Too much is bad: increasing numbers of livestock and conspecifics reduce body mass in an avian scavenger

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Abstract. Individual traits such as body mass can serve as early warning signals of changes in the fitness prospects of animal populations facing environmental impacts. Here, taking advantage of a 19-yr monitoring, we assessed how individual, population, and environmental factors modulate long-term changes in the body mass of Canarian Egyptian vultures. Individual vulture body mass increased when primary productivity was highly variable, but decreased in years with a high abundance of livestock. We hypothesized that carcasses of wild animals, a natural food resource that can be essential for avian scavengers, could be more abundant in periods of weather instability but depleted when high livestock numbers lead to overgrazing. In addition, increasing vulture population numbers also negatively affect body mass suggesting density-dependent competition for food. Interestingly, the relative strength of individual, population and resource availability factors on body mass changed with age and territorial status, a pattern presumably shaped by differences in competitive abilities and/or age-dependent environmental knowledge and foraging skills. Our study supports that individual plastic traits may be extremely reliable tools to better understand the response of secondary consumers to current and future natural and human-induced environmental changes.

Key words: body mass; density dependence; grazing; individual traits; NDVI; vulture.

INTRODUCTION

The complex relationships between climate, vegetation, and the dynamics of animal populations have generated great interest in ecological research (Simard et al. 2010), with a growing focus on individual indicators as early warning signals of changes in demographic parameters of animal populations facing environmental impacts (Clements and Ozgul 2016). Among these indicators, body mass has been widely used as an indicator of animal fitness, mainly of primary consumers (Pettorelli et al. 2007, Couturier et al. 2009, Rioux Paquette et al. 2014, Duncan et al. 2015). However, there is comparatively much less information regarding secondary consumers, although primary productivity is known to influence population dynamics of different groups, from arthropods to large vertebrates (Buschke et al. 2011, Deichmann et al. 2012, Pierce et al. 2012). In addition, research on body condition (i.e., body mass) of secondary consumers and its relationship to ecosystem-

level processes can improve our understanding of the effects of human-induced environmental change on food webs (Coulson et al. 2011).

Anthropogenic modifications of primary productivity at ecosystem-level, notably through agriculture and livestock farming, can aggravate the consequences of climatic impacts on wild animals (Darkoh 2003, Beschta et al. 2013), also disrupting species interactions across trophic levels (Rosenblatt 2018). The negative consequences of livestock expansion (Ellis 2011) are exacerbated in oceanic islands, where the introduction of domestic ungulates has also led to high extinction rates of native fauna and flora (Coblentz 1978, Chapuis et al. 1994). However, in some island systems, introduced ungulates have been deeply rooted in their ecosystems for millennia (Zeder 2008), even becoming keystone species in the food webs when native herbivores became extinct (Hunter 1992, Gangoso et al. 2006).

Farming practices have favored the establishment of a win-win relationship between humans and avian scavengers that feed on livestock carcasses (O'Neal 2015), also promoting the occurrence of traditionally abundant vulture populations in different archipelagoes, from Macaronesia and the Mediterranean (Donázar et al. 2005) to the Indian Ocean (Gangoso et al. 2013). In

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these closed ecological scenarios, cascading climate-driven effects across different trophic levels and intraspecific competition for resources (Carrete et al. 2006, Fernández-Bellón et al. 2016, Heuck et al. 2017) may determine fluctuations of vulture populations and individual body condition. However, we still do not know the relative importance of climate-driven biotic interactions and human-induced modifications of the ecosystems in relation to individual- and population-level factors in these processes.

Here, we test how changes in primary productivity, trophic resources and density-dependent factors may modulate changes in individual body mass of an insular scavenger, taking advantage of a unique long-term monitoring (19 yr) program of the endemic Canarian Egyptian vulture (*Neophron percnopterus majorensis*). We predict (Table 1) that vultures will gain body mass in periods of high and/or very variable primary productivity, because this would in turn increase the availability of natural food resources (carcasses of wild primary consumers). We also expect that vulture body mass will increase in periods of high availability of livestock carcasses. In contrast, vulture body mass will decrease in parallel with the overall population increase due to density-dependent factors. Because bird sex and age determine foraging strategies in this population, with females and immature individuals relying more on predictable resources (García-Heras et al. 2013, van Overveld et al. 2018), we predict that body mass of females and immature vultures will be more affected by livestock abundance and intraspecific competition than by changes in landscape-scale primary productivity. Disentangling the complex relationships among ecosystem-level factors, population structure, and individual characteristics that determine animal body condition will help define management strategies for this and other ecologically similar endangered populations.

METHODS

Field procedures

The population of Canarian Egyptian vultures was intensively monitored in Fuerteventura Island from 1999 to 2017. Complete censuses were carried out annually by means of intensive surveys of all those areas susceptible of holding territorial vultures. In addition, all fledglings were ringed and several adult and immature birds were captured and ringed each year. Fledglings were captured at nests whereas immature and adult birds were captured in baited places using cannon nets. Thus, in 2017, of 311 individuals (148 breeders and 163 non-breeders) 89.7% were banded (121 and 158 birds respectively). During the whole study period, a total of 394 individuals were captured, of which 123 were recaptured. Capture effort was intensified in 2015 ($n = 77$) aimed at tagging individuals with GPS trackers. The highest frequency of captures took place in May–June ($n = 225$)

and September–October ($n = 107$), while no captures were made in July, August, or December (Appendix S1; Fig. S2). Accordingly, these captures were distributed into two categories: breeding and non-breeding Season (February–June and September–January, respectively).

All birds were weighed using a Pesola scale (± 5 g). Only a very small number of birds used to have full crops during handling (two of 116 individuals, 1.7%, examined between 2013 and 2015). In fact, Egyptian vultures usually vomit after being captured, as other scavengers do when facing predators (O’Neal 2015), so this circumstance would not affect our results. Wing chord length (*Wing*) was measured using a 100-cm rule to the nearest mm. Wing chord length is a reliable and widely used proxy for body size (Ashton 2002, Van Buskirk et al. 2010, Rioux Paquette et al. 2014). The age of the individuals captured was known either because they were ringed as fledglings or because at the time of first capture they were immature with a distinctive transition plumage. Following (Forsman 2007), we distinguished five plumages between fledgling and adult age. Adult birds were those having acquired the fifth plumage (≥ 6 yr old). We discarded recently fledged young whose condition mainly depends on their recent development history. Data on the annual breeding vulture population size (Population) were considered as an estimator of intraspecific competence for food resources (van Overveld et al. 2018). See Appendix S1 for details on the study area and species.

Primary productivity and food resource availability

We used the Normalized Difference Vegetation Index (NDVI) derived from satellite sensors as a proxy for vegetation productivity and biomass (Pettorelli et al. 2005, De La Maza et al. 2009) and, consequently, for availability of wild primary consumers to vultures. We used a gridded daily NDVI data set from the NOAA Climate Data Record (CDR) of Advanced Very High Resolution Radiometer (AVHRR; Vermote et al. 2014). The NDVI products are computed from an atmospherically corrected bidirectional surface reflectance that has been masked for water, clouds, heavy aerosols, and cloud shadows. Per-pixel quality assessment metadata were used to check the product performance to measure the NDVI throughout the years. We first calculated mean monthly values of NDVI for the study period (Appendix S2). From this, we estimated five different variables: primary productivity in each year (annual NDVI), in the month of the vulture capture (NDVI-month), and monthly average NDVI of the two and six months before the capture (NDVI2month and NDVI6-month, respectively), as well as the coefficient of variation of the mean values in these periods (CVNDVI2month and CVNDVI6month). We used these different NDVI variables to evaluate the relative importance of NDVI average, seasonality and potential time-lag effects (Sloat et al. 2018).

TABLE 1. Hypotheses, variables, and predictions tested for long-term changes in body mass (BM) of individual Egyptian vultures of the Canary Islands.

Measure	Calculation/	Measurement	Prediction		Source
			Immature	Adults	
Individual characteristics					
Sex	male/female	molecular†	Females have higher BM because the existence of reversed sexual dimorphism.	Females have higher BM because the existence of reversed sexual dimorphism.	Donázar et al. (2002)
Age	yr	ring lecture, plumage features	Aged vultures (more experienced birds) present higher BM.	NA	Chastel et al. (1995)
Wing	mm	ruler	Large birds show higher BM than small birds.	Large birds show higher BM than small birds.	Rioux Paquette et al. (2014)
Spatial and temporal constraints					
Season	breeding (Feb–Jun); non-breeding (Aug–Jan)	fate of capture	Vultures have higher BM during the non-breeding than breeding season because they rely more on predictable resources and, in adults, lack of breeding constraints.	Vultures have higher BM during the non-breeding than breeding season because they rely more on predictable resources and, in adults, lack of breeding constraints.	Milenkaya et al. (2013), van Overveld et al. (2018)
Territory	yes/no	fieldwork	NA	Territorial individuals have less BM because of reproductive constraints.	Houston (1976)
Main food resources					
Livestock	annual census of number of ungulate heads	Canarian Government censuses‡; own data	BM increases in periods with more livestock because goat carcasses are the main food source for vultures.	BM increases in periods with more livestock because goat carcasses are the main food source for vultures.	Medina (1999), Gangoso et al. (2006)
Intraspecific competition (density dependence)					
Population	annual number of active territories	fieldwork	Larger population sizes enhance competition and result in decreases in BM.	Larger population sizes enhance competition and result in decreases in BM.	Fernández-Bellon et al. (2016)
Primary productivity and vegetation biomass					
NDVI	The NDVI is computed as $(\text{NIR} - \text{Red})/(\text{NIR} + \text{Red})$ where NIR and Red are the amount of near-infrared and red light, respectively, reflected by a surface and measured by satellite sensors.	average value of monthly values§	Absence or little effect on immature vultures because of dependence on livestock and feeding stations.	Positive effect on adult vultures because of dependence on more unpredictable wild carcasses.	van Overveld et al. (2018)
CVNDVI		coefficient of variation of average value of monthly values§	Higher CV would determine higher BM as insurance against resource fluctuation.	Higher CV would determine higher BM as insurance against resource fluctuation.	Wardle et al. (2012)

Note: NA, not applicable; NDVI, normalized difference vegetation index.

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‡http://www.gobiernodecanarias.org/istac/temas_estadisticos/sectorprimario/agricultura/ganaderia/

§https://data.noaa.gov/cgi-bin/iso?id=gov.noaa.ncdc:C00813_R.

Availability of livestock carcasses (Livestock) was estimated from livestock numbers assuming that an increase in domestic ungulates leads to an increase in the number of carcasses available for vultures (Fillios et al. 2010, Margalida and Colomer 2012). We obtained the annual number of goat and sheep held in farms on Fuerteventura from governmental databases up to 2014 and author data from 2015 to 2017 (see *Data Availability* and databases *available online*).⁵ Despite European sanitary regulations implemented in 2004–2005 (Donázar et al. 2009, Margalida and Colomer 2012, Margalida et al. 2014), carcass removal from farms has been only partially implemented in the study area: during 2015 we performed 94 interviews to farmers; 57 of them (61%) admitted that they left livestock carcasses near their exploitations. Because overgrazing may be an important factor affecting primary productivity (Pandey and Singh 1992, Gangoso et al. 2006), we analyzed how both livestock numbers and precipitation influenced annual NDVI. As expected (Sloat et al. 2018, Liang and Gornish 2019), primary productivity was positively affected by rainfall, while livestock numbers exerted a negative effect (see Appendix S2 for details).

Data analyses

We assessed variation in the Egyptian vultures' body mass (g) as a function of individual, population, and environmental characteristics (see data in Appendix S4). We split the database according to two broad age categories: immature (first–fourth plumage: up to fifth calendar year) and adult birds (fifth plumage: $\geq$ sixth calendar year). We performed separate linear mixed models (LMM) with identity link function for immatures and adults, where individual Body mass was included as the response variable. Explanatory variables (Table 1) described the period of capture (Season) and individual characteristics (Sex, Age, and Wing). Age was fitted only for immature birds. For adults, a previous analysis confronting Age and Body mass using only individuals with known age showed no correlation ($r_s = 0.149$, $P = 0.184$, $n = 81$). Consequently, in the final models for adult birds we included all the individuals over six years old even if their exact age was unknown. Wing accounts for potential variability associated with body size (Rioux Paquette et al. 2014). As these authors explain, although the use of body condition indices (e.g., regression residuals) is widespread, it has been suggested that body mass alone often outperforms condition indices as a measure of fat content in bird species. Consequently, they propose to use body mass as a proxy for condition, while including a size covariate (wing length in our case) to effectively correcting mass for size (see Rioux Paquette et al. 2014). The variable Territory, which describes whether the vultures were territorial breeders in the year of capture, was also included in

models for adult birds. In addition, we tested the effects of availability of food resources (Livestock and those variables related to NDVI) and density dependence (Population). Finally, because the study species presents reversed sexual dimorphism, with females being slightly larger (6.1%) than males (Appendix S4) and both sexes differ in foraging strategies (van Overveld et al. 2018), we included the two-way interactions between *Sex* and all other variables (Table 1). In all models, the variable Individual was included as a random term to account for repeated measurements of the same bird. All continuous variables were scaled prior to analyses. Models were fitted with all possible combinations of explanatory variables, except for pairs of variables with a Spearman's correlation coefficient higher than |0.5| to avoid collinearity (Graham 2003).

We used Akaike Information Criterion corrected for small sample sizes (AIC_c ; Sugiura 1978) for model selection. We considered as statistically equivalent those models with $\Delta AIC_c < 2.0$ and used model averaging to deal with model selection uncertainty (Burnham and Anderson 2002). We discarded models including uninformative parameters, namely those whose 85% confidence intervals overlapped with 0 (Arnold 2010). All analyses were carried out in R statistical software (R Core Team 2017) using the stats package for LM and confidence intervals, lme4 (Bates et al. 2014) for the LMM analysis, AICcmo-dav (Mazerolle 2019) for model ranking, and MuMIn (Barton 2017) for model averaging.

RESULTS

Individual variation in the Egyptian vultures' body mass depended on Sex, Wing, Age, and Season (Fig. 1). Strong variations in body mass across years during the study period were also apparent (Fig. 2). Only one model was retained for immature birds, whereas for adults we obtained five candidate models (Appendix S3). Final models (averaged models for adults) showed some common patterns for both age classes (Table 2, Fig. 3). Thus, Body mass was higher for females and for individuals with larger body size (Wing). However, the interaction between these two variables indicated that the effect of Wing on Body mass was strong for females and almost non-existent for males. We also found a negative effect of Livestock numbers and a positive effect of the CVNDVI6month on the body mass of both age groups (Fig. 3). With regard to other variables, however, immatures and adults showed divergent patterns. Immatures gained mass with Age and during the non-breeding Season, but seasonal effects were not apparent in adults. In addition, the number of conspecifics (Population) negatively affected the mass of adults, but not of immatures. Finally, within the adult fraction, territorial birds showed higher body mass than non-territorial individuals (Fig. 3).

DISCUSSION

We found that oscillations in the availability of food (livestock and natural prey) and vulture population

⁵ http://www.gobiernodecanarias.org/istac/temas_estadisticos/sectorprimario/agricultura/ganaderia/

FIG. 1. Variation in body mass (g) for immature (2–5 yr old) and adult (≥ 6 yr old), left and right columns, respectively. Variation is shown for male (white) and female (gray/black), from top to bottom, with respect to the territorial status (only adults), breeding season (B, breeding; Non-B, Non-breeding), age, and wing length. The line within boxes indicates the median, the edges of the boxes the first (Q1) and third (Q3) quartiles, and the whiskers extend 1.5 times the interquartile range. Photo credit: Manuel de la Riva.

density were key determinants explaining temporal changes in vultures' body mass. Importantly, the relative strength of individual, population and resource availability factors on body mass changed with life stage (i.e., immature vs. adults) and territorial status of adult birds, a pattern presumably shaped by differences in competitive abilities and/or age-dependent environmental knowledge and foraging skills (van Overveld et al. 2018). Even though this vulture population strongly depends

on livestock carcasses as their main food source, a negative relationship was unexpectedly found between numbers of goat/sheep and average body mass of both adults and immatures.

Environmental effects: NDVI and livestock

Rather than a direct link between vulture body mass and landscape-scale primary productivity (and

FIG. 2. Long-term changes in body mass of male (black points and line) and female (white points and gray line) Egyptian vultures captured across the study years (1998–2017). The upper panel shows data from immature birds (2–5 yr old), while the lower panel shows data from adults (≥ 6 yr old). The lines connect annual means. Photo credit: Manuel de la Riva.

presumably a higher density of primary consumers; Schaub et al. 2005), a strong positive relationship was found between body mass and natural oscillations of local vegetation (i.e., high coefficient of variation of NDVI). More specifically, broad oscillations of NDVI (reflecting periods with both high and low primary productivity) may lead to greater mortality rates of wild herbivores such as rabbits and rodents, but also birds, for instance, due to unexpected drops in food available to these animals (short periods of rainfall followed by droughts; see Soudijn and de Roos 2017). Consequently, we could hypothesize that high variance in NDVI would lead to an overall increase in the availability of natural carcasses of wild herbivores that are a common food resource in the diet of island and mainland populations of Egyptian vultures, especially during the breeding season (Medina 1999, Margalida et al. 2012; see *Data Availability*). Within this scenario, the gain of mass by vultures during such unstable environmental conditions would fit within the so-called “fat storage strategy” (Wardle et al. 2012, Gołowski et al. 2015), as has also been observed in

bird populations from arid islands where food and water availability is intermittent (Grant 1965). In addition, fat storage can provide a reservoir of carotenoids (Negro et al. 2001, Metzger and Bairlein 2011), which are known to be essential immune stimulant and antioxidant micronutrients for this and other scavenger species (Negro et al. 2002, Blanco et al. 2013).

The negative relationship between livestock numbers and body mass is, however, surprising. We expected that fat reserves would accumulate under conditions of food bonanza, allowing vultures to build up an insurance against potential future food shortage or alternatively, to increase their investment during highly demanding periods such as reproduction (Weber et al. 1998). However, it is possible that in periods of food abundance (when future food prospects are generally good), vultures may trade-off fat storage against the benefits of being more agile (Lima 1986). On the other hand, while agility may confer important benefits while hunting (e.g., raptors) or escaping from predators (e.g., songbirds; Stankowich and Blumstein 2005, Macleod et al. 2008), this may not be true for a species such as the Egyptian vulture. They have very few natural predators (i.e., no records of predated Egyptian vultures exist on the Canary islands) and typically travel and search for carrion using soaring flight with little energy expenditure (Ruxton and Houston 2004). Furthermore, even though livestock densities showed strong fluctuations (between 70,000 and 150,000 animals), given an annual livestock mortality rate of $\sim 10\%$, as in other areas with similar pastoral regimes (Margalida and Colomer 2012), this suggests that many carcasses have been available to vultures during the study period, even when livestock numbers reached minimum values. Hence, it is unclear why vultures would adaptively reduce their weight only in response to extreme high livestock densities, especially because the presence of many carcasses would allow vultures to reduce food searching efforts and flight activity.

As an alternative scenario, we therefore propose that an increase in cattle numbers and associated grazing pressure may have impacted vegetation structure and landscape-scale primary productivity (Liang and Gornish 2019), likely affecting other primary consumers on which vultures forage (Margalida et al. 2012). Indeed, in accordance with other studies (Sloat et al. 2018, Liang and Gornish 2019) we found that primary productivity was not only determined by precipitation (as would be expected), but also negatively affected by livestock numbers. Thus, our results would indicate that wild prey represents essential, but highly underestimated, resources, whose availability would affect vulture condition and fitness (Margalida et al. 2012). Wild prey may have also a qualitative importance linked to the fact that remains of small animals, including bones, provide essential micronutrients such as calcium (Reynolds and Perrins 2010) that are present to a much lesser extent in the soft tissues of ungulates (Houston 1978). It would deserve to

TABLE 2. Estimates and standard errors resulting from the top ranked model of body mass for immature (≤ 5 yr old) and from model averaging of selected models for adult birds (≥ 6 yr old).

Variable	Estimate	SE	7.5%	92.5%	RI
Immatures					
(Intercept)	2259.06	17.15	2234.3	2283.9	
Age	37.68	9.28	24.29	51.07	
CVNDVI6month	34.14	9.14	20.88	47.35	
Livestock	−30.48	9.89	−44.76	−16.17	
Season	143.05	19.04	115.59	170.53	
Sex	−76.21	20.8	−106.49	−46.1	
Sex $\times$ wing	−84.1	19.74	−112.57	−55.62	
Wing	112.91	16.86	88.4	137.43	
Adults					
(Intercept)	2419.79	26.32	2380.96	2457.85	
CVNDVI6month	47.04	12.44	29.35	65.43	1
Livestock	−31.78	21.66	−63.17	−9.72	0.84
Population	−25.26	23.06	−63.49	−8.68	0.69
Sex	−115.3	39.03	−170.71	−57.16	1
Sex $\times$ wing	−61.19	43.34	−127.12	−19.64	0.83
Territory	−46.91	35.05	−101.19	−13.78	0.82
Wing	108.96	21.99	76.23	140.88	1

Notes: See Table 1 for a full description of each explanatory variable. Confidence intervals (7.5–92.5%) of the estimates are also shown. RI shows the relative importance of each variable calculated as the sum of the Akaike weights over all of the models in which the term appears; this parameter is not shown for immatures because only one model was retained. Reference values of factorial explanatory variables (Sex, Territory, and Season) are shown for males, territorial adults and non-breeding season.

be investigated, however, why vultures do not compensate their weight loss (if due to the absence of natural prey) by an increase in the consumption of livestock.

Individual and population effects

As predicted by allometric relationships between size and mass in birds (Nudds 2007), we found that females (the largest) were also heavier compared to males. Interestingly, within each sex, a stronger relationship was found between body size and mass in females, suggesting that these traits are under stronger selection in the larger, but also more dominant sex. In females, individual performance may strongly depend on competitive skills. This allows them to feed more at predictable resources, while males in general avoid feeding in highly competitive resource environments (García-Heras et al. 2013, van Overveld et al. 2018). In line with this suggestion, taking into account effects of age on dominance rank, body size was positively correlated with dominance in females, but not in males (see *Data Availability*).

The effect of age on body mass of immature birds may reflect an improvement in their foraging skills over time, especially to locate carcasses of wild animals. Given the high annual rate of immature survival in our population (98%; see Badia-Boher et al. 2019), we believe this pattern is due to acquired experience, rather than selective disappearance of lighter individuals (Forslund and Pärt 1995, Sanz-Aguilar et al. 2008). Within the adult fraction, territorial birds showed higher body mass than non-territorial ones (Fig. 3). This seems counterintuitive

because the high energetic demands of reproduction usually lead to marked weight losses in birds (Ricklefs 1974), including vultures (Houston 1976). Again, the explanation for this pattern seems to be related to individual competitive abilities. Territorial birds are on average of higher dominance rank compared to non-territorial ones (Penteriani et al. 2011, Tapia and Zuberogitia 2018, van Overveld et al. 2018), which may provide a competitive advantage during food exploitation at predictable feeding sites and/or their territories may be located in food-rich areas. In addition, territorial adults may represent a subset of high-quality birds with well-developed foraging skills and environmental knowledge, allowing them to perform better in periods of high abundance of natural prey. While the body mass of adult vultures showed no response to seasonality, immatures were heavier during the non-breeding season. Seasonal variation in body mass among immatures could be linked to large-scale movements and energetically costly prospective activities that these birds perform during the population breeding season (van Overveld et al. 2018). At the end of this period, almost the entire non-breeding population concentrates in communal roosts and exploits more predictable resources and overall flight activity of vultures outside the breeding season is much lower (Donazar et al. 2002, van Overveld et al. 2018).

The finding of the effect of population growth over the study period on body mass is remarkable. Density-dependent processes have been invoked as regulators of body mass in other vertebrates (e.g., fishes; Dunham and Vinyard 2011) and there are numerous studies

FIG. 3. Changes in body mass as predicted by the generalized linear mixed models (GLMMs) fitted for immature and adult data in relation to variables evaluating long-term changes in primary productivity (Table 2). CVNDVI6: coefficient of variation of monthly values (daily averages) during the six months prior to the capture. Livestock: numbers of head (goats and sheep) in Fuerteventura Island. Breeding season: B, breeding; Non-B, non-breeding. Models were fitted for values corresponding to females. We applied the average of the range values for the rest of the variables fitted into the model.

indicating that in very dense populations, the individual condition worsens (Vincent et al. 1995, Saidapur and Girish 2001, MacDonald et al. 2002, Rogers et al. 2009). Although increasing competition for food resources is known to shape population parameters in growing populations of other vultures (Carrete et al. 2006, Fernández-Bellón et al. 2016), the overall importance of these processes in bird populations is largely unknown. We found that population size negatively affected vultures' body mass, but only within the adult fraction of the population. It could be hypothesized that this effect is mainly driven by competition for natural food resources. The absence of a density-dependent effect in immatures is intriguing and suggests age-specific differences in resource competition, as well as energetic costs associated with sexual and social competition for mates/territories and resource defense. Moreover, immatures rely more on predictable resources such as feeding stations

and large farms despite their overall low social position (van Overveld et al. 2018). It would be interesting to address in future studies whether wild prey could become a key factor limiting population growth, despite the presence of an overabundance of goats.

Synthesis and perspectives

The influence of human-mediated transformation on grazing biomes through livestock pressure jointly interacts with climatic conditions to determine the landscape-scale primary productivity. Currently, populations of three endemic scavengers (Egyptian vultures, Ravens, and Common Buzzard) in the study area largely depend on goat carcasses, as occurs in other insular systems (Gangoso et al. 2006, 2013). Thus, increasing livestock numbers would be expected to favor vulture body condition. Our study, however, shows that small wild prey

may represent an underestimated component in the diet of Egyptian vultures (Margalida et al. 2012). As such, high livestock numbers and associated overgrazing effects can even have a negative influence on vultures' body condition, with potential important consequences on individual fitness (Stearns 1992, Williams 2012). These conflicting effects of livestock production must be taken into account in conservation programs for obligate and facultative scavenger species whose diet also includes wild primary consumers, especially in a context where worldwide grazing pressure is growing exponentially. Therefore, assuming that higher livestock densities result in direct positive effects for endangered vulture populations can be a manifest error. An integral management strategy will be required to allow the maintenance of biodiversity in grazed areas, especially on islands sensitive to drought events and regions where the effects of environmental modifications, including climate change, are expected to be strong (Arévalo et al. 2012).

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2125/full>

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.02v6wwq0d>