Biological Conservation 164 (2013) 123–128

Contents lists available at SciVerse ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Waterbird demography as indicator of wetland health: The French-wintering common snipe population

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ARTICLE INFO

Article history:
Received 26 November 2012
Received in revised form 15 April 2013
Accepted 21 April 2013

Keywords:
Capture–recapture
Common snipe
Sustainable harvest
Climate change
Leslie matrix
Drainage
Flyway approach to conservation
Multistate model

ABSTRACT

The population dynamics of waterbirds constitute an indicator of wetland conservation status. However, waterbird population censuses are difficult to implement because the individuals are very mobile within their range, and some species are elusive or breed in remote areas. Therefore, demographic models based on the estimation of survival and breeding success appear as a reliable alternative to population censuses. Here we present this model-based approach in the case of the French-wintering snipe population (*Gallinago gallinago*), which breeds mainly in Northern and Eastern Europe. Using a multi-state model to accommodate the mobile nature of waterbirds, we estimate snipe survival using a joint analysis of capture–recapture and ring-recovery data. Then, we use matrix population models to estimate the minimum recruitment rate required to maintain the population at its current size and derive a chart for using age-ratio of ringed birds as indicator of population trend. Although we call for more data collection in order to reduce uncertainty, we conclude that occasional declines are likely after years with poor breeding success, but that the French-wintering snipe population is on average stable. Individual-based monitoring data and population modeling make it possible to use waterbirds as indicator species at the flyway scale.

1. Introduction

Wetland degradation (drainage and pollution) is one of the first consequences of landscape anthropization (Baldock, 1984). Yet wetlands provide ecosystem services that are essential to our societies (denitrification, flood water retention, etc.; Gleason et al., 2008); thus wetland preservation represents a major conservation challenge (Ramsar-Convention-Secretariat, 2010). A distinctive suite of birds are specialized on wetlands and need them to breed, roost and feed. These birds can be used as indicator species for the conservation status of the wetlands that correspond to their species-specific habitat requirements. For example, the assemblage of species that use reedbeds depend on water levels and reed harvesting (Graveland, 1999; Barbraud et al., 2002; Polak et al., 2008); see also Davidson and Stroud (2006), DeLuca et al. (2008), Paillisson et al. (2002). Several historically abundant species are currently among the fastest declining species in the world (Amano et al., 2010; Greenberg et al., 2011), suggesting that wetland degradation can jeopardize even common species' survival. Here we focus on a particularly widespread European waterbird, Common snipe *Gallinago gallinago* (snipe hereafter). Snipes inhabit all types of freshwater marshes, migrate on a broad front, and are not restricted to coastal areas as are most other waders that winter in Europe. A large part of the northern and eastern European population winters in France, making the French-wintering population an indicator of wetland health along this flyway (Dodman and Boere, 2010). Recent trends from some breeding population surveys are currently raising concerns for this species (BirdLife-International, 2012). In addition, snipe is a gamebird with a French hunting bag reaching 250,000–300,000 birds annually (Tesson and Leray, 2000). This hunting bag has decreased recently, further suggesting population decline. A proper quantification of the European snipe population dynamics thereby appears necessary to inform the status of this indicator species. This quantification can also be used to aid decision-making about sustainable hunting.

Large-scale population censuses yet remain very challenging in snipes as in most other waders (Amano et al., 2010; Davidson and Stroud, 2006), because of the large breeding and wintering ranges that encompass remote areas, of the long-range migrations and of the short-term response to fluctuations in water levels. Snipes further challenge field biologists because of their elusive nature.

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0006-3207/$ - see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.biocon.2013.04.015

Therefore, process-based population models that separate the demographic processes of survival, fecundity, and movement constitute reliable alternatives to pattern-based models based on population censuses (Beissinger and Westphal, 1998). To document survival probability and harvest rates, a nation-wide ringing program has been set in place in recent years in France (starting during the 1999/2000 hunting season). Recaptures of live birds and recoveries of dead birds have been recorded, which provide information about the survival of snipes that winter in France. These data are typically analyzed using capture–recapture–recovery models (e.g., Gauthier and Lebreton, 2008). Snipe behavior, however, challenges typical assumptions of capture–recapture–recovery models. Although snipes do exhibit site-fidelity both within and across winters when the conditions allow (Davies, 1977; Spence, 1988), when the conditions are unfavorable (droughts, floods, and freezing conditions) they undertake within-winter movements that are similar to nomadism; they track water levels and avoid areas that become unsuitable. This is a behavior typical to most waterbirds, including ducks (Roshier et al., 2002), gulls (McNichols, 1975), and raptors (Martin et al., 2006). From a modeling standpoint, both recapture and recovery probabilities are influenced by this behavior: snipes that exit the area where they were ringed are unlikely to land in another ringing area, and will thus not be subject to recapture anymore. Snipe hunting is more evenly distributed across space, so that snipes that escape recapture by ringers may still be reported by hunters. To address that issue, we designed multistate capture recapture models (Lebreton et al., 2009) that allowed marked individuals to transit between a state "In ringing area" subject to recapture and a state "Out of ringing area" not subject to recapture. By doing so, we estimated survival while accounting for possible movements of individuals between these states. Hereafter we describe this model and its implementation. Then we use matrix population models to discuss the implication of our data and findings for the characterization of snipe population trend.

2. Materials and methods

2.1. Field procedures and data selection

Two methods of capture were used. Most snipes were caught with mist-nets at dawn or dusk in marshes or meadows. The remaining records were obtained during daytime with traps placed along the water line of ponds or in intensively used feeding sites. Age determination (hatch year bird or adult) was made after examination of wing and tail feathers (CICB and OMPO, 2002; Wlodarczyk et al., 2008). A total of 10,721 snipes were ringed between 1999 and 2011, of which 563 were recaptured later and 584 were recovered by hunters. From this extensive dataset we selected the records corresponding to birds ringed between November and February, i.e., we excluded birds most likely to still be migrating. We also excluded recaptures occurring outside of this period. We discarded records when the age at ringing was not recorded (c. 250 records) as well as records from the Mediterranean region (c. 200 records) because many of these birds came from a more southerly flyway (breeding areas in central Europe). This selection yielded a final dataset containing records from 4029 snipes (1420 ringed as adults, 2609 ringed as hatch-year birds). Of these, 113 were recovered by hunters and 150 were recaptured at least once during a hunting season different from the season during which they were ringed. The maximum number of encounters per individual was 3. Annual survival probability was estimated from November 1st to October 31st the following year. The 12 month period starting on November 1st following the birth of an individual is hereafter termed its "Hatch year".

2.2. Goodness of fit tests

We tested the goodness of fit of the Cormack–Jolly–Seber model (Lebreton et al., 1992) to the recapture data only (not the recovery data). We used the "overall test" in software U-CARE (Choquet et al., 2009a) for that purpose. This test can be divided into components (Pradel et al., 2005). Among these components, the test for short-term transience (component 3.SR testing for a difference in encounter probability between previously captured and newly-marked snipes) and the test for short-term trap-dependence (component 2.CT testing for a difference in the probability to be encountered in hunting season $t+1$ between the snipes captured during season t and those not captured that season), when they are both significant, suggest individual or spatial heterogeneity in recapture probability (Péron et al., 2010). Such heterogeneity would for example be expected if ringed snipes were a mixture of migrants and resident wintering birds.

2.3. Multistate capture–recapture–recovery model: general structure

Based on our understanding of snipe movement behavior, we considered two "live" states, namely state 1 "alive and in a ringing area" and state 2 "alive and out of ringing areas". As typically done when combining recapture and recovery data (Gauthier and Lebreton, 2008; Hénaux et al., 2007), these two states were complemented by two "Just dead" states, which represented individuals available for recovery, and a state "Long dead", which represented individuals dead for more than 1 year. The diagram representation of this model is presented in Online Appendix. Each year, birds in state 1 had the probability $1-f_1$ to move to state 2, where f_1 is called state-fidelity; and birds in state 2 had the probability $1-f_2$ to return to state 1. At first capture, all birds were in state 1. Survival probability was denoted S. In matrix notation, this model is represented by the survival-transition matrix Φ of which the (i,j)th cell represents the probability to be in state j at time $t+1$ if in state i at time t:

$$\Phi = \begin{bmatrix} Sf_1 & S(1-f_1) & 1-S & 0 & 0 \\ S(1-f_2) & Sf_2 & 0 & 1-S & 0 \\ 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix} \tag{1}$$

The model is then fully specified by describing the observation process (Online Appendix). The observation matrix P can also be used for this purpose. It has in its (i,j)th cell the probability to record event j if in state i. Possible events are $j=1$ for "individual not recorded", $j=2$ for "individual captured and alive", and $j=3$ for "individual shot and reported as such":

$$P = \begin{bmatrix} 1-p & p & 0 \\ 1 & 0 & 0 \\ 1-r_1 & 0 & r_1 \\ 1-r_2 & 0 & r_2 \\ 1 & 0 & 0 \end{bmatrix} \tag{2}$$

where p and r denote recapture and (state-dependent) recovery probabilities respectively.

An additional complexity had to be accommodated: ringing occurred throughout a protracted period in winter, and was simultaneous with hunting. Thus, an individual ringed early in the season was exposed to mortality risks for a longer period than an individual ringed late in season. To accommodate that feature we used a monthly formulation of capture–recovery models (Péron et al., 2012a). We denoted $\tilde{s}_w$ the monthly winter survival. For an individual ringed in November, the probability to survive up to the end of

Table 1
Model selection for the effects of geographic zone (coastal vs. interior), year, and age (first year vs. adult) on model parameters. Model #1 is the most complex "umbrella" model. Phrases indicated in bold indicate selected model simplifications (e.g., Age+Year when in bold indicates that the Zone effect is dropped from the preferred model). np is the number of parameters in the model, AIC is the Akaike information criterion. Because the data was deemed too sparse to support a model selection including all the typically included combinations of effects (Lebreton et al., 1992), we devised a step-wise approach. For each step, there was a starting model that depended on the previous steps. We computed the difference in AIC between this starting model and other models in the subset considered at this step. This difference is denoted ΔAIC$^{(s)}$ for step #s. We also computed the overall difference in AIC compared to the overall preferred model (Model 19). This difference is denoted ΔAIC without superscript. Structures that were selected at each step are underlined.

Model#	Winter survival	Summer survival	Fidelity	Recapture	Recovery					
1. Selection for the effect of zone (comparison point: Model 1)						np	Deviance	AIC	ΔAIC$^{(1)}$	ΔAIC
1	Age+Zone+Year	Age+Year	Age+Zone+Year	Age+Zone+Year	Fidelity+Age+Zone+Year	81	2777.00	2939.00	0	24.08
2	Age+Year	Age+Year	Age+Zone+Year	Age+Zone+Year	Fidelity+Age+Zone + Year	80	2799.92	2959.92	20.92	45.00
3	Age+Zone+Year	Age+Year	Age+Year	Age+Zone+Year	Fidelity+Age+Zone+Year	79	2779.83	2937.83	−1.16	22.92
4	Age+Zone+Year	Age+Year	Age+Zone+Year	Age+Year	Fidelity+Age+Zone+Year	80	2777.01	2937.01	−1.99	22.09
5	Age+Zone+Year	Age+Year	Age+Zone+Year	Age+Zone+Year	Fidelity+Age+Year	80	2787.65	2947.65	8.66	32.74
2. Selection for the effect of year (comparison point: Model 4)						np	Deviance	AIC	ΔAIC$^{(2)}$	ΔAIC
4	Age+Zone+Year	Age+Year	Age+Zone+Year	Age+Year	Fidelity+Age+Zone+Year	80	2777.01	2937.01	0	22.09
6	Age+Zone	Age+Year	Age+Zone+Year	Age+Year	Fidelity+Age+Zone+Year	67	2796.17	2930.17	−6.84	15.25
7	Age+Zone+Year	Age	Age+Zone + Year	Age+Year	Fidelity+Age+Zone+Year	68	2796.80	2932.80	−4.21	17.88
8	Age+Zone+Year	Age+Year	Age+Zone	Age+Year	Fidelity+Age+Zone+Year	67	2800.57	2934.57	−2.44	19.66
9	Age+Zone+Year	Age+Year	Age+Zone+Year	Age	Fidelity+Age+Zone+Year	67	2806.02	2940.02	3.01	25.10
10	Age+Zone+Year	Age+Year	Age+Zone+Year	Age+Year	Fidelity+Age+Zone	67	2812.35	2946.35	9.34	31.43
11	Age+Zone	Age	Age+Zone	Age+Year	Fidelity+Age+Zone+Year	42	2839.20	2923.20	−13.81	8.28
3. Selection for the effect of age (comparison point: Model 11)						np	Deviance	AIC	ΔAIC$^{(3)}$	ΔAIC
11	Age+Zone	Age	Age+Zone	Age+Year	Fidelity+Age+Zone+Year	42	2839.20	2923.20	0	8.28
12	Zone	Age	Age+Zone	Age+Year	Fidelity+Age+Zone+Year	41	2839.28	2921.28	−1.91	6.37
13	Age+Zone	.	Age+Zone	Age+Year	Fidelity+Age+Zone+Year	41	2839.52	2921.52	−1.68	6.60
14	Age+Zone	Age	Zone	Age+Year	Fidelity+Age+Zone+Year	41	2842.19	2924.19	0.99	9.27
15	Age+Zone	Age	Age+Zone	Year	Fidelity+Age+Zone+Year	41	2840.04	2922.04	−1.16	7.12
16	Age+Zone	Age	Age+Zone	Age+Year	Fidelity+Zone+Year	41	2839.29	2921.29	−1.91	6.37
17	Zone	.	Age+Zone	Year	Fidelity+Zone+Year	38	2839.90	2915.90	−7.29	0.99
4. Selection for the effect of fidelity (comparison point: Model 17)						np	Deviance	AIC	ΔAIC$^{(4)}$	ΔAIC
17	Zone	.	Age+Zone	Year	Fidelity+Zone+Year	38	2839.90	2915.90	0	0.99
18	Zone	.	Age+Zone	Year	Zone+Year	37	2847.19	2921.19	5.29	6.28
19	Fidelity+Zone	.	Age+Zone	Year	Fidelity+Zone+Year	39	2836.92	2914.92	−0.99	0
5. Selection for linear trend in time effect (comparison point: Model 17)						np	Deviance	AIC	ΔAIC$^{(5)}$	ΔAIC
17	Zone	.	Age+Zone	Year	Fidelity+Zone+Year	38	2839.90	2915.90	0	0.99
20	Zone	.	Age+Zone	LYear	Fidelity+Zone+LYear	14	2934.96	2962.96	47.06	48.05

winter (February 29) was then $\tilde{s}_w^4$, while an individual ringed in February was assigned a first winter survival probability of $\tilde{s}_w$. Then we introduced the probability to survive from the end of February to the beginning of November, denoted s_s and called "summer survival" hereafter for practicality (although the period spanned from late winter to early autumn). Individuals dying in "summer" were not subject to recovery. In brief, annual survival probability was $S = \tilde{s}_w^4 \cdot s_s$.

2.4. Biological hypotheses and model selection

In waders and other gamebirds, survival often varies with age. Hatch year birds exhibit lower survival and higher vulnerability to hunting than adults (Sandercock, 2003). Between-year variation is also commonplace, reflecting in particular the effect of weather on survival (Péron et al., 2011; Sandercock, 2003). Lastly, we investigated a potential difference between the interior and coastal zones (see map in Online Appendix). The winter is milder on the coast than in the interior, potentially allowing better survival, but on the other hand hunting pressure is believed to be higher on the coast (as suggested by spatial variation in hunting bags and in hunting practices; Tesson and Leray, 2000). For each of the six sets of model parameters (survival in winter, survival in summer, state-fidelity, recapture probability, recovery probability), we thereby considered the following effects: full time variation (one parameter per year); age effect (hatch year vs. adults); coarse geographic variation (coastal zone vs. interior zone). Out of the large number of possible combinations of these effects, we selected a set of 17 models representing a sequential selection for the effects of zone, then year, and age (Table 1). Our approach was to start from the most complex model and then simplify it by comparing its Akaike Information Criterion (AIC) with that of simpler models in a stepwise fashion (see the caption of Table 1 for further details). We used the usual difference of two AIC points to choose between models (Burnham and Anderson, 2002). Once a preferred model was obtained, we considered variation around this model, namely, we tentatively replaced the full year effects acting on recapture, recovery or survival probabilities by logit-linear trends (representing a gradual increase or decrease in parameter value with time). A linear trend is expected both because of the sampling design (increasingly numerous locations were included and the effort was initially focused around a few high-hunting pressure locations) and because of ongoing changes in the wintering habitat of snipes. We also tried removing the state-specificity in recovery probability, representing a homogenous hunting pressure across areas with and without ringing effort; as well as adding state-specificity in survival probability, representing a heterogeneous survival probability across areas with and without ringing effort. Lastly we investigated whether our multistate approach was indeed supported by the data by merging the two states "in ringing area" and "out of ringing area" and comparing the AIC.

Model building and fitting was performed using E-SURGE (Choquet et al., 2009b).

2.5. Matrix modeling, recruitment rate and population trend

Most snipes breed in their first year of life. To describe snipe population dynamics we thus needed two age classes only: “first-year birds” and “adults”. Accordingly we built a two age-class, pre-breeding-census matrix model (Caswell, 2000; chapter 2). In this model, population stability (population growth rate of one) occurs if and only if the number of 1-year old recruits perfectly compensates the deaths of breeding adults. This translates into:

$$R_{MIN} = 1 - S \tag{3}$$

where R is the recruitment rate (number of female offspring that reach 1 year of age, per breeding female) and S is the annual adult survival rate estimated from our data.

The best information available about recruitment rate in the French-wintering snipe population is probably the age ratio among captured birds. This metric is however affected by the fact that migration phenology differs between hatch year and later years. We considered the range 30–70% as plausible for the November 1st value of the percentage of hatch-year birds (age-ratio). Our unpublished data indicate 60% as the most plausible value, with lower values believed to correspond to unsuccessful breeding seasons. Furthermore age-ratio in autumn needs to be corrected for uneven sex-ratio (the wintering population is female-biased; unpublished data). We considered that recruitment occurred on May 1st. Summer survival probability in Eq. (4) was thus raised to the power corresponding to the number of months of exposure. Dividing the number of female offspring that recruited (left pair of brackets) by the number of females that produced those recruits (right pair of brackets), recruitment rate was then computed as:

$$R(AR) = [AR \cdot (1 - SR_{HY}) \cdot \tilde{s}_w^4 \cdot \tilde{s}_s^{2/8}]\left[\frac{(1 - AR) \cdot (1 - SR_{AD})}{\tilde{s}_s^{6/8}}\right]^{-1} \tag{4}$$

where AR is the proportion of hatch year birds in the November population, SR_{HY} is the proportion of males among hatch year birds (taken to be 0.45; unpublished data), SR_{AD} is the proportion of males among adults birds (taken to be 0.32; unpublished data), and $\tilde{s}_s$ and $\tilde{s}_w$ are as estimated from our data. Sampling uncertainty linked to the relative sparseness of the data was accounted for in a parametric bootstrap (Davison and Hinkley, 1997) producing a confidence interval for $R(AR)$. The bootstrap was performed within the variation for survival estimates, but sex-ratios were treated as fixed values.

3. Results

3.1. Goodness of fit tests

The global goodness-of-fit test was non-significant ($\chi^2_{29} = 28.79$, $P = 0.48$, $\tilde{c} = 0.99$), suggesting that the recapture process was unlikely to be subject to major individual or spatial heterogeneity. However, the component corresponding to short-term trap dependence was very significant and in the direction of trap shyness. Since our multistate model was aimed at accommodating movements in and out of the ringing areas (which possibly explained the trap shyness), and since the overall test was not significant, we did not correct for over-dispersion in the model selection procedure.

3.2. Model selection

Results of the model selection are presented in Table 1. The effect of geographic zone was retained in winter survival and state-fidelity but not in recapture probability (first section in Table 1). The effect of year was discarded in survival and state-fidelity probabilities but retained in recapture and recovery probability (second section in Table 1). Age-effects were discarded in all parameters except state-fidelity, (third section in Table 1). Removing state-specificity in recovery probability decreased the support from the data (Model 18 vs. Model 17), and adding state-specificity in survival slightly increased it (Model 19 vs. Model 17: difference in AIC less than two points, indicating incertitude about the presence of state-specificity in survival). Replacing year-effects by linear trends decreased the support (Model 20 vs. 17). The preferred model at the end of the model selection procedure had the effect of geographic zone on winter survival and site-fidelity, the effect of age on site-fidelity, the effect of year on recovery and recapture, and the effect of state (within/outside ringing sites) on survival and recovery probabilities.

3.3. Parameter estimates from the preferred model

Annual survival estimates were 0.52 in the coastal zone and 0.44 in the interior. This probability could be decomposed into the “summer” survival probability of 0.63 (95% confidence interval: [0.45, 0.78]) for an 8 month period, and the winter survival probability. In state 1 monthly winter survival probability was 0.95 (95% CI [0.87, 0.98]) and 0.92 (95% CI [0.79, 0.97]) for the coastal and interior zones respectively. In state 2 monthly winter survival probability was estimated at a very low 0.20 and 0.12 in the coastal and interior zones respectively, albeit with large 95% CI ([0.005, 0.91] and [0.003, 0.86]), which overlapped with the confidence intervals for the estimates in state 1. As per our model selection, hatch year birds survived as well as adults birds.

Recapture probability was 0.03 on average over years (estimated range [0, 0.05]). Recovery probability in state 1 was 0.060 on average over years (estimated range [0.002, 0.11]). Recovery probability in state 2 was higher than in state 1 although large uncertainty remained: average estimate over years 0.69, estimated range [0.18, 0.96]. Point estimate of fidelity to state 1 was lower in hatch year than adult birds, especially on the coast, although large uncertainty remained (estimate for hatch year: 0.84 with 95% CI [0.29, 0.98]; estimate for adults 0.92 with 95% CI [0.44, 0.99]). Fidelity to state 2 was estimated at 100% for all zones and age-classes (boundary estimate indicating that snipes that transitioned to state 2 never returned to state 1). Overall, the model was thus akin to a mixture of a state with low hunting pressure (state 1) and a state with high hunting pressure (state 2).

3.4. Non-preferred model without the multistate structure

The model without distinction between a state “in ringing location” and a state “out of ringing location” is not in Table 1 but had 9.5 AIC points more than the preferred model. The multistate structure was thereby supported by the data. The survival estimates were however relatively robust to the choice of model in the present study. Point estimates for annual survival probabilities from the non-preferred model without the multistate structure were 0.49 and 0.45 in the coastal and interior zones respectively (vs. 0.52 and 0.44 in the preferred model).

3.5. Matrix modeling and computation of recruitment rate

The minimum number of offspring required for population stability was $R_{MIN} = 0.48$ recruited female per breeding female on the

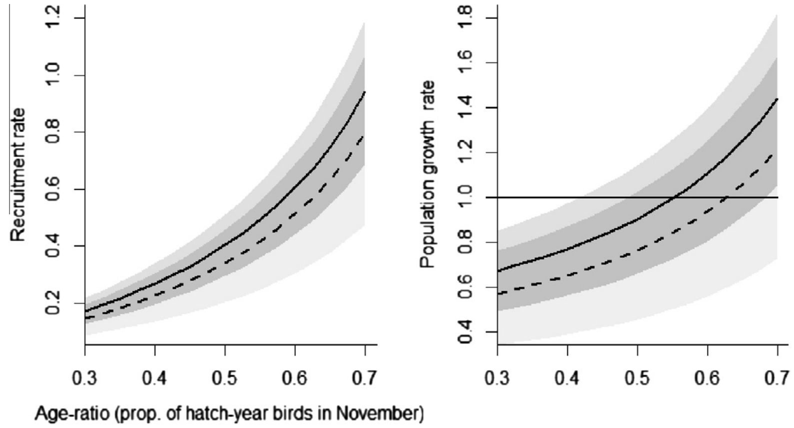

Fig. 1. (a) Recruitment rate (female offspring that reach 1 year of age per breeding female) and (b) Population growth rate, estimated for varying values of November age ratio (proportion of hatch year birds in the November population). Plain lines: coastal zone; Dashed lines: interior zone. Gray areas: 95% confidence intervals from a parametric bootstrap within the estimated sampling (co)variation in survival probabilities; the darkest area represents overlaps in the confidence intervals.

coast and $R_{MIN} = 0.56$ in the interior. The actual recruitment rate computed from Eq. (4) varied from a pessimistic 0.18 if the proportion of hatch-year birds in November was 0.30 to an optimistic 0.97 if that proportion was 0.70 (Fig. 1a). Proportions of hatch-year birds below 0.54 on the coast and 0.61 in the interior were associated with population decline, although large uncertainties remained (Fig. 1b).

4. Discussion

In an elusive and mobile species of wader, we used ring recoveries and recapture data to build a population model and make inference about population trend. We argue that in other species with similar characteristics (most migratory gamebirds) this approach is more effective than census data, because the latter are rendered unreliable when birds unpredictably move out of survey areas or escape detection. Here, for the French wintering snipe population, we provide an updated estimate of yearly survival and use age-ratio data to infer that the population is stable, although we call for more data collection to reduce uncertainty.

4.1. Survival estimation and data collection

The spatial scale of our study is much larger than the scope of earlier works on snipe demography (national ring-recovery scheme vs. localized capture–recapture program, e.g., Spence, 1988). This constitutes an improvement compared to previous estimations of snipe and other wader survival. Nevertheless, with increasing spatial scope also came new issues. In particular the existence of a huge matrix surrounding ringing locations, where snipe could still be reported by hunters but had no chance to be recaptured, called for a multistate type of model. But even then, snipes may some time after their first capture choose to winter in locations with altogether no hunting and no ringing, or with no reporting of rings. French-ringed snipes are for example very rarely reported from south of the Pyrenees. This can induce a downward bias in survival because permanent emigration to completely unmonitored areas is confounded with death even when using a multistate model (the issue of "apparent survival" which is described in full by Burnham, 1993). Second, ringing effort was concentrated around a few areas. In particular the locality of Braud-et-Saint-Louis contributed >17% of ringing records while the other 347 localities contributed an average 0.25% each. In other words, the individuals included in this analysis might not be representative of the whole French-wintering population. To confirm or infirm this, (1) efforts should be made towards documenting the probability that French-banded snipes shot in another country are reported; and (2) ringing and recapture effort in France should be extended to areas known *not* to host a significant number of hunters (e.g., large protected areas). The solution towards which our multistate model converged was indeed a situation with one state with low recovery probability (state 1), and one state with low survival and high recovery probability (state 2). The existence of locations with strong hunting pressure and of others with low reporting rate might explain this result; under this explanatory hypothesis, state-fidelity parameters would capture spatial heterogeneity in recovery rate rather than movement probabilities.

4.2. Population trend

Our point estimates indicate that population declines may occasionally occur after a year of poor breeding success, but that on average the population is stable (Fig. 1: for a proportion of 0.60 hatch-year birds in November as commonly observed, the point estimate of the growth rate is above 1). We note however that much more data will be necessary to confirm these conclusions with tighter confidence intervals, and that our matrix population models did not include age-specificity in breeding success. First-year breeders were assumed to experience the same breeding success as adults, although in many species they are less successful. Thus, Eq. (3) gives an optimistic estimation of R_{MIN}. In any case, threats such as wetland drainage, scrub encroachment, urbanization, and other habitat modification may not be as strong in the breeding range of the French-wintering population as they are in other parts of the range (Baines, 1988; Grishanov, 2006). Population resilience may also come from compensatory density-dependence and the natural response of breeding females to temporal variability in wetland habitat quality (Péron et al., 2012b).

4.3. Recommendations

Based on our data and analysis, ringing data (recoveries and recaptures) constitute a relevant alternative to census data, which can prove unreliable in waterbirds. The obvious drawbacks of the approach are the field effort which increases dramatically compared to a census-based study, and the relative complexity of the statistical analysis. In terms of monitoring, the examination of our own data leads us to recommend some form of stratified sampling in which areas with different land use and land ownership are all represented. The current approach of mostly working near hunting locations can lead to datasets biased towards low survival probabilities. We recommend concentrating the ringing effort on the wintering period to avoid ringing many transients that bring less demographic information. Using a hunting pressure index as a predictor of survival probability is an option which has been attempted in woodcocks (Péron et al., 2012a) but there are multiple challenges: hunting bags are not valid proxies because the population sizes from which they are harvested are generally unknown; and indexes based on ringing data are by construction correlated to the recovery and survival estimates (Péron et al., 2012a). Lastly, complexifying the model (adding the multistate structure) was warranted because of the expected spatial heterogeneity in recapture probability: there was a large matrix surrounding ringing areas where snipes could escape recapture effort while still being subjected to hunting. Even if we later found that neglecting this aspect had little impact on survival estimates in the present analysis, we note that this was largely due to the sparseness of the dataset which led to imprecise point estimates. It has been shown elsewhere that neglecting the multistate structure of a dataset can lead to biased survival estimates (Lebreton and Pradel, 2002). In conclusion, we recommend mark-recapture–recovery data, multistate analyses, and matrix population models for the study of the conservation status of waders and other animal species that can serve as indicator species, but for which reliable censuses are difficult to implement.

Acknowledgements

We thank all the ringers of the ONCFS/FNC/FDC snipe network and the hunters who returned their rings. Three anonymous reviewers provided helpful comments.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.04.015.

References

Amano, T., Szekely, T., Koyama, K., Amano, H., Sutherland, W.J., 2010. A framework for monitoring the status of populations: an example from wader populations in the East Asian–Australasian flyway. Biol. Conserv. 143, 2238–2247.

Baines, D., 1988. The effects of improvement of upland, marginal grasslands on the distribution and density of breeding wading birds (Charadriiformes) in Northern England. Biol. Conserv. 45, 221–236.

Baldock, D., 1984. Wetland drainage in Europe: the effects of agricultural policy in four EEC countries. Institute for European Environmental Policy; International Institute for Environment and Development, London.

Barbraud, C., Lepley, M., Mathevet, R., Mauchamp, A., 2002. Reedbed selection and colony size of breeding Purple Herons Ardea purpurea in southern France. Ibis 144, 227–235.

Beissinger, S.R., Westphal, M.I., 1998. On the use of demographic models of population viability in endangered species management. J. Wildl. Manage. 62, 821–841.

BirdLife-International, 2012. Species Factsheet: *Gallinago gallinago*. <http://www.birdlife.org> (22/08/2012).

Burnham, K.P., 1993. A theory for combined analysis of ring recovery and recapture data. In: Lebreton, J.D., North, P.H. (Eds.), Marked Individuals in the Study of Bird Population. Birkhäuser Verlag, Basel, Switzerland, pp. 199–213.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information–Theoretic Approach, second ed. Springer-Verlag, New York.

Caswell, H., 2000. Matrix Population Models: Construction, Analysis and Interpretation, second ed. Sunderland, Massachusetts.

Choquet, R., Lebreton, J.D., Gimenez, O., Reboulet, A.M., Pradel, R., 2009a. U-CARE: utilities for performing goodness of fit tests and manipulating CApture–REcapture data. Ecography 32, 1071–1074.

Choquet, R., Rouan, L., Pradel, R., 2009b. Program E-SURGE: a software application for fitting multievent models. In: Thomson, D.L., Cooch, E.G., Conroy, M.J. (Eds.), Modeling Demographic Processes in Marked Populations. Springer, New York, pp. 845–865.

CICB-&-OMPO, 2002. Key to Ageing and Sexing of the Common Snipe *Gallinago gallinago* by the Study of Feathers. CIC & OMPO, Paris.

Davidson, N.C., Stroud, D.A., 2006. African–Western Eurasia flyways: current knowledge, population status and future challenges. In: Boere, G.C., Galbraith, C.A., Stroud, D.A. (Eds.), Waterbirds Around the World. The Stationery Office, Edingburgh, UK, pp. 63–73..

Davies, M., 1977. Wintering snipe in middlesex. Ringing Migr. 1, 173–177.

Davison, A.C., Hinkley, D.V., 1997. Bootstrap Methods and their Applications. Cambridge University Press, Cambridge.

DeLuca, W.V., Studds, C.E., King, R.S., Marra, P.P., 2008. Coastal urbanization and the integrity of estuarine waterbird communities: threshold responses and the importance of scale. Biol. Conserv. 141, 2669–2678.

Dodman, T., Boere, G.C., 2010. The Flyway Approach to the Conservation and Wise use of Waterbirds and Wetlands: A Training Kit. Wings Over Wetlands Project, Wetlands International and BirdLife International, Ede, The Netherlands.

Gauthier, G., Lebreton, J.D., 2008. Analysis of ring-recovery data in a multistate capture–recapture framework. Can. J. Statist. – Revue Canadienne De Statistique 36, 59–73.

Gleason, R.A., Laubhan, M.K., Euliss Jr., N.H., 2008. Ecosystem services derived from wetland conservation practices in the United States Prairie Pothole Region with an emphasis on the U.S. Department of Agriculture Conservation Reserve and Wetlands Reserve Programs. U.S. Geological Professional Paper 1745.

Graveland, J., 1999. Effects of reed cutting on density and breeding success of Reed Warbler Acrocephalus scirpacaeus and Sedge Warbler A-schoenobaenus. J. Avian Biol. 30, 469–482.

Greenberg, R., Demarest, D.W., Matsuoka, S.M., Mettke-Hofmann, C., Evers, D., Hamel, P.B., Luscier, J., Powell, L.L., Shaw, D., Avery, M.L., Hobson, K.A., Blancher, P.J., Niven, D.K., 2011. Understanding declines in Rusty Blackbirds. In: Wells, P.V. (Ed.), Boreal Birds of North America: A Hemispheric View of their Conservation Links and Significance. Studies in Avian Biology, vol. 41, University of California Press, Berkeley, CA, pp. 107–126.

Grishanov, D., 2006. Conservation problems of migratory waterfowl and shorebirds and their habitats in the Kaliningrad region of Russia. In: Boere, G.C., Stroud, D.A. (Eds.), Waterbirds Around the World. The Stationery Office, Edingburgh, UK, pp. 63–73.

Hénaux, V., Bregnballe, T., Lebreton, J.D., 2007. Dispersal and recruitment during population growth in a colonial bird, the great cormorant *Phalacrocorax carbo sinensis*. J. Avian Biol. 38, 44–57.

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

Lebreton, J.D., Nichols, J.D., Barker, R.J., Pradel, R., Spendelow, J.A., Caswell, H., 2009. Modeling individual animal histories with multistate capture–recapture models. In: Caswell, H. (Ed.), Advances in Ecological Research, vol. 41. Academic Press, London, pp. 87–173.

Lebreton, J.D., Pradel, R., 2002. Multistate recapture models: modelling incomplete individual histories. J. Appl. Statist. 29, 353–369.

Martin, J., Nichols, J.D., Kitchens, W.M., Hines, J.E., 2006. Multiscale patterns of movement in fragmented landscapes and consequences on demography of the snail kite in Florida. J. Anim. Ecol. 75, 527–539.

McNichols, M.K., 1975. Larid site tenacity and group adherence in relation to habitat. Auk 92, 98–104.

Paillisson, J.M., Reeber, S., Marion, L., 2002. Bird assemblages as bio-indicators of water regime management and hunting disturbance in natural wet grasslands. Biol. Conserv. 106, 115–127.

Péron, G., Crochet, P.-A., Choquet, R., Pradel, R., Lebreton, J.-D., Gimenez, O., 2010. Capture–recapture models with heterogeneity to study survival senescence in the wild. Oikos 119, 524–532.

Péron, G., Ferrand, Y., Choquet, R., Pradel, R., Gossmann, F., Bastat, C., Guénézan, M., Bauthian, I., Julliard, R., Gimenez, O., 2012a. Spatial heterogeneity in mortality and its impact on the population dynamics of Eurasian woodcocks. Popul. Ecol. 54, 305–312.

Péron, G., Ferrand, Y., Gossmann, F., Bastat, C., Guénézan, M., Gimenez, O., 2011. Escape migration decisions in Eurasian Woodcocks: insights from survival analyses using large-scale recovery data. Behav. Ecol. Sociobiol. 65, 1949–1955.

Péron, G., Nicolai, C.A., Koons, D.N., 2012b. Demographic response to perturbations: the role of compensatory density dependence in a North American duck under variable harvest regulations and changing habitat. J. Anim. Ecol. 81, 960–969.

Polak, M., Kasprzykowski, Z., Kucharczyk, M., 2008. Micro-habitat nest preferences of the great bittern, Botaurus stellaris, on fishponds in central-eastern Poland. Ann. Zool. Fenn. 45, 102–108.

Pradel, R., Gimenez, O., Lebreton, J.D., 2005. Principles and interests of GOF tests for multistate capture–recapture models. Animal Biodiv. Conserv. 28, 189–204.

Ramsar-Convention-Secretariat, 2010. Ramsar Handbooks for the Wise use of Wetlands, fourth ed. Gland, Switzerland.

Roshier, D.A., Robertson, A.I., Kingsford, R.T., 2002. Responses of waterbirds to flooding in an arid region of Australia and implications for conservation. Biol. Conserv. 106, 399–411.

Sandercock, B.K., 2003. Estimation of survival rates for wader populations: a review of mark-recapture methods. Wader Study Group Bull. 100, 163–174.

Spence, I.M., 1988. Mortality of Snipe estimated from a mark and recapture study. Ringing Migr. 9, 27–31.

Tesson, J.-L., Leray, G., 2000. Enquête nationale sur les tableaux de chasse à tir saison 1998–1999. La bécassine des marais et la la bécassine sourde. Faune Sauvage, Cahiers techniques vol. 251, pp. 160–167 (in French).

Wlodarczyk, R., Kaczmarek, K., Minias, P., Janiszewsky, T., 2008. Ageing and sexing of the Common Snipe *Gallinago gallinago gallinago*. Wader Study Group Bull. 115, 45–49.