COOPERATIVE BREEDING IN THE VULTURINE GUINEAFOWL (*Acryllium vulturinum*) AT MPALA RESEARCH CENTER, LAIKIPIA COUNTY KENYA

BY

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DECLARATION

Declaration by the student

This thesis is my original work and has not been presented for a degree in any other University for any awards.

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DEDICATION

To mum -Lucy, thanks for all the support.

ABSTRACT

Cooperative breeding is widely reported across the animal kingdom. In birds, it is thought to be more common in altricial species (where chicks are dependent in the nest after hatching), with few described cases in precocial species (where chicks move independently straight after hatching). The study examined cooperative breeding in a precocial species, the vulturine guineafowl (*Acryllium vulturinum*), at the Mpala Research Centre, Laikipia Kenya. The aim of the study was to investigate whether vulturine guineafowl breed cooperatively, and, if so, how help is distributed among group members. To achieve this, the study determined who breeds, quantified the investments by females during incubation, and observed who is closely associated to the chicks. The study determined whether non-breeders provide care at same levels to parents, and whether they pay any costs to helping. By following colour-banded females, the study found that multiple females can breed within each group, with each female attending to her own nest. Data from sixteen incubating females fitted with solar-powered high-resolution GPS tags revealed high female attendance, with females spending 97.6% of the incubation period on the nest. In one social group of vulturine guineafowl where all individuals were colour-banded, males were over-represented among the individuals that were detected with clutches more than expected by chance, and detailed observations found that these individuals exhibited cooperative breeding behaviour including caring for the chicks by covering them, calling them if they find a food resource and guarding them. In three focal clutches from this group, the study found no overlap among individuals that were significantly associated with each clutch, suggesting that helpers specialized on specific clutches. Focal follows of clutches found that helpers provide a substantial amount of care, and as a result none of the mothers provided the majority of the care to the chicks. Finally, helping was costly, focal follows showed that helpers expressed a significant reduction in time spent foraging while providing allo-parental care ($P<0.01$). In conclusion, vulturine guineafowl are cooperative breeders, and express cooperative breeding that is combined with an unusual plural-breeding social system. Future research on this system could focus on determining the factors that drive helpers to specialize on specific clutches, which could reveal important insights into the fine-scale drivers of cooperative breeding.

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LIST OF ABBREVIATIONS

COV- Cover

CPO- Within group guarding

GLM- Generalized linear Model

GPS- Global Positioning System

GRD- Guarding

VGF-Vulturine Guineafowl

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CHAPTER ONE

INTRODUCTION

1.1 Background information

In some species of birds, mammals, fish and invertebrates more than two adults contribute towards raising young (Koenig, 2017) known as cooperative breeding (Cockburn, 2002). Typically, cooperatively breeding groups consist of a breeding pair and one or more ‘helpers. The latter are usually offspring from previous breeding attempts that have delayed their own dispersal and help in rearing their younger siblings (Clutton-brock, 2002). However, in a considerable proportion of cooperatively breeding species, groups contain either unrelated helpers or multiple co-breeding pairs; thus, there may be multiple evolutionary routes to cooperative breeding (Riehl, 2013).

As cooperative breeding appears to be a suboptimal reproductive strategy for helpers or co-breeders, cooperative breeding behaviour has received considerable empirical (Koenig & Stacey, 1990) and theoretical (Emlen, 1982; Komdeur, 2000; Shen *et al*., 2017) attention, across a plethora of species, over the past five decades. Nevertheless, the question why some individuals forego independent breeding in favour of helping others, or co-breeding, remains unanswered (Koenig, 2017). This is despite a multitude of comparative studies over the past several decades (Arnold & Owens, 1998, 1999; Jetz & Rubenstein, 2011). In fact, opposing ecological correlates of cooperative breeding have been found in different taxa (Gonzalez *et al*., 2013; Rubenstein & Lovette, 2007). Perhaps, studies to date have struggled to find an overarching, interspecific driver of cooperative breeding due to the lack of breadth in studies of cooperative breeders. For example, in birds, cooperative breeding is mostly characterized as helping at the nest by non-parents, despite care often continuing long after the nest period, such as via continued provisioning of offspring. Furthermore, although avian cooperatively breeding groups in most species comprise a breeding pair with additional, non-breeding helpers—who are typically adult offspring from previous breeding seasons (Dickinson *et al*., 1996)—cooperative breeding systems can encompass a hugely diverse range of both social and genetic group structures (Lin *et al*., 2019). Thus, new insights may be gained by studying candidate species that may breed cooperatively but have different social structures and understudied taxa like the northern ground hornbill (*Bocorvus abyssinicus*) that has a complex structure (Kemp *et al*., 2020).

Cooperative breeding is most commonly described in altricial species (Cockburn, 2006; Lukas & Clutton-Brock, 2012). In contrast, much fewer precocial species appear to breed cooperatively (Cockburn, 2006). A possible explanation is that the effect of helping behaviours on offspring fitness in precocial species is reduced due to the advanced developmental stage, and early independence in terms of feeding, of precocial chicks (Cockburn, 2006). Alternatively, the lack of evidence for cooperative breeding in precocial species could be because classical examples of cooperative breeding in birds primarily consider helping at the nest (Brown 1974; Emlen 1982), rather than other forms of help that may occur after chicks leave the nest. In other words, cooperative breeding in precocial-breeding species may have remained disproportionately undetected.

Cooperative breeding behaviours may be more challenging to detect in species that do not have extended nestling periods, as is the case for precocial species. However, there are many ways in which helpers may still contribute to raising offspring in such species. For example, in some precocial species, such as trumpeters (*Psophia spp*.), helpers may contribute to both incubating the eggs of the dominant female, nest building as well as providing food for the chicks (Sherman, 1995). Even post hatching, there are many ways in which helpers may increase the survival of offspring without providing care at the nest. For example, helpers may protect chicks from predators or the abiotic environment (such as covering chicks with their wings to provide shade or warmth), identifying and providing food for chicks or maintaining vigilance to provide chicks with more time to forage (Hale, 2006). However, identifying such forms of cooperative breeding requires more careful observations than what is necessary for describing helping at the nest.

One reason why precocial species have not been considered as candidates for cooperative breeding could also be because the independence of the young necessitates less help, meaning that breeding females would gain less overall benefit from receiving help. However, this logic could be mistaken. Due to high predation risk to ground nesting birds (Thompson & Raveling, 1987), females of precocial species, which typically nest on the ground, rarely leave the nest and thus forego feeding for the duration of 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. Similarly, female red jungle fowl (*Gallus gallus*) lose 10–20% of body mass during incubation. Accordingly, reproduction in precocial species may carry substantial costs for the female (Sockman, 2003). Costs of incubation are also evident in species where multiple individuals contribute to incubation. Given the substantial costs associated with egg laying and incubation to females, 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.

One group of non-passerine birds with precocial young, in which some studies of cooperative breeding have been conducted, are Galliformes. For example, in the bar-throated partridge (*Arborophila brunneopectus*), helpers locate food for chicks and contribute to both territory vigilance as well as defending chicks against predators (Wang *et al.*, 2017). Similarly, in the group-living wood quail (*Odontophorus guttatus*) helpers defend the group's territory against neighbours during the breeding season (Hale, 2006). While an extensive review on cooperative breeding in birds (Riehl, 2013) describes only one presumed case of cooperative breeding in Galliformes, the aforementioned studies suggest that cooperative breeding could be more common in Galliformes, and in precocial species more generally, than is currently viewed. Thus, Galliformes potentially represent an ideal order in which to explore cooperative breeding, and how it might be expressed away from the nest.

Vulturine guineafowl (*Acryllium vulturinum*) are large, terrestrial birds that live in stable groups of approximately 15-55 individuals (Papageorgiou *et al*., 2019). Given the social organization of this species—forming large groups that containing adults, subadults and juveniles—they are a good candidate for breeding cooperatively, yet no formal studies have thus far been carried out. Vulturine guineafowl pairs form at the beginning of the breeding season, followed by females laying, and independently incubating, a clutch of 13-15 eggs in a scrape on the ground (Johnson, 2002). Vulturine guineafowl chicks are precocial, with the mother and chicks typically (re)joining their social group very soon after hatching. During the first few weeks of life chicks are highly vulnerable to predation, meaning that they likely benefit from protection offered by helpers. Moreover, initial observations of vulturine guineafowl groups suggest that non-parents exhibit helping behaviours towards chicks, such as attracting chicks to food resources and sheltering the chicks. Accordingly, vulturine guineafowl appears to be an excellent candidate species for studying cooperative breeding in a precocial species. Some of the findings from April 2018 to March 2019 were published in Papageorgiou *et al*. (2019), and revealed that vulturine guineafowls form plural breeding groups with multiple breeding units which will return into the same group after the breeding season. That study also uncovered that group membership was highly stable across years and groups contain multiple breeding pairs.

1.2 Problem statement

In avian species, cooperative breeding is broad and studied comprehensively.

Most studies done on cooperative breeding are about species which are usually under-developed and require parental care before they can stand, walk and survive by themselves, known as altricial species. By contrast bird species where chicks are well developed when hatched and are able to stand and walk on their own, referred to as precocial species, are rarely studied in the context of cooperative breeding. The Galliformes order consists predominately of precocial species and to date there is scarce information known about co-operative breeding in Galliformes.

Therefore, there is need for further research on cooperative breeding systems in non-passerines. The breeding systems in the Galliformes order have been largely unexplored and in particular for the vulturine guineafowl, for which there has not been any published peer-reviewed articles up to date.

1.3 Objectives of the study

1.3.1 General objective

To characterize cooperative breeding in the vulturine guineafowl

1.3.2 Specific Objectives

1. To determine who breeds within a social group of the vulturine guineafowls
2. To determine the investments of females during incubation
3. To determine who contributes to rearing the chicks
4. To determine if chicks will receive more care from helpers and if the care provided will be greater for the dominant females
5. To assess the costs paid by helpers rearing chicks

1.4. Hypotheses (H)

Q1. H_0: All reproductive age members of the group breed

H_1: Some individuals forgo breeding in order to provide help

Q2 H_0: Both parents contribute to incubation

$H1_1$: The breeding female contribute significantly more to incubation than the breeding male

Q3. $H1_0$: There are no significant associations between non-breeding group members and clutches

HI_1: Some non-breeding group members associate significantly with clutches

If $H1_1$ is true, then

$H2_0$: There is no difference in associations to clutches between males and females

$H2_1$: Males are much more likely to associate significantly with clutches than the females are.

Q4. $H1_0$: Breeding females provide the majority of care to the clutch

$H1_1$: Helpers provide the majority of the overall care to the clutch

If $H1_1$ is true then

$H2_0$: All females receive equal help from helpers

$H2_1$: The dominant female receives disproportionately more help from helpers

Q5. $H0_1$: Helpers have the same food intake rates when helping versus not helping

$H1_1$: Helpers have a significantly lower food intake rate while helping

1.5 Justification and significance of the study

Understanding cooperative breeding in different environments is a key area in research that could shed more light on how ecology can influence breeding systems (Guindre-parker & Rubenstein, 2018). Even though the mystery about why non-breeding, subordinate group members help dominant individuals while foregoing their own procreation remains largely unsolved, research on cooperative breeding continues to captivate ecologists and provide insights into cooperation in animal societies (Koenig, 2017). Studies suggest that cooperative breeding could be more common in Galliformes, and in precocial species more generally, than it is currently viewed. Such data are crucial as several studies have relied on large scale data bases about cooperative breeding in birds to test hypotheses. These data bases are likely to be largely incomplete because they are highly biased towards the altricial species. There is need for cooperative breeding studies to take a broader taxonomic scope and group living Galliformes are needed because they are assumed to not breed cooperatively though it is untested. There is also evidence that reproductive effort of females in Galliformes is extremely high.

They tend to have high nest attendance which could promote helping as being very beneficial. Nonetheless, an extensive review on cooperative breeding on birds (Riehl, 2013) describes only one presumed case of cooperative breeding in Galliformes Szechenyi's monal-partridge (*Tetraophasis szechenyii*).

CHAPTER TWO

LITERATURE REVIEW

2.1 Reproductive skew in cooperative breeders

A crucial determinant of inclusive fitness is whether an individual has access to reproductive opportunities (Dickinson & Hatchwell, 2009). 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). However, there are many factors that may prevent individuals from breeding either in groups or independently. For example, direct reproductive suppression by socially dominant individuals may prevent subordinates from reproducing (Huchard *et al*., 2016). Subordinate members of a group can sustain a high reproductive skew where they suppress reproduction to avoid inbreeding for example in the paired babbler (*Turdoides bicolor*) (Ridley, 2011)**.** Furthermore, individuals may not have access to reproductive opportunities. This may be due to lack of suitable breeding sites such as in the case of acorn woodpeckers (*Melanerpes formicivorus*) (Koenig *et al*., 2016). Alternatively, biased sex ratios may result in a lack of potential reproductive partners (Cockburn, 1998). Accordingly, reproductive skew may range from low to high, where most individuals reap similar direct fitness or a small subset of individuals gain the vast majority of direct fitness, respectively (Magrath & Heinsohn, 2000).

2.2 Female incubation effort in birds

In birds, the relative contribution of males versus females to reproductive activities may vary widely at multiple stages of reproduction, such as nest building and offspring provisioning. One stage of reproduction during which males and females generally vary widely is incubation (Matysioková & Reme, 2014). In some species males provision incubating females with food, as is seen in meadow pipits (*Anthus prantensis*) (Halupka, 2013) and snow buntings (*Plectrophenax nivalis*) (Lyon & Montgomerie, 2013). Alternatively, both sexes may contribute to incubating the eggs (Lislevand, 2014).

Females may also receive no aid from their mates, which is the case in wood ducks (*Aix sponsa*) (Hepp *et al*., 2006). In precocial species, females typically spend the vast majority of the incubation period on the nest (Persson & Göransson, 1999; Thompson & Raveling, 1987). Accordingly, in contrast to altricial species, females in precocial species typically experience considerable reductions in body condition through the production and incubation of the large clutches that are typical of such species (Meijer & Siemers, 1993; Moreno, 1989). The high costs of incubation may be particularly pronounced in Galliformes, for example in ring necked pheasants (*Phasianus colchicus*) females attend the nest nearly 100% of the time during incubation and, in doing so, lose up to 19% of their body mass (Persson & Göransson, 1999). Similarly, female red jungle fowl (*Gallus gallus*) lose 10–20% of body mass during incubation (Meijer & Siemers, 1993). Due to their ground-nesting nature and associated high predation risk (Thompson & Raveling, 1987), helmeted guineafowl (*Numida meliagris*) females rarely leave the nest, which is likely to reflect a substantial cost borne by reproductive females (Sockman, 2003). The costs of incubation in precocial species are not only evident when solely the breeding female incubates, but also in those where multiple individuals contribute to incubation. For example, in white winged choughs (*Corcorax melanorhampos*) females do not lose body mass during incubation – instead, these costs are borne by young helpers contributing to incubation by losing body mass in proportion to the amount of incubation they perform (Heinsohn & Cockburn, 1994).

Due to the severe depletion of breeding females' resources (e.g. body fat) during incubation, females must trade-off investing their limited resources into current reproduction versus improving their condition for future reproduction (Giudice *et al*., 2015). Thus, there is scope for non-breeding individuals to benefit breeding female's current and/or future chicks by helping. For example, in helmeted guineafowl (*Numida meleagris*) helpers may offset the cost to breeding females though enhanced food provision rates to chicks (Van Niekerk, 2010). Thus, cooperative breeding may be more prevalent in precocial species than is currently thought. As further evidence that cooperative breeding may be under reported in precocial species, as reviewing literature since the tabulation of data by Wang & Kimball in 2016 has revealed a further 9 species from 33 originally described as being cooperative breeders (Wang & Kimball, 2016). The pattern is similar with Galliformes, with now 7 species, up from the 2 species described five years ago, (Appendix 1; Table 6).

2.3 Male-biased helping behaviour in cooperatively breeding birds

As avian sex ratios in some species (Donald 2007; Székely *et al.* 2014) and philopatry (Clarke *et al.*, 1997) are generally male-biased, and dispersal is predominately female-biased (Greenwood, 1980), helpers are generally more likely to be males rather than females. For example, in the case of bell miners (*Manorina melanophrys*) where there is male biased helping (Clarke *et al.*, 2002). Further, when there is a shortage of females in the population due to male biased adult sex ratio, it prevents male helpers breeding and favours cooperative breeding behaviour to arise (Zeng *et al.*, 2016). In multiple breeding pairs of the meerkats (*Suricata suricata*) dominant individuals contribute significantly less than subordinate individuals in carrying out different cooperative breeding activities (Clutton-Brock *et al.*, 2004). However, not all animal societies have exclusive reproduction by dominant individuals, and how helping is distributed among multiple reproductive units in such societies remains unknown.

Due to their terrestrial, gregarious and ground-nesting nature, Galliformes experience a high predation risk especially at a young age. Thus, the precocial young still require extensive parental care after hatching (Van Niekerk, 2010). While it is typical for female Galliformes to receive no help during incubation, other group members may perform helping behaviours post-hatching. In helmeted guineafowl (*Numida meleagris*), the male is thought to help care for the chicks during the day, allowing the female to forage and regain body condition lost during incubation while the female cares for the chicks during the night. Patterns of associations and help between helpers and juveniles remain understudied in plurally breeding birds.

2.4 Investment of females into parental care

Parental care is common among most species in the animal kingdom (Gonzalez-Voyer & Kolm, 2010). Females have to trade off investing their limited resources into raising current offspring versus maintaining condition and investing in future offspring. When many helpers are available, females should provide greater pre-natal investment (e.g., into having larger or more eggs) and less into postnatal care (Yamamoto, 2015). Such effects should be particularly true in precocial species where there is greater scope for indirect fitness benefits of helping by enhancing the survival of the young (Van Niekerk, 2010).

Individuals' contributions to helping behaviour may vary substantially. For example, meerkat pups can receive as little as 3% of their food items from some helpers and as much as 23% from other helpers, which varies according to helpers' foraging success (Clutton-Brock & Manser, 2011). In meerkats, mothers also provide disproportionately less parental care (relative to other group members) when their pups are younger, highlighting the costs borne from maternal investments (Brotherton *et al.*, 1996).

In altricial birds, helpers provide a substantial amount of the parental care, but not necessarily the majority. For example, in bell miners (*Manorina melanophrys*), young nestlings receive most of their food from parents, while older nestlings receive most of their food from helpers (te Marvelde *et al.*, 2009) meaning that parents (and females in particular) provide the majority of the parental care. While precocial chicks may not require the same overall intensity of care as altricial chicks, the particularly high costs incurred by females during laying and incubation may set the scene for cooperative breeding to be a selective advantage. In such cases, it should be observed that the provisioning of parental care by mothers post-hatching should represent a relatively small amount of the overall care that chicks receive. However, the relative contribution of breeding females versus their helpers has not been quantified in precocial birds.

2.5 The costs of breeding in cooperatively breeding species

To conclude that a behaviour can be considered as cooperative, it is necessary to demonstrate that it is costly to the actor and beneficial to the recipient. Several studies of cooperative breeders have shown that helpers incur costs by rearing offspring that are not theirs. For example, in meerkats (*Suricata suricata*) helping behaviours, such as babysitting, pup protection, allo-lactation, pup feeding and teaching (Clutton-Brock & Manser, 2011), result in helpers foregoing foraging activities and thus incurring associated growth costs (Russell *et al.*, 2003). Similarly, in wood mice (*Apodemus sylvaticus*), restricted foraging time and associated weight loss causes helpers to be unable to reproduce successfully, but leads to increased survival of the offspring they help (Gerlach & Bartmann, 2002). In the pied kingfisher (*Cerylr rudis*), where helpers are either primary or secondary, the primary helpers tend to have a lower survival rate as compared to the secondary helpers, who have a survival rate equal to that of the breeding pair

(Reyer, 1980). In some species, it hard to elucidate why some helpers give most care for the young with whom they are not related (Kingma, 2017).

Some species do not have opportunity costs of helpers, as is the case in long-tailed tits (*Aegithalos caudatus*), because most of the helpers are unsuccessful breeders (Hatchwell, 1988). One challenge for studying cooperative breeding in precocial bird species is detecting costs of helping. In species that live in groups, one way to achieve this is by recording the opportunity cost borne by providing alloparental care. The more parental care given by helpers the less the helpers have to invest in their offsprings (Downing *et al*., 2021). That is, at any given moment, do current helpers pay a cost by being prevented from performing behaviours necessary for their own maintenance, such as limited foraging.

CHAPTER THREE

MATERIALS AND METHODS

3.1. Study area

The study is based at the Mpala Research center (Figure 1), a 48,000-acre property located to the north west of Mt. Kenya. It is between latitude 0^0.15'N to 0^0.30'N and longitude 36^0.45' to 37''E. Mpala gently slopes from the south west (1850m) to the north east (1550m) above sea level. Mpala is characterized by semi-arid savanna habitat that is representative of the vast areas in Africa. Rainfall averages from 500-600mm per year, occurring predominately in two rainy seasons, while temperature ranges from 25^0-33^0 C (maximum) and 12^0-17^0C (minimum) (Young *et al*., 2003). Mpala is along a rainfall gradient with the southwest receiving an annual of 600 mm and the northeast 500 mm of rainfall. Red soils predominate on more sloping topographies, with approximately 10% of Mpala underlain by black cotton soils. The soils are described as well drained, moderately deep to very deep, dark reddish brown, sandy clay to clay loam (Young *et al*., 1995). The natural vegetation is mainly *Acacia* scrubland and the riverbanks are dominated by *Acacia xanthophloea*. The red soils support a predominantly grassy bushland vegetation cover types with some patches of Acacia woodlands and open grasslands. The bushes are largely of *Acacia mellifera* and *Acacia etbaica* while on the black cotton soils vegetation cover is grassland patched with bushes of *Acacia drepanalobium* and some *Acacia mellifera* (Odadi, 2012). The native biodiversity in Mpala consists of approximately 600-800 plant species, more than 300 bird species, and at least 70 mammal species including 28 species of large herbivores, 19 species of large carnivores, and insectivorous mammals. Mpala also has rodents, bats and butterflies (Young *et al*., 1997).

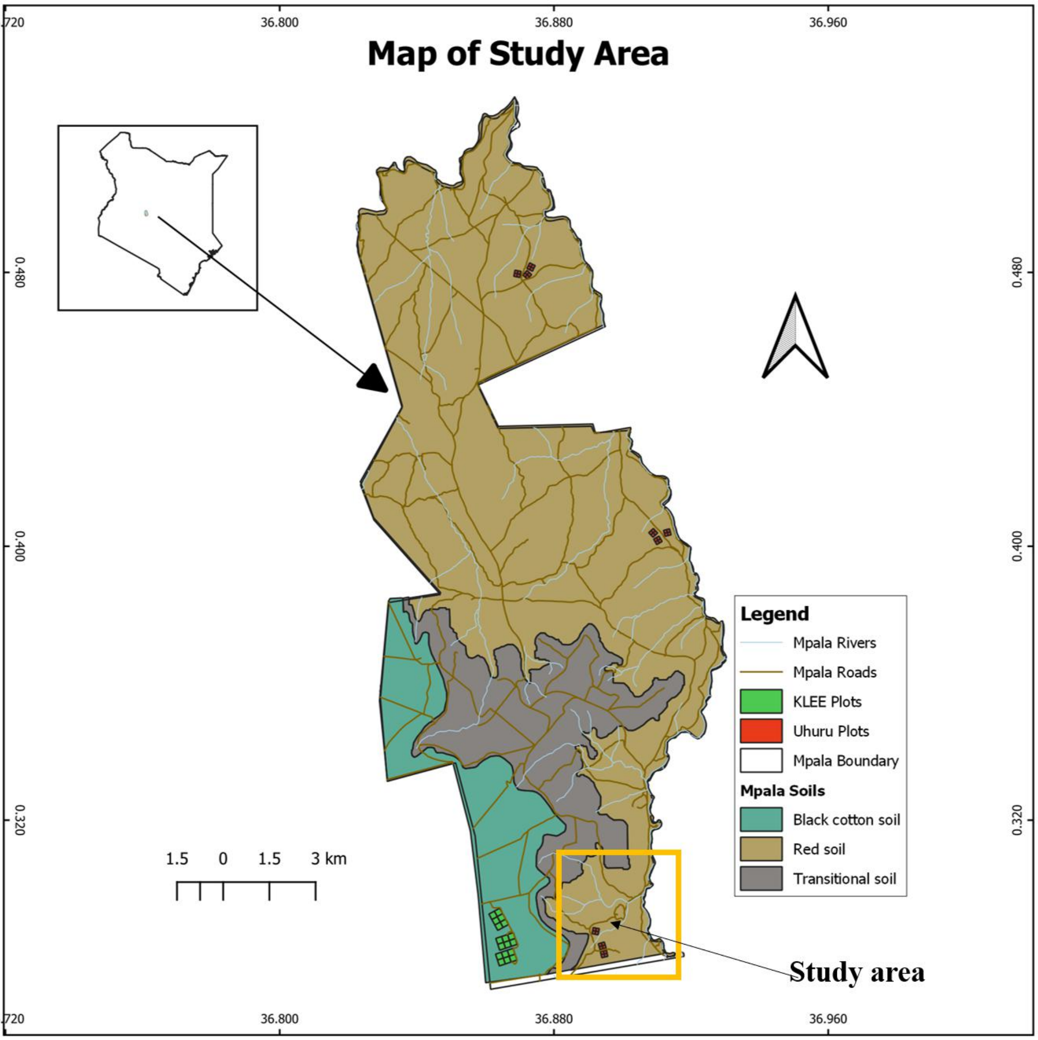

Figure 1. Map showing location of the study area

(Source: Author, 2021)

3.2 Study population

The study population is composed of 18 groups of vulturine guineafowls that reside in an area of approximately 500ha, at the southern part of Mpala research center, Laikipia county Kenya (Figure 2). The study population was established in August 2016, forming a large ongoing project in which most of the vulturine guineafowl in the local population have been trapped using big walk-in traps. Birds were then ringed with stainless steel rings from the National Museums of Kenya and a unique combination of four plastic colour bands fitted on each tarsus on the tibio tarsus for field identification. Vulturine guineafowl can be sexed in the field, with adult males, adult females and juveniles distinguished based on size, plumage and behaviour (Plates 1&2). The study population also consists of three habituated groups that can be followed on foot and observed at close range. Like in other groups, all individuals in the habituated groups were marked with colour bands, and some individuals (both male and females) were fitted with solar-powered GPS tags.

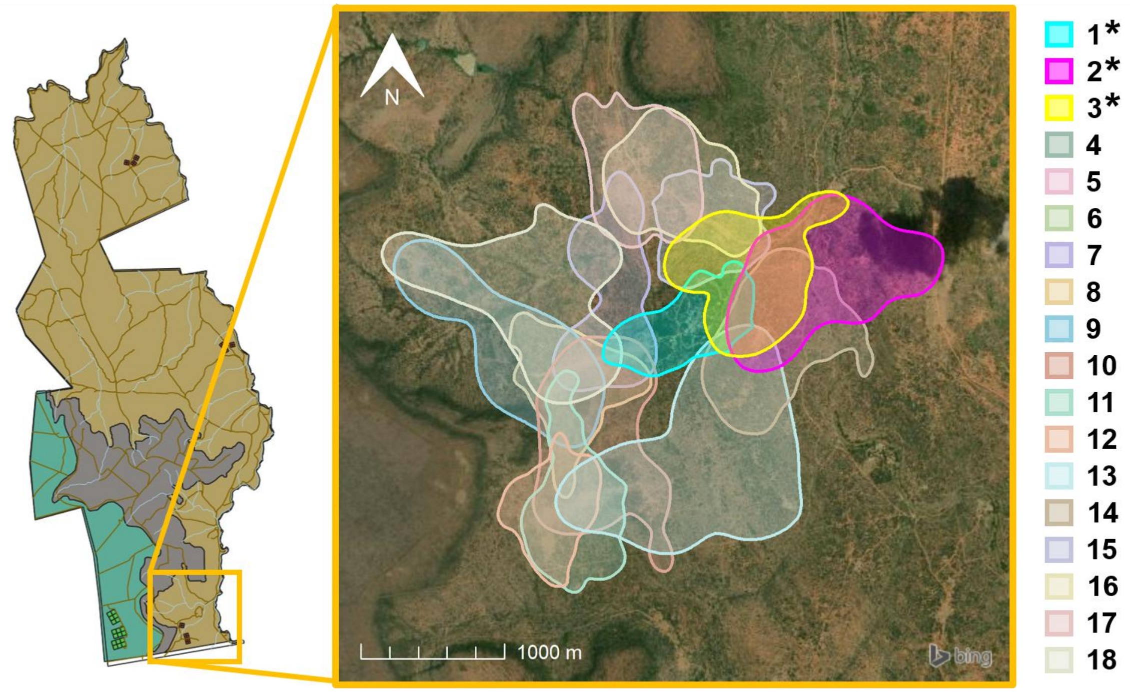

Figure 2: Home range of 18 study groups, with the three habituated groups (numbers 1 to 3) highlighted.

(Source: Author, 2021)

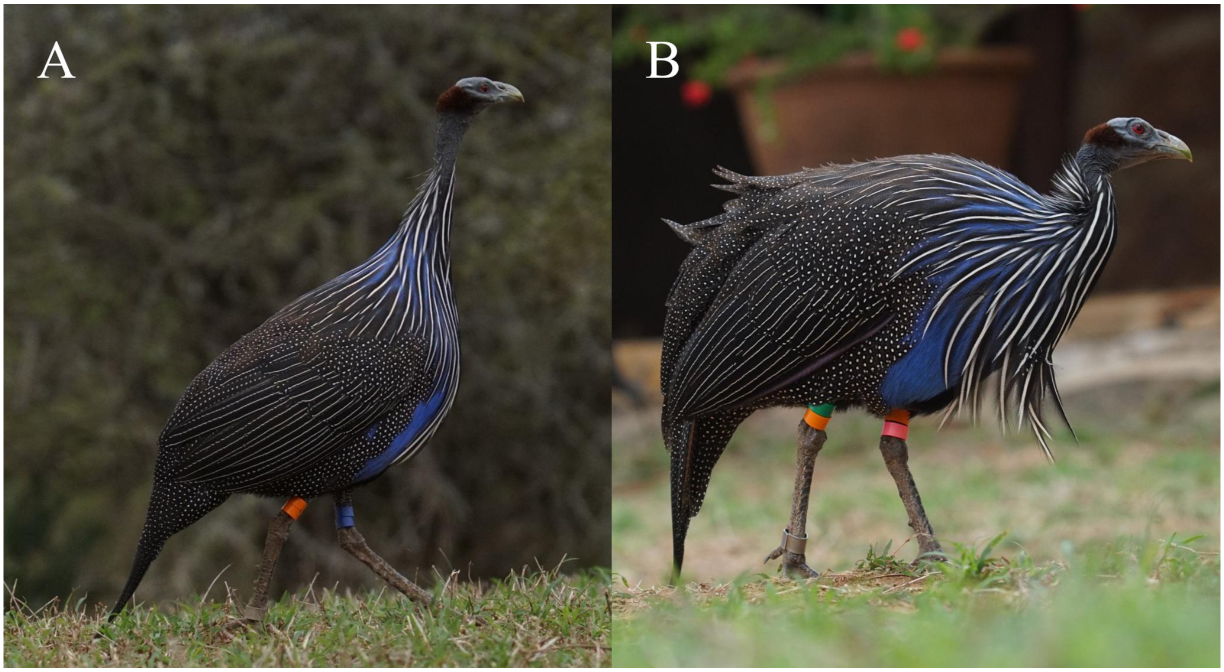

Plate 1: (A) male VGF (B) female VGF.

(Source: Author, 2021)

The male VGF is characterized by having a longer tarsus and a bigger breast. The female VGF has a short tarsus and smaller breast. The male VGF is larger than the female VGF in size.

Plate 2: Adult VGF and juveniles

(Source: Author, 2021)

3.3 Time frame

The majority of the study (objective 1, 3, 4 & 5) was conducted from 9th September 2019 to 14th February 2020, at which time there was one breeding event in which only one of the habituated groups reproduced successfully (hence these objectives were conducted on one group). For objective 2, data additional data were included from a large breeding season that occurred in May 2018, allowing sufficient GPS tracking data from females across three groups. The reproductive season was divided into three periods. The pre-breeding, breeding, and post-breeding periods. The pre-breeding period was defined as a period of one month prior to the observation of the first pair, and was used to establish a baseline for the social dynamics of the study group. The breeding period was the period from the start of pair formation until all chicks had hatched, which monitored incubation behaviour and observed non-breeding individuals to understand their group structure. Finally, the post-breeding season was a period of 2 months after the chicks hatched, during which collected information was collected on the chicks' behaviour and social associations.

3.4 Data collection

3.4.1 Determining which members of the social group of vulturine guineafowls breed

Vulturine guineafowls form large social groups during the non-breeding season. During this time, vulturine guineafowls have a steep dominance hierarchy, with dominant individuals monopolizing access to food resources. At the beginning of the rainy season—when this species breeds—pair formation begins, which may be several weeks in advance of the female laying the first egg. However, not all individuals in the group subsequently breed (or attempt to breed). Predictions are that the individuals who are highest in the hierarchy are more likely to breed because these can maintain better body condition and secure mates by displacing competitors.

Vulturine guineafowl social groups temporarily split during the breeding season, forming pairs and females lay eggs, which they subsequently incubate. Until recently, it was not known how groups of vulturine guineafowls are formed and what social structure characterizes wild populations. Data was collected for a period of 6 months (September 2019 to February 2020) on who breeds in these social groups. Paired individuals consisting of one male and one female which isolated themselves from their social group were recorded. Females were followed to their nest to record when incubation started and how many survived the first two weeks

As part of the long-term data collected on the vulturine guineafowl population dominance interactions for one habituated group were collected. To determine which members of a group breed when conditions became suitable (that is, rainy seasons), all individuals that formed pairs within the habituated group were noted, and their nests located. Pairs were defined as a female and an associated male which moved together (that is, less than 5m apart) and away from the group (that is, more than 20m from other group members). Before considering two birds to be a pair, they had to be observed moving together for the whole day, and recorded even if they paired for a single day.

3.4.2 Determining females' investment during incubating

Ground-nesting birds are typically at greater risk of nest predation than cavity or shrub nesters (Storch, 2014). Additionally, the chances of predation are likely to increase if there is regular movement to and from the nest; for example, if the female leaves the nest to forage or if parents alternate incubating. Avoiding detection by predators, which is critical for female and nest survival (Troscianko *et al.*, 2016), is especially difficult in brightly-coloured species (Götmark, 1997). Given that vulturine guineafowl breed in scrapes on the ground (Johnson, 2002) and are brightly-coloured, predictions are that first, only one individual will contribute to incubation and second, to minimize movement to and from the nest, that the incubating individual(s) will remain on the nest with few, if any, recesses during the incubation period. Should females be found to remain on the nest with minimal feeding breaks throughout the 25-day incubation period, females can be expected to incur considerable reductions in body mass, which cooperative helping behaviour by non-breeding individuals may subsequently offset.

In order to investigate the costs associated with nesting and incubation, positional data was collected from 16 incubating females which had previously been fitted with solar-powered, high-resolution GPS tags which operated daily from 0600h to 1900h. These data were collected in 2 breeding seasons (n=13 nests from May 2018, n=3 nests from November 2019). Nest coordinates were extracted from the GPS data as the mean latitude and longitude of each stationary detection for a given female during incubation.

3.4.3 Determining who are the closest associates to the chicks

Due to the male-biased sex ratios observed in birds generally, males likely face more restricted opportunities to breed independently (Leedale *et al.*, 2018). 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). The importance of direct and indirect benefits in helpers providing help can be determine the adaptability of cooperative breeding behavior (Kingma *et al.*, 2011). As these patterns of sex-biased dispersal and resulting sex bias in the population coincide with those observed in vulturine guineafowl, the prediction is that help will be given predominantly by the non-breeding male group members.

To determine associations between group members and chicks, group composition data in the morning (0600hrs-0930hrs) and evening (1700-1900hrs) for an average of four days in a week was collected. For this particular question, the central habituated group in the study area was targeted. Each time members of this group were encountered in an entity composed of adults or both adults and chicks, the identity of every adult bird present was recorded as well as the total number of adults and chicks present in each of the clutch encountered. The time from the start of observation of the group and the end time of the observation were recorded. A pair of binoculars were used to identify the unique combination of colour bands on the adults and the chick tag on one subadult, recording the data into a notebook.

Group observations were divided into two categories, single or subgroup. 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 meters of each other but more than 10m from other individuals), then these were recorded as a subgroup within the broader group.

Although chicks were not individually-marked, the clutches (N=3) were identifiable because they were not synchronized in time, meaning that there was a clear size difference between chicks from each clutch. From these differences, chicks from the same clutch remained together the vast majority of the time. One exception was for two clutches that hatched on the same day that became mixed together, however the mother from one of these clutches was predated, and these were from then-on recorded as being part of the clutch of the remaining mother which adopted the surviving chicks. Observations were collected when chicks were 1-4 months old, from the end of 2019 to the beginning of 2020.

3.4.4 Determining if chicks will receive significantly more care from helpers than from mothers and if the amount of care provided by helpers will be significantly greater for offspring of more dominant females

Plurally breeding groups provide an ideal setting to explore how helping behaviour by non-breeders is shared between the broods of multiple females with differing social status. It was predicted that females should receive help from previous offspring, and that more dominant females should receive more help, given that helpers usually help kin and such females likely have more close relatives within the social group.

In addition to collecting group composition data (see Question 3), interactions were recorded by through all-occurrence sampling of the habituated group. Because clutches were often apart, observation effort was distributed equally across the clutches over the whole study period. Four categories of interactions between adults and chicks in each clutch were recorded. The first is guarding behaviour (GRD), whereby individual A stays more than 20 meters from the rest of the group members with X number of chicks. The second is a within-group chick guarding behaviour (CPO), whereby individual A who is the actor does not allow Y adult group members to approach X chicks. The third behaviour is chick feeding behaviour (CFD) (Plate 3A), whereby individual A does some soft trills (that is, type of vocalizations) and calls the chicks to food. The final behaviour is chick covering (COV) (Plate 3B), whereby individual A covers X chicks under its wings for a certain period of time and for this behaviour the duration (in minutes) of each COV event was recorded. The actor of each interaction, the identity of the recipient clutch, and the length of the event in the case of COV events were recorded.

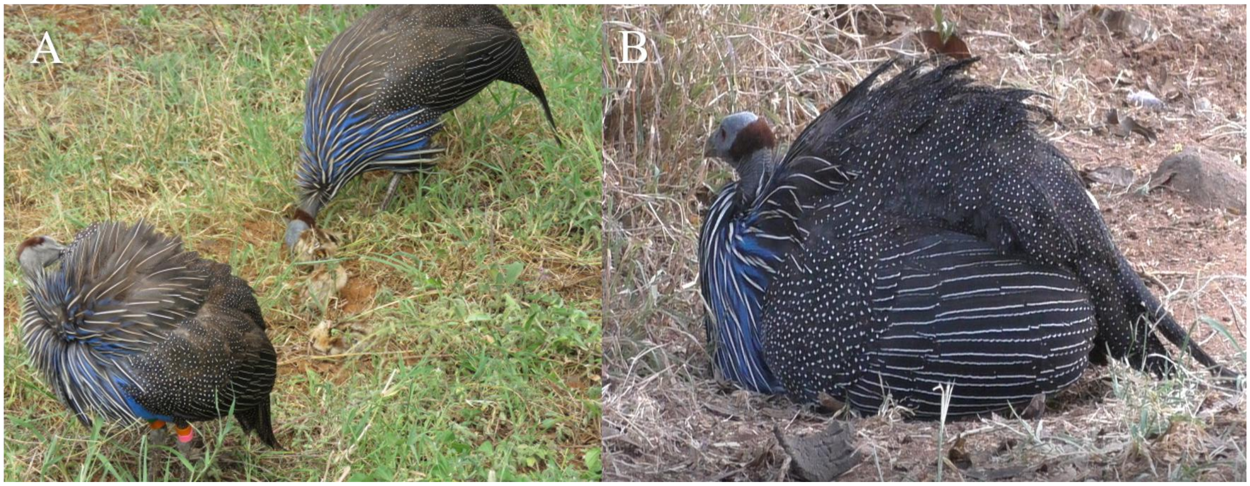

Plate 3: (A) Chick feeding behaviour (CFD) by an adult male, and (B) chick covering behaviour (COV) by an adult male.

(Source: Author, 2021)

3.4.5 Determining if helpers pay any cost by caring for the chicks

The helping behaviour of non-breeders—such as providing chicks with food, vigilance against predators and covering the chicks for warmth—are likely to carry costs, such as reduced food intake rates (Heinsohn & Cockburn, 1994). Additionally, helpers might pay costs by being less mobile, due to covering or attending to chicks, and hence encountering fewer resources than non-helpers. Moreover, helpers may even lose weight if helping involves a large investment in the young (Norberg, 1981). Whether vulturine guineafowl helpers forego foraging opportunities when carrying out helping behaviour will be investigated, and it is predicted that helpers will have reduced food intake rates relative to surrounding, non-helper group.

To investigate if individuals pay a cost while engaging in cooperative breeding behaviour, videos from one habituated group when chicks younger than five weeks were present (from 5th November 2019 to 1st December 2019) were recorded. From these videos, activity budgets for sessions when an individual could be tracked on the frame without getting lost due to occlusion or due to the movement of the person holding the camera were recorded. A new session would start if the focal individual started presenting a cooperative breeding behaviour (that is, covering the chicks under the wings, coded as COV) and would end when they stopped performing COV. Sessions when the focal individual was not engaged in cooperative breeding behaviour were recorded. For each session of a focal individual, the seconds she or he was involved in foraging as it was pecking on the ground or on a plant (herein foraging duration) but also if the bird was covering the chicks under her/his wings (COV) were recorded.

To further describe the COV behavior, apart from the video tracking, The presence and the duration of COV was recorded. In total, 71 occasions when covering under the wings was performed was recorded, and the duration of COV in minutes was also recorded for 27 out of these 71 occasions.

3.5 Data analysis

3.5.1 Determining which members of the social group of vulturine guineafowls breed

The hierarchical ranks of all members of the group were calculated using randomized Elo-ranking (Sánchez-Tójar *et al.*, 2017) to determine within-group dominance ranks. Elo scores work by giving individuals more positive values if they win an interaction against another individual, and more negative values when they lose. First, the probability that the winner of an interaction should win was calculated using the following function:

$$P\ (\text{winner should win}) = 1 / (1 + \exp(\sigma * x))$$

where sigmoid is a fixed parameter ($\sigma=0.001$) and x is the absolute difference in Elo scores between the two individuals (these were all initiated to equal 0). The winner's score was then updated using the equation score_new = score + (1-p)*200, and the loser's score was updated using the equation score_new = score - (1-p)*200. These calculations were done using the aniDom package in *R*.

Finally, the breeding pairs and the membership composition of the habituated group during the November 2019 breeding were tabulated, and evaluated against the ranks.

3.5.2 Investments made by females during incubating

Using GPS data from 265 daily tracks of incubating females, the following measures were calculated: the percent of the incubation period spent attending to the nest, the time of day when excursions occur, the length of time spent away from the nest, and maximum distance from the nest. This measure per excursion was calculated, and calculated an overall frequency at which excursions occurred. The percent of time spent incubating was calculated for each female as the summed duration of all periods in which the female was detected at the nest divided by the summed durations of all detections at the nest and away. Length of time spent away was simply calculated as the difference, in minutes, between the first and last detection of a given excursion. Due to the fact that not all females were tracked on every day of the incubation period (2 tags from 2018 were programmed to only record data every 4th day, and some tags' batteries fell below the level at which data could be collected), a subset of females (n=8) that produced data for every day of the full period to estimate frequency-related measures was used.

Because the need for females to leave the nest should be greater, the longer they remain at the nest, the relationship between incubation day and the number of excursions was tested. To do this, a Binomial generalized linear model (GLM) where the dependent variable was whether an excursion occurred or not on a given day (1= yes, 0=no) and the independent variable was nest-day (that is, number of days since start of incubation for a given nest) was used. The identity of each female was fitted as a random effect.

Females were said to be attending to the nest when detected within 10 meters of the calculated nest position, and were marked as making an excursion away from the nest when they were further than 10 meters.

A 10-meter threshold was used because the stationary behaviour and dense brush generated an increase in GPS positioning error, which could place points that appeared to be away from the nest when in fact the female had remained on the nest. To avoid including the initial movements of the female to the nest before incubation, or away after chicks had hatched, data from the first or last day of the incubation period was not analyzed.

Group members were considered to be visiting the nest when recorded within 5 meters of the nest at any point during the incubation period. The identity of all visitors, as well as the timing and duration of each unique visit, were recorded. Nesting females were not included in the list of potential visitors to their own nests, but were still included as potential visitors at the nests of other females from the same group. In total, 2279 daily tracks across 55 individuals were used to investigate three elements of any potential nest visits: the identity of the visitor, the duration of the visit, and whether or not that visit occurred while the female was making an excursion away from the nest.

Finally, whether members of the same social group attended nests during incubation was assessed. Movements of individuals belonging to three groups in which all members that were GPS-tagged (n=11 nests belonging to females from these groups) were analyzed.

3.5.3 Determining who are the closest associates to the chicks

Group composition data was used to calculate the frequencies of attendance of each group member to each of the three clutches.

This rate was calculated by dividing the number of subgroups that the individual was observed in that comprised the clutch by the total number of subgroups that the individual was observed, limited to groups in which there was an observation of that clutch (because not all clutches were observed in a given sampling day). For example, if an individual was observed 10 times in different groups that contained clutch A, of which 8 times it was in a subgroup with clutch A, the rate of attendance of the individual to clutch A was 0.8.

The individuals who were the primary associates of each clutch were determined using a simple permutation test. The permutation test consisted of randomizing the subgroups that the focal chicks were contained to determine which adults were observed with the chicks more often than expected by chance. The permutation test worked as follows: for each day K observations were randomly allocated of the chicks to subgroups observed on that day, where K corresponds to the number of subgroups the chicks were observed in that day. Each individual's rate of attendance from these permuted data was re-calculated (that is, they remained in the same subgroup, but the chicks were moved between subgroups for the purpose of the permutation test). The permutation test therefore maintained the number of times each individual and each clutch were 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, the individuals who's observed values was higher than 95% of the values generated by the permutation procedure ($P \leq 0.05$) were extracted.

The individuals as having significantly higher attendance to that clutch than expected by chance were recorded. This process was repeated for all three clutches.

Significant attendance to each clutch by each group member as a network was plotted. From these data, information such as age and sex distribution of the primary helpers, and whether individuals specialized on helping one more clutch than the other was extracted. To test whether males were disproportionately represented as helpers, a two-sample proportion test that compared the proportion of males to females among the helper and non-helper category (excluding mothers) was performed**.**

3.5.4 Determining if chicks will receive significantly more care from helpers than from mothers and if the amount of care provided by helpers will be significantly greater for offspring of more dominant females

Interaction data to characterize the relative contribution of each significant associate to the clutch was used. To determine whether the mother provided most of the care or not, and (if not) how help received varied between clutches first, the number of each interaction directed towards a focal females' chicks was extracted. Because GRD and CPO were similar behaviours, and expressed relatively rarely, they were combined into one behaviour. For each of that females' significant helpers (and the female herself), the number of interactions they provided from the 4 behaviours was calculated. Raw number of interactions observed because each helper was observed relatively equal number of times and all had an equal opportunity to be observed while providing help in each sample (Hoppitt & Farine, 2017). Box plots on which the mother's value for the care given was marked and plotted (Figures 13-16). Because the mothers clearly did not give the majority of the care to their chicks, comparison of the mother to other helpers statistically was not done

Significant difference in the care given by the helpers of the different clutches was tested. Two-sample test for equality of proportions to contrast the proportion of total help given to each of the brood by the mother was used. That is, the number of helping events of cover and food provisioning by the mother out of the total number of helping events given by the significant helpers which included the mother were provided. This comparison across the three pairs of clutches was performed. Significant effects mean that the difference in the proportion of help given by the mother was significantly lower in one clutch than the other

3.5.5 Determining if helpers pay any cost by caring for the chicks

Using the data extracted from the videos, the proportion of the time spent foraging (response variable) was examined as to whether it was predicted by whether the focal individual was involved in COV (1) or not (0) (binary independent variable). A Generalized Linear Model of a binomial family was run.

CHAPTER FOUR

RESULTS

4.1 The breeding members of vulturine guineafowls

The results in Table 1 show that 6 females in a social group that bred during the breeding season of November 2019. The dominance hierarchy for both males and females are listed in their respective columns, with numbers 1 to 8 representing the ranks, whereby 1 is the most dominant and 8 being the least dominant. Males paired with the particular females are highlighted. One out of the five nests were predated on and 4 out of the 6 females chicks hatched and survived the first 2 weeks.

Table 1. Vulturine guineafowl breeding members of a habituated group.

	Dominance rank of female (1=highest, NA=not available)	**Male(s) paired with**	**Dominance rank of male(s) (1=highest, NA=not available)**	**Nest predation (T=True, F=False)**	**Chicks hatched and survived two weeks (T=True, F=False, NA=not available)**
	1	WKOW	1	F	T
	NA	KKRK, YOKO	2, 4	T	NA
	NA	RROR, WBKR	5, 3	F	F
	NA	WBKR, YOKO, WKOR, OOBB	3, 4, 8, 6	F	T
	NA	YOKO, WORR, YGBW	4, 13, 17	F	T
	NA	WBKR, YOKO	3, 4	F	T

4.2 Investments females make when incubating

Females spent, on average, 97.6% (SD= 2.35%, range=90.9–100) of the incubation period at the nest. Excursions were typically quite short, averaging only 36 minutes in length (SD=37.1, range=0–245) (Figure 3A) with females travelling up to 288 meters from the nest (mean=120.8, SD=46.7) (Figure 3B). Excursions occurred at all hours between 0600-1600, with the majority taking place in the early afternoon between 1200h and 1400h (Figure 3C). From the subset of 8 females for which were able to record the full incubation period, females made on average 10 excursions (range 4–21) over the course of the 24-day incubation period, typically making only one excursion per day on the days in which they did leave the nest (Figure 3D). Lastly, there was no significant effect of the number of days since the start of incubation on whether or not a female made an excursion (P=0.797, Table 2).

Group members were recorded visiting a female's nest on 45 occasions. Almost all visits occurred on either day 0 (the day on which the female began incubating) or on the hatching day of a given nest (Figure 4). Only 6 of the 45 visits occurred between days 1 and 22. Visits lasted for 24.6 minutes on average (SD=37.9, range: 3 seconds–150 minutes). For all incubating females, the most frequent visitors were males. In 2 instances, the most frequent visitor was also a male which had previously been identified as the breeding partner of the female in question. None of the detected visits occurred during the same time when a nesting female was on an excursion. No cases of other females visiting the incubating female were detected.

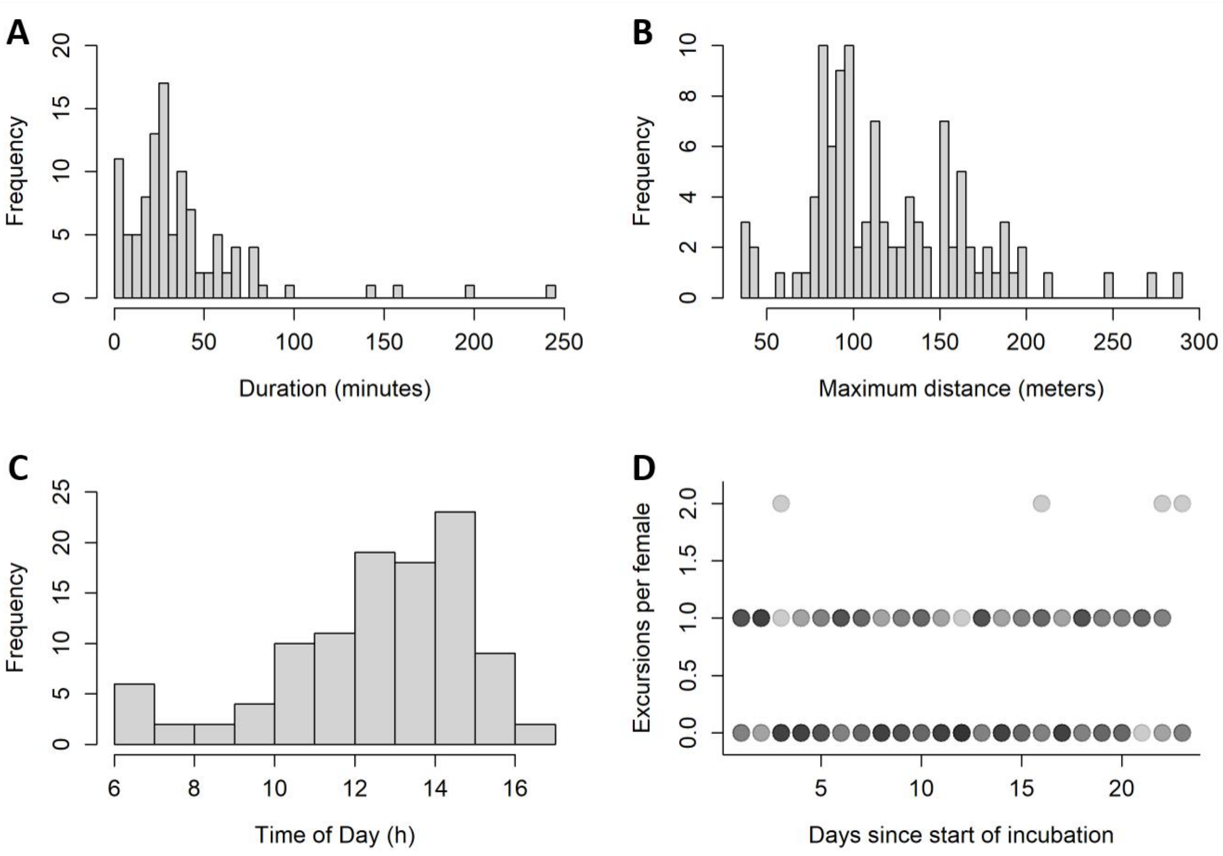

Figure 3: A) Distribution of the durations of excursion time in minutes. B) Maximum distance travelled from the nest per excursion. C) Distribution of the time of the day when incubating females took excursions away from the nest. D) Excursions per female

Table 2. Generalized linear mixed model fit by maximum likelihood for a final model

	Estimate	Std. Error	Z value	Pr(>|z|)
Intercept	-0.3178	0.4807	-0.661	0.509
Number of days since start of incubation	0.0068	0.0266	0.257	0.797

Random effects

Groups	**Name**	**Variance**	**Std.dev**
Female ID	**Intercept**	0.894	0.9453

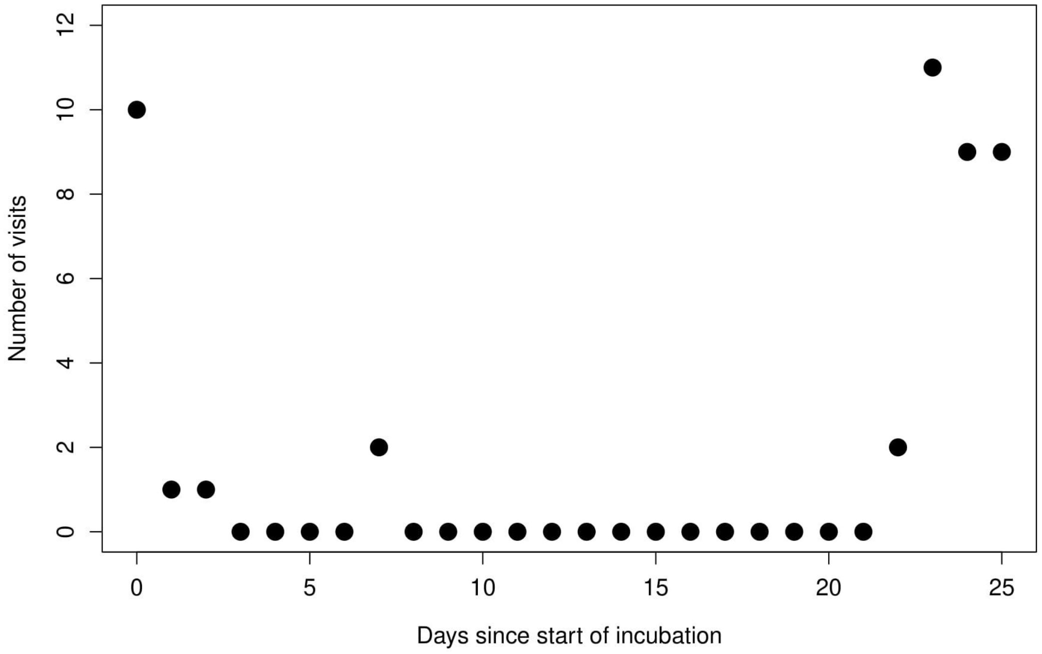

Figure 4: Number of visits by other group members than the incubating female detected at each day of the incubation period.

4.3 Closest associates to the chicks

There were three key insights from the analysis for objective 3. First, each clutch had a number of individuals that were observed with the clutch more than expected by chance, but that not all individuals were consistently detected with a clutch (Figure 5). Second, there was no overlap amongst the individuals that were significantly associated with each clutch indicating that each clutch had a distinct set of associates. Third, there was a strong male bias amongst helpers in YOBK's clutch had 7 associates (6 males and 1 female), WOBY's clutch had 6 associates (5 males and 1 female), and GOBO's clutch had 3 associates (all males). By contrast, the 16 individuals that did not associate with the brood more than expected by chance were more represented by females. Finally, the one known male offspring (CT311, a 1-year-old male whose mother was YOBK) significantly helped its mother. The results in Table 3 show that overall, males were significantly disproportionately overrepresented among the associates as compared to the females (χ^2= 7.407, df= 1, P=0.006).

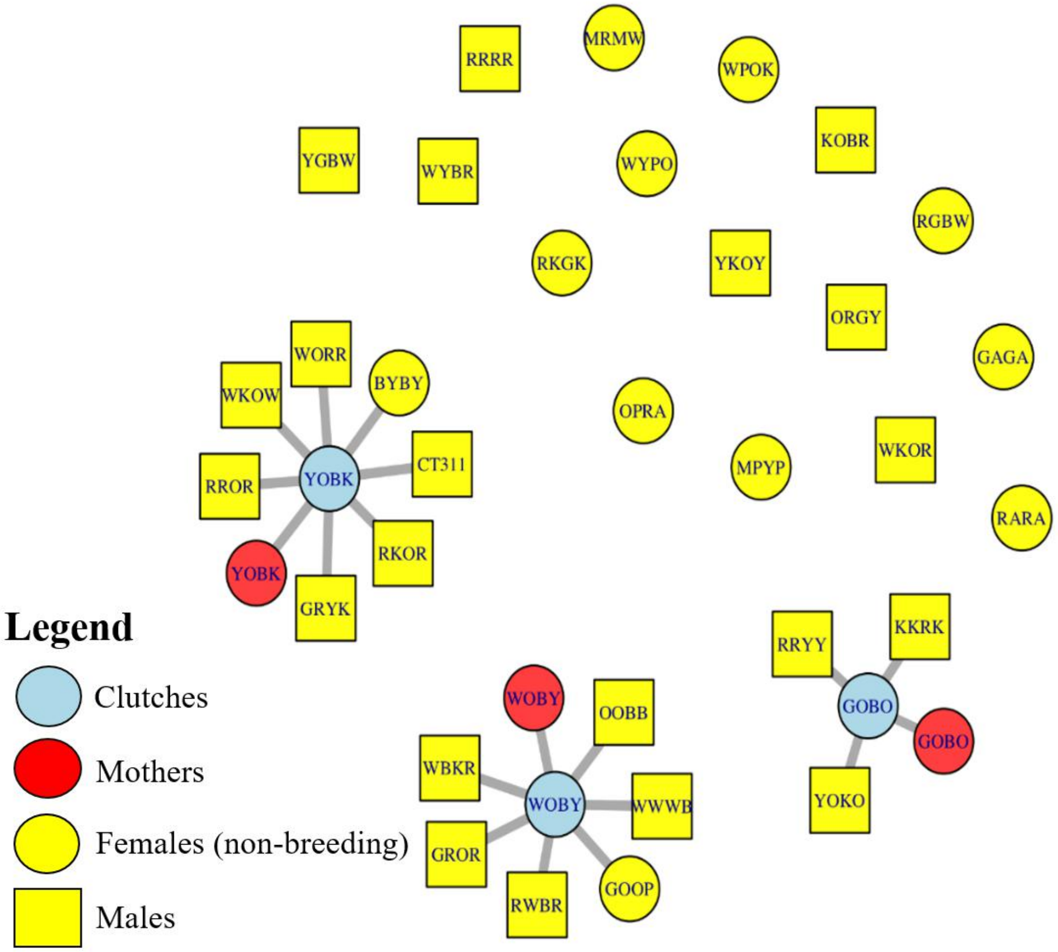

Figure 5: Network of attendance to each clutch.

Table 3. 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 clutches.

Mean 1	Mean 2	X^2	DF	P	95%CI
0.133	0.778	7.407	1	0.006	-1.000–-0.234

4.4 Chicks receive significantly more care from helpers than mothers and the amount of care provided by helpers will be significantly greater for offspring of more dominant females

Mothers did not provide a disproportionate amount of the care towards their offspring. In none of the three clutches, nor across any of the interaction types, were mothers consistently giving the most care (Figures 6-8). Further, mothers also did not spend more time covering the chicks (COV) than the helpers. For example, out of the 20 cover events recorded for YOBK's chicks, the mother was found to cover chicks for only 1 minute and also contributed in only 42 of the 330 CFD events and 1 out of 7 GRD+CPO events. However, not all females received the same amount of help from helpers. YOBK, the dominant female, received disproportionately significantly more help in food provisioning (CFD) and cover (COV) than the other two females ($P<0.05$), but there were no statistical differences in the help received among WOBY and GOBO (Table 4). The chicks from YOBK's clutch also received a much higher number of helping interactions overall (YOBK=446 vs. WOBY=92 and GOBO=85). However, YOBK's clutch was observed more than WOBY's and GOBO's clutch, hence contributing to some of these differences. No observations were made for COV interactions in the GOBO clutch, meaning that comparisons cannot be drawn effectively.

Table 4: 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 clutches. Significant values are shown 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	-0.190–0.1310	0.839
	COV	0.600	0.000	0.365	1	-0.179–1.000	0.56

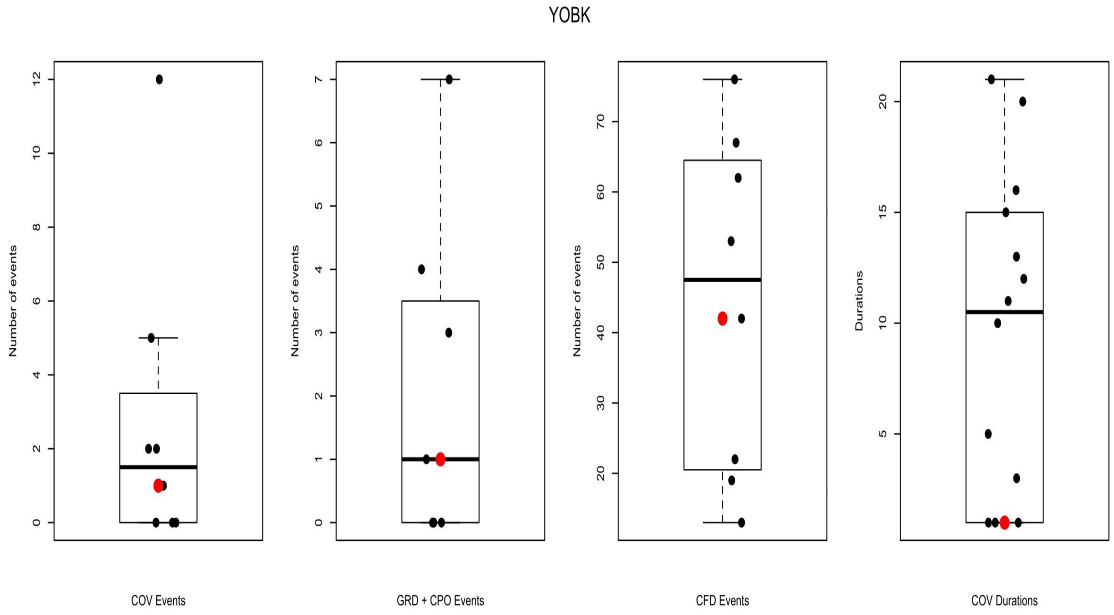

Figure 6. Amount of help given by the mother and helpers for the YOBK clutch.

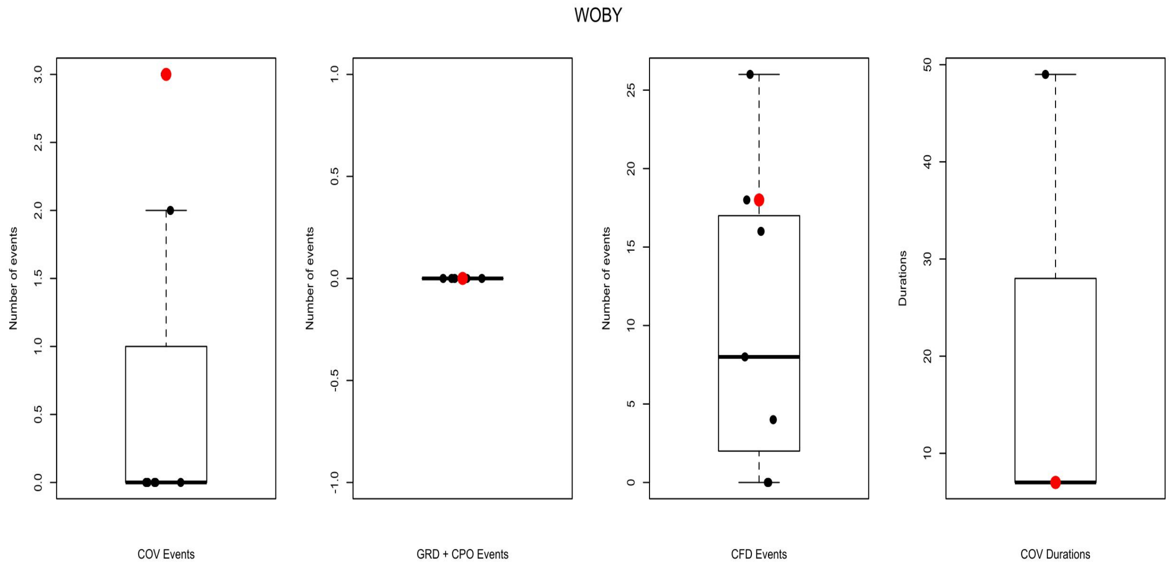

Figure 7: Amount of help given by the mother and helpers for the WOBY clutch.

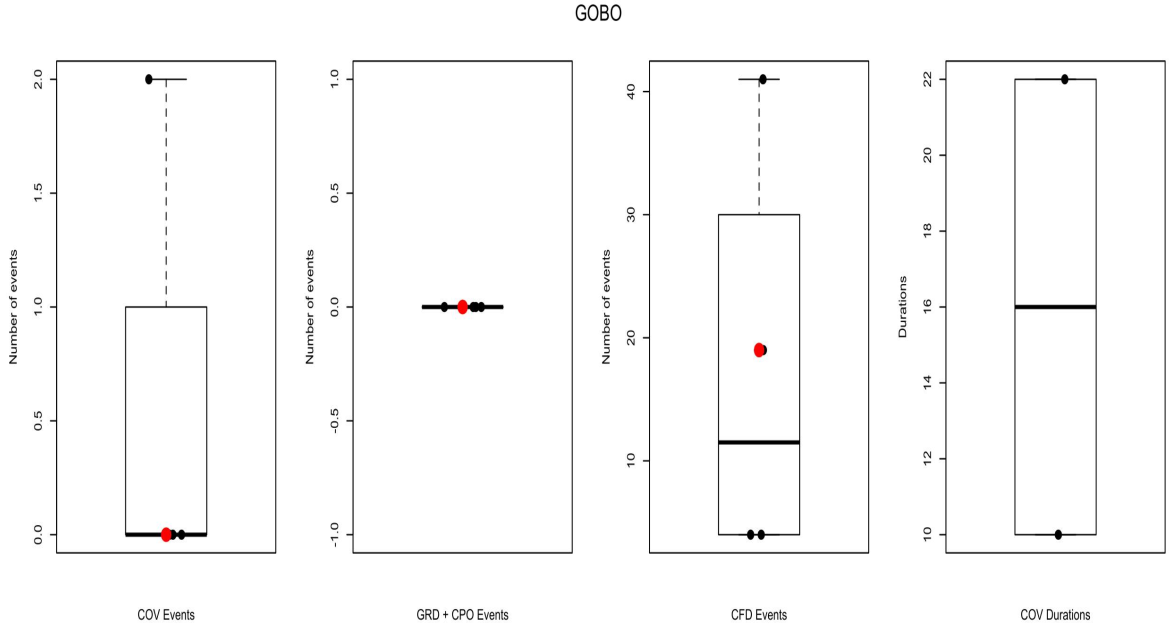

Figure 8: Amount of help given by the mother and helpers for the GOBO clutch.

4.5 Costs paid by helpers caring for the chicks

Based on 27 observations of COV behaviour, when the duration of COV was accurately recorded, birds perform this behaviour on average for 16.091 minutes (range=1–60 minutes). Based on the video data, birds pecked on average 0.093 times per second when they were not performing the COV behaviour (range=0–1.47) and pecked on average 0.009 times per second when they were performing the COV behaviour (range=0–0.097). This means that, on average, a bird performing a key helping behaviour missed 81.129 pecks (89.787 pecks over 16.091 minutes when not helping versus 8.689 pecks over 16.091 minutes when helping), thereby potentially reducing their foraging intake (based on pecks) by 90%.

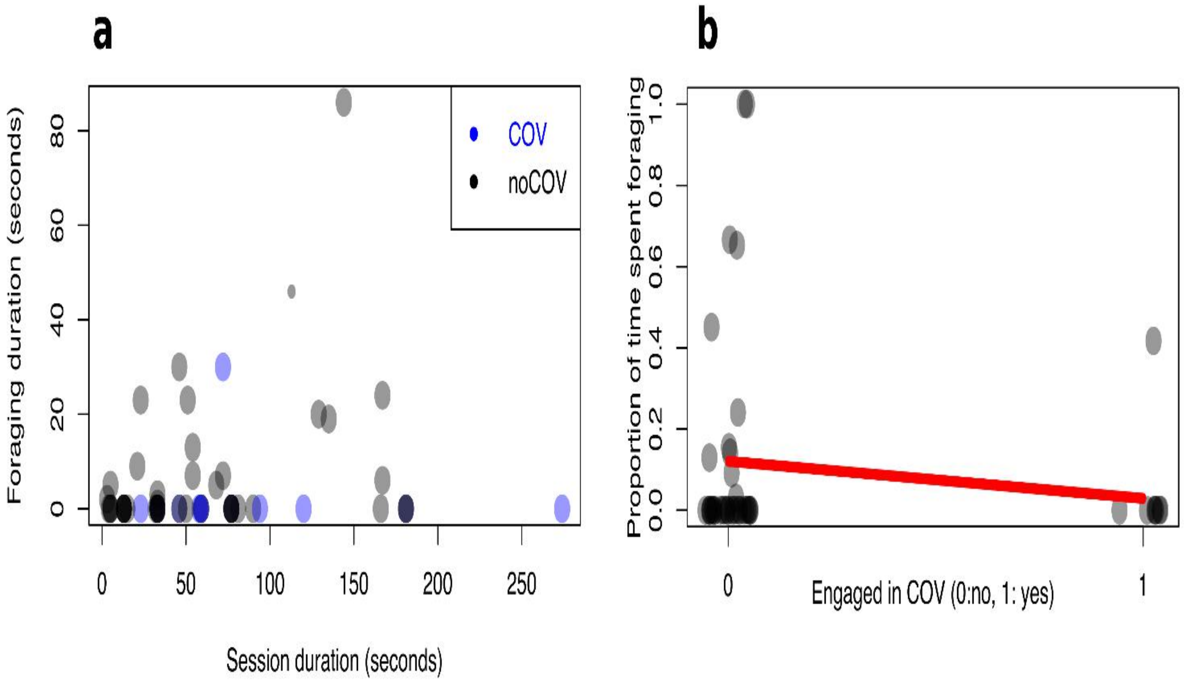

Figure 9: **(a) Raw data (b) Proportion of time spent foraging.**

The raw data shows the duration of each video session on the axis and the foraging duration in seconds for each video session on the y axis (Figure 12 a). Blue dots represent instances of COV behaviour while the black dots represent no COV. Proportion of time spent foraging (Figure 12b) on the y axis while engaged in COV behaviour (1) or when not engaged in COV (0). The x coordinates in b are jittered for better visualization.

Table 5. The proportion of the time spent foraging (response variable) was predicted by whether the focal individual was involved in COV (1) or not (0) (binary independent variable).

	Estimate	**Standard error**	**Z Value**	**Pr(>|z|)**
Intercept	-1.988	0.058	-34.174	< 0.001
Engaged in COV (0:no, 1: yes)	.526	0.194	-7.856	<0.001

The table shows the model coefficients: - standard errors, Z statistic and associated p values. The estimates for being engaged in COV were generated using a binomial generalized linear model.

CHAPTER FIVE

DISCUSSION

5.1. Members of the social group of vulturine guineafowls that breed

Different species of animals that exhibit cooperative breeding behavior vary from being a breeding pair with helpers to multiple breeding units who may be either polygamous and polyandrous (Kathleen, 2018). There is no clear understanding of the drivers that give rise to multiple breeding units in the vulturine guineafowls. Multiple breeding individuals have been studied in a particular mammal species known as the golden lion tamarins (*Leontopithecus rosalia*) (Dietz & Baker, 1993) who are cooperative breeders since the adults care for the young ones regardless of how many they are (Goldizen, 1989). This is similar to the vulturine guineafowls since they form multiple breeding pairs during the breeding season and provide care to the offspring after hatching. A study on the grey wolves (*Canis lupus*) showed that breeding by multiple individuals should be possible if there is a sufficient availability of resources. Vulturine guineafowl breed during the wet season when there are adequate food resources, and because of low within-group competition many individuals can reproduce at the same time. The study also highlighted the variance that can emerge in terms of who is successful. In this particular breeding season, the dominant male was successful since the female he was paired with was successful and the chicks survived. By contrast, the beta male was not successful since the female he was paired with was predated on during the incubation phase. The third male in the hierarchy was successful and the chicks survived. This was an exceptional case since the female he was paired with was predated a day after she came back with chicks but her clutch mixed with that of another subordinate female in the group. Whether the link between survival of offspring and dominance in vulturine guineafowl is non-random will require many more seasons of data. Studies on wolves (Cassidy & Forever, 2015; Peterson *et al*., 2016) showed that subordinate females that breed may lose their offspring very early because of lack of help and infanticide.

5.2 Investment's females make during incubating

The results show that female vulturine guineafowls invest highly during the incubation phase with them spending a lot of time on the nest with minimal excursions. If they make excursions, they do not travel far away from their nest location. They tend to make excursions anytime of the day but most of the excursion are usually around midday. The females received very few, if any, visitors during incubation and these were mostly detected during the first and last day of incubation. Incubation by the vulturine guineafowl was performed solely by the female. A similar study conducted in a Galliforme species on the reproductive and mating strategies of the northern bob white quail (*Colinus virginianus*) discovered that both males and females participate in the incubation process (Burger *et al*., 1995). The results indicated that female guineafowl spent a large percentage of their time on the nest. With so much time spent on the nest, the females potentially incurred a great cost in terms of lost foraging opportunities. Though they may make few excursions during the incubation period, these were fairly short and likely not enough to maintain optimal body condition. During the incubation phase, the females' excursions typically occurred in the afternoon when it was hot. This case is also demonstrated in the northern bob white (*Colinus virginianus*) which took 0-3 recesses per day from mid-day to late afternoon (Burnam *et al*., 2012) with the longest break taking 42 minutes.

Species vary in how many visitors females receive while incubating. Female Kalij pheasants (*Lophura leucomelanos*) sit on the nest alone for the entire incubation period of 26 days and no visitor was recorded in close proximity to the nest (Severo, 2013). In the Florida scrub jays, speculations suggest that female helpers stay close to the nesting female to help in incubation and brooding (Hailman *et al*., 2010). In the vulturine guineafowl, 12 visits—including 6 that were not on day zero or the hatch day—were less than 10 seconds, which might have been false positives in which the visitors were just passing by the nest area. However, 4 of the visits detected were over 1 hour long, but all of these took place on the hatch day of the nest being visited. One exception is on day 22 when the female was in the true incubation phase. The visit lasted 20 minutes and was from a male that was paired up with the female. In a similar study on the helmeted guineafowl (*Numida meliagris*) the study showed that the male stays near the nest guarding the female on the first few days of incubation (Elbin *et al*., 1986). That study showed that the male stayed at the nest past day zero, which does not seem to be the case in the vulturine guineafowl males.

This study was the first to use GPS tracking to collect data on one important stage in the life of birds: nest attendance. Numerous studies rely on direct observation, such as in studies on the helping and social behaviours of foxes made using field observation method (Aguiar & Moro-Rios, 2009), while camera traps are increasingly used, and more efficient, method especially in areas that are difficult to access and also ensures continuous sampling (Trolliet *et al*., 2014). The limitation in using such methods is that they are very time consuming—both through the field observations or in analyzing the camera trap data. However, the method still requires some optimization. One challenge encountered was that the GPS tags collected fewer data through the entire incubation period as the females spent most of their time (97%) on the nest, which was also under cover and thereby reducing the solar exposure to charge the tags. As a result, tags collected sparser data, which could have under-estimated the times that females left the nest. Alternatively, the coarser data also suffered from higher GPS error, which could have overestimated how often the females leave the nest. Finally, birds that left the nest more might have the likelihood of recharging their tags, and therefore be over-represented in the data. Future studies should carefully consider the battery capacity of GPS tags before using them to collect nest attendance data.

5.3 Closest associates to the chicks

The results show that vulturine guineafowls exhibited cooperative breeding behaviours like food provisioning, cover and guarding with the significant associates of each clutch—and subsequently those who helped most—being predominately male group members. Each clutch had between 3 and 8 individuals that were observed with them more often than expected by chance, and that these provided more care (overall) than the mother did. The results of this study are consistent with other cooperatively breeding Galliformes, for example a study of the northern bob white (*Colinus virginianus*) showed that helpers can contain either males, females or a mixture of both males and females (Orange *et al*., 2016). However, vulturine guineafowl contrast with passerines, such as the splendid fairy wrens (*Malarus splendens*) in which an increase in the number of female helpers increase the broods productivity while an increase in the number of males does not (Brooker & Rowley, 1995), resulting in a larger representation of females helping the brood as compared to males. However, despite tending to be quite social not all Galliformes are cooperative breeders. For example, in the California quail (*callipepia californica*), most broods are reared by parents alone (Lott, 1999). In other studies, males in the Centrolenidae family of glass frogs do not accept unrelated clutches but spend days watching the embryos without attending to them in any ways (Aguilar *et al*., 2021). As opposed to other cooperative breeding birds, the superb fairy wrens (*Malurus cyaneus*) helpers are usually not related to the offsprings that they provide care to (Dunn *et al*., 1995).

By studying the social network of the helpers and the broods they were helping, the results showed that the helpers were brood specific, which suggests that this species differs in the structure of helping from many others. This appears to be unlike helping in other species. For example, in a study conducted on the Barrow's goldeneye (*Bucephala islandica*), a duck species that has precocial young, the offspring from multiple adults are merged so that they could benefit equally from the care provided by the members of the group (Eadie & Lyon, 1998).

5.4 Chicks receive significantly more care from helpers than mothers and the amount of care provided by helpers will be significantly greater for offspring of more dominant females

One striking result was that not all females received help equally. YOBK, who has been the dominant female over most of the period that this group has been studied, received much more help from her helpers than either of the other two females. Comparison of the proportion of care given by mothers among the three broods showed that there was a significant difference between YOBK and the other two females (YOBK gave disproportionately less care). However, what was consistent across all three clutches is that mothers did not provide the majority of care to their chicks. The large amount of help given by non-parents is perhaps unusual. A study on the grey wolves (*Canis lupus*) revealed that breeding females spend more time guarding the offspring than the rest of the group members (Ausband *et al*., 2016). One reason why female vulturine guineafowl received so much help could be because of the high cost they pay during incubation—meaning that they have to prioritize recovering their body condition.

5.5 Costs paid by helpers caring for the chicks

The results showed that the vulturine guineafowls performing a key helping behaviour potentially reduced their foraging intake for the benefit of the offsprings. Cooperative breeding behaviours are usually identified through food provisioning by different individuals, especially at the nest for altricial species. In the study, four cooperative behaviours given by non-parents to offspring were identified, including food provisioning, guarding, cover for the chicks, and within group guarding behaviour. These behaviours are consistent with those observed by helpers in other precocial species (Du Plessis *et al*., 1995). The most evident form of cooperative breeding behaviour given by vulturine guineafowl helpers was calling the chicks for food by making soft trills. In the same observation period, 639 such interactions were observed, compared to only 56 of the other interactions combined. This is not unexpected, as assisting chicks to forage probably represents the lowest-cost help that can be given. Helping was costly to helpers. However, few studies have investigated the costs of care to helpers. In meerkats (*Suricata suricatta*), helpers lose weight when they participate in cooperative breeding activities such as baby feeding and feeding the young (Russell *et al*., 2003). In white winged coughs (*Corcorax melanorhamphos*) which are cooperative breeders, helpers suffer costs from provisioning help in addition to costs they incur by choosing to remain in their natal territory (Heinsohn & Cockburn, 1994). Cooperatively breeding vulturine guineafowls incur costs that are a limitation to their provisioning effort.

CHAPTER SIX

CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusion

This study provides the evidence of cooperation in vulturine guineafowl, and captures a cooperative social system that is distinct from previously published systems. Recent studies on Galliformes indicate that cooperative breeding might be more common in precocial species than earlier comprehended. Group living in many Galliformes may also contribute significantly to the evolution of cooperative breeding behaviour.

Objective 1: All females in the group can reproduce though more dominant females are likely to attempt breeding.

Objective 2: Results indicate that females carry out the incubation role all alone but after hatching, they rejoin the group back with chicks. They received visitors but this was mostly during the first and last days of incubation.

Objective 3: Help is provided non-randomly, with most help coming from the non-dispersing sex, that is, the males and each clutch having a distinct set of helpers. It’s unclear who the helpers actually are but one outstanding observation the only subadult male in the group was among the primary helpers of his mother’s clutch, who was the dominant. The three clutches had multiple males that helped in rearing the chicks.

Objective 4: Helpers provided the same amount of care as the mother on average as the most dominant female received more help as compare to the other clutches. The helpers brooded the chicks by covering them under the wings and they were also guarding the young against intruders.

Objective 5: Helping was costly for individuals and they ended up reducing the amount of time they took to forage so that they can help in caring for the chicks. With this they will gain direct fitness.

6.2 Recommendation

6.2.1 Recommendations for further research.

This thesis found strong evidence for cooperative breeding in a Galliforme. It is therefore recommended that more studies are needed done on cooperative breeding in non-passerines, and especially among the Galliformes and other altricial species. Because many Galliformes are social, cooperative breeding is likely to be much more widespread in these species than currently thought.

It is recommended that more studies are conducted, and behavioural observations collected, in plural breeding species. Specifically, it is recommended that more studies investigate how social rank of breeders affects reproductive success, especially among males as these are philopatric. Such insights are important for understanding how indirect fitness might be gained via paternal routes, which are usually linked with much greater kinship uncertainty.

This thesis found that females invest a lot into reproduction, especially during incubation. It is recommended that more studies are carried out on the reproductive behaviour of Galliformes, as female investment (or lack of help received during incubation) may indicate which species could breed cooperatively. At present, most studies on Galliformes have been carried out in the northern hemisphere, and therefore greater focus should be placed on African and Asian species in this family.

This thesis also has recommendations for management and conservation of vulturine guineafowl. Specifically, management of group members should ensure that helpers are also protected, as this thesis has shown that they give the majority of the care for the young. Young males are particularly important, as these are the significant helpers of each brood, and without them broods may not survive, and therefore groups may go extinct.

Because helping is costly, it is recommended that any conservation actions ensure that helpers have access to sufficient resources in order to survive and offset the costs of helping. Thus, habitat protection, including of both cover and open areas on which birds forage, is essential, as vulturine guineafowl spend most of their foraging time on open glades but also require cover for protection from predators. Conserving such a habitat matrix will ensure long term survival of the vulturine guineafowl species.

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APPENDICES

Appendix 1. Cooperative breeding in precocial species

Table 6: Present evidence for cooperative breeding in some precocial species (adapted from Wang and Kimball 2016).

Updated information (reviewed in this thesis) is given by superscripts, with references given in the table footnotes.

COMMON NAME	SCIENTIFIC NAME	STATUS
EGYPTIAN GOOSE	*ALOPOCHEN AEGYPTIACA*	NON-COOPERATIVE
BRAZILIAN TEAL	*AMAZONETTA BRASILIENSIS*	NON-COOPERATIVE
NORTHERN PINTAIL	*ANAS ACUTA*	NON-COOPERATIVE
AMERICAN WIGEON	*ANAS AMERICANA*	NON-COOPERATIVE
WHITE - CHEEKED PINTAIL	*ANAS BAHAMENSIS*	NON-COOPERATIVE
BERNIER’S TEAL	*ANAS BERNIERI*	NON-COOPERATIVE
CAPE TEAL	*ANAS CAPENSIS*	NON-COOPERATIVE

CHESTNUT TEAL	*ANAS CASTANEA*	NON-COOPERATIVE
BROWN TEAL	*ANAS CHLOROTIS*	NON-COOPERATIVE
NORTHERN SHOVELER	*ANAS CLYPEATA*	NON-COOPERATIVE
EURASIAN TEAL	*ANAS CRECCA*	NON-COOPERATIVE
CINNAMON TEAL	*ANAS CYANOPTERA*	NON-COOPERATIVE
BLUE-WINGED TEAL	*ANAS DISCORS*	NON-COOPERATIVE
EATON'S PINTAIL	*ANAS EATONI*	NON-COOPERATIVE
RED BILLED TEAL	*ANAS ERYTHRORHYNCHA*	NON-COOPERATIVE
FALCATED DUCK	*ANAS FALCATA*	NON-COOPERATIVE
YELLOW BILLED TEAL	*ANAS FLAVIROSTRIS*	NON-COOPERATIVE
BAIKAL TEAL	*ANAS FORMOSA*	NON-COOPERATIVE
MOTTLED DUCK	*ANAS FULVIGULA*	NON-COOPERATIVE

YELLOW BILLED PINTAIL	*ANAS GEORGICA*	NON-COOPERATIVE
MELLER'S DUCK	*ANAS MELLERI*	NON-COOPERATIVE
CAMPBELL TEAL	*ANAS NESIOTIS*	NON-COOPERATIVE
EURASIAN WIGEON	*ANAS PENELOPE*	NON-COOPERATIVE
RED SHOVELER	*ANAS PLATALEA*	NON-COOPERATIVE
PUNA TEAL	*ANAS PUNA*	NON-COOPERATIVE
GARGANEY	*ANAS QUERQUEDULA*	NON-COOPERATIVE
AUSTRALASIAN SHOVELER	*ANAS RHYNCHOTIS*	NON-COOPERATIVE
AMERICAN BLACK DUCK	*ANAS RUBRIPES*	NON-COOPERATIVE
CHILOE' WIGEON	*ANAS SIBILATRIX*	NON-COOPERATIVE
CAPE SHOVELER	*ANAS SMITHII*	NON-COOPERATIVE
AFRICAN BLACK DUCK	*ANAS SPARSA*	NON-COOPERATIVE

GADWALL	*ANAS STREPERA*	NON-COOPERATIVE
PACIFIC BLACK DUCK	*ANAS SUPERCILIOSA*	NON-COOPERATIVE
YELLOW BILLED DUCK	*ANAS UNDULATA*	NON-COOPERATIVE
SILVER TEAL	*ANAS VERSICOLOR*	NON-COOPERATIVE
HAWAIIAN DUCK	*ANAS WYVILLIANA*	NON-COOPERATIVE
HORNED SCREAMER	*ANHIMA CORNUTA*	NON-COOPERATIVE
GREATER WHITE FRONTED GOOSE	*ANSER ALBIFRONS*	NON-COOPERATIVE
GREY-LAG GOOSE	*ANSER ANSER*	NON-COOPERATIVE
PINK FOOTED GOOSE	*ANSER BRACHYRHYNCHUS*	NON-COOPERATIVE
SWAN GOOSE	*ANSER CYGNOIDES*	NON-COOPERATIVE
LESSER WHITE FRONTED GOOSE	*ANSER ERYTHROPUS*	NON-COOPERATIVE
BEAN GOOSE	*ANSER FABALIS*	NON-

		COOPERATIVE
BEAR-HEADED GOOSE	*ANSER INDICUS*	NON-COOPERATIVE
MAGPIE GOOSE	*ANSERANAS SEMIPALMATA*	COOPERATIVE
LESSER SCAUP	*AYTHYA AFFINIS*	NON-COOPERATIVE
REDHEAD	*AYTHYA AMERICANA*	NON-COOPERATIVE
HARDHEAD	*AYTHYA AUSTRALIS*	NON-COOPERATIVE
BAER’S POCHARD	*AYTHYA BAERI*	NON-COOPERATIVE
MADAGASCAR POCHARD	*AYTHYA INNOTATA*	NON-COOPERATIVE
GREATER SCAUP	*AYTHYA MARILA*	NON-COOPERATIVE
CANVASBACK DUCK	*AYTHYA VALISINERIA*	NON-COOPERATIVE
MUSK DUCK	*BIZIURA LOBATA*	NON-COOPERATIVE
CANADA GOOSE	*BRANTA CANADENSIS*	NON-COOPERATIVE
CACKLING	*BRANTA*	NON-

GOOSE	*HUTCHINSII*	COOPERATIVE
BARNACLE GOOSE	*BRANTA LEUCOPSIS*	NON-COOPERATIVE
RED-BREASTED GOOSE	*BRANTA RUFICOLLIS*	NON-COOPERATIVE
NENE	*BRANTA SANDVICENSIS*	NON-COOPERATIVE
BUFFLE HEAD	*BUCEPHALA ALBEOLA*	NON-COOPERATIVE
COMMON GOLDEN EYE	*BUCEPHALA CLANGULA*	NON-COOPERATIVE
BARROW’S GOLDEN EYE	*BUCEPHALA ISLANDICA*	COOPERATIVE
MUSCOVY DUCK	*CAIRINA MOSCHATA*	NON-COOPERATIVE
WHITE-WINGED DUCK	*CAIRINA SCUTULATA*	NON-COOPERATIVE
RINGED TEAL	*CALLONETTA LEUCOPHRYS*	NON-COOPERATIVE
CAPE BARREN GOOSE	*CEREOPSIS NOVAEHOLLANDIAE*	NON-COOPERATIVE
NORTHERN SCREAMER	*CHAUNA CHAVARIA*	NON-COOPERATIVE
SOUTHERN	*CHAUNA*	NON-

SCREAMER	*TORQUATA*	COOPERATIVE
ROSS'S GOOSE	*CHEN ROSSII*	NON-COOPERATIVE
AUSTRALIAN WOOD-DUCK	*CHENONETTA JUBATA*	NON-COOPERATIVE
KELP GOOSE	*CHLOEPHAGA HYBRIDA*	NON-COOPERATIVE
ANDEAN GOOSE	*CHLOEPHAGA MELANOPTERA*	NON-COOPERATIVE
UPLAND GOOSE	*CHLOEPHAGA PICTA*	NON-COOPERATIVE
ASHY-HEADED GOOSE	*CHLOEPHAGA POLIOCEPHALA*	NON-COOPERATIVE
RUDDY-HEADED GOOSE	*CHLOEPHAGA RUBIDICEPS*	NON-COOPERATIVE
LONG-TAILED DUCK	*CLANGULA HYEMALIS*	NON-COOPERATIVE
COSCOROBA SWAN	*COSCOROBA COSCOROBA*	NON-COOPERATIVE
BLUE WINGED GOOSE	*CYANOCHEN CYANOPTERA*	NON-COOPERATIVE
WANDERING WHISTLING DUCK	*DENDROCYGNA ARCUATA*	NON-COOPERATIVE

BLACK-BELLIED WHISTLING DUCK	*DENDROCYGNA AUTUMNALIS*	NON-COOPERATIVE
FULVOUS WHISTLING DUCK	*DENDROCYGNA BICOLOR*	NON-COOPERATIVE
PLUMED WHISTLING DUCK	*DENDROCYGNA EYTONI*	NON-COOPERATIVE
HARLEQUIN DUCK	*HISTRIONICUS HISTRIONICUS*	NON-COOPERATIVE
BLUE DUCK	*HYMENOLAIMUS MALACORHYNCHOS*	NON-COOPERATIVE
HOODED MAGANSER	*LOPHODYTES CUCULLATUS*	NON-COOPERATIVE
CRESTED DUCK	*LOPHONETTA SPECULARIOIDES*	NON-COOPERATIVE
SURF SCOTER	*MELANITTA PERSPICILLATA*	NON-COOPERATIVE
TORRENT DUCK	*MERGANETTA ARMATA*	NON-COOPERATIVE
SMEW	*MERGELLUS ALBELLUS*	NON-COOPERATIVE
ORINOCO GOOSE	*NEOCHEN JUBATA*	NON-COOPERATIVE
RED-	*NETTA RUFINA*	NON-

CRESTED POCHARD		COOPERATIVE
MASKED DUCK	*NOMONYX DOMINICUS*	NON-COOPERATIVE
BLUE-BILLED DUCK	*OXYURA AUSTRALIS*	NON-COOPERATIVE
SPUR-WINGED GOOSE	*PLECTROPTERUS GAMBENSIS*	NON-COOPERATIVE
STELLER'S EIDER	*POLYSTICTA STELLERI*	NON-COOPERATIVE
HARTLAUB'S DUCK	*PTERONETTA HARTLAUBII*	NON-COOPERATIVE
SALVADORI'S TEAL	*SALVADORINA WAIGIUENSIS*	NON-COOPERATIVE
KNOB BILLED DUCK	*SARKIDIORNIS MELANOTOS*	NON-COOPERATIVE
SPECTACLED EIDER	*SOMATERIA FISCHER*	NON-COOPERATIVE
BRONZE WINGED DUCK	*SPECULANAS SPECULARIS*	NON-COOPERATIVE
FRECKLED DUCK	*STICTONETTA NAEVOSA*	NON-COOPERATIVE
SOUTH AFRICAN SHELDUCK	*TADORNA CANA*	NON-COOPERATIVE

COMMON SHELDUCK	*TADORNA TADORNA*	NON-COOPERATIVE
WHITE-BACKED DUCK	*THALASSORNIS LEUCONOTUS*	NON-COOPERATIVE
DWARF CASSOWARY	*CASUARIUS BENNETTI*	NON-COOPERATIVE
EMU	*DROMAIUS NOVAEHOLLANDIAE*	NON-COOPERATIVE
WRYBILL	*ANARHYNCHUS FRONTALIS*	NON-COOPERATIVE
SURFBIRD	*APHRIZA VIRGATA*	NON-COOPERATIVE
RUFOUS BELLIED SEED SNIPE	*ATTAGIS GAYI*	NON-COOPERATIVE
WHITE-BELLIED SEED SNIPE	*ATTAGIS MALOUINUS*	NON-COOPERATIVE
UPLAND SAND PIPER	*BARTRAMIA LONGICAUDA*	NON-COOPERATIVE
DOUBLE STRIPED THICK KNEE	*BURHINUS BISTRIATUS*	NON-COOPERATIVE
SPOTTED THICK KNEE	*BURHINUS CAPENSIS*	NON-COOPERATIVE
BUSH STONE CURLEW	*BURHINUS GRALLARIUS*	NON-COOPERATIVE

EURASIAN STONE CURLEW	*BURHINUS OEDICNEMUS*	NON-COOPERATIVE
WATER THICK KNEE	*BURHINUS VERMICULATUS*	NON-COOPERATIVE
SHARP-TAILED SANDPIPER	*CALIDRIS ACUMINATA*	NON-COOPERATIVE
RED KNOT	*CALIDRIS CANUTUS*	NON-COOPERATIVE
CURLEW SANDPIPER	*CALIDRIS FERRUGINEA*	NON-COOPERATIVE
STILT SANDPIPER	*CALIDRIS HIMANTOPUS*	NON-COOPERATIVE
WESTERN SANDPIPER	*CALIDRIS MAURI*	NON-COOPERATIVE
PECTORAL SANDPIPER	*CALIDRIS MELANOTOS*	NON-COOPERATIVE
ROCK SAND PIPER	*CALIDRIS PTILOCNEMIS*	NON-COOPERATIVE
SEMIPALMATED SANDPIPER	*CALIDRIS PUSILLA*	NON-COOPERATIVE
TEMMINICK’S STINT	*CALIDRIS TEMMINCKII*	NON-COOPERATIVE
GREAT KNOT	*CALIDRIS TENUIROSTRIS*	NON-COOPERATIVE

WILLET	*CATOPTROPHORUS SEMIPALMATUS*	NON-COOPERATIVE
KENTISH PLOVER	*CHARADRIUS ALEXANDRINUS*	NON-COOPERATIVE
COMMON RINGED PLOVER	*CHARADRIUS HIATICULA*	NON-COOPERATIVE
JAVAN PLOVER	*CHARADRIUS JAVANICUS*	NON-COOPERATIVE
GREAT SAND PLOVER	*CHARADRIUS LESCHENAULTII*	NON-COOPERATIVE
RUFOUS CHESTED PLOVER	*CHARADRIUS MODESTUS*	NON-COOPERATIVE
NEW ZEALAND DOTTEREL	*CHARADRIUS OBSCURUS*	NON-COOPERATIVE
CHESTNUT BANDED PLOVER	*CHARADRIUS PALLIDUS*	NON-COOPERATIVE
KITTLITZ’S PLOVER	*CHARADRIUS PECUARIUS*	NON-COOPERATIVE
MALAYSIAN PLOVER	*CHARADRIUS PERONII*	NON-COOPERATIVE
LONG BILLED PLOVER	*CHARADRIUS PLACIDUS*	NON-COOPERATIVE
RED-CAPPED PLOVER	*CHARADRIUS RUFICAPILLUS*	NON-COOPERATIVE

SAINT HELENA PLOVER	*CHARADRIUS SANCTAEHELENAE*	NON-COOPERATIVE
SEMIPALMATED PLOVER	*CHARADRIUS SEMIPALMATUS*	NON-COOPERATIVE
MADAGASCAR PLOVER	*CHARADRIUS THORACICUS*	NON-COOPERATIVE
KILDEER	*CHARADRIUS VOCIFERUS*	NON-COOPERATIVE
WILSON’S PLOVER	*CHARADRIUS WILSONIA*	NON-COOPERATIVE
BANDED STILT	*CLADORHYNCHUS LEUCOCEPHALUS*	NON-COOPERATIVE
SUBANTARCTIC SNIPE	*COENOCORYPHA AUCKLANDICA*	NON-COOPERATIVE
CHATHAM SNIPE	*COENOCORYPHA PUSILLA*	NON-COOPERATIVE
INDIAN COURSER	*CURSORIUS COROMANDELICUS*	NON-COOPERATIVE
CREAM-COLOURED COURSER	*CURSORIUS CURSOR*	NON-COOPERATIVE
BURCHELL’S COURSER	*CURSORIUS RUFUS*	NON-COOPERATIVE
SOMALI COURSER	*CURSORIUS SOMALENSIS*	NON-COOPERA

		TIVE
TEMMINICK'S COURSER	*CURSORIUS TEMMINCKII*	NON-COOPERATIVE
CRAB PLOVER	*DROMAS ARDEOLA*	NON-COOPERATIVE
BLACK FRONTED DOTTEREL	*ELSEYORNIS MELANOPS*	NON-COOPERATIVE
RED KNEED DOTTEREL	*ERYTHROGONYS CINCTUS*	NON-COOPERATIVE
BEACH STONE-CURLEW	*ESACUS GIGANTEUS*	NON-COOPERATIVE
GREAT STONE-CURLEW	*ESACUS RECURVIROSTRIS*	NON-COOPERATIVE
EURASIAN DOTTEREL	*EUDROMIAS MORINELLUS*	NON-COOPERATIVE
SPOON-BILLED SANDPIPER	*EURYNORHYNCHUS PYGMEUS*	NON-COOPERATIVE
PUNA SNIPE	*GALLINAGO ANDINA*	NON-COOPERATIVE
SOUTH AMERICAN SNIPE	*GALLINAGO PARAGUAIAE*	NON-COOPERATIVE
GIANT SNIPE	*GALLINAGO UNDULATA*	NON-COOPERATIVE
GREY	*GLAREOLA*	NON-

PRANTICOLE	*CINEREA*	COOPERATIVE
SMALL PRANTICOLE	*GLAREOLA LACTEA*	NON-COOPERATIVE
ORIENTAL PRANTICOLE	*GLAREOLA MALDIVARUM*	NON-COOPERATIVE
BLACK WINGED PRANTICOLE	*GLAREOLA NORDMANNI*	NON-COOPERATIVE
ROCK PRANTICOLE	*GLAREOLA NUCHALIS*	NON-COOPERATIVE
MADAGASCAR PRANTICOLE	*GLAREOLA OCULARIS*	NON-COOPERATIVE
COLLARED PRANTICOLE	*GLAREOLA PRATINCOLA*	NON-COOPERATIVE
CHATHAM OYSTERCATCHER	*HAEMATOPUS CHATHAMENSIS*	NON-COOPERATIVE
MAGELLANIC OYSTERCATCHER	*HAEMATOPUS LEUCOPODUS*	NON-COOPERATIVE
GREY-TAILED TATTLER	*HETEROSCELUS BREVIPES*	NON-COOPERATIVE
WANDERING TATTLER	*HETEROSCELUS INCANUS*	NON-COOPERATIVE
PHEASANT TAILED JACANA	*HYDROPHASIANUS CHIRURGUS*	NON-COOPERATIVE

COMB-CRESTED JACANA	*IREDIPARRA GALLINACEA*	NON-COOPERATIVE
WATTLED JACANA	*JACANA JACANA*	NON-COOPERATIVE
NORTHERN JACANA	*JACANA SPINOSA*	NON-COOPERATIVE
BROAD-BILLED SANDPIPER	*LIMICOLA FALCINELLUS*	NON-COOPERATIVE
SHORT-BILLED DOWITCHER	*LIMNODROMUS GRISEUS*	NON-COOPERATIVE
LONG-BILLED DOWITCHER	*LIMNODROMUS SCOLOPACEUS*	NON-COOPERATIVE
ASIAN DOWITCHER	*LIMNODROMUS SEMIPALMATUS*	NON-COOPERATIVE
MARLED GODWIT	*LIMOSA FEDOA*	NON-COOPERATIVE
HUDSONIAN GODWIT	*LIMOSA HAEMASTICA*	NON-COOPERATIVE
PLAIN’S WANDERER	*PEDIONOMUS TORQUATUS*	NON-COOPERATIVE
RED PHALAROPE	*PHALAROPUS FULICARIUS*	NON-COOPERATIVE
RED-NECKED PHALAROPE	*PHALAROPUS LOBATUS*	NON-COOPERATIVE

DIADEMED PLOVER	*PHEGORNIS MITCHELLII*	NON-COOPERATIVE
RUFF	*PHILOMACHUS PUGNAX*	NON-COOPERATIVE
GREY PLOVER	*PLUVIALIS SQUATAROLA*	NON-COOPERATIVE
MAGELLANIC PLOVER	*PLUVIANELLUS SOCIALIS*	NON-COOPERATIVE
EGYPTIAN PLOVER	*PLUVIANUS AEGYPTIUS*	NON-COOPERATIVE
CHRISTMAS SANDPIPER	*PROSOBONIA CANCELLATA*	NON-COOPERATIVE
JERDON’S COURSER	*RHINOPTILUS BITORQUATUS*	NON-COOPERATIVE
AUSTRALIAN PAINTED SNIPE	*ROSTRATULA AUSTRALIS*	NON-COOPERATIVE
GREATER PAINTED SNIPE	*ROSTRATULA BENGHALENSIS*	NON-COOPERATIVE
AMERICAN PAINTED SNIPE	*ROSTRATULA SEMICOLLARIS*	NON-COOPERATIVE
BUKIDNON WOOD DUCK	*SCOLOPAX BUKIDNONENSIS*	NON-COOPERATIVE
AUSTRALIAN PRANTICOLE	*STILTIA ISABELLA*	NON-COOPERATIVE

BUFF BREASTED SANDPIPER	*TRYNGITES SUBRUFICOLLIS*	NON-COOPERATIVE
FYNBOS BUTTONQUAIL	*TURNIX HOTTENTOTTUS*	NON-COOPERATIVE
RED-BACKED BUTTON QUAIL	*TURNIX MACULOSUS*	NON-COOPERATIVE
BLACK-BREASTED BUTTONQUAIL	*TURNIX MELANOGASTER*	NON-COOPERATIVE
MADAGASCAR BUTTONQUAIL	*TURNIX NIGRICOLLIS*	NON-COOPERATIVE
SPOTTED BUTTONQUAIL	*TURNIX OCELLATUS*	NON-COOPERATIVE
BUFF-BREASTED BUTTONQUAIL	*TURNIX OLIVII*	NON-COOPERATIVE
PAINTED BUTTON QUAIL	*TURNIX VARIUS*	NON-COOPERATIVE
LITTLE BUTTONQUAIL	*TURNIX VELOX*	NON-COOPERATIVE
WORCESTER'S BUTTONQUAIL	*TURNIX WORCESTERI*	NON-COOPERATIVE
BLACKSMITH	*VANELLUS*	NON-COOPERA

LAPWING	*ARMATUS*	TIVE
GREY-HEADED LAPWING	*VANELLUS CINEREUS*	NON-COOPERATIVE
CROWNED LAPWING	*VANELLUS CORONATUS*	NON-COOPERATIVE
RIVER LAPWING	*VANELLUS DUVAUCELII*	NON-COOPERATIVE
SOCIABLE LAPWING	*VANELLUS GREGARIUS*	NON-COOPERATIVE
SENEGAL LAPWING	*VANELLUS LUGUBRIS*	NON-COOPERATIVE
YELLOW-WATTLED LAPWING	*VANELLUS MALARBARICUS*	NON-COOPERATIVE
SPOT-BREASTED LAPWING	*VANELLUS MELANOCEPHALUS*	NON-COOPERATIVE
ANDEAN LAPWING	*VANELLUS RESPLENDENS*	NON-COOPERATIVE
SABINE’S GULL	*XEMA SABINI*	NON-COOPERATIVE
TEREK SANDPIPER	*XENUS CINEREUS*	NON-COOPERATIVE
AFRICAN OPENBILL	*ANASTOMUS LAMELLIGERUS*	NON-COOPERATIVE
ASIAN	*ANASTOMUS*	NON-

OPENBILL	*OSCITANS*	COOPERATIVE
BLACK-NECKED STORK	*EPHIPPIORHYNCHUS ASIATICUS*	NON-COOPERATIVE
SADDLE BILLED STORK	*EPHIPPIORHYNCHUS SENEGALENSIS*	NON-COOPERATIVE
JABIRU	*JABIRU MYCTERIA*	NON-COOPERATIVE
MARABOU STORK	*LEPTOPTILOS CRUMENIFERUS*	NON-COOPERATIVE
GREATER ADJUTANT	*LEPTOPTILOS DUBIUS*	NON-COOPERATIVE
LESSER ADJUTANT	*LEPTOPTILOS JAVANICUS*	NON-COOPERATIVE
SUN BITTERN	*EURYPYGA HELIAS*	NON-COOPERATIVE
KAGU	*RHYNOCHETOS JUBATUS*	COOPERATIVE
WATTLED GUAN	*ABURRIA ABURRI*	NON-COOPERATIVE
VULTURINE GUINEAFOWL	*ACRYLLIUM VULTURINUM* [a]	COOPERATIVE [A]
CONGO PEAFOWL	*AFROPAVO CONGENSIS*	NON-COOPERATIVE
BARBARY	*ALECTORIS*	NON-

PARTRIDGE	*BARBARA*	COOPERATIVE
CHUKAR	*ALECTORIS CHUKAR*	NON-COOPERATIVE
ROCK PARTRIDGE	*ALECTORIS GRAECA*	NON-COOPERATIVE
PHILBY’S PARTRIDGE	*ALECTORIS PHILBYI*	NON-COOPERATIVE
RED LEGGED PARTRIDGE	*ALECTORIS RUFA*	NON-COOPERATIVE
AUSTRALIAN BRUSHTURKEY	*ALECTURA LATHAMI*	NON-COOPERATIVE
CHEST-NUT NECKLACED PARTRIDGE	*ARBOROPHILA CHARLTONII*	NON-COOPERATIVE
GREEN LEGGED PARTRIDGE	*ARBOROPHILA CHLOROPUS*	NON-COOPERATIVE
TAIWAN PARTRIDGE	*ARBOROPHILA CRUDIGULARIS*	NON-COOPERATIVE
ORANGE-NECKED PARTRIDGE	*ARBOROPHILA DAVIDI*	NON-COOPERATIVE
WHITE NECKLACED PARTRIDGE	*ARBOROPHILA GINGICA*	NON-COOPERATIVE
RED-BREASTED PARTRIDGE	*ARBOROPHILA HYPERYTHRA*	NON-COOPERATIVE

HILL PARTRIDGE	*ARBOROPHILA TORQUEOLA*	NON-COOPERATIVE
GREAT ARGUS	*ARGUSIANUS ARGUS*	NON-COOPERATIVE
HAZEL GROUSE	*BONASA BONASIA*	NON-COOPERATIVE
CHINESE GROUSE	*BONASA SEWERZOWI*	NON-COOPERATIVE
RUFFED GROUSE	*BONASA UMBELLUS*	NON-COOPERATIVE
CALIFORNIA QUAIL	*CALLIPEPLA CALIFORNICA*	COOPERATIVE
FERRUGINOUS PARTRIDGE	*CALOPERDIX OCULEUS*	NON-COOPERATIVE
CHEER PHEASANT	*CATREUS WALLICHI*	NON-COOPERATIVE
GUNNISON GROUSE	*CENTROCERCUS MINIMUS*	NON-COOPERATIVE
GREATER SAGE-GROUSE	*CENTROCERCUS UROPHASIANUS*	NON-COOPERATIVE
CRESTED BOBWHITE	*COLINUS CRISTATUS*	NON-COOPERATIVE
SPOT-BELLIED BOBWHITE	*COLINUS LEUCOPOGON*	NON-COOPERATIVE

YUCATAN BOBWHITE	*COLINUS NIGROGULARIS*	NON-COOPERATIVE
NORTHERN BOBWHITE	*COLINUS VIRGINIANUS* [b]	COOPERATIVE [B]
BLUE BILLED CURASSOW	*CRAX ALBERTI*	NON-COOPERATIVE
BLUE CURASSOW	*CRAX ALECTOR*	NON-COOPERATIVE
RED BILLED CURASSOW	*CRAX BLUMENBACHII*	NON-COOPERATIVE
YELLOW-KNOBBED CURASSOW	*CRAX DAUBENTONI*	NON-COOPERATIVE
BARE-FACED CURASSOW	*CRAX FASCIOLATA*	NON-COOPERATIVE
WATTLED CURASSOW	*CRAX GLOBULOSA*	NON-COOPERATIVE
GREAT CURASSOW	*CRAX RUBRA*	NON-COOPERATIVE
BLUE EARED PHEASANT	*CROSSOPTILON AURITUM*	NON-COOPERATIVE
TIBETAN EARED PHEASANT	*CROSSOPTILON HARMANI*	COOPERATIVE
SPRUCE GROUSE	*DENDRAGAPUS CANADENSIS*	NON-COOPERATIVE

SIBERIAN GROUSE	*DENDRAGAPUS FALCIPENNIS*	NON-COOPERATIVE
SOOTY GROUSE	*DENDRAGAPUS FULIGINOSUS*	NON-COOPERATIVE
DUSKY GROUSE	*DENDRAGAPUS OBSCURUS*	NON-COOPERATIVE
BEARDED WOOD PARTRIDGE	*DENDRORTYX BARBATUS*	NON-COOPERATIVE
GREY WINGED FRANCOLIN	*FRANCOLINUS AFRICANUS*	NON-COOPERATIVE
AHANTA SPURFOWL	*FRANCOLINUS AHANTENSIS*	NON-COOPERATIVE
WHITE THROATED FRANCOLIN	*FRANCOLINUS ALBOGULARIS*	NON-COOPERATIVE
DOUBLE-SPURRED SPURFOWL	*FRANCOLINUS BICALCARATUS*	NON-COOPERATIVE
MOUNT CAMEROON FRANCOLIN	*FRANCOLINUS CAMERUNENSIS*	NON-COOPERATIVE
CAPE SPURFOWL	*FRANCOLINUS CAPENSIS*	NON-COOPERATIVE
CHESTNUT-NAPED SPURFOWL	*FRANCOLINUS CASTANEICOLLIS*	NON-COOPERATIVE
CLAPPERTON'S SPURFOWL	*FRANCOLINUS CLAPPERTONI*	NON-COOPERATIVE

COQUI FRANCOLIN	*FRANCOLINUS COQUI*	NON-COOPERATIVE
ERCKEL’S SPURFOWL	*FRANCOLINUS ERCKELII*	NON-COOPERATIVE
FINSCH’S FRANCOLIN	*FRANCOLINUS FINSCHI*	NON-COOPERATIVE
BLACK FRANCOLIN	*FRANCOLINUS FRANCOLINUS*	NON-COOPERATIVE
GREY STRIPPED SPURFOWL	*FRANCOLINUS GRISEOSTRIATUS*	NON-COOPERATIVE
SWAMP FRANCOLIN	*FRANCOLINUS GULARIS*	NON-COOPERATIVE
HILDEBRANDT’S SPURFOWL	*FRANCOLINUS HILDEBRANDTI*	NON-COOPERATIVE
HEUGLIN’S SPURFOWL	*FRANCOLINUS ICTERORHYNCHUS*	NON-COOPERATIVE
JACKSON’S SPURFOWL	*FRANCOLINUS JACKSONI*	NON-COOPERATIVE
LATHAM’S FRANCOLIN	*FRANCOLINUS LATHAMI*	NON-COOPERATIVE
YELLOW-NECKED SPURFOWL	*FRANCOLINUS LEUCOSCEPUS*	NON-COOPERATIVE
RED WINGED FRANCOLIN	*FRANCOLINUS LEVAILLANTII*	NON-COOPERATIVE

ORANGE RIVER FRANCOLIN	*FRANCOLINUS LEVAILLANTOIDES*	NON-COOPERATIVE
NAHAN’S PARTRIDGE	*FRANCOLINUS NAHANI*	NON-COOPERATIVE
NATAL SPURFOWL	*FRANCOLINUS NATALENSIS*	NON-COOPERATIVE
HANDSOME SPURFOWL	*FRANCOLINUS NOBILIS*	NON-COOPERATIVE
DJIBOUTI SPURFOWL	*FRANCOLINUS OCHROPECTUS*	NON-COOPERATIVE
GREY BREASTED SPURFOWL	*FRANCOLINUS RUFOPICTUS*	NON-COOPERATIVE
SCHEGEL’S FRANCOLIN	*FRANCOLINUS SCHLEGELII*	NON-COOPERATIVE
CRESTED FRANCOLIN	*FRANCOLINUS SEPHAENA*	NON-COOPERATIVE
SHELEY’S FRANCOLIN	*FRANCOLINUS SHELLEYI*	NON-COOPERATIVE
SCALY SPURFOWL	*FRANCOLINUS SQUAMATUS*	NON-COOPERATIVE
RING NECKED FRANCOLIN	*FRANCOLINUS STREPTOPHORUS*	NON-COOPERATIVE
SWAINSON’S SPURFOWL	*FRANCOLINUS SWAINSONII*	NON-COOPERATIVE

SWEISTRA'S SPURFOWL	*FRANCOLINUS SWIERSTRAI*	NON-COOPERATIVE
SRI LANKA'S SPURFOWL	*GALLOPERDIX BICALCARATA*	NON-COOPERATIVE
PAINTED SPURFOWL	*GALLOPERDIX LUNULATA*	NON-COOPERATIVE
RED SPURFOWL	*GALLOPERDIX SPADICEA*	NON-COOPERATIVE
RED JUNGLE FOWL	*GALLUS GALLUS*	NON-COOPERATIVE
GREEN JUNGLE FOWL	*GALLUS VARIUS*	NON-COOPERATIVE
CRIMSON HEADED PARTRIDGE	*HAEMATORTYX SANGUINICEPS*	NON-COOPERATIVE
BLOOD PHEASANT	*ITHAGINIS CRUENTUS*	NON-COOPERATIVE
WILLOW PTARMIGAN	*LAGOPUS LAGOPUS*	NON-COOPERATIVE
WHITE TAILED PTARMIGAN	*LAGOPUS LEUCURA*	NON-COOPERATIVE
ROCK PTARMIGAN	*LAGOPUS MUTA*	NON-COOPERATIVE
MALEEFOWL	*LEIPOA OCELLATA*	NON-COOPERATIVE

SNOW PARTRIDGE	*LERWA LERWA*	NON-COOPERATIVE
HIMALAYAN MONAL	*LOPHOPHORUS IMPEJANUS*	NON-COOPERATIVE
CHINESE MONAL	*LOPHOPHORUS LHUYSII*	NON-COOPERATIVE
SCLATER’S MONAL	*LOPHOPHORUS SCLATERI*	NON-COOPERATIVE
BULWER’S PHEASANT	*LOPHURA BULWERI*	NON-COOPERATIVE
SIAMESE FIREBACK	*LOPHURA DIARDI*	NON-COOPERATIVE
EDWARD’S PHEASANT	*LOPHURA EDWARDSI*	NON-COOPERATIVE
CRESTLESS FIREBACK	*LOPHURA ERYTHROPHTHALMA*	NON-COOPERATIVE
VIETNAMESE PHEASANT	*LOPHURA HATINHENSIS*	NON-COOPERATIVE
SUMATRAN PHEASANT	*LOPHURA HOOGERWERFI*	NON-COOPERATIVE
KALIJ PHEASANTS	*LOPHURA LEUCOMELANOS*[c]	COOPERATIVE [C]
SILVER PHEASANT	*LOPHURA NYCTHEMERA*	NON-COOPERATIVE

SWINHOE’S PHEASANT	*LOPHURA SWINHOII*	NON-COOPERATIVE
MALEO	*MACROCEPHALON MALEO*	NON-COOPERATIVE
MADAGASCAR PARTRIDGE	*MARGAROPERDIX MADAGASCARIENSIS*	NON-COOPERATIVE
NEW GUINEA SCRUBFOWL	*MEGAPODIUS AFFINIS*	NON-COOPERATIVE
SULA MEGAPODE	*MEGAPODIUS BERNSTEINII*	NON-COOPERATIVE
PHILLIPINE MEGAPODE	*MEGAPODIUS CUMINGII*	NON-COOPERATIVE
TONGAN MEGAPODE	*MEGAPODIUS PRITCHARDII*	NON-COOPERATIVE
ORANG FOOTED SCRUBFOWL	*MEGAPODIUS REINWARDT*	NON-COOPERATIVE
TANIMBAR MEGAPODE	*MEGAPODIUS TENIMBERENSIS*	NON-COOPERATIVE
BLACK PARTRIDGE	*MELANOPERDIX NIGER*	NON-COOPERATIVE
ALAGOAS CURASSOW	*MITU MITU*	NON-COOPERATIVE
SALVIN’S CURASSOW	*MITU SALVINI*	NON-COOPERA

		TIVE
HELMETED GUINEAFOWL	*NUMIDA MELEAGRIS* [d]	COOPERATIVE [D]
BLACK-FRONTED WOODQUAIL	*ODONTOPHORUS ATRIFRONS*	NON-COOPERATIVE
VENEZUELAN WOOD-QUAIL	*ODONTOPHORUS COLUMBIANUS*	NON-COOPERATIVE
TACARCUNA WOOD-QUAIL	*ODONTOPHORUS DIALEUCOS*	NON-COOPERATIVE
STARRED WOODQUAIL	*ODONTOPHORUS STELLATUS*	NON-COOPERATIVE
GORGETED WOOD-QUAIL	*ODONTOPHORUS STROPHIUM*	NON-COOPERATIVE
HORNED GUAN	*OREOPHASIS DERBIANUS*	NON-COOPERATIVE
MOUNTAIN QUAIL	*OREORTYX PICTUS*	NON-COOPERATIVE
CHACO CHACHALACA	*ORTALIS CANICOLLIS*	NON-COOPERATIVE
GREY-HEADED CHACHALACA	*ORTALIS CINEREICEPS*	NON-COOPERATIVE
RUFOUS-HEADED CHACHALACA	*ORTALIS ERYTHROPTERA*	NON-COOPERATIVE

WEST MEXICAN CHACHALACA	*ORTALIS POLIOCEPHALA*	NON-COOPERATIVE
RUFOUS VENTED CHACHALACA	*ORTALIS RUFICAUDA*	NON-COOPERATIVE
BUFF-BROWED CHACHALACA	*ORTALIS SUPERCILIARIS*	NON-COOPERATIVE
PLAIN CHACHALACA	*ORTALIS VETULA*	NON-COOPERATIVE
RUFOUS BELLIED CHACHALACA	*ORTALIS WAGLERI*	NON-COOPERATIVE
HELMETED CURASSOW	*PAUXI PAUXI*	NON-COOPERATIVE
HORNED CURASSOW	*PAUXI UNICORNIS*	NON-COOPERATIVE
WHITE-WINGED GUAN	*PENELOPE ALBIPENNIS*	NON-COOPERATIVE
WHITE BROWED GUAN	*PENELOPE JACUCACA*	NON-COOPERATIVE
DUSKY LEGGED GUAN	*PENELOPE OBSCURA*	NON-COOPERATIVE
CHESTNUT BELLIED	*PENELOPE OCHROGASTER*	NON-COOPERA

GUAN		TIVE
BAUDO GUAN	*PENELOPE ORTONI*	NON-COOPERATIVE
CAUCA GUAN	*PENELOPE PERSPICAX*	NON-COOPERATIVE
WHITE CRESTED GUAN	*PENELOPE PILEATA*	NON-COOPERATIVE
CRESTED GUAN	*PENELOPE PURPURASCENS*	NON-COOPERATIVE
TIBETAN PARTRIDGE	*PERDIX HODGSONIAE*	COOPERATIVE
GREY PARTRIDGE	*PERDIX PERDIX*	NON-COOPERATIVE
BANDED QUIAL	*PHILORTYX FASCIATUS*	NON-COOPERATIVE
TRINIDAD PIPING GUAN	*PIPILE PIPILE*	NON-COOPERATIVE
GERMAN’S PEACOCK PHEASANT	*POLYPLECTRON GERMAINI*	NON-COOPERATIVE
MOUNTAIN PEACOCK PHEASANT	*POLYPLECTRON INOPINATUM*	NON-COOPERATIVE
HAINAN PEA COCK PHEASANT	*POLYPLECTRON KATSUMATAE*	NON-COOPERATIVE
MALAYAN PEACOCK-	*POLYPLECTRON MALACENSE*	NON-COOPERA

PHEASANT		TIVE
STONE PARTRIDGE	*PTILOPACHUS PETROSUS*	NON-COOPERATIVE
KOKLASS PHEASANT	*PUCRASIA MACROLOPHA*	NON-COOPERATIVE
CRESTED ARGUS	*RHEINARDIA OCELLATA*	NON-COOPERATIVE
LONG BILLED PARTRIDGE	*RHIZOTHERA LONGIROSTRIS*	NON-COOPERATIVE
TAWNY-FACED QUAIL	*RHYNCHORTYX CINCTUS*	NON-COOPERATIVE
CRESTED PARTRIDGE	*ROLLULUS ROULOUL*	NON-COOPERATIVE
REEVE’S PHEASANT	*SYRMATICUS REEVESII*	NON-COOPERATIVE
COOPER PHEASANT	*SYRMATICUS SOEMMERRINGII*	NON-COOPERATIVE
RED BILLED BRUSH-TURKEY	*TALEGALLA CUVIERI*	NON-COOPERATIVE
BLACK BILLED BRUSH TURKEY	*TALEGALLA FUSCIROSTRIS*	NON-COOPERATIVE
BROWN COLLARED BRUSH-TURKEY	*TALEGALLA JOBIENSIS*	NON-COOPERATIVE

CAUCASIAN GROUSE	*TETRAO MLOKOSIEWICZI*	NON-COOPERATIVE
BLACK BILLED CAPERCAILLIE	*TETRAO PARVIROSTRIS*	NON-COOPERATIVE
BLACK GROUSE	*TETRAO TETRIX*	NON-COOPERATIVE
WESTERN CAPERCAILLIE	*TETRAO UROGALLUS*	NON-COOPERATIVE
ALTAI SNOWCOCK	*TETRAOGALLUS ALTAICUS*	NON-COOPERATIVE
CHEST-NUT THROATED PARTRIDGE	*TETRAOPHASIS OBSCURUS*	NON-COOPERATIVE
SZECHENYII'S MONAL PARTRIDGE	*TETRAOPHASIS SZECHENYII*	COOPERATIVE
GREATER PRAIRIE CHICKEN	*TYMPANUCHUS CUPIDO*	NON-COOPERATIVE
LESSER PRAIRIE CHICKEN	*TYMPANUCHUS PALLIDICINCTUS*	NON-COOPERATIVE
SHARP TAILED GROUSE	*TYMPANUCHUS PHASIANELLUS*	NON-COOPERATIVE
UDZUNGWA FOREST PARTRIDGE	*XENOPERDIX UDZUNGWENSIS*	NON-COOPERATIVE
STRIPED CRAKE	*AENIGMATOLIMNAS*	COOPERATIVE

	MARGINALIS	
UNIFORM CRAKE	*AMAUROLIMNAS CONCOLOR*	NON-COOPERATIVE
BROWN CRAKE	*AMAURORNIS AKOOL*	NON-COOPERATIVE
BLACK TAILED CRAKE	*AMAURORNIS BICOLOR*	NON-COOPERATIVE
BLACK CRAKE	*AMAURORNIS FLAVIROSTRA*	COOPERATIVE
ISABELLINE-BUSH HEN	*AMAURORNIS ISABELLINA*	NON-COOPERATIVE
PLAIN BUSH-HEN	*AMAURORNIS OLIVACEA*	NON-COOPERATIVE
SAKALAVA RAIL	*AMAURORNIS OLIVIERI*	NON-COOPERATIVE
WHITE BREASTED WATER HEN	*AMAURORNIS PHOENICURUS*	NON-COOPERATIVE
CHESTNUT HEADED CRAKE	*ANUROLIMNAS CASTANEICEPS*	NON-COOPERATIVE
BLACK BANDED CRAKE	*ANUROLIMNAS FASCIATUS*	NON-COOPERATIVE
SNORING RAIL	*ARAMIDOPSIS PLATENI*	NON-COOPERATIVE
LIMPKIN	*ARAMUS GUARAUNA*	NON-COOPERA

		TIVE
INACCESSIBLE ISLAND RAIL	*ATLANTISIA ROGERSI*	NON-COOPERATIVE
BLACK CROWNED CRANE	*BALEARICA PAVONINA*	NON-COOPERATIVE
GREY CROWNED CRANE	*BALEARICA REGULORUM*	NON-COOPERATIVE
MADAGASCAR WOOD RAIL	*CANIRALLUS KIOLOIDES*	NON-COOPERATIVE
GREY-THROATED RAIL	*CANIRALLUS OCULEUS*	NON-COOPERATIVE
SWINHOE'S RAIL	*COTURNICOPS EXQUISITUS*	NON-COOPERATIVE
SPECKLED RAIL	*COTURNICOPS NOTATUS*	NON-COOPERATIVE
YELLOW RAIL	*COTURNICOPS NOVEBORACENSIS*	NON-COOPERATIVE
AFRICAN RAIL	*CRECOPSIS EGREGIA*	NON-COOPERATIVE
CORN CRAKE	*CREX CREX*	NON-COOPERATIVE
ZAPATA RAIL	*CYANOLIMNAS CERVERAI*	NON-COOPERATIVE
EURASIAN	*FULICA ATRA*	COOPERA

COOT		TIVE
CARIBBEAN COOT	*FULICA CARIBAEA*	NON-COOPERATIVE
HORNED COOT	*FULICA CORNUTA*	NON-COOPERATIVE
RED KNOBBED COOT	*FULICA CRISTATA*	COOPERATIVE
GIANT COOT	*FULICA GIGANTEA*	COOPERATIVE
WHITE WINGED COOT	*FULICA LEUCOPTERA*	NON-COOPERATIVE
RED FRONTED COOT	*FULICA RUFIFRONS*	NON-COOPERATIVE
WATERCOCK	*GALLICREX CINEREA*	NON-COOPERATIVE
LESSER MOORHEN	*GALLINULA ANGULATA*	NON-COOPERATIVE
COMMON MOORHEN	*GALLINULA CHLOROPUS*	COOPERATIVE
SPOT FLANKED GALLINULE	*GALLINULA MELANOPS*	NON-COOPERATIVE
TASMANIAN NATIVEHEN	*GALLINULA MORTIERII*	COOPERATIVE
TRISTAN MOORHEN	*GALLINULA NESIOTIS*	COOPERATIVE
MAKIRA	*GALLINULA*	COOPERA

WOODHEN	*SILVESTRIS*	TIVE
WEKA	*GALLIRALLUS AUSTRALIS*	NON-COOPERATIVE
GUAM RAIL	*GALLIRALLUS OWSTONI*	NON-COOPERATIVE
SLATY-BREASTED RAIL	*GALLIRALLUS STRIATUS*	NON-COOPERATIVE
WHOOPING CRANE	*GRUS AMERICANA*	NON-COOPERATIVE
SARUS CRANE	*GRUS ANTIGONE*	NON-COOPERATIVE
SANDHILL CRANE	*GRUS CANADENSIS*	NON-COOPERATIVE
WATTLED CRANE	*GRUS CARUNCULATUS*	NON-COOPERATIVE
COMMON CRANE	*GRUS GRUS*	NON-COOPERATIVE
RED CROWNED CRANE	*GRUS JAPONENSIS*	NON-COOPERATIVE
SIBERIAN CRANE	*GRUS LEUCOGERANUS*	NON-COOPERATIVE
BROLGA	*GRUS RUBICUNDA*	NON-COOPERATIVE
WHITE	*GRUS VIPIO*	NON-

NAPPED CRANE		COOPERATIVE
DEMOISELLE CRANE	*GRUS VIRGO*	NON-COOPERATIVE
BARE-EYED RAIL	*GYMNOCREX PLUMBEIVENTRIS*	NON-COOPERATIVE
BALD-FACE RAIL	*GYMNOCREX ROSENBERGII*	NON-COOPERATIVE
TALAUD RAIL	*GYMNOCREX TALAUDENSIS*	NON-COOPERATIVE
DRUMMER RAIL	*HABROPTILA WALLACII*	NON-COOPERATIVE
NKULENGU RAIL	*HIMANTORNIS HAEMATOPUS*	NON-COOPERATIVE
RED AND WHITE CRAKE	*LATERALLUS LEUCOPYRRHUS*	NON-COOPERATIVE
GALAPAGO'S CRAKE	*LATERALLUS SPILONOTUS*	NON-COOPERATIVE
JUNIN RAIL	*LATERALLUS TUEROSI*	NON-COOPERATIVE
RUFOUS FACED CRAKE	*LATERALLUS XENOPTERUS*	NON-COOPERATIVE
LEWIN'S RAIL	*LEWINIA PECTORALIS*	NON-COOPERATIVE

NEW GUINEA FLIGHTLESS RAIL	*MEGACREX INEPTA*	NON-COOPERATIVE
OCELLATED CRAKE	*MICROPYGIA SCHOMBURGKII*	NON-COOPERATIVE
COLOMBIAN CRAKE	*NEOCREX COLOMBIANA*	NON-COOPERATIVE
PAINT BILLED CRAKE	*NEOCREX ERYTHROPS*	NON-COOPERATIVE
WOOD’S FORD RAIL	*NESOCLOPEUS WOODFORDI*	NON-COOPERATIVE
AFRICAN FINFOOT	*PODICA SENEGALENSIS*	NON-COOPERATIVE
TAKAHĒ	*PORPHYRIO HOCHSTETTERI*	COOPERATIVE
ASH-THROATED CRAKE	*PORZANA ALBICOLLIS*	NON-COOPERATIVE
HENDERSON CRAKE	*PORZANA ATRA*	COOPERATIVE
SORA	*PORZANA CAROLINA*	NON-COOPERATIVE
WHITE-BROWED CRAKE	*PORZANA CINEREA*	NON-COOPERATIVE
YELLOW-BREASTED CRAKE	*PORZANA FLAVIVENTER*	NON-COOPERATIVE
BAND-	*PORZANA*	NON-

BELLIED CRAKE	*PAYKULLII*	COOPERATIVE
SPOTTED CRAKE	*PORZANA PORZANA*	NON-COOPERATIVE
BAILLON'S CRAKE	*PORZANA PUSILLA*	NON-COOPERATIVE
DOT-WINGED CRAKE	*PORZANA SPILOPTERA*	NON-COOPERATIVE
SPOTLESS CRAKE	*PORZANA TABUENSIS*	NON-COOPERATIVE
GREY-WINGED TRUMPETER	*PSOPHIA CREPITANS*	COOPERATIVE
PALE-WINGED TRUMPETER	*PSOPHIA LEUCOPTERA*	COOPERATIVE
DARK-WINGED TRUMPETER	*PSOPHIA VIRIDIS*	COOPERATIVE
RED-LEGGED CRAKE	*RALLINA FASCIATA*	NON-COOPERATIVE
FORBES'S FOREST RAIL	*RALLINA FORBESI*	NON-COOPERATIVE
MAYR'S FOREST RAIL	*RALLINA MAYRI*	NON-COOPERATIVE
CHESTNUT FOREST CRAKE	*RALLINA RUBRA*	NON-COOPERATIVE

RED-NECKED CRAKE	*RALLINA TRICOLOR*	NON-COOPERATIVE
BOGOTÁ RAIL	*RALLUS SEMIPLUMBEUS*	NON-COOPERATIVE
PLAIN-FLANKED RAIL	*RALLUS WETMOREI*	NON-COOPERATIVE
ROUGET'S RAIL	*ROUGETIUS ROUGETII*	COOPERATIVE
STREAKY-BREASTED FLUFFTAIL	*SAROTHRURA BOEHMI*	NON-COOPERATIVE
SLENDER-BILLED FLUFFTAIL	*SAROTHRURA WATERSI*	NON-COOPERATIVE
SUBDESERT MESITE	*MONIAS BENSCHI*	COOPERATIVE
GREAT BLUE TURACO	*CORYTHAEOLA CRISTATA*	COOPERATIVE
GREY GO-AWAY-BIRD	*CORYTHAIXOIDES CONCOLOR*	COOPERATIVE
WHITE-BELLIED GO-AWAY-BIRD	*CORYTHAIXOIDES LEUCOGASTER*	COOPERATIVE
ROSS'S TURACO	*MUSOPHAGA ROSSAE*	NON-COOPERATIVE
VIOLET TURACO	*MUSOPHAGA VIOLACEA*	NON-COOPERATIVE
RUWENZORI TURACO	*RUWENZORORNIS JOHNSTONI*	NON-COOPERATIVE

RED-CRESTED TURACO	*TAURACO ERYTHROLOPHUS*	NON-COOPERATIVE
ARABIAN BUSTARD	*ARDEOTIS ARABS*	NON-COOPERATIVE
AUSTRALIAN BUSTARD	*ARDEOTIS AUSTRALIS*	NON-COOPERATIVE
BLACK BUSTARD	*EUPODOTIS AFRA*	NON-COOPERATIVE
NORTHERN BLACK KORHAAN	*EUPODOTIS AFRAOIDES*	NON-COOPERATIVE
BLUE BUSTARD	*EUPODOTIS CAERULESCENS*[6]	COOPERATIVE
BUFF-CRESTED BUSTARD	*EUPODOTIS GINDIANA*	NON-COOPERATIVE
HARTLAUB'S BUSTARD	*EUPODOTIS HARTLAUBII*	NON-COOPERATIVE
LITTLE BROWN BUSTARD	*EUPODOTIS HUMILIS*	NON-COOPERATIVE
BLACK-BELLIED BUSTARD	*EUPODOTIS MELANOGASTER*	NON-COOPERATIVE
RÜPPELL'S KORHAAN	*EUPODOTIS RUEPPELLII*	NON-COOPERATIVE
RED-CRESTED BUSTARD	*EUPODOTIS RUFICRISTA*	NON-COOPERATIVE

SAVILE'S BUSTARD	*EUPODOTIS SAVILEI*	NON-COOPERATIVE
BENGAL FLORICAN	*HOUBAROPSIS BENGALENSIS*	NON-COOPERATIVE
HEUGLIN'S BUSTARD	*NEOTIS HEUGLINII*	NON-COOPERATIVE
GREAT BUSTARD	*OTIS TARDA*	NON-COOPERATIVE
AGAMI HERON	*AGAMIA AGAMI*	NON-COOPERATIVE
MALAGASY POND HERON	*ARDEOLA IDAE*	NON-COOPERATIVE
JAVAN POND HERON	*ARDEOLA SPECIOSA*	NON-COOPERATIVE
DWARF IBIS	*BOSTRYCHIA BOCAGEI*	NON-COOPERATIVE
WATTLED IBIS	*BOSTRYCHIA CARUNCULATA*	NON-COOPERATIVE
HADADA IBIS	*BOSTRYCHIA HAGEDASH*	NON-COOPERATIVE
OLIVE IBIS	*BOSTRYCHIA OLIVACEA*	NON-COOPERATIVE
SPOT-BREASTED IBIS	*BOSTRYCHIA RARA*	NON-COOPERATIVE

AMERICAN BITTERN	*BOTAURUS LENTIGINOSUS*	NON-COOPERATIVE
EURASIAN BITTERN OR GREAT BITTERN	*BOTAURUS STELLARIS*	NON-COOPERATIVE
CATTLE EGRET	*BUBULCUS IBIS*	NON-COOPERATIVE
STRIATED HERON	*BUTORIDES STRIATA*	NON-COOPERATIVE
GREEN HERON	*BUTORIDES VIRESCENS*	NON-COOPERATIVE
GREAT EGRET	*CASMERODIUS ALBUS*	NON-COOPERATIVE
SHARP-TAILED IBIS	*CERCIBIS OXYCERCA*	NON-COOPERATIVE
LITTLE BLUE HERON	*EGRETTA CAERULEA*	NON-COOPERATIVE
SLATY EGRET	*EGRETTA VINACEIGULA*	NON-COOPERATIVE
AMERICAN WHITE IBIS	*EUDOCIMUS ALBUS*	NON-COOPERATIVE
SCARLET IBIS	*EUDOCIMUS RUBER*	NON-COOPERATIVE
SOUTHERN BALD IBIS	*GERONTICUS CALVUS*	NON-COOPERA

		TIVE
NORTHERN BALD IBIS, HERMIT IBIS, OR WALDRAPP	*GERONTICUS EREMITA*	NON-COOPERATIVE
JAPANESE NIGHT HERON	*GORSACHIUS GOISAGI*	NON-COOPERATIVE
CINNAMON BITTERN OR CHESTNUT BITTERN	*IXOBRYCHUS CINNAMOMEUS*	NON-COOPERATIVE
STRIPE-BACKED BITTERN	*IXOBRYCHUS INVOLUCRIS*	NON-COOPERATIVE
LITTLE BITTERN OR COMMON LITTLE BITTERN	*IXOBRYCHUS MINUTUS*	NON-COOPERATIVE
MADAGASCAR IBIS	*LOPHOTIBIS CRISTATA*	NON-COOPERATIVE
GREEN IBIS	*MESEMBRINIBIS CAYENNENSIS*	NON-COOPERATIVE
INTERMEDIATE EGRET	*MESOPHOYX INTERMEDIA*	NON-COOPERATIVE
CRESTED IBIS	*NIPPONIA NIPPON*	NON-COOPERATIVE
BLACK-CROWNED NIGHT	*NYCTICORAX NYCTICORAX*	NON-COOPERATIVE

HERON		
BARE-FACED IBIS	*PHIMOSUS INFUSCATUS*	NON-COOPERATIVE
CAPPED HERON	*PILHERODIUS PILEATUS*	NON-COOPERATIVE
ROSEATE SPOONBILL	*PLATALEA AJAJA*	NON-COOPERATIVE
AFRICAN SPOONBILL	*PLATALEA ALBA*	NON-COOPERATIVE
YELLOW-BILLED SPOONBILL	*PLATALEA FLAVIPES*	NON-COOPERATIVE
ROYAL SPOONBILL	*PLATALEA REGIA*	NON-COOPERATIVE
WHITE-FACED IBIS	*PLEGADIS CHIHI*	NON-COOPERATIVE
WHITE-SHOULDERED IBIS	*PSEUDIBIS DAVISONI*	NON-COOPERATIVE
RED-NAPED IBIS	*PSEUDIBIS PAPILLOSA*	NON-COOPERATIVE
HAMERKOP	*SCOPUS UMBRETTA*	NON-COOPERATIVE
WHISTLING HERON	*SYRIGMA SIBILATRIX*	NON-COOPERATIVE
GIANT IBIS	*THAUMATIBIS*	NON-

	GIGANTEA	COOPERATIVE
RUFESCENT TIGER HERON	*TIGRISOMA LINEATUM*	NON-COOPERATIVE
FOREST BITTERN	*ZONERODIUS HELIOSYLUS*	NON-COOPERATIVE
CLARK'S GREBE	*AECHMOPHORUS CLARKII*	NON-COOPERATIVE
WESTERN GREBE	*AECHMOPHORUS OCCIDENTALIS*	NON-COOPERATIVE
HORNED GREBE OR SLAVONIAN GREBE	*PODICEPS AURITUS*	NON-COOPERATIVE
GREAT CRESTED GREBE	*PODICEPS CRISTATUS*	NON-COOPERATIVE
HOODED GREBE	*PODICEPS GALLARDOI*	NON-COOPERATIVE
YELLOW-LEGGED TINAMOU	*CRYPTURELLUS NOCTIVAGUS*	NON-COOPERATIVE
BROWN TINAMOU	*CRYPTURELLUS OBSOLETUS*	NON-COOPERATIVE
SMALL-BILLED TINAMOU	*CRYPTURELLUS PARVIROSTRIS*	NON-COOPERATIVE
TEPUI TINAMOU	*CRYPTURELLUS PTARITEPUI*	NON-COOPERATIVE

TATAUPA TINAMOU	*CRYPTURELLUS TATAUPA*	NON-COOPERATIVE
PALE-BROWED TINAMOU	*CRYPTURELLUS TRANSFASCIATUS*	NON-COOPERATIVE
BRUSHLAND TINAMOU	*NOTHOPROCTA CINERASCENS*	NON-COOPERATIVE
CHILEAN TINAMOU	*NOTHOPROCTA PERDICARIA*	NON-COOPERATIVE
TACZANOWSKI'S TINAMOU	*NOTHOPROCTA TACZANOWSKII*	NON-COOPERATIVE
WHITE-BELLIED NOTHURA	*NOTHURA BORAQUIRA*	NON-COOPERATIVE
CHACO NOTHURA	*NOTHURA CHACOENSIS*	NON-COOPERATIVE
DARWIN'S NOTHURA	*NOTHURA DARWINII*	NON-COOPERATIVE
SPOTTED NOTHURA	*NOTHURA MACULOSA*	NON-COOPERATIVE
LESSER NOTHURA	*NOTHURA MINOR*	NON-COOPERATIVE
PATAGONIAN TINAMOU	*TINAMOTIS INGOUFI*	NON-COOPERATIVE
PUNA TINAMOU	*TINAMOTIS PENTLANDII*	NON-COOPERATIVE

WHITE-THROATED TINAMOU	*TINAMUS GUTTATUS*	NON-COOPERATIVE

Species added to the list are:

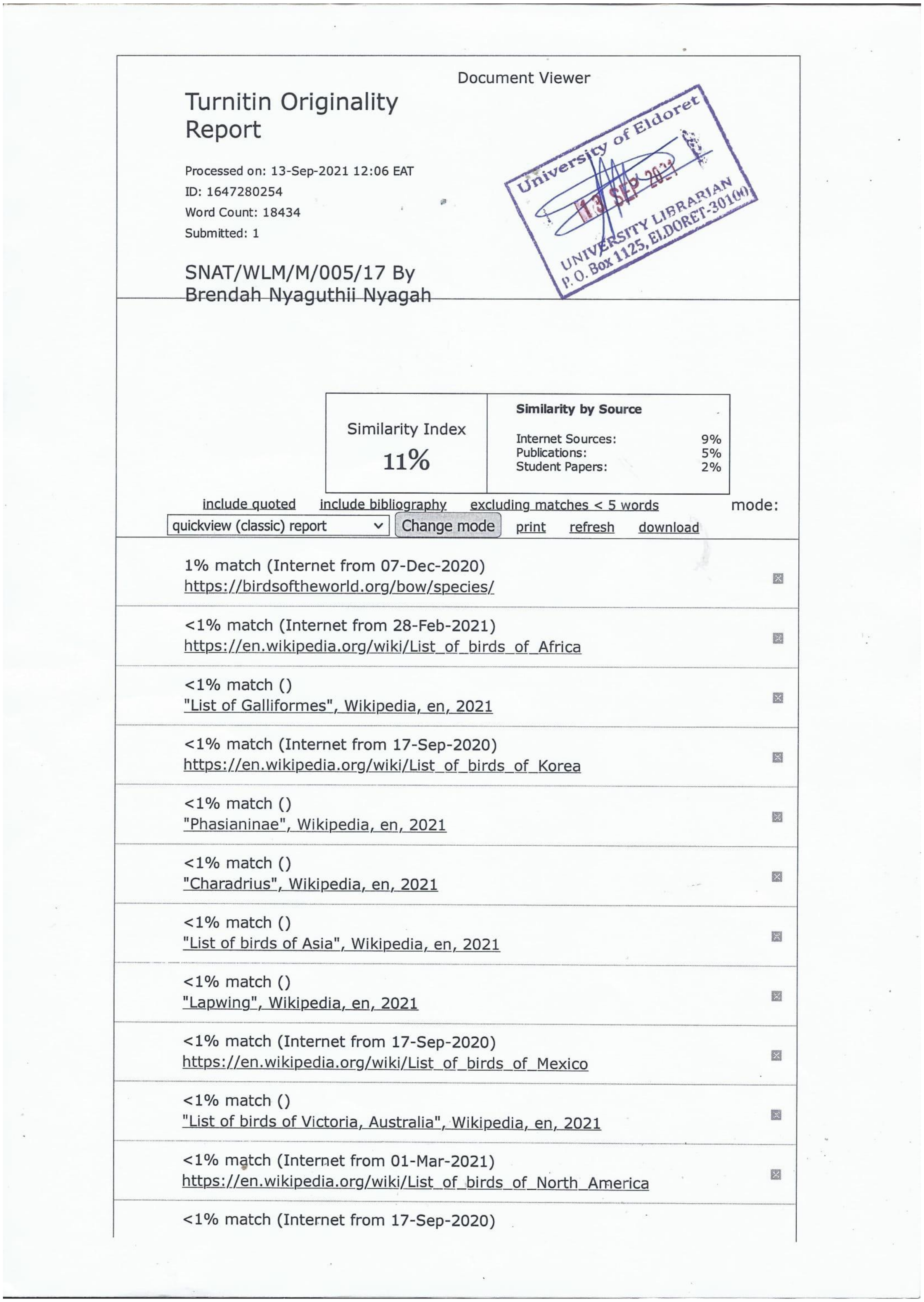
Acryllium vulturinum [a]- This study

Colinus virginianus [b]- (Orange *et al*., 2016)

Lophura leucomelanos [c]- (Severo, 2013)

Numida meleagris [d]- (Van Niekerk, 2010)

Appendix 2: Similarity report



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