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Author for correspondence:

Wolfgang Goymann

e-mail: goymann@orn.mpg.de

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Male-only care and cuckoldry in black coucals: does parenting hamper sex life?

Ignas Safari^{1,2,3}, Wolfgang Goymann^{1,2} and Hanna Kokko⁴

¹Max-Planck-Institut für Ornithologie, Abteilung für Verhaltensneurobiologie, Eberhard-Gwinner-Straße 6a, 82319 Seewiesen, Germany

²Coucal Project, PO Box 26, Chimala, Tanzania

³Department of Conservation Biology, University of Dodoma, PO Box 338, Dodoma, Tanzania

⁴Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland

iD IS, 0000-0001-5157-5398; WG, 0000-0002-7553-5910; HK, 0000-0002-5772-4881

Providing parental care often reduces additional mating opportunities. Paternal care becomes easier to understand if trade-offs between mating and caring remain mild. The black coucal *Centropus grillii* combines male-only parental care with 50% of all broods containing young sired by another male. To understand how much caring for offspring reduces a male's chance to sire additional young in other males' nests, we matched the production of extra-pair young in each nest with the periods during which potential extra-pair sires were either caring for offspring themselves or when they had no own offspring to care for. We found that males which cared for a clutch were not fully excluded from the pool of competitors for siring young in other males' nests. Instead, the relative siring success showed a temporary dip. Males were approximately 17% less likely to sire young in other males' nests while they were incubating, about 48% less likely to do so while feeding nestlings, followed by 26% when feeding fledglings, compared to the success of males that currently did not care for offspring. These results suggest that real-life care situations by males may involve trade-off structures that differ from, and are less strict than those frequently employed in theoretical considerations of operational sex ratios, sex roles and parenting decisions.

1. Introduction

Investment into offspring care results in a resource allocation conflict, if parental investment that benefits offspring reduces a parent's ability to invest into self-maintenance or further mating opportunities [1–4]. This conflict is intensified when there is a high likelihood of caring for unrelated offspring. In most animals, females provide more care than males [5–8]. Several hypotheses have been proposed to explain this phenomenon, including certainty of genetic parentage which is typically higher for females than males [1,4,6]. There should be selection against male care when females mate with multiple males and thus are likely to produce sets of offspring that are fathered by more than one male [1,6,9,10]. Indeed, several meta-analyses suggest that male contributions to care decline with increasing rates of paternity loss, particularly so in bird species with altricial young [11–14].

However, it is difficult to disentangle cause and effect, because both confidence in paternity and the degree of paternal care can influence each other [15–18]. Confidence in paternity may increase paternal investment [19–21], but at the same time, males engaged in paternal care may be limited in time and energy to pursue extra-pair copulations, leading to low rates of paternity loss in the population as a whole [15–18]. There is behavioural evidence suggesting that these constraints exist: males of most monogamous and biparental birds engage in extra-pair matings during the fertile period of their social mate or while she is incubating, but hardly do so once their nestlings have hatched [22–26]. Also, males of classical polyandrous birds with male-only

care are less likely to copulate with females while parenting (e.g. wattled jacana, *Jacana jacana* [27], northern jacobins, *Jacana spinosa* [28], spotted sandpiper, *Actitis macularia* [29]). As a consequence, rates of extra-pair paternity in most classical polyandrous shorebirds with male-only care are similar or even lower than those of socially monogamous shorebirds with biparental care [30–33]. By contrast, polygynous shorebirds with female-only care have a high proportion of broods with multiple genetic fathers [33–35].

In some polyandrous bird species with male-only care, males that have already received a clutch to care for may attempt to achieve further copulations with the female who laid the eggs (e.g. [36,37]), presumably to sire some offspring in the nest of the subsequent male [38]. Therefore, paternal care may not necessarily prevent males from copulating with their mate, who is laying a clutch for one of her other partners, or from seeking extra-pair copulations with other females. To understand the evolution of parenting (and in particular its costs), it is thus important to quantify the degree to which caring for offspring reduces a male's prospects of siring additional young in nests of other males. We investigate this pertinent question that has triggered several theoretical reviews (e.g. [39–41]) and a mathematical model [42], using classically polyandrous black coucals as a model system. We match the occurrence of extra-pair young (i.e. offspring in the nest of a focal male that were not sired by him) with the availability of each potential sire. We ask whether availability, modelled as a time-varying propensity to sire eggs, varies depending on the state of each potential sire. The 'state' refers to whether the male, on a given day, is in the mating pool because it has no clutch to care for (in the parental care literature this is called the 'time-in', e.g. [6,10,43]), or in the various stages of caring for young (incubation, or feeding of nestlings or fledglings; so-called 'time-out' [6,10,43]).

The black coucal is an excellent model to study trade-offs between paternal care and the pursuit of additional fertilizations, because it is the only known bird species combining exclusive paternal care for altricial young with a high degree of paternity loss [44,45]. Female black coucals defend large territories and form a polyandrous social group with up to five males. Females do not provide any parental care and remain in the mating pool ('time-in') for the entire breeding season of three to four months. There are no indications for a trade-off between mating and defending a territory in females [46]. By contrast, each male incubates his clutch for a period of two weeks, and broods and feeds the nestlings and fledglings for another 2 + 2 weeks [46–48]. Hence, a male black coucal endures a 'time-out' period (*sensu* [43]) of about six weeks. Paternal care thus requires a significant time and energy investment [48,49], with the potential loss of mating opportunities. At first sight, this may appear to be a very special case applying only to polyandrous species with male-only care, but in fact, it applies to a broad range of mating systems in which males contribute to offspring care. For example, males of socially monogamous species with biparental care face a similar trade-off between parenting and seeking additional matings. This problem is particularly pertinent in species with a long breeding season and a low breeding synchrony among females. In such a situation additional mating opportunities arise frequently and it is important to know how strict the 'time-out' for males may be. The strictness of such 'time-outs' of

males has important implications for the concept of operational sex ratios (OSR): if there is no complete 'time-out' of incubating or offspring-feeding males, they cannot be assumed to be unavailable for matings, which should be incorporated in future OSR modelling.

Based on the heavy parental investment of male black coucals, theory, at first sight, predicts low extra-pair paternity. Yet 50% of all broods contain at least one offspring sired by a male other than the social father, with 17.3% of offspring not sired by the carer [44]. Males lose paternity to other males from within the social group of their polyandrous female (co-mates, *sensu* [27]), but also to males from polyandrous groups of other females (extra-group males). Similar to other simultaneously polyandrous birds (e.g. [27,50,51]), the black coucal data suggest that extra-pair fertilizations mainly result from sneaky copulations rather than stored sperm [44,45].

The evolution of male care becomes easier to understand when caring does not strictly prevent males from gaining mating opportunities elsewhere [7]. To estimate the degree to which caring reduces such opportunities, we used maximum-likelihood modelling whereby each egg (with known genetic paternity) was linked to the breeding-cycle state of each potential sire at the time of egg-laying. The stricter the 'time-out', the larger the reduction in siring ability (which we model as a propensity) of a male caused by incubation, feeding nestlings, or feeding fledglings, compared with the baseline propensity of a male that is not engaged in any of these parental activities. We used an information-theoretic approach with model averaging to estimate these reductions.

Our approach takes advantage of the high potential reproductive rate of female black coucals: individual females lay up to eight clutches per season [44,46], and females appear limited by the number of available males rather than by their egg production rate. Thus, whenever a female is laying a clutch for one of her mates, there are males within and outside her 'harem' group in different stages of the breeding cycle (i.e. without a clutch to care for, incubating, feeding nestlings or fledglings) that could potentially act as extra-pair sires. This allows us to estimate relative propensities over time as a function of each male's current activities. Our model also takes into account that males might be more likely to sire extra-pair young within their own females' social group rather than outside this group. In a separate analysis, we checked the extent to which this may have been owing to proximity effects.

2. Material and methods

(a) Field methods

We studied black coucals breeding in partially flooded grassland in the Usangu wetland (8°41' S 34°5' E; 1000 m above sea level) in Mbeya Region of south-western Tanzania. Data were collected during 12 breeding seasons (typically January–June) in 2001–2002, 2005–2006, 2008 and 2010–2016. Coucals were caught with mist-nets, a small blood sample (less than 50 μ l) taken and stored in Queen's lysis buffer [52] for genetic sexing and parentage analysis. Then, birds were measured, banded and fitted with radio-transmitters (for details see [46]).

Nests were found through behavioural observations and radio-tracking (for details see [46,48]). Each nest was assigned to the male attending it and the female holding the territory in which the nest was found. Males usually start incubating after

the first or the second egg has been laid, while the female continues to lay eggs daily until the clutch (typically four eggs, range = 2–8) is completed. Therefore, the eggs hatch asynchronously according to the laying order, creating noticeable size hierarchies among the nestlings. For nests found after clutch completion, we estimated the laying date of the first egg by backdating from the observed hatching date, assuming an incubation period of 15 days [46]. When the nestlings were 4–5 days old, we took a small blood sample for genetic sexing and parentage analysis.

(b) Parentage analysis

Adults and offspring were genetically sexed [53] and genotyped for parentage and sibship analysis (for further details see [44]). Offspring in the nest of a focal male that were not sired by him were considered to be extra-pair young (defined from the perspective of the social father). Extra-pair young were sired by either another male within the social group of the polyandrous female (i.e. a co-mate of the social father, *sensu* [27]) or by a male from outside the female's social group (i.e. an extra-group male). Even though female black coucals have sperm storage tubules [54] our previous analyses suggest that the last male which copulated with the female has precedence in siring offspring [44]. For our main analysis, we thus assume that offspring were sired by a male who copulated with the female shortly before the respective egg was fertilized.

(c) Scoring parental activities and distances between territories

For the laying period of each genotyped clutch, we scored the breeding status of each male that could have been a potential sire of each respective egg as either being free of parental activities, incubating his own clutch, feeding his own nestlings or feeding his own fledglings. The laying period of a clutch was defined as the range of days from the laying of the first to the last egg of the respective clutch. A male was considered to be free from parental duties if he did not have an active nest, and the fledging from a previous nest happened at least two weeks ago. We noted the number of offspring that each male sired in the respective clutch, and whether he was the social father of the clutch, a male within the social group of the female who laid the focal clutch (i.e. a co-mate of the social father), or an extra-group male. Furthermore, we included the distance (in metres) from the centre of the home range of each male to the female who laid the focal clutch. Distance matrices between all adults were generated from the coordinates of the centre of the home range of each individual using GEOGRAPHIC DISTANCE MATRIX GENERATOR v.1.2.3 [55].

(d) Sample size

Our analysis is based on a sample of 162 black coucal clutches from 96 different females and 142 different social fathers. The sampled clutches contained a total of 560 genotyped offspring of which 75 young from 57 clutches were extra-pair [44]. In addition to the 142 social fathers, other 62 males whose clutches were predated at various stages before the offspring could be sampled for DNA were also included in the pool of potential extra-pair sires in the respective breeding seasons. Each egg has multiple potential fathers, and assuming that all known males that were present in the study area could potentially sire the young, our analysis includes activities of, on average, 19.9 males at the time that is relevant for each egg.

(e) Statistical analyses

In our first (main) analysis, we took advantage of all eggs with known paternity, where the social situation around the nest was known on the day the egg was laid. The social situation encompasses the activities of all potential (i.e. alive) extra-pair sires (categories are: free from parental duties, incubating, feeding nestlings, or feeding fledglings; figure 1) as well as the status of each male relative to the female who laid the egg (social father, within-group male, or extra-group male, figure 1). In the second, separate analysis, we investigate the effect of the distance from a male's home range centre to the female who laid the clutch.

The main analysis uses a model comparison approach to contrast the performance of $6 \times 3 + 2 = 20$ candidate models (figure 1), each using a specific assumption structure that relates the social situation present in the population to the realized parentage of the focal egg. Models differ from each other in up to four respects: (i) whether the social father is assumed to have better paternity prospects in early-laid rather than late-laid eggs in his nests (and whether this relationship is assumed to be linear or nonlinear), (ii) whether within-group males have better prospects than extra-group males, (iii) whether parenting activities of potential extra-pair sires (either within- or extra-group) cause reductions of siring propensities, and (iv) whether parenting activities matter on the day the focal egg was laid (basic assumption, all models without subscripts), or on the same day near the beginning of the laying sequence of the focal nest, regardless of the focal egg's own lay day: this is day 0 (i.e. the day before the first egg was laid) for models A_0 , B_0 , C_0 , D_0 , E_0 , G_0 , and day 1 (i.e. the day the first egg was laid) for models A_1 , B_1 , C_1 , D_1 , E_1 , G_1 . These alternatives allow us to explore the possibility that sperm from a copulation that occurred some days ago has the potential to sire e.g. the fourth or fifth hatchlings of the broods (the chicks for which extra-pair paternity was at its highest [44]). Models F and N (the null model where all males have equal chances to sire any egg) do not use information of extra-pair male activities and thus corresponding model variants F_0 , F_1 , N_0 or N_1 do not exist. Note that our phrases 'better prospects' above merely indicate an *a priori* plausible direction for an effect; the estimation procedure also allows prospects to worsen under these conditions (unexpected effects were not found in reality, but we imposed no constraints that would have precluded finding them).

The models used for Akaike information criterion (AIC) [56] estimation had the following structure. We considered the dataset of all eggs that had known sires ($n = 560$). For each egg, we recorded the social situation (as explained in detail in the electronic supplementary material) that was relevant to determine the availabilities of potential sires. Here, 'potential' encompasses the set of males that were alive and were part of this study for the respective breeding season, and thus could have competed to become the biological sire. The modelling procedure uses information about male group identity (i.e. social father with a certain number of eggs in his nest, another within-group male, or an extra-group male relative to the focal nest) as well as male activities to estimate the *relative propensity* of each male to be the sire of an egg laid on a specific day into a specific nest.

We do not pre-assign any other propensities than a social father's first-egg propensity, which is 1. This is necessary simply to set a scale, as propensities are always interpreted in a relative manner: doubling the propensity doubles the expected number of occasions that a male in this state is observed to sire an egg. Thus, in an example that allows particularly easy predictions: if social fathers always had five times the propensity of any within-group male (the latter thus have a relative propensity of 0.2), and there was never any extra-group paternity, and group size was always 4, then each social father can be said to have five 'lottery tickets' against one ticket per each of his (three)

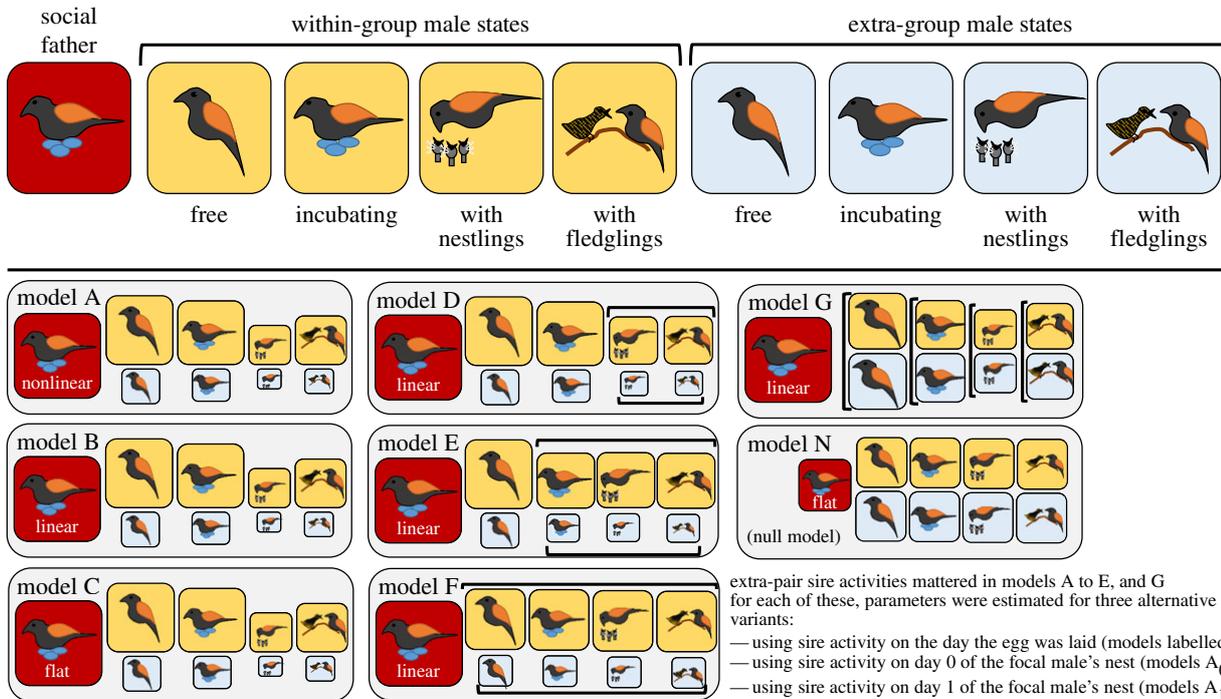


Figure 1. The structure of the models that were fitted to the data. The vignettes in the top row explain the visual notation: dark red, the social father; light brown, a within-group male who can be in one of four different states; light blue, an extra-group male (likewise in four possible states). Below, each model uses a different assumption of how propensities to sire an egg depend on (i) the social father's number of eggs: nonlinearly, linearly, or not at all ('flat' relationship), (ii) extra-pair male state including parenting activities and/or within- or extra-group status. Whenever vignettes differ in size, the estimation procedure allows estimated propensities to differ between these male states (note that the sizes chosen for the vignette illustrations indicate this flexibility, rather than pre-assigned assumptions of certain male classes having larger propensities than others). Brackets indicate that the estimated propensities were not allowed to vary by the respective model. Note also that the real dataset typically had cases with more than one male sharing the same state (e.g. two or more within-group males free from parenting activities); each male is then assigned the same propensity that associates with this state.

within-group competitors. This case would predict observed datasets to have each egg being sired by a within-group male with probability $(1 + 1 + 1)/(5 + 1 + 1 + 1) = 37.5\%$, and the same answer is obtained by scaling the social father's propensity to 1, as long as the others scale accordingly: $(0.2 + 0.2 + 0.2)/(1 + 0.2 + 0.2 + 0.2) = 37.5\%$.

The estimation of the propensities for the real-life data begins with guesses (e.g. 0.2 above), from which the procedure forms predictions (e.g. the 37.5% above) for each social situation encountered. The guesses then converge towards best-fitting values with a maximum-likelihood method (visually depicted as searching for the size of vignettes, within each model structure in figure 1, that together produce the highest likelihood of producing the observed data when we view vignette size as proportional to the number of 'lottery tickets'; see the electronic supplementary material for mathematical details). Using our toy example above again, if real data confirmed that all groups have four males but the observations indicated 40% (rather than 37.5%) extra-pair paternity, the likelihood of observing this data is maximized when the within-group male propensities are 0.22222 (relative to the social father's propensity of 1). This estimate would then be used to score the performance of the model using standard AIC criteria [57], and the different models (figure 1) are contrasted against each other in terms of performance. In reality, the observed data offers more information than an aggregate measure 'certain percentage of extra-pair paternity', and most of our real models also included more detail than the above toy example: they also included the possibility that a social mate's propensity is lower for later laid eggs (modelled with a slope of the decline, a , and its exponent, b , figure 2 and table 1), as well as variations in other males' propensities depending on their activities. How likelihoods are computed for these more complicated scenarios is described in

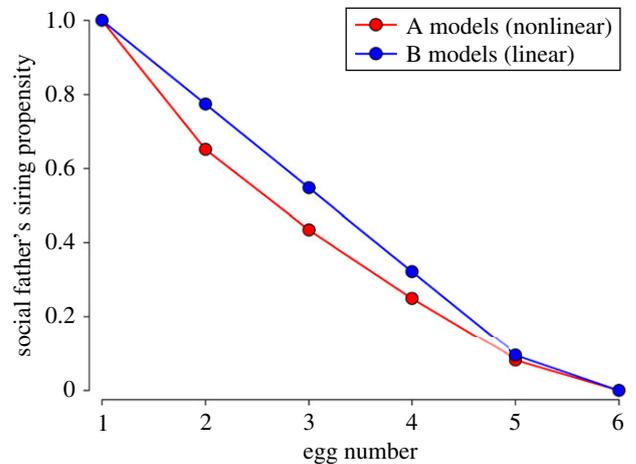


Figure 2. The social father's propensity to sire eggs declines steeply with egg number in the best-supported models (blue, all B; red, all A models; the slight variations in a and b values within a model type lead to functions that are so similar that they are indistinguishable in this figure). A lower ceiling of 0 is applied to the functions $1 - a(n - 1)$ (the linear B models) and $1 - a(n - 1)^b$ for the nonlinear A models (n denotes the n th egg laid in the focal nest).

the electronic supplementary material. We also included a null model (labelled 'N') that assumes every male to have equal chances to fertilize any egg.

We thereafter also asked, in a separate analysis, whether distance to the focal female helped to explain which extra-pair males gained paternity. We did not incorporate distance in our main model above, because precise distance data had not been

Table 1. Results of all models, with AIC, Δ AIC and model weight w , and the remaining columns represent the maximum likelihood estimates for parameters that determine each male's siring propensity in each setting (values without decimals are assumptions imposed by a particular model rather than estimates). (Models within Δ AIC < 2 are in bold; the horizontal line distinguishes between models with some (Δ AIC < 3) and virtually zero support. A social father's propensity to sire the n th egg in his nest is modelled as $1 - a(n-1)^b$ or 0 if this is negative (note that b is 1 for linear models, predicting no success for 6th or later eggs in B models; our dataset only had 1 such egg and it was extra-pair). The propensities of free within-group males (WGM) or free extra-group males (EGM) can be used as in the table. To get the propensities of incubating or feeding males, the values given in the parenting columns are used to multiply these 'free' baselines. To use an example from the best-performing model B₁: a social father's 3rd egg when there is also a nestling-feeding WGM male competitor is estimated with the social father and this particular competitor having relative paternity chances $1 - 0.2261 \times 2 = 0.5478$ and $0.0639 \times 0.4695 = 0.0300$, respectively.)

model	AIC	Δ AIC	w	a	b	free WGM	free EGM	incubating	feed nestlings	feed fledg.
B₁	550.05	0	0.2969	0.2261	1	0.0639	0.0005	0.8456	0.4695	0.7004
B	551.04	0.9875	0.1812	0.2261	1	0.0634	0.0005	0.7907	0.5890	0.7173
B₀	551.11	1.0598	0.1748	0.2261	1	0.0627	0.0005	0.8364	0.5515	0.8451
A₁	551.32	1.2698	0.1573	0.3488	0.6981	0.0536	0.0004	0.8446	0.4699	0.6995
A	552.29	2.2444	0.0967	0.3499	0.6959	0.0532	0.0004	0.7924	0.5880	0.7173
A ₀	552.37	2.3169	0.0932	0.3497	0.6963	0.0526	0.0004	0.8358	0.5511	0.8458
D ₁	577.16	27.1137	<0.0001	0.0383	1	0.1138	0.0009	0.7793	0.4761	0.4761
D	578.12	28.0685	<0.0001	0.0374	1	0.1130	0.0009	0.7373	0.5554	0.5554
D ₀	578.39	28.3428	<0.0001	0.0389	1	0.1134	0.0009	0.7103	0.5400	0.5400
E	580.14	30.0873	<0.0001	0.0018	1	0.1183	0.0009	0.6506	0.6506	0.6506
E ₁	580.17	30.1181	<0.0001	0.0016	1	0.1155	0.0009	0.7122	0.7122	0.7122
F	580.69	30.6396	<0.0001	0.0020	1	0.1030	0.0008	1	1	1
E ₀	580.81	30.7582	<0.0001	0.0015	1	0.1148	0.0009	0.7290	0.7290	0.7290
C1	581.05	31.0007	<0.0001	0	1	0.1202	0.0009	0.7398	0.4336	0.6801
C	582.18	32.1336	<0.0001	0	1	0.1197	0.0009	0.6776	0.5613	0.6593
C0	582.47	32.4164	<0.0001	0	1	0.1211	0.0009	0.6657	0.4973	0.6887
G	859.88	309.8269	<0.0001	0.2252	1	0.0050	0.0050	0.7310	0.7310	0.7310
G ₁	860.13	310.0823	<0.0001	0.2251	1	0.0049	0.0049	0.7509	0.7509	0.7509
G ₀	860.92	310.8727	<0.0001	0.2250	1	0.0048	0.0048	0.8406	0.8406	0.8406
N	3315.83	2765.8	<0.0001	0	1	1	1	1	1	1

recorded for all the potential sires. For the subset where this was available, we did not use an AIC approach, as we were interested in the simpler question of whether extra-pair siring occurs over all male–female distances present in the population or only over a subset of short distances.

3. Results

(a) Impacts of different social and paternal care states

Four (out of 20) models had AIC scores within Δ AIC < 2 of each other (in order of declining support: models B₁, B, B₀ and A₁ (table 1). A further two (A and A₀) were within the Δ AIC < 3 range. All other 14 models were extremely poorly supported, with the null model being the least supported.

When the best model (B₁) is not the only well supported one, it is essential to discuss properties of the data that all models with good or moderate support agree on, as well as the differences that remain between them. All supported models, regardless of whether one restricts attention to the top four or considers all six with at least moderate support (table 1), agreed on (i) the social father's declining ability to retain paternity of late-laid eggs, (ii) the status of a male

being an important predictor of siring propensities (social father $>$ within-group male $>$ extra-group male), and (iii) parenting activities having a detrimental effect on siring prospects of males, though with no stage leading to zero (or near zero) success. The models differed with respect to the precise shape of the decline of the social father's paternity when new eggs are added to his brood (figure 2; note that the linear B models outperformed the nonlinear A models, but only with a narrow margin), and with respect to the day when the activities of extra-pair males matter. The best model (B₁) considers the day when the first egg was laid in the focal nest, but models that base predictions on another day perform almost equally well if they otherwise use the assumption set of the B models.

Estimates for within-group male siring propensities were between 5% and 7% of the social father's first-egg propensity (table 1, e.g. 0.0639 in the best model B₁). This indicates that extra-pair males have low chances to sire the first eggs entering a male's nest, but since the social father's own propensity declines rapidly with egg number (with less than 10% of the original propensity left by the time a fifth egg is laid, figure 2), within-group male propensities are sufficient to make them very serious competitors for late-laid eggs (for example, 0.0639 for a within-group male versus 0.0956 for

the social father for the fifth egg of a clutch according to the best model; the latter value is calculated as $1 - 0.2261 \times 4$, table 1 for details on the calculation). All models agreed on extra-group males having very low (but still non-zero) propensities to sire eggs, between 0.0004 and 0.0005 of the social father's first-egg propensity (table 1).

The above numbers do not yet take into account reductions in siring due to extra-pair sires' own parenting activities. The estimates for these are in the last three columns of table 1. All supported models agree that all stages of parenting reduce siring propensities ('free' propensities are always multiplied by a factor < 1), and that this reduction is strongest when the male is feeding nestlings. Model averaging across the six supported models with model weights w , a male experiences a drop of $1 - 0.8278 \approx 17.2\%$ of paternity chances when incubating compared with his 'free' propensity (range 15.4%–21.9% among the six best models, table 1), while feeding nestlings leads to $1 - 0.5246 \approx 47.5\%$ reduction (range 41.1%–53.1%), and feeding fledglings reduces siring propensities by $1 - 0.7438 \approx 25.6\%$ (range 15.5%–30.1%). Overall, no stage of parenting led to near-zero siring prospects (last three columns of table 1), which would have been the outcome if the 'time-out' caused by parenting was strict. Note that our method is able to exclude the possibility of any of these results being a spurious correlation arising from synchronous breeding activities—e.g. fewer eggs being available to be fertilized when many males are feeding nestlings—because the analysis is conducted on a per-egg basis, and all likelihood calculations are thus based on males making use of siring opportunities that did exist in reality.

While the agreement between models produces clear results regarding the effect of parenting, the models do not unambiguously differentiate between possible scenarios of sperm storage. All timing choices for measuring the activity of males yielded models with at least moderate support (table 1: models with and without subscripts can be found near the top). The best model (B_1) offers a mixed message: extra-pair males' parenting activities matter at the time when the first egg is laid in the focal nest, but this combines with the social father's siring success decreasing rapidly for late-laid eggs. The former message implies that the set of male activities which occur when early eggs are laid in a nest have an impact on paternity of late eggs (indicative of some delay between copulation and fertilization), but the latter fact suggests a role for later copulations that occur while the social father is preoccupied with his nest that has received its first eggs. As a whole, these findings can be reconciled in a view of moderately short-term sperm storage (a few days) with some stochasticity in the outcome (variable numbers of copulations with different males, or some variation in the time lag between copulation and fertilization).

(b) Distances between males and females and likelihood of siring extra-pair offspring

For a large subset of data (sample size indicated in figure 3), we had sufficient male location data to establish a distribution for the distance of the male's home range centre to that of their social female (the curve with red dots gives the cumulative distribution, figure 3) as well as other females alive in the same year (curve with triangles). Males sired extra-pair young in nests of their co-mates over the entire

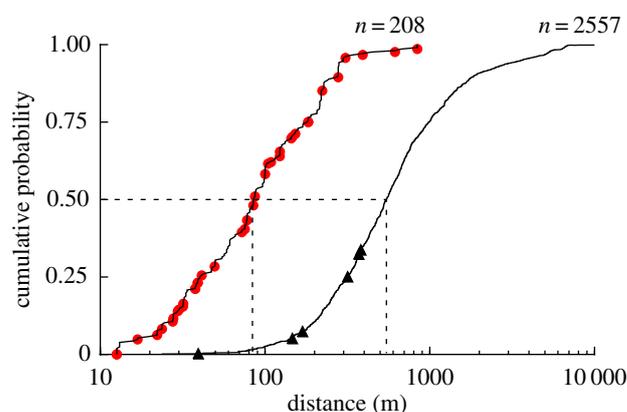


Figure 3. Cumulative distance distribution from the center of the home ranges of individual males to those of females when the male and the female were part of the same social group (curve with red dots) or different groups (curve with black triangles). Dots and triangles, respectively, mark cases with extra-pair young production. Dotted lines show the distance medians for all data (85 m for within-group individuals, 548 m for extra-group). Beyond 382 m distance, extra-group males had no success. Greater distances than those of within-group males are not solely responsible for the meagre siring success of extra-group males, as the total n for extra-group male availability at < 382 m is 870 (with 6 successes as indicated), while the within-group male availability at this range is 201 (with 40 successes as indicated), thus success for extra-group males is clearly lower (z -test, $P < 0.001$).

range of distances, while the rare siring successes of extra-group males were confined to males residing close to the focal extra-group female (figure 3).

4. Discussion

How much does parenting reduce the success of male coucals as sires in nests other than their own? We conducted an information-theoretic approach to estimate how male ability to obtain paternity in other males' nests fluctuates over time as a function of parental care at their own nests. All supported models produced a clear pattern, with males being maximally 'busy' (=least able to sire elsewhere) when they were feeding nestlings, and least busy when they did not have a nest to care for at all. Our approach estimated that incubating reduces siring prospects by approximately 17%, feeding nestlings reduced it by approximately 48%, and the reduction went back to approximately 26% when feeding fledglings. Thus, as a whole our analysis provides evidence for a very 'leaky' time-out of males as a result of parental care: its nature is a temporary and incomplete dip in competitiveness for fertilizing eggs in other males' nests, rather than a complete exclusion from the pool of males competing for such opportunities as assumed in classical models of OSR and care roles [43].

Our results also show male black coucals to be particularly serious competitors for paternity in other males' nests when the female lays additional eggs to an already existing clutch, and when the males are members of the same social group (i.e. associated with the same female). Extra-group members, even when focusing on the subset of males who reside relatively close to a female other than their social partner, obtained paternity at a very low rate. Contrastingly,

males belonging to the same social group never ceased to pose a threat to each other's paternity, regardless of how advanced the activities at their own nest were. This threat did not disappear, although it diminished, during the time when the potential extra-pair sire was incubating or provisioning nestlings or fledglings. Our results are consistent with the hypothesis that nestling provisioning in altricial species entails higher limitations to male extra-pair activities than other care stages [12,14]. The suggestion that male incubation constitutes a stronger constraint than nestling provisioning [13,15] was not supported by our data.

Males rarely sired extra-pair young with a female other than their social partner, suggesting that the established social relationships between a female and her 'harem' males have an influence on mating patterns that go beyond a mere proximity effect. Because a female black coucal regularly moves throughout her large territory, each of her 'harem' males can readily access her during the entire breeding season. This setting promotes intense competition among co-mates whenever the female is laying a clutch for one of them. The recipient of the clutch attempts to guard her intensively [47], but once she has laid the first or the second egg for his clutch, the male starts incubating, which prevents efficient guarding while she continues to complete his clutch. Our results suggest that the effect is a continual reduction in paternity with each subsequent egg laid (figure 2; note that the nonlinear model formulation was flexible enough to detect cases where paternity remains near intact for, e.g. first three eggs and declines thereafter, but the best-fitting nonlinear model instead suggests a more immediate drop as egg numbers increase).

In other words, 'harem' males frequently succeed in fertilizing some subsequent eggs of the clutch, and this includes males already caring for their own respective clutches. The time budgets of caring males play a role here. Males are known to frequently interrupt incubation (mean = 6, range 2 to 12 pauses per day) and typically spend about 40 min off-nest during such pauses [48]. Our results suggest that incubation prevents intense mate-guarding (thus the female can add extra-pair eggs to an incomplete clutch) but does not prevent an incubating male from acquiring paternity in others' nests. We do not know whether this is achieved because a female approaches a male sitting on a nest, or because males use their brief times off the nest to look for the female in addition to foraging. Our methods did not assign a systematic, clear role to the exact time point when male activities matter most, as a determinant of model performance; males only rarely changed state precisely between two alternative time points in the data, which—perhaps together with a stochastic delay between copulations (unobserved by us) and fertilization—explains our inability to distinguish precisely between timing alternatives. Time budget constraints may become more severe after a clutch has hatched, as the schedule of provisioning the young is not only physiologically and energetically demanding [49] but also leaves less time to rest, forage or mate [48]. Still, in our analyses, chances to sire young (as evidenced by paternity gains) do not drop to zero during this time either, which might indicate a role for active visits by females seeking fertilizations.

It is informative to compare a male black coucal's trade-off situation to that of other taxa where paternal care prevails. Among fish species that provide care for young, male care is much more common than female care [8,57]. Although not

the sole argument (e.g. [58]), it appears plausible for such fishes that a 'time-out' caused by male care is often not a good way to characterize the mating dynamics: females often prefer caring males, who through care increase, rather than decrease, their current mating opportunities (e.g. [7,57–59]). Furthermore, energetic costs of many fish-specific forms of parental care (such as fanning eggs) do not rise steeply, or at all, with the number of offspring in the nest. This is different for birds with altricial young, such as the black coucal, where more mouths to be fed increase the costs of parenting [48,49]. Despite this, we have shown that male black coucals experience only limited damage to their pursuit of additional mating opportunities—in the form of siring eggs cared for by other males—even if they perform parenting duties. In this sense, coucals are more 'fish-like' than the dramatic difference in the form of care might suggest, and the explanation for male willingness to perform care might have similar root causes of limited (if any) trade-offs between caring and gaining paternity elsewhere, at least in the current mating season.

Numerous previous studies, mostly from socially monogamous biparental species, have focused on understanding how males time their extra-pair mating activities in relation to the fertility stage of their respective social partners or other available females [22,24,25]. We are not aware of any previous study that compared propensities to sire extra-pair young in relation to the temporal dynamics of parental care states of individual males, despite the question of extra-pair paternity and breeding synchrony, in general, attracting much interest (e.g. [60,61]). Behavioural evidence from other bird species (including socially monogamous biparental birds, e.g. fairy martins, *Hirundo ariel* [25], hooded warblers, *Wilsonia citrina* [26] and classically polyandrous birds with male-only care, e.g. spotted sandpiper, *Actitis macularia* [29]), suggests that similar processes as in the male-only care coucals could play a role: while parenting males are less likely to engage in extra-pair mating activities, parenting does not prevent them from engaging in such activities if fertile females are available—though species-specific details will depend on breeding synchrony, territoriality and also female behaviour. If detailed time-stamped behavioural data are available for such species, our method could be applied to biparental care situations too, as it would be easy to incorporate female care state as another variable in biparental systems. This would allow the field to move from qualitative to quantitative interpretations of 'time-in' and 'time-out' periods. It would indeed be interesting to know whether the 'leaky', i.e. gradual, pattern of 'time-in' and 'time-out' periods that we identified in coucals applies to many species in which males contribute to parental care without being the sole provider; this could also help in comparison of synchronous and asynchronous breeding activities. Further work could also lift some of the limitations of our approach: we assumed, for example, that each egg laid formed an independent contribution to information about availabilities. Merging our style of analysis with, e.g. an analysis of local networks (see methods of [61]) would be a fruitful further research avenue, where sufficient data are available.

In conclusion, our analysis provides evidence for a 'time-out' of males as a result of parental care, but its nature is a temporary and incomplete drop-out in competition for fertilizing eggs in other males' nests, rather than a complete exclusion from the mating pool. The degree to

which males drop out from the mating pool depends on the parenting stage. To the best of our knowledge, this is the first detailed quantitative description of the reproductive 'time-out' propensities of males while caring for young. Such empirical results are of eminent importance to evaluate how well theoretical and mathematical models of 'time-out' describe the trade-offs between mating and parenting in males and to understand potential differences in absolute and relative reproductive 'time-out' of males and females within the OSR framework.

Ethics. This research adhered to the local guidelines regarding animal experimentation of Germany and Tanzania. The ethical approval and research permits to conduct this study were obtained from the Tanzania Wildlife Research Institute (TAWIRI) and the Tanzanian Commission for Science and Technology (COSTECH).

Data accessibility. Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.m906r59> [62].

Authors' contributions. I.S. collected field data, conducted parentage analyses, scored male social states and parental care activities, calculated distances between territories and drafted the initial manuscript. W.G. designed the study, collected field data and co-drafted the

manuscript. H.K. conceived the idea to look at male activities, conducted the statistical analyses and co-drafted the manuscript. All authors critically revised and approved the final version of the manuscript.

Competing interests. The authors declare that they do not have any conflict of interest.

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