AGE-DEPENDENT SURVIVAL OF ISLAND VS. MAINLAND POPULATIONS OF TWO AVIAN SCAVENGERS: DELVING INTO MIGRATION COSTS

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ABSTRACT

Large terrestrial long-lived birds (including raptors) are typically sedentary on islands, even when they are migratory on the mainland. Density-dependent variation in the age at first breeding has been described as responsible for the long-term persistence of long-lived bird populations on islands. However, sedentary island populations may also benefit from higher survival rates derived from the absence of migration costs, especially for young individuals. Thus, sedentary island populations can mimic a natural experiment to study migration costs. We estimated the age-dependent survival of two sedentary raptors on Menorca Island (Egyptian vultures *Neophron percnopterus* and red kites *Milvus milvus*) and compared these estimates with those reported for other migratory and sedentary populations. In Menorca, Egyptian vultures, but not red kites, showed low levels of human-related mortality resulting in extremely high survival probabilities, probably due to different diet choices and behavioral patterns. Juvenile Egyptian vultures and red kites in the studied population had lower survival probabilities than adults. This difference, however, was smaller than those reported for mainland migrant populations, which showed a lower juvenile survival rate. In fact, between-population comparisons suggested that survival of the young in migrant populations may be triggered by mortality factors in wintering areas. In contrast, adult survival may respond to mortality factors in breeding areas. Our results suggest that raptor species that become sedentary on islands may benefit from higher pre-breeder survival prospects in comparison with their mainland migrant counterparts. This fact, in combination with an earlier age at first reproduction, may facilitate their persistence.

Keywords: *Neophron percnopterus*, *Milvus milvus*, multievent, radiotracking, demography.

INTRODUCTION

How isolated populations of long-lived terrestrial vertebrates persist in the long-term is a central topic in research in ecology, evolution and the conservation of insular systems (Morris and Doak 2002; Whittaker and Fernández-Palacios 2007). Although numerous animal populations have become extinct or are currently threatened as a consequence of human activities, intrinsic traits of animal species are strongly associated with extinction risks (Boyer 2010). Conservative life-history strategies distinctive of long-lived organisms (i.e., long generation time) involve higher extinction risks when persecution or predation occurs (Owens and Bennett 2000). Long-lived animals typically present low fecundity, high survival, a delayed accession to reproduction and age-dependent vital rates (i.e., survival and productivity) (Newton 1989; Forslund and Pärt 1995). Consequently, their population growth rate is highly sensitive to changes in both adult (Sæther and Bakke 2000) and cumulative pre-breeder survival (Sergio et al. 2011). Adult survival is generally higher and less variable than juvenile survival (Sæther and Bakke 2000; Sanz-Aguilar et al. 2014). Juveniles have to deal with inexperience in foraging skills (Greig et al. 1983) and territory defense or poorer competitive abilities (Forero et al. 1999). In addition, long-lived terrestrial animals show limited dispersal opportunities and small population sizes, which increase their chances of extinction through environmental and/or demographic stochasticity processes (Lande 1988; Morris and Doak 2002; Whittaker and Fernández-Palacios 2007).

Within this scenario, it may be hypothesized that the persistence of island populations can be linked to fundamental changes in key demographic parameters. Additionally, island populations represent natural experiments in which dispersal is limited (Whittaker and Fernández-Palacios 2007). In this respect, it is key that large, insular terrestrial long-lived birds with deferred sexual maturity are generally sedentary (raptors and ciconiiforms) in contrast with those populations of the mainland, which tend to be migratory (Donazar et al

2005; Ferrer et al. 2011). Island populations are especially subject to inbreeding depression and/or density-dependence problems (Lande 1988; Brouwer et al. 2009). It has been proposed that sedentary island birds can gain experience earlier and recruit at younger ages than their migratory counterparts facilitating their persistence (Ferrer et al. 2004, 2011). However, whether sedentary island populations benefit from the absence of migration costs in terms of survival is unexplored (Sanz-Aguilar et al. 2012). In fact, juvenile and adult survival in several migratory long-lived raptor species has been shown to be influenced by both migration and environmental conditions at wintering grounds (Grande et al. 2009; Mihoub et al. 2010; Klaassen et al. 2014; Sergio et al. 2014). Migration between wintering and breeding grounds is recognized as a critical period for the survival of young birds (Mihoub et al. 2010; Sanz-Aguilar et al. 2012; Sergio et al. 2014). By using the most seasonally suitable habitats, individuals are expected to improve their fitness by increasing future fecundity and/or survival (Berthold 2001). However, the benefits of migration may be balanced by costs associated with the migratory process (Alerstam et al. 2003), and survival can be jeopardized by adverse environmental conditions during migration and/or at wintering areas (Schaub et al. 2005; Newton 2006; Grande et al. 2009; Carrete et al. 2013; Klaassen et al. 2014; Sergio et al. 2014). Moreover, studies on partial migratory long-lived species such as the white stork *Ciconia ciconia* or the greater flamingo *Phoenicopterus roseus* revealed an increased juvenile survival for resident or short-distance wintering individuals (Schaub et al. 2004; Sanz-Aguilar et al. 2012), although the opposite result was found in merlins (*Falco columbarius*) (Warkentin et al. 1990).

The aim of this study is to describe the relationship between age-dependent survival and sedentary/migratory habits of two long-lived scavenger raptors inhabiting island (i.e., sedentary populations) and mainland areas (i.e., migrant populations). The selected species are the Egyptian vulture *Neophron percnopterus*, and the red kite *Milvus milvus*, a globally

endangered and near threatened species, respectively (BirdLife International 2014). Egyptian vultures from mainland European populations are long-distance migrants wintering in the sub-Saharan Sahel region (López-López et al. 2014). Red kites are resident in most of their Western European range, but birds from northeastern and central Europe typically winter in the south; mainly in Iberia and France (Schaub 2012). On the contrary, the two species are resident on islands both in the Mediterranean (Balearic Islands) and in Macaronesia (Canary and Cape Verde archipelagos, Donazar et al. 2002, 2005). We estimate the survival rates of the species on Menorca Island, a small Mediterranean island, and compare the obtained values with those reported for other sedentary populations (Mallorca and Canary islands, Donazar et al. 2002; Tavecchia et al. 2012; Tenan et al. 2012) and mainland migrant populations (continental Spain and Switzerland, (Grande et al. 2009; Kéry and Schaub 2012; Sanz-Aguilar et al. 2015). Our main hypothesis is that survival rates should consistently differ between island and mainland populations of the two species due to the absence of migration costs in island populations. We specifically predict that: 1) resident populations inhabiting islands should present a higher survival rate; 2) because migration imposes higher costs during the first years of life, differences in survival rates should be higher for the immature fraction of the populations; 3) given that Egyptian vultures have a later recruitment and lower fecundity than red kites (Newton et al. 1989; Carrete et al. 2009; Cortés-Avizanda et al. 2009; Tenan et al. 2012), we expect a lower variability of survival between age classes and between populations for Egyptian vultures (Sæther and Bakke 2000).

METHODS

Study species

Egyptian vultures and red kites are highly opportunistic species, foraging on small wild prey and on carcasses of small and medium-sized animals (Donazar 1993). Non-breeders typically aggregate around predictable food resources (e.g., landfills or vulture restaurants)

(Donázar et al. 1996; López-López et al. 2013). Given their larger body size, Egyptian vultures can feed on larger items than red kites. Egyptian vultures are able to reproduce at three years of age (own data) but typically recruit from five years of age onwards (Carrete et al. 2009; Sanz-Aguilar et al. 2015), whereas red kites, able to breed in their first year, typically recruit at two-three years of age (Newton et al. 1989; Tenan et al. 2012). The two species in both island and mainland populations are subject to the same key anthropogenic mortality causes: poisoning, electrocution and direct persecution (Donázar et al. 2002; Hernández and Margalida 2009; Knott et al. 2009; Smart et al. 2010; Tavecchia et al. 2012). Additionally, on mainland populations wind-farm collision is an important mortality factor (Carrete et al. 2009; Schaub 2012; Bellebaum et al. 2013; Sanz-Aguilar et al. 2015).

Study area and data collection

The study was carried out on Menorca Island (Balearic Archipelago, 39°58'00''N 4°05'00''E, 701Km²) (Fig. 1). The Egyptian vulture population comprised around 50 breeding pairs in 1989, which declined to 39 pairs in 1999 and increased again to 51 in 2004 (authors' own data). From 2004 to 2014, the breeding population was stable at around 50 pairs (authors' own data). Egyptian vultures are mainly distributed on ravines and marine cliffs on the eastern part of the island (De Pablo 2002). 135 breeding pairs of red kites bred on the island in the mid-1980's, but an intense decline due to poisoning and electrocution led to a minimum number of 6 breeding pairs in 1998 (De Pablo 2004). Since then, the population has increased to 27 breeding pairs in 2014 distributed throughout the island (authors' own data). Exceptional individual exchanges with the neighboring Mallorca Island have been recorded for the red kite (3 individuals) but not for the Egyptian vulture (authors' own data).

From 1998 to 2005, 45 first-year, 2 second-year and 8 adult Egyptian vultures of unknown age were captured and marked with PVC rings with a unique alpha-numeric code

allowing for long-distance identification and equipped with a radiotransmitter (TW3 2xAA and TW3 AA, BIOTRACKS LTD) mounted on a Teflon backpack harness. Transmitters had a life expectancy of 3-7 years and weighed <5% of bird body weight. Additionally, 21 first-year Egyptian vultures were only marked with PVC rings. Individual age was determined on the basis of plumage characteristics (Cramp and Simmons 1977). Resightings of live individuals without active radio-signals (n=15) and/or without radiotransmitters (n=8) were recorded during population monitoring, and dead individuals with (n=5) and without radiotransmitters (n=3) were recovered.

From 1999 to 2010, 153 fledgling red kites were marked and equipped with a radiotransmitter (TW3 AA BIOTRACKS LTD) mounted on a Teflon backpack harness. Transmitters had a life expectancy of 2-4 years and weighed <5% of bird body weight.

Individuals of both species were radio-tracked weekly until the end of battery life, the loss of the radio signal, their death and/or the end of the study (December 2012). When a bird radio-signal was lost, we flew the entire island in a small aircraft trying to relocate marked birds. Moreover, the radio-signal frequencies of lost individuals were also tracked by a research team on the neighboring island of Mallorca, which allowed the location and tracking of 3 red kites that moved to Mallorca. 73 red kites were recovered dead during the study period. Causes of mortality were determined by necropsy and pathology procedures (Hernández and Margalida 2009). They were classified as follows: poisoning, electrocution, wind farm collision, natural deaths (including drowned birds and birds with broken bones or muscle injuries) and unknown cause (when decomposition of the carcass did not allow a precise determination of cause of death).

Survival modeling

To take advantage of all the available information collected in the field we designed two capture-recapture multievent models able to combine multiple sources of information to

estimate individual survival (Pradel 2005). For the Egyptian vultures, the multievent model (see model details in Online Resource 1) allowed the combination of radiotracking, resighting and recovery data. Individuals with active radiotransmitters presented perfect resighting and recovery probabilities ($=1$), whereas those without active radio signal detection and recovery were estimated by the model proposed in Tavecchia et al. (2012). The model allowed the estimation of simultaneous survival and radio signal functioning probabilities (Tavecchia et al. 2012) (see details in Online Resource 1). As only 8 vultures were recovered dead (one adult by poisoning, 2 first-year individuals due to natural causes, and 2 first-year individuals, 2 subadults and 1 adult due to unknown causes), we did not take into account different mortality causes in our multievent model. Given that goodness-of-fit (GOF) has not yet been developed for multievent models, capture–recapture analysis of Egyptian vulture data began with the assessment of the GOF of the Arnason-Schwarz multisite model to the data (Pradel et al. 2005) using program U-CARE 2.3.2 (Choquet et al. 2009a). We began our model selection with a general model considering 8 age classes for radio signal functioning transition parameters and 7 age classes for survival transition parameters, which were selected on the basis of previous knowledge of the species (i.e., differences between 6 age classes found by Grande et al. (2009) and the maximum expected radiotransmitter battery life: 7 years). We first simplified the structure of the radiotransmitter functioning parameter and then modeled survival probabilities as a function of age. We considered different age structures (levels) and models with a linear as well as quadratic function of age (covariates) on survival.

As very few red kites were identified using their ring code once the radio signals were lost ($n=2$) we discarded these observations and used known fate radiotracking data on live and dead encounters to estimate individual survival with a specific multievent model. This multievent model allowed the combination of live radiotracking with recovery data specifying the different causes of mortality (Tavecchia et al. 2012) (see details in Online Resource 2). As

we only used known fate data (i.e., radiotracking) for red kites, no GOF was necessary (White and Burnham 1999). We limited the maximum number of age classes considered to three (juveniles “i.e., first year”, subadults “i.e., second year” and adults “i.e., from third year onwards”) because of the low numbers of observations of individuals older than four years due to the radiotransmitter battery life and based on previous knowledge of the species (Smart et al. 2010; Kéry and Schaub 2012; Schaub 2012; Tavecchia et al. 2012; Tenan et al. 2012). We first tested differences in survival probabilities and then differences in mortality causes between age classes.

Models were built and fit to the data using the program E-SURGE 1.6.3 (Choquet et al. 2009b). Model selection was based on Akaike’s Information Criterion adjusted for the effective sample size, AICc (Burnham and Anderson 2002). In addition, for each model j , we calculated the Akaike weight, w_j , as an index of its relative plausibility (Burnham and Anderson 2002). Estimates were obtained by model averaging in which each model contributed to the final estimate according to its w_j (Burnham and Anderson 2002).

Comparison of survival with other populations

We investigated the extent of age-dependent survival differences among different populations with available survival estimates (and SE) of the studied species in other insular and mainland regions of Western and central Europe and Macaronesia (Fig. 1-2). We used Z-tests (Zar 1999), as estimates across datasets were independent.

For the Egyptian vulture we used the estimates obtained for the migrant Ebro population (ϕ age 1-2=0.72 (0.02), ϕ age 3-4=0.78(0.03), ϕ age 5=0.60 (0.05), ϕ breeders=0.83 (0.02), (Grande et al. 2009)), the migrant Andalusia population (ϕ non-breeders age 1-5=0.73 (0.04), ϕ breeders=0.94 (0.04), (Sanz-Aguilar et al. 2015)) and the resident Canary population (ϕ age1-5=0.887 (0.045), ϕ age>5 & breeders =0.897 (0.098), (Donázar et al. 2002)).

We compared red kite survival probabilities obtained in this study with those of the neighboring population of Mallorca (ϕ age 1=0.72 (0.08), ϕ age 2=0.82 (0.09), ϕ age >2=0.79 (0.09), (Tavecchia et al. 2012)), and the partial but mainly migratory Swiss population (ϕ age 1=0.41 (0.14) , ϕ age 2= 0.66 (0.07), ϕ age >2= 0.84 (0.03), (Kéry and Schaub 2012)).

RESULTS

Egyptian vulture survival

The overall goodness-of-fit test of the Arnason-Schwarz multisite model was not statistically significant ($\chi^2 = 4.263$, d.f. = 19, $p = 0.999$). We began model selection by testing different age structures in radio signal functioning probabilities (models Mv 1-Mv 6, Table 1). The structure of the radio signal functioning parameter that minimized AICc considered 8 age classes (i.e., 8 years) and a linear decreasing trend over time in the probabilities of radiotransmitter functioning (model Mv 4, Table 1). More complex or simpler structures did not reduce AICc: no radiotransmitter functioned longer than 7 years and the model predicted an accumulated probability of radiotransmitter functioning in its 8th year of 0 (results not shown). We selected the structure of model Np4 to test for differences in survival between age classes (Models Mv 4, Mv 7- Mv 12, Table 1) and to test for linear and quadratic age effects on survival (Models Mv 13 - Mv 14, Table 1). The best model in terms of AICc included 2 age classes on survival probabilities: a differential survival between first-year and older birds (Model Mv 11, Table 1). However, this model was close in terms of AICc to other models (Models Mv 11-Mv 13). Model averaged survival estimates (and SE) were: ϕ non-breeders age 1=0.92 (0.04), ϕ non-breeders age 2=0.99 (0.01), ϕ non-breeders age 3=0.97 (0.02), ϕ non-breeders age > 3=0.99 (0.01), and ϕ breeders of unknown age=0.98 (0.02) (Fig. 2). Resighting probabilities ranged from 0 to 0.31 (results not shown) and recovery probability was 0.43 (SE=0.33).

Red kite survival

The modeling of age effects on survival probabilities of red kites showed that first-year birds (i.e., juveniles) presented a different survival rate than older birds because the models considering no age-effects (Model Mm 4, Table 2) or no differences between juveniles and subadults (2 years old) were rejected in terms of AICc (Model Mm 3, Table 2). The models considering equal survival of adults (older than 2 years old) and subadults (Model Mm 2, Table 2) or full age differences (Model Mm 1, Table 2) were close in terms of AICc. Consequently, we used both structures of survival (Model Mm 1-Mm 2, Table 2) to model the probabilities of the different mortality causes. The best models included differences in mortality causes between young birds (including juveniles and subadults) and adults (Models Mm 6 and Mm 9, Table 2). However, models considering no age effects on the probabilities of dying due to the different mortality causes were also close in terms of AICc (Models Mm 7 and Mm 10, Table 2). Model averaged survival estimates (and SE) were: ϕ juveniles (age 1)=0.54 (0.04), ϕ subadults (age 2)=0.83 (0.04) and ϕ adults (age ≥ 3)=0.84(0.05) (Fig. 2). Model averaged estimates of mortality causes showed that birds mainly died by poisoning, followed by electrocution, unknown and natural causes and wind farm collision (Fig. 3). Although confidence intervals overlap, mortality by poisoning seemed to be higher for adults than for subadults and juveniles (Fig. 3).

Comparison of survival with mainland and other island populations

Non-breeding Egyptian vultures from sedentary populations (aged 1 to 7), Menorca and Canary, survived significantly better than individuals from the Ebro or the Andalusia migrant populations (Fig. 2, Table 3). Non-significant differences in breeder survival between adult breeders from Andalusia, Menorca and Canary were found but breeders from the Ebro population had a lower survival than breeders from Menorca and Andalusia (Fig. 2, Table 3). Survival in the migrant populations (Andalusia and Ebro) only differed significantly for non-

breeders aged 5 and breeders, being higher for the Andalusia population (Fig. 2, Table 3). Survival in the resident populations (Menorca and Canary) only differed significantly for non-breeders aged 2, 4 and 5, being higher for the Menorca population (Fig. 2, Table 3).

We did not find significant differences in red kite adult survival (birds older than 2 years old) between the three considered populations (Fig. 2, Table 4). Subadult survival in Menorca birds was significantly higher than in the Swiss population and similar to survival on Mallorca Island, which presented intermediate values and no differences from the Swiss population (Fig. 2, Table 4). Juvenile survival was significantly higher in Mallorca than in Menorca or Swiss populations, which showed no significant differences (Fig. 2, Table 4).

DISCUSSION

Our study demonstrates that insular sedentary populations of long-lived birds had higher survival rates, especially among young birds, than their mainland migrant counterparts. Moreover, these differences were consistent among two different species inhabiting Mediterranean and Macaronesian archipelagos. This result is in agreement with the observed higher survival rates of resident and short-distance migrant individuals among partial migratory mainland populations of other long-lived birds such as white storks (Schaub et al. 2004), greater flamingos (Sanz-Aguilar et al. 2012) and spoonbills *Platalea leucorodia leucorodia* (Lok et al. 2013). In fact, no density-dependent effects on the survival of the Seychelles warbler *Acrocephalus sechellensis* (Brouwer et al. 2009) or survival differences between resident populations of blue tits *Parus caeruleus* on Corsica Island and the French mainland (Blondel et al. 1992) were found. This suggests that migratory behavior may play a more important role in avian survival than insularity per se.

Age-related improvement in survival expectancies is typical among long-lived birds, such that juveniles have higher mortality rates than adults (Newton 1989). Accordingly, we found that juvenile (i.e., first-year) Egyptian vultures and red kites in the studied population

had lower survival probabilities than adults. The relative difference between juvenile and adult breeder survival on Menorca Island, however, was smaller (Egyptian vultures =5%, red kites= 36%) than those reported for migrant populations (Andalusia Egyptian vultures =22%, Ebro Egyptian vultures =12%, Swiss red kites=52%) (Grande et al. 2009; Kéry and Schaub 2012; Sanz-Aguilar et al. 2015). Similarly, and in accordance with the results obtained for the studied population, sedentary populations of Egyptian vultures in the Canary Islands and red kites on Mallorca Island also showed small differences between juvenile and adult survival (1% and 9%, respectively, (Donazar et al. 2002; Tavecchia et al. 2012)). In summary, age had a milder influence on survival rates in sedentary island populations because of the higher survival probabilities shown by the youngest fraction of the populations.

Egyptian vultures are more long-lived and have a lower fecundity than red kites. Survival differences between age classes were lower for the Egyptian vulture than for the red kite (see above), which is in accordance with the life-history fast-slow continuum (Sæther and Bakke 2000). The red kite population on Mallorca Island, however, showed small survival differences between juveniles and adults (9%, Tavecchia et al. 2012). High juvenile survival rates have been reported for sedentary raptor populations supplemented with food (Sarrazin et al. 1994; Oro et al. 2008) because it can buffer the effect of illegal poisoning and other mortality factors (Oro et al. 2008, 2013; Tavecchia et al. 2012). We are confident that this was the most plausible explanation for the high survival rate of juvenile red kites in Mallorca (Tavecchia et al. 2012; Tenan et al. 2012). In fact, these rates were the highest ever reported for this species (see Newton et al. 1989; Knott et al. 2009, Smart et al. 2010; Kéry and Schaub 2012; Bellebaum et al. 2013). On the contrary, on Menorca Island there are no supplementary feeding programs. This could explain the differences in juvenile survival between neighboring islands even when the relative incidence of human-induced mortality factors (poisoning and, to a lesser extent, electrocution) was very similar (Tavecchia et al. 2012; Tenan et al. 2012).

298 That said, it should be noted that even given the high levels of human-induced mortality,
299 juvenile and subadult survival of red kites in both Balearic islands (Mallorca and Menorca)
300 were higher than those found for individuals from the Swiss migrant population (Kéry and
301 Schaub 2012), which is not affected by illegal poisoning in its breeding area (Knott et al.
302 2009).

303 Non-breeding Egyptian vultures in Menorca showed higher survival rates than in any
304 other studied population (Donazar et al. 2002; Grande et al. 2009; Sanz-Aguilar et al. 2015).
305 The survival differences between island populations may be due to additional mortality
306 factors (causalities with power lines) heavily affecting Egyptian vultures at Canary Islands
307 (Donazar et al. 2002). Contrary to red kites, Egyptian vultures in Menorca were scarcely
308 affected by non-natural human-related mortality. This may be due to different non-exclusive
309 factors: 1) red kites are distributed throughout the island whereas Egyptian vultures are
310 concentrated on the eastern side where illegal poisoning is less common (authors' own
311 observations); 2) the diet of Egyptian vultures relies more heavily on livestock carcasses and
312 less so on small game than red kites (Congost and Muntaner 1974; authors' own data); and 3)
313 Egyptian vultures use trees and cliffs instead of power lines for communal roosting (Congost
314 and Muntaner 1974; authors' own data).

315 In contrast to juvenile survival, differences in adult/breeder survival between migrant
316 populations were probably more closely related to local human-related mortality factors in
317 breeding areas (Carrete et al. 2009; Hernández and Margalida 2009; Smart et al. 2010; Schaub
318 2012). There is no doubt that long-distance migration entails costs (Alerstam et al. 2003),
319 including mortality during migration (Newton 2006) and/or at wintering areas (Schaub et al.
320 2005; Sergio et al. 2011). However, migratory mortality costs may be much more important
321 for young and inexperienced individuals (Mihoub et al. 2010; Sanz-Aguilar et al. 2012;
322 Sergio et al. 2014). In fact, Egyptian vultures from the Andalusia and Ebro breeding

populations, showed differences in adult survival but not in juvenile and pre-breeding survival. Pre-breeder survival was probably dependent on environmental conditions in their common African wintering areas thus equally affecting individuals from all of the Iberian populations (Grande et al. 2009; Carrete et al. 2013; Sanz-Aguilar et al. 2015).

Small sedentary populations on islands face reduced fitness due to inbreeding depression (Lande 1988). Genetic diversity has been shown to negatively affect recruitment (i.e., delayed reproduction) and breeding success in the Egyptian vulture in the Canary Islands (Agudo et al. 2012). Similarly, the species also presents a very low breeding success on Menorca Island (authors' own data). However, these detrimental effects on productivity may be compensated for by high survival expectancies such as those demonstrated by our results. This fact, in combination with an earlier age at first reproduction among sedentary long-lived birds on islands (Ferrer et al. 2011), may facilitate their persistence and be responsible for the very high densities reached in populations without human-related mortality (Bannerman et al. 1968; De Pablo 2004; Gangoso et al. 2013). In fact, there are numerous small populations of raptors on islands that have persisted with low numbers for at least more than a century (Bannerman et al. 1968; Walter 1990) and even the studied population of red kites is recovering from a minimum population size of 6 breeding pairs. For its part, the Egyptian vulture population on Menorca has remained stable around 50 breeding pairs over the last 10 years (which is the maximum population size ever recorded on this island, authors' own data). None of the vultures marked as young were observed breeding during the study period, which also suggests that density-dependence processes influencing recruitment are acting in this population (Ferrer et al. 2011). In conclusion, although small populations are always subject to environmental and demographic stochasticity effects, our study highlights the potential of persistence of long-lived raptors on islands due to their high survival prospects in the absence of human-related mortality factors.

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356

CONFLICT OF INTEREST

357 The authors declare that they have no conflict of interest.

358

ETHICAL APPROVAL

359 All applicable institutional and/or national guidelines for the care and use of animals were

360 followed.

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Table 1. Modeling of radiotrasmmitter functioning (η), survival (ϕ), resighting and recovery probabilities of Egyptian Vultures on Menorca Island. Notation, np: number of parameters; Dev: relative deviance; AICc: Akaike information criterion corrected for sample size; Δ AICc: the AICc difference between the current model and that with the lowest AICc value; w : Akaike's weight. Model notation: numbers indicate the number of age classes "a" considered, A indicates a linear age trend and A² a quadratic age trend. Note that all models considered constant adult survival, constant recovery probabilities and time-dependent resighting probabilities. The model with the lowest AICc is in bold.

Model	η	ϕ	np	Dev	AICc	Δ AIC	w
Mv 1	a7	a7	36	437.4	520.27	15.14	0.00
Mv 2	A7	a7	31	442.59	512.53	7.40	0.01
Mv 3	a8	a7	37	436.24	521.76	16.63	0.00
Mv 4	A8	a7	31	441.98	511.92	6.79	0.01
Mv 5	a6	a7	35	438.89	519.13	14.00	0.00
Mv 6	A6	a7	31	444.22	514.15	9.02	0.00
Mv 7	A8	a6	30	442.27	509.68	4.55	0.03
Mv 8	A8	a5	29	442.79	507.69	2.56	0.07
Mv 9	A8	a4	28	443.23	505.65	0.52	0.20
Mv 10	A8	a3	27	446.42	506.37	1.24	0.14
Mv 11	A8	a2	26	447.63	505.13	0.00	0.26
Mv 12	A8	a1	25	452.37	507.45	2.32	0.08
Mv 13	A8	A7	26	449.12	506.63	1.50	0.12
Mv 14	A8	A ² 7	27	447.92	507.87	2.74	0.07

Table 2. Modeling of survival (ϕ) and mortality probabilities by different causes (ω) of red kites on Menorca Island. Notation, np: number of parameters; Dev: relative deviance; AICc: Akaike information criterion corrected for sample size; Δ AICc: the AICc difference between the current model and that with the lowest AICc value; w : Akaike's weight. Model notation: j=juveniles (age 1), sa=subadults (age 2), ad=adults (age $\geq$ 3), = and $\neq$ indicate no differences and differences between the age classes considered, respectively. The model with the lowest AICc is in bold.

Model	ϕ	ω	np	Dev	AICc	Δ AIC	w
Mm 1	j $\neq$ sa $\neq$ ad	j $\neq$ sa $\neq$ ad	13	439.61	466.46	7.09	0.01
Mm 2	j $\neq$ sa=ad	j $\neq$ sa $\neq$ ad	12	439.88	464.61	5.24	0.03
Mm 3	j=sa $\neq$ ad	j $\neq$ sa $\neq$ ad	12	453.42	478.14	18.77	0.00
Mm 4	j=sa=ad	j $\neq$ sa $\neq$ ad	11	460.72	483.33	23.96	0.00
Mm 5	j $\neq$ sa=ad	j $\neq$ sa=ad	10	443.25	463.77	4.39	0.05
Mm 6	j$\neq$sa=ad	j=sa $\neq$ ad	8	443.04	459.38	0.00	0.41
Mm 7	j $\neq$ sa=ad	j=sa=ad	6	448.36	460.56	1.18	0.23
Mm 8	j $\neq$ sa $\neq$ ad	j $\neq$ sa=ad	11	442.99	465.60	6.22	0.02
Mm 9	j $\neq$ sa $\neq$ ad	j=sa $\neq$ ad	9	442.77	461.19	1.81	0.17
Mm 10	j $\neq$ sa $\neq$ ad	j=sa=ad	7	448.09	462.35	2.98	0.09

Table 3. Comparison of the Egyptian vulture average non-breeder (NB) and breeder (B, aged ≥ 5) survival estimates (Z-test) among the populations of Menorca (ME, sedentary), Andalusia (AN, migratory), Ebro (EB, migratory) and Canary (CA, sedentary). Significant effects (two-sided $p < 0.05$) are in bold.

	ME vs. AN	ME vs. EB	ME vs. CA	AN vs. EB	AN vs. CA	EB vs. CA
NB age 1	3.52	4.52	0.60	-0.16	-2.51	-3.02
NB age 2	6.30	11.99	2.05	0.00	-2.51	-3.02
NB age 3	5.35	5.24	1.61	-1.00	-2.51	-1.89
NB age 4	6.24	6.56	2.04	-1.00	-2.51	-1.89
NB age 5	6.23	7.59	2.04	2.03	-2.51	-4.14
B	0.81	4.77	0.80	2.46	0.41	-0.67

Table 4. Comparison of the red kite average survival estimates (Z-test) among the populations of Menorca (ME, sedentary), Mallorca (MA, sedentary) and Switzerland (SW, migratory). Significant effects (two sided $p < 0.05$) are in bold.

	ME vs MA	ME vs SW	MA vs SW
Juveniles (age 1)	-2.02	0.93	1.96
Subadults (age 2)	0.10	2.23	1.46
Adults (age ≥ 3)	0.49	-0.02	-0.54

Figure 1. Study areas and species. Survival rates were estimated for Egyptian vultures (EV) and red kites (RK) living in 1: Menorca Island. Results were compared with those obtained in other studies from 2: Mallorca Island, 3: Canary Fuerteventura Island, 4: Ebro Valley, 5: Andalusia, 6: Switzerland.

Figure 2. Population specific age-dependent survival estimates (and 95% CI) of Egyptian vultures (A) and red kites (B). Sedentary populations are denoted with black symbols and migratory populations with empty symbols.

Figure 3. Probabilities of juvenile, subadult and adult red kite mortality (and 95% CI) by the different causes considered (poisoning, electrocution, collision, natural and unknown causes).

Figure 1

Figure 2

Figure 3