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Reintroducing endangered raptors: a case study of supplementary feeding and removal of nestlings from wild populations

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ABSTRACT

1. Supplementary feeding is a common practice to raise reproductive output in raptors and other species; nevertheless, its application in conservation has only recently been critically discussed. Here we analyse the effect of supplementary feeding in territorial raptors, taking advantage of two long-term data sets for the Spanish imperial eagle (*Aquila adalberti*) and bearded vulture (*Gypaetus barbatus*). In both species, supplementary feeding was used over four years, allowing the extraction of eggs or nestlings for reintroduction programmes.

2. Both populations increased during the last 20 years. In 2001 only 10 Spanish imperial eagle pairs were found in Sierra Morena, increasing to 91 pairs in 2015 (810% of increase). The Bearded vulture population in Aragon increased from 15 occupied territories in 1988 to 67 in 2012 (347% of increase). Density-dependent breeding productivity on habitat heterogeneity was established in both populations.

3. Results of Generalised linear mixed model (GLMM) analysis with relative productivity as the dependent variable, species and supplementary feeding as fixed factors and territory as random factor, showed a significant effect of supplementary feeding on relative productivity in both species as well as in the interaction between territory and supplementary feeding. This implied a different response among territories to supplementary feeding. Birds in poor quality territories with low productivity levels responded more strongly to supplementary feeding than birds in territories with higher levels of natural productivity.

4. A reintroduction programme based on supplementary feeding and extraction of nestlings costs eight times less than the same program based on captive breeding, and takes ten years less.

5. *Synthesis and applications.* Supplementary feeding in territorial raptors could be useful in two situations: (i) in an episodic main prey collapse and (ii) in poor quality territories in a high density population, to produce extra young for reintroduction programmes. For greatest efficiency, supplementary feeding needs to be targeted at the poorer territories in which the reproductive rate has the potential to be raised by provision of extra food. The extra young produced can then be used in reintroduction programmes in which their chances of recruiting to a breeding population are high.

Keywords: cost analysis, habitat heterogeneity hypothesis, reintroduction, relative productivity, supplementary feeding, translocation, Spanish imperial eagle, bearded vulture, raptor, nestling

Introduction

Supplementary feeding is a common practice to raise reproductive output in raptors and other bird species, either for experimental or for conservation purposes (e.g. California condor, Wilbur, Carrier & Borneman 1974; sparrowhawk, Newton & Marquiss 1981; various vulture species, Terrasse 1985; common kestrel, Wiehn & Korpimaki 1997; Spanish imperial eagle, Gonzalez *et al.* 2006; Ferrer & Penteriani 2007; bearded vulture, Margalida 2010). Despite the widespread use of this technique over the last 50 years, particularly in endangered species, its application in conservation has only recently been critically discussed (Cortés-Avizanda *et al.* 2016), revealing important differences in evaluation of the technique. Some claim major beneficial effects at the population level, but others little or no effect (Carrete et al. 2006, Gonzalez *et al.* 2006, Margalida 2010, Margalida *et al.* 2016, Oro *et al.* 2008).

Additional potential problems with this technique have been suggested; for example, that predictable human-provided food sources could increase the survival of individuals that would otherwise disappear as a result of natural selective processes, favouring some kind of artificial selection (Blanco 2006). It is further claimed that such human-based food supplies could lead to an uncertain future for some populations, functional guilds, and, ultimately, communities (Cortés-Avizanda *et al.* 2016). In these studies, supplementary food is viewed as representing a major modification of the natural distribution of resources, the consequences of which may reach the ecosystem level, potentially influencing vegetation and abiotic components such as soil nutrients and water.

Evaluations of food provision projects could depend partly in the way in which food is provided. One type aims to feed large numbers of birds in one place, e.g. at rubbish dumps or by design, e.g. at 'vulture restaurants' (Cortés-Avizanda *et al.* 2016). At such communal feeding stations, food provision usually takes place year round, and over many successive years, all the time providing sufficient food for many birds. In conservation terms, such programmes are aimed mainly to increase overall population size, but often also have educational or tourism values.

In a second type, supplementary feeding is targeted at particular territorial pairs within a population, and is done for only a limited period each year. Typically, food is placed every day or two close to the nests of selected pairs for part or all of the breeding cycle from before laying to independence of young, depending on the objective. The usual aims are to increase clutch size or prevent nestling deaths by increasing nutritional condition of adults. For this reason, cainistic species (which often show brood reduction through aggressive interactions among nestlings) are frequently targeted, so as to increase overall productivity (Ferrer & Penterian 2007; Morandini & Ferrer 2015). This technique works particularly well in populations where territories vary in quality, where

provisioning can be concentrated in the poor-quality territories, in which the occupants readily respond by producing extra young, bringing their brood sizes up to those typical of good territories. Consequently, by providing food in poor territories, the total productivity of the population can be raised. These "extra young" could enable a depleted population to expand more rapidly, or could be used in reintroduction programmes for other areas, all without reducing the reproduction of the existing population below its natural level (Ferrer *et al.* 2014, 2016).

Here we analyse the effect of supplementary feeding on territorial raptors, taking advantage of long-term data sets for the Spanish imperial eagle (*Aquila adalberti*) and bearded vulture (*Gypaetus barbatus*). In both species, supplementary feeding was used over several years to increase productivity, allowing the extraction of eggs or nestlings for reintroduction programmes. Breeding performance was density-dependent in relation to habitat heterogeneity in both species (Ferrer & Donazar 1996, Ferrer *et al.* 2014, Morandini *et al.* 2017). Some (high quality) territories showed consistently high productivity and others consistently low productivity. At low population levels, mainly high quality territories were occupied, but as numbers grew more poor territories were occupied, lowering the overall production per pair in a density dependent manner. Differences in quality between territories have been explained by differences in food availability, degree of human disturbance, mortality factors and other differences (Newton & Marquiss 1976; Newton 1991; Ferrer & Donazar 1996; Ferrer & Bisson 2003). However, food availability is one of the most common factors limiting territory quality and also one of the easiest to manipulate. Our aims here are to determine the effect of supplementary feeding on the number of extra-young produced and toanalysethe cost of this procedure in comparison to the alternative method of captive breeding. On the basis of these findings, we make recommendations for the use of targeted supplementary feeding in the future.

Materials and Methods

Study species

The Spanish imperial eagle is one of the rarest eagles in the world (Vulnerable in the IUCN Red List), with around 500 breeding pairs in 2016 (National Working Group, unpublished data 2016), located entirely in the Iberian Peninsula. The species is a large (2500-3500 g), long-lived raptor with a maximum recorded lifespan of 22 years, and delayed maturity (adult plumage at 4–5 years old; Ferrer, 2001). It is monogamous, sedentary and territorial, with a low annual productivity averaging 0.75 chicks/pair (range 0-4; Ferrer & Calderón 1990). Reproduction usually lasts 8 months from February, when laying starts, until October when the latest juveniles leave the natal area (Ferrer, 2001). This species is considered to be a facultative cainist. The monitored nests were at the

northern limit of Andalusia (≈38°22'N 3°50'W), in the Sierra Morena, occupying a large part of the southern Iberian Peninsula and a wide altitudinal range (0-2000 m.a.s.l.), with a dry-humid Mediterranean climate (annual rainfall: 300-2000 mm, average annual temperature: 9-19ºC). The landscape consisted of a mosaic of Mediterranean forests, scrublands and grasslands in hilly and mountainous areas, crops in lowlands and coastal wetlands. A reintroduction program has been running in Cádiz province (south of Spain) since 2003.

The bearded vulture is another large (4,500-7,000 g) long-lived territorial raptor, with a maximum recorded lifespan of 32 years (Lopez-Lopez et al. 2013; Ferrer et al. 2014 and references therein), and delayed maturity (adult plumage at 5–7 years old), that breeds in sparsely distributed territories in mountainous regions (Donázar, Hiraldo & Bustamante 1993). Annual productivity in Spain averages 0.65 young per pair (range 0-1). The species is an obligate cainist, laying two eggs but raising at most one young. The species feeds mainly on large fresh bones of ungulates which it swallows whole or in pieces. Its numbers and breeding range declined throughout Europe during much of the twentieth century (Hiraldo, Delibes & Calderón 1979; Mingozzi & Estève 1997), and three reintroduction programs are currently underway, one in Switzerland and two in Spain (Ferrer et al. 2014). The only surviving bearded vulture population in the Spanish Pyrenees is composed of 186 reproductive units (mostly pairs, but some polyandrous trios), 78 of them in the region of Aragon (Spanish bearded vulture working group unpublished data).

Data collection and supplementary feeding
For the Spanish imperial eagle, data were derived from a total of 91 different territories in the Sierra Morena from 2012 to 2015 (n=325 breeding attempts). We considered a territory as occupied when it held a pair showing breeding behaviour (nest construction, defence or incubation). All nests were monitored from the beginning of the breeding season (January–February, during the courtship and nest site selection stages; Ferrer, 2001) until the last chick left the natal territory. Productivity was calculated as the number of fledglings per territorial pair per year. Supplementary food in the form of domestic rabbits (around 400 g.) was provided to individual pairs. Technical assistants deposited 1–2 rabbits each day on ledges unreachable by terrestrial carnivores, at a medium distance of 340 m from the nest. The eagles readily accepted this supplementary food. Feeding started in February and finished in June, when the young were large, and was provided to 35 different territories, some in more than one year (n=86). Young from these nests were removed at 35-45 days old. In territories where food was provided, the occupants had a history of poor breeding.

The whole bearded vulture population in the Aragonese Spanish Pyrenees area (approx. 7600 km^2) was monitored for 25 years from 1988 to 2012 inclusive. Each year, all known territories

as well as other potential breeding areas were carefully searched for birds, nests or other signs of occupancy during the breeding season (November to August). Occupied territories were located on the basis of territorial or courtship activity and breeding parameters were then recorded on later visits (see Margalida *et al.* 2003). At the population level, productivity was measured as the mean number of fledglings raised per territorial pair, including breeding failures and taking into account that no more than one nestling could be reared per breeding attempt. Supplementary feeding was conducted over 4 years (2007–2010) with the aim of improving the physical condition of particular breeders in the pre-laying period and stimulating the laying of viable eggs. Feeding started on 31 October and finished on 31 March, about 30 days after egg laying. Technical assistants deposited 15–18 kg of bones (acquired from a slaughter house) each day on ledges unreachableby terrestrial carnivores, at a medium distance of 1118 m from the nest. During the 4 years, around 5,108 kg of bones were supplied, divided among 11 different territories. In order to avoid competition with other more generalist scavengers, such as griffon vultures *Gyps fulvus* or corvids, a specific diet was provided for individual reproductive units based on sheep and goat bones. Supplementary feeding was provided to 11 different territories which had a history of poor breeding success (n=22 breeding attempts). The young were removed at different ages (from 10-45 day-old), and hand-reared for later release. In some cases, eggs were removed before hatching.

Financial Cost analyses

In order to analyse the relative financial costs of alternative approaches to obtaining young for release, we compared the budget of two typical captive breeding programmes, one of bearded vultures, conducted by the Gypaetus Foundation in Spain (http://www.gypaetus.org/), and other of Spanish imperial eagles, operated by the Migres Foundation (www.fundacionmigres.org/es/), with the cost of two supplementary feeding and extractions programs, one with bearded vultures conducted by Fundación para la Conservación del Quebrantahuesos in the Pyrenees (http://www.quebrantahuesos.org/), and the other affecting Spanish imperial eagles in Andalucía conducted by the Andalusia Environmental administration(https://www.juntadeandalucia.es/medioambiente/portal_web/web/temas_ambient ales/biodiversidad/0_conservacion_biodiversidad/planes_conservacion_recuperacion/Programas%2 0de%20actuacion/programa_actuacion_aguila_imperial_%20anexo_II.pdf).

We also estimated the annual cost of a standard reintroduction program, using data from the following programs developed in Spain: Spanish imperial eagle reintroduction in Cádiz (Madero & Ferrer 2002; Muriel *et al.* 2011) and Bearded vulture reintroduction (http://www.gypaetus.org/) in

Cazorla (Simón *et al*. 2005). Obviously the costs could change through time, but it is the relative costs of the different procedures that are important here.

Statistical analyses

For the calculation of productivity values for territories, we controlled for a potential year effect by subtracting mean annual productivities from the original data on breeding success (relative productivity, Ferrer & Bisson 2003; Penteriani, Balbontin & Ferrer 2003; Horváth *et al.* 2014). Hatching date was given a numerical value by considering the earliest hatching date of each year as day 1. We tested for trends in response to supplementary feeding with linear analysis using the F-ratio statistic to find whether the slope of the data was significantly different from zero. Variances of the linear models were tested for homogeneity using Cochran's C statistic. Generalized linear models (GLM) with normal distribution function were used to examine differences in relative productivity among territories, as well as to compare productivity in the same territories with and without supplementary feeding. To avoid potential pseudo-replication due to the high potential for strong site-fidelity and pair-fidelity in these long-lived species, a generalized linear mixed model (GLMM) was conducted with territories as a random effect. In this case, relative productivity was considered as the dependent variable over the years. To remove the effect of territory quality, we compared productivity parameters in the same territory with and without supplementary feeding with a nonparametric Wilcoxon Matched Pairs Test. To analyze for potential deleterious effects on the productivity of supplemented pairs in the years following supplementation, paired comparisons using the Wilcoxon Matched Pairs Test were conducted. Statistical significance was set at P< 0.05, and analyses were conducted using the Statistica 8.0 package (Statsoft Inc., Tulsa, OK, USA).

Results

Supplementary feeding and extractions

Both populations increased during recent decades. In 2001 only 10 Spanish imperial eagle pairs were found in Sierra Morena, increasing to 91 pairs in 2015, an overall increase of 810%. The Bearded vulture population in Aragon increased from 15 occupied territories in 1988 to 67 in 2012, which represents an increase of 347%. Density-dependent breeding productivity on habitat heterogeneity was established in both populations (Ferrer *et al.* 2014, 2016; Morandini et al. 2017).

Results of GLMM analysis with relative productivity as the dependent variable, and species and supplementary feeding as fixed factors and territory as a random factor, are presented in Table 1. No differences between species were found (P=0.890), including in their response to supplementary feeding (P=0.367). However, in both species a significant effect of supplementary

feeding on relative productivity was found (P=0.013). This productivity did not seem to be affected by territories alone (P=0.192), but by the interaction between territory and supplementary feeding (P=0.030). This implied a different response among territories to supplementary feeding.

To control for potential interaction effects, paired comparisons of the same territories with and without supplementary feeding were conducted. Relative productivity emerged as significantly higher when supplementary food was provided (Wilcoxon Matched Pairs Test; Z=2.906, n=45, P=0.003). To measure differences in the intensity of response to supplementary feeding by territory we subtracted relative productivity without supplementary feeding from the values obtained in the same territory under supplementation. No difference in the intensity of response between species was found (ANOVA; F= 0.642, P=0.427). However, in both species differential response among territories was significantly related to the mean productivity of those territories without supplementation. Poor quality territories with low productivity levels responded more strongly to supplementary feeding than did territories with higher levels of natural productivity (r=-0.435, n=45, P=0.002; Fig 1).

A highly significant relationship between relative productivity without supplementation and hatching date was found (r = -0.2474, n=222, P= 0.0002), with pairs laying later in the season producing few nestlings. Selecting only those nests with hatching dates earlier than the median value for the total population (34 days) and repeating the GLMM for relative productivity with supplementary feeding as a fixed factor and territory as a random factor, any effect of supplementary feeding disappeared, showing that earlier nests did not respond to supplementary feeding in a significant way (relative productivity without supplementary feeding =0.533, and with supplementary feeding =0.582, F=0.090, P=0.764). These were the best territories, as judged by their productivity over a period of more than 15 years.

To estimate the potential over-production of young with supplementary feeding in both species, we compared mean productivity in poor quality territories in years with and without supplementation (Table 2). To produce 10 extra young per year in Spanish imperial eagles we needed to supplement 20 poor quality territories per year (10/(1.3430-0.8373)), and 37 territories in the case of the bearded vulture (10/(0.4135-0.1436)). With 10 released young per year over 10 years we could achieve a viable new reintroduced population of both species (Morandini & Ferrer 2017).

Paired comparisons by territories of the natural relative productivity without supplementation against the relative productivity the year after a supplementation of food was conducted, revealed no effect in subsequent productivity (Wilcoxon Matched Pairs Test; Z=0.495, n=49, P=0.619). The implication was that good breeding associated with food supplementation in one year was not followed by poorer-than-expected breeding in the following year.

Financial Costs

The annual cost of supplementary feeding and extraction programmes, including employment of two technicians during five months per year, averaged 28,833 €. Reintroduction annual cost, including transmitters and rings for the released birds, information dissemination, technicians, food and other costs was between 59,000 € per year and 100,000 € /year depending on the programme, with a mean cost of 78,000 € per year for both species.

Considering only the annual cost of maintenance of the captive programme, the Spanish imperial eagle mean annual budget in the period 2005-2011 was 275,000€ in salaries and 86,000 € in facility running expenses, giving a total annual cost of 361,000 €. The bearded vulture program budget, using mean values from 1996-2014, was 300,000 € in salaries and 120,000 € in operation costs, giving a total annual cost of 420,000 €. Consequently, annual mean cost for these two captive programmes was 390,500 €, about five times more than the supplementary feeding programmes.

As is usual, however, both captive breeding programmes started with young individuals as breeding stock. Owing to the deferred sexual maturity of these species, both programmes needed a long period of years before they could produce young for releases. In the bearded vulture this initial period was 10 years, and in the Spanish imperial eagle it was 7 years. Obviously, these pre-production periods must be included in the total cost of captive breeding programmes. Consequently, a reintroduction program based on captive bearded vultures as the source of young needs 10 years of pre-production plus the necessary years of releases in the reintroduction. Assuming a standard reintroduction period of 10 years of releases, we need to include 20 years of operating costs for the facility (7,81 millions) plus 10 years of the reintroduction cost (780,000 €); giving a total of 8,590,000 €.

Alternatively, a reintroduction based on supplementary feeding and extractions would cost 10 years of supplementations (288,830 €) plus 10 years of releases (780,000 €), that is a total cost of 1,068,830 €. In other words, a programme based on supplementary feeding and extraction costs 8 times less than the same program based on captive breeding, and takes 10 years less.

Discussion

We showed that supplementary feeding is an effective technique for improving significantly the productivity of certain territories when correctly applied. Selecting poor quality territories, supplementary feeding increased by 160% the mean annual productivity in the Spanish imperial eagles and by 288% in the bearded vultures. However, using relative productivity, no differences between species in response to supplementary feeding were found, suggesting that our findings could be applied to yet other species of similar life history.

According to the theory of habitat heterogeneity, as breeding density increases and good territories become occupied first, an increasing proportion of new pairs have to settle in poor quality habitat for breeding. In these conditions, the population operates as a source-sink system with poor quality territories, mostly unproductive, being maintained by the high quality territories with adults producing more young than are needed to replace themselves (Ferrer & Donazar 1996).

Our results demonstrated that in a high-density population, food supplementation in sink territories produced a significant increase in productivity. In both species, the intensity of response to supplementary feeding was stronger in those territories with lower productivity without intervention, suggesting that birds in poor territories were limited by food availability. Consequently, the selection of specific territories for food supplementation is critical in achieving an increase in the total production of young. This in turn requires prior knowledge of the population, so that poor territories can be identified. The highly significant relationship between productivity and hatching date provides us with an easy and accurate way of distinguishing between territories of different quality. Selecting territories where laying is later in the season for the provision of supplementary food, could significantly increase the final number of young produced, on the basis on minimal prior information.

This resulting surplus of young produced can then be removed without any obvious effect on the donor population. Alternatively, we can leave these extra young in their natal population, increasing the stock of floaters, though the demographic value of these extra young is higher in well-designed reintroduction programmes in new but suitable areas (Morandini *et al.* 2017). Even if supplementary feeding is not able to produce the minimum necessary number of annual extra young to release (in order to guarantee a successful reintroduction program; Morandini & Ferrer 2017), it can allow us to reduce to a minimum the impact of repeat extractions in the donor population (Ferrer *et al.* 2014).

Consequently, supplementary feeding could be most usefully applied in two different situations: (i) in an episodic main prey collapse, as occurred in Doñana National Park in 1991, when a new viral disease decreased by 7-fold the normal density of the wild rabbit *Oryctolagus cuniculus*, the main prey of the Spanish imperial eagle (Ferrer, Newton & Muriel 2013); and (ii) in poor quality territories in a high density population to produce extra-young for reintroduction programmes. Suggestions to extend this technique to most or all the pairs in a population due to the beneficial effect on productivity (Gonzalez *et al.* 2006) may not be the best strategy, because some of the territories may already be producing at maximum rate. For greatest efficiency, supplementary feeding needs to be targeted at the poorer territories in which the reproductive rate has the potential to be raised by provision of extra food. The extra young produced can then be most

effectively used in reintroduction programmes in which their chances of recruiting to a breeding population are high.

Some authors have suggested that food provisioning would constitute a major modification of the natural distribution of resources at the ecosystem level, leading to 'an uncertain future for populations, functional guilds, and, ultimately, communities' (Cortés-Avizanda *et al.* 2016). We consider this to be erroneous; if one considers 'natural' as not human-influenced, there is already in Europe nothing like a natural distribution of resources. Perhaps in vulture restaurants some care must be taken over potential effects of prolonged and predictable provisioning of food but this is not the case for the temporary supplementary feeding of targeted breeding pairs. For positive effect of supplementary feeding at vulture restaurants on a highly endangered raptor species, *Egyptian vulture* sees López-López, García-Ripollés & Urios (2014).

A potential unintended consequence of supplementary feeding might be a decrease of productivity or survival of the adults involved, owing to exhaustion after raising extra young (Blanco, 2006). However, in our study no effects of food provision on subsequent productivity in the same territories the following year without supplementation were found, indicating that that there was no reproductive cost to the parents in feeding extra young. Supplementary feeding and extraction of young could actually have benefited the parents because of the shorter period devoted to young removed well before their normal fledging time. Usually, young are extracted when they are around 40 days old, whereas the usual dependence period in eagles, for example, takes around 130 days (Ferrer, 2001). Unfortunately, we could not measure the survival of the adults, but note that all the territories in which adults were fed contained the same number of adults the following year. None of the territories involved contained only single adults or no adults.

Our financial cost analysis demonstrated that, for a reintroduction programme, production of young from supplementary feeding and extraction is around 8 times cheaper than production of young in a captive breeding programme. When captive breeding is used as a source of young for reintroduction, account must be taken, in such a long-lived species, of the lengthy period in captivity before individuals taken early in their lives start to breed. In the case of bearded vultures, according to the Gypaetus Foundation (electronic bulletins 2008-2012), the program started in 1996, and the first releases were made ten years later in 2006. Obviously, this ten-year budget is part of the total cost of the programme. Even if the adults for breeding were donated free of charge by zoos (thus eliminating the pre-breeding costs for the reintroduction programme, so that breeding could begin immediately), the programme for reintroduction would still be about five times more expensive than a programme based on supplementary feeding.

Another consideration is the actual capacity of production in captivity of young per year, which greatly affects the duration and hence the cost of any reintroduction program (Morandini & Ferrer 2017). Again, using the information provided by the Gypaetus foundation, during the ten years of releases, 37 individuals have been set free (3.7 per year). According to simulations, with this number of young per year, releases need to continue for more than 23 years to achieve a viable population (see Ferrer *et al.* 2014, Morandini & Ferrer 2017). Consequently, the real total cost of this approach based in captive breeding would be 14,680,500 € (33 years of operating cost: 12,886,500 € plus 23 years of released: 1.794000 €), against 1,068,830 € using our suggested approach (extracting wild young from food supplemented nests). In other words, in an standard reintroduction program releasing 10 young per year during 10 years, each one of the released young bred in captivity costs around 146,805 € and each young coming from a food-supplemented wild population that we released costs 10,680 €.

Captive breeding programmes may be the only option when the remaining wild populations are so small that extractions would not be possible or if no wild populations remain. Additionally, we sometimes have captive animals that could not themselves be released but could be useful for producing young for release. Nevertheless, when we are planning a reintroduction program, differences in the total cost of the two alternative strategies (breeding in captivity versus the harvesting of wild nestlings) can be so great as to settle any argument over methodology.

Authors' contributions

MF, VM and IN conceived the ideas and designed methodology; GB and VM collected the data; MF analysed the data; MF and IN led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility

Databases are available in Digital CSIC repository http://dx.doi.org/10.20350/digitalCSIC/8512 (Ferrer *et al.* 2017).

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Table 1: Examination of any significance in response of productivity to supplementary feeding in the two species. No differences between species were found, including in their response to supplementary feeding. A significant effect of supplementary feeding on relative productivity was found. Relative productivity did not seem to be affected by territories alone, but by the interaction between territory and supplementary feeding. This implied a different response among territories to supplementary feeding.

	Factors	df-Factor	MS - Factor	df - Error	MS - Error	F	P
(1)Species	Fixed	1	0.022296	164.6890	1.168583	0.019080	0.8907
(2)Supplementary feeding	Fixed	1	6.435504	158.0235	1.040051	6.187684	0.0139
(3)Territory	Random	168	1.129538	20.6699	0.812563	1.390092	0.1929
1*2	Fixed	1	0.524861	46.1736	0.633368	0.828683	0.3673
2*3	Random	38	0.664224	298.0000	0.436578	1.521433	0.0302

Table 2: Paired comparisons of productivity in the same territories with and without supplementary feeding. In both species, significantly higher relative productivity was found when supplementary food was provided (Wilcoxon Matched Pairs Test; Z=2.906, n=45, P=0.003)

Species	Mean productivity without supplementary feeding	Mean productivity with supplementary feeding	Increment
Aquila adalberti	0.8373	1.3430	60.40%
Gypaetus barbatus	0.1436	0.4135	187.95%

Fig 1: Linear regression between relative productivity of territories and response of these same territories when supplementary feeding is conducted. Poor quality territories with low productivity levels respond more strongly to supplementary feeding than those with higher levels of natural productivity (r=-0.435, n=45, P=0.002).