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Use of mixture models to characterize site quality in philopatric animals: a case study with Bonelli's eagle

C. Chevallier¹, P-A. Crochet¹, N. Vincent-Martin², A. Ravayrol³ & A. Besnard¹

¹ UMR 5175, Centre d'Ecologie Fonctionnelle et Evolutive, Montpellier, France

² Conservatoire d'espaces naturels de PACA, Ecomusée de la Crau, Boulevard de Provence, Saint Martin de Crau, France

³ La Salsepareille, Clermont l'Hérault, France

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Correspondence

Aurélien Besnard, Centre d'Ecologie, Fonctionnelle et Evolutive, UMR 5175, 1919 route de Mende, 34293 Montpellier cedex 5, France. Tel: 0033467613280; Fax: 0033467412138
Email: aurelien.besnard@cefe.cnrs.fr

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Abstract

The French population of the Bonelli's eagle *Aquila fasciata* has suffered a sharp decline over the last decades, resulting in the implementation of several conservation actions since 1990. In parallel, a capture–recapture (CR) program has been conducted to monitor the population. Field practitioners suspected that certain breeding sites were responsible for most of the adult deaths and were interested in confirming this hypothesis in order to focus their actions on these particular sites. Our study sought to determine whether there was indeed a quantifiable difference in the quality of the eagle's breeding sites. Since Bonelli's eagles are highly faithful to their breeding site, we tested whether the turnover of breeding individuals observed at different sites resulted from a mixture of two different turnover rates. We also used the recent multi-event CR modeling approach to test whether or not we could detect adult survival heterogeneity in the population. Our study revealed that there was a difference in breeding-site quality a decade ago, before large efforts were made to insulate high-voltage power lines, but failed to detect a difference in breeding-site quality more recently. No survival heterogeneity was detected. These counterintuitive results could be due to a lack of statistical power or because the conservation actions performed over the last 20 years cloud the issue. When no *a priori* information is available on habitat quality differences, we advocate for the use of a mixture modeling approach since it is consistent and fairly general.

Introduction

Understanding the population dynamics of endangered species is often a prerequisite to setting up efficient conservation actions. Viability of the population is influenced by the overall quality of the habitat, but it also depends crucially on habitat heterogeneity and how the individuals deal with that heterogeneity (Suhonen *et al.*, 2010). Indeed, habitat selection by individuals influences their breeding performance and/or survival (Sergio *et al.*, 2006; Arroyo *et al.*, 2009), which influences the viability of the whole population (Murphy, Freas & Weiss, 1990). Moreover, habitat heterogeneity can generate a negative feedback on population growth rate when individuals are forced to occupy low-quality site as global population size increases (Rodenhouse, Sherry & Holmes, 1997). This hypothesis, named the 'site-dependence hypothesis', has been demonstrated in some species and advocate for the use of habitat quality in time-series models exploring population dynamic (Krüger & Lindström, 2001). When demographic parameters such as fecundity or survival are estimated, population viability analyses (PVA) are powerful tools to predict the

future evolution of the population (Morris & Doak, 2002) or to identify key life stages or demographic processes that can be targeted for efficient management (Crouse, Crowder & Caswell, 1987; Caswell, 2001; Morris & Doak, 2002). In the past, PVA were conducted on single populations, but recent developments have meant these modeling tools now allow spatial aspects to be included (Carroll & Miquelle, 2006; Mashinski *et al.*, 2006; Naujokaitis-Lewis *et al.*, 2009), which enables the exploration of the dynamic of systems in which connected (sub)populations exhibit different internal dynamics [see software META-X (Grimm *et al.*, 2004), RAMAS, (Schtickzelle & Baguette, 2004)]. Most of these analyses concerned fragmented populations where local (sub)populations inhabited habitats of different quality. Few studies have dealt with habitat heterogeneity on a smaller scale (Vogeli *et al.*, 2010), such as territories or individual breeding sites. However, individual habitat selection influences individual performance (Sergio *et al.*, 2006; Arroyo *et al.*, 2009), in turn eventually influencing the viability of the whole population (Murphy *et al.*, 1990). Understanding how heterogeneity in site quality impacts population dynamics is then crucial for setting up efficient

conservation actions (Chauvenet *et al.*, 2010; Oliver *et al.*, 2010). Indeed, because the budgets for conservation actions are always limited, it is important to optimize their allocation (Murdoch *et al.*, 2007). When site quality is heterogeneous, this optimization involves determining if site quality can be improved, at what cost and what the return on investment would be in terms of improvement of population growth rate (Pidgeon, Radeloff & Mathews, 2006). For instance, it is not clear if improving low-quality sites would have more or less impact than a similar improvement to mid-quality sites. When factors that influence site quality can be modified by management action, improvement of lower-quality sites can indeed become an efficient conservation strategy. A search for such optimal effort allocation can take advantage of the whole body of PVA theory.

However, determining the quality of sites is always challenging. Current practice consists of comparing vital rates (i.e. survival or fecundity) between different habitats (see, e.g. [Perlut *et al.*, 2008](#)). But this approach necessitates some prior information on habitat quality to allow *a priori* classification of sites into groups that can be compared for the demographic traits measured. The difficulty is that habitat heterogeneity can remain unclear to human perception either because it is related to factors that we cannot assess (such as physiology, for instance) or because it occurs at too small or too large a spatial scale. For instance, birds of prey occupy large territories that encompass a large heterogeneity in habitats. This makes it impossible to make an *a priori* determination if a breeding territory is likely to be good or bad. One solution may be to use some characteristics that have been demonstrated to be good proxy of habitat quality such as occupancy in birds ([Sergio & Newton, 2003](#)).

Our study proposes an alternative approach relying on the recent implementation of mixture models in capture–recapture (CR). This approach allows the determination of whether some individual heterogeneity exists on demographic parameters without any *a priori* idea regarding which individuals occur in which type of habitat (bad or good). We took advantage of this advance in methodology to determine whether there were good and bad territories for the Bonelli's eagle.

Bonelli's eagle *Aquila fasciata* is a large bird of prey globally classified as endangered (IUCN, 2001). The French population occupies the southern part of the country, from the eastern Pyrenees to Provence (CEN-LR, 2004; Hernandez-Matias *et al.*, 2009). This population has suffered a sharp decline from about 80 breeding pairs in 1960 to only 23 in 2002 (CEN-LR, 2004). In 2009, the French population had a total of 29 breeding pairs and, although this population appears to be stable or even slightly increasing, such a low number means that its future remains largely insecure (CEN-LR, 2004). As a consequence, the species is also listed as endangered on the French Red List (http://www.uicn.fr/IMG/pdf/Liste_rouge_France_Oiseaux_de_metropole.pdf) and is the object of a dedicated action plan (Plan National d'Action or PNA) funded by French authorities and managed by local nongovernmental associations. Since 1990, the species has been subject to a CR

program to better understand the species' local population dynamics. During this period, opportunistic discoveries of eagles that had been electrocuted or shot led to an initiative to insulate electric power lines in the species' range and to an awareness campaign to target hunters and to increase local acceptance of a species traditionally seen as a nuisance to small game species, for example, rabbit *Orytolagus cuniculus* and red-legged partridge *Alectoris rufa*.

Even if much progress has been made to protect the population, field managers suspect that some breeding sites are still particularly dangerous for adult birds, because they induce a high mortality rate because of the breeding birds' proximity to high-voltage power lines or their sensitivity to direct human destruction. Because adult survival is the main factor driving population dynamics in long-lived birds such as the Bonelli's eagle, high mortality rates of breeding birds could be one of the main factors driving the species' decline in France. Unfortunately, the actual cartography of the power lines is not available to directly test their effect on site quality (it is classified as sensitive data by the company) and if it can be collected by field research, the past cartography is impossible to collect. The power lines locations have sharply evolved over the last 20 years in the area (lines burying, insulation/mitigation, development of large lines, highly variable in space and time).

The aim of this study was thus to try to identify the 'good' breeding sites (ensuring a high survival probability) versus 'bad' breeding sites (related to a low survival probability) for the French Bonelli's eagle population. The main questions we addressed were first, do 'good/bad' sites really exist in the French population, and second, if so, what are these sites? We used two complementary analyses to address these questions. Both approaches relied on the fact that Bonelli's eagle is highly faithful to its breeding site (Bosch *et al.*, 2010). Because of this site fidelity, the replacement of one or two individuals on a previously occupied breeding site nearly always indicates the death of the resident bird(s). In a first analysis, we compared turnover rates for various breeding sites to determine their relative quality in terms of adult survival. In a second analysis, we explored whether two groups of individuals could be identified in the population: one group with high survival probability, occupying good-quality sites; the other with low survival probability, occupying bad-quality sites. This second analysis was performed using recent multi-event CR methods that allow the detection of individual heterogeneity on demographic parameters such as survival rates ([Pradel, 2005](#)).

Materials and methods

Bonelli's eagle, French population

Bonelli's eagle (Veillot, 1822) is a large bird of prey with a wingspan of more than 1.50 m and a weight of about 2 kg (Del Hoyo, Elliott & Sargatal, 1994). The subspecies *A. fasciata fasciata* ranges from southern Europe and North Africa to eastern India and southern China (Del

Hoyo *et al.*). Its life strategy is characterized by a late first-reproduction age [3 or 4 years old, (Hernandez-Matias *et al.*, 2010)], a low fertility rate (Saether, Ringsby & Roskaft, 1996; Hernandez-Matias, Real & Pradel, 2011a) and a high adult survival rate [0.87; (Hernandez-Matias *et al.*, 2011b)], and thus it can be considered a 'survival species' (Saether *et al.*, 1996). Its home range is about 30 km² (Carrete *et al.*, 2002) for adults. Adults are present throughout the year in the vicinity of their breeding areas, while juveniles and immature birds stray sometimes quite far from their natal site (Real & Manosa, 2001; Balbontin, 2005; Cadahia, Urios & Negro, 2007). This wandering behavior induces high mortality in the first age classes as a result of collision or electrocution by electric power lines (Carrete *et al.*, 2002; Real *et al.*, 2005). Adults show a strong site and pair bond tenacity (Bosch *et al.*, 2010).

Data collection

CR data were collected for the French Bonelli's eagle population between 1990 and 2009. Since 1990, most of the chicks born in France (450 out of a total of 478 chicks known to have fledged) have been individually banded with two different rings before fledging: one plastic ring (*Darvic*) with alphanumeric codes that can be read with the aid of a telescope from a distance of up to 200 m, and one metal ring provided by the French ringing center. Recaptures, defined as resightings of the rings, have occurred throughout the French Mediterranean area (in the regions of Languedoc–Roussillon, Provence–Alpes–Côte d'Azur and Rhône–Alpes), conducted by volunteers, with a special effort concentrated on breeding sites. Some dead birds ($n = 43$) have also occasionally been recovered. Monitoring effort of known pairs is very high, ensuring that almost all individuals breeding on known territories have been identified. Every year, searches for new breeding sites are carried out, but newly colonized sites are probably not all detected immediately, thus a few breeding attempts may have escaped detection. However, the proportion of fledged chicks missed due to the fact that this is certainly very low.

In addition to CR data, data on site occupancy were also collected for all monitored sites, including sites where one or both adults were unringed (which mostly occurred at the beginning of the study period before intensive ringing efforts began). Data on turnover rates for sites with unringed adults are likely to underestimate true turnover rates as some cases of adult replacement might have gone unnoticed where the old and new birds had similar plumage features (see Discussion).

Statistical analysis

Throughout our analyses, we modeled heterogeneity of site or individuals by using mixture modeling that aimed at testing whether the observations are generated by a mixture of two groups with distinct parameters of their probability distributions. Such a mixture is expected when two types of sites exist with high and low turnover probabilities or

hosting individuals with high or low survival probabilities. Pledger (2005) showed that such an approach also adequately models more continuous heterogeneity. In addition, Gimenez and Choquet (2010) warn against the use of random individual effects in CR modeling because of methodological issues. The mixture approach thus allows us to model both turnover heterogeneity and survival heterogeneity in the same framework.

Turnover analysis

In order to investigate the presence of heterogeneity in adult survival, we tested whether the number of new birds arriving on a breeding site already occupied the year before followed a mixture of two Poisson distributions or not. Because several conservation programs have been set up over the last 20 years, especially from 1997, when numerous insulations of high-voltage power lines were carried out, we suspected that turnover rates on the breeding sites might be different before and after 1997. Thus, we performed the mixture analysis on the whole dataset as well as on two data subsets, the period before 1997 and the period after 1997. The analyses were performed using a modified code of the 'Eyes: Normal Mixture Model' example provided in Winbugs (Spiegelhalter *et al.*, 1996) and based on a method proposed by Diebolt & Robert (1994). The code was modified to deal with Poisson distributions (available in Supporting Information Appendix S1). This code included an offset, which in our study is the number of years each site was occupied. This offset allows modeling the number of new birds recruited on a site relative to the duration of its utilization by pairs, that is the turnover rate. The parameterization of the model included a parameter called 'theta', which is the difference between the two rates of the Poisson distributions. When the confidence interval limits of the 'theta' included zero, we rejected the hypothesis that the data was generated by a mixture of two distinct distributions.

Survival analysis

The modeling context of our survival analysis was a special case of CR multi-state approaches (Arnason, 1972, 1973) that allowed combining data from resightings of live animals and dead recoveries (Lebreton & Pradel, 2002). This standard Arnason–Schwartz model does not account for between-individual heterogeneity. However, two methods have been proposed to overcome this issue: random individual effects (Cam *et al.*, 2002) and mixture models with discrete classes of individuals (Pledger, Pollock & Norris, 2003). We used the latter approach here in a framework based on a recent generalization of CR multisite models: the multi-event models (Pradel, 2005). Multi-event models allow taking into account a discrete, hidden individual heterogeneity structure on the parameters of a multisite CR model (Pradel, 2009), thus making the implementation of Pledger *et al.* (2003) models straightforward. Such an approach has already been successfully used to detect heterogeneity in capture probabilities (Crespin *et al.*, 2008) or breeding dispersal (Peron *et al.*,

Table 1 Matrixes used in E-surge to model the capture–recapture data of the French Bonelli’s eagle population

	Good	Bad	Just dead	Long dead	
Initial state	π	$1-\pi$	0	0	
Transition between states	Good	\emptyset_g	0	$1-\emptyset_g$	0
	Bad	0	\emptyset_b	$1-\emptyset_b$	0
	Just dead	0	0	0	1
	Long dead	0	0	0	1
State	Event		0	1	2
	Good	$1-p$	P	0	
	Bad	$1-p$	P	0	
	Just Dead	$1-\lambda$	0	λ	
	Long Dead	1	0	0	

‘Good’ and ‘bad’ represents the quality of the breeding sites; ‘just dead’ is the state reached just after the death of an individual where dead individuals can be recovered; ‘long dead’ is the state in which dead individuals stay in the long term and is considered here as a non-observable state.

\emptyset_g and \emptyset_b are the survival probabilities in ‘good’ and ‘bad’ sites respectively, P and λ are resighting and recovery probabilities. π is the initial proportion of individuals breeding in ‘good’ sites. Events are ‘0’ when an individual is not seen in a given year, ‘1’ when it is seen alive and ‘2’ when it is found dead.

2010). In our study, the hidden state of the individuals corresponds to the quality of their breeding site (‘good’ or ‘bad’), which determines the survival probability of the birds breeding there. Because birds can be resighted or recovered, we used a special parameterization of the model with two dead states: ‘Just Dead’ is the state reached just after the death of an individual, where dead individuals can be recovered; ‘Long Dead’ is the state in which dead individuals stay in the long term and is considered here as a non-observable state (animals cannot be recovered in the ‘Long-Dead’ state) (Lebreton, Almeras & Pradel, 1999). Each individual could thus belong to two out of four underlying states: ‘good’, ‘bad’, ‘Just Dead’ or ‘Long Dead’ (see Table 1). The ‘events’ are here the observation status of the individuals *i.e.* ‘not seen’, ‘resighted’ and ‘recovered’. All models were fully described by first considering the vector of probabilities of the initial state, then linking states at successive sampling occasions by the matrix of survival/transition probabilities, exactly like in multistate models, while the events were linked to states by the matrix of event probabilities. These three matrixes are shown in Table 1.

Because Bonelli’s eagle does not breed before the age of 3–4 years (Hernandez-Matias *et al.*, 2010) and because monitoring mostly focused on breeding sites, individual detection probabilities were expected to change with age. Moreover, as usual in long-lived birds, survival probabilities are also probably age-dependent (Weimerskirch, 1992;

Martin, 1995; Dreiss *et al.*, 2010). We thus built three sets of models: one with four age classes on both survival and resighting probabilities, one with four age classes on survival probabilities and three age classes on resightings, and one with four age classes on survival probabilities with classes 2 and 3 having the same survival [following the best model from Hernandez-Matias *et al.*, (2011b)] and three age classes on resighting probabilities. Heterogeneity structure was tested on adults only, because the focus of our study on heterogeneity in site quality relates to breeding territories only. It was tested on both periods (1990–1997 and 1997–2009), and separately on each period both for survival probabilities and initial state probabilities. All combination of age-class structures on survival and resightings and heterogeneity on adult survival were tested. The full set of models fitted thus included 48 models. Model selection was performed using the quasi Akaike information criterion (QAIC) and QAIC weights (Akaike, 1973; Burnham & Anderson, 2004). The goodness-of-fit (GOF) of the Cormack–Jolly–Seber (CJS) model was assessed using contingency tables on live animals with the software U-CARE 2.2.2 (Pradel, Gimenez & Lebreton, 2005; Choquet *et al.*, 2009a).

We used the program E-surge 1.1.1 (Choquet, Rouan & Pradel, 2009b) to obtain maximum likelihood estimates of the parameters and to perform model selection.

Results

Turnover analysis

The dataset included 35 breeding sites and totaled 530 breeding attempts over the whole period (1990–2009), including 88 breeding adult replacement events. The number of replacements varied between sites and ranged from 0 to 6. The annual turnover rate on breeding sites ranged from 0 to 0.66.

The analysis conducted on the whole dataset did not reject the null hypothesis that the number of replacements followed a single Poisson distribution ($\theta = 1.96$ [–0.55–14.82]). On the contrary, the analysis conducted separately for the two periods (before and after 1997) significantly detected a mixture of Poisson distributions during the first period ($\theta = 6.05$ [0.526–19.12], mean turnover rate on ‘good’ sites <0.01., mean turnover rate on ‘bad’ = 0.22, proportion ‘good’/‘bad’ sites: 0.36/0.64, Fig. 1), but not during the second period ($\theta = 3.27$ [–0.25–17.37], mean turnover rate 0.14). The mean turnover decreased slightly after 1997, although not significantly (mean turnover rate before 1997: 0.18 ± 0.02 , after = 0.14 ± 0.2 , χ^2 test $P = 0.2$).

Survival modeling

The CJS model fitted the data adequately (GOF test: $\chi^2_{24} = 5.44$, $P = 1$). The dataset combined 450 ringed birds, 585 resightings and 43 recoveries over the whole period (1990–2009). The two best models, which are identical in

terms of AIC values, included a three age-class structure on resighting probabilities, and identical survival probabilities for age classes 2 and 3 (Table 2). The best model also included a difference in survival probabilities for the first three age classes before and after insulation of power lines,

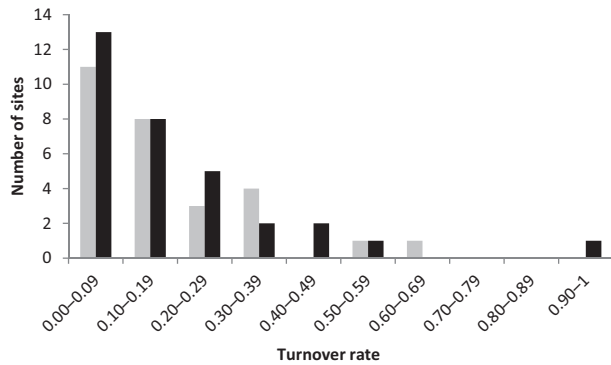


Figure 1 Frequency of annual turnover rate on breeding sites between 1990 and 2009 of the French Bonelli’s eagle population. Grey indicates 1990–1997 and black indicates 1997–2009.

while the second-best models included this effect on the four age classes. The first model including heterogeneity has an AIC of 3.77 superior to the best model (Table 2). The sum of QAIC weights of all models including a heterogeneity structure on survival probabilities is 0.21. This low value suggests that this effect is poorly supported by the data.

The parameter estimations of the best model are shown in Table 3. As expected, the survival and the resighting probabilities increased with age. The survival probabilities also increased during the second period for the first three age classes. In the second-best model, the adult survival probabilities are different between the two periods before and after 1997, but their confidence intervals are partially overlapping [0.78 (0.42–0.95) during the first period, and 0.87 [0.79–0.92] during the second period].

Discussion

We detected the existence of two different turnover rates among breeding sites during the first 10 years of the study, but the effect disappeared during the second 10-year period. However, we failed to detect the existence of two groups of

Table 2 Multi-event models fitted to the capture–recapture data of the French Bonelli’s eagle population over the 1990–2009 period

Rank	QAICc	ΔQAICc	AIC weight	Initial State	Survival			Resightings
					Effect on age classes 1,2 and 3	Age 2 = Age 3	Effect on age class 4	
1	1204.93	–	0.41	.	Two-period	Yes	.	p(3)
2	1206.58	1.65	0.18	.	Two-period	Yes	Two-period	p(3)
3	1208.69	3.77	0.06	.	Two-period	Yes	H1&2	p(3)
4	1208.7	3.77	0.06	.	Two-period	No	.	p(3)
5	1210.13	5.21	0.03	.	Two-period	No	.	p(4)
6	1210.31	5.38	0.03	Two-period	Two-period	Yes	H1&2	p(3)
7	1210.4	5.47	0.03	.	Two-period	No	Two-period	p(3)
8	1210.56	5.63	0.02	.	.	Yes	.	p(3)
9	1210.81	5.88	0.02	.	Two-period	Yes	Two-period + H1&2	p(3)
10	1211.28	6.36	0.02	.	.	Yes	Two-period	p(3)
11	1211.86	6.93	0.01	.	Two-period	No	Two-period	p(4)
12	1212.21	7.28	0.01	Two-period	Two-period	Yes	Two-period + H2	p(3)
13	1212.48	7.55	0.01	.	Two-period	No	H1&2	p(3)
14	1212.49	7.56	0.01	.	.	No	.	p(3)
15	1212.63	7.7	0.01	Two-period	.	Yes	Two-period + H1	p(3)
16	1212.75	7.82	0.01	Two-period	Two-period	Yes	Two-period + H1	p(3)
17	1212.75	7.82	0.01	Two-period	Two-period	Yes	Two-period + H1&2	p(3)
18	1212.89	7.97	0.01	Two-period	Two-period	No	Two-period + H1	p(3)
19	1213.19	8.26	0.01	.	.	No	Two-period	p(3)
20	1213.75	8.83	0	.	.	No	.	p(4)
21	1214.04	9.11	0	.	Two-period	No	H1&2	p(4)
22	1214.25	9.33	0	.	.	Yes	H1&2	p(3)
23	1214.37	9.44	0	.	.	Yes	Two-period + H1&2	p(3)
24	1214.5	9.57	0	Two-period	.	No	Two-period + H1	p(3)
25	1214.52	9.59	0	Two-period	Two-period	No	Two-period + H1	p(4)
26	1214.65	9.72	0	.	.	No	Two-period	p(4)
27	1214.7	9.77	0	.	Two-period	No	Two-period + H1&2	p(3)
28	1214.85	9.92	0	Two-period	.	Yes	H1&2	p(3)

‘.’ means constant; ‘Two-period’ means that the parameters were different before and after 1997; ‘H1&2’ means that heterogeneity was assumed on survival during the two periods, ‘H1’ only during the first period and ‘H2’ only during the second period; ‘p(4)’ means that the resighting probabilities were fitted with four age classes while p(3) means they were fitted with three age classes; ‘QAIC’ means quasi Akaike information criterion.

Table 3 Parameter estimation provided by the best multi-event model obtained by the analysis of capture–recapture data of the French Bonelli's eagle population over the 1990–2009 period

Parameter	Age class	Probability	Confidence intervals	Standard error
Survival first period (1990–1997)	1	0.35	0.21; 0.51	0.08
	2	0.44	0.28; 0.62	0.09
	3	0.44	0.28; 0.62	0.09
Survival second period (1997–2009)	1	0.49	0.35; 0.63	0.07
	2	0.62	0.50; 0.72	0.06
	3	0.62	0.50; 0.72	0.06
Survival both periods	4	0.86	0.77; 0.91	0.03
Recovery	All	0.11	0.09; 0.15	0.02
Resighting	1	0.09	0.05; 0.15	0.02
	2	0.19	0.12; 0.29	0.04
	3	0.46	0.38; 0.54	0.04

individuals exhibiting different survival probabilities with the CR approach either in the first or second period. Thus, our results partially confirmed the suspicion of field practitioners working on the conservation of the French Bonelli's eagle population that some breeding sites may be more dangerous than others. However, it appears that this was mainly the case before large-scale conservation efforts for the species had been made.

Good and bad sites were detected during the first monitoring period. Ten sites were considered as 'good' and 18 as 'bad'. These sites were identified, but the discussions with the field managers confirmed that no clear covariate could explain the observed differences in turn-over rates between these two classes of sites. Detailed examination of these sites' characteristics may be interesting, unfortunately the cartography of the power lines and the shooting pressure, which are the two main factors known to impact the species, are not available for the past period.

About one-third of the breeding sites were considered as exhibiting no replacement, while two-thirds were exhibiting a replacement every 5 years on average (0.2 turnover rate). The sites with no turnover were the 10 sites (over 28) occupied by the same breeding pair over the 8-year period of 1990–1997 and one site occupied 4 years and never occupied after that. For a species whose usual mortality rate is about 10% [survival probability is around 0.9 in stable or increasing populations (Hernandez-Matias *et al.*, 2011a)], we might expect a mean yearly turnover rate of 0.19 ($1 - 0.9 \times 0.9$) on the breeding sites, which translates into a 0.185 probability of no-turnover over an 8-year period. The expected number of sites with no change is about five (0.185×28.0 occupied sites), that is half the observed number. In addition, this expected turnover rate for a population with a high survival probability is indeed the one we observed in bad sites. This is probably due to the fact that turnover rate is underestimated during the early study period (see Data collection in Material and Methods section). This is unlikely to bias our conclusions on site heterogeneity although as this should equally effects sites independently of their quality. On the worst of case, this bias would be conservative as it would reduce the true differences in turnover rates between good and bad sites.

During the second period, no heterogeneity was detected. However, the mean observed turnover rate decreased only slightly between the first and second period. This result suggests that the bad sites may have slightly improved during the second period, leading to a reduction of the difference in turnover rates between 'good' and 'bad' sites, which in turn makes it more difficult to detect a mixture of distributions in the dataset for this second period. Considering the fact that there was much fewer unringed birds during the second period, and hence that the turnover rates were probably much less underestimated, this slight change in observed rates probably reflects a stronger change in real turnover rates.

This hypothesis is strengthened by the multi-event CR analysis, which demonstrated that survival probabilities increased for all age classes after 1997. The increase of survival is around 40% for the first three age classes. The difference is less marked for adult survival than for juveniles and immature birds, as it only increased 10%. However, in a long-lived species such as the Bonelli's eagle, a 10% increase in adult survival potentially leads to a significant increase in population growth rate. Such improvement in survival may be related to a general improvement in site quality, limiting our statistical power to detect any current differences between sites. We did not detect adult survival heterogeneity in the first period as could have been expected after turnover analyses. However, in this period only few adults were ringed, and our power to detect heterogeneity was probably low.

Besides the problem of statistical power, we can hypothesize that classifying only two types of site is probably too simplistic. We suspect that breeding-site quality follows a continuum from good to bad, both of which may occur in low proportion, passing through mid-quality sites, which may be in high proportion. Our methodological choice of searching for a two-group mixture may be unable to deal with such a continuum, although mixture models are known to be powerful tools for dealing with such continuums (Cubaynes *et al.*, 2012). Lastly, the initiatives implemented by the Bonelli's National Action Plan were mostly conducted at a local scale and sometimes over short periods. These actions may have resulted in progressive improve-

ment of mean quality heterogeneous in time and space that masked any general pattern of good-/bad-quality sites.

What can explain the change in turnover rate before and after 1997? After 1997, the Bonelli's National Action Plan had implemented several programs to improve habitats by opening vegetation structure, increasing food availability and insulating high-voltage power lines. We have demonstrated in another paper that the mortality rate induced by electrocution decreased between the first and second period for all age classes and is responsible for the improvement in survival; for instance, it fell from 0.13 to 0 in adults (Besnard *et al.*, unpubl. data). Because the other actions are not expected to improve adult survival much, it is likely that insulation of power lines close to breeding sites is the main factor responsible for the improvement of low-quality sites. Other factors may also have contributed, but are more difficult to prove. For example, direct intentional destruction (mainly shooting) has long been, and still is, a problem, as proven by the occasional discovery of shot birds. Indirect evidence for a reduction of persecution comes from the improving relationships between hunting organizations and conservationists (several National Action Plan members, pers. comm.), but recoveries of shot birds are too rare to confirm this reduction (there have only been three recoveries of shot birds: one in 2001, one in 2002 and one in 2006). Moreover, as for the causes of differences between good and bad sites during the first period, it is here impossible to unambiguously conclude that changes in electrocution and shooting pressure is the main cause of change in turn-over rates because no precise information regarding electric line types on territories and hunting practices are available.

Field managers suspected that some sites were more dangerous than others; however, the differences in turnover rates during the first period may be explained by at least two alternative hypothesis: first, because several birds were unringed during the first period, a higher divorce rate inducing increased breeding dispersal on low-quality sites would similarly inflate the turnover rate; second, individuals of low quality with innate higher mortality rate may be more likely to occupy low-quality sites again generating a higher turnover rate on these sites independently of any extrinsic sources of danger/mortality.

The first aim of our study was to identify a few key sites where the limited budgets allocated to the protection of the species should be invested preferentially after 10 years of conservation action. Although this study failed to statistically identify dangerous sites during the recent period, it clearly showed that there was a large variability in turnover rates on the breeding sites. Therefore, two options remain for managers. The first should be to continue comprehensive action over the area (such as insulation of power lines, for instance). The second is to invest more money on the sites that exhibit the highest turnover rates, even if it cannot be statistically proven that these sites are more dangerous than others.

When no *a priori* information is available on habitat quality differences at the intrapopulation level, we advo-

cate for the use of a mixture modeling approach, because it is consistent and fairly general. When heterogeneity can be demonstrated, use of the recent spatial PVA developments offers a great opportunity to improve the modeling of local dynamics and to explore alternative management scenarios. Note that programs such as E-Surge (Choquet *et al.*, 2009b) can provide probabilities of each individual belonging to low- or high-quality sites when models with heterogeneity are selected, allowing identification of low-quality sites. However, this mixture modeling approach applies to studies of highly philopatric species, because the method does not currently allow for movements of individuals between groups of low or high survival. It is also currently only applicable to long-lived species, for which several breeding occasions occur. In addition to territorial long-lived species such as the focus of this study, these methods are well suited for many other situations, such as the study of discrete patches of nests, parts of colonies or subpopulations (Schooley & Branch, 2007), for which it is difficult to make *a priori* assessments of habitat typology.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Example of Winbugs code for Poisson mixture.

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