Chapter 15
Importance of Long-Term Studies to Conservation Practice: The Case of the Bearded Vulture in the Pyrenees

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Abstract Detailed, long-term scientific studies are necessary for conservation purposes, but with the main handicap to have the continual economic support required for them. Behavioural and conservation biology studies need long-term projects to achieve robust data, but managers, administrations and policy-makers need, in most cases, immediate results. Here I show several examples of the research obtained from a long-term study (1987–2014) in one of the most threatened species in Pyrenean mountains, the bearded vulture (*Gypaetus barbatus*), highlighting the importance of such long-term research. The results show how long-term studies are necessary to identify conservation problems, to understand demographic changes on populations and priorities to apply conservation measures. The study's findings allowed the identification of the negative density-dependent effects on fecundity, the lack of recolonization of new territories outside the current distribution area and the increase in polyandrous trios, suggesting an initial optimal habitat saturation. From a management point of view, the studies show that supplementary feeding sites (SFS) can have detrimental effects on fecundity but increases pre-adult survival. Also, illegal poisoning is increasing, and the demographic simulations suggest a regressive scenario in population dynamics if this factor is not eliminated. More recently, anthropogenic activities through human health regulations that affect habitat quality can suddenly modify demographic parameters. The results obtained about changes in nest-site selection, mating system and demographic parameters can only be achieved through long-term studies,

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suggesting the importance of long-term research to provide accurate information to managers and policy-makers to optimise the application of conservation measures.

Keywords Conservation measures · *Gypaetus barbatus* · Long-term studies · Management · Policy-makers · Pyrenees · Threatened species · Vulture

15.1 Introduction

Detailed, long-term scientific studies of long-lived species although necessary are relatively unusual (Clutton-Brock and Sheldon 2010; Mills et al. 2015, 2016), with the main handicap to require a continual economic support (Birkhead 2014). On the other hand, Ph.D. projects, as well managers, administrations and policy-makers need, in most cases, immediate results. As a result, funding agencies usually operate on short-term funding cycles, making it difficult to maintain the continual levels of support required for long-term research.

Nevertheless, such studies are essential to understanding the factors that drive population size and dynamics and to provide crucial information for conservation. Thus, long-term monitoring of wild populations is necessary to obtain the information needed for conservation purposes. For example, some demographic and ecological processes require long-term monitoring. Those relevant for conservation include the need to estimate variation in demographic parameters over time, which affect geometric population growth and establish population trends. For example, the near extinction of some long-lived species as the Condor of California (*Gymnogyps californianus*) related to lead intoxication (Mee and Hall 2007) and the sudden regressive trend on three Asian vulture species during the last decade as consequence of the intoxication by a veterinary drug (Oaks et al. 2004; Green et al. 2004) show the importance of long-term monitoring and the estimation of demographic parameters for conservation practice.

The identification of conservation problems through long-term studies to help threatened species applying most appropriate measures constitutes a valuable tool for managers and practitioners. Accordingly, the discipline of conservation biology needs to be integrated into policy decisions to be effective, assuring that results obtained are immediately applied.

In the case of threatened species, the identification and application of measures to improve the conservation status and population trend are a priority for conservation biologists and policy-makers. This is the case of the bearded vulture (*Gypaetus barbatus*), a long-lived, flashing endangered species that provides critical ecosystem services such as disease and pest control (Margalida et al. 2011a; Margalida and Colomer 2012; Donázar et al. 2016), indirect greenhouse emissions regulation (Morales-Reyes et al. 2015, 2017) or cultural inspiration and recreational activities (Donázar et al. 2016). In Europe, a total of 215 territories have been documented in mountainous ecosystems (del Hoyo et al. 1994; Margalida 2010a), 130 of which are present on the southern face of the Pyrenees (Spain). In this region, several management and conservation actions have been carried out during the last 30 years to improve the status of the species. The historical decline in Europe has been associated with anthropogenic actions, mainly poisoning and direct persecution (Margalida et al. 2008a; Margalida 2010a). Significant human and economic efforts have been dedicated to recovering this threatened species in Europe to reverse its negative population demographic trend (i.e. conservation programmes and reintroduction projects), through funds provided by several life projects, administrations and NGOs (Schaub et al. 2009; Margalida 2010a).

Here, I show several examples of the research obtained from a long-term study in this threatened species inhabiting mountain biomes, in this case, the Pyrenees (Spain, France and Andorra). The primary goal is to highlight, based on some case study examples (see Carrete et al. 2006a, b; Margalida et al. 2008a, 2014a; Oro et al. 2008), the importance of long-term studies to obtain accurate data for conservation purposes.

15.2 A Long-Term Study Initiated in 90s

In 1992, a search for the SCI papers indexed as "*Gypaetus barbatus*" showed that until this year, only seven papers had been published about the species. The main information was provided on books (Hiraldo et al. 1979; Heredia and Heredia 1990; Mundy et al. 1992) and the unpublished thesis by Chris J. Brown about the subspecies *Gypaetus barbatus meridionalis* in Southern Africa (Brown 1988). General aspects of breeding ecology were provided, but several essential aspects of the ecology and demography were lacking. Under this scenario, the Spanish Ministry of Environment and the autonomous governments of Catalunya, Navarra and Aragón started different conservation actions in this difficult to study species. At the beginning of 90s, under the recovery plan for the bearded vulture applied by the different administrations (Navarra, Catalunya and Aragón) and a Life project, Spain started with the regular monitoring and study of the breeding biology of the species (see Heredia and Heredia 1990; Margalida and Heredia 2005). With this background, the main goals were as follows (see Margalida 2010a):

- Describe the behaviour, demography and ecology of the bearded vulture
- Evaluate the conservation measures already implemented and the future problems that the conservation of the species will have to confront
- Identify the factors causing the species' decline
- Develop management recommendations for its recovery
- Optimise the management of bearded vulture populations from the standpoint of conservation biology.

15.3 Long-Term Changes in Nest-Site Selection and Distribution

15.3.1 Importance of Nest Selection Studies for Conservation

Nest-site selection studies are a valuable tool that provides information about the suitability and limitations for the future population growth and geographic expansion of a species. Explanatory and predictive models are powerful instruments in the study of spatial distributions of populations, and their use is growing exponentially in animal ecology (Guisan and Zimmermann 2000; Guisan et al. 2002, 2013; Rushton et al. 2004; Oppel et al. 2012). Models establish statistical relationships between a response variable, such as the presence or absence of the species, and a set of explanatory variables that usually quantify environmental characteristics such as climate, landscape features and degree of human influence (e.g. Bustamante and Seoane 2004; Guisan and Thuiller 2005; Gavashelishvili and McGrady 2006; Addison et al. 2013; Guisan et al. 2013). This procedure has been regularly employed in wildlife conservation, mainly to determine the probability of future site occupation for expanding populations (Mladenoff et al. 1995; Buckland et al. 1996; Jerina et al. 2003; Hirzel et al. 2004) and to examine habitat suitability for released populations within reintroduction programmes (Bustamante 1998). The accuracy of predictive models is strongly dependent on population equilibrium, biotic interactions and stochastic local events. While such complexity frequently limits the generality of the results (Guisan and Zimmermann 2000; Guisan et al. 2002, 2013), an increasing number of studies take this into account (e.g. Fielding and Haworth 1995; Lindenmayer et al. 1995; Rodriguez and Andrén 1999). Predictive models are a potentially valuable tool to detect long-term trends in those key variables capable of explaining the distribution of organisms. In the case of the bearded vulture, the restricted distribution of the isolated Pyrenean region was a concern from a conservation perspective by making the species more vulnerable to extinction threats. As a consequence, we examined the long-term variation in how individuals select nesting cliffs all over the Spanish Pyrenees (see details in Margalida et al. 2008a). We focussed on variables indicating a high probability of cliff occupancy as determined by a previously published model (Table 15.1, see Donázar et al. 1993; Margalida et al. 2008a).

15.3.2 The Compacting Process on Pyrenean Bearded Vultures

Although the breeding population increased from 53 to 93 territories between 1991 and 2002, the breeding range surprisingly expanded only slightly. New and old nesting cliffs had similar habitat features in relation to topography, altitude and

Table 15.1 Variables used to characterise bearded vulture nesting cliffs and random cliffs. In random cliffs, distances were measured from a point in the centre of the cliff (modified from Donázar et al. 1993 and Margalida et al. 2008a)

Topography

Relief: Topographic irregularity index. A total number of 20 m contour lines, cut by four 1 km lines starting from the nest in directions N, S, E and W.

Cliff local characteristics

Altitude: Altitude of the nest above the sea-level (m).

Cliff: Cliff height, measured as the number of the 20-m contour cuts by a 50-m line perpendicular to the cliff face at nest level.

Orientation: Orientation of the cliff face at the level of the nest. Orientations were scored in increasing shelter from cold, humid winds from the NW which are dominant in the area: 1= NW, 2 = N or W, 3 = NE or SW, 4 = E or S, 5 = SE.

Environmental characteristics of the surrounding area

Forest: Extension (%) of forested areas in a 1 000 m radius around the nest.

Distance Village: Distance to the nearest inhabited village (km).

Inhabitants: Number of inhabitants in the nearest village.

Human disturbance

Kilometres roads: Kilometres of paved and unpaved roads in a 1 000 m radius of the nest.

Distance paved road: Shortest linear distance between the nest and the closest paved road (km).

Distance road: Shortest linear distance between the nest and the closest road, paved or unpaved (km).

Height paved road: Altitudinal difference between the nest and the closest paved road, measured at the point the road is closer to the nest (m). If the nest is lower than the road, a negative value is obtained.

Height road: Altitudinal difference (m) between the nest and the closest road (paved or unpaved). If the nest is lower than the road a negative value was obtained.

Intraspecific relationships

Nearest neighbour: Linear distance between the nest and the closest nest of the nearest neighbour (km).

degree of human influence, but the distance between occupied cliffs was reduced (from 11.1 to 8.9 km). As a result, the probabilities of occupation predicted by the model were lower for newly colonised sites. Interestingly, the cliffs located in peripheral zones, without no previous bearded vulture territories, tended to be smaller (mean height) and were usually located in less steep and lower altitude zones. Also, they were closer in both, distance and altitude, to roads and they had a greater neighbouring human population. The new territories occupied from 1991 to 2002 showed similar habitat characteristics to those occupied before 1991. The only exception was the variable "nearest neighbour" distance. New territories were situated at a significantly smaller distance to other occupied territories than they were before. In relation to randomly selected cliffs, new nest sites were in areas that were more rugged, and in cliffs that were higher than average. In addition, new nesting cliffs were not significantly further from the nearest occupied nest (mean: 8.9 km) than random cliffs (mean: 8.1 km) with similar when comparing old nests to randomly selected cliffs.

The application of models including the variable "nearest neighbour" determined that newly occupied cliffs had intermediate probability values between old nesting cliffs and randomly selected cliffs. Therefore, during the last years, bearded vultures have been selecting a similar kind of cliff as previously chosen in relation to topography and distance from human habitation, the main factors affecting cliff selection. The distance between neighbouring territories decreased in parallel with the increase in population density (from 4.4 to 2.5 territories/1000 km^2 during 1991–2002).

15.3.3 Why Bearded Vultures Do not Extend Their Distribution Range?

Our study suggests that territory compression may occur without serious modification of nesting habitat quality. Our findings show that the selection of nest sites has not changed with the population increase of the Pyrenean bearded vulture. For those variables determining the probability of cliff occupancy (ruggedness, altitude and distance to the nearest human habitation), newly established territories between 1991 and 2002 had similar values to those of traditional territories occupied previously. These new pairs, however, occupied cliffs in between the existing old territories so that the distance between neighbours has reduced by around 20%, which proves territory shrinkage (Both and Visser 2000; Ridley et al. 2004). Cliffs remaining unoccupied by bearded vultures after 1991 in the periphery of the Pyrenees had both lower values in key variables (e.g. relief, altitude, distance to a village) and lower probability of occupancy than those occupied in the Pyrenean range during the same period. These findings seem to contradict what would be expected from a distribution by despotic competition, classically described for birds of prey and other territorial birds (Newton 1998). It could be argued that there is still availability of good-quality breeding sites in the Pyrenees and that, consequently, the population has not reached the saturation threshold necessary to observe the occupation of marginal territories by newly established birds. This argument holds true if the comparison is limited to the examination of the quality of nesting cliffs where no long-term changes were appreciable. A different picture, however, arises when the distance between neighbouring territories is considered. Since this variable was significant in the model fitted in 1991, we can deduce that saturation is taking place and that there is a decrease in territorial quality via a reduction in the distance between breeding pairs. In parallel, it has been demonstrated that the productivity of the Pyrenean population has sharply declined during the last decade as a consequence of the increasing breeding density (Carrete et al. 2006a; Margalida et al. 2014b), a clear symptom of population crowding, as is the appearance of unusual mating systems (Bertran and Margalida 2003; Carrete et al. 2006b; Bertran et al. 2009).

The packing process could also be motivated by the scarcity of suitable breeding places in mountain areas surrounding the Pyrenees. As our analyses demonstrate, potential nesting cliffs in those regions are of lower quality (regarding altitude, topography and human influence) than those existing within the central mountain range. Human presence is known to strongly affect the distribution patterns of bearded vultures and other large raptors, not only respect to the safety of breeding nest sites (Donázar et al. 1993; Margalida et al. 2007a), but also with regard to foraging grounds (Bautista et al. 2004; Gavashelishvili and McGrady 2006). Previous analyses have shown that the breeding success of Pyrenean bearded vultures is affected by human activities and infrastructures (Donázar et al. 1993; Arroyo and Razin 2006) as occurs in other vulture species (Zuberogoitia et al. 2008; Margalida et al. 2011b; but see Oppel et al. 2016). Therefore, it is reasonable to think that the low probability of cliff occupancy outside the Pyrenees is determined, at least partially, by the intense human influence on these peripheral mountain regions. In this sense, the Pyrenees could progressively become more of an ecological island for the bearded vulture surrounded by areas that are inadequate due to the increasingly human influence on the environment. If these factors prevent the population from increasing in numbers and expanding, the risk of extinction in this population will remain high as a consequence of stochastic demographic and environmental phenomena and the limited genetic variability (Godoy et al. 2004).

The relatively low quality of sites in nearby mountains may prevent the expansion of the breeding range, but conspecific attraction and supplementary feeding may also play a role. Our study confirmed that monitoring changes in key variables relevant to habitat selection are useful in determining long-term trends in settlement patterns in heterogeneous environments. The results also suggest that the available nest-site selection model may accurately predict cliff occupancy by bearded vultures in those areas where the distance to the nearest neighbour is not limiting. In particular, the model may be useful in establishing priority areas for reintroduction.

15.4 Changes in Mating System and Population Regulation

15.4.1 Cooperative Breeding

In many bird species, a proportion of mature individuals in the population does not breed (i.e. floaters), mainly because all suitable territories are occupied (Newton 1992). These individuals are a reservoir for the recruitment of new breeders and, therefore, are important for the regulation of the population (López-Sepulcre and Kokko 2005). However, delaying reproduction has a fitness cost, even for a long-lived species, and mature birds may try to enter into the reproductive population by alternative routes: individuals may occupy poor-quality territories (Rodenhouse et al. 1997), or enter into an occupied high-quality territory as a helper (Hatchwell and Komdeur 2000).

Cooperative breeding is a breeding system in which more than a pair of individuals shows parent-like behaviour towards young of a single nest. In its broadest sense, it includes reproductive systems varying from helping by non-breeding offspring to various forms of polygamy, in which more than one male or female share breeding status (Brown 1987; Cockburn 1998; Hatchwell and Komdeur 2000). This is the case of the bearded vulture in the Pyrenees, a species considered monogamous but with several polyandrous territories found since the beginning of the 80s (Heredia and Donázar 1990; Bertran et al. 2009). The copulation behaviour suggests that most of these territories are formed by two males and a female (Bertran and Margalida 2002a, 2003, 2004) but also polyandrous quartets have been described (Margalida et al. 1997).

15.4.2 *Contrasting Hypotheses to Explain Changes in Reproductive System*

Several hypotheses have been proposed to explain the evolution of this reproductive system. According to the *ecological constraints hypothesis*, cooperative breeding appears when opportunities for independent breeding are limited because of ecological factors, such as low availability of resources or high risk of mortality during dispersal. The *life-history hypothesis*, however, states that cooperative breeding is a consequence of certain life-history traits of a species, such as low adult mortality, that reduce the opportunities for independent breeding. Beyond their differences, both hypotheses stress that direct fitness benefits of looking for independent breeding opportunities do not outweigh the indirect fitness benefits of helping relatives (Pen and Weissing 2000). Although the evolution of cooperative breeding has often been attributed to kin selection (Emlen 1991; Emlen et al. 1991), there is increasing evidence that helpers can be unrelated to the young they are raising (Cockburn 1998; Heg and van Treuren 1998). Other rewards, such as staying in a restricted area to increase their probabilities to acquire a high-quality territory (Heg and van Treuren 1998; Kokko and Sutherland 1998) or, as in polygamous units, to have some chance of breeding (Hartley and Davies 1994) should tempt birds to join an existing breeding pair rather than search for an unlikely opportunity of independent reproduction in a saturated environment.

15.4.3 *What Happened with the Pyrenean Population? The Polyandrous Emergence*

The analysis of the role of habitat saturation in the mating system of bearded vultures, a territorial and usually monogamous raptor, was assessed by Carrete et al. (2006a). Because the bearded vulture population increased progressively since

1970s (less than 40 breeding territories) until the 90 breeding pairs monitored in 2002 and this increment was within a restricted geographical range (the Pyrenees), so crowding mechanisms severely reduced territory suitability and fitness of territorial birds (Carrete et al. 2006a; Margalida et al. 2008a). In parallel to the increase in population size, some territories became occupied by polyandrous trios (Heredia and Donázar 1990). This fact raised the question of what are the consequences of this behavioural change for dominant breeders as well as for the whole population (Fig. 15.1). Currently, the proportion of polyandrous trios in Spanish Pyrenees is around 35% of the breeding population.

Polyandrous trios tended to appear in traditional territories (i.e. territories occupied before 1988) where productivity tended to be higher when occupied by breeding pairs (see details in Carrete et al. 2006b, Fig. 15.2). However, these high-quality territories became less productive when they received a third individual, suggesting that the appearance of another adult could trigger conflicts that affect reproduction among individuals from the same territory. Accordingly, the addition of a new individual decreased pair's productivity and that this was true even when considering density-dependent effects of the increase of the population over time.

The social organisation of a population is the consequence of the decisions made by individuals to maximise their fitness. Carrete et al. (2006b) found that a substantial proportion of unpaired birds become potential breeders by either entering high-quality territories or by forming polyandrous trios as a strategy to increase their individual performance. Thus annual increases in the number of breeding territories were associated with the proportion of trios, suggesting that the

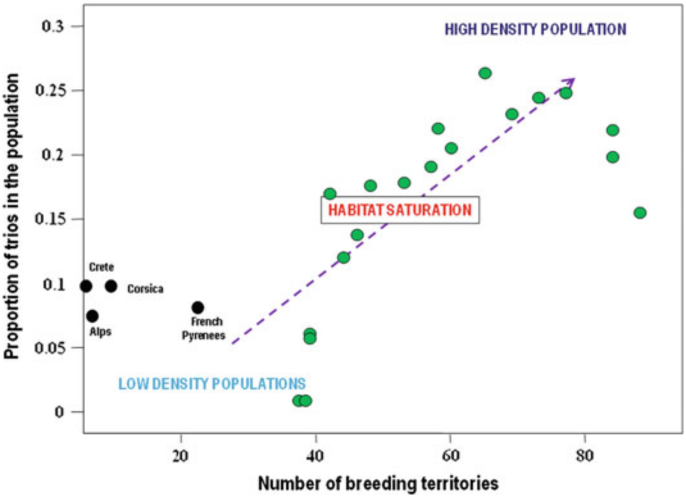

Fig. 15.1 Number of breeding territories and proportion of trios in the Spanish population of bearded vultures (*green dots*) compared with other populations (*black dots*) (modified from Carrete et al. 2006a)

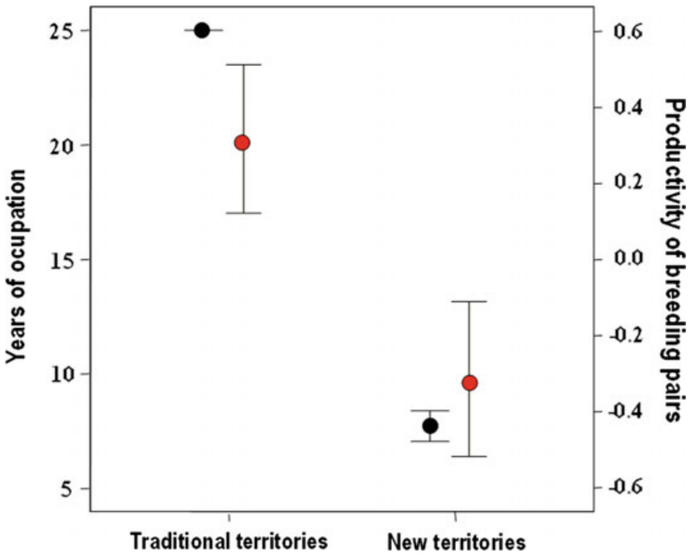

Fig. 15.2 Differences (mean ± s.e.) in time since territory formation (*black dots*) and mean standardised productivity of territories when occupied by breeding pairs (*red dots*) between traditional and new territories (modified from Carrete et al. 2006b)

progressive saturation of the population could be related to their formation. In this sense, the appearance of another adult could trigger conflicts that affect reproduction among individuals from the same territory (Bertran et al. 2009). Accordingly, after fitting territory and year into models to control for the density-dependent decay in the productivity of the population during the study period, we found that the formation of trios in some territories caused productivity depression in the whole population. The decision of some individuals to enter into breeding trios as subordinates also had clear adverse consequences to population demography.

Bearded vultures entered the breeding pool by occupying poor-quality territories (Carrete et al. 2006b) or by queuing in high-quality territories to wait until they are available. Therefore, trio formation may be a strategy for intruders to increase their fitness prospects by mating with a female or by increasing their likelihood of inheriting a high-quality territory when the dominant male dies. Reproductive success of previous owners was compromised when territories changed to trios, suggesting that the third individual was costly. Intruders, however, are not evicted by owners (Bertran and Margalida 2002b), perhaps because trios arise from uncommon ecological constraints and thus the energy invested in an unusually developed agonistic behaviour could be higher than the costs of accepting them (Clutton-Brock and Parker 1995; Hamilton and Taborsky 2005).

Intraspecific variation in mating systems may be determined by ecological features of the environment (Heg and van Treuren 1998) or by conflicts of interest between individuals (Davies and Hartley 1996). The Spanish population of bearded vultures is highly restricted spatially, and both the reproductive and non-reproductive fractions of the population coexist. The decision of some individuals to get into a trio as a subordinate also has clear adverse consequences for the whole population. However, since it appears as a result of ecological constraints, this behaviour could be reversed through management.

15.4.4 Conservation Implications Related with the Apparition of Polyandrous Formations

This unusual mating behaviour is thus compromising the conservation effort directed to this endangered species; management to encourage floaters to settle in other suitable but unoccupied areas may be beneficial. Our findings have direct implications for conservation. To our knowledge, this would be another example of the detrimental effects of food supplementation programmes on the conservation of threatened species (Robertson et al. 2006). Reducing food supply or progressively moving feeding stations outside of the Pyrenees may encourage floaters to settle in other areas where they could find breeding opportunities (see Margalida et al. 2008a, 2013). The translocation of floaters of the endangered Seychelles magpie-robin *Copsychus sechellarum* from a population-saturated island to an unoccupied one was a successful conservation strategy, since individuals become breeders (Kokko and Sutherland 1998). A similar situation could be expected if ecological and behavioural cues exposed in this paper are linked to direct conservation actions for this endangered vulture.

15.5 Density-Dependent Productivity Depression and Supplementary Feeding Management

Two different hypotheses relate density-dependent changes in demographic parameters to population regulation in territorial species. The *interference hypothesis* suggests that reductions in fecundity and/or survival coinciding with an increase in population size are caused by a homogeneous reduction in the quality of available resources due to an increase in agonistic encounters between individuals (Dhondt and Schillemans 1983; Sillett et al. 2004). The *habitat heterogeneity hypothesis*, however, suggests that the progressive occupation of low-quality territories as density increases causes a decline in the average per capita productivity and/or survival of a population even when its variation increases, leading to density-dependent regulation (Rodenhouse et al. 1997; Krüger and Lindström 2001; Sergio and Newton 2003). Here, dominant or early-arriving individuals occupy high-quality areas and, by means of territorial behaviour, relegate subordinate or late-arriving individuals to inferior territories or, when these places are also occupied, to a non-breeding lifestyle (Newton 1998). This pre-emptive settlement pattern, coupled with habitat heterogeneity and density-dependent changes in demography, has been defined as site-dependent population regulation (Rodenhouse et al. 1997). This mechanism, which complements and, in certain kinds of species, may even preclude local crowding mechanisms, can generate negative feedback at all population sizes, sometimes independently of local population densities (Rodenhouse et al. 1997).

The behaviour of floaters may also be a potential regulatory factor (López-Sepulcre and Kokko 2005). These "surplus" individuals that form a buffer against population fluctuations may harm breeding performance through intraspecific conflicts. The establishment of supplementary feeding points within the distribution area of the breeding population has been the most significant management action in terms of time and effort undertaken to help the bearded vulture in the Spanish Pyrenees from the 80s. These sites concentrate a substantial fraction of the floater population. In this sense, the spatial and temporal overlap between the breeding and non-breeding population fractions may affect the fitness of territorial birds by increasing intraspecific interactions.

15.5.1 Density-Dependent Productivity Depression Associated to Supplementary Feeding Sites (SFS)

From 1978 to 2002 the bearded vulture population in the Spanish Pyrenees increased from 38 to 91 breeding pairs. During the same period, the mean annual productivity of the population declined from 0.8 to 0.37 young/territorial pair. Variability among territories was responsible for a large proportion of this decline. However, this variability was not related to habitat heterogeneity per se. Habitat quality index (i.e. an index obtained by considering only relief, altitude and distance to villages) dropped by 13% during the study period, while the same index including distance to the nearest breeding pair declined by 20%. Thus, while the increase in population resulted in some pairs occupying intrinsically poorer territories, the proximity between conspecific breeding pairs seemed to be the most important factor reducing habitat quality and, therefore, productivity.

Productivity in traditional territories (those occupied at least since 1978) was better and more stable than in new ones (those occupied from 1988 onwards, when the population started to increase) initially, from 1988 to 1993. However, these differences lessened and disappeared all together in the final years (1994–2002), when territories became more homogeneous regarding productivity. Accordingly, we found that although the intrinsic quality of traditional territories remained relatively constant through time, a rise in the number of breeding pairs may have increased intraspecific interactions, thereby reducing the other quality index.

Even when all territories are not equally affected, the distances to both the nearest conspecific pair and the nearest supplementary feeding points have a negative effect on productivity. Although there is a certain degree of variability in their responses, territories located near supplementary feeding points that are also near to other bearded vultures breeding territories had lower productivity than territories with less conspecific pressure.

15.5.2 Habitat Heterogeneity and Population Regulation

The above evidence suggests that, in accordance with other studies on territorial raptors (e.g. Krüger and Lindström 2001; Sergio and Newton 2003; Carrete et al. 2006a), habitat heterogeneity plays a key role in the population regulation of bearded vultures. As the Pyrenean bearded vultures are not individually marked, we cannot tell whether habitat heterogeneity is a consequence of sites possessing different suitabilities for reproduction or survival (Breininger and Carter 2003; Lambrechts et al. 2004; Carrete et al. 2006a). However, our findings that productivity declined and its variation increased as bearded vulture populations increased from 38–91 pairs (during 1987–2002) are new and relevant to both basic and applied ecology because they show that population regulation is not merely a result of interference (i.e. ideal free distribution) or pre-emptive use of space. Moreover, traditional discussions on density dependence in territorial systems are mainly based on data obtained from populations in demographic equilibrium, where crowding mechanisms are usually precluded. Our data, collected throughout a period of population growth, show that when high-density situations are encouraged, demographic density dependence in territorial birds can occur because of the combined effects of site quality (ideal despotic distribution) and crowding mechanisms (ideal free distribution). Moreover and no less importantly, we also show that non-breeding birds can make up a significant fraction of the whole population and that their effects on breeding individuals as scramble competitors must be taken into account (López-Sepulcre and Kokko 2005).

Age differences could be proposed as an alternative hypothesis to explain productivity variation between territories (Forslund and Pärt 1995), where inexperienced birds occupying new territories increase their productivity through years and senescence promotes a progressive decay of productivity in traditional sites (Margalida et al. 2008b). Even when we were not able to test age effect on reproduction (Bearded vultures are not individually marked), and therefore we cannot discard it, our data are reliably showing that habitat heterogeneity and interference play a role in productivity depression, explaining a substantial percentage of deviance.

The density of conspecific competitors has been shown to affect territory size in several bird species negatively (see review in Newton 1998), independently of food availability (e.g. Arcese and Smith 1988; Stamps 1990). Although we have no information on either home range size or its change with density, our results suggest that this bearded vulture population may have suffered a process of territorial compression associated with an increase in the number of breeding pairs (nearly 25% reduction in the mean nearest neighbour distance between 1987 and 2002, Margalida et al. 2008a). This fact may be affecting the productivity of the population (see Carrete et al. 2006a). Moreover, Donázar et al. (1993) did not find any relationship between breeding success and distance to conspecific breeding pairs, suggesting that productivity was not limited by any density-dependent mechanism before 1991. Consequences of territory compression have been explored in other species, where increases in density are accompanied by increases in aggressive behaviour among territorial animals and costs associated with territory defence (e.g. Calsbeek and Sinervo 2002; Mougeot et al. 2003; Sillett et al. 2004). In these cases, territory shrinkage and territorial disputes associated with high-density situations affected reproduction and had fitness costs for territorial animals (Gordon 1997; Calsbeek and Sinervo 2002; Ridley et al. 2004), as in our bearded vulture population. However, we found that not all territories were equally affected by increases in the number of breeding pairs. Territories located in high-density situations became less productive and more unpredictable than territories located far away from conspecific pairs, indicating that in the present situation proximity to other breeding pairs could be the main factor promoting territory quality and also, to some extent, habitat heterogeneity in this closed population.

15.5.3 Effects of Supplementary Feeding Sites on Breeding Output

Proximity to supplementary feeding points where non-breeding birds congregate was also detrimental for reproduction (Fig. 15.3). For species with delayed maturity such as many long-lived raptors, spatial segregation between dispersing and breeding birds is a common feature (Newton 1979). This is because preparation for reproduction governs preferences among breeders, while food is the main driving force underlying habitat selection patterns in dispersing birds (e.g. Bustamante et al. 1997; Brown 1997; Mañosa et al. 1998; Hirzel et al. 2004). In our study area, however, the high availability of food resources associated with supplementary feeding points allows a great number of non-breeding bearded vultures—which otherwise would be occupying different areas (Brown 1997; Xirouchakis and Nikolakalis 2002; Hirzel et al. 2004; Margalida et al. 2011a)—to coexist within the spatial distribution of the breeding population. Contrary to the social behaviour observed in other species in which floaters and territorial birds may coexist in areas of high food supply (e.g. Blanco and Tella 1999), bearded vultures are territorial birds that defend exclusive breeding areas against both conspecifics and heterospecific birds (e.g. Bertran and Margalida 2002b; Margalida and Bertran 2000, 2005). Thus, high concentrations of floaters around breeding territories—as

Fig. 15.3 Supplementary feeding sites congregate bearded vultures of different age classes (A. Margalida)

happens near supplementary feeding points (see Sesé et al. 2005; Margalida et al. 2011a)—may increase the time being spent in agonistic encounters and, therefore, reduce breeding success. Moreover, conspecific crowding can be a significant stressor that may alter glucocorticosteroid release, causing both physiological and behavioural changes that may affect population dynamics (Rotllant et al. 1998; Creel 2001; Romero 2004).

In conclusion, these results suggest that vulture populations are regulated as postulated by the site-dependency hypothesis: as the population increases, average productivity decreases because progressively poorer territories are used. The combined effects of the shrinkage of territories and the presence of floaters around supplementary feeding points seem to be the main causes of productivity decline and are therefore the main determinants of territory quality. This has conservation implications, especially concerning the role of supplementary feeding points.

15.5.4 Management Implications for Conservation Plans

The establishment of supplementary feeding points for the management of vulture populations has been used during reintroduction programmes to maintain birds close to release areas (Griffon Vultures, *Gyps fulvus*, in France; Sarrazin et al. 1996), to increase food supply (Piper et al. 1999), or even as a potential solution to reduce poisoning (California Condor, in the United States; Meretsky et al. 2000).

Our results suggest that these management actions aimed at increasing the number of breeding pairs within the present distribution of the species and those attracting nonbreeders within the spatial range of the breeding population of bearded vultures should be reconsidered. In particular, the strategy of food supplementation should be reviewed because it seems to be one of the main potential factors promoting the congregation of non-breeding birds around breeders. Decisions to disperse or to remain in the local population are influenced by local intraspecific competition (Clarke et al. 1997; Perrin and Mazalov 1999; Gandon and Michalakis 2001; Lambin et al. 2001; Serrano et al. 2004). Thus high food availability within the geographical range of the breeding population could be keeping dispersing birds in their natal areas. The expected consequences of reducing food availability would be both an increase in the movements of floaters outside the distribution range of breeding birds, thereby reducing direct interactions in territories located near feeding points, and a geographical expansión of the breeding population to other suitable areas, as is proposed in the Recovery Plan of the species in Spain. Supplementary feeding sites were opened on the basis of their importance in increasing juvenile survival (Heredia and Heredia 1990). In this sense, direct evidence of a causal link between food supplementation and juvenile survival is lacking, although suggested according to the behaviour and survival values obtained (Oro et al. 2008; Margalida et al. 2011a, 2014b). Juvenile populations may have increased as a result of other factors such as an increase in wild ungulate populations (Razin and Bretagnolle 2003) or the reduction in direct human persecution through legislation since early 1980.

15.6 Demography: Effects of Poisoning and Supplementary Feeding

The provision of supplementary food at artificial or supplementary feeding stations or "vulture restaurants" (hereafter SFS), a well-established management tool in the conservation of scavenger populations (Cortés-Avizanda et al. 2010; Moreno-Opo et al. 2015; Cortés-Avizanda et al. 2016), appears to be a potentially useful solution worldwide. SFS has frequently been used to facilitate the recolonization of abandoned areas (Mundy et al. 1992), or to provide safe food sources in areas where carcasses are baited with poisons to control carnivores (e.g. Wilbur et al. 1974) or livestock has been treated with veterinary drugs (Gilbert et al. 2007). To the contrary, adverse effects of artificial feeding stations on demographic parameters of some species (Carrete et al. 2006a) are a concern and prompt us to correctly assess their effect on the demography of target populations.

The relevance of SFS for population viability through increments in the survival rates of non-territorial birds challenges the theoretical low sensitivity of population growth rates to this parameter expected among long-lived species (Saether and Bakke 2000). Conversely, SFS appear to be discouraging population expansion outside the Pyrenees and have been related to habitat saturation processes (Margalida et al. 2008a), which are triggering negative population effects such as reductions in productivity and changes in mating behaviour (Carrete et al. 2006a). Taking into account the life-history characteristics of the species and based on the general hypothesis of positive effects of predictable food supply on survival, we predict that increments in the illegal use of poison during recent decades (Hernández and Margalida 2008, 2009; Margalida 2012; Mateo-Tomás et al. 2012) have decreased survival rates of bearded vultures. However, this effect would have been buffered by the use of SFS, the use of which varies considerably among individuals although a general pattern is associated with age (young birds are more frequently seen at SFS than older ones, Margalida et al. 2011c). Population projections under different management scenarios in which poisoning have been combated with a variable degree of effectiveness are also presented.

15.6.1 Relationship Between Supplementary Feeding and Survival

We assessed the role of supplementary feeding on bearded vulture's survival. The best survival model obtained using the MARK program accounts for 85% of the weight of all models and included the effects of age (young or adults), time and the intensity of use of SFS on survival, and of age on recapture rates. Interestingly, the addition of the individual covariate describing the intensity of use of SFS significantly improved the models. However, the use of SFS decreased with bird age, even after controlling for individual variability (see Oro et al. 2008). Thus, survival was equal for birds of ages up to 4 years old (the age classes more frequently seen at SFS) and remained constant over time (0.944) even after the recent increment in the illegal use of poison. Conversely, survival of older birds ($\geq$ 5 years old) decreased linearly with time (Fig. 15.4), with an average value of 0.878. Other models, including a higher number of age classes (results not shown) or different combinations of age and time, behaved worse. Thus, the results support the hypothesis of improvement of survival rates associated with the use of SFS. Indeed, survival estimates for the two most important age classes at the beginning of the study period (1987) when the use of illegal poison was less marked, but SFS were not available, were 0.787 and 0.961 for young (the age class using SFS) and adults, respectively.

Ecological theory predicts that survival of long-lived species should increase gradually with age because (1) individuals improve their competitive skills or change from vagrant lifestyles to more sedentary ones after territory acquisition

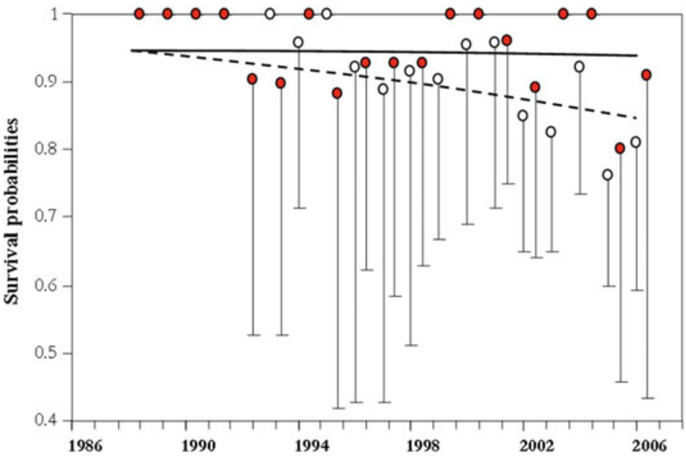

Fig. 15.4 Variation in survival rates of adult (>5 years and older; *white dots*) and young birds (4 years and younger; *red dots*) with time and age using the parameters obtained with the model ($\phi_{(1\_4+5)+T}$, p_A). Mean values and 95% lower confidence intervals are shown, as well as the linear negative trends for adults (*dashed line*) and young (*solid line*). Survival rates estimated as 1 were actually estimable parameters, i.e. years in which all individuals survived. Note that the two trends were parallel in the logit scale (modified from Oro et al. 2008)

and/or (2) natural selection progressively eliminates low-quality individuals (Tavecchia et al. 2001). Even when the underlying mechanisms may be of great interest in understanding the evolution of life histories, it is tough to correctly separate one mechanism from another (Tavecchia et al. 2001; Sanz et al. 2008). All in all, consequences for population dynamics are similar: population growth rates among long-lived species are expected to be highly sensitive to changes in adult survival (Real and Mañosa 1997; Oro et al. 2008; Ortega et al. 2009; Hernández-Matías et al. 2013; Margalida et al. 2015), so natural selection might have minimised variation in this parameter to ensure population stability (Saether and Bakke 2000). However, our results show how survival of bearded vultures changes through a bird's lifespan in an unnatural way, with non-adult birds (<5 years old) having higher and more constant estimates than adults (0.944 and 0.878, respectively, Fig. 15.4). Two main aspects seem to have been directly responsible for this outcome, namely the opening of SFS (directly tested through individual and age-specific frequencies of visits), and the increasing use of illegal poison to control predators (indirectly tested through a temporal trend in survival). Thus, human activities, both through apparently well-intentioned and malicious actions, can perturb evolutionary forces promoting unexpected changes in survival patterns and, therefore, demographic dynamics.

15.6.2 *Population Trajectories Under Different Management Scenarios: Which Are the Demographic Effects of SFS?*

We built a prospective stochastic age-structured population model (only for females) to explore the functional dependence of λ (the population growth rate) on the demographic rates of the study population. This kind of perturbation analysis allows us to identify potential management targets because variations in demographic parameters with high sensitivity (or elasticity) produce large changes in λ. We also built a retrospective stochastic population model to detect whether parameters used in the prospective model were reliable and described with certainty the behaviour of the population. Here, we used the same structure and number of replications as that of the prospective model but run over the period for which data were collected (20 years), setting the initial population size to that estimated in 1985 (i.e. 37 breeding females).

The current combination of demographic parameters of the Spanish bearded vulture population (scenario 1, Table 15.2) gave a $\lambda = 0.961$. When we explored how this rate changed within a range of different combinations of survival scenarios (all other vital rates remained equal as in further prospective models), we found that the population increased ($\lambda > 1$) only with very high values of adult survival. To the contrary, λ showed low sensitivity to changes in survival of non-adult individuals.

Retrospective analysis showed that simulations performed using actual survival estimates (scenario 1, Table 15.2) fitted quite well with the observed dynamics of the breeding population (mainly at the end of the time series, Fig. 15.5a), despite the uncertainty of the demographic estimates of the model, and the way they

Table 15.2 Survival and reproductive parameters used in Monte Carlo simulations for estimating extinction risk in prospective models for the bearded vulture in the Spanish Pyrenees. In brackets, SE of the estimates (see details in Oro et al. 2008)

Parameters	Supplementary feeding sites			No supplementary feeding sites	
	Poisoning		No poisoning	Poisoning	No poisoning
	Scenario 1	Scenario 2	Scenario 3	Scenario 4	Scenario 5
Young survival	0.944 (0.012)	0.944 (0.012)	0.944 (0.012)	0.787 (0.018)	0.787 (0.018)
Adult survival	0.878 (0.014)	$\phi_{(t)} \cdot 0.264 + \mathit{rand} \cdot 0.241^{\xi}$	0.961 (0.019)	0.878 (0.014)	0.961 (0.019)
Fertility§	0.7359e-0.0056·PD*				

$^{\xi}$ Initial value$_{t=1}$ = 0.961

*Density-dependence function (PD = population density)

§*Source* Carrete et al. (2006a, b)

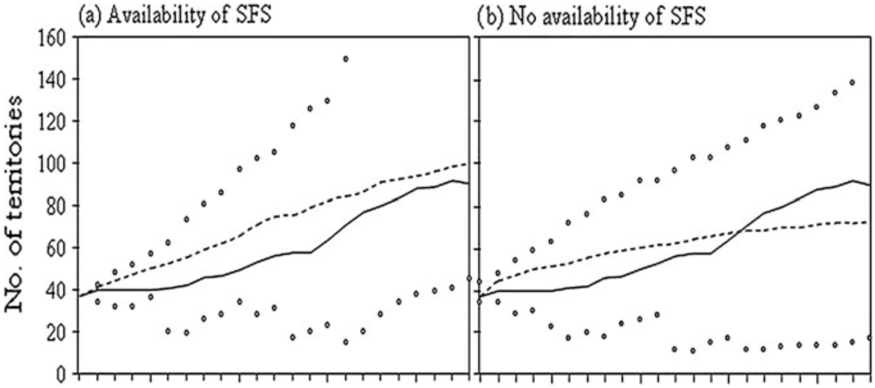

Fig. 15.5 Retrospective analysis of the dynamics of the Spanish population of bearded vultures in the Pyrenees during 1985–2007. Simulations were carried out using estimated values of **a** actual survival rates, i.e. with the effects of poison and SFS; and **b** survival with poison effects but without SFS. *Dashed lines* show the mean value of stochastic trajectories using Monte Carlo simulations, while open dots are the maximum and minimum values of that run. For comparison, we show the observed number of breeding territories through time (*solid lines*) from Oro et al. (2008)

potentially changed with population density (both positively and negatively; author's unpublished data). Retrospective simulations without the positive effects of SFS on young survival but no effects of poison on adult survival rates yielded a lower number of territories than observed in the study population (71 vs. 80 territories, Fig. 15.5). However, population trends were quite similar in all cases (scenario 1: $\lambda = 0.961$, scenario 5: $\lambda = 1.000$, observed: $\lambda = 1.048$) suggesting that population consequences of the progressive reduction in adult survival rates could have been buffered by increments in young survival rates associated with the use of SFS.

15.6.3 Availability of SFS

We envisaged that the illegal use of poison continues affecting survival rates of vultures using the survival rates of pre-adult and adult birds estimated by the best-selected model (see Oro et al. 2008), which were lower than expected likely due to the effect of illegal poison. Thus, we performed a second set of simulations considering that the temporal dynamics of poisoning are dominated by fluctuations, both short and long term, with positive temporal autocorrelation (coloured environmental noise, Inchausti and Halley 2003). Finally, we simulated the behaviour of our population under effective management actions reducing the impact of poisoning, using actual adult survival estimates obtained in our study area but without poison effects.

The three scenarios considered within this group of simulations showed different patterns associated with the effects of poison on survival. When the survival of adults decreases because of the illegal use of poison and survival of young increases due to their use of SFS (scenarios 1 and 2, Fig. 15.6), population trajectories decreased over the years (scenario 1: $\lambda = 0.961$; scenario 2: $\lambda = 0.932$). However, extinction probabilities were not equal in the first and the second scenarios. When the impact of poison was stochastic with no clear trend over time (scenario 1 Table 15.2), probabilities of extinction were nil, although some trajectories attained the quasi-extinction threshold (scenario 1 Table 15.2, Fig. 15.6). Conversely, ARIMA analysis indicated that the way in which illegal poisoning impacted our bearded vulture population (i.e. the colour of the environmental noise) depended on the age class considered. For instance, the decrease of survival among birds older than 4 years during 1986–2007 ($a = 0.264$, $b = 0.241$) showed a long-term temporal autocorrelation (i.e. red noise), whereas for birds up to 4 years old ($a = -0.018$, $b = 0.250$) survival exhibited a short-term temporal autocorrelation

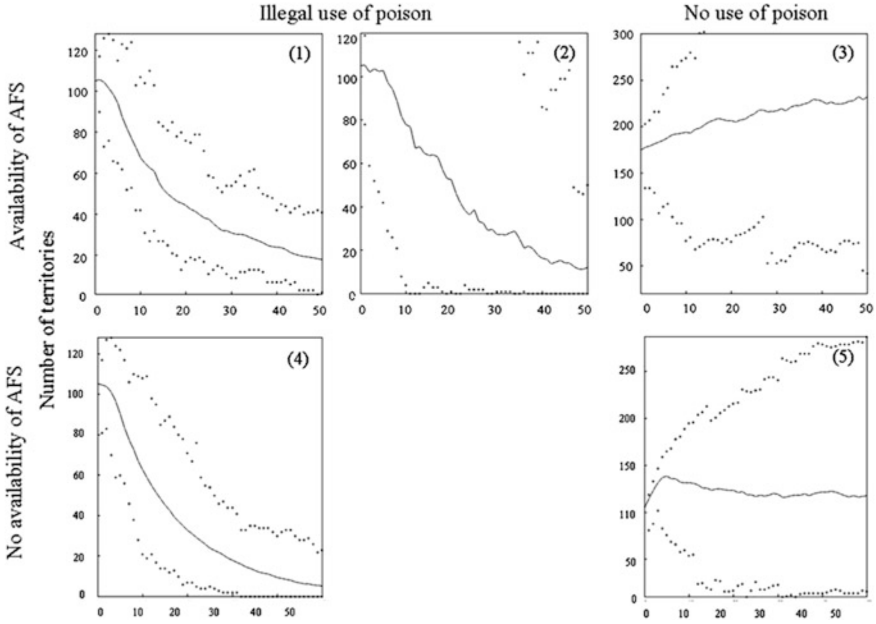

Fig. 15.6 Stochastic population projections estimated through Monte Carlo simulations (50 years of temporal window, 500 runs) for some of the scenarios considered: (1) actual values of adult survival without temporal autocorrelation in the use of poison, (2) and (4) actual values of adult survival with temporal autocorrelation in the use of poison, (3) no impact of poison, assuming that young and adult survival were equal, and (5) no impact of poison, assuming that survival of young, and adults were the same t (see Oro et al. 2008 for details). *Lines* are mean values of the stochastic runs for each time step, while *dots* show the maximum and minimum values of those runs. Projections were carried out on the density of females of any age, which have different scales in each graph

(i.e. blue noise). This temporal autocorrelation in the impact of poison, the most realistic situation (scenario 2 Table 15.2), increased the extinction probabilities of the whole population, with a maximum value over a time horizon of 50 years ($p_e(t = 50) = 1$, mean extinction time: 10.2 years, see scenario 2 Table 15.2, Fig. 15.6). Note that for these two poison-impacted scenarios the mean trajectories were quite similar, except for the largest variability expected in population trajectories when the impact of poison was temporally correlated (scenario 2 Table 15.2, Fig. 15.6). Interestingly, both mean trajectories were relatively stable in early years, probably due to the buffer capacity of recruits resulting from very high young survival.

Increments in the survival rate of adult birds up to that expected when the illegal use of poison was near nil combined with a high survival rate of young (maintained through SFS) predicted a marked increment in the number of breeding territories ($\lambda = 1.014$; Fig. 15.6).

15.6.4 No Availability of SFS

This group of simulations allowed us to disentangle the actual usefulness of SFS to mitigate the effects of illegal poison on population persistence.

Populations suffering from negative effects of illegal poisoning on survival rates but not managed with SFS showed a lower population growth rate and a slightly higher probability of extinction in the time horizon of 50 years than its most conservative counterpart (scenario 1: $\lambda = 0.961$; scenario 4: $\lambda = 0.932$; Fig. 15.6). However, in a scenario of no use of illegal poisoning and no SFS, population numbers are somewhat lower although still rather stable (scenario 5: $\lambda = 1.000$; scenario 3: $\lambda = 1.016$).

Population projections under scenarios of illegal poisoning did not forecast a positive outcome for the most important European core of this species. When the impact of poison on adult survival was stochastic, probabilities of extinction for the population were nil, although some trajectories achieved the quasi-extinction threshold. Of even greater concern, extinction probabilities for the population increased when the effect of illegal poisoning on adult survival followed a temporal autocorrelation, the most probable scenario. Conversely, population projections run with the survival of adults not affected by illegal poisoning predicted better situations, with larger population increments in scenarios of maintenance of SFS, when survival rates of young birds are also improved. The counter-scenario, no use of illegal poisoning and no availability of SFS, predicts slightly lower population sizes but with near stable trajectories. Consequently, an important management action intuitively used to reduce the negative effects of illegal poisoning such as the opening of SFS as appear to be not as effective as expected in saving threatened populations from future negative trends. As in many other long-lived species, survival of adults is the key demographic parameter contributing most to the projected population growth rate (e.g. Saether and Bakke 2000), and management actions should be directed to improve it. However, in the short term, SFS can maintain a large floater surplus that may delay population decline. It is understood that the eradication of the illegal use of poison is neither easy nor time efficient, and hence measures taken to allow more time for the application of proper and more effective management actions can be a useful instrument for conservation. Thus, efforts to determine adequate tools to reduce poisoning risk among adults are important as well. In this sense, experimental work is needed to test the effectiveness of smaller, less predictable SFS located near breeding territories to enhance adult survival while avoiding large aggregations of non-adult birds in their surroundings.

It is worth noting that the reliability of predictive models depends on the robustness of demographic rates and the number of known parameters for each age class. In our case, survival estimates by age classes and fecundity were available and reliable. Nevertheless, some parameters were unknown, mainly the recruitment curve and how it changed with variations in density (Tavecchia et al. 2007). Thus, the structure of the model was a compromise between complexity (due to known demographic patterns such as age-dependent survival or density-dependent fecundity) and simplicity (due to the unknown parameters such as the percentage of breeders at each age class). However, several goals to ensure the maximum reliability at the predictive power of extinction risk were achieved in our modelling by incorporating uncertainty in parameter estimates and stochasticity in population dynamics (Lande et al. 2003). Finally, it is important to note that demographic consequences of artificial increments in survival are limited to those included in our hypothetical scenarios. Complex aspects linked to alterations in natural selection pressures should also be taken into account since a large proportion of young, that in more “natural” situations would have died (low-quality individuals; Tavecchia et al. 2001; Sanz et al. 2008), are now potentially recruited into the breeding population. Moreover, if only SFS-maintained birds are progressively selected, the population can become more dependent on human-supplied food than previously thought.

15.6.5 Usefulness of Supplementary Feeding Sites for the Conservation of Endangered Populations

Supplementary feeding of wild birds is a widespread practice that may alter the natural dynamics of food supply, representing a major intervention in avian ecology. Indeed, supplementary feeding has the potential to change long-term population dynamics and distribution ranges of many species (for a revision see Robb et al. 2008). Therefore, policy-makers and managers have found in supplementary feeding actions a common, straightforward solution to many different conservation challenges of endangered populations, including increasing breeding success (e.g. González et al. 2006; Margalida 2010b; Margalida et al. 2017), providing safe food in areas where carcasses are poisoned or contaminated with veterinary drugs (e.g. Gilbert et al. 2007), promoting the recolonization of abandoned areas (Mundy et al. 1992) and aiding in reintroduction programmes (Chamberlain et al. 2005).

To our knowledge, the Spanish population of bearded vultures represents one of the few cases for which both positive and negative outcomes of artificial feeding sites have been carefully weighed using a population dynamics approach (Fig. 15.7). Recent studies have shown that supplementary feeding can have several adverse effects on this population such as territory compression and coexistence between breeders and floaters (Carrete et al. 2006b; Margalida et al. 2008a), and changes in the mating system reducing territory quality (because of intraspecific interactions) and population productivity (Carrete et al. 2006a). Present results, however, support their usefulness as temporal tools to maintain individuals while more complex objectives such as the eradication of illegal poisoning from the field are achieved. However, the maintenance of SFS should not distract managers from prioritising the long-term viability of this and many other species by eradicating illegal poison use. Taking into account that one of the main threats to this population is its restricted geographic range, SFS can be utilised as a very specific tool for the recovery of the population in peripheral areas, to promote the colonisation of suitable unoccupied areas outside the Pyrenees. Although beyond the scope of this chapter and awaiting scientific support, this latter possibility should be considered a potentially positive aspect of SFS on species conservation.

Fig. 15.7 Adult bearded vulture feeding in a supplementary feeding station in the Catalonian Pyrenees (A. Margalida)

15.7 Effects of Changes in Sanitary Policies in Demographic Parameters

Any factor that disturbs the balance between fecundity and survival will be particularly hazardous for species with slow lifestyles (Owens and Benett 2000; Cardillo et al. 2004). For example, the recent and sudden appearance of non-natural mortality factors related to the ingestion of veterinary drugs (i.e. diclofenac) or the increase in the use of illegal poison baits severely affected populations of Old World vultures (Green et al. 2004, 2006; Virani et al. 2011; Margalida 2012; Margalida et al. 2014c). In parallel, a recent change in European health policy may be exacerbating the precarious status of these large species. Coinciding with the outbreak of bovine spongiform encephalopathy in 2001, scavenger food resources have been reduced because farmers were forbidden from retaining certain dead livestock (Donázar et al. 2009a; Margalida et al. 2010).

Considering the importance of such information for managers and conservationists, our purpose was to test if two human-induced activities (i.e. illegal use of poison baits and regulations in the availability of domestic carcases) can modify life-history traits in a threatened vulture population. Some assessment of food resources and their relation to population dynamics (Colomer et al. 2011; Margalida et al. 2011a; Margalida and Colomer 2012; Martínez-Abraín et al. 2012) and behavioural changes (Zuberogoitia et al. 2010; Margalida et al. 2011d, 2014b) has been documented. In this sense, although food availability can also influence life-history traits and the scientific literature on this topic in birds is abundant (Lack 1968; Western and Ssemakula 1982; Oro et al. 1999, 2004), to our knowledge few studies have attempted to relate the effects of human-induced activities on life-history traits in long-lived raptor species (Martínez-Abraín et al. 2012, Hernández-Matías et al. 2015). The outbreak of bovine spongiform encephalopathy began in 2001, the restrictive legislation forced the closure of 80% of feeding stations (Donázar et al. 2009a; Cortés-Avizanda et al. 2010; Margalida et al. 2014b) and obliged the collection of domestic ungulates to be destroyed. These measures were not implemented effectively until 2005 (Donázar et al. 2009a, 2010; Margalida et al. 2010) when the recovery of dead livestock was collected from farms and most of the feeding stations (80%) closed. Thus, we considered the period 1994–2004 as the “before policy implementation period” (noted as BPI) and 2005–2011 the “after policy implementation period” (noted as API) (Margalida et al. 2012). During the BPI remains of domestic ungulates were present in the field and food availability was considered sufficient to cover the energetic requirements of avian scavengers (Margalida et al. 2011a). However, during API the carcases of domestic animals progressively had to be collected from farms and destroyed in authorised plants (Donázar et al. 2009a; Morales-Reyes et al. 2015). The monitoring of several regions suggested that more than 80% of remains of Ovis/Capra were collected, whereas this proportion reached nearly 100% for the remains of Bos/Equus.

We analysed breeding parameters (during 1994–2011) and survival probabilities (during 1987–2011) to determine if changes in the availability of food supply and/or the effects of illegal poisoning are important anthropogenic mortality factors affecting this population, and whether they can modify life-history traits in a long-lived species. We tested the hypothesis that the reduction in the availability of food resources in the ecosystem (as consequence of a sudden reduction of domestic carcasses in the field from 2005 and the closure of several feeding stations) should decrease survival probabilities, specially that of juveniles and subadults, which are more dependent on this food resource than are older birds (Oro et al. 2008).

15.7.1 Influence of Health Policies on Demographic Parameters

Between 1994 and 2011 we monitored 510 breeding attempts with a total of 298 clutches being laid. The average number of pairs that annually began breeding was 59% (range 42–71%, n = 18) with a similar trend between years, being the proportions of pairs that started breeding before and after policy change similar (57 vs. 61%, Fig. 15.8).

We documented egg-laying dates on 258 occasions, without significant differences between years. However, when we compared egg-laying dates before and after policy change, we found a significant delay following the reduction in food supplies (average 8 January vs. 12 January, t = 2.44, P = 0.016, Fig. 15.9).

We observed a total of 104 clutches of which 57% consisted of a single egg (remainder held two eggs). The proportion of single-egg clutches increased through time and differed before and after policy change (single-egg clutches: 39.4% vs. 69.6%, Fig. 15.10).

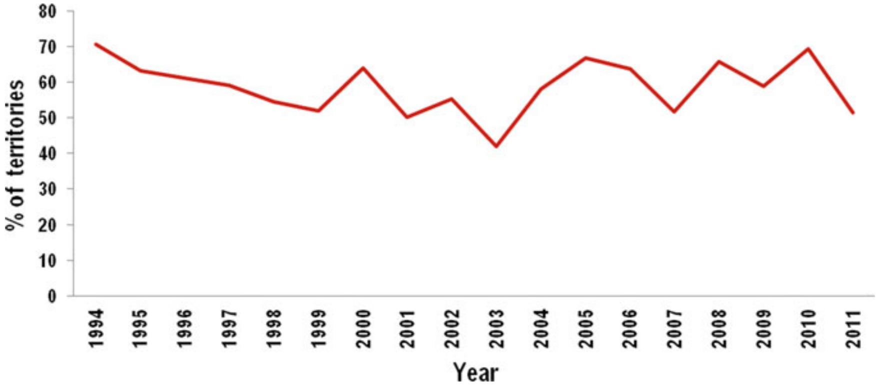

Fig. 15.8 Inter-annual variation in the percentage of bearded vulture territories that had breeding pairs (Margalida et al. 2014a)

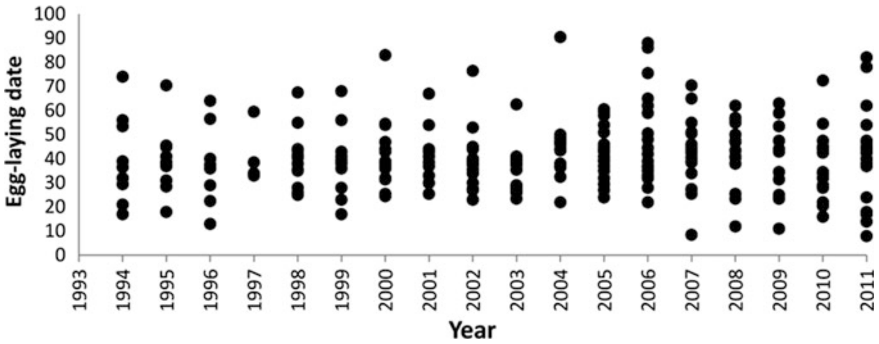

Fig. 15.9 Inter-annual variation in laying dates in the bearded vulture. 0 = 1st December (Margalida et al. 2014a)

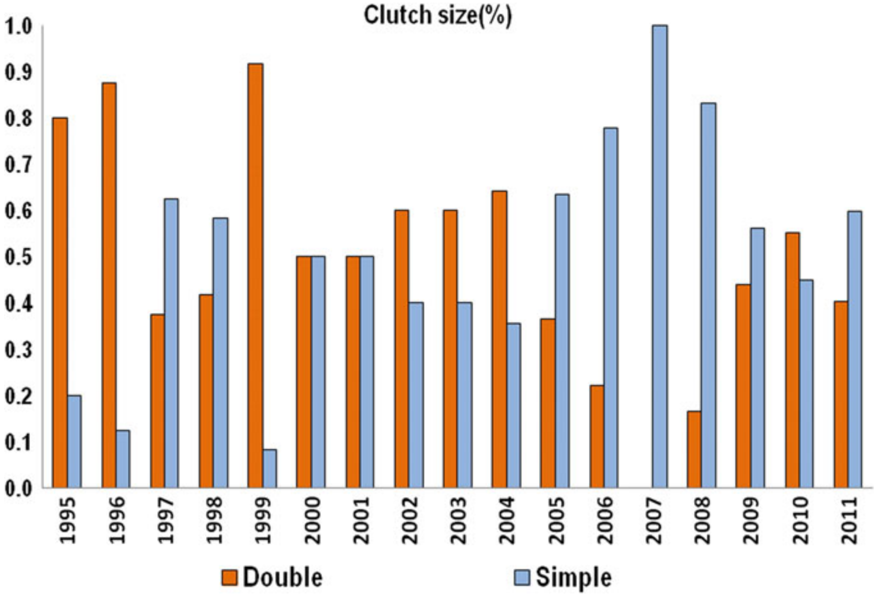

Fig. 15.10 Variation in the clutch size in the bearded vulture in the Pyrenees. *Orange columns* double (2-egg clutches); *blue columns* simple (1-egg clutches) (Margalida et al. 2014a)

Productivity and fledging rate decreased slightly through time, and both values decreased before policy changes, although the differences were not statistically significant (Productivity: 0.37 vs. 0.29; Fledging rate: 0.54 vs. 0.46, Fig. 15.11).

Between 1994 and 2011 we documented a total of 65 cases of mortality. Survival decreased with time in all age classes (adults, >6 years old: $r_s = -0.60$, $P = 0.0091$; subadults, 4–5 years old: $r_s = -0.56$, $P = 0.0147$; juveniles, 1–3 years old: $r_s = -0.48$, $P = 0.042$, $n = 18$). Annual survival differences did not coincide

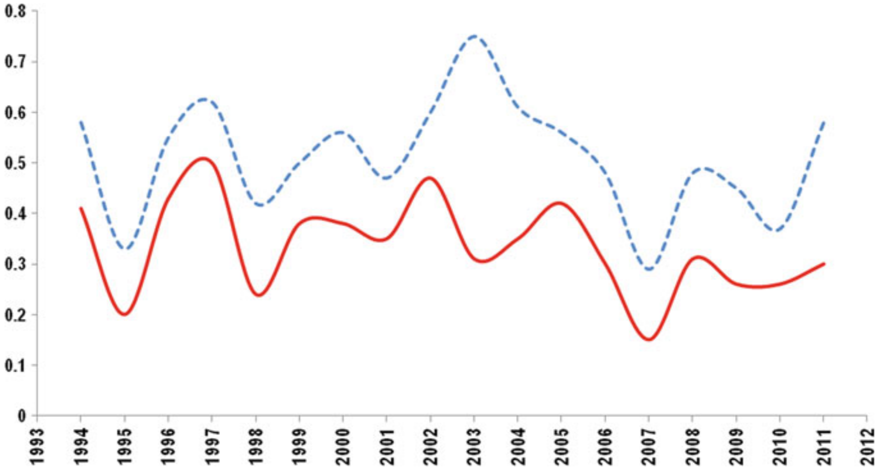

Fig. 15.11 Inter-annual variation in the number of young fledged from all monitored nests (productivity, *red line*) and the number of young fledged from successful nests (fledging rate, *broken line*) in the bearded vulture (Margalida et al. 2014a)

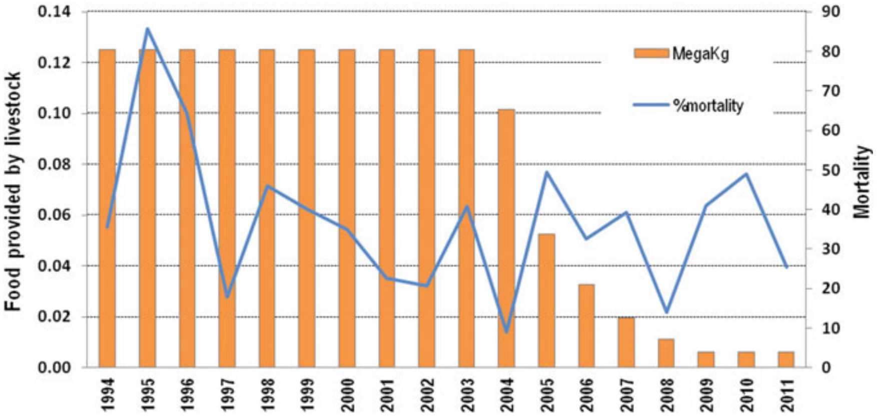

Fig. 15.12 Inter-annual variation in the food biomass (bones) provided by domestic ungulates and adult survival of the bearded vulture (for more details see Margalida et al. 2014a)

with policy change in juvenile and adult age classes (juveniles: 0.975 vs. 0.981; adults: 0.978 vs. 0.946), but did with subadults (0.920 vs. 0.902, P = 0.0059). This coincides with changes in the number of carcasses provided by domestic ungulates that decreased progressively from 2003 ($r_s = -0.91$, $P = 0.0001$, n = 18, Fig. 15.12).

15.7.2 *Effects of Illegal Poisoning and Reduced Food Supplies on Adult and Pre-adult Survival*

The model garnering the greatest support (model 1) showed that the closure of some feeding stations slightly changed survival and did so differently for juveniles (1–2 years old, the age class exploiting feeding stations with higher frequency) and immature (2–3 years old) and subadults (4–5 years old), whereas adults (>6 years old) showed a temporal decline in survival over the study. Survival of juveniles slightly decreased from 0.975 to 0.957, that of immatures and subadults from 0.917 to 0.906, whereas adult survival decreased from 0.975 in 1987–0.901 in 2011 (Table 15.3).

15.7.3 *Contradictions Between Health and Biodiversity Policies*

Recent changes in European health regulations provoked apparent contradictions between the application of sanitary and conservation policies (i.e. to eliminate corpses avoiding the presence of carrion in the field vs. to conserve scavenger species; Donázar et al. 2009b; Margalida et al. 2010). Implementation of the sanitation policy appears to have undermined conservation goals, as evidenced by, for example, in the same area with Eurasian griffon vultures in which an annual decrease in breeding success, reduced population growth, increased mortality on young age classes and changes in diet and behaviour is observed (Donázar et al. 2009b, 2010; Zuberogoitia et al. 2010; Margalida et al. 2011d, 2014c). Our results confirm these observations with empirical, long-term data on another vulture species. After sanitation policies had been enacted, the threatened Pyrenean bearded vulture population had reduced survival, especially of subadult individuals, and adults bred later and less successfully than before policy implementation. In this sense, additional conservation actions, such as supplementary feeding, can buffer the negative effects of policy change on demographic parameters (Oro et al. 2008). However, because supplementary feeding can also have detrimental effects (Carrete et al. 2006b; Robb et al. 2008; Cortés-Avizanda et al. 2016), this tool should only be used as a precautionary measure until the recovery of the previous scenario (i.e. availability of domestic carcases in the field) is achieved.

According to our results, reduction of food supply does not affect the proportion of pairs that start breeding, and so the decision to breed or not was influenced by the change in carcase disposal legislation. Among the European scavenger guild, bearded vultures seem to be the least sensitive to the effects of food limitations (Margalida and Colomer 2012). Their specialised diet based on bone remains implies a foraging resource for which only conspecifics can compete, which lasts

Table 15.3 List of the 15 models explaining bearded vulture survival with lowest QAICc values. Age of individuals was grouped into eight age classes, the last grouping 6-year-old birds and older (see methods). Models referring to 2005 deal with a tipping point in that year, after which API was in short supply probably affecting survival. Models considering different groupings of age classes were noted by their first and age class considered; for instance, a model grouping birds of 2 year and 3 year old was noted as 2 year_3 year. Np = number of identifiable parameters; Δ_i = QAICc difference value between the best model and model i; w_i = weight of model i (Margalida et al. 2014a)

No.	Np	Deviance	QAICc	Δ_i	w_i	Hypothesis tested on survival by time and age
1	28	921.148	979.148	0	0.41	Only two values: before and after 2005 differently for juveniles (1 year) and immature and subadults (2 year_5 year); for adults, trend with time
2	28	922.572	980.636	1.488	0.19	Temporal trend in survival only for adults (>5 year old); the two other age classes considered have constant survival and different for juveniles (1 year) and immatures and subadults (2 year_5 year)
3	28	923.76	981.823	2.675	0.11	Only two values: before and after 2005, but differently for juveniles, immature and subadults (2 year_5 year) and adults
4	28	924.045	982.109	2.961	0.09	Two values: before and after 2005 but only for adults; other age classes had constant survival but different for juveniles (1 year) and immature and subadults (2 year_5 year)
5	28	924.561	982.624	3.476	0.07	Two values: before and after 2005 but only for adults; other age classes had constant survival (1 year_5 year)
6	25	931.319	982.965	3.817	0.06	Constant (all age classes the same survival)
7	27	928.733	984.625	5.477	0.03	Two values: before and after 2005 but only for adults; other age classes had the same constant survival
8	27	928.757	984.675	5.527	0.03	Only two values: before and after 2005 but differently for juveniles, immature and subadults (1 year_5 year) and adults

(continued)

Table 15.3 (continued)

No.	Np	Deviance	QAICc	Δ_i	w_i	Hypothesis tested on survival by time and age
9	31	921.023	985.553	6.405	0.01	Only survival of old subadults and adults (>5 year old) had a temporal trend; other age classes have constant survival and different for each age
10	29	930.044	990.258	11.11	0.00	Only two values: before and after 2005 differently for juveniles (1 year) and immature and subadults (2 year_5 year); for adults, a temporal trend before 2005 and another temporal trend (different slope) after 2005
11	41	904.715	991.165	12.017	0.00	Change only with age
12	29	931.077	991.291	12.143	0.00	Only two values: before and after 2005 but differently for juveniles (1 year) and immature, and subadults (2 year_5 year); for adults, survival had a temporal trend until 2006 and then remained constant
13	30	929.903	992.272	13.124	0.00	Only adult survival changes with time; other age classes had constant survival and grouped differently for juveniles (1 year), immatures (2 year_3 year) and subadults (4 year_5 year)
14	84	810.319	997.854	18.706	0.00	Change with time and age, but recapture equal for all ages except for juveniles
15	94	797.367	1010.411	31.263	0.00	Change with time and age

ten times longer than meat remains and is very nutritious, being an advantage compared to a meat-based diet (Houston and Copsey 1994; Margalida 2008a, b). Thus, although the proportion of pairs that do not start laying annually is important (range 29.4%–58.1), the decision to start breeding, which could be influenced by the physical condition of the individual (Jenouvrier et al. 2005), appears not to compromise the reproduction of bearded vultures. This suggests that, in this isolated population, several buffering mechanisms (e.g. changes in the structure of breeding age, low dispersal movements and/or the availability of natural food) may contribute to maintain stable the proportion of pairs that start laying (Sergio et al. 2011; Oro et al. 2012; Margalida et al. 2013). In this sense, the carcass disposal policy does not seem to affect population movements because pre-adult individuals remained in the study area without greater pre-dispersal movements (Margalida et al. 2013). Thus, a possible explanation is related to the high food availability in the Pyrenees (Margalida et al. 2011a). With respect to non-natural mortality, although mortality factors affect mostly adult age classes (Margalida et al. 2007b; Oro et al. 2008), this seems to play no role in the start of breeding. Thus, buffering capacity through ecological and behavioural processes such as positive feedback from conspecific attraction could explain this regular pattern (Margalida et al. 2011d; Oro et al. 2012).

During the last six years, the proportion of double clutches seemed to decrease in parallel with laying dates. Large avian species often show obligate brood reduction (two eggs laid but only one chick survives) in which siblicide (when more that 90% of last-hatched chicks die, Simmons 1988) may occur, even when food supplies are abundant. The second egg thus serves as insurance against loss of the first egg from infertility, predation, or damage, rather than as a means of rearing two chicks (Stinson 1979; Anderson 1990; Mock et al. 1990). According to Winkler et al. (2002), there is a strong effect of laying date on clutch size, and earlier breeding may lead to larger clutch sizes. An increase of food resources could increase clutch size in fratricide facultative species (Korpimaki and Wiehn 1998), but in obligate fratricide species such as bearded vultures, the second egg seems to be an adaptive mechanism serving as an insurance egg to avoid breeding failure if the first egg does not hatch (Stinson 1979; Margalida et al. 2004). In this respect, in several species, including the bearded vulture, it seems that single-egg clutches are related to old or young females (Frey et al. 1995). According to our results, the increase of single-egg clutches could be related to a reduction in food supply or the stress that changes in food availability could provoke in individuals (i.e. increasing their foraging effort or the agonistic interactions as a consequence of a greater competence for the resources) and the effects of mate loss with the incorporation of less experienced individuals.

15.7.4 The Impact of Policies Decisions on Breeding Ecology and Conservation

The conservation implications of these results suggest that anthropogenic activities modifying habitat quality through human health regulations (i.e. a reduction in food availability) can alter demographic parameters and increase the probability of illegal poison bait consumption thus increasing non-natural mortality. The shifts in demographic parameters can have important conservation consequences, being necessary to adopt preventive mitigation measures on targeted species. As a result, preventive management measures such as supplementary feeding can be effective until more flexible sanitary legislation allows increased trophic availability, minimising the detrimental effects that food shortages and illegal poisoning can cause.

15.8 Concluding Remarks

Scientists and managers generally work at different timescales (Linklater 2003). Managers often need to respond quickly to immediate problems, whereas scientists can sometimes take years to generate appropriate information. This is the case of the bearded vulture in the Pyrenees, a species at which administrations invested substantial economic and human resources in recovering their populations. As our results show, long-term studies are necessary to identify conservation problems, to understand demographic changes on populations and priorities to apply conservation measures. Thanks to the long-term studies, we identified a saturation in the region of optimal habitat for the species, reflected in negative density-dependent effects on fecundity (Carrete et al. 2006a), the lack of recolonization and expansion beyond the current range of new territories (Margalida et al. 2008a) and the increase in polyandrous trios (Carrete et al. 2006b). Also, supplementary feeding sites (SFS) can have detrimental effects on fecundity (Carrete et al. 2006a), despite increasing pre-adult survival (Oro et al. 2008; Margalida et al. 2014b). Thus, as a management action, SFS should be moved into peripheral areas. In this sense, the recent network of protection areas for the feeding of necrophagous species of European interest (PAFs) suggests that these areas may be more efficient for breeders than for floaters, whose home ranges can be considerably larger (Margalida et al. 2016; Morales-Reyes et al. 2017). In the case of bearded vultures, the overlap of core areas (k50%) of breeders with PAFs reached 90.6%, while the overlap was only 64.2% for floaters (Morales-Reyes et al. 2017). The long-term monitoring has revealed how illegal poisoning, the most important non-natural mortality factor (Margalida 2012), is increasing over time and the demographic simulations suggest a regressive scenario in population dynamics if this factor is not eliminated (Oro et al. 2008). Anthropogenic activities through human health regulations that affect habitat quality can also suddenly modify demographic parameters (Margalida et al. 2014c). Our findings suggest a delay in laying dates and a regressive trend in clutch size, breeding success and survival following the policy change. Finally, the recent approved veterinary use of diclofenac in Spain (Margalida et al. 2014c) can threaten the scavenger guild community. This new risk requires a programme of monitoring of non-steroidal anti-inflammatory drug contamination of ungulate carcases available to vultures and of moribund and dead obligate and facultative avian scavengers would be needed to be confident that a damaging level of contamination is not present (Green et al. 2016). The ecosystem services provided by vultures (Moleón et al. 2014; Morales-Reyes et al. 2015) and the conservation of biodiversity implies that managers and policy-makers need to balance the demands of public health protection and the long-term conservation of biodiversity.

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