Release success of captive bred Cape Vultures (*Gyps coprotheres*) in the Magaliesberg Mountains, South Africa

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ABSTRACT

The Cape Vulture, *Gyps coprotheres,* is currently classified as 'endangered'. Endemic to southern Africa, its population has declined continuously over the past 40 years. The species is facing multiple anthropogenic threats. Notably, birds frequently collide with power lines and some cannot be released after treatment. This has led to the establishment of a captive breeding population with the hope that captive bred young can supplement wild populations and re-establish a now-abandoned breeding colony in the Magaliesberg Mountains, South Africa. This study aimed to follow the breeding behaviours of the captive colony and assess the appropriateness of chick rearing conditions. The study also aimed to monitor the behaviour, physical condition and dispersal of ten captive bred vultures after release in relation to their age.

Behavioural observations of captive adult breeding and parental behaviours were conducted to establish whether chicks developed under comparable conditions to wild chicks. A high percentage of total colony copulation attempts (22 %) were extra-pair copulations. Four paired males formed ephemeral extra-pair relationships, two of which were homosexual. Chicks fledged earlier than wild chicks, on average at 128 days old.

Wild and captive bred birds were observed at carcasses to compare competitive and feeding behaviours. Older birds, both wild and captive, fed the most efficiently. Preliminary evidence suggests females are more dominant and have higher display rates than males. Captive bred juvenile and four year old birds' competitive and feeding behaviours (interaction rate, feeding rate, display rate, dominance, aggressiveness, and feeding efficiency) were the closest to, but still generally below, average values for same-aged wild birds. An index of body condition, body mass, and the prevalence of fault bars on the rectrices were used to assess their physical condition.

After eight months, none of the ten birds had moved more than 8 km from the release site, nor had they foraged away from the vulture restaurant on site. Although altitude records of > 3100 m were recorded, their flight skills seemed inadequate.

Future management considerations include the initiation of a pre-release exercise regime, the establishment of an acclimatization enclosure removed from the breeding site, and a varied or reduced post-release feeding schedule. Fledglings should be relocated and housed at the release enclosure until they are four years old.

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CHAPTER 1: INTRODUCTION

1.1 General context: African vulture crisis

Africa is on the verge of a continent wide vulture crisis. All of Africa's nine vulture species are declining at alarming rates (Ogada and Buij 2011, Ogada et al. 2015), placing them in critical danger of extinction with projected population declines between 70 and 97 % over the next three vulture generations (Ogada et al. 2015). Researchers fear the results of Africa's declining vulture populations will negatively affect ecosystems, human health, and national economies, as was seen with India's vulture crisis in the late 2000's (Pain et al. 2003, Ogada et al. 2012). While the loss of over 97 % of India's vultures was attributed mainly to the use of the veterinary drug diclofenac on cattle (Pain et al. 2008), African vultures are facing extinction from numerous threats, the majority of which are directly or indirectly the results of man, requiring a multi-organizational and transnational conservation approach. However, it has been predicted that a single threat alone such as power line electrocutions or wind turbine collisions could cause and/or accelerate the extinction of Cape Vultures *Gyps coprotheres* (20-35 years and 140 years, respectively, to extinction in study region; Boshoff et al. 2011, Rushworth and Krüger 2014).

Within the context of these impending cataclysmic population collapses, VulPro initiated a Cape Vulture captive breeding programme in 2011 from the large resident non-releasable population at a rehabilitation centre in South Africa. The first chicks produced from this breeding programme are the focus of this study. These chicks were released as part of a supplementation programme to boost the existing Magaliesberg population. This study has far reaching implications for future reintroduction efforts where the species is now locally extinct, i.e. Namibia, as well as the management of breeding and release programmes of all African vulture species.

1.2 *Gyps* vultures

Of the fifteen Old World vulture species, eight are classified in the genus *Gyps,* the closest relatives to the Cape Vulture. All *Gyps* species are large-bodied, long lived, slow to reach maturity, slow to achieve breeding success, and have low reproduction rates (Mundy et al. 1992).

There are six *Gyps* vultures which are colonial cliff nesters. The Cape Vulture *G. coprotheres* and Rüppell's Vulture *G. rueppellii* occur only in Africa (Mundy et al. 1992). The Himalayan Griffon *G.*

himalayensis, Indian Vulture *G. indicus*, and Slender-billed Vulture *G. tenuirostris* occur only in Asia and the Indian subcontinent (Mundy et al. 1992) and have all recently undergone drastic population declines (Pain et al. 2008). The widely distributed Griffon Vulture *G. fulvus* is stable throughout Europe and central Asia, but faces numerous threats in northern Africa (BirdLife International 2015b).

Two *Gyps* species are distinguished by their smaller body size and are solitary breeders which nest in trees. The African White-backed Vulture *G. africanus* is distributed widely throughout sub-Saharan Africa. The White-rumped Vulture *G. bengalensis* was historically distributed through the Indian subcontinent and southern Asia and has also recently undergone drastic population contractions (Pain et al. 2008). Historically, these species used to be in the genus *Pseudogyps*, but molecular studies now suggest that this genus should not be recognized (Seibold and Helbig 1995, Johnson et al. 2006).

Recent research suggests all *Gyps* species show similar response to toxins, specifically lead (Naidoo et al. 2012) and non-steroidal anti-inflammatory drugs (NSAIDs, Naidoo et al. 2009). The similarities in physiology across *Gyps* species have allowed researchers to study veterinary drug toxicity from trials performed on what was considered relatively stable African *Gyps* populations and translate the findings to management plans for the highly threatened Asian *Gyps* vultures (Pain et al. 2008).

All *Gyps* vultures share ecological and behavioural traits which make them susceptible to the same anthropogenic threats and mortality risks. For example, their propensity to feed in large congregations makes them susceptible to mass poisoning events from toxic veterinary drugs or poisoned carcasses. Their high wing loading (Pennycuick 1971) and reliance on thermal updrafts for flight put them at high risk of electrocution because they are often forced to roost on power line poles when they are unable to reach a cliff face due to poor wind conditions (pers. observations). Due to these behavioural similarities, as well as similar breeding ecologies and life history traits, the findings in this thesis have implications for breeding and release programmes of all *Gyps* species, especially within the African context.

1.3 Cape Vulture conservation status

There is a need for a standardized global census for all Cape Vulture breeding colonies within one breeding season to establish an updated global breeding count. Despite intensive conservation and research efforts over the past thirty years, the range and population of the Cape Vulture continues to decline (Benson 2004, Boshoff and Anderson 2007, Wolter et al. 2016). Historically, the Cape Vulture was widespread in Namibia and much of the former Cape Province in South Africa. The global population underwent drastic declines circa 1900 from rinderpest, game herd destruction, the Anglo-Boer War, conversion of grazing land to cultivation, and poisoning incidences (Boshoff and Vernon 1980). The species' range expanded from 1950 to 1975, with the largest concentration existing in the Eastern Cape grasslands (Boshoff and Vernon 1980). As a result of overgrazing and a decline in livestock, Cape Vulture distribution again contracted around 1975 (Boshoff and Vernon 1980). The IUCN Red List currently classifies the Cape Vulture as 'Endangered' because the small population is likely to continue to decline (Birdlife International 2015b).

The most recent global population estimates in 2006 suggest 8,000 to 10,000 individuals remain in the wild (BirdLife International 2015b). The two largest colonies are located in Blouberg and Kransberg, both in Limpopo Province, South Africa (Wolter et al. 2012). The species' breeding range extends into Botswana and Lesotho but breeding no longer occurs in Namibia, Swaziland, and Zimbabwe (Piper 2004, Wolter et al. 2012). The last reported census in Mozambique recorded only five breeding pairs in 2002 (Ara Monadjem pers. comm.).

Major and well-documented threats to the species include poisoning, electrocution, collisions with electricity cables, and harvesting for traditional superstitious beliefs or 'muti' (Phipps et al. 2013, Pfeiffer et al. 2014). Vultures are often the unintentional victims of carcasses baited with poison for 'problem' carnivores such as hyenas and jackals (Ogada 2014). There has been a recent surge in intentional poisoning from poachers who lace large mammal carcasses with poison with the intention of wiping out vultures who signal the presence of the dead carcasses to law enforcement (Kerri Wolter pers. comm.)

Electrocutions and collisions with power line structures are a widespread threat for vultures throughout South Africa (van Rooyen 2004). Electrocutions are typically fatal and unsafe structures have the potential to impact the population on a large scale. Up to 400 birds were recorded dead under one powerline transect 75 km outside of the Magaliesberg, an incident which likely contributed to the decline and subsequent extinction of the Roberts' Farm breeding colony (Verdoorn et al. 1998). Collisions with power line wires are the leading cause of vulture injuries at VulPro's rehabilitation centre in South Africa (Naidoo et al. 2011.).

A relatively smaller yet profuse threat is the demand for animal parts for 'muti' trade, specifically vulture heads, brains, or feet. This trade stems from local superstitious beliefs that consumption of these parts gives the consumer clairvoyant powers or that they provide relief from headaches and allergies (Cunningham and Zondi 1991, Mundy et al. 1992, Beilis and Esterhuizen 2005, Mander et al. 2007). Pfeiffer et al. (2014) surveyed residents in the Eastern Cape Province, South Africa who attributed the largest source of vulture mortality in the region to their use in traditional medicine (31 % of respondents). There is ample evidence, both via word-of-mouth and physical, i.e. electrocuted vultures found under power line structures with missing head and feet as well as rescued live birds, that community beliefs around the Magaliesberg create a demand for vultures in the 'muti' trade (pers. observations).

Other less well known but important threats to the species include direct persecution, drowning in farm reservoirs, habitat loss and a general decrease in food supply (Piper 2004, Boshoff and Anderson 2007).

In southern Africa and globally, vulture restaurants have been implemented as a proactive conservation method to provide poison-free meat and bone fragments to wild vultures (Piper 2004, Piper 2006) and to reduce their need to expand their foraging range which exposes individuals to poisoning events (Gilbert et al. 2007, Kane et al. 2015). There are 166 active registered vulture restaurants scattered across southern Africa but some of these only supply food once or twice per year (VulPro vulture restaurant database, August 2015). The region surrounding the Magaliesberg colonies is exceptional in that there are six active feeding sites within 50 km of the Cape Vulture colonies which cumulatively provide food daily. Wolter et al. (2016) suggests the regular supply and large mass of carrion provided in the Magaliesberg has contributed to the stabilization of the local Cape Vulture breeding population.

1.4 *Gyps* vulture captive breeding

VulPro's Cape Vulture breeding and supplementation programme is the first for *Gyps* species in Africa. The National Zoological Gardens (NZG) in Pretoria, South Africa has been successfully breeding Cape Vultures for many years but only started contributing the offspring to supplementation efforts in 2015. While VulPro's programme was a regional pioneer, successful captive breeding and reintroduction programmes have been instituted for four other *Gyps* species in eight countries (Figure 1, see Appendix 1 for details).

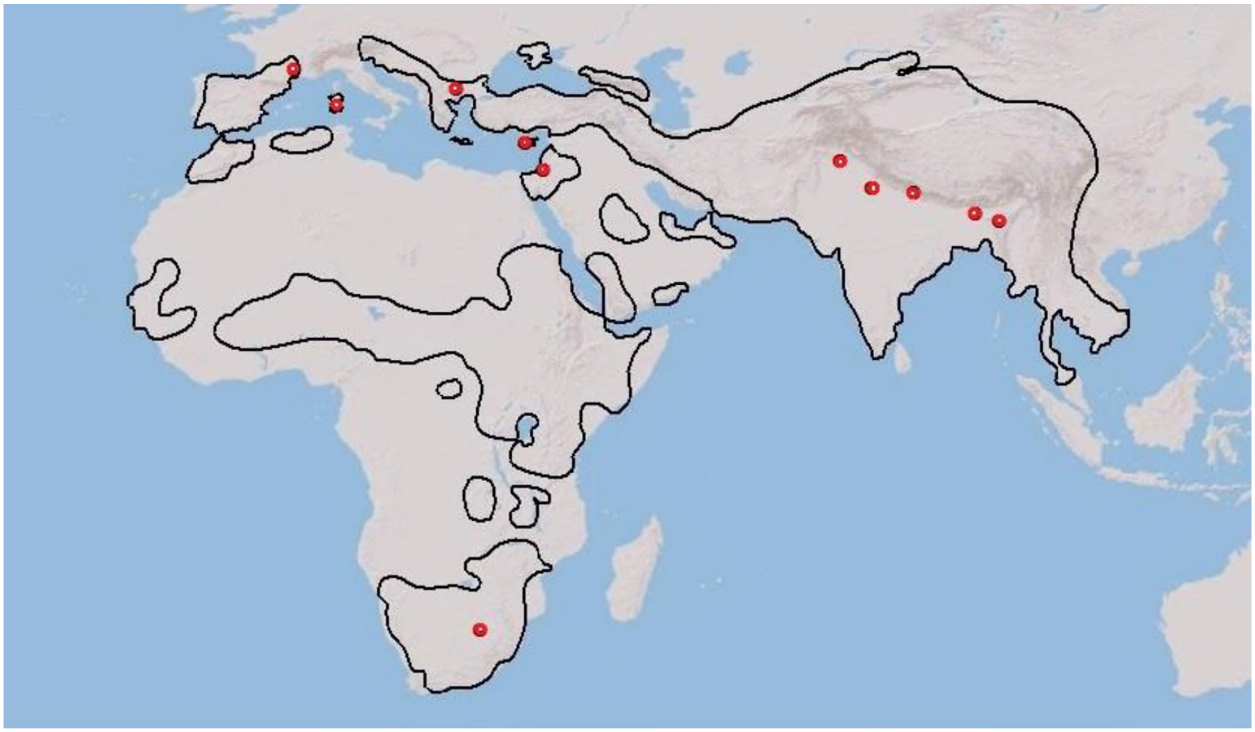


Figure 1: World map displaying the traditional range of all eight *Gyps* species (black outline, Mundy et al. 1992) and all *Gyps* breeding, reintroduction, or translocation programmes (red circles).

The majority of efforts are focused on the Griffon Vulture *Gyps fulvus* across Europe. The most studied and successful *Gyps* conservation programme released 61 Griffon Vultures between 1981 and 1986 into the Grand Causses region, southern France (Terrasse et al. 2004). The reintroduced population has recolonized the region and continues to grow, reaching over 300 breeding pairs in 2011 (Bosè et al. 2012). Starting in 2011, Cypriot Griffon Vulture populations were supplemented by individuals from Crete (Kassinis 2013). Since 1992, 115 Griffon Vultures have been captive bred and released in Israel (Hatzofe 2013), while 113 individuals have been reintroduced in Bulgaria between 2009 and 2013 (Dobrev and Stoychev 2013).

The most recently established *Gyps* breeding programmes were initiated on the Indian subcontinent following a drastic population crash of three species: White-rumped Vulture, Indian Vulture, and Slender-billed Vulture (Green et al. 2007). There are currently five captive breeding centres in India, Nepal, and Pakistan (Khan and Murn 2011) which house 248 individuals removed from the wild for breeding purposes (Ishtiaq et al. 2015). As of 2013, 90 chicks have been bred in captivity. Releases have not yet occurred in the region due to the lack of a safe food supply, but are planned for the near future (Toby Galligan pers. comm.)

1.5 Thesis layout

This study records the breeding ecology of VulPro's captive Cape Vulture population and holistically follows captive bred birds through the first eight months post-release. These observations were designed to aid management decisions for captive breeding and release programmes. Ultimately, the aim of my research is to maximize the number of offspring suitable for the release programme and maximize individual survival while minimizing resource use. Specifically, this study addresses the question: What is the best age to release captive bred Cape Vulture chicks?

CHAPTER 4 follows the rearing of five chicks in VulPro's 2014 breeding season. Each successive chapter investigates one behavioural or physiological aspect used to measure release success: body condition (**CHAPTER 5**), intraspecific competition and food intake (**CHAPTER 6**), and ranging (**CHAPTER 7**).

1.5.1 Hypotheses

I hypothesize that the older Cape Vultures reared in the 2011-2013 broods, or the post-fledging sub-group, will integrate into wild populations at a faster rate, compared with fledglings reared in 2014.

Specifically, I expect juvenile vultures to disperse more rapidly than older birds. I expect older vultures to roost within wild colonies earlier than fledglings. Older vultures will be more efficient at feeding and will therefore maintain higher body condition, better feather condition (fewer fault bars) and display greater weight gain post-release compared to fledglings. If age is a determining factor in wild vulture competitive behaviours, I suspect older vultures will adopt comparable behaviours to wild Cape Vultures of the same age at an earlier date, compared with fledglings.

CHAPTER 2: STUDY AREA

2.1 VulPro

VulPro is a non-profit organization, created in 2007, dedicated to the conservation of all southern African vulture species. VulPro is a multi-faceted conservation organization which conducts research, rehabilitation, captive breeding, educational programmes, and actively works with landowners and businesses to mitigate all threats.

Captive bred birds were released at the breeding facility which straddles North West and Gauteng provinces, South Africa at 25°42’40.86” S, 27°57’13.28” E. VulPro currently houses over 100 non-releasable vultures, the majority of which are Cape Vultures injured by power line collisions or electrocutions (Naidoo et al. 2011). The nine hectare centre also contains a rehabilitation facility, multiple breeding enclosures, and a vulture restaurant which provides carcasses on an almost daily basis. An education centre on site facilitates presentations to school groups and the general public. Guided tours are also available by appointment. The organization’s focus is now shifting to their captive breeding programme as the directors believe this programme will be crucial for all species’ survival (Kerri Wolter pers. comm.).

2.2 Magaliesberg Mountains

The Cape Vulture supplementation project centres on the Magaliesberg Mountains Protected Environment. Under the current level of protection, the region supports conservation, tourism, and livestock production, while moderating unsustainable development. In June 2015, UNESCO declared the region a Biosphere Reserve with the aim of reducing the impact of bordering developments (Magaliesberg Biosphere 2015)

The Magaliesberg is a stunning mountain range that runs east – west for approximately 200 km, arcing from Pilansberg in North West Province to Pretoria in northern Gauteng Province (Figure 2, Carruthers 1990). The south facing escarpment forms a natural demarcation between the northern highveld and southern bushveld biomes and is the most distinctive feature of the range. Gentle northern slopes are carved by slow flowing mountain spring streams creating deep *kloofs*, or canyons. The Magaliesberg region receives rainfall from summer thunderstorms, averaging 681 mm annually (Carruthers 1990).

The Magaliesberg region is classified as an Important Bird Area by BirdLife International (BirdLife International 2015a). The Magaliesberg Biosphere Reserve alone hosts 443 species of birds, almost half of the total avian species found in South Africa (Magaliesberg Biosphere 2015) including breeding pairs of Verreaux's Eagles *Aquila verreauxii* and one Black Stork *Ciconia nigra* pair which nests in a shallow cliff cavity in the middle the Skeerpoort Cape Vulture colony (BirdLife South Africa 2015).

The Magaliesberg range displays a high degree of plant and animal endemism such as southern African endemic reptiles Kalahari tent tortoise *Psammobates oculiferus*, Duerden's burrowing asp *Atractaspis dierdeni*, and Distant's thread snake *Leptotyphphlops distanti*, threatened endemic invertebrates such as Stobbia's Fruit Chafer beetle *Ichnestoma stobbiai*, and regionally endemic threatened plants such as *Aloe peglerae* and *Delosperma leendertziae* (Gauteng C-Plan 3.3 2011, BirdLife South Africa 2015).

The region boasts unique human history dating back millions of years to early hominids. This, in addition to its unique and old geological formations, benign climate, and rugged terrain, generate the regions' allure as a tourist destination (Magaliesberg Biosphere 2015).

Small scale cattle farms are the most common land use surrounding the mountains, as well as tourism-based small business. Urbanization, including tourism and commercial and industrial development, is increasing especially surrounding the Hartbeespoort Dam in the east of the mountain range (BirdLife International 2015a). The construction of eco-estates, housing complexes, government sponsored low-cost housing schemes and makeshift housing complexes around VulPro in the last 5 years has increased the likelihood that birds will have a fatal interaction with the sprawling power line grid as well as fatal interactions with community members who illegally target and kill birds for the 'muti' trade (Pfeiffer et al. 2014 and pers. observation).

2.3 Cape Vulture breeding colonies in the Magaliesberg

The south facing cliffs of the Magaliesberg Mountains, located in North West and Gauteng Provinces, South Africa support one extinct and two active breeding colonies of Cape Vulture (Figure 2). VulPro's release programme aims to supplement these populations and hopes to re-establish the extinct Roberts' Farm colony.

The Magaliesberg colonies have been monitored since the 1950's but not continuously or with standardized methods. VulPro has conducted standardized annual breeding censuses since

2006 (Whittington-Jones et al. 2011). Wolter et al. (2007 and 2016) report a recovery trend in the population of Cape Vultures in the Magaliesberg Mountains over the last three years.

The Magaliesberg Cape Vultures account for 12 % of the global population as of 2013 (Wolter et al. 2013), based on two colonies at Skeerpoort and Nooitgedacht.

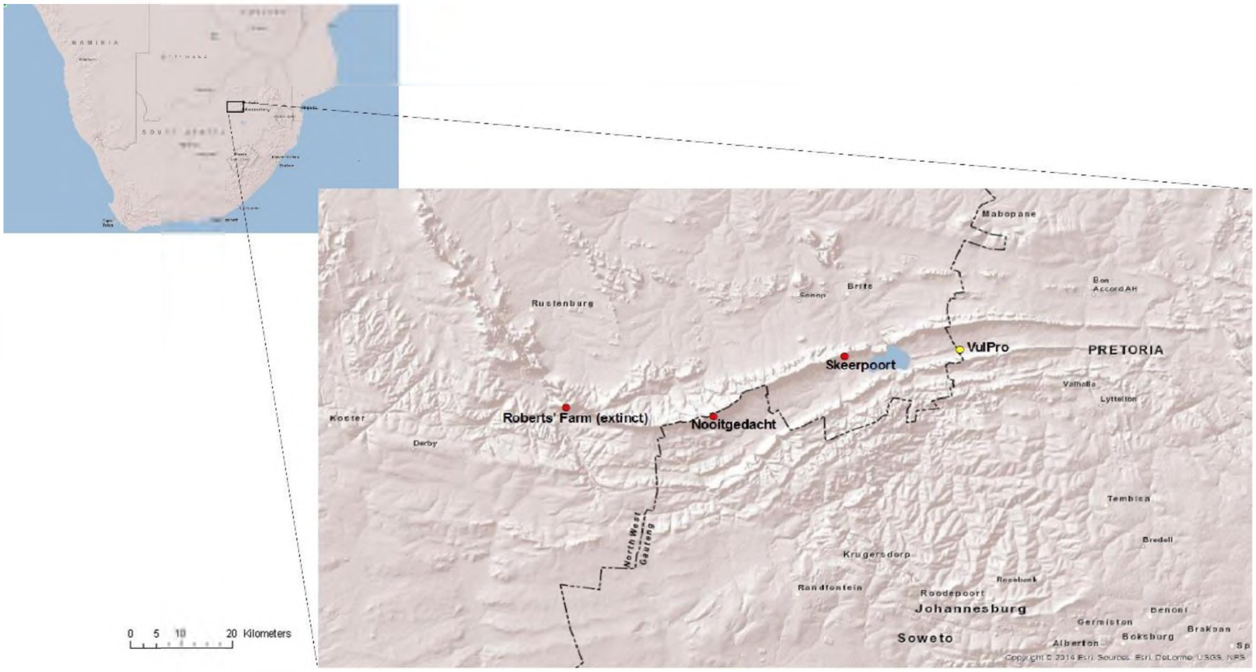


Figure 2: Map of the Magaliesberg Mountain range and surrounding area displaying three Cape Vulture breeding colonies (red dots) in relation to VulPro NPO (yellow dot).

The Skeerpoort colony (25°45’01.20” S, 27°45’27.90” E) overlooks Hartbeespoort Dam and contains the majority of breeding pairs in the Magaliesberg range. The population appears to be stable but has fluctuated reaching a maximum of 331 pairs in 2008 and a minimum of 200 pairs in 2012 (Wolter et al. 2016). The colony contained approximately 400 breeding pairs in 1997 (Verdoorn et al. 1998) but the variation may be attributed to different counting methods and observers.

The Nooitgedacht colony (25°51’18.52” S, 27°32’15.26” E) is midway between the Skeerpoort colony to the east and Roberts’ Farm colony to the west. It is the only Cape Vulture colony located within the boundaries of Gauteng Province. The colony is unique in that it contains a sub-colony on an eastern facing cliff face. The colony has undergone drastic fluctuations in recent decades. In 1967 the construction of micro-wave transmission lines on top of the cliff caused its 67 breeding pairs to abandon the site. The site was used only for roosting until 1989 when landowners initiated a vulture feeding site, luring vultures from other locations to utilize the cliff face. The first successful breeding attempt since 1967 was recorded in 1991. Prior to 1967 there is no record of the vultures using the eastern facing sub-colony; the birds first started roosting there in 1994. Breeding site attendance increased steadily to approximately 120 breeding pairs in 1997 (Verdoorn 1998). Since 2006, the colony has fluctuated between a minimum of 74 pairs in 2012 and maximum of 125 pairs in 2010 (Wolter et al. 2016).

Roberts' Farm (25°49'57.40" S, 27°17'18.83" E) is the westernmost Cape Vulture colony in the mountain range. The colony historically contained 155 breeding pairs in 1988, but by 1995 the colony had declined to twenty one pairs. This drastic decline is attributed to a string of electrocutions in 1995 in which possibly up to 400 Cape Vultures were killed 75 km southwest of the colony (Verdoorn et al. 1998). The colony declined further to five pairs in 2011. All pairs abandoned the site in 2012 and no breeding has been recorded since (Wolter et al. 2016).

The history of the Roberts' Farm colony decline is summarized in Figure 3. Some caution must be used when comparing historical data to more recent counts. Methods were standardized from 1981 to 1991 as well as from 2006 to 2014, but are not directly comparable.

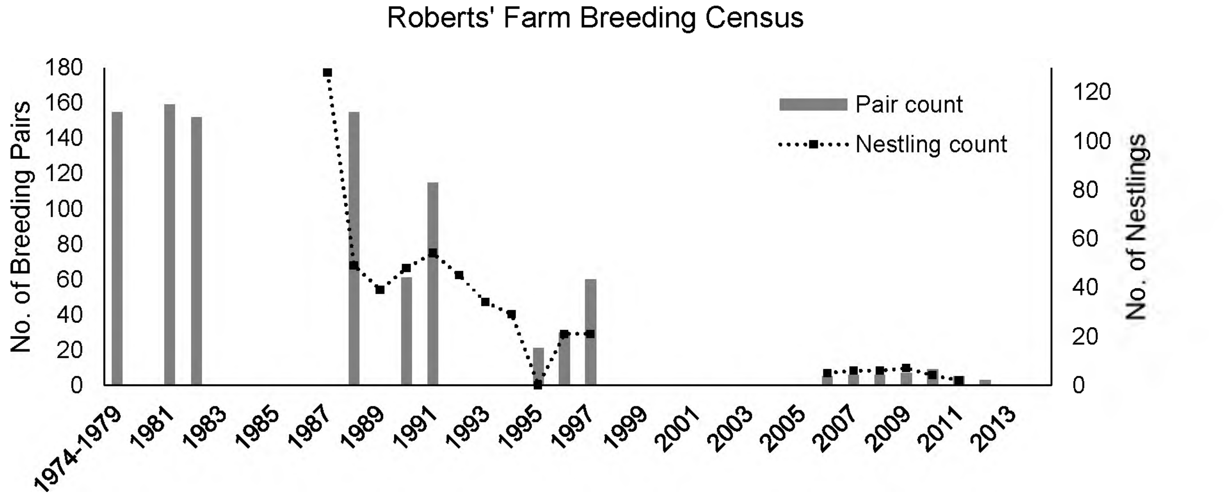


Figure 3: A summary of all available breeding pair and nestling counts for the Roberts' Farm colony from 1974-2014. Data was summarized from Verdoorn 1990, Verdoorn and Becker 1992, Verdoorn et al. 1992, Verdoorn et al. 1998, Wolter et al. 2007, Whittington-Jones et al. 2011, and Wolter et al. 2016.

CHAPTER 3: INDIVIDUAL CHICK HISTORIES

Ten captive bred Cape Vultures were released in February 2015 with ages ranging from one to four years at the time of release (Table 1). Age classes of Cape Vultures are defined as follows: juveniles six months to one year old, immatures two to four years old, sub-adults five to six years old, and adults seven years and older. All birds were genetically sexed by the National Research Foundation via the amplification of the Chromo Helicase DNA binding (CHD1) gene using the P2 / P8 primer set (Griffiths et al. 1998).

Three individuals were bred at the National Zoological Gardens (NZG) in Pretoria, South Africa while seven were bred at VulPro NPC in North West Province, South Africa. All released individuals were monitored using the same behavioural and GPS tracking methods. However, the collaboration between VulPro and the NZG only formed in 2014, thus there is no data concerning the rearing methods and pre-release conditions of NZG birds. An additional two birds, raised at VulPro in 2014, were included in the captive breeding ecology study (**CHAPTER 4**) but were not released with the others due to a lack of available GPS units (see Table 1 for details).

Table 1: Details of each individual studied within the captive breeding and release programmes.
*chick 008 went missing on 24 July and is presumed dead.
CTT = Cellular Tracking Technologies LLC., MTI = Microwave Telemetry, Inc.

Chick ID	Origin	Hatch Date	Age at release (years)	Sex	Released in 2015?	Days free-ranging over study period	GPS type
000	VulPro	25 July 2012	3	Male	Yes	258	CTT backpack
001	VulPro	2 July 2012	3	Female	Yes	258	CTT backpack
002	VulPro	2 July 2013	2	Female	Yes	22	CTT backpack
003	VulPro	2 August 2013	2	Female	Yes	258	CTT backpack
004	VulPro	20 July 2014	1	Male	No	0	CTT backpack
005	VulPro	30 June 2014	1	Female	Yes	258	CTT backpack
006	VulPro	23 June 2014	1	Male	Yes	258	CTT backpack
007	NZG	23 July 2013	2	Male	Yes	258	MTI backpack
008	NZG	22 August 2011	4	Male	Yes	160 *	MTI backpack
012	VulPro	30 June 2014	1	Female	Yes	258	CTT backpack
013	VulPro	6 August 2014	1	Male	No	0	CTT backpack
026	NZG	20 July 2012	3	Male	Yes	235	MTI patagial (1 month) then CTT backpack

All birds were parent raised with no direct human contact. Vultures were handled only for tagging, collection of samples and body condition assessment, and transport between facilities and/or enclosures. All birds were regularly exposed to people for husbandry matters, i.e. when providing food and cleaning water baths, as well as to the public from outside the enclosures. The degree of public exposure varied drastically by site. As the NZG is a popular tourist and local destination, birds at the NZG were exposed to the public daily. VulPro is not open to the public, but chicks were exposed to small groups of people between 3 and 10 times per month during guided tours.

Birds raised at the NZG spent their entire lives inside a large mixed-vulture species (Cape and African White-backed Vultures) flight enclosure before being transported to VulPro in December 2014, two months before release. At VulPro they were housed in a 40 m x 9 m mixed-vulture species (Cape, African White-backed, and Lappet faced Vultures) enclosure with both releasable and non-releasable rehabilitated birds. Birds raised at VulPro spent the first six months of their lives with their parents in a 40 m x 18 m breeding enclosure with only adult and sub-adult Cape Vultures. At six months old, chicks were moved to VulPro's rehabilitation enclosure where they could socialize with birds of different ages. The breeding enclosure and the rehabilitation enclosure are 10 m apart, allowing birds to see and hear one another.

All birds were released on 15 February 2015 at VulPro's facilities. One at a time birds were removed from the rehabilitation enclosure and placed in the adjacent 'open' enclosure where VulPro houses non-releasable African White-backed and Cape Vultures which are unable to fly due to power line collision injuries. The birds were not encouraged to fly; all of them remained on the ground in the open enclosure for a few hours before leaving the enclosure and exploring the rest of the property, including VulPro's vulture restaurant.

The amount of time birds spent free-flying over the study period varied because two birds displayed inadequate flight within the first few weeks after release (Table 1). Bird 002 and 026 were placed back into the rehabilitation enclosure for monitoring for varying lengths of time to investigate the cause of the poor flight.

It was clear 002's flight was inadequate very early. She was re-captured on 21 February and assessed by a veterinarian. X-rays revealed a hairline fracture in her left radius (Appendix 4), likely the result of her initial reactions to the GPS backpack harness in which she collided with perches in the rehabilitation enclosure when she attempted to forcefully 'flip' herself over backwards. She was monitored in the rehabilitation enclosure for 4 weeks and re-released on 30 March; however, her flight still proved inadequate as she was never seen to fly higher than 5 m. She was taken back into captivity on 17 April where she remained for 7 months with no improvement in flight. In November a health assessment revealed a flesh wound on her right wing caused by the patagial tag (Appendix 5). This tag was removed, wound treated, and she was re-released on 30 November. At the time of writing (May 2016), she still fails to gain height in flight and roosts on lower structures than most chicks (5 m versus 9 m).

Bird 026 was released with a patagial GPS device from Microwave Telemetry Inc. This device has been deployed on California Condors (*Gymnogyps californianus,* Brandt et al. 2013) in the United States and Lappet-faced Vultures (*Torgos tracheliotos*) and other Cape Vultures at VulPro with great success (unpublished data). However, after poor flight strength and lack of ability to gain height in flight, 026's patagial device was removed and replaced with a Cellular Tracking Technologies LLC GPS device with a backpack harness. He was re-released on 01 April and his flight improved but not drastically, as he was still seen with low and poor flight for several weeks. Like individual 002, he has never been seen to perch on the taller enclosures on the property (9 m), but his GPS unit has recorded him at heights of 65 m.

Bird 008 disappeared on 24 June 2015, 160 days post-release, coinciding with the malfunction of his GPS unit. Unfortunately his GPS unit never transmitted and his body was never found. The cause of his disappearance was never identified, but he is presumed dead.

CHAPTER 4: CAPTIVE BREEDING ECOLOGY

4.1 Introduction

4.1.1 Wild Cape Vulture breeding behaviours

Cape Vultures are obligate colonial cliff nesting breeders. Colonies vary in size, but can be substantial; the largest colony at Blouberg, Limpopo Province, South Africa, contained 861 breeding pairs in 2013 (Benson 2015).

Each pair rears only one offspring per year. Wild birds have been recorded to lay a second replacement egg if the first is broken or abandoned early in the season. The breeding season is long, up to ten months of the year, as chicks are slow to mature and have a long post-fledging dependence period. Nest building begins in March and chicks fledge around December. Nest building, incubation, and chick care is shared between the pair. Nestlings are constantly guarded by one parent while the other forages (Mundy et al. 1992).

The majority of our knowledge of Cape Vulture breeding behaviour comes from intensive studies conducted in the Magaliesberg and Potberg colonies in the 1970's and 1980's (see Robertson 1985, Robertson 1986a, Robertson 1986b, and Mundy et al. 1992). In these studies, the sex of each bird was determined only by behaviours, i.e. position during copulation. Only a few birds were individually recognizable, making it difficult for researchers to assess the extent of extra-pair copulations and the exact degree of sex variation in parental involvement in chick care.

The objectives of this study were to record the rearing conditions of releasable birds to determine how closely these conditions match those of wild birds, specifically those of sex-biased parental duties and social interactions.

4.1.2 VulPro's captive breeding programme

VulPro initiated a captive breeding programme for the Cape Vulture in 2011 with seven breeding pairs. The breeding enclosure has since doubled in size and now contains thirteen breeding pairs in the 2015 season.

VulPro's captive breeding protocols are described in detail by Wolter et al. (2014b) and are summarized here. Adult and sub-adult Cape Vultures (five years and older) are housed in a 40 m x 18 m flight cage with an artificial, south facing cliff which was specifically designed to facilitate easy movement of flightless birds (Figure 4). Beginning in early March, *Rhus lancea* branches and long dried grasses are provided for pairs to build nests on their chosen ledges. The goal is to allow each pair the opportunity to incubate, hatch, and raise their chick independent of human intervention. Yet for most pairs (nine of ten pairs in 2014) some human intervention is required. Usually eggs are removed the day they are laid and replaced with wooden dummy eggs unless the parents are extremely aggressive, the parents have proven their ability to safely incubate a dummy egg and raise a chick in past years, or removal of the egg has caused rejection of chicks in past years. Eggs are artificially incubated at 50 % relative humidity and 37.5 °C and turned by hand 3 times per day. Each year two or three pairs are chosen to double clutch, i.e. remove their egg without providing a replacement which prompts the pair to continue to copulate and lay a replacement egg. Eggs are returned to the parents as soon as the chick internally pips, i.e. breaks into the air cell, before breaking the outer shell. The parents then assist the hatching process.

Figure 4: VulPro's Cape Vulture breeding enclosure with an artificial cliff face specially designed to facilitate the movement of flightless vultures.

4.2 Methods

The breeding enclosure was monitored for 511 hours over 333 days between 7 March 2014 and 7 March 2015. There were 24 days of observation missed in November. Otherwise, missed observation days were scattered through the year with only five days missed during the peak breeding season (April - September). Observation time periods were categorized as morning

(6h00 – 11h00), mid-day (11h00 – 15h00), and evening (15h00 – 19h00). Observations were equalized across time periods every three days or more frequently when possible.

Monitoring took place from the same location 30 m from the cliff face. This position was outside of the enclosure to reduce habituation of chicks but provided a full view of each cliff ledge. Individuals were recognized by patagial tags or otherwise unique markings with the aid of binoculars. A total of 37 of 41 individuals were genetically sexed by the National Research Foundation via the amplification of the Chromo Helicase DNA binding (CHD1) gene using the P2 / P8 primer set (Griffiths et al. 1998).

4.2.1 Copulations

The breeding enclosure contained 41 sub-adult (between 5 and 7 years old) and adult birds (7 years or older) including ten breeding pairs. Only these ten pairs which succeeded in producing an egg are included in the pair copulation analysis. Two couples formed pair bonds but only successfully bred in the following 2015 season. The copulations of these two pairs are not included in either the pair or extra-pair analyses.

Interactions were considered copulation attempts if one individual mounted another or one bird showed an interest in copulating through foreplay behaviours, i.e. crowding or following another individual in anticipation of mounting. Successful copulations were confirmed by witnessed cloacal contact, tail swiping by the male on top, or an ejaculatory pause. The duration of foreplay behaviours, mountings, and cloacal contact were recorded with a stop watch.

4.2.2 Incubation

The time an incubating parent lost and re-established body contact with the egg was noted to the nearest 30 seconds. An egg was considered un-incubated as soon as the parent lost body contact with the egg, even if it continued to tend to the egg. Complete incubation records are available for 7 pairs only. Incubation periods for other pairs were not recorded for various reasons: the pair continually rolled the dummy egg out of the nest (pair #2), the pair’s egg was infertile and their dummy egg was rolled out of the nest and abandoned at incubation day 15 (pair #3), or the identity of the incubating bird was routinely impossible to record (pair #4).

Independent two sample t-tests were conducted using R (R Core Team 2013, version 3.2.0) to assess sex differences in incubation duties. Values are presented as mean ± SD.

4.2.3 Brooding

Scan samples were conducted every ten minutes to record the proximity of each parent relative to the chick and 'nest ledge' (see Table 2 for codes). The 'nest ledge' was the space routinely defended from intruding neighbours and never exceeded 2 m beyond the nest. These observations were made from 3 September 2014, when the oldest chick was nine weeks old, until the chicks were removed from the enclosure in late December.

Table 2: Codes used to quantify the proximity of each parent to the chick.

Code	Description
Brooding	The chick is in the nest and the parent is standing on the nest, or; the chick is on its nest ledge and the parent is touching the chick (i.e. preening or feeding).
Present	The chick is on its nest ledge, the parent is within 2 metres of the chick but not brooding.
Not present	The chick is on its nest ledge, the parent is more than 2 metres from the chick.
Out of nest	The chick is not present on its nest ledge.

4.2.4 Fledging

Chicks raised on the cliff were considered fledged from their first excursion to the ground. In all cases this event coincided with a visit to a carcass. Chicks raised on the ground were considered fledged upon their first visit to a carcass. Each chick's age at fledging was compared to its body condition and mass using Pearson product-moment correlation analyses in R (R Core Team 2013, version 3.2.0, see **CHAPTER 5** for body condition data).

4.2.5 Parental feedings and post-fledging dependence period (PFPD)

Parental feedings were noted *ad libidum.* Feedings that occurred five minutes or more apart were considered separate feeding sessions. Independent two sample t-tests were conducted using R (R Core Team 2013, version 3.2.0) to assess sex differences in feeding duties. Values are presented as mean ± SD.

Before each chick was considered independent enough to be moved out of the enclosure away from their parents, it was confirmed each chick was routinely able to obtain food from carcasses by assessing their crop content (see Houston 1976 or **CHAPTER 6** for crop size categories and methods).

4.3 Results

4.3.1 Pair copulations

A total of 1,142 copulation attempts were recorded among ten breeding pairs, 59 % (n = 669) of which were successful. These copulations occurred throughout the year with a peak of both total interactions (Figure 5) and successful copulations (Figure 6) on 4 May and 13 May, respectively, fifteen and six days before the average egg lay date (19 May 2014, n = 10 eggs).

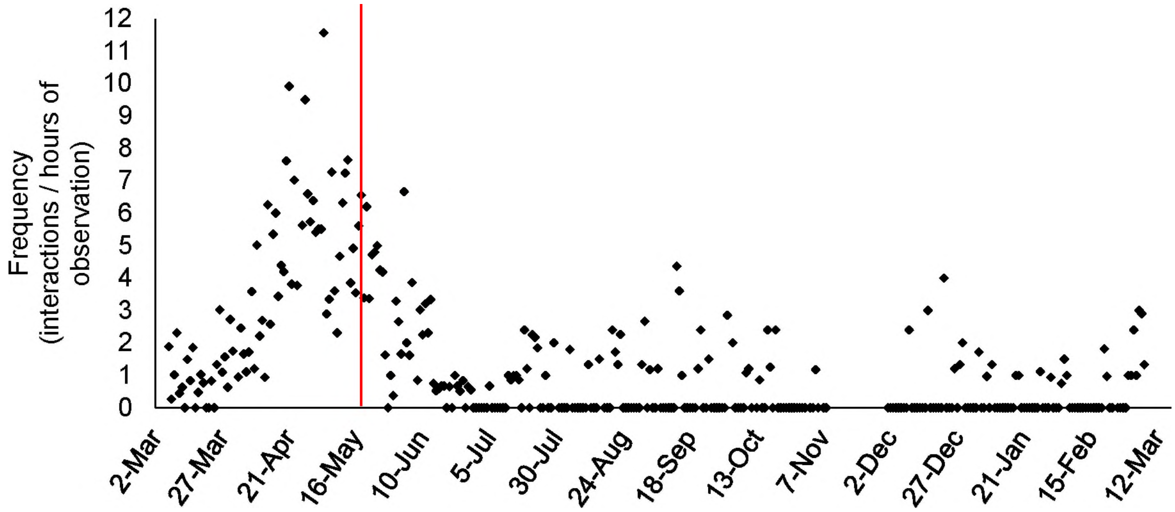


Figure 5: Frequency of total pair interactions per day for VulPro's ten breeding pairs including foreplay, unsuccessful mountings, and successful copulations. The colony's average egg lay date (19 May) is noted with a red line.

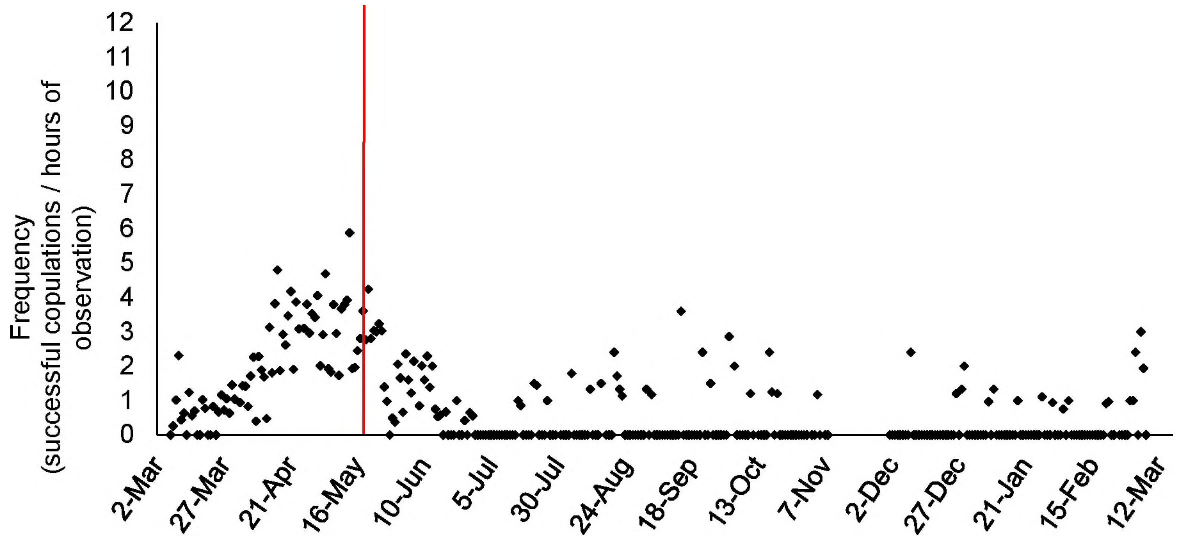


Figure 6: Frequency of successful copulations per day for VulPro's ten breeding pairs. The average egg lay date (19 May) is noted with a red line.

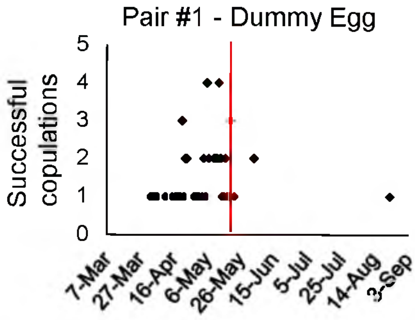
The majority of copulations, 81 % (n = 921) occurred on the pair's nest ledge. The remaining interactions occurred either on the ground in front of the nest (ground nesting pairs only, n = 81) or on roost ledges adjacent to the nest ledge (n = 140). Pairs which copulated on roost ledges were forced to do so because copulation attempts on their nest ledge were routinely interrupted by neighbouring birds.

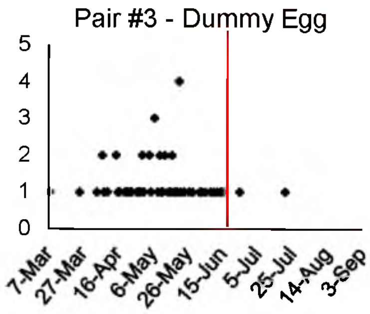
A loud raspy call accompanied 99 % (n = 1,128) of copulation attempts. The identity of the caller was confirmed during 482 interactions. In all instances the call was made by the male.

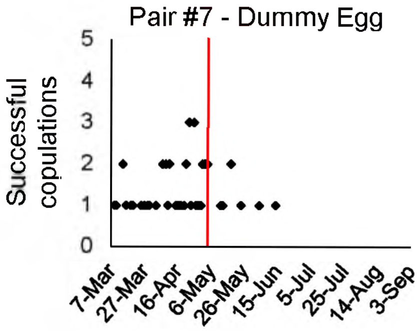
Only 10 % (n = 109) of all interactions involved discernible foreplay behaviours. In 30 instances foreplay did not proceed to mounting or copulation. The most common foreplay behaviours were conducted by the male and include crowding (n = 36) or following the female (n = 30), preening (n = 19) or grabbing the female's ruff (n = 24), and vocalizing (n = 36). Rarely the female was seen preening the male (n = 2). On one occasion the male fed the female a piece of dried meat which he brought to the nest.

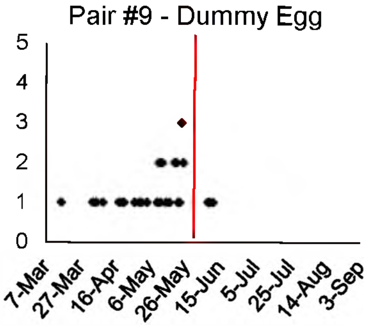
Seasonal fluctuations in successful copulations varied by pair (Figure 7). On one extreme, pair #8 copulated only between 29 March and 26 April and stopped immediately after laying their egg. Alternatively, pair #2 copulated successfully year round even while a dummy egg or chick (only one at a time) was present in the nest. Pairs were more likely to continue copulating post-egg lay when eggs were removed for artificial incubation (6 of 8 pairs). When eggs remained with the pair for natural incubation, only 1 pair (of 2) copulated post-egg lay and only on one occasion.

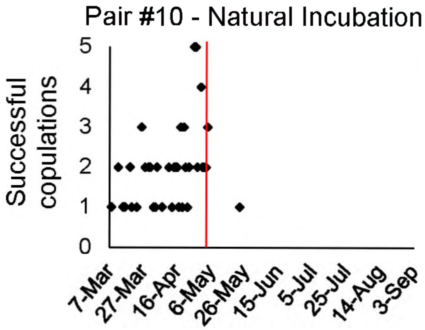
For 9 of the 10 pairs, there was a peak in frequency of successful copulations before egg lay. This peak was defined as the earliest day with the highest frequency of copulations for each pair and was on average 13 days pre-egg lay (Figure 7; 13 ± 8 days, range 1-28 days, n = 9).

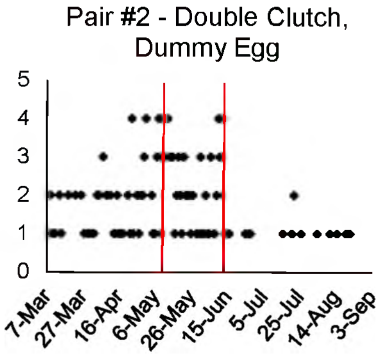

Pair #1 - Dummy Egg

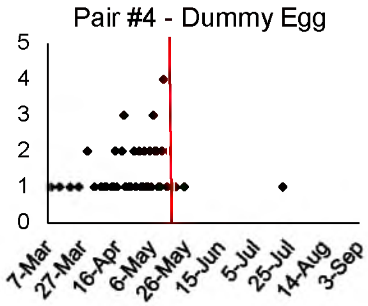

Pair #3 - Dummy Egg

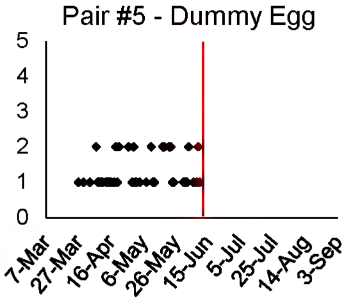

Pair #7 - Dummy Egg

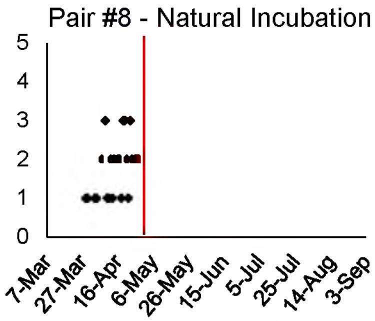

Pair #9 - Dummy Egg


Pair #10 - Natural Incubation


Pair #2 - Double Clutch, Dummy Egg







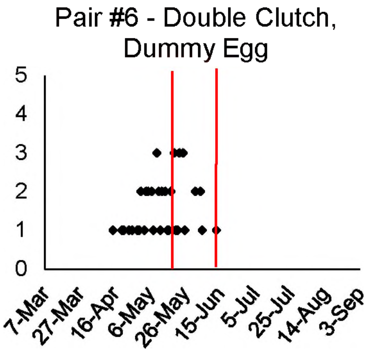


Figure 7: Daily successful copulations for each pair during the peak breeding season. Egg lay dates are noted with red lines.

4.3.2 Extra-pair copulations

Extra-pair copulations (EPCs) within VulPro's colony were variable; both breeding and non-breeding individuals were involved in hetero- and homosexual encounters. All individuals in the enclosure except one non-breeding male, 40 birds in total, were involved in an EPC or EPC attempt.

EPCs accounted for 22 % of all colony interactions. EPC interactions were frequent within the peak breeding season with 331 EPCs occurring between 15 April and 29 October (Figure 8). The majority of EPCs occurred between mid-April and mid-July (n = 324). The highest frequency of EPCs in the colony, 16 interactions in one day, occurred the same day as the average egg lay date (19 May 2014, n = 10 eggs).

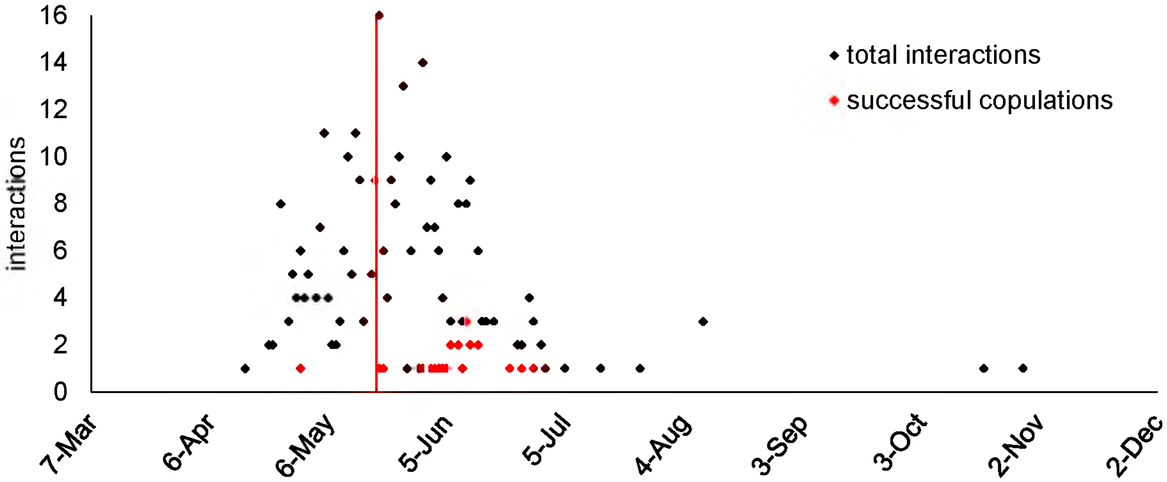


Figure 8: The seasonal occurrence of all EPCs. The average egg lay date (19 May) is noted with a red line.

The majority of EPCs involved at least one member of a breeding pair (95 %, n = 315). Both breeding males and breeding females were equally involved in EPCs (male n = 157, female n = 158). However, interactions with breeding females never resulted in cloacal contact; the females protested by pecking the male off her back or walking away.

Homosexual interactions accounted for 37 % (n = 121) of the total. All female-female interactions (n = 35) were instigated by one non-breeding female. None of these female-female encounters resulted in cloacal contact.

Only 7 % of extra-pair interactions (n = 23) resulted in cloacal contact, most (n = 21) involving one of four breeding males. These four males formed ephemeral relationships with a single individual, two males and two females. These extra-pair partners (EPPs) routinely roosted on the pair's nest ledge or nearby and attempted to build a nest with the pair or with the breeding male at a separate roost location (Figure 9). EPPs were occasionally tolerated by the breeding female at the nest site, but were often chased away. Aggressions towards the EPP increased in the later period of egg incubation and chick development, eventually leading to aggressive interactions with the breeding male.

Figure 9: A breeding female incubates her egg while tolerating the presence of her mate's male extra-pair partner roosting on the nest ledge (pair #6).

Copulations within these extra-pair relationships were tightly temporally constrained around the egg lay date of the original pair, most occurring within five and twenty five days of the initial copulation attempt (Figure 10). However, one breeding male (#9) attempted copulations with his EPP in late October, 150 days from his initial copulation attempt. Within each extra-pair relationship, copulations occurred either pre-egg lay or post-egg lay but not both. Even though copulations did not continue outside of peak breeding season, the two homosexual extra-pair relationships (pair #6 and #9) continued in the same fashion the following breeding season with successful copulations witnessed in extra-pair #9. The two heterosexual extra-pair relationships did not continue, however this can likely be attributed to a drastic reduction in observation time and the fact that female EPP #5 died in June 2015.

It is possible that sperm was transferred in homosexual encounters: the average duration of cloacal contact in successful homosexual encounters was slightly higher than the average duration of cloacal contact in pair copulations (pair = 13 ± 7.3 sec, n = 669; EPC = 14.9 ± 12.1 sec, n = 17).

All but eleven EPCs occurred on roost ledges or on the ground. Interactions occurred on nest ledges when a male mounted a breeding female on her nest ledge (n = 8) or when EPP #6 mounted the breeding male while he was incubating his egg (n = 3, Figure 10).

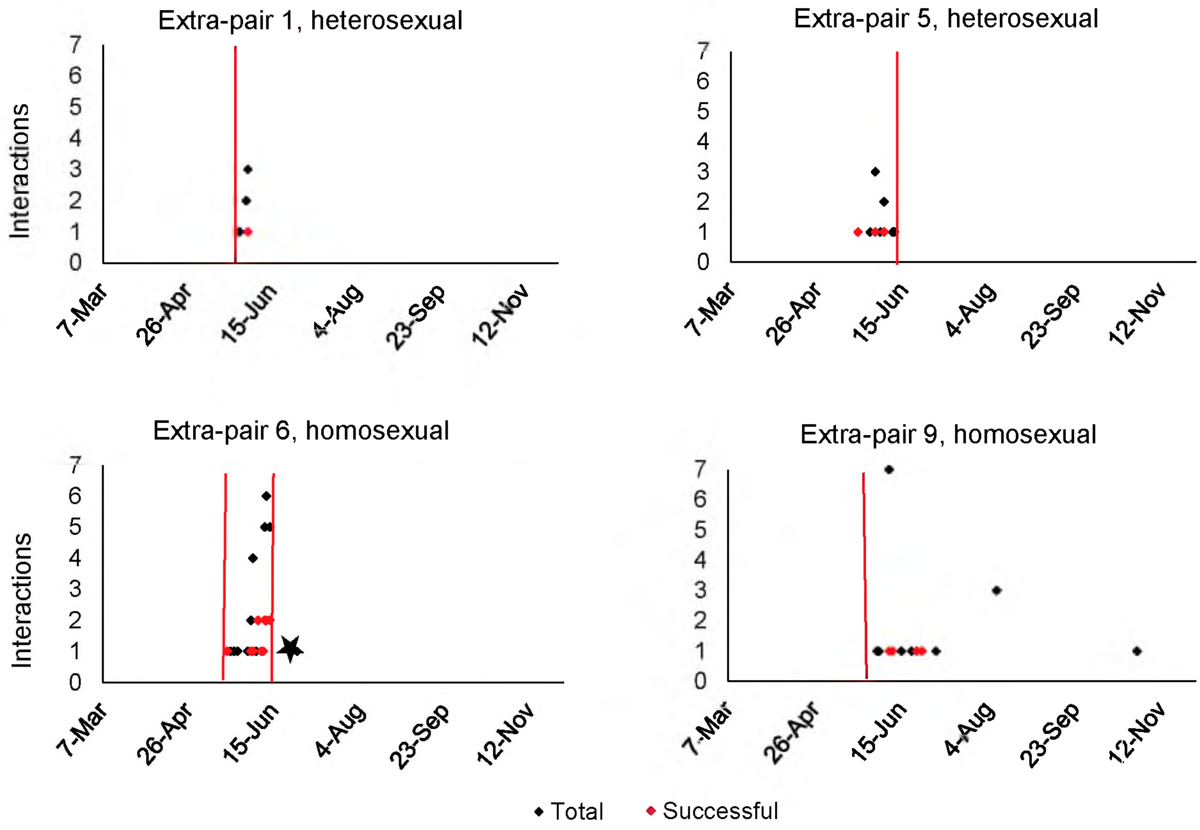


Figure 10: The seasonal occurrence of EPCs involving four breeding males with their extra-pair partners (EPPs). The original pairs' egg lay dates are noted with red lines. ★Three attempted copulations in extra-pair #6 occurred post-egg lay and were role reversed: the EPP attempted to mount the breeding male as he was incubating his egg.

Of the seventeen males involved in homosexual encounters, eight individuals were involved in both roles: mounting and being mounted. Five males were only seen on the bottom, three males only on top. The only homosexual copulations resulting in cloacal contact occurred within the two semi-permanent extra-pair relationships. In these relationships, both of the breeding males were always observed mounting the EPP, with the exception of three occasions when the EPP mounted male #6 while incubating; the EPP was sharply rejected.

Aggressive interactions were frequent during the breeding season and often occurred on breeding ledges. Unpaired individuals frequently attempted to steal nesting material from pairs, resulting in low intensity interactions occasionally involving body contact or biting, rarely serious injury. One breeding male routinely attempted to nest and copulate with a neighbouring breeding female. On six occasions he mounted her without protest on her nest ledge. These six encounters were all disrupted by the female's partner or other neighbours before cloacal contact.

Fights in one cliff section were a daily occurrence due to the close (vertical) proximity of three nests. Pair copulation attempts in this section often failed from neighbour harassment. Two of the three males belonging to these highly disturbed nests had EPPs (pair #5 and #6). A third male (pair #9) with an EPP built his nest on the ground at a location which was easily accessible to intruders.

The two breeding males which formed homosexual extra-pair relationships (pair #6 and #9) succeeded in raising a chick, while the two breeding males which formed heterosexual extra-pair relationships (pair #1 and #5) did not successfully raise a chick. Pair #1's egg rolled out of the nest the morning it was laid and broke. Pair #5's egg was infertile.

4.3.3 Incubation

The sharing of incubation duties varied between pairs (Figure 11). Females incubated eggs between 25.3 and 68.3 % of the observation period, males between 26.8 and 74.0 %. When averaged, there was no statistically significant difference in incubation duties between sexes (male = 51.3 ± 16.0 %, female = 43.7 ± 14.8 %., t = -0.997, p = 0.339, df = 12).

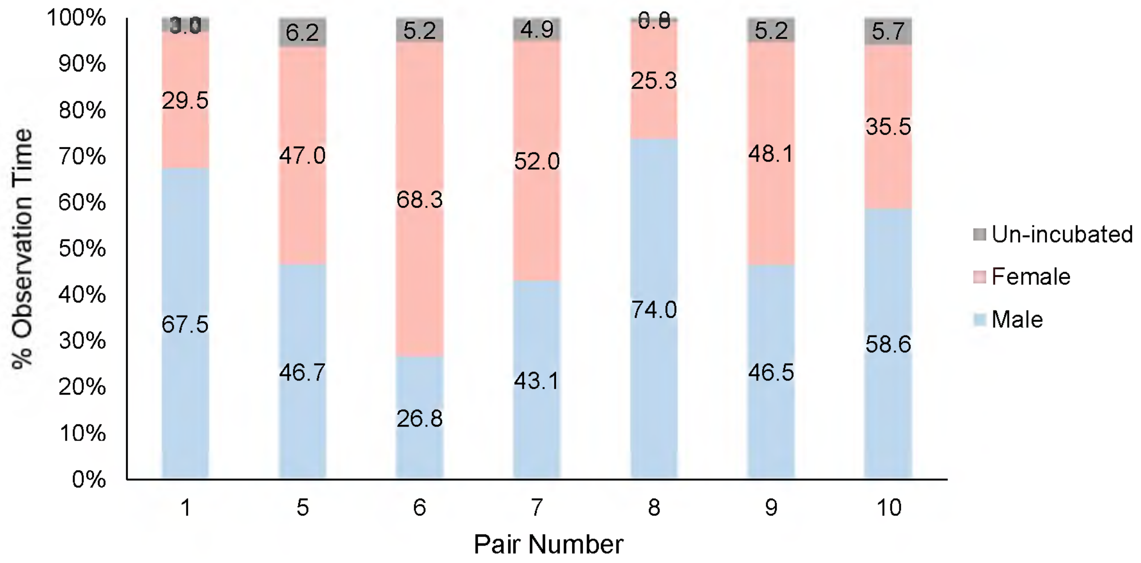


Figure 11: Percentage of observation time eggs were incubated by the male, female, or left un-incubated.

Eggs were incubated closely and rarely exposed except when the parent stood up to stretch, turn the egg, defend the nest from an intruder, or when parents changed over at the nest. Eggs were rarely left un-guarded. Eggs were left un-incubated between 0.8 and 6.2% of the observation periods. The pairs which incubated their eggs the most closely (pairs #1 and #8, un-incubated time 3.0 and 0.8 % respectively) are two of VulPro's most experienced breeding pairs, suggesting successful egg incubation and guarding comes with age and experience. This season was the first year both pairs #6 and #9 successfully bred, yet the length of time their eggs were left un-incubated was not the highest of the colony. According to this sample, naturally incubated eggs can withstand up to 5.7 % time exposed. Pairs #8 and #10 incubated their eggs naturally and successfully produced chicks with 0.8 and 5.7 % of total time un-incubated.

Regular change-overs for each pair at the nest were witnessed ranging between 0.6 and 2.3 per day (Table 3). These figures include both visually confirmed and assumed change-overs, i.e. when the opposite parent was seen on the nest later in the day.

Table 3: Summary of each pair's incubation duties (duration) and change over count.

Pair #	1	5	6	7	8	9	10
days observed	48	52	53	55	54	54	48
observation time (min)	5849	4230	4023	8063	8636	5826	6748
Male (min)	3948.5	1974.5	1076.5	3476	6390.5	2708.5	3954
Female (min)	1726	1988.5	2746	4189.8	2184	2802	2397
Egg un-incubated (min)	177	261.5	210.5	395.5	72.5	302.5	385
Change-overs:							
total (witnessed and assumed)	69	56	31	116	30	56	108
total / day	1.4	1.1	0.6	2.1	0.6	1.0	2.3

4.3.4 Brooding

Chicks were closely brooded at all times until around six weeks old. A single Cape Vulture parent brooded an average of 60 % of the observation period in week four and five. A single parents' brooding gradually decreased to 10 % or less at thirteen weeks old. Both parents were present, either brooding or standing, on the nest ledge approximately 70 % of the observation period until the chicks were seventeen weeks of age. At this time chicks started to explore their surroundings and leave the nest ledge (Figure 12).

Chicks were rarely left alone on the nest ledge. One chick (004) is the exception to this rule. Pair #9 left the chick alone for 3 % of the observation time at seven weeks old and again at eight weeks old. At ten weeks old, the chick was left alone for 23 % of the observation period. At thirteen weeks old the chick was left alone 60 % of the observation period. The male of this pair was hand raised and the female often roosted at a separate ledge. The fact that this nest location was on the ground with little risk of the chick falling may have created a greater sense of security for the parents. It was possible (and common) for them to be more than 2 m away from the chick and still quickly run to the nest site to defend the chick if disturbed. Two other chicks were first left unguarded at fifteen and twenty weeks old. The remaining two chicks were never seen left alone while on the nest ledge.

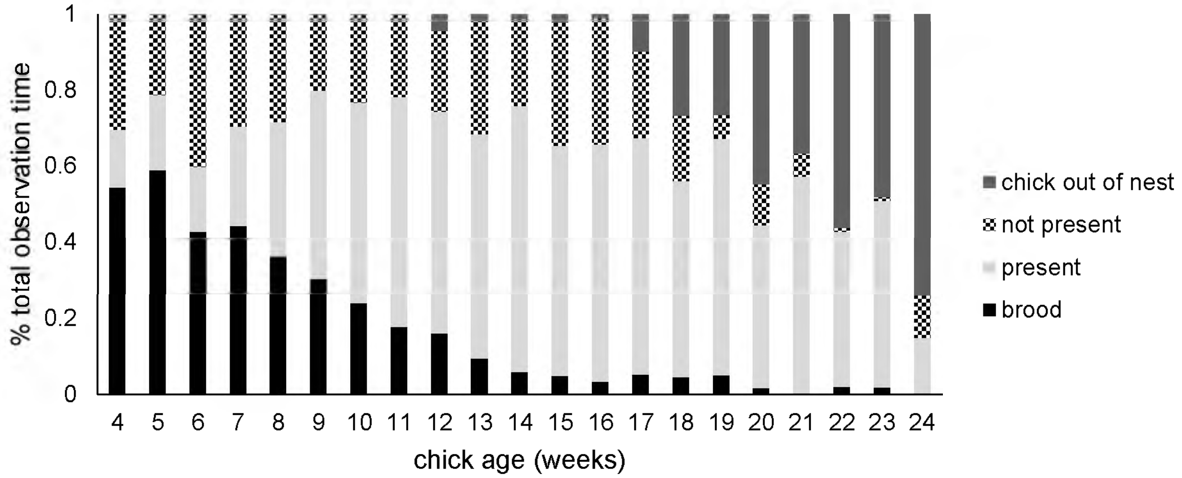


Figure 12: Spatial relationship: single adult to chick. The average percentage of observation time an adult spent brooding, present, not present, or when the chick was off the nest ledge. Values represent the average of all parents, both males and females, for five pairs.

4.3.5 Fledging

Determining the fledge date of each chick is complicated by the captive setting. VulPro's breeding cliff is specially designed with steps to facilitate movement of birds with reduced or no flight abilities. Fledging occurs gradually as the chicks hop to the ground, explore the enclosure, and visit a carcass all without taking flight. Measuring this milestone is also complicated by the variation in nest locations, i.e. some chicks were raised on the cliff and others were raised on the ground, greatly reducing the chicks' motivation to attempt a long flight. Chicks raised on the ground often walked and explored the enclosure before they were able to fly.

The average fledging age for VulPro's brood was 128 days old (SD = 9.7 days, range 115 -142, n = 5). Two chicks raised on the ground, chick 004 and 006, fledged an average of thirteen days younger than chicks raised on the cliff. Likewise, males fledged an average of thirteen days younger than females (Table 4, male $\bar{x}$ = 123 days, female $\bar{x}$ = 136 days).

Table 4: Fledge dates for chicks raised in 2014.

chick ID	fledge date	fledge age (days)	nest location	sex
004	12-Nov	115	ground	male
006	27-Oct	126	ground	male
013	12-Dec	128	cliff	male
005	7-Nov	130	cliff	female
012	19-Nov	142	cliff	female

Early fledge dates did not correlate with body condition score (BCS, all chicks had BCS of 3 upon removal from breeding enclosure) or body mass, although mass measures were only available for three chicks (r = -0.05, p = 0.967, df = 1, see **CHAPTER 5** for body condition analysis).

A chick was considered spatially independent when it spent ≥ 50% of the observation period off the nest ledge. The two chicks which hatched later in the season as a result of double clutching, chicks 004 and 013, were two of the three youngest to gain spatial independence. Chick 004 was the youngest to achieve spatial independence at only seventeen weeks old. All other chicks achieved spatial independence at twenty and twenty one weeks old (Figure 13).

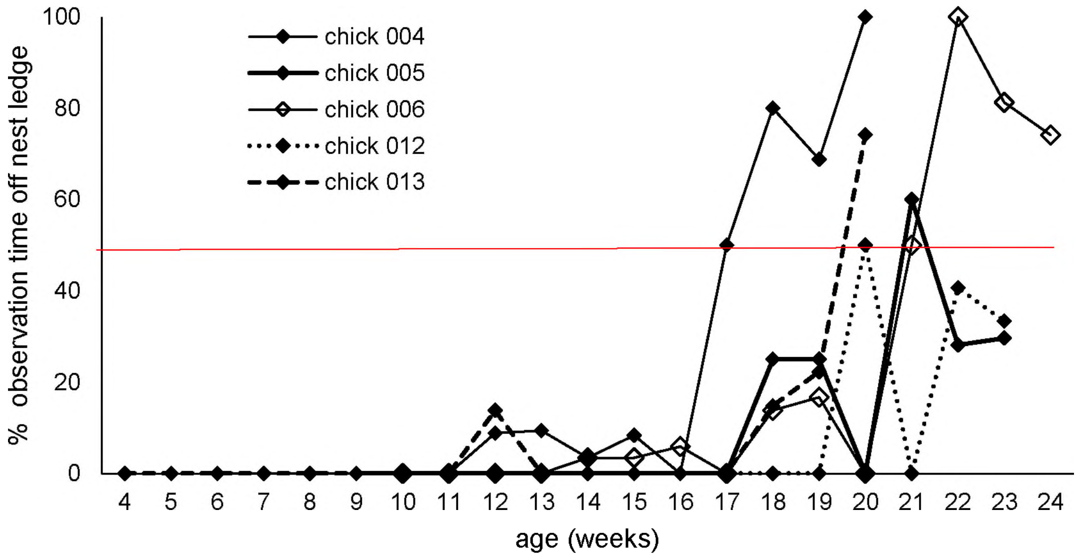


Figure 13: Spatial independence of each chick throughout development. Chicks were considered spatially independent from their parents when they spent ≥ 50% of the observation time off the nest ledge.

4.3.6 Parental feedings and the post-fledging dependence period (PFDP)

Feeding rates are summarized in Table 5. Chicks were fed most frequently when young. By the time all chicks were six months old, no parents were seen to regurgitate food even though the chicks would often beg by pecking at the parents' beak and face while making a loud raspy scream.

Feeding duties were shared evenly between sexes. Males were seen feeding the chick more frequently than females, but this difference was not significant (Table 5, male feeding rate = 0.22 ± 0.10, female = 0.17 ± 0.06, t = -1.062, p = 0.324, df = 8).

During the PFDP, each chick regularly visited carcasses at the entrance to the enclosure 30 m from the cliff face. They would feed or pick at the carcasses, display, compete, and interact with other individuals. Chicks were never seen to fill their crops and rarely filled them to half full (see Houston 1976 or **CHAPTER 6** for crop size categories). Often chicks were seen picking at unbroken skin or bone for several minutes without ingesting meat.

Table 5: Feeding rates (number of feeding events / hour observation) for each chick, grouped by chick age and parent sex.

	Pair 9 chick 004			Pair 7 chick 005			Pair 8 chick 006			Pair 10 chick 012			Pair 6 chick 013			mean feed rate, single parent
Chick age	hrs observ	♂ feed rate	♀ feed rate	hrs observ	♂ feed rate	♀ feed rate	hrs observ	♂ feed rate	♀ feed rate	hrs observ	♂ feed rate	♀ feed rate	hrs observ	♂ feed rate	♀ feed rate	
1 week	8.1	0.00	0.37	10.7	0.37	0.56	12.2	0.08	0.00	10.7	0.47	0.37	4.7	0.00	0.21	0.2
1 mo.	25.9	0.08	0.50	30.3	0.40	0.53	41.3	0.07	0.05	30.3	0.56	0.36	21.2	0.33	0.28	0.3
2 mos.	24.5	0.29	0.16	21.3	0.42	0.28	23.0	0.17	0.13	21.3	0.56	0.28	23.7	0.38	0.30	0.3
3 mos.	23.1	0.26	0.26	23.8	0.42	0.08	24.0	0.17	0.13	23.8	0.13	0.25	22.5	0.27	0.18	0.2
4 mos.	11.3	0.44	0.00	22.1	0.23	0.05	22.7	0.04	0.13	22.1	0.23	0.00	6.1	0.33	0.00	0.1
5 mos.	15.0	0.00	0.00	6.4	0.31	0.00	10.0	0.00	0.00	6.4	0.31	0.00	21.2	0.05	0.05	0.1
6 mos.	25.4	-	-	21.1	0.00	0.00	16.7	0.00	0.00	21.1	0.00	0.00	28.1	-	-	0.0
total	133.2			135.7			149.8			135.7			127.5			

4.4 Discussion

4.4.1 Comparison to wild Cape Vulture behaviors and other studies

The peak of pair copulation frequency 13 days pre-egg lay in VulPros' colony is comparable to wild Cape Vultures (peak the month before egg lay, Robertson 1986b) and Griffon Vultures (peak between 21 and 7 days before egg lay, Margalida and Bertran 2010).

In VulPro's colony, the degree of human disturbance to each pair varied by method of egg incubation, i.e. replacing with a dummy egg or leaving for natural incubation. Stressful encounters, for example removal of the egg, have the potential to negatively affect a wide array of behaviors in vertebrates (Wingfield et al. 1997) and could explain the higher frequency of post-egg lay copulations in some pairs in this colony. Subcutaneous implants of corticosterone (a hormone naturally produced during stressful encounters) in wild Pied Flycatchers *Ficedula hypoleuca* reduced the frequency in which parents fed their chicks, resulting in reduced breeding success. Further implants resulted in birds abandoning nests and territories altogether (Wingfield et al. 1997). It is important to keep in mind that what is 'stressful' differs between individuals and species. Carlstead and Shepherdson (1994) suggest potentially 'stressful' environmental enrichment for captive animals may positively alter reproductive behaviours and success.

Extra-pair copulations (EPCs) are common behaviours in birds and have been noted in nearly every avian family (Westneat et al. 1990). Multiple studies have found EPCs to result in successful fertilization, with up to 60 % of Mallard progeny resulting from EPCs (Evart and Williams 1987) but the genetic importance of EPCs in wild Cape Vultures is unknown. The high amount of successful EPCs involving VulPro's breeding males suggests EPCs may be part of a fixed mating strategy for male reproduction (Westneat et al. 1990). But this association is less clear for breeding females, of which the vast majority sharply rejected EPC attempts.

It could be that the high frequency of EPCs (and high proportion relative to pair copulations) is a result of the captive setting. Captive birds are forced to share communal roosting space off the breeding cliff, where the majority of unsuccessful EPC occurred. Møller (1987) describes a positive relationship between density and occurrences of EPCs in colonial Barn swallows *Hirundo rustica*. Although this relationship is not necessarily linear, especially in territorial species when neighbouring nesting sites become saturated, further increases in density do not necessarily result in increased opportunities for EPCs.

22 % of all the colony's copulation interactions were extra-pair copulations (EPCs), a much higher proportion than observed in the wild (Cape Vulture 4 %, Robertson 1986b; Griffon Vulture 3.3 %, Xirouchakis and Mylonas 2007). While the contexts of wild and captive EPCs are comparable, i.e. both forced and unforced and mostly off of nest ledges, all wild EPCs were considered to be chance encounters (Robertson 1986b). The semi-permanent extra-pair relationships formed by breeding males in VulPro's colony have not been noted behaviourally in the wild. However, there is indirect evidence for their existence as nests in several wild colonies have been noted with two eggs (1 % of nests in the Magaliesberg, Mundy et al. 1992). In some cases both eggs were fertile. One nest had two eggs over three consecutive years. Two eggs in one nest at the Roberts' Farm colony had the same hatch date, suggesting they were laid by different females (Mundy et al. 1992). To that fact, the shortest duration between VulPro's females' first and second clutches was twenty five days (unpublished data). None of VulPro's breeding females accepted copulation attempts from males beyond their partner, suggesting that Cape Vultures are genetically monogamous.

The two homosexual pairings in VulPro's colony are not explained by a sex bias. The colony sex ratio was close to equal with twenty one males, eighteen females, and two individuals of unidentified sex. Additionally, overcrowding likely did not influence this behaviour as the artificial cliff face and enclosure had extra space for additional pairs and nests, confirmed with the occupation of three more nest sites the following season.

Homosexual mountings are common in social animals and have been noted in many bird species (Bagemihl 1999). They are rarely noted in observations of raptors but have been witnessed in polyandrous trios of Bearded Vulture *Gypaetus barbatus* (Bertran and Margalida 1999, Bertran and Margalida 2002). The occurrence of extra-pair relationships noted here may be explained by the more accurate individual identification compared to wild studies. The behaviours of the extra-pair partner (EPP, male or female) at the nest and the breeding female were indistinguishable as long as the presence of the EPP remained uncontested by a pair member. If tolerance of these EPP individuals also happens in the wild, these relationships may go unnoticed. This is especially true on wild ledges with high nest density common in many Cape Vulture colonies; the density of nests can certainly be higher than these captive breeding ledges (pers. observation).

Based on the occurrence of extra-pair relationships within highly disturbed areas of the artificial cliff, it is possible that homosexual mountings and semi-permanent extra-pair relationships help regulate aggressive encounters within the colony (Bertran and Margalida 2003). In wild colonies, it is common for pairs to build nests in close proximity to another (less than 2 m away). If the disturbance of nests influences the male's likelihood to accept an extra-pair relationship, it might be expected to see this behaviour in wild colonies on heavily used, congested ledges. Further research should investigate the occurrence and extent of these extra-pair relationships in captivity, as well as their existence and context in the wild.

Incubation change-over rate observed of 0.6 to 2.3 per day is higher than the average rate seen in wild colonies (0.5 per day, Mundy et al. 1992). However, this is expected as captive birds are not constrained by a need to forage and are able to spend more time at their nest.

Using the criteria of first visit to a carcass as well as spatial independence, four of the five chicks fledged earlier than the average wild Cape Vulture (140 days old, Robertson1986a*,* Mundy et al. 1992). The earliest chicks to fledge were raised on ground nests and were also male. Determining the effect of sex versus nesting location on fledging dates is impossible with this small sample.. Wild Cape Vulture chicks were witnessed returning to their nest ledge as late as 221 days after their first flight. Some wild chicks received food from their parents as late as 210 days after fledging and were fed on average one day out of every 3.5 days during the PFDP (Robertson 1985, Mundy et al. 1992). This contrasts strongly with the truncated PFDP seen in this colony where no chick was seen to be fed at six months old (approximately 60 days after fledging) and two chicks were not fed at five months old (approximately 30 days after fledging). Future research should investigate parental and captive bred chick behaviors during this time to determine why captive parents are less supportive and what, if any, effects this may have on post-release social or feeding behaviors.

4.4.2 Management considerations

Many of the characteristics of Cape Vulture copulations noted by Robertson (1986b) were verified in these observations of VulPro's captive population. Captive Cape Vultures copulate successfully year round, share incubation duties between sexes, engage in extra-pair copulations, and are able to raise physically healthy chicks. These numerous similarities suggest that the basic requirements for successful reproduction are met, i.e. nutrition, ambient climate, substrates for nesting and parental behaviors.

The high proportion of EPCs in the captive colony highlights the need for stringent behavioural monitoring every year. These behaviours should be monitored and social situation altered if aggressions increase or breeding success is negatively affected. As wild nests have been recorded with two eggs (conceivably from different females), it is possible this circumstance will arise within the programme. Chick parentage is critical information for determining the utility of an individual within other captive breeding programmes or within the supplementation programme (IUCN/SSC 2013, Ishtiaq et al. 2015). Because egg laying occurs at night or very early in the morning, the identity of the egg layer is likely only to be verified by video recording, yet supplementary information from behavioural monitoring can be helpful in this regard.

CHAPTER 5: BODY CONDITION

5.1 Introduction

Fully understanding the health of captive bred, released individuals is critical for managing the population both pre-release and post-release. International guidelines dictate that the release of captive bred individuals should only be undertaken if managers are certain chicks are free from non-endemic contagious diseases and are behaviourally and physically healthy enough to have an equal chance of survival as their wild-born counterparts (IUCN/SSC 2013). Monitoring health post-release is essential to identifying underlying causes of mortalities and to mitigating mortalities when possible (IUCN/SSC 2013). Several reintroduction programmes have reported starvation as a cause of death, especially in young Andean Condors *Vultur gryphus* (Wallace and Temple 1987b), California Condors *Gymnogyps californianus* (Woods et al. 2007), and Griffon Vultures *Gyps fulvus* (Terrasse 2005) soon after release.

Captive bred Cape Vulture health was assessed through measurements of body condition, body mass, and a count of fault bars on single rectrices. These measurements were conducted while in captivity to determine suitability for release as well as several times post-release, documenting changes in body condition across time.

5.1.1 Body condition score (BCS) and body mass

There are numerous ways to measure the body condition of birds. Body mass alone is a poor indication of condition in vultures, as there is a high amount of individual variation in size (Houston 1976). Kirk and Gosler (1994) measured the relative mass of South American vultures using biometric scaling to assess variations in body condition based on migratory behaviour and competitive interference at carcasses.

Fat scoring is one of the oldest used body condition scoring techniques (Labocha and Hayes 2012). Houston (1976) found dissected wild breeding Rüppell's Vultures to have visible fat deposits ranging from thin sheets in the abdominal mesentery to, when in high amounts, thick deposits inside the legs and under the skin. A few captive Cape Vultures at VulPro show an excessive enthusiasm for feeding, causing visible fat deposits on their heads and necks. These individuals require a tailored diet. Assessing internal fat levels, while pertinent for captive populations, requires the bird to be euthanized.

The body condition score (BCS) scale described below was used in this study because it is a quick tool that can be used in the field to inspect both protein (breast muscle) and fat levels (although only in high levels on the head and neck). It has been used at VulPro during rehabilitation of all vulture species to judge the initial condition of injured birds as well as their suitability for release, and is used by other facilities as a quick way to routinely monitor the condition of captive birds (Rehse 2014).

This study aimed to monitor the health of birds before and after release to 1) determine if body mass and condition of captive bred birds is comparable to those seen in wild individuals of the same age, thereby assessing their suitability for release, 2) quantify changes in body condition based on husbandry (captive vs. free-flying), and 3) assess if bird age significantly affects the change in body condition between pre-release and final measurements.

5.1.2 Fault bar analysis

Fault bars are visible deformations in feathers which occur during feather growth. The deformation of barbules causes damage of varying degrees in the vane producing translucent strips or ripples which run almost perpendicular to the rectrix (Jovani and Blas 2004). Fault bars can also be seen on the upper surface of the rachis (Camiña and Yosef 2012). Stressful events, i.e. predator interactions, noisy traffic in wild settings or handling in captivity, are known causes of fault bars (King and Murphy 1984). However the causes are likely multifactorial and may include malnutrition (Camiña and Yosef 2012). Mundy et al. (1992) suspected dietary deficiency to be the cause of fault bars in nestling vultures, although this has not been empirically tested with any species of vulture.

Across species, nestling feathers show more fault bars than adults (crow, Slagsvold 1982; hawks and owls, Hawfield 1986; sparrow, Serrano and Jovani 2005). White stork *Circonia circonia* nestlings have up to three times as many fault bars as adults (Jovani and Blas 2004). Even within a single species and age class, individual variations in stress tolerance may produce repeated occurrences of fault bars year after year in the same bird (Bortolotti et al. 2002).

Severe fault bars weaken feathers and can lead to feather breakage, ultimately affecting the flight and fitness of the bird (Swaddle et al. 1996). The analysis of captive birds' fault bars can provide insight into how individuals are physiologically responding to environmental conditions and feeding regimes and has the potential to help determine an individual's suitability for release.

This analysis was conducted to determine 1) the general condition of the individual's feathers pre-release and 2) if the comparison of feathers collected during pre-release and final measurements, analysed in conjunction with other behavioural and physiological traits, may provide a proximate measure of the birds' ability to adapt to the unpredictable life outside of captivity.

5.2 Methods

5.2.1 Body condition score and body mass

Each individual's overall health, condition, and flying abilities were visually monitored on a daily basis. Age classes are defined as follows: juveniles six months to one year old, immatures two to four years old, sub-adults five to six years old, and adults seven years and older.

BCS was assessed by the same experienced observer (Kerri Wolter) using a scale from 1 to 5. This scale reflects the amount of flesh felt around the mid-point of the keel in addition to visual inspection of fat levels on the head and neck. A healthy bird scores between 3 and 4, a thin bird 2 to 2.5, and an emaciated bird 1.5 or less. A score of 4.5 or 5 is overweight and has only been recorded in captivity.

Body mass was calculated by placing the bird in a specially designed bag on a hanging spring scale (Wolter et al. 2014a). Mass was always recorded as the final measurement during handling in the hope that the birds would regurgitate any food in their crops. When the birds did not regurgitate before weighing, the size of their crop was noted and mass was reduced based on Houston's (1976) illustrated guide of known mass crop content (see section 6.2.2 for crop size categories).

Wild Cape Vulture body mass data was available from unrelated research, collected between January 2007 and July 2013 (Kerri Wolter, unpublished data). Birds were weighed on a standing scale (Wolter et al. 2014a). All values are represented as mean ± SD.

The initial BCS of VulPro's juveniles was recorded when they were removed from the breeding enclosure and relocated to the rehabilitation enclosure two months before release (Table 6). The initial BCS of birds bred at the NZG was recorded during their translocation to VulPro's property two months before release (Table 6).

Physical measurements of condition (mass and BCS) and biological samples were taken again during the fitting of patagial tags and GPS tracking devices between seven and seventeen days pre-release (Table 6). Also during this time a drop of blood was taken from the tarsus vein using a 23 gauge needle and transferred to FTA paper. Each individual was genetically sexed by the National Research Foundation via the amplification of the Chromo Helicase DNA binding (CHD1) gene using the P2 / P8 primer set (Griffiths et al. 1998).

Final BCS measurements were taken when birds were recaptured around eight months post-release (between 255 and 274 days after pre-release measurements, Table 6). Measures of BCS were taken more frequently for some individuals post-release ('interim' measurements, Table 6) if they required handling for other purposes, i.e. maintenance of GPS units or retrieval from outside VulPro's property. Recaptures were conducted using a walk-in capture enclosure at VulPro's restaurant (Wolter et al. 2014a).

BCS for bird 008 was only possible 162 days after pre-release measurements. His final body mass was not recorded before he went missing. Two additional birds (004 and 013), raised in 2014 at VulPro, were not intended for release but were included in BCS analysis to determine the effect of captivity on body condition of vultures with the same rearing conditions. Released bird 002 was recaptured and placed in captivity 61 days post-release. Her final measurements, and those of non-released captive bred juveniles 004 and 013, were taken while in captivity.

Table 6: The dates on which body condition score and body mass were recorded for captive bred released and captive birds. Dashes indicate no data was collected.
(*) Measurements were taken in captivity.

Chick ID	Initial measurement	pre-release measurement	interim measurement	final measurement	days between pre-release and final measurements
008	11-Dec-14	6-Feb-15	18-Jul-15	-	162
000	-	29-Jan-15	-	22-Oct-15	266
001	-	29-Jan-15	-	20-Oct-15	264
026	11-Dec-14	7-Feb-15	13-Jun-15	20-Oct-15	255
003	-	29-Jan-15	-	20-Oct-15	264
007	11-Dec-14	5-Feb-15	-	18-Oct-15	255
012	17-Dec-14	5-Feb-15	18-Jul-15	18-Oct-15	255
005	17-Dec-14	2-Feb-15	26-Aug-15	23-Oct-15	263
006	17-Dec-14	30-Jan-15	29-Aug-15	31-Oct-15	274
002	-	29-Jan-15	7-May-15*	28-Oct-15*	272
004	17-Dec-14	-	-	28-Oct-15*	315
013	30-Dec-14	-	-	28-Oct-15*	302

BCS and mass data distributions were checked for normality using Shapiro-Wilk tests. One-way ANOVA tests were then performed to determine if BCS and body mass, as well as changes in BCS and body mass over time, differed with age. Independent two sample t-tests were performed to determine the effect of captivity on single records of BCS as well as BCS or body mass change over time. Each bird's change in BCS and change in mass were compared using Pearson product-moment correlation analyses. All analyses were performed in R (R Core Team 2013, version 3.2.0). Values are presented as mean ± SD.

5.2.2 Fault bar analysis

During pre-release measurements, one central rectrix was cut just above the termination of the vane. Fault bars were counted over the entire length of the feather if any of the following conditions were present: a) visible deformation of barbules causing the vane to ripple b) more severe deformation of the barbules creating a 'window' in the vane, and c) presence of a white bar on the upper surface of the rachis (Figure 14).

No feathers were cut during final measurements because ten of twelve individuals' central rectrices were actively moulting. Bird 026's central rectrix had not yet started to moult. No final data were available for bird 008. Fault bars were counted while the bird was in hand if the feather had grown over half the total length. Bird 000 and bird 003's rectrices were just beginning to emerge from the sheath, making a count impossible. Bird 012 was moulting eight of her fourteen rectrices at the time of recapture (growing rectrices from left to right 1, 2, 7, 8, 9, 10, 13, and 14).

The distributions of fault bar count data were tested for normality using Shapiro-Wilk tests. One-way ANOVA tests were then conducted to determine if there was any difference in fault bar occurrence based on bird age (years). Each individual's fault bar count was compared to BCS using Pearson product-moment correlation analyses. Average feeding rates for juvenile chicks raised at VulPro (see Table 5) were compared to pre-release fault bar counts using Pearson product-moment correlation analyses. Analyses were conducted in R (R Core Team 2013, version 3.2.0). Values are represented as mean ± SD.

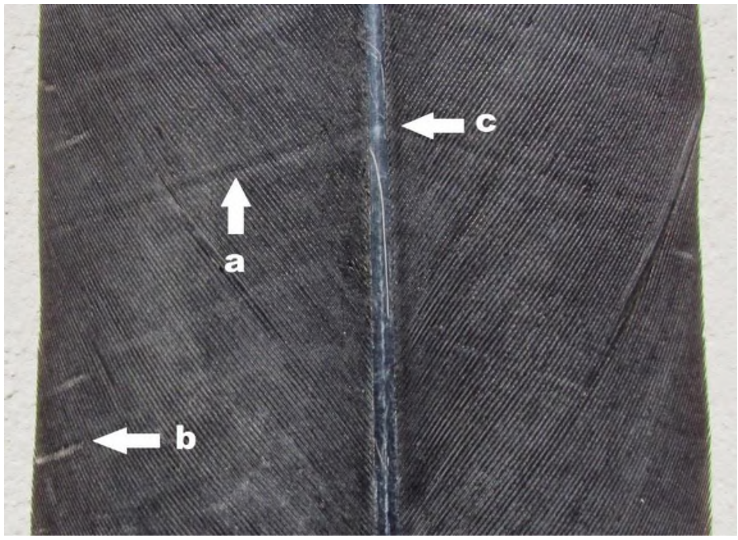


Figure 14: Cape Vulture rectrix showing multiple fault bars noted by (a) deformation of barbs causing the vane to ripple (b) deformation of the barbs creating a 'window' in the vane, and (c) a white bar on the upper surface of the rachis.

5.3 Results

5.3.1 Body condition score

None of the released birds' body condition measures varied statistically significantly by age for both pre-release and final measurements (pre-release BCS: $F_{3,6} = 1.333$, $p = 0.362$, n = 10; final BCS : $F_{3,6} = 0.202$, $p = 0.891$, n = 10; pre-release mass: $F_{3,6} = 4.394$, $p = 0.724$, n = 10; final mass: $F_{2,6} = 1.878$, $p = 0.246$, n = 9).

Age similarly had no statistically significant effect on an individuals' change in BCS or change in mass between pre-release and final records (BCS change: $F_{3,6} = 3.889$, $p = 0.089$, n = 10; mass change: $F_{2,6} = 2.296$, $p = 0.196$, n = 9).

All juveniles had BCS 3 at the time of initial measurements at 6 months old. Likewise, immature birds, two to four years old, from the NZG had a BCS 3 or 3.5 at the time of initial measurements when translocated to VulPro. Between this initial record and pre-release records (range 44 to 58 days), while in captivity at VulPro four of six birds' BCS increased to BCS 4. The BCS of three year old bird 026 and fledgling 006 remained constant during this time (Table 7, Figure 15).

Captivity was a statistically significant factor influencing an individual's BCS for final measures (captive = 3.8 ± 0.3, released = 3.2 ± 0.5, $t = -2.683$, $p = 0.028$, df = 10) and was near statistically significant for each birds' change in BCS between pre-release and final records (captive = 0.67 ± 0.58, released = -0.44 ± 0.53, $t = -2.949$, $p = 0.055$, df = 8).

Between pre-release and final records, six of nine released individuals decreased BCS by 0.5 or 1. Two individuals (juvenile 012 and three year old 026) maintained their BCS, while one individual (three year old 000) increased by 0.5. Alternatively, all three captive birds increased BCS by 0.5 or 1 (Table 7).

Juvenile 006's final BCS was 2.5. This low condition is not outside values seen in the wild; however, it is the lowest recorded for any released individual. It is noteworthy that he had a much higher BCS 4 when he was captured only two months prior (29 Aug 2015) for GPS unit replacement (Figure 15, Table 7). There is no explanation for this relatively sudden drop in condition. He was monitored over that period and was feeding normally. However, comparison with other body condition measures (see section 5.3.2.4) confirm there was a recent decline in his health.

008 was recaptured 5 days prior to his disappearance to trim the dorsal feathers surrounding his GPS unit. While his final BCS decreased by 1 from pre-release measurements, he was still within healthy range and his GPS harness fit nicely. There were no indications that he was ill or in poor condition which might give insight into his subsequent disappearance.

Table 7: Body condition score and mass for each individual during initial, pre-release, and final measurements. Dashes indicate missing data.

(*) Measurements were taken in captivity.

		BCS				**mass (kg)**	
Chick ID	Age	initial	pre-release	interim	final	pre-release	final
008	4	3	4	3	-	7.2	-
000	3	-	3.5	-	4	9.2	9.5
001	3	-	3.5	-	3	8.7	8.5
026	3	3	3	3	3	8.7	9.25
003	2	-	4	-	3	8.4	9
007	2	3.5	4	-	3	7.9	8
012	1	3	4	3	4	9	9.5
005	1	3	4	4	3.5	9.4	10.5
006	1	3	3	4	2.5	8.2	9
004	1	3	-	-	4*	-	10.5*
013	1	3	-	-	4*	-	11.5*
002	2	-	3.5	4*	3.5*	9	11*

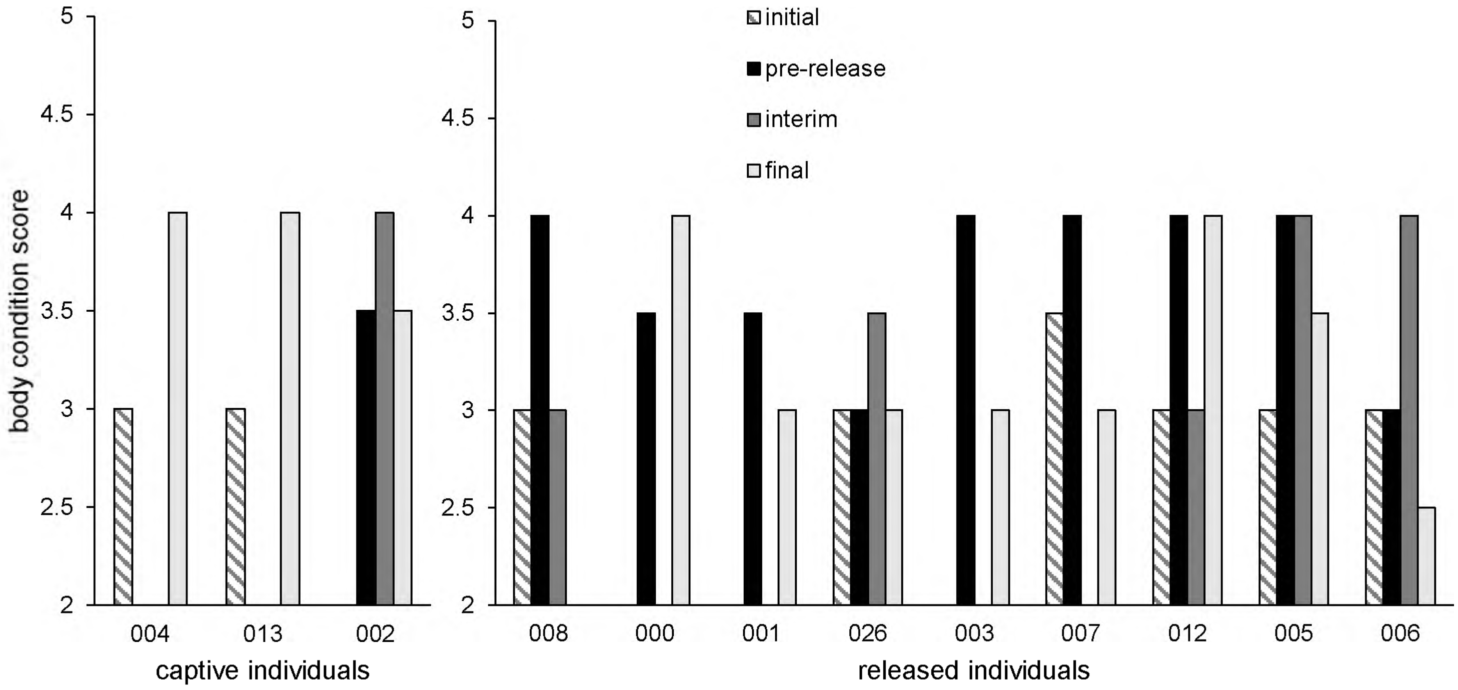


Figure 15: Body condition score for individuals over the course of 9 months. 'Initial' measurements were taken approximately two months pre-release, 'pre-release' measurements between 7 and 17 days pre-release, 'interim' measurements while the chicks were free-flying, and 'final' measurements eight months after the release event.

5.3.2 Body mass

Mean measures of wild Cape Vulture body mass were available for juveniles (8.3 ± 1.3 kg, n = 38), sub-adults (9.1 ± 1.5 kg, n = 34) and adults (9.3 ± 1.4 kg, n = 94) (Kerri Wolter, unpublished data). No data were available for wild immatures aged two to four years old.

All three juveniles' pre-release body mass measures were within the wild juvenile mean ± SD (Table 7). All juveniles gained mass, up to 1 kg, post-release. One female juvenile, bird 005, gained mass post-release to 10.5 kg. Her mass is well outside the wild juvenile range, meeting the outer limit of wild sub-adult mass range. This female's mass is comparable to her heavy captive contemporaries and makes her the heaviest released individual. All two year old birds and two three year old birds gained mass between records. Only one individual lost body mass (only 0.2 kg, three year old bird 001).

A final body mass measurement was not recorded for bird 008 before he disappeared. He was the oldest bird but also the lightest within a healthy BCS 3 to 4.

Measures of body mass change were only available for one captive bird, making analyses comparing released to captive bird mass impossible. However, this two year old gained twice as much mass as any other released bird during the same period.

5.3.3 Fault bar analysis

5.3.3.1 Pre-release measurements

The mean fault bar count in VulPro's fledglings was ten times higher than VulPro's immature birds (Table 8; fledglings = 5 ± 3.6 bars, n = 5; immatures = 0.5 ± 1 bars, n = 4). The mean fault bar count in immature birds from the National Zoological Garden's (NZG) population was higher than VulPro's fledglings (7.3 ± 8.5 bars, n = 3). When feathers from birds from both facilities were analysed collectively, there was no statistically significant difference in fault bar counts based on age ($F_{3,8} = 0.361$, $p = 0.783$, n = 12).

Table 8: Count of fault bars from feathers collected during pre-release and final measurements. Dashes indicate missing data or where central rectrices had not yet moulted.

(*) Fault bar counts were taken while in captivity.

breeding facility	chick ID	age	pre-release	$\bar{x}$	final	$\bar{x}$
National Zoological Gardens	007	2	4	7.3	0	0
	008	4	1		-	
	026	3	17		-	
VulPro	000	3	0	0.5	moult	0
	001	3	0		0	
	002	2	2		0*	
	003	2	0		moult	
	004	1	2	5	1*	4.4
	005	1	10		8	
	006	1	1		13	
	012	1	6		0	
	013	1	6		0*	

All birds from the NZG displayed fault bars. The feather with the most fault bars (seventeen) belonged to three year old 026. VulPro's fledgling 012's feather displayed the most severe fault bars. While her rectrix remained intact, fault bars on her primary feathers caused breaks in multiple locations.

The frequency in which VulPro's vulture parents were seen feeding their chicks varied between pairs (see section 4.3.7, Table 5). There was a slight significant correlation between feeding rates (averaged for each chick with both parents) and fledgling fault bar counts, however this is opposite of expected. Increased feeding rates correlated with higher fault bar counts (r = 0.83, p = 0.083, df =3).

5.3.3.2 Final measurements

Juveniles raised at VulPro had the highest average count of fault bars during final measurements (4.4 ± 5.9 bars, n = 5). In fact, three juveniles were the only individuals with rectrices showing fault bars. However, fault bar counts did not vary statistically significantly by age ($F_{2,5}$ =0.661, p = 0.556, n = 8). The highest fault bar counts (eight and thirteen) belonged to released individuals. Captive bird 004 displayed one.

5.3.3.3 *Comparison between pre-release and final measurements*

Every individual's fault bar count decreased at the final measurement regardless of remaining in captivity or being released, with one exception. Released juvenile 006's fault bar count increased from one to thirteen. Juvenile 005's fault bar counts remained consistently high during both pre-release and final measurements.

It is interesting to note that bird 012's pre-release fault bars were the most severe, causing multiple primary feathers to break. While her final measurement showed zero fault bars, she is the same individual who was actively moulting an unusual number of rectrices.

5.3.3.4 *Comparison to other body condition measures*

Fault bar counts did not correlate with BCS during pre-release ($r = 0.14$, $p = 0.695$, df = 8) or final measurements ($r = -0.16$, $p = 0.710$, df = 6). Four individuals with high fault bar counts had BCS in the healthy range (3 to 4). However, in one instance BCS and fault bar counts were comparable. Bird 006's BCS deteriorated from 4 to 2.5 in two months at the time of moult, with the newly grown feather showing twelve more fault bars than the previous feather. There is no concrete explanation for 006's drop in condition or increase in fault bars. In this time frame he did not venture outside of VulPro's property (see **CHAPTER 7**) and showed no indication of change in feeding or other behaviours.

5.4 Discussion

5.4.1 Body condition score and body mass

All chicks were within healthy or normal range of BCS and mass during final measurements showing they were able to adapt to an environment with increased feeding competition, increased exercise, and variable, potentially stressful conditions when exploring outside the release site.

Increased feeding competition has been shown to have a negative impact on the body condition in vultures. The body condition of resident Turkey Vultures *Cathartes aura*, which tended to have smaller overall body size relative to migrants, decreased during migration influx (Kirk and Gosler 1994). Large body size certainly proves to be an advantage, as larger cathartid vultures (overall body size and mass) are more dominant than smaller individuals of the same species, providing them greater access to food resources (Wallace and Temple 1987a, Kirk and Gosler 1994). At VulPro, feeding competition increased for captive bred chicks post-release as they had to learn to compete with hundreds of wild individuals at a carcass. All chicks tended to be less dominant than same-aged wild conspecifics; however, they had regular access to a high quality diet and all individuals were able to feed to sustain good body condition (see **CHAPTER 6**).

Both increase in caloric intake and reduction in exercise, i.e. captivity, have correlated with increased breast muscle thickness in other bird species (mute swans *Cygnus olor*, Sears 1988; mallards *Anas platyrhynchos,* Arsnoe et al. 2011). Most Cape Vultures, regardless of age, gained BCS in a relatively short time after being introduced to VulPro's flight enclosure (Figure 14). This could be a result of moving birds from an environment with higher feeding competition to one with lower feeding competition. All birds' previous enclosures contained more than double the inhabitants of VulPro's rehabilitation enclosure. Feeding regimes likely did not effect this BCS increase, as both VulPro and NZG chicks were previously allowed constant daily access to carcasses. Alternatively, VulPro's rehabilitation enclosure was given carcasses three times per week, with food being available only five or six days / week. The general decrease in released birds' BCS from initial to final measurements is not surprising, as birds exercised more frequently to access high roosting spots and thermals and explore outside the release property (see **CHAPTER 7**).

The thickness of the pectoral muscle can be used as a general measure of protein reserves, as it corresponds to pectoral lean dry muscle mass (Sears 1988) which is correlated with total lean dry mass in many species (*Accipiter gentilis*, Macström and Kenward 1981; *Lagopus lagopus*, Brittas and Macström 1982). The BCS used in this study assessed the thickness of the pectoral muscle around the keel as well as visual inspection of subcutaneous fat levels around the head and neck. A measure of absolute (unscaled) body mass usually has a fairly strong correlation with fat mass (Labocha and Hayes 2012). However, there was no correlation in this study between BCS and body mass, or between changes in each individual's BCS and mass overtime. Similarly, no correlation was found between mass and breast muscle thickness in mute swans (Sears 1988). This is likely because fat stores are typically depleted before protein reserves (Carpenter et al. 1993, Jenni et al. 2000). While the BCS used here may be a quick method to assess an individual's general condition, the scale is likely too crude to interpret health more in depth than 'healthy', 'unhealthy', or 'grossly unhealthy'. Additionally, this method has its limitations because the repeatability of this measure is dependent on it being conducted by the same experienced observer. Future research should attempt to empirically validate a condition index, i.e. a measure by which to scale body mass, appropriate for *Gyps* vultures. This validated index could then be used in conjunction with the field-friendly BCS used in this study to investigate its validity.

5.4.2 Fault bar analysis

Mundy et al. (1992) suspected dietary deficiency to be the cause of fault bars in nestling vultures. Camiña and Yosef (2012) showed that changes in nation-wide carcass availability and vulture restaurant management practices in Spain coincided with a notable decrease in that year's Griffon Vulture nestling fault bar counts. Conversely, studies which have attempted to experimentally (nutritionally and behaviourally) induce fault bars conclude stressful interactions, such as handling, and not nutritional deficiencies, cause significant fault bars (King and Murphy 1984, Negro et al. 1994). Fault bars on rectrices of wild nestling Osprey had no connection to food shortages or feeding rank within the brood (Machmer et al. 1991).

The cause of higher pre-release fault bar counts in immature captive bred Cape Vultures could similarly not be attributed to reduced feeding frequency; however, diet quality varied between feeding regimes at VulPro and the NZG. Birds at the NZG are fed twice daily with beef pieces and calcium supplements (Sarah Chabangu, head bird curator, pers. comm.). VulPro provides whole carcasses of game and livestock species to the rehabilitation enclosure (feeding immature birds) approximately three times per week but food is often left over and available for multiple days, up to six days per week. Nutritional deficiency cannot be ruled out as a cause for high fault bars in birds from the NZG, but drastic difference in housing conditions (noisy environment with high exposure to the public) suggests captive Cape Vulture faults bars may be induced by stress.

Among chicks raised at VulPro, pre-release fault bar counts corroborate findings in other species that fault bar occurrence his highest among nestlings/juveniles (Slagsvold 1982, Hawfield 1986, Jovani and Blas 2004, and Serrano and Jovani 2005). Chick 005 maintained high fault bar counts during both pre-release and final measurements with no obvious or individualized stressors or change in diet, confirming similar findings that fault bar counts can be comparable in some individuals with particularly low or high stress tolerance across years (Bortolotti et al. 2002).

Most fault bar counts did not correlate with any other measure of body condition, suggesting fault bar counts are not, if considered independently, a good indicator of body condition or suitability for release. Yet, the assessment of fault bars and feather condition in conjunction with other condition measures may help identify individuals which are in a physiologically weakened state or are more prone to reacting negatively to stressful encounters.

5.4.3 Management considerations

When fitting GPS backpack style harnesses, one must consider the fact that captive bred chicks are likely to lose body condition post-release. Upon final investigations, all chicks' GPS harnesses fit appropriately, i.e. not too loose to risk entanglement of limbs and not too tight to be restrictive, because this factor was kept in mind when fitting the harnesses; they were fit tightly.

Chick 002 was placed in captivity seven days post-release due to a lack of flight, likely caused by a hairline fracture in her left radius (see **CHAPTER 3** and Appendix 4). VulPro staff believe this injury occurred immediately after the chick was released into the flight enclosure with her newly fitted GPS unit and backpack style harness. She, and two other individuals, reacted violently to the harness by doing back flips and stumbling around the enclosure with wings out for up to twenty minutes. They all became accustomed to the harness within a half hour without human intervention. Her fracture healed and she was re-released forty five days after the original release event. However, she still failed to gain much distance or height in flight, even though her flight appeared strong and symmetrical. She was again placed in captivity sixty one days after the original release event after she was unable to escape dogs on the property. Over the subsequent six months she was monitored closely in captivity with no signs of high flight or perching on high perches. While collecting post-release measurements, her patagial tags were removed revealing a deep flesh injury on the leading edge of her left wing (Appendix 5) which was caused over time by the patagial tag. She was one of the first individuals to be fitted with a new style of patagial tag. As she had already worn a differently shaped tag, the new tag was placed into her existing piercing. The original piercing was too close to the bend in her wing to accommodate the new style tag, yet this issue was not detected at the time of fitting. After the problem patagial tag was removed, within 8 days she perched on a high perch for the first time.

These cases emphasize the lasting negative impact that routine yet invasive measures such as fitting patagial tags and GPS harnesses can have on a bird's condition and survival, and the importance of having a trained professional install tested devices and critically evaluate each case individually.

CHAPTER 6: INTRA-SPECIFIC COMPETITIVE BEHAVIOURS

6.1 Introduction

Wild vultures in South Africa are increasingly reliant on vulture restaurants for food. The Magaliesberg vultures are no exception. Six vulture restaurants in the region cumulatively provide food on a daily basis for the wild population of 320 breeding pairs, non-breeding residents, and vagrants (Wolter et al. 2016). Carcass availability at VulPro's vulture restaurant has become reliable to the point that wild individuals congregate on the property daily in the absence of food and wait until food is delivered.

A single Cape Vulture may find itself competing against 400 hungry birds for a modest-sized carcass. To survive, chicks must not only learn competitive skills to gain access to food, but also to feed as efficiently as possible. This is especially the case for captive bred chicks feeding at VulPro's restaurant. Starvation has been a confirmed cause of post-release death in several vulture captive breeding and release programmes (Wallace and Temple 1987b, Woods et al. 2007, Terrasse 2005).

Vulture restaurants have been implemented strategically to influence ranging and to observe the behavioural integration of released individuals in captive breeding programmes. Wallace and Temple (1987b) assessed behavioural integration of released Andean Condors in Ecuador by counting the number of interactions 'won' at a carcass and comparing results to wild individuals. Extensive studies have been conducted in France comparing wild and captive bred Griffon Vultures to determine if sex, age, or origin had any effect on competitive behaviours (Bosè and Sarrazin 2007, Bosè et al. 2012, Duriez et al. 2012).

A vulture's crop is a great physiological advantage. The elastic pouch in the digestive tract anterior to the stomach acts as a food storage unit in which large *Gyps* vultures are able to store up to one-fifth of their body weight (Houston 1976). Cape Vultures can store up to 1.6 kg of meat in the crop and stomach, enough food in to sustain them for more than one day if food is sparse (Komen 1991, Komen and Brown 1993). After consuming approximately 600 grams of meat, the crop distends past the chest contour feathers providing an easy visual tool to estimate food intake (Houston 1976).

This is the first in depth study to assess competitive behaviours of wild Cape Vultures at a carcass. Mundy et al. (1992) summarized a few preliminary observations and questioned age-related dominance. Early findings suggest that adults 'dominate' younger birds when feeding close to colonies (around the Magaliesberg and Potberg), yet further afield this trend was not always clear, suggesting there may be a 'home field advantage' for breeding adults close to their colony. A study at VulPro's vulture restaurant showed adult female Cape Vultures initiated 64 % of feeding events. Immatures only began feeding (males 4 % of events, females 14 % of events) when adult females were not present, suggesting there are differences in aggression or dominance based on age and / or sex (Vermuelen 2014).

Observations of competitive behaviours and daily food intake were conducted with the aims of determining 1) behavioural variations between age classes and sex within the wild population, 2) behavioural variations between wild birds and captive bred chicks, 3) the behavioural integration, or lack thereof, of each captive bred chick, and 4) if captive bred chicks are able to feed adequately post-release.

6.2 Methods

6.2.1 Focal sampling

Competitive behaviours were recorded by focal sampling (Altmann 1974) at VulPro's vulture restaurant (25°42'40.86" S, 27°57'13.28" E) inside a south-facing permanent hide. Carcasses of varying sizes were placed 20 m from the hide. Only individually recognizable birds marked with patagial tags or colour rings were followed to avoid pseudo replication. Age classes are defined as follows: juveniles six months to one year old, immatures two to four years old, sub-adults five to six years old, and adults seven years and older.

Observations of a focal individual were started at random under the conditions that food was still available for consumption and the focal subject's crop was less than half full (see section 6.2.2 for crop size categories). Each individual was followed for up to 30 minutes using binoculars while comments were dictated to a video recording using a GoPro Hero 3+ camera. Behaviours were classified using a species-specific ethogram adapted from prior Griffon Vulture behavioural research (Bosè and Sarrazin 2007, Table 9). Videos were later reviewed to verify and finally transcribe all interactions onto data sheets.

Feeding rate, interaction rate, aggressiveness, dominance, and display rate were calculated according to the methods of Bosè and Sarrazin (2007). Feeding rate is the ratio of time spent feeding to total observation time. Interaction rate is the ratio of number of interactions to total observation time. Aggressiveness is the ratio of number of attacks to total observation time. Display rate is the ratio of number of displays to total observation time. Dominance is the ratio of number of attacks 'won' to total observation time.

Each interaction was classified as a 'win' or 'lose' for the focal subject based on the movement of birds in relation to the carcass using a constant 20 metre diameter circle around the feeding site. The focal subject 'won' if an interaction resulted in a supplant, avoidance, or change in a behaviour state moving the other individual farther from the carcass, i.e. Waiting to Outside, Feeding to Waiting, or Feeding to Outside (see Table 9). The focal subject 'lost' if it was supplanted, avoided another bird, or changed its behaviour state moving away from the carcass. The outcome was a 'draw' if neither individual avoided, supplanted, or changed its behaviour state.

Each individual's crop size was noted at the beginning and end of the sample (see section 5.2.2 for crop size categories). Feeding 'efficiency' was calculated using the following formula.

$$\text{Efficiency} = \frac{\text{crop contents at end (g)} - \text{crop contents at start (g)}}{\text{Time observed (min)}}$$

Table 9: Ethogram of Cape Vulture (CV) behaviours, adapted from Bosè and Sarrazin's (2007) Griffon Vulture ethogram.

Class	Behaviour	Code	Description
State	Waiting	w	CV is within 10 metre radius of centre of restaurant but not feeding.
	Feeding	fd	CV enters its head into the carcass or clearly eats a piece of flesh.
	Outside	o	CV is outside of 10 metre radius from centre of restaurant.
	Moving	mov	CV is moving: walking, running, or flying.
High Intensity Interaction	Lunge	lung	CV lunges or jumps towards the receiver.
	Contact Jump	jump	CV jumps upon the receiver's back.
	High Intensity Peck	hip	CV forcefully pecks the receiver's head, neck, or back.
	Talon Contact	tc	CV makes contact to the receiver with its talons.
	Bite	bite	CV bites any part of the receiver's body (not just the feathers).
Low Intensity Interaction	Low Intensity Peck	lip	CV lightly or slowly pecks at the receiver or; CV pecks a body part other than the receiver's head, neck, or back.
	Feather	fe	CV pulls the receiver's feathers with its beak.
	Supplant	sup	CV approaches the receiver within 1 metre and the receiver immediately moves outside 1 metre of CV.
	Avoid	av	Sender advances from outside 3 metres in a straight line toward CV, but CV moves before the sender can get within 1 metre.
	Cower	zz	CV flinches or moves less than 1metre away from the receiver.
Display	Wing Display	wd	CV opens wings.
	Talon Display	td	CV lifts its leg and directs the spread talons toward the receiver.
	Approach	zu	CV advances in a straight line toward the receiver and comes within 1 metre of the receiver.
	Near	na	CV advances from outside 3 metres in a straight line toward the receiver but stops before coming within 1 metre of the receiver.

6.2.1.1 Wild vulture behaviours

91 individuals were observed systematically at VulPro's vulture restaurant during 63 feeding events between 22 March 2014 and 14 May 2015. The duration of observations ranged from 14 to 30 minutes with 95 % of samples lasting 20 minutes or longer. Feeding events took place throughout the day between 8h30 and 15h15.

Each individual's age was determined by the age at tagging. All individuals were wild captured or wild-rehabilitated between 2005 and 2015. Juvenile and immature plumage is distinctive, allowing for more accurate age determination. Adult age estimates should be considered minimum values because plumage becomes monotypic around seven years old (Mundy et al. 1992, Table 10).

Table 10: Sample sizes of (W) wild captured and (R) wild-rehabilitated individuals, detailed by minimum estimated year of age.

	Juvenile	Immature			Sub-adult	Adult	
age (years)	1	2	3	4	5-6	7-10	10+
W	0	2	11	7	1	27	7
R	14	5	9	4	1	1	2
TOTAL	14	7	20	11	2	28	9

68 wild individuals were sexed based on visual inspection of head and bill shape (29 males, 38 females). Female Cape Vultures tend to have narrower, rounder heads with longer bills than males (see Naidoo et al. 2011 for explanatory pictures).

To assess the benefits of being aggressive, a chi-squared test was used to analyse the association between who initiated interactions and the outcome (win, lose, or draw). All behavioural parameters were tested for correlation among the entire sample (n = 91 except for 'efficiency' where n = 25).

Shapiro-Wilk tests revealed behaviour values did not follow the normal distribution, so data were square root transformed. The sub-adult and adult age classes were combined into one 'adult category because only two sub-adults had been sampled. One-way ANOVA tests were performed in R (R Core Team 2013, version 3.2.0) to determine if behavioural parameters varied based on age class. When this was found to be the case, Tukey HSD tests were used to determine which age classes varied significantly. Independent two sample t-tests were performed to determine if behaviours differed by sex. Values are presented as mean ± SD.

6.2.1.2 Captive bred vulture behaviours

Captive bred individuals were followed as often as possible at VulPro's vulture restaurant, between 3 and 7 samples per chick (Table 11). Equalizing samples across time was not always possible due to bird behaviours or feeding schedules. Bird 002 was not sampled past April because she was placed back in captivity.

Table 11: Focal sample sizes for each captive bred bird detailed by age and month post-release.

age (years)	4	3			2			1			
	008	000	001	026	002	003	007	005	006	012	TOTAL
February	1	1	1	2	1	1	3	2	2	1	15
March		1	2			2	1	1	1	1	9
April	1	1		1	2	1		1	1	1	9
May		1	1	1		2	2	2	1	3	13
June		1		1							2
July	3	1	2	2					1		9
TOTAL	5	6	6	7	3	6	6	6	6	6	57

There were 57 observation periods during 29 feeding events in the first six months post-release, between 17 February and 23 July 2015. Feeding events took place throughout the day between 6h30 and 15h15. The duration of observations ranged between 6 and 30 minutes, with 88 % of observations (n = 50) lasting 20 minutes or longer.

The sex of each bird was determined genetically via the amplification of the Chromo Helicase DNA binding (CHD1) gene using the P2 / P8 primer set (Griffiths et al. 1998).

All behavioural parameters were tested for correlation among the entire sample (n = 57 except for 'efficiency' where n = 49). To avoid pseudo replication, one randomly chosen full length sample (30 minute) was chosen for each chick. The distributions of behaviour values were tested for normality using Shapiro-Wilk tests. One-way ANOVA tests were performed to determine if captive bred bird behaviours differ by age. When this was found to be the case, Tukey HSD tests were used to determine which ages' behaviour values varied significantly. To determine if behaviours vary by sex, independent two sample t-tests were performed on the same subset of data. All analyses were performed in R (R Core Team 2013, version 3.2.0).

6.2.1.3 Wild vs. captive bred vulture behaviours

Values for each behaviour were averaged among wild individuals of the same age (years). This provided an 'expected' range of values (wild mean ± SD) with which to compare same-aged captive bred behaviour values.

First, each individual captive bred chicks' behaviours were averaged over the first six months post-release and compared to same-aged wild averages to assess individual birds' performance. Secondly, these mean captive bred bird behaviour values were then averaged within each age (years) and compared to wild same aged behaviour value means using a Mann-Whitney U Test in R (R Core Team 2013, version 3.2.0) to determine if some age groups of released birds performed more closely to their wild counterparts than others.

To determine if captive bred bird behaviours improved with time, i.e. if they adopted more wild-type behaviours over time, behaviour values for individuals were averaged within each month post-release and compared to the range of 'expected' values for each behaviour and age group (wild mean ± SD).

6.2.2 Food intake

To assess each individual's food intake and ability to feed itself, crop bulge size was recorded after feeding, independent of focal sampling. These measurements were taken as often as possible, ranging from 3 to 23 times each month between 1 week pre-release (in VulPro's rehabilitation enclosure) and 6 month post-release (at VulPro's vulture restaurant or while roosting on VulPro's property). Only the maximum size record for each day was used in analysis.

Crop size categories were adapted from Houston's (1976) descriptions of crop size and shape after feeding captive Rüppell's Vultures known masses of food. The categories and approximate mass of meat consumed are as follows 1) empty ≤ 400 g 2) slit 600 g 3) quarter 750 g 4) third 850 g 5) half 1,000 g 6) three quarters 1,200 g 7) full 1,500+ g.

A half crop was considered an adequate crop level for each day, providing individuals enough calories for two days (adult requirements per day range from 484 g / day (inactive) to 581 g / day (active or foraging), Komen and Brown 1993). To obtain a measure of each bird's ability to adequately feed, I assessed the ratio of counts a bird filled its crop to half or more versus the total count of crop bulges recorded each month. The distributions crop size data were tested for normality using Shapiro-Wilk tests. One-way ANOVA tests were performed in R (R Core Team 2013, version 3.2.0) to determine if birds' propensity to fill their crops varied by age. Independent two-sample t-tests were performed to determine if each birds' ability to fill its crop varied by origin (NZG or VulPro).

6.3 Results

6.3.1 Wild vulture behaviours

A total of 3,166 intraspecific interactions were recorded, 39 % (n = 1,250) of which were initiated by the focal subject (Table 12). The outcomes of interactions (win, lose, or draw) were significantly associated with whether or not the individual initiated or received the interaction ($x^2 = 745.56$, $df = 2$, $p < 0.001$). An individual was far more likely to win if it initiated the interaction.

Table 12: Summary of interaction counts between wild Cape Vultures, detailed by outcome and whether the focal subject initiated or received the interaction. Values in parentheses note the percentage of the total.

outcome	subject initiated	subject received	total interactions
lose	72 (6)	789 (41)	861 (27)
draw	802 (64)	1062 (56)	1864 (59)
win	376 (30)	65 (3)	441 (14)

For wild birds, all behaviours except 'efficiency' were positively correlated with each other at a statistically significant level ($p < 0.01$ and $p < 0.001$, Table 13). 'Efficiency' was negatively correlated with all other behaviours except dominance. The only behaviour which was statistically significantly correlated with 'efficiency' was display rate ($p < 0.01$, Table 13).

Table 13: Spearman correlation coefficients for behaviours of all wild individuals (efficiency n = 25, all others n = 91). Levels of statistical significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	feeding rate	interaction rate	aggression	display rate	dominance	efficiency
feeding rate	1	0.35***	0.32**	0.31**	0.41***	-0.27
interaction rate		1	0.83***	0.61***	0.60***	-0.26
aggression			1	0.68***	0.78***	-0.27
display rate				1	0.53***	-0.52**
dominance					1	0.01
efficiency						1

Feeding efficiency varied significantly by age class (n = 25, $F_{2,22} = 10.56$, $p < 0.001$, Figure 16a) with adults being the most efficient feeders. Juveniles and adults had highly significant differences in efficiency ($p < 0.001$), yet no statistical difference was detected between the efficiency scores of immatures and adults.

Feeding rate also varied significantly by age class (n = 91, $F_{2,88} = 5.207$, $p < 0.01$, Figure 17). Specifically, the difference between immature and adult feeding rates was significant ($p < 0.01$). There were no statistically significant differences in display rate, interaction rate, aggressiveness, or dominance between age classes (display rate n = 91, $F_{2,88} = 1.402$, $p = 0.252$; interaction rate n = 91, $F_{2,88} = 0.716$, $p = 0.492$; aggressiveness n = 91, $F_{2,88} = 0.928$, $p = 0.399$; dominance n = 91, $F_{2,88} = 0.654$, $p = 0.522$; Figure 17).

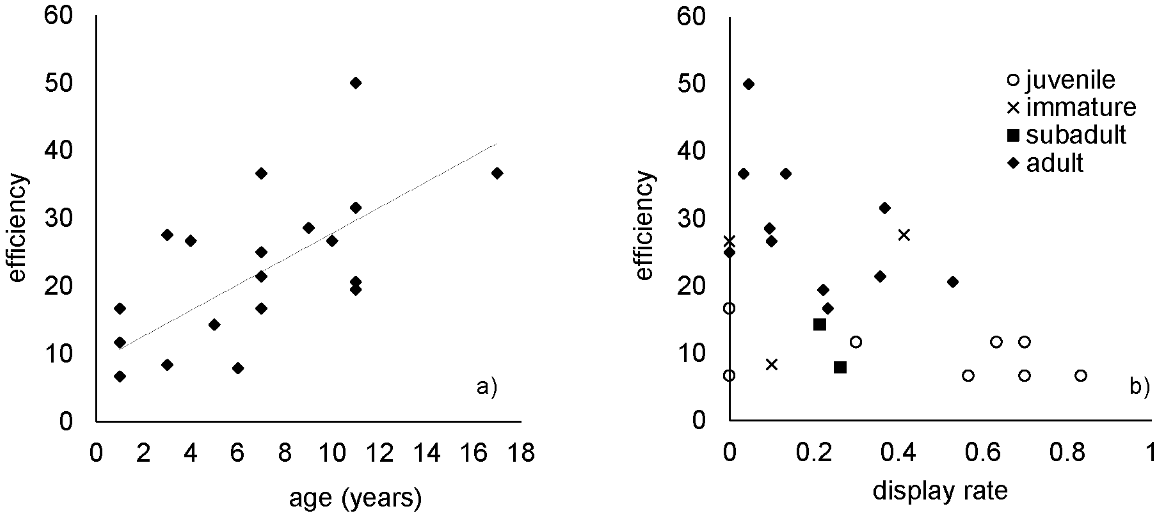


Figure 16: Relationship between feeding efficiency and age for wild Cape Vultures (a, n = 25, $F_{2,22} = 10.56$, $p < 0.001$). Relationship between display rate and feeding efficiency in wild Cape Vultures, detailed by age class (b, n = 25).

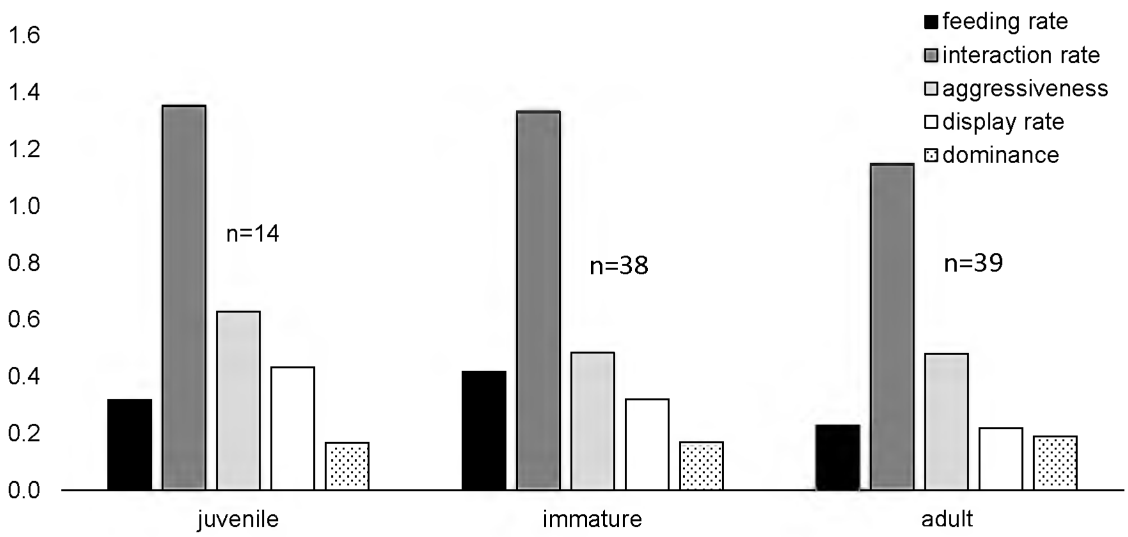


Figure 17: Mean behavioural parameters for each age class of wild Cape Vultures, with the 'adult' group including birds age 5 years and older. Feeding rate is statistically significant between age classes (n = 91, $F_{2,88} = 5.207$, $p < 0.01$), specifically between immatures and adults ($p < 0.01$).

Display rate was significantly higher for females than males (male = 0.19 ± 0.19, female = 0.37 ± 0.34, $t = 2.727$, $p < 0.01$, df = 65). No other behavioural parameter showed statistically significant differences between sexes, although dominance values were close to being significantly different (male = 0.14 ± 0.14, female = 0.21 ± 0.18, $t = 1.857$, $p = 0.068$, df = 65).

6.3.2 Captive bred vulture behaviours

For captive bred vultures, all behaviours except 'efficiency' were positively correlated with each other at a statistically significant level ($p < 0.01$ and $p < 0.001$, Table 14). 'Efficiency' was negatively correlated with all other behaviours. The only behaviour which was significantly correlated with 'efficiency' was feeding rate ($p = 0.019$, Table 14).

Table 14: Spearman correlation coefficients for behaviours of captive bred individuals (efficiency n = 49, all others n = 57). Levels of statistical significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	feeding rate	interaction rate	aggression	display rate	dominance	efficiency
feeding rate	1	0.51***	0.64***	0.46***	0.38**	-0.33*
interaction rate		1	0.76***	0.50***	0.45***	-0.10
aggression			1	0.78***	0.74***	-0.24
display rate				1	0.73***	-0.21
dominance					1	-0.14
efficiency						1

Females were significantly more dominant than males (male = 0.04 ± 0.04, female = 0.14 ± 0.06, $t = 3.198$, $p = 0.016$, df = 8). There was no statistically significant difference in any other behaviour mean values based on sex.

For captive bred vultures, feeding efficiency varied significantly with age (n = 10, $F_{3,6} = 11.82$, $p = 0.006$). Specifically, efficiency was significantly different between the 4 year old and all other ages (1 year olds, p = 0.011; 2 year olds, $p < 0.01$; 3 year olds, $p < 0.01$). Feeding rates also varied significantly with age (n = 10, $F_{3,6} = 8.717$, $p = 0.013$). Specifically, feeding rates were significantly different between juveniles and 2 year olds (p = 0.019), as well as between juveniles and 3 year olds ($p = 0.023$). All other behaviours did not differ significantly with age (dominance n = 10, $F_{3,6} = 0.194$, $p = 0.897$; display rate n = 10, $F_{3,6} = 0.678$, $p = 0.597$, aggressiveness n = 10, $F_{3,6} = 1.275$, $p = 0.365$, interaction rate n = 10, $F_{3,6} = 2.66$, $p = 0.142$).

6.3.3 Wild vs. captive bred vulture behaviours

When assessing each released bird's performance individually, individual juvenile averages were closer to wild juvenile averages more consistently than older birds (Figure 18). Older bird behaviours varied by individual, with some performing more closely to wild averages than others within a single age group (higher performance: birds 001 and 002; lower performance: birds 000, 003, and 007). Two year old birds had the overall lowest performance; two individuals never scored above 50% of wild average for any behaviour (Figure 18).

All captive bred behaviour values for all ages were below wild averages, except juvenile feeding rates which were above average wild values (captive = 0.36 ± 0.10, wild = 0.32 ± 0.27, Table 15). The interaction rate of two year olds was the only behaviour in which was significantly different from wild averages (captive n = 3, mean = 0.71 ± 0.18, wild n = 7, mean = 1.52 ± 0.60, $W(8) = 1$, $p = 0.033$, Table 15).

Table 15: Averaged Cape Vulture behaviour values detailed by age and origin. The number of individuals sampled, noted in parentheses, is consistent for all behaviours except efficiency which is noted separately. Dashes indicate missing data.

* Statistically significant difference from the wild mean. (*W* (8) = 1, *p* = 0.033).

Age (years)		feeding rate	interaction rate	aggression	display rate	dominance	efficiency
1	wild (14)	0.32	1.36	0.63	0.43	0.17	9.44 (9)
	captive (3)	0.36	0.84	0.41	0.29	0.09	13.11 (3)
2	wild (7)	0.37	1.52	0.58	0.39	0.17	--
	captive (3)	0.12	0.71 *	0.23	0.16	0.08	11.45 (3)
3	wild (20)	0.38	1.32	0.46	0.29	0.18	17.96 (2)
	captive (3)	0.13	0.65	0.19	0.13	0.07	11.24 (3)
4	wild (11)	0.46	1.06	0.33	0.22	0.10	26.67 (1)
	captive (1)	0.30	1.26	0.32	0.04	0.02	26.02 (1)

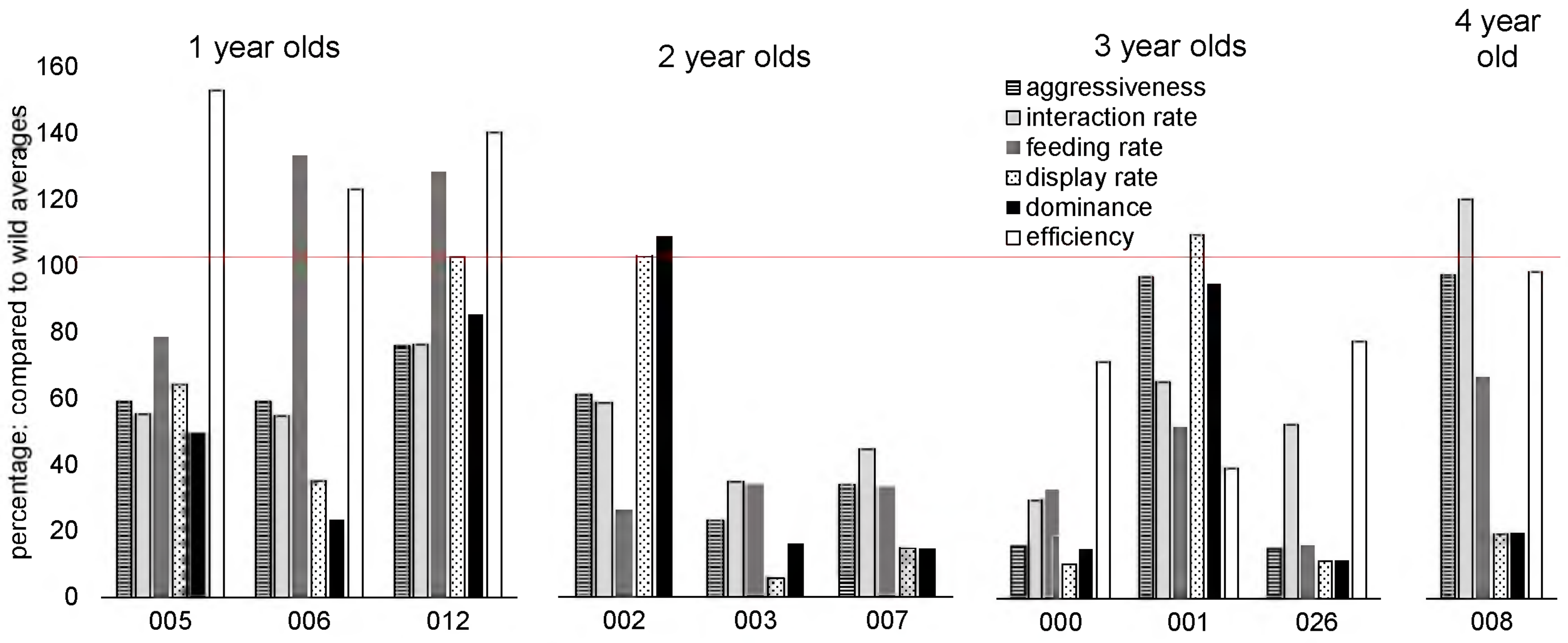


Figure 18: Performance measures for individual captive bred bird behaviours, averaged across samples taken in the first 6 months post-release. Values above (or below) 100 indicate higher (or lower) than average wild performance (taken from same–aged wild values). Measures of efficiency were not available for wild two year old birds.

As a general trend, juveniles showed an increase in behaviour values within the first six months post-release, i.e. they displayed more behaviours within 'normal' wild value range over time (interaction rate, display rate, dominance, aggressiveness, and feeding rate). All other age groups digressed. Two year olds had the strongest negative trend across time (Figure 19).

Bird 008, the oldest at four years old, showed the closest approach to wild behaviours: 100% of his behaviour values were within the wild range (mean ± SD) after the third month post-release. However this decreased to 60% of values in the sixth month. One year olds also showed high levels of integration with 75% to 80% of behaviours within the wild range in the first, fourth, and sixth months post-release and were the only age class to increase behavioural parameters within a wild range of values over time. Two year olds were the worst at integrating into wild behaviour, displaying the lowest values inside the wild range (7% and 15%, second and fourth month post-release respectively, Figure 19).

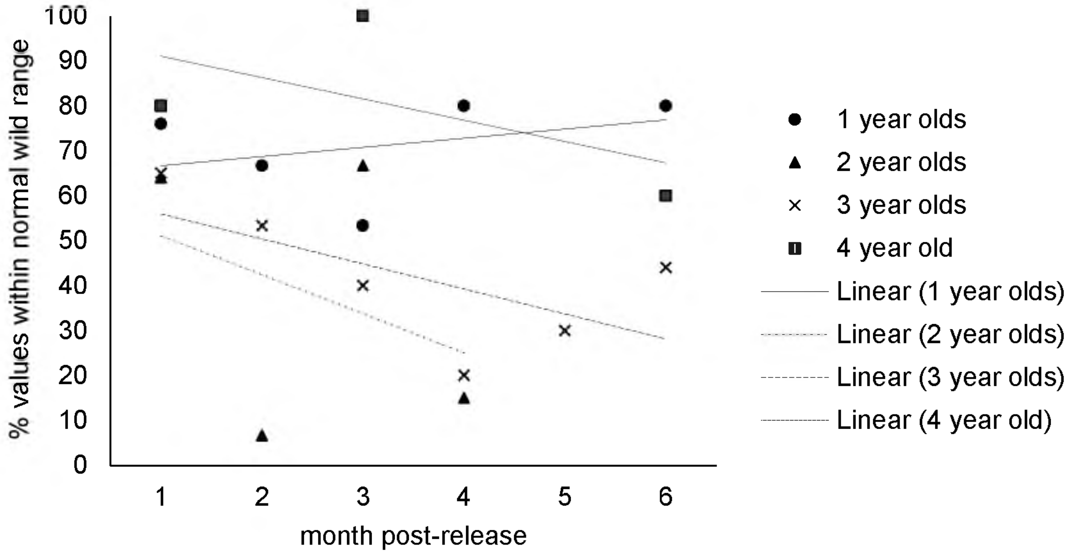


Figure 19: Captive bred bird performance over time: The percentage of captive bred bird behaviour values that fell within the acceptable range (mean ± SD) of same-aged wild behaviours, detailed by month post-release and bird age. Values include interaction rate, display rate, dominance, aggressiveness, and feeding rate.

6.3.3 Food intake

All released individuals managed to feed at VulPro's restaurant to survive the first six months post-release. However, there were age-related differences in abilities. Notably, the eldest individual, 008, was more likely to fill his crop consistently over time.

When values were averaged monthly, each bird improved in filling their crop regardless of age (Figure 20). There was a slight difference in feeding abilities based on age, although these differences were not statistically significant pre-release (in the enclosures), six months post-release, or when all post-release values were averaged (pre-release n = 10, $F_{3,6}$ = 1.961, p = 0.221; post-release n = 10, $F_{3,6}$ = 1.439, p = 0.321; average n = 10, $F_{3,6}$ = 2.459, p = 0.16). Juveniles never filled their crops more than 30% of observations pre-release, i.e. while housed in the enclosure. Birds two years and older filled their crops between 14 and 57% of observations pre-release.

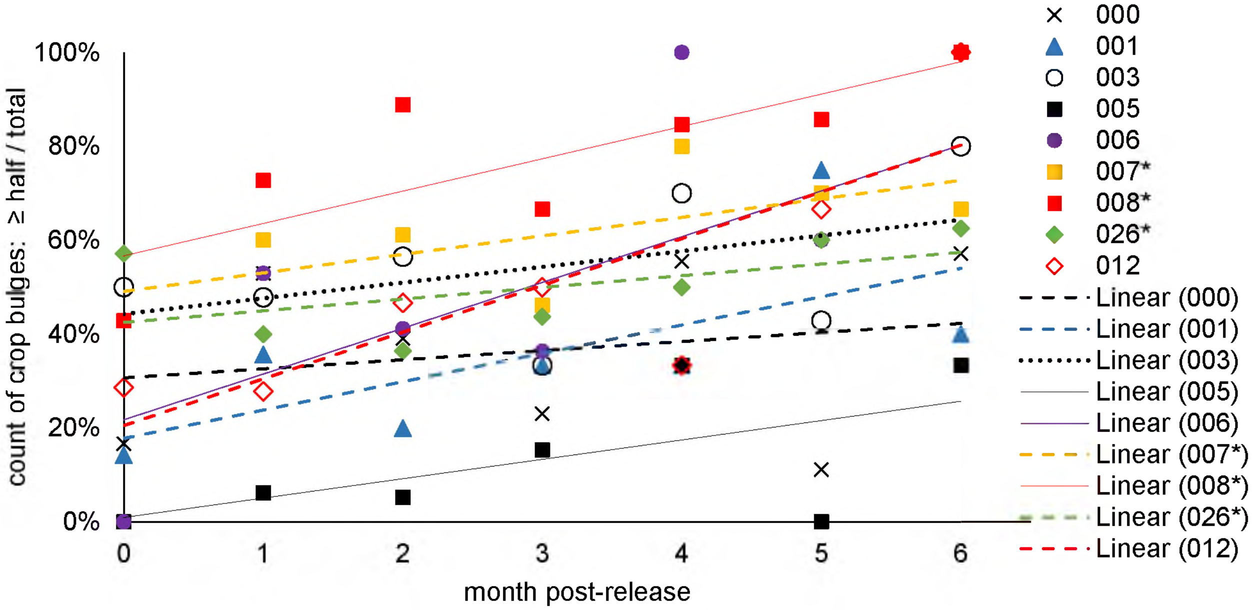


Figure 20: Measures of food intake for each bird 1 week pre-release through 6 months post-release. Values represent the count of crop bulges half or greater / total number bulges recorded.
(*) Individuals raised at the National Zoological Gardens.

Birds raised from the National Zoological Gardens were more likely to fill their crops compared to birds raised at VulPro. Origin was a significant factor in a bird's propensity to fill its crop soon after translocation to VulPro, or 'pre-release' (VulPro = 20 ± 18 %, NZG = 48 ± 8 %, t = -3.273, p =

0.012, df=8) but became a non-significant factor six months post-release (VulPro = 68 ± 27 %, NZG = 77 ± 21 %, t = -0.550, *p* = 0.605, df = 8) or when all measures were averaged across time (VulPro = 41 ± 14 %, NZG = 63 ± 14 %, t = -2.247, *p* = 0.087, df =8).

6.4 Discussion

6.4.1 Comparison to other studies

Several studies observed feeding dynamics in African vulture scavenging guilds, but these have typically focused on their roles as scavengers or interactions between species (Houston 1974, Anderson and Horwitz 1979, Kruuk 1967, Brown and Jones 1989). To my knowledge, the only studies on intraspecific feeding competition in African vultures have been conducted with the Lappet-faced Vulture *Torgos tracheliotos* (Bamford et al. 2010) and a study with very small sample size in the Cape Vulture (44 interactions, Mundy et al. 1992). There are ample studies providing comparisons to Griffon Vulture intraspecific interactions, specifically comparing wild and reintroduced populations in France (Bosè and Sarrazin 2007, Bosè et al. 2012, Duriez et al. 2012).

Variations in vulture restaurant placement, abundance, and management practices have been shown to effect the scavenging behaviour (Deygout et al. 2009, Deygout et al. 2010, Duriez et al. 2012) and health of vulture and raptor populations (Robb et al. 2008, Camiña and Yosef 2012). Studies of competitive interactions between Cape Vultures are limited (Mundy et al. 1992), but pertinent as the supplementation programme aims to utilize strategically placed vulture restaurants to attract birds back to abandoned breeding sites.

The Cape Vulture's expert ability to feed successfully and quickly was highlighted by Brown and Jones' (1989) observations at a Namibian vulture restaurant in which 88 % of birds left with full crops, while every individual (59 total) consumed at least 1 kg of meat. Results here show that both wild and captive bred Cape vultures' feeding efficiency increases as they age, as was suggested in other studies with African *Gyps* species (Houston 1976).

Bosè and Sarrazin (2007) found higher interaction rate, aggressiveness, and dominance in old adult Griffon Vultures versus all other age classes. The authors attributed this to the fact that old adults often landed first, providing them access to food under less competitive circumstances, ultimately allowing them more time to interact. This variation by age was not seen in wild or captive bred Cape Vultures and may be a result of VulPro's predictable and reliable carcass provisioning, as birds roost on the property and start to feed together as soon as food is deposited with high competitive interference. Another study, while the sample size was small, agreed with my findings that Cape Vultures' ability to dominate one another do not vary by age: immatures are just as easily able to dominate adults as the reverse (Mundy et al. 1992).

A strict hierarchy exists among Andean Condors aligned by sex and age, correlating to larger body size, with older males sitting at the top of hierarchies (Wallace and Temple 1987a, Donázar et al. 1999). Body size also helps determine a Turkey Vulture's chance at winning encounters; larger migrant Turkey Vultures dominated smaller residents of the same species at a carcass (Kirk and Gosler 1994). Slightly larger female White-headed Vultures are dominant over males (Mundy et al. 1992). With the absence of sexual dimorphism and equal sharing of reproductive investment in the Cape Vulture, the presence of sex biased competitive behaviours is somewhat surprising. Although the high female display rate in wild Cape Vultures was also noted in Griffon Vultures (Bosè and Sarrazin 2007). Preliminary assessments of intraspecific competition between Lappet-faced Vultures, which show little sexual dimorphism in body size, also suggest a sex bias, with older males having the highest probability of 'winning' interactions (Bamford et al. 2010).

The correlation between feeding rate and display rate was significant in both wild and captive bred Cape Vultures, as is also the case in wild Griffon Vultures (Bosè and Sarrazin 2007). However, having access to food (feeding rate) and the amount of food ingested (efficiency) are not comparable measures. Both wild and captive bred Cape Vulture feeding rates and efficiency were negatively correlated. Displaying more frequently makes an individual more likely to win an interaction (higher dominance) giving them more access to food, but it does not guarantee they are able to consume it. Bosè and Sarrazin (2007) suggest that displays convey greater competitive abilities and therefore should increase with higher competitive pressures, i.e. larger group size. This rationale also applies across age groups where levels of efficiency vary. Juvenile birds display more often because they are less efficient feeders and therefore must gain relatively more access to a carcass to consume the same mass of food as older birds.

It is noteworthy that no bird managed to forage successfully or feed outside of VulPro's restaurant the first six months post-release (see **CHAPTER 7** for ranging details). I believe the almost daily food availability on site affected behaviours and contributed to a sense of complacency. Birds roosted daily at the restaurant on the ground or on top of bordering enclosures. They had the option to feed at their leisure in the early morning or late afternoon with less competition, contributing to the lower than wild average interaction rates, feeding rates, aggressiveness, dominance, and display rates during feeding event focal samples.

The youngest captive bred Cape Vultures (juveniles) learned to adopt wild-type behaviors over time but the eldest individual at four years old displayed overall the highest proportion of behaviors within the wild range. Studies of reintroduced captive bred Andean Condors similarly found older birds integrated more quickly than juveniles by showing comparable numbers of encounters ‘won’, relative to same-aged wild individuals, around six months post-release (Wallace and Temple 1987b). The eldest individual’s advanced performance was also shown by his high food intake values, a fact which may be compounded by the fact that he was removed from his birthplace and translocated to VulPro two months before release. This suggests translocation from the birthplace to a separate release site may be an important protocol to prompt desirable feeding behaviour. Based solely on the competitive abilities and feeding efficiency seen in individuals within this sample, future releases should be conducted with older individuals.

6.4.2 Sources of error and biases

Many people who work closely with Cape Vultures can rapidly identify sex differences based on head shape and routinely use this method to sex individuals in the field (Vermuelen 2014). Xirouchakis and Poulakakis (2008) have shown the closely related Griffon Vulture can be sexed with 94.1 % accuracy based on head length, head width, bill length, and bill-cere length. However, this method has not been verified empirically with the Cape Vulture. The significant differences in display rate and dominance seen between sexes must be examined with caution. Observations of head shape were made from a distance of 20 m during focal sampling, not from empirical measurements. The fact that display rates were higher for wild females and not captive bred females, and dominance was higher for captive bred females but not (significantly) for wild females, suggests either the head shape sexing method is not entirely reliable, sample sizes were too small, or that captive bred chick behaviours do not mimic wild type behaviors based on sex. The wild subsample of individuals which could be sexed was biased toward females (38 females, 29 males). If a sex bias in behaviours exists and the entire sample of wild birds was skewed with more females, this bias would affect averaged wild behaviour values and may therefore explain why captive bred males tended to have lower behaviour values compared to wild averages.

There are numerous factors not accounted for in these analyses which likely affect vulture behaviours and these warrant further in-depth analysis. The average number of Cape Vultures present varied by feeding event, ranging from 7 to 125 birds (captive bred samples) or 10 to 257 birds (wild samples). Studies in France showed that an increased number of vultures present correlated to a decrease in individual Griffon Vulture feeding rates (Bosè et al. 2012). At VulPro, the mass of food present and number of carcasses provided also varied by feeding event. All of these factors can influence the competitive pressure on any one individual. The mass of food present, up to a certain threshold, was shown to affect the mean number of vultures that decide to land (Bosè and Sarrazin 2007). I suspect the number of carcasses and the spatial spread of carcasses are equally important in population feeding dynamics and should be addressed.

6.4.3 Future research and management considerations

The sex and age of the conspecific with which each focal subject interacted was not recorded, making analyses of hierarchies impossible. Recording these variables would be helpful in further understanding the social dynamics between individuals, and has implications for measuring the success of captive bred chick integration.

Future behavioural research should be conducted with released birds after they are translocated to an acclimatization site off breeding premises. Additionally, reducing the frequency of feeding events at the release site approximately two months post-release may encourage foraging flights (Lieberman 1987) and may affect the integration rates or competitive abilities of released chicks.

CHAPTER 7: RANGING BEHAVIOURS

7.1 Introduction

Major technological advances in GPS satellite tracking technologies occurred around 2004 which revolutionized the study of raptor behaviour, allowing high resolution data to be collected at frequent intervals over many years (Meyberg and Meyberg 2007). The Cape Vulture has been the subject of several GPS-based studies over the last decade in order to assess the effect of power line transects on ranging behaviour (Phipps et al. 2013), predict the impact of pending wind energy developments (Rushworth and Krüger 2014), and study the range patterns of a declining peripheral population in Namibia (Bamford et al. 2007).

To my knowledge, data from eighteen Cape Vultures tracked with GPS devices has been published: twelve adults, five immatures, and one juvenile (Bamford et al. 2007, Phipps et al. 2013, and Rushworth and Krüger 2014). At least another twenty two individuals have been fitted with GPS units and these data are being prepared for publication.

Notably, from the above mentioned studies, home range size varies greatly between adults and younger birds. The overall foraging range, calculated as minimum convex polygons (MCPs), showed adult home ranges were on average 121,655 km^2, while immature ranges were on average 492,300 km^2 (Phipps et al. 2013). Another study showed home ranges were an order of magnitude higher for immatures than adults in Namibia (adults 21,320 km^2 vs. immatures 482,276 km^2, Bamford et al. 2007). It is suspected that immature and juvenile birds, who are less efficient feeders, forage widely to avoid intraspecific competition with adults at carcasses (Mundy et al. 1992, Duriez et al. 2012, and **CHAPTER 6**). Adult Cape Vultures' foraging range is relatively restricted to the area surrounding their breeding colonies. The proportion of adults present at feeding sites varies in relation to the distance from the breeding colony; the proportion of adults reduced from 91 % within 40 km of the colony to 14% between 240 and 350 km from the colony (Richardson 1984, Piper 1994).

Based on the long distance ranging displayed by wild young Cape Vultures, I expected extensive movements from the released captive bred chicks. The objectives of utilizing GPS devices on captive bred chicks in this study were to 1) determine the rate of dispersal from the release site between released chicks of varying ages, 2) compare captive bred chick ranging behaviours with wild counterparts and 3) constantly monitor chicks' locations to mitigate threats and mortalities.

7.2 Methods

7.2.1 GPS units and patagial tags

Each bird was fitted with GYPAETUS model patagial tags from Maquia Ambientales Serveis, Spain. These PVC-based, durable, no-fade tags are visible from both dorsal and ventral surfaces of the wing. The tag pair weighs 64 g, an average of 0.75 % of each bird's mass.

Birds captive bred at VulPro (n = 7) were fitted with solar-powered 75 g CTT-1080a GPS-GSM tracking devices, produced by Cellular Tracking Technologies (CTT), Pennsylvania USA. Locality, altitude, speed, and functional variables (voltage, etc.) were recorded every fifteen minutes from 04h00 to 16h00 GMT. Birds raised at the National Zoological Gardens were fitted with 70 g GPS-PTT backpack devices (n = 2) and a 50 g GPS-PTT patagial device (n = 1) from Microwave Telemetry, Inc. (MTI), Columbia, Maryland, USA. Locality, speed, altitude and functional variables were recorded every two hours from 05h00 to 17h00 GMT. All backpack devices were placed on the birds using a specially designed Teflon® harness (Wolter et al. 2014a).

All devices were fitted between seven and seventeen days before release. The total mass added, including devices, mounting packs and patagial tags, weighed between 101 g (MTI patagial device) and 189 g (CTT backpack device), accounting for between 1.2 and 2.5 % of each individual's body mass. Total mass of the device and mounts were approximated as each harness was tailored to each individual during fitting.

7.2.2 Range Analysis

Bird locations were analysed over 258 days, between the 15 February 2015 and 31 October 2015. When GPS coordinates placed an individual further than 50 m outside VulPro's perimeter fence or higher than 200 m above ground level (AGL), the movement was noted as an excursion.

The horizontal dilution of precision (HDOP) was verified for every excursion data point. MTI device horizontal data is accurate to ± 18 m. CTT device horizontal data is accurate to ± 2 m. Approximations of flight height AGL were made by subtracting the GPS altitude data from Google Earth altitude records at each fix location. VulPro is located approximately 1,280 m above sea level (ASL). MTI device altitude data is accurate to ± 22 m. CTT device altitude data is accurate to ± 3 m.

7.3 Results

There was an overwhelming lack of movement from each bird. Individuals were occasionally observed as they ranged outside the property. It was clear that a lack of flight stamina caused them to land on the ground; flapping became weaker and birds were often visibly exhausted and panting upon landing. On six occasions, birds which ranged outside the property required human intervention to ensure their safety. When deciding to collect a grounded bird, the terrain and land ownership was first assessed to determine the risk level from human or dog attack. If birds were grounded in safe areas, they were left to manage their own travel or return.

Two year old 002 was recaptured and placed in captivity between day 15 and 43 post-release, and then again permanently at 61 days post-release for treatment of a wing injury. In the two months in which she was free-flying, she never left VulPro's property. All other individuals explored outside the release site between one and ten occasions for varying lengths of time (Table 16, see Appendix 6 for excursion details).

Table 16: Count of each chick's excursions detailed by month.

chick ID	005	006	012	002	003	007	000	001	026	008
age	1	1	1	2	2	2	3	3	3	4
February		2	2					2		
March	2	1	2		1		1	1		1
April	1	1					1	1	2	
May		1	1			1		1	1	
June		1					2			
July	1	1					2	1	1	1
August	1	1	1							
September		1	1					3		
October		1						1		
TOTAL	5	10	7	0	1	1	6	10	4	2

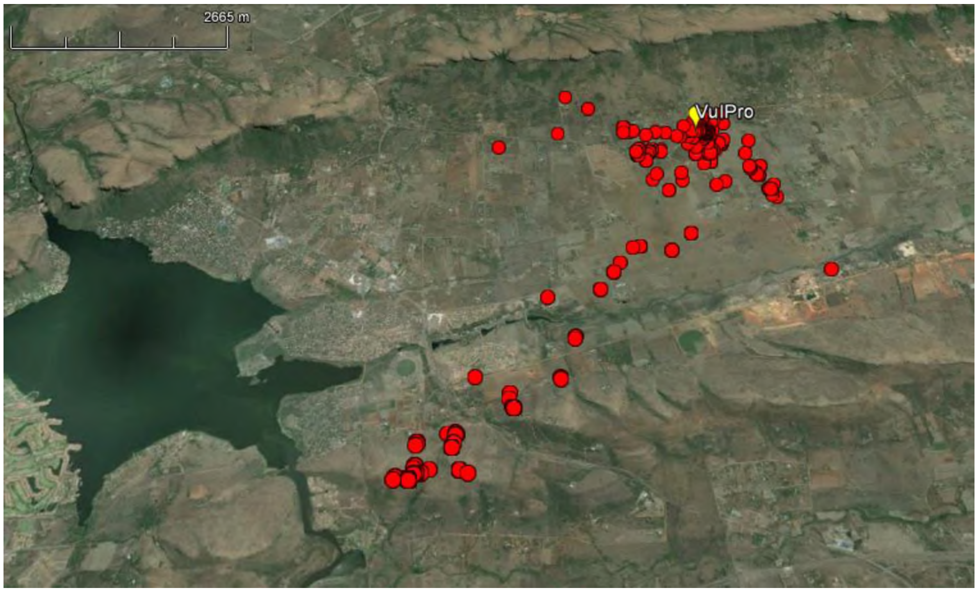
One and three year olds ranged outside the property the most frequently. Juvenile 006 was the first to venture outside the property two days post-release. He reached 0.55 km outside of the property before he landed on the ground, requiring intervention to bring him back safely. Bird 006 subsequently ventured outside the most frequently with ten excursions. His final seven trips did not require human intervention; he returned to VulPro on his own.

Two juveniles, one two year old, and two three year olds spent at least one night roosting outside the release site (Table 17). Three year old 000 spent four nights outside VulPro, the longest duration of any excursion. He was re-sighted the second day inside an eco-estate, grounded in a marshy area in a dense group of reeds. It was impossible for him to fly from his location so he was flushed onto shorter grass where he took off only to land in a neighbouring farm. The terrain was open with no vegetation, so he was left alone to depart in his own time. Within a few hours he took flight and landed on a power line structure nearby, where he remained until flying back to VulPro a few days later.

Only excursions from individuals 006 and 001 required human intervention. These six instances all happened in the first three months post-release. Bird 001 required retrieval after being grounded in an unsafe area in mid-May. He was encouraged by VulPro staff to fly elsewhere or perch higher, only to land five metres next to a busy road and petrol station before he was captured and taken back to VulPro. His excursion was the last to require intervention; all birds made a total of 22 trips after this date and found their own way back.

Three year old 001 ranged the farthest, 7.95 km southwest of VulPro (Table 17 and Figure 22). The day of departure and the following day were exceptionally windy. He became grounded at the crest of a ridge where he waited for three nights (Figure 21). During this time he attempted a few short flights but was unable to move large distances and remained grounded in the area. His return flight to VulPro lasted under a half hour and presumably coincided with more favourable flight conditions.

Figure 21: Cumulative movements of bird 001 eight months post-release.

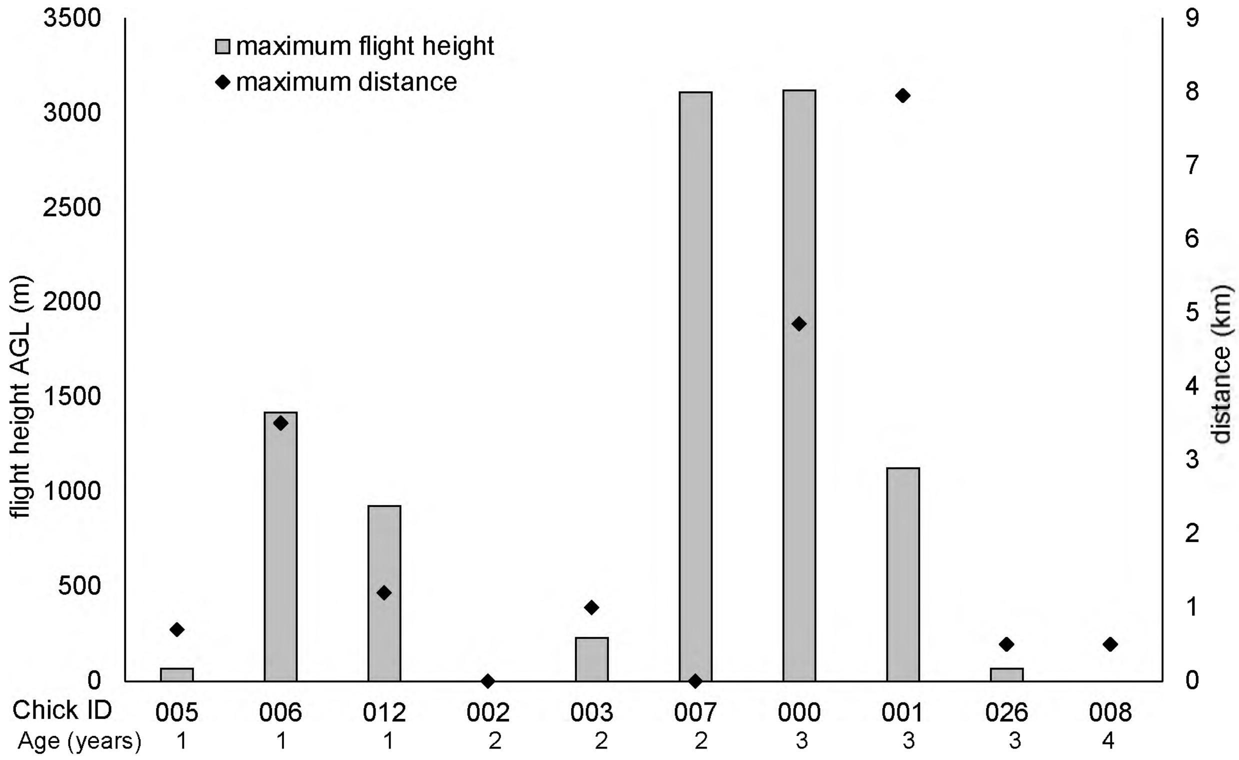


The most adept individual was three year old 000. He never required assistance to return safely to VulPro on any of his six excursions. He had the highest recorded flight height (3,120 m AGL) and second longest flight distance (4.85 km, Table 17).

Table 17: Overview of excursions including maximum distance travelled and maximum flight height.

chick ID	005	006	012	002	003	007	000	001	026	008
age	1	1	1	2	2	2	3	3	3	4
overnight trips	0	3	1	0	1	0	3	4	0	1
day trips	5	7	6	0	0	1	3	6	4	1
total excursions	5	10	7	0	1	1	6	10	4	2
max. flight height (m AGL)	65	1420	925	0	230	3110	3120	1125	65	0
max. distance (km)	0.70	3.50	1.20	0	1.00	0	4.85	7.95	0.50	0.50

Figure 22: Maximum flight height and distance travelled for each individual.



Two year old 007 had the second highest flight height at 3,110 m AGL. However, he was never recorded outside the property. Many birds, including 000 and 007, were seen to take flight with wild vultures from the restaurant, join them low in a thermal, and then return to the restaurant. Four birds were recorded flying > 1,000 m AGL on twelve occasions (birds 000, 001, 006, and 007). Another, bird 012, was recorded flying at 925 m AGL. The fastest of these high flights was made by bird 006 at 87 km per hour.

7.4 Discussion

The flight heights recorded from these captive bred individuals are the highest on record for Cape Vultures. Mendelsohn and Diekmann (2007) report Cape Vultures in Namibia reach peak flight height at 700 to 1,000 m AGL during long-distance flights. More typical flight heights occur while foraging and range from 200 to 500 m AGL (Mundy et al. 1992, Mendelsohn and Diekmann 2007). Pennycuick's (1971) extensive studies of thermal soaring flight recorded a Rüppell's Griffon Vulture at approximately 1,550 m AGL (3,050 m above sea level), but notes thermals can grow to 3,000 m AGL or higher by 15h00 when conditions are at their peak. The records noted here of flight heights 3,120m and 3,110 m AGL were recorded at 13h00 and 11h00 local time. Vultures are among the few birds which have made record flights worldwide, including soaring Bearded Vultures at 7,315 m and a Rüppell's Vulture which collided with a commercial aircraft at 11,200 m ASL (Laybourne 1974). As the flight records in this study were almost double previous known records for the species, VulPro's recent GPS data from three wild Cape Vultures in the Eastern Cape and the Magaliesberg area were investigated. All displayed maximum flight heights near or exceeding those of captive bred chicks. One wild vulture over the course of nine minutes started from a roosting position on the crest of a ridge and slowly gained altitude to reach approximately 5,330 m AGL before landing again (Kerri Wolter, unpublished data).

Five individuals were never recorded above 250 m AGL. Bird 002 sustained a wing injury, but there is no explanation for the lack of high flight in three other individuals. Bird 026 was originally released with a patagial GPS device. He was recaptured 23 days post-release because his flight seemed laboured and he never flew more than 4 m above the ground. A slight wing asymmetry was noted in captivity which was resolved immediately after removing the patagial GPS device. He was re-released with a backpack GPS device after 11 days in captivity. His flight remained poor for approximately one month until he was able to reach a higher (6 m) perch, which he then routinely accessed. At the time of writing, he has still not managed to join other chicks on the top of an enclosure (9 m), although one GPS record places him flying 65 m AGL 250 m outside VulPro's property.

Brown (1985) proposed Cape Vulture range size provides a direct measure of the ease with which an individual can find food. Deygout et al. (2009) modelled the impact that spatial and temporal changes in restaurant provisioning had on vulture scavenging efficiency, i.e. the distance travelled in search of food. Indeed, they found the distribution of resources had a substantial impact on scavenging and that the model was best described with the existence of 'trapliners', or birds which regularly rely on previously acquired personal information. In other words, vultures become accustomed to regular feeding sites and habitually visit active feeding sites where food is regularly supplied.

The overwhelming lack of captive bred bird ranging is likely due to the fact that VulPro provides food on an almost daily basis. Captive bred chicks have always had food provided for them and have never needed to rely on social networks to acquire food. Other successful reintroduction programmes temporally and spatially stagger proffered food around the release site to encourage dispersal and 'teach' foraging (Lieberman et al. 1987, Wallace and Temple 1987b). In response to this protocol, flight distances of released captive bred Andean Condors in Colombia increased from < 1 km to about 10 km after the first six months post-release, with sustained flights of 1.5 – 16 km after the first 6 months (Lieberman et al. 1993).

Future research should investigate the effects of various feeding regimes within the supplementation programme, specifically in the Magaliesberg Mountains, on post-release ranging patterns. Similarly, variations in feeding regimes should be considered and evaluated in the context of the Magaliesberg Mountains to determine their effects on wild foraging behaviors (Deygout et al. 2009, Deygout et al. 2010) and restaurant utility in attracting wild birds to selected regions, i.e. colonies to be re-established (Mihoub et al. 2009).

CHAPTER 8: CONCLUSION

8.1 Comparison to other vulture breeding and reintroduction programmes

The main objective of this research was to determine the best age to release the species, maximizing individual survival while minimizing conservation resource use. The release of vultures at VulPro's breeding facility was conducted to avoid potentially unnecessary costs associated with acclimatization enclosure construction and to reduce the use of staff and monetary resources. However, my results confirm that methods used in other vulture reintroduction programmes, i.e. releasing from a removed acclimatization enclosure and temporal and spatial staggering of post-release feedings, should be implemented to avoid the few behavioural issues seen in this programme. VulPro's property is not an appropriate release site for captive bred Cape Vultures.

The pioneering Griffon Vulture reintroduction programme released four fledglings which rapidly left the area (Sarrazin et al. 1994). Introductions then proceeded to house individuals in a captive breeding acclimatization enclosure until release at adulthood, with great success. Griffon Vultures released as adults remained in the region to colonize local breeding sites, with successful breeding occurring as early as a few months post-release (Terrasse et al. 2004).

The eldest released Cape Vulture at four years old, bird 008, disappeared five months post-release coinciding with the malfunction of his GPS unit. It was only his second venture off the property. He likely had poor flight stamina even though his short-distance flights were strong. He was an adept and efficient feeder and was in good health at the time of disappearance. He is presumed dead and is the only chick lost in the programme. This is comparable to the high observed adult (older than five years old) Griffon Vulture mortality in reintroductions in France which were attributed to the dispersal of mates, the energetic costs of learning to fly, consequences of captivity, learning to compete for food at carcasses, and the difficulties in learning foraging flight, especially in bad weather conditions (Terrasse et al. 2004). High adult mortality was observed in the first year post release, yet when survival was assessed over periods longer than one year, the protocol of releasing adults remained the most efficient (98% adult survival over many years; vs. 74 % adult first year post-release; Sarrazin et al. 1994). Subsequent Griffon Vulture reintroductions never allowed an individual to remain in captivity past five years of age, with the release of three year old birds proving very successful (Terrasse et al. 2004). The California Condor release programme in Arizona showed higher survival for individuals released when older than one year, although none of these birds were older than three years old when released (95 % older than one year vs. 73 % younger than one year survival first year post-release; Woods et al. 2007). In a pilot study, four adult condors, eight and nine years old, were released; two were killed by coyotes within the first month post-release likely due to improper roosting site location. The other two were returned to captivity (Woods et al. 2007).

When modelling the parameters involved in reintroductions of long-lived species, Sarrazin and Legendre (2000) concluded the release of adults was the most effective strategy, mainly because of the higher reproductive rate. Extinction probabilities were lower when releasing adults rather than juveniles. In contrast, other models which incorporated genetic effects concluded releasing juveniles might positively affect long term persistence (Robert et al. 2004). With all of these in mind, in the context of reintroductions, Mihoub et al. (2009) recommends preferentially releasing adults to create an artificial social context for species which rely on social cues for settlement. A reintroduction programme's failure or success is highly dependent on the dispersal of released individuals which are attracted to conspecifics in the closest and largest populations (Le Gouar et al. 2008). These models assume a reintroduction context where no wild conspecifics already exist. In the context of the Magaliesberg supplementation programme, selecting suitable breeding habitat for the location of the acclimatization enclosure, in conjunction with decoy vultures on the cliff, may provide adequate social cues; housing captive birds at prime breeding habitat will attract wild, free-ranging birds to the location (Mihoub et al. 2009).

8.2 Management implications and recommendations

Within two days of bird 008's disappearance, searches were initiated using VHF transmitters, foot, and driving surveys in the vicinity where he was expected to be grounded. Remains of a Cape Vulture were found, the victim of a dog attack which occurred the same weekend as bird 008's disappearance. Neighbours were aware of the attack and claimed the dogs' owner likely sold the bird into the 'muti' trade. Genetic analysis performed at the NZG (using both nuclear and mitochondrial markers) confirmed the remains did not belong to the missing individual.

This supplementation programme is facing a great challenge that other vulture reintroduction programmes in Europe or the Unites States do not encounter. When birds become grounded, there is a real threat they will soon be found by dogs or people. The human population around VulPro is growing and within this community it is not uncommon for members to capture or club grounded birds to sell their body parts into the 'muti' trade. The high propensity for these captive bred birds to land on the ground, coupled with their relative habituation to people, is the biggest behavioural challenge this programme faces. Efforts were made to ‘haze’ any bird found on the ground in inappropriate areas at VulPro. Very quickly, within one month, individuals reduced grounding behaviour and increased the distance allowed between themselves and people. In light of these behaviours and threats, VulPro’s property is not a suitable nor safe release site for captive bred chicks.

The presence of power line structures can influence wild vulture ranging behaviour, as the poles are often used as roost sites (Phipps et al. 2013). The situation is both positive and negative for wild vultures; their foraging ranges have expanded with increased electrical infrastructure, yet some poles pose a threat of electrocution (the amount of risk depends on the structure design). There are multiple power line transects approximately 300 m east of VulPro’s property that have caused numerous vulture electrocutions and collisions. The lines have since been mitigated with measures to make them visible to vultures leaving the restaurant, and are still commonly used by wild vultures. Bird 003’s only excursion involved roosting on these structures over three nights. Bird 000 also roosted on power line structures over multiple excursions (Appendix 8). Electrocutions were major sources of mortalities in both California Condor (Woods et al. 2007) and Griffon Vulture (Terrasse et al. 2004) released populations. Power line aversion behavioural programmes, in which chicks are conditioned to avoid perching on power line structures using charged ‘mock’ poles inside their enclosures, have been used successfully in California Condor reintroduction efforts (Cohn 1999). As powerline electrocutions and collisions are a leading cause of vulture mortalities in South Africa and within the Magaliesberg region (Naidoo et al. 2011, Boshoff et al. 2011), a similar behavioural aversion programme should be implemented in the breeding enclosure and acclimatization enclosure in an attempt to reduce these mortalities.

Many raptor rehabilitation programmes implement pre-release flight training or fitness regimes to ensure individuals are able to hunt and to increase the likelihood of survival in the wild (Holz et al. 2006). The exercise methods vary depending on the species and injury, but cage flight exercises have been shown to increase post-release survival in many raptor species (Greene et al. 2004). While vultures do not need agility in flight to hunt or kill prey, they require prolonged flapping flight to access thermals (pers. observation), exercise which is especially difficult after feeding when their wing loading is higher (Mundy et al. 1992, Bamford et al. 2009). Williams (2015) showed other vultures with high wing loadings, Griffon Vultures and Andean Condors, displayed flapping flight between 4 and 16 % of ‘classifiable’ flight time. While flapping flight is a small fraction of vulture flight time budget, it is not possible to practice more than a few wing beats in a large flight enclosure. Captive bred chicks will have never experienced prolonged flapping flight before release. VulPro has a high rehabilitation success rate without implementing any fitness regimes. Released rehabilitated Cape Vultures have a 75 % mean annual survival rate (Monadjem et al. 2014). However, in another study, ten of eleven birds which had spent more than a year in captivity at VulPro were recovered dead or in a weakened state (Bartels et al. 2007). Rehabilitated birds, as well as captive bred chicks, are simply observed in their large flight enclosure (40 x 9 x 9 m) to assess their suitability for release (Naidoo et al. 2011). While this may be adequate to assess the flight abilities of wild individuals held in captivity for a limited amount of time, the lack of flight skill and stamina exhibited by captive bred birds, especially in the first three months post-release, suggest active training may be beneficial to help them prepare for a life outside a flight cage.

Other successful vulture reintroduction programmes have utilized an acclimatization enclosure separate from the breeding facility, where vultures are housed for a varying lengths of time, up several years, before release (Hatzofe 2001, Woods et al. 2007, Sarrazin 2013). I recommend a new site be implemented, located on the top of a Magaliesberg cliff or nestled onto the cliff face itself. This site would achieve multiple objectives. 1) A new release enclosure located on or very near the cliff face would introduce birds to thermal updrafts and wind currents they do not routinely encounter in the breeding enclosure or restaurant at VulPro. 2) A vulture restaurant slightly removed (1 km away) from the release site would force birds to forage, increasing their fitness soon after release. 3) Temporal staggering of feeding events, which is not currently possible at VulPro's restaurant, may encourage longer distance foraging flights and therefore increase fitness. 4) Lastly, a new release site farther removed from the dense human habitation in the vicinity of VulPro would reduce the risk that birds become targeted when grounded near the release site.

Unfortunately, the oldest individual was lost to the programme and the cause of disappearance or death was not verified. However, his behavioural integration, coupled with his tendency to remain in the area suggest release at age of sexual maturity (four to five years old, Robertson 1983) is the best method for release of this species. Individuals should be translocated to the above mentioned acclimatization enclosure around seven months of age and be housed there with minimal human interaction until the time of release.

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These protocols were developed by K. Wolter. This publication was prompted by the need for peer-reviewed protocols for my research and other conservation efforts. K. Wolter wrote the original manuscript which I then contributed to and edited for publication.

Wolter, K., W. Neser, and **M.T. Hirschauer**. 2014 (*b*) Cape Vulture captive breeding protocols. Version 1.0. Accessed online 18 September 2014. <www.vulpro.com>

These protocols emerged out of my 2014 breeding season monitoring efforts as part of my thesis research. The protocols were written to be a resource for other vulture breeding facilities. K. Wolter managed the breeding programme and developed the majority of the protocols. I added and adapted protocols and was the lead author of the manuscript.

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K. Wolter and W. Neser collected all data between 2010 and 2013. K. Wolter and I collected all 2014 data. I synthesized the data and prepared the manuscript.

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APPENDICES

Appendix 1: Details of global *Gyps* vulture breeding, reintroduction, and translocation efforts.

country	coordinating organization(s)	location(s)	website	species	captive breeding or translocation	reintroduction or supplementation
France	Fonds d'Intervention pour les Rapaces and the Parc National des Cevennes	Causses and southwestern Alps		*G. fulvus*	CB and TL	Re
Italy	World Wide Fund for Nature, Lega Italiana Protezione Uccelli - BirdLife, Fonds d'Intervention pour les Rapaces, Legambiente Sardinia	eastern Alps, Appenines, Sicily, Sardinia, Pollino National Park		*G. fulvus*	TL	Re
Israel	Israel Nature and Parks Authority	Mt. Carmel		*G. fulvus*	CB	Re
Cyprus	Game Fund, Cyprus	Limassol	http://www.gypas.org/en/index.html	*G. fulvus*	TL	Sup
Bulgaria	Green Balkans Stara Zagora Non-Profit Organisation	Stara Planina and Kresna Gorge	http://www.greenbalkans.org/birdsofprey/life/	*G. fulvus*	TL	Re
India	Bombay Natural History Society	Haryana, West Bengal and Assam	http://www.save-vultures.org/	*G. bengalensis*, *G. indicus*, *G. tenuirostris*	CB	Re (planned)
Pakistan	World Wildlife Fund Pakistan	Changa Manga	http://www.save-vultures.org/ ; http://www.wwfpak.org/species/Vulture.php	*G. bengalensis*	CB	Re (planned)
Nepal	Department of National Parks and Wildlife Conservation, the National Trust for Nature Conservation, Bird Conservation Nepal	Chitwan National Park	http://www.save-vultures.org/ ; http://www.birdlifenepal.org/	*G. bengalensis*, *G. indicus*, *G. tenuirostris*	CB	Re (planned)
South Africa	VulPro	Magaliesberg Mountains	http://www.vulpro.com/	*G. coprotheres*	CB	Sup

Appendix 2: Data from wild Cape Vulture focal samples.

#	sample date	sample time	sample duration (min)	bird ID	estimated sex	minimum age (years)	CV present at start	CV present at end
1	3/22/2014	12:34:38	30	no tag		2	6	34
2	3/22/2014	12:22:09	20	B533	male	3	19	7
3	4/7/2014	12:43:45	24	B609	female	3	50	33
4	4/6/2014	14:14:52	21	B648	male	1	10	12
5	4/15/2014	13:01:48	28	B420	male	4	22	15
6	4/18/2014	11:28:45	30	C196	female	1	36	42
7	6/1/2014	13:18:22	30	B545	male	7	8	11
8	6/1/2014	13:19:47	30	B540		3	14	17
9	6/2/2014	12:13:56	30	B584	female	4	24	34
10	6/9/2014	11:10:46	30	B427	female	4	21	29
11	6/9/2014	11:12:43	30	B511	female	9	19	48
12	6/9/2014	11:21:02	23	B150	male	14	24	41
13	7/19/2014	8:35:55	30	B607	male	3	48	>100
14	7/19/2014	9:02:22	29	B611		3	>100	80
15	7/19/2014	10:38:37	30	B653		4	70	71
16	7/15/2014	13:08:00	25	C174		3	56	65
17	7/19/2014	10:38:41	30	B518	male	3	70	62
18	8/10/2014	13:24:43	30	CR-R-YB	female	15	20	36
19	8/6/2014	13:41:21	30	B622	male	2	95	40
20	8/6/2014	13:49:11	22	B672	male	10	83	43
21	7/22/2014	13:43:04	30	016E	male	3	38	27
22	7/23/2014	12:38:26	30	B601	female	3	80	49
23	7/25/2014	11:46:29	30	B632	female	2	53	74
24	7/25/2014	13:22:12	30	C156		4	39	41
25	8/3/2014	11:25:05	20	B370		4	56	79
26	8/9/2014	13:34:46	30	B442	male	8	36	50
27	8/9/2014	13:34:16	30	B700		4	31	46
28	8/9/2014	13:35:16	30	B423	female	4	37	46
29	8/9/2014	14:11:36	27	B533	male	3	54	36
30	8/15/2014	12:03:12	30	B538	male	7	89	110
31	8/15/2014	13:10:05	24	B677	female	10	69	40
32	8/17/2014	9:45:21	30	B552		9	18	24
33	8/17/2014	10:35:38	30	B603	male	3	64	56
34	8/17/2014	10:50:38	21	C142	male	4	53	57
35	8/18/2014	14:43:27	24	B374	female	9	31	24
36	8/23/2014	8:43:02	30	B535		9	68	115
37	8/21/2014	11:48:46	21	B375	female	3	100	178
38	8/24/2014	8:21:20	30	B539		3	170	280

39	8/21/2014	12:12:41	25	B630	female	2	180	132
40	8/22/2014	10:58:15	30	B509	male	9	80	154
41	8/23/2014	9:10:05	28	B376	female	9	94	113
42	8/24/2014	7:54:35	30	B512	male	9	65	180
43	8/30/2014	11:27:42	30	B556	male	3	27	26
44	9/2/2014	10:12:50	30	B380	male	3	40	70
45	9/3/2014	10:06:20	25	B434	male	10	65	115
46	9/4/2014	14:44:37	26	B507	female	9	37	30
47	9/5/2014	14:24:17	30	B614	female	3	67	30
48	9/8/2014	10:50:46	30	B554	male	9	25	54
49	9/8/2014	11:02:11	27	B445	female	8	42	65
50	9/11/2014	9:44:06	23	B326	male	23	17	50
51	9/19/2014	9:51:53	25	B621		2	139	138
52	9/22/2014	10:08:55	30	C165		3	180	146
53	9/23/2014	9:30:57	29	B696	male	8	40	150
54	9/28/2014	11:22:04	30	B592	female	4	160	100
55	10/1/2014	6:27:48	30	B382		7	70	125
56	10/4/2014	8:39:16	30	B604	female	2	100	122
57	10/4/2014	8:09:16	30	B559	female	9	60	100
58	10/5/2014	9:18:24	30	B654	female	10	121	140
59	10/7/2014	10:50:35	30	B371	female	3	70	143
60	10/14/2014	8:04:38	29	B517	female	7	67	114
61	10/17/2014	8:36:03	29	B379	female	3	263	250
62	10/17/2014	7:58:18	30	C202	male	2	60	256
63	10/23/2014	8:28:14	24	B510		9	161	233
64	10/23/2014	7:53:59	30	B369	female	9	45	161
65	10/24/2014	10:25:18	30	B661	female	10	125	87
66	12/6/2014	13:27:41	30	020E		1	160	90
67	1/12/2015	9:51:13	30	019E	female	1	60	80
68	1/12/2015	10:37:26	30	B574		7	95	130
69	1/15/2015	9:58:16	21	B505	female	9	100	35
70	1/15/2015	9:36:46	30	B508		7	90	115
71	1/16/2015	10:40:23	30	022E	female	1	100	78
72	2/3/2015	9:54:35	30	B598	female	4	82	140
73	2/10/2015	13:42:09	30	022	male	1	43	24
74	2/14/2015	10:43:33	30	018	female	1	17	57
75	2/20/2015	9:00:34	30	017	male	1	9	100
76	2/26/2015	13:46:12	30	B616	female	3	44	30
77	3/1/2015	9:31:20	19	B383	female	6	140	120
78	3/4/2015	9:13:24	30	Rings BGY/YBSAF		17	30	87
79	3/13/2015	7:08:15	30	021	female	1	13	13
80	3/13/2015	9:26:17	30	024	female	1	118	120
81	3/13/2015	7:08:14	30	011	female	1	13	13

82	3/13/2015	7:18:14	30	016	male	1	13	16
83	3/14/2015	11:10:25	19	B665		11	140	154
84	3/20/2015	13:42:14	30	023		1	55	38
85	3/24/2015	13:23:05	17	B513		11	45	55
86	4/3/2015	12:37:06	18	B657		11	96	114
87	4/8/2015	13:12:04	22	B695	male	11	50	26
88	4/8/2015	13:21:04	14	027	female	5	50	26
89	4/11/2015	10:44:08	28	029	male	7	35	55
90	5/14/2015	14:40:34	24	018E	female	7	20	25
91	5/14/2015	14:28:34	30	C230		1	32	20

#	feeding rate	interaction rate	aggressiveness	display rate	dominance	crop difference (g)	feeding efficiency
1	0.20	0.73	0.17	0.07	0.10		
2	0.05	1.05	0.15	0.05	0.10		
3	0.33	0.71	0.08	0.13	0.04		
4	0.62	1.05	0.29	0.00	0.05		
5	0.46	0.68	0.04	0.00	0.04		
6	0.10	0.53	0.03	0.00	0.00		
7	0.17	1.17	0.43	0.27	0.07		
8	0.23	1.47	0.60	0.43	0.20		
9	0.60	1.30	0.27	0.13	0.07		
10	0.63	0.93	0.30	0.40	0.17		
11	0.60	0.83	0.27	0.00	0.23		
12	0.57	1.22	0.57	0.13	0.52		
13	0.20	1.50	0.23	0.30	0.13		
14	0.52	1.48	0.21	0.31	0.07		
15	0.00	0.23	0.03	0.00	0.00		
16	0.68	1.48	0.80	0.64	0.48		
17	0.47	1.63	0.67	0.20	0.17		
18	0.60	1.43	0.70	0.43	0.47		
19	0.27	0.97	0.40	0.07	0.03		
20	0.14	0.45	0.09	0.00	0.05		
21	0.60	0.87	0.40	0.30	0.20		
22	0.70	1.57	0.13	0.10	0.07		
23	0.73	1.97	0.93	0.60	0.23		
24	0.50	1.00	0.33	0.10	0.07		
25	0.50	1.25	0.65	0.30	0.00		
26	0.43	0.70	0.17	0.13	0.00		

27	0.73	1.23	0.70	0.43	0.33		
28	0.83	1.23	0.43	0.73	0.17		
29	0.41	0.74	0.22	0.22	0.15		
30	0.07	1.07	0.20	0.10	0.03		
31	0.21	0.67	0.42	0.29	0.04		
32	0.17	1.10	0.60	0.07	0.23		
33	0.40	1.30	0.30	0.20	0.07		
34	0.24	1.48	0.29	0.19	0.05		
35	0.54	1.17	0.38	0.33	0.38		
36	0.07	0.70	0.27	0.07	0.20		
37	0.19	1.05	0.43	0.05	0.14		
38	0.27	1.10	0.47	0.03	0.20		
39	0.28	1.24	0.32	0.56	0.08		
40	0.13	2.03	1.13	0.60	0.23		
41	0.29	1.54	0.82	0.39	0.29		
42	0.03	0.53	0.13	0.10	0.07		
43	0.77	1.27	0.37	0.10	0.20		
44	0.33	2.30	0.83	0.23	0.13		
45	0.16	0.96	0.04	0.04	0.04		
46	0.50	2.42	1.42	1.46	0.46		
47	0.53	2.13	1.00	1.00	0.53		
48	0.20	1.83	0.47	0.17	0.20		
49	0.67	1.30	0.48	0.37	0.19		
50	0.04	0.78	0.17	0.04	0.04		
51	0.32	2.44	0.68	0.80	0.12		
52	0.27	1.07	0.37	0.07	0.03		
53	0.21	3.41	1.41	0.14	0.45		
54	0.10	0.77	0.30	0.17	0.13		
55	0.07	0.97	0.43	0.43	0.23		
56	0.77	1.83	1.20	0.57	0.57		
57	0.37	0.57	0.27	0.03	0.07		
58	0.07	0.43	0.37	0.10	0.10	800	26.67
59	0.47	2.30	1.17	1.00	0.53		
60	0.03	1.03	0.38	0.03	0.03		
61	0.10	0.93	0.48	0.41	0.21	800	27.59
62	0.03	1.43	0.33	0.10	0.07		
63	0.13	1.08	0.42	0.13	0.17		
64	0.03	0.47	0.20	0.20	0.07		
65	0.07	1.27	0.40	0.23	0.10		
66	0.10	0.93	0.50	0.53	0.13		
67	0.07	1.60	0.57	0.70	0.07	350	11.67
68	0.23	1.23	0.53	0.13	0.30	1100	36.67
69	0.10	0.48	0.38	0.10	0.05	600	28.57

70	0.13	0.43	0.17	0.23	0.10	500	16.67
71	0.37	2.33	1.30	0.70	0.30	200	6.67
72	0.47	1.53	0.30	0.00	0.10	800	26.67
73	0.13	0.47	0.20	0.00	0.00	200	6.67
74	0.47	0.93	0.47	0.30	0.10	350	11.67
75	0.10	2.17	1.23	0.77	0.47		
76	0.13	0.43	0.23	0.10	0.03	250	8.33
77	0.21	1.84	1.16	0.26	0.58	150	7.89
78	0.10	0.37	0.13	0.03	0.03	1100	36.67
79	0.83	1.53	0.77	0.70	0.37	200	6.67
80	0.10	1.83	1.10	0.83	0.10	200	6.67
81	0.73	2.07	1.33	0.33	0.50		
82	0.53	1.97	0.60	0.63	0.20	350	11.67
83	0.11	1.68	0.74	0.37	0.47	600	31.58
84	0.17	1.27	0.37	0.57	0.07	200	6.67
85	0.71	3.29	1.76	0.53	0.47	350	20.59
86	0.17	1.89	0.33	0.22	0.06	350	19.44
87	0.14	0.68	0.36	0.05	0.18	1100	50.00
88	0.29	1.07	0.50	0.21	0.21	200	14.29
89	0.36	1.57	0.32	0.36	0.04	600	21.43
90	0.04	0.33	0.21	0.00	0.13	600	25.00
91	0.13	0.30	0.07	0.00	0.00	500	16.67

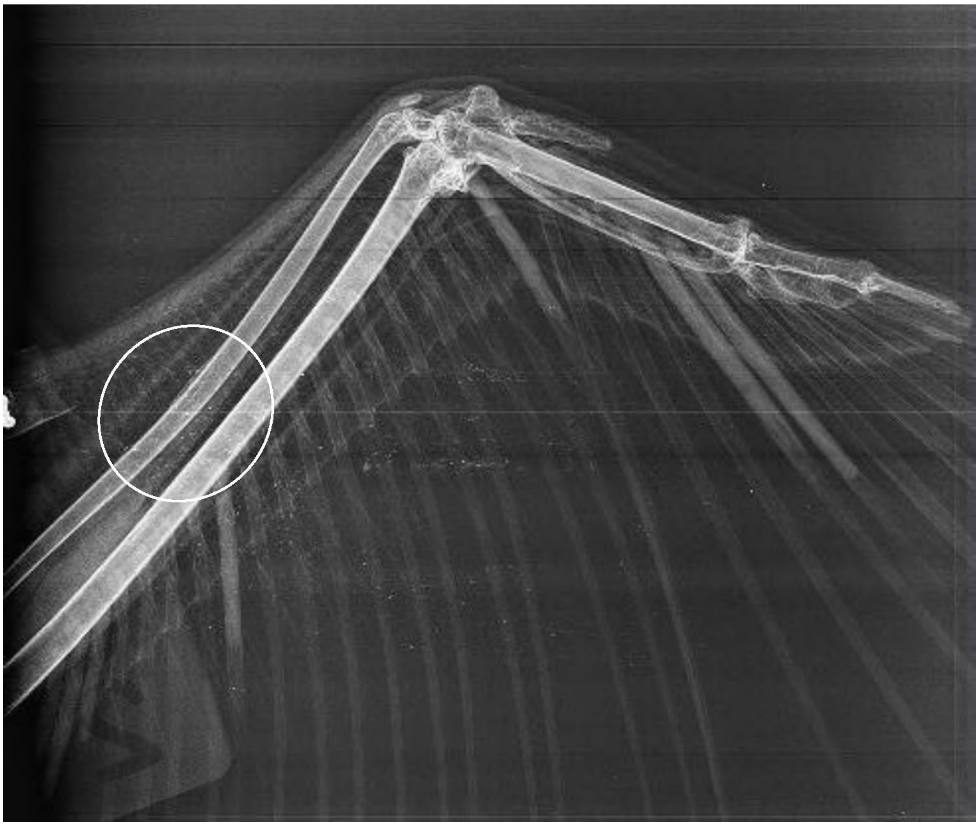
Appendix 3: Data from captive bred Cape Vulture focal samples.

#	sample date	sample duration (min)	bird ID	average CV present	feeding rate	interaction rate	aggressiveness	display rate	dominance	crop difference (g)	feeding efficiency
1	17-Feb-15	30	002	16	0.13	1.27	0.47	0.57	0.27	350	11.67
2	17-Feb-15	30	003	16	0.20	0.80	0.07	0.03	0.03	800	26.67
3	17-Feb-15	20	012	13	0.35	1.45	0.75	0.25	0.25	200	10.00
4	17-Feb-15	30	026	13	0.23	1.40	0.10	0.07	0.03	600	20.00
5	17-Feb-15	30	005	13	0.70	1.17	0.67	0.40	0.27	600	20.00
6	20-Feb-15	30	006	55	0.03	0.43	0.03	0.00	0.00	0	
7	20-Feb-15	30	026	102	0.07	1.10	0.07	0.07	0.00	200	6.67
8	20-Feb-15	30	007	70	0.07	1.03	0.33	0.00	0.03	350	11.67
9	22-Feb-15	30	001	62	0.07	1.27	0.33	0.43	0.13	350	11.67
10	22-Feb-15	20	007	88	0.05	0.90	0.25	0.05	0.05		
11	24-Feb-15	20	000	7	0.35	0.90	0.00	0.05	0.00	400	20.00
12	25-Feb-15	30	005	75	0.10	0.47	0.30	0.30	0.07	0	
13	1-Mar-15	30	003	145	0.07	0.47	0.17	0.00	0.00	100	3.33
14	26-Feb-15	30	008	44	0.40	0.60	0.13	0.00	0.00	400	13.33
15	3-Mar-15	30	012	15	0.73	1.93	0.80	0.93	0.20	200	6.67
16	14-Mar-15	30	005	109	0.40	1.23	0.57	0.43	0.07	0	
17	18-Mar-15	30	000	107	0.07	0.20	0.03	0.03	0.03	400	13.33
18	18-Mar-15	30	001	107	0.17	0.60	0.37	0.33	0.20	150	5.00
19	24-Mar-15	30	003	38	0.00	0.23	0.10	0.03	0.00	0	
20	30-Mar-15	30	001	36	0.07	0.23	0.07	0.10	0.13	0	
21	30-Mar-15	30	007	36	0.23	0.47	0.07	0.00	0.00	400	13.33
22	30-Mar-15	30	006	36	0.27	0.37	0.10	0.03	0.03	200	6.67
23	2-Apr-15	30	002	85	0.00	0.97	0.40	0.60	0.10	0	
24	2-Apr-15	30	026	85	0.03	0.60	0.00	0.03	0.00	0	
25	8-Apr-15	12	012	22	0.33	0.58	0.25	0.25	0.08	150	12.50
26	8-Apr-15	30	005	31	0.00	0.13	0.03	0.00	0.00	0	

27	8-Apr-15	30	002	17	0.17	0.47
28	9-Apr-15	30	000	44	0.20	0.53
29	13-Apr-15	30	003	17	0.30	0.87
30	24-Feb-15	30	007	7	0.27	0.90
31	24-Feb-15	30	006	7	0.30	0.73
32	13-Apr-15	30	008	17	0.33	1.30
33	13-Apr-15	23	006	17	0.78	0.87
34	5-May-15	30	007	69	0.07	0.53
35	5-May-15	25	012	69	0.48	1.08
36	11-May-15	30	005	47	0.30	1.33
37	11-May-15	21	026	76	0.00	0.10
38	11-May-15	30	001	72	0.07	0.20
39	12-May-15	30	000	96	0.00	0.07
40	12-May-15	27	003	113	0.00	0.33
41	12-May-15	30	007	101	0.07	0.27
42	14-May-15	10	012	31	0.10	0.30
43	28-May-15	30	003	128	0.20	0.50
44	29-May-15	12	005	61	0.00	0.17
45	29-May-15	19	006	35	0.26	0.68
46	29-May-15	22	012	57	0.45	0.86
47	17-Jun-15	30	000	125	0.03	0.50
48	17-Jun-15	30	026	125	0.00	0.27
49	6-Jul-15	30	000	73	0.10	0.13
50	6-Jul-15	30	001	73	0.33	0.43
51	6-Jul-15	30	006	73	0.90	1.37
52	15-Jul-15	29	001	160	0.48	2.41
53	16-Jul-15	30	026	97	0.07	0.63
54	17-Jul-15	11	008	81	0.00	0.55
55	22-Jul-15	6	008	35	0.33	3.50
56	23-Jul-15	11	008	45	0.45	0.36
57	23-Jul-15	30	026	95	0.03	0.73

0.20	0.07	0.20	350	11.67
0.17	0.00	0.07	150	5.00
0.27	0.03	0.10	150	5.00
0.40	0.23	0.03	200	6.67
0.47	0.30	0.03	400	13.33
0.43	0.03	0.10	200	6.67
0.39	0.00	0.00	200	8.70
0.07	0.07	0.03	500	16.67
0.52	0.64	0.28	350	14.00
0.67	0.53	0.10	200	6.67
0.05	0.00	0.05	0	
0.07	0.10	0.03	200	6.67
0.03	0.00	0.00	0	
0.04	0.00	0.00	0	
0.07	0.00	0.00	200	6.67
0.00	0.10	0.00	250	25.00
0.17	0.03	0.03	350	11.67
0.00	0.00	0.00	200	16.67
0.47	0.21	0.11	400	21.05
0.55	0.50	0.05	250	11.36
0.10	0.03	0.03	0	
0.00	0.03	0.00	0	
0.10	0.07	0.03	0	
0.27	0.13	0.10	150	5.00
0.77	0.37	0.07	250	8.33
1.55	0.83	0.45	200	6.90
0.10	0.03	0.03	0	
0.27	0.18	0.00	0	
0.67	0.00	0.00	150	25.00
0.09	0.00	0.00	650	59.09
0.17	0.00	0.03	450	15.00

Appendix 4: Chick 002 x-ray showing hairline fractured radius 11 days after injury. 26 February 2015.



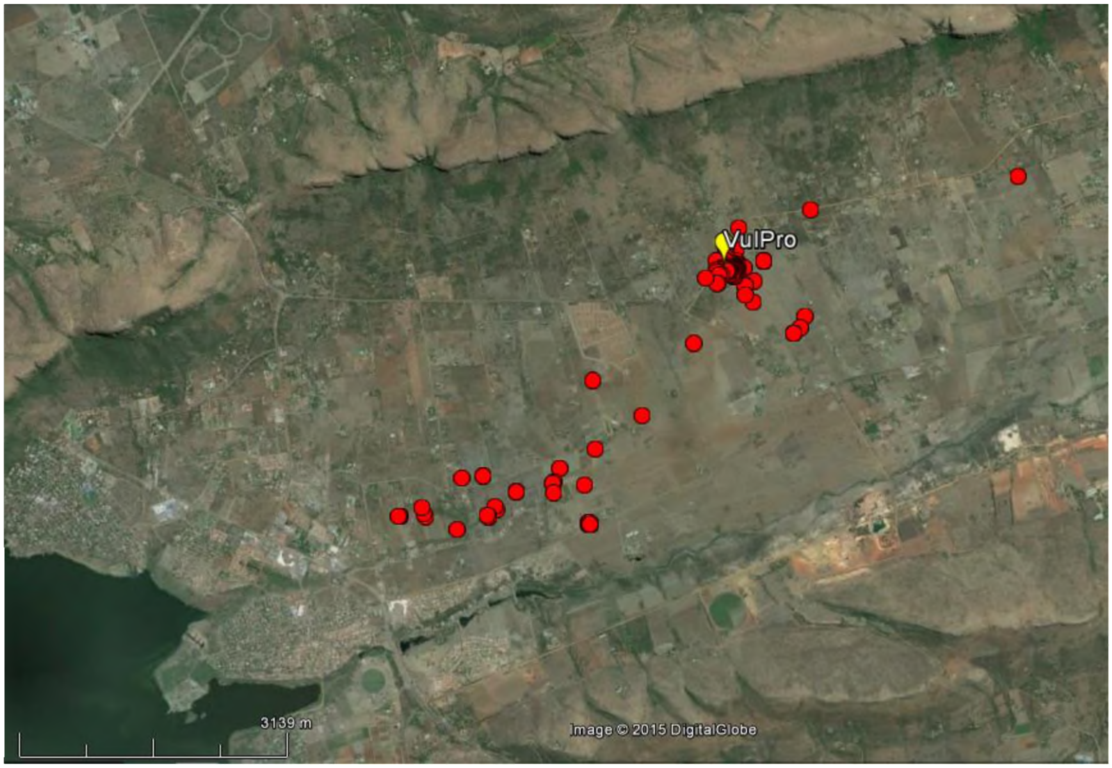
Appendix 5: Chick 002's wing injury caused by improper placement of patagial tag, 28 October 2015.

Appendix 6: Details of each excursion for all chicks over the first eight months post-release.

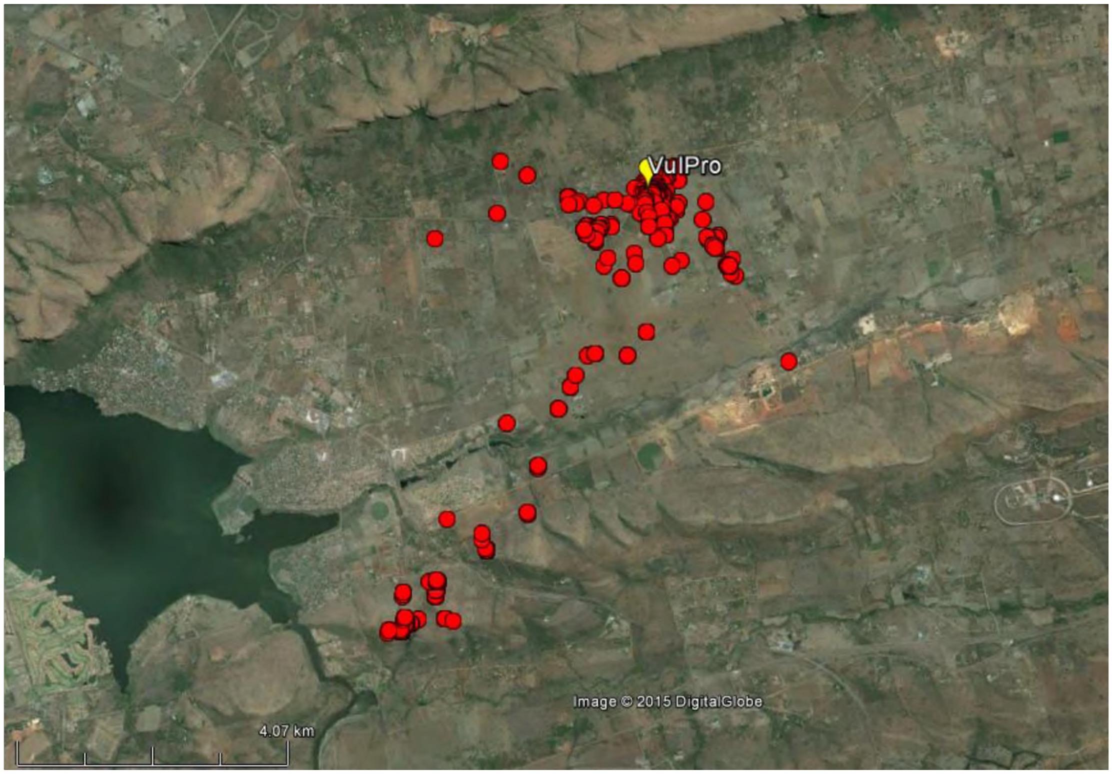
Bird ID		005	006	012	002	003	007	000	001	026	008
Age		1	1	1	2	2	2	3	3	3	4
Excursion	date	17-Mar	17-Feb	19-Feb		10-Mar	28-May	19-Mar	18-Feb	15-Apr	8-Mar
1	duration	1 day	1 day	1 day		2 nights	1 day	1 day	1 night	1 day	1 day
	max. distance (km)	0.1	0.55	0.55 km		1	0	3.55	0.45	0.25	0.5
	max. flight height (m)	0	0	0		230	3,110	3,120	0	65	0
	human intervention	no	yes	no		no	no	no	yes	no	no
2	date	28-Mar	23-Feb	22-Feb				23-Apr	22-Feb	21-Apr	24-Jul
	duration	1 day	1 night	1 day				1 night	1 day	1 day	GPS failure
	max. distance (km)	0.65	3.5	1.2 km				1.15 km	0.35	0.5	
	max. flight height (m)	0	580	150				0	0	0	
	human intervention	no	yes	no				no	no	no	
3	date	7-Apr	10-Mar	12-Mar				20-Jun	2-Mar	12-May	
	duration	1 day	1 night	1 day				1 day	2 nights	1 day	
	max. distance (km)	0.4	3.1	0.9 km				0	1.8	0.3	
	max. flight height (m)	0	1,420	525				510	0	45	
	human intervention	no	yes	no				no	yes	no	
4	date	22-Jul	1-Apr	23-Mar				26-Jun	11-Apr	26-Jul	
	duration	1 day	2 nights	1 day				3 nights	1 day	1 day	
	max. distance (km)	0.7	2.6	0.65				3.6	0.5	0.15	
	max. flight height (m)	0	1,160	925				0	0	0	
	human intervention	no	no	no				no	no	no	
5	date	18-Aug	1-May	11-May				14-Jul	12-May		
	duration	1 day	1 day	1 day				4 nights	1 day		
	max. distance (km)	0.5	0.75	0.4 km				4.85	1.75		
	max. flight height (m)	0	1090	530				0	0		
	human intervention	no	no	no				no	yes		
6	date		12-Jun	13-Aug				31-Jul	22-Jul		
	duration		1 day	1 day				1 day	3 nights		
	max. distance (km)		0.6	0.5				0.45	7.95		
	max. flight height (m)		300	0				120	610		
	human intervention		no	no				no	no		

Bird ID		005	006	012	002	003	007	000	001	026	008
Age		1	1	1	2	2	2	3	3	3	4
Excursion	date		28-Jul	19-Sep					3-Sep		
7	duration		1 day	4 nights					1 day		
	max. distance (km)		1.4	GPS failure					1.2		
	max. flight height (m)		420	GPS failure					410		
	human intervention		no	no					no		
8	date		29-Aug						20-Sep		
	duration		1 day						1 night		
	max. distance (km)		0.3						7.65		
	max. flight height (m)		385						220		
	human intervention		no						no		
9	date		19-Sep						26-Sep		
	duration		1 day						1 day		
	max. distance (km)		0.25						2.6		
	max. flight height (m)		0						1125		
	human intervention		no						no		
10	date		4-Oct						19-Oct		
	duration		1 day						1 day		
	max. distance (km)		0.2						2.3		
	max. flight height (m)		0						595		
	human intervention		no						no		

Appendix 7: Cumulative range maps for each chick over first 8 months post-release: 15 February 2015 – 31 October 2015.

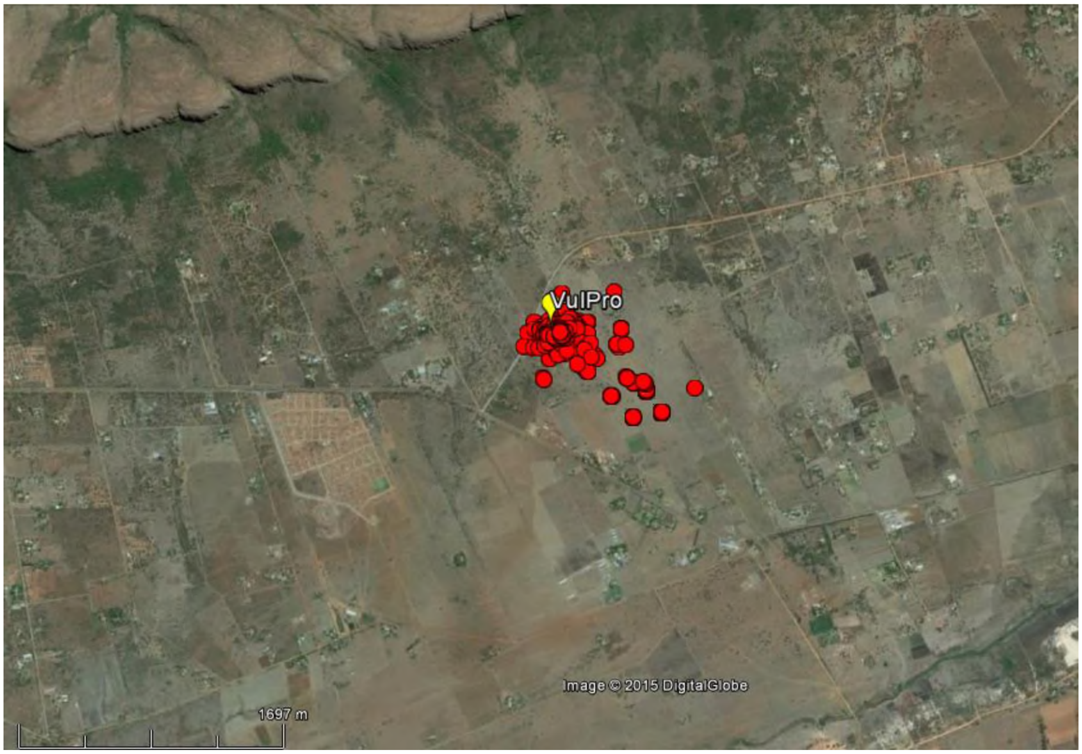


Chick 000

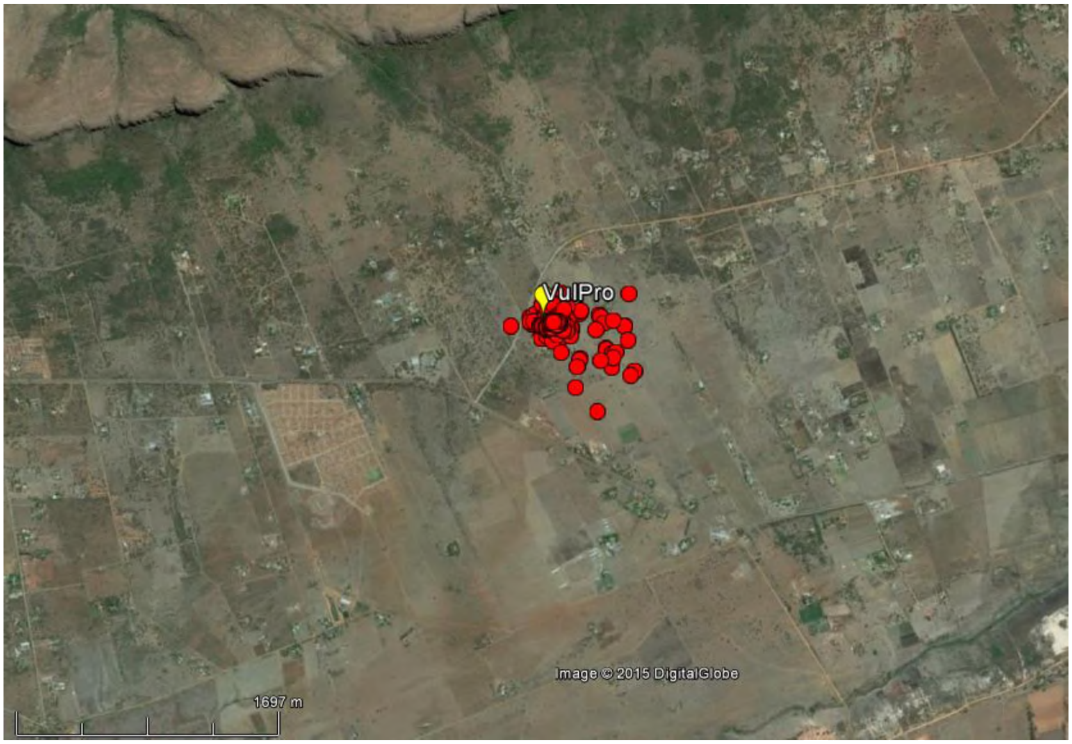


Chick 001

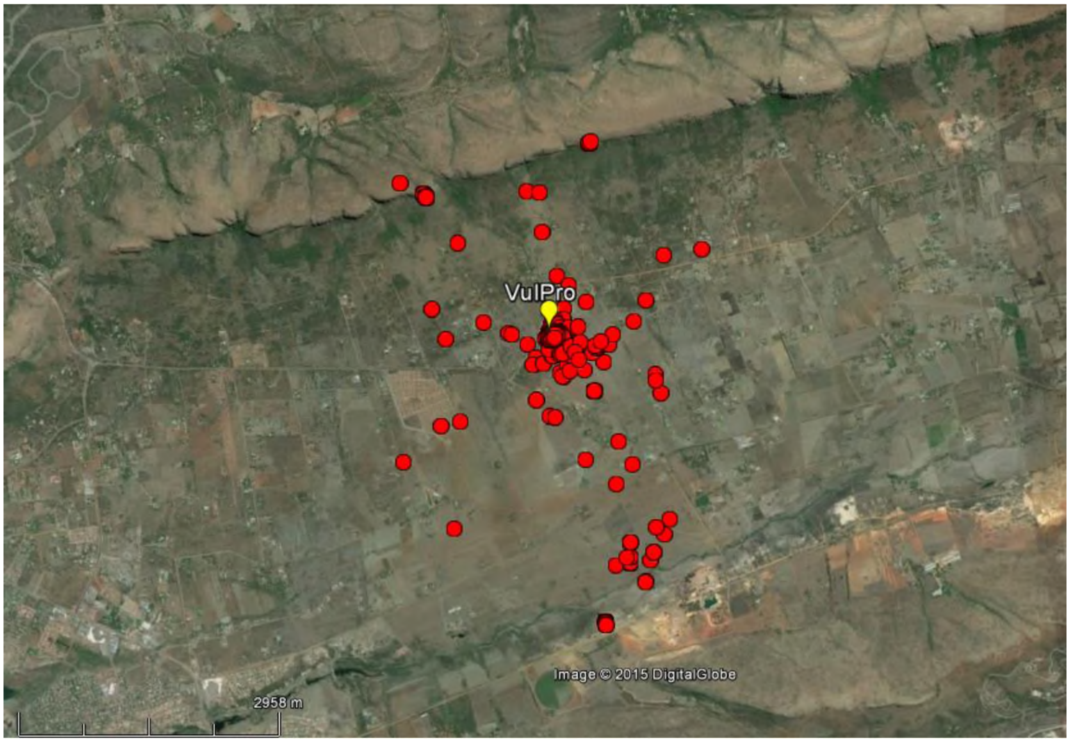
Chick 002



Chick 003



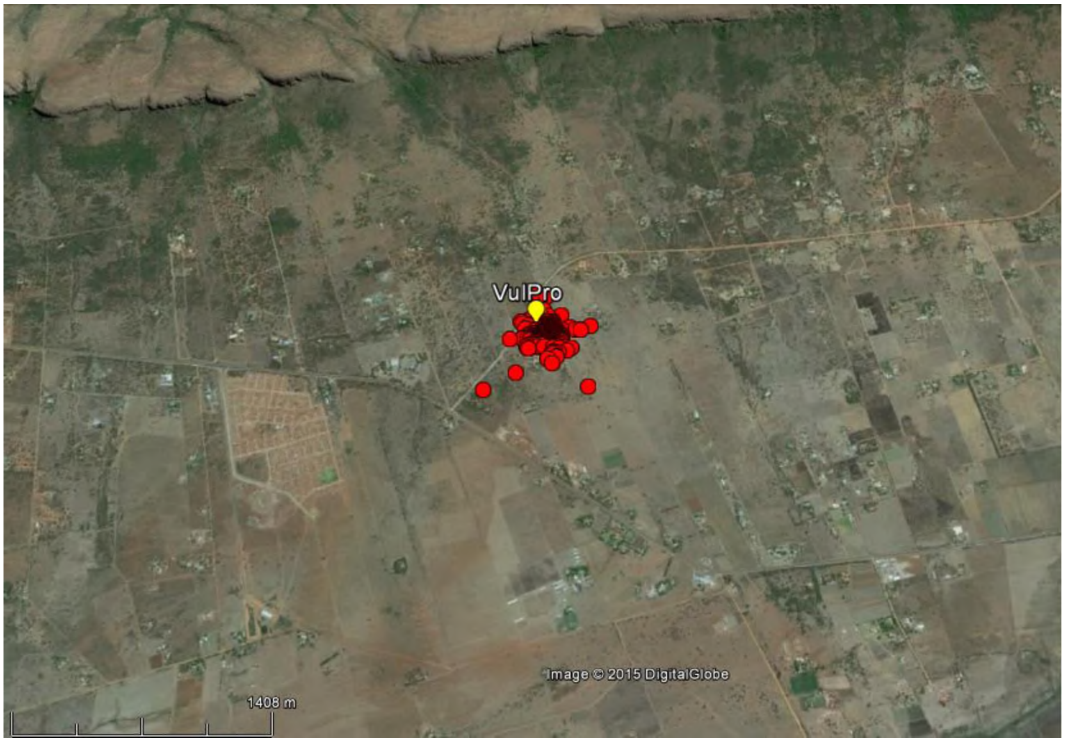
Chick 005



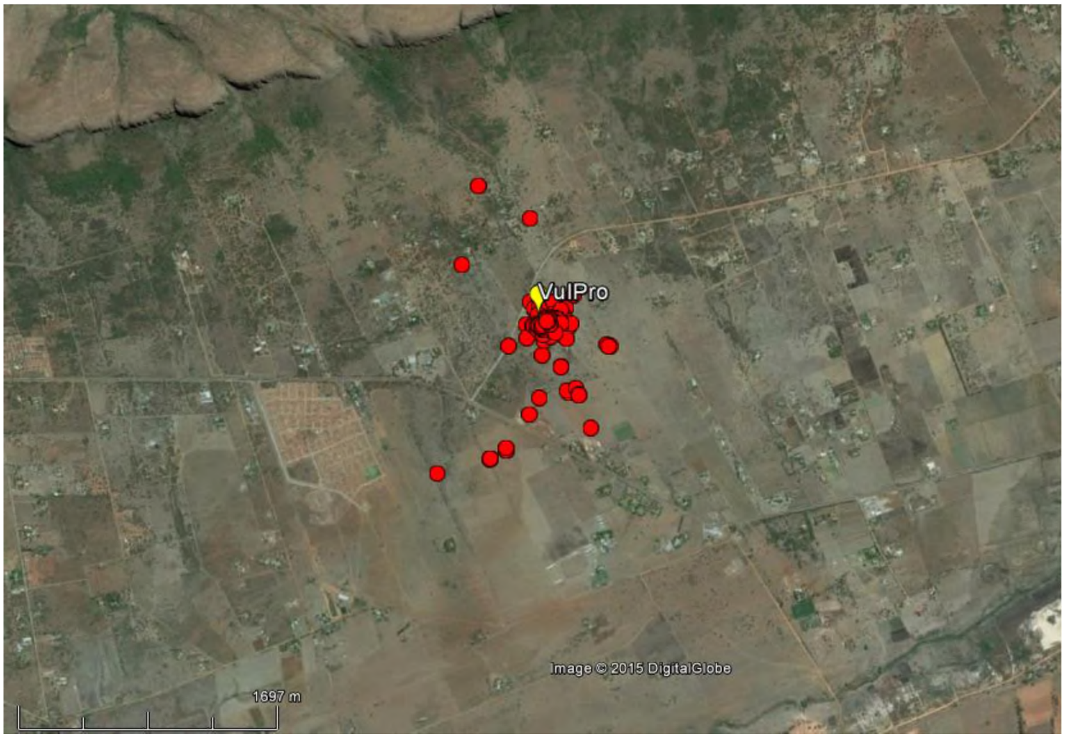
Chick 006

Chick 007

Chick 008



Chick 026



Chick 012

Appendix 8: Chicks 003 and 000 roosting on power line structures.