

FORUM

Supplementary feeding and young extraction from the wild are not a sensible alternative to captive breeding for reintroducing bearded vultures *Gypaetus barbatus*

Antoni Margalida^{1,2*}, José M. Martínez³, Amaia Gómez de Segura⁴, Maria A. Colomer⁵, Raphaël Arlettaz^{2,6} and David Serrano⁷

¹Department of Animal Production (Division of Wildlife), Faculty of Life Sciences and Engineering, University of Lleida, 25198 Lleida, Spain; ²Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, Baltzerstrasse, 6, 3012 Bern, Switzerland; ³Sección de Biodiversidad, Servicio Provincial de Agricultura, Ganadería y Medio Ambiente de Huesca, Gobierno de Aragón, C/General Lasheras, 8, 22071 Huesca, Spain; ⁴Oficina Comarcal Agroambiental del Sobrarbe, Servicio Provincial de Agricultura, Ganadería y Medioambiente, Departamento de Agricultura, Ganadería y Medio Ambiente, Gobierno de Aragón, C/Samper, 4, E-22430 Boltaña, Spain; ⁵Department of Mathematics, Faculty of Life Sciences and Engineering, University of Lleida, 25198 Lleida, Spain; ⁶Swiss Ornithological Institute, Valais Field Station, Rue du Rhône 11, 1950 Sion, Switzerland; and ⁷Department of Conservation Biology, Estación Biológica de Doñana, EBD-CSIC, Avda de Américo Vespucio s/n, Isla de la Cartuja, E-41092 Sevilla, Spain

Summary

1. Reintroduction programmes need regular assessments of their achievements and cost-efficiency so as to adapt management strategy. Ferrer *et al.* argue that the reintroduction of the bearded vulture, which has so far relied upon the release of captive-reared chicks, could instead use the extra number of young produced by supplementary feeding on poor-quality territories in the Pyrenees. They argue that this strategy would not affect the donor population while being much cheaper than a captive breeding programme. We question this assertion based on several grounds.

2. Ferrer *et al.* used incorrect data when estimating the effects of supplementary feeding on the production of young. Our reanalyses using the same data source but corrected for missing values show effect sizes of low magnitude and with substantial uncertainty, questioning any positive effect of supplementary feeding on productivity. Moreover, Ferrer *et al.*'s experiment actually lacks a genuine statistical control due to weak temporal stability in territory quality: we demonstrate that average productivity of territories of low-quality during the baseline period (2001–2006) might actually have been increasing during the 'treatment' period (2007–2010) even without food supplementation due to a possible regression to the mean effect.

3. Our demographic reanalysis furthermore suggests that the donor population would not be that resilient to the extraction of young, resulting in trajectories far less optimistic (53–56 pairs in a time horizon of 50 years) than the 70 pairs reported. We also suggest that the costs of a captive breeding programme are substantially lower than suggested by Ferrer *et al.*

4. *Synthesis and applications.* The management recommendations proposed by Ferrer *et al.* appear unjustified. We thus urge governmental agencies to avoid making strategic political decisions and deploying conservation action on such a flawed base. We do not question here the utility of experimental approaches in reintroduction biology, but advocate independent assessment of study designs, data handling and quantitative analyses, notably when extraction of individuals from endangered populations is proposed as the best alternative option.

Key-words: captive breeding, density-dependent productivity, population dynamics, reintroduction, supplementary feeding, young-removal

*Correspondence author. E-mail: amargalida@prodan.udl.cat

Introduction

Reintroduction programmes need regular assessments of their achievements and cost-efficiency in order to adaptively redefine their strategic objectives and methodological approaches (McCarthy & Possingham 2007; McCarthy, Armstrong & Runge 2012). The outcome of this evaluation routine will optimally lead to a reallocation of scarce resources such as workforce, financial investments and even the organisms available for reintroduction (McCarthy, Armstrong & Runge 2012).

In a recent article, Ferrer *et al.* (2014), focusing on a population of bearded vultures *Gypaetus barbatus* inhabiting the Central Pyrenees (ca. 70 breeding units), claim that (i) artificial supplementary feeding can boost productivity (number of young fledged per territory and year) in suboptimal habitat, with the potential to produce an extra seven young annually in the 15 poorest quality territories; (ii) reintroduction operations elsewhere can use these extra young without affecting the viability of the donor population; and (iii) a targeted supplementary feeding programme plus the translocation of these extra young would be seven times cheaper than the current reliance on the captive breeding programme developed in Europe. This is a welcome exercise towards more systematic integration of modern adaptive management principles into reintroduction efforts (McCarthy, Armstrong & Runge 2012; Nichols & Armstrong 2012). In effect, although reintroduction has become a common tool for restoring the populations of large and threatened terrestrial vertebrates (Seddon, Armstrong & Maloney 2007; Ewen *et al.* 2012), we still much too often lack proper evaluations of the relevance of different option sets (McCarthy, Armstrong & Runge 2012). This is a serious handicap given that the management of emblematic species such as the bearded vulture usually requires substantial financial support, thus being under intense political scrutiny and public criticism.

The bearded vulture went extinct in most of its former Western Palearctic range but has been successfully reintroduced in the Alps from captive stock (Schaub *et al.* 2009). Making use of this exceptional momentum, new reintroduction projects have been launched recently in Mediterranean Europe, notably in Andalusia, also based on individuals stemming from captivity, and in the Cantabrian Mountains. In the latter case, clutches have been removed from the wild Pyrenean population in Aragon to release captive-reared young into the wild.

Focusing on the population of bearded vultures inhabiting Aragon, Ferrer *et al.* (2014) wondered whether the capture and release of the extra young that are produced by this free-ranging, in some places artificially fed population would represent a good alternative to captive breeding. They conclude that relying on the extra wild-born young produced in food-supplemented territories would be a safe and much cheaper alternative to captive breeding for future reintroduction programmes. They argue

that this strategy would reduce the costs of human interventions, increase the probability of success, be void of any demographic impact on the donor population and receive a wide support from the public. Yet, we believe that there are major flaws in the study by Ferrer *et al.* (2014), which cast important doubts about their management recommendations. In this paper, we would like to discuss several controversial aspects of their analyses, which, according to our own in-depth appraisal, invalidate their conclusions.

As a departure point, we used the same information that Ferrer *et al.* claim to have used. These data were officially provided by the Regional Governments of both Aragón (demographic data, clutch removal operations and supplementary feeding scheme) and Andalusia (expenditure of the captive breeding programme).

Can supplementary feeding increase productivity?

That supplementary feeding can be a useful tool to improve on breeding parameters (e.g. clutch size and fledgling success) has been documented for several raptors (Newton 1998; González *et al.* 2006). For the bearded vulture, the available information suggests that supplementary feeding can indeed improve pre-adult survival (Oro *et al.* 2008; Margalida, Colomer & Oro 2014). However, surplus feeding does not seem to influence breeding success, even when specific food is provided in a targeted manner to the territories during chick-rearing (Margalida 2010). Ferrer *et al.* (2014), on the contrary, claim that artificial feeding carried out well before the egg-laying period can dramatically increase productivity in suboptimal territories, reporting a sevenfold increase in the production of young under such circumstances. To reach these high figures, Ferrer *et al.* compared the reproductive output in 10 territories during two time periods: one with (2007–2010) and one without (2001–2006) supplementary feeding. Yet, in-depth scrutinizing of the data at hand reveals that the design was not as well balanced as suggested. First, it is said that the supplementary feeding programme was applied during 2007–2010 in 10 territories, but the official information says that artificial feeding started only in 2008 (Table 1). Secondly, supplementary feeding was not applied all the years in all 10 territories: it was implemented in only five territories in 2008, eight in 2009 and eight in 2010. Thirdly, four clutches and one chick were removed from these experimental territories for captive-rearing so that the final breeding outcome for these territories is only theoretical (Table 1). Thus, only 17 out of the 40 'experimental' breeding events could actually be used to estimate the effects of supplementary feeding on productivity (Table 1). Still, Ferrer *et al.* report that sample size for supplementary feeding was 40.

First, we conducted exactly the same analysis as Ferrer *et al.*, comparing productivity of the 10 territories in 2001–2006 vs. 2007–2010, irrespective of whether they

were food-supplemented or not, but according to the official data provided by the authorities, the very same as used by Ferrer *et al.*, but accounting for the correct categorization of data points explained above. Ferrer *et al.* showed that supplementary feeding increased productivity by 694% (from 0.078 to 0.541 fledglings/territory). In contrast, we obtained a change in average productivity per territory from 0.12 in 2001–2006 to 0.22 in 2007–2010. Estimates clearly differ radically for both ‘control’ and ‘treatment’ periods. The difference we found is not only of much lower magnitude (183% vs. 694%) than in the paper from Ferrer *et al.*, but had also weak statistical support (estimate: 0.7536, 95% CI: –0.7259 to 2.2332, $P = 0.31$, see more details in Appendix S1, Supporting Information).

Secondly, we performed a proper analysis that accounts for the aforementioned categorization discrepancies and discards missing data (i.e. performed by taking into account if territories were food-supplemented or not in a given year instead of comparing time periods) for the whole period (2001–2010). This analysis yielded productivity values of 0.12 and 0.29, for non-supplemented and supplemented territories, respectively, a difference which was also subject to considerable statistical uncertainty (estimate: 1.3466, 95% CI: –0.4262 to 3.1194, $P = 0.13$, Appendix S1).

Importantly, however, these slight apparent increases in productivity could be merely due to a lack of genuine statistical controls. In effect, Ferrer *et al.* used territories with very low productivities, then supposedly supplemented them, and finally compared the average productivity between the supplemented and the non-supplemented periods. This design, where the same territories were used for comparison, rests on the assumption that they exhibit high temporal consistency in productivity. Otherwise, average productivity may increase just by chance due to

the boundary imposed by choosing territories of poor quality that have only a narrow margin to decrease productivity, but a wide margin to increase it. To explore this possibility, we chose the 15 worst territories each time in five 6-year periods (from year 2000 onwards and after excluding the experimental territories) and then compared their productivity with that of the same territories during the four following years. We obtained increments in average productivity that ranged 179.6–462.9% (see Appendix S2), so that some increment in productivity would have been expected even in the absence of food supplementation. This regression to the mean phenomenon can be avoided by comparing an appropriate control to increases in the experimental group (Kelly & Price 2005). Therefore, the experiment should have included as controls other territories of poor quality not receiving the supplementation treatment because of the critical assumption of high temporal consistency in territory quality, and this design constraint was not fulfilled (see below).

Ferrer *et al.* (2014) further argued that the discrepancy between the positive effect they claimed to find vs. the lack of effect in the study of Margalida (2010) resides in the fact that ‘food provision started well before [egg] laying [in their “experiment”], thereby increasing the proportion of pairs that laid (...)’. However, surprisingly they did not compare the probability of egg-laying between supplemented and non-supplemented territories. We calculated these figures and obtained, again based on official data, average values of 0.65 and 0.53 for territories with and without supplementation, respectively, a difference that has again very low if any statistical support (estimate: 0.3652, 95% CI –0.7385 to 1.4689, $P = 0.51$, Appendix S1), and that would be subject to the same regression to the mean fallacy. For all these reasons, it is highly questionable whether supplementary feeding had any positive impact at all on breeding output.

Table 1. Overview of the supplementary feeding (SF) programme carried out in 10 territories in the Aragonese Pyrenees

Year	Territory	2008		2009		2010				
		SF	Clutch	Fledgling	SF	Clutch	Fledgling	SF	Clutch	Fledgling
1997	4		0	0	Yes	0	0		1	Removed
1988	35		1	0		1	0	Yes	1	1
1988	36	Yes	1	1	Yes	0	0	Yes	–	0
1988	38	Yes	1	1	Yes	1	0		1	1
1988	39		0	0	Yes	0	0	Yes	0	0
1996	40	Yes	Removed		Yes	1	0	Yes	1	0
1999	49		0	0		0	0	Yes	0	0
1992	51	Yes	Removed		Yes	Removed		Yes	Removed	
1988	55		–	–	Yes	1	1	Yes	0	0
2003	58	Yes	1	1	Yes	0	0	Yes	1	0
			5	3		8	7		7	7

The year of occupancy, the identification code in the official data set and the breeding output of each territory are reported. In Table 1, grey are marked the territories and years when SF was conducted, specifying whether the clutch or the chick had been removed. The last line includes the number of food-supplemented territories that can be used per year to estimate egg-laying rates and productivity, respectively. Data provided by the Government of Aragón.

Population dynamics and density-dependent effects

Because animal population management guidance is usually reliant on the outcome of population viability analysis (PVA), data quality, repeatability and reproducibility are fundamental issues (Ellison 2010; Pe'er *et al.* 2013). We first performed modelling with the same parameters and scenarios of Ferrer *et al.* (see table 1 in Ferrer *et al.* 2014 and first column in table 2), using VORTEX v. 10.0.7.3. (Appendix S3), and obtained very different population trajectories. Our simulations yielded a negative impact in any scenario of extraction, either with (17–37% decline in 10–22 years) or without (37–46% in 10–22 years) the production of seven extra fledglings per year during the food supplementation period (Fig. 1). In a time horizon of 50 years, the average number of breeding pairs oscillated between 53 and 56 (Fig. 1), in contrast with Ferrer *et al.*

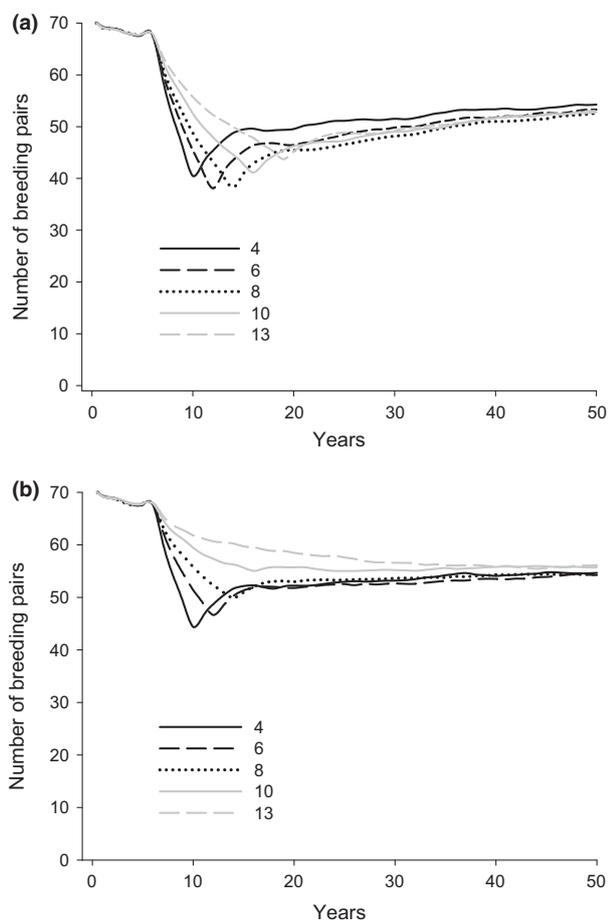


Fig. 1. Outcome of Vortex simulations carried out based on the data used by Ferrer *et al.* (2014) (see table 1 in Ferrer *et al.* and first column of table 2). The scenarios considered by Ferrer *et al.* with different combinations of young removed per year and years of extraction (4 years–26 young, 6 years–18 young, 8 years–14 young, 10 years–10 young and 13 years–7 young) were simulated. Population trajectories are shown for each scenario without (a) and with (b) the hypothetical production of seven extra young per year during the years of extraction.

who reported a maximum potential of 70 breeding pairs in all simulations.

We furthermore disagree with the demographic approach by Ferrer *et al.* (2014) regarding the parameter values they retained for modelling age at first breeding and juvenile survival (see details in Table 2). Simulations based on more reliable and updated parameters (see second column of Table 2) provided strong evidence that the expected trajectories would be far less optimistic than those shown by Ferrer *et al.* (2014) (Fig. 2), corroborating the predictions by Oro *et al.* (2008) (see Fig. 5 therein). Although we are confident that our population projections are more realistic than in Ferrer *et al.*, we recognize that more advanced modelling techniques that fully incorporate uncertainty may improve substantially their realism (Bakker *et al.* 2009; Armstrong & Reynolds 2012). For example, although adult survival is quite well estimated in the Pyrenean population, PVAs are highly sensitive to uncertainty in this parameter (see Appendix S3, Figure S3), to an extent that errors may introduce further substantial uncertainty in model projections.

Finally, Ferrer *et al.* (2014) suggest that the density-dependent productivity regulation in the Aragonese Pyrenees mainly results from an increase in the proportion of poor territories occupied as the population grew, while reproductive units on first occupied territories maintained a high mean productivity. This means, within the logic of the habitat heterogeneity hypothesis (HHH), that the low-quality territories chosen for the supplementation experiment should be new territories with significantly lower values in productivity. According to official data, however, eight out of the ten territories that were food-supplemented were in fact old territories (i.e. occupied for more than 15 years backwards), which again contrasts with the categorization by Ferrer *et al.* (2014). Our analysis of the data available for the population as a whole shows that there is indeed no evidence for any HHH operating nowadays in Pyrenean bearded vultures. First, new and old territories do not differ in mean annual productivity, with 0.37 and 0.38, respectively (estimate: 0.04226, 95% CI –0.8593 to 0.9438, $F_{1,369} = 0.01$, $P = 0.93$; Fig. 3), as already suggested by Carrete, Donazar & Margalida (2006) for the period 1994–2002. Secondly, while testing for temporal consistency in territory productivity by means of repeatability analyses (Nakagawa & Schielzeth 2010), we found R -values ≤ 0.25 (Appendix S4), indicating that between-territory differences in productivity show low consistency. In other words, the weak constant spatial pattern over time across territories also suggests HHH to only be a minor mechanism responsible for driving the drop in productivity observed in the population.

Captive breeding vs. translocation of wild-born young

Although it seems obvious that translocations generally are less expensive than traditional captive breeding

Parameter	Ferrer <i>et al.</i>	Updated parameters
Inbreeding depression	–	No
Environmental Variation concordance of reproduction and survival	–	No
Mating system	–	Long-term monogamy
Carrying capacity	70 pairs	70 pairs
Mean age of first successful breeding*	7 years	11 years
Maximum age of reproduction	32 years	32 years
Maximum number of broods per year	1 brood	1 brood
Maximum progeny per brood	1 young	1 young
Sex ratio at birth	50%	50%
Productivity	0.6 at low density 0.35 at high density	0.6 at low density 0.35 at high density
Annual juvenile mortality in Pyrenees		3.4% (SD 1.5) [‡] (1 year old)
Annual pre-adult mortality in Pyrenees	3.9% (SD 1.8) [†] (1–6 years old)	9.8% (SD 0.7) [‡] (2–5 years old)
Annual adult mortality	13% (SD 1.4) (>6 years old)	6.8% (SD 1.9) [‡] (>5 years old)

Table 2. Life history parameters used to simulate population trajectories of bearded vultures. The parameters used by Ferrer *et al.* and the updated parameters are shown

*The parameter to be introduced in Vortex is mean age of first successful breeding. This has been estimated to occur in the Pyrenean population at a median age of 11 years (Antor *et al.* 2007; López-López *et al.* 2013), a substantially later age than that used by Ferrer *et al.*

[†]Ferrer *et al.* (2014) set juvenile/pre-adult mortality at 21% for 1- to 6-year-old birds (see Table 1 therein). Although this parameter is usually presented in the literature on an annual basis (and is the way it should be introduced in Vortex), early modelling exercises with annual mortality rates of 21% evidenced dramatic population declines (results not shown), so we assumed that this is total mortality between 1 and 6 years of age. This corresponds to annual survival estimates of $\sqrt[6]{(100 - 21)/100} = 0.961$, that is 3.9% mortality, a rate not achieved in any of the studies cited by Ferrer *et al.* for the Pyrenean population. Oro *et al.* (2008) estimated annual juvenile survival (1–4 years old) at 0.944 in the Pyrenees, which would correspond to 21% total mortality between 1 and 4 [$100 \times (1 - 0.944^4)$], but not between 1 and 6 years as Ferrer *et al.* parameterized. Due to the unknown origin of this parameter, we conservatively assumed that 3.9% annual mortality was the parameter used.

[‡]Annual survival probabilities of juveniles (1-year old), subadults (2–5 years old) and adults (>5 years old) were obtained from Margalida, Colomer & Oro (2014) by averaging survival estimates from the last 5 years for which data were available in the Pyrenees (2007–2011). This is justified by the fact that some parameters changed after the massive closure of feeding stations, and also because adult survival showed a temporal regressive trend (Oro *et al.* 2008; Margalida, Colomer & Oro 2014). The annual survival values are 0.966 (SD 0.015) for juveniles, 0.902 (SD 0.007) for pre-adults (2–5 years old) and 0.932 (SD 0.019) for adults.

programmes, the lack of detailed, disaggregated financial information about inherent costs in Ferrer *et al.* (2014) precludes any rigorous comparative assessment. According to Ferrer *et al.* (2014), capturing, temporarily raising and translocating by hacking seven extra chicks obtained from wild nests would cost approximately €100 000 per year, but the authors do not provide an accurate detailed description about how this calculation was done. On the other hand, they claim that € 700 000 per year would be necessary for the maintenance of a captive breeding programme. However, the cost of the captive breeding programme carried out in Andalusia in 2013 amounted to € 206 000 according to official sources (Government of Andalusia; Appendix S5); a substantially lower sum.

Another argument against captive breeding raised by Ferrer *et al.* is that ‘the probability of success is often lower in reintroduction programmes using captive born

animals owing to factors such as lower survival rates, inappropriate behaviour or poor adaptation to local conditions’. Yet, the survival of first year and older bearded vultures released to the wild from captive stock has been proven, by the means of elaborated population dynamic mark–resighting modelling, to be as high as 0.89 and 0.96, respectively (Schaub *et al.* 2009), whereas the overall Alpine reintroduction programme is one the most successful species restoration programmes ever carried out world-wide. This crucial study, unfortunately, is not considered by Ferrer *et al.* (2014).

Conclusions

Unfortunately, the welcome initiative of Ferrer *et al.* (2014) is a failed exercise to improve ex-situ conservation and restoration action for such a highly threatened and

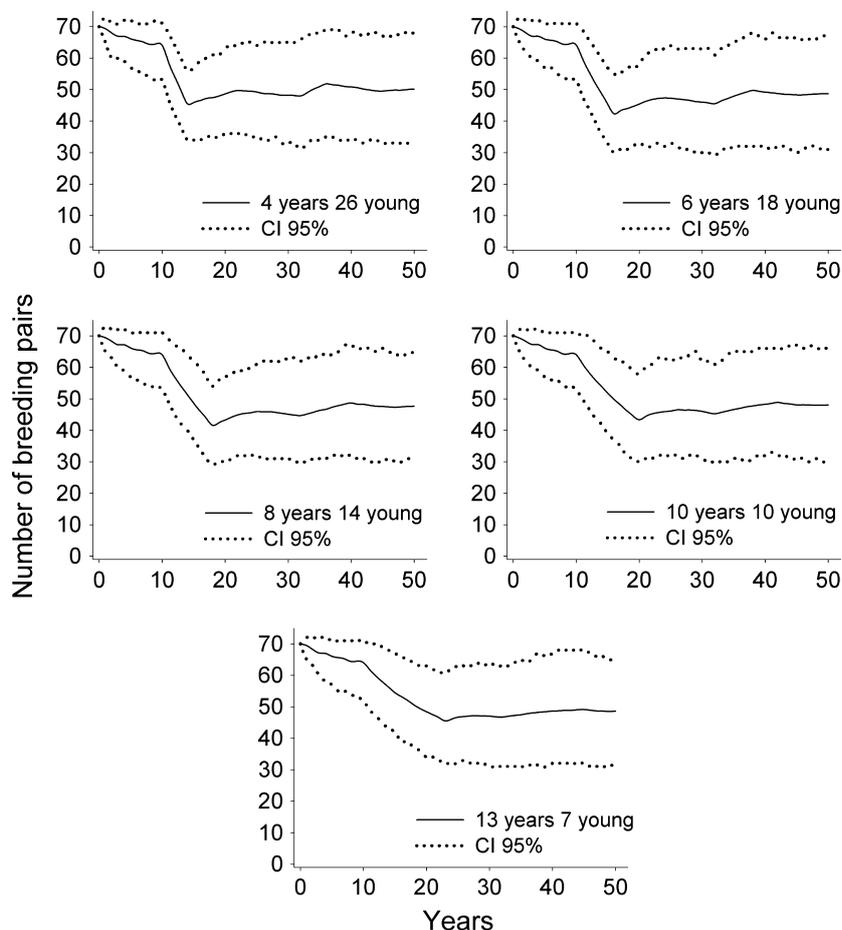


Fig. 2. Outcome of Vortex simulations (CI 95%) of the donor population of bearded vultures using updated life history parameters (Table 2). The scenarios considered by Ferrer *et al.* with different combinations of young removed per year and years of extraction (4 years–26 young, 6 years–18 young, 8 years–14 young, 10 years–10 young and 13 years–7 young) were simulated.

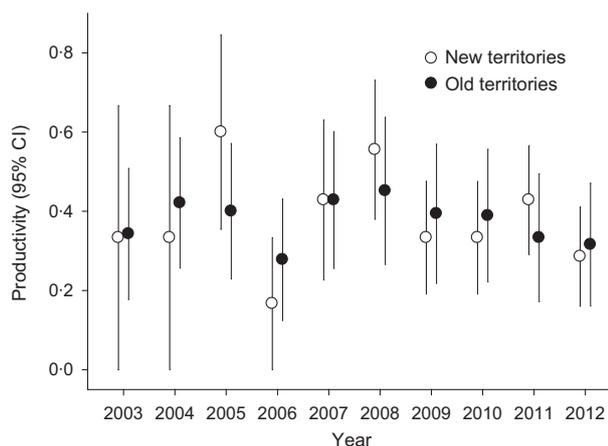


Fig. 3. Average annual productivity within the so called old (occupied before 1997) and new territories (occupied after 2002) from 2003 to 2012.

emblematic species as the bearded vulture. Our reanalyses of the same original data set provided to Ferrer *et al.* clearly challenge their conclusions because (i) supplementary feeding cannot be proven to increase breeding performance based on currently available data and research; (ii) any demographic projections suggest a future negative population impact in case of extractions carried out at the

levels suggested by Ferrer *et al.*; and (iii) the argument by Ferrer *et al.* that the wild extraction strategy would be seven times cheaper than conventional captive breeding is too simplistic, being based on figures which do not seem to add up. We thus urge governmental agencies to avoid making strategic decisions and implementing conservation actions on such a flawed base.

Field experiments are desirable in reintroduction biology to illuminate causal inference and properly assess management alternatives (McCarthy, Armstrong & Runge 2012). In order to avoid misguided action plans, we suggest that independent assessments, even of published peer-reviewed studies, are systematically carried out, notably when extraction of individuals from endangered populations is suggested as the best alternative. Such assessments have to critically evaluate study designs and data handling, and make sure that quantitative inference is rooted in state-of-the-art statistical analyses and modelling techniques that fully incorporate uncertainty.

Acknowledgements

Data from the Aragonese breeding population were kindly provided by M. Alcántara (Jefe del Servicio de Biodiversidad, Dirección General de Conservación del Medio Natural, Departamento de Medio Ambiente, Government of Aragon). Data from the captive programme in Andalusia were kindly provided by R. Arenas (Jefe del Servicio de Gestión del Medio

Natural, Consejería de Medio Ambiente, Government of Andalusia). The comments of two anonymous reviewers, V. Bretagnolle, J.A. Donazar, T. Pärt and D. Oro greatly improved the manuscript. J.M. Martínez was supported by the Government of Aragón (projects RB34045 and RB44037). A. Margalida was supported by a Ramón y Cajal research contract from the Ministry of Economy and Competitiveness (RYC-2012-11867).

Data accessibility

Raw data have not been archived because they belong to the Government of Aragón and contain sensitive information on an endangered species listed in the National Catalogue of Threatened Species of Spain.

References

- Antor, R.J., Margalida, A., Frey, H., Heredia, R., Lorente, L. & Sesé, J.A. (2007) First breeding age in captive and wild Bearded Vultures *Gypaetus barbatus*. *Acta Ornithologica*, **42**, 114–118.
- Armstrong, D.P. & Reynolds, M.H. (2012) Modelling reintroduced populations: the state of the art and future directions. *Reintroduction Biology: Integrating Science and Management* (eds J.G. Ewen, D.P. Armstrong, K. Parker & P. Seddon), pp. 165–222. Blackwell Publishing Ltd, Oxford.
- Bakker, V.J., Doak, D.F., Roemer, G.W., Garcelon, D.K., Coonan, T.J., Morrison, S.A., Lynch, C., Ralls, K. & Shaw, R. (2009) Incorporating ecological drivers and uncertainty into a demographic population viability analysis for the island fox. *Ecological Monographs*, **79**, 77–108.
- Carrete, M., Donazar, J.A. & Margalida, A. (2006) Density-dependent productivity depression in Pyrenean Bearded Vultures: implications for conservation. *Ecological Applications*, **16**, 1674–1682.
- Ellison, A.M. (2010) Repeatability and transparency in ecological research. *Ecology*, **9**, 2536–2539.
- Ewen, J.G., Armstrong, D.P., Parker, K. & Seddon, P. (2012) *Reintroduction Biology: Integrating Science and Management*. Blackwell Publishing Ltd., Oxford.
- Ferrer, M., Newton, I., Muriel, R., Báguena, G., Bustamante, J., Martini, M. & Morandini, V. (2014) Using manipulation of density-dependent fecundity to recover and endangered species: the bearded vulture *Gypaetus barbatus* as an example. *Journal of Applied Ecology*, **51**, 1255–1263.
- González, L.M., Margalida, A., Sánchez, R. & Oria, J. (2006) Supplementary feeding as an effective tool for improving breeding success in the Spanish imperial eagle (*Aquila adalberti*). *Biological Conservation*, **129**, 477–486.
- Kelly, C. & Price, T.D. (2005) Correcting for regression to the mean in behaviour and ecology. *The American Naturalist*, **166**, 700–707.
- López-López, P., Zuberogoitia, I., Alcántara, M. & Gil, J.A. (2013) Philopatry, natal dispersal, first settlement and age of first breeding of Bearded Vultures *Gypaetus barbatus* in central Pyrenees. *Bird Study*, **60**, 555–560.
- Margalida, A. (2010) Supplementary feeding during the chick-rearing period is ineffective in increasing the breeding success in the bearded vulture (*Gypaetus barbatus*). *European Journal of Wildlife Research*, **56**, 673–678.
- Margalida, A., Colomer, M.A. & Oro, D. (2014) Man-induced activities modify demographic parameters in a long-lived species: effects of poisoning and health policies. *Ecological Applications*, **24**, 436–444.
- McCarthy, M.A., Armstrong, D.P. & Runge, C. (2012) Adaptive management of reintroduction. *Reintroduction Biology: Integrating Science and Management* (eds J.G. Ewen, D.P. Armstrong, K. Parker & P. Seddon), pp. 256–289. Blackwell Publishing Ltd, Oxford.
- McCarthy, M.A. & Possingham, H.P. (2007) Active adaptive management for conservation. *Conservation Biology*, **21**, 956–963.
- Nakagawa, S. & Schielzeth, H. (2010) Repeatability for Gaussian and non-Gaussian data: a practical guide for ecologists. *Biological Reviews*, **85**, 935–956.
- Newton, I. (1998) *Population Limitation in Birds*. Academic Press, London.
- Nichols, J.D. & Armstrong, D.P. (2012) Monitoring for reintroductions. *Reintroduction Biology: Integrating Science and Management* (eds J.G. Ewen, D.P. Armstrong, K. Parker & P. Seddon), pp. 223–255. Blackwell Publishing Ltd, Oxford.
- Oro, D., Margalida, A., Carrete, M., Heredia, R. & Donazar, J.A. (2008) Testing the goodness of supplementary feeding to enhance population viability in an endangered vulture. *PLoS One*, **3**, e4084.
- Pe'er, G., Matsinos, Y.G., Johst, K., Franz, K.W., Turlure, C., Radchuk, V. et al. (2013) A protocol for better design, application, and communication of population viability analyses. *Conservation Biology*, **27**, 644–656.
- Schaub, M., Zink, R., Beissmann, H., Sarrazin, F. & Arlettaz, R. (2009) When to end releases in reintroduction programmes: demographic rates and population viability analysis of bearded vultures in the Alps. *Journal of Applied Ecology*, **46**, 92–100.
- Seddon, P.J., Armstrong, D.P. & Maloney, R.F. (2007) Developing the science of reintroduction biology. *Conservation Biology*, **21**, 303–312.

Received 18 December 2014; accepted 18 September 2015

Handling Editor: Tomas Pärt

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Comparison of breeding parameters between supplemented and non-supplemented territories.

Appendix S2. Changes in productivity of the poorest territories between periods.

Appendix S3. Population modelling and sensitivity analysis.

Appendix S4. Repeatability analyses of productivity in bearded vultures.

Appendix S5. Costs of the captive breeding programme in Andalusia.