks in a sex-role reversed bird species. *Behav. Ecol.* **21**: 1147-1155.
- 841 Gelman, A., Su, Y.-S., Yajima, M., Hill, J., Pittau, M. G., Kerman, J., Zheng, T. & Dorie, V. (2014) Data
842 analysis using regression and multilevel/hierarchical models. Vol. Version 1.7-07. pp. CRAN,
843 CRAN R repository.
- 844 Goymann, W. & Helm, B. (2015) Seasonality of life histories in tropical birds: Circannual rhythms and
845 *Zeitgeber*. In: *Annual, lunar, and tidal clocks. Patterns and mechanisms of nature's enigmatic*
846 *rhythms*, (Numata, H. & Helm, B., eds.). pp. 247-275. Springer, Tokyo.
- 847 Goymann, W., Kempnaers, B. & Wingfield, J. 2005. Breeding biology, sexually dimorphic development
848 and nestling testosterone concentrations of the classically polyandrous African black coucal,
849 *Centropus grillii*. *J. Ornithol.* **146**: 314-324.
- 850 Goymann, W. & Wingfield, J. C. 2004. Competing females and caring males. Sex steroids in African
851 black coucals, *Centropus grillii*. *Anim. Behav.* **68**: 733-740.
- 852 Goymann, W., Wittenzellner, A., Schwabl, I. & Makomba, M. 2008. Progesterone modulates aggression
853 in sex-role reversed African black coucals. *Proc. Royal Soc. B* **275**: 1053-1060.
- 854 Goymann, W., Wittenzellner, A. & Wingfield, J. C. 2004. Competing females and caring males.
855 Polyandry and sex-role reversal in African black coucals, *Centropus grillii*. *Ethology* **110**: 807-
856 823.

- 857 Graul, W. D., Derrickson, S. R. & Mock, D. W. 1977. The evolution of avian polyandry. *Am. Nat.* **111**:
858 812-816.
- 859 Hoyt, D. F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. *Auk* **96**: 73-77.
- 860 Irwin, M. P. S. 1985. Interrelationships among african species of *Centropus* (Cuculidae). *Ostrich* **56**: 132-
861 134.
- 862 Jenni, D. 1974. The evolution of polyandry in birds. *Am. Zool.* **14**: 129-140.
- 863 Jenni, D. A. & Collier, G. 1972. Polyandry in the American Jacana (*Jacana spinosa*). *Auk* **89**: 743-765.
- 864 Jennions, M. D. & Kokko, H. (2010) Sexual selection. In: *Evolutionary behavioral ecology*, (Westneat, D.
865 F. & Fox, C. W., eds.). pp. 343-364. Oxford University Press, Oxford, New York.
- 866 Kokko, H. & Jennions, M. (2012) Sex differences in parental care. In: *The evolution of parental care*,
867 (Royle, N. J., Smiseth, P. T. & Kölliker, M., eds.). pp. 101-116. Oxford University Press, Oxford.
- 868 Kokko, H. & Jennions, M. D. 2008. Parental investment, sexual selection and sex ratios. *J. Evol. Biol.* **21**:
869 919-948.
- 870 Kraaijeveld, K., Kraaijeveld-Smit, F. J. L. & Komdeur, J. 2007. The evolution of mutual ornamentation.
871 *Anim. Behav.* **74**: 657-677.
- 872 Kruschke, J. R. 2013. Bayesian estimation supersedes the t test. *J. Exp. Psychol.* **142**: 573-603.
- 873 Kvarnemo, C. (2010) Parental care. In: *Evolutionary behavioral ecology*, (Westneat, D. F. & Fox, C. W.,
874 eds.). pp. 451-467. Oxford University Press, Oxford, New York.
- 875 Ligon, J. D. 1993. The role of phylogenetic history in the evolution of contemporary avian mating and
876 parental care systems. *Curr. Ornithol.* **10**: 1-46.
- 877 Ligon, J. D. 1999. *The evolution of avian breeding systems*. Oxford University Press, Oxford.
- 878 Liker, A., Reynolds, J. D. & Székely, T. 2001. The evolution of egg size in socially polyandrous shorebirds.
879 *Oikos* **95**: 3-14.
- 880 Maurer, G. 2008. Who cares? Males provide most parental care in a monogamous nesting cuckoo.
881 *Ethology* **114**: 540-547.
- 882 Maurer, G., Double, M. C., Milenkaya, O., Susser, M. & Magrath, R. D. 2011. Breaking the rules: sex
883 roles and genetic mating system of the pheasant coucal. *Oecologia* **167**: 413-425.
- 884 Maurer, G., Smith, C., Süsser, M. & Magrath, R. D. 2008. Solo and duet calling in the pheasant coucal:
885 sex and individual call differences in a nesting cuckoo with reversed size dimorphism. *Austral.*
886 *J. Zool.* **56**: 143-149.
- 887 Maxson, S. J. & Oring, L. W. 1980. Breeding season time and energy budgets of the polyandrous spotted
888 sandpiper. *Behaviour* **74**: 200-263.
- 889 Muck, C., Kempnaers, B., Kuhn, S., Valcu, M. & Goymann, W. 2009. Paternity in the classical
890 polyandrous black coucal (*Centropus grillii*)--a cuckoo accepting cuckoldry? *Behav. Ecol.* **20**:
891 1185-1193.
- 892 Murray, B. G. 2001. Are ecological and evolutionary theories scientific? *Biol. Rev.* **76**: 255-289.
- 893 Nakagawa, S. & Schielzeth, H. 2013. A general and simple method for obtaining R² from generalized
894 linear mixed-effects models. *Meth. Ecol. Evol.* **4**: 133-142.
- 895 Olsen, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C.,
896 D'Amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H.,
897 Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P. & Kassem, K. R. 2001. Terrestrial
898 ecoregions of the world: A new map of life on earth. *BioScience* **51**: 933-938.

- 899 Osborne, D. R. 1982. Replacement nesting and polyandry in the wattled jacana, *Jacana jacana*. *Wilson*
900 *Bull.* **94**: 206-208.
- 901 Owens, I. P. F. 2002. Male-only care and classical polyandry in birds: phylogeny, ecology and sex
902 differences in remating opportunities. *Phil. Trans. Royal Soc. B* **357**: 283-293.
- 903 Queller, D. C. 1997. Why do females care more than males? *Proc. Royal Soc. B* **264**: 1555-1557.
- 904 Rappole, J. H. & Tipton, A. R. 1991. New harness design for attachment of radio transmitters to small
905 passerines. *J. Field Ornithol.* **62**: 335-337.
- 906 Reynolds, J. & Szekely, T. 1997. The evolution of parental care in shorebirds: life histories, ecology, and
907 sexual selection. *Behav. Ecol.* **8**: 126-134.
- 908 Reynolds, J. D., Goodwin, N. B. & Freckleton, R. B. 2002. Evolutionary transitions in parental care and
909 live bearing in vertebrates. *Phil. Trans. Royal Soc. B* **357**: 269-281.
- 910 Ridley, M. 1978. Paternal care. *Anim. Behav.* **26**: 904-932.
- 911 Rowan, M. K. 1983. *The doves, parrots, louries and cuckoos of southern Africa*. David Philip Publisher,
912 Cape Town.
- 913 Schwagmeyer, P. L., Clair, R. C. S., Moodie, J. D., Lamey, T. C., Schnell, G. D. & Moodie, M. N. 1999.
914 Species differences in male parental care in birds: A reexamination of correlates with paternity.
915 *Auk* **116**: 487-503.
- 916 Shuster, S. M. & Wade, M. J. 2003. *Mating systems and strategies*. Princeton University Press,
917 Princeton.
- 918 Slotow, R. 1996. Black coucal *Centropus grillii* egg volume predicts their polyandrous mating system. *J.*
919 *Avian Biol.* **27**: 171-173.
- 920 Sokal, R. R. & Rohlf, F. J. 1995. *Biometry*, 3 ed. W.H. Freeman and Company, New York.
- 921 Sorenson, M. D. & Payne, R. B. (2005) A molecular genetic analysis of cuckoo phylogeny. In: *The*
922 *cuckoos*, (Payne, R. B., ed.). pp. 68-94. Oxford University Press, Oxford.
- 923 Tallamy, D. W. 2000. Sexual selection and the evolution of exclusive paternal care in arthropods. *Anim.*
924 *Behav.* **60**: 559-567.
- 925 Tarboton, W. R. 1992. Aspects of the breeding biology of the African jacana. *Ostrich* **63**: 141-157.
- 926 Tarboton, W. R. 1995. Polyandry in the African Jacana: The roles of male dominance and rate of clutch
927 loss. *Ostrich* **66**: 49-60.
- 928 Thioulouse, J., Chessel, D., Dolédec, S. & Olivier, J. M. A.-a. m. a. a. g. d. s. 1997. ADE-4: a multivariate
929 analysis and graphical display software. *Statistics and Computing* **7**: 75-83.
- 930 Thomas, G. H., Szekely, T. & Reynolds, J. D. (2007) Sexual conflict and the evolution of breeding systems
931 in shorebirds. In: *Adv. Study Behav.* **37**: 279-342.
- 932 Trumbo, S. T. (2012) Patterns of parental care in invertebrates. In: *The evolution of parental care*,
933 (Royle, N. J., Smiseth, P. T. & Kölliker, M., eds.). pp. 81-100. Oxford University Press, Oxford.
- 934 van Someren, V. G. L. 1956. Days with birds. *Fieldiana Zoology* **38**: 1-520.
- 935 Vernon, C. J. 1971. Notes on the biology of the black coucal. *Ostrich* **42**: 242-258.
- 936 Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies.
937 *Ecology* **70**: 164-168.
- 938 **Tables**

939 Table 1. Predicted differences between classically polyandrous black coucals (BC) and socially
 940 monogamous white-browed coucals (WBC; see text for details).

Category	Trait	Prediction
morphology	sexual dimorphism	BC > WBC
	wing load, tail length	BC < WBC
	cloacal protuberance (sperm comp.)	BC > WBC
	egg size	BC < WBC
population parameters	species density	BC > WBC (Goymann et al. 2005) BC < WBC (Owens, 2002)
	territory size	♀BC > ♂BC & WBC
	adult sex ratio	♂-bias in BC, unbiased in WBC
breeding biology	length of breeding season	BC < WBC
	clutch size, nestling number	BC < WBC
	nestling sex-ratio	♂-bias in BC, unbiased in WBC
reproductive success	nest predation	BC > WBC
	reproductive rate	♀BC > ♂BC & WBC
	reproductive success	♀BC > ♂BC & WBC more variable in ♀BC than ♂BC
	superabundant food resources	occasional polyandry in WBC

941

942

943 Table 2. Number of male partners per female black coucal and per female white-browed coucal

number of ♂ partners:	per ♀ black coucal	per ♀ white-browed coucal
0	0	0
1	1	56
2	11	0
at least 2	17	0
3	13	0
4	4	0
5	1	0
total no of ♀♀	47	56

944

945

946 Table 3. Summary of biometric measures of adult coucals (mean \pm 95 % confidence interval, range;
 947 sample size; BC = black coucal, WBC = white-browed coucal).

	Female BC	Male BC	Female WBC	Male WBC
bill (mm)	25.7 \pm 0.5 (21.2-36.0; 139)	23.4 \pm 0.3 (20.2-30.3; 95)	28.9 \pm 0.7 (22.7-32.2; 31)	27.9 \pm 0.4 (24.8-31.2; 51)
body mass (g)	165.9 \pm 2.9 (122-214; 140)	98.0 \pm 1.6 (78-120; 94)	153.8 \pm 4.8 (124-183; 31)	136.1 \pm 3.3 (117-165; 51)
tarsus (mm)	42.4 \pm 0.3 (38.7-46.6; 142)	38.9 \pm 0.3 (34.4-42.8; 96)	42.0 \pm 0.7 (38.4-44.9; 31)	41.1 \pm 0.2 (39.2-43.4; 50)
claw of 4 th toe (mm)	25.7 \pm 0.6 (16-42; 139)	24.0 \pm 0.6 (17-39; 95)	17.5 \pm 0.8 (12-22; 31)	16.8 \pm 0.6 (12-23; 51)
wing (mm)	176.9 \pm 1.0 (160-190; 140)	157.5 \pm 1.3 (140-180; 94)	165.0 \pm 2.2 (151-177; 31)	156.7 \pm 1.5 (144-167; 51)
tail (mm)	177.0 \pm 1.3 (156-199; 131)	159.4 \pm 0.7 (125-180; 90)	213.7 \pm 4.3 (195-242; 31)	201.0 \pm 2.5 (181-220; 51)
cloacal protub. (mm ³)	302.1 \pm 32.3 (139)	879.2 \pm 106.8 (94)	188.8 \pm 41.3 (31)	296.2 \pm 50.5 (51)
wing load (g/cm ²)	0.530 \pm 0.009 (140)	0.397 \pm 0.005 (92)	0.566 \pm 0.019 (31)	0.554 \pm 0.012 (49)

948

949 Table 4. Posterior mean number of eggs per clutch, number of nestlings and fledglings, and periods
 950 (days) of incubation and nestlings (BC = black coucal, WBC = white-browed coucal, CrI= 95% credible
 951 interval, d=days)

Trait	Species (N)	Mean [95% CrI]	Mode (range)	Statistics
number of eggs	BC (189)	4.18 [3.83-4.54]	4 (2-7)	F=0.01; marginal $R^2_{\text{glmm}}=0.01$
	WBC (117)	4.19 [3.84-4.53]	4 (1-6)	conditional $R^2_{\text{glmm}}=0.22$
			Julian date	F=1.20; $\beta=-0.002$ [-0.006- 0.002]
number of nestlings	BC (143)	3.60 [3.18-4.03]	4 (1-6)	F=1.03; marginal $R^2_{\text{glmm}}=0.01$
	WBC (97)	3.43 [3.02-4.86]	4 (1-6)	conditional $R^2_{\text{glmm}}=0.22$
			Julian date	F=0.39; $\beta=-0.002$ [-0.006- 0.004]
number of fledglings	BC (87)	3.33 [2.81-3.87]	4 (1-5)	F=6.04; marginal $R^2_{\text{glmm}}=0.05$,
	WBC (57)	2.83 [2.30-3.36]	4 (1-5)	conditional $R^2_{\text{glmm}}=0.18$
			Julian date	F=0.27; $\beta=0.001$ [-0.008-0.004]
incubation period (d)	BC (8)	15.2 [14.3-16.2]	(13-17)	$F_{1,31}=2.339$; adjusted $R^2=0.04$
	WBC (24)	16.1 [15.5-16.6]	(14-18)	
nestling period (d)	BC ♀ (51)	12.8 [12.2-13.4]	(8-17)	F=15.02; marginal $R^2_{\text{glmm}}=0.13$
	BC ♂ (44)	12.3 [11.7-12.9]	(9-17)	conditional $R^2_{\text{glmm}}=0.56$
	WBC ♀ (51)	13.9 [13.3-14.5]	(10-17)	sex difference: F=0.80
	WBC ♂ (56)	14.0 [13.4-14.6]	(9-17)	

952 Abbreviations: BC = black coucal, WBC = white-browed coucal, CrI= 95% credible interval, d=days

953

955 Table 5. Posterior mean body mass (including 95% credible intervals) in relation to the percentage of
 956 adult body mass when leaving the nest (BC = black coucal, WBC = white-browed coucal, CrI= 95%
 957 credible interval)

Species and sex (N)	posterior mean body mass [95% CrI]	% adult body mass	Statistics
BC ♀ (71)	75.9 [72.9–79.0] g	45.7	species: F=138.25
BC ♂ (68)	65.6 [62.5–68.7] g	66.9	sex: F=33.58
WBC ♀ (66)	94.2 [91.1–97.4] g	61.2	species * sex: F=4.438
WBC ♂ (72)	89.5 [86.4–92.5] g	65.8	marginal $R^2_{\text{glimm}}=0.47$; cond. $R^2_{\text{glimm}}=0.62$

958

959

960 Table 6. Differences in the variance [95% confidence interval] of reproductive success (var = variance,
 961 N = number)

species	sex	var N of nests	var N of eggs	var N of nestlings	var N of fledglings
black coucal	female	4.8 [2.8 – 9.9]	72.0 [41.5 – 147.8]	45.3 [26.1 – 93.1]	23.1 [13.3 – 47.5]
	male	0.8 [0.5 – 1.5]	11.3 [7.6 – 19.8]	8.8 [5.5 – 15.4]	7.2 [4.5 – 12.8]
white-browed	female	1.4 [0.8 – 3.0]	22.7 [13.7 – 52.4]	14.5 [8.4 – 30.9]	14.5 [8.8 – 32.5]
coucal	male	1.3 [0.9 – 2.3]	20.9 [13.9 – 38.2]	13.8 [9.3 – 24.7]	13.3 [8.9 – 23.8]

962

963 **Figure legends**

964 Fig. 1. (a) Body mass, (b) length of the 4th claw, (c) wing load, and (d) tail length of female black coucals
965 (BC fem; N = 131 – 142), male black coucals (BC male; N = 90 – 96), female white-browed coucals
966 (WBC fem; N = 31) and male white-browed coucals (WBC male; N = 50 – 51). Large black and white
967 triangles and error bars indicate posterior mean estimates and their 95 % credible intervals for black
968 and white-browed coucals, respectively. Small open jittered triangles (black coucals pointing upwards,
969 white-browed coucals pointing downwards) indicate values of individual measurements. For exact
970 sample sizes of each variable see Table 3.

971

972 Fig. 2. (a) Volume of the cloacal protuberance of female (N = 139) and male black coucals (N = 94) and
973 female (N = 31) and male white-browed coucals (N = 49). (b) Mean and 95 % credible intervals of
974 protuberance volumes of male black and white-browed coucals during different stages of the breeding
975 cycle (for an explanation of symbols, error bars and abbreviations see Fig. 1).

976

977 Fig. 3. (a) Egg volume of black (N = 339) and white-browed coucals (N = 126; for an explanation of
978 symbols, error bars and abbreviations see Fig. 1). (b) Egg-volume of black (red) and white-browed
979 coucals (blue) in relation to female body mass (species regression lines with shaded areas indicating
980 95 % credible intervals).

981

982 Fig. 4. Territory sizes of female (N = 82) and male (N = 59) black coucals, and female (N = 31) and male
983 (N = 54) white-browed coucals (for an explanation of symbols, error bars and abbreviations see Fig. 1).

984

985 Fig. 5. Lengths of the breeding seasons of coucals in 2011, 2012, 2013 and 2014 in relation to rainfall
986 (dark-grey spikes; there was no rainfall outside the time indicated in the graphs). The grey horizontal

987 bars indicate periods of active nests of white-browed coucals, each line representing one pair. The
988 black horizontal bars indicate periods of active nests of black coucals, each line representing one male,
989 and clumped lines without spaces in between indicating nests of males belonging to one female. The
990 grey shading in the background indicates the period during which researchers were present to check
991 nests.

992

993 Fig. 6. Time interval between subsequent nests (nesting interval) depending on the fate of the previous
994 nest (egg-predation, nestling-predation, successfully fledged) in female (left; N = 29/22/39) and male
995 (center; N = 9/1/19) black coucals and pairs of white-browed coucals (right, N = 8/12/34). The intervals
996 for female black coucals represent a conservative estimate and are likely to be lower in reality (see
997 main text). For an explanation of symbols, error bars and abbreviations see Fig. 1.

998

999 Fig. 7. (a) Number of eggs laid/incubated per season in individual female black coucals (BC female;
1000 N = 24), male black coucals (BC male; N = 36) and pairs of white-browed coucals (WBC pairs; N = 51).
1001 (b) Number of nestlings per season in individual female (N = 24) and male black coucals (N = 36) and
1002 pairs of white-browed coucals (N = 54). (c) Number of fledged young per season in individual female
1003 (N = 24) and male black coucals (N = 35) and pairs of white-browed coucals (N = 54). The values for
1004 female black coucals represent an underestimation (see main text). For an explanation of symbols,
1005 error bars and abbreviations see Fig. 1.

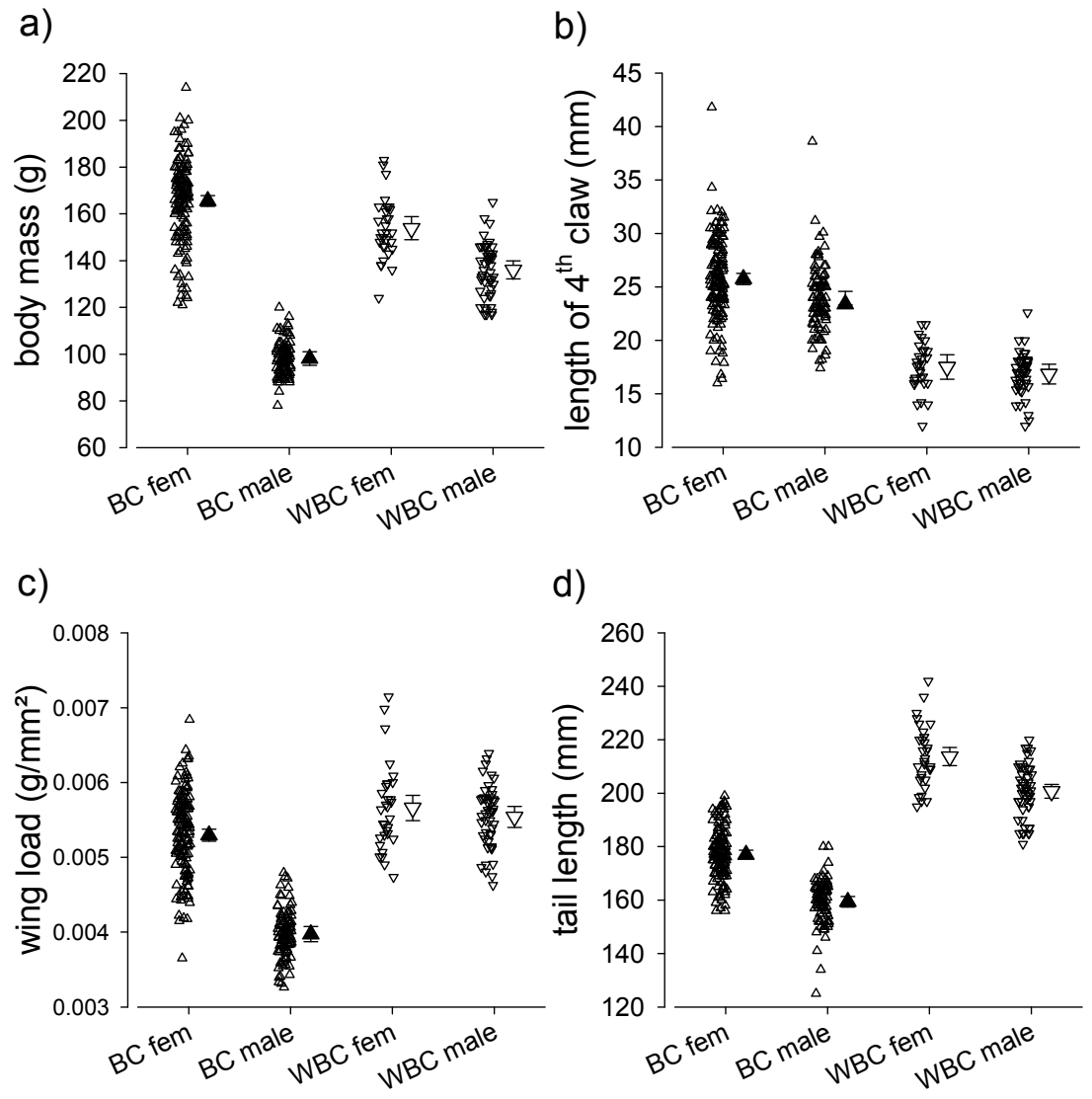
1006

1007 Fig. 8) Specific environmental factors (green) may facilitate the evolution a classical polyandrous
1008 mating system. When food abundance is high (enabling a single parent to raise a clutch) and nest
1009 predation is substantial, selection may favor males (blue) that incubate and females (pink) that gather
1010 resources for quick replacement clutches. If the nest fails both partners benefit from being able to
1011 rapidly replace the lost clutch. This is particularly important, when the breeding season is short. If the

1012 nest is successful, the male can raise the clutch on his own and the female is free to use her resources
1013 and produce a new clutch for a new mate, if such a mate is available. Additional selective forces (in
1014 lilac) may enhance subtle sex differences in behavior, size and mortality, leading to a fixation of sex-
1015 roles. Specifically, large females relative to males may be better in egg-laying and/or defending high
1016 quality territories to attract additional males. Such selection for larger female relative to male body
1017 size could result in higher female mortality in the fledgling phase (lower body mass relative to adult
1018 mass) and during migration (higher wing load) compared to males, resulting in a stronger male-biased
1019 adult sex ratio (ASR). A strongly male biased ASR increases selection on females to enhance mating
1020 effort and on males to invest in parental care. Because small males relative to females may be more
1021 efficient in provisioning offspring (i.e. better maneuverability and energy expenditure due to lower
1022 wing load) there may be selection for smaller body size in males than females. The associated decrease
1023 in wing load may enhance male survival during migration, which could further increase the male-bias
1024 in the adult sex ratio (for details see main text).

1025

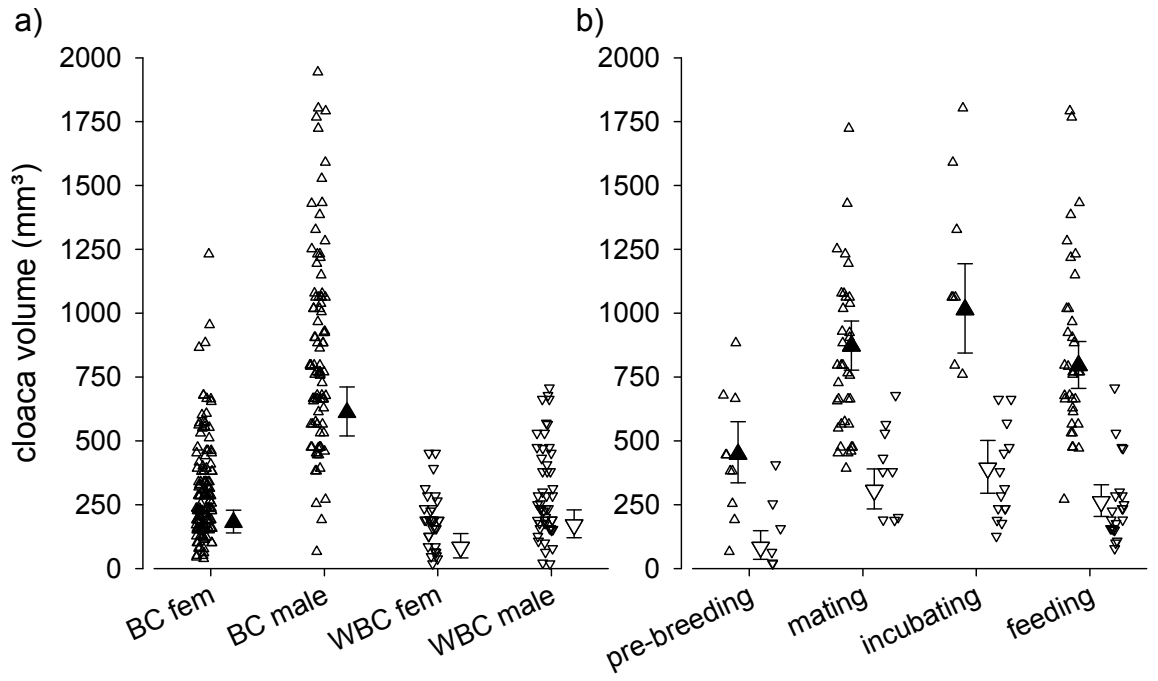
1026



1027

1028 Figure 1

1029

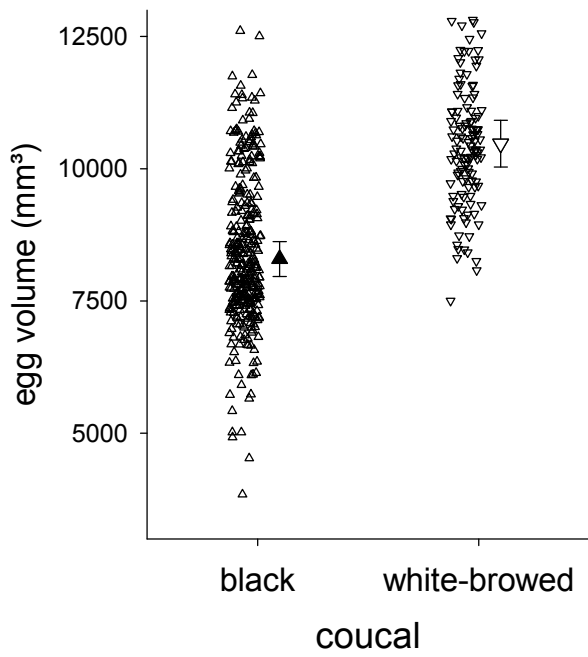
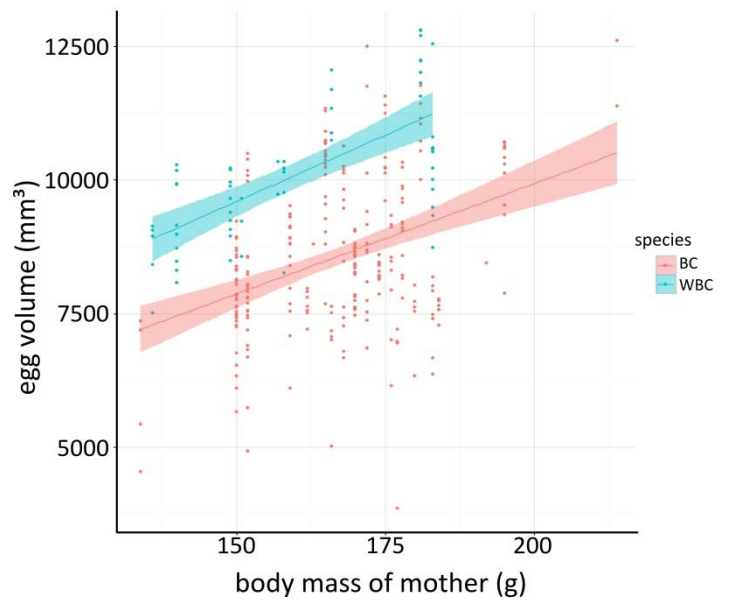


1030

1031 Figure 2

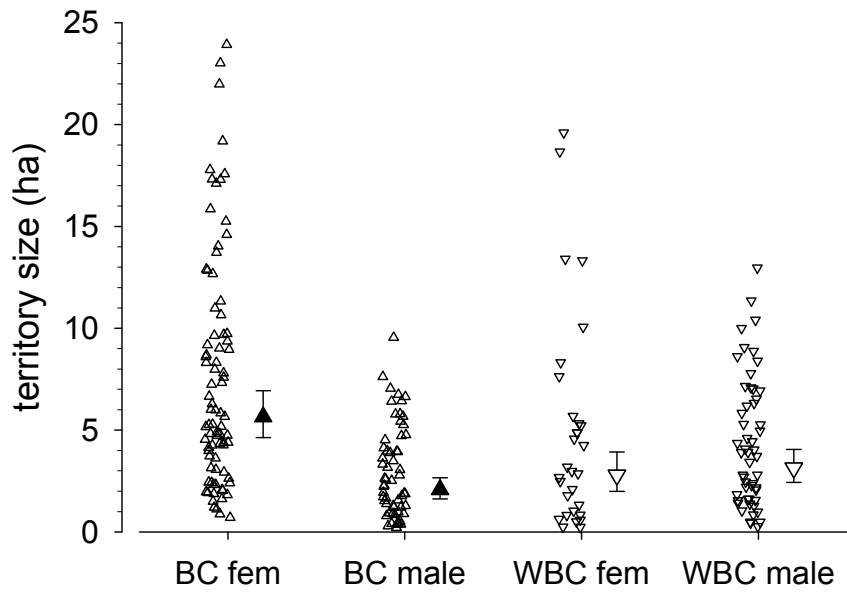
1032

1033



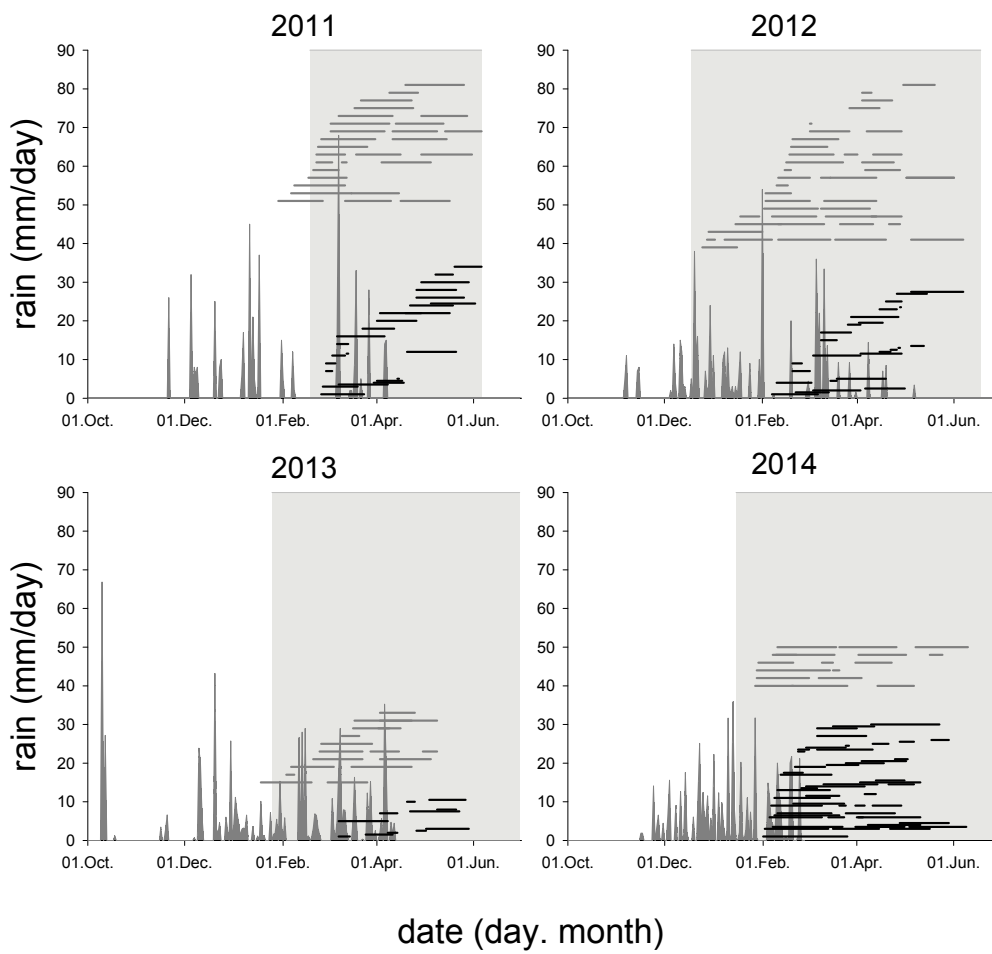
1034

Figure 3



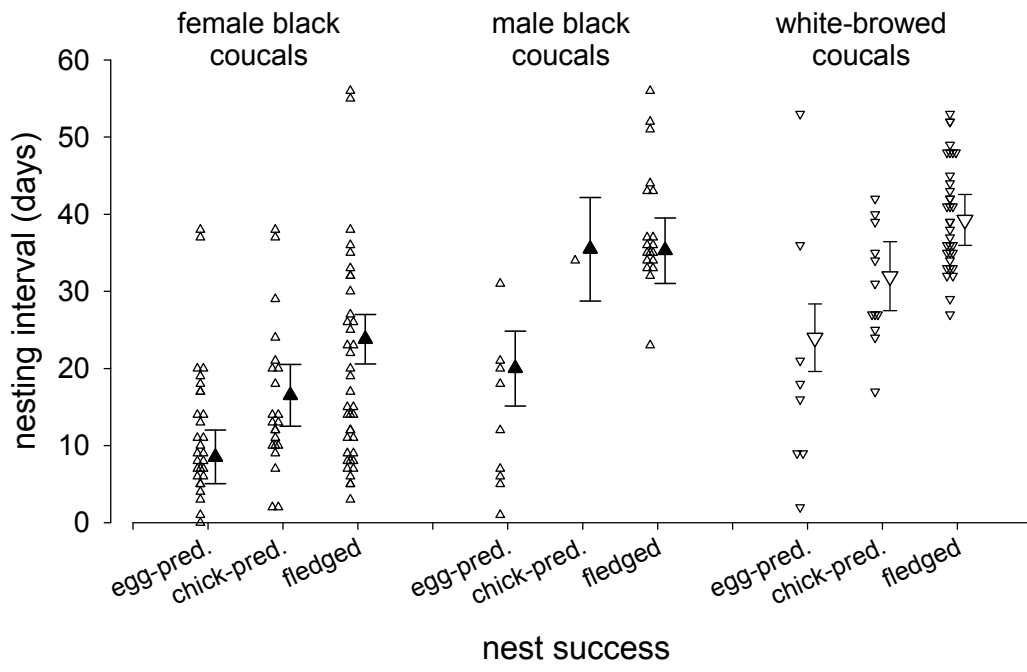
1035

1036 Figure 4



1037

1038 Figure 5

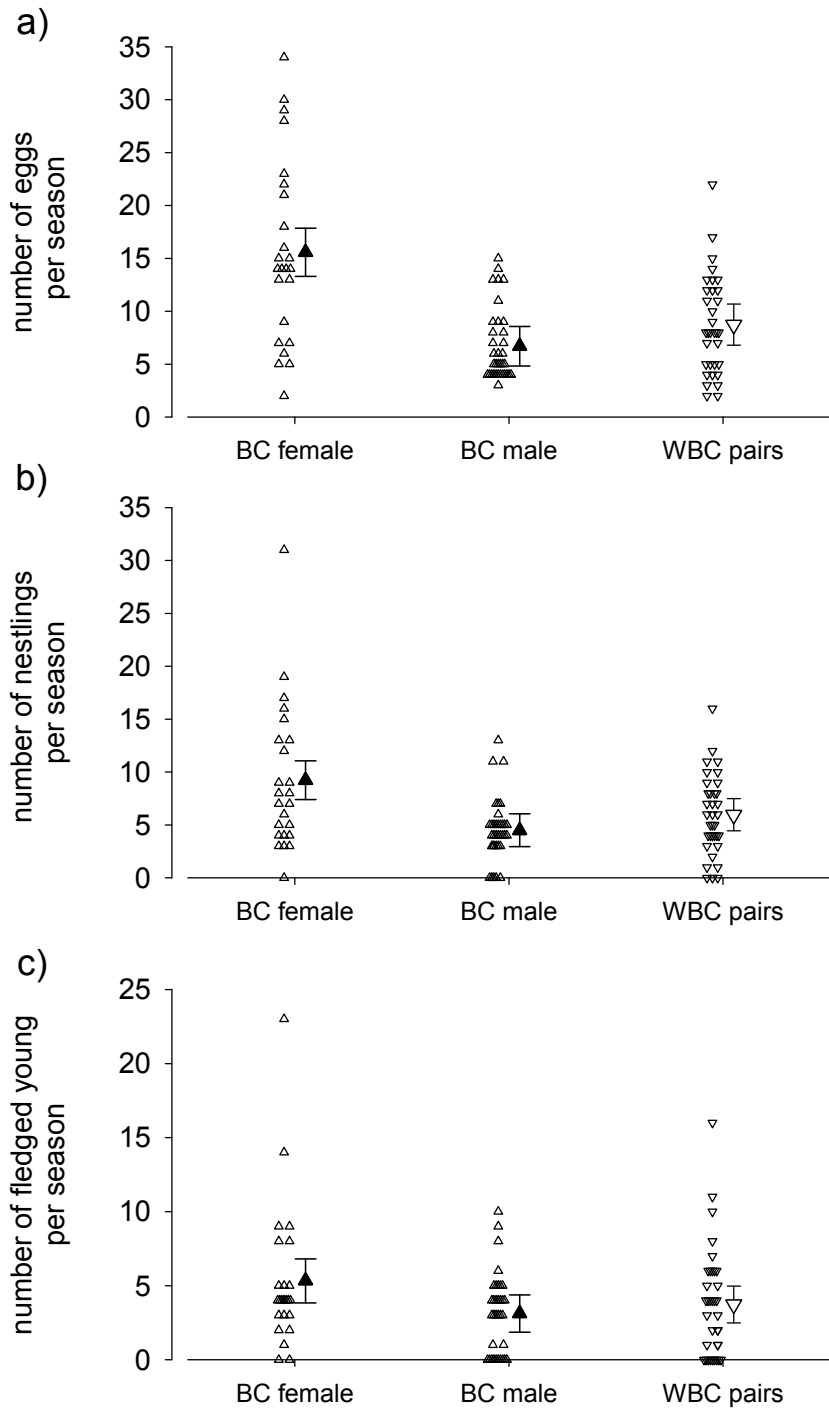


1039

1040 Figure 6

1041

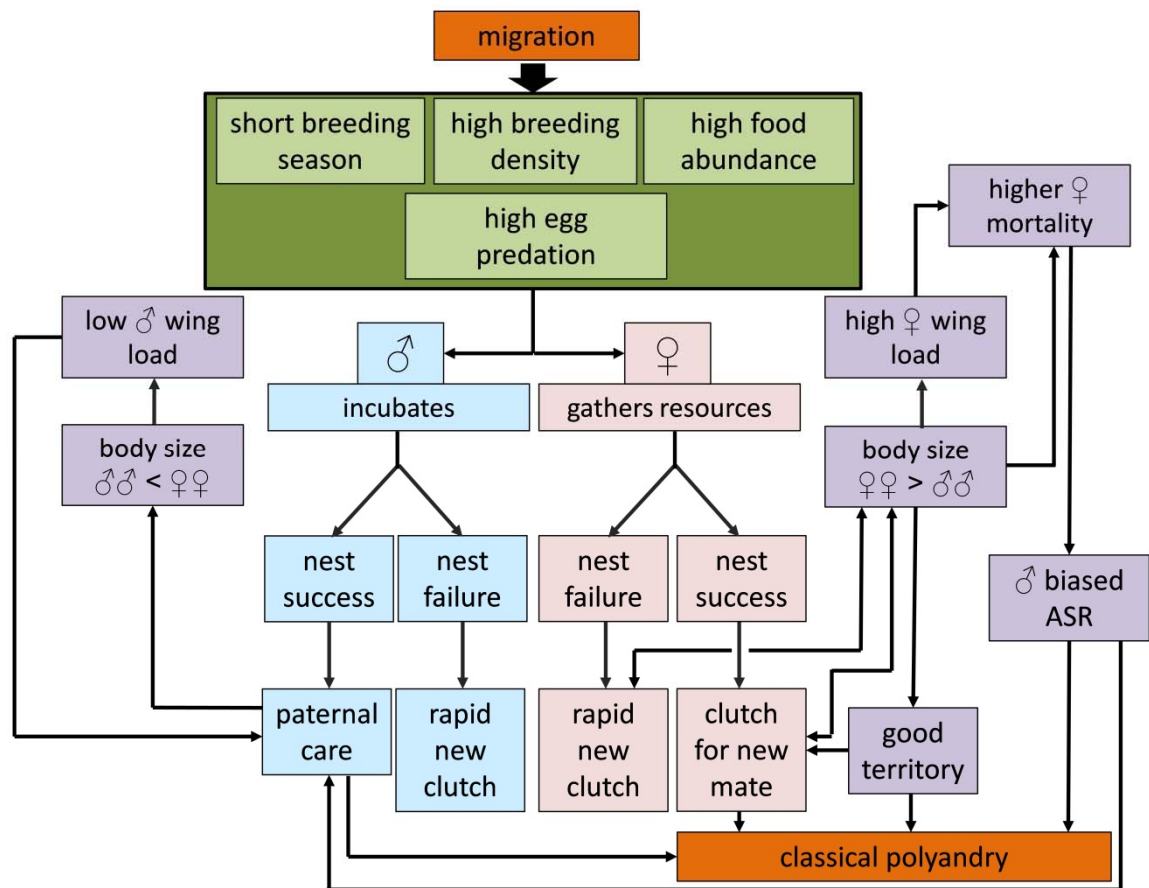
1042



1043

1044 Figure 7

1045



1046

1047 Figure 8

1048