ÉCOSCIENCE 14 (4): 432-439 (2007)

Potential contributions of capture–recapture to the estimation of population growth rate in restoration projects[1]

Roger PRADEL[2], CEFE/CNRS, 1919 Route de Mende, 34293 Montpellier Cedex 05, France, e-mail: roger.pradel@cefe.cnrs.fr
Pierre-Yves HENRY, Département Écologie et Gestion de la Biodiversité USM301/UMR7179, Muséum National d'Histoire Naturelle, 1, avenue du Petit Château, 91800 Brunoy, France.

Abstract: Estimation of population growth rate is central to evaluating a restoration plan. The follow-up of individually recognizable animals, known as capture–recapture, is a means of collecting the data necessary for such estimation. This alternative method can easily be put in practice during restoration projects because reintroduced animals can be tagged before release. Population growth rate can then be estimated directly from capture–recapture data (Pradel, 1996). The method also enables evaluation of the demographic processes responsible for variation in population size. We examine three examples and conclude with a discussion of the potential of this approach.
Keywords: *Ciconia ciconia*, declining population, *Hieraaetus fasciatus*, *Phoenicopterus roseus*, population growth rate, reintroduction.

Résumé : L'estimation du taux de croissance de la population est centrale dans l'évaluation d'un plan de restauration. Le suivi d'animaux identifiables individuellement, méthode connue sous le nom de capture-recapture, permet d'obtenir les données nécessaires à une telle estimation. Cette méthode alternative peut facilement être utilisée dans les projets de restauration puisque les animaux réintroduits peuvent être marqués avant d'être relâchés. Le taux de croissance de la population peut alors être estimé directement à partir des données de capture-recapture (Pradel, 1996). De plus, cette méthode permet d'évaluer les processus démographiques responsables des variations dans la taille de la population. Nous examinons trois exemples et concluons avec une discussion sur le potentiel de cette approche.
Mots-clés : *Ciconia ciconia*, *Hieraaetus fasciatus, Phoenicopterus roseus*, population décroissante, réintroduction, taux de croissance de la population.

Nomenclature: Throughout, latin binomials are those used by the original authors.

Introduction

The aim of a restoration plan is to establish or reinforce a population that should be able to sustain itself subsequently. This aim may be pursued through a range of more or less direct measures (from habitat management to the introduction of new individuals). Whatever the means used, the obvious measure of the success or failure of a restoration plan is the achieved population growth rate (ρ). However, assessment of population growth rate (PGR) determines only whether the restoration was successful ($\rho > 1$) or not ($\rho < 1$), not the reasons for it. Knowledge of these reasons is important in order to modify the restoration plan as it proceeds or to draw lessons for future restoration enterprises. Therefore, as argued by Robert, Couvert & Sarrazin (2007), demography, which mediates all factors affecting population size, should be closely looked at as well.

It happens that one of the best ways of studying demography in the wild (see Caswell, 2001, for a review), namely the follow-up of individually marked animals, known as the capture–recapture method (CR hereafter), also permits direct estimation of the realized PGR (Pradel, 1996). CR thus provides a very complete tool for monitoring a restoration project. Additionally, it can easily be put in practice during restoration projects by marking introduced animals before they are released. In the next section, we compare this method to more traditional methods for estimating PGR. In section on *Three short case studies*, we examine some real examples drawn from our experience. Finally, we conclude by drawing lessons from the examples and discussing more generally the advantages and shortcomings of the CR approach.

Comparison of capture–recapture to other methods for estimating population growth rate

PGR can be estimated by a purely phenomenal approach that consists of comparing successive census data or by a purely analytical approach whereby the demographic mechanisms are examined one by one before being put together in, for example, a Lotka–Leslie matrix model to derive the PGR. The CR approach, as we will see, falls somewhere in the middle because it provides direct assessment of PGR but also offers some opportunity to study the mechanisms.

Comparison of successive counts is arguably the most natural approach. However, besides offering no insight at all into the mechanisms responsible for population change,

---

[1] Rec. 2007-04-02; acc. 2007-04-02.
Associate Editor: François Sarrazin.
[2] Author for correspondence.

this approach presents a number of practical difficulties. One obvious difficulty is that detecting all animals present in a population is rarely feasible; hence, knowledge of the absolute population size will remain most of the time out of reach. A related problem is that detectability is often very heterogeneous among individuals, such that a sometimes very large fraction of the population remains elusive. Population counts are thus almost certainly partial and hence should be considered an index of abundance, like track counts, counts of nests, and so on. Indices of abundance, and hence partial counts, can indeed be used to estimate PGR if their relationship to abundance is known, but unfortunately this is rare (Williams, Nichols & Conroy, 2002). Even in the most favourable case, where the index can be deemed proportional to abundance, estimating PGR as the ratio of successive indices carries statistical difficulties. Because the indices represent the population size with some stochastic error, the successive estimates of PGRs obtained in this way are negatively correlated. Under these circumstances, the sensitivity of PGR to a covariate cannot be examined easily.

The CR approach does not suffer from these limitations. Detectability is taken into account, and PGR is directly a parameter of the CR models, so any correlation between the successive PGR estimates is automatically taken into account. Heterogeneity of detectability is the only one of the above-mentioned problems not addressed in the original CR model (Pradel, 1996). However, this model can be generalized to accept a mixture of individuals with different capture probabilities (R. Pradel & P.-Y. Henry, in prep.) Even without this improvement, it has long been known that parameters that are ratios of numbers of animals, such as PGRs or survival rates, are only weakly affected by capture heterogeneity. For instance, Figure 1 contrasts, for an increasing degree of heterogeneity, the large bias in the CR estimate of population size with the small bias in the estimate of annual survival (Carothers, 1973). The PGR estimator, being a ratio of ratios (see Pradel, 1996), is expected to be even more robust to recapture heterogeneity than the survival estimator. This has indeed been verified at least once, on the northern spotted owl (*Strix occidentalis caurina*) populations of the western United States. Hines and Nichols (2002) found that the bias remained very low (less than 5%) through a range of different scenarios. It is worth noting that capture heterogeneity did tend to give the false impression that PGR was decreasing near the end of the time series (see Figure 4 in Hines & Nichols, 2002). Hence, caution should be taken when investigating trends in PGR: a positive trend can be trusted, but a negative trend could be spurious and should be double-checked. One way to do so is to retain only some of the first study years and to repeat the analysis on the truncated data set. If the trend is spurious and due to capture heterogeneity, then the PGR estimates for the new "last years" of the study should be affected in turn and thus estimated below the values obtained for the same years with the complete data set. If the trend is real, similar PGR estimates for the same years should arise in both analyses.

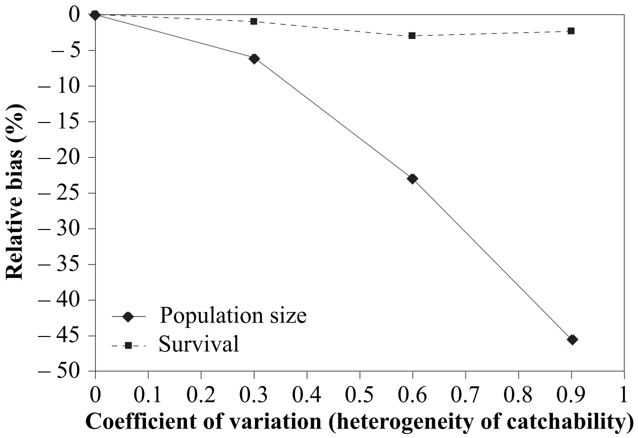

FIGURE 1. When heterogeneity of catchability increases, population size is more and more underestimated. Survival is underestimated but to a much lesser extent (from Carothers, 1973, Table 4).

But one of the main attractions of the CR approach is that, unlike census data, it provides access to the mechanisms responsible for changes in population size. For instance, population size may remain constant because survival is very high and there is virtually no reproduction (or immigration), such that the same animals are present all the time. This is what is expected for long-lived species such as cetaceans, chelonians, or procelariiforms. On the other hand, there might be a huge turnover, with virtually every animal present at the beginning of the study dying before its end, but with their losses compensated for by similar numbers of new recruits (as in many short-lived species). Because the new animals, unlike the old ones, are unmarked, the 2 different scenarios can be distinguished by CR, whereas they are indistinguishable with census data. The marked animals can be thought of as a tracer poured into a liquid; a strong turnover dilutes them much more than a weak one.

This emphasis on the mechanisms is at the core of the analytical approach to the estimation of PGR, which is the common alternative to census data. In the analytical approach, one seeks to measure the flows of animals in and out of the population due to immigration and birth on one side, emigration and death on the other side. The results are generally gathered in a population matrix model from which the asymptotic PGR, λ, can be deduced (see, for instance, Caswell, 2001). This approach has a theoretical flavour as it serves generally to examine different scenarios and yields, not the *realized* PGR (ρ), like the CR approach, but the *theoretical* asymptotic PGR (λ) reached when all things remain equal for an indefinite but very long time. This is a profound difference, and one not stressed enough in our view; this difference justifies the use of a different notation for the CR PGR estimate, as in the original paper (Pradel, 1996). The completely analytical approach is in fact very demanding, and in practice some aspects of the population dynamics are so difficult to quantify that the poor quality of the estimates there may hamper the method as a whole. Particularly demonstrative in this respect is the study of the northern spotted owl populations in the western United States. Researchers concluded after 5 y of comparing the population matrix approach to the direct estimation of PGR using marked individuals that the CR approach was superior, and they used it exclusively afterwards (Courtney *et al.*, 2004). Among the most problematic aspects were estimation of breeding propensity (a component of fecundity), immigration, and emigration. For species with larval stages, we can add to this list fecundity of breeders and early survival. Each of these aspects deals with elusive stages or individuals. The CR approach is not very useful for this type of individuals, but it does enable estimation of the gross inflow and outflow, lumping together local recruits and immigration with respect to the former, and deaths and emigration with respect to the latter, and thus permitting at least identification of the broad area where a problem may occur. For more detailed information, protocols such as multi-site sampling (Nichols & Pollock, 1990) and the robust design (Nichols *et al.,* 2000) are worth considering. The CR approach has now been used several times with many different species (see Table I). We examine hereafter 3 unpublished examples taken from our experience.

Three short case studies

White stork population of Baden-Württenberg (Germany)

The first example concerns the white stork (*Ciconia ciconia*) population of Baden-Württenberg (western Germany) during the years 1956–1971. This was a period when all Western European populations of the species were declining (Bairlein, 1991). This spectacular decline has been well documented. As there was an ongoing ringing program in the Baden-Württenberg population at the time, it is possible to try to detect the decline through CR data. The ringing scheme consisted of visiting the nests and ringing the young before they could fledge. Later, when ringed white storks returned as adult breeders, they could be followed over the years. These re-observations of marked individual animals constitute the time series that are used for studying the changes in population size hereafter. Note that since data are available only on individuals ringed at nest, estimates of PGR are representative only of the fraction of the population that is of local origin. More precisely, the method estimates the growth rate of the *marked fraction* of the population. Its application yields a point estimate of the average annual PGR over the entire period that is lower than 1, hence pointing to a decline, but the 95% confidence interval contains 1, so the analysis is not conclusive (Table II, first row). This is at first surprising given the sharp decline known to have occurred. There are in fact 2 problems with this calculation. First, there is evidence that the decline did not start before the early 1960s, so a different time window would be more appropriate for detecting the decline. Second and more important, the conditions for the correct application of the method are not met. Ideally, the ringed animals should represent a random fraction of the breeders. However, because of the ringing protocol, during the first years of the study ringed storks are necessarily young storks. And because they are younger than average, recruitment, and hence PGR, is overestimated. Under the assumptions of constant survival and recruitment probabilities, constant population size, and constant marking effort, it can be shown that the estimated population growth rate is $\hat{\lambda}_i = (1\text{-}\phi^{i+1})/\ (1\text{-}\phi^{i})$, where *i* is the number of time steps since the beginning of the study (Henry, 1999). Based on this formula and given the survival rate of the species, it can be determined that the ringed fraction becomes representative of the breeders as a whole only after the first 4 y of the study. After setting aside the first 4 y, the average annual PGR estimated for the period 1961–1971 does demonstrate a sharply decreasing population, declining by 10% each year (Table II, second row). Note that if unmarked individuals encountered while searching for marked individuals had been counted, all of the years could have been used (see Nichols & Hines, 2002, for details). We will come back to this in the discussion.

Table I. Direct estimation of the realized population growth rate from capture-recapture data.

Group	Reference
Birds	Sandercock & Beissinger (2002)
	Dreitz *et al.* (2002)
	Cam *et al.* (2003)
	Jenouvrier, Barbraud & Weimerskirch (2003)
	Franklin *et al.* (2004)
	Boyce, Irwin & Barker (2005)
	Piersma *et al.* (2005)
	Noon & Blakesley (2006)
	Dinsmore, White & Knopf (2005)
	Lampila *et al.* (2006)
	Peery, Becker & Beissinger (2006)
Mammals	Boulanger, Himmer & Swan (2004)
	Lima *et al.* (2001)
	Mizroch *et al.* (2004)
	Brongo, Mitchell & Grand (2005)
	Clark, van Manen & Pelton (2005)
	Lehmkuhl *et al.* (2006)
	Hoyle, Pople & Toop (2001)
	Ozgul *et al.* (2006)
Reptiles	Webb, Brook & Shine (2002a)
	Iverson *et al.* (2006)
	Lowe (2003)
	Converse, Iverson & Savidge (2005)
	Dodd, Ozgul & Oli (2006)
	Webb, Brook & Shine (2002b)
	Sasso *et al.* (2006)
Fish	Pine, Allen & Dreitz (2001)
Mollusks	Villella, Smith & Lemarie (2004)

It is also possible to investigate the reasons for the decline. The primary parameter to suspect when the population size of a long-lived species changes dramatically is the survival rate (Lebreton, 1978). Adult survival rate in the neighbouring Alsace population has been found to be highly sensitive to the conditions prevailing in the wintering Sahelian zone as measured by the rainfall amount at Mopti (Mali) (Kanyamibwa *et al.,* 1990). Given that the Baden-Württenberg population shares the same wintering grounds, we checked whether its adult annual survival was also driven by the same covariate and found that it was ($[\phi_x, p, \gamma_t]$ *versus* $[\phi_t, p, \gamma_t]$: $\Delta AIC_c = -11.43$, see Table III for explanation of model notation). The rainfall amount at Mopti explained 51% of the temporal variation in survival and was

Table II. CR estimate of the annual population growth rate (PGR) for the Baden-Württenberg white stork population over 2 time periods. The estimate in the first row, which includes the first years of the study, is biased upwards due to fact that the ringing scheme targeted youngs at the nest (see text).

Period	Estimated PGR	95% confidence interval	
1956–1971	0.986	0.956	1.02
1961–1971	0.897	0.865	0.93

highly significant ([ϕ_x, *p*, γ_t] *versus* [ϕ, *p*, γ_t]: $\chi^2(1) = 18.96$, $P < 0.0001$). Thus, the drought in the Sahel zone must have impacted this population as well as the Alsace population through its effect on the survival rate. However, the PGR itself was not correlated to the rainfall covariate ([ϕ_t, *p*, ρ_x] *versus* [ϕ_t, *p*, ρ_t]: $\Delta\text{AIC}_c = + 19.83$), prompting an examination of recruitment. Although the proportion of new recruits decreased during the 1960s (see Figure 2), precipitating the decline, the drought does not seem to be responsible for this decline (models ϕ_t, *p*, γ_x and ϕ_t, *p*, f_x are both far from the best model: $\Delta\text{AIC}_c = + 32.05$ and + 38.74, respectively). The decline in recruitment is actually best described by a linear negative trend in per-capita recruitment rate (best model: ϕ_x, *p*, f_T). This could possibly be linked to deteriorating conditions on the breeding grounds. However, the per-capita recruitment rate is not simply related to fecundity because white storks do not start to breed before age 3 and knowledge of the survival of young would be needed to draw any conclusions.

THE FRENCH COLONY OF THE GREATER FLAMINGO (CAMARGUE, SOUTHERN FRANCE)

The Fangassier colony of the greater flamingo (*Phoenicopterus roseus*) in southern France has been managed since 1970 to provide a permanent breeding site to the Western Mediterranean population of the species (see, *e.g.,* Tavecchia *et al.,* 2001 for more details). As a result, the species has dramatically recovered in the region. Since 1984, observations of ringed individuals at the colony have been routine (ringing started in 1950 and became systematic in 1977), as have annual censuses of the number of breeding pairs. The colony growth rate has been estimated both by CR and as the ratio of successive censuses (Henry, 1999). The second approach is known to produce negatively correlated estimates of successive PGRs because the same census number is used as numerator in one year and denominator the next year (if population size is underestimated, the first PGR will tend to be underestimated but the second will tend to be overestimated). This may be the reason for the seesaw appearance of the census-estimated PGR shown in Figure 3. By contrast, the CR-estimated PGR appears smooth on the same figure. The really important point, however, is that the 2 approaches do not target exactly the same population. We already know that the marked individuals become representative of the general breeding population only after some time has elapsed (see section on *White stork population of Baden-Württenberg* [*Germany*]). This has been taken into account here. However, the question of the origin of the marked individuals remains. Individuals ringed outside of the Camargue colony can be observed breeding there, but ringing on the other colonies is much more recent and has been done on an irregular basis. Thus, these individuals cannot be used for the analysis. They could possibly be used in a comprehensive analysis of the different colonies, but unfortunately, unlike the estimation of movement and recruitment for instance (Spendelow *et al.,* 2002), there is currently no model for the estimation of PGR in a metapopulation context. Therefore, we opted for a CR analysis of locally ringed animals only. Thus, the CR approach describes the dynamics of the autochthonous component of the breeding population only, while the cen-

TABLE III. Some CR models fitted to the Baden-Württenberg white stork population. Parameters are ϕ, annual survival probability; *p*, detection probability; *g*, proportion of old individuals in the population; ρ, realized population growth rate; and *f* , per capita recruitment rate, *i.e.*, percentage of new individuals at $i + 1$ per individuals present at *i*. Effects considered are *t*, time variation; *T*, linear time trend; and *x*, rainfall amount as covariate. ΔAIC*c* is the difference in Akaike Information Criterion adjusted for small sample size between the current and the best model.

Model	ΔAIC_c	Number of parameters	Deviance
ϕ_x, p, f_T	0	5	3087.14
ϕ_x, p, γ_t	2.68	19	3060.99
ϕ_x, p, γ_T	4.99	5	3092.13
$\phi_t, p, \gamma_t = \phi_t, p, \rho_t = \phi_t, p, f_\text{t}$	14.11	33	3042.63
ϕ, p, γ_t	19.55	18	3079.95
ϕ_t, p, γ_x	32.05	19	3090.36
ϕ_t, p, ρ_x	33.94	19	3092.26
ϕ_t, p, f_x	38.74	19	3097.05

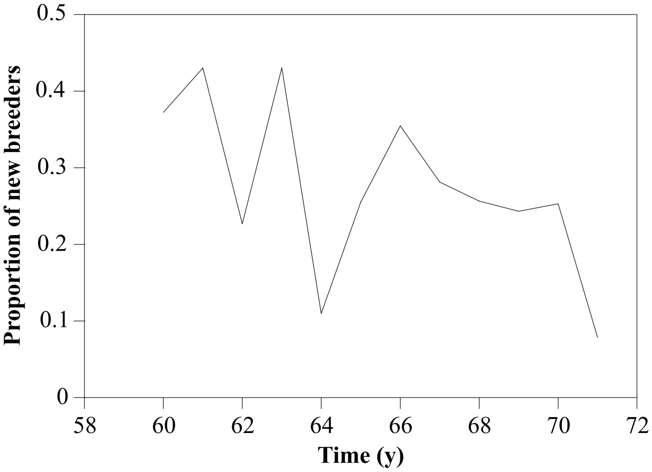

FIGURE 2. Estimated proportions of first-time breeders among the breeders in the white stork population of Baden-Württenberg. This proportion declines over the study period. Estimates for the first 4 y of the study are not shown because they are biased (see text).

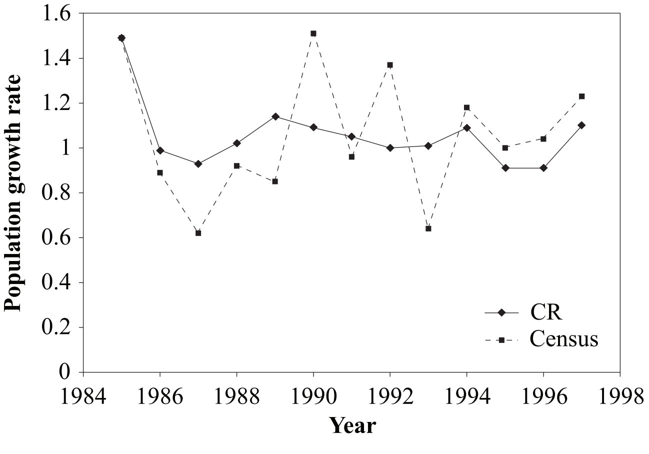

FIGURE 3. Comparison of estimates of the greater flamingo Fangassier colony growth rate derived from census data and from capture–recapture data (reproduced from Henry, 1999).

sus approach is comprehensive. The ups and downs of the census curve could thus alternatively represent mass movements of allochthonous flamingos joining, then leaving, the colony. Near the end of the study, the 2 curves come into close agreement except that the CR curve is shifted downward. This discrepancy could be due to the bias in the CR estimates expected near the end of a study when there is a strong heterogeneity of capture (see section on *Comparison of capture–recapture to other methods for estimating population growth rate*).

The Bonelli's eagle in southern France

The Bonelli's eagle (*Hieraaetus fasciatus*) is rare in France (some 25 breeding pairs) and the object of a national restoration plan (Cheylan, Ravayrol & Cugnasse, 2003). With very small populations, it is not uncommon for the census to come very close to exhaustiveness. It is believed that virtually every potential nest site is known, and each is visited several times every year. However, because of demographic stochasticity, an increase (or a decrease) in population size may occur by mere chance. Thus, although population size is known very accurately, the effectiveness of the restoration effort is difficult to ascertain. The estimation of demographic parameters suffers from the same problem: because of the limited number of individuals, estimates of demographic parameters from capture–recapture data remain imprecise. It is thus important to gather every bit of information, hence to follow the individuals as closely as possible. However, this need comes into conflict with the need to protect the few remaining individuals. Each year, the young Bonelli's eagles are ringed before fledging with traditional metal bands. Because the reading of metal rings is very difficult and very time-consuming, there has been some consideration of using more conspicuous marks such as alar tags. However, the idea has been abandoned for the moment due to concerns about the mark possibly being harmful to the birds. In order to improve the precision of the estimates of annual survival rate, the possibility of reading the ring numbers twice a year was then contemplated, the idea being that, as the number of individuals cannot be increased, the information collected on each of them has to be augmented. One of us (R.Pradel) examined the improvement in terms of precision that could be expected from this new protocol. To this end, simulations were run under 3 realistic scenarios in terms of true annual survival and encounter probabilities. As the gain in precision also depends on the model applicable, it was assumed that a model with constant survival should fit for this long-lived species but that encounter probability was so liable to variation that a model with time-varying encounter probabilities should be considered as well as the one with constant encounter probabilities. Among the combination of scenarios and models, the best gain produced by the additional reading session every year was a 20% decrease of the standard deviation (see Table IV). Thus, given how difficult it is to read a ring, the new protocol does not seem worth the effort. *A posteriori*, this is not surprising because, given the relatively high survival and encounter probabilities with this species, the intermediate reading does not add much information. The conclusion might have been entirely different with a short-lived species or a much lower encounter probability. Here, a greater precision of demographic parameter estimates seems attainable only by incorporating the censuses in the CR analysis. This is still a matter of methodological research.

Table IV. Improvement in precision of survival probability estimates for the Bonelli's eagle in France achieved with 2 visits per year instead of 1. Scenario 1: 90% annual survival, 90% encounter probability; scenario 2: 90% annual survival, 70% encounter probability; scenario 3: 75% annual survival, 70% encounter probability. In reality, although annual survival (ϕ) may be deemed constant, encounter probability (p) is likely to vary by year. We thus considered that the analysis should be conducted under both assumptions: encounter probability constant (p) or variable (p_t).

Scenario	Analysis model	Decrease in σ_ϕ
scenario 1	(ϕ, p_t)	13.00%
scenario 1	(ϕ, p)	8.80%
scenario 2	(ϕ, p_t)	21.20%
scenario 2	(ϕ, p)	17.30%
scenario 3	(ϕ, p_t)	17.40%
scenario 3	(ϕ, p)	12.60%

Discussion

The demographic mechanisms underlying changes in population size can be identified only through the following of individual animals. This can be achieved by means of a variety of devices, such as metal or colour rings, pit tags, or radio transmitters, with which the animals may be equipped. The most capable versions of these devices enable the animals to be tracked continuously and at a distance. However, these devices tend to be disturbing (and costly) and as such are not well suited to the monitoring of a fragile population. The passive tags seem a better compromise because their potential impact is better known and limited. However, passive tags do not guarantee that the equipped animal will be contacted, even if present. There is thus a need to resort to models acknowledging imperfect detection for the analysis of the data. This methodology is well developed for the study of survival. The same also holds for the study of recruitment provided the protocol is adequate (see below). But the direct study of PGR, which is of prominent interest to managers of small or endangered populations, remains to be improved in several ways. The refined CR analyses of survival or recruitment that can be carried out (see, for instance, Tavecchia *et al.,* 2001 for the greater flamingo) have no equivalent for PGR. Neither the age of the individuals nor the metapopulation context can currently be taken into account in a PGR analysis of CR data.

For this reason, despite the fact that taken alone they provide absolutely no information on the turnover of individuals, censuses, and more generally the gathering of indices of abundance, should not be abandoned. For one thing, such indices provide an estimate of the balance between influx and outflux. Thus, if the capture–recapture protocol permits only the estimation of, say, survival, the availability of an index of abundance will render the recruitment attainable as well. Also, when information is limited (very small populations), availability of an index of abundance is very valuable: by complementing the information brought by capture–recapture data, such indices enable more precise estimation of vital rates. Yet another situation where censuses are instrumental is when the ringed animals belong to a subset of the population that has a dynamics distinct from that of unringed animals (section on *The French colony of the greater flamingo* [*Camargue, southern France*]), especially when locally born animals are ringed but immigrants are not. In such cases, the availability of both sources of information is required to distinguish how each component behaves. The precise way in which the 2 kinds of information may be combined is still a matter of research, but there are already some well-identified directions, *e.g.,* the Kalman filter (Besbeas *et al.,* 2002). In the case of the Bonelli's eagle, greater precision of demographic parameter estimates might have been achieved by incorporating the censuses in the analysis (section on *The Bonelli's eagle in southern France*).

We have seen that some very common protocols like the marking of young at the nest (sections on *White stork population of Baden-Württenberg* [*Germany*] and on *The French colony of the greater flamingo* [*Camargue, southern France*]) are inadequate for the direct study of PGR and corrections have to be applied (Henry, 1999). This is because during the first years of the studies the ringed individuals were not representative of the population as a whole. For one thing, they were younger than average. Also, temporal variation in the marking effort confounded later variation of recruitment. These problems are solved if the field protocol includes counting the number of unmarked observed while searching for marked individuals, such that marked and unmarked are sampled with the same probability. During data analysis, the unmarked are then treated as individuals captured and not released (Nichols & Hines, 2002; Dreitz *et al.,* 2002, for an example). This trick provides the growth rate of the population as a whole, and problems due to time variation in the marking effort and the transitory difference in age structure between the marked fraction of the population and the population as a whole are solved. If we had had yearly counts of unmarked breeding white storks or greater flamingos, we would have used this method.

The origin of individuals is another potential problem, assuming especial importance in a restoration context: a change in population size due to recruitment of locally born individuals, *i.e.,* from the managed area, has very different implications than an identical change due to immigration from populations out of managers' reach. For instance, the rapid increase in population size of the Audouin's gull colony at the Ebro delta in Spain could not have been possible without immigration from other, distant colonies (Oro & Pradel, 1999). Thus, a manager may seek to distinguish changes of the PGR due to local recruitment from changes due to immigration. This can be partially solved with Pradel's model, where the contribution of adult-disperser immigration can be separated from the contribution of *in situ* reproduction and local survival (Nichols *et al.,* 2000; Nichols & Hines, 2002). Use of a robust design model, parameterized so that recruitment of immigrants can be distinguished from local recruitment (Nichols & Pollock, 1990), should enable identification of the contributions of both types of individual to the overall PGR (Dreitz *et al.,* 2002; Nichols & Hines, 2002). Finally, another type of distinction is obviously central when new individuals are introduced into an existing population. There are then 2 kinds of individuals around—the native and the introduced ones, with potentially very different characteristics and behaviour (see Letty, Marchandeau & Aubineau, 2007)—and the introduced animals are more likely to be marked. Following these animals will first teach us how introduced animals fare during the transitory period after release when they have to adapt to a new environment. This will permit adaptation of the reintroduction procedures. But later on, if the reintroduction is to be a success, the introduced animals will have to settle in the population and, past the transitory period, become fully part of it. Also, they and their descendants will become a significant, if not dominant, part of the population. It is thus interesting to monitor these animals over the long term as well. Of course, this can be complemented with the marking of native animals. It can be very instructive to compare the performances of native and introduced animals, especially to see if they differ over the long term.

Acknowledgements

We thank the Station Biologique de la Tour du Valat and the Collectif Bonelli for providing data and two anonymous referees for their constructive comments.

Literature cited

Bairlein, F., 1991. Population studies of white storks *Ciconia ciconia* in Europe, with reference to the western population. Pages 207–229 *in* C. Perrins, J.-D. Lebreton & G. Hirons (eds.). Bird Population Studies: Relevance to Conservation and Management. Oxford University Press, Oxford.

Besbeas, P., S. N. Freeman, B. J. T. Morgan & E. A. Catchpole, 2002. Integrating mark–recapture–recovery and census data to estimate animal abundance and demographic parameters. Biometrics, 58: 540–547.

Boulanger, J., S. Himmer & C. Swan, 2004. Monitoring of grizzly bear population trends and demography using DNA mark–recapture methods in the Owikeno Lake area of British Columbia. Canadian Journal of Zoology, 82: 1267–1277.

Boyce, M. S., L. L. Irwin & R. Barker, 2005. Demographic meta-analysis: Synthesizing vital rates for spotted owls. Journal of Applied Ecology, 42: 38–49.

Brongo, L. L., M. S. Mitchell & J. B. Grand, 2005. Long-term analysis of survival, fertility, and population growth rate of black bears in North Carolina. Journal of Mammalogy, 86: 1029–1035.

Cam, E., L. Lougheed, R. Bradley & F. Cooke, 2003. Demographic assessment of a Marbled Murrelet population from capture–recapture data. Conservation Biology, 17: 1118–1126.

Carothers, A., 1973. The effects of unequal catchability on Jolly-Seber estimates. Biometrics, 29: 79–100.

Caswell, H., 2001. Matrix Population Models: Construction, Analysis and Interpretation. 2nd Edition. Sinauer Associates, Sunderland, Massachusetts.

Cheylan, G., A. Ravayrol & J.-M. Cugnasse, 2003. Programme de baguage de l'Aigle de Bonelli en France. Compte-rendu pour 2002 – 13e année. Faune de Provence, 21: 86–87.

Clark, J. D., F. T. van Manen & M. R. Pelton, 2005. Bait stations, hard mast, and black bear population growth in Great Smoky Mountains National Park. Journal of Wildlife Management, 69: 1633–1640.

Converse, S. J., J. B. Iverson & J. A. Savidge, 2005. Demographics of an ornate box turtle population experiencing minimal human-induced disturbances. Ecological Applications, 15: 2171–2179.

Courtney, S., J. Blakesley, R. Bigley, M. Cody, J. Dumbacher, R. Fleischer, A. B. Franklin, J. Franklin, R. Gutiérrez, J. Marzluff & L. Sztukowski, 2004. Scientific Evaluation of the Status of the Northern Spotted Owl. Sustainable Ecosystems Institute, Portland, Oregon.

Dinsmore, S. J., G. C. White & F. L. Knopf, 2005. Mountain plover population responses to black-tailed prairie dogs in Montana. Journal of Wildlife Management, 69: 1546–1553.

Dodd, C. K., A. Ozgul & M. K. Oli, 2006. The influence of disturbance events on survival and dispersal rates of Florida box turtles. Ecological Applications, 16: 1936–1944.

Dreitz, V. J., J. D. Nichols, J. E. Hines, R. E. Bennetts, W. M. Kitchens & D. L. Deangelis, 2002. The use of resighting data to estimate the rate of population growth of the snail kite in Florida. Journal of Applied Statistics, 29: 609–623.

Franklin, A. B., R. J. Gutiérrez, J. D. Nichols, M. E. Seamans, G. C. White, G. S. Zimmerman, J. E. Hines, T. E. Munton, W. S. LaHaye, J. A. Blakesley, G. N. Steger, B. R. Noon, D. W. H. Shaw, J. J. Keane, T. L. McDonald & B. Susan, 2004. Population dynamics of the California spotted owl (*Strix occidentalis occidentalis*): A meta-analysis. Ornithological Monographs, 54: 1–110.

Henry, P.-Y., 1999. Les modèles statistiques de capture–recapture et l'étude du taux de multiplication en biologie des populations. M.Sc. thesis, Université Montpellier II, Montpellier.

Hines, J. E. & J. D. Nichols, 2002. Investigations of potential bias in the estimation of λ using Pradel's (1996) model for capture–recapture data. Journal of Applied Statistics, 29: 573–587.

Hoyle, S. D., A. R. Pople & G. J. Toop, 2001. Mark–recapture may reveal more about ecology than about population trends: Demography of a threatened ghost bat (*Macroderma gigas*) population. Austral Ecology, 26: 80–92.

Iverson, J. B., S. J. Converse, G. R. Smith & J. M. Valiulis, 2006. Long-term trends in the demography of the Allen Cays Rock Iguana (*Cyclura cychlura inornata*): Human disturbance and density-dependent effects. Biological Conservation, 132: 300–310.

Jenouvrier, S., C. Barbraud & H. Weimerskirch, 2003. Effects of climate variability on the temporal population dynamics of southern fulmars. Journal of Animal Ecology, 72: 576–587.

Kanyamibwa, S., A. Schierer, R. Pradel & J.-D. Lebreton, 1990. Changes in adult annual survival in a Western European population of White Stork (*Ciconia ciconia*). Ibis, 132: 27–35.

Lampila, S., M. Orell, E. Belda & K. Koivula, 2006. Importance of adult survival, local recruitment and immigration in a declining boreal forest passerine, the willow tit *Parus montanus*. Oecologia, 148: 405–413.

Lebreton, J.-D., 1978. Un modèle probabiliste de la dynamique des populations de Cigogne blanche *C. ciconia* en Europe occidentale. Pages 277–343 *in* J. Legay & R. Tomassone (eds.). Biométrie et Écologie. Société Française de Biométrie, Paris.

Lehmkuhl, J. F., K. D. Kistler, J. S. Begley & J. Boulanger, 2006. Demography of northern flying squirrels informs ecosystem management of western interior forests. Ecological Applications, 16: 584–600.

Letty, J., S. Marchandeau & J. Aubineau, 2007. Problems encountered by individuals in animal translocations: Lessons from field studies. Écoscience, 14: 420–431.

Lima, M., N. C. Stenseth, N. G. Yoccoz & F. M. Jaksic, 2001. Demography and population dynamics of the mouse opossum (*Thylamys elegans*) in semi-arid Chile: Seasonality, feedback structure and climate. Proceedings of the Royal Society of London, B, 268: 2053–2064.

Lowe, W. H., 2003. Linking dispersal to local population dynamics: A case study using a headwater salamander system. Ecology, 84: 2145–2154.

Mizroch, S. A., L. M. Herman, J. M. Straley, D. A. Glockner-Ferrari, C. Jurasz, J. Darling, S. Cerchio, C. M. Gabriele, D. R. Salden & O. Von Ziegesar, 2004. Estimating the adult survival rate of central North Pacific humpback whales (*Megaptera novaeangliae*). Journal of Mammalogy, 85: 963–972.

Nichols, J. D. & J. E. Hines, 2002. Approaches for the direct estimation of λ, and demographic contributions to λ, using capture–recapture data. Journal of Applied Statistics, 29: 539–568.

Nichols, J. D. & K. H. Pollock, 1990. Estimation of recruitment from immigration *versus* in situ reproduction using Pollock's robust design. Ecology, 71: 21–26.

Nichols, J. D., J. E. Hines, J.-D. Lebreton & R. Pradel, 2000. Estimation of contributions to population growth: A reverse-time capture–recapture approach. Ecology, 81: 3362–3376.

Noon, B. R. & J. A. Blakesley, 2006. Conservation of the northern spotted owl under the northwest forest plan. Conservation Biology, 20: 288–296.

Oro, D. & R. Pradel, 1999. Recruitment of Audouin's gull to the Ebro Delta colony at metapopulation level in the western Mediterranean. Marine Ecology Progress Series, 180: 267–73.

Ozgul, A., K. B. Armitage, D. T. Blumstein & M. K. Oli, 2006. Spatiotemporal variation in survival rates: Implications for population dynamics of yellow-bellied marmots. Ecology, 87: 1027–1037.

Peery, M. Z., B. H. Becker & S. R. Beissinger, 2006. Combining demographic and count-based approaches to identify source–sink dynamics of a threatened seabird. Ecological Applications, 16: 1516–1528.

Piersma, T., K. G. Rogers, H. Boyd, E. J. Bunskoeke & J. Jukema, 2005. Demography of Eurasian golden plovers *Pluvialis apricaria* staging in the Netherlands, 1949–2000. Ardea, 93: 49–64.

Pine, W. E., M. S. Allen & V. J. Dreitz, 2001. Population viability of the Gulf of Mexico sturgeon: Inferences from capture–recapture and age-structured models. Transactions of the American Fisheries Society, 130: 1164–1174.

Pradel, R., 1996. Utilization of capture–mark–recapture for the study of recruitment and population growth rate. Biometrics, 52: 703–709.

Robert, A., D. Couvert & F. Sarrazin, 2007. Integration of demography and genetics in population restorations. Écoscience, 14: 463–471.

Sandercock, B. K. & S. R. Beissinger, 2002. Estimating rates of population change for a neotropical parrot with ratio, mark–recapture and matrix methods. Journal of Applied Statistics, 29: 589–607.

Sasso, C. R., J. Braun-McNeill, L. Avens & S. P. Epperly, 2006. Effects of transients on estimating survival and population growth in juvenile loggerhead turtles. Marine Ecology Progress Series, 324: 287–292.

Spendelow, J. A., J. D. Nichols, J. E. Hines, J.-D. Lebreton & R. Pradel, 2002. Modeling postfledging survival and age-specific breeding probabilities in species with delayed maturity: A case study of Roseate Terns at Falkner Island, Connecticut. Journal of Applied Statistics, 29: 385–405.

Tavecchia, G., R. Pradel, V. Boy, A. R. Johnson & F. Cézilly, 2001. Sex- and age-related variation in survival and cost of first reproduction in Greater Flamingos. Ecology, 82: 165–174.

Villella, R. F., D. R. Smith & D. P. Lemarie, 2004. Estimating survival and recruitment in a freshwater mussel population using mark–recapture techniques. American Midland Naturalist, 151: 114–133.

Webb, J. K., B.W. Brook & R. Shine, 2002a. Collectors endanger Australia's most threatened snake, the broad-headed snake *Hoplocephalus bungaroides*. Oryx, 36: 170–181.

Webb, J. K., B. W. Brook & R. Shine, 2002b. What makes a species vulnerable to extinction? Comparative life-history traits of two sympatric snakes. Ecological Research, 17: 59–67.

Williams, B. K., J. D. Nichols & M. J. Conroy, 2002. Analysis and Management of Animal Populations. Academic Press, San Diego, California.