

Environmental and Social Correlates, and Energetic Consequences of Fitness Maximisation on Different Migratory Behaviours in a Long-lived Scavenger

Jon Morant (✉ jon_morant@hotmail.com)

Sociedad de Ciencias Aranzadi <https://orcid.org/0000-0001-5702-2348>

Martina Scacco

Max Planck Institute of Animal Behavior: Max-Planck-Institut für Verhaltensbiologie

Kamran Safi

Max Planck Institute of Animal Behavior: Max-Planck-Institut für Verhaltensbiologie

Jose María Abad Gómez

Junta de Extremadura

Toribio Álvarez

Junta de Extremadura

Ángel Sánchez

Junta de Extremadura

W. Louis Phipps

Vulture Conservation Foundation

Isidoro Carbonell Alanís

SALORO

Javier García

Universidad de León: Universidad de León

Javier Prieta

SEO/BirdLife: Sociedad Española de Ornitología

Iñigo Zuberogoitia

Science Society: Sociedad de Ciencias Aranzadi

Pascual López-López

Universidad de Valencia: Universitat de Valencia

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Abstract

Partial migration is one of the most widespread migratory strategies among taxa. Investigating the trade-off between environmental/social factors - fitness and energetic consequences – is essential to understand the coexistence of migratory and resident behaviours. Here, we compiled field monitoring data of wintering population size and telemetry data of 25 migrant and 14 resident Egyptian Vultures *Neophron percnopterus* to analyse how environmental and social factors modulate resident population size, compare fitness components (i.e., survival and reproduction), and energetic consequences between migratory and resident individuals across wintering and non-wintering seasons. We observed that food availability positively correlated with the wintering population size and that subadult birds increased linearly with censused adult birds. Residents exhibited higher survival probabilities, but lower breeding activity and higher energy expenditure, less flight efficiency, and lower activity due to shorter winter-day lengths. On the contrary, migratory birds showed lower survival but more breeding attempts but spent less energy and flew more efficiently at longer distances, benefitting from longer days in African wintering quarters. These results suggest that anthropogenic food mediated social attraction could modulate population dynamics and promote residency. Food availability may benefit resident individuals enhancing their survival which may offset higher energy expenditure. Migrant birds, on the contrary, may compensate for the higher costs in terms of survival by a reduction in the energy cost, which may benefit future breeding. Our results offer new insights to understand how species benefit from one strategy or another and that the coexistence of both migratory forms is context-dependent.

1. Introduction

The drivers of animal movement and its consequences pose some of the most challenging questions in ecology research. Among the various forms and realisations of animal movement, migration is the most conspicuous phenomenon and has attracted scientists' attention for centuries. Animal migration is defined as a bidirectional and repeated movement between two different places, usually breeding and wintering areas, with a residency period in each location (Hansson and Akesson 2014). One of the most widespread strategies in migratory species is partial migration, in which part of the population remains in the breeding grounds while some individuals move to a distinct place to overwinter (Chapman et al. 2011a). The life-histories of individuals, in species simultaneously exhibiting these two well-marked behaviours, are subject to (and shaped by) different environmental, social and evolutionary forces (Lunberg 2013). Disentangling which factors determine the stability and persistence of these two strategies is crucial to understand the emergence of the migratory behaviour (Turbek et al. 2019).

Environmental (e.g., climate, resources) and social cues (e.g., location or presence of other individuals) are among the most influencing factors modulating migratory behaviour in partial migratory species (Shaw and Couzin 2013). Therefore, changes in these factors may favour migration or residency, and ultimately affect survival and reproduction (Buchan et al. 2019). Among the environmental cues, milder winters and higher food availability during winter could favour residency at higher latitudes, which increases individual survival and enables early reproduction and higher breeding success (Meller et al.

2016; Gilroy 2017). On the contrary, migration could be more advantageous by abandoning the resource-depleted regions during the non-breeding season which could increase both the chances of survival and reproduction (Winger et al. 2019; Winger and Pegan 2020). In terms of social cues, in long-lived species, the decision to migrate or not may come from learning or following more experienced individuals which could enhance the survival of less-skilled individuals (e.g., juveniles; Mellone et al. 2011; Teitelbaum et al. 2016). These findings show that despite the great progress that has been made in understanding the contribution of survival and reproduction to the maintenance of these two migratory behaviours, less attention has been paid to their energetic consequences. Energy expenditure is a key link between behaviour and overall fitness (Grémillet et al. 2018), therefore addressing energetic consequences of different migratory strategies is of paramount interest.

The recent advent of high-resolution Global Positioning Systems (GPS) in combination with tri-axial acceleration data, have allowed researchers to study how much energy is spent by animals during crucial periods of their annual cycle (i.e., breeding season; Grémillet et al. 2018), estimate how expensive or efficient it is to move depending on their kinematic patterns (i.e., flapping flight; Williams et al. 2020) and even investigate which factors limit activity duration (Pokrovsky et al. 2021). Integrating this energetic perspective into the study of migratory strategies could help to understand 1) the indirect energetic consequences of changes in those environmental and social factors that modulate migration and residency, 2) the trade-offs between fitness (e.g., survival and reproduction) and energy expenditure of both strategies and, 3) whether migratory or residency affect movement efficiency and activity duration. Overall, these three aspects could help explain the relative contribution of environmental conditions, social factors, fitness and energy expenditure, to the coexistence and persistence of these two strategies in partial migratory species (Gilroy 2017). This is of great importance to predict not only how current and future environmental changes could impact populations but also to design effective conservation measures that account for within-species behavioural migratory diversity and preserve species functionality and their role in ecosystems (Gilroy et al. 2016).

Here, we untangle from a mechanistic perspective which factors modulate and shape both migratory and residency strategies in a long-distance soaring migrant, the Egyptian Vulture *Neophron percnopterus*, by combining field monitoring and GPS tracking data of a partially migratory population in Spain. This endangered species ranges across southern Europe, northern Africa, the Middle East and Central and South Asia (BirdLife International 2020). While migratory individuals regularly travel >4,000 km between their northern breeding and southern wintering grounds by using several distinct migratory flyways (Phipps et al. 2019; Buechley et al. 2021), other individuals overwinter in southern and south-western Spain (García et al. 2000; Morant et al. 2020). The Egyptian Vulture is an obligate scavenger that frequently consumes both carrion from livestock and wild ungulates (Donázar 1993). The species exhibit complex social behaviour forming large individual congregations outside the breeding season at highly preferred feeding stations (e.g., farms) and nearby temporary roosting sites (García-Alfonso et al. 2020; van Overveld et al. 2020a). Altogether, these traits make it an ideal study species to assess how different migratory strategies coexist.

We firstly investigate the correlates underlying the partial migratory strategy observed in the Egyptian Vulture population overwintering in south-west Spain. Secondly, we investigate the consequences of either residency or migration and aim to identify the factors that balance between the costs and benefits associated with both strategies. We therefore hypothesize that: 1. there should be a relationship between the number of resident individuals and environmental conditions (e.g., temperature and food) and social factors (e.g., conspecific attraction); 2. different strategies (migration and residency) should differ in terms of reproduction (e.g., number of breeding years and number of successful breeding years) and survival; and 3. that differences in reproductive output and survival should be offset by different energetic requirements. Finally, 4. We expect that both migratory strategies yield different outcomes in terms of energy expenditure, flight efficiency and activity duration during winter.

2. Materials And Methods

2.1. FIELD MONITORING DATA

We gathered data from two different annual censuses of the wintering Egyptian vulture population in Cáceres, Extremadura, Spain (see Supp. Mat. Appendix S1 for details). We accessed to two sources of data: 1) data from the Spanish Ornithological Society, in which the wintering population was monitored on a yearly basis by censusing individuals (without differentiation of age classes) in January between 2006 and 2019; 2) our own monitoring project, where the wintering population was monitored twice monthly from December to February between 2014 and 2019 with adults and subadults classified according to plumage characteristics (more details in Morant et al. 2020). In the first case, censuses were carried out in one roosting site until 2014. From 2014 onwards, four additional wintering roosting sites were discovered and censused taking advantage of GPS tracking of some individuals that were tagged in 2014 ($n=5$, see Morant et al. 2020 for details). It was not possible to record data blind because our study involved focal animals in the field.

2.2. MOVEMENT DATA

We used data from 39 Egyptian Vultures belonging to three different populations in the Iberian Peninsula, namely: Extremadura, Duero/Douro and Castilla-La Mancha/Valencia (see Supp. Mat Figure. S1). Of the 39 birds, seven ($n=6$ adults and $n=1$ juvenile) were captured and tagged in Castellón and Guadalajara provinces (Spain) between 2007 and 2009 with a solar-powered GPS tag from Microwave Telemetry (Columbia, Maryland, USA), 19 ($n=11$ adults, $n=5$ subadults, $n=3$ juveniles) were captured in Cáceres (Extremadura, Spain) between 2014 and 2020, and fitted with solar-powered GSM-GPS-ACC transmitters ($n=16$) (E-obs GmbH, Munich, Germany) and Ornitela ($n=3$) devices, while 16 were equipped in Duero/Douro (Bragança, Portugal; Zamora, Spain; Salamanca, Spain) with Ecotone-Skua ($n=3$ adults, $n=1$ subadults, $n=2$ juveniles) (Ecotone skua), and Ornitela ($n=2$ adults, and $n=5$ juveniles) devices (see Supp Mat Table 1 for details). GPS fixes and associated data were acquired at temporal resolutions ranging from one location per 5 minutes to one location every 2 h, with dormancy periods during the night (from 22.00 p.m. to 4.00 a.m.) (see López-López et al. 2014, Phipps et al. 2019 and Morant et al. 2020 for more

details on the tagged individuals; see also Supp Mat Table S1.). Individual ages at deployment were estimated in calendar years based on plumage traits of different age classes. We classified juveniles as individuals in the first calendar year, immatures as individuals in the second to fifth calendar year and adults as individuals in the sixth calendar year or older (Forsman 2016). The sex of individuals was determined by using molecular sexing techniques (Fridolfsson et al. 1999).

Table 1

Estimates for fixed terms of the best models of environmental and social correlates, breeding and survival and energetic consequences. For the breeding, survival and environmental correlates models, Migratory type and Age class were coded as a factor, being "Migrant", and "Adult" the reference values for statistical comparisons. Significant values are highlighted in bold. Abbreviations: SE= Standard error.

Hypotheses	Predictors	Estimate \pm SE	z value	P-value
Social correlates	Number of adults	0.184 \pm 0.002	3.649	<0.001
Breeding	Migratory behaviour (resident)	-0.722 \pm 0.324	-2.228	0.025
	Tracking years	0.310 \pm 0.088	13.547	<0.001
	Migratory behaviour (resident)	-0.600 \pm 0.359	-1.669	0.095
	Tracking years	0.323 \pm 0.090	3.565	<0.001
Survival	Migratory behaviour (resident)	9.97e-8 \pm 1.07	-15.1	<0.001
	Age class (Juvenile)	33.8 \pm 1.13	3.12	0.001
	Age class (Subadult)	0.831 \pm 0.805	-0.242	0.801
	Migratory behaviour (resident)*Age class (Juvenile)	-	-	-*
	Migratory behaviour (resident)*Age class (Subadult)	1.91e+4 \pm 1.07	15.3	<0.001
Energy expenditure	Migratory behaviour (resident)	0.665 \pm 0.122	5.436	<0.001
	Season (Winter)	-0.388 \pm 0.028	-13.474	<0.001
	Flight behaviour (Others)	-1.677 \pm 0.026	-63.208	<0.001
	Migratory behaviour (resident)*Season (Winter)	0.235 \pm 0.034	6.879	<0.001
	Migratory behaviour (resident)*Flight behaviour (Others)	-0.653 \pm 0.031	-20.792	<0.001
Flight efficiency	Cumulative daily distance	4.6e-05 \pm 2.3e-04	0.203	0.839

* No Juveniles for the class resident are found at the end of the established period in the survival analyses.

Hypotheses	Predictors	Estimate \pm SE	z value	P-value
	Migratory behaviour (resident)	-0.025 \pm 0.170	-0.151	0.879
	Season (Winter)	-0.420 \pm 0.034	-12.286	<0.001
	Cumulative daily distance*Migratory behaviour (resident)	0.003 \pm 0.0003	12.732	<0.001
	Cumulative daily distance *Season(Winter)	0.002 \pm 0.0003	6.897	<0.001
	Migratory behaviour (resident) *Season(Winter)	0.723 \pm 0.034	21.179	<0.001
Activity duration	Day length	0.805 \pm 0.034	23.222	<0.001
	Season (Winter)	12 \pm 3.734	3.215	0.001
	Migratory behaviour (resident)	6.731 \pm 0.953	7.057	<0.001
	Day length * Season (Winter)	-1.060 \pm 0.327	-3.235	0.001
	Day length * Migratory behaviour (resident)	-0.380 \pm 0.393	-9.677	<0.001
	Season (Winter)*Migratory behaviour (resident)	-2.494 \pm 3.800	-6.563	<0.001
	Day length* Season (Winter)*Migratory behaviour (resident)	2.226 \pm 0.334	6.650	<0.001
* No Juveniles for the class resident are found at the end of the established period in the survival analyses.				

All captured individuals were equipped with yellow and red alphanumeric plastic rings, metal rings and a GPS transmitter. All transmitters weighed 24–63 g, <3% of body mass, which is below the recommended limits to avoid adverse effects (Bodey et al. 2018) and were attached using backpack or leg-loop harness systems. All the GPS and accelerometry data were automatically incorporated and downloaded from the online Movebank data repository (www.movebank.org; Wikelski and Kays 2019).

Birds were divided into “migrant” (n=24) (i.e., birds that exhibited usual migratory behaviour overwintering in the African quarters; Supp Mat. Figure S2A; see for example García-Ripollés et al. 2010) and “resident” (n=12) (i.e., birds that did not migrate and remained in the Iberian Peninsula during the study period; Supp Mat. Figure S3B; see Morant et al. 2020 for details). Two of the tagged birds, initially resident, exhibited migratory behaviour the following wintering season, when they left the breeding grounds to migrate to Africa. Therefore we considered them resident during the period they remained in the study area and

migrant after this period in our analyses (see also Supp Mat Table S2. for details of individuals used in each analysis).

2.3 ENVIRONMENTAL AND SOCIAL CORRELATES OF MIGRATORY BEHAVIOUR

We analysed the relationship between the number of resident birds during winter and different environmental factors, namely; 1) early-winter temperature in the current season (i.e., mean temperature between Nov-Dec), 2) mid-winter temperature recorded in the previous year (i.e., mean temperature between Dec-Feb) (see Meller et al. 2016 for a similar approach); 3) food abundance in the study area (e.g., livestock numbers). We also added 4) breeding population size in the study area. Temperature information was recorded for 2006-2019 (Agencia Estatal de Meteorología 2020). Livestock numbers, including cows, pigs (both from intensive and extensive farming systems), goats and sheep were obtained from the annual census conducted in the study area (data provided by the regional government, Junta de Extremadura). Data of breeding population size was obtained from the annual systematic surveys carried out in Cáceres between 2006-2019 by rangers during the breeding period (April-August) (data provided by the regional government, Junta de Extremadura).

We then investigated how the above-mentioned factors influenced the number of wintering vultures by computing Spearman correlation tests between the number of wintering individuals at the roosting sites recorded in the censuses between 2006 and 2019 and the environmental conditions in the respective years.

To investigate the effect of the social factors, we modeled the number of wintering subadults recorded in the census carried out between 2014 and 2019 wintering seasons (Nov-Feb) as a function of the number of adults recorded in the same censuses. We ran Generalized Linear Mixed Models (GLMMs) with Poisson distribution error and log-link function and we entered the year as a random factor in our model to account for the effects of a repeated census every year. We estimated marginal and conditional R^2 by using “piecewiseSEM” R package to assess the models’ overall explanatory power (i.e., for fixed and random factors).

2.4 BREEDING AND SURVIVAL CONSEQUENCES OF MIGRATORY BEHAVIOUR

We estimated the number of breeding years of each tagged individual (i.e., number of years that an individual had bred independently of the breeding output since the tagging date) and successful breeding years (i.e., number of years an individual had bred and raised at least one chick since the tagging date).

We only selected data from adult individuals (>5 calendar years) since subadult individuals do not usually breed (Serrano et al. 2021). We used data recorded during field monitoring during the breeding season for each individual and year. Individuals’ nests were identified by using GPS locations and later confirmed in the field. Breeding status (i.e., breeding/non-breeding) of each individual was confirmed

during April-June, when the tagged individual and its pair were observed copulating, arranging the nest and incubating. Breeding success of tagged individuals was confirmed when at least one chick was successfully raised at the end of the breeding period (August; see Morant et al. 2019 for details). If the breeding information (i.e., breeding and breeding success) from tagged individuals could not be confirmed during the fieldwork (e.g., due to logistic or economic limitations), we used the “nestR” package (Picardi et al. 2020) to assess breeding output for each individual and breeding season (see Supp. Mat. Appendix S2 for details).

To construct our survival database, we gathered data on each GPS-tagged individuals’ survival at the end of the study period, in our case, 28th February 2021. We estimated the number of days between the first and the last tagging date. For each individual we assigned a binary value as event indicator, being 0 if an individual was alive at the time of the last GPS location (28th February 2021) or 1 if an individual had died. We also recorded individuals’ age (namely age class) for those who were alive at the end of the study period and of the dead individuals (i.e., corresponding to the last GPS location date where casualties occurred). In case there was no clear evidence of individual death (e.g., picture of the dead individual or reliable information from collaborators or official entities), we could reliably separate deaths from cases of transmitter-failure based on three simple indicators extracted from the tags (see Supp Mat Appendix S3). Although we cannot rule out the possibility of some effect, we assume that tagging with the transmitters had a negligible impact on individuals’ absolute survival (e.g., Bodey et al. 2018; Buechley et al. 2021).

We used the breeding dataset to examine whether different migratory strategies exhibited differences on reproduction. We modeled the number of cumulated breeding years and the number of successful breeding years as a function of migratory type (migrant and resident) by running Generalized Linear Models (GLMs) with Poisson error distribution and log-link function. To elucidate the effect of time on the decision of breeding and on breeding success, we also included the number of tracking years as a covariate in our models. We ran separate models for the number of cumulative breeding years and breeding success.

We evaluated the effect of migratory behaviour (migrant and resident) on daily survival by running Cox regression models with right-censored data (Pollock et al. 1989). We also entered age class (adult, subadult and juvenile) at the end of the study period to account for the effects of age-specific variation on survival. We measured the interaction between migratory behaviour and age class. The model was fitted by using “survival” package (Therneau 2018).

In the case of the breeding model (i.e., GLM), we explored the overdispersion of selected models using the AER package (Kleiber and Zeileis 2008) to ensure that our model did not violate the assumption of Poisson distribution (i.e., variance and the mean are the same). We also computed the overall explanatory power of the selected model (D^2) by using “modEva” package (Barbosa et al. 2015) to inspect the proportion of variation explained by our best models. In the case of the survival models, we checked the

overall explanatory power by using the “Rsq.ad” function which measures the proportion of variance explained by the best models.

2.5 ENERGETIC CONSEQUENCES OF MIGRATORY BEHAVIOUR

We investigated the energetic consequences of adopting one migratory strategy or other. In particular, we examined differences in energy expenditure, flight efficiency and activity duration among migratory and resident birds.

2.5.1 ENERGY EXPENDITURE

We estimated the energy expenditure in two different seasons (non-winter: March-Oct, and winter: Nov-Feb) using the Overall Dynamic Body Acceleration (hereafter ODBA), calculated from the tri-axial accelerometry data (hereafter ACC) (Shepard et al. 2008; Gleiss et al. 2011). We used birds from which ACC data was recorded (migrant=9, resident=13). ODBA can be considered a proxy of energy expenditure since it is positively associated with oxygen consumption and carbon dioxide production (Wilson et al. 2006, 2019) and the mechanical work produced by muscles and internal organs (Gleiss et al. 2011; Bishop et al. 2015). Furthermore, the daily, integrative summary of daily energy expenditure from ODBA is even more effective when the parts with high-energy locomotion (e.g., flapping flight) are modelled separately from other behaviours (Duriez et al. 2014; Stothart et al. 2016).

ACC data were collected in bursts on three axes (X—sway, Y—surge, Z—heave) for a duration of 2-3 s every 5-10 min at 20 Hz from Ornitela and E-Obs devices, respectively (see Supp Mat. Table S1). Firstly, we estimated the energy expenditure calculated as the average ODBA value for each burst of 2-3s along the three axes (X, Y, Z). We transformed raw acceleration data into physical unit “g” (Laich et al. 2011) by using “moveACC” package (Scharf 2018). To this end, we assigned the calibration values of intercept and slope provided by manufacturers for each device type (Ornitela and E-Obs, respectively). We then estimated the average ODBA value (in gravitational units) for each burst. We finally estimated the mean daily ODBA by averaging the ODBA values per day, for each individual, year, month and day (see Wilson et al. 2019).

Secondly, we estimated the flight type (flapping or non-flapping) for each burst, by extracting wingbeat frequency from the ACC data (O’Mara et al. 2018). Finally, we classified each wing beat frequency as flapping or non-flapping. We identified and removed outliers in wingbeats (being <2 or >6 beats per second), representing about 1% of all bursts classified as flapping (see also O’Mara et al. 2018 for a similar approach).

We analysed the energy expenditure (i.e., mean daily ODBA) among the two migratory behaviours and flight types (i.e., flapping and not flapping flight). We also considered season (i.e., wintering and non-wintering periods) to account for differences among different periods in our model. We ran GLMMs with Gaussian distribution including cumulative daily ODBA as response variable, and migratory type, flight

type and season as covariates. We consider the interaction between 1) migratory behaviour and flight type, and 2) between migratory behaviour and season covariates.

2.5.2 FLIGHT EFFICIENCY

We calculated flight efficiency based on the percentage of time spent daily in flapping flight in relation to the daily distance travelled during non-winter and wintering seasons. We selected flapping flight since it is considered the costliest activity in soaring birds, given the disproportionate energy expenditure compared to all other behaviours (e.g., Williams et al. 2020).

We estimated the percentage of time spent flapping by counting the daily flapping events for each individual from the former energy expenditure database (see section 2.5.1). Flight types were extracted from the ODBA database, whereas the cumulated distance was estimated from the GPS data. Given that individuals tagged with different devices had different sampling schedules (5 min fix recording period for E-Obs devices and 30 min for Ornitela devices from some birds; see Supp Mat Table S1), we resampled our database to 30 min period and excluded superburst periods (<5 s). We estimated the cumulative daily distance, which is the distance covered in one day (or the sum of the distance covered in each 30 min segment), by using the “amt” package (Signer et al. 2019). Flight efficiency was then calculated as the ratio between daily percentage of flapping flight and daily distance.

To analyse whether there were differences in flying efficiency among migratory and resident birds in wintering and non-wintering periods, we modelled the daily percentage of time spent flapping as a function of daily cumulative distance (km) and migratory behaviour (migrant and resident). Since we expect that the highest difference among both migratory behaviours would occur in winter, we also included season (wintering and non-wintering period) as a factor in our model. We considered the interaction between cumulative distance, migratory behaviour and season in our model. We used a beta regression model and considered the proportion of time spent flapping ranging from 0 to 0.5 (i.e., 0-50%). We ran a glmmTMB model implemented in the “glmmTMB” package with beta family and logit link (Brooks et al. 2017).

2.5.3 ACTIVITY AND DAY LENGTH

To compare the activity duration between migrant and resident individuals, we followed the procedure proposed by Pokrovsky et al. (2021). We first calculated the mean ODBA values for each hour, and then we summed all the values to get daily estimates of ODBA value for each day. We also used the GPS data to estimate the day length by using “geosphere” package (Hijmans 2016). We then joined both datasets to the most proximal timestamp. For estimating how many hours the tagged vultures remained active, we counted the number of hours that were greater than a certain threshold of activity. This threshold was estimated as mean ODBA for the non-moving bird. We considered birds as non-moving when 1) two consecutive GPS coordinates were equal, 2) there were at least six ODBA bursts between these GPS values, and 3) the movement among these two points did not exceed the mean location error of the GPS devices (this being for Ornitela of ± 3.4 meters and ± 1.9 meters for e-obs tagged individuals; see Fleming

et al. 2020). We used 20 measurements from 7 different birds for each migratory type. The average values of the activity threshold were 0.067 and 0.051 for migrant and resident birds, respectively.

We inspected the consequences of migratory strategy across seasons and different day lengths in terms of the number of hours that Egyptian Vultures remain active. We thus modelled the activity duration (in hours) by running linear mixed-effects models (LMMs) in which migratory behaviour (migrant and resident), season (winter and non-wintering periods) and day length were entered as covariates. We considered the interaction among these three variables to ascertain which migratory behaviour is more beneficial across seasons (assuming that for instance longer days in Africa may benefit migrants in winter).

In the three analyses, individual identity and year were entered as random terms to account for the measures of the same individuals and within the same year. For the energy expenditure and activity duration model, we estimated marginal and conditional R^2 by using “piecewiseSEM” R package to assess the model’s overall explanatory power. In the case of the flight efficiency model (i.e., glmmTMB), the proportion of the total variance explained by the fixed and random terms was estimated by using performance package (Lüdecke et al. 2020).

Spatial and statistical analyses were done in R version 4.0.0 (R Core Team, 2020). In all analyses the models were compared by using the Akaike Information Criterion (AIC; Burnham and Anderson, 2002), corrected for small sample sizes (AICc). The best model was that with the lowest AICc value. All models with a difference of $\Delta AICc < 2$ were compared to the best model (Burnham and Anderson, 2002). For the best model, homogeneity of variance and normality of residuals was inspected by using “ggresid” package to check the goodness-of-fit of our best models (Goode and Rey, 2019). All tests were two-tailed, statistical significance was set at $p < 0.05$, and all means were given together with standard error.

3. Results

3.1 ENVIRONMENTAL AND SOCIAL CORRELATES

We found that the livestock numbers were the only environmental covariates significantly correlated to the number of resident individuals during winter. The number of wintering individuals was positively correlated to the number of cattle ($\rho = 0.63$, $P = 0.022$) but negatively correlated to the number of goats and sheep ($\rho = -0.65$, $P = 0.017$ and $\rho = -0.56$, $P = 0.045$, respectively) (Figure 1A-C). The number of pigs intensively and extensively managed were also negatively correlated but the relationship was not significant ($\rho = -0.48$, $p = 0.094$ and $\rho = -0.42$, $p = 0.16$, respectively) (Figures 1D and E). We neither found significant correlation with breeding population size ($\rho = -0.49$, $p = 0.088$; Figure 1F) and early and mid-winter temperatures during winter ($\rho = 0.44$, $p = 0.13$ and $\rho = 0.17$, $p = 0.58$, respectively) (Figures 1G and H).

We observed that social factors greatly influenced the number of subadults censused at roosting sites. Our results showed a significant relationship between the number of subadults and number of adults (Supp Mat Table S3; Table 1). The number of subadults increased linearly together with the number of adults, explaining almost 49% of the total variance of the model (Figure 2).

3.2. BREEDING AND SURVIVAL CONSEQUENCES OF MIGRATORY BEHAVIOUR

Overall, our results showed that migrant birds bred significantly more often than resident birds (mean= 2.63 years, SD=1.92, and mean = 1.09 years, SD= 1.04, respectively) (Supp Mat Table S3; Table 1; Figure 3A), and that the number of breeding years increased together with the tracking years for both migratory behaviours (Figure 3B). Migratory and resident birds experienced similar breeding success (mean= 1.95 years, SD=1.61, and mean = 0.91 years, SD= 0.83, respectively) (Supp Mat Table S3; Table 1; Figure 3C). Not surprisingly, in both migratory behaviours the number of successful breeding years also increased with the number of tracking years (Figure 3D).

We observed a total of 13 casualties of the tagged birds (33% of all tagged birds) at the end of the study period, of which 12 were migratory birds and one was a resident bird. The casualties occurred in Spain and Portugal (n=2) and the rest of them in African quarters (n=11). Our results showed a significant difference in survival probability between migratory behaviour and between age classes (Supp Mat Table S3; Table 1). Resident birds exhibited higher survival rates than migrants for all age classes (mean= 0.9, SD=0.09, and mean=0.71, SD=0.16, respectively; Figure 4A and 4B). Moreover, survival of juvenile birds was significantly lower (mean= 0.50, SE=0.19) compared to that of subadults and adults (mean=0.75, SE=0.17, and mean=0.79, SE=0.1, respectively) (Figure 4C).

3.3 ENERGETIC CONSEQUENCES OF MIGRATORY BEHAVIOUR

In general, Egyptian Vultures spent much less energy in winter than in the non-winter seasons. Migrant birds spent less energy compared to resident birds in costly flight types like flapping, particularly in winter (mean=3.02 g, SD=1.62 and mean=3.93 g, SD=1.66 g, respectively) (Supp Mat Table S3; Table 1; Figure 5A). Migrant and resident birds spent similar energy in other flight behaviours (i.e., soaring, gliding) than resident birds in both non-wintering and wintering seasons (mean=1.65 g, SD=0.469 g, and mean=1.55 g, SD=0.518 g, respectively) (Table 1). Overall migrant birds spent less time flapping relative to the distance they covered compared to the resident birds during non-wintering period and further peaking in the wintering season (Supp Mat Table S3; Table 1; Figure 5B). Moreover, resident birds exhibited a less efficient flight during the wintering season in Iberian Peninsula compared to migrant birds (mean=4.8%, SD=2.73%, and mean=2.63%, SD=2.31%, respectively). Finally, overall, we found that activity duration significantly increased with day length which varied along with seasons and migratory behaviour (Table 1). Migrant and resident birds exhibited similar activity duration in the non-wintering season when both

remained in the Iberian Peninsula and thus, shared similar day length values (mean=12.6 hours, SD=2.95, and mean= 13.4, SD=2.54, respectively; Figure 5C and D). On the contrary, we found significant differences between migratory behaviour in winter, when migrant birds exhibited higher activity values during winter than resident birds (mean=11.4, SD=2.49, and mean=10.6, SD=2.22, respectively; Figure 5C and D).

4. Discussion

In this study we disentangled the causes and consequences of migratory behaviour in a long-distance partial migratory bird, the Egyptian Vulture. We showed that environmental (food) and social (attraction to conspecifics) cues are primary correlates of variation in wintering population size across time. Interestingly, we observed that migrants exhibited higher breeding activity (i.e., number of breeding years) than resident individuals, whereas residents showed higher survival probabilities than migrant individuals. We found that overwintering in the breeding grounds seemed to be energetically more expensive than migrating. Overall, resident birds spent more energy and flew less efficiently during winter than migrants. Furthermore, daily activity duration of residents was lower due to the short days during winter in the Iberian Peninsula. In summary, our findings showed that optimal migratory strategy is context-dependent. Residency may be advantageous in terms of resource availability and survival, but it is energetically costly. On the contrary, migration is less costly and may allow individuals to invest more energy in reproduction which may explain the observed high breeding rates and lower survival probabilities. Therefore, our results suggest that the coexistence of different migratory behaviours may be balanced by a complex trade-off between fitness and optimal energy allocation shaped by environmental and social factors.

4.1 THE ROLE OF ENVIRONMENT AND SOCIALITY

Global change has become one of the most influencing factors on partial migratory species in recent decades (e.g., Gill et al. 2019; Van Doren et al. 2021). Species rapidly respond to milder winters and increasingly predictable and available food pulses at higher latitudes by shortening migratory routes and even by remaining in the breeding areas during winter (Haest et al. 2019; Nuijten et al. 2020; Riotte-Lambert and Mathiopoulos 2020 and references therein). However, our results showed that responses of birds are more influenced by proximate factors such as a significant increase in food availability and social cues rather than the climate (e.g., temperature). Indeed, it is known that anthropogenic food subsidies may greatly influence changes in migratory patterns in social species (Oro et al. 2013). The White Stork (*Ciconia ciconia*) is one such example that has become resident in Europe (e.g., Rotics et al. 2017; Arizaga et al. 2018), due to the increase of year-round available food sources at rubbish-dumps (Gilbert et al. 2016). Our results showed that adult Egyptian Vultures may attract subadults and less experienced individuals by remaining in a particular place where resources are abundant and predictable (see Morant et al. 2020). This pattern has also been observed in White Storks (see also Rotics et al. 2016) and other sedentary populations of Egyptian Vultures where collective foraging in areas of high food predictability and availability (e.g., farms) could benefit individuals with lower social status, such as

juveniles or subadults (García Alfonso et al. 2020; van Overveld et al. 2020b). Overall, our results evidence that migratory decisions at the population level might be influenced by the environment (e.g., food availability), and modulated by sociality.

4.2 FITNESS MAXIMISATION

Recent studies on fitness benefits of migration or residency strategies yield clear evidence that in terms of survival residency is more beneficial than migration (Buchan et al. 2019). Our results are in agreement with these findings and suggest that improved climate conditions and year-round resource availability could contribute to the observed higher survival rates (e.g., Satterfeld et al. 2018). In fact, we found that all age classes exhibited higher survival rates in residents as compared to migrants. Hence, residency could be particularly beneficial for immature and juvenile birds that exhibited higher mortality rates associated with migration (see Grande et al. 2009; Sanz-Aguilar et al. 2017). However, Buechley et al. (2021) found that migratory Egyptian Vultures experienced higher survival rates at African wintering grounds. The higher survival at non-breeding grounds, linked to the fact that juvenile Egyptian Vultures spend the first years of their lives in African grounds until reaching adulthood (Donázar 1993), showed that a certain parity might exist among survival rates among migratory and non-migratory birds that could contribute to the coexistence of both behavioural strategies (Gilroy 2017).

Our findings showed a clear breeding advantage for migrant birds. However, it could be expected that resident birds could increase breeding performance due to their earlier access to best-breeding sites and earlier reproduction (Pulido and Bethold 2010). According to our results, it is also possible that in resident birds specific components of fitness are maximized (i.e., survival) at the expense of reproduction. Migrants, on the contrary, may allocate more resources towards reproduction while they are subjected to direct mortality costs of migration (Soriano-Redondo et al. 2020; Buechley et al. 2021). However, the observed similar breeding success between migrants and residents may indicate a clear advantage towards residents, since improved conditions during breeding season can result in better productivity for both migrants and residents, in addition to improved survival for residents (see for example Griswold et al. 2011). In this context, maximisation of certain fitness components could occur if some individual traits such as physical condition are compromised due to unfavourable conditions experienced in winter (Chapman et al. 2011b).

Overall, our results showed a complex trade-off between survival and reproduction which could lead to a selection of an optimal strategy that maximises certain fitness components for migratory behaviour (Chapman et al. 2011b). More importantly, they may indicate that migratory and resident species have different life-history strategies (e.g., migratory species live faster than resident ones) that promotes the coexistence among both forms (Soriano-Redondo et al. 2020).

4.3. IMPACT OF MIGRATORY BEHAVIOUR ON ENERGY ALLOCATION

Overall, we observed that residency is more energetically costly than migration, particularly during the wintering season. These results are contrary to previous studies showing that residency in breeding grounds in Europe could increase survival probability and decrease energy expenditure (see Flack et al. 2016; Rotics et al. 2017). We observed that resident individuals invested more effort flying in wintering ground than migrants, particularly they invested more time in costly flight types like flapping for the same travelled distance. These results suggest that migratory birds experienced better flying conditions and can travel farther by using gliding and soaring flights which minimize travel costs (see for example Rotics et al. 2016). Moreover, resident individuals exhibited lower activity duration due to shorter daylight hours in the Iberian Peninsula (Pokrovski et al. 2021). Therefore, our findings may indicate that the decision to stay may offset the higher energy spent in wintering grounds with harsher conditions (Rotics et al. 2018). However, residents may also compensate for the higher energy expenditure by reducing their wintering foraging areas and exploiting highly predictable food resources such as farms close to their roosting sites (Supp Mat Figure S3 and Table S4; see also Morant et al. 2020 and Soriano-Redondo et al. 2021).

5. Conclusions

We showed that the resident populations of Egyptian Vultures are influenced by the increased resource availability in wintering grounds. Interestingly, our results suggest that such change in environmental conditions could be amplified by species-specific behavioural traits such as attraction to conspecifics (van Overveld et al. 2020a, 2020b). We also observed that each migratory form may maximise a certain fitness component (i.e., survival or reproduction). Resident individuals may maximize their survival by exploiting predictable and easily available trophic resources (e.g., farms, López-López et al. 2014; Morant et al. 2020) that compensates for the higher energy cost of moving in unfavourable conditions during winter. Migrant individuals could benefit from more seasonal and unpredictable resources but better environmental conditions in African wintering quarters that improve their flight capacities (e.g., reducing flapping flight due to higher availability or thermals; Flack et al. 2016) and more daylight hours to forage (e.g., due to longer days in Africa in winter; Pokrovski et al. 2021). In summary, our results reveal a complex trade-off between fitness components between migrant and resident behaviours which could offset the energetic consequences of selecting one strategy or the other. Taken together, these insights could help better understand coexistence of both migratory forms in partial migratory species.

Declarations

Capture, banding and monitoring of Egyptian Vultures were conducted under permits and following the protocols approved by the “Dirección General de Medio Ambiente (Consejería de Agricultura, Desarrollo Rural, Población y Territorio”, Government of Extremadura, licenses numbers: CN0011-17-AAN, CN0020-15-AAN) and following the protocols approved by the “Servicio de Conservación de la Naturaleza y Áreas Protegidas” (Government of Extremadura), following the approved guidelines. All procedures regarding animal manipulation and tagging were strictly performed in accordance with relevant guidelines and regulations of the “Patrimonio natural y de la biodiversidad” (Article 61 of Law 42/2007, Spanish Ministry

of the Ecological Transition) and “Catálogo Regional de Especies Amenazadas de Extremadura” (Article 8 of Decree 37/2001 of 6 March).

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COMPETING INTERESTS

The authors declare that they have no conflict of interest.

ETHICS APPROVAL

All procedures regarding animal manipulation and tagging were strictly performed in accordance with relevant guidelines and regulations of the “Patrimonio natural y de la biodiversidad” (Article 61 of Law 42/2007, Spanish Ministry of the Ecological Transition).

DATA AND CODE AVAILABILITY

The data used to perform all the analyses is archived in Zenodo and is available at the following link: <https://zenodo.org/record/5837571>.

AUTHORS CONTRIBUTION

J.M. conceived of the presented idea, developed the theory and performed the computations; J.M., M.S., K.S., I.Z., L.P., and P.L-L. prepared the database and taking responsibility for logical interpretation and presentation of the results; J.M.A.G, J.P., I.C., J.G., L.P., and P.L-L. conducted fieldwork; A.S., T.A., and P.L-L. obtained funding. All authors took part in the preparation of the manuscript and gave their final approval for submission and publication.

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Figures

Figure 1

Spearman correlations between censused Egyptian vultures on roosting sites throughout thirteen wintering seasons (2006–2019) and; (A-E) number of livestock censused; (F) breeding population size in the study area; and (G-H) early and mid-winter temperatures (°C). Black dots represent the raw data points. The shaded areas represent 95% confidence intervals.

Figure 2

Relationship between the number of Egyptian vulture subadults and number of adults censused in roosting sites (n=5) throughout five wintering seasons (2014–2019). Black dots represent the raw data points. The shaded area represents the 95% confidence interval. R^2 showed the marginal variance explained by the model.

Figure 3

Predicted values of the significant variables included in the best models of breeding. Figure A represents the cumulative breeding years for each migratory type throughout the study period. Figure B shows the effect of time on the cumulative and successful breeding years from the tracked birds. Differences between migrant and resident birds on successful breeding years are shown in the figure C. The figure D shows trends in successful breeding years respecting the time birds were tracked. Black dots represent the raw data points. The bars (Figure A and C) and shaded areas (Figure B and D) represent 95% confidence intervals.

Figure 4

Survival analysis results for different migratory behaviours x Age class (A), migratory behaviour (B) and Age class (C) by using ox regression method for GPS-tracked individuals (n=39) during the study period. The upper plot shows each migration strategy's survival probability throughout time (in days) since the first tracking day. Each step in the lines represents the death of an individual in each case. The shaded area represents 95% confidence interval.

Figure 5

Differences between migrant and resident birds in energy expenditure (expressed as cumulative daily ODBA in gravitational units [g]) among different flight behaviours in non-winter and wintering seasons of (A) and percentage of time spent daily in flapping flight respecting to the cumulative daily distance among migrant and resident birds during non-winter and wintering seasons (B). In figure A, the horizontal line in the box plot represents the mean, whilst the standard deviation is shown as error bars. Shaded areas represent 95% confidence intervals in figure B. Colored dots represent the raw data points. Photo Credits of Egyptian Vultures by Jon Morant and Miguel Ángel Muñoz Memole.

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