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Using manipulation of density-dependent fecundity to recover an endangered species: the bearded vulture (*Gypaetus barbatus*) as an example

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Summary

1. Endangered species subjected to reintroduction programs often occur as small and isolated populations with local high density and depressed fecundity. Variation in territory quality may lead to this low fecundity owing to increasing occupation of sub-optimal territories as population density grows, known as the habitat heterogeneity hypothesis (HHH). In this context, food supplementation in poor territories may be used to produce extra young which could be allocated to reintroduction programs.

2. We analyze the density-dependent fecundity pattern and the underlying mechanism in a small population of bearded vultures (*Gypaetus barbatus*) in Aragón (NE Spain). We then examine the viability of a hypothetical reintroduction program using extra young produced by supplementary feeding on poor territories and the effect on the donor population by means of population simulations. We also compare the economic cost of such a reintroduction program in relation to the cost of a traditional captive breeding program.

3. The wild population showed clear negative density-dependent fecundity regulation driven by the HHH mechanism, with territories acting as a ‘source-sink’ system. Simulations showed that extractions for translocations had no relevant long-term effects on the donor population viability, but a marked population reduction during the extraction period. However, the implementation of supplementary feeding to produce extra young for translocation lessened significantly this expected initial population reduction.

4. Likewise, analyses showed that the annual budget of a captive breeding program for this species could be seven times more expensive than the translocation of extra young produced by food supplementation.

5. *Synthesis and applications.* Reintroduction programs are increasingly used as effective conservation techniques. Released individuals may be provided by captive breeding programs, which have often been relatively expensive and entailed various problems, or by translocation of wild-reared individuals, which may be subjected to public criticism and potential effects on donor populations. In this respect, raising fecundity by means of supplementary feeding in heterogeneous populations was shown to be a relatively cheap source of young for reintroductions, also avoiding negative effects on donor populations and public opinion.

Keywords: cost analysis, habitat heterogeneity hypothesis, population viability analysis, reintroduction, site-dependence hypothesis, supplementary feeding, translocation

Introduction

The two main ways of obtaining a sustainable source of young to undertake a reintroduction program are breeding in captivity and extraction from wild populations. However, many endangered species, persist as small relatively isolated populations but at high local density (IUCN 2012). This is a common pattern in some large species, such as raptors, that have suffered from human persecution and habitat destruction in the past (Ferguson-Lees & Christie 2003). Species showing this type of distribution are often subject to reintroduction programs aimed at extending the current range and numbers of the species and, consequently, their expected persistence time (IUCN 1998; Seddon 2010). Remaining high-density populations of endangered species often show low fecundity, resulting from density-dependent processes (Nicholson 1933; Lack 1954; Sinclair 1989; Newton 1998). This fact complicates one of the methods used in reintroduction programs: the extraction of free-living young for release in other areas. Because fecundity is low, public opinion is often against extractions, making sensible management difficult, especially if extractions can put the donor population at risk. On the other hand, using young from a pre-existing captive population avoids any effects on potential wild donor populations.

Density-dependent effects in the regulation of bird populations, especially fecundity, are well described (Cooch *et al.* 1989; Newton 1994, 1998; Ferrer & Donazar 1996; Rodenhouse, Sherry & Holmes

1997; Penteriani, Gallardo & Roche 2002; Penteriani, Balbontín & Ferrer 2003; Kokko, Harris & Wanless 2004; Ferrer, Newton & Casado 2006, 2008). Two major mechanisms have been proposed (Fretwell & Lucas 1970). The first is called the habitat heterogeneity hypothesis (HHH) (Dhondt, Kempenaers & Adriaensen 1992; Ferrer & Donazar 1996), or site-dependence hypothesis (Rodenhouse, Sherry & Holmes 1997). In such situations, at low population densities, individuals select optimal territories. As density increases, an increasing proportion of individuals are relegated to poorer territories, where breeding is less successful, lowering the mean per capita fecundity of the population as a whole (Andrewartha & Birch 1954; Brown 1969).. The second potential mechanism is named the individual adjustment hypothesis (IAH) or interference competition hypothesis. In this situation (Lack 1966, Fretwell & Lucas 1970; Dhondt & Schillemans 1983), density-dependent depression of fecundity is envisaged to affect all individuals of the population to a similar extent. It can arise from a general depression in food supplies, or an increased frequency of aggression and interference among territorial pairs, resulting in a hostile social environment that leads to a relatively uniform reduction in breeding performance across the population. Under this hypothesis, as density rises, all or most individuals (or territories) should show reduced fecundity (Fernandez, Azkona & Donazar 1998).

According to both hypotheses, mean fecundity declines as density rises (Ferrer & Donazar 1996). But from a conservation point of view, the two mechanisms have different effects. In a high density population under HHH, a fraction of the territories are producing most of the young, contributing disproportionately to the recruitment and persistence of the population ("sources" according to Ferrer & Donazar 1996). Under IAH, however, the production of young is more uniformly distributed among territories (Ferrer, Newton & Casado 2008). Under the heterogeneity hypothesis, the destruction of a fraction of the population would have tremendous effects on population viability if high quality territories were affected or small effects if only poor territories were affected. Under IAH the effect should be proportional to the fraction affected.

Variation in the quality of territories is the main driver of fecundity according to the HHH. Differences in productivity among 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). Food availability seems to be both one of the most common factors limiting territory quality and one of the easiest to manipulate. Supplementary feeding is a common practice in raptors and other species to raise reproductive output, either for experimental or 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, González *et al*. 2006, Ferrer & Penteriani 2007; bearded vulture, Margalida 2010). In a high density population, food supplementation in ’sink’ territories could lead to an ‘overproduction’ of young that are not strictly necessary to maintain the population. Although these extra young could increase the resilience of the original population, keeping surplus birds nearby in case of population decline, the demographic values of these extra young would be higher in a well-designed reintroduction programme in a new but suitable area. This holds especially when the donor population operates under the HHH, because in this situation the aim is to produce extra young from territories that would otherwise be mostly unproductive. Those extra young can then be used in reintroduction programs, for example, releasing them in areas where they might not otherwise settle, but without affecting the trend of the donor population. Under the IAH, it is much less predictable whether or not donor territories would produce young naturally in any particular year, so some supplementary feeding could be ineffective, and the impacts of removal on the donor population would be much less certain.

The only surviving bearded vulture (*Gypaetus barbatus*) population in the Spanish Pyrenees is composed of 150 reproductive units (mostly pairs, but some polyandrous trios), 78 of them in the region of Aragon. In this Aragonese population, we analyzed fecundity to find whether the observed density dependence was operating as expected on HHH or IAH. This finding enabled us to evaluate the potential for producing extra young using a supplementary feeding program, and whether a reintroduction program could be undertaken without affecting the viability of the donor population. Finally, the cost of such a procedure was compared against a typical program of captive breeding for release.

Material and methods

SPECIES AND POPULATION

The bearded vulture is a large long-lived territorial raptor, with delayed maturity (adult plumage at 5–7 years old), that breeds in sparsely distributed territories in mountainous regions (Donázar *et al.* 1993). Its numbers and breeding range declined throughout Europe during much of the twentieth century (Hiraldo, Delibes & Calderón 1979; Tucker & Heath 1994; Mingozzi & Estève 1997; Grubac 2002). The clutch generally consists of two eggs, but only one chick survives due to obligate cainism (Brown 1977; Thaler & Pechlaner 1980; Heredia & Heredia 1991). The species feeds mainly on large bones of ungulates which it obtains from fresh carcasses and swallows whole or in pieces.

In Spain, where the bulk of the current European population is located, the species reached its lowest levels in the 1970s, when fewer than 40 occupied breeding territories remained in the Pyrenees. After a period of stability up to 1987, the population of this vulture increased to 90 occupied territories by 2002 (Heredia & Margalida 2002) and to 150 by 2011 (Spanish bearded vulture working group unpublished data). However, this increase occurred only within a restricted geographical area, leading to a rise in population density (Donázar *et al.* 2005).

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. Territories occupied for more than 15 years (i.e. since 1997) were considered as first occupied territories in the analyses. In general, once a territory was occupied, it remained occupied throughout the remaining period of study.

SUPPLEMENTARY FEEDING

In order to avoid competition with other more generalist scavengers, such us griffon vultures (*Gyps fulvus*) or corvids, a specific diet was provided for individual reproductive units based on sheep and goat bones. These were the 3rd and 4th metatarsal and metacarpal together with the remaining limb up to the finger bones. They were collected from authorized slaughter houses, where under official regulations, these materials are considered as surplus waste. In all cases, the bones were conveyed by veterinary officials in watertight barrels to the feeding point.

Supplementary feeding was conducted over four 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. Supplementary feeding started on 31 October and finished on 31 March, about 30 days after egg laying. Some 350 working days and 980 hours were dedicated to this operation. Technical workers walked to the nesting areas to deposit 15-18 kg of bones each day, at a medium distance of 1118.5 ± 999.1 m (range: 50-3900 m, n = 14) from the nest. The food was placed on ledges supposedly unreachable by other carnivores, but on at least 7 occasions other species were seen at the food (*Corvus corax, Corvus corone, Gyps fulvus, Milvus milvus, Vulpes vulpes, Martes martes*). Nevertheless, the most frequently observed species using the food was by far the bearded vulture. Only the local pair visited each feeding site, and indeed no more than one or two bearded vultures were seen there at one time. Around 5108 kg of bones were supplied during the four years, divided among 10 different territories. The selected experimental territories where considered as low quality or “sink” territories because they had a laying rate (number of years with egg laying per number of monitored years) below the population mean (0.69 layings per year). They were also accessible by car even during heavy snow, and the topography allowed access on foot close to the nest.

SIMULATIONS

We conducted simulations to analyze the viability of a hypothetical reintroduction program, based on the extra young produced by supplementary feeding. We used Vortex simulation software (Vortex, version 9.72, Lacy *et al.* 2005). Vortex is an individual-based model for population viability analyses (PVA). It models population dynamics as discrete, sequential events that occur according to probabilities defined by the user and modelled as constants or random variables that follow specified distributions. The events used for modelling describe the typical life cycle of sexually reproducing, diploid organisms. The method is particularly suitable for species like the one we modelled here, with low fecundity, long lifespan, small population size, estimable age-specific fecundity and survival rates, and mainly monogamous breeding (Lacy 2000). In fact, Vortex has already been used to analyze the viability of bearded vulture populations (Bustamante 1996, 1998).

Using previously published estimates of fecundity and mortality rates for the species (Bustamante 1998; Margalida *et al.* 2003; Oro *et al.* 2008; Table 1), we conducted several simulations for different scenarios. For each scenario, we performed 1000 replicates during a simulated 50-year period. We selected this period because it is the double of the known reproductive life for this species (age at first breeding 7 years, maximum age of reproduction 32 years, see table 1). Negative density-dependent fecundity was considered in all the simulations (Table 1). The equation that *Vortex* uses to model density dependence is: $P(N)=P(0)-[P(0)-P(K)N/K^{B}]$. were $P(N)$ is the percentage of females that breed when the population size is N, $P(K)$ is the percentage that breed when the population is at carrying capacity (K), and $P(0)$ is the percentage that breed when the population is close to zero . The exponent B can be any positive number and determines the shape of the curve relating the percentage breeding to population size, as the population becomes large. If $B = 1$, the percentage breeding changes linearly with population size. If $B = 2$, $P(N)$ is a quadratic function of N. As can be seen in Figure 2, the relationship between number of pairs and fecundity was significantly linear, so a value of $B=1$ was selected for modeling purposes.

First, we examined the dynamics of released bearded vultures in a simulated reintroduction program. We calculated the number of juveniles that would be available to release each year and the number of years required to achieve a new population. We estimated juvenile mortality (from 1 to 6 years old) using data from the reintroduction program conducted by the Gypaetus Foundation in Spain (http://www.gypaetus.org/, Table 1). We consider a new population as successfully established when the probability of extinction during 50 years (that is twice the reproductive life) was less than 0.001 ($P < 0.001$) and it showed a positive trend in population size. We simulated reintroduction programs lasting from 2 to 13 years in duration, calculating the minimum number of juveniles we would have to release each year assuming a 1:1 sex ratio. A population ceiling of 70 pairs was considered in these simulations because the selected area for potential reintroduction in Picos de Europa Mountains is of similar size to the Aragones population.

Second, we simulated the effect on the Aragonese bearded vulture population of repeated extractions of the minimum number of young needed for a successful reintroduction according to previous simulations, with and without food supplementation. In these simulations a population ceiling of 70 breeding pairs was considered. Juvenile mortality (between 1 and 6 year of age) used was derived from published data of this population (Table 1). Simulations started with an age distribution of a stable population.

COST ANALYSIS

In order to analyse the relative financial costs of alternative approaches to obtaining young for reintroduction, we compared the budget of a typical captive breeding program, namely the one conducted by the Gypaetus Foundation in Spain (http://www.gypaetus.org/), with the cost of a supplementary feeding program (like the one conducted by Fundación para la Conservación del Quebrantahuesos in the Pyrenees; http://www.quebrantahuesos.org/), plus the necessary care of the extracted young until the age of release. We also estimated the annual cost of a standard reintroduction program, based on young taken from unfed wild pairs, using data from the following programs developed in Spain: Osprey reintroductions in Huelva and Cádiz (Muriel *et al.* 2010), 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

We tested for trends in fecundity 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 binomial distribution and logit link function were used to examine differences in productivity among territories as well as to compare productivity in the same territories with and without supplementary feeding. Statistical significance was set at $P < 0.05$ and analyses were conducted using the STATISTICA 8.0 package (Statsoft Inc., Tulsa, USA).

Results

DENSITY-DEPENDENT FECUNDITY

The population of bearded vultures in Aragon increased throughout the 25-year study period from 29 occupied territories in 1988 up to 78 in

2012 (Fig. 1), which represents an increase of 269%. During the same period, the trend in fecundity was significantly negative, decreasing from a mean value of 0.56 young per occupied territory during the first 8 years to 0.36 during the last 8 years (r = -0.663, n = 22, $P < 0.001$; Fig. 1). In addition, a significant negative relationship between fecundity and number of breeding pairs was found (r = -0.655, n = 22, $P < 0.001$; Fig. 2), suggesting the action of a density-dependent fecundity process.

Significant differences of fecundity among territories were found (GLM with binomial distribution and logit link function; Wald statistic = 156.45, $P < 0.001$), with some territories showing consistently high values of fecundity throughout the study, and others consistently low values. Comparing fecundity between those territories occupied for longer than 15 years and recently occupied territories, using only the last 10 years, a significant difference was found (GLM with binomial distribution and logit link function; Wald statistic = 4.73, $P = 0.029$, Fig. 3), with higher fecundity in old territories (mean = 0.372 young per territory and year) than in recently occupied ones (mean = 0.288). In other words, the decline in mean fecundity was caused by the progressive addition of less productive territories to the population, the occupants of which bred poorly throughout.

SUPPLEMENTARY FEEDING

Comparing the production of chicks in the 10 selected poor territories between the periods with (2007-2010) and without (2001-2006) supplementary feeding, highly significant differences were found. Average annual production of young in those 10 nests during the 6 years without supplementary food was 0.078 against 0.541 during the 4 years with supplementary food. This significant change (GLM with binomial distribution and logit link function; Wald statistic = 8.617, P = 0.003), represents a seven-fold (693.6 %) increase in the expected number of young per nest. On the other hand, territories without supplementary food showed no significant change in average production between those two periods (GLM with binomial distribution and logit link function; Wald statistic = 2.758, P = 0.948). From these results, we can predict that supplementary feeding in all the 15 poorest territories of the population (i.e. those with an average annual egg laying rate below the population mean, i.e. 0.69 laying events per year), whose mean annual production of young per pair was 0.103 (total annual young = 1.545) would become 0.541 x 15 = 8.115 young (between 5 and 11; P = 0.05), roughly equivalent to 7 extra young per year.

SIMULATIONS

The number of young released necessary to obtain a new successful population (with a probability of extinction of $P<0.001$ during 50 years) varies from 54 per year over two years to 4 per year over 23 years (Fig. 4), with number of young per year showing a significant negative exponential relationship with number of years (r = - 0.788, P < 0.001).

Consequently, as we reduce the number of young released each year, the number of years necessary to obtain a successful population increases exponentially. Analysing only the cases between 2 and 13 years, a significant effect of number of young per year on the final size of the simulated population was found (r = - 0.614, P = 0.033), with higher mean population levels as the number of young released per year increased, thereby shortening the reintroduction period. After 50 years, the mean final population size in simulations with 54 young released during two years was 33.1 breeding pairs against 22.7 when releasing 7 young during 13 years (Fig. 5). Therefore, if we only released the 7 extra young produced by supplementary feeding we would need at least 13 years of releases to obtain a new population with a probability of extinction of P < 0.001.

In simulating the effect on the donor population of the removal of nestlings, we only considered extractions of up to 26 young per year, as this is roughly the mean number of young produced by the whole population of Aragon each year. Consequently, only extraction programmes of 4 or more years were simulated. As shown in Fig. 6, the effect on the donor population varies significantly according to the extraction program (r = - 0.896, P < 0.001).

As the extraction period lengthened, the size of the modelled donor population after 50 years became lower. If we removed 26 young over each of four successive years, the mean donor population size after 50 years became 246 individuals, against 184 if we removed 7 young during each of 13 successive years. However, the number of breeding pairs was the same at the end of all these simulations (70, i.e. maximum possible; Fig. 6). The magnitude of temporary decreases in the number of breeding pairs in donor populations was related to the length of the extraction period ($r = 0.941$, $P = 0.017$), ranging between 36.3% (from 70 to 44.57 pairs) in four-year extraction programmes to 13.7% in 13 year programmes. In any case, the probability of extinction of the donor populations was always below 0.001.

Conducting the same simulations under a supplementary feeding program (i.e. assuming that we are able to produce 7 extra young), again the probability of extinction was lower than 0.001 for all the scenarios (Fig. 7). The effect of different extraction programs on the donor population was consistently less than in the previous simulations, and the length of the extraction programs had no influence on the final donor population size ($r = 0.330$, $P = 0.385$). Temporal reduction in number of breeding pairs varies from 18.2% (from 70 to 57.24 pairs) in four-year extraction programs to 0% in 13-year programs. In fact, extractions varying from 10 young over 10 years to 7 young over 13 years seem to have no effect on the size of the donor population (Fig. 7).

ANALYSIS OF LIKELY COSTS

We compared the relative costs of a captive breeding program producing 7 young bearded vultures per year against the alternative approach of supplementary feeding of wild birds in poor territories. The annual cost of a captive breeding program for this species, as currently running in Andalusia, Spain (http://www.gypaetus.org/), is 700,000 €, including the cost of the releases in the Cazorla mountains (SE Spain) where an average of 2.7 young per year have been released during the last 6 years. This gives a total budget of 9,100,000 € to maintain the program during the necessary 13 years, releasing at least 7 young per year, to obtain a self-sustaining population in the new area, assuming that the production of 7 young per year would not increase the current budget.

In contrast, the cost of the supplementary feeding program in the Aragonese Pyrenees plus the additional cost of raising the extracted 7 young until their release by hacking, together with all other associated costs of the program, give an estimated annual budget of 100,000 €, which is seven times less than the approach based on captive breeding. Using the supplementary feeding technique, the total cost of a reintroduction program during the 13 necessary years would be 1,300,000 €. In other words, for the money needed for a captive breeding and release program, we could conduct up to seven different reintroduction programmes using this new approach, providing that sufficient young were available.

A major component of the total cost is the number of years needed to maintain a programme. According to our simulations, a 4-year program would be successful providing that 26 young were available per year. This means that during 4 consecutive years we would have to remove almost all the young of the donor population (without supplementary food). Although no risk of extinction for the donor population would exist, some effects on the size of the total population would be expected during the first 10 years until it had fully recovered (see Figs. 6, 7). The total budget needed, however, would be 400,000€, that is almost 23 times less than the money needed for the actual captive breeding and release program.

Discussion

Our studied population of bearded vultures in the Aragonese Pyreenes showed density-dependent fecundity regulation, as suggested by the highly significant negative relationship found between mean fecundity and density. The fact that first occupied territories showed higher fecundity throughout than newly-occupied ones is in accordance with the HHH as the main driver of density-dependent fecundity in this population. As expected under the HHH, the decrease in mean fecundity over the years was mainly due to an increase in the proportion of poor territories occupied as the population increased, while reproductive units on first occupied territories maintained a high mean fecundity (e.g. Newton 1991; Dhondt, Kempenaers & Adriaensen 1992; Kempenaers & Dhondt 1992; Ferrer & Donazar 1996; Krüger & Lindström 2001; Sergio & Newton 2003). Significant fecundity differences among territories support this pattern as well. In this situation, the population can be viewed as a source-sink system, with sink territories being maintained due to ‘overproduction’ of young in source territories (Pulliam & Danielson 1991; Ferrer & Donazar 1996). Other authors have previously suggested that this bearded vulture population was under HHH regulation, at least partially (Carrete, Donazar & Margalida 2006).

Nevertheless, some other factors would explain why old territories show a consistently higher fecundity than recently-occupied ones. For example, old territories could be occupied by older and/or higher quality breeders than new territories so that age-differences would confound any effects of territory quality. This seems improbable, however, due to a general trend in long-lived raptor species with deferred maturity to increase the mean age at first breeding as population density increases (Ferrer *et al.* 2004). This tendency has already been suggested for the growing population of the bearded vulture in the Pyrenees (Antor *et al.* 2008). Furthermore, in the longest occupied territories much turnover of breeders would have been expected in the 25-year study period, because every few individuals would have been expected to live to the maximum possible breeding age. Lastly, even if an age effect was operating and the positive effect of food supplementation depended on inexperienced individuals more than on territory quality, it could not have affected the results or the rationale behind the simulations. As long as some territories responded to supplementary feeding by increasing fecundity, the extraction of those ’extra young‘ would have had the same effect on the viability of the donor population, regardless of whether it resulted from territory quality, breeder quality or both.

Supplementary feeding increased fecundity in poor territories by more than 690%. This contrasts with an earlier study by Magalida (2010) who found no such effect. However, Margalida (2010) provided supplementary food only from hatching and during the following two months, so it could not have affected egg laying. In our case, food provision started well before laying, thereby increasing the proportion of pairs that laid and thus their fecundity. For supplementary feeding to be effective, it must be applied at the right time. If the main objective is to increase the proportion of Bearded Vulture pairs laying eggs, supplementary feeding must start well before laying in order to affect female condition,(for general discussion of efficacy of management techniques see Ferrer & Hiraldo 1991).

Cost analyses, based on recent comparative price levels, show that the use of captive breeding as a source of young for a reintroduction program is seven times more expensive than extraction of overproduced young from a food-supplemented wild population. The necessary maintenance of the facility, year-round labour costs and food supply for the captive animals, account for those differences. In addition, the probability of success is often lower in reintroduction programs using captive-born animals owing to factors such as lower survival rates, inappropriate behaviour or poor adaptation to local conditions (reviews in, Griffth *et al.* 1989; Beck *et al.* 1994; Snyder *et al.* 1996; Wolf *et al.* 1996).

In all the scenarios examined, extractions of young had non-significant effects on the viability of the donor population with or without stimulating extra production of young by means of supplementary feeding in poor territories. Nevertheless, in the absence of appropriate food supplementation during the extraction period, the simulated donor population was significantly affected, losing breeding pairs. This temporary decrease in population size had no effect on the extinction probability over 50 years, but the simulated population took some years to recover its previous size, which could have negative effects on public opinion, hampering support for the programme. Moreover, population size was more affected as the extraction period lengthened, suggesting that extractions of young would be best concentrated into a period as short as possible.

On the other hand, using food supplementation in target territories, the expected production of extra young allowed their removal without any effect on the donor population, in either the short-term or long term. Using these extra young, a 13-year reintroduction could be started with a probability of extinction for both the donor and the new population of $P < 0.001$. This would help to avoid any negative public perception of the management plan and would be cheaper than a captive breeding and release program, but must be maintained for at least 13 years. Probably a combination of both strategies would be the best compromise option, i.e. an overproduction of young and the removal of additional young in order to reduce the duration of the program.

Many endangered species could benefit from this approach, especially those that now exist as isolated but dense populations. Extending the overall distribution, and increasing the connectivity between subpopulations, could be one of the most effective conservation measures that could be undertaken. Reintroduction programmes of various animals have increased greatly during the last 25 years, and will probably be increasingly used in the future (Seddon *et al.* 2007). In this context, the use of population dynamics theory applied to conservation could reduce the costs of these interventions, increase the probability of success, and avoid problems related to negative impacts on donor populations and public opinion.

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Table 1. Summary of parameter values used in Vortex for the simulations of trends in the donor population and in the hypothetical reintroduced population. Based on data from Bustamante (1998), Margalida *et al*. (2003), Oro *et al*. (2008)

Parameter	**Value**
Age of first breeding	7 years
Maximum age of reproduction	32 years
Maximum number of broods per year	1 brood
Maximum progeny per brood	1 young
Sex ratio at birth	50%
Fecundity rate (density dependence)	0.6 at low density
	0.35 at high density
Juvenile mortality in Pyrenees (1-6 years)	21% (SD 1.8)
Annual adult annual mortality (>6 years old)	13% (SD 1.4)
Juvenile mortality of released birds (1-6 years)	50% (SD 1.2)

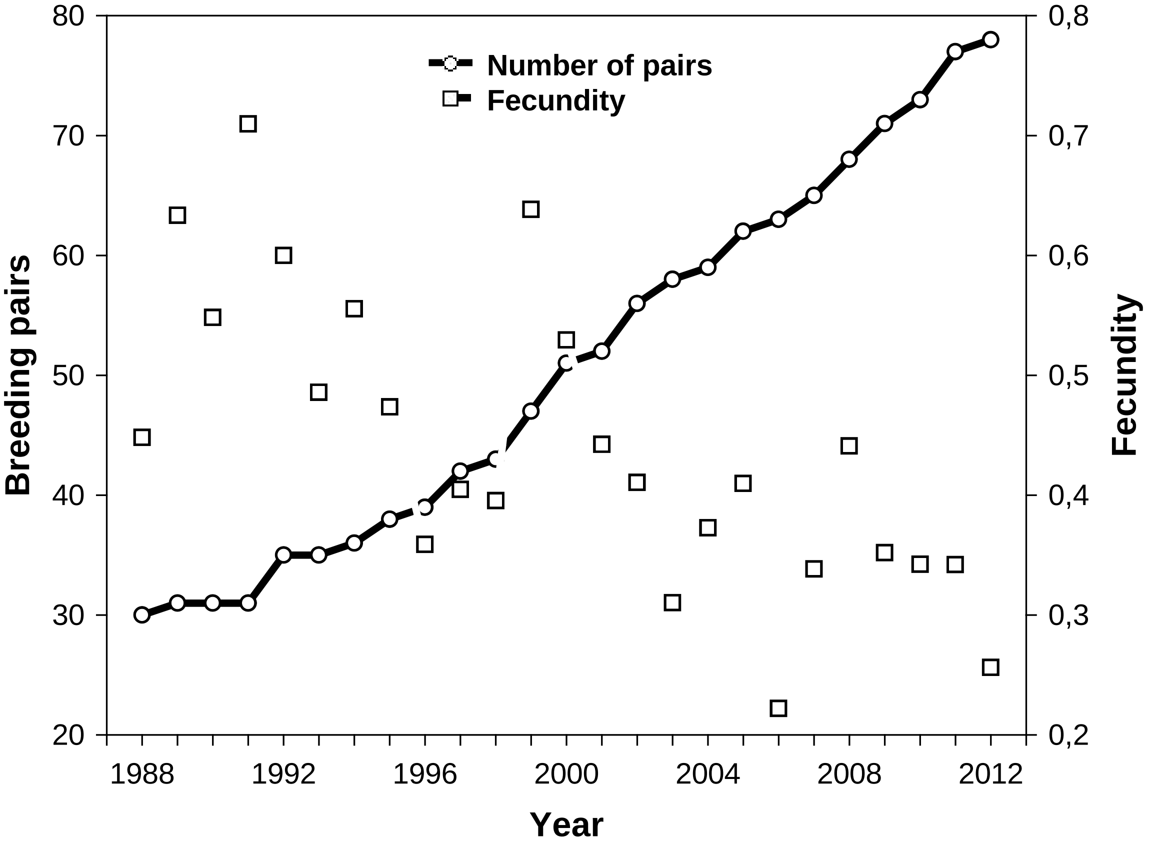

Fig. 1. Growth of the population (number of occupied territories) and average fecundity (fledglings per year) of the bearded vulture in Aragon (Spanish Pyrenees) throughout the study period (1988-2012, inclusive).

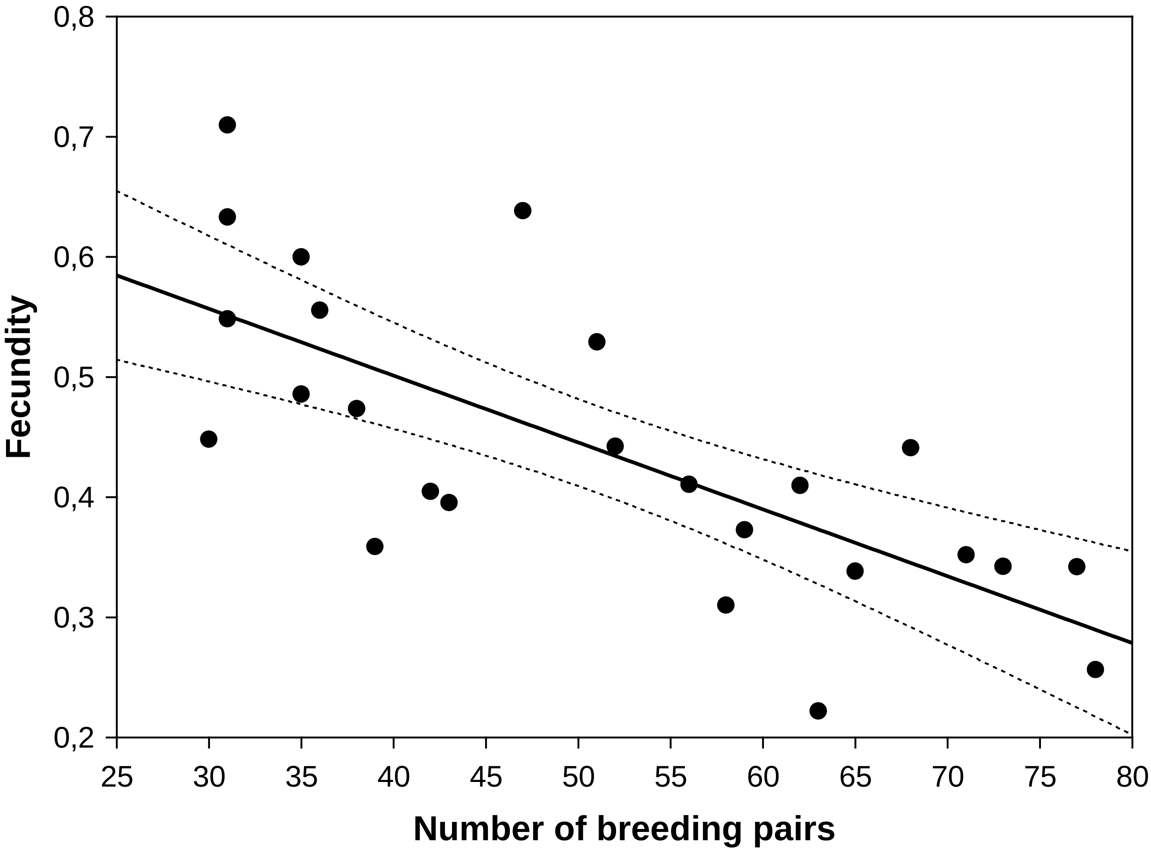

Fig. 2. Significant negative relationship between density and mean fecundity (*r* = -0.717, *n* = 25, *P* < 0.001) in the bearded vulture population of Aragon (Spanish Pyrenees). Dotted lines represent 95% confidence intervals. Fecundity is measured as the mean number of young produced per reproductive pair or unit.

Fig. 3. Significant (GLM Binomial distribution and logit link function, Wald statistic = 4.73, *P* = 0.029) differences in fecundity between old territories (those occupied more than 15 years ago) and new ones (less than 10 years ago).

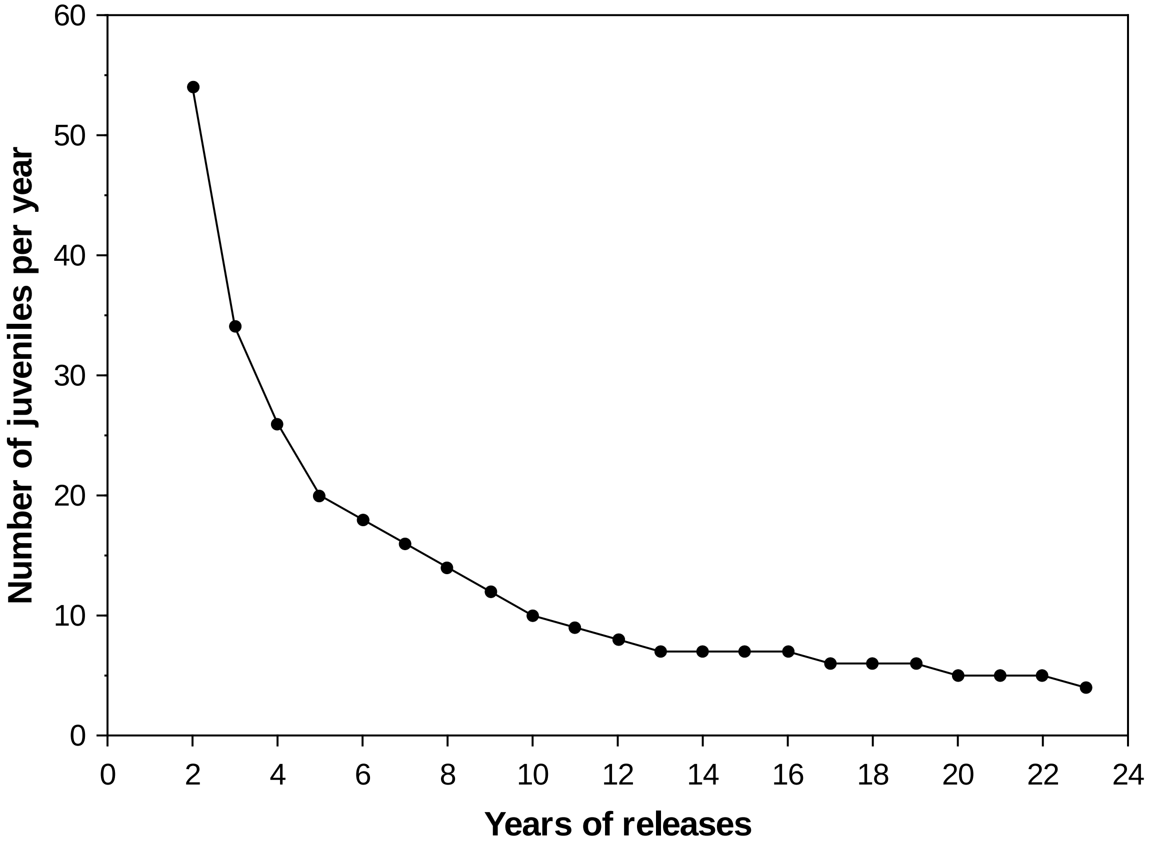

Fig. 4. Negative exponential relationship between number of young released per year and number of years necessary to obtain a probability of extinction below 0.001 in a simulation period of 50 years.

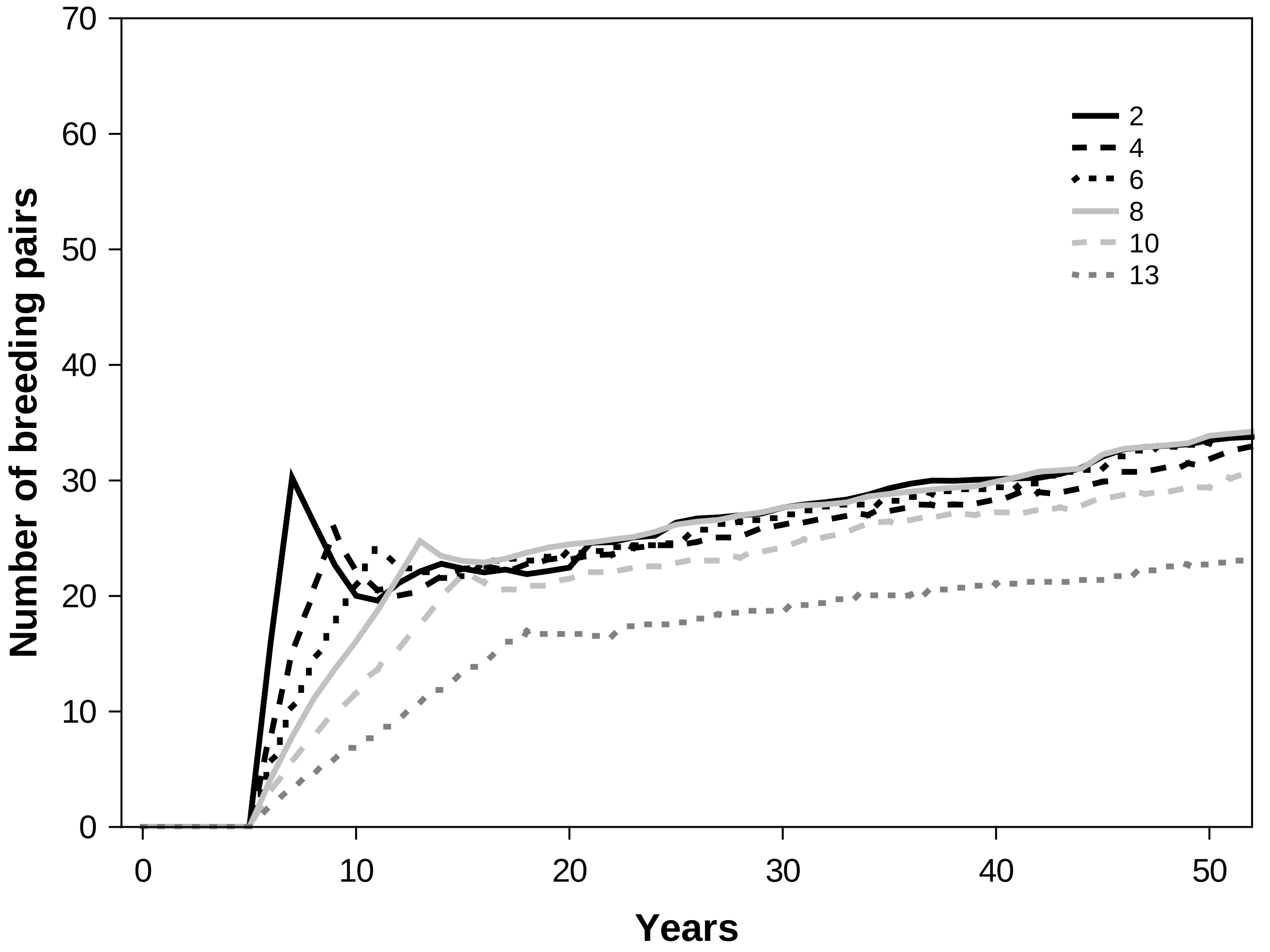

Fig. 5. Trajectories of new populations according different combinations of young released per year and duration of the releases (2 years-54 young, 4 years-26 young, 6 years-18 young, 8 years-14 young, 10 years-10 young and 13 years-7 young).

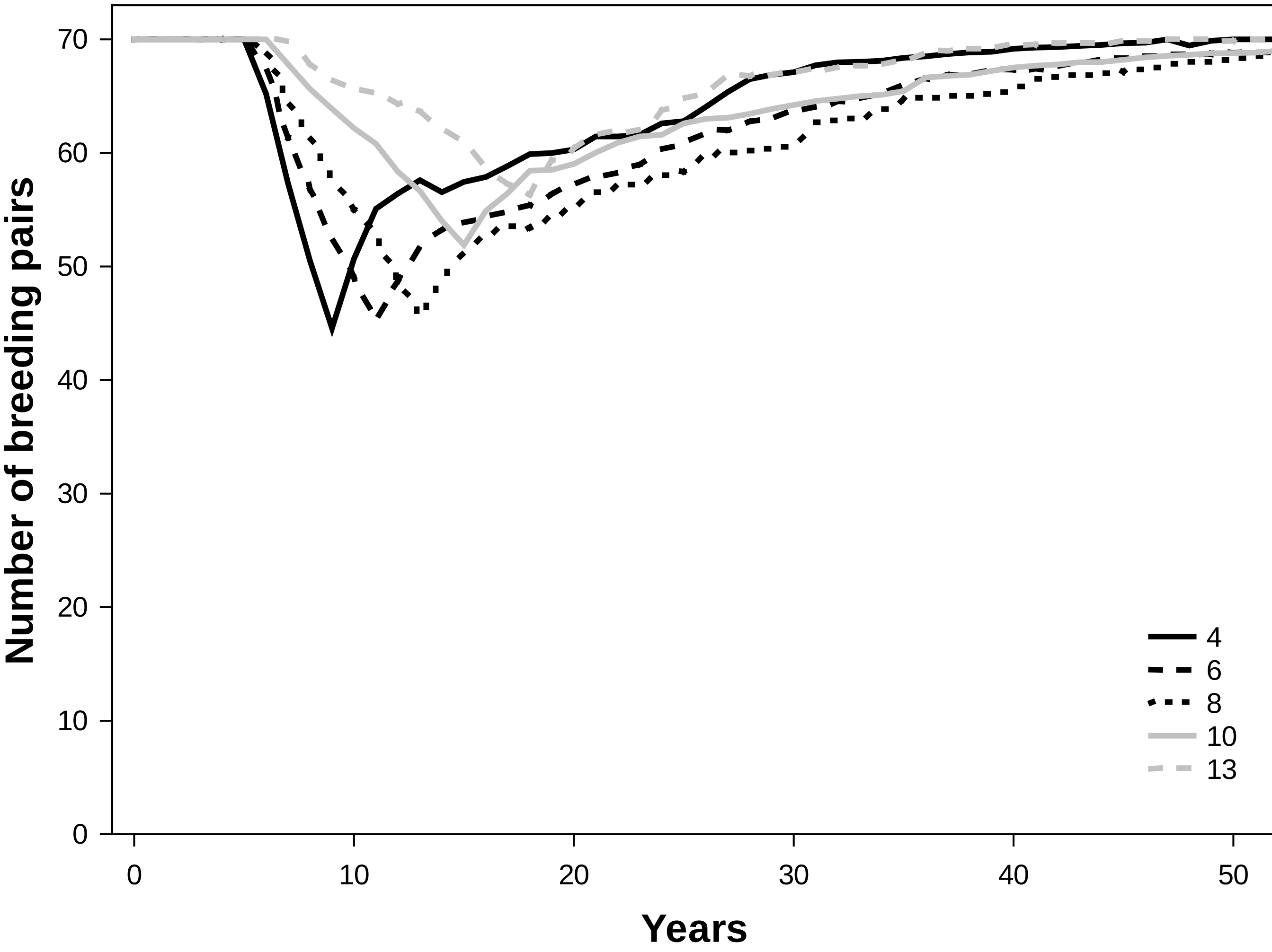

Fig. 6. Effect of different combinations of young removed per year and number of years of extraction on the number of breeding pairs in the donor population without a supplementary feeding programme (4 years-26 young, 6 years-18 young, 8 years-14 young, 10 years-10 young and 13 years-7 young).

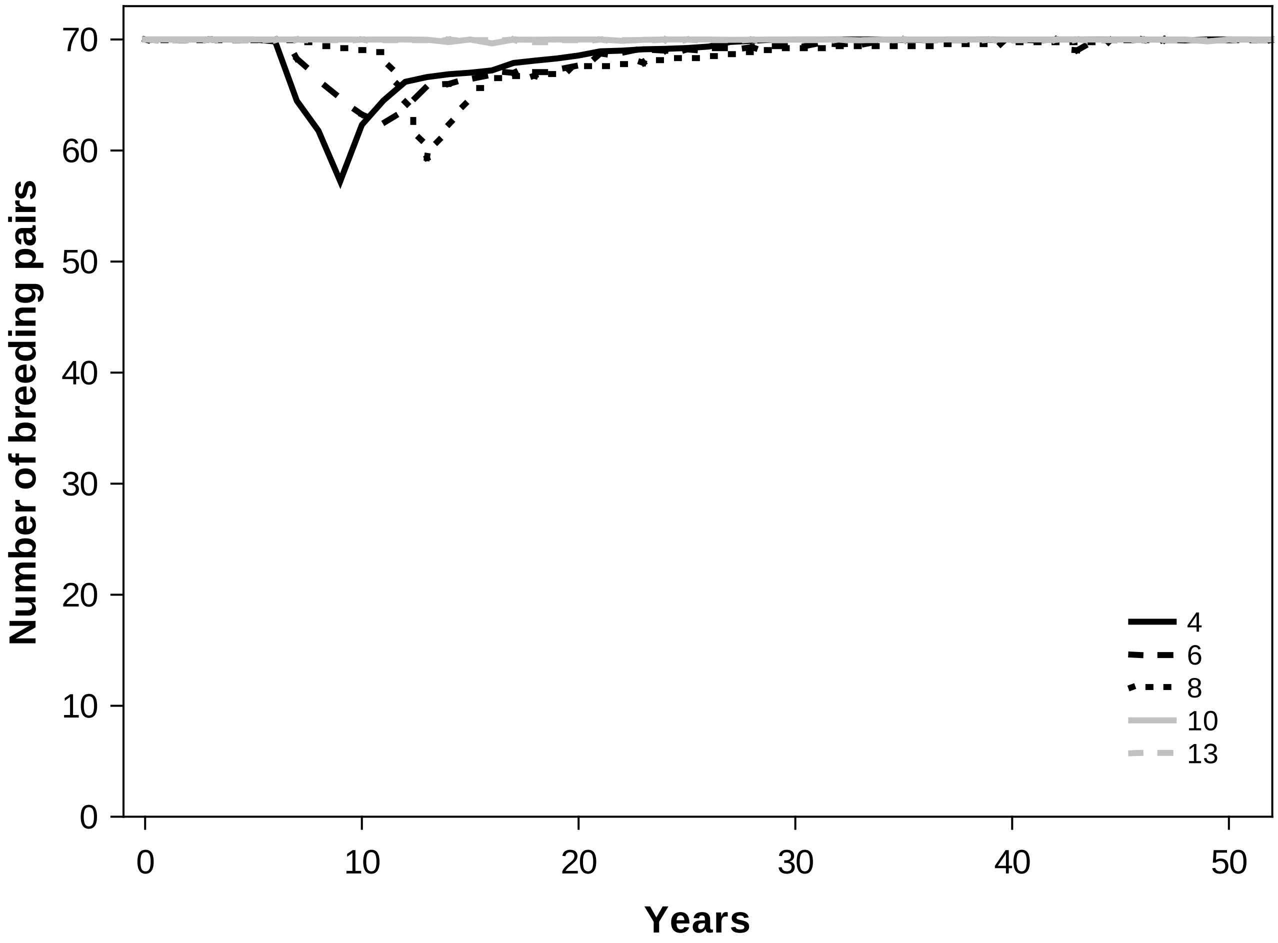

Fig. 7. Effect of different combinations of young removed per year and number of years of extraction on number of breeding pairs of the donor population with a supplementary feeding programme producing an extra 7 young per year (4 years-26 young, 6 years-18 young, 8 years-14 young, 10 years-10 young and 13 years-7 young).