

Abundance Estimation With a Transient Model Under the Robust Design

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ABSTRACT A common situation in capture–mark–recapture (CMR) studies on birds and other organisms is to capture individuals not belonging to the studied population only present during the short time of the capture session. Presence of such transient individuals affects demographic parameter estimation from CMR data. Methods exist to reduce biases on survival estimates in the presence of transients and have been shown to be particularly efficient within the Robust Design framework (several secondary capture sessions within a short time interval during which the studied population can be assumed closed). We present a new model to estimate population size accounting for transients. We first used simulated data to show that the method reduces positive biases due to transients. In a second step, we applied the method to a real CMR dataset on a reed warbler (*Acrocephalus scirpaceus*) population. Population size estimates are reduced by up to 50% when correcting for the presence of transients. Many field studies on managed animal populations use capture–recapture methodology to obtain crucial parameters of the focal population demography. The resulting data sets are used either to estimate population size ignoring the presence of transients, or to estimate vital rates, accounting for transients but overlooking abundance estimation. Our method conciliates these 2 approaches. (JOURNAL OF WILDLIFE MANAGEMENT 72(5):1203–1210; 2008)

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Capture–mark–recapture (CMR) studies are essential for estimating demographic parameters. Among these parameters, population size and apparent survival rate are the most frequently studied (Seber 1992). One specific CMR design, the Robust Design, allows estimation of both parameters simultaneously (Pollock 1982). Under this design, 2 sampling periods, primary and secondary, are distinguished. Consecutive primary sampling periods are separated by sufficient time (typically 1 yr for vertebrates) so that the sampled population is expected to change through gains (birth and immigration) and losses (death and emigration) during these periods. Capture–recapture data summarized over primary periods are analyzed using models developed for open populations, such as the classical Cormack–Jolly–Seber model (CJS), and allow estimation of survival (Cormack 1964, Jolly 1965, Seber 1965, Lebreton et al. 1992).

Each primary period i ($i = 1, 2, \dots, k$) includes l_i secondary sampling periods separated by time intervals short enough for the population to be closed to gains or losses. Data from the secondary periods within a primary period can be analyzed using capture–recapture models developed for closed populations, such as those summarized by Otis et al. (1978), and allow estimation of population size. Such data can provide robust estimation of capture rates for each primary capture period and, thus, more precise estimates of survival rates among primary capture periods. In particular,

survival estimates are less affected by heterogeneity of capture probabilities among individuals because there are multiple opportunities to capture the animal within a primary session (Pollock 1982, Kendall et al. 1995).

Unfortunately, the assumption of closure (i.e., absence of death, recruitment, and dispersal events) within a primary period is rarely met because captured individuals are a sample of the entire population present at a site, which is a mixture of local individuals (e.g., local breeders) and transient individuals that do not belong to the studied population. Transients may have various origins depending on species and population considered (e.g., migrants stopping over at the study site, neighboring residents that are occasional visitors to the studied site, or prospecting nonbreeders). Transients also have the property of being caught only once during a primary capture occasion and never subsequently recaptured during secondary occasions. Although individuals that are captured several times can a posteriori be identified as residents, it is impossible to distinguish between residents and transients among individuals caught only once within a primary session.

Presence of transient individuals biases estimates of demographic parameters when using classical CMR models. Because transients are never recaptured, they cause an underestimation of survival when using open population models (Pradel et al. 1997). The impact of transients on population size estimates is 2-fold. First, the local population size estimate is biased positively by presence of transients that do not belong to the studied population in

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the sample of captured animals. Second, because they are captured only once, transients negatively bias the capture probability estimate in closed population models, which again inflates the population size estimate.

Detection of transients is straightforward with open population models; apparent survival rate is lower for newly captured individuals than for recaptures (Pradel et al. 1997). Survival ratio estimates are an estimate of the proportion of residents among newly captured individuals, which is based on the assumption of constant survival among resident individuals in a given site. Transients are frequently found in breeding bird populations sampled by mist-netting. For instance, DeSante et al. (1999) analyzed data from hundreds of North American passerine populations and showed that on average, 50% of newly caught individuals were transients.

Methods to obtain unbiased survival estimates accounting for transients exist, but no method is yet available for reducing bias due to transients in abundance estimates (Pradel et al. 1997, Hines et al. 2003). One possibility for reducing bias is to estimate the number of transients and remove them from the total population size estimate. However, this approach would require making unrealistic assumptions such as a limited number of transient individuals and equal capture probabilities between transient and resident individuals. For mobile organisms like birds, it could be assumed that transients come from a nearly infinite population, each of these individuals having a nearly zero capture probability.

Here, we develop statistics to account for transients. We used the transient rate, estimated from primary periods, to correct the statistics from secondary periods. This correction allows for estimation of population size. Our method is built on the ad hoc approach of Hines et al. (2003) to estimate the transient rate and uses the Jackknife estimator to estimate the resident population size (Burnham and Overton 1979).

METHODS

Using Transient Capture–Recapture Model Under the Robust Design

We closely followed the ad hoc approach developed by Hines et al. (2003). Within a given primary period, we first classified all recaptured individuals from previous primary capture occasions as residents (see Fig. 1). In addition, among newly captured individuals in primary period i , we identified as residents those that were captured more than once among the l_i secondary sessions. We assigned to the unknown group newly captured individuals captured only once during the primary period i . Note that we did not use potential recaptures in any subsequent primary period to retrospectively update the status of unknown individuals. Indeed, because only surviving individuals can be recaptured, reclassifying unknown individuals as resident because they are retrapped in subsequent primary occasions would substantially bias all parameter estimates.

Hines et al. (2003) suggested that individuals could be classified as resident only after a minimum interval of time

between first capture and recapture within the considered primary period. Hines et al. (2003) gave as an example an individual recaptured on a study site after $\geq d$ days (e.g., $d = 10$) and defined as a resident. We do not consider such a refinement here, but it can be easily incorporated in our proposed method. We pooled data over secondary sampling periods to one capture indicator for each primary period before analysis in Program MARK (White and Burnham 1999). When using MARK, we considered 2 distinct groups (resident and unknown individuals). Survival rates for each group are computed. Individuals with resident status are analyzed with a classical CJS model (Cormack 1964, Jolly 1965, Seber 1965). The unknown group is analyzed using Pradel et al.'s (1997) model. The transient model (Pradel et al. 1997) yields an estimate of the resident rate $(1 - \tau)$ that is 1 minus the proportion of transients among individuals, thanks to both unknown and resident survival estimations with

$$(1 - \tau) = \frac{\phi_{unk}}{\phi_{res}}, \quad (1)$$

where ϕ_{unk} = survival of unknown category, and ϕ_{res} = survival of resident category.

Note that our parameter τ is different from that defined in Pradel et al. (1997) because it is applied to a smaller subset of individuals. Direct estimation of the resident rate may be obtained with specific software (TMSURVIV; Kendall and Hines 1999) but may also be obtained using the MARK framework with an appropriate design matrix and a log link (see Appendix).

Incorporating Transient Rate Estimates Into the Estimation of Population Size

We adopted the approach of Hines et al. (2003) to create a new population size estimator.

We are the first to develop a model estimating abundance adjusted for transients.

The basic estimator of population size is

$$\hat{N}_t = \frac{n_t}{\hat{p}_t}, \quad (2)$$

where \hat{p}_t = estimate of encounter probability and n_t = number of birds captured in year t .

Here we estimated \hat{p}_t for each year t using either an open-population capture–recapture model such as proposed in the JS model (Jolly 1965, Seber 1965) or a Robust Design (CJS; Pollock 1982) model. Because the transient rate estimated by Pradel et al.'s (1997) model is only an estimate of the transient rate of the subset of newly captured individuals rather than of the entire captured population, it cannot be applied directly to this population size estimate.

An estimate for resident abundance in year t is

$$\hat{N}_{tr} = \frac{n_{t,r}}{\hat{p}_{t,r}} + \frac{n_{t,r}(1 - \hat{\tau}_t)}{\hat{p}_{t,r}} = \frac{n_{t,r} + n_{t,u}(1 - \hat{\tau}_t)}{\hat{p}_{t,r}}, \quad (3)$$

where $n_{t,r}$ = number of birds captured in year t that are known to be resident because they were captured in a

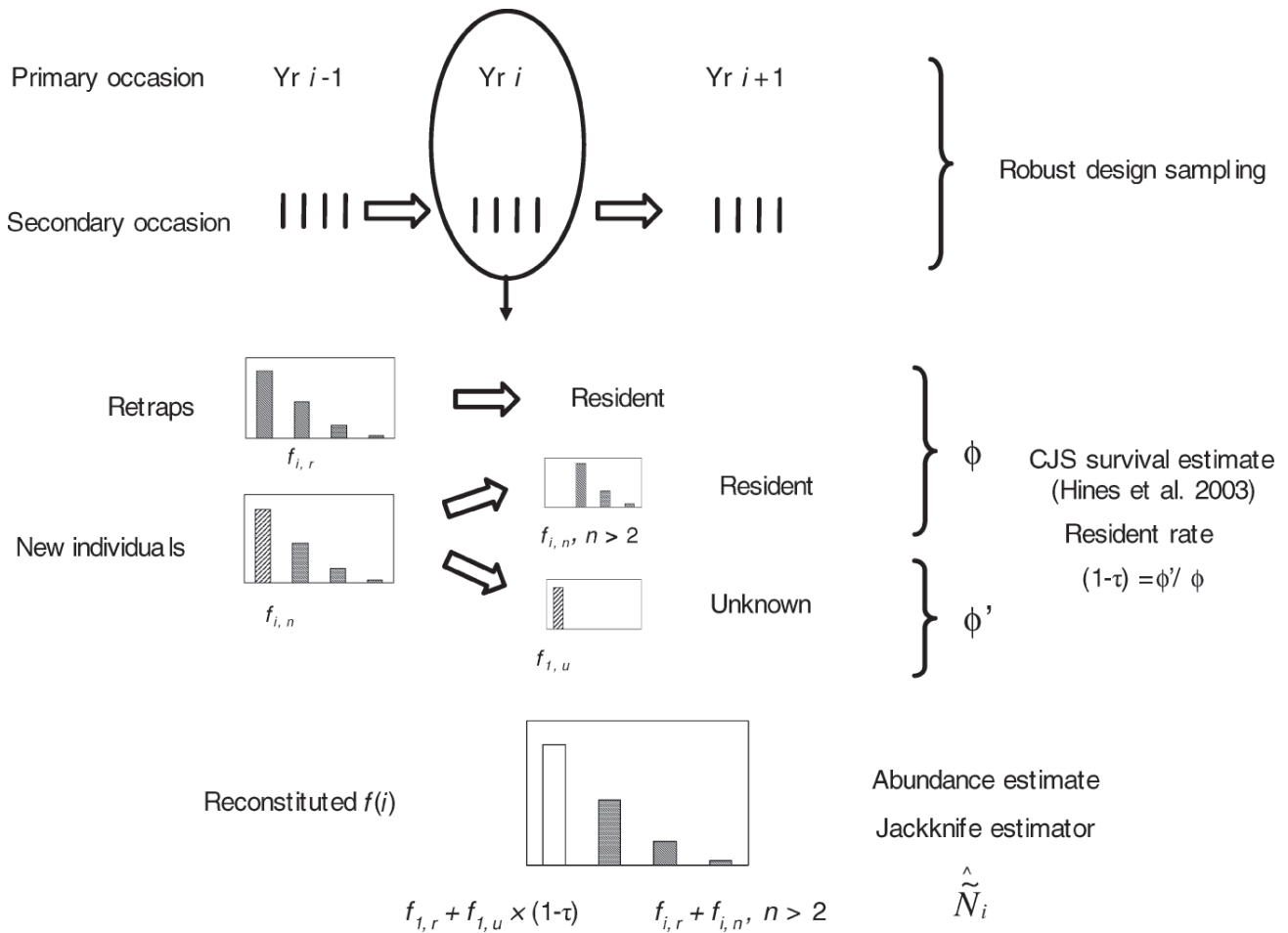


Figure 1. Diagram summarizing the method. Variables: $f_{i,r}$: frequency of individuals recaptured in year i and first captured before year i ; $f_{i,n}$: frequency of newly captured individuals in year i ; $f_{i,u}$: frequency of individuals captured only once in year i (individuals of the unknown group); $f_{i,n}, n > 2$: frequency of individuals captured more than once in year i (individuals of the resident group); ϕ' = survival of the unknown group; ϕ = survival of the resident group; τ = transient rate; $1 - \tau$ = resident rate; \hat{N}_i = population size estimation in year i , with modified model $M_{b\tau}$ taking into account transients.

previous year, $n_{t,u}$ = number of birds captured in year t that were never captured before and are, therefore, of unknown status, $\hat{p}_{t,r}$ = probability that a resident individual is captured in year t estimated by the Pradel et al. model, and $\hat{\tau}_t$ = transient rate estimated by the Hines et al. model. Note that it is not possible to estimate abundance for the first and last year, for which one of the estimated parameters is missing. To improve precision of the estimates in the robust design (i.e., produce smaller SEs), the Hines et al. (2003) approach may be applied by using number of captures within primary sampling periods to classify individuals into resident or unknown status (see above).

The modified abundance estimator is then

$$\hat{N}'_{t,r} = \frac{n'_{t,r} + n'_{t,u}(1 - \hat{\tau}'_t)}{\hat{p}_{t,r}}, \quad (4)$$

where $n'_{t,r}$ = number of birds captured in year t that are known to be residents because they were captured in a previous year or captured >1 time in year t , $n'_{t,u}$ = number of birds captured in year t that were never captured in

previous years and were not captured >1 time in year t , $\hat{\tau}'_t$ = transient rate estimated by the Hines et al. model, and $\hat{p}_{t,r}$ = probability that a resident is captured in year t , estimated by the Pradel et al. model.

To improve precision of the estimates and obtain an estimate for the first year of the study, capture probability can be estimated from secondary occasions using closed population models, which may be achieved by focusing on capture probabilities originating from the subset of residents of previous primary periods (i.e., recaptures). Use of this subset for estimating capture probabilities may, however, be a substantial source of bias and uncertainty under certain circumstances. First, if number of recaptures is small, focusing on residents will further reduce sample size. In the case of passerine population studies based on mist-netting, only 20% of individuals caught in a given year are recaptures from the previous year (e.g., DeSante et al. 1999). Second, using only recaptures of resident individuals may lead to biased estimates in the presence of capture heterogeneity because recaptures from previous years will be biased toward individuals whose capture probabilities are

higher than average. In addition, although the robust design allows estimating population size each year, because the transient rate estimation is computed using survival estimates (Pradel et al. 1997), it is not possible to estimate the resident population size for the first year. Because these different limitations may be important, we based our approach on the Jackknife estimator.

The Minimum Sufficient Statistic (MSS) of the Jackknife estimator relies only on capture frequencies f_1, \dots, f_t , that is, the number of individuals caught exactly 1, 2, ... t times during the i secondary periods of a primary capture period (Fig. 1). The estimator is a linear function of the k first capture frequencies (Jackknife estimator of k^{th} order; Burnham and Overton 1979). For order k , the Jackknife estimator $N_{b,k}$ is

$$\hat{N}_{b,k} = \sum_{j=1}^t a_{j,k} f_j \quad (5)$$

$$\text{Var}(\hat{N}_{b,k}) = \sum_{j=1}^t a_{j,k}^2 f_j - \hat{N}_{b,k} \quad (6)$$

where the $a_{j,k}$ are functions of t .

The testing procedure of Burnham and Overton (1979) allows selection of an appropriate order for the Jackknife estimator.

Our basic idea is to modify the MSS using the estimated transient rates (Hines et al. 2003). We propose to use the Hines et al. (2003) approach but using modified f_1 as follows:

$$\tilde{f}_1 = f_{1,R} + f_{1,U}(1 - \hat{\tau}) \quad (7)$$

where \tilde{f}_1 is the modified number of individuals captured exactly once, $f_{1,R}$ is the number of individuals with resident status captured exactly once (i.e., recaptures from previous primary occasions), $f_{1,U}$ is the number of individuals with unknown status captured exactly once, and $(1 - \hat{\tau})$ is the resident rate estimated using the Hines et al. (2003) approach.

The modified Jackknife estimator accounting for transients $\tilde{N}_{b,k}$ is

$$\tilde{N}_{b,k} = a_{1,k} \tilde{f}_1 + \sum_{j=2}^t a_{j,k} f_j \quad (8)$$

$$\text{Var}(\tilde{N}_{b,k}) = a_{1,k}^2 [f_{1,R} + f_{1,U} \text{var}(1 - \tau)] + \sum_{j=2}^t a_{j,k}^2 f_j - \tilde{N}_{b,k} \quad (9)$$

As far as we can see, the Jackknife is the only estimator that remains reliable under the above conditions because it is the only way to incorporate extra information properly (only one MSS needs to be modified contrary to all other estimators in Otis et al. [1978], for which ≥ 2 MSS would need to be modified). Moreover, the Jackknife accounts for capture

heterogeneity, a problem often encountered in bird CMR studies. We called this new model $M_{b\tau}$.

Simulation Study

We applied our proposed method to simulated datasets. Simulated data mimicked a capture–recapture experiment of passerines using mist-netting. We simulated a Robust Design scheme with 4 primary periods, each one made of 4 secondary sampling periods. Survival rate between subsequent primary periods corresponding to 1 year was 60%. We fixed the resident population size to $N = 100$ individuals. At the beginning of each primary period, we replaced dead individuals with new individuals to keep population size constant. We fixed expected individual annual recapture to 0.50 (which corresponded to a 0.159 probability of recapture during each secondary period). We added 40 captured transient individuals (i.e., individuals captured only once during the whole simulated study) at each primary period. We considered 4 scenarios: 1) a first situation in which recapture probability was the same for all individuals ($p^* = 0.50$), 2) a trap-shy model mimicking a learning behavior of trap avoidance with a reduction of $r = 40\%$ ($P_{\text{second capture}} = 0.4 P_{\text{first capture}}$), 3) a scenario with some heterogeneity in capture probability among individuals, wherein the intrinsic capture probability of each individual was drawn from a Beta distribution with mean $\bar{p} = 0.5$ and standard deviation (SD) = 0.032, and 4) same as scenario 3, with SD = 0.1. We generated 500 simulated datasets for each scenario.

We split individuals into 2 groups using the Hines et al. (2003) approach described above. The model we used for estimating the transient rate assumed constant survival and capture rates through time. We allowed estimated transient rates to vary among primary periods. Indeed, at each primary occasion, the class of individuals known to be resident increased because it depended partly on the number of captures in preceding primary periods. Consequently, the estimated proportion of residents intrinsically increased through time although number of captured transient individuals and resident population size were kept constant.

We used 4 approaches to estimate population size in the 4 scenarios we considered: 1) Model 1: the omniscient approach. In this case, simulated data do not include any transient individuals so there is no transient issue. Under this approach we used the uncorrected M_b model. 2) Model 2: the new approach, modified M_b model, called $M_{b\tau}$. In this case, data include transient individuals and we used the $M_{b\tau}$ model, which account for presence of transients. 3) Model 3: a new approach, the Jolly–Seber (J–S) estimator corrected for transient rate (eq 3). In this case, data include transient individuals and we used the basic estimator of population size. 4) Model 4: the naïve approach, the classical M_b model. In this case, data include transient individuals and we used the uncorrected M_b model.

Case Study

We applied the method to CMR data from the French avian monitoring program (Julliard and Jiguet 2002), which

Table 1. Survival and capture probability models sorted by increasing Akaike's Information Criterion adjusted for small sample size (AIC_c). The ΔAIC_c is the difference in AIC_c between the current and the best model. Data come from a dataset on a reed warbler population located in the north of France (Pas-de-Calais), 1996–2003.

Model ^a	AIC_c	ΔAIC_c	No. parameters	Deviance
$[\phi_t, \tau_t, p_t]$	352.40	0	15	37.06
$[\phi_t, \tau_t, p_g]$	353.77	1.37	16	34.14
$[\phi_t, \tau_t, p_{g+t}]$	354.44	2.04	16	34.81
$[\phi_t, \tau_t, p_{g+t}]$	361.43	9.03	22	28.7
$[\phi_t, \tau_t, p_t]$	363.74	11.33	15	46.25
$[\phi_t, \tau_t, p_t]$	365.72	13.13	21	35.20
$[\phi_t, \tau_t, p_g]$	373.79	21.39	10	66.91
$[\phi_t, \tau_t, p_t]$	376.97	24.57	9	72.18

^a ϕ = apparent survival rate, p = capture rate, τ = transient probability, t = model with time-dependence, $.$ = constant model, g = group (resident vs. unknown).

is similar to the Constant Effort Site program in the United Kingdom (Peach et al. 1998) or Monitoring Avian Productivity and Survivorship program in the United States (DeSante et al. 1999). The protocol follows a robust design, with temporal standardization; numbers and dates of visits were similar across years. Three secondary capture sessions were conducted in May–June. Net positions on study sites were constant within and among primary periods. All individuals were banded, sexed, and aged. Recaptures were recorded, including all within-day recaptures. The data we present come from a specific program on reed-bed passerines. Such surveys may help managers to evaluate the impact of habitat management on the bird community. Because they are of strong conservation concern in Europe and an important proportion of wetland habitats, reed beds are thus found in protected areas (Van der Putten 1997). In most cases, these wetlands are not at equilibrium, and some management is needed to ensure persistence of this habitat type. To allow density comparison among sites, the spatial distribution of capture devices is standardized.

We focused on an 8-year dataset on a reed warbler (*Acrocephalus scirpaceus*) population located in the north of France (Pas-de-Calais). We present estimates of population size only for 4 years with $M_{b\tau}$ and M_b models.

We built 8 models: $[\phi_t, \tau_t, p_t]$, $[\phi_t, \tau_t, p_g]$, $[\phi_t, \tau_t, p_t]$, $[\phi_t, \tau_t, p_{g+t}]$, $[\phi_t, \tau_t, p_t]$, $[\phi_t, \tau_t, p_g]$, $[\phi_t, \tau_t, p_t]$, $[\phi_t, \tau_t, p_{g+t}]$ (Table 1), using log link (Appendix). We assessed the fit of the most general model $[\phi_t, \tau_t, p_{g+t}]$ to the data with a bootstrap goodness-of-fit test (GOF; White and Burnham 1999). We based selection of the best model on Akaike's Information Criterion corrected for small sample size (AIC_c ; Anderson and Burnham 1999).

RESULTS

Simulation Study

In the first scenario, capture probability was the same across individuals. When transients were present, we found that estimates from $M_{b\tau}$ were not different from the true population size (Fig. 2). The uncorrected M_b overestimated population size by as much as 100%. Estimates from the J–

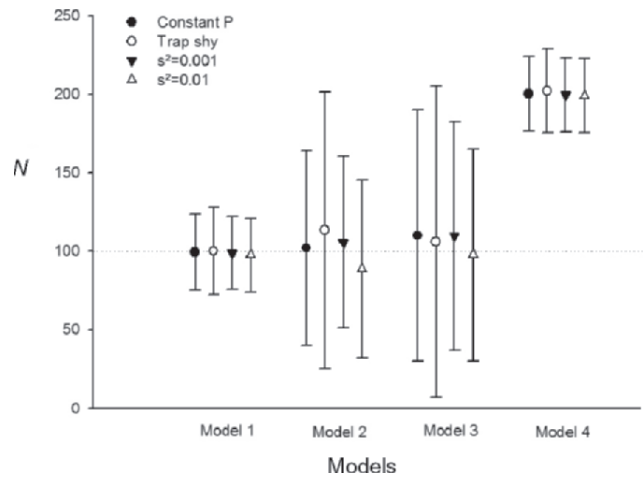


Figure 2. Population size estimates under different models $\pm 95\%$ confidence interval from 500 simulations and under 4 scenarios. Dashed line is the actual population size.

- (i) The omniscient approach.
 Model 1: M_b model without transient individuals in the data set.
 (ii) The new approach, M_b model modified.
 Model 2: $M_{b\tau}$ model (eq 7) year 1, 2 and 3 with transient individuals in the data set.
 (iii) The new approach, basic estimator of population size.
 Model 3: Jolly–Seber estimator corrected for transient rate (eq 4) year 2 and 3 with transient individuals in the data set. The year 1 cannot be estimated.
 (iv) The naïve approach, the classical M_b model.
 Model 4: M_b model with transient individuals in the data set.
 (1) Scenario 1: recapture probability constant ($P = 50\%$).
 (2) Scenario 2: Trap-shy model (reduction of capture probability $r = 40\%$).
 (3) Scenario 3: Heterogeneity in capture probability with variance $s^2 = 0.001$.
 (4) Scenario 4: Heterogeneity in capture probability with variance $s^2 = 0.01$.

S estimator appeared unbiased (i.e., not different from the true population size) but were less precise than $M_{b\tau}$ (i.e., larger SE). In the second scenario with trap-shy behavior, $M_{b\tau}$ overestimated population size (Fig. 2). Again, the uncorrected M_b overestimated the population size by about 100%. Estimates from the J–S estimator seemed to be unbiased (i.e., not different from the true population size) although less precise than $M_{b\tau}$ (i.e., SE was large). In the third and fourth scenarios, individuals had heterogeneous capture probability (scenario 3: SD = 0.032; scenario 4: SD = 0.1). Results indicate that the estimates of population size with $M_{b\tau}$ or the J–S estimator decreases as variance in capture probability increases (Fig. 2). Model M_b overestimated population size by about the same magnitude as previously in both scenarios.

In each scenario we found larger standard error for population size estimates for the first primary period, presumably due to the small number of resident individuals identified during the first primary period. In subsequent primary periods, some of the captured individuals were already identified as resident in the previous occasions so that the precision of the estimates was improved.

Case Study

We considered the fit of the model $[\phi_t, \tau_t, p_{g+t}]$ adequate (GOF test, $P = 0.08$). According to AIC_c , 2 models $[\phi_t, \tau_t,$

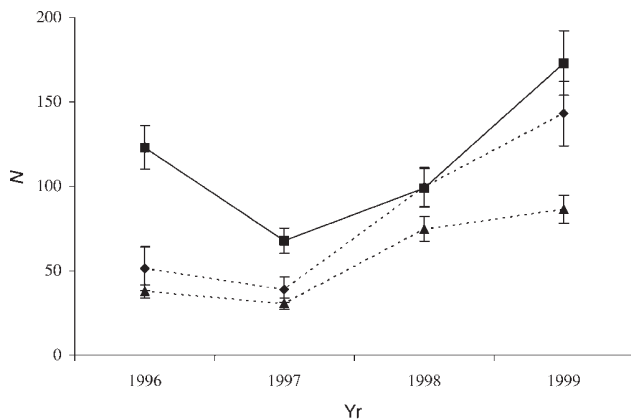


Figure 3. Yearly population size estimates, between 1996 and 1999, of reed warbler (*Acrocephalus scirpaceus*) from a French Constant Effort Site located in north of France (Pas-de-Calais), accounting for the presence of transients with model $M_{b\tau}$ and compared with M_b . The dotted line is the population size estimate accounting for transients, using estimates from a model with different capture probabilities for the unknown and resident groups (diamonds) or from a model with same capture probabilities for the unknown and resident groups (triangles). The solid line is the population size estimate not accounting for transients.

p_i] and $[\phi_i, \tau_i, p_g]$, with time-dependence on survival, were selected (Table 1). Temporal variations in survival rates thus appeared to be not negligible. There was no difference between these 2 models based on AIC_c ($[\phi_i, \tau_i, p_i]$ and $[\phi_i, \tau_i, p_g]$; $\Delta AIC_c < 2$). Individuals classified as resident, based on multiple captures within the primary period during which they were first caught, tended to have a higher capture rate than did residents from the unknown group ($p = 0.618$, $SE = 0.1144$, $n = 341$ for residents and $p = 0.287$, $SE = 0.136$, $n = 88$ for unknown individuals).

First, the resident population size estimated after transient correction ($M_{b\tau}$ model) was smaller than without corrections (M_b model). Estimates of resident population size (averaged across yr) from model $M_{b\tau}$ were 29% and 50% lower than estimates obtained from M_b model when $M_{b\tau}$ was respectively run with $[\phi_i, \tau_i, p_g]$ and $[\phi_i, \tau_i, p_i]$ (Fig. 3). Second, estimates obtained with the $M_{b\tau}$ model were more precise than those from the M_b models. Indeed, estimates of SE from model $M_{b\tau}$ were on average 46% lower with the $[\phi_i, \tau_i, p_g]$ model and 54% lower with the $[\phi_i, \tau_i, p_i]$ model than were estimates obtained with the model M_b , which may be due to the improved precision of the estimate for single capture frequency. Estimates for 1998 were close between the classical and the transient models. This was due to a low transient rate estimate for 1998 ($\tau = 0.04$, $SE = 0.345$).

DISCUSSION

We developed a new method to estimate abundance accounting for biases due to presence of transients in the study population. We developed our method within the Robust Design framework and it uses the estimate of transient rate developed by Hines et al. (2003).

The different scenarios we considered in simulated datasets with and without heterogeneity in capture probability

between individuals and trap-shy response allowed us to validate the $M_{b\tau}$ model. Indeed, simulated data showed that the $M_{b\tau}$ model allows substantial reduction of the positive bias on estimates of population size due to transients, although it decreases the precision of estimates (SEs from $M_{b\tau}$ models were around 3 times higher than SEs from M_b models). The method also can be applied with the modified Jolly–Seber estimator. Estimates obtained with the J–S estimator are valid and robust to different sources of heterogeneity among individuals (recapture rates). However, we showed that with data similar to birds sampled with mist nets, estimates obtained with the J–S estimator were less precise than the $M_{b\tau}$ estimates, regardless of the scenario. Such difference in precision (approx. 20%) should be lower in cases of higher survival and recapture rates. However, such estimates suffer from the same limitations as the classical J–S estimator (see Seber 1992). In particular, it is not possible to estimate population size in the first year of monitoring due to the impossibility of estimating capture probability.

Several estimation models exist with different biological assumptions and statistical constraints. We chose the model M_b for different reasons, based on underlying ecological assumptions and statistical robustness. First, birds generally show capture heterogeneity among individuals, partly due to transients but also because some individuals have a greater propensity to be captured than others. Moreover, bird populations often exhibit trap responses that are difficult to distinguish from intrinsic capture heterogeneity. It is therefore preferable to use the M_b model, which accounts for capture heterogeneity (Otis et al. 1978). Further, model M_b uses the Jackknife estimator, a fairly robust estimator when capture heterogeneity occurs (Otis et al. 1978). The Jackknife has been demonstrated to be the most robust population size estimator in small mammal studies and has also been suggested as the most appropriate estimator for estimate of community size (Hallet et al. 1991, Manning et al. 1995, Boulanger and Krebs 1996, Boulanger et al. 1998). The Jackknife estimator has been tested and compared with other estimators such as those developed by Chao (Chao 1987, Chao et al. 1992, Lee and Chao 1994), who concluded that the Jackknife estimator is the best estimator in situations with heterogeneity and adequate data. Finally, all estimators have more or less systematic biases. The Jackknife is known to underestimate population size, in particular when many individuals are captured only once, which can be due to low capture probability and sparse data, presence of transients, or capture heterogeneity (Chao 1988, 1989; Pradel et al. 1997; Julliard et al. 1999). However, the Jackknife estimator was shown to be the estimator with the most consistent biases when abundance varies. All other estimators show increasing negative biases with increasing population size (Boulanger and Krebs 1996).

Variance of the population size estimate (eq 9) is underestimated by a factor of 2 as compared with the actual variance of estimated population sizes. Further analyses suggested that this bias comes from not taking into account the covariance between the 2 probabilities X and Y , with

X = probability of being captured only once and Y = probability of being captured more than once. Because these 2 probabilities are clearly not independent, a term of covariance needs to be added to our formula. Unfortunately, we are unable to mathematically formalize this covariance. Despite some attempts to explicitly represent different groups (resident population captured only once, resident population captured more than once, and transient population) using multinomial functions, we could not obtain any unbiased equation for variance due to the lack of information on the transient population. Development of an unbiased estimator of the variance of population size estimates in the presence of transients thus remains a challenging task.

Because a_1 values in equation 8 are much larger than a_i values for $i > 1$, the Jackknife estimator is mostly sensitive to the relative number of individuals captured only once within a primary period and having an unknown status. Noticeably, this group of individuals depends on prior capture effort. The more capture sessions during a year, the smaller the unknown group because the chance of correctly assigning residents to the resident group increases. Indeed, a resident is defined as an individual captured more than once during a primary occasion. Similarly, individuals with unknown status are relatively more frequent in the first year of the study. Consequently, interpreting transient rates is more complicated if the number of capture sessions is variable. The same number of secondary periods in each primary session of the robust design reduces this problem. This is only true when an adequate interval between the secondary sampling periods is provided. The size of this interval should be based on knowledge of the species, with proper time lag durations to avoid misclassification yet keep the benefit of precision (Hines et al. 2003).

The method proposed by Hines et al. (2003) assumes that capture probabilities are equal for the 2 groups (residents and unknowns). However, birds may be present in the study site for various reasons, thus leading to heterogeneity of capture probabilities. Individuals with particularly high capture probabilities are likely to be classified as resident, and conversely, individuals with low probabilities will be classified as unknown. Thus, the hypothesis of equal capture probability between groups is unlikely. Imposing equal capture probabilities for resident and unknown groups can lead to bias in the estimate of transient rate, because this assumption causes an overestimate of capture probability for all the individuals in the population when heterogeneity is present. Survival estimates will be biased low and the transient probability will be biased high for the unknown group. We tested these predictions by allowing differences in capture probabilities among groups in model $[\phi_s, \tau_s, p_g]$. However, models with p_r and p_g did not differ ($\Delta AIC_c < 2$; Table 1) although estimated capture probabilities for residents were twice as high as the unknowns. We may have failed to detect differences in capture probabilities among groups because of small sample size or because of only a small difference. We recommend using transient rate estimates

from models accounting for group variation of capture probabilities to account for the bias due to transients.

MANAGEMENT IMPLICATIONS

Many field studies on managed animal populations use capture–recapture methodology to obtain crucial parameters of the focal population demography (Williams et al. 2002). Inferences from these studies are hindered by the presence of transient individuals. Our method to estimate abundance of local populations accounting for the presence of transients is, thus, useful. Although we have focused on estimates of bird population, our method can be applied to any organism monitored with a Robust Design in which transient individuals occur (e.g., newts, Perret et al. 2003; bats, Sendor and Simon 2003).

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APPENDIX: DIRECT ESTIMATE OF TRANSIENT RATE USING PROGRAM MARK

We considered a 4-year capture–mark–recapture study, using the Robust Design, which allowed classification of individuals into the unknown (*U*) or the resident (*R*) group. To estimate the transient rate and appropriate standard errors, we parameterized survival as follows (Parameter Index Matrix formatted for Program MARK):

U-group			R-group		
1	5	6	4	5	6
	2	6		5	6
		3			6

We then used the following design matrix:

Parameter no.	β_1	β_2	β_3	β_4	β_5	β_6
1	1	0	0	1	0	0
2	1	1	0	0	1	0
3	1	0	1	0	0	1
4	1	0	0	0	0	0
5	1	1	0	0	0	0
6	1	0	1	0	0	0

$\beta_1 = \text{Intercept}$

If a log link is used, the β_i ($i = 4, 5, 6$) are exactly equal to log-transformed resident rate ($1 - \tau$). The resident rate ($1 - \tau$) and its associated standard error can be directly calculated from the appropriate β as

$$(1 - \tau) = \exp(\beta)$$

$$SE(1 - \tau) = (1 - \tau)SE(\beta)$$

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