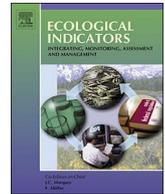




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European policies on livestock carcasses management did not modify the foraging behavior of a threatened vulture



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ABSTRACT

Policy decisions have the potential to affect biodiversity conservation and modify, among other factors, animal demography, behavior and ecological processes. This became manifest in Europe in the past decade in light of the appearance of bovine spongiform encephalopathy (BSE). However, the obvious effects of policy decisions on foraging behavior are lacking. Here, we use data from a long-term study (1992–2015) of the ecology of the bearded vulture *Gypaetus barbatus* in the Pyrenees to assess whether or not the implementation of health policies in the period 2006–2011 really did affect this vulture's foraging behavior and breeding success. To test this, we used the frequency of nest changeovers (between 1992 and 2015) as a surrogate for the time invested in searching for and obtaining food. Additionally, between 2006 and 2015 we monitored the movements of 20 bearded vultures with GPS satellite transmitters. Our findings show no differences between annual home range sizes and/or the time used to search for food either before, during or after the imposition of health regulations. No differences between periods (during or after health regulations) were found in the use of supplementary feeding sites (SFS). An analysis of food available indicates that this similarity of use in different periods could be explained by the high habitat quality in the Pyrenees and the good availability of trophic resources. Our results suggest that diet plasticity and habitat quality compensate for the sudden effects of food shortages and so question the true usefulness of SFS in buffering a quantitative food deficit. We discuss the implications of these results from both ecological and conservation perspectives.

1. Introduction

An assessment of the effects of anthropogenic activity on ecosystem dynamics is often complex since these effects may not manifest themselves until several years after the original human impact has occurred (Vitousek et al., 1997; Robertson et al., 2012). In addition, the dearth of previous long-term datasets that can assess objectively the relationships between human actions and ecosystem effects hampers any adequate evaluation of this cause/effect relationship (Robertson et al., 2012); this lack thus highlights the need for long-term studies (Mills et al., 2015). This scenario becomes evident when sudden changes due to policy decisions affecting habitat quality (e.g. food availability) occur, a good example of which was the 2001 outbreak of bovine spongiform encephalopathy in Europe that brought out into the open contradictions between sanitary and environmental policies (Tella, 2001; Donazar et al., 2009a,b; Margalida et al., 2010). In Spain, home to > 90% of all European vulture species' individuals, the feeding

resources of both facultative and obligate scavenger species were suddenly limited by the application of health policies that, as a precautionary measure, obliged the carcasses of domestic animals to be collected and then transformed or destroyed in authorized plants, thereby reducing substantially (around 80%) the food available for obligate and facultative scavenger species (Donazar et al., 2009a,b; Cortés-Avizanda et al., 2010). Furthermore, the closure of several supplementary feeding sites (hereafter SFS) or 'vulture restaurants' accentuated the sudden changes occurring in the availability of trophic resources (Donazar et al., 2010; Blanco, 2014; Llana and López-Bao, 2015).

The new laws were implemented from 2002 onwards with the entry into force of Regulation EC 1774/2002 and were strongly enforced in Spain in, above all, 2005–2011. Nevertheless, since 2012 new regulations have made sanitary policies more flexible and have partially reversed the previous situation (EC 142/2011, Royal Decree 1632/2011; Margalida et al., 2012) by allowing farmers to leave extensive

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livestock carcasses in specific areas (*Protected Areas for the Feeding of Scavengers* – PAFs- implemented since 2013–2014; see Morales-Reyes et al., 2017) and/or feeding sites (Margalida et al., 2012).

The detrimental effects of the initial policies regarding scavenger species were highlighted by several studies that described shifts in dietary habits (Donazar et al., 2010; Blanco 2014; Llaneza and López-Bao, 2015), changes in behavioural ecology (Zuberogoitia et al., 2010; Margalida et al., 2011) and a fall in demographic parameters (Margalida et al., 2014). More recently it have been also documented additional detrimental effects related with the new regulations, as those affecting the greenhouse-gas emissions associated with the transport of carcasses (Morales-Reyes et al., 2015). However, it is still unknown how these policies will affect foraging behaviour, a serious shortfall given the importance of this information from management and conservation perspectives. In addition, Spain have an important network of supplementary feeding sites (Moreno-Opo et al., 2015; Cortés-Avizanda et al., 2016), being a good scenario for evaluating whether an intensification in the use of supplementary feeding sites occurred after food shortages and whether this affected the feeding and foraging movements of obligate scavengers (Deygout et al., 2009; Montsarrat et al., 2013).

Foraging occupies a substantial amount of the daily time budget of avian scavengers. The spatial and temporal unpredictability of food resources obliges individuals to explore extensive surface areas and optimal foraging behaviour is influenced by the quality of the foraging patch and the fitness of the individual (Houston and McNamara, 1986; McNamara and Houston, 1986). This uncertainty provokes a trade-off between energy gains and survival (Olsson et al., 2002). Limitations in food supplies may force animals to evaluate trade-offs between survival and fitness (Olsson et al., 2002) and so food availability is an important driver of home foraging ranges (DeVault et al., 2004; Carrete and Donazar, 2005; Kertson and Marzluff, 2011). The potential effects of food shortages on the use of space by vultures have not yet been determined but could be useful for managers and policy-makers. For example, changes in the use of space could determine just how important SFS are as tools for compensating a reduction in food supplies and/or how these effects are linked to demographic parameters (see Margalida et al., 2014). Nevertheless, the ways in which food shortages affect foraging and act as a key driver of animal space use have not been resolved. Resource distribution and temporal availability affects movement ecology but also individual life history and has a demographic impact on population dynamics (Nathan et al., 2008). According to ecological theory, birds may need to use a greater variety of food resources when the abundance of their preferred prey becomes scarcer (Bell and Ford, 1990).

We used data from a long-term study of the breeding ecology of bearded vultures that began in 1992. Thus, we had at our disposal information on nest changeovers and foraging behaviour that coincided with the food-shortage period, i.e. the Policy-Implementation Period (PI) in 2005–2011, as well as the pre- and post- food-shortage period, i.e. the No-Policy-Implementation Period (NPI) that encompasses the rest of the study period (1992–2004 and 2012–2015).

We hypothesized that if food shortages affect habitat quality and by extension breeding behaviour, foraging movements would vary according to the availability of resources and could, additionally, affect breeding parameters. Thus, hypothesis 1 was that health policies regulate food availability and affect home range size and daily movements, which means that home ranges and daily movements are larger when food availability is lower (during PI). This implies that the time invested in searching for food could affect breeding output. The species would respond to changes in food availability by increasing its consumption of alternative prey items and/or visiting SFS more frequently, albeit without modifying substantially the area it exploited and the time invested in finding food. Thus, a second hypothesis (hypothesis 2) was that SFS can buffer the effects of food shortages as individuals could use these predictable sites more frequently during PI and, consequently, modify their feeding and foraging patterns asso-

ciated with these points. As a result, a reduction in food availability could lead to greater use of SFS during PI, because these sites provide predictable food resources in a spatial and temporal scale. In addition, food shortages also could provoke differences between the PI and NPI periods in the presence of individuals at these sites — but without necessarily affecting the amount of time invested in searching for food during the incubation or chick-rearing periods or having any effect on breeding output.

To test this, we used three indicators 1) the frequency of changeovers during incubation and chick-rearing as a surrogate of the time invested searching for food. Thus, comparing the frequency of changeovers between PI (2005–11) and NPI (1992–1994 and 2012–2015) we can assess whether or not the foraging time varied as a response to the implementation of health policies; 2) the kernel and minimum convex polygon (MCP) estimators of home ranges to assess if there were differences between the PI (2006–2011) and NPI (2012–2015) periods in terms of the use of space, i.e. the foraging areas visited; and 3) the percentage of locations near SFS as a surrogate of a higher/lower use of these predictable food-resource sites in the PI (2006–2011) and NPI (2012–2015) periods. Additionally, we assessed the potential effects of changes in food availability on breeding output during this period by comparing productivity and breeding success during the PI and NPI periods.

2. Material and methods

2.1. Study area and data collection

The southern side of the Pyrenees (SW Europe) has been intensively monitored as part of the recovery plan for this species executed in the Spanish Autonomous Communities of the Basque Country, Navarre, Aragon and Catalonia that includes programs to monitor population trends, breeding parameters and survival rates (including a specific capture-mark-resighting subprogram).

In 1992–2015, all known territories located in the eastern Pyrenees (range 15–44 territories) were visited (2–3 visits/month) to search for signs of occupancy (territorial and/or courtship activity, nest arrangement/building) and to record reproductive parameters. Observations began in September–October, coinciding with the start of nest-building and sexual activity (Bertran and Margalida, 1999), and ended during fledging (June–August).

2.2. Bearded vulture capture and tracking

In 2006–2013 a total of 20 bearded vultures were fitted with satellite transmitters. Birds were captured using radio-controlled bow-nets at feeding sites ($n = 16$) or as fledglings in nests ($n = 1$), or were individuals from official wildlife recovery centres that were subsequently released ($n = 3$). Birds were assigned to one of four age-classes as per previous studies (Margalida et al., 2016): juvenile (birds during their first year of life), immature (2–3 years), sub-adult (4–5 years) or adult (≥ 6 years). Individuals were sexed from blood samples, while territoriality, breeding status and annual breeding success were assessed by field observations.

Solar-powered 70-gr (GPS/PTT) satellite transmitters (Microwave Telemetry, Inc. Columbia, MD) were used to track movements. Transmitters were attached to a backpack harness made from 0.64-cm Teflon ribbon (Bally Ribbon Mills, Bally, PA) and were programmed to collect GPS locations (18 m manufacturer's estimated error) every hour from 6:00 to 21:00 UTC; the only exception were two non-territorial adults that were programmed to transmit a fix every two hours. The average number of fixes collected per day for all tracked birds was 5.1 ± 2.9 (range per individual was 3.6 ± 2.4 – 7.5 ± 3.0).

2.3. Scenarios considered

We considered the periods 1992–2004 and 2012–2015 as the No-Policy-Implementation Period (NPI) and 2005–2011 as the Policy-Implementation Period (PI). During NPI, remains of domestic ungulates were present in the field and food availability was considered sufficient to cover the energy requirements of avian scavengers (Margalida and Colomer, 2012). However, during PI, the carcasses of livestock were progressively collected from farms and destroyed in authorized plants (Donazar et al., 2009a,b). Monitoring in several regions suggested that 80% of *Ovis/Capra* remains and nearly 100% of *Bos/Equus* remains were removed from the field (Margalida et al., 2014).

2.4. Changeover frequency and breeding output

To assess the time an individual invested in foraging for food we used two variables providing estimates of the availability of food present in each period (NPI vs PI) as surrogates of habitat quality. For NPI we used data from nine nests monitored intensively in 1993–2000 and for PI we used seven of these same nests monitored in 2006–2011. Foraging time during incubation was considered as the time invested by an individual after changeover in obtaining food, resting and returning to the nest. This was measured in minutes as the time elapsed between leaving the nest and returning to take over incubation duties. During this period the food obtained is for the adults as at this stage no prey is needed for the nest. Foraging time during rearing was considered as the time invested by an individual during the chick-rearing period (i.e. after hatching) between changeover and returning to the nest with a food item. At this stage adults may use foraging time to obtain food for themselves or for the chick. Given that during the first weeks of a chick's life one adult is always present at the nest, we only considered changeovers during the first two months after hatching, a period during which feeding frequency and food delivery to the nest is similar (Margalida and Bertran, 2000).

To compare the effects on breeding output, we took the values obtained for productivity (chicks fledged divided by territories monitored) and breeding success (chicks fledged divided by territories with egg-laying) in the eastern Pyrenees (Catalonia) between 1992 and 2015. For the NPI period we monitored breeding output at 15–19 pairs per year during 1992–2004 and 39–44 during 2012–2015. For the PI period (2012–2015) the range of breeding attempts monitored was 34–44.

2.5. Movement modelling

To study temporal variation in bearded vulture movement ecology we compared the PI and NPI periods, namely, data obtained in 2006–2011 and 2012–2015. We used annual home range estimator and daily movement parameters. First, we calculated the 90% (K90) and the 50% kernel (K50) density contours. K90 represents the home range and the K50 the core area of activity. A minimum convex polygon (MCP) is typically used as a measure of the maximum area of activity. We used dynamic kernel models in the *adehabitatHR* package to calculate use distributions (UD; Worton 1989). This package was run in R software (v 2.14; R Development Core Team 2005 <http://www.r-project.org/>) in combination with ArcGIS 9.1 (ESRI 2003) to build UD surfaces. Annual UDs were estimated for each bird using the ad hoc method as a smoothing parameter. The resolution of UD surfaces was established at 1 ha. Data for birds with fewer than 50 localizations per year were removed from the analyses.

We selected two parameters to describe daily bearded vulture movement patterns: the cumulative distance travelled per day and the maximum distance reached per day. The cumulative distance travelled per day (km) was calculated summing the straight-line distances between successive locations on the same day. The maximum distance reached per day (km) was calculated as the maximum distance from the

initial daily location to any location reached on the same day. To calculate both parameters we only used days with seven or more locations. All data of tracked bearded vultures during their juvenile stage were discarded because their movement patterns are very different from other non-territorial birds and are still dependent on their parents' territory (Margalida et al., 2016). All values are presented as mean \pm standard deviation (sd).

2.6. Assessment of food available vs food needed

We used the Eastern Pyrenees in Catalonia as a case study because detailed recent studies of food resources and breeding parameters for bearded vultures are available for this region (Margalida and Colomer, 2012; Margalida et al., 2014). We divided the study area into 10 sub-areas in which detailed census data for bearded vultures and wild and domestic ungulates are available; these areas also included peripheral areas visited by the vultures (for more details see Margalida and Colomer, 2012). The study area contains a total of 10 supplementary feeding sites (SFS) for bearded vultures (the supplied remains are principally sheep extremities) and nine additional sites for other avian scavengers (carcasses and other types of remains, Moreno-Opo et al., 2015). We obtained data on demographic parameters and biomass from Margalida and Colomer, (2012) (based on censuses carried out by staff from the Departament de Medi Ambient i Habitatge of the Generalitat de Catalunya), as well as from the literature (for more details see Margalida and Colomer, 2012) and personal observations. The year was divided into two periods: *Breeding*, from October to June, and *Non-breeding*, from July to September. *Breeding* includes the pre-laying period (nest-building and sexual activity) and the reproductive period (egg-laying in December–February and fledging in June–August), which coincides with the presence of transhumant livestock in mountain areas (Olea and Mateo-Tomás, 2009). During the *Non-breeding* period, that is, the post-fledging period, the quantity of livestock in the mountain areas increases significantly as a consequence of transhumant livestock. Thus, due to temporal differences, food availability differs between seasons, being greater during the summer. Nonetheless, the energetic requirements of avian scavengers are higher during the breeding season (winter and spring).

To compare the total potential biomass that bearded vultures need with the food available in the ecosystem, the annual energetic requirements of individuals – determined using their standard metabolism (King and Farner, 1961; Donazar, 1993; Prinzing et al., 2002; Prinzing et al., 2002) – was multiplied by the number of individuals present in the region (see Margalida and Colomer, (2012)).

We compared the hypothetical biomass provided (transformed in megacalories) by domestic and wild ungulates during PI and NPI. The NPI scenario corresponds to a period of ecosystem functioning prior to the application of sanitary regulations (Donazar et al., 2009a,b; Margalida et al., 2010) in which all carcasses of domestic and wild ungulates were available for the avian scavenger guild. The PI scenario, on the other hand, reflects a situation in which approximately 80% of all animal carcasses were removed from the field. First, we calculated the biomass provided by each subzone with respect to the megacalories necessary to cover the energetic requirements of the bearded vulture territories present in each subzone. This allowed us to obtain a picture of the surplus – or lack – of biomass from a spatial point of view without taking into account the biomass provided by SFS.

2.7. Effects of supplementary feeding sites

A total of 107 SFS were located in the distribution range of bearded vultures in Spain and France. We evaluated the effects of SFS presence on bearded vulture movements in two ways: firstly, we calculated the percentage of bearded vulture locations inside buffers of 0.5 km, 1 km and 5 km around each SFS (see Margalida et al., 2016), and, secondly, calculated the number of SFS located inside the annual UD surfaces of

tracked bearded vultures. We used the core area (K50) and home range (K90) and, additionally, calculated the 20% kernel (K20), which allowed us to determine each bearded vulture's areas of greatest use (Margalida et al., 2016). In the case of territorial adults, K20 was not estimated due to the absence of SFS.

2.8. Statistical performance

We evaluated the effect of territorial status (territorial vs non-territorial) and period (NPI vs PI) on the size of home range estimators (K90 and K50) and movement parameters (mean cumulative distance daily travelled and maximum distance reached per day) using generalized linear mixed models (GLMM; Zuur et al., 2007). We built models that included the interaction between the two factors (territorial status*HR estimators; territorial status*movement parameters); to avoid pseudoreplication, individual identity was included as random factor. For GLMM we used a Gamma error distribution and the log link using the *lme4* package (Bates et al., 2015) in R software (version 2.14). To compare variance in annual home range estimators and movement parameters we used an F-test. Differences invested in foraging time during incubation and rearing for each period were tested with a Mann-Whitney *U* test and an analysis of variance (ANOVA).

To assess the frequency of use of SFS in the two periods (NPI vs PI) we used a paired Wilcoxon rank sum test to study differences in territorial status in the percentage of locations at 0.5 km, 1 km and 5 km from a SFS, and the number of SFS inside K20, K50 and K90.

To assess the differences between the biomass (expressed in megacalories) available in the two periods, NPI vs PI, we used a *t*-test. All statistical procedures were performed using R software.

3. Results

3.1. Temporal variation in bearded vulture movements

We found no relationship in bearded vultures between annual home range size and the regulation period (GLMM for K90 $t = 0.36$; $P = 0.72$; K50 $t = -0.30$; $P = 0.76$; MCP $t = 0.79$; $P = 0.43$; Table 1, Supplementary Material Fig. S1) neither between movement parameters and regulation periods (GLMM for cumulative distance $t = -1.29$; $P = 0.19$; Maximum distance $t = -0.67$; $P = 0.54$; Table 1, Supplementary Material Fig. S2), nor between the interaction between territorial status and the regulation period (Regulation*Territorial status) for all previous parameters (GLMM K90 $t = -0.58$; $P = 0.56$; K50 $t = -0.14$; $P = 0.88$; MCP $t = 0.30$; $P = 0.76$; Cumulative distance $t = -1.29$; $P = 0.19$; Maximum distance $t = -0.67$; $P = 0.54$).

3.2. Mean time foraging during incubation and rearing

When we compared mean foraging time in the two periods (NPI vs PI), i.e. the time invested in changeovers as surrogates of time searching for food, no differences were found in foraging time either during incubation (Mann-Whitney *U* test, $z = 0.53$, $P = 0.60$) or during rear-

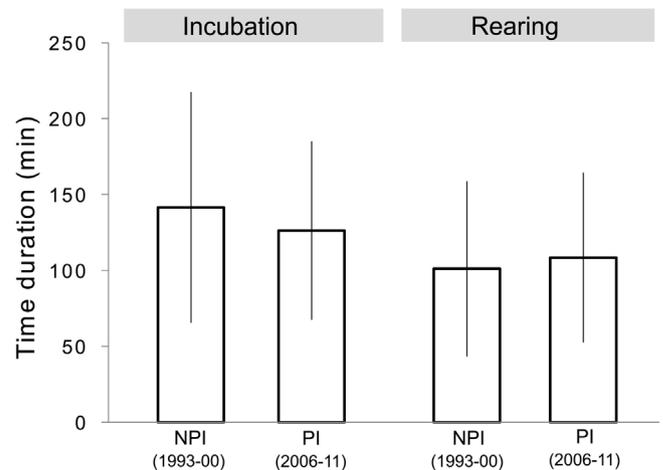


Fig. 1. Differences in changeover duration during incubation and chick-rearing in the policy periods (NPI: Non-Policy Implementation Period; PI: Policy-Implementation Period). Bearded vulture breeding pairs monitored intensively during NPI (1992–2000; $n = 9$) and during PI (2006–2011; $n = 7$).

ing (Mann-Whitney *U* test, $z = -0.83$, $P = 0.20$, Fig. 1).

3.3. Effects on breeding output

Although differences were not statistical significant (Productivity: ANOVA $F = 2.08$, $df = 2, 21$, $P = 0.15$; Breeding success: $F = 2.21$, $df = 2, 21$, $P = 0.14$), productivity and breeding success reached their lowest values during the PI period (Fig. 2).

3.4. Estimates of available vs needed food resources

In the study area there are 10 bearded vultures SFS that are supplied with sheep remains (extremities), the average amount of food provided per site/year being $2598.2 \pm SD = 1404.16$ kg. In addition, nine other vulture restaurants for other avian scavengers exist at which carcasses and other remains are provided regularly. The average amount of food provided per site/year is 1531.8 ± 1084.16 kg. Without taking into account this surplus biomass and only considering the natural biomass offered by the ecosystem, PI implied a significant reduction in the amount of food available in both *Non-breeding* ($t = 5.20$, $P = 0.0006$) and *Breeding* periods ($t = 4.54$, $P = 0.0014$, Table 2). Nevertheless, the availability of food is substantially higher in all studied areas than the energetic requirements of the breeding bearded vulture population (Table 2). In the food-shortage period (PI), the needed vs available energetic requirements in the *Non-breeding* period were 414.4 vs 5879.4 megacalories for the total breeding population (36 territories); the results were similar for the *Breeding period*: 947.2 vs 7707.5 megacalories. Thus, the natural food supply – that is, excluding the food provided by SFS – in the study area during PI was 10 times greater than the energetic requirements needed for the breeding population.

Table 1

Annual home range estimators for bearded vultures in the Pyrenees according to the Policy-Implementation Period (PI) and the Non-Policy-Implementation Period (NPI) and to territorial status (non-territorial birds NT; territorial birds T). We show the number of tracked birds according to their territorial status in each period (Indv) and the total number of tracked birds according to their territorial status and year (n). The minimum convex polygon (MCP) and the utilization density kernel of 90% and 50% (K90 and K50 respectively) are shown in km². The cumulative distance travelled per day (Cum Dist) and maximum distance reached per day (Max Dist) are shown in km. The Policy-Implementation Period (PI) was from 2005 to 2011 and Non-Policy-Implementation Period (NPI) was from 1992 to 2004 and from 2012 to 2015.

Status	Period	Indv	n	MCP	K90	K50	Cum Dist	Max Dist
Non Territorial	PI	12	31	12,266 ± 8038	11,328 ± 6713	3392 ± 2297	41.8 ± 31.0	24.5 ± 25.5
	NPI	12	22	14,778 ± 8504	12,063 ± 5513	3142 ± 1854	38.9 ± 37.3	23.2 ± 27.1
Territorial	PI	5	12	605 ± 576	71 ± 73	16 ± 17	19.2 ± 15.3	5.8 ± 5.7
	NPI	6	13	1211 ± 1979	57 ± 36	13 ± 9	23.7 ± 21.7	8.4 ± 13.1

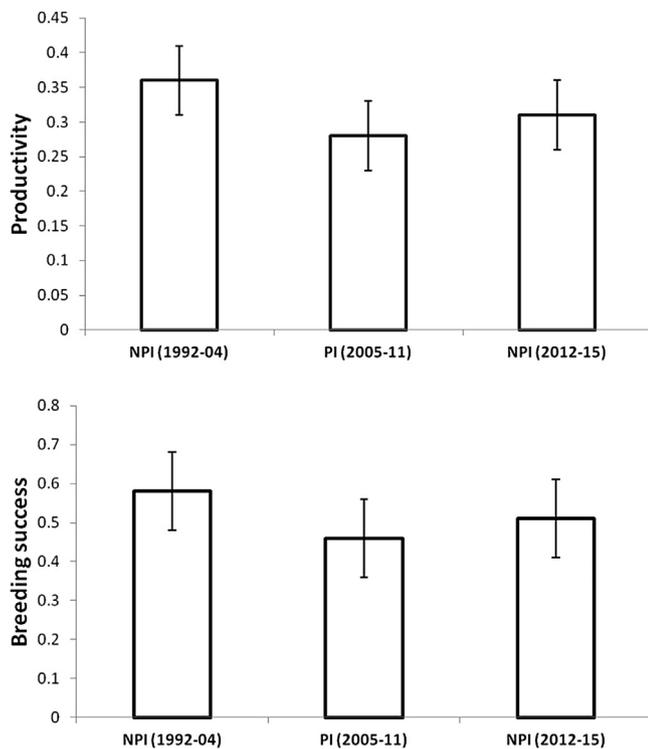


Fig. 2. Differences in productivity and breeding success of the studied bearded vulture population (range 15–44 territories/year, see details in Methods) in the policy periods (PI: Policy-Implementation Period; NPI: Non-Policy Implementation Period).

Table 2

Spatial and temporal distribution of the (expressed in megacalories) needed and available energetic resources for the breeding bearded vulture population in the eastern Pyrenees according to the two policy implementation periods (PI: Policy-Implementation Period; NPI: Non-Policy-Implementation Period). Area refers to the regions of Catalonia with the number of breeding pairs present in brackets (see Margalida and Colomer, 2012). The Breeding period was considered as October–May and the Non-breeding period as June–September (see Material and Methods). Data do not include food provided at Supplementary Feeding Sites.

Area	Necessary Non-breeding	Available Non-breeding		Necessary Breeding	Available Breeding	
		NPI	PI		NPI	PI
VA (2)	22.4	1276.2	1243.0	51.2	941.6	874.4
AR (6)	67.2	344	212.8	153.6	453.4	308.8
PJ (9)	100.8	1251.4	851.8	230.4	1904.8	1147.5
PS (8)	89.6	1090.7	873.6	204.8	1076.2	803.6
AU (7)	78.4	836.3	589.8	179.2	1276	784.3
C (0)	0	272.6	203.8	0	372.3	260.5
R (1)	11.2	710.2	570.7	25.6	826.1	631.5
B (1)	11.2	1011.0	608.3	25.6	1935.5	1195.8
S (1)	11.2	904.5	472.2	25.6	1823.0	1030.7
N (2)	22.4	595.7	253.4	51.2	1290.7	670.4

3.5. Influence of supplementary feeding sites

In non-territorial individuals, no differences were found in the use of SFS in the NPI and PI periods at 0.5 km (Wicoxon test, $z = -0.07$, $P = 0.94$), 1 km ($z = -0.78$, $P = 0.43$) or 5 km ($z = -0.99$, $P = 0.32$), or in relation to the number of SFS situated inside UD kernels at K90 ($z = -1.33$, $P = 0.18$), K50 ($z = -1.20$, $P = 0.23$) or K20 ($z = -0.81$, $P = 0.42$) (Table 3, Figs. 3 and 4). The same result was obtained for territorial individuals: 0.5 km ($z = -0.56$, $P = 0.58$), 1 km ($z = -0.71$, $P = 0.48$) and 5 km ($z = -0.07$, $P = 0.95$) and in relation to the space use at K90 ($z = -0.57$, $P = 0.57$) and K50 ($z = -1.58$, $P = 0.11$) (Figs. 3 and 4).

Table 3

Differences in number of supplementary feeding sites (SFS) inside the utilization density kernel of 20%, 50% and 90% (K20, K50 and K90 respectively) and percentage of locations at 0.5 km, 1 km and 5 km from bearded vulture SFS. Data for territorial and non-territorial birds are given in terms of the PI and NPI periods.

	0.5 km	1 km	5 km	K20	K50	K90
Non-territorial						
NPI	1.78%	3.17%	29.31%	2.32	6.31	21.42
PI	2.01%	3.76%	29.61%	2.88	8.06	22.15
Territorial						
NPI	2.74%	5.21%	53.56%	0.00	0.00	0.55
PI	2.37%	7.01%	78.06%	0.00	0.25	0.83

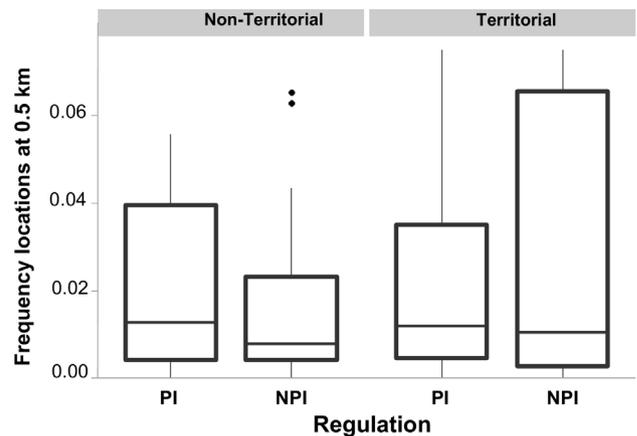
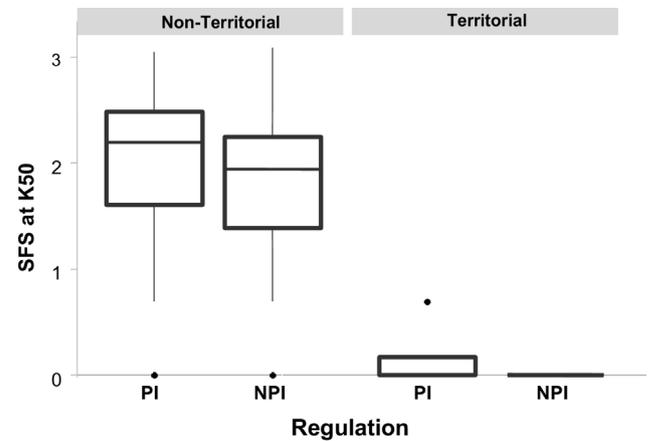


Fig. 3. Comparisons of number of supplementary feeding sites (SFS) inside UD kernel 50% (K50) and frequency of locations at 0.5 km of a SFS between policy periods (PI: Policy-Implementation Period; NPI: Non-Policy-Implementation Period) and territorial status (NT: non-territorial; T: territorial).

4. Discussion

Our findings show no differences between annual home range sizes, daily movements and/or the time used to search for food either before, during or after the imposition of health regulations. In addition, no differences between periods were found in the use of SFS. The analysis of food resources available indicates that the absence of differences in home ranges, movement parameters, and the similar use of SFS in different regulatory periods could be explained by the high availability of trophic resources in the Pyrenees. Accordingly, our results suggest that diet plasticity and habitat quality compensate for the sudden effects of food shortages and so question the true usefulness of SFS for bearded vultures in buffering a quantitative food deficit.

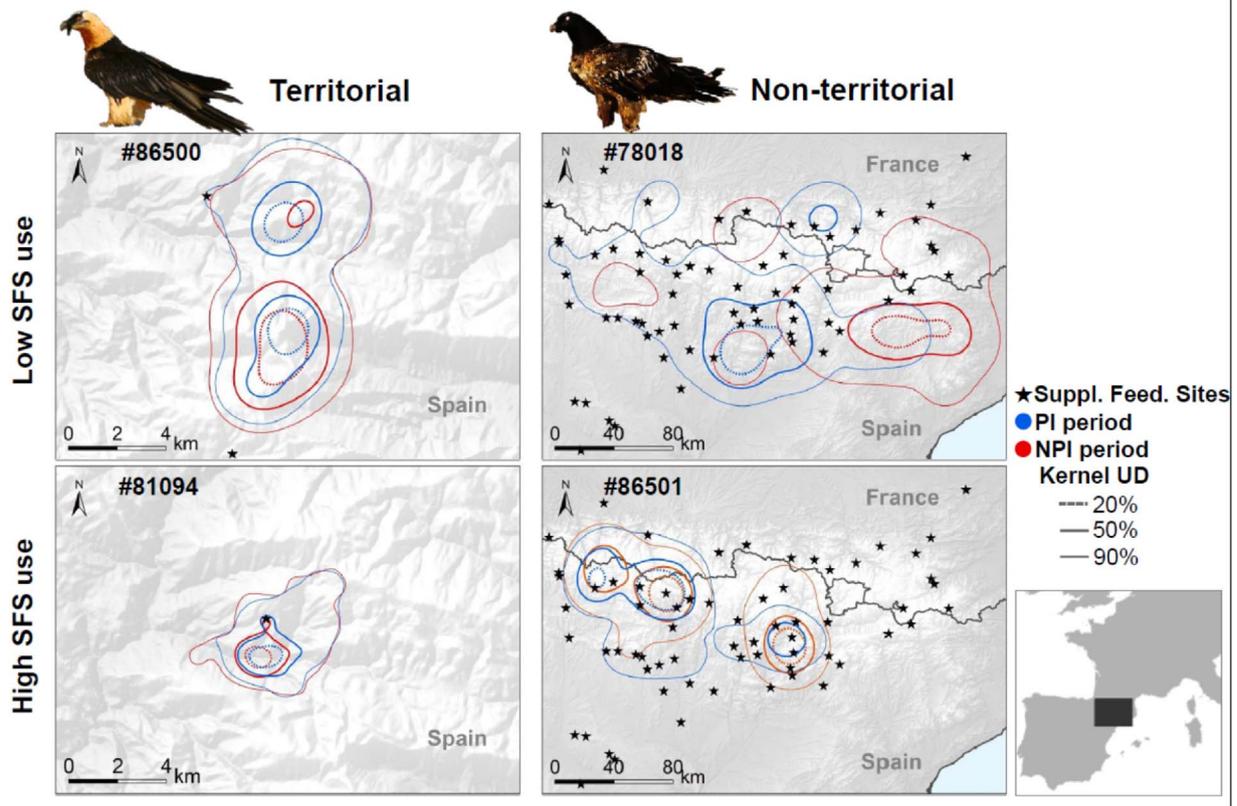


Fig. 4. Comparison of home range estimators (UD kernel K20, K50 and K90) between four bearded vultures (two territorial and two non-territorial) according to policy periods (PI: Policy-Implementation Period; NPI: Non-Policy-Implementation Period). Individuals for each territorial status group were selected according to their use of supplementary feeding sites SFS; one with low use of SFS (at least one policy period with number of SFS inside K50 = 0) and other with higher use of SFS (SFS inside K50 > 0).

4.1. Effects of food shortages on bearded vulture movements

Our findings reject hypothesis 1 and suggest that the food shortages caused by health policies did not substantially affect either foraging behaviour or breeding output in bearded vultures. A possible explanation is that, although the obligate recovery of carcasses provoked a reduction by 80% of food availability (Cortés-Avizanda et al., 2010; Margalida et al., 2014), the presence of carrion during this period in remote areas was still regular and partially buffered the effects of the health-policy restrictions. This finding was confirmed by a comparison of the animal biomass available in the study area and the energetic requirements of the breeding population. Our results suggest that the Pyrenees is a high-quality habitat due to the important populations of wild ungulates that provide an important food resource for both breeding and floater populations (Margalida and Colomer, 2012). Accordingly, food availability in the Pyrenees – independently of food shortages and the biomass provided by the SFS – is substantially higher than the food required by the breeding bearded vulture population. Although this assessment of food availability was carried out in the eastern Pyrenees, the ecological characteristics and agro-grazing systems practiced in other parts of the Pyrenees are similar and so our results can be extrapolated to other parts of these mountains (e.g. Gortázar et al., 2000), thereby enabling us to discuss the relative importance of SFS and their management.

Under a scenario of food shortages, the most aggressive and abundant members of the European avian scavenger guild (i.e. griffon vultures *Gyps fulvus*) can competitively displace other species and monopolize food resources (Cortés-Avizanda et al., 2010; Moreno-Opo et al., 2015). This was shown by a resource partitioning study of the supplementary feeding sites used by facultative and obligate avian scavengers (Moreno-Opo et al., 2016). Food characteristics, morpho-

logical traits and landscape variables seem to explain differences in species' use of these sites and griffon vultures were found to be the commonest species at experimentally provided carrion (Cortés-Avizanda et al., 2010; Moreno-Opo et al., 2015). However, other obligate vulture species may be less affected by sudden changes in food availability (Margalida and Colomer, 2012). For instance, during PI obligate scavengers such as griffon vultures modified their feeding habits as a result of the sudden shift in food availability (Donázar et al., 2010), while species with diet plasticity such as the Egyptian vulture *Neophron percnopterus* maintained their diet spectrum regardless of changes in health policies (Donázar et al., 2010). Thus, it has been suggested that SFS play an important role in compensating for quantitative deficits in food availability buffering the negative effects of food shortages on demographic parameters (Oro et al., 2008; Margalida et al., 2014).

4.2. Can SFS modify spatial ecology of bearded vultures?

According to optimal foraging theory, individuals should try to maximize net energetic gain by increasing energy intake rate and reducing searching or handling costs (Emlen, 1966; Charnov, 1976; Brown 1988; Van Gils et al., 2015). Thus, SFS as sites with high food availability should be preferentially selected to reduce search time or home range and increase food consumption (Monsarrat et al., 2013). However, in contrast to this prediction, our results regarding the use of SFS suggest that both territorial and non-territorial individuals used the SFS in a similar way during the PI and NPI periods. This could be explained by the fact that the amount of available natural food is substantially higher than the amount needed to cover the energetic requirements of the breeding population. It is important to note that resource consumption by the floater population was not estimated in

this assessment. Because our estimate is conservative and only considers domestic and wild ungulates but no other alternatives present in this species' diet spectrum (see Margalida et al., 2009), we can speculate that natural food resources continue to be abundant enough to feed the overall bearded vulture population in the Pyrenees (breeding and non-breeding) given that their availability is 10-times greater than the energetic requirements needed for the breeding population. Thus, our findings suggest that, although predictable food sources can be frequently consumed and are useful for increasing pre-adult survival and/or breeding success in vultures (Oro et al., 2008; Garcia-Heras et al., 2013; López-López et al., 2014; Margalida et al., 2014), they do not seem to be that important for territorial individuals. This coincides with the home ranges of bearded vultures in which intensive core areas of K20 and K50 do not seem to be substantially influenced by the presence of SFS (see also Margalida et al., 2016). Thus, if food resources are sufficient in the Pyrenees to cover the energetic requirements of the breeding and non-breeding population, and given the knowledge of their detrimental effects on fecundity (Carrete et al., 2006a) and other additional associated economic and environmental costs (Oro et al., 2013; Fielding et al., 2014; Cortés-Avizanda et al., 2016), the usefulness of the SFS for this species has to be called into question. Territorial bearded vulture adults moved on average 24 km per day, although breeding individuals moved an average maximum distance per day of 8 km within home ranges of about 60 km² (Margalida et al., 2016). This implies that breeding bearded vultures seem to obtain their energetic resources in a smaller area than other obligate avian scavengers (Moreno-Opo et al., 2010; Kane et al., 2016) and even bearded vultures in South Africa (Kruger et al., 2014). Given a diet based mainly on wild and domestic ungulates (mean 66%, range 47.5–78.1%, Margalida et al., 2009) and the fact that food remains remain in good condition for several weeks (Houston and Copley, 1994), we can affirm that quantitatively (Table 2) bearded vultures in the Pyrenees have enough food resources (Margalida and Colomer, 2012). This assertion is also supported by the forecasted population trend under scenarios of food shortages in which Egyptian and bearded vultures are the species least likely to be affected by changes in habitat quality (i.e. food available) caused by novel sanitary policies (Margalida and Colomer, 2012).

4.3. Influence of food shortages on breeding output

Food shortages could affect breeding output if food quality diminishes. For example, in bearded vultures, meat remains during the first weeks of chicks' lives seem to be important for breeding success (Margalida et al., 2009). Our results indicate that although minimal values were obtained during PI, no differences were found in breeding parameters, which suggests that, apparently, food shortages and the potential changes in dietary spectrum are not the main factor limiting reproduction. Specific supplementary feeding programs to increase breeding output failed to increase breeding success and similar values were obtained in territories with supplementary feeding and those with no supplementary feeding (Margalida et al., 2017). In addition, the breeding output of this population seems regulated by density-dependent mechanisms (Carrete et al., 2006b). However, supplementary feeding can be a useful tool to reduce illegal poisoning and declines in demographic parameters as survival (Gilbert et al., 2007; Oro et al., 2008). Additional variables affecting breeding output are related to the increase in polyandrous formations that increase reproduction costs (Carrete et al., 2006b), human disturbance (Arroyo and Razin, 2006), adult mortality due to illegal poisoning (Margalida et al., 2008; Margalida et al., 2012; Berny et al., 2015; Mateo-Tomás et al., 2012; Ogada et al., 2015) and lead poisoning (Hernández and Margalida, 2009). Thus, breeding output is affected by several factors, thereby making it difficult to disentangle the main factors that influence reproduction.

Another characteristic of bearded vulture ecology is their specialized diet that reduces competition with heterospecifics (Moreno-Opo

et al., 2015). Thus, under a scenario of food shortages, the diet plasticity of this species can allow individuals to adapt their foraging strategies without modifying their use of space. This was shown to be the case in the Egyptian vulture, a species with a similar dietary breadth. Donazar et al. (2010) identified dietary shifts in griffon vultures but not in Egyptian vultures, the latter exploiting the same prey and in similar proportions in the same study area over a period of 20 years. According to the alternative prey hypothesis (Angelstam et al., 1984; Pöysä et al., 2016), individuals could synchronize fluctuations in their main and alternative prey groups as generalist predators do (Lourenço et al., 2015). This is plausible, although other environmental factors give rise to the very high dietary variability of opportunistic vultures (Costillo et al., 2007), thereby masking the effects of closing the feeding sites.

4.4. Conservation implications

Our results suggest that food shortages in the Pyrenees triggered by new sanitary legislation did not affect substantially foraging movements of bearded vultures. Thus, current resource distribution and temporal availability of food are not key drivers of the use of space by bearded vultures. If we assume that, quantitatively, food resources are abundant and that the new and more flexible health regulations will facilitate the presence of carrion resources in ecosystems (Morales-Reyes et al., 2017), the network of SFS should be revised. A good example are the recently established protected areas for feeding scavengers (PAFs) in Spain, which provide food from livestock in a more natural way and so reduce the over-predictable nature of SFS (Morales-Reyes et al., 2017). Thus, future studies should assess the true role of SFS as means of optimizing management and conservation decisions.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2017.04.048>.

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