Available online at www.sciencedirect.com
SCIENCE DIRECT®
Biological Conservation 122 (2005) 89–97
BIOLOGICAL CONSERVATION
www.elsevier.com/locate/biocon

Factors affecting population dynamics of Eurasian woodcocks wintering in France: assessing the efficiency of a hunting-free reserve

Olivier Duriez [a,b,*], Cyril Eraud [a,c], Christophe Barbraud [d], Yves Ferrand [e]

[a] *Office National de la Chasse et de la Faune Sauvage, CNERA Avifaune Migratrice, Station de Chizé, 79360 Villiers-en-Bois, France*
[b] *Laboratoire d'Ecologie, UMR 7625, bâtiment A, 7éme étage, case 237, 7 quai St. Bernard, Université Paris 6, 75005 Paris, France*
[c] *Equipe Ecologie Evolutive, UMR-CNRS 5561 Bio Géo Sciences, Université de Bourgogne, 6, Bd Gabriel, 21000 Dijon, France*
[d] *CNRS – Centre d'Etudes Biologiques de Chizé, 79360 Beauvoir-sur-Niort, France*
[e] *Office National de la Chasse et de la Faune Sauvage, CNERA Avifaune Migratrice, 5 rue de St. Thibaut, BP 20 St. Benoist, 78612 Le-Perray-en-Yvelines cedex, France*

Received 20 April 2004; received in revised form 30 June 2004; accepted 13 July 2004

Abstract

The Eurasian woodcock *Scolopax rusticola* is a migratory bird of major importance for hunting, which is susceptible to habitat loss and the stochastic effects of severe winter weather. Conservation issues mostly concerned regulation of hunting, but the efficiency of hunting-free reserves has never been investigated. We studied causes of mortality and survival probabilities of 98 radio-tagged woodcocks in a reserve with no hunting and in an adjoining hunting area in Brittany (France). Predation, mostly by mammalian predators on fields at night, was similar among adults and yearlings, while hunting mortality was more important in yearlings. Overall winter survival probabilities were 0.86 ± SE 0.07 in adults and 0.63 ± SE 0.07 in yearlings. Survival probabilities of both age classes increased as birds spent more time in the reserve. Equality of predation in both reserve and hunting areas suggests an additive mortality due to hunting over the winter. Population matrix models predicted that such low survival probabilities cannot sustain long term viable populations. These results call for caution in the harvesting of woodcock populations wintering in western France and could be a forewarning of a decline. The regulation of hunting by setting bag limits or reducing the length of shooting seasons, or the creation of reserves might be appropriate tools for the sustainable management of woodcock populations.

Keywords: Eurasian woodcock; *Scolopax rusticola*; Game species; Survival; Hunting effect; Predation; Population matrix model

1. Introduction

Sustainable use of biodiversity is a key element of recent environmental laws such as the EC Birds Directive in 1979 or the Rio Convention in 1992. Hunting, as a recreational practice, can have various effects on bird populations, leading in some case to annihilation (Newton, 1998). Although the impact of hunting disturbance on birds, especially waterbirds, has received much attention (Evans and Day, 2002; Gill and Sutherland, 2000; Madsen, 1998a,b; Tamisier et al., 2003), to our knowledge, assessing the efficiency of hunting-free reserves on survival of migratory birds has rarely been investigated. In game species, protected areas are designed to preserve some individuals for future reproduction and to ensure viability of populations. However, reserves are often created according to political criteria (land property,

* Corresponding author. Tel.: +33 5 65 60 77 40; fax: +33 5 49 09 68 80.
E-mail addresses: o.duriez@wanadoo.fr, chize@oncfs.gouv.fr (O. Duriez).

0006-3207/$ - see front matter © 2004 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2004.07.002

ideology, tourism) in addition to, and sometimes instead of, biological interests. Indeed, protected areas are also often surrounded by areas of intense human activities, including hunting, because animals are more abundant. In this context, to ensure that management both optimises wildlife preservation and recreational opportunities, measures are needed to minimise impacts of hunting on reserves. It is therefore necessary to assess the efficiency of the reserve structure to achieve its goals (maintaining a sufficiently high number of individuals until the end of the hunting season) and to establish sustainable management plans. Optimal reserves must take into account the behaviour of the target species, especially in case of highly mobile species such as birds. For example, in ducks, individuals often roost in the protected areas (mainly large lakes) during the day, but disperse at night in the surrounding hunting area (small ponds) to forage (Tamisier and Tamisier, 1981). In this case, an optimally managed reserve would also offer protected nocturnal foraging habitats (Fox and Madsen, 1997). One mean of testing the efficiency of reserve is to compare survival probabilities in both protected and hunted areas, controlling for potentially confounding factors.

Eurasian woodcocks *Scolopax rusticola* are solitary migratory waders with a wide breeding range over the Eurasian continent, but with populations concentrated along the Atlantic and Mediterranean coasts in winter (Cramp and Simmons, 1983). The woodcock is an important quarry species and is hunted in the majority of European countries (estimated annual bag between 3 and 4 million birds in Europe; Ferrand and Gossmann, 2001). French hunters kill between 30% and 40% of the total bag in Europe (shooting about 1,200,000 woodcocks every winter), and the interest for woodcock hunting has recently increased because of the scarcity of other wild small game species such as partridges and rabbits (Ferrand and Gossmann, 2000). In addition to hunting, woodcock populations are threatened by the loss of their wintering habitats (decrease of the surface areas of permanent meadows and hedges, increase of less suitable coniferous forests; Pain and Pienkowski, 1997). However, the size of the woodcock population and its trend remain poorly known in Europe, except in France where the breeding and wintering population appear rather stable in the last 15 years (Ferrand and Gossmann, 2001), and in Switzerland where the breeding population is clearly decreasing (Estopey, 2001a,b). The conservation status of the woodcock in Europe was established as 'vulnerable in winter' (Heath et al., 2000; Tucker and Heath, 1994) but the trend was recently revised as 'stable' (Wetlands International, 2002). In this context, estimating survival rates in different parts of the breeding and wintering range is essential, in order to define sustainable management practices (bag limit, reserves). Annual survival rates of 0.47 for yearlings (<1 year old) and 0.58 for adult birds were found in Great Britain (Hoodless and Coulson, 1994), but were much lower for birds wintering in France (0.34 for yearlings and 0.44 for adults, with a mean life expectancy of 1.25 years; Tavecchia et al., 2002). Tavecchia et al. (2002) found that temperature and rainfall influenced winter survival and argued that stochastic events such as severe winter conditions might drive populations to a low level from which it would be difficult to recover. These very low survival rates, increased hunting pressure, sensitivity to climate fluctuations and loss of habitats raise the issue of the long-term viability of this species.

Most studies dealing with survival rates in woodcocks were based on ring recoveries (Hoodless and Coulson, 1994; Tavecchia et al., 2002) or age ratios of bags (Fadat, 1993). Indeed, because of the faithfulness of wintering woodcocks, age-ratios are linked both to reproduction success and hunting pressure (Fadat, 1981), without any possibility to separate these two factors. Anyway, these methods suffer biases toward hunting and underestimation of other causes of mortality. An alternative method is the use of radio-telemetry that has the advantage of conferring upon individuals a recapture rate equal to 1, allowing a simplification of survival parameters estimates (White and Garrott, 1990). Moreover, radio-tagging enables us to determine the cause of death, and to quantify the impact of predation, which has not been possible hitherto. In the present paper, we analysed data on radio-tagged woodcocks living inside and outside a hunting-free reserve to investigate: (1) What are the causes of mortality, and what is the impact of predation? (2) What are the survival probabilities in wintering woodcocks? (3) What is the real efficiency of reserves and what proportion of a population can be protected by a reserve?

2. Methods

2.1. Study area

The study was carried out in Brittany (48°30′ N, 3°28′ W; Western France) during three consecutive winters (1999–2000, 2000–2001, and 2001–2002; hereafter called 2000, 2001 and 2002 winters, respectively). The study was conducted from 1st December to 22nd February (12 weeks), including a major part of the hunting period in France (1st October–28th February in 2000 and until 20th February in 2001 and 2002). The study area was ca. 1800 ha and encompassed a forest (the Beffou forest) and a surrounding bocage (a characteristic landscape of Northern France consisting of small irregular fields interspersed by hedges and copses). Meadows grazed by cattle prevailed (70% of fields) and the remaining fields were cereal stubbles and winter cereal leaves. The Beffou forest was composed mainly by three habitat

Table 1
Sample sizes, exposure days and sources of mortality of 98 radio-tagged woodcocks during a three-year study of winter survival in Brittany

Season	Age-class	*n*	Exposure days	Source of mortality			Migration
				Predation	Hunting	Unknown	
1999–2000	Adult	14	840	1	0	3	10
	Yearling	13	660	3	3	3	5
2000–2001	Adult	12	503	2	1	2	7
	Yearling	27	1069	2	6	5	14
2001–2002	Adult	9	373	0	0	1	8
	Yearling	23	1057	2	2	4	15
Overall	Adult	35	1716	3	1	6	25
	Yearling	63	2786	7	11	11	34
Total	–	98	4502	10	12	17	59

types: closed-canopy deciduous woodland (30–100 years old, including mainly beech *Fagus sylvatica* and Oaks *Quercus robur* and *Quercus sessiliflora*), closed-canopy coniferous woodland (30–100 years old, including mainly Sitka spruce *Picea sitchensis*, Common silver fir *Abies alba*, Scots pine *Pinus sylvestris* and Maritime pine *Pinus pinaster*) and young beech-oak plantations (10–30 years, with dense shrub strata). The climate is under oceanic influence, characterised by rain, wind and mild temperatures in winter (January, mean rainfall: 100 mm; mean temperature: 4.5 °C; source Météo France). Woodcock hunting was prohibited in the Beffou forest since 1995. However, hunting was allowed in the bocage and private woods, sometimes directly adjacent to the forest. Hence, for further purposes, the forest will be called the ''reserve'' and the remaining area the ''hunting area''. Hunting occurred mainly on weekends but was legal six days per week. Woodcock hunters are generally solitary and helped with their dog.

2.2. Data collection

Woodcocks were captured on feeding sites at the beginning of the night (range 18:00–24:00) using a spotlight and a landing net (Gossmann et al., 1988). Birds were fitted with a metal and a colour ring and aged (1st year vs. adult) according to wing feather characteristics and moult status (Clausager, 1973; Fadat, 1994). A total of 105 woodcocks were captured and monitored.

Each bird was fitted with a radio-transmitter (Biotrack® TW3), weighting from 7 to 12 g (2–4% of body mass) according to the battery size. All the birds in 2000 and 7 in 2001 were fitted with radio-tags maintained on the back with a Teflon ribbon two-loop backpack harness (Kenward, 1987). Seven woodcocks died of starvation because the bill was jammed in the upper loop of the harness (probably when preening). Consequently, during winters 2001 and 2002, the radio-tags were glued on the back and maintained with a single-loop harness (passing on the belly and behind the wings; McAuley et al., 1993). The single-loop harness did not cause any mortality. Some woodcocks were resighted or recovered in the study area in the following winters. Only one bird tracked on the winter 2000 was recaptured and tracked in 2002, but only the data from the winter 2000 were included in the analysis to avoid pseudoreplication. Hence, after excluding the seven birds died, data from 98 independent individuals were available for analyses (Table 1).

Birds were located to the nearest 10 m by day and 50 m by night 2–5 times per week until their death or departure on migration, which started at the end of February until early April, as previously described with ringing data (Ferrand and Gossmann, 2001; Hoodless, 2002). Locations were plotted on a 1/10,000 map using a GIS package (Arcview 3.2, ESRI, Redlands, USA). The status of the birds (alive or dead) was assessed according to their behaviour. When no movement or activity was recorded for two consecutive days and nights, birds were flushed to check if they were still alive. Otherwise, we searched for the radio-tags.

Mortality was assigned to hunting when hunters brought back the radio-tag, or when the radio-tag was found with obvious signs of knife-cutting on the harness. Mortality was assigned to predation when the radio-tag was found with remains of the body, was buried, or had tooth marks and a chewed antenna (fox *Vulpes vulpes*) or when it was surrounded by scissors-like cut feathers (mustelids or feral cats). When cues were lacking, mortality source was defined as unknown. From late February, lost signals were attributed to departure on migration.

The pattern of site use in woodcocks was such that many individuals changed their diurnal site several times during the study period, switching from the reserve to hunting areas (Duriez, 2003). Therefore, for each individual the pattern of site use was defined as the proportions of radio-tracking locations in reserve and hunting area.

2.3. Survival analyses

Survival probabilities of radio-tagged woodcocks throughout the study period were estimated by using "known fates" models implemented in the software MARK (White and Burnham, 1999). For analyses, we considered the "week" as the time unit and each bird as an independent sample unit. We assumed that survival was constant over time because our sample size was not sufficient for analyses combining time effect. We tested whether survival probability was related to age, year, pattern of site use, mass and date of capture, including additive and interaction terms. Age and year were introduced in models as groups and, site use, mass (in g) and date of capture (for each year, day 1 = 1st December) as standardized individual covariates. Pattern of site use was defined as the per cent (%) of locations in the reserve area. We used the Akaike Information Criteria (AIC_c) to select the most parsimonious model (Anderson and Burnham, 1999): $AIC_c = -2\log \ \mathrm{Dev} + 2K + 2K(K+1)/(n-K-1)$, where Dev is the Deviance (and not s) of the model, K the number of parameters and n the effective sample size. We assumed equal fit of two models when difference in AIC_c values (ΔAIC_c) between the models was <2. Model selection was performed in two steps. Firstly, we used a step-down approach (Lebreton et al., 1992) to select the most parsimonious factorial model that fitted the data, starting with the model Age*Year as the global model. Secondly, the effect of each covariate was tested when separately added to the previously selected model.

2.4. Population matrix model

Modelling of population trajectories was conducted using a Leslie matrix using the software ULM (Legendre and Clobert, 1995). The matrix structure followed Tavecchia et al. (2002) and consisted in a female-based model with two age-classes (yearlings and adults) and a post-breeding census. The initial population size was $n_1 = 100$ yearlings + $n_2 = 100$ adults. We assumed constant 1:1 sex-ratio σ at fledging and an equal female fecundity f in both age classes (2 fledglings; Hoodless and Coulson, 1998). In species with first breeding attempts occurring when individuals are one year old such as in woodcock, the population growth rate is highly sensitive to post-fledging survival. Because post-fledging survival s_0 is an unknown parameter (Hoodless and Coulson, 1998), models were fitted with several values of s_0, ranging from 0.5 to 0.9. The transition matrix was the following:

$$\begin{bmatrix} S_{ew}S_{lw}S_0\sigma f & S_{ew}S_{lw}S_0\sigma f \\ s & v \end{bmatrix},$$

where s and v are annual survival probabilities for yearlings and adults, respectively. Annual survival probability was a product of summer survival s_s (from 1st March to 30th September: 0.590 ± SE 0.041; Tavecchia et al., 2002), early winter survival s_{ew} (from 1st October to 30th November: derived from the monthly survival s_1 0.918 ± SE 0.024 in yearlings and s_2 0.959 ± SE 0.012 in adults; Tavecchia et al., 2002) and late winter survival s_{lw} (from 1st December to 28th February; s_3 for yearlings and s_4 for adults estimated in the present study). The model was deterministic (age structure, survival probability and breeding success constant over time) and assumed full reproduction at one year. We ran models for 100 generations.

3. Results

3.1. Causes of mortality and site use

Over the three seasons, 59 woodcocks survived to the hunting season and went on migration (loss of signal in spring) (Table 1). The hunting mortality concerned mostly yearlings (91%) and 70% of birds predated were yearlings (Table 1), although there was no significant difference in the causes of mortality between ages (Fisher's exact test $P = 0.293$). Predation was only due to terrestrial predators: four cases were attributed to foxes *Vulpes vulpes* and six cases to feral cats or mustelids (Stone marten *Martes foina* or Marten *Martes martes*). Seven cases attributed to martens, cats or foxes were found in the fields or hedges. Only one case attributed to fox and two attributed to marten were found in the forest.

To investigate the effect of hunting on survival and the efficiency of the reserve, we looked at the per cent (%) of diurnal locations in the reserve (Fig. 1). More than half of the birds spent all their winter in the reserve, but the remaining half was submitted to possible hunting for a variable amount of time, and 30% of birds spent >50% of their time in the hunting area (woodlands or hedges). The per cent (%) of locations in the reserve did not differ among ages and years (GLM with bino-

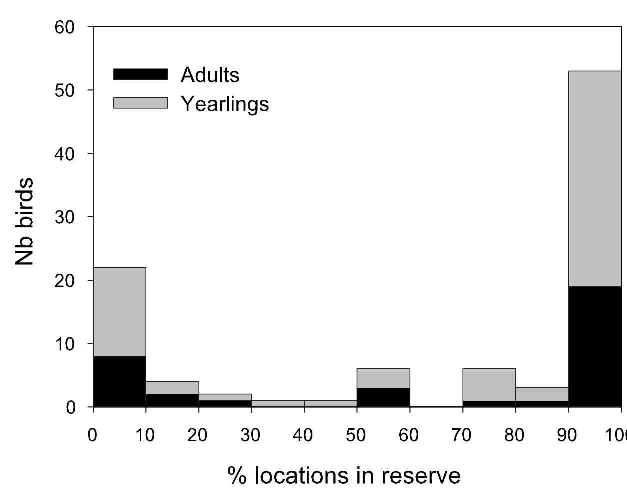

Fig. 1. Per cent of locations spent in the reserve for each of the 98 woodcocks monitored, between age classes.

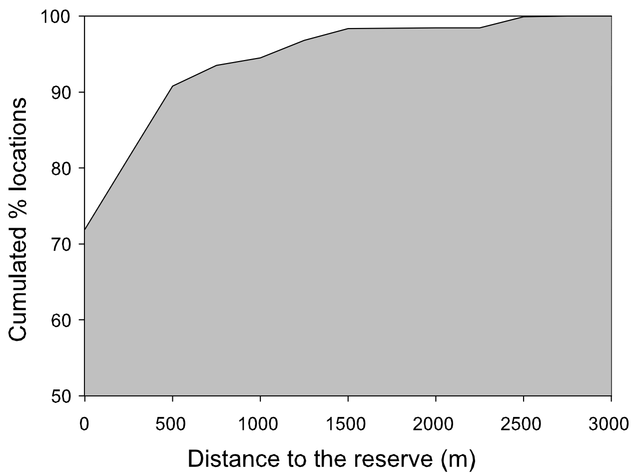

Fig. 2. Cumulated per cent (%) of diurnal locations according to the distance to the strict reserve of the Beffou forest (calculated using buffer zones incremented by 250 m-steps extending the reserve).

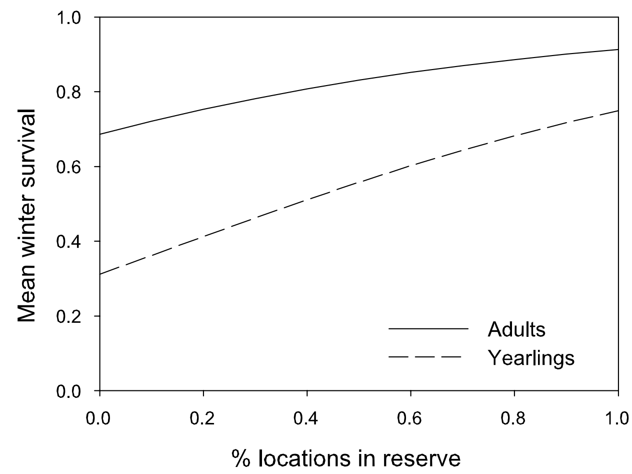

Fig. 3. Mean survival probabilities over the winter (from 1st December to 22nd February) in Brittany, for adult (solid line) and young (dashed line) woodcocks, according to the per cent (%) locations spent in reserve. These results are based on model S{Age + Reserve} fitted on a dataset including 98 radio-tagged birds.

mial error: $F_{1,94} = 0.64$, $P = 0.42$ for age; $F_{2,95} = 2.19$, $P = 0.12$ for year; Fig. 1). While 72% of locations occurred in the reserve, 91% of locations were located within 500 m from the reserve boundaries and 95% within 1 km (Fig. 2).

3.2. Survival probabilities

Model selection showed that the model S{Age + Reserve} had the lowest AIC_c (Table 2). When deriving survival parameters in this model ((weekly survival)$^{12 \text{ intervals}}$ over the 12 weeks of the study period) for age only, mean winter survival probability was 0.863 ± SE 0.066 in adults and 0.627 ± SE 0.073 in yearlings. For both age classes, survival probability increased as birds spent more time in reserve (Fig. 3; slope = 0.596 ± SE 0.209, $P < 0.05$). In the model S{Age*Reserve}, the slopes were 0.150 ± SE 0.348 (ns) and 0.776 ± SE 0.249 ($P < 0.05$) for adults and yearlings, respectively. Increasing the over-dispersion factor up to 2 did not modify the two top ranking models, showing robustness of models to over-dispersion (Table 2).

3.3. Population matrix model

The population matrix model was adjusted to include both the effects of age and per cent (%) locations in reserve on winter survival. Therefore, in yearlings, winter survival was s_{ew}. s_3 with $s_{ew} = s_1^2$ (to account for the tow months of October and November) and we calculated different values for s_3 ((weekly survival)^{12} to account for the 12 weeks of study from 1st December to 22nd February) according to the per cent (%) locations in reserve (from 0 to 100). Similarly, in adults, winter survival was s_{ew}. s_4 with $s_{ew} = s_2^2$ and different values for s_4 were calculated according to the per cent (%) locations in reserve. Changes in population growth rates λ according to different values of per cent (%) locations in reserve and s_0 are given in Fig. 4. Results showed that a reserve can help to maintain a population stable

Table 2
Results of model selection investigating the effects of age, year, date of ringing, mass at ringing and per cent (%) locations in reserve on survival probabilities, based on 98 radio-tagged woodcocks wintering in Brittany

Model	AIC_c	ΔAIC_c	AIC_c weight	K	Dev	C-hat		
						1	1.5	2
S{Age + Reserve}	190.749	0	0.73418	3	184.715	1	1	1
S{Age*Reserve}	193.560	2.81	0.18005	3	187.526	2	2	2
S{Age}	196.693	5.94	0.03759	2	192.676	3	3	4
S{Age*Year}	198.541	7.79	0.01492	6	186.423	4		
S{.}	198.684	7.94	0.01389	1	196.678		4	3
S{Year}	199.990	9.24	0.00723	3	193.656			
S{Age*Date of ringing}	200.152	9.40	0.00667	3	194.119			
S{Age*Mass}	200.547	9.80	0.00547	3	194.513			

K is the number of parameters and Dev is the deviance of the model. The three columns on the right represent the ranking of the four first models for three values of the overdispersion factor C-hat.

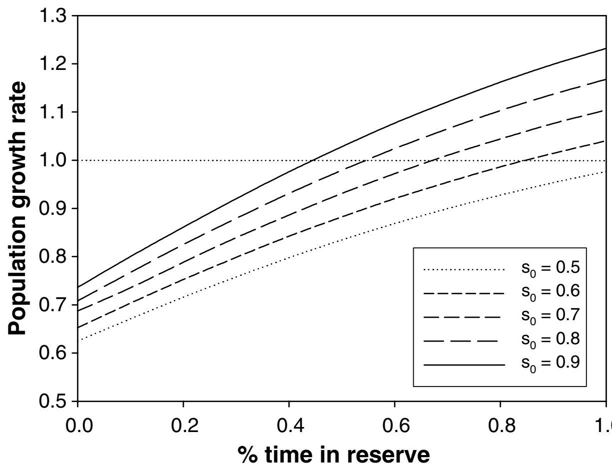

Fig. 4. Modelled population growth rates of woodcocks wintering in France according to the per cent (%) of time they spent in reserve areas and for different values of post-fledging survival (s_0).

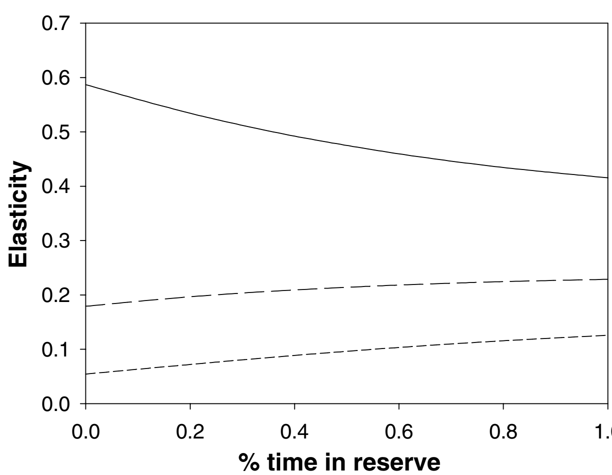

Fig. 5. Elasticities of the population growth rate to changes in the matrix entries according to the per cent (%) of time spent in the reserve, for post-juvenile survival $s_0 = 0.6$. Results are given for adult survival (solid line), adult fecundity (long-dashed line) and yearling fecundity (short-dashed line).

($\lambda = 1$) only if $s_0 > 0.6$. Elasticity analysis showed that the most important parameter influencing woodcock population dynamics when $s_0 = 0.6$ was the adult survival, followed by yearling survival, adult fecundity and yearling fecundity (Fig. 5). For values of s_0 ranging from 0.5 to 0.7, results were similar and adult survival was still the most important parameter.

4. Discussion

4.1. Causes of mortality

Predation was an important cause of mortality in wintering woodcocks (10.2% of birds, Table 1). Predation has not been quantified in previous studies because the datasets were mostly built on hunting recoveries (Hoodless and Coulson, 1994). The probability of recovering a predated woodcock marked only with a leg ring must be very low owing to the bird's cryptic plumage and use of woodland habitat. Conversely, the predation probability in our dataset was perhaps overestimated because of the handicap potentially caused by carrying a radio-tag (time lag in the escape behaviour) (Bro et al., 1999), although the extra-load never exceeded 4% of the body weight that is usually advised (Caccamise and Hedin, 1985).

Predation mostly occurred in fields outside the forest. Because the predators involved (foxes, cats and mustelids) are mainly nocturnal, this predation probably occurred mostly at night, when the majority of woodcocks were in the fields. For some birds living in hedges, the predation possibly occurred in the diurnal site, because predators are also known to follow hedges (Harris and Woollard, 1990). The circumstances of the three predated woodcocks found in the forest were particular. One of them was found only 40 m from the forest edge and the bird could have been killed in fields and brought to the forest by the predator. The two other cases were probably killed in the forest but it happened during the three-week frost spell in December 2001, while most of the woodcocks remained in the forest at night. Therefore, we believe that, under usual climatic conditions, the forest is the safer habitat for woodcocks from a predation point of view and that it is risky for woodcocks to frequent fields at night. Thus, it is unlikely that woodcocks frequent fields at night to lower predation risk, as suggested for the American woodcock *Scolopax minor* by Connors and Doerr (1982). The benefit to use the fields at night is likely to be food-related (Duriez, 2003; Granval and Bouché, 1993). The absence of predation by raptors could be explained by the absence of potential predators (Goshawks *Accipiter gentilis*, Peregrine *Falco peregrinus*, Eagle-Owl *Bubo bubo*) and the only nocturnal raptors present (Barn Owl *Tyto alba*, Tawny owl *Strix aluco* and Long-eared owls *Asio otus*) cannot kill woodcocks.

In our study, hunting and predation mortalities were similar. However, the relatively low hunting pressure in our study site due to the presence of the reserve, which represented one third of the study area, and the effect of hunting on survival probabilities, suggest that in areas without reserves, mortality due to hunting might be higher than mortality due to predation. The hunting mortality in yearlings was high compared to adults, despite no difference in the proportion of age-classes frequenting the reserve. This probably reflected greater knowledge of the study area by adults. Owing to the great fidelity to their wintering quarter (Fadat, 1993; Hoodless and Coulson, 1994; Wilson, 1983), woodcocks which spend their first winter in an area free from hunting are more likely to survive and visit the same place in following winters. This difference between adult and yearling hunting mortality suggests that population dynamics estimates based on age-ratio bag statistics (Fadat, 1993) are not valid. According to our dataset, the commonly observed ratio of 70% of yearlings shot in France does not mean that 70% of the wintering woodcocks are yearlings in this country.

Frost weather is known to increase woodcock mortality (Tavecchia et al., 2002). However, climate in Brittany is oceanic and frost spells are rare. Except a three-weeks frost spell in December 2001, there was never more than four consecutive days of frost during our study period. The reduced mortality in both age-classes in 2002 contradicts the hypothesis of climatic events affecting survival probabilities in our dataset.

4.2. Population dynamics

Our survival probabilities calculated from radio-tracking data and the values calculated on hunting recoveries for woodcocks wintering in Brittany by Tavecchia et al. (2002) were similar for adults (0.86 and 0.88, respectively, for a 3-month survival) but were 14% lower for yearlings (0.63 and 0.77, respectively). In the closely related American woodcock, age-specific difference was found in annual survival (Krementz et al., 2003), but not in winter survival (Krementz et al., 1994; Krementz and Berdeen, 1997). The low winter survival rates in American woodcocks (0.65–0.72) are considered to be one cause of the general decline of this species, in addition to suitable habitat loss (Krementz et al., 1994; Krementz and Berdeen, 1997; Pace, 2000). The similar winter survival probabilities found in young Eurasian woodcocks, even near a hunting-free reserve, could be a forewarning of a possible decline of populations.

The mortality probability increased by 23% in adults and 44% in yearlings if they spent all the winter in the hunting area compared to the reserve. This confirms the efficiency of reserves to protect woodcocks, as already suspected from the high ratio of adult birds shot in a forest that remained as a reserve for several years (Fadat, 1995). The selected model S{Age + Reserve} suggests an additive effect of hunting mortality over the winter period considered. If the hunting mortality was compensatory, we would not expect such a difference in survival between the reserve and the hunting area (Newton, 1998).

The population matrix model shows that the population growth rate λ increases with the proportion of time that birds in the population spend in reserve. For populations submitted to hunting on their wintering quarter, post-fledging survival s_0 should be above 0.6 to maintain a constant population level. Post-fledging survival should be a critical demographic parameter in woodcocks because they breed in their first year and the average life expectancy of the birds wintering in France is only 1.25 years (Tavecchia et al., 2002). Even the prohibition of hunting and the creation of numerous reserves could not help to stabilize populations if $s_0 < 0.6$. In case of a total absence of reserves in France and of a hunting pressure similar to our study area, the population would be declining even if $s_0 = 1$. In the north-eastern part of France, the hunting pressure is very low compared to western France (Ferrand and Gossmann, 2000). Moreover, the elasticity analysis suggests that adult survival is the most important parameter to consider for a sustainable management of woodcock populations. Decrease in adult survival was shown to be the most important parameter to explain a decline in a Semipalmated sandpiper *Calidris pusilla* population (Hitchcock and Gratto-Trevor, 1997). The more individuals spend time outside reserve, the more λ decreases, and the more adult survival is an important parameter.

Our results cannot pretend to be definitive because our sample size was small and we need further studies on winter and summer survival in other regions or countries with less intensive hunting. Our demographic simulations considered that woodcocks only produced one clutch per year, but if a fraction of the population produced two clutches (not proved hitherto but theoretically possible), population trends could be different. Future work must focus on breeding biology, breeding success and juvenile survival in the main breeding range (Russia, Fenno-Scandia, Central Europe).

4.3. Implications for management

The low annual survival probabilities of woodcocks (Tavecchia et al., 2002) compared to other shorebirds (usually between 0.60 and 0.90; compilation from Piersma et al. (1996)), and the possible additive effect of hunting in winter found in this study, suggest caution in the harvesting of populations wintering in France and possibly other western European countries. Implications for management would be the limitation of hunting and/or the creation of reserves. The limitation of hunting could be a time limit (days without hunting, or reduction of the hunting season) or a bag limit. Ideally, a bag limit should not be fixed but adapted to the local conditions encountered each season (e.g., frost spell, low abundance of migratory birds) and overall adjusted to the breeding success and summer survival in adults and chicks. These last two parameters are crucial because woodcocks (especially chicks) are known to be very sensitive to weather conditions such as drought (Tavecchia et al., 2002).

This study showed that reserves are efficient tools to protect wintering woodcocks but in their current shape, their efficiency is not optimal. Indeed, the Beffou reserve only hosts 72% of woodcock locations. Their efficiency could be increased by the integration of the movements occurring between the reserve (forest), the hunting area (woods and hedges), and the nocturnal feeding meadows. Because hunters were often patrolling very close to the reserve boundaries in our study site, to be truly efficient, reserves in bocage landscape should include a buffer zone with low and controlled hunting pressure in the surrounding woods and hedges, as suggested for wildfowl by Fox and Madsen (1997) and Guillemain et al. (2002). A buffer zone of 500 m or 1 km wide would protect 91% or 95% of locations, respectively (Fig. 2). Otherwise, the reserve area would play a role of a source for a surrounding sink (hunted) area.

Acknowledgements

This study was funded by the Office National de la Chasse et de la Faune Sauvage. We are very grateful to all the persons involved in the fieldwork: François Gossmann, Hervé Jamin, Jean-Pierre Richard, Yannick Chaval, Jean-Luc Chil, Sébastien Descamps, Cédric Guyot, Julie Le Bihan, Frédérique Leroy, Jérôme Marie, and Sophie Alary. Many thanks to Hervé Fritz for useful discussions. We are grateful for the logistic facilities provided by the Côtes d'Armor Regional Council ("Conseil Général des Côtes d'Armor", landowner of the Beffou forest) and Jean-Claude Fornasier (National Forest Service "Office National des Forêts", manager of the forest). Many thanks to all the farmers for allowing a free access to their fields. This manuscript was improved by the comments from two anonymous referees.

References

Anderson, D.R., Burnham, K.P., 1999. General strategies for the analysis of ringing data. Bird Study 46, 261–270.

Bro, E., Clobert, J., Reitz, F., 1999. Effects of radiotransmitters on survival and reproductive success of gray partridge. Journal of Wildlife Management 63, 1044–1051.

Caccamise, D.F., Hedin, R.S., 1985. An aerodynamic basis for selecting transmitters loads in birds. Wilson Bulletin 97, 306–318.

Clausager, I., 1973. Age and sex determination of the woodcock (*Scolopax rusticola*). Danish Review of Game Biology 8, 1–18.

Connors, J.I., Doerr, P.D., 1982. Woodcock use of agricultural fields in coastal North Carolina. In: Dwyer, T.J., Storm, G.L. (Eds.), Woodcock Ecology and Management. Vol. Report 14. U.S. Fish and Wildlife Service, pp. 139–147.

Cramp, S., Simmons, K.E.L., 1983. *Scolopax rusticola* woodcock. In: Cramp, S., Simmons, K.E.L. (Eds.), Handbook of the Birds of Europe, the Middle East and North Africa. Vol. III Waders to Gulls. Oxford University Press, Oxford, pp. 444–457.

Duriez, O., 2003. Individual wintering strategies in the Eurasian woodcock *Scolopax rusticola*: energetic trade-offs for habitat selection. Université de Paris VI, PhD Thesis, Paris. Available at: <http://tel.ccsd.cnrs.fr/documents/archives0/00/00/35/09/index_fr.html>.

Estopey, F., 2001a. Le déclin de la population de Bécasse des bois *Scolopax rusticola* du Jorat (Vaud, Suisse). Nos Oiseaux 48, 83–93.

Estopey, F., 2001b. Suivi démographique des populations nicheuses de Bécasse des bois *Scolopax rusticola* en Suisse Occidentale de 1989 à 2000. Nos Oiseaux 48, 105–112.

Evans, D.M., Day, K.R., 2002. Hunting disturbance on a large shallow lake: the effectiveness of waterfowl refuges. Ibis 144, 2–8.

Fadat, C., 1981. Age ratios des tableaux de chasse de bécasses (*Scolopax rusticola*) – Signification biologique et utilisation pour la bonne gestion des populations bécassières. Bulletin Mensuel de l'Office National de la Chasse numéro spécial scientifique et technique 20, 141–172.

Fadat, C., 1993. Survival of Eurasian woodcocks estimated from the age ratio of specimens in hunting bags at wintering sites. In: Longcore, J.R., Sepik, G.F. (Eds.), 8th American Woodcock Symposium. U.S. Fish and Wildlife Service, Biological Report 16, p. 134.

Fadat, C., 1994. La Bécasse des bois. Brochure technique de l'Office National de la Chasse, Paris.

Fadat, C., 1995. La Bécasse des bois en hiver. Ecologie, Chasse, Gestion. Maury presse, Clermont-l'Hérault, France.

Ferrand, Y., Gossmann, F., 2000. La bécasse des bois – Enquête nationale sur les tableaux de chasse à tir saison 1998–1999. Faune Sauvage 251, 96–105.

Ferrand, Y., Gossmann, F., 2001. Elements for a woodcock (*Scolopax rusticola*) management plan. Game and Wildlife Science 18, 115–139.

Fox, A.D., Madsen, J., 1997. Behavioural and distributional effects of hunting disturbance on waterbirds in Europe: implications for refuge design. Journal of Applied Ecology 34, 1–13.

Gill, J.A., Sutherland, W.J., 2000. Predicting the consequences of human disturbance from behavioural decisions. In: Gosling, L.M., Sutherland, W.J. (Eds.), Behaviour and Conservation. Cambridge University Press, Cambridge, UK, pp. 51–64.

Gossmann, F., Ferrand, Y., Loidon, Y., Sardet, G., 1988. Méthodes et résultats de baguages des Bécasses des bois (*Scolopax rusticola*) en Bretagne. In: Havet, P., Hirons, G. (Eds.), 3ème Symposium Européen sur la Bécasse et la Bécassine, Paris, 14–16 October 1986, pp. 34–41.

Granval, P., Bouché, M.B., 1993. Importance of meadows for wintering Eurasian woodcock in the west of France. In: Longcore, J.R., Sepik, G.F. (Eds.), 8th American Woodcock Symposium, Vol. 16. U.S. Fish and Wildlife Service, Biological Report 16, p. 135.

Guillemain, M., Fritz, H., Duncan, P., 2002. The importance of protected areas as nocturnal feeding grounds for dabbling ducks wintering in western France. Biological Conservation 103, 183–198.

Harris, S., Woollard, T., 1990. The dispersal of mammals in agricultural habitats in Britain. In: Bunce, R.G.H., Howard, D.C. (Eds.), Species Dispersal in Agricultural Habitats. Belhaven Press, pp. 159–188.

Heath, M., Borggreve, C., Peet, N., (Eds.), 2000. European Bird Populations: Estimates and Trends. Birdlife International, Cambridge, UK.

Hitchcock, C.L., Gratto-Trevor, C., 1997. Diagnosing a shorebird local population decline with a stage-structured population model. Ecology 78, 522–534.

Hoodless, A.N., Coulson, J.C., 1994. Survival rates and movements of British and Continental woodcocks *Scolopax rusticola* in the British Isles. Bird Study 41, 48–60.

Hoodless, A.N., Coulson, J.C., 1998. Breeding biology of the woodcock *Scolopax rusticola* in Britain. Bird Study 45, 195–204.

Hoodless, A.N., 2002. Eurasian woodcock *Scolopax rusticola*. In: Wernham, C.V., Toms, M.P., Marchant, J.H., Clarck, J.A., Siriwardena, G.M., Baillie, S.R. (Eds.), The Migration Atlas: Movements of the Birds of Britain and Ireland. T. & A. D. Poyser, London, pp. 319–322.

Kenward, R.E., 1987. Wildlife Radio Tracking. Academic Press, London.

Krementz, D.G., Seginak, J.T., Smith, D.R., Pendleton, G.W., 1994. Survival rates of American woodcock wintering along the Atlantic coast. Journal of Wildlife Management 58, 147–155.

Krementz, D.G., Berdeen, J.B., 1997. Survival rates of American woodcock wintering in the Georgia piedmont. Journal of Wildlife Management 61, 1328–1332.

Krementz, D.G., Hines, J.E., Luukkonen, D.R., 2003. Survival and recovery rates of American woodcock banded in Michigan. Journal of Wildlife Management 67, 398–407.

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. Ecological Monographs 61, 67–118.

Legendre, S., Clobert, J., 1995. ULM, a software for conservation and evolutionary biologists. Journal of Applied Statistics 22, 817–834.

Madsen, J., 1998a. Experimental refuges for migratory waterfowl in Danish wetlands. I. Baseline assessment of the disturbance effects of recreational activities. Journal of Applied Ecology 35, 386–397.

Madsen, J., 1998b. Experimental refuges for migratory waterfowl in Danish wetlands. II. Tests of hunting disturbance effects. Journal of Applied Ecology 35, 398–417.

McAuley, D.G., Longcore, J.R., Sepik, G.F., 1993. Techniques for research into woodcock: experiences and recommendations. In: Longcore, J.R., Sepik, G.F. (Eds.), 8th American Woodcock Symposium, Vol. 16. U.S. Fish and Wildlife Service, Biological Report 16, pp. 5–13.

Newton, I., 1998. Population Limitation in Birds. Academic Press, San Diego, USA.

Pace, R.M., 2000. Winter survival rates of American woodcock in South Central Louisiana. Journal of Wildlife Management 64, 933–939.

Pain, D.J., Pienkowski, M.V., 1997. Farming and Birds in Europe. Academic Press, London.

Piersma, T., van Gils, J., Wiersma, P., 1996. Family Scolopacidae. In: del Hoyo, J., Elliott, A., Sargatal, J. (Eds.), Handbook of the Birds of the World. Vol. 3. Hoatzin to Auks. Lynx edicions, Barcelona, pp. 444–534.

Tamisier, A., Tamisier, M.C., 1981. L'existence d'unités fonctionnelles démontrées chez les sarcelles d'hiver en Camargue par la radiotélémétrie. Revue d'Ecologie (Terre et Vie) 35, 563–579.

Tamisier, A., Béchet, A., Jarry, G., Lefeuvre, J.-C., Le Maho, Y., 2003. Effets du dérangement par la chasse sur les oiseaux d'eau – Revue de littérature. Revue d'Ecologie (Terre et Vie) 58, 435–449.

Tavecchia, G., Pradel, R., Gossmann, F., Bastat, C., Ferrand, Y., Lebreton, J.-D., 2002. Temporal variation in annual survival probability of the Eurasian woodcock *Scolopax rusticola* wintering in France. Wildlife Biology 8, 21–30.

Tucker, G.M., Heath, M.F. (Eds.), 1994. Birds in Europe: Their Conservation Status. Birdlife International, Cambridge, UK.

Wetlands International, 2002. Eurasian woodcock. In: Waterbird Population Estimates. Wetlands International Global Series No. 12, Wageningen, The Netherlands, p. 164.

White, G.C., Garrott, R.A., 1990. Analysis of Radio-tracking Data. Academic Press, San Diego.

White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 (suppl.), 120–129.

Wilson, J., 1983. Wintering site fidelity of woodcock in Ireland. In: Kalchreuter, H. (Ed.), 2nd European Woodcock and Snipe Workshop. International Waterfowl Research Bureau, Fordingbridge, UK, pp. 18–27.