Cooperative breeding in a plural breeder: the vulturine guineafowl (*Acryllium vulturinum*)

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ABSTRACT

Cooperative breeding is widely reported across the animal kingdom. In birds, it is hypothesised to be most common in altricial species (where chicks are dependent on parental care in the nest after hatching), with few described cases in precocial species (where chicks are more independent immediately after hatching). However, cooperative breeding may also be more difficult to detect in precocial species, and therefore has been overlooked. In this study, we investigate whether vulturine guineafowl (*Acryllium vulturinum*)—which have precocial young—breed cooperatively and, if so, how help is distributed among group members. Using data collected from colour-banded individuals in one social group of vulturine guineafowl over three different breeding seasons, we found that multiple females can simultaneously attempt to breed within a group. Broods had close adult associates and most of these associates exhibited four distinct cooperative breeding behaviours: babysitting, within-group chick guarding, covering the chicks under the wings and calling the chicks for food. Further, we found that helping is significantly male-biased, that helpers provided most of the care to each brood, that breeding females differed in how much help they received, and that helpers pay a foraging cost when providing care. Our results confirm that vulturine guineafowl are cooperative breeders, which they combine with an unusual plural-breeding social system. Our study also adds to growing evidence that cooperative breeding may be more widespread among species with precocial young than previously thought, thereby providing a counterpoint to the altriciality-cooperative breeding hypothesis.

Keywords: Cooperation, Galliformes, helping, precocial breeding, vulturine guineafowl

INTRODUCTION

In some species of birds, mammals, fish and invertebrates more than two adults contribute towards raising offspring, which is known as cooperative breeding. Typically, groups of cooperatively breeding individuals consist of a breeding pair and one or more 'helpers'. The latter are usually offspring of the breeding pair from previous breeding attempts that delayed dispersal, and help in rearing their younger siblings (Clutton-Brock, 2002). As cooperative breeding seems to be a suboptimal reproductive strategy for helpers, it has received considerable empirical (W. D. Koenig & Stacey, 1990; Walter D. Koenig & Dickinson, 2016) and theoretical (Emlen, 1982; Hatchwell & Komdeur, 2000; Shen et al., 2017) attention over the past five decades. In birds, cooperative breeding has primarily been described among altricial species (Cockburn, 2006; N. Wang & Kimball, 2016), and the relative paucity of cases among species with precocial young has led to the hypothesis that there exists a link between altriciality and

cooperative breeding (Walter D. Koenig & Dickinson, 2016). However, cooperative breeding has been mostly characterised as helping at the nest by non-parents, despite the energetic costs for parents being higher during the post fledging care compared to the nestling period such as via continued provisioning of offspring. New insights on the link between cooperative breeding and altriciality may thus be gained by extending the scope of studies of cooperative breeding.

The disparity in the presence of cooperative breeding between altricial and precocial species could be because species with precocial offspring—which are more independent straight after hatching—have less need for help. However, this logic may be flawed. Due to high predation risk of the eggs to ground-nesting birds (Thompson & Raveling, 1987), females of ground-nesting precocial species typically have very high nest attendance rates, thus foregoing feeding during incubation. For example, female ring-necked pheasants (*Phasianus colchicus*) attend their nest nearly 100% of the time during incubation and, in doing so, lose up to 19% of their body mass (Persson & Göransson, 1999). Given the substantial costs associated with egg laying and incubation to breeding females, reducing the effort by the breeding female would allow her to recover from her natal investment, and thereby to produce more chicks (the load lightening hypothesis) (Crick, 1992; Hatchwell, 1999), while enhanced care can increase chick survival rates (Heinsohn, 2004). Thus, there is substantial scope for non-breeding individuals to gain sufficient indirect fitness by reducing the effort of related females.

An alternative reason for the limited evidence for cooperative breeding in precocial species is because classical examples of cooperative breeding in birds primarily consider helping at the nest, rather than other forms of help that may occur after chicks leave the nest. If this is the case, then cooperative breeding may have been disproportionately undetected in precocial species. While helping at the nest provides parents and/or chicks with obvious benefits, there are many ways in which helpers can contribute to raising offspring in precocial species. For example, in trumpeters (*Psophia spp.*), which have precocial offspring, helpers contribute to nest building and incubation of eggs as well as providing chicks with food. Even without attending the nest, helpers can still contribute to increasing offspring survival or reduce parental investment post-hatching. For example, helpers may protect chicks from predators or the abiotic environment (such as covering chicks with their wings to provide shade or warmth), identify and provide food for chicks, or maintain vigilance to allow chicks more time to forage. However, such forms of cooperative breeding can be more difficult to detect and require more careful observations than what is necessary for describing helping at the nest. Beyond the challenge of quantifying the benefits to chicks and costs to helpers, it can also be difficult to follow precocial chicks in their natural environment as it requires following them on foot for a long period of time, in addition to the fact that the chicks will run, hide or go to inaccessible areas. Groups also need to be habituated,

and the habituation process is not that common in bird species. Thus, species in which helpers do not attend a nest may be less likely to be studied for their helping behaviour. Together, these factors could have led to a general under-reporting of cooperative breeding in species with precocial young.

One group of birds with precocial young in which evidence for cooperative breeding is increasing is Galliformes. To date, support for the existence of cooperative breeding has been found in nine species of Galliformes. In five species, the buff-throated partridge (*Arborophila brunneopectus*) (Wang et al., 2017), black-breasted wood quail (*Odontophorus guttatus*), Kalij pheasants (*Lophura leucomelanos*) (Zeng et al., 2016), Tibetan eared pheasants (*Crossoptilon crossoptilon*) and white eared pheasants (*Crossoptilon harmani*) (Lu & Zheng, 2005), the evidence for cooperative breeding is relatively strong. In these species, helpers were found to show food to the chicks, remain vigilant against predators and care for the chicks by expressing agonistic interactions among conspecific intruders. In four species, the California quail (*Callipepla californica*) (Lott, 1999), northern bobwhite (*Colinus virginianus*) and scaled quails (*Callipepla squamata*) (Orange et al., 2016) and marbled quail (*Odontophorous gujanensis*) (Skutch, 1947) the evidence remains largely anecdotal. The phylogenetic distance between these species, and among other species that breed cooperatively and have precocial young, suggests that cooperative breeding could be more common in Galliformes—and in precocial species more generally—than previously thought. This is likely because Galliformes have received little attention from researchers relative to many other groups of birds in the context of cooperative breeding. Thus, Galliformes represent an excellent taxonomic group in which to explore cooperative breeding, and how cooperative breeding behaviours might be expressed away from the nest.

Vulturine guineafowl are large, terrestrial Galliformes that live in stable groups of approximately 13-65 individuals, with groups associating preferentially with other groups to form a multilevel society (Papageorgiou et al., 2019). Given that social groups contain many adults, sub-adults and juveniles (Papageorgiou et al., 2019), vulturine guineafowl are a good candidate for being both plural and cooperative breeders, the former being defined as living in stable social groups containing multiple reproductive males and females. Vulturine guineafowl also have extreme sex-biased dispersal—all males remain in their natal groups (Klarevas-Irby et al., 2021)—setting the scene for high within-group relatedness among males, which could drive indirect fitness benefits of cooperative breeding (Hamilton, 1964). Furthermore, a recent comparative analysis suggests that the same environmental conditions might promote both cooperative breeding and multilevel societies (Camerlenghi et al., 2022). If cooperative breeding is present in vulturine guineafowl, we predict that helping is most strongly expressed by males as these are the philopatric sex. We also test what share of the care is given by mothers versus helpers, and whether the latter pay a cost to helping. In terms of costs, we expect that

helpers should forego other activities, such as foraging, when providing help. By employing a heterogenous approach to our study of cooperative breeding in the vulturine guineafowl, we are able to provide new evidence for the presence of cooperative breeding behaviour in an under-represented group of precocial species.

METHODS

Study species

Although they live in large groups with stable membership for most of the year, vulturine guineafowl form pairs at the beginning of the breeding season (Papageorgiou et al., 2021), after which the pairs move separately from the remaining group with the male mate-guarding the female. This is followed by the female laying—and independently incubating—a clutch of 13-15 eggs in a scrape on the ground (Johnson, 2002). (We note that our field observations suggest clutch sizes are smaller and more variable than the literature suggests, ranging from 7 to 12 eggs across 14 nests found). While the female incubates, the male re-joins the group, and can re-pair with a new female. Vulturine guineafowl chicks are precocial, with the mother and chicks typically re-joining the social group (or part of their social group) very soon after hatching. As in other guineafowl species (Del Hoyo et al., 1994), vulturine guineafowl females appear to receive no help during incubation. Although information about this remains anecdotal, we have never observed evidence suggesting otherwise (e.g., via GPS tracking and a few nests monitored using camera traps). Chicks are highly vulnerable to predation during the first few weeks of life, meaning that they could benefit from protection offered by helpers.

Study group and field data collection

Our study is focused on a long-term habituated social group living mostly within the fenced area of the Mpala Research Centre (MRC), in Laikipia county, Kenya, and forms part of a long-term study population of vulturine guineafowl at the MRC. Mpala is characterised by semi-arid savanna habitat with rainfall averaging between 500 and 600 mm per year, occurring predominantly in two rainy seasons (Young et al., 2003). The natural vegetation is mainly *Acacia* scrubland, and vulturine guineafowl specialise on the red soils that are dominated by *Acacia mellifera* and *Acacia etbaica*. The study group was first colour-banded, and tracked with GPS (He et al., 2022), in September 2016. Group size over the study period ranged from 30-35 adults. In the wet seasons spanning October to December 2019, April to May 2020, and October to November 2020, we recorded breeding activity within the study group. This involved following pairs that split from the main group, finding and monitoring the nests, and observing care behaviours post-hatching. Pairs were defined as a female and an associated male who moved together (that is, typically less than 5 m apart) and away from the group (that is, more than

20 m from other group members, but generally much further). Before considering two birds to be a pair, they had to be observed moving together for the whole day, but all pairs were recorded even if they were paired only for a single day. By following pairs, we eventually located and monitored the nests of all breeding females. When the clutch was expected to hatch (25 days after the start of incubation), we searched for the female and chicks.

We also collected data on associations between group members and broods by recording group composition data in the morning (0600 hrs - 0930 hrs) and evening (1700-1900 hrs) for an average of four days per week. Each time members of the group were encountered, the identity of every adult bird present was recorded, as well as the total number of banded and unbanded adults, and the number of chicks present from each of the broods. All birds that were present together in an area (that is, within sight of each other and behaving cohesively) were considered to be part of the same group, and given the same group identifier. Within these individuals, if some were more spatially clustered (e.g., within 2 metres of each other but more than 10m from other individuals), then these were recorded as a subgroup within the broader group (or as pairs, if they remained distinctly separate for the entire day).

Although chicks could not initially be marked individually, broods (up to N=3 per season) were generally identifiable because they hatched asynchronously, meaning that there was a clear size difference between chicks from different broods. From these differences, we ascertained that those chicks from the same brood remained together the vast majority of the time. There were two exceptions. First, during the first season, two broods hatched on the same day and became mixed together after the mother from one of these broods was predated during the night very shortly after hatching and we classified this as adoption. The surviving chicks were from then on recorded as being part of the brood of the remaining mother. Second, during the second season, two broods hatched near synchronously and merged together, with their helpers also overlapping in the same subgroup. We therefore found a corresponding increase in overlap among the helpers over the second and third season, but we cannot know whether the patterns we observed are common or not when broods are very close in age. Association data, between helpers and broods, were collected for each breeding season when chicks were 0–4 months old.

In addition to collecting association data, we observed and recorded cooperative breeding interactions via all-occurrence sampling (Altmann, 1974) over the three seasons. Specifically, we found four types of cooperative breeding interactions between adults and chicks. The first is babysitting behaviour (BBS), whereby individual A stays more than 20 metres from the rest of the group members with some or all of chicks. The second is within-group chick guarding behaviour (GRD), whereby an individual does not

allow other adult group members to approach the chicks. The third behaviour is chick covering (COV) (Figure 1A), whereby an individual covers chick under its wings. The final cooperative breeding behaviour is chick feeding (CFD) (Figure 1B), whereby an individual performs soft trills (a type of vocalisation) calling the chicks to a food item. For each interaction, we recorded the identity of the actor, the identity of the recipient brood, the event duration in the case of cover events, and the number of chicks involved in each interaction. Because broods often moved separately through the group's home range, we aimed to distribute our observation effort evenly across broods over each season.

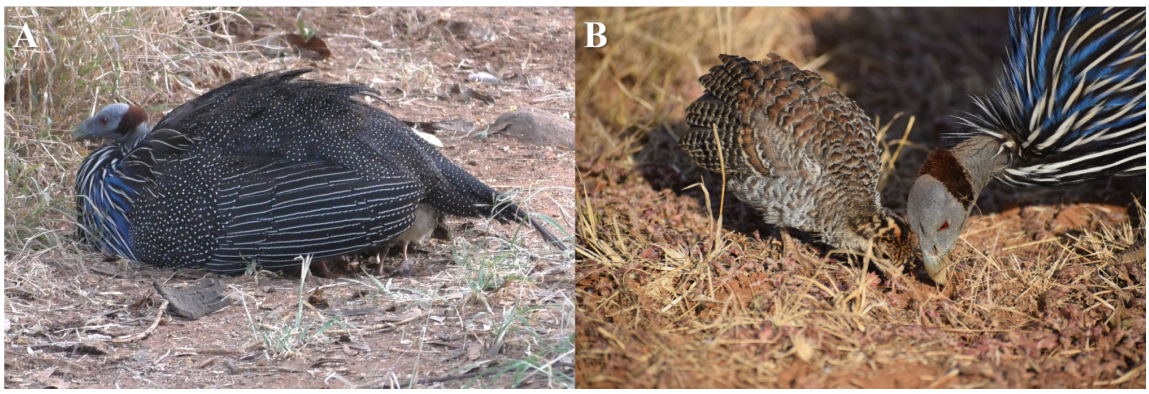

Figure 1. Examples of cooperative breeding behaviours. (A) Chick covering behaviour by an adult male and (B) chick feeding behaviour by an adult male.

Finally, to quantify whether helpers pay a cost by engaging in cooperative breeding behaviour, we recorded videos during a period when the chicks were younger than five weeks (in the final season). From these videos, we were able to quantify the foraging activity by birds in each recording session for the duration that an individual could be tracked in the frame without moving out of the frame (due to occlusion or due to the movement of the person holding the camera). A new session would start if the focal individual started covering the chicks under the wings and would end when they stopped performing the behaviour. Each time we recorded an individual covering the chicks, we also recorded another focal individual who was not engaged in cooperative breeding behaviour. For each focal observation, we counted the number of pecks the individual made (pecking on the ground or on a plant) divided by the length of the focal observation, and whether or not the individual was covering the chicks under its wings or not.

Data analysis

Who helps and who receives most help?

We used a social network approach to identify the main helpers for each group in each of the three seasons. Using the group composition data, we calculated the rate of attendance of each group member to each brood. This rate was calculated by dividing the number of subgroups that the individual was observed in that comprised the brood by the total number of subgroups that the individual was observed in, limited to group composition observations containing that brood (because not all broods were observed in a given sampling day). For example, if an individual was observed 10 times in different groups that contained brood A, of which 8 times it was in a subgroup with brood A, the rate of attendance of the individual to brood A was 0.8.

To identify which individuals occurred with the brood more than expected by chance, we used a simple permutation test (Farine, 2017) which consisted of randomising the subgroups that the focal chicks were contained in. The permutation test worked as follows: for each day, K observations of the chicks were randomly allocated to subgroups observed on that day, where K corresponds to the number of subgroups the chicks were originally observed in that day (thus, all potential helpers remained in the same subgroup, but the chicks were moved between subgroups for the purpose of the permutation test). The rate of attendance for each individual was re-calculated from these permuted data. The permutation test therefore maintained the number of times each individual and each brood was observed, and the same number of total groups and subgroups. This permutation procedure was repeated 1000 times, thereby generating a distribution of rate of attendance values for each individual. From this distribution, we extracted the identities of the individuals whose observed rate of attendance was higher than 95% of the rates generated by the permutation procedure (i.e., significant at $P \leq 0.05$ using a one-tailed test). These individuals were recorded as having significantly higher attendance to that brood than expected by chance. This process was repeated for all broods in all seasons. Finally, to test whether males were disproportionately represented as helpers, we conducted a two-sample proportion test that compared the proportion of males to females among the helper and non-helper category (excluding mothers) in each of the three seasons**.**

We used the cooperative breeding interaction data to characterise the relative contribution of each significant associate to the brood. From these data, we determined whether the mother provided most of the care or not, and (if not) how help received varied between broods. First, we counted the number of each interaction directed towards a focal females' chicks. Because babysitting and within-group guarding behaviours were expressed relatively rarely, they were combined into one category for analysis. Mothers clearly did not give the majority of the care to their chicks, so we then tested whether

some females received more help than others in each of the three seasons. As we did not have an equal opportunity to observe each brood, and difference can lead to spurious outcomes (Hoppitt & Farine, 2018), we used a two-sample test for equality of proportions. We thus conducted pairwise contrasts of the proportion of total help each mother gave to the chicks in her brood. This comparison was performed across the broods within each of the three seasons. Significant effects mean that the difference in the proportion of help given by the mother was significantly lower in one brood than the other.

Finally, we tested whether males gave overall more help than females. To do this, we counted the number of chick feeding interactions for each individual in each season as they were the most prevalent compared to other interactions. We then constructed a generalised linear mixed model with a Poisson error distribution, sex as the only predictor of the count of chick feeding interactions per individual per season, and individual identity and season as nested random effects. We excluded mothers from this analysis. While we could not explicitly account for differences in the number of observations, in practice every individual had the same opportunity to be observed helping each time we collected data. Thus, under random feeding, we would not expect our model to produce a significant difference.

Do helpers pay a cost for helping?

Using the data extracted from the videos, we quantified the proportion of the time spent foraging (response variable), and tested whether this was predicted by whether the focal individual was involved in covering chicks under the wings behaviour (1) or not (0) (binary independent variable). To do this, we used a general linear model with a binomial error distribution. Ideally, we would have accounted for repeated observations of some individuals using mixed models, but we unfortunately could not always identify the individual recorded, and on only three occasions could we do so while an individual was covering the chicks. However, the data were relatively well distributed amongst individuals (average 2.25 observations per individual, when the identity was known). We thus do not expect repeated observations to have a major impact on our conclusions.

RESULTS

Multiple females breed in groups of vulturine guineafowl

Multiple female group members bred in each of the three breeding seasons (Table 1). Among these, there was some consistency in which females attempted to breed, with two females attempting to breed in all three seasons. Others were only observed breeding in later seasons, suggesting that they might have been recently recruited into the group and we observed their first reproduction. Overall, it appears

that reproduction is open to all female group members, with the exception of females that have not yet dispersed.

Table 1: Females in each of the three seasons that successfully bred (had chicks) and the number of helpers (significant associates with the brood) that assisted their brood if they successfully hatched (Y=Yes, N=No).

Season 1 (May 2019)			**Season 2 (May 2020)**			**Season 3 (Nov 2020)**		
Female	Successful	Number of helpers	Female	Successful	Number of helpers	Female	Successful	Number of helpers
BYYO[1]	N	NA	GOOP	Y	28	GAGA	Y	10
GOBO	Y	3	MRMW[4]	N	NA	GOOP	Y	10
GOOP[2]	Y	NA	RARA[5]	N	NA	MGYB[8]	N	NA
RGBW	N	NA	RGBW	Y	28	MRMW[9]	N	NA
ROOR[3]	Y	NA	WOBY[6]	N	NA	RKGK	Y	14
WOBY	Y	6	WYPO[7]	N	NA	YOBK	Y	7
YOBK	Y	7	YOBK	Y	11			

[1]BYYO was predated during incubation.
[2]GOOP's chicks were all predated by the second week.
[3]ROOR was predated the first night after re-joining the group.
[4]MRMW's nest was predated by a white-tailed mongoose.
[5]RARA dumped her eggs on MRMW's nest, which was later on predated.
[6]WOBY was predated during incubation.
[7]WYPO's nest was predated during incubation.
[8]MGYB's nest was predated on the third day of the egg-laying period.
[9]MRMW's nest was predated after she abandoned it during incubation.

Males provide most care while mothers provide a small proportion of the total care to the offspring

There were three key insights from the analysis in the first season. First, each brood had a number of individuals that were observed with the brood more than expected by chance, and not all individuals were consistently detected with a brood. Second, there was relatively little overlap amongst the individuals that were significantly associated with each brood, indicating that each brood had a distinct set of associates. Third, there was a strong male bias amongst associates (Table 2). The patterns of who attended to each brood was a bit more mixed in the second and third seasons.

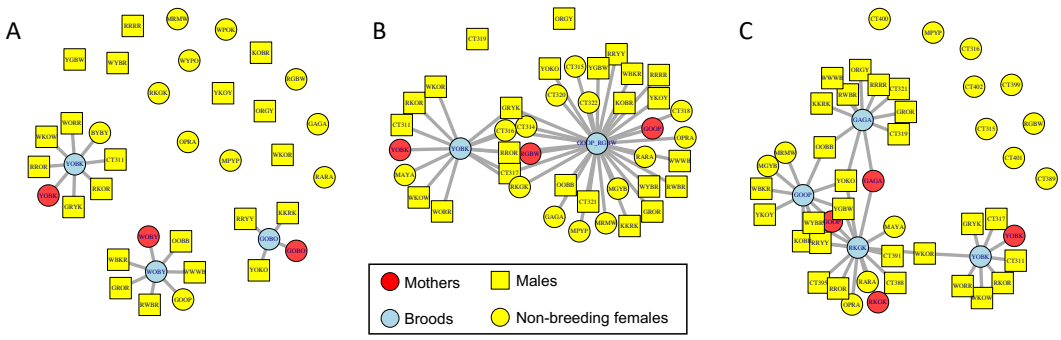

Figure 2. Social networks of attendance to the broods in (A) May 2019, (B) May 2020 and (C) Nov 2020 breeding seasons. ROOR was predated and her chicks joined the WOBY brood in May 2019, while the broods of GOOP and RGBW merged during the May 2020 season.

Table 2. **Males are significantly more associated with the broods than females.** Results of the two-sample test for equality of proportion of males among the non-associated individuals versus males among the significant associates of the three broods, in each of the three seasons.

	Proportion of significant associates					
Season	***Male***	***Female***	X^2	***DF***	***P***	***95%CI***
1	0.667	0.182	4.987	1	0.023	0.111 – 0.858
2	0.815	0.889	0.063	1	0.801	-0.327 – 0.178
3	1	0.455	13.63	1	0.0002	0.187 – 0.904

Mothers also consistently provided a small proportion of the total care that their offspring received. For example, in the first season, out of the 20 cover events recorded for YOBK's chicks, the mother was found to cover chicks in one event for only one minute. She also contributed only 42 of the 330 chick feeding events and one out of seven between group guarding and within-group guarding events. However, not all females received the same amount of help from helpers. YOBK, a female who is known to have successfully bred before, generally received more help in food provisioning and covering chicks under the wings than the other females (see Supplementary Tables S1-S3), whereas there were fewer differences in the help received among the other mothers (see Supplementary Tables S4-S9). YOBK received more help with chick provisioning in each of the other two seasons, with the exception of one female (GAGA) in the third season (see Supplementary Table S7). As cover interactions were relatively rare, some comparisons could not be drawn effectively. There were no instances of babysitting and guarding behaviours in the first season for two mothers as well as the third season for all the mothers.

Overall, males provided significantly more helping interactions than females. Of the 2506 chick feeding interactions given by non-breeding individuals that we recorded across the three seasons, 2451 were given by males. This translates to an estimated 32.7 times more interactions per individual per season for males relative to females (Table 3).

Table 3. Males provide significantly more help than females. Results of the generalised linear mixed model comparing the number of chick-feeding interactions performed by male and female non-breeders across the three seasons.

	Coefficient	***SE***	***Z***	***P***
Intercept	-0.703	0.569	-1.235	0.217
Sex (M)	3.487	0.507	6.880	<0.001
	Random effect	***Variance***	***SD***	
	Actor	2.146	1.465	
	Season	0.433	0.658	

Helpers pay foraging costs while helping

Based on 27 observations of covering chicks under the wings, where the duration of cover was accurately recorded, birds performed this behaviour on average for 16 minutes (range=1–60 minutes). From the video data, we estimated that birds pecked on average 0.10 times per second when they were not performing the cover behaviour (range=0–1.47) and pecked on average 0.01 times per second when they were performing the cover behaviour (range=0–0.01), a significant difference (Table 4). This means that, on average, a bird performing a key helping behaviour missed 81 pecks (90 pecks over 16 minutes when not helping versus 9 pecks over 16 minutes when helping), thereby potentially reducing their foraging intake (based on pecks) by 90%.

Table 4. Helpers pay a foraging cost when helping. The proportion of the time spent foraging (response variable) was predicted by whether the focal individual was involved in chick covering behaviour. The estimates for peck rates as a function of being engaged in cover (1) or not (0) were generated using a binomial general linear model.

	Estimate	***SE***	***Z***	***P***
Intercept	-1.988	0.058	-34.174	< 0.001
Engaged in cover (0:no, 1: yes)	0.526	0.194	-7.856	< 0.001

DISCUSSION

In this study, we provide the first evidence for cooperative breeding in the vulturine guineafowl (*Acryllium vulturinum*) and, to our knowledge, the tenth known case in Galliformes. Vulturine guineafowl groups contain multiple females (we observed up to 8 breeding females out of 13 adult female group members) that can attempt to reproduce, meaning that they are also clearly plural breeders, with a similar social and reproductive system to the sympatric superb starling (*Lamprotornis superbus*) (Rubenstein, 2006). We found that helpers provide the majority of the care and pay a foraging cost when doing so. As in most avian cooperatively breeding birds, we found that helping associations and helping interactions were very male biased. Overall, vulturine guineafowl have the common hallmarks of plural cooperative breeding species.

Helpers relieve the parents of the offspring from the burden of workload, hence increasing the latter's energy as well as enhancing their survival (Downing et al., 2021). The major driving force behind the evolution of cooperative breeding behaviour are the benefits accrued from inclusive fitness (Richardson et al., 2002). A crucial determinant of inclusive fitness is whether an individual has access to reproductive opportunities (Dickinson & Hatchwell, 2004). In group-living species, if all group members can breed then there is likely no benefit to foregoing reproduction in order to raise others' offspring, as is the case in cooperative breeders (Emlen, 1982). The importance of direct and indirect benefits in helpers providing help can be determined by the adaptability of cooperative breeding behaviour (Kingma, 2017). There is scope for non-breeding individuals in precocial species to gain sufficient indirect fitness through cooperative breeding, for example via load lightening or enhancing offspring care (Heinsohn, 2004), to overcome the costs of not breeding themselves. Additionally, in birds females typically disperse while males are usually philopatric, meaning that non-breeding males—in contrast to females—are likely to be related to breeders and their offspring, and may thereby gain indirect fitness by helping (Finn, 2017). Help provided by unrelated individuals requires direct fitness benefits that might be acquired through group augmentation (Wright et al., 2010) as well as via bogus-reciprocity (Connor, 1986; Ligon & Ligon, 1978). By paying to stay and help, helpers promote the formation of social ties as a way of securing being part of the group and benefit from living in one, as well as improving the helper's reputation in the group thereby enhancing their chances of future breeding (Wright, 2007). Cooperatively breeding vulturine guineafowl conform to these hypothesised patterns of cooperative breeding. Helpers are likely to increase the reproductive success of the female or enhance the female's survival through reducing her need to care directly for the chicks. Specifically, we found that the female only provides a small proportion of all the chick caring interactions, which is likely to be important for her to regain the body condition she lost through laying and attending to the nest. Further, as female vulturine guineafowl may breed twice per year—as we found with several females

being successful in both May 2020 and November 2020 (Table 1)—helping might be key to females regaining body condition in time for the next reproductive opportunity by reducing the inter-birth interval (Ridley & Raihani, 2008). Thus, our study provides further support for a number of general hypotheses surrounding cooperative breeding.

There is considerable variation in the structure of cooperatively breeding groups among species, ranging from a single breeding pair with associated helpers to multiple breeding units, which may be polygamous or polyandrous (Ausband, 2018). We still have no clear understanding of the drivers that give rise to multiple breeding units in the vulturine guineafowl. The vulturine guineafowl form multiple breeding pairs during the breeding season and non-breeding group members provide care to the offspring after hatching. This is similar to golden lion tamarins (*Leontopithecus rosalia*) which have multiple breeding individuals in which adults care for offspring regardless of how many offspring there are in a cooperative polyandrous group (Dietz & Baker, 1993; Goldizen, 1989). Vulturine guineafowl breed during the wet season when there are temporary increases in resource abundance (both food and safe nesting sites) that allow many individuals to reproduce at the same time. Our study also highlights the variance that can emerge in terms of who is a successful breeder, with many clutches predated during incubation or early in the life of chicks. We ruled out dominance as a determinant for the breeding success in females, firstly because the structure of the female dominance hierarchy is not very clear relative to the males (Dehnen et al., 2022) and secondly because GOOP, who consistently lost dominance interactions and performed many subordinate interactions, was one of only three females to (attempt to) breed in all three seasons. However, more data are needed to more explicitly evaluate the link between breeding and dominance, and whether factors such as experience might drive variation in nesting rates and nest success among females.

In this study, we identified four juvenile-directed cooperative behaviours by non-parents, including babysitting (BBS), chick feeding (CFD), covering the chicks under the wings (COV), and within-group guarding behaviour against other adults (GRD). These are consistent with cooperative breeding behaviours exhibited in other precocial species (Du Plessis et al., 1995). For example, Kalij pheasants (*Lophura leucomelanos*) have different cooperative breeding behaviours which include caring for chicks, vigilance against predators and agonistic interactions among conspecific intruders (Zeng et al., 2016). Similarly, helpers in the buff-throated partridge (*Arborophila brunneopectus*) care for the chicks by showing food and remaining vigilant against intruders (Wang et al., 2017). Such behaviours are clearly beneficial to chicks, but may not be immediately obvious to observers, and typically require following groups at small distances to make close observations. Doing so was made substantially easier

436 by our study group being habituated to our presence and due to their home range being centred within a
437 fenced area that was safe to walk in.
438
439 The associates of each brood were predominantly male group members, and they typically provided
440 more care than the mother did. These results are consistent with those reported in other cooperatively
441 breeding Galliformes. One exception in our data was the second breeding season, although this season
442 was notable for having many failed nests, which could have stimulated help from females. Why males
443 attend to broods more than females in vulturine guineafowl, given that subadult females can remain in
444 their natal territory for several years before dispersing (Klarevas-Irby et al., 2021), remains unknown.
445 This pattern has been observed widely in other species (Green et al., 2016). Further, we found that even
446 though some females were detected as significant associates of the brood, male helpers still provided
447 nearly 98% of all the chick feeding interactions (excluding those from the mothers), which also suggests
448 that 'female helpers' offer few benefits to the chicks. This is consistent with the sympatric grey-crowned
449 babbler (*Pomatostomus temporalis*), where only the number of male helpers increased reproductive
450 success (Blackmore & Heinsohn, 2007).
451
452 By studying the social network of individual helpers and the broods, we showed that helpers appeared
453 to be generally brood specific. One striking result was that not all females received help equally: one
454 female, YOBK, which also bred in previous seasons, received consistently more help than other females
455 across the three seasons. One reason for this could be that this female had more male offspring in the
456 group. For example, CT317, a male that helped YOBK's brood in the second and third seasons, was
457 part of the brood that she cared for in the first season. This pattern is mirrored by patterns of consistency
458 in helping by other males. For example, YKOY was not detected as a helper in the first season, when
459 GOOP did not successfully breed, but was significantly associated with her brood in the following two
460 seasons. Thus, it is likely that—consistent with many other species (Cockburn, 2006)—help is given by
461 male offspring from previous broods. This would be facilitated in vulturine guineafowl by very high
462 natal philopatry by males (Klarevas-Irby et al., 2021).
463
464 A consistent pattern that emerged across all three seasons is that mothers did not provide the majority
465 of care to their chicks. The large amount of help given by non-parents is perhaps unusual (Green et al.,
466 2016). For example, in purple gallinules (*Porphyrio martinicus*), breeding adults provide the majority
467 of the care to chicks, which are sub precocial (Hunter, 1987), while both male and female purple
468 gallinules participate in the incubation process (Gross & Tyne, 1929). One reason why female vulturine
469 guineafowl receive so much help may be because of the high cost they pay during incubation—meaning
470 that recovering their body condition might compromise the amount of care they can provide to the

current brood, which is then offset by the help provided by other individuals. Further, care involves not only food provisioning, vigilance against predators and agonistic behaviours against intruders (Clutton-Brock & Manser, 2016) but also learning so as to enhance foraging skills (Heinsohn, 1991).

Cooperative breeding behaviours are identified mostly through food provisioning by different individuals, especially at the nest for altricial species. The most frequent form of cooperative breeding behaviour given by vulturine guineafowl helpers was calling the chicks to food by making soft trills. More chick feeding interactions were observed across the three seasons compared to all the other cooperative breeding interactions combined. Helping is also likely to be costly to helpers, given that they express a demonstrable reduction in food intake to provide care to the chicks while the rest of the group is foraging—they forage less when providing cover than when not providing cover. However, few studies have investigated the costs of care to helpers (Covas et al., 2022; Cram et al., 2015; Guindre-Parker & Rubenstein, 2018a, 2018b; Mendonça et al., 2020). In meerkats (*Suricata suricatta*), helpers lose weight when they participate in cooperative breeding activities such as feeding the young (Russell, 2003). Similarly, in white winged choughs (*Corcorax melanorhamphos*), helpers suffer mass loss from performing incubation, in addition to costs they incur by choosing to remain in their natal territory (Heinsohn & Cockburn, 1994). While we report that vulturine guineafowl helpers incur some foraging costs, our data do not yet allow us to quantify the total extent of the costs they bear. It may be that, for adult males, these are relatively small costs that they are willing to pay when their own reproductive attempts have failed (e.g., due to lack of breeding opportunities).

Further behavioural studies are needed on cooperative breeding in non-passerines, species with precocial young, and plural breeders. Specifically, we suggest that future research investigates what determines the relative reproductive success of males and females, especially in species where nest predation is high and where, subsequently, which females succeeds in bringing chicks back to the brood may be relatively random. Such insights are important for understanding how indirect fitness might be gained via paternal routes, which are usually linked with much greater kinship uncertainty. Finally, further studies are needed on the reproductive behaviours of precocial species, where female investment (or lack of help received) during incubation, together with high levels of sociality, may be an indicator of which species breed cooperatively.

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ETHICS

Ethical approval was granted by the Max Planck Society's Ethikrat Committee. Data were collected with permission from, and in collaboration with, the Kenya National Science and Technology Council (NACOSTI/P/16/3706/6465), the National Environment Management Authority (NEMA Access Permit NEMA/AGR/68/2017), the Kenya Wildlife Service, the National Museums of Kenya, Dr. Peter Njoroge, and the Mpala Research Center.

CONFLICT OF INTEREST

The authors declare no conflict of interest

AUTHOR CONTRIBUTIONS

DRF and DP conceived the study. DRF, DP, JK, and BN designed the study. BN and DP collected the data. DRF, DP, JK, and BN analyzed the data. DRF, TD, and BN drafted the manuscript. All the authors contributed to the final manuscript.

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Data were collected with permission from, and in collaboration with, the National Commission for Science, Technology, and Innovation (NACOSTI), the National Environment Management Authority (NEMA), the Kenya Wildlife Service (KWS), the National Museums of Kenya (NMK), Peter Njoroge, the Mpala Research Centre. In addition, we thank the vulturine guineafowl team members, especially Wismer Cherono and Deborah Molitor for assistance with data collection and the Farine lab for discussions about the study.

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673 **SUPPLEMENTARY MATERIALS FOR:**

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675 **Cooperative breeding in a plural breeder: the vulturine guineafowl (*Acryllium***
676 ***vulturinum*)**

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679 **Table S1**. Overview of two-sample tests for equality of proportions, comparing the proportion of help given by
680 the mother relative to the help given by helpers across the three broods in season 1. Significant values are shown
681 in bold.

Pairwise comparison	Interaction type	Mean 1	Mean 2	χ^2	DF	95% CI	P
YOBK-WOBY	CFD	0.250	0.119	7.480	1	0.075–0.245	**0.006**
	COV	0.600	0.454	6.020	1	-0.006–1.000	**0.014**
GOBO-YOBK	CFD	0.280	0.119	10.658	1	0.040–0.281	**0.001**
	COV	0.000	0.045	2.708^{e-31}	1	-0.178–0.870	1
WOBY-GOBO	CFD	0.250	0.279	0.041	1	-0.190–0.131	0.839
	COV	0.600	0.000	0.365	1	-0.179–1.000	0.56

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685 **Table S2**. Overview of two-sample tests for equality of proportions, comparing the proportion of help given by
686 the mother relative to the help given by helpers across the three broods in season 2. Significant values are shown
687 in bold.

Pairwise comparison	Interaction type	Mean 1	Mean 2	χ^2	DF	95% CI	P
YOBK-GOOP	CFD	0.067	0.2333	4.1074	1	-0.316-0.0178	**0.042**

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Table S3. Overview of two-sample tests for equality of proportions, comparing the proportion of help given by the mother relative to the help given by helpers across the three broods in season 3. Significant values are shown in bold.

Pairwise comparison	Interaction type	Mean 1	Mean 2	χ^2	DF	95% CI	P
YOBK-RKGK	CFD	0.339	0.068	61.489	1	0.205-0.337	**4.450^{e-15}**
	COV	0.333	0.000	2.341	1	-0.0719-0.739	0.126
YOBK-GOOP	CFD	0.168	0.068	15.064	1	0.0544-0.146	**0.001**
YOBK-GAGA	CFD	0.100	0.068	1.923	1	-0.010-0.073	0.166

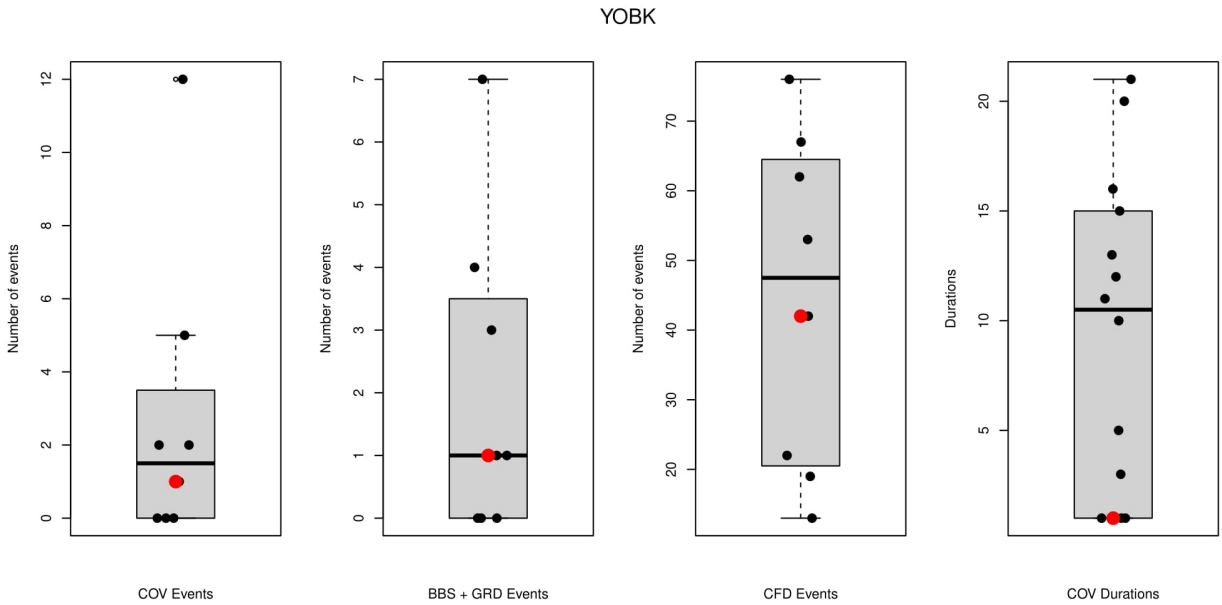


Figure S1. Amount of help given by the mother (red points) and helpers (black points) for the YOBK brood in season 1.

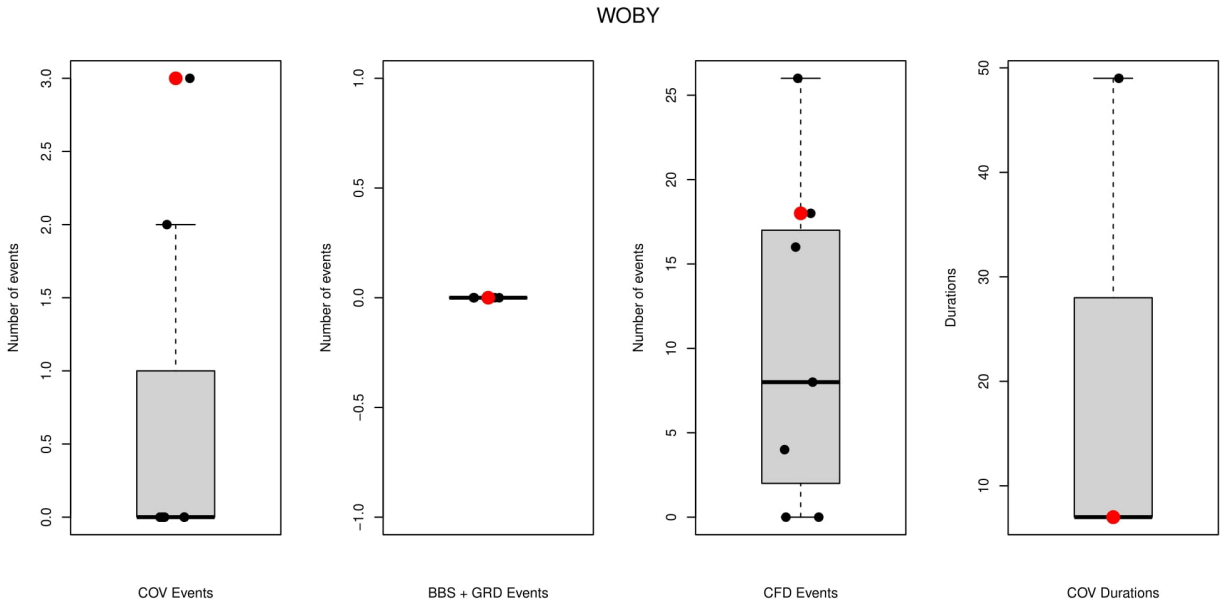


Figure S2. Amount of help given by the mother (red points) and helpers (black points) for the WOBY brood in season 1.

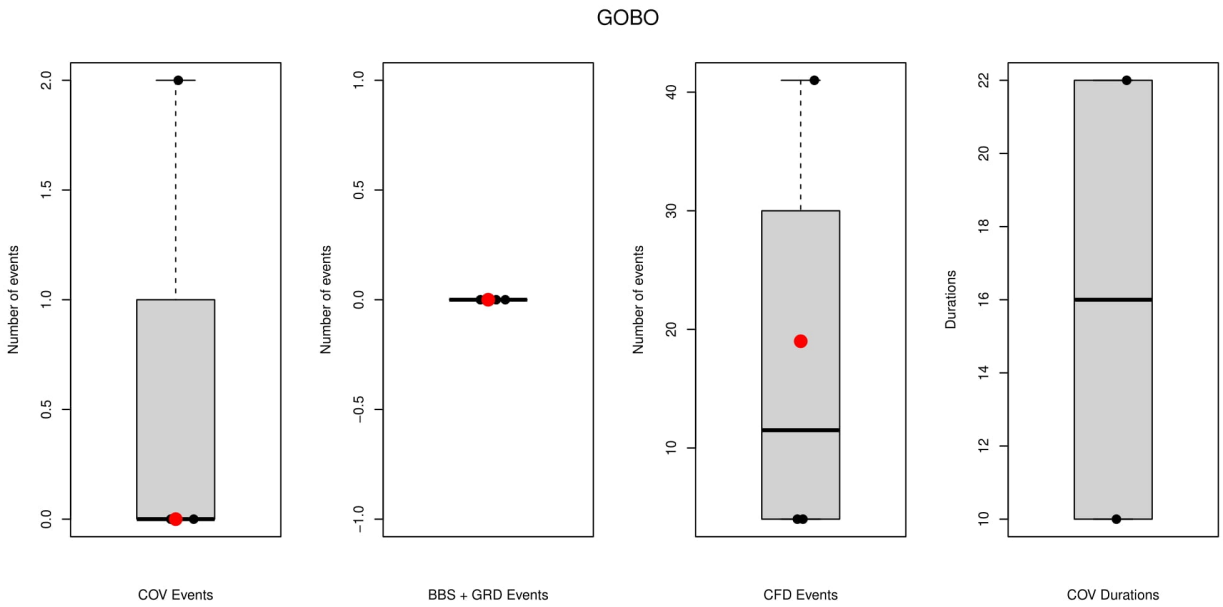


Figure S3. Amount of help given by the mother (red points) and helpers (black points) for the GOBO brood in season 1.

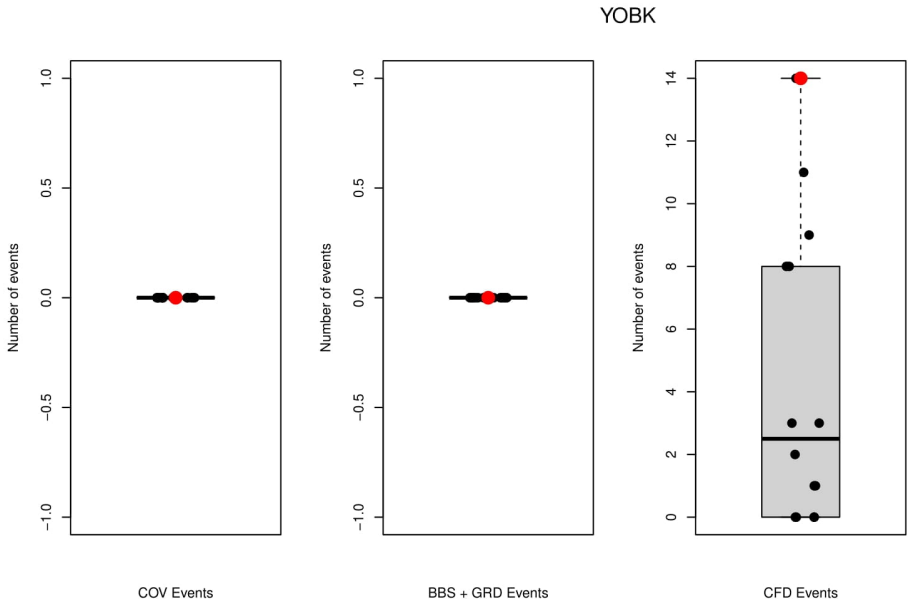


Figure S4. Amount of help given by the mother (red points) and helpers (black points) for the YOBK brood in season 2.

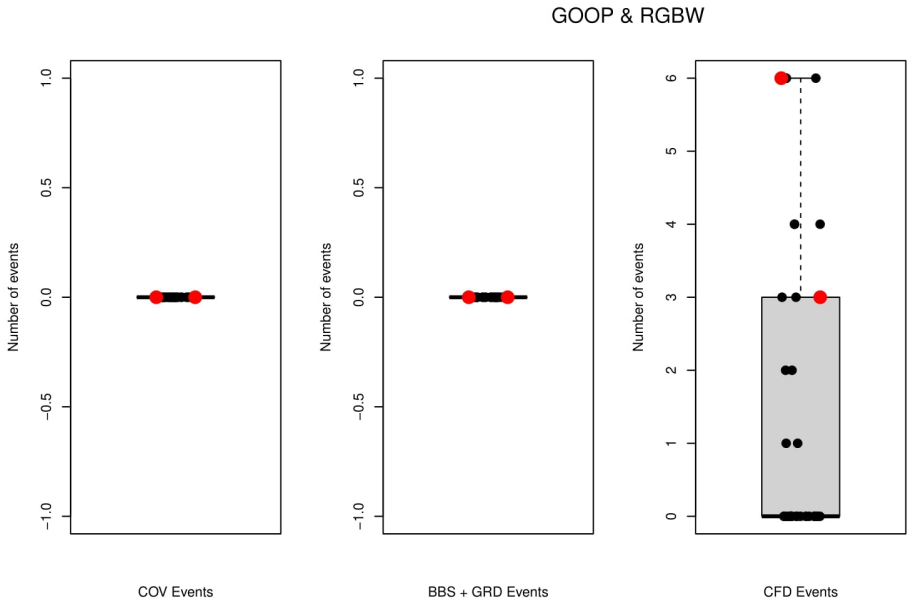


Figure S5. Amount of help given by the mother (red points) and helpers (black points) for the GOOP (and chicks from RGBW) brood in season 2.

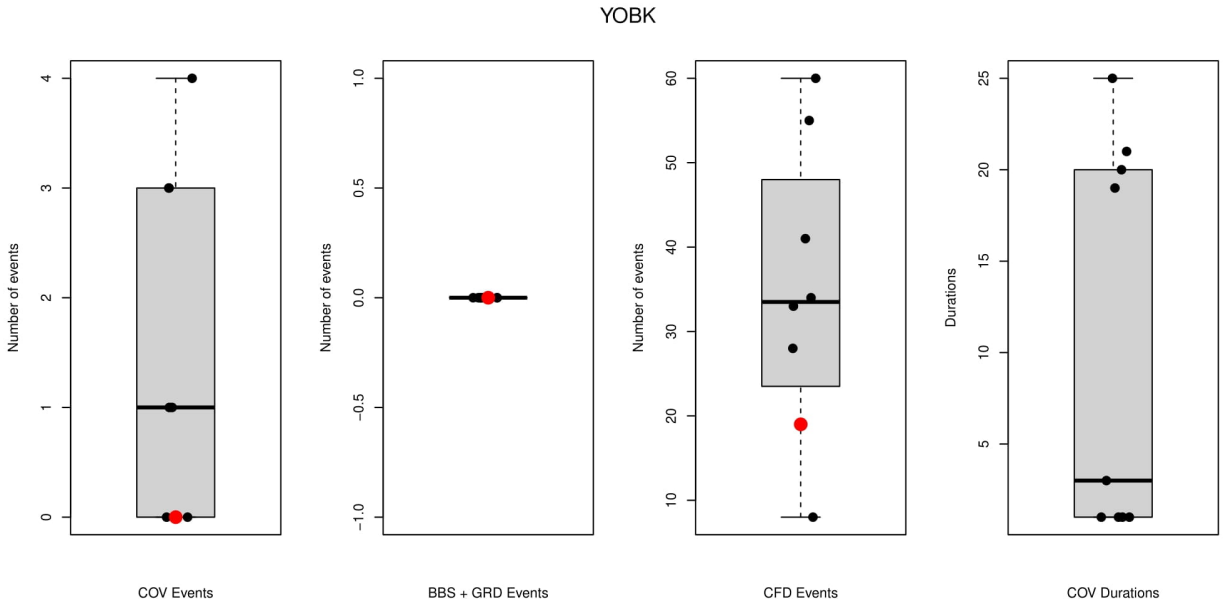


Figure S6. Amount of help given by the mother (red points) and helpers (black points) for the YOBK brood in season 3.

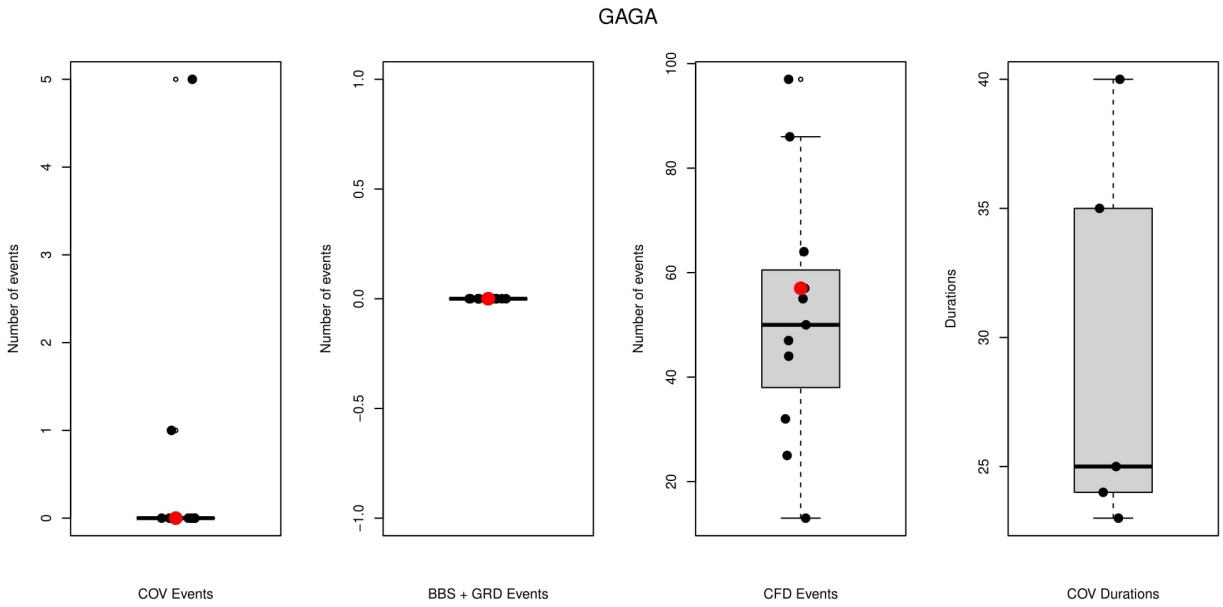


Figure S7. Amount of help given by the mother (red points) and helpers (black points) for the GAGA brood in season 3.

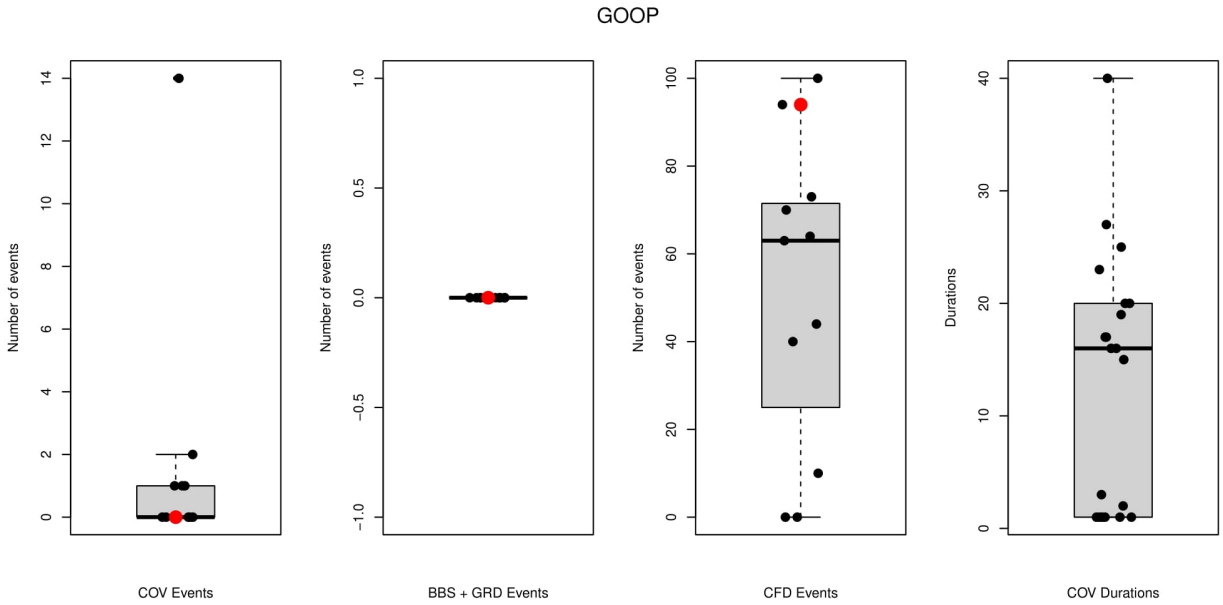


Figure S8. Amount of help given by the mother (red points) and helpers (black points) for the GOOP brood in season 3.

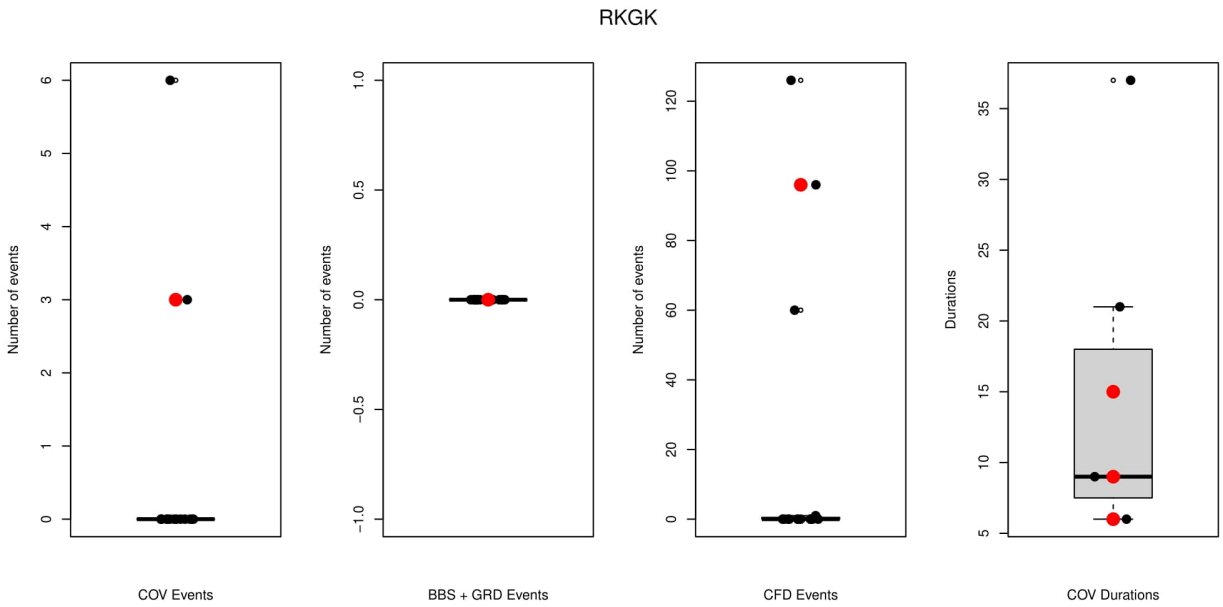
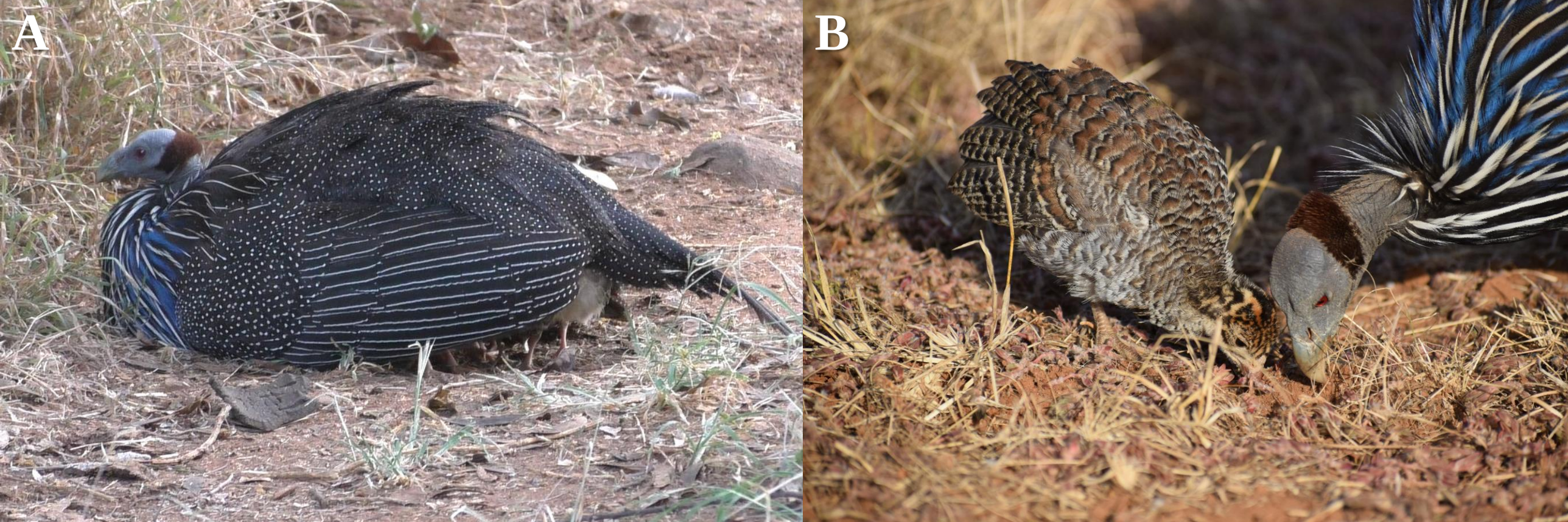
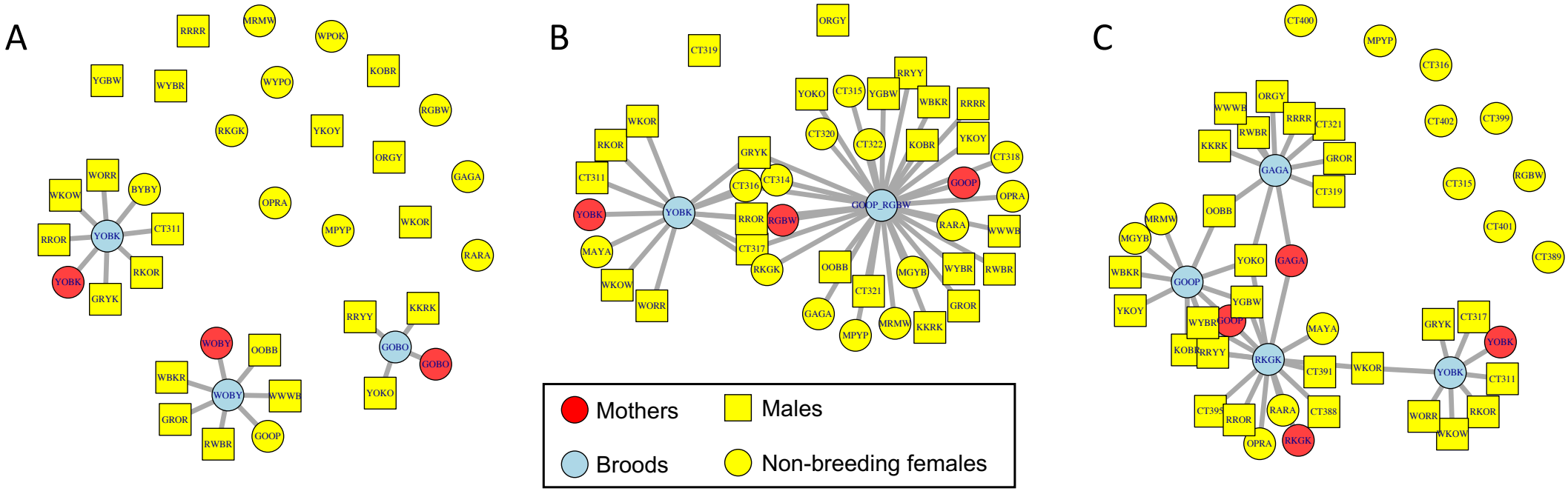


Figure S9. Amount of help given by the mother and helpers for the RKGK brood in season 3.


A
B


A
RRRR
MRMW
WPOK
YGBW
WYBR
WYPO
KOBR
RGBW
RKGK
YKOY
ORGY
GAGA
WORR
WKOW
BYBY
OPRA
YOBK
CT311
RROR
MPYP
WKOR
RARA
YOBK
RKOR
GRYK
RRYY
KKRK
GOBO
GOBO
YOKO
WOBY
OOBB
WBKR
WOBY
WWWB
GROR
GOOP
RWBR
B
ORGY
CT319
RRYY
YOKO
CT315
YGBW
WBKR
RRRR
WKOR
CT320
CT322
KOBR
YKOY
RKOR
GRYK
CT318
CT311
CT316
CT314
GOOP
OPRA
YOBK
YOBK
GOOP_RGBW
RROR
RGBW
RARA
WWWB
CT317
MAYA
RKGK
OOBB
MGYB
WYBR
RWBR
WKOW
CT321
GROR
WORR
GAGA
MPYP
MRMW
KKRK
C
CT400
MPYP
CT316
WWWB
ORGY
RRRR
CT321
CT402
CT399
RWBR
KKRK
GAGA
GROR
CT319
CT315
RGBW
OOBB
MRMW
CT401
MGYB
YOKO
GAGA
CT389
WBKR
GOOP
YGBW
YKOY
WYBR
GOOP
MAYA
GRYK
CT317
YOBK
KOBR
RRYY
RKGK
CT391
WKOR
YOBK
CT311
CT395
RROR
RARA
CT388
WORR
RKOR
OPRA
RKGK
WKOW
Mothers
Males
Broods
Non-breeding females