Effects of age, territoriality and breeding on survival of Bonelli's Eagle *Aquila fasciata*

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Survival typically contributes most to population trends in long-lived birds and its accurate estimation is therefore vital for population management and conservation. We evaluated the effects of age, territoriality and reproduction on survival in Bonelli's Eagle *Aquila fasciata* through multistate capture-mark-recapture analyses on a long-term dataset. Monitoring was carried out in southeast France (1990–2008) and involved the surveying of territorial Eagles, the marking of fledged chicks, and the recording of resightings and recoveries of marked non-territorial and territorial birds. Survival improved with age, but territoriality was not retained in the best model; yearly survival was estimated at 0.479 for fledglings (to 1 year of age), 0.570 for 1- and 2-year-olds, and 0.870 for 3-year-old and older individuals. The second best model supported a further increase in survival from 3-year-olds (0.821) to older individuals (0.880). In the third best supported model, territoriality enhanced survival, but only in 2-year-olds (0.632 vs. 0.562 for non-territorial). We found no correlation between the previous breeding stage and future survival, consistent with the long lifespan of the study species. Nevertheless, 4-year-old and older successful breeders were more likely to breed the following year than failed adult breeders (0.869 vs. 0.582), suggesting that the cost of reproduction is small in comparison with the variation in quality among individuals or their territories.

Keywords: birds of prey, *Hieraaetus fasciatus*, life history, raptors, vital rate estimation.

Life-history traits are the main determinants of population dynamics, and thus the understanding of life histories is central to basic and applied ecology. In long-lived birds, survival makes the highest contribution to population growth rate (Roff 1992, Sæther & Bakke 2000). Therefore, survival estimation is a prerequisite for effective population management and conservation of target long-lived species (Wisdom *et al.* 2000, Sibly & Hone 2002).

Survival generally improves with age in birds (Newton 1979, Sæther & Bakke 2000, Tavecchia *et al.* 2001, Beauplet *et al.* 2006), a fact that can

be explained by age-related improvements in foraging ability, diet choice and access to better territories (Pärt 2001, Rutz *et al.* 2006, Daunt *et al.* 2007), or by the greater proportion of low-quality individuals early in life (i.e. the selection hypothesis; Mauck *et al.* 2004). On the other hand, life-history theory predicts a negative correlation between effort in the current reproductive attempt and future survival and/or fecundity (i.e. the cost of reproduction hypothesis; Roff 1992). Consequently, non-manipulative studies in this field have focused on analysing the existence of the predicted trade-off in natural populations using multistage models in which survival may depend on the age and reproductive stage of individuals

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(Tavecchia *et al.* 2001, Moyes *et al.* 2006, Sanz-Aguilar *et al.* 2008). In contrast, the role of stages defined on the basis of individuals' behavioural traits in life-history variation has received less attention. However, if behaviourally defined stages (e.g. territorial stage) have a significant effect on survival or reproduction, knowledge of how these stages of individuals interact with age in determining their vital rates may contribute to a better understanding of the processes shaping both population dynamics and life-history evolution.

Bonelli's Eagle *Aquila fasciata* is a territorial accipitrid that is irregularly distributed from Southeast Asia through the Middle East to the western Mediterranean (del Hoyo *et al.* 1992). Its European population has been estimated at 920–1100 pairs, of which *c.* 80% are found in the Iberian Peninsula (BirdLife International 2004). The species has undergone a dramatic decline in numbers and range in recent decades and is now listed as endangered in Europe (Rocamora 1994, BirdLife International 2004, Ontiveros *et al.* 2004, Real 2004). The main factor thought to have caused this decline is a demographic imbalance related to decreased fecundity and, especially, increased adult and pre-adult mortality (Real & Mañosa 1997, Real *et al.* 2001, Carrete *et al.* 2002, Soutullo *et al.* 2008), mainly caused by electrocution and persecution (Real *et al.* 2001). However, other factors such as the loss of suitable habitat caused by changes in land use (Balbontín 2005, Carrete *et al.* 2005, Martínez *et al.* 2008), a decline in its main prey populations (Real 1991, Villafuerte *et al.* 1995, Ontiveros *et al.* 2004) and competition with the Golden Eagle *Aquila chrysaetos* (Fernández & Insausti 1990, López-López *et al.* 2004, Carrete *et al.* 2006) have also had a negative effect on the populations of this raptor.

Like other eagle species, Bonelli's Eagle is long-lived and monogamous, and exhibits delayed maturity, small clutch size and low annual productivity (del Hoyo *et al.* 1992, Real & Mañosa 1997, del Moral 2006). Once the dependence period (i.e. post-fledgling) ends, Bonelli's Eagles enter a transient nomadic phase – the dispersal period – which may last for several years before they are recruited into a territory (Newton 1979, Real & Mañosa 2001), usually between the third and fourth years of life (Hernández-Matías *et al.* 2010).

Given its life-history strategy, survival is a key life-history trait that has important consequences for the species' population dynamics and conservation status (Newton 1979, Sæther & Bakke 2000). Accordingly, previous demographic analyses of Bonelli's Eagle populations have suggested that survival, either in adults (Real & Mañosa 1997, Carrete *et al.* 2005) or in pre-adults (Soutullo *et al.* 2008), is the main vital rate regulating populations. Nevertheless, data on survival rates in Bonelli's Eagles based on marked individuals are scarce. Survival estimates usually require the continuous monitoring of the fate of individually marked subjects over a long period of time, such as capture-mark-recapture (CMR) methods (Lebreton *et al.* 1992, Williams *et al.* 2002, Sandercock 2006). Survival estimation is a challenge in species such as eagles in which individuals are difficult to capture, mark, recapture and re-sight. In fact, most previous estimates of adult survival in Bonelli's Eagle (Real & Mañosa 1997, Carrete *et al.* 2005) were calculated using the turnover rate (based on age, assessed by plumage) of territorial individuals. However, Hernández-Matías *et al.* (2011) estimated survival using both the turnover rate and CMR methods and showed that the turnover-rate method systematically overestimates adult survival if it is not properly corrected for biasing factors such as the proportion of non-observable replacements (e.g. the replacement of an adult-plumaged territorial eagle by another adult-plumaged eagle).

Data on pre-adult survival are also scarce and no available estimates based on CMR methods exist (Real & Mañosa 1997, Arroyo *et al.* 1998, Balbontín *et al.* 2003, Soutullo *et al.* 2008). The main shortcomings of these previous studies result from basing survival estimates on a small number of individuals and failing to account for several confounding factors in the analysis, such as the probability of resighting and/or tag loss, thereby biasing survival estimates (Lebreton *et al.* 1992, Williams *et al.* 2002, Zens & Peart 2003, Lindberg & Walker 2007).

In Bonelli's Eagle, the acquisition of a territory represents a marked change in lifestyle: territorial birds are sedentary and exhibit strong fidelity to their territories (Bosch *et al.* 2010), whereas non-territorial birds perform long-distance movements to dispersal areas (Real & Mañosa 2001, Cadahía *et al.* 2010), consistent with the view that non-territorial birds have to confront less predictable environments and are more exposed to novel risks (Clobert *et al.* 2001). The habitat features selected by non-territorial birds differ from those selected by territorial birds (Mañosa *et al.* 1998,

Balbontín 2005, Cadahía *et al.* 2010); likewise, the main causes of mortality also differ between territorial and non-territorial Eagles (Real *et al.* 2001). In fact, data on survival in Bonelli's Eagles demonstrate considerably higher survival in territorial (i.e. mostly adult) in comparison with non-territorial (i.e. mostly pre-adult) birds (e.g. Real & Mañosa 1997, Soutullo *et al.* 2008). Nevertheless, it remains unknown whether observed improvements in survival are caused by the age of the individuals or by their territorial stage.

In this study, our first objective was to provide robust estimates of age-dependent survival in Bonelli's Eagle, a prerequisite if management and conservation strategies of this endangered species are to be properly implemented. To do so, we applied CMR methods to a dataset from a long-term ongoing monitoring project (initiated in 1990) carried out on a population of Bonelli's Eagles in southeast France. All territories in the population were surveyed: the plumage-age and identity of territorial birds were recorded, most fledged chicks were tagged, and resightings and dead recoveries of both non-territorial and territorial birds were recorded. Additionally, we assessed whether the territorial stage of individuals interacts with age in determining survival probabilities. Finally, we assess whether the breeding stage of territorial birds (either successful or failed) is related to the probabilities of survival and of breeding successfully in the following year.

METHODS

Field data

The study area was located in Provence and Languedoc-Roussillon (southeast France) at the northwestern limit of the species' distribution. The study population remained roughly stable at 23–29 territorial pairs during the study period (1990–2008). During the study period, most of the chicks fledged ($n = 423$) were tagged at the nest with both metal and coded darvic bands. Additionally, all known territories were intensively monitored to obtain the occupation status, identity, plumage-age and sex of the territorial birds ($n = 35$ territories; see Hernández-Matías *et al.* 2010). The monitoring of territories included intensive efforts aimed at detecting territorial birds with metal bands, as some individuals lose their darvic bands (Hernández-Matías *et al.* 2011 and see below). Addition-

ally, territorial birds from the only neighbouring population (Catalonia, northeastern Spain) were intensively monitored during the study period. In both France and Catalonia, territorial birds were classified from their plumage-ages as young, immature, subadult or adult, corresponding, respectively, to first-year, second-year, third-year and fourth-year or older birds (Parellada 1984); sex was established on the basis of behaviour and body size, as the study species shows marked reversed sexual dimorphism (del Hoyo *et al.* 1992). The two main dispersal areas used by non-territorial birds are La Camargue and La Crau (Cheylan *et al.* 1996), both of which were located within our study area. These areas were intensively surveyed by birdwatchers and by the managers of the reserves in question, who contributed most of the observations of non-territorial Bonelli's Eagles used in this study. The reliability of all the observations was evaluated and validated by the coordinator of the banding programme. Marked birds found dead (recoveries) were also recorded. In total, 119 birds were resighted at least once, of which 75 were non-territorial (34 recovered dead) and 44 territorial (three recovered dead). None of the territorial birds had been previously recorded as non-territorial.

Estimates of survival and the cost of reproduction

Capture-recapture multistate models (Lebreton *et al.* 1992, 1999, Pradel 2005) were run to assess whether survival depended on the age and the territorial stage of individuals, and whether successful reproduction decreased future breeding success and survival (hereafter referred to as analyses A and B, respectively). In analysis B, all individuals considered were territorial and so we also assessed whether previous experience in the territory (either more or less than a year in the territory) determined the probabilities of both future breeding success and survival. We estimated three types of parameters: the probability of resighting a marked bird over time t (p); the probability that a marked bird survived from year t to year $t + 1$ (Φ); and the probability that a marked bird in a given state in year t is in another state in year $t + 1$ (ψ). ψ was used to model either (i) darvic-band loss and territorial stage transitions (analysis A) or (ii) the breeding-state transition of territorial birds, i.e., the probability of switching from successful to failed breeding and vice versa (analysis B). The

three parameters (p, Φ, ψ) were estimated from encounter histories using maximum likelihood procedures with the program E-SURGE (Choquet *et al.* 2009a). The goodness-of-fit of the Cormack–Jolly–Seber (CJS) model was assessed using contingency tables with the program U-CARE 2.2.2 (Pradel *et al.* 2005, Choquet *et al.* 2009b).

Model parameterization

E-SURGE allows transition and encounter matrices and initial state vectors to be defined in more than one step, and we used this flexibility to define the transition matrix in several steps. In analysis A, we estimated separately: the probability that a bird alive at t survived to $t + 1$ (Φ), the probability that a non-territorial bird at t had acquired a territory in $t + 1$ (ψ_{terr}), and the probability that a live tagged bird at t had lost its tag at $t + 1$ (ψ_{untag}). To do so, we considered seven states: 'alive non-territorial with darvic band', 'alive non-territorial without darvic band', 'alive territorial with darvic band', 'alive territorial without darvic band', 'non-territorial recently died' (either with or without darvic band), 'territorial recently died' (either with or without darvic band) and 'long dead'. Dead individuals were assumed to be retrievable during the interval in which they died, but no later. The state 'recently died' is observable, and once an individual is detected as 'recently died', the model subsequently considers that this individual will be in the state 'long dead', which cannot be observed. In analysis B, we estimated separately: the survival probability (Φ) and the probability of breeding successfully at $t + 1$ (ψ_{breed}) in relation to the breeding success at t. To do so, we considered four states: 'successful breeder', 'failed breeder', 'recently died' and 'long dead'. In analysis B, darvic band loss was not considered because, due to intense resighting efforts, the probability of resighting territorial birds, whether tagged or untagged, was the same (Hernández-Matías *et al.* 2011).

Time intervals and definition of the resighting probability

A large proportion of observations of non-territorial birds occurred in winter, whereas most observations of territorial birds were from the breeding season. To account for this source of heterogeneity in resightings, in analysis A we pooled all observa-

tions of non-territorial birds into two periods of 6 months each (February–July and August–January) to construct individual capture-resighting histories. Thus, this model considered 10 age-classes, and survival probabilities were estimated as half-year survival rates. Nevertheless, half-year survival rates in the same year were forced to be equal in the model (except in the first year of life) and, to facilitate the interpretation, we report only yearly survival rates in the Results section, which were calculated from half-year survival rates using the Delta method (Powell 2007). We considered the two periods of the first year of life separately because most observations in August–January were of first-year birds, and so at this age only the separate estimation of half-year survival rates was possible. ψ_{untag} and p were modelled for each half-year, while ψ_{terr} was modelled for transitions from August–January to February–July, and was fixed at zero for transitions from February–July to August–January.

In the case of territorial birds, most of the observations were from the breeding period (all territories were surveyed in that season) and were assigned to the corresponding 6-month period (February–July). There were so few observations of territorial birds in the period August–January that we decided they were not worth keeping in the analysis. Consequently, the resighting probability of territorial birds in winter was fixed at zero. In analysis B, we used time intervals of 1 year, and only observations made during the breeding period in monitored territories were used to construct individual capture-resighting histories. In both analyses, pooling half-year or year periods as discrete time units may potentially cause a violation of CMR model assumptions, although the resulting biases are expected to be small (Hargrove & Borland 1994).

Model selection

In analysis A, the initial model considered survival (Φ) to be fully age- and stage-dependent with an additive effect of time; ψ_{terr} and ψ_{untag} were age-dependent, while p was dependent on the territorial stage, the 6-month period (be it August–January or February–July), the darvic band state (lost or otherwise) and the life status (a resighting of a living bird or a recovery of a dead individual). Model selection was conducted in steps that analysed successively ψ_{untag}, p and

ψ_{terr}, while keeping the other parameters as in the initial model. Once a suitable structure for transition and resighting probabilities had been selected, we evaluated the effect of time on survival by comparing the full model with the fully age-dependent model. Then, we analysed the effect of survival in relation to age and territorial stage. In some models, survival was taken to be equal in the second and the third years of life to improve the precision of the survival estimates (by enlarging the sample size), given that during this period most Eagles are non-territorial and have a similar life-style.

In analysis B, we initially fixed survival according to the results of analysis A and evaluated (i) the effect of age on the initial breeding success state (i.e. the first occasion the individual was territorial) and (ii) the transition probability in breeding state in relation to age, observed territorial experience and breeding state in $t - 1$. Once we had identified the best model, we assessed whether including the effects of both territorial experience and previous breeding stage on survival improved the fit. The effects of time on breeding stage transition probabilities were not evaluated because our sample size was too small.

In both analyses A and B, the effect of sex was evaluated by comparing the best model (obtained by following the steps described above) with a similar model that considered the effect of sex on survival probability (both analyses) and on the transition probability between breeding states (analysis B). Due to the small sample size, we could not evaluate complex full models including sex.

Model selection was made on the basis of Akaike's information criterion corrected for small sample size (AICc), the model with the smallest AICc value being considered to have the greatest support. Models were considered to be statistically equivalent when the difference in AICc (ΔAICc) was < 2 (Burnham & Anderson 2002).

RESULTS

Age- vs. stage-dependent survival (analysis A)

The CJS model fitted the data adequately (GOF test: $\chi^2_{53} = 32.59$, $P = 0.988$). Overall, stage-structured models performed worse than age-only-structured models (sum of AICc weights 0.33 vs. 0.67; Table 1). In the best model that considered

Table 1. Effects of age and territoriality on the survival of Bonelli's Eagle. In all models, it was assumed that adult survival is reached by the age of 4 years. The first part of the analysis considered different groupings of the five age-classes, each class being identified by the age of the bird at its beginning. The second part further considered potential differences in survival between territorial and non-territorial Eagles: 'te' indicates territorial; 'nt' non-territorial. Model definition describes the structure of the probabilities of survival (Φ), of resightings of alive individuals (p), and recoveries of dead individuals (λ), and the probabilities that a non-territorial bird at t had acquired a territory at $t + 1$ (ψ_{terr}), and that a live tagged bird at t had lost its tag at $t + 1$ (ψ_{untag}). 'tag' means individual with darvic band and 'untag' without darvic band. A space separates age- and territory-classes with the same survival; a comma separates classes with different survivals.

Model definition	np	Deviance	AICc	AICc weight
Age-dependent survival				
$\Phi_{(0,1\ 2,3\ 4)}\ \psi_{\text{terr}\ (0,1,2,3\ 4)}\ \psi_{\text{untag}}\ p_{(\text{nt tag, nt untag, te})}\ \lambda$	13	1304.28	1330.91	0.330
$\Phi_{(0,1\ 2,3,4)}\ \psi_{\text{terr}\ (0,1,2,3\ 4)}\ \psi_{\text{untag}}\ p_{(\text{nt tag, nt untag, te})}\ \lambda$	14	1304.02	1332.75	0.131
$\Phi_{(0,1,2,3\ 4)}\ \psi_{\text{terr}\ (0,1,2,3\ 4)}\ \psi_{\text{untag}}\ p_{(\text{nt tag, nt untag, te})}\ \lambda$	14	1304.26	1332.99	0.117
$\Phi_{(0,1,2,3,4)}\ \psi_{\text{terr}\ (0,1,2,3\ 4)}\ \psi_{\text{untag}}\ p_{(\text{nt tag, nt untag, te})}\ \lambda$	15	1304.01	1334.85	0.046
$\Phi_{(0,1,2\ 3,4)}\ \psi_{\text{terr}\ (0,1,2,3\ 4)}\ \psi_{\text{untag}}\ p_{(\text{nt tag, nt untag, te})}\ \lambda$	14	1306.35	1335.09	0.041
$\Phi_{(0,1,2\ 3\ 4)}\ \psi_{\text{terr}\ (0,1,2,3\ 4)}\ \psi_{\text{untag}}\ p_{(\text{nt tag, nt untag, te})}\ \lambda$	13	1311.67	1338.30	0.008
$\Phi_{(0,1\ 2\ 3\ 4)}\ \psi_{\text{terr}\ (0,1,2,3\ 4)}\ \psi_{\text{untag}}\ p_{(\text{nt tag, nt untag, te})}\ \lambda$	12	1319.95	1344.50	0.000
Stage-dependent survival				
$\Phi_{(0,\ 1\ 2nt,\ 2te,\ 3\ 4)}\ \psi_{\text{terr}\ (0,1,2,3\ 4)}\ \psi_{\text{untag}}\ p_{(\text{nt tag, nt untag, te})}\ \lambda$	14	1304.15	1332.89	0.123
$\Phi_{(0,\ 1\ 2nt\ 3nt,\ 2te\ 3te,\ 4)}\ \psi_{\text{terr}\ (0,1,2,3\ 4)}\ \psi_{\text{untag}}\ p_{(\text{nt tag, nt untag, te})}\ \lambda$	14	1305.50	1334.24	0.062
$\Phi_{(0,\ 1\ 2nt,\ 2te,\ 3,\ 4)}\ \psi_{\text{terr}\ (0,1,2,3\ 4)}\ \psi_{\text{untag}}\ p_{(\text{nt tag, nt untag, te})}\ \lambda$	15	1303.90	1334.74	0.049
$\Phi_{(0,\ 1,\ 2nt\ 2te,\ 3\ 4)}\ \psi_{\text{terr}\ (0,1,2,3\ 4)}\ \psi_{\text{untag}}\ p_{(\text{nt tag, nt untag, te})}\ \lambda$	15	1304.02	1334.87	0.046
$\Phi_{(0,\ 1,\ 2nt\ 3nt,\ 2te\ 3te,\ 4)}\ \psi_{\text{terr}\ (0,1,2,3\ 4)}\ \psi_{\text{untag}}\ p_{(\text{nt tag, nt untag, te})}\ \lambda$	15	1305.48	1336.32	0.022
$\Phi_{(0,\ 1,\ 2nt,\ 2te,\ 3,\ 4)}\ \psi_{\text{terr}\ (0,1,2,3\ 4)}\ \psi_{\text{untag}}\ p_{(\text{nt tag, nt untag, te})}\ \lambda$	16	1303.79	1336.75	0.018
$\Phi_{(0,\ 1,\ 2nt,\ 2te,\ 3nt,\ 3te,\ 4)}\ \psi_{\text{terr}\ (0,1,2,3\ 4)}\ \psi_{\text{untag}}\ p_{(\text{nt tag, nt untag, te})}\ \lambda$	17	1303.30	1338.38	0.008
$\Phi_{(0,\ 1,\ 2nt\ 3nt\ 4nt,\ 2te\ 3te\ 4te)}\ \psi_{\text{terr}\ (0,1,2,3\ 4)}\ \psi_{\text{untag}}\ p_{(\text{nt tag, nt untag, te})}\ \lambda$	14	1318.56	1347.30	0.000
$\Phi_{(\text{nt, te})}\ \psi_{\text{terr}\ (0,1,2,3\ 4)}\ \psi_{\text{untag}}\ p_{(\text{nt tag, nt untag, te})}\ \lambda$	11	1329.22	1351.68	0.000

the effect of age but not of territorial stage (AICc weight = 0.33; Fig. 1a), yearly survival was constant over the study period and was estimated at 0.479 (95% CI = 0.357–0.605) for fledglings (to 1 year of age), 0.570 (95% CI = 0.462–0.672) for 1- and 2-year-olds, and 0.870 (95% CI = 0.790–0.923) for 3-year-old and older individuals. This suggests that 13.7% of fledglings survived to the age of 4 years and that *c.* 16.9% of fledglings survived to territorial recruitment (assuming the recruitment rates estimated by Hernández-Matías *et al.* 2010). The second best supported model (AICc weight = 0.13) indicated that survival was lower for 3-year-olds (0.821, 95% CI = 0.529–0.949) than for older individuals (0.880, 95% CI = 0.786–0.936). In the third best supported
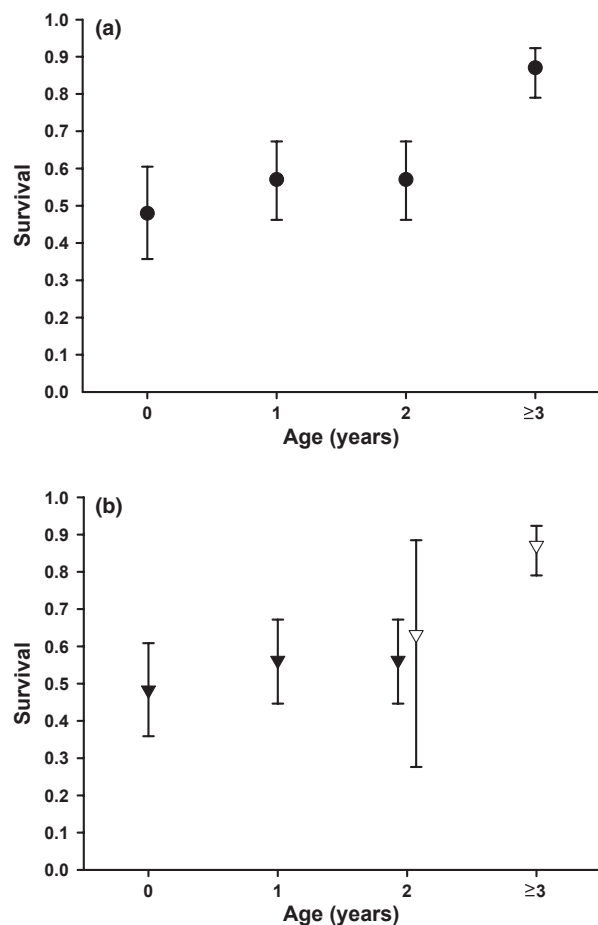
model (AICc weight = 0.12), which was the best model considering the effect of territorial stage (Fig. 1b), differences according to territorial stage occurred only in 2-year-olds, being lower for non-territorial (0.562, 95% CI = 0.446–0.672) than for territorial birds (0.632, 95% CI = 0.276–0.885).

Regarding the sex effect, a model equivalent to the above best model but including the effect of sex on survival probability for all age classes received least support; on the other hand, a model considering the effect of sex on survival of the oldest birds only performed almost as well as the above best model (ΔAICc = 0.2) and thus suggests that older females (Φ = 0.903; 95% CI = 0.807–0.954) survived better than older males (Φ = 0.801; 95% CI = 0.649–0.897).

In the best-supported model in Table 1, tag loss occurred at a constant rate of 0.059 (95% CI = 0.038–0.092) every half-year. The resighting probability differed between tagged and untagged non-territorial Eagles (0.040, 95% CI = 0.026–0.063 and 0.006, 95% CI = 0.001–0.048, respectively), but did not differ in territorial birds (0.614, 95% CI = 0.505–0.713; see Hernández-Matías *et al.* 2011). The probability of recovering a dead individual in the year of death, whether territorial or non-territorial, was 0.109 (95% CI = 0.080–0.143).

Effects of the current breeding stage on future breeding and survival (analysis B)

The CJS model fitted the data adequately (GOF test: $\chi^2_{21} = 8.166$, $P = 0.994$). The best model indicated that the future breeding state of territorial birds was determined by age and the previous breeding state (Table 2). Adult (i.e. 4-year-old and older birds) successful breeders were more likely to breed successfully the following year than adult failed breeders (0.869, 95% CI = 0.691–0.951 vs. 0.582, 95% CI = 0.330–0.798). Two- and 3-year-old (i.e. non-adult) successful breeders showed a markedly lower tendency to breed successfully the following year (0.318, 95% CI = 0.105–0.650) than adult successful breeders. Additionally, non-adults whose breeding attempt failed showed a slightly higher probability of successful breeding the following year (0.404, 95% CI = 0.124–0.765) than successful breeders of the same age. Our results suggest that the effect of sex on the transition between breeding stages was weak (ΔAICc = 4.7 with respect to the best-supported model).

Figure 1. Survival according to best supported models for (a) age-dependent and (b) stage-dependent survival in Table 1. In (b) territorial and non-territorial birds are represented by open and full triangles, respectively. Error bars represent 95% confidence intervals.

Table 2. Effect of age, breeding and territorial experience on transition probabilities between breeding states (Ψ) and on survival (Φ). Probabilities of capture were estimated separately for resightings of live individuals (p) and recoveries of dead individuals (λ). The models considered a maximum of four age classes (from 2 to 5 years old), two states of territorial experience ('ne': first-year territorial; 'ex': at least second-year territorial) and two breeding states ('fa': failed breeder; 'su': successful). The nomenclature follows that of Table 1, but we allowed combinations of the breeding and territorial states (e.g. 3ne_su: 3-year old non-experienced territorial that succeeded in reproduction). The first part of the analysis considers survival according to the results of analysis A in the text ($\Phi_{(2,\ 3\ 4)}$). Once we had identified the best model, in the second part of the analysis we assessed whether including the effects of both territorial experience and the previous breeding stage on survival improved the fit.

Model definition	np	Deviance	AICc	AICc weight
Modelling transition probability between breeding stages				
$\Psi_{(2fa\ 3fa,\ 2su\ 3su,\ 4fa\ 5fa,\ 4su\ 5su)}\ \Phi_{(2,\ 3\ 4)}\ p\ \lambda$	11	320.06	344.87	0.432
$\Psi_{(ne,\ ex\_fa,\ ex\_su)}\ \Phi_{(2,\ 3\ 4)}\ p\ \lambda$	10	325.43	347.74	0.103
$\Psi_{(2,\ 3fa,\ 3su,\ 4fa\ 5fa,\ 4su\ 5su)}\ \Phi_{(2,\ 3\ 4)}\ p\ \lambda$	12	321.26	348.61	0.067
$\Psi_{(ne\_fa,\ ne\_su,\ ex\_fa,\ ex\_su)}\ \Phi_{(2,\ 3\ 4)}\ p\ \lambda$	11	325.15	349.96	0.034
$\Psi_{(fa,\ su)}\ \Phi_{(2,\ 3\ 4)}\ p\ \lambda$	9	331.13	351.00	0.020
$\Psi_{(2,\ 3fa,\ 3su,\ 4fa,\ 4su,\ 5fa,\ 5su)}\ \Phi_{(2,\ 3\ 4)}\ p\ \lambda$	14	319.73	352.34	0.010
$\Psi_{(2,\ 3ne\_fa,\ 3ne\_su,\ 3ex\_fa,\ 3ex\_su,\ 4fa\ 5fa,\ 4su\ 5su)}\Phi_{(2,\ 3\ 4)}\ p\ \lambda$	14	320.49	353.11	0.007
$\Psi_{(ne,\ ex)}\ \Phi_{(2,\ 3\ 4)}\ p\ \lambda$	9	334.96	354.84	0.003
$\Psi_{(ne\_fa,\ ne\_su,\ ex)}\ \Phi_{(2,\ 3\ 4)}\ p\ \lambda$	10	334.79	357.10	0.001
$\Psi_{(2,\ 3,\ 4,\ 5)}\ \Phi_{(2,\ 3\ 4)}\ p\ \lambda$	11	332.76	357.57	0.001
$\Psi_{(2,\ 3ne\_fa,\ 3ne\_su,\ 3ex\_fa,\ 3ex\_su,\ 4ne\_fa\ 5ne\_fa,\ 4ne\_su\ 5ne\_su,\ 4ex\_fa\ 5ex\_fa,\ 4ex\_su\ 5ex\_su)}\ \Phi_{(2,\ 3\ 4)}\ p\ \lambda$	16	319.60	357.71	0.001
$\Psi_{(2,\ 3ne,\ 3ex,\ 4ne\ 5ne,\ 4ex\ 5ex)}\ \Phi_{(2,\ 3\ 4)}\ p\ \lambda$	14	329.93	362.54	0.000
Modelling survival probability				
$\Psi_{(2fa\ 3fa,\ 2su\ 3su,\ 4fa\ 5fa,\ 4su\ 5su)}\ \Phi_{(2,\ 3ne\ 4ne,\ 3ex\ 4ex)}\ p\ \lambda$	12	319.25	346.61	0.181
$\Psi_{(2fa\ 3fa,\ 2su\ 3su,\ 4fa\ 5fa,\ 4su\ 5su)}\ \Phi_{(2,\ 3fa\ 4fa,\ 3su\ 4su)}\ p\ \lambda$	12	319.77	347.12	0.140

Models equivalent to the above best-supported model but including the effect of the territorial experience and the previous breeding state on survival performed least well and showed ΔAICc of 1.74 and 2.25, respectively (Table 2). In these models, survival of 2-year-olds was estimated at 0.769 (95% CI = 0.301–0.963) and 0.775 (95% CI = 0.297–0.965), respectively. The model including territorial experience suggested that 3-year-old and older non-experienced Eagles had lower survival than experienced Eagles of the same age (0.761, 95% CI = 0.500–0.910 vs. 0.865, 95% CI = 0.753–0.931). Finally, the model including the effect of previous breeding state suggests that failed breeders survived better than successful breeders (0.883, 95% CI = 0.629–0.971 vs. 0.825, 95% CI = 0.687–0.910).

DISCUSSION

We report for the first time survival estimates from birth to adulthood based on CMR methods in the endangered Bonelli's Eagle. In our best-supported model, yearly survival was estimated at 0.479 for fledglings (to 1 year of age), 0.570 for 1- and 2-year-olds, and 0.870 for 3-year-old and older individuals. In addition, a model that fitted the data similarly well supported a survival value for 3-year-olds still lower than that for older individuals (0.821 and 0.880, respectively). Our estimates covered a fairly long period of time (1990–2008) and were corrected for several potential biases such as tag loss and imperfect detection of marked birds, be they territorial or non-territorial. As in other studies restricted to a geographical area smaller than the actual distribution of the study species, permanent emigration outside our study area could have potentially confounded our survival estimates (Lebreton *et al.* 1992). However, the territorial birds from the only adjacent population (in Catalonia) were also intensively monitored during the study period (e.g. Real & Mañosa 1997, 2001, Hernández-Matías *et al.* 2010) and indeed two of the territorial birds included in our analyses were detected in that population. Furthermore, the kernel of natal dispersal in Bonelli's Eagles suggests that *c.* 95% of Eagles born in France are recruited into these two populations (A. Hernández-Matías and J. Real, unpubl. data). This kernel was fitted by maximum likelihood procedures on the basis of natal dispersal distances of 52 Eagles banded as chicks in France and Catalonia and corrected for monitoring effort, which was estimated for any given dispersal distance interval in a range of

450 km (50 km width) as the probability of detecting a marked bird on the basis of the proportion of monitored territories per year and the distance at which territorial birds were monitored. Therefore, the confounding effect on our study of permanent emigration should be small.

Previous reports of survival for non-territorial Bonelli's Eagles provided estimates of 0.36–0.50, 0.40, 0.69 and 0.5 during the first year of life in, respectively, central Spain (Arroyo *et al.* 1998), Catalonia (Real & Mañosa 1997), Andalusia (southern Spain, based on Balbontín *et al.* 2003, Balbontín 2004) and eastern Spain (Soutullo *et al.* 2008). The last three studies also provide values for survival during the second year of life, estimated at 0.41, 0.72 and 0.21, respectively. These estimates were based on return rates and thus they are potentially biased by the confounding effect of the resighting probability, while the small sample size may also have limited the precision of these survival estimates. Nevertheless, the values of first-year survival in these studies match our results fairly well, suggesting that survival rates at this age are similar throughout Bonelli's Eagle populations in France and northeastern, eastern and central Spain, but are considerably higher in the healthy southern Spanish population. These results are consistent with the view that non-breeding Bonelli's Eagles (usually under 3 years of age) from West European populations share several dispersal areas (Cheylan *et al.* 1996, Real & Mañosa 2001, Balbontín & Ferrer 2009, Cadahía *et al.* 2010) and thus are exposed to similar environmental conditions, although birds from some populations do have an apparent tendency to use the nearest dispersal areas more intensively. Data from sightings and recoveries of marked birds in our population indicated that dispersing birds mostly concentrate in French Mediterranean coastal areas (Cheylan *et al.* 1996), particularly in the Crau plain (Bouches-du-Rhône). Nevertheless, there are also several records of birds from France dispersing into central and southern Spain (Cheylan *et al.* 1996, N. Vincent-Martin and A. Ravayrol, unpubl. data) and two (of 34) individuals from France and four (of 19) individuals from Catalonia marked at fledgling were later resighted as territorial birds in, respectively, Catalonia (Hernández-Matías *et al.* 2010) and France (J. Real and A. Hernández-Matías, unpubl. data), which also supports the idea that the survival rates of birds dispersing from France, and at least from some Iberian populations, may be similar.

In contrast, previous adult survival estimates from seven local populations in West Europe were markedly different, with values ranging from 0.839 to 0.967 (Real & Mañosa 1997, Carrete *et al.* 2005, Soutullo *et al.* 2008). Due to the high sensitivity of the population growth rate to adult survival, some of these populations showed contrasting population trends (del Moral 2006). However, it is likely that these estimates overestimated true survival rates as they were calculated using the turnover rate (mostly based on the plumage-age of territorial Eagles). With the same dataset as used here, Hernández-Matías *et al.* (2011) employing CMR methods estimated adult survival at 0.88 for the period 1999–2008 and showed that without suitable corrections the turnover rate method overestimated survival by *c.* 5.6%; this bias may be even stronger in populations with lower mortality levels where there is a high proportion of unobservable replacements.

As expected, we found an improvement in survival rates as Eagles aged, a finding widely reported in other long-lived birds (Sæther & Bakke 2000, Tavecchia *et al.* 2001, Beauplet *et al.* 2006). This pattern can be explained by age-related improvements in foraging ability, diet choice and access to better territories (Pärt 2001, Rutz *et al.* 2006, Daunt *et al.* 2007). This observed pattern could also be explained by the selection hypothesis (Cam & Monnat 2000, Mauck *et al.* 2004, Tavecchia *et al.* 2005), which states that selection acts on a cohort early in life, leaving only the highest-quality individuals to survive to old age.

A non-mutually exclusive explanation is that territorial life improves survival in eagles (Kokko & Sutherland 1998, Penteriani *et al.* 2005). Our CMR analyses revealed a marked improvement in survival between the first and second years of life, and especially between the third and fourth years of life, which fits well with the pattern of territory acquisition in the population studied (correlation between the proportion of territorial birds (based on data in Hernández-Matías *et al.* 2010) and survival: $r_s = 0.975$, $P = 0.005$, $n = 5$ age-classes). In agreement with this idea, the best model integrating the effect of both age and territorial stage on survival suggested that 2-year-old territorial individuals survived better than non-territorial ones of the same age. However, the overall support for stage-structured models was lower than that for age-only-structured models (sum of AICc weights of 0.33 vs. 0.67), suggesting that the effect

of age was more relevant than the effect of territorial stage. However, the sample of territorial 2-year-olds was relatively small (because most birds acquire a territory at the age of 3 years), and few non-territorial older birds were recorded (due to their low numbers and the low resighting probabilities), so the effect of territorial stage on survival may be stronger than we detected. Additionally, our results show a tendency for territorial birds to survive better if they have at least 1 year of previous experience in the territory, which may be because experience confers on individuals higher competence to exploit their territory (Martínez et al. 2006).

Our results give some support to the idea that females of more than 3 years of age survive better than males of the same age (mostly territorial Eagles), but we did not find sex-specific survival differences in younger age classes (also see Hernández-Matías et al. 2011). In Bonelli's Eagle, adult mortality is mostly caused by electrocution and direct persecution by man (Real et al. 2001). A possible explanation is that females are less exposed to mortality risks because during the breeding period they remain longer at the nest or in the breeding area, as they dedicate more effort than males to incubation duties and care of the chicks (but see Ferrer & Hiraldo 1992).

Life-history implications

In territorial birds such as Bonelli's Eagle, breeding performance may be linked to both territory and individual quality (Pärt 2001, Penteriani et al. 2003, Carrete et al. 2006, Sergio et al. 2009). Thus, we found that successful experienced breeders were more likely to breed successfully the next year compared with failed experienced breeders, suggesting that the cost of reproduction is small in comparison with the variation in quality between individuals and their territories. If low-quality territories are more easily accessible to young individuals, there may be a trade-off between recruiting early and trying to recruit into a good-quality territory (Kokko & Sutherland 1998, Grande et al. 2009). In this sense, Krüger (2005) showed in a Goshawk Accipiter gentilis population that females starting to breed at the age of 1 year suffered a very high fitness cost if they were in a poor-quality territory, although fitness costs were small when they were in a good-quality territory. In our study, we show in the case of non-experienced birds (i.e.

birds with no previous experience of their territory) that successful breeders have a slightly higher probability of failing to reproduce the following year than unsuccessful breeders, which can be interpreted as an indication of the cost of first reproduction (Cam & Monnat 2000, Tavecchia et al. 2001, Sanz-Aguilar et al. 2008).

The delayed onset of reproduction may indeed be the result of a limitation on territory acquisition (Brommer et al. 1998, Newton 1998, Cooper et al. 2009). Accordingly, increased opportunities for recruitment amongst non-breeders result in first breeding attempts occurring at a younger age in many territorial birds, as observed in experimental studies in which adult territorial individuals were removed (reviewed by Newton 1992), in growing populations (Margalida et al. 2008) or in those subject to high adult mortality (Ferrer et al. 2003). By recruiting earlier, individuals may benefit from having the opportunity to begin their breeding careers sooner and thus improve their fitness (McGraw & Caswell 1996, Oli et al. 2002). Birds may also gain more experience with their mate and/or knowledge of local features of the territory (Bradley et al. 1990, Beletsky & Orians 1991), which is also expected to improve their breeding performance in future years. Additionally, territoriality may itself improve individual survival, above all if the environmental features of the territories are more favourable to survival than the features of the dispersal areas used by non-territorial birds. Interestingly, the potential interference between behaviourally defined stages (such as the territorial stage) and key vital rates including survival or reproduction may add an important source of heterogeneity and help explain the processes shaping life-history evolution within species, populations and individuals from the same population.

Implications for conservation

Obtaining robust estimates of survival is a necessary step towards understanding the demographic dynamics of Bonelli's Eagle populations (Morris & Doak 2002) and is thus a prerequisite if the management and conservation strategies designed for this species are to be successfully implemented. After the severe decline documented in recent decades, most Bonelli's Eagle populations have stabilized and in some cases have even increased their numbers, although some populations in northwestern Spain are on the brink of extinction (Fernández

et al. 1998, del Moral 2006). Despite these contrasts, the relationships between these trends and dynamics at a metapopulation level are not yet well understood (Real & Mañosa 1997, Soutullo *et al.* 2008), partly because previous information on non-adult survival and natal dispersal patterns was scarce, but probably also because previous adult survival estimates may have been biased (Hernández-Matías *et al.* 2011). In this sense, our study offers robust estimates of survival from birth to adulthood. Given that most West European populations share dispersal areas, we expect that the survival of non-territorial Eagles will be similar in all populations, although we lack empirical data to confirm this idea. Currently, information on the number of breeding pairs and their productivity is obtained for most West European populations every year or every few years (e.g. del Moral 2006). Therefore, it would represent a considerable step forward if long-term ringing schemes (similar to that used in this study) were to be extended to other populations; this would allow us to estimate survival over time, to improve knowledge of the geographical areas and the risks faced by dispersing Eagles and to identify the natal dispersal patterns of these populations. Collecting such information would provide the basis for developing suitable demographic models, identifying the target vital rates in this species and thus for optimizing decision-making in the implementation of sustainable management and conservation measures.

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