Short communication

Long-term relationship between diet breadth and breeding success in a declining population of Egyptian Vultures Neophron percnopterus

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Between 2000 and 2009 we studied the diet and breed-
ing success of Egyptian Vultures Neophron percnopterus
in southern Spain. Wild species accounted for 74.9% of
prey items (n = 1071) with a predominance of mammals
(62.3%), followed by birds (20.8%) and reptiles
(13.1%). Spatially, the diet was highly varied and not
restricted to carcasses of livestock; wild Rabbits Oryctola-
gus cuniculus accounted for 54% of the overall remains.
The spatial variability may reflect regional and local dis-
parity in the availability of main prey. The temporal rela-
tionship between variation in trophic diversity and
Vulture nesting productivity (both values showing a
long-term decrease) might suggest a causal link between
variation in diet and reproductive output. We hypothe-
size that high turnover rates could explain productivity
variation as a consequence of the recruitment of less
experienced individuals to the breeding population. This
could in turn generate covariation between diet and
reproductive output.

Keywords: breeding output, dietary breadth, for-
aging efficiency, population dynamics, Spain.

Long-term studies of diet allow researchers to test spe-
cific hypotheses about the fecundity consequences of
resource acquisition. Identifying the causes of variation
in breeding productivity and their relationship to diet is
a key achievement in successful population management
(Marshall et al. 2002, Katzner et al. 2005, Margalida
et al. 2009, Whitfield et al. 2009) because it enables
improvement of conservation measures (Katzner et al.
2005, Arroyo & García 2006, Oro et al. 2008, Margalida
et al. 2009, Whitfield et al. 2009), and prediction of the
population effects of such interventions (Donázar et al.
2010, Margalida et al. 2011).

According to ecological theory, birds may need to use
a greater variety of food resources when the abundance of
their preferred prey declines (Bell & Ford 1990). Thus,
diet breadth should expand when the preferred resources
are scarce and a negative relationship between diet diver-
sity and breeding performance would be expected (Wat-
son 1997, Elmhagen et al. 2000). However, a positive
relationship between diet specificity and breeding pro-
ductivity may occur when there is marked spatial and
temporal variation in the availability of preferred
resources (Korpimäki 1992, Arroyo & García 2006).

Here, we use long-term monitoring of a declining
population of Egyptian Vultures Neophron percnopterus
in southern Spain to examine long-term variability in its
breeding parameters and diet. Despite the urgent need
for well-informed conservation planning, studies on the
trophic requirements of this species are scarce and most
of them date back over 20 years (Donázar 1993, but see
Donázar et al. 2010). Our specific objectives were (1) to
describe diet composition and its variation in relation to
local environmental variability and (2) to examine the
association between breeding productivity and diet
breadth. Based on our results, we suggest that high turn-
over rates derived from unusual human-induced mortal-
ity are driving covariation between diet specificity and
demographic performance.

METHODS

Study area

The study was carried out in Andalusia (southern Spain;
Fig. 1) between 2000 and 2009. During this period, the
number of occupied territories declined from 33 to 23 (a

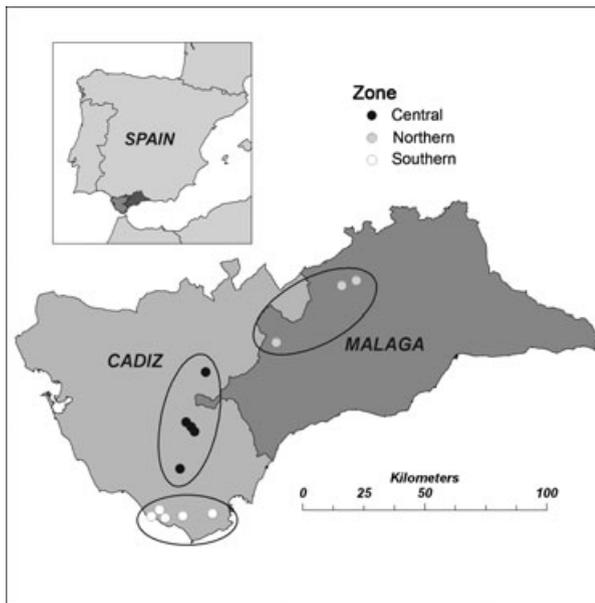*Corresponding author.
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Figure 1. Study area and location of the Egyptian Vulture breeding territories according to the three zones considered.

3.4% annual decline). The study area is characterized by abundant domestic livestock and the presence of six supplementary feeding stations (Benítez et al. 2009). The study area was sub-divided into three main zones (Fig. 1): the Northern zone (65 000 km^2), with low human population density, with nests between 500 and 1000 m asl; the Central zone (78 000 km^2), again little populated and with nests between 100 and 500 m asl; and the Southern zone (33 000 km^2), well populated and with nests located from sea level to 500 m asl.

Surveys and prey collection

Productivity (number of chicks fledged divided by the number of pairs checked) and dietary habits were studied in a sample of 13 territories (i.e. 57% of the current population). We collected prey remains from nests during June–July coinciding with the ringing of the chicks. The territory was the sampling unit. Only territories with a minimum sample size of 20 prey items per year were considered (see Moleón et al. 2009, Whitfield et al. 2009). Under this criterion and after pooling data across years, there was no correlation between the number of prey items collected and diet breadth ($r_s = $)0.30, $P > 0.05$, $n = 13$) or between the cumulative number of prey items collected for the whole population in a year and the annual diet breadth ($r_s = $)0.09, $P > 0.05$). Consequently, to compare diet breadth between regions, we pooled prey items across years for each territory. Mate loss was monitored by documenting replacements through rings and plumage characteristics.

Statistical analyses

We used correspondence analysis to assess differences in dietary variation across the three zones: Northern ($n = 3$ territories), Central ($n = 5$) and Southern ($n = 5$). We classified prey items into six main taxonomic categories: birds, amphibians, reptiles, fish, mammals and 'other prey' (e.g. carrion, eggs, pellets). We calculated the dietary specialization in each territory with the Levins index of diet breadth using the 62 prey species that we could identify accurately (Levins 1968; Supporting Information Table S1). The Levins index was calculated for each territory as $B \frac{1}{4} 1 = \sum_{i \frac{1}{4} 1}^{n} p_i^2$; where p_i is the proportion of prey in different categories. To compare diet breadth samples with different numbers of prey categories, we calculated the standardized food niche breadth following Colwell and Futuyma (1971): $B_{sta} = (B_{obs}$) $B_{min}) / (B_{max}$) $B_{min})$, where B_{min} is the minimum niche breadth possible ($n = 1$), B_{obs} is the number of prey types observed, and $B_{max} = N$. This index ranged from 0 to 1 with higher values corresponding to a broader diet.

One-way ANOVA and Scheffé post-hoc tests were used to examine differences in the average percentage (log-transformed) of the three most important taxonomic categories considered (mammals, birds and reptiles). We used Spearman's rank correlation coefficient and regression analyses to assess the relationship between different covariates and chi-square tests to test for spatial and temporal variation in the frequency of individual turnover in vulture territories.

Generalized linear mixed models (GLMMs, McCullagh & Searle 2000) implemented in R 2.1.1 (R Development Core Team, http://www.r-project.org) were used to test how territory-specific breeding productivity varied with the Levins index and year as covariates. Territory identity was fitted as a random factor. GLMMs permit the use of suitable error distributions and some of the limitations of conventional regression models were avoided by using the Poisson distribution as an error function. We built multivariate models using a backward removal procedure and selected the model with the lowest Akaike information criterion (AIC). Statistical significance was set at $a = 0.05$ for all analyses and all values are presented as means ± sd.

RESULTS

Diet spectrum

Between 2000 and 2009 we identified 1071 prey items from 13 Egyptian Vulture territories (Table 1, Table S1). Wild mammals, birds and reptiles accounted for 74.9% of the diet. Wild Rabbits Oryctolagus cuniculus were the dominant prey (mean percentage occurrence = 53.98 ± 14.67%; range 36.7–83.1%) among the 18 mammal species identified. Among bird prey (32 species

Table 1. Occurrence (%) of main prey categories in the diet of breeding Egyptian Vultures in the three studied zones of southern Spain. Ranges in parentheses.

Prey category	Northern zone (n = 3 territories)	Central zone (n = 5 territories)	Southern zone (n = 5 territories)	Total (n = 13 territories)
Fish	1.4 (0–4.1)	1.1 (0–5.6)	0.4 (0–2.3)	0.9 (0–5.6)
Amphibians	0.6 (0–1.9)	0	3.2 (0–7.1)	1.4 (0–7.1)
Reptiles	5.2 (1.9–10.2)	5.5 (0–12.3)	25.4 (9.9–48.1)	13.1 (0–48.1)
Birds	22.2 (14.3–31.4)	16.1 (12.2–25.9)	24.7 (14.9–39.3)	20.8 (12.2–39.3)
Mammals	67.2 (58.8–73.3)	76.4 (64.8–85.7)	45.4 (25.3–64.9)	62.3 (25.3–85.7)
Other Prey	3.4 (2–5.9)	0.9 (0–2.1)	0.9 (0–2)	1.5 (0–5.9)
n*	186	394	491	1071

*Cumulative number of identified prey items.

identified), doves Columba spp. dominated (3.45 ± 2.5%; range 0–8.7%), followed by domestic hens (3.45 ± 2.9%; range 0–10.7%, n = 13). Finally, three reptile species were identified, with Lacerta lepida being the most frequent item (7.6 ± 10.88%; range 0–39.2%).

Spatial and inter-territorial differences in diet

Factor I of the correspondence analysis explained 62% of the variance separating birds, amphibians, fish and reptiles from mammals and other prey (Fig. 2). Factor II explained 19% of the variance and separated mammals
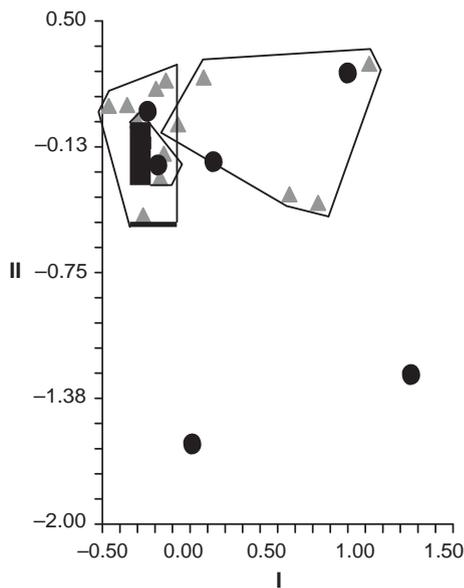
Figure 2. Variation in the diet of breeding Egyptian Vultures in southern Spain. Plot of factors I and II of the correspondence analyses: areas of each zone delimited by minimum polygon: N: Northern; C: Central; S: Southern. Prey categories are shown by black circles and territories by grey triangles.

and reptiles from the other categories. Mammals was the most important category in the three zones, although their importance decreased in the Southern zone ($F_{2,12} = 7.10$, P = 0.012) where reptiles were dominant ($F_{2,12} = 6.44$, P = 0.015).

Spatial and temporal differences in productivity and their relationship to diet diversity and mate loss

There were no differences in productivity among zones (Northern: 0.61 ± 0.22 chicks fledged/pair/year, n = 3 territories; Central: 0.88 ± 0.17, n = 5; Southern: 0.92 ± 0.17, n = 5; $F_{2,12} = 0.68$, P = 0.53). However, mean territory-level diet breadth varied significantly between zones (Northern: 7.55 ± 1.22; Central: 3.57 ± 0.94; Southern: 8.09 ± 0.94, $F_{2,12} = 6.50$, P = 0.015). Mate losses also varied spatially, with more replacements taking place in the Central zone (v_2^2 ¼ 13:51; P = 0.0012). The annual trend in the frequency of mate losses was significant and positive ($r_s = 0.547$, P = 0.014, n = 9). Over time, mean annual productivity declined over the study period ($r_s = $⟩0.74, P = 0.002, n = 10, Fig. 3). Annual trophic diversity co-varied positively with productivity, both values declining over time ($r_s = 0.597$, P < 0.05). At the territory level,
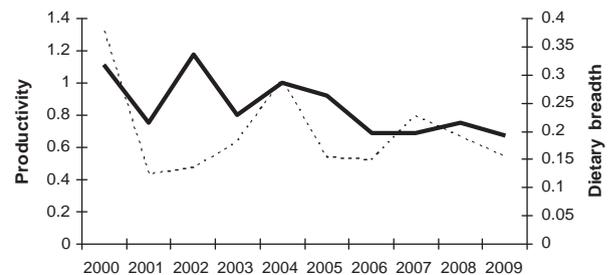
Figure 3. Variations in productivity (continuous line) and dietary breadth (standardized food niche breadth, dashed line) during 2000–2009.

productivity correlated positively with dietary breadth (GLMM $F = 1.32$, df = 133, $P < 0.001$). A year effect was also marginally significant ($F = $ ⟩0.063, df = 133, $P = 0.068$).

DISCUSSION

Rabbits, reptiles and other small- to medium-sized vertebrates dominated the diet of breeding Egyptian Vultures in southern Spain. Livestock formed a relatively minor proportion of the diet despite its abundance in the study area and its use in supplying supplementary feeding stations (Benítez et al. 2009). Thus, the effects of food shortages on breeding and population dynamics of Egyptian Vultures as a consequence of sanitary legislation restrictions (Donázar et al. 2009, Margalida et al. 2010) are probably less detrimental than for other avian scavengers. Although it may underestimate the importance of large mammals (Sánchez-Zapata et al. 2010), the analysis of prey remains has been used to assess relationships between diet and breeding performance in other facultative scavengers (Whitfield et al. 2009) and should be valid for comparative purposes within populations because it seems reasonable to assume that the same detection biases should equally affect all territories. Thus, the observed variability between zones of our study area probably reflects differential availability of resources and highlights Egyptian Vultures as opportunistic scavengers.

We found a significant and positive relationship between breeding productivity and diet diversity. Similar results were found for generalist predators and facultative scavengers such as Golden Eagles Aquila chrysaetos (Whitfield et al. 2009) and also for obligate scavengers such as Bearded Vultures Gypaetus barbatus (Margalida et al. 2009). We concur with Whitfield et al. (2009) that diet specificity could be a consequence of variations in prey availability, rather than a substantial cause of variation in reproductive success. In addition, in our study area, population and productivity have been declining for the last 20 years, in parallel with diet breadth; however, factors other than prey availability may be responsible for these trends.

During recent decades, Iberian Egyptian Vultures have been subject to high mortality rates due to illegal poisoning (Carrete et al. 2007, Hernández & Margalida 2009) and, more recently, collisions with wind turbines (Carrete et al. 2009). We suggest that such strong drivers of mortality may not only be responsible for population declines but may also indirectly promote variations in productivity and diet composition mediated by the artificially inflated recruitment of less experienced individuals to the breeding population (Carrete et al. 2006), as has been suggested for other raptor species (Pedrini & Sergio 2001, Margalida et al. 2008). In fact, most mate losses observed in our study area took place in the Central zone, which was the area with the lowest diet breadth. In addition, their frequency increased with time. Foraging efficiency mediated by age and breeding experience would thus add a new piece to the puzzle of the diet specificity (Watson 1997, Katzner et al. 2005) and prey availability (Whitfield et al. 2009) hypotheses.

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SUPPORTING INFORMATION

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

Table S1. Occurrence (n) of prey items identified in the diet of breeding Egyptian Vultures in the three studied zones of southern Spain.

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