# Quick Methods for Evaluating Survival of Age-Characterizable Long-Lived Territorial Birds

**ARTICLE** *in* JOURNAL OF WILDLIFE MANAGEMENT · MAY 2011

Impact Factor: 1.61 · DOI: 10.1002/jwmg.102

Antonio Hernandez-Matias
University of Barcelona

Roger Pradel
Centre d'Ecologie Fonctionnelle et Evolutive

The Journal of Wildlife Management 75(4):856–866; 2011; DOI: 10.1002/jwmg.102

*Research Article*

# Quick Methods for Evaluating Survival of Age-Characterizable Long-Lived Territorial Birds

**ANTONIO HERNÁNDEZ-MATÍAS,**[1] *Conservation Biology Group, Departament de Biologia Animal, Universitat de Barcelona, Av Diagonal 645, Barcelona 08028, Spain*

**JOAN REAL,** *Conservation Biology Group, Departament de Biologia Animal, Universitat de Barcelona, Av Diagonal 645, Barcelona 08028, Spain*

**ROGER PRADEL,** *Centre d'Ecologie Fonctionnelle et Evolutive, Centre National de la Recherche Scientifique, 1919 Route de Mende, 34293 Montpellier Cedex 5, France*

**ABSTRACT** Survival is a key life-history trait in animals. However, most methods of survival estimation require substantial human and economic investment in the long term, particularly in species occurring in low densities, the case of most endangered species. An alternative to traditional recapture (CR) methods is estimation of adult survival based indirectly on either age ratios (AGR) or turnover rates (TOR) in territorial species. These 2 methods are applicable to bird species in which recruited individuals enter into the breeding population whilst still exhibiting the external traits that distinguish those animals from experienced adults. The main advantages of these methods are that survival can be easily estimated for all monitored individuals after just 1 or 2 breeding seasons and that disturbance to the species is minimized. The main constraints of indirect methods are that the assumptions are more restrictive than in CR methods, and survival estimates, although comparable between sites and years, may be biased. We used data from a long-term monitoring survey of 2 populations of the endangered Bonelli's eagle (*Aquila fasciata*), one in Catalonia (NE Spain) and the other in Provence and Languedoc-Roussillon (SE France). We evaluated survival estimates using the AGR and TOR methods and compared them with CR methods and provide suitable corrections for refining survival estimates based on indirect methods. In Catalonia (2002–2008), survival was estimated at 0.84 by CR methods (SE = 0.047; $n = 25$ radio tagged eagles), at 0.86 by the corrected AGR method (SE = 0.011; $n = 558$ bird $^{*}$ year), and at 0.86 by the corrected TOR method (SE = 0.022; $n = 547$ bird $^{*}$ year). In France (1999–2008), survival was estimated at 0.88 by CR methods (SE = 0.040; $n = 45$ darvic banded eagles), at 0.87 by the corrected AGR method (SE = 0.015; $n = 443$ bird $^{*}$ year), and at 0.87 by the corrected TOR method (SE = 0.015; $n = 438$ bird $^{*}$ year). All analyses suggest that females survive better than males and that individuals from the French population survive better than individuals from the Catalan population. We conclude that indirect methods, which should not be regarded as a substitute of CR methods, will allow wildlife managers and researchers to estimate accurately adult survival in a territorial species over a short period of time and to monitor survival across populations over large geographic ranges and over time.

**KEY WORDS** *Aquila fasciata*, birds of prey, Bonelli's eagle, endangered species, *Hieraaetus fasciatus*, population monitoring, raptors, survival, vital rate estimation.

Wildlife managers are often required to make rapid and difficult decisions regarding populations of threatened or endangered species (Burgman 2005). Survival is a major determinant of animal population dynamics (Sæther and Bakke 2000) and thus the acquisition of accurate estimates of survival is a necessary step towards the understanding and prediction of species' future demographic fates (Morris and Doak 2002). Consequently, survival estimation is a prerequisite if the management and conservation strategies of target species are to be properly implemented.

In bird populations, survival estimation usually involves monitoring the fates of individually marked subjects repeatedly or over long periods of time (Lebreton et al. 1992, Williams et al. 2002, Murray and Patterson 2006, Sandercock 2006). However, survival estimation may be a challenge in species in which individuals are difficult to capture, mark, or recapture or resight or whenever conservation decisions dependent on survival estimates must be made in the short term. The problems involved in capturing animals have been partially solved by concentrating marking efforts during the periods of animals' life-cycles in which individuals can be most easily caught (e.g., nestlings) or by using non-invasive methods such as acoustic (Vögeli et al. 2008) and genetic tagging (Rudnick et al. 2005, Kenward et al. 2007) and individual recognition through morphological features (Lank and Dale 2001). The problem of resighting in highly mobile species has been overcome by means of telemetric devices attached to individuals, which enable birds to be localized remotely on local and even global scales (Kenward et al. 2002, McIntyre et al. 2005). However, most of the above methods require serious long-term human and economic investment, particularly in species with low return

Received: 4 December 2009; Accepted: 13 October 2010

---

[1] *E-mail: ahernandezmatias@ub.edu*

rates, whether they are a product of long-distance dispersal patterns or slow life-history strategies, and in species occurring in low numbers or densities, the case of most endangered species. In such cases, survival can usually only be estimated for short time periods or over a small sample of individuals, thus leading to potentially biased survival estimates.

An alternative to recapture methods is estimation of adult survival in territorial species through indirect methods based on either age ratios (AGR) or turnover rates (TOR). These 2 methods are applicable to species in which at least some recruiting individuals enter the breeding population whilst still exhibiting the external traits (individuals not in full adult plumage) that distinguish them from experienced adult birds. The AGR method consists of estimating adult survival as the proportion of individuals exhibiting adult traits in the breeding fraction of a population (Newton 1979, Rohwer 2004, Sandercock 2006) and so one year of monitoring is enough to obtain a yearly estimate of adult survival. The TOR method consists of estimating adult mortality from turnover rates of territorial birds based on plumage-ages (Real and Mañosa 1997, Watson 1997, Carrete et al. 2005). Essentially, in the latter technique, when a bird is observed to have disappeared from or to have been replaced in its territory on the basis of its plumage-age, it is assumed to have died; thus, $\geq 2$ years of monitoring are required. The main advantages of the AGR and TOR methods are: 1) survival can be estimated for a whole population rather than for just a small set of marked individuals, as logistic, human, and economic requirements are considerably lessened; 2) population survival estimates can be obtained after monitoring for only 1 or 2 breeding seasons; 3) comparable survival estimates can be attained for several populations across large geographic regions and time spans; and 4) disturbances can be minimized, as it is not necessary to either tag individuals or access nests. The main constraints of these indirect methods are: 1) assumptions are more restrictive than for recapture methods (see Assumptions of Indirect Methods, below); 2) survival estimates, although comparable among sites and years, may be biased; and 3) individual variation in survival probability cannot be taken into account.

Bonelli's eagle (*Aquila fasciata*) is a good model for evaluating these indirect methods in a long-lived species because, like other eagles, it is territorial and shows strong site tenacity and is characterized by a slow life-history strategy (del Hoyo et al. 1992). Thus, its population dynamics are greatly determined by adult survival (Real and Mañosa 1997, Carrete et al. 2005; but see Soutullo et al. 2008). However, survival is difficult to estimate in eagles because of their low breeding densities (Newton 1979) and the inherent difficulty in capturing, tagging, and subsequently resighting individual birds (Kenward et al. 2002). This issue is particularly relevant as roughly one-third of all eagle species are listed as threatened or endangered (International Union for Conservation of Nature 2010). In fact, Bonelli's eagle has suffered a dramatic decline both in range and numbers in recent decades in Europe, which has been linked with low adult survival rates (Rocamora 1994, Real and Mañosa 1997, Real 2004). However, most previous adult survival estimates on this species are based on indirect methods and so survival estimates may be potentially biased.

In this study, our objective was to evaluate survival estimates obtained through AGR and TOR methods and compared them with survival rates estimated from the recapture of individually tagged endangered Bonelli's eagles (*Aquila fasciata*). Additionally, we developed suitable corrections for indirect methods, which allowed us to refine survival estimates, thereby making them comparable with those calculated using recapture methods.

## STUDY AREA

We studied 2 Bonelli's eagle populations, one in Catalonia (NE Spain) and the other in Provence and Languedoc-Roussillon (SE France), hereafter the Catalan and French populations, respectively. The French population was located at the north-western limit of the species' distribution, whereas the Catalan population was located immediately south of the first. Comprehensive censuses of these populations established that the Catalan population consisted of 74 territorial pairs in 1994, a figure that gradually dropped to 65 pairs in 2000, but which has remained almost constant since (Real et al. 2004). The French population remained roughly constant at 23–29 territorial pairs during the whole study period.

## METHODS

We used both the recapture and indirect methods to calculate survival estimates for the periods 2002–2008 and 1999–2008 in, respectively, the Catalan and the French populations. In France, we used additional monitoring data gathered over a longer period of time (1992–2008) to obtain survival estimates using the TOR method and then estimated the proportion of uncorrected survival that corresponded to true mortality (i.e., NRSA parameter), which is needed to correct survival estimates with the TOR method (see details below). We used this longer period because information was available on the plumage-age of both the tagged territorial birds that died and the birds that replaced them. These tagged territorial birds included birds we marked and also territorial eagles tagged as fledglings during previous studies (e.g., Real and Mañosa 2001) or non-systematically tagged as adults by wildlife managers or for environmental impact assessments.

### Field Methods

The key information for applying the indirect methods is the plumage-age of a sample of territorial birds in the population during $\geq 1$ year (AGR) or 2 years (TOR; see Fig. 1). Additionally, the combined information of plumage-age and the sex of territorial birds is required to correctly apply the TOR method. We intensively monitored a sample of territories from both populations to gather data on occupation status (i.e., whether a suitable area was occupied by territorial eagles; see Real and Mañosa 1997), identity (if banded), plumage-age, and sex of territorial birds (Catalonia: 61 territories; France: 35 territories). Surveys included $\geq 3$ visits during the breeding season (from Jan to Jul). We considered a bird territorial in one year when we observed

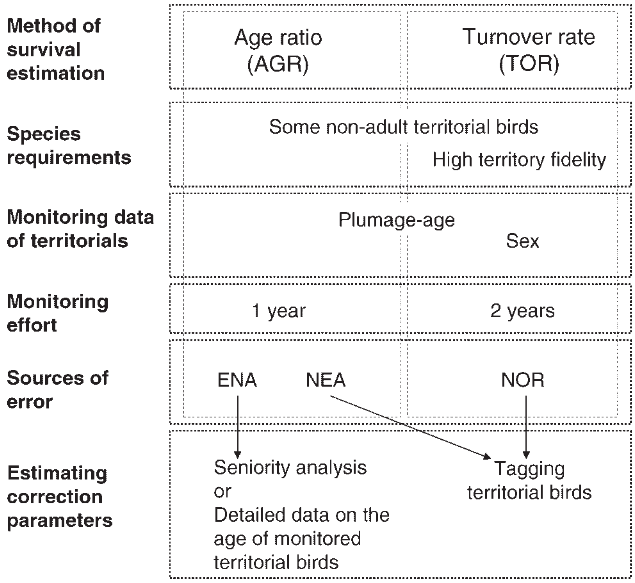

**Figure 1.** Representation of the main requirements for estimation of adult survival based on the age-ratio (AGR) and the turnover-rate (TOR) methods in terms of species requirements, the monitoring data needed for territorial birds, and the monitoring effort. Additionally, we indicate sources of error for each method, as well as the data needed to estimate the correction parameters (ENA: proportion of experienced non-adults; NEA: proportion of non-experienced adults; NOR: proportion of non-observable replacements).

it mated on several occasions during the breeding season and regularly exhibiting territorial behavior, such as roosting at the breeding area (defined as a radius of 750 m from the nest, see Bosch et al. 2010), flight display, nest-building, courting, and breeding. We determined age and sex of individuals in the breeding area to ensure that the territorial birds we were studying were actually holding the monitored territory. We classified territorial birds from their plumage-ages as young (first-year), immature (second-year), subadult (third-year), or adult (fourth-year or older; Parellada 1984; J. Real, University of Barcelona, unpublished data). We determined sex based on behavior (e.g., courtship, copulation, incubation) and body size, as Bonelli's eagles show marked reversed sexual dimorphism (del Hoyo et al. 1992). Based on the data for territorial birds, for each year we calculated the number of territorial birds exhibiting non-adult plumage ($N_{\text{non-ad}}$), number of territorial birds exhibiting full adult plumage ($N_{\text{ad}}$), and number of territorial birds that were not replaced ($N_{\text{non-rep}}$) for males, females, and both sexes combined. We established replacement events by comparing the plumage-age of birds of each sex in the same territory during 2 consecutive years.

In France, as part of a long-term study based on individual banding initiated in 1990, chicks were marked at the nest (40–50 days old) with an alphanumeric coded darvic band, which can be read through a telescope from a distance of up to 200 m. From 1990 to 2008, 423 fledglings were marked. We did not consider records of banded territorial birds before 1999 for survival estimation in capture-resighting analyses because the sample size was too small. Given that darvic-band loss was not uncommon, monitoring also included an intensive effort to detect territorial birds wearing metal bands, which involved feeding and observation from hides of territorial birds suspected of having been replaced.

In Catalonia, during 2002–2005 we trapped 25 eagles from 14 territories with a radio-controlled bow-net trap developed by V. G. Matarranz (Subdirección General para la Biodiversidad–Ministerio de Medio Ambiente). We equipped 22 eagles with a back-pack transmitter with an activity switch (TW-3 32–40 g, Biotrack Ltd., Wareham, Dorset, BH20 5AX, United Kingdom) with a 2- to 3-year life-span; we provided 3 additional birds with solar-powered Global Positioning System (GPS) satellite transmitters (Microwave PTT-100 45 g Argos/GPS, Microwave Telemetry Inc., Columbia, MD) fitted with a Teflon harness with a rupture point (Garcelon 1985). From January to June, we located eagles using either an Icom R10 receiver (Icom Inc, Osaka, Japan) or telemetrically on a daily basis using the Argos system. The monitoring of eagles' movements confirmed that birds were actually holding the territories where we captured them (see Bosch et al. 2010). When we did not detect a territorial eagle by either radio receiver or satellite, we located it visually to check that it was still equipped with its darvic or metal bands.

Eagles were tagged under permission of Servei de Fauna (Generalitat de Catalunya) in Catalonia, and Centre de Recherches par le Baguage des Populations d'Oiseaux (Museum National d'Histoire Naturelle) in France.

### Survival Estimates Based on Recapture Methods

We computed survival and recapture models using a capture-resighting approach (Lebreton et al. 1992). Given that these models consider time in discrete units, we used time intervals of one year, and we used all observation made during the breeding period of each year in monitored territories to construct individual capture-resighting histories. Following Lebreton et al. (1999), we applied multi-state models, which allow information from both live individuals and birds found dead to be considered and may thus improve precision of survival estimates (Kendall et al. 2006). We used multi-state models to obtain estimates of 3 types of parameters: probability of resighting a marked bird over time $t$ ($p$), probability that a marked bird survived from time $t-1$ to time $t$ ($\Phi$), and probability that a marked bird in a given state at time $t-1$ is in another state at time $t$ ($\psi$). In our approach we used $\psi$ to model tag loss, that is, either the loss of darvic bands in France or the exhaustion of transmitter batteries in Catalonia. We estimated these 3 parameters simultaneously from encounter histories by maximum likelihood procedures with the program E-SURGE (Choquet 2007, Choquet et al. 2009). E-SURGE allows transition and encounter matrices and initial state vectors to be defined in >1 step. We used this flexibility to define the transition matrix in 2 steps, the first to model the probability that a bird alive at $t-1$ survived to $t$ ($\Phi$) and the second to model the probability that a live tagged bird then became untagged ($\psi$). We explicitly included the state "dead" in the model structure and split it into 2 categories: "just dead" and "long dead" in recognition of the fact that we would not observe dead individuals in the future.

We assessed goodness-of-fit of the Cormack–Jolly–Seber model through contingency tables using the program U-CARE 2.2.2 (Pradel et al. 2003, Choquet et al. 2005). We selected models based on Akaike's Information Criterion corrected for small sample size (AICc), selecting the model with the smallest AICc value (Burnham and Anderson 2002). We conducted model selection in steps, first by analyzing transition and resighting probabilities while keeping survival parameters fully time dependent and then, once we had selected a suitable structure for transition and resighting probabilities, by analyzing the effect of survival. In Catalonia, we used 5-state models ("alive" and "just dead" when the radio transmitter was working, "alive" and "just dead" when it was not working, and "long dead"). On the basis of the models considering yearly variation in survival ($\Phi_t$) and state-dependent resighting probabilities ($p_{5\ \mathrm{sta}}$), we first studied whether the time elapsed since tagging was related to the probability of transition from battery working to not working (models 1–3 in Table 1). Secondly, we evaluated whether resighting probability differed among states (models 2 and 4 in Table 1). Finally, we computed models considering effects of time and sex on probability of survival (models 4–11 in Table 1). The inspection of parameter estimates for survival-time dependent models allowed us to group years into periods of constant survival. In France, we used 4-state models ("alive with darvic band," "alive without darvic band," "just dead," and "long dead"). On the basis of models considering the yearly variation in survival ($\Phi_t$) and state-dependent resighting probabilities ($p_{4\ \mathrm{sta}}$), we first studied whether the time elapsed since tagging was related to the probability of transition from darvic-tagged to untagged (models 1–5 in Table 2). Secondly, we evaluated whether resighting probability differed among states (models 1 and 6 in Table 2) and, finally, we computed models accounting for effects of time and sex on probability of survival (models 6–9 in Table 2).

### Assumptions of Indirect Methods

Just as in recapture methods (Lebreton et al. 1992, Sandercock 2006), indirect methods assume that the fate of birds (e.g., whether they live or die) is independent among individuals, and in the case of permanent emigration, may lead to an underestimation of survival rates. Moreover, indirect methods—like any other population level method—do not correct for individual heterogeneity (Williams et al. 2002).

The AGR method also assumes that both the rate of population growth and its age distribution are stable. Additionally, this method assumes that both the replacement of territorial birds is always performed by non-adult individuals and that all non-adult individuals are recruiting birds. Consequently, in species with delayed maturity, survival estimates may be biased, both because adult–adult replacement may cause an overestimation of survival and because presence of non-adult birds recruited in previous years may lead to an underestimation of this parameter. On the other hand, the TOR method is only applicable to territorial socially monogamous birds with between year breeding site tenacity and assumes that replacements are always carried out by non-adult individuals. Consequently, adult survival estimates may be biased because adult–adult replacement may cause an overestimation of this parameter.

### Survival Estimates Based in Indirect Methods

We calculated yearly estimates of survival for males, females, and both sexes together in both populations using the 2 indirect methods. We summarized yearly survival rates as geometric mean survival rates, which we then compared with survival rates estimated on the basis of recapture methods during the same periods. Additionally, we estimated survival rates for both sexes together over a longer period to calculate NRSA (see below).

**Table 1.** Estimation of resighting ($p$), radio transmitter state transition ($\Psi$), and survival ($\Phi$) probabilities for tagged Bonelli's eagle from Catalonia, Spain, 2002–2008. We modeled transition probabilities according to the time elapsed since tagging and considering 2, 3, and 4 age classes ($\Psi_{2y}$, $\Psi_{3y}$, and $\Psi_{4y}$, respectively). We estimated resighting probabilities for 5-state models ($p_{5\ \mathrm{sta}}$): "alive" and "just dead" with the radio transmitter working, "alive" and "just dead" with the radio transmitter not working, and "long dead" and 4-state models ($p_{4\ \mathrm{sta}}$): "alive," "just dead" with the radio transmitter working, "just dead" with radio transmitter not working, and "long dead." We estimated survival probabilities considering constant ($\Phi_i$), sex- ($\Phi_{\mathrm{sex}}$), and time- ($\Phi_t$) dependent effects. Time-dependent models considered survival to vary yearly ($\Phi_t$) or to be constant in 2 periods (2002–2007 and 2008: $\Phi_{t(2\ \mathrm{periods})}$). For each model, we give model notation and definition, deviance, the number of estimable parameters (np), and the Akaike's Information Criterion corrected for small sample size ($\mathrm{AIC_c}$).

| Model | Definition | np | Deviance | $\mathrm{AIC_c}$ |
|---|---|---|---|---|
| Modeling transition probabilities | | | | |
| 1 | $\Psi_{2y}\ \Phi_t\ p_{5\ \mathrm{sta}}$ | 11 | 129.37 | 156.67 |
| 2[a] | $\Psi_{3y}\ \Phi_t\ p_{5\ \mathrm{sta}}$ | 12 | 120.96 | 148.91 |
| 3 | $\Psi_{4y}\ \Phi_t\ p_{5\ \mathrm{sta}}$ | 13 | 120.67 | 151.34 |
| Modeling resighting probabilities | | | | |
| 4[a] | $\Psi_{3y}\ \Phi_t\ p_{4\ \mathrm{sta}}$ | 11 | 120.96 | 146.25 |
| Modeling survival probabilities | | | | |
| 5 | $\Psi_{3y}\ \Phi_i\ p_{4\ \mathrm{sta}}$ | 7 | 129.87 | 145.20 |
| 6 | $\Psi_{3y}\ \Phi_{\mathrm{sex}}\ \mathrm{p}_{4\ \mathrm{sta}}$ | 8 | 128.93 | 146.66 |
| 7 | $\Psi_{3y}\ \Phi_{t\ +\ \mathrm{sex}}\ p_{4\ \mathrm{sta}}$ | 12 | 120.08 | 148.03 |
| 8 | $\Psi_{3y}\ \Phi_{t(2\ \mathrm{periods})}\ p_{4\ \mathrm{sta}}$ | 8 | 124.89 | 142.63 |
| 9 | $\Psi_{3y}\ \Phi_{t(2\ \mathrm{periods})\ +\ \mathrm{sex}}\ p_{4\ \mathrm{sta}}$ | 9 | 124.09 | 144.28 |
| 10 | $\Psi_{3y}\ \Phi_{t(2\ \mathrm{periods})\ *\ \mathrm{sex}}\ p_{4\ \mathrm{sta}}$ | 10 | 121.82 | 144.54 |
| 11[a] | $\Psi_{3y}\ \Phi_{\mathrm{f\ \&\ m\ (02–07)\ +\ m\ (08)}}\ p_{4\ \mathrm{sta}}$ | 8 | 121.83 | 139.57 |

[a] Models selected at each step.

**Table 2.** Estimation of resighting ($p$), darvic-band state transition ($\Psi$), and survival ($\Phi$) probabilities for tagged Bonelli's eagle from France, 1999–2008. We modeled transition probabilities according to time elapsed since tagging and considering 1, 2, 3, 4, or 5 age classes ($\Psi_i$, $\Psi_{2y}$, $\Psi_{3y}$, $\Psi_{4y}$, and $\Psi_{5y}$, respectively). We estimated resighting probabilities for 4-state models ($p_{4\text{ sta}}$): "alive with darvic band," "alive without darvic band," "just dead," and "long dead" and 3-state models ($p_{3\text{ sta}}$): "alive," "just dead," and "long dead." We estimated survival probabilities using constant ($\Phi_i$), sex- ($\Phi_{\text{sex}}$), and time- ($\Phi_t$) dependent effects. For each model, we give model notation and definition, deviance, number of estimable parameters (np), and the Akaike's Information Criterion corrected for small sample size (AIC$_c$).

| Model | Definition | np | Deviance | AIC$_c$ |
|---|---|---|---|---|
| Modeling transition probabilities | | | | |
| 1[a] | $\Psi_i\ \Phi_t\ p_{4\text{ sta}}$ | 14 | 229.90 | 263.43 |
| 2 | $\Psi_{2y}\ \Phi_t\ p_{4\text{ sta}}$ | 15 | 229.32 | 265.72 |
| 3 | $\Psi_{3y}\ \Phi_t\ p_{4\text{ sta}}$ | 16 | 229.26 | 268.62 |
| 4 | $\Psi_{4y}\ \Phi_t\ \mathrm{p}_{4\text{ sta}}$ | 17 | 228.52 | 270.90 |
| 5 | $\Psi_{5y}\ \Phi_t\ p_{4\text{ sta}}$ | 18 | 228.52 | 274.02 |
| Modeling resighting probabilities | | | | |
| 6[a] | $\Psi_i\ \Phi_t\ p_{3\text{ sta}}$ | 13 | 230.92 | 261.64 |
| Modeling survival probabilities | | | | |
| 7 | $\Psi_i\ \Phi_{t\,+\,\text{sex}}\ p_{3\text{ sta}}$ | 14 | 229.85 | 263.37 |
| 8[a] | $\Psi_i\ \Phi_{\text{sex}}\ p_{3\text{ sta}}$ | 6 | 236.29 | 249.29 |
| 9[a] | $\Psi_i\ \Phi_i\ p_{3\text{ sta}}$ | 5 | 237.15 | 247.85 |

[a] Models selected at each step.

We calculated survival using the age-ratio method ($S_{\text{AGR}}$) as follows (Rohwer 2004):

$$S_{\text{AGR}(t-1\rightarrow t)} = \frac{N_{\text{ad}(t)}}{N_{\text{ad}(t)} + N_{\text{non-ad}(t)}}$$

where $N_{\text{non-ad}(t)}$ is the number of territorial non-adults at time $t$, and $N_{\text{ad}(t)}$ is the number of territorial adults at time $t$.

We calculated survival using the turnover rate method ($S_{\text{TOR}}$) as follows (Real and Mañosa 1997):

$$S_{\text{TOR}(t-1\rightarrow t)} = \frac{N_{\text{non-rep}(t)}}{N_{\text{total}(t-1)}}$$

where $N_{\text{non-rep}(t)}$ is the number of territorial birds at $t - 1$ that were not replaced and had not disappeared at $t$ (on the basis of the plumage-age of individuals), and $N_{\text{total}(t-1)}$ is the total number of territorial birds at $t - 1$. We did not consider replacements of marked birds when the new individual exhibited the same (for adults) or the following (for non-adults) age-class plumage as the previous territory holder because our aim was to evaluate this method when there are no marked individuals in the monitored territories.

## Corrections for the Indirect Methods

Survival estimates using the indirect methods may be biased due to presence of experienced non-adults (ENA) or non-experienced adults (NEA) in the AGR method or by presence of non-observable replacements (NOR) in the TOR method (Fig. 2). To correct for these biases it is necessary to have more detailed demographic data derived from marked individuals. Most of the correction parameters are based on rates (Table 3), so we estimated their corresponding standard errors as the square root of the variances, which we calculated from the following equation:

$$\text{Var}(\hat{\pi}) = \frac{\pi \times (1-\pi)}{N_\pi}$$

where $\pi$ is the raw estimate of the rate and $N_\pi$ the sample size from which we estimated it. In those cases in which the correction parameter is a function of other variables, we used the delta method to obtain the formula for estimating variance (see below).

To calculate the corrected estimate of survival using the AGR method and its variance we used the following expressions:

$$S_{\text{AGR-C}} = [S_{\text{AGR}} \times (1-\text{NEA})] + [(1-S_{\text{AGR}}) \times \text{ENA}]$$

$$\begin{aligned}\text{Var}(S_{\text{AGR-C}}) &= \left[[(1-\text{NEA})-\text{ENA}]^2 \times \text{Var}(S_{\text{AGR}})\right] \\ &\quad + \left[(-S_{\text{AGR}})^2 \times \text{Var}(\text{NEA})\right] \\ &\quad + \left[(1-S_{\text{AGR}})^2 \times \text{Var}(\text{ENA})\right]\end{aligned}$$

where NEA is the proportion of non-experienced adults, and ENA is the proportion of experienced non-adults.

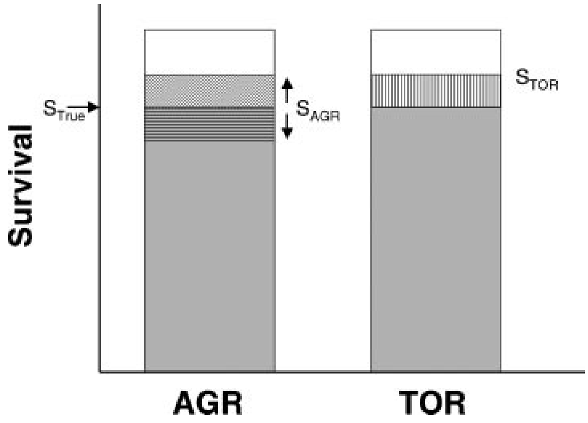

**Figure 2.** Representation of expected biases in adult survival estimations based on the age-ratio (AGR) and the turnover-rate (TOR) methods. True survival ($S_{\text{True}}$) is represented by the gray area of the graphic and true mortality by the white area. Survival estimates using AGR methods ($S_{\text{AGR}}$) may be underestimated for non-adults with previous breeding experience (horizontal lines) and overestimated for adults without previous breeding experience (oblique lines). Survival estimates using TOR methods ($S_{\text{TOR}}$) may be overestimated for non-observable replacements (vertical lines).

**Table 3.** Parameters for correcting survival estimated by indirect methods in Bonelli's eagle populations from France, 1999–2008, and Catalonia, 2002–2008. Parameter estimate (PAR), standard error (SE), and sample size (*n*) of each parameter are indicated.

| | Catalan population | | | French population | | |
|---|---|---|---|---|---|---|
| **Ratios to correct indirect methods** | **PAR** | **SE** | ***n*** | **PAR** | **SE** | ***n*** |
| Age ratio method (AGR) | | | | | | |
| Experienced territorial non-adults (ENA) | 0.153 | 0.084 | 165[a] | 0.111 | 0.061 | 83[a] |
| Non-experienced territorial adults (NEA)[b] | 0.066 | 0.034 | 75 | 0.066 | 0.034 | 75 |
| Turnover rate method (TOR) | | | | | | |
| Non-observable replacements (NOR) | 0.526 | 0.114 | 19 | 0.222 | 0.097 | 18 |
| Uncorrected survival due to non-observable replacements (NRSA) | 0.074 | 0.047 | 638[c] | 0.019 | 0.015 | 879[c] |

[a] Sample size indicates the number of non-adult individual * year that we used to estimate the proportion of each class age to the total number of non-adult territorial birds ($R_i$).

[b] Estimated from seniority probability for adult individuals in Hernández-Matías et al. (2010).

[c] Sample size indicates the number of non-adult individual * year that we used to estimate the uncorrected $S_{\mathrm{TOR}}$.

To estimate the NEA and ENA proportions we used a previous study on Bonelli's eagle by Hernández-Matías et al. (2010) based on the same data set as we used here. Hernández-Matías et al. (2010) provide seniority estimates (Pradel et al. 1997), which are defined as the probability that a territorial bird of age i is experienced ($\gamma_i$). Additionally, we estimated the proportion of each class age for the total of non-adult territorial birds ($R_i$ for i = 2- and 3-year-olds, which are the possible ages of ENA birds in the Bonelli's eagle). Thus, we estimated the ENA and its variance as follows:

$$\mathrm{ENA} = \sum (\gamma_i \times R_i)$$

$$\mathrm{Var(ENA)} = \sum \left[\left(\gamma_i^2 \times \mathrm{Var}(R_i)\right) + \left(R_i^2 \times \mathrm{Var}(\gamma_i)\right)\right]$$

whereas we directly applied NEA and its variance using the seniority estimate for adult birds provided by Hernández-Matías et al. (2010; see Table 3).

To calculate the corrected yearly estimates of survival using the TOR method and its variance we used the following expressions:

$$S_{\mathrm{TOR\text{-}C}} = S_{\mathrm{TOR}} \times (1-\mathrm{NRSA}) \times (1-\mathrm{DWA})$$

$$\begin{aligned}\mathrm{Var}(S_{\mathrm{TOR\text{-}C}}) &= \left[[(1-\mathrm{NRSA}) \times (1-\mathrm{DWA})]^2 \times \mathrm{Var}(S_{\mathrm{TOR}})\right] \\ &+ \left[[(-S_{\mathrm{TOR}}) \times (1-\mathrm{DWA})]^2 \times \mathrm{Var(NRSA)}\right] \\ &+ \left[[(-S_{\mathrm{TOR}}) \times (1-\mathrm{NRSA})]^2 \times \mathrm{Var(DWA)}\right]\end{aligned}$$

where NRSA is the proportion of $S_{\mathrm{TOR}}$ that correspond to mortality (area with vertical lines in Fig. 2). We estimated NRSA and its variance from the ratio of non-observable replacements (NOR) as:

$$\mathrm{NRSA} = \frac{[\mathrm{NOR} \times (1-S_{\mathrm{TOR}})]}{[(1-\mathrm{NOR}) \times S_{\mathrm{TOR}}]}$$

$$\begin{aligned}\mathrm{Var(NRSA)} &= \left[\left[\frac{(1-S_{\mathrm{TOR}})}{\left[S_{\mathrm{TOR}} \times (1-\mathrm{NOR})^2\right]}\right]^2 \times \mathrm{Var(NOR)}\right] \\ &+ \left[\left[\frac{(-\mathrm{NOR})}{[S_{\mathrm{TOR}}{}^2 \times (1-\mathrm{NOR})]}\right]^2 \times \mathrm{Var}(S_{\mathrm{TOR}})\right]\end{aligned}$$

To estimate NOR we used data from tagged territorial individuals that were known to be dead and for which the age-plumage of the new territorial bird was known. It is important to note that the value of $S_{\mathrm{TOR}}$ needed to estimate NRSA should be calculated without considering apparent deaths that lead to territorial abandonment and with the same period used to estimate NOR. In declining populations, it is also necessary to correct yearly $S_{\mathrm{TOR}}$ estimates for the yearly proportion of monitored birds that resulted in the abandonment of a territory (DWA). An advantage of the corrections for the TOR method as opposed to the AGR method is that the information needed to correct the bias is more easily gathered. It is noticeable that $S_{\mathrm{TOR\text{-}C}}$ can be directly estimated from NOR without the needing to estimate NRSA. However, this may produce biases when the uncorrected $S_{\mathrm{TOR}}$ differs between the period for which data on known replacements is available and the period for which we want to estimate survival.

## RESULTS

### Survival Estimates by Recapture Methods

*Catalonia.*— During the period 2002–2008, we found 8 out of 25 radiotagged birds dead, and we considered 2 others to be dead because their satellite transmitter suddenly stopped sending locations and we never resighted the birds. By the end of the study we confirmed only 9 tagged eagles to be still alive. The Cormack–Jolly–Seber (CJS) model explained the data adequately (goodness-of-fit test: $\chi^2_{3\ \mathrm{df}} = 5.000$, $P = 0.172$). All best models included the effect of the time elapsed since tagging on the probability of the transition from the state "transmitter working" to that of "not working" (first year: 0.10, second year: 0.27, third year: 0.87 in model 11 in Table 1), which agreed with the estimated duration of the radio devices provided by the manufacturer. Additionally, models considering the effect of radio state in the resighting probability for alive individuals indicated very high values ($P = 1$ in models 1–3 in Table 1) both for individuals with working transmitters and those with non-working transmitters. Therefore, we estimated resighting probabilities of live individuals as one parameter when modeling survival probabilities (models 4–11 in Table 1). Probability of recovering a dead individual was higher for individuals with working transmitters than for individuals with non-working transmitters in all models ($P = 0.82$ [95% CI: 0.49–0.95] and $P = 0.40$ [95% CI: 0.10–0.80], respectively, in model 11 in Table 1).

The model considering constant survival between sexes and years estimated this value at 0.78 (SE = 0.049, 95% CI: 0.67–0.86; model 5 in Table 1). A similar model considering survival dependent on sex (model 6 in Table 1) indicated higher survival for females ($\Phi = 0.83$, SE = 0.068, 95% CI: 0.66–0.93) than for males ($\Phi = 0.74$, SE = 0.068, 95% CI: 0.59–0.85). Nevertheless, the best model (model 11 in Table 1) indicated that survival, estimated at 0.84 (SE = 0.047, 95% CI: 0.72–0.91), remained constant for females in the whole study period and for males in the period 2002–2007, but that male survival crashed dramatically in 2008 ($\Phi = 0.40$, SE = 0.155, 95% CI: 0.16–0.70). This extremely low value for male survival may be biased by the small number of males that were still alive at the end of the study period.

*France.*— During the period 1999–2008, 39 eagles were recruited into a territory and we found 2 individuals dead. The CJS model explained the data adequately (goodness-of-fit test: $\chi^2_{16\ \mathrm{df}} = 7.458$, $P = 0.963$). Models considering the effect of the time elapsed since banding on tag-loss probability did not have a better fit than models considering a constant yearly rate of tag loss, which we estimated at 0.07 (95% CI: 0.02–0.25; model 9 in Table 2). Analyses reveal that resighting probability of birds that lost their darvic bands ($P = 0.64$, 95% CI: 0.46–0.79; in model 1 in Table 2) was similar to those that kept their darvic bands ($P = 0.50$, 95% CI: 0.31–0.67). Accordingly, a model considering the same resighting probability for either birds that lost their darvic tag or birds that did not performed better than a model considering different resighting probabilities for either tagged or untagged birds (model 6 vs. model 1 in Table 2). This result can be explained by the efforts made by fieldworkers to detect marked birds with metal bands in their territories. We estimated resighting probability for birds recovered dead at 0.17 (95% CI: 0.04–0.49; model 9 in Table 2).

The best model indicated that survival remained constant over time and did not differ between sexes, and we estimated it at 0.88 (SE = 0.040, 95% CI: 0.78–0.94; model 9 in Table 1). Nevertheless, the model considering the effect of sex on survival probability (model 8 in Table 2) was <2 $\mathrm{AIC_c}$ points from the best model, thereby suggesting that females ($\Phi = 0.91$, SE = 0.046, 95% CI: 0.77–0.97) survived better than males ($\Phi = 0.84$, SE = 0.070, 95% CI: 0.65–0.93).

### Survival Estimates Using Indirect Methods

In both populations the uncorrected estimates of survival calculated by indirect methods provided higher values than estimates by recapture methods (Catalonia: AGR method: 0.91 [SE = 0.013, $n = 558$ bird $*$ year]; TOR method: 0.93 [SE = 0.012, $n = 547$ bird $*$ year]; France: AGR method: 0.93 [SE = 0.012, $n = 443$ bird $*$ year]; TOR method: 0.93 [SE = 0.012, $n = 438$ bird $*$ year]). Nevertheless, the proposed corrections for estimates of survival calculated by indirect methods provided similar values of survival to those estimated by recapture methods (Fig. 3A and B). In the Catalan population, the corrected estimate of survival was calculated at 0.86 by the AGR method (SE = 0.011, 95% CI: 0.84–0.88) and 0.86 by the TOR method (SE = 0.022, 95% CI: 0.81–0.90), whereas in the French population, the corrected estimate of survival was calculated at 0.87 by the AGR method (SE = 0.015, 95% CI: 0.84–0.90) and 0.92 by the TOR method (SE = 0.013, 95% CI: 0.89–0.94). The main discordance we found in the corrected estimates of the indirect methods corresponds to the TOR estimate in the French population, in which we estimated the NRSA parameter at 0.019 using data of 18 known deaths of territorial birds recorded during the period 1992–2008. However, we would expect to find similar values to the NEA parameter, which was estimated by Hernández-Matías et al. (2010) with recapture methods at 0.066 for the same period. In fact, when applying the NEA value instead of the NRSA parameter $S_{\mathrm{TOR\text{-}C}}$ is estimated at 0.87 (SE = 0.015, 95% CI: 0.84–0.90).

Both recapture and indirect methods suggested that females survived better than males both in the Catalan (F: $S_{\mathrm{AGR\text{-}C}} = 0.87$ [SE = 0.021], $S_{\mathrm{TOR\text{-}C}} = 0.87$ [SE = 0.024], Fig. 3E; M: $S_{\mathrm{AGR\text{-}C}} = 0.86$ [SE = 0.020], $S_{\mathrm{TOR\text{-}C}} = 0.85$ [SE = 0.025], Fig. 3C) and French populations (F: $S_{\mathrm{AGR\text{-}C}} = 0.89$ [SE = 0.017], $S_{\mathrm{TOR\text{-}C}} = 0.93$ [SE = 0.016], Fig. 3F; M: $S_{\mathrm{AGR\text{-}C}} = 0.86$ [SE = 0.020], $S_{\mathrm{TOR\text{-}C}} = 0.90$ [SE = 0.018], Fig. 3D).

## DISCUSSION

Our results show that both the age-ratio and the turnover-rate methods are useful for monitoring adult survival over time and space in populations of bird species that show morphologically age-characterizable breeding individuals. In most raptor populations, some individuals become territorial before exhibiting full adult plumage and so we expect that these indirect methods can be widely applied to this group (Newton 1979, Gerrard et al. 1992, Krueger 1997, Watson 1997, Whitfield et al. 2004). In our study, the uncorrected survival estimates for Bonelli's eagle using indirect methods show the same trends as estimates using recapture methods, that is, females survive better than males and eagles from the Catalan population survive less well than birds from the French population.

The assumptions of the indirect methods may constrain their application and they obviously are not substitutes for traditional recapture methods (see above). Nevertheless, their relatively low cost in comparison with recapture methods make them useful tools when rapid management

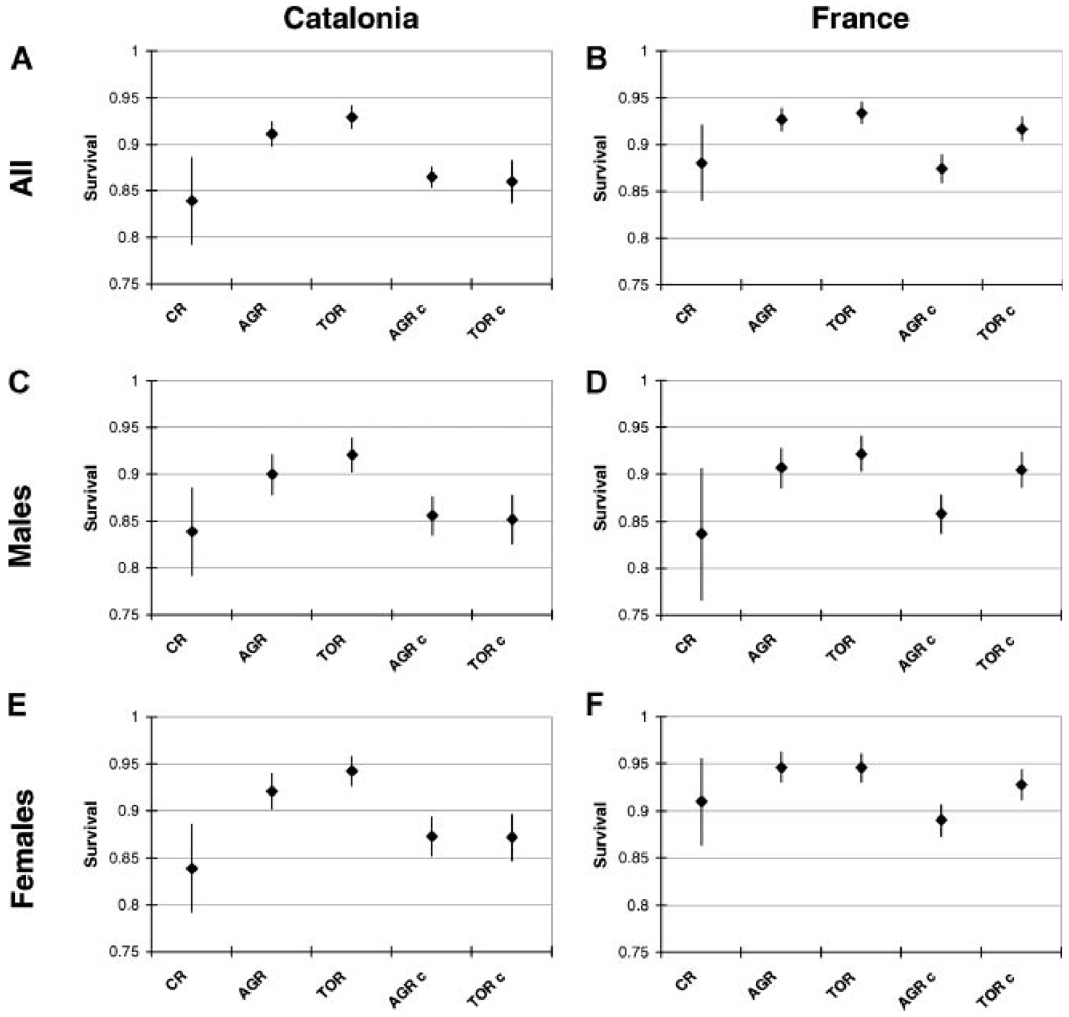

**Figure 3.** Survival estimates using recapture (CR), uncorrected and corrected age-ratio (AGR and AGR-C, respectively) methods, and uncorrected and corrected turnover-rate (TOR and TOR-C, respectively) methods for territorial Bonelli's eagles from the Catalan and the French population, 2002–2008 and 1999–2008, respectively. For each method, we show survival values and their associated standard errors for females (E, F), males (C, D), and both sexes combined (A, B).

or conservation decisions have to be taken on a target species for which survival data is not available. Additionally, given the possibility of estimating survival across broad spatial and time scales, these described indirect methods can be powerful tools for monitoring spatial and temporal variations in survival in bird populations, particularly in long-lived territorial species in which between-year territory based monitoring is feasible. Without corrections, these 2 indirect methods overestimate true survival in the study populations of the endangered Bonelli's eagle. However, the corrections we proposed allow reliable survival estimates to be obtained that can be applied in demographic models for investigating current and future population trends.

### Accuracy of Survival Estimates by Recapture Methods

We assumed that the survival estimates using the recapture of adult Bonelli's eagles were not biased. Survival estimation may be biased if it is based on a small number of individuals (Williams et al. 2002, Lindberg and Walker 2007). Our study species breeds at low densities and the studied populations were small (Real et al. 2004), so the sample-size problem is unavoidable, even though we in fact monitored a sizeable fraction of the individuals in the population (e.g., nearly all fledged chicks in France). Our results indicate that the reencounter probability was high in both populations, which is to be expected in a territorially conspicuous species such as Bonelli's eagle with high territorial tenacity, and thus we assume that our adult survival estimates are correct.

Radiotagging has the inherent advantage that all live and most dead individuals can be easily found. On the other hand, it requires a concerted effort in terms of equipment, the trapping of individuals, and the monitoring of territories (Kenward et al. 2002). Moreover, the relatively short useful life-span of radio transmitters means that survival estimates can only be achieved over short time periods and that continuous high investment is unavoidable. Hazard heterogeneity may potentially cause a bias in survival estimation if radiotagging is concentrated over a short period of time and monitoring for survival estimate lasts for a longer period of time (Zens and Peart 2003). This source of bias could potentially have affected our survival estimates of radiotagged birds at the end of the study period (2006–2008). However, we did not find any increase in survival during these years, as would be expected if hazard heterogeneity of the sample had biased our results, and so the error introduced by this effect was probably negligible.

Marking nestlings with darvic bands and the subsequent monitoring of territories was also highly effective in detecting tagged individuals. However, tag loss was not rare and it would have been preferable to have marked birds with more resistant bands. In the French population, we surveyed most territories by using bait to attract eagles so that darvic or conventional metal bands could be read. Therefore, reencounter probabilities did not differ between darvic-tagged and untagged individuals. This technique may potentially cause a bias in the estimation of resighting probability if some birds are more prone to visit bait than others. In our study, though, all eagles surveyed by this method were successfully attracted to the bait and so this problem does not apply here.

Finally, we benefited from the high flexibility of current methods and software to model reencounter histories considering the complexity of the system under study. This allowed us to incorporate into our models information regarding birds observed alive or found dead (Lebreton et al. 1999), as well as several effects such as time-dependent tag-loss probability and state-specific reencounter probabilities that may potentially cause a violation of the model's assumptions (Kendall et al. 2006, Sandercock 2006). All the above arguments support the idea that our survival estimates, based on recapture methods, were accurate and reliable.

### Constraints of the Indirect Methods

The main constraint associated with the use of the indirect methods is their associated assumptions (see Methods). Indirect methods are designed to estimate survival in the territorial fraction of a population and so are not suitable for estimating survival of non-territorial birds. Moreover, indirect methods are only suitable if the age of territorial individuals can be determined morphologically and assigned to $\geq 2$ categories (e.g., morphologically non-adult vs. adult birds). Although this requirement is normally fulfilled in long-lived species, this method is also potentially applicable to the many short-lived species that are also distinguishable as first-year adults (Svensson 1992). For example, the age-ratio method has been successfully applied for calculating survival estimations of museum-collected individuals of several passerine species (Ricklefs 1997, Rohwer 2004). On the other hand, in healthy and stable populations of territorial long-lived birds characterized by a high adult survival, a large pool of non-breeding adult floaters, and a large proportion of adult-plumaged recruits (Ferrer and Penteriani 2008), the indirect methods are not suitable to detect short-term variations in survival. However, if a decline in survival continues for several years, indirect methods (even without corrections) are able to detect such a decline (see Balbontín et al. 2003, Ferrer et al. 2003).

The age-ratio method can potentially be applied to non-territorial species. However, the application of this method is rather restrictive, as variations in the rate of population change or in age distribution may bias survival estimates (Rohwer 2004, Murray and Patterson 2006). In the event that additions or deletions to the population in question are due to the non-adult fraction of the breeding population, a simple correction consists of multiplying the survival estimate by the rate of population change between $t - 1$ and $t$. However, if dealing with net emigration or immigration of adult individuals, accurate data is needed and the proposed formulas for the survival estimation have to be modified to correct for these biases. In territorial species such as Bonelli's and other eagle species that exhibit temporal stability in their choice of breeding sites, estimating survival in one population may be successful if the same territories are repeatedly monitored in consecutive years, thereby enabling survival of the population to be estimated over time.

The turnover-ratio method can only be applied to species for which survival is estimated in terms of territories, as a replacement of a territorial bird can only be established by comparing the same territory over 2 consecutive seasons (Real and Mañosa 1997, Watson 1997). Eagles are a suitable group for applying this method, as most eagle species are long-lived and territorial and show strong site tenacity; furthermore, their population growth is constrained by nest-site availability (Newton 1979) and non-breeding eagles preferentially recruit in previously occupied territories (Hernández-Matías et al. 2010). On the other hand, territory-based estimates of survival may be biased in territorial species with high levels of breeding dispersal. This dispersal problem may be overlooked in survival estimates at population level if dispersing birds replace a true death in a monitored territory. However, if a bird occupies a previously unoccupied territory or moves away from the study area, the survival estimate is underestimated.

In the present study, we addressed the most important biases expected to affect survival estimates when using indirect methods in long-lived monogamous territorial species. To correct survival when estimated using the turnover-rate method, first, it is necessary to know the proportion of NOR, which mostly correspond to adult-adult replacements. This information should be collected by tagging a sample of territorial birds and then by monitoring their presence in their territories over time. In the case of Bonelli's eagle, both radiotracking and darvic bands are suitable for estimating this parameter. When a tagged territorial individual is known to have died, it is thus easy to know the age of the replacement eagle, and we also recorded this information in our study. Alternatively, individual identification through DNA tagging (e.g., Rudnick et al. 2005) would allow the NOR parameter to be estimated if combined with monitoring data. Once the NOR parameter is known, the proportion of the uncorrected survival estimate that does not correspond to true survival (NRSA) can be estimated from the NOR parameter and the uncorrected survival estimate. However, these 2 parameters should be estimated over the same time period to avoid biases in the NRSA estimation, given that changing the NRSA has an important effect on the corrected survival estimate. In France, our estimated NRSA is extremely low (1.87%) and matches neither the estimated NRSA in Catalonia (7.45%) nor the NEA parameter in France (6.58%), which were expected to show similar values. Nevertheless, when applying the NEA parameter instead of the NRSA to estimate the corrected survival from France, the survival value matches fairly well with that obtained by recapture methods (87.3% and 88.0%, respectively), which highlights the importance of having the best possible data concerning the parameters used to correct survival estimates employing the indirect methods. This issue also applies to sex-specific survival estimation. Here, we applied the same correction parameters to both males and females, based on limitations in sample sizes. Nevertheless, it is worth noting that sex-specific differences in correction parameters may bias sex-specific survival estimates. In fact, only one 1 of 4 territorial females known to have died in Catalonia during the study period was replaced by a non-adult female, compared to 8 out of 15 males, further supporting the notion that males have lower adult survival rates than females in this population.

Regarding the age-ratio method, the necessary data for correcting its potential biases may be more difficult to collect, as comprehensive recapture data for individually recognizable birds marked as fledgings are required to obtain age-specific seniority probabilities (Hernández-Matías et al. 2010). Alternatively, the fraction of non-adult birds that are experienced could be derived from monitoring data if detailed data on the age of monitored territorial birds exists, and the proportion of non-experienced territorial adults could be indirectly calculated from the ratio of adult-adult replacements (i.e., the NRSA parameter from the turnover-ratio method), for which the necessary data could be collected more easily.

Finally, the indirect methods cannot account for individual variation in survival probability and thus its association with relevant covariates is limited. The indirect methods allowed us to estimate sex-specific survival probabilities. According to the recapture methods, our results suggest that females show higher survival probability than males (Newton 1986), although our uncorrected estimates might be biased if biasing factors differ between sexes (e.g., recruitment age, floater population size; Heeb et al. 1999, Dale 2001). On the other hand, the turnover-rate method can be applied to obtain survival probabilities at territorial level, which can thus be related to territorial characteristics such as density of power lines and pressure from hunting.

## MANAGEMENT IMPLICATIONS

The age-ratio and the turnover-rate methods we described in this report are useful to monitor adult survival across populations and over time (also see Newton 1979, Ferrer 1993, Watson 1997), particularly when the application of traditional capture-recapture methods is not feasible. To apply the indirect methods we described detailed information on the plumage-age and sex of territorial birds must be recorded. Thus, data collection should only be conducted by experienced fieldworkers. This information should be established on the basis of repeated observations of territorial birds in the breeding area or preferably at the nest site, to avoid monitoring birds that do not correspond to the birds holding the monitored territory. Monitoring should encompass a representative sample of the areas used by the population.

Uncorrected estimates of survival derived from the 2 indirect methods may be biased (see Results), so we highlight the need to use suitable corrections to obtain accurate survival estimates. To minimize the effort needed to estimate the magnitude of the sources of error, we recommend combining basic monitoring with data from intensive monitoring campaigns using tagged individuals. In populations where capturing territorial individuals is not feasible, genetic analyses of naturally shed feathers found in the nest as a means of recognizing territory owners will allow these parameters to be estimated (Rudnick et al. 2005). Once samples exist from several years or from populations for which information on uncorrected survival and sources of error is available, we recommend looking for correlations between easily measurable characteristics of the population (e.g., the proportion of territorial birds showing non-adult plumage) and the sources of error (e.g., the proportion of non-observable replacements). Knowledge of these correlations will allow the magnitude of the sources of error to be extrapolated, even in populations for which information regarding recognizable individuals is not available (A. Hernández-Matías and J. Real, University of Barcelona, unpublished data).

## ACKNOWLEDGMENTS

Comments from K. Titus, M. J. Bechard, F. R. Thompson, and an anonymous referee greatly improved previous versions of the manuscript. In France, data were provided by the "Plan National d'Action de l'Aigle Bonelli" managed by the Ministère de l'Ecologie, de l'Energie, du Développement durable et de la Mer (MEEDDM), with the collaboration of the Espaces Naturels de Provence (CEEP), CORA and Conservatoire des Espaces Naturels du Languedoc-Roussillon. We thank N. Vincent-Martin and A. Ravayrol for his invaluable help in preparing the data bases, and M. Lecacheur. In Catalonia, A. Tintó, R. Bosch, F. Parés, R. Amo, and many other observers provided invaluable help in fieldwork tasks, V. García M. captured the eagles, and C. Castell greatly contributed to the achievement of this study. M. Lockwood revised the English. This study was supported by the Spanish Ministerio de Educación y Ciencia through projects CGL2007-64805/BOS, and CGL2004-03189, and grant SAB-2006-0014/Roger Pradel, the French MEEDDM, Oficina Tècnica de Planificació i Anàlisi Territorial–OTPAT (Diputació de Barcelona), and Fundació Miquel Torres (Bodegas Miquel Torres).

## LITERATURE CITED

Balbontín, J., V. Penteriani, and M. Ferrer. 2003. Variations in the age of mates as an early signal of changes in population trends? The case of Bonelli's eagle in Andalusia. Biological Conservation 109:417–423.

Bosch, R., J. Real, A. Tintó, E. Zozaya, and C. Castell. 2010. Home-ranges and patterns of spatial use in territorial Bonelli's Eagles *Aquila fasciata*. Ibis 152:105–117.

Burgman, M. A. 2005. Risks and decisions for conservation and environmental management. Cambridge University Press, Cambridge, United Kingdom.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Carrete, M., J. A. Sánchez-Zapata, J. F. Calvo, and R. Lande. 2005. Demography and habitat availability in territorial occupancy of two competing species. Oikos 108:125–136.

Choquet, R. 2007. E-SURGE 1.0 user's manual. Centre d'Ecologie Fonctionnelle et Evolutive-Centre National de la Recherche Scientifique, Montpellier, France.

Choquet, R., L. Rouan, and R. Pradel. 2009. Program E-SURGE: a software application for fitting Multievent models. Pages 845–865 *in* D. L. Thomson, E. G. Cooch, and M. J. Conroy, editors. Modeling demographic processes in marked populations. Series: environmental and ecological statistics, Vol. 3. Springer, New York, New York, USA.

Choquet, R., A. M. Reboulet, J. D. Lebreton, O. Gimenez, and R. Pradel. 2005. U-CARE 2.2 user's manual. CEFE, UMR, 5175. CNRS, Montpellier, France.

Dale, S. 2001. Female-biased dispersal, low female recruitment, unpaired males, and the extinction of small and isolated bird populations. Oikos 92:344–356.

del Hoyo J., A. Elliott, and J. Sargatal. editors. 1992. Handbook of the birds of the world, Vol. 2. New World Vultures to Guineafowl, Lynx Edicions, Barcelona, Spain.

Ferrer, M. 1993. El Águila imperial. Serie Eurofauna, Editorial Quercus, Madrid, Spain. [In Spanish].

Ferrer, M., and V. Penteriani. 2008. Non-independence of demographic parameters: positive density-dependent fecundity in eagles. Journal of Applied Ecology 45:1453–1459.

Ferrer, M., V. Penteriani, J. Balbontin, and M. Pandolfi. 2003. The proportion of immature breeders as a reliable early warning signal of population decline: evidence from the Spanish imperial eagle in Doñana. Biological Conservation 114:463–466.

Garcelon, D. K. 1985. Mounting backpack telemetry packages on bald eagles. Institute for Wildlife Studies, Arcata, California, USA.

Gerrard, J. M., P. N. Gerrard, P. N. Gerrard, G. R. Bortolotti, and E. H. Dzus. 1992. A 24-year study of Bald Eagles on Besnard Lake, Saskatchewan. Journal of Raptor Research 26:159–166.

Heeb, P., I. Werner, A. C. Mateman, M. Kölliker, M. W. G. Brinkhof, C. M. Lessells, and H. Richner. 1999. Ectoparasite infestation and sex-biased local recruitment of hosts. Nature 400:63–65.

Hernández-Matías, A., J. Real, R. Pradel, A. Ravayrol, N. Vincent-Martin, and F. Bosca. 2010. Determinants of territorial recruitment in Bonelli's eagle (*Aquila fasciata*) populations. Auk 127:173–184.

International Union for Conservation of Nature. 2010. IUCN Red List of Threatened Species. Version 2010. 4. <www.iucnredlist.org>. Accessed 18 Jan 2011.

Kendall, W. L., P. B. Conn, and J. E. Hines. 2006. Combining multistate capture–recapture data with tag recoveries to estimate demographic parameters. Ecology 87:169–177.

Kenward, R. E., T. Katzner, M. Wink, V. Marcstrom, S. Walls, M. Karlbom, R. Pfeffer, E. Bragin, K. Hodder, and A. Levin. 2007. Rapid sustainability modeling for raptors by radiotagging and DNA-fingerprinting. Journal of Wildlife Management 71:238–245.

Kenward, R. E., S. P. Rushton, C. M. Perrins, D. W. MacDonald, and A. B. South. 2002. From marking to modelling: dispersal study techniques for land vertebrates. Pages 50–71 *in* J. M. Bullock, R. E. Kenward, and R. S. Hails, editors. Dispersal ecology. Blackwell, Oxford, United Kingdom.

Krueger, O. 1997. Population density and intra- and interspecific competition of the African Fish Eagle Haliaeetus vocifer in Kyambura Game Reserve, southwest Uganda. Ibis 139:19–24.

Lank, D. B., and J. Dale. 2001. Visual signals for individual identification: The Silent "Song" of Ruffs. Auk 118:759–765.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case-studies. Ecological Monographs 62:67–118.

Lebreton, J. D., T. Almeras, and R. Pradel. 1999. Competing events, mixtures of information and multistratum recapture models. Bird Study 46:39–46.

Lindberg, M. S., and J. Walker. 2007. Satellite telemetry in avian research and management: sample size considerations. Journal of Wildlife Management 71:1002–1009.

McIntyre, C. L., M. W. Collopy, and M. S. Lindberg. 2005. Survival probability and mortality of migratory juvenile golden eagles from interior Alaska. Journal of Wildlife Management 70:717–722.

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology. Theory and practice of population viability analysis. Sinauer Associates, Sunderland, Massachusetts, USA.

Murray, D. L., and B. R. Patterson. 2006. Wildlife survival estimation: Recent advances and future directions. Journal of Wildlife Management 70:1499–1503.

Newton, I. 1979. Population ecology of raptors. T & A.D. Poyser, Berkhamsted, United Kingdom.

Newton, I. 1986. The Sparrowhawk. T. and A.D. Poyser Ltd, London, United Kingdom.

Parellada, X. 1984. Variació del plomatge i identificació de l'àliga cuabarrada (*Hieraaetus fasciatus* fasciatus). Pages 70–79. *in* Rapinyaires mediterranis, Vol. 2. CRPR, Barcelona, Spain. [In Catalan].

Pradel, R., A. R. Johnson, A. Viallefont, R. G. Nager, and F. Cézilly. 1997. Local recruitment in the Greater Flamingo: A new approach using capture–mark–recapture data. Ecology 78:1431–1445.

Pradel, R., C. M. A. Wintrebert, and O. Gimenez. 2003. A proposal for a goodness-of-fit test to the Arnason-Schwarz multisite capture-recapture model. Biometrics 59:43–53.

Real, J. 2004. Aguila–azor perdicera, *Hieraaetus fasciatus*. Pages 154–157 *in* A. Madroño, C. González, and J. C. Atienza, editors. Libro Rojo de las Aves de España. Dirección General para la Biodiversidad-SEO/Birdlife, Madrid, Spain. [In Spanish].

Real, J., and S. Mañosa. 1997. Demography and conservation of western European Bonellís eagle *Hieraaetus fasciatus* populations. Biological Conservation 79:59–66.

Real, J., and S. Mañosa. 2001. Dispersal of juvenile and immature Bonelli's Eagles in northeastern Spain. Journal of Raptor Research 35:9–14.

Real, J., A. Tintó, A. Borau, A. Beneyto, and X. Parellada. 2004. Àliga perdiguera *Hieraaetus fasciatus*. Pages 182–183 *in* J. Estrada, V. Pedrocchi, L. Brotons, and S. Herrando, editors. Atles dels Ocells Nidificants de Catalunya (1999–2002). Institut Català d'Ornitologia and Lynx Editions, Barcelona, Spain. [In Catalan].

Ricklefs, R. E. 1997. Comparative demography of new world populations of Thrushes (Turdus ssp.). Ecological Monographs 67:23–43.

Rocamora, G. 1994. Bonelli's eagle *Hieraaetus fasciatus*. Pages 184–185 *in* G. M. Tucker and M. F. Heath, editors. Birds in Europe: Their conservation status. Birdlife conservation series, No. 3. Birdlife International, Cambridge, United Kingdom.

Rohwer, S. 2004. Using age ratios to infer survival and despotic breeding dispersal in hybridizing Warblers. Ecology 85:423–431.

Rudnick, J. A., T. E. Katzner, E. A. Bragin, O. E. Rhodes, and J. A. Dewoody. 2005. Using naturally shed feathers for individual identification, genetic parentage analyses, and population monitoring in an endangered Eastern imperial eagle (Aquila heliaca) population from Kazakhstan. Molecular Ecology 14:2959–2967.

Sæther, B. E., and O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81:642–653.

Sandercock, B. K. 2006. Estimation of demographic parameters from live-encounter data: a summary review. Journal of Wildlife Management 70:1504–1520.

Soutullo, A., P. López-López, and V. Urios. 2008. Incorporating spatial structure and stochasticity in endangered Bonelli's eagle's population models: Implications for conservation and management. Biological Conservation 141:1013–1020.

Svensson, L. 1992. Identification guide to European passerines. British Trust for Ornithology, Stockholm, Sweden.

Vögeli, M., P. Laiolo, D. Serrano, and J. L. Tella. 2008. Who are we sampling? Apparent survival differs between methods in a secretive species. Oikos 117:1816–1823.

Watson, J. 1997. The Golden Eagle. T & A D Poyser, London, United Kingdom.

Whitfield, D. P., A. H. Fielding, D. R. A. Mcleod, and P. F. Haworth. 2004. The effects of persecution on age of breeding and territory occupation in golden eagles in Scotland. Biological Conservation 118:249–259.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, California, USA.

Zens, M. S., and D. R. Peart. 2003. Dealing with death data: individual hazards, mortality and bias. Trends in Ecology and Evolution 18:366–373.

*Associate Editor: Marc J. Bechard.*