


Cooperative and plural breeding by the precocial Vulturine Guineafowl

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Cooperative breeding in birds is thought to be more common in altricial species, with few described cases in precocial species. However, cooperative breeding may also be more difficult to detect in precocial species and could have been overlooked. We investigated whether precocial Vulturine Guineafowl *Acryllium vulturinum* breed cooperatively and, if so, how care is distributed among group members. We collected data from 51 uniquely marked individuals (27 males, 24 females), of which 13 females bred at least once over three different breeding seasons. We found that broods had close associates comprising both adults and subadults that exhibited four distinct cooperative breeding behaviours: babysitting, chick guarding, covering the chicks and calling the chicks to food. Further, we found that offspring care is significantly male-biased, that non-mother individuals provided most of the care that each brood received, that breeding females differed in how much help they received and that carers pay a foraging cost when providing care. In line with many other birds, we found that females received help from their sons. Our results confirm that Vulturine Guineafowl are cooperative and plural breeders and add 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, multilevel societies, precocial species.

In some bird (Arnold & Owens 1998), mammal (Clutton-Brock 2006), fish (Kölliker 2012) and invertebrate (Russell & Lummaa 2009) species, more than two adults contribute to raising offspring by providing alloparental care, which is

known as cooperative breeding. Cooperative breeding has received considerable empirical (Stacey & Koenig 1990, Koenig & Dickinson 2016) and theoretical (Emlen 1982, Hatchwell & Komdeur 2000, Shen *et al.* 2017) attention over the past five decades. In birds, cooperative breeding is thought to be more prominent among altricial species (where chicks depend on care in the nest after hatching) (Cockburn 2006, Wang *et al.* 2017). A

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recent review found that cooperative breeding is found in 11% of species with altricial young, but only 4% of species with precocial young (where chicks are more independent immediately after hatching) (Scheiber *et al.* 2017). The relative lack of cases of cooperative breeding among species with precocial young has led to the hypothesis that there exists a link between altriciality and cooperative breeding because precocial chicks require less care (Ligon & Burt 2004, Wang & Kimball 2016). However, cooperative breeding is known to occur in distantly related precocial species, implying that it has evolved several times in precocial species (Wang & Kimball 2016) and that other factors may be driving the perceived difference.

The apparent disparity in frequency of cooperative breeding between altricial and precocial species could be because species with precocial offspring have less need for care. However, this logic may be flawed as it overlooks the significant costs to females and risk to offspring in precocial species. First, females in precocial species typically invest almost twice as much energy into their eggs as altricial species (Ar & Yom-Tov 1978), suggesting a large energetic investment in laying the clutch. Secondly, due to the high predation risk to the eggs of ground-nesting birds (Thompson & Raveling 1987), females of ground-nesting precocial species typically have very high nest attendance rates, potentially foregoing feeding entirely during incubation. For example, female Common Pheasants *Phasianus colchicus* attend their nest intensively and, as a result, suffer a 19% reduction in body mass after the incubation period (Breitenbach & Meyer 1959). By caring for chicks after hatching, non-breeding individuals may provide benefits to breeding females of precocial species by allowing them to produce larger clutches and facilitate recovery during the post-hatching period: the 'load-lightening' hypothesis (Hatchwell 1999, Crick 2008). Furthermore, given that chicks of most precocial species have lower survival probabilities than adults, additional offspring care could substantially enhance chick survival in such species (Heinsohn 2004). Accordingly, there is substantial scope for the fitness of females and chicks to be enhanced through cooperative care in precocial species, and hence for non-breeding individuals to gain sufficient indirect fitness.

An alternative reason for the limited evidence for cooperative breeding in precocial species is that

classical examples of cooperative breeding in birds primarily consider offspring care at the nest, rather than other forms of care that may occur after chicks leave the nest. If this is the case, cooperative breeding may have been disproportionately undetected in precocial species. Although provisioning chicks at the nest provides parents and/or chicks with obvious benefits, there are ways in which individuals can contribute to raising offspring in precocial species. For example, in Trumpeters *Psophia* spp., non-breeders contribute to nest-building and incubation, as well as feeding chicks after leaving the nest (Sherman 1995). Even without attending to the nest, group members can still enhance offspring survival and reduce parental investment after chicks have hatched. For example, group members may protect chicks from predators or the abiotic environment (such as providing chicks with shade (Cuthbert 1954) or warmth (Bartholomew 1966)), identify and provide food for chicks, or maintain vigilance to allow chicks more time to forage. Such benefits of cooperative breeding are, however, likely to be more difficult to detect and measure in precocial species (Cockburn 2006). Beyond the challenge of quantifying the benefits to chicks and costs to individuals providing care, it can also be difficult to study precocial chicks in their natural environment. Doing so requires following groups and chicks closely for long periods, during which time they can be highly mobile, and may range in areas which are inaccessible to human observers or in concealing habitats. 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 and increasing evidence for cooperative breeding is Galliformes. To our knowledge, cooperative breeding has been found in nine species of Galliformes. In five species, the evidence for cooperative breeding is relatively strong. These are the Buff-throated Monal-Partridge *Tetraophasis szechenyii* with one breeding pair and one to three helpers (Wang *et al.* 2017), Spotted Wood Quail *Odontophorus guttatus* with two to nine adult helpers (Hale 2006), Kalij Pheasants *Lophura leucomelanos* (Zeng *et al.* 2016, Lone *et al.* 2024) with one to nine individual helpers, Tibetan Eared Pheasants *Crossoptilon harmani* with up to 10 individuals in a social group and White Eared Pheasants *Crossoptilon crossoptilon*, which move in large flocks (Lu & Zheng 2005). In these species, helpers were found

to show food to chicks, remain vigilant by monitoring their surroundings to check for predators and care for chicks by guarding them from conspecific intruders. In four species the evidence for cooperative breeding remains more anecdotal. These are the California Quail *Callipepla californica* where helpers consist of at least two females and multiple males (Lott 1999), Northern Bobwhite *Colinus virginianus* and Scaled Quail *Callipepla squamata* with flocks of up to 30 individuals (Orange *et al.* 2016) and Marbled Wood Quail *Odontophorus gujanensis* with at least five adults helping the chicks (Skutch 1947). However, the phylogenetic distance between these species (Ligon & Burt 2004, Guan *et al.* 2022) and among other species that breed cooperatively and have precocial young suggests that cooperative breeding could be more common in Galliformes and other precocial species than previously thought. This is also likely because Galliformes have received disproportionately less attention from researchers relative to many other groups of birds (Xu *et al.* 2011). Hence, Galliformes represent an excellent taxonomic group for exploring cooperative breeding, and how cooperative breeding behaviours might be expressed away from the nest.

The Vulturine Guineafowl *Acryllium vulturinum* is a large (~1.6 kg), terrestrial galliform that lives in a complex society. During the non-breeding seasons, Vulturine Guineafowl form spatiotemporally stable social units consisting of approximately 13–65 individuals, and these social units can exhibit preferential associations with other social units to form larger, higher level social units (i.e. a multilevel society, see Papageorgiou *et al.* (2019) for more details). Stable social units during the non-breeding season contain many adults, subadults and juveniles, with these probably representing members of multiple breeding subunits (Papageorgiou *et al.* 2019). This means that Vulturine Guineafowl are a good candidate for being both plural and cooperative breeders, the former being defined as living in stable social units containing multiple reproductive males and females. Vulturine Guineafowl also have extreme sex-biased dispersal with all males remaining in their natal social units (Klarevas-Irby *et al.* 2021). This sets the scene for high relatedness among males within the same social unit, 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).

Our study characterizes the incidence and structure of cooperative breeding in the Vulturine Guineafowl. We combine data on social associations between colour-marked individuals and broods and link these associations to direct observations of the care given to each brood by carers. We also test what share of offspring care is given by mothers versus carers, and whether the latter pay a foraging cost when providing care, and by tracking cohorts across years we test whether care is provided by previous, non-reproductive offspring. By employing a diversified approach combining behavioural data and social network analyses, we provide new evidence for the presence of cooperative breeding behaviour in an under-studied group of precocial species.

METHODS

Study species

While Vulturine Guineafowl live in stable social units for most of the year (Ogino *et al.* 2023), they can exhibit short-term changes in within-unit social associations (Fig. 1) when conditions are suitable for breeding (rainy seasons). First, breeding pairs split off from the rest of the social unit and remain separate from the other members of the social unit, with the male mate-guarding the female, for up to several weeks. Non-breeding individuals remain largely cohesive, although they may split into clusters for minutes to hours (e.g. two subsets of the non-breeding individuals might forage on opposite sides of a large open area). During this period, breeding females forage intensively and then begin laying a clutch of 8–15 eggs in a scrape on the ground.

At the onset of incubation, males return to the remaining members of the social unit and may re-pair with a new female. Incubation and the timing of hatching is typically asynchronous among females from the same social unit. As in other guinea fowl (Del Hoyo *et al.* 1994), female Vulturine Guineafowl receive no help during incubation.

Vulturine Guineafowl chicks are precocial and highly vulnerable to predation during the first few weeks of life; hence, they may benefit from any protection offered by adults and subadults. Soon

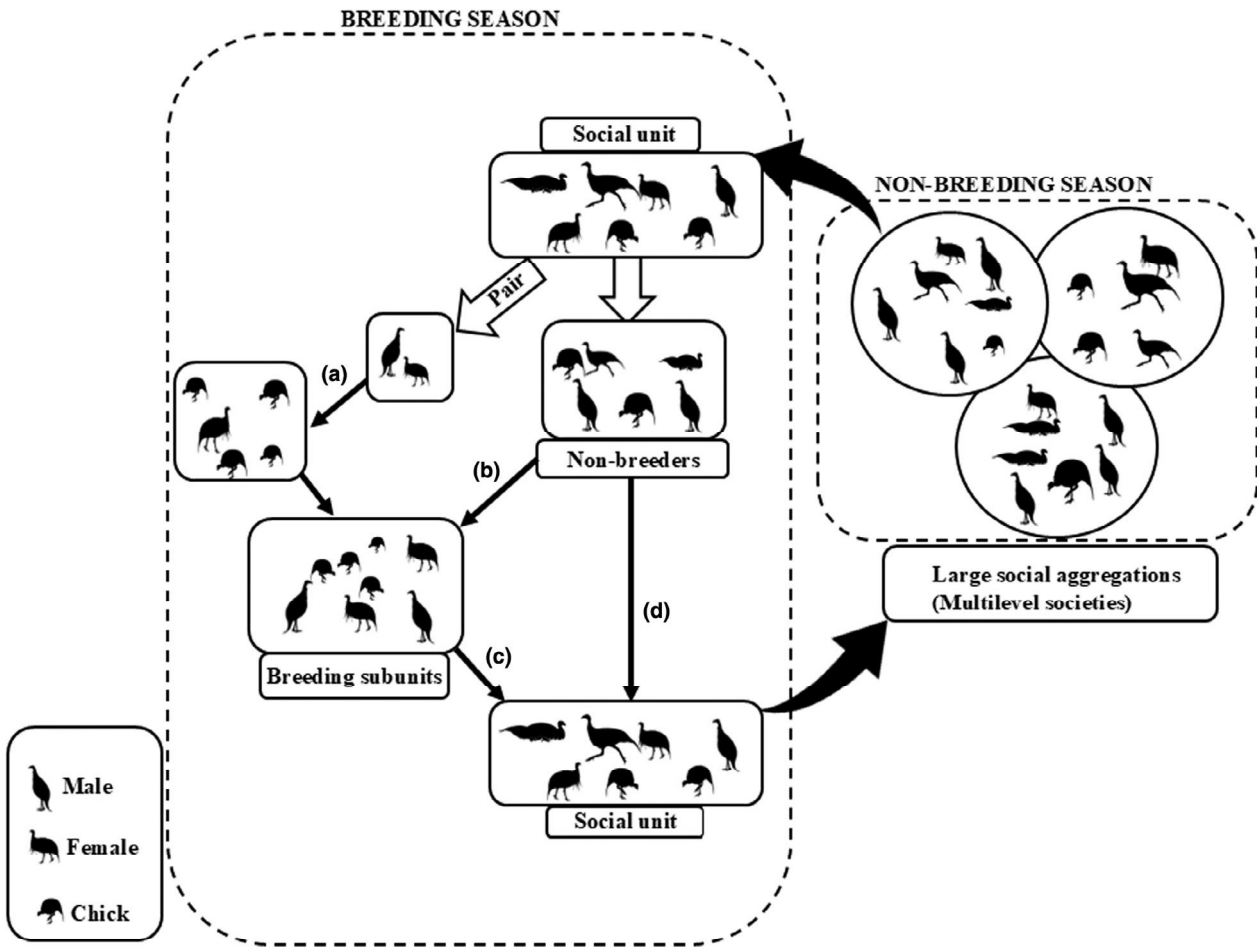


Figure 1. Social structure of the Vulturine Guinea-fowl. During the breeding season, pairs split off from the rest of the social unit and move separately from the rest of the group. (a) The male mate-guards the female for several weeks and during this period the female lays a clutch of eggs and starts incubating. (b) After hatching, non-breeders and other members of the social unit join the mother, form smaller breeding subunits and provide care for the chicks. (c) Breeding subunits re-form into a stable social unit. (d) The rest of the non-breeders re-form into a stable social unit. During the non-breeding season, social units aggregate forming multilevel societies.

after hatching, mothers and chicks typically re-join the social unit. However, there is then often an increase in the splitting of the unit into smaller social subunits. We predicted that these subunits would be stable and represent breeding subunits.

Study area, study population and field data collection

Our study took place at Mpala Research Centre (MRC) (0°17'32.67"N, 36°53'54.45"E), in Laikipia County, Kenya. At MRC, we have been conducting a long-term GPS-tracking study of a population of Vulturine Guinea-fowl since 2016.

Mpala is characterized by semi-arid savanna habitat with rainfall averaging 500–600 mm per year, occurring predominantly in two rainy seasons (Young *et al.* 2003). The natural vegetation is mainly *Acacia* scrubland, and Vulturine Guinea-fowl specialize on the red soils dominated by *Acacia mellifera* and *Acacia etbaica*.

Mpala is rich in predators and megafauna so research is conducted in vehicles, preventing close observation and following of birds. One exception to this is a 0.3-km² fenced compound that is regularly visited by up to three social units. One of these social units (the 'Mpala group') has become accustomed to human presence, and the females

reproduce within or nearby the fenced compound and spend at least part of their day foraging (with their chicks after breeding) in this area, allowing close observations. The members of this social unit were first colour-banded and tracked with GPS (He *et al.* 2022) in September 2016. For the present study, we collected data from 51 uniquely marked individuals (27 males and 24 females) from the habituated social unit living within the fenced compound at Mpala.

Our study spanned three wet seasons: November 2019 to January 2020, May to August 2020 and November 2020 to January 2021 (following this period, a prolonged drought prevented this group from breeding again until July 2023). Data collection involved following pairs after they had split from the main social unit, finding and monitoring the nests, and observing care behaviours post-hatching. Nest monitoring was conducted *ad hoc* (taking care to minimize disturbance and avoid making the nest detectable by predators). Pairs were defined as a female and an associated male that moved together (typically <5 m apart) and away from the other birds (at least 20 m from the nearest birds, 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. When the clutch was expected to hatch (25 days after the start of incubation), we searched for the female and chicks to collect data on cooperative breeding interactions.

After chicks hatched, we collected data on associations between adult (and immature) guineafowl and broods by recording data on the composition of groups observed in the field in the morning (6:00–9:30 AM) and evening (5:00–7:00 PM) for an average of 4 days per week. Our aim was to determine the membership of breeding subunits, within the long-term stable social unit, using social network analysis. Groups were defined as a set of individuals that were observed within sight and/or close proximity (<1.5 m) to each other or were moving in a coordinated manner. Each time a group of guineafowl was encountered (irrespective of whether chicks were present), we recorded the identity of every banded bird present, the identity of the brood (if present), as well as the total number of banded adults, unbanded adults and chicks present. We assigned a unique group identifier to each observation (and to all individuals observed therein). Within each group observation, we also

recorded any subgroups, which were defined as clear spatial clusters of individuals that were separated from (by >5 m), but otherwise moved cohesively with, other guineafowl. The number of individuals in each group and especially subgroup could vary within and across days as members of the social unit engaged in different breeding-related activities, hence our use of social networks to infer the breeding subunits.

Although chicks could not be marked individually before they were one month old, broods were generally identifiable because they hatched asynchronously, so chick size differed markedly between broods. Based on these differences, we could identify and assign a unique identifier (using the identity of their social mother) to the chicks representing each brood in each breeding season. Adults observed associating with a breeding female and her chicks also moved mostly independently from other broods (hence our prediction that they formed breeding subunits). However, we observed two exceptions to this rule when multiple nests hatched at the same time and broods with similarly sized chicks merged. In these cases, we re-assigned the chicks that merged under a shared identifier with uncertain maternity (i.e. treating them as one social brood belonging to both females). Association data between adults and broods were collected for each breeding season until chicks were three months old, by which time the stable social unit had generally re-formed.

In addition to collecting association data (group composition), we observed and recorded four types of cooperative breeding interactions (babysitting, chick guarding, covering the chicks and calling the chicks to food; Table 1) via all-occurrence sampling (Altmann 1974). Chick covering and chick-feeding behaviours are illustrated in (Fig. 2). 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, we aimed to distribute our observation effort for recording cooperative breeding interactions evenly across broods over each season.

We defined any individual that was engaging in any cooperative breeding behaviour as a 'carer'. In other species, carers have been reported to include non-parents (e.g. older siblings from previous years; Ligon & Ligon 1978), unrelated individuals (Clutton-Brock 2002) or social parents. Due to a

Table 1. Types of cooperative breeding interactions between adults and chicks.

Interaction	Code	Description
Babysitting	BBS	An individual stays more than 20 m from the rest of the other individuals with one or more chicks for more than 5 min.
Guarding	GRD	An individual does not allow other adults to approach one or more chicks.
Cover	COV	An individual covers one or more chicks under its wings.
Chick-feeding	CFD	An individual performs soft trills (a type of vocalization), calling chicks to a food item.

lack of genetic data on kinship, we can only conclude whether a given female is the social mother of the brood or any associated carers.

To quantify whether carers incur costs, we analysed videos of carer behaviour when engaging in cooperative interactions versus not. Videos were recorded using a Panasonic HC-V800 High-Definition Video Camera. To avoid observer influence, a focal brood was followed from between 2 and 5 m distance. From the videos, we quantified foraging activity by birds in each recording session for the duration that an individual could be tracked without moving out of frame (due to occlusion or due to the movement of the person holding the camera). A new session started when at least two individuals were in the frame and one focal individual (focal carer) started covering the

chicks, and ended when they stopped. For each period in which a focal carer covered the chicks, we also recorded another focal individual (focal forager) that was not engaged in cooperative breeding behaviour. For each focal observation, we counted the number of pecks the focal forager made (pecking on the ground or on a plant) and divided these by the length of the focal observation. Observations were started when the birds left the roost in the morning and ended after 2 h or when the birds moved to inaccessible areas.

Data analysis

Which individuals provide care and who receives the most care?

We used a social network approach to identify the main members of each breeding subunit in each of the three seasons and linked this information to our observations of caring behaviours. For each individual we calculated the rate of attendance to each brood. This rate was calculated by dividing the number of subgroups that contained both the focal individual and a given brood by the total number of observations in which the individual and brood were observed. For example, if an individual was observed in 10 group associations that contained brood A, of which it was in the same subgroup as the brood in eight of these, the rate of attendance of the individual to brood A would be 0.8. This approach represents a strict test of social choices relative to opportunity (Farine & Carter 2022) which was important because our observations were limited to areas where we could

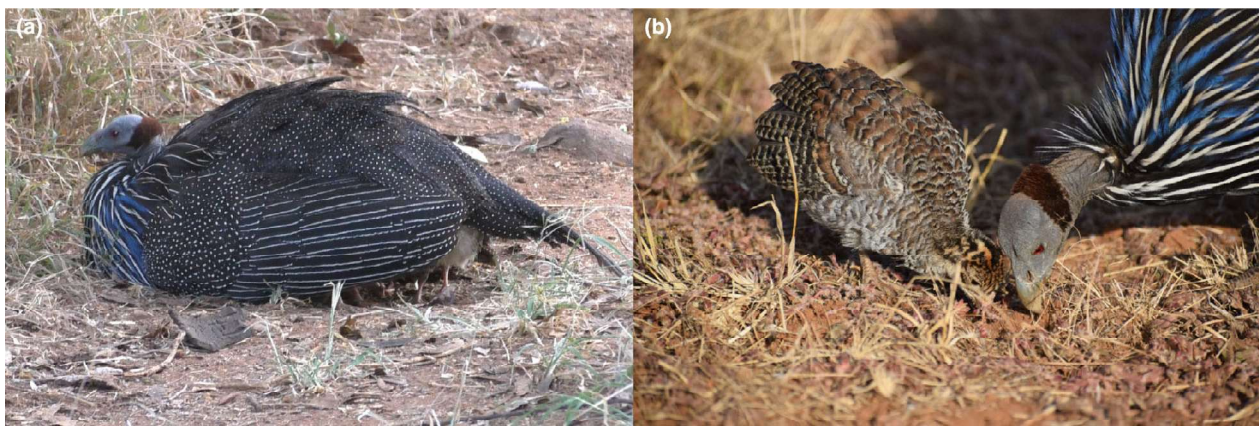


Figure 2. Examples of cooperative breeding behaviours. (a) Chick covering behaviour by an adult male and (b) chick-feeding behaviour by an adult male.

observe birds and these may have reflected shared spatial preferences among individuals (Webber *et al.* 2023).

To identify which individuals occurred with which brood more than expected by chance (Farine 2017), we used a permutation test by randomizing the subgroup that contained the focal brood, as follows:

- 1 K observations were randomly assigned to subgroups observed that day, maintaining the original number of subgroups per day across three seasons.
- 2 Chicks were permuted between subgroups within the same group observation.
- 3 Rate of attendance was recalculated from the permuted data for each individual.
- 4 The total number of observations for each individual and brood as well as the subgroups and observations were maintained.
- 5 To generate a distribution of the rate of attendance for each individual the permutation procedure was repeated 1000 times.
- 6 A one-tailed test ($P \leq 0.05$) considered individuals whose observed rate of attendance was higher than 95% of the permuted rates significant.

Finally, to test whether males were disproportionately represented as carers, we conducted a two-sample proportion test that compared the proportion of males to females among the carer and non-carer categories (excluding mothers) in each of the three seasons.

We used the cooperative breeding interactions data to characterize the relative contribution of each significant associate to each brood. From these data, we determined whether the mother provided most of the care or not, and whether care received varied between broods. First, we recorded the occurrence of each interaction (Table 1) directed towards the brood of a focal female. Because babysitting and within-group guarding behaviours were rarely expressed (21 events), they were combined into one category for analysis. Mothers clearly did not give most of the care to their chicks (Table S4), 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 differences can lead to spurious outcomes (Hoppitt & Farine 2018), we used a two-sample test for equality of proportions. Less frequently

sampled broods could, for example, appear to have more care given by mothers if different individuals conduct the care at different times. We therefore conducted pairwise contrasts of the proportion of total care 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 care given by the mother was significantly lower in one brood than the other.

Finally, we tested whether males gave more help than females. To do this, we focused on chick-feeding interactions as they were the most prevalent. We obtained the count for each carer in each season as the response variable. We then constructed a generalized 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.

Do non-mother individuals pay a cost for caring?

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 (i.e. either the focal carer or focal forager) was involved in the COV (wing-covering) 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 it was not always possible to 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 among individuals (average 2.25 observations per individual, when the identity was known). For this reason, we do not expect repeated observations to have a major impact on our conclusions.

Statistical analysis

All analyses were performed in R version 3.5.1 (R Development Core Team 2018).

RESULTS

Over the three breeding seasons, we collected data from 51 adults and subadults, of which 13 were

females that attempted to breed. From these, 10 females had broods that survived long enough to collect enough data for our analysis (Table 1). Among these, there was some consistency in which females attempted to breed, with two of our study females attempting to breed in all three seasons (see Dehnen *et al.* (2023) for more exploration of the propensity and consequences of females breeding). Others were only observed breeding in later seasons, which to the best of our knowledge was their first reproduction after natal dispersal. Observation effort ranged from 70 to 1133 min per brood (mean 627.40 ± 352.78 standard deviation (sd)). These observations were split across 10–43 morning and/or afternoon observation sessions per brood (mean 22.80 ± 10.50 sd).

Carers are predominantly male, and include non-breeders

There were four key insights from our analyses of significant associates (Fig. 3). First, not all group members consistently associated with all broods, but each brood was associated with a subset of individuals that were observed with that brood more than would be expected by chance. Secondly, there was relatively little overlap among the individuals that were significantly associated with each brood, indicating that each brood had a distinct set of associates. In other words, birds formed breeding groups during the chick-rearing period. Thirdly, there was a significant male bias among associates (Table 2), and only one non-breeding female was observed providing care (a subadult female). Finally, multiple lines of evidence suggest that significant associates (and individuals that provide care) include non-breeding carers, including (Fig. 3) individual males that (1) were not sexually mature at the time of helping (and not fully grown), (2) were helping their social mothers and (3) helped before ever having been observed forming a pair with a female.

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

Mothers provided a small proportion of the total care that their offspring received. For example, in the first season, of the 20 cover events recorded for one brood (assigned to female YOBK, named after her colour-bands), the social mother was

found to cover chicks in one event for only 1 min. The social mother also contributed to only 42 of the 330 chick-feeding events and one out of seven guarding events. However, not all females received equal help from carers. YOBK, a previously successful breeder, generally received more assistance with food provisioning and chick care than others (see Tables S1–S3). Other mothers showed fewer disparities in care received (see Tables S1–S3 and Figs S1–S9). YOBK consistently received more help with chick food provisioning across seasons compared with other females, except for one instance where another female (GAGA) received similar levels of help in the third season (see Table S3 and Fig. S7). As cover interactions were relatively rare, some comparisons could not be made with confidence. 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 care 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).

Non-mother individuals pay foraging costs while performing covering behaviours

Based on 27 observations of covering chicks, where cover duration data were available, individuals performed this behaviour on average for 16 min (range 1–60 min). 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 10-fold and significant difference (Table 4).

DISCUSSION

Our study provides the first evidence for cooperative breeding in the Vulturine Guineafowl. We detected stable breeding subunits consisting of social mothers and carers. Had we studied the social behaviour of Vulturine Guineafowl only during the breeding period, each of these breeding subunits might easily be considered as a separate

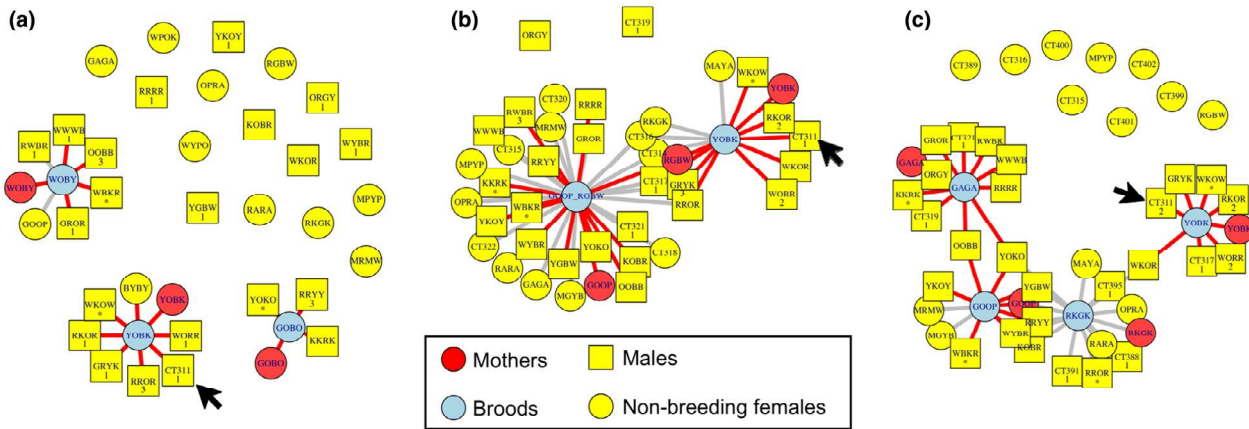


Figure 3. Social networks of attendance to the broods in (a) November 2019, (b) May 2020 and (c) November 2020 breeding seasons. Edges represent significant associates of each brood while red edges represent associates that were also observed engaging in caring behaviours. Numbers represent levels of evidence for males being carers as: (1) caring before being sexually mature, (2) caring for the chicks of their social mother and (3) caring before being observed engaging in any reproductive behaviours. For example, male CT311 – marked with an arrow on the figure – was only 6 months old in the first season (November 2019), and, at that time, was less than 50% the size of an adult male (~800 g versus 1.6 kg). Males marked with an asterisk (*) were observed paired with the female of the broods that they associated with significantly. ROOR is not shown here as she was depredated before associations could be measured; however, her chicks joined the WOBY brood in November 2019, while the broods of GOOP and RGBW merged during the May 2020 season. Each of the non-significantly associated males in November 2019 were observed giving care at least once, but none of the non-significantly associated males in May 2020 were observed giving any care. The alphanumeric codes inside each coloured polygon correspond to the field markings (colour band combination or wing tag number) identifying each individual.

Table 2. Males are significantly more likely than females to be associated with the broods. Results of the two-sample test for equality of proportions comparing the proportion of males with that of females among the significant associates of the three broods, in each of the three seasons. Values represent the model estimates of the proportion of males and females that were significantly associated with the brood. Positive significant effects suggest that a higher proportion of males are significant associates. The non-significant result in Season 2 was due to the merging of two broods causing almost all group members to join this mixed brood (with the exception of the birds attending to the YOBK brood, see Fig. 3).

Season	Proportion of significant associates		χ^2	df	P	95% CI
	Male	Female				
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 to 0.178
3	1	0.455	13.63	1	0.0002	0.187–0.904

Table 3. Results of the generalized linear mixed model comparing the number of chick-feeding interactions performed by male and female non-breeders across the three seasons. sd, standard deviation; se, standard error.

	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
Individual identity		2.146		±1.465
Season		0.433		±0.658

Table 4. Results of the binomial general linear model comparing the proportion of the time spent foraging (response variable) between focal individuals that were involved in chick covering behaviour and those that were not. Individual identity is not included in this model because we could not always identify the individual recorded. Data were collected only during the first breeding season. se, standard error.

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

group (and not the lowest tier in a multilevel society, *sensu* Papageorgiou *et al.* (2019)). However, we know that this species lives in large, cohesive social units in the non-breeding season, and here we confirm that these comprise multiple breeding subunits, meaning also that Vulturine Guinea-fowl are plural breeders. We found that carers provide most of the care that chicks receive. As in other avian cooperative breeders where providing care is male-biased (Riehl 2013), we found that caring associations and caring interactions were strongly male-biased in the Vulturine Guinea-fowl, with evidence suggesting that most care is given by sub-adult and non-reproductive males towards the chicks of their social mother. Overall, Vulturine Guinea-fowl exhibit the common hallmarks of plural, cooperatively breeding species, with similarities in terms of social and reproductive system to the sympatric, but altricial, Superb Starling *Lamprotor-nis superbus* (Rubenstein 2006).

In species that breed cooperatively, individuals usually help to raise offspring that are not their own. By helping, individuals can gain direct fitness benefits through routes including parentage of offspring (Richardson *et al.* 2002), territory inheritance (Kingma 2017), group augmentation (Ligon & Ligon 1978, Wright *et al.* 2010) or 'pay-to-stay' benefits (Wong & Balshine 2011). In contrast, indirect fitness benefits may be accrued by helping kin, and can manifest through enhanced offspring number (Blackmore & Heinsohn 2007) or survival (Hatchwell *et al.* 2004), as well as increased parental survival (Downing *et al.* 2021) or reproductive rate (Russell 2003). Male birds are typically philopatric (Greenwood 1980), meaning that non-breeding males (unlike dispersing females) are likely to be related to breeders and their offspring, and may thereby gain indirect fitness by helping (Dickinson & Hatchwell 2004). In species where breeders make a substantial investment in reproduction, additional offspring care from such group

members could generate indirect fitness benefits, such as greater offspring survival or enhanced parental current or future reproductive investment, that outweigh the costs of helping.

In cooperatively breeding Vulturine Guinea-fowl, non-breeding helpers are likely to enhance the survival of chicks and of breeding females by assuming some of the costs associated with caring for the chicks. We found that breeding females only provide a small proportion of all the chick-caring interactions, which may be important for females to regain body condition lost through laying and attending to the nest. Further, as female Vulturine Guinea-fowl may breed twice per year (several females bred successfully in both May 2020 and November 2020 (Table 5)) if conditions are suitable, additional caring may be key to females regaining body condition in time for the next reproductive opportunity by reducing the inter-hatch interval (Ridley & Raihani 2008). For non-reproductive, philopatric males, increasing the number of breeding attempts and the survival of offspring should represent a significant source of indirect fitness benefits, which may explain (or be further explained by) the surprisingly long period until birds reach sexual maturation (which is evident from birds only reaching full adult size more than a year after hatching).

There is considerable variation in the structure of cooperatively breeding groups among species, ranging from a single breeding pair with associated carers to multiple breeding units, which may be polygamous or polyandrous (Stacey & Koenig 1990, Koenig & Dickinson 2016). We still have no clear understanding of the drivers that give rise to multiple breeding subunits in Vulturine Guinea-fowl. When conditions are suitable for breeding, several breeding pairs form from otherwise stable social units and non-breeding members of the social unit provide care to the offspring after hatching. This is similar to Golden Lion

Table 5. Females in each of the three seasons that bred (and had their chicks hatched (Y = yes, N = no)), the number of significant associates with the brood if they successfully hatched (NA = data not available) and the number of eggs laid by the females (UNK = unknown).

Season 1 (November 2019)				Season 2 (May 2020)				Season 3 (November 2020)			
Female	Hatched	Number of associates	Number of eggs ^a	Female	Hatched	Number of associates	Number of eggs ^a	Female	Hatched	Number of associates	Number of eggs ^a
BYYO ^b	N	NA	10	GOOP	Y	28	9	GAGA	Y	10	13
GOBO	Y	3	8	MRMW ^e	N	NA	8	GOOP	Y	10	9
GOOP ^c	Y	NA	UNK	RARA ^f	N	NA	UNK	MGYB ⁱ	N	NA	UNK
RGBW	N	NA	8	RGBW	Y	28	UNK	MRMW ^j	N	NA	9
ROOR ^d	Y	NA	UNK	WOBY ^g	N	NA	UNK	RK GK	Y	14	UNK
WOBY	Y	6	UNK	WYPO ^h	N	NA	UNK	YOBK	Y	7	8
YOBK	Y	7	8	YOBK	Y	11	UNK				

^aNumber of eggs is given only when clutches were complete (i.e. female started incubation). ^bBYYO was depredated during incubation. ^cGOOP's chicks were all depredated by the second week. ^dROOR was depredated the first night after re-joining the study group. ^eMRMW's nest was depredated by a white-tailed mongoose. ^fRARA dumped her eggs on MRMW's nest, which was later depredated. ^gWOBY was depredated during incubation. ^hWYPO's nest was depredated during incubation. ⁱMGYB's nest was depredated on the third day of the egg-laying period. ^jMRMW's nest was depredated after she abandoned it during incubation.

Tamarins *Leontopithecus rosalia* which have multiple breeding individuals and in which adults care for offspring regardless of how many offspring there are in a cooperative polyandrous group (Goldizen 1989, Dietz & Baker 1993).

Vulturine Guineafowl breed during the wet season when there are temporary increases in resource abundance (both food and safe nesting sites) that can allow many individuals to reproduce simultaneously. Our study also highlights variance in breeding success, with many clutches and females depredated during incubation or early in the life of chicks (Table 5). This variance makes it unlikely that dominance acts as a major determinant of breeding success, with female dominance hierarchies being less structured than those of males (Dehnen *et al.* 2022). However, more data are needed to more explicitly evaluate the link between breeding and dominance, and whether factors such as previous experience might drive variation in nesting rates and nest success among females (Dehnen *et al.* 2023).

In this study, we identified four juvenile-directed cooperative behaviours by non-parents, comprising babysitting, chick feeding, covering the chicks and within-group chick-guarding behaviour against other adults. These are consistent with cooperative breeding behaviours exhibited in other precocial species (DuPlessis *et al.* 1995). For example, cooperative breeding behaviours of Kalij Pheasants include caring for

chicks, vigilance against predators and agonistic interactions among conspecific intruders (Zeng *et al.* 2016). Similarly, helpers in the Buff-throated Monal-Partridge care for the chicks by identifying 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 short distances to make close observations. Doing so in our study was made substantially easier by having many birds habituated to our presence and due to their home-range incorporating a fenced area that was safe to walk in while making the close observations needed to identify cooperative breeding behaviours.

The associates of each brood were mostly males, and they typically provided more care than the mother did. These results are also consistent with those reported in other cooperatively breeding Galliformes. One exception in our data was the second breeding season, although this season was notable for having many failed nests, which could have stimulated care from females that were still too young to disperse and breed themselves. Why males attend to broods more than females in Vulturine Guineafowl, given that subadult females can remain in their natal territory for several years before dispersing (Klarevas-Irby *et al.* 2021), remains unknown, but this pattern has been observed widely in other species (Green *et al.* 2016). Further, we found that although some

females were detected as significant associates of the brood, male carers provided nearly 98% of all chick-feeding interactions (excluding those from the mothers). This is consistent with the Grey-crowned Babbler *Pomatostomus temporalis*, where only the number of male helpers increased reproductive success (Blackmore & Heinsohn 2007). Hence, male-biased helping behaviour may reflect the importance of kinship in reproduction by Vulturine Guinea fowl, given that males are philopatric in their group.

By studying the social network of individual carers and broods, we showed that carers appeared to be generally brood-specific. Among these, we found several lines of evidence supporting the hypothesis that Vulturine Guinea fowl carers include non-breeding males. This includes subadult males that provide care before they are fully grown or sexually mature (e.g. CT311, Fig. 3) and subadults. Others (e.g. CT317, a male that cared for YOBK's brood in the second and third seasons) were part of the brood that their social mothers cared for during the first season and were subsequently observed providing care for the same female's brood in later seasons. Further, the significant associates with each brood were relatively consistent over years. For example, YKOY was not detected as a significant carer in the first season, when GOOP did not successfully breed, but was significantly associated with her brood in the following two seasons. Hence, care is neither given randomly nor opportunistically, and a substantial proportion of the care that we observed came from individual males that were unlikely to have any brood paternity.

A consistent pattern that emerged across all three seasons was that mothers provided a minority of care to their chicks. The large amount of help given by non-mothers is perhaps unusual (Green *et al.* 2016). For example, in Purple Gallinules *Porphyrio martinica*, breeding adults provide most care to chicks, which are subprecocial (Hunter 1987), while both male and female Purple Gallinules participate in incubation (Gross & Van Tyne 1929). One reason why female Vulturine Guinea fowl receive so much help in raising their offspring may be the high cost they pay during incubation, meaning that recovering their body condition might compromise the amount of care they can provide to the current brood, which is then offset by the care provided by other individuals. Further, care involves not only food

provisioning, but also maintaining vigilance against predators and agonistic behaviours against intruders (Clutton-Brock & Manser 2016), and providing opportunities for learning to enhance foraging skills (Heinsohn 1991, Cant *et al.* 2016). Finally, substantial care by non-mothers is likely to be beneficial because females have several opportunities to breed each year due to the presence of two rainy seasons.

Cooperative breeding behaviours are likely to be costly to carers (Cram *et al.* 2015, Mendonça *et al.* 2020, Covas *et al.* 2022). For example, in Meerkats *Suricata suricatta*, helpers lose weight when they participate in cooperative breeding activities, such as feeding the young (Russell 2003). Similarly, White-winged Chough *Corcorax melanorhamphos*, helpers lose weight when performing incubation, in addition to the costs they incur by choosing to remain in their natal territory (Heinsohn & Cockburn 1994). Our study aligns with this body of evidence, demonstrating that individuals spend less time foraging when engaging in cooperative breeding behaviours relative to individuals that do not provide care. We acknowledge that individuals may not always directly trade off care for foraging, for example if they provide care when satiated, and so pay a potentially lower cost to helping. However, our observations often began early in the morning (c. 6:00 AM), as birds left the roost, where in almost all cases carers immediately provided care before undertaking any foraging themselves. Hence, although the overall costs that helpers pay are likely to be smaller than those in altricial species (e.g. provisioning chicks at a nest), Vulturine Guinea fowl must still allocate time for caring behaviours into their budget that is independent from their foraging time budget.

Conclusions

Further behavioural studies on cooperative breeding are needed 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, which may result in hatching success being relatively random among females. Such insights are important for understanding how indirect fitness might be gained via paternal routes, which are usually linked with much greater kinship uncertainty. In the Vulturine Guinea fowl, the

harsh climates of Kenya combined with a short inter-wet seasonal cycle may also have set the scene for helping, as mothers can reproduce again before their male offspring reach sexual maturity (which in Vulturine Guineafowl is also delayed). 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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AUTHOR CONTRIBUTIONS

Brendah Nyaguthii: Conceptualization; methodology; data curation; formal analysis; writing – original draft; writing – review and editing; investigation; visualization. **Tobit Dehnen:** Methodology; writing – review and editing; data curation. **James A. Klarevas-Irby:** Conceptualization; methodology; formal analysis; data curation; writing – review and editing; visualization. **Danai Papageorgiou:** Conceptualization; methodology; formal analysis; data curation; writing – review and editing; visualization. **Joseph Kosgey:** Writing – review and editing; supervision. **Damien R. Farine:** Supervision; funding acquisition; conceptualization; methodology; formal analysis; writing – review and editing; investigation; project administration; visualization.

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ETHICAL NOTE

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 Centre.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

Data Availability Statement

The data supporting the findings of this study and the code are available at <https://doi.org/10.6084/m9.figshare.28158335.v1>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Amount of care given by the mother and carers for the YOBK brood in season 1.

Figure S2. Amount of care given by the mother and carers for the WOBY brood in season 1.

Figure S3. Amount of care given by the mother and carers for the GOBO brood in season 1.

Figure S4. Amount of care given by the mother and carers for the YOBK brood in season 2.

Figure S5. Amount of care given by the mother and carers for the GOOP (and chicks from RGBW) brood in season 2.

Figure S6. Amount of care given by the mother and carers for the YOBK brood in season 3.

Figure S7. Amount of care given by the mother and carers for the GAGA brood in season 3.

Figure S8. Amount of care given by the mother and carers for the GOOP brood in season 3.

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

Table S1. Overview of two-sample tests for equality of proportions, comparing the proportion of care given by the mother relative to the help given by carers across the three broods in season 1.

Table S2. Overview of two-sample tests for equality of proportions, comparing the proportion of care given by the mother relative to the care given by carers across the three broods in season 2.

Table S3. Overview of two-sample tests for equality of proportions, comparing the proportion of care given by the mother relative to the care given by carers across the three broods in season 3.

Table S4. Overview of the total number of different interactions across three different seasons from different mothers in the study group.