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Relative contribution of local demography and immigration in the recovery of a geographically-isolated population of the endangered Egyptian vulture

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ARTICLE INFO

ABSTRACT

In a context of increasing concern for biodiversity conservation but decreasing resources devoted to species management, measuring the impact of actions is critically needed so as to optimise conservation practices. Long-term longitudinal data collected on marked individuals allow for an assessment of the demographic response of a population to conservation actions while accounting for potential confounding factors. This study focused on the recovery of a geographically-isolated population of the endangered Egyptian vulture in south-eastern France, which experienced food shortages induced by major changes in habitat and sanitary legislation limiting the abandonment of dead animals in the field. The survival rates and population dynamics of the Egyptian vulture were computed, following the implementation of supplementary feeding stations, while accounting for the potential variation in environmental conditions on wintering grounds, reproduction and immigration. An integrated population model (IPM) was used to combine capture–resighting data with recoveries of dead birds, breeding surveys and counts of territorial pairs over a 16-year period. Results showed that the implementation of vulture restaurants improved the local survival rates and successfully stabilised the local demography of Egyptian vultures; this despite a reduction in average fecundity due to compensatory density feedback. Moreover, throughout the study period, about two thirds of the new recruits into the breeding population were immigrants, suggesting immigration constantly sustained the Egyptian vulture population in south-eastern France. However, we did not detect any effect of vulture restaurants on the immigration rate, indicating that the improvement of local survival by vulture restaurants remained the main driver of the positive shift in the population dynamics. This study highlights the positive impact of vulture restaurants on Egyptian vulture population restoration by compensating for natural food limitations. It also points out the methodological importance of estimating immigration for understanding population dynamics and that large-scale monitoring and internationally-concerted conservation should be promoted.

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1. Introduction

An important amount of human and financial resources is currently spent on a growing number of conservation actions aiming at stopping the decline of species worldwide (Ferraro and Pattanayak, 2006). The impact of conservation actions needs to be carefully evaluated so as to ensure that the targeted species or populations are actually benefiting from the conducted actions and that the dedicated resources are therefore helping to reach conservation objectives. Such evaluations are also critically needed to develop evidence-based conservation strategies (Sutherland et al., 2004). Yet, they are relatively rare and conservation actions continue to be applied using subjective criteria (but see Ferrer and Hiraldo, 1991). Consequently, some actions are widely used based on a perceived merit which has not been properly measured (Margoluis et al., 2009; Sutherland et al., 2004).

Supplementary feeding station for scavenger populations (hereafter vulture restaurants) is a typical example of a conservation action which is widely used without systematic evaluation (Piper, 2005). The action consists of dispatching carcasses of livestock over vulture foraging areas to counteract the decrease of food supply induced by pastoralism decline and sanitary regulation limiting the abandonment of dead animals in the

field. These actions are also supposed to facilitate the recolonization of abandoned areas and to provide alternative food sources to compensate for carcasses treated with veterinary drugs or used as poisoned bait (Cortés-Avizanda et al., 2010; Oro et al., 2008). Unfortunately, there is still little information available to improve the design of the vulture restaurants and their positive impact on population dynamics (Cortés-Avizanda et al., 2010; Grande, 2006; but see Ferrer et al., 2014).

To build evidence in animal conservation, a common method consists in measuring the population in terms of population size (Margolius et al., 2009). However, individual counts may suffer from a detection bias and uncertainty is rarely appropriately accounted for. In addition, this phenomenological approach does not allow for the identification of underlying processes, and therefore leaves potential confounding factors, which could generate changes in population dynamics regardless of implemented conservation actions, undetected (Ferraro and Pattanayak, 2006). A demographic approach is considered as a powerful alternative for evaluating the impact of conservation action, because it identifies the relative contribution of local fecundity- and survival-related traits to the population response using the estimations of key demographic parameters which are based on longitudinal surveys of marked animals (Frederiksen et al., 2014).

The validity of a demographic approach in evaluating conservation is however dependent on the spatial scale at which endangered populations exchange individuals. Usually, survival and reproduction are estimated from local monitoring assuming that the focal population is closed or that emigration equilibrates immigration. However, evidence is increasing that immigration plays a crucial role in restoring populations which are intrinsically declining despite an apparent stability (Brown and Collopy, 2012; Schaub et al., 2010, 2012; Tempel et al., 2014). Thus, the spatial scale at which conservation actions are evaluated should take these immigration and emigration fluxes into account. Additionally, the development and implementation of conservation programmes should likewise be aware or include these factors.

Concerning vulture restaurants, quantitative analyses of their effects on demographic parameters are rare and sometimes contradicting. In some contexts, supplementary feeding seem to have enhanced the survival of immature bird only (+60% for juvenile Cape griffons, Piper et al., 1999; +20% for pre-adult Bearded vultures, Oro et al., 2008). Whereas in other contexts, they appeared ineffective in reducing griffon vultures mortality which was caused by poisoning in Spain (Martínez-Abraín et al., 2012). Concerning the reproductive performance, territorial pairs of Egyptian vultures near restaurants appeared more productive (Grande, 2006; Liberatori and Penteriani, 2001) while fecundity decreased in a bearded vulture population due to a compensatory feedback (Carrete et al., 2006). These heterogeneous findings imply that the impact of supplementary feeding still needs to be evaluated for different species and ecological contexts.

In this study, we assessed the impact of vulture restaurants which were put in place to rescue a small population of Egyptian vultures *Neophron percnopterus* (≤30 pairs) in south-eastern France after a strong decline from a hundred pairs present in 1900. The recovery in population size was observed following the implementation of vulture restaurants (Fig. 1), and has led to the impression that the restaurants are effective. Yet, the recovery could have been driven by confounding factors, e.g. improved conditions on wintering grounds through climate and primary productivity change (Grande et al., 2009). Furthermore, as many species of large raptors, the Egyptian vulture has undergone dramatic reduction and fragmentation of its range, leading to geographically isolated populations. The French population we studied is isolated from other known Spanish populations at the northern limit of the species distribution range. Nonetheless, some resightings of vultures ringed in Spain and recruited in south-eastern France suggest demographic exchanges between populations. Additionally, a regular immigration is likely to have promoted the recent recovery of the Catalan population (Tauler et al., 2015). Therefore, it is not unlikely that a significant immigration rate from the Spanish neighbourhood hide a declining local
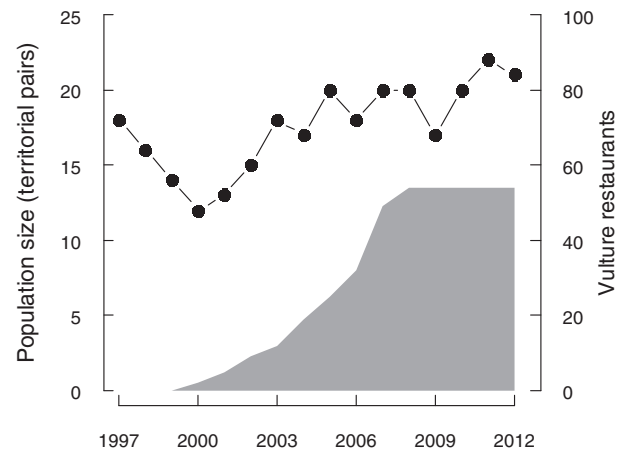

Fig. 1. Variation of the observed population size between 1997 and 2012, measured in number of territorial pairs (black dots). The progressive implementation of vulture restaurants is represented by the grey polygon.

dynamics in south-eastern France (e.g. Schaub et al., 2010). Likewise, it could also have reinforced the recovery of the population from a stable local dynamics otherwise.

Our objective in this study was therefore to determine the contribution of several demographic processes in the perceived recovery of this Egyptian vulture population following the implementation of vulture restaurants. To achieve this, we combined multiple sources of data from a 16-year monitoring encompassing the conservation programme (Capture–Mark–Resighting, recoveries of dead birds, breeding surveys and counts of territorial pairs) into a single integrated population model (IPM; Schaub and Abadi, 2011). We parameterized our IPM using existing knowledge on Egyptian vulture life histories (Cortés-Avizanda et al., 2009; Grande et al., 2009), so as to quantify the relative contribution of survival, reproduction and immigration in the recent observed recovery and to assess to what extent these demographic parameters were influenced by the onset of supplementary feeding.

2. Methods

2.1. Egyptian vultures in south-eastern France

The Egyptian vulture is a medium-sized and long-lived raptor characterized by a late onset of reproduction and a high elasticity of population growth rate to adult survival (García-Ripollés and López-López, 2011; Grande et al., 2009). French Egyptian vultures winter in the Sahel region between Mauritania and Senegal (Meyburg et al., 2004). Fledglings spend their first summer in Africa before initiating the seasonal migration after 2–3 years old (Grande et al., 2009). There is a high variability in the age at which vultures acquire a territory (i.e. recruit, from 3 to 11 years old; birds are called floaters before recruitment) but most of them recruit at around 6 years old (Grande, 2006). Once territorials, they are mostly faithful to their breeding site. Breeding pairs can raise one sometimes two fledgling per year (Cortés-Avizanda et al., 2009). Survival rates are known to increase with age and territorial status (Grande et al., 2009).

The Egyptian vulture has been recently listed among the 100 most worldwide threatened birds (30th rank in the EDGE list of the Zoological Society of London; edgeofexistence.org). In Europe, population decline has been putatively attributed to mortality induced by poisoning and electrocution (García-Ripollés and López-López, 2011) and to the reduction in pastoralism and the setting up of sanitary regulations that have reduced the availability of carcasses in the wild (Margalida et al., 2010; Martínez-Abraín et al., 2012). The south-eastern French population of Egyptian vultures suffered from a steep decline in numbers of pairs (from ~100 in 1900 to 12 in 2000, Orabi, 2008) and in its breeding range. It is situated on either sides of the Rhone valley (Map in

Supporting Information Appendix A), occupying open habitats such as scrubland and limestone hills with cliffs for nesting. It now appears geographically isolated from the nearest ensemble of breeding areas, the French Pyrenees (72 territorial pairs in 2012), by the unsuitable Aude and Garonne valleys (Appendix A). Between 2003 and 2008, the south-eastern French population benefited from a European LIFE Nature programme (LIFE03 NAT/F/000103). The main conservation action consisted in the implementation of vulture restaurants. Vulture restaurants are small open fenced places weekly supplied by butchery offal or sheep carcasses mostly in spring (March–April–May). They are widely used in Mediterranean countries for the conservation of vulture species: griffon *Gyps fulvus*, cinereous *Aegypus monachus*, bearded *Gypaetus barbatus* and Egyptian vultures *Neophron percnopterus* (Cortés-Avizanda et al., 2010). In south-eastern France, the first restaurant was set up in 1999 and the LIFE programme enabled to progressively increase their number until 54 (Fig. 1), spread over the current and historical breeding areas. At the same time, the number of territorial pairs increased from 12 territorial pairs in 2000 to 21 in 2012, suggesting a positive impact of vulture restaurants on population dynamics.

In order to properly assess this impact, a systematic breeding survey started in 1997. Each spring, territorial pairs were monitored and a survey of the entire zone allowed the detection of new ones. We defined this count of territorial pairs as population size. Repeated visits at occupied breeding sites between March and July enabled to record the number of fledglings produced per pair (hereafter fecundity). Capture–Resighting (CR) data were collected from 1997 to 2012. During this period, 151 chicks have been ringed at the nest with a metal ring and three plastic coloured rings, whose unique combination can be read using a telescope at a distance up to 200 m. Resighting data (171 events from 66 individuals) consist in i) resightings across the study area which was intensively monitored by different organizations, and ii) recoveries of dead birds (n = 9). Among resightings, 11 individuals were identified despite the loss of one of their coloured rings (metal ring identification, unique combination of two rings, previously known territorial birds). Since no data could have been obtained from birds having emigrated towards the Pyrenees or Spain, the analysis of the Capture–Resighting data estimated local survival (or apparent survival, i.e. the combination of true survival and permanent emigration).

2.2. Demographic modelling and integrated population model

Our approach consisted in integrating all available information sources in a single modelling framework so-called Integrated Population Model (IPM; Besbeas et al., 2002; Schaub and Abadi, 2011). Our IPM was made of a Multi-State Capture–Recapture model (MSCR) estimating local survival, a Fecundity model estimating the variation in fecundity, and a Matrix Population model (MPM) projecting the size of the population over time (Fig. B.1.1 in Appendix B). We used a demographic approach that investigates the influence of vulture restaurants on local survival (using MSCR) and its consequence on population dynamics (using MPM). We chose to build a single IPM structure (Hilborn and Mangel, 1997), parameterized according the available scientific evidence on Egyptian vulture demography (Cortés-Avizanda et al., 2009; García-Ripollés and López-López, 2011; Grande et al., 2009).

Local survival rates were estimated using CR data with a multi-state approach allowing the combination of resightings (live individuals) and recoveries (dead individuals; Lebreton et al., 2009). This type of models also permits to simultaneously model survival, recruitment and ring loss probabilities (Tavecchia et al., 2012). The modelling of ring loss was especially important here to avoid any negative bias in survival estimates, as vultures species are known to get rid of their coloured rings (Le Gouar et al., 2008; Grande et al., 2009). The multi-state approach consisted in the deconstruction of the vulture demography in a succession of states and their associated observations (Lebreton et al., 2009). In our case, vultures in a given year could be in one of these 9 states: fledgling, floater having one, two or three coloured rings, territorial

having one, two or three coloured rings, recently dead and recovered, long dead. They could be observed as fledgling, floater having one, two or three coloured rings, territorial having one, two or three coloured rings, recently dead and recovered, dead and not recovered, or not observed at all. From one year to another, individuals could move among states according to transition probabilities describing survival, recruitment within a territorial pair, ring loss, and recovery following death (see state-transition and observation matrices in Appendix B.1). We parameterized survival and resighting probabilities as time-invariant, with no difference between sexes (Grande et al., 2009). Survival and resighting probabilities depended on the age and the status (floater or territorial) of an individual. The resighting probability varied according to three age classes for floaters (age 1, age 2, age 3 +) and a single class for territorials (Grande et al., 2009). We checked whether the resighting probability of floaters (only the class of age 3 + to have enough data) increased over time as a consequence of the implementation of vulture restaurants, where camera-traps were installed to identify ringed individuals. Ring loss was accounted for by estimating the resighting probabilities of floaters (only the class of age 3 +) and territorials having lost at least one coloured ring independently from birds having all their rings. The probability to survive to age *i* varies according to four classes for floaters (age 1–2, age 3–4, age 5, age 6 +) and a single class for territorials (Grande et al., 2009). Since estimation of the variation in the probability of becoming territorial was not available, we assumed that it varied according to age classes (same categorisation as for survival) but remained constant through time. This probability was fixed at 0 for age 1–2, recruitment at this age having never been observed in our population.

Our aim was to test for a linear relationship between local survival rates and the number of vulture restaurants implemented during the survey. To achieve this, we fitted the number of available restaurants each year as a continuous covariate in both floater and territorial birds (Appendix B.1). Uncontrolled environmental variation may have altered survival irrespective of conservation actions. Indeed, such effect of environmental variation on survival was found at both breeding and wintering grounds (Grande et al., 2009). We accounted for potential confounding factors by estimating the influence (on both floater and territorial survival) of the variation in primary production measured by the Normalized Difference Vegetation Index as a proxy for food availability on wintering grounds (see Appendix C for details on NDVI extraction). High NDVI values indicate high primary productivity (associated to wet winters). We assumed that the implementation of vulture restaurants outweighed the variation of resource availability in the breeding area.

We estimated the annual variation in average fecundity using a Poisson model linking the number of fledglings produced each year to the estimated number of territorial pairs (Kéry and Schaub, 2012). In addition, we tested for a linear compensatory density-feedback of population size on fecundity, as frequently observed in long-lived including scavengers (Carrete et al., 2006; García-Ripollés and López-López, 2011).

We then built a post-breeding matrix population model (Fig. B.1.1.; Caswell, 2001). This MPM was female-based, assuming an even sex-ratio and similar demographic rate between sexes (Grande et al., 2009). We defined a compartment of floaters with five stages from age 1 to 5, and a sixth stage including territorial birds of any age. The transitions incorporated demographic stochasticity by sampling survival using a binomial distribution and fecundity using a Poisson distribution. However, we did not model random annual variation around parameters to limit model complexity. We used this MPM with demographic rates estimated by the MSCR and Fecundity model to project the asymptotic population growth rate in different management situations (before/after the implementation of vulture restaurants, with/without a density feedback on fecundity). Finally, the population size projected by the MPM was compared to the annual count of territorial pairs under a Poisson distribution. The potential mismatch between count predictions and observations was used in the IPM to estimate the number of immigrants recruited each year as territorials (Szostek et al., 2014). The IPM estimated an average immigration rate with

random annual variation. This immigration rate was defined as the number of female immigrants newly recruited in year $t + 1$ per number of territorial females in year t (Abadi et al., 2010). We also tested for a positive linear relationship between the immigration rate and the number of vulture restaurants, which could potentially have attracted dispersers.

Finally, we used a Bayesian framework to analyse the IPM, combining the joint likelihood with prior probability distributions to obtain posterior distributions of the target parameters (see Appendix B for more details). We first specified informative priors chosen from literature for demographic rates to help convergence and then checked the sensitivity of each parameter by changing for uninformative priors. The priors of the covariates effects on vital rates were uninformative but centred on zero. These effects were considered significant when the 95% of their posterior distribution did not overlap zero (Grosbois et al., 2008). We applied Markov Chain Monte Carlo (MCMC) methods to simulate observations from the posterior distributions with software WinBUGS (Lunn et al., 2000) that was run from R with package R2WinBUGS (Sturtz et al., 2005). We specified a burn-in of 50 000 and simulated 100 000 samples subsequently thinned by a factor 10 and ran 2 chains with different starting values. Inferences were therefore based on 5000 samples constituting the posterior distributions. The convergence of the Markov chains was satisfactory in each case ($\hat{R} < 1.05$). Models and associated BUGS code are detailed in supplementary materials (Appendix B.1 & B.2).

3. Results

3.1. The impact of vulture restaurants on local survival and fecundity

Local survival of Egyptian vultures increased with the number of restaurants implemented in south-eastern France (Fig. 2). Both floater and territorial vultures benefited from an about 11% improvement of their survival between 1997 and 2012 (Table 1). This main result was robust to the detection of an expected improvement of the resighting probability of floater birds during the survey period, due to the progressive implementation of camera traps at restaurants (Table 1). Moreover, it accounted for changes in resource availability at wintering grounds due to climate variation, using NDVI as a proxy. Indeed, the survival of floaters was significantly lower during wet winters (i.e. years with
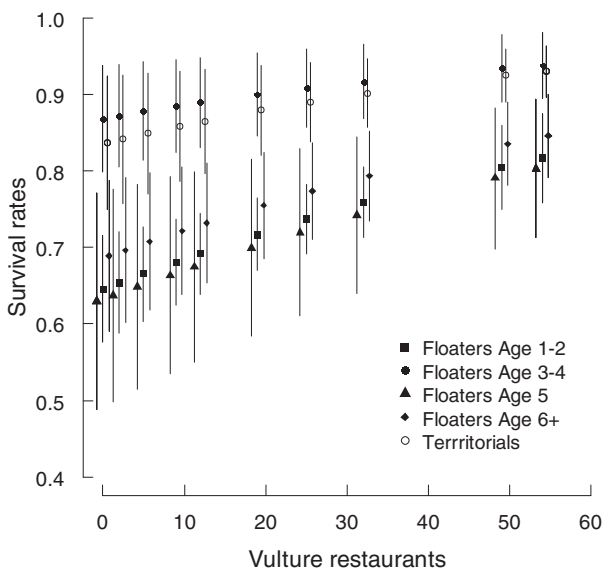

Fig. 2. Effect of vulture restaurants on class-specific survival rates. These are predictions of the relationships estimated by the integrated population model, with associated standard deviation. Points are moved on the X axis to improve visibility. See Table 1 and Appendix B.1 for more details on formulation and parameterisation of relationships.

Table 1

Parameter estimation (mean, SD and quartiles) from the integrated population model of Egyptian vultures in south-eastern France. Transition probabilities used in the IPM are separated from the coefficient of the potential effects acting on them. Remote-sensed and yearly averaged Normalized Difference Vegetation Index (NDVI) is used as a proxy of primary productivity in wintering grounds.

Notation	Parameter	Mean	SD	2.50%	97.50%
Probabilities					
S_{12}	Survival of floaters until age 1 and 2	0.742	0.046	0.652	0.830
S_{34}	Survival of floaters until age 3 and 4	0.910	0.051	0.793	0.986
S_5	Survival of floaters until age 5	0.724	0.107	0.508	0.923
S_{6+}	Survival of floaters until age 6 and more	0.778	0.062	0.645	0.888
S_T	Survival of territorials of all ages	0.893	0.050	0.775	0.970
p_1	Resighting of floaters of age 1	0.026	0.015	0.005	0.062
p_2	Resighting of floaters of age 2	0.152	0.042	0.081	0.243
p_{3+}	Resighting of floaters of age 3 and more	0.325	0.045	0.241	0.417
p_T	Resighting of all territorials	0.965	0.032	0.883	0.999
α_{34}	Recruitment at age 3 and 4	0.024	0.014	0.005	0.058
α_5	Recruitment at age 5	0.124	0.054	0.040	0.248
α_{6+}	Recruitment at age 6 and more	0.199	0.056	0.103	0.320
r	Recovery of recently dead birds	0.087	0.027	0.043	0.146
L	Annual loss of one ring	0.068	0.016	0.042	0.103
p_{LF}	Resighting of floaters having lost a ring	0.232	0.099	0.088	0.467
p_{LT}	Resighting of territorials having lost a ring	0.938	0.056	0.792	0.998
Coefficient					
p_{time}	Temporal increase of floater resighting	0.082	0.051	−0.012	0.182
$NDVI_F$	NDVI variations on floater survival	−0.126	0.054	−0.233	−0.020
$NDVI_T$	NDVI variations on territorial survival	0.011	0.014	−0.162	0.410
Food	Vulture restaurants on survival	0.016	0.007	0.002	0.031
Fec	Average number of fledgling per pair	0.777	0.053	0.676	0.884
DDFec	Density feedback on fecundity	−0.050	0.024	−0.011	−0.015
Im	Immigration rate	0.081	0.047	0.011	0.189
ImFood	Vulture restaurants on immigration	−0.008	0.049	−0.104	0.085
λ_{IPM}	Population growth rate	1.015	0.010	0.995	1.036

high NDVI values; Fig. 3). However, we did not find such effect on the survival of territorials (Table 1).

The annual number of fledglings produced decreased following the implementation of vulture restaurants (−26%), suggesting the occurrence of a compensatory density feedback impacting the average fecundity of the population (Fig. 3; Table 1 and Table B.3.1).

All significant effects highlighted by our model were identifiable and insensitive to change in prior distributions (Appendix B.3).

3.2. Vulture population dynamics and the contribution of immigration

The improvement of survival shifted the projected population dynamics, using locally estimated demographic parameters, from a declining to a stable population ($\lambda_{1997–2003} = 0.927$ [95%CI: 0.870–0.988] *vs.* $\lambda_{2003–2012} = 1.008$ [0.971–1.025]; Fig. 4). This shift occurred in 2004–2005 and coincided with the start of the LIFE programme in 2003. When the increase of territorial survival (11%) was modelled on the population dynamics projected with local demographic parameters estimated in 2000 (population size at the beginning of restaurant implementations), the projected growth rate increased from 0.945 to 1.005, suggesting that the increase in survival of territorial birds accounted for most of the change in the observed population growth rate. Noteworthy, this positive effect of vulture restaurants would have been partially masked if individuals having lost one of their coloured rings (annual probability of ring loss at 6.8%) had not been accounted for (Table 1, Fig. 4).

The projection of the local population dynamics did not match the observed recovery of the population ($\lambda_{1997–2012} = 0.972$ [0.949–0.996] *vs.* $\lambda_{Obs} = 1.012$; Fig. 4). The IPM including immigration
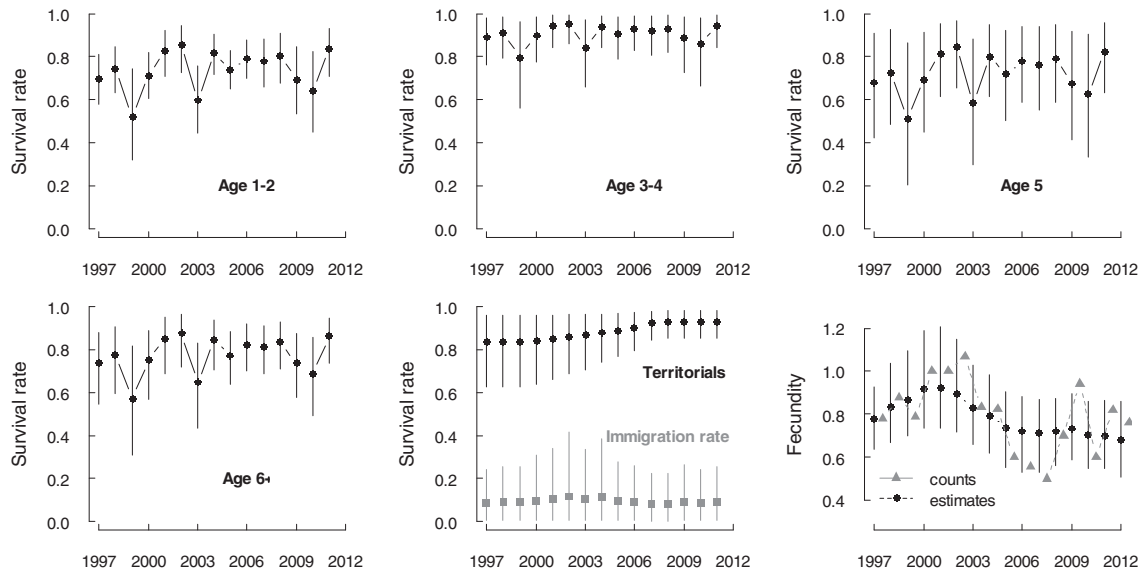
Fig. 3. Annual variations of the demographic rates (survival, fecundity and immigration, estimated with 95% CI) of the Egyptian vulture population. The estimation of floater survival (until age 1–2, age 3–4, age 5, age 6 and more) depended on variation in NDVI values at wintering grounds and on the progressive implementation of vulture restaurants. The survival of territorial birds only increased with the number of vulture restaurants. The immigration rate (in grey square) randomly varied around 8%. The variation of fecundity is negative density-dependent. Estimates of the Fecundity model are in black and compared to the annual measure in grey triangle.

($\lambda_{IPM} = 1.015$ [95%CI: 0.995–1.036]; Fig. 4 and Table 1), estimated that between 1 and 2 female immigrants were recruited annually (1.693 ± 0.297; Table B.3.1), corresponding to an average immigration rate of 0.081 ± 0.047 (Fig. 3 and Table 1). This estimated number of immigrants exceeded by around 1.6 times the number of local recruits, the latter remaining relatively low throughout the study, despite the improvement of survival rates (mean number of local recruits: 1.063 ± 0.182; Table B.3.1). This probably arose from the decrease of average fecundity. Indeed, when the observed decrease in fecundity was modelled on the population dynamics projected with the survival improvement

as above, the increase in projected growth rate was reduced (0.945 to 0.987 *vs.* 1.005). If immigration can be considered as an important driver of the Egyptian vulture population in south-eastern France, we did not detect any effect of vulture restaurants on the immigration rate (Table 1 and Fig. 3), indicating that the improvement of local survival by vulture restaurants remained the main driver of the positive shift in the population dynamics.

4. Discussion

The implementation of vulture restaurants appeared as an effective conservation action for the globally endangered Egyptian vulture in south-eastern France. Unravelling the demography for evaluating the impact of this conservation action, we identified two main processes underpinning the observed recovery of the population: 1) the implementation of vulture restaurant improved local survival rates enough to have halted the population decline, and 2) a reinforcement of the dynamics by immigrants recruited in the population (probably constant through time). The observed recovery took place whereas the average fecundity substantially decreased due to a compensatory density feedback.

4.1. The impact of vulture restaurants on Egyptian vulture population dynamics

Although the use of supplementary feeding with vulture restaurants have received considerable attention as a way to preserve species from poisoning and from starvation after sanitary legislation (Cortés-Avizanda et al., 2010; Margalida et al., 2010), few studies analysed their impact on survival rates. A 60% increase in the survival of juvenile Cape griffons was identified after the implementation of vulture restaurants (Piper et al., 1999). An experimental setting confirmed that providing safe food halved the mortality rate of Asian vultures due to veterinary drug poisoning (Gilbert et al., 2007). Finally, supplementary feeding increased pre-adult survival by 20% (Oro et al., 2008), while the closure of restaurants after sanitary legislation reduced the survival of birds irrespective of their age (Margalida et al., 2014). To date, their impact on Egyptian vulture survival has not been directly quantified.

Here, we found that the implementation of supplementary feeding improved vulture local survival rates by about 11%. Given that
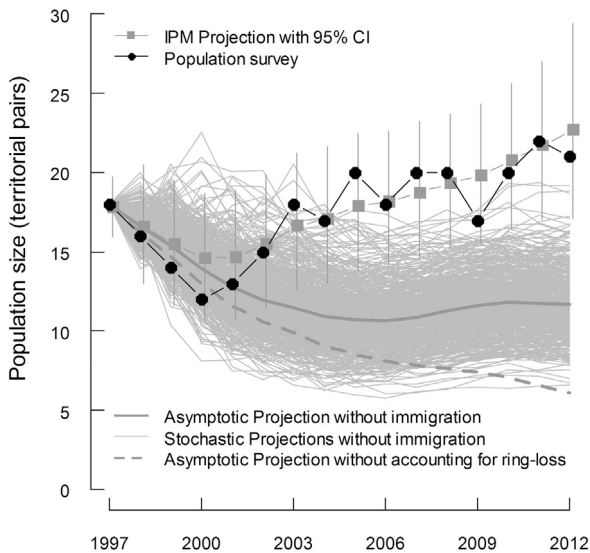

Fig. 4. Projections of the Egyptian vulture population trend compared to the count of territorial pairs monitored between 1997 and 2012. The prediction of the integrated population model (IPM, which accounts for immigration) and its 95% confidence interval match the observed trend of the population size. To compare with a model that does not account for immigration, we drew 500 stochastic projections and the asymptotic projection of the Matrix Population Model (MPM) using local survival estimated by the Multi-State Capture–Resighting model (MSCR for survival) and the annual measure of fecundity. Finally, we added an asymptotic projection of a similar model in which the resightings of birds having lost their ring was referred as not seen in order to mimic a situation where ring loss was not accounting for by any kind of doubled-marking.

immigration remained apparently constant throughout the study period, this improvement in survival can be considered as the main factor responsible for the halt of the historical decline of the Egyptian vulture population in south-eastern France. This conclusion is in line with the fact that survival of territorial adults is the main driver of the species dynamics, as in other long-lived raptors (Oro et al., 2008; Tauler et al., 2015). This first empirical evidence of the benefit of vulture restaurants on the survival of Egyptian vultures confirms the predictions of a previous population viability analysis suggesting that a 10% increase in survival entailed by supplementary feeding would lead to a positive population trend (García-Ripollés and López-López, 2011). The increase in local survival can be due to two non-mutually exclusive processes: an improvement of true survival and/or the reduction of permanent emigration. Indeed and as a consequence of the implementation of the conservation action, the study area might have become more attractive to local birds, therefore reducing their probability to disperse outside the study area, but also to immigrant birds. Indeed, conspecific attraction is an important mechanism driving habitat selection in birds (Oro et al., 2008; Szostek et al., 2014). Interspecific attraction may also have played a role as the number of griffon vultures in south-eastern France increased throughout the study period following a reintroduction programme. Griffon vultures are known to favour the presence of Egyptian vultures by facilitating the detection of carcasses and ensuring their cutting up (Cortés-Avizanda et al., 2010). However, the bulk of the Egyptian vulture in south-easter France currently breeds in areas without griffon vultures.

Before building our inferences, we carefully evaluated potential confounding factors in the identification of conservation benefits. First, trans-Sahara migrants, such as the Egyptian vulture, are known to be affected by environmental variations in wintering grounds (Grande et al., 2009; Mihoub et al., 2010). We found that the survival of territorial individuals was not affected by environmental conditions in Africa. In addition, we found that survival of floaters was lower during wet winters (inducing higher primary productivity) in the Sahel region. These results are not consistent with those found by Grande (2006) in Spain, showing that survival was increased for both floaters and territorial individuals following wet winters. In this study however, the potential effects of poisoning and supplementary feeding were not accounted for and their effects may have been absorbed by the NDVI covariate. Our results rather suggested that wet winters may reduce the mortality of cattle and other animals which in turn reduce the availability of carcasses for Egyptian vultures.

Second, we detected an improvement in resighting probabilities through time due to the set-up of camera traps at vulture restaurants. Not accounting for this would have overestimated the effect of supplementary feeding. Third, not integrating individuals having lost at least one ring would have prevented the identification of the restaurant effect. On the other hand, integrating them in the data set without explicitly accounting for ring loss would have underestimated survival and overestimated immigration. The implementation of a proper double-marking system (i.e. two strictly identical tags, each of them allowing the identification of individuals) for vultures and other large raptors, would be of great values for any demographic analyses (see also Le Gouar et al., 2008).

4.2. Compensatory density feedback on fecundity

Contrary to its benefit on survival, the conservation action did not succeed in one of its objectives, i.e. the increase of vulture fecundity. Yet, a higher fecundity of territorial pairs closed to vulture restaurants had already been shown in this species (Grande, 2006; Liberatori and Penteriani, 2001). On the contrary, such benefit has not been identified in griffon and bearded vultures (Carrete et al., 2006; Martínez-Abraín et al., 2012). Moreover, vulture restaurants can favour compensatory density feedback on fecundity at the population level (Carrete et al., 2006; Ferrer et al., 2014). Here, we detected a similar compensatory

density feedback and two alternative mechanisms can explain this: the aggregation of floaters inducing an increased level of interference (individual adjustment hypothesis) or the colonisation of new low-quality habitats (heterogeneous habitat hypothesis; e.g. Ferrer et al., 2014). Intra-specific competition by interference may increase competition for food access on a restaurant between floaters and the neighbour territorial pair. A spatial heterogeneity in food supplementation at restaurants may also increase the divergence of reproductive performances between pairs. In our case, the density feedback induced a 26% decrease in fecundity during the recovery period (from 0.92 to 0.68 fledgling per territorial pairs). We showed that this reduced fecundity buffered the benefit of survival improvement. While the benefit on survival might encourage the use of vulture restaurants for other populations of Egyptian vultures, this second result suggests that their spatial setting and possibly their supply frequency remain to be improved to limit the onset of the compensatory feedback (Cortés-Avizanda et al., 2010). Focusing the food supply on poor quality territories may be a relevant option to be tested in the field, once the local determinants of fecundity have been understood (Ferrer et al., 2014).

4.3. The importance of immigration for the dynamics of endangered vulture populations

The projected population trend based on locally-estimated demographic parameters indicated a halt of the historical decline and a stabilisation around a dozen of territorial pairs. This did not match the count of territorial pairs, which progressively increased to 21 pairs in 2012. Results from the IPM highlighted that immigration was responsible for about two-third of the recruitment and was therefore an important driver of Egyptian vulture population dynamics in south-eastern France. We estimated annually about 1.6 immigrants per local recruit, corresponding to an immigration rate of 8%. Overall, our analysis brings us to the conclusion that the studied population was demographically connected with surrounding populations despite its relative geographic isolation at the northern range margin of the species' distribution. We also provided a direct quantification of this connexion from local monitoring data in line with a recent prediction of viability analyses suggesting that the annual immigration of 1 or 2 birds should have partly driven the increase of the Catalan population (Tauler et al., 2015). These results contrast with the general idea that Egyptian Vulture was considered highly philopatric according to CR data (average natal dispersal distance: 36 ± 42 km; range = 0–150 km; n = 22; Grande, 2006), and as a consequence, population viability analyses were conducted assuming closed populations (García-Ripollés and López-López, 2011; Sanz-Aguilar et al., 2015). However, the paucity of CR surveys in Pyrenees and Iberian Peninsula implied a low detection of long-distance dispersers whereas some birds could disperse among populations, as showed by the increasing proportion of non-ringed birds seen at restaurants and the recent identification of three Spanish birds recruited in south-eastern France (authors' unpublished data). Our study highlights the impact of those few birds dispersing among populations and our findings participate to the growing evidence for the crucial role played by immigration in shaping bird population dynamics (Altwegg et al., 2014; Brown and Collopy, 2012; Schaub et al., 2012; Tempel et al., 2014), especially in long-lived raptors (Hernández-Matías et al., 2013; Schaub et al., 2010; Tauler et al., 2015).

What are the consequences of this awareness in terms of conservation practices? Some populations apparently stable would decline without the supply of immigration (Brown and Collopy, 2012; Schaub et al., 2010, 2013). Immigration can therefore hide declining local demography and actual threats on population from the manager's eyes. In our case, ignoring immigration may have over-emphasised the success of the conservation action by focusing on population counts. Thus, the fact that immigration supply depends, at least partly, on processes occurring outside of managed areas challenges the idea that local conservation actions could entirely determine population dynamics (Tempel

et al., 2014). In our case, the vulture population could not have increased despite conservation actions in absence of immigration. Indeed, a decline of source populations or an increasing mortality of dispersing birds, for instance at wind farms or power lines, could reduce the availability of potential recruits, while evidence is growing for the importance of floaters in the persistence of long-lived bird populations (Ferrer and Penteriani, 2008; Penteriani et al., 2011). Alternatively, emigration could also decrease and partially compensate for a potential reduction in immigration (Runge et al., 2006). Investigating the mechanisms underlying immigration and emigration may therefore be useful if we want to rapidly to mitigate new threats (sensus adaptive management strategy; Salafsky et al., 2002). In our case, the implementation of vulture restaurants may have retained dispersing birds attracted by food resources and/or mate availability (Oro et al., 2008; Szostek et al., 2014). Immigration has been recently shown to have the potential to regulate isolated bird populations (Schaub et al., 2013). We did not find evidence for any relationship between immigration and population size or the number of vulture restaurants. Yet, the statistical power to detect such a relationship was probably quite low in our case, because of the restricted population size and the relative short time period available for a long-live species (16 years of data, generation time of 8.5 years).

Increasing the scale of monitoring to reach broad-scale assessments would be therefore of great value for understanding the demography of mobile species such as long-lived raptors or colonial seabirds (Hernández-Matías et al., 2013; Oro, 2003). As a first step, sharing monitoring data would help in quantifying long-distance demographic exchanges and their consequences on each population dynamics using multi-site CR models or IPM (Kéry and Schaub, 2012). For instance, the western Europe populations of Bonelli's eagles seems to constitute a dynamical source-sink system, on which conservation action could be prioritized in favour of source populations (Hernández-Matías et al., 2013). In this study, French Bonelli's eagles isolated at the northern margin of the species distribution range appeared to behave like a sink population supported by immigrants from south of Spain. Although being similarly isolated at range-margin, the Egyptian vulture population in south-eastern France cannot be considered as a sink population, since its local demography is predicted to be stable, or even slightly increasing, in the absence of immigration. This seems also to be the case for the neighbour Catalan population (Tauler et al., 2015). On the contrary, the declining Spanish core population had lower survival rates compared to the French and Catalan populations (Fig. B.3.2; Grande et al., 2009). Thus, range-margin populations cannot be systematically considered as sink without a proper understanding of the local vs. global (locals and immigrants) demography. Otherwise, any prioritization of conservation actions could be misled.

4.4. Conclusion

By improving local survival and population dynamics of the Egyptian vulture in south-eastern France, ongoing food supplementation seems to ensure short-term viability of the population until a new system of dispatched natural quartering is implemented and/or the recovery of wild ungulate populations (Margalida et al., 2011). However, the spatial setting of restaurants may be improved to limit the onset of the compensatory feedback (Ferrer et al., 2014). Finally, we hope to have raised the issue of distinguishing the relative contribution of immigration (global) and local population dynamics in evaluating conservation programmes. The highlighted importance of immigration calls for cross-border joint effort in monitoring population for sharing knowledge, building scientific evidence and optimising the use of resources (Hernández-Matías et al., 2013; Oro, 2003).

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2015.07.008.

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