Variation in age-structured vital rates of a long-lived raptor: Implications for population growth

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Abstract

Age-structured variation in multiple vital-rates is a fundamental determinant of population growth, with important implications for conservation management. However, for many long-lived vertebrates such as birds of prey, such variation has been usually examined in shorter-lived species. Here, we investigate the pattern of age-related variation in fitness components and its repercussions on population growth for a migratory raptorial bird, the black kite (Milvus migrans), with a longer lifespan than most other previous model species. Both survival and offspring production varied along the lifespan in conjunction with the sequence of major life history stages: they were lowest during the initial years of life, increased steeply during the period of progressive incorporation of floaters in the breeding sector of the population (age 2–6), levelled off between 7 and 11 years of life, declined with senescence after age 12, and increased again for the few high-quality individuals capable of reaching age 18–25. This pattern was more gradual, asymmetrical and protracted than in shorter-lived species. Matrix modelling estimated a stationary growth rate, which was more sensitive to changes in survival in early life rather than to survival in adult life, contrary to expectations for long-lived species. Our results highlight: (1) a growing appreciation of the importance of juvenile survival for population dynamics, (2) the need for caution on the generalization that population-trends of long-lived species are primarily determined by adult survival, and (3) that the trajectory of the breeding populations of migratory species may be determined by environmental variation experienced in early life in staging areas located far away from breeding areas.

Zusammenfassung

Die altersbedingte Variation bei vielen Vitalparametern ist ein fundamentaler Faktor bei der Bestimmung des Populationswachstums mit wichtigen Auswirkungen auf das Naturschutzmanagement. Dennoch wurde bei langlebigen Wirbeltieren, wie z. B. Greifvögeln, diese Variation gewöhnlich nur bei kurzlebigeren Arten untersucht. Hier untersuchten wir die Muster der altersbedingten Variation der Fitness-Komponenten und ihre Rückwirkungen auf das Populationswachstum bei einem ziehenden Greifvogel mit einer längeren Lebenserwartung als die bisher untersuchten Modellarten, dem Schwarzmilan

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Introduction

Obtaining robust estimates of age- or stage-dependent vital rates and population structure is essential for the study of population functioning (Caswell 2001; Sibly, Hone, & Clutton-Brock 2003). For example, individuals of different age and experience may survive at different rates in response to the same environmental stressors, so that population variation can only be explained by taking into account the effect of an age-by-time interaction on vital rates (e.g. Saether et al. 2000). As a consequence, detailed knowledge of age-related variation in vital rates is a fundamental pre-requisite for effective population management and conservation (Wisdom, Mills, & Doak 2000; Sibly & Hone 2002).

Advances in demography in the last decades have recurrently highlighted two novel aspects. First, there is a growing appreciation of the differential contribution of different vital rates and their variability to population growth (Saether & Bakke 2000; Wisdom et al. 2000; Caswell 2001). Such contribution varies along a continuum ranging from short-lived species, for which fecundity is a major determinant of population dynamics, to long-lived species, whose population growth is usually thought to be most dependent on adult survival (Heppell, Caswell, & Crowder 2000; Saether & Bakke 2000). Second, a growing emphasis on long-term studies facilitates increasing access to datasets on individual life histories long enough to cover the variation in vital rates along the whole lifespan of the target species. In turn, this allows to capture a more realistic picture of population dynamics even for longer-lived species, whose demography has been traditionally elusive to model.

Despite the above, and with the exception of some mammalian herbivores and seabird species (e.g. Gaillard, Festa-Bianchet, & Yoccoz 1998; Schreiber & Burger 2002), comprehensive analyses of age-related variation in multiple vital rates are still rare for many long-lived animal groups, largely because of the enormous amount of field effort necessary to describe the fates of large numbers of individuals composing the population. One such group includes birds of prey, despite the importance of such species in terms of ecological role and threatened status, and despite the great attention and funding traditionally devoted to these charismatic taxa. With few exceptions (e.g. Green, Pienkowski, & Love 1996; Kenward, Marcström, & Karlbom 1999; Ferrer, Otalora, & García-Ruiz 2004; Whitfield, Fielding, Mcleod, & Haworth 2004; Anthony et al. 2006), comprehensive demographic analyses on these species have mainly focused on smaller-sized, shorter-lived species (e.g. Newton & Rothery 1997; Hakkarainen, Korpinimay, Koivunen, & Ydenberg 2002; Altweeg, Roulin, Kestenholz, & Jenni 2003; Karell, Ahola, Karstinen, Zolei, & Brommer 2009). Even among these, we are aware of only one study which has provided a comprehensive picture of variation in multiple vital rates along the whole lifespan of the study species (Newton & Rothery 1997). More commonly, fitness components are reported for the first years of life, but pooled altogether for all the older age-classes. This is mostly done because the exact age of older birds is unknown (e.g. individuals were marked when adult) or is available for only a small fraction of individuals. All the above leaves open the question of whether the patterns observed so far on shorter-lived species also apply to larger, longer-lived ones. For the latter, existing information reflects the daunting task of collecting data over several decades, and is mainly obtained from introduced or artificially maintained populations (Green et al. 1996; Sarrazin & Legendre 2000), it typically concerns only one fitness component (e.g. Oro, Margalida, Carrete, Heredia, & Donáz 2008; Grande et al. 2009), is based on one or two coarse age classes (e.g. comparison of immatures vs. adults; Kenward et al. 1999; Ferrer et al. 2004; Sulaw, Robert, Köppen, Hauff, & Krone 2010), or is indirectly or partially estimated thorough various assumptions or modelling simulations (e.g. Wootton & Bell 1992; Kenward et al. 1999; Whitfield et al. 2004; Krüger, Grünkorn, & Struwe-Juhl
2010). Such lack of comprehensive information is particularly important because longer-lived species are frequently threatened and population management is increasingly based on population viability analyses that use educated guesses or parameters borrowed from other populations (Wootton & Bell 1992; Katzner, Bragin, & Milner-Gulland 2006; Krüger et al. 2010).

Here, we use a data-rich sample to provide a comprehensive account of age-structured variation in multiple vital rates and of its repercussions on population dynamics for a long-lived raptorial species, the black kite (*Milvus migrans*, maximum observed lifespan of 25 years). In particular, we (1) examine age-related variation in offspring production and survival, (2) estimate the population growth of the population through deterministic matrix modelling, and (3) assess the contribution of different age-dependent vital rates to population growth. We show that larger species may be characterized by more complex variation in fitness components across age-classes than previously appreciated and that assumptions on age-dependent parameters might lead to incorrect or oversimplified management guidelines. For example, current generalizations about the importance of adult survival for population growth may not hold systematically across all long-lived species, and the pre-breeding stage of the life-cycle, i.e. before the age of full recruitment, might play a more important role than generally assumed (see also Whitfield et al. 2004; Katzner et al. 2006).

**Materials and methods**

**Study species and data collection**

We studied the black kite, a medium-sized, migratory raptor (adult body mass in our population ∼700–1200 g; Sergio, Blas, Forero, Donazar, & Hiraldo 2007) in a 430 km² plot located in Doñana National Park (south-western Spain). In this population, the age of first territorial establishment ranges between 1 and 7 years and the maximum recorded lifespan is 25 years (Blas, Sergio, & Hiraldo 2009; unpublished data). Observed breeding and natal dispersal distances are short (median 302 m and 4800 m, respectively) and intensive, spatially extensive multi-year surveys suggest an extremely low rate of emigration to other populations (Forero, Donázár, & Hiraldo 2002). This ensures that modelled survival should not be confounded or biased by emigration.

In all analyses, we employ data collected between 1986 and 2009. Since 1986, the nestlings were marked with a white Darvic ring with a black three-character alphanumeric code, which can be read by telescope from a distance. Even if ringing activities started earlier (since 1964), it was only after 1989 that a standard protocol for systematic resighting was established (Sergio, Blas, & Hiraldo 2009). We analysed 6543 reencounters of 4581 kites born in Doñana National Park and marked as nestlings at the time of fledgling. As a consequence, we know the exact chronological age of all birds in the dataset. Encounters included birds resighted on their territories, on carrion-baits or at communal roosting sites. Birds of different age or breeding status may be differentially detected by each of these methods: readings at territories mostly recorded breeders, readings at roost-sites mainly included non-breeding, younger individuals, while ring-readings at carrion-baits included birds of all ages and status (Sergio et al. 2009). Because the type of resighting (on territory, at carrion-baits or at roost-sites) was recorded only since 1996, all three encounter types were pooled in a single dataset and analysed together. This probably increased the level of recapture heterogeneity (see section ‘Results’), but allowed us to include in the analysis data collected before 1996, thus increasing the number of old birds in the analysis. When a marked bird was detected on a territory, the area was visited weekly to locate its nest and to record clutch size and the number of chicks raised to fledging age (40–45 days old, Blas et al. 2009). No further ring-readings were conducted during such nest checks (i.e. such territories did not receive a subsequent higher ring-reading effort).

**Modelling survival and encounter probabilities**

Survival and reencounter probabilities were modelled simultaneously as a function of age, year of observation, and their statistical interactions, and estimated by maximum likelihood methods (Lebreton, Burnham, Clobert, & Anderson 1992). Hereafter, the effect of the year of observation is defined as “time” and noted ‘t’ to conform to classical terminology in survival analyses (Lebreton et al. 1992). Following Catchpole, Morgan, Coulson, Freeman, and Albon (2000), we first considered the effect of age alone to detect the best age structure. In doing so, we modelled one parameter at a time while keeping the others as general as possible (e.g. Grosbois & Tavecchia 2003). Once the best age structure was detected, we considered the effect of the year of observation within each age class. Finally, we built additive models to verify whether year-to-year variation had a similar effect in all age classes (parallel variation of survival across ages).

Model notation was complex because a given effect can be important for one age class or parameter, but not for others. We choose a model notation similar to the one used in Catchpole et al. (2000), in which each modelled parameter was separated by a “/” symbol. The model assuming a full age effect (22 age classes) for the survival probability, \( \phi \), and for the reencounter probability, \( p \), was then denoted \( \phi_0/\ldots/\phi_{22}/p_0/\ldots/p_{22} \). The subscript indicates the age of the bird and the symbol “/” indicates that all ages in between were modelled separately. To simplify model structure, we grouped in a single class the age parameters with similar values. In model notation, such age-classes will be denoted by the first and the last age of the class joined by the under score symbol “_”. For example, a model assuming only two age classes for survival, the first including ages from 0 to 10 and the second from 11 to 24, will be denoted as...
\( \phi_{0,10}/\phi_{11,24} \). The effect of year of observation was denoted in parentheses after the parameter as \( \phi_{0,10}(t)/\phi_{11,24}(t) \). When the two parameters were assumed to vary in parallel over time (i.e., no interaction effect), the notation was \( \phi_{0,10}(t)/\phi_{11,20}(t) \). We began the analysis of encounter histories by a goodness of fit test (Choquet, Reboulet, Lebreton, Gimenez, & Pradel 2003) of a general model including the effects of age, year of observation and their statistical interaction on survival and recapture probabilities, noted as \( \phi_{0}(t)/.../\phi_{22}(t)/p_{0}(t)/.../p_{22}(t) \).

Model selection was based on the Akaike’s Information Criterion (AIC, Burnham & Anderson 2002) calculated as the model deviance plus twice the number of estimable parameters in the model. The AIC value for each model was calculated using the program M_SURGE (Choquet, Reboulet, Pradel, Gimenez, & Lebreton 2003). In addition, we calculated the AIC weight of each model as a measure of its relative ‘plausibility’ (Burnham & Anderson 2002). Models with similar AIC values should be considered equivalent. During the early stages of the analysis, when our interest was mainly in detecting the correct age-structure, we simply retained the model with the highest AIC weight. However, when estimates were used to parameterise the transition matrix (see below), their values were derived as a weighted mean using the weight of each model (i.e., model averaging, Burnham & Anderson 2002).

**Modelling breeding performance**

We employed the number of fledged young per breeding attempt, denoted \( F \), as a measure of reproductive performance and investigated its age-structure through multiple regression (GLM with Poisson errors and a log-link structure). Model notation and selection were the same as detailed above for the survival analyses. Data were available for 1380 nesting attempts by known-age individuals.

**Matrix population model and perturbation analyses**

The age-dependent values of survival and fertility were included into an age-structured demographic matrix, \( M \) (Caswell 2001; Appendix A). The matrix \( M \) describes the transition of the population between two consecutive years, \( t \) and \( t+1 \). The matrix is of dimension \( n \times n \) where \( n \) corresponds to the number of age classes detected. The asymptotic population growth, \( \lambda \), is calculated as the dominant eigenvalue of \( M \) (Caswell 2001). In a stable population, \( \lambda \) is equal to 1, while lower values indicate a declining trend. To account for the stochastic variation of parameters, the value, \( \alpha_j \), of each vital rate for the age class \( j \), was randomly drawn from a truncated normal distribution, \( tN(\pi_j, \sigma_j) \), with probability mean \( \pi \) and variance \( \sigma^2 (\pi_j) \) and its variance were derived by the analysis of individual based information; Appendix A). We also included demographic stochasticity, the variation due to the random process of mortality and reproductive success within the population by using a value, \( \theta_j \), drawn from a binomial distribution \( B(\theta_j, \alpha_j) \), with probability \( \alpha \) and population size \( P \) for each class \( j \), following Katsner et al. (2006). Because the Doñana population is around 1500 individuals, \( P \) was assumed to be 100 individuals for each age class. The population growth rate including stochasticity, noted \( \lambda_s \), and its variance were calculated as the average values from 1000 simulations. We compared these values with the deterministic population growth rate (\( \lambda_d \)), which was estimated using the average values \( \pi_j \) and \( \sigma_j^2 \). The 95% confidence interval of \( \lambda_d \) can be calculated combining parameter variances with their respective sensitivity (Lande 1988). The difference of the two population growth rates, as the parameter notation suggests, is that \( \lambda_d \) was calculated using the average values of the parameters while \( \lambda_s \) was calculated by randomly drawing each parameter value from its estimated distribution. Finally, we used perturbation analyses to calculate the sensitivity, \( S \theta \), and elasticity, \( E \theta \), of the population growth rate to a given parameter \( \theta \) (Caswell 2001). Sensitivity is the change in population growth rate in response to an absolute change of a given parameter \( \theta \), while elasticity is the change in the population growth rate in response to a proportional change of a given parameter \( \theta \). All analyses were implemented with program R (R Development Core Team 2009).

**Results**

**Age-structured survival**

The goodness-of-fit test of the general model \( \phi_{0}(t)/.../\phi_{22}(t)/p_{0}(t)/.../p_{22}(t) \) indicated a large residual deviance \( \chi^2_{183} = 261.60, p < 0.0001 \). This lack of fit was probably due to the inclusion of different types of resighting, which might have increased the heterogeneity in encounter probability across individuals. As a consequence, deviances were typically inflated and were scaled using a variance inflator factor \( \hat{c} = \chi^2/d.f. = 261.60/183 = 1.42 \). Note that recapture heterogeneity can be partially accommodated in capture–recapture models by modifying the encounter histories (Pradel 1993; Tavecchia, Minguez, De León, Louzao, & Oro 2008). However, by doing this, recapture and survival cannot be fully age-dependent simultaneously as the model including trap-dependence and transient-effects becomes parameter redundant (Tavecchia, Pradel, Genovart, & Oro 2007). Because recapture and survival are expected to change with age, we preferred to correct model deviances by a scale parameter.

The retained model-structures for encounter probabilities and for survival were not the same (Table 1). Encounter probabilities and survival increased constantly with age, but recapture had a more complex age-structure than survival. The effect of time was retained in all age-classes (Table 2). For survival, virtually all the top models gave indication of a complex age-structure incorporating a survival-decline in
Table 1. Models of encounter probability (A), age-structured survival (B) and offspring production (C) (number of nestlings raised to fledging age, see text). (A) and (B) are based on capture–recapture data for 4581 black kites marked as fledglings, and (C) is based on 1380 nesting attempts by individuals of known age sampled in Doñana National Park (Spain). **Notation:** np, number of parameters in the model; AIC, Akaike’s Information Criterion; ΔAIC, difference in AIC-value between the target model and the model with the lowest AIC; AICw, Akaike weights; φ, survival probability; p, reencounter probability; F, number of fledged young. The best model (highest AIC weight) is highlighted in bold. See section ‘Materials and methods’ for details. For conciseness of presentation, we report only the 10 best competing models. The complete list of models is available on request from the authors.

<table>
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<tr>
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<th>ΔAIC</th>
<th>AICw</th>
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<td>219</td>
<td>8868.00</td>
<td>0</td>
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<td>p1/p2/3p6/7_16/17p20/21 22</td>
<td>6</td>
<td>219</td>
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<td>2.41</td>
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<td>p1/p2/3p6/7_13/p14_16/p17_20/p21 22</td>
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<td>220</td>
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<td>4.15</td>
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<td></td>
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<td></td>
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<td>22.20</td>
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<td></td>
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<td>5</td>
<td>233</td>
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<td>233</td>
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<td>(C) Offspring production</td>
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<td>F1 2/F3 6/7 25</td>
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</table>

*Age modelled as a continuous variable.

Table 2. Model structure and percentage of explained variance. Variations in survival among-years were more pronounced for younger birds than for adults. The percentage of variance explained by variations among-years (%) decreased with age. **Notation:** DEV, model deviance; AIC, Akaike’s Information Criterion.

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<th>Model</th>
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</table>
Fig. 1. Variation in (A) survival and (B) offspring production (number of nestlings raised to fledging age) across age-classes of black kites in Doñana National Park (Spain). Survival estimates are based on 6543 reencounters of 4581 kites marked as fledglings. Estimates of offspring production are based on 1380 nesting attempts by kites of known age. All estimates are means ± 1 SE.

older ages (Table 1). According to the best model, survival was minimal in the first year of life, it increased steeply after age 2, it levelled-off for ages 7–11, it declined after age 12 and increased again for the few individuals capable of reaching ages older than 18 (Fig. 1A). For the oldest age class, survival and encounter probabilities were estimated to be 1.00. While this is an unrealistic value for survival probably exaggerated by the small sample size (only 18 individuals belonged to this group), it does suggest that survival may be high for this tail of the population. Accumulation of larger samples in future years will allow more realistic estimates of survival rates of very old birds. We did not consider this issue further in our population model.

Age-structured breeding performance

In the best model (Table 1C), breeding output was minimal for first and second year birds, intermediate for individuals of 3–6 years of age, it peaked at ages 7–11 and declined slightly after age 12 (Fig. 1B, Appendix A).

Population model and perturbation analyses

The stochastic population growth rate $\lambda_s$ was 0.991 (se = 0.024; 95% CI: 0.941–1.037), which suggested a stable population. A regression of nest counts on year also yielded a stable trend in numbers (slope = 0.009 ± 0.003). The value of $\lambda_d$, calculated using a deterministic model, indicated a similar result ($\lambda_d = 0.991$, se = 0.015; 95% CI: 0.961–1.021). As expected, the variation associated with the stochastic value was larger than the one calculated through the deterministic model. Both elasticity and sensitivity analyses gave the same indications with values decreasing with age (Fig. 2). The population growth rate was least sensitive to changes in the average value of fledglings production ($E(F) = 0.143; S(F) = 0.224$) and most sensitive to variations in average survival probability ($E(\phi) = 0.857; S(\phi) = 1.08$; Fig. 2). However, when considering survival during different stages of the life cycle, the population growth rate was more affected by an overall change in survival parameters up to age 7 (the maximum age of first breeding) than by changes in survival during the later years of life (all parameters considered: $E(\phi_{0-6}) = 0.61; E(\phi_{7-22}) = 0.37$, respectively).

Discussion

We showed a detailed, comprehensive pattern of age-structured variation in multiple vital rates for a raptorial species with a maximum lifespan of 25 years. Both reproduction and survival rates varied in a more complex manner.
along the lifespan of the population than previously reported for shorter-lived raptors (e.g. Korpinäkkä 1992; Newton & Rothery 1997; Karell et al. 2009). Survival showed a very abrupt increase from the first to the second year of life, suggesting a very strong mortality-peak and selection-episode during the first migration and wintering stages. Later variations in survival were never as abrupt, but fitted well the sequence of major life-history stages of the species: (1) survival was rather stable between ages 2 and 6, which is the period of progressive incorporation of floating individuals into the breeding population (Sergio et al. 2009); (2) it increased and reached a plateau at age 7–11, when virtually all individuals have recruited into the breeding population and breeding performance is highest (Blas et al. 2009); (3) it declined to lower senescent levels between ages 12 and 17; and (4) it increased again to very high levels after 18 years of life. The survival of this last age-class was not considered in population modelling as it refers to only few individuals. Mortality plateaus like this are increasingly found in data-rich samples, for example in human demography (Pletcher & Curtsanger 1998). Although this has important implications for the evolution of senescence (Weitz & Faser 2001), it has little influence on population dynamics and will be examined in more detail after the accumulation of larger samples in the future. Fledglings production followed a pattern rather similar to the one depicted for survival: (1) it was extremely low during the initial breeding attempts in the first 2 years of life; (2) it increased to higher levels for ages 3–6 when many birds in the population were still breeding for the first time(s) and accumulating experience (Blas et al. 2009); and (3) it levelled-off at maximum levels after age 7. Compared to previous studies on similar taxa, the above-described pattern highlights two important points. First, previous studies have usually pooled all adult-individuals (aged >1–2 years old) in a single age-class. This may obscure much variation in age-structured vital rates as well as the relative importance of different phases of the life-cycle in determining population growth rates, potentially leading to oversimplified views of population functioning (e.g. Zabel & Levin 2002) and, ultimately, to incorrect management guidelines (see below).

Second, previous analyses on shorter-lived species have reported steep improvement and deterioration of fitness components with age (e.g. Newton & Rothery 1997). Such dynamic, rapid changes may not apply to longer-lived species, which may be characterized by more gradual, complex and protracted variations in vital rates, as seen in various seabirds (e.g. Newton 1989; Nisbet 2001). For example, restraint strategies, by which individuals refrain from costly activities, may be more viable for longer-lived animals and dilute the costs of reproduction through optimal allocation of age at first breeding (e.g. Weimerskirch 1992). In agreement with this idea, similarly complex variations in survival along multiple age-stages has been reported by the only other study which examined detailed, age-related variation in survival for a long-lived raptor, the Egyptian vulture (Neophron percnopterus, Grande et al. 2009). This is even more remarkable given that the study did not cover the whole lifespan of the species (Grande et al. 2009). All the above suggests that our current picture of raptor demography may be over-simplified and biased towards the life-history strategies of shorter-lived species. Longer-lived eagles and vultures, which are more frequently imperilled and in need of robust management plans, may need modelling exercises based on more complex and realistic demographic estimates (see Kelly & Durant 2000 for similar reasoning).

Results of the elasticity analyses suggested that the stationary growth rate of the population was most dependent on survival in the first few years of life. Although our results are consistent with those reported in two previous studies on raptors (e.g. Whitfield et al. 2004: golden eagles Aquila chrysaetos, Katzner et al. 2006: imperial eagles Aquila heliaca), they were rather surprising given that long-lived species are usually expected to show higher elasticities for adult than for juvenile (i.e. before full recruitment) survival (Saether & Bakke 2000; Stahl & Oli 2006), as also observed in many previous studies on birds of prey (Wootton & Bell 1992; Hiraldo, Negro, Donázár, & Gaona 1996; Seamans & Gutiérrez 2007; Karell et al. 2009). We showed that changes in survival probability in the first 7 years of life (i.e. up until all birds are recruited in the breeding population; Sergio et al. 2009), affected the population growth rate more than changes in subsequent survival. The discrepancy of these results with previous studies could be caused by different reasons. The large sample used here, nearly unique in a study on long-lived raptors, allowed us to describe fine-scale variations in vital rates, otherwise frequently masked by a lack of statistical power. In this sense, we believe that our conclusions could apply to many other raptor species. However, we cannot exclude that the differences found are the results of specific biological processes acting in our population. For example, the marked mortality-peak in early life of this population may have accentuated the importance of survival in such early life stages. Also, the fact that improvements in performance in this population are promoted by positive selection for high-quality phenotypes in early life (Blas et al. 2009; Sergio et al. 2009) may contribute to exaggerate the importance of early processes of recruitment and survival at the population level. Finally, it should be noted that sensitivity and elasticity analyses are based on the analytical properties of the matrix model, among these the convergence to a stationary age distribution (Caswell 2001). In highly dynamic systems, this might lead to minor differences with other studies, such as those based on simulations (e.g. Katzner et al. 2006). However, given the small year-to-year variation in most parameters considered, we believe that in our case these differences were negligible. Whatever the mechanism causing the discrepancy with earlier studies, such results have three major implications: (1) they contribute to a growing awareness of the importance of survival in early life on population persistence and variation (e.g. Gaillard et al. 1998; Whitfield et al. 2004; Penteriani, Otalora, Sergio, & Ferrer 2005; Katzner et al. 2006); (2) they
stress how generalizations about the importance of different vital rates for population management should be taken with caution and, whenever possible, examined in detail for the species in question; and (3) they show that migratory populations like ours, where the initial years of life may be spent on another continent, may be regulated by factors operating far from the breeding quarters (e.g. Greenberg & Marra 2005). This may make their conservation management extremely challenging.

In conclusion, our population was characterized by a pronounced mortality-bottleneck in early life, followed by gradual improvements in performance, a mid-life plateau, and a less abrupt progression of senescence than observed in shorter-lived raptors. Unexpectedly, the population trajectory was found to be largely determined by survival before the age of full recruitment, which, in turn, may be affected by factors operating far from the breeding quarters. The appreciation of such complexity may be a key progress for conservation, given that management of vulnerable species is increasingly based on viability modelling (e.g. Kauffman, Frick, & Linthicum 2003; Schaub, Pradel, & Lebreton 2004; Katzner et al. 2006), which is often based on educated guesses or on parameters taken from other populations (Kelly & Durant 2000).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.baae.2010.11.004.

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