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# Long-term data indicates that supplementary food enhances the number of breeding pairs in a Cape Vulture *Gyps coprotheres* colony

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## Summary

The number of vultures is declining in many parts of the world due to numerous threats, such as poisoning and collisions with power-lines as well as the lack of adequate food sources. Vulture restaurants, i.e. supplementary feeding stations, have become a widespread conservation tool aimed at supporting vulture colonies. However, it is poorly understood how vulture restaurants influence population dynamics and whether they affect breeding success of vulture populations. We used a 12-year dataset from a breeding colony of the Cape Vulture *Gyps coprotheres* and a nearby vulture restaurant in South Africa to investigate the effect of supplementary food on population dynamics and breeding success. We found a significantly positive effect of supplementary food during the nest-building stage on the number of breeding pairs. However, breeding success, i.e. the proportion of successful nests, did not depend on supplementary food during the incubation and rearing stage. Especially during the critical rearing stage, the amount of food supplied might not have been sufficient to meet food demands of the colony. Still, our results indicate that carefully managed vulture restaurants might stabilise vulture colonies and can therefore aid vulture conservation.

## Introduction

Vultures are highly threatened in many parts of the world. Major threats are direct human impacts, such as poisoning, persecution, harvesting and killing for use in traditional medicine (Allan 1989, Oaks *et al.* 2004, Bamford *et al.* 2007, Ogada *et al.* 2012). Furthermore, vultures are indirectly threatened by human activities, e.g. by changes of sanitary regulations (Donázar *et al.* 2009, Margalida *et al.* 2010), the use of pharmaceuticals (Margalida *et al.* 2014), lead poisoning (Gangoso *et al.* 2009, Hernández and Margalida 2009), drowning in farm reservoirs (Anderson 2000), electrocution (Van Rooyen 2000), or collision with power lines (Ledger and Annegarn 1981, Boshoff *et al.* 2011) and wind farms (Carrete *et al.* 2012, Martínez-Abrain *et al.* 2012).

In addition the loss and transformation of natural habitat and breeding sites (Boshoff and Vernon 1980, Naidoo *et al.* 2011) have caused declines in vulture populations in many parts of the world. These are accompanied by the disappearance of large ungulate herds and changes in farming practice, leading to a decrease in the food supply for vultures (Boshoff and Vernon 1980, Naidoo *et al.* 2011). Some populations of vultures have become dependent on domestic livestock as their main food source (Vernon 1999, Gilbert *et al.* 2002, Margalida *et al.* 2011a; but see Kane *et al.* 2014).

Supplementary feeding stations ("vulture restaurants" or "food bonanzas") are seen as the key conservation intervention for vulture conservation in Europe, America and southern Africa (Gilbert *et al.* 2007, Cortés-Avizanda *et al.* 2010). In South Africa about 18% of supplementary food for vultures is supplied from state-managed protected areas and the majority (82%) comes from private commercial livestock farmers (Piper 2004). The main aim of supplementary feeding is to provide a regular supply of poison-free food to discourage vultures from feeding from uncontrolled sources (Anderson and Anthony 2005, Piper 2005, Gilbert *et al.* 2007, Margalida *et al.* 2014). Further, vulture restaurants are frequently used for long-term population monitoring, even though the resulting data have to be interpreted with caution (Margalida *et al.* 2011b). In spite of all these benefits there are still some aspects of potential conflict. For instance, vulture restaurants attract facultative scavengers, which may in turn act as predators on vultures and other species (Piper 2005, Cortés-Avizanda *et al.* 2010, Yarnell *et al.* 2015). Potentially, the success of vulture restaurants can also put the animals at risk of mass poisoning, e.g. through carcasses of animals that had been treated with non-steroidal anti-inflammatory drugs (Piper 2004, Oaks *et al.* 2004). Moreover, incorrect placement of feeding sites could expose vultures to threats such as power lines (Piper 2004).

The few studies that have investigated the direct effects of artificial restaurants on vulture breeding dynamics have found both positive (Piper *et al.* 1999, Vlachos *et al.* 1999, Oro *et al.* 2008, García-Ripollés and Lopez-Lopez 2011, Margalida *et al.* 2014) and negative effects (Carrete *et al.* 2006). In Bearded Vultures *Gypaetus barbatus*, the amount of available food is, along with low human population density and low vegetation cover, a major determinant of the selection of breeding sites (Gavashelishvili and McGrady 2006, Margalida *et al.* 2007), and supplementary feeding enhances both the number of breeding pairs and breeding success rates in Black Vultures *Coragyps atratus* (Vlachos *et al.* 1999). In contrast, in Bearded Vultures, the average number of fledglings raised per breeding pair declines with proximity to feeding stations, potentially owing to increased numbers of floaters and decreasing territory size (Carrete *et al.* 2006). The variability of these results might be due to the fact that effects of supplementary feeding vary with the breeding stage considered. Studies on other raptor species showed that supplementary feeding during breeding or in the pre-breeding season tends to improve breeding success due to a higher attentiveness and better body conditions of the breeding birds (Hansen 1987, Gehlbach and Roberts 1997). Supplementary feeding during the chick-rearing stage has been found to have a positive influence on survival rate and breeding success (González *et al.* 2006, Oro *et al.* 2008). A better understanding of the effects of supplementary feeding during different breeding stages is essential for the effectiveness of vulture restaurants as a conservation tool.

In our study, we examined the impact of supplementary feeding at a vulture restaurant on a breeding colony of the endangered Cape Vulture *Gyps coprotheres* over a 12-year period in KwaZulu-Natal, South Africa. We investigated the influence of supplementary feeding during different stages of breeding (i.e. pre-season, nest-building, incubation and rearing) on the number of breeding pairs and on breeding success (i.e. numbers of eggs incubated and large chicks). We predicted that there would be a positive relationship between supplementary feeding before egg-laying and the number of breeding pairs, assuming that the birds would enter the breeding season in a better body condition. We further predicted that breeding success would be positively correlated with the amount of food supplied at the vulture restaurant during critical phases of breeding (incubation and rearing).

## Methods

### *The study species*

The Cape Vulture is endemic to southern Africa (Bamford *et al.* 2007) and it is classified as "Vulnerable" on the IUCN Red List (Anderson 2000, IUCN 2014). There are approximately 3,700 breeding pairs of Cape Vultures in South Africa (Cape Vulture Task Force pers. comm.). Range and population size of the species have markedly decreased over the last century, due to low reproductive and survival rates and human-induced threats (Boshoff and Vernon 1980, Piper *et al.* 1981, Bamford *et al.* 2007, Monadjem *et al.* 2012). As it is one of the heaviest (8–10 kg) vultures in South Africa and plays an important role for the region by scavenging carcasses, the Cape Vulture is regarded as a flagship species for vulture conservation in southern Africa (Mundy *et al.* 1992, Piper *et al.* 1999).

The Cape Vulture feeds on the soft tissue of medium to large animals. An adult bird needs c. 1.5 kg of food every three days (Mundy *et al.* 1992). Activity range estimations of the species, obtained from observations, marking and satellite tracking, range from 1,940 km$^2$ to 482,000 km$^2$ (Robertson and Boshoff 1986, Bamford *et al.* 2007, Phipps *et al.* 2013).

The Cape Vulture is a social feeder and is the only South African vulture species nesting colonially on cliffs (Mundy *et al.* 1992). Up to 80% of a colony have been found to be involved in breeding each year, while the reasons for birds not breeding are unknown (Mundy *et al.* 1992, Piper 1994). The Cape Vulture starts copulating 2–3 months before eggs are laid (Mundy *et al.* 1992). Between May and June, the female lays a single egg (Mundy *et al.* 1992; average date 24 May, calculated across data from nine colonies). The periods of copulation and egg-laying are henceforth combined as nest-building stage. Males and females share incubation equally during the 52–54 day incubation period (incubation stage; calculating from average egg-laying date, the major incubation period is June to July; Mundy *et al.* 1992). During the rearing stage (August to December) the egg and the nestling are vulnerable to predation by both avian predators, such as Black Eagles *Aquila verreauxii*, crows *Corvus* spp., or White-necked Ravens *C. albicollis*, and mammalian predators such as chacma baboons *Papio ursinus* (Mundy *et al.* 1992). After an average nestling period of 140 days, the birds begin to fledge in November to December (Piper *et al.* 1981, Mundy *et al.* 1992).

Overall, a family (i.e. two adult birds and one nestling) is estimated to require 230 kg of meat during the entire nestling period (Komen and Brown 1993). Two to three months after hatching (end of September to end of October, when calculated from average laying date; see above), the nestling requires about 900 g of food each day (Komen 1991, Mundy *et al.* 1992). Owing to the high demand, this period is critical in food supply (Mundy *et al.* 1992).

### *The study colony*

The study was conducted at the Mzimkhulu colony in southern KwaZulu-Natal, South Africa (30°39′43.63″S, 30°14′39.30″E). The colony is situated on private land of M. Neethling, 22 km from the Indian Ocean on rugged sandstone cliffs overlooking the Mzimkhulu River. The landscape in the coastal area around the colony is characterised by sugar-cane farming. Livestock farming in KwaZulu-Natal is mainly based in the Midlands, c.200 km to the north-west (Ngcobo and Dladla 2002).

The roosts have been occupied at least since the 1960s (M. N. pers. obs.). The colony is spread across several nesting sites along the length of the cliff face that has been used to varying degrees over the years. In 2012 the colony comprised c.120 birds, with 49 active breeding pairs. Only a small number of the birds are individually marked, thus immigration and emigration rates or survival rates are unknown. Main predators at the colony are White-necked Ravens (M. N. pers. obs.). Black Eagles are also well-known predators at Cape Vulture colonies in general (Mundy *et al.* 1992), but are not regularly observed here. A vulture restaurant site is in close proximity to the colony (Mzimkhulu vulture restaurant; 30°39′44.43″S, 30°14′40.80″E). The distance to the nearest known vulture restaurant apart from this is c.90 km (VulPro pers. comm.). The distance from the nearest known colony (Msikaba colony) is c.70 km.

### *Determination of nest numbers and breeding success*

Monitoring of the colony began in 2001 and consisted of biannual counts for the entire study period. During this time, the breeding sites and roosting ledges were observed from six observation points by two or more counters using binoculars and telescopes. Sets of reference photographs were taken of the cliffs from each observation point. Nesting sites were marked on these photographs so that they could be tracked through the nesting season and the use of nesting sites was monitored over time. The dataset we used for this study contained the combined monitoring results of all six observation points from 12 years of observations spanning 2001 to 2012 (Figure 1).

The first count was conducted in June each year to record the number of breeding pairs at the beginning of the breeding season. All the nests with incubating adults were counted. Nests that had failed before the first count were not recorded. The second count was conducted in late September each year to record the number of failed nesting attempts and surviving nestlings up to that stage. Breeding success was calculated as the number of nests with large nestlings at the September count as a proportion of the number of nests occupied by incubating adults at the beginning of the breeding season in June. As the last count in the season was done in September, we do not have information about later survival of the nestlings before fledging. We are thus aware that our measure is not an exact representation of annual breeding success, as some of the large chicks might still die before they fledge, however, according to our monitoring experience (M. N., R. U. pers. obs.), mortality of chicks on the nest is low once they are large, which is why we assume that our measure is representative of the exact breeding success.

In addition, we calculated the total size of the population based on Piper (1994) as 2*breeding pairs*1.25). We are aware that this only gives a rough estimate of the population size, as it does not account for non-breeding floaters settling at the colony at times of high food supply.

## *Supplementary food*

The vulture restaurant is situated on private land about 200 m away from the edge on top of the breeding cliff. It has been run continuously by M. N. since the year 2001. Carcasses (domestic cows, pigs, and plains zebras *Equus burchelli*) have been provided by surrounding livestock farmers and the local nature conservation organization Ezemvelo KZN Wildlife. Feeding is irregular, driven by the availability of mortalities in the surrounding area. Birds from the colony and from the nearest colony at Msikaba frequently use the restaurant site all year round, as could be confirmed by resightings of tagged birds. Moreover, large numbers of birds that potentially do not breed at the colony are regularly observed (M. N., D. G. S. pers. obs.).

The restaurant database we used for this study included the kind of carcass (e.g. pig, cow) together with the date, covering the years 2001–2012. We used an average weight for each carcass type obtained from several sources (Jungius 1971, Bowland *et al.* 2001, Ogunsanmi and Taiwo 2001, Fick *et al.* 2006, Kirby *et al.* 2008, Grey-Ross *et al.* 2009, Kamler *et al.* 2013). These average weights were used to calculate the amount of supplementary food in kilograms provided during the different breeding stages (pre-season, nest-building, incubation, rearing stage; see above).

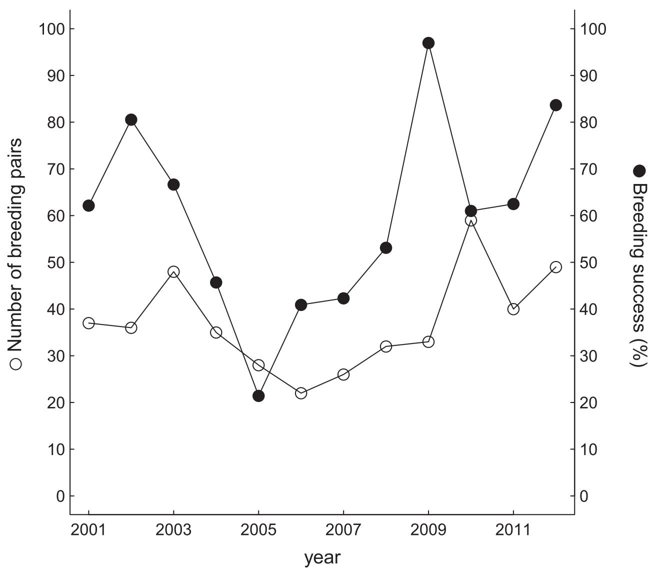


Figure 1. Number of breeding pairs (white) and breeding success (black; number of nestlings as a percentage of nests built) of the Cape Vulture *Gyps coprotheres* across 12 years (2001–2012) of supplementary food provision at the Mzimkhulu vulture restaurant, South Africa.

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## *Rainfall data*

Abundant rainfall has been shown to have a negative effect on the egg-laying date of Cape vultures (Mundy *et al.* 1992, Robertson and Boshoff 1986). Moreover, rainfall of the pre-season or of the breeding season may have both positive and negative effects on the breeding success of raptor species (Monadjem and Bamford 2009, Väli 2012, Anctil *et al.* 2014). Thus, we included the amount of rainfall as a covariate in the analyses. Rainfall data came from a nearby farm (within 5 km of all the roost sites) where it was measured daily for the duration of the study period by M. N. (Figure 2).

## *Data*

For the analyses we constructed a dataset including the study year (2001 to 2012), month, number of breeding pairs counted at the beginning of the breeding season, annual breeding success (i.e. number of large nestlings divided by the number of initial nests), estimated population size, the amount of supplementary food (kg per month) as well as average monthly rainfall (mm). To assess the effect of supplementary food during different breeding stages, we divided the dataset into the following stages: (1) pre-season, i.e. January and February, (2) the nest-building stage, as the time during copulation and egg-laying between March and June; (3) the incubation stage, representing the time of incubation from June to July; and (4) the rearing stage, which was the time after hatching, with young nestlings during August and September. The months October to December were omitted from the rearing stage as the count of large chicks took place in September, and we do not have information of the fate of nestlings after that. For each stage, we summed the total amount of supplementary food provided and calculated the total amount of rainfall. The total population size of the colony in each year was calculated from the number of breeding pairs. As we intended to use the number of breeding pairs as a dependent variable in our analyses, we refrained from using the per capita amount of food (i.e. amount of food/population size) as an explanatory variable, but used the absolute amount of food instead.

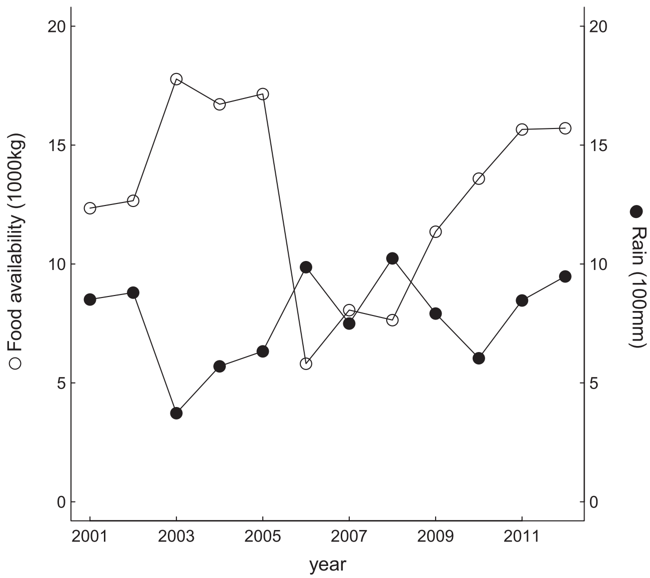


Figure 2. Food availability (1,000 kg; white) and rainfall (100 mm; black) at the study colony of the Cape Vulture *Gyps coprotheres* across 12 years (2001–2012) of supplementary food provision at the Mzimkhulu vulture restaurant, South Africa. Note that food amount in kg was multiplied by 1,000 and rainfall in mm by 100 for graphical presentation only.

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In a first analysis, we tested whether the total amount of supplementary food and total rainfall during the pre-season or during the nest-building stage had an influence on the number of breeding pairs using a generalized linear model (model formula: NumberOfNests~ RainPreSeason+ FoodPreseason+RainNestbuilding+FoodNestbuilding). Owing to overdispersion of our model, we used a quasi-Poisson error structure (Crawley 2007). In a second analysis, we tested whether the amount of supplementary food provided and total rainfall during the pre-season or during the incubation and during the rearing stage had an effect on breeding success (model formula: BreedingSuccess~ RainPreSeason+FoodPreSeason+RainIncubationAndRearing+FoodIncubation+ FoodRearing). As breeding success is the proportion of successful nests at the end of the breeding season, we used a generalized linear model with a quasi-binomial error distribution.

For both analyses, we selected the best model set starting from a global model including all predictor variables (see model formulas above). Model selection was performed using QAICc (package MuMIn). We then averaged parameter estimates and their significance across the set of best models (delta QAICc < 2; Symonds and Moussalli 2011). All statistical analyses were performed with R 3.0.1 (R Development Core Team 2013).

We are aware that large birds might react to long-term changes in conditions rather than to short-term changes. Thus, we did separate analyses including the amount of food supplied and the amount of rainfall during the entire pre-season year (focal year – 1, months January to December) instead of the pre-season in the models depicted above. Results remained qualitatively similar, except for a positive effect of rain in the previous year on breeding success (see the online Supplementary Material for further details).

## Results

The population size during the study period ranged from 55 birds in 2006 to 148 birds in 2010 (mean = 93 ± 27 standard deviation, mean ± SD hereafter). During the study period, the number of breeding pairs ranged from 22 in 2006 to 59 in 2010 (37 ± 11). The mean breeding success was 60% (± 21%) with a minimum of 21% in the year 2005 and a maximum of almost 97% in 2009 (Fig. 1).

### *Influence of supplementary food on the number of breeding pairs*

During the nest-building stage a minimum amount of 2,640 kg food was supplied in 2008 and a maximum amount of 9,080 kg food in 2003 (5,440 kg ± 1,800 kg; Figure 2). Model selection revealed that the amount of supplementary food during the nest-building stage and pre-season rainfall were the only variables contained in the set of best models (delta QAICc < 2; Table 1). Model averaging then revealed that the amount of supplementary food during the nest-building stage had a positive effect on the number of breeding pairs ($z = 2.86$; $P = 0.004$; Figure 3). The amount of rainfall during the pre-season had a significantly negative effect on the number of breeding pairs ($z = 2.19$; $P = 0.028$).

### *Influence of supplementary food on breeding success*

Food supply during the incubation stage ranged from a minimum of 1,670 kg supplied in 2004 to a maximum of 6,710 kg in 2010 (3,380 kg ± 1,530 kg). The amount of supplementary food for the rearing stage ranged from 0 kg in 2007 to 3,640 kg in 2010 (1,550 kg ± 1,080 kg). The best model identified with the help of QAICc was the null model including only the intercept and none of the predictor variables (Table 2).

## Discussion

Our 12-year data set showed a significantly positive influence of the provision of supplementary food during the nest-building stage on the number of breeding pairs. Contrary to our expectations, the provision of supplementary food during incubation and rearing stages was not related

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Table 1. Model selection table showing the set of the five best models testing for an effect of the total amount of supplementary food and total rainfall during the pre-season or during the nest-building stage on the number of breeding pairs. Parameter estimates of the respective variables, QAICc-values, delta (difference between QAICc of the respective model and the best model) as well as QAICc-weights are given. QAICc-values of models used for model averaging of parameter estimates and their significance are highlighted in bold-face type.

| Model number | Food during pre-season | Food during nest-building | Rain during pre-season | Rain during nest-building | QAICc | Delta QAICc | QAICc weights |
|---|---|---|---|---|---|---|---|
| 1 | - | 0.00 | - | - | 56.80 | **0.00** | 0.35 |
| 2 | - | - | -0.00 | - | 58.60 | **1.78** | 0.14 |
| 3 | - | 0.00 | -0.00 | - | 58.60 | **1.80** | 0.14 |
| 4 | - | - | -0.00 | -1.23 | 59.10 | 2.34 | 0.11 |
| 5 | 0.00 | 0.00 | - | - | 60.10 | 3.28 | 0.07 |

to the annual breeding success. Furthermore, rainfall during the pre-season had a negative effect on the number of breeding pairs.

### *Influence of supplementary feeding on nest building and breeding success*

Our results showed a significantly higher number of breeding pairs in years with a larger quantity of supplementary food. This result is in line with a study by Hansen (1987) who showed an increase of breeding density in a Bald Eagle *Haliaeetus leucocephalus* population due to supplementary feeding.

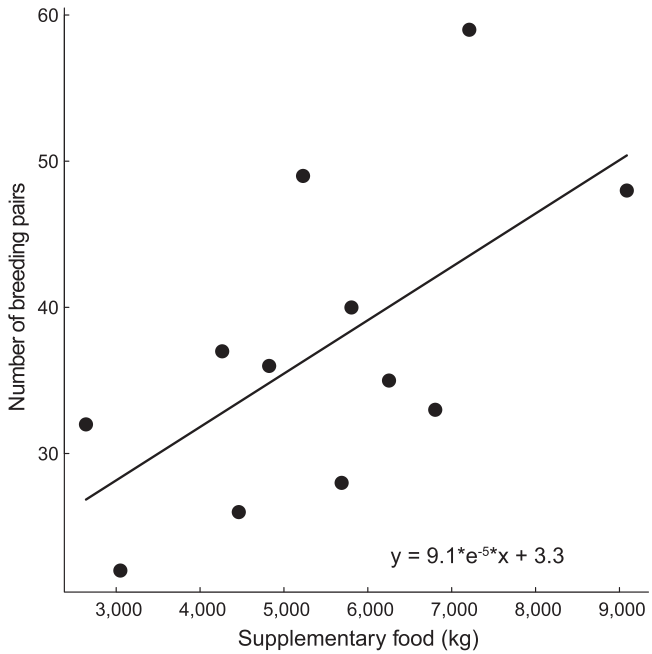


Figure 3. Effect of supplementary food during the nest-building stage on the number of breeding pairs of the Cape Vulture *Gyps coprotheres* during 12 years (2001–2012) of supplementary food provision at the Mzimkhulu vulture restaurant. The formula gives the relationship among the number of breeding pairs (y) and the amount of supplementary food (x; in kg) as derived from a model-averaging of parameter estimates (for statistical details see results).

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Table 2. Model selection table showing the set of the five best models testing for an effect of the amount of supplementary food provided and total rainfall during the pre-season or during the incubation and during the rearing stage had an effect on breeding success. Parameter estimates of the respective variables, QAICc-values, delta (difference between QAICc of the respective model and the best model) as well as QAICc-weights are given. QAICc-values of models used for model averaging of parameter estimates and their significance are highlighted in bold-face type.

| Model number | Food during pre-season | Food during incubation | Food duirng rearing | Rain during pre-season | Rain | QAICc | Delta QAICc | QAICc weights |
|---|---|---|---|---|---|---|---|---|
| 1 | - | - | - | - | - | 16.70 | **0.00** | 0.48 |
| 2 | - | - | - | -0.00 | - | 19.90 | 3.16 | 0.10 |
| 3 | | | | - | 0.00 | 20.10 | 3.32 | 0.09 |
| 4 | - | 0.00 | - | - | - | 20.30 | 3.52 | 0.08 |
| 5 | 0.00 | - | - | - | - | 20.30 | 3.53 | 0.08 |

Moreover, it is known that food abundance has a positive influence on the number of breeding pairs in Ferruginous Hawks *Buteo regalis* and Tawny Owls *Strix aluco* (Southern 1970, Smith *et al.* 1981). As mature Cape Vultures settle at one colony, and most likely their natal one (Mundy *et al.* 1992), the positive effect on the number of breeding pairs found here is unlikely to be caused by the attraction of a higher number of breeders in years of high food supply. An explanation for this result could be that the parental birds enter the nest-building period in a better body condition due to the additional food. Consequently a larger number of breeding pairs are able to lay eggs (Hansen 1987, Gehlbach and Roberts 1997). In general, as the number of breeding pairs was positively related to the number of fledglings at the end of the breeding season in our study ($r = 0.84$, $P < 0.001$), a larger quantity of supplementary food during the nest-building stage could potentially be a tool to stabilise a vulture colony. Yet, the interplay of supplementary feeding with other factors influencing breeding success, e.g. stage-specific survival rates, weather conditions, disturbance or demographic variability need to be elucidated before management recommendations can be made (Donázar *et al.* 1993, Arroyo and Razin 2006).

Contrary to our expectations we found neither an effect of supplementary food during the incubation stage, nor during the rearing stage on the annual breeding success, i.e. on the proportion of successful nests at the end of the breeding season. This result disagrees with a number of other studies on raptors that showed higher egg survival rates and hatching success due to supplementary feeding (Hansen 1987, Gehlbach and Roberts 1997, González *et al.* 2006). A reason for the contrasting result found in our study could be that the focal species of the aforementioned studies are all facultative scavengers that lay more than one egg. For these species, supplementary feeding increases the number of fledglings per brood by e.g. reducing sibling aggression (González *et al.* 2006). Our study species is a specialised obligate scavenger with a clutch size of one. Thus, there is no gradual effect of supplementary feeding on breeding success of single pairs, but merely a decision between survival or death of the only chick. Added to this, the contrasting results may arise from the strong variation in population size during our study period and owing to external factors not measured here. For example, one known source of variation in population size was a poisoning incident in 2005, when a horse that had been treated with veterinary drugs was accidentally supplied as food (M. N. pers. obs.). This is believed to have resulted in the decrease in this Cape Vulture population from 70 birds in 2005 to 55 in 2006. Despite this, additional analyses excluding the year 2005 in the analyses of breeding success, and the year 2006 in the analyses of the number of nests, revealed qualitatively similar results as the initial models. Thus, the decrease in the population did not influence the overall findings of our study.

Our results are in line with a study by Margalida (2010) on Bearded Vultures, that also found that supplementary feeding during the rearing stage is ineffective in increasing breeding success. Vultures breeding close to a vulture restaurant may be exposed to higher predation pressure and more interspecific competition at the feeding site (Anderson and Anthony 2005). As a consequence of higher food availability, vulture restaurants may attract predatory species such as crows or ravens, which may act as predators of vulture eggs and chicks and as food competitors

(Anderson and Anthony 2005). The degree of competition with this facultative scavenging community may thereby vary with the type of carcass supplied (Moléon *et al.* 2015). Moreover, especially in years with high food availability high numbers of floaters might use the restaurant. While breeding birds have to return to their nest, floaters can occupy the feeding site for a longer time. This may in turn increase intraspecific competition for food (Carrete *et al.* 2006). The interplay of these factors might attenuate potential positive effects of supplementary feeding on breeding success. Moreover, assuming that a chick needs 900 g of food per day (Mundy *et al.* 1992) during the phase of maximum food demand, the average demand of the chicks alone at our colony should be c.2,000 kg (average of 37 nests across years). In contrast, the average food supply during the rearing stage at the study restaurant was 1,550 kg. This indicates that the amount of food provided during the chick-rearing stage may not have been sufficient to have a positive effect on breeding success. To meet their demands, the birds rely on other food sources at greater foraging distances.

### *Influence of rainfall*

Our results showed a significantly lower number of breeding pairs in years with high rainfall during the pre-season (January/February). This is in line with other studies that showed that Cape Vultures and other scavenging bird species are sensitive to rainfall (Mundy *et al.* 1992, Robertson and Boshoff 1986, Monadjem and Bamford 2009, Anctil *et al.* 2014). After months with heavy rainfall, birds can start the breeding season in a lower body condition, and thus fewer pairs start breeding. In contrast to this, high amounts of rainfall during the year preceding the breeding year led to high breeding success (Tables S1, S2). While explanations for this pattern remain speculative and could potentially be related to habitat quality and higher natural food availability in the landscape, these results show that long-term abiotic conditions may be an important driver of vulture population dynamics.

### *Potential implications for vulture conservation*

We are aware of several limitations inherent to our data. First, we have no information about the availability of food in the surroundings of the study colony apart from the study restaurant. Yet fluctuations in food availability are likely to have a strong impact on the dependence of the colony on the adjacent restaurant (Moreno-Opo *et al.* 2015). More detailed analyses of the foraging activity of the birds, e.g. obtained with the help of satellite transmitters, would be useful to assess the importance of the study restaurant in comparison to other unknown food sources. Moreover, we are aware that our conclusions are based on the analyses of one colony and restaurant site only. There are only few cases where a restaurant is adjacent to a colony and even fewer where the exact amount of food supplied has been recorded over a long time period. Despite these limitations, our results showed a significantly higher number of breeding pairs in years with a larger amount of supplementary food during the nest-building stage. If this conclusion holds for other colonies as well, vulture restaurants could be used as a successful conservation tool, since feeding during the nest-building stage can increase the number of breeding pairs and ultimately the number of offspring. However, we found no influence on annual breeding success, i.e. on the proportion of successful nests. Thus, the amount of food provided at a restaurant which relies on irregular food supply may not fulfil a colony´s demands for food during critical breeding stages. A possible recommendation for the study restaurant would be to increase the amount of food provided during these times of food deficiency (see also Kane *et al.* 2014), but thorough investigations on the interplay between intra- and interspecific competitors are necessary before phrasing such recommendations. Moreover, despite the lack of an overall effect, a high amount of supplementary food might be critical for breeding success during years with particularly unfavourable breeding conditions, e.g. due to food scarcity or weather extremes. Finally, our measure of breeding success was based on the number of large chicks towards the end of the breeding season. Thus, the potential positive effects of supplementary food on offspring survival in the first months after fledging still need to be investigated.

To conclude, it is important to ensure that supplementary feeding programs are extensively managed and only poison-free and good quality food is supplied. Meeting these standards, the provision of supplementary food at restaurants has the potential to be an effective tool to support vulture colonies.

## Supplementary Material

To view supplementary material for this article, please visit https://doi.org/10.1017/S0959270915000350

## Acknowledgements

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