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Temporal variation in annual survival probability of the Eurasian woodcock *Scolopax rusticola* wintering in France

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The Eurasian woodcock *Scolopax rusticola* is an important quarry species hunted all over its range. Some authors have reported local declines in both wintering and breeding woodcock numbers. In order to investigate whether these possible declines are the result of a negative trend in survival, we analysed 3,312 recoveries of 15,839 woodcocks ringed in France during 14 consecutive winters (1984/85-1997/98). We distinguished between winter (October-February) and summer (March-September) recoveries in order to estimate survival and recovery rate separately for each period because selective pressures during these two periods are likely to be different. Survival varied according to year during both winter and summer. Winter survival probability covaried positively with mean winter nocturnal temperature and ranged from 0.74 (SE = 0.057) during the winter of 1985/86 to 0.83 (SE = 0.042) during the winter of 1994/95. Mortality of first-year birds was 22% higher than that of adults in any year. Results from a second analysis in which we compared survival of birds ringed during 1991-1997 in the three main woodcock wintering areas along the French Atlantic coast suggested a threshold effect of weather conditions. Mean winter survival covaried with temperature and rainfall mainly in the northernmost regions where weather conditions are more severe. We did not find any particular trend in survival probability that could explain the possible declines in woodcock numbers. However, the generally low adult annual survival, and the negative influence of stochastic events such as severe winter conditions might drive populations to a level from which it would be difficult to recover. Results of a two-age-class demographic model are discussed together with implications for management.

Key words: Eurasian woodcock, management, meteorological covariables, recovery, seasonal survival

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A wide range of possible causes might be responsible for changes in the abundance of a particular species. In general terms, these factors act on population size by influencing individual reproductive success and/or survival probability (Begon & Mortimer 1986, Newton 1998). In birds, factors responsible for changes in survival probability other than individual characteristics such as age or sex, can be broadly divided into two categories: those linked to natural processes, e.g. weather conditions or predator pressure, and those linked to human activity, e.g. habitat fragmentation or harvesting. These selective pressures might vary from region to region and their potential influence on demographic parameters are sometimes difficult to detect, in particular in highly mobile species whose individuals move over a wide geographic range. For instance survival probability of the white stork *Ciconia ciconia* breeding in France is influenced by the level of rainfall on their wintering ground in the Sahel region (Kanyamibwa, Schierer, Pradel & Lebreton 1990, Barbraud, Barbraud & Barbraud 1999). Variations in survival probability of the song thrush *Turdus philomelos* in Britain were partially correlated with winter weather conditions (Thomson, Baillie, & Peach 1997). Nevertheless, this relationship explained only part of the decreasing trend in survival, and Thomson et al. (1997) concluded that some undetected sources of mortality could be acting in other part of the species' distribution range.

The Eurasian woodcock *Scolopax rusticola* is a solitary wader that breeds mainly in mixed or deciduous woodlands (Cramp 1985). The major proportion of the western Eurasian population migrates to breed in the northeastern part of the continent (Clausager 1974, Cramp 1985, Hagemeijer & Blair 1997). Some authors have reported recent declines in both wintering and breeding areas (Fadat 1989, 1994, Hagemeijer & Blair 1997), but the actual status of the population is still under debate (Asbirk, Berg, Hardeng, Koskimies & Petersen 1997, Ferrand & Gossmann 2000). Whether the possible declines are the result of a negative trend in demographic parameters has been poorly investigated. There are several ongoing ringing programmes for this species, and an insight into the population dynamics of the woodcock can be obtained from recoveries of individually ringed birds. We used flexible models for capture-recovery data (Brownie, Anderson, Burnham & Robson 1985) to investigate whether survival of woodcocks wintering in France varied according to the age of the birds, and whether it was influenced by winter temperature and/or winter rainfall. We then investigated a possible trend in the survival parameters over years. An estimate of survival probability over the summer period was obtained by formulating the recovery model on the basis of monthly survival. We finally examined spatial heterogeneity of survival among the main wintering areas in France.

Material and methods

Data set and recovery models

Woodcocks in France are mainly migratory. High numbers can be found during winter particularly along the northern and western Atlantic coast. Since 1984, the French Office National de la Chasse et de la Faune Sauvage has coordinated a long-term winter ringing programme of woodcocks that in 1991 was extended to all main wintering areas throughout the country. We used data of birds captured, ringed and released on their wintering grounds from November to March for 14 consecutive winters (1984/85-1997/98). Birds were classified as adults and yearlings, respectively, according to plumage characteristics (Clausager 1973, Gossmann, Ferrand, Loidon & Sardet 1988). Annual survival, from 1 October to 30 September, was estimated by maximum likelihood procedures from age-dependent recovery tables (see Brownie et al. 1985 for a detailed description of recovery analysis) using the computer programme MARK 1.7 (White & Burnham 1999). Estimation of survival was complicated by the fact that releases were spread over the hunting season (Table 1), which in France lasts from 15 September to 28-29 February. In-season banding violates the assumption that mortality during the releasing period should be negligible. In

Table 1. Number of adult and yearling woodcocks ringed in each month of release. Birds released after March were considered released during the summer season (see text for details).

Month	Adults	Yearlings
November	1789	3831
December	1735	2941
January	1050	1717
February	711	1032
March	456	577
Total	5741	10098

addition, the survival of newly marked birds relates to a period shorter than one year and is thus not directly comparable to a yearly survival. This heterogeneity cannot be handled simply by considering a specific survival parameter for newly marked birds, because the initial recovery and survival rates, when specific, cannot be identified separately without additional information (Lakhani & Newton 1983, Anderson, Burnham & White 1985, Freeman, Morgan & Catchpole 1992). In order to overcome the identifiability problem, we took advantage of the in-season banding protocol by reformulating the model in terms of monthly survival. First, woodcocks were grouped according to the month of release (November, December, January, February and March). We then considered two different monthly survivals, s_w for 'winter' (1 October - 29 February) and s_s for 'summer' (1 March - 30 September). This way, four out of the five classes concerned birds released during the winter period (November, December, January and February). The last class (March) concerned birds released at the beginning of the summer period, just after the end of the hunting season. Over the respective periods, both survivals were assumed to be constant. The annual survival, S, can thus be written as the product S_wS_s of the survival probability during the winter and summer seasons, or as $s_w{}^5s_s{}^7$. The initial survival probabilities of birds released in different months can similarly be expressed in terms of monthly survival probabilities (Table 2). These relationships, which can be linearised by a log transformation, render all parameters identifiable. We checked this last point using the method described by Catchpole & Morgan (1997).

Table 2. Survival within the same year (starting from 1 October) of woodcocks released at different periods; s_w = monthly survival during winter (1 October - 28-29 February), s_s = monthly survival during summer (1 March - 30 September).

Birds released in	
November	$s_w{}^{3.5}\ s_s{}^{7}$
December	$s_w{}^{2.5}\ s_s{}^{7}$
January	$s_w{}^{1.5}\ s_s{}^{7}$
February	$s_w{}^{0.5}\ s_s{}^{7}$
March	$s_s{}^{6.5}$
Previous year	$s_w{}^{5}\ s_s{}^{7}$

Model notation was complicated by the presence of the two periods. A classical notation for recovery models is S(x), λ(y) where S is the survival parameter, λ the ring recovery rate, x (respectively y) a descriptor of the factors acting on S (respectively λ) and of the way they interact. For instance, S(a+t), λ(p) depicts a model where survival varies with age and time while λ varies with the periods (hunting versus breeding seasons). Additionally, the '+' between a and t means that the effects of age and time are cumulative. If they interacted, the notation would be 'a*t' (see also Lebreton, Burnham, Clobert & Anderson 1992). In the present study, we adapted the notation to accommodate the specific situations considered (two different monthly survival probabilities). 's' (lowercase) will always denote the monthly survival. The basic ring recovery rates considered will be λd_w, λi_w and λ_s, i.e. those pertaining to the winter period of the year of release (direct recovery rate), to subsequent winters (indirect recovery rates) and to the summer season, respectively. We assumed that the recovery rates during the summer period of the year of release did not differ from those in subsequent years. Indeed, the direct recovery rate has been found to be higher than the indirect recovery rate, probably because recoveries made near the banding area are more readily reported (Brownie et al. 1985). Here, most of the recoveries during the summer period are made on the breeding grounds in northeastern Europe far away from the winter banding sites, which justifies that direct and indirect recovery summer rates are not distinguished.

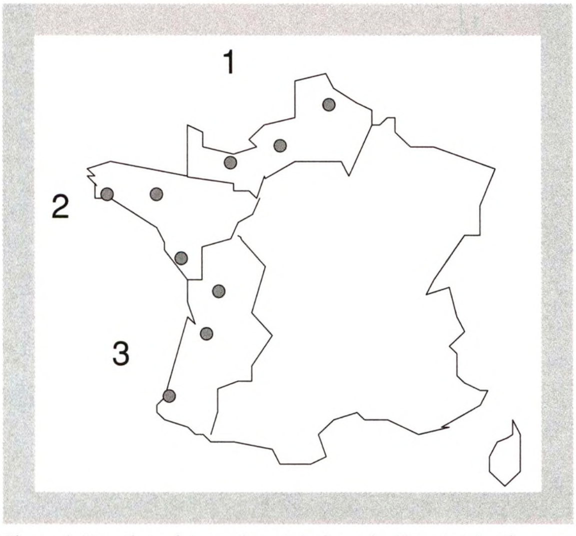

Figure 1. Location of the regions 1-3 along the French Atlantic coast used to detect spatial heterogeneity of parameters. Grey dots indicate where meteorological data were recorded within each region.

Meteorological data

Annual winter (November-February) mean rainfall and mean nocturnal temperature over the study period were obtained from METEO FRANCE on nine locations along the French Atlantic coast (three locations in each of the three coastal regions; Fig. 1). The general mean of these nine stations was taken as an external variable to investigate a possible relationship with woodcock survival in the overall data set. In a second analysis, the relationship at a regional level was investigated using the mean of the three stations within each region (Fig. 2).

Survival analysis

We first analysed survival and recovery rate at country scale (whole data set) over the whole study period. This allowed us to test for the influence of weather conditions and/or age on survival. However, some large-scale or comparative ring recovery studies on birds have shown spatial heterogeneity in survival and recovery rates (Nichols, Williams & Caithness 1990, Krementz, Baker & Nichols 1997). Since woodcocks are extremely faithful to their wintering site both within and between years (Wilson 1982, Hoodless & Coulson 1994), we investigated spatial heterogeneity of parameters by considering the three main wintering areas along the French Atlantic coast separately (see Fig. 1). We restricted this second analysis to a shorter period (1991-1997) for which the three data sets were of similar size. Model selection followed a modified Akaike's information criterion (QAICc; Burnham & Anderson 1998) given by the comupter programme MARK 1.7.

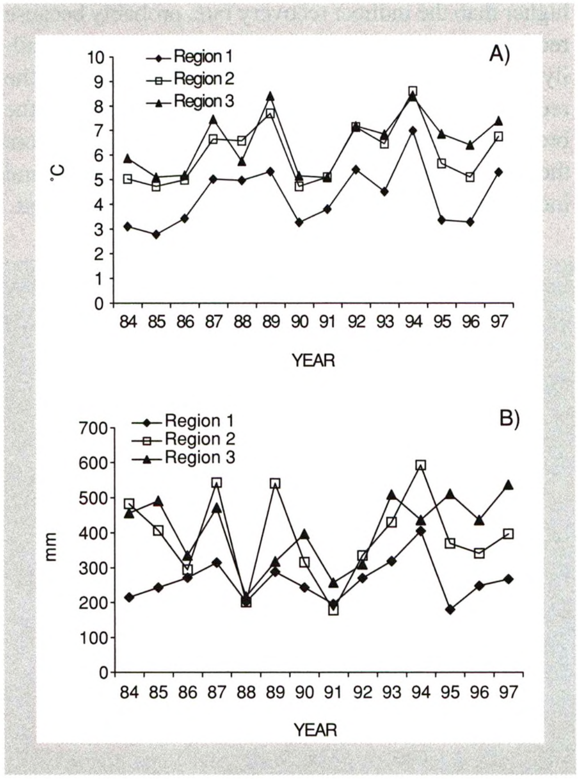

Figure 2. Variation in mean winter (November-February) nocturnal temperature (A) and rainfall (B) for the wintering regions 1-3 during 1984-1997.

Influence of weather condition on survival

In testing the influence of several main effects and their interactions on survival probabilities and/or on recovery rate there is a general risk of building biologically unrealistic or overparameterised models (Anderson & Burnham 1999). To avoid this risk, we fitted relatively few models based on biologically realistic assumptions. Moreover, time effect in recovery rate was tested twice during the selection procedure (the first time in the presence of other effects and the second time in a more parsimonious environment). This was because the necessary log-link function tends to generate unrealistic estimates (>1) in highly parameterised models (as the computer programme MARK 1.7 does not allow different link functions for survival and recovery rate). The model selection procedure started by assessing the fit of the model $S_w(a*t*g)\ S_s(t*g)\ \lambda d_w(.)\lambda i_w(.)\lambda s(.)$ assuming age (two classes) and time (14 occasions) variation in survival for each of the five release-classes independently (noted g). The winter direct, λd_w, indirect, λi_w, and the summer, λ_s, recovery rates were assumed to be constant. In theory, the residual deviance of recovery models for large data sets should be approximately χ^2-distributed (White & Burnham 1999). However, in practice data are commonly overdispersed (see for example Siriwardena, Baillie & Wilson 1999). A variance inflation coefficient, $\hat{c}$ (Lebreton et al. 1992), to account for this lack of fit can be easily estimated by dividing the model deviance by its number of degrees of freedom (difference between the number of cells in the recovery matrices and the number of model parameters). The $\hat{c}$ coefficient is then used to scale the deviance of all models and calculate their QAICc (Burnham & Anderson 1998). We used $\hat{c}$ calculated from model 1. If the lack of fit was actually due to overdispersion, its estimated value should be approximately the same for all structurally valid models. To check this point $\hat{c}$ was estimated for each model fitted.

Spatial heterogeneity of parameters

We grouped the main wintering areas along the French Atlantic coast into three main bio-geographic regions (see Fig. 1). Within each region hunting pressure, habitat availability and habitat quality were assumed to be

Table 3. Elimination of non-significant effects in recovery rate (λ) and monthly woodcock survival during the winter (s_w) and the summer (s_s) periods. Effect of winter temperature and rainfalls are denoted θ and π, respectively. a = age, t = time, g = release-based class. The selected model (10) is in italics.

Model	Survival	Recovery rate	QAICc	np	$\hat{c}$
1	$s_w(a*t*g)$, $s_s(t*g)$	$\lambda d_w(.)\lambda i_w(.)\ \lambda s(.)$	12372.67	184	1.886
2	$s_w(a*t)$, $s_s(t)$	$\lambda d_w(.)\lambda i_w(.)\ \lambda s(.)$	12194.04	45	1.881
3	$s_w(a*t)$, $s_s(t)$	$\lambda_w(.)\lambda_s(.)$	12194.28	44	1.882
4	$s_w(a*t)$, $s_s(t)$	$\lambda_w(t)\lambda_s(.)$	12212.83	57	1.882
5	$s_w(a+t)$, $s_s(t)$	$\lambda_w(.)\lambda_s(.)$	12182.29	31	1.882
6	$s_w(a+t)$, $s_s(t)$	$\lambda_w(t)\lambda_s(.)$	12193.20	44	1.881
7	$s_w(a+t)$, $s_s(t)$	$\lambda_w(T)\lambda_s(.)$	12175.54	32	1.881
8	$s_w(a)$, $s_s(t)$	$\lambda_w(T)\lambda_s(.)$	12173.45	19	1.882
9	$s_w(a+\theta+\pi)$, $s_s(t)$	$\lambda_w(T)\lambda s(.)$	12163.19	21	1.880
10	*$s_w(a+\theta)$, $s_s(t)$*	*$\lambda_w(T)\lambda_s(.)$*	12162.76	*20*	1.881
11	$s_w(a+\pi)$, $s_s(t)$	$\lambda_w(.)\lambda_s(.)$	12173.32	20	1.882
12	$s_w(a+\theta+T)$, $s_s(t)$	$\lambda_w(.)\lambda_s(.)$	12173.40	21	1.882
13	$s_w(a+\theta)$, $s_s(t)$	$\lambda_w(t)\lambda_s(.)$	12176.09	32	1.881
14	$s_w(a+\theta)$, $s_s(.)$	$\lambda_w(T)\lambda_s(.)$	12168.55	7	1.883

homogeneous. The first region included the areas of Pas-de-Calais and Normandy; the second region the Bretagne and the Pays-de-la-Loire; the third included the Aquitaine and the Charente-Maritime (see Fig. 1). The three regions, hereafter called region 1, 2 and 3, respectively, spanned a gradient of latitude (at about 50°N, 47°50'N and 45°N, for region 1, 2 and 3, respectively; see Fig. 1). We began by fitting a model similar to the one retained for the overall data set. We then fitted models accounting for winter temperature (noted θ), winter rainfall (π) and temperature + rainfall (noted θ + π) and estimated how much variation of survival probability was explained by each factor. As in the previous analysis, a variance inflation coefficient ($\hat{c}$) was used to scale each model deviance.

Results

Influence of age and weather conditions on survival (overall data set)

Out of 15,839 woodcocks marked (5,741 adults), 3,312 (20.9%) were recovered during 1984-1997; of these 3.7% were recovered during the summer period. Model selection started by fitting the model $s_w(a*t*g)$ $s_s(t*g)$ $\lambda d_w(.)$ $\lambda i_w(.)\lambda_s(.)$ (see Model 1 in Table 3). The variance inflation coefficient, $\hat{c}$, calculated for this model was 1.886 and was used to scale all subsequent model deviances. A first significant reduction in QAICc was obtained by linking the five release-based groups on the basis of a common monthly survival (Model 2). A simpler model was obtained by equating the direct and indirect winter recovery rates (the two models were equivalent) and by omitting the interaction term between age and time on winter survival (Model 3). At this stage we tried to fit a more general model assuming a time-dependent winter recovery rate (Model 4). However, this model yielded unrealistic values for the first two recovery rates and had a higher QAICc anyway (even when unrealistic estimates were fixed at 1). We built an intermediate model in which the variation in λ was modelled as a linear trend, noted T (Model 7). This model, in which recovery rate was decreasing with time, had a lower QAICc value and it was retained (see Table 3). The final step was to test whether time variation in winter monthly survival was correlated with mean winter nocturnal temperature (θ) and/or mean winter rainfall (π) by means of models in which parameters were linked to an external variable (Lebreton et al. 1992). Much of the difference in deviance (52.7%) between models 7 and 8 was explained by variation in the mean winter temperature along the Atlantic coast (Model 10). According to this model there was a positive relationship between winter monthly survival and temperature. While mean winter temperature explained much of the variation

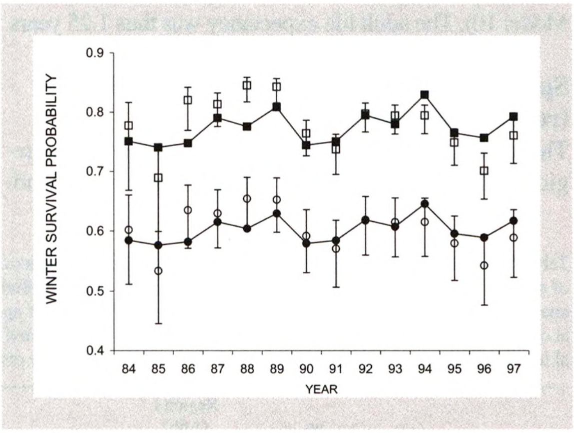

Figure 3. Woodcock survival probability over winter (October-February) during 1984-1997 for adults (□) and first-year birds (○) as estimated from the model $s_w(a+t)$ $s_s(t)$ $\lambda_w(T)$ $\lambda_s(.)$ and the model $s_w(a+q)$ $s_s(t)$ $\lambda_w(T)$ $l_s(.)$ (adults = ■, first-year birds = ●) in which the survival probability is dependent on mean winter temperature. Bars show 95% confidence intervals.

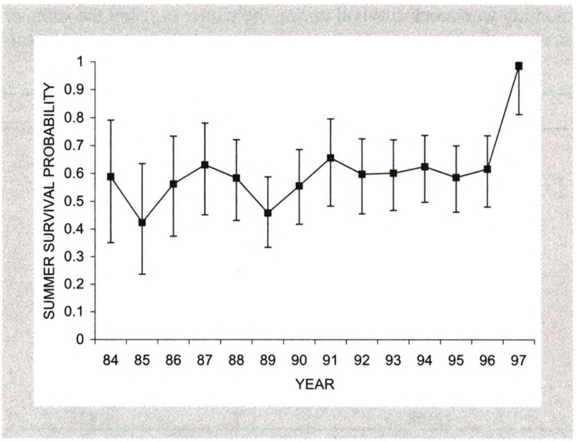

Figure 4. Woodcock survival probability over summer (March-September) during 1984-1997 as estimated from the model ($s_w(a+\theta)$ $s_s(t)$ $\lambda_w(T)$ $\lambda s(.)$).

Table 4. Movements of woodcocks within the French Atlantic coast; see text for definition of regions of banding.

	Region of recovery			
Region of banding	1	2	3	Total
1	688	56	24	768
2	24	1383	28	1435
3	0	6	392	398

over time, winter rainfall explained only 9% (when tested alone) despite the fact that the two variables were positively correlated ($r^2 = 0.42$, $t_{40} = 5.33$, $P < 0.01$).

Mean monthly winter survival was 0.95 (SE = 0.012) for adult and 0.90 (SE = 0.024) for first-year birds, respectively (from Model 8). These values correspond to an over winter survival probability, $s_w{}^5$, of 0.77 (95% c.i.: 0.66-0.85) for adult birds and 0.59 (0.43-0.73) for first-year birds (Fig. 3). Mean summer survival probability, $s_s{}^7$, according to Model 14 was 0.59 (95% c.i.: 0.51-0.66; Fig. 4). We did not find any evidence for a negative linear trend in woodcock survival (Model 12 was not retained). However, if any, it would be a slight positive trend (slope of the logit linear equation ± SE of Model 12: b = 0.02 ± 0.009). The annual survival ($s_w{}^5 s_s{}^7$) was 0.44 and 0.34 for adults and first-year birds, respectively (estimated as the geometric mean from Model 10). The adult life expectancy was thus 1.25 years.

Spatial heterogeneity of survival probability (reduced data sets)

The small proportion of birds (6%) recovered in a region different from the one in which they were banded confirmed that long-distance movements between wintering areas were rare (Table 4) and justified a separate analysis for each region. Regions were located on a north-south gradient of latitude along which the pattern of weather conditions was likely to differ. Indeed, the correlation between mean winter temperature and rainfall differed among regions, being strong in the northernmost region ($r^2 = 0.50$, $t_{14} = 3.47$, $0.005 < P < 0.002$) and weaker in the most southern areas ($r^2 = 0.29$, $t_{14} = 2.23$, $0.02 < P < 0.01$ and $r^2 = 0.06$, $t_{14} = 0.87$, $0.20 < P < 0.50$ for regions 2 and 3, respectively). Under the hypothesis that temperature and/or rainfall affected woodcock survival, we predicted that this relationship would be strongest in region 1 where weather conditions were more severe (see Fig. 2). Survival was modelled separately for each region (period 1991-1997) beginning with the model $s_w(a+t)$ $s_s(.)$ $\lambda(T)$ $\lambda s(.)$. To avoid overparameterisation summer survival was assumed to be constant in all models for the reduced data sets. The influence of winter temperature and rainfall on winter woodcock survival differed according to region (Tables 5 and 6). As predicted, the strongest correlation was detected in the most northerly wintering region. This latitudinal gradient in the correlation between weather conditions and survival suggests a 'threshold effect' of weather conditions on survival, especially for rainfall that explained only 9% of the time variation in the overall data set, but 65% in the most northerly region (see Table 6). Monthly survival among the three regions was difficult to compare because the model retained in each zone was not the same (see Table 6). However, a mean value can be estimated by weighing each year-specif-

Table 5. Spatial influence of weather variables on monthly woodcock winter survival as measured by contrasting models with additive effect of age (a), time (t), winter temperature (θ) and rainfall (π). Modified deviances (model deviance/ $\hat{c}$) of retained models are in italics. In each analysis $\hat{c}$, estimated from the model assuming additive effect of age and time, is given in parentheses at the top of the table. In the analysis at country level (France; 1984-1997) summer survival was assumed to vary over time, whereas it was assumed constant in analyses at regional level (regions 1, 2 and 3; 1991-1997). In both analyses winter recovery rate was modelled as a linear function of time.

	np	Region I (1.66)	Region 2 (1.94)	Region 3* (1.00)	France (1.89)
$s_w(t+a)$	12	2205.15	3137.94	*2911.42*	12111.28
s_w $(a+\theta)$	7	2211.20	*3144.43*	2925.07	12147.71
s_w $(a+\pi)$	7	*2208.87*	3147.10	2927.97	12162.20
s_w $(a+\theta+\pi)$	8	*2208.77*	3142.45	2924.40	12151.33
s_w (a)	6	2215.78	3148.26	2930.00	12166.92

* Parameters for 1991 and 1992 were assumed to be equal to make the model function converge.

Table 6. Proportion (in %) of temporal variation in woodcock survival (with delta deviance given in parentheses at the top of the table) explained by weather variables according to region (1-3) and country (France); θ = temperature, π = rainfall.

	Region 1 (10.63)	Region 2 (12.03)	Region 3 (18.58)	France (24.08)	Df
θ	43.1	37.1	26.5	52.7	1
π	65.0	11.2	10.9	8.9	1
π+θ	66.0	56.3	30.1	59.5	2

ic estimate by the inverse of the variance (Table 7). The mean monthly winter survival appears to be lower in the most northerly region (region 1), whereas summer survival values are similar (see Table 7).

Discussion

Influence of weather conditions on woodcock survival

Winter survival of Eurasian woodcocks during 1984-1997 appeared to be positively correlated with winter weather conditions (rainfall and nocturnal temperature) recorded along the French Atlantic coast. These results are consistent with those found at more northern latitudes for a species with a similar diet, the song thrush (Thomson et al. 1997). It is very likely that severe winter conditions influence bird mortality by interacting with food availability. However, we do not know whether cold and dry winters decrease woodcock survival by increasing mortality from starvation, or by rendering birds more sensitive to predation or hunting pressure. Probably both hypotheses are true, but recovery models cannot distinguish between natural and hunting-caused mortality. The separate analysis of recoveries of birds ringed in the three main wintering areas along the French Atlantic coast showed a spatial heterogeneity of survival parameters. Other ringing studies have shown that survival probability in birds, and by consequence selective pressures acting on mortality, have an important spatial component (Nichols et al. 1990, Krementz et al. 1997). In our study absolute values of survival were difficult to compare because the retained model changed according to the region considered. However, the influence of weather conditions clearly varied according to latitude. In particular, although the influence of temperature was retained at country level, the effect of rainfall was not, and this appeared to be important in the most northerly region. Our result suggests a 'threshold effect' of dry conditions. Under the hypothesis that hunting pressure over the French Atlantic coast is similar, a 'threshold effect' of weather condition might be sufficient to generate a geographic variability in survival.

At country scale, mean annual survival for adult and first-year birds ringed in winter in France was 0.44 and 0.34, respectively. For woodcocks ringed in Britain, Hoodless & Coulson (1994) found a value of 0.58 for adult and 0.47 for first-year birds using a recovery

Table 7. Mean monthly woodcock survival during 1991-1997 from models retained in each of the regions (1-3) and the whole of France. Mean seasonal values are estimated by weighing the year specific estimates for the inverse of their variance ($\sum_i \Phi_i \frac{1}{\sigma_i^2} / \sum_i \frac{1}{\sigma_i^2}$). Summer values are the same for adult and first-year birds. Standard errors are given in parentheses.

Region	1		2		3		France	
Model	s_w (a+π)		s_w (a+θ)		s_w (a+t)		s_w (a+θ)	
Year	Adult	First-year	Adult	First-year	Adult	First-year	Adult	First-year
1991	0.870 (0.040)	0.799 (0.055)	0.953 (0.027)	0.913 (0.051)	0.963 (0.011)	0.920 (0.012)	0.944 (0.014)	0.898 (0.026)
1992	0.890 (0.033)	0.818 (0.050)	0.961 (0.022)	0.921 (0.046)	0.963 (0.011)	0.920 (0.012)	0.955 (0.011)	0.909 (0.024)
1993	0.903 (0.029)	0.830 (0.047)	0.958 (0.024)	0.912 (0.048)	0.967 (0.008)	0.923 (0.011)	0.956 (0.012)	0.905 (0.024)
1994	0.927 (0.024)	0.852 (0.043)	0.967 (0.019)	0.926 (0.043)	0.982 (0.004)	0.934 (0.008)	0.963 (0.010)	0.916 (0.022)
1995	0.865 (0.042)	0.795 (0.056)	0.955 (0.026)	0.915 (0.050)	0.978 (0.004)	0.934 (0.008)	0.948 (0.013)	0.902 (0.025)
1996	0.884 (0.035)	0.812 (0.051)	0.953 (0.027)	0.9123 (0.051)	0.950 (0.006)	0.907 (0.009)	0.946 (0.013)	0.900 (0.025)
1997	0.889 (0.033)	0.817 (0.050)	0.960 (0.023)	0.919 (0.047)	0.952 (0.005)	0.909 (0.008)	0.955 (0.011)	0.908 (0.024)
Mean weighed value								
Winter	0.898	0.821	0.959	0.918	0.974	0.925	0.953	0.906
Summer	0.958		0.918		0.93		0.967	

model with constant parameters. However, the period of release was not taken into account and simple comparisons of absolute values must be looked at with caution. Nevertheless, a comparison with the adult longevity of other species of Scolopacidae (del Hoyo, Elliot & Sargatal 1996) or with early results on woodcock recoveries (Hemery, Jarry, Le Toquin & Nicolau-Guillaumet 1978, Gossmann, Ferrand & Bastat-Lequerré 1994) confirm that survival of Eurasian woodcocks wintering in France is generally low, probably due to the high hunting pressure in France. Indeed, the absolute number of woodcocks harvested, the relative number of woodcocks killed per hunter and the proportion of first-year birds in France are among the highest found in Europe (Ferrand & Gossmann 1998, Ferrand 2000). A striking result of our study is that monthly survival during summer was comparable with monthly survival during winter. This cannot be due simply to the fact that our summer period included 15 days of winter hunting (15-30 September) because only two out of the 124 summer recoveries came from the last 15 days of September. Most of the population wintering in France is migratory and moves to breed in eastern Europe. In these areas, summer hunting is allowed (Fokin & Blokhin 2000) which gives a total harvesting period of almost one year.

Finally, the recovery rate decreased over the study. Although we were not able to test for a full specific time effect but only for a linear constraint, this kind of negative trend has also been found in other long-term recovery studies (Wernham & Peach 1999, Frederiksen & Bregnballe 2000). However, we cannot explain whether this result is due to a bias in large recovery models or to a real effect (e.g. hunters being less prone to report rings).

Woodcock population dynamics and management

In contrast to recovery rate, we did not find any clear trend in survival probability that could explain a general decrease in woodcock numbers. However, the estimated adult life expectancy (1.25 years for an adult bird) was low. Whether this low value might jeopardise woodcock populations must be investigated by a demographic model including breeding output parameters. Such models are difficult to build because important parameters such as chick and post-fledging survival probabilities are lacking (Hoodless & Coulson 1998). Hoodless & Coulson (1998) estimated a value of 1.8 (0.38-3.2) fledged chicks per breeding females. By a simple deterministic demographic model (two-age-class Leslie matrix; Appendix I) in which population growth rate has been fixed at 1, it is possible to estimate the monthly survival of post-fledged woodcocks needed to maintain a constant population level. According to the matrix model, this monthly value should be between 0.90 and 1.00 (values calculated using 1.6 and 0.9 fledged females per breeding female, respectively; see Appendix I). Thus, post-fledging survival must be higher than 97% of adult survival. Unless mean annual breeding output is greater than 1.6 fledged female per breeding female, and fledgling survival and adult survival are equal, results indicate that the woodcock population is declining. Yet conclusions for the European woodcock population are difficult to draw because the survival parameters used in the model come from birds wintering in France only (i.e. a small part of the species' distribution area). At the scale of France the number of wintering woodcocks might be kept constant by continuous immigration of first-year birds (i.e. birds born by adults wintering elsewhere). This is supported by the fact that the age ratio (proportion of adult to first-year birds) in France is among the highest found in Europe (Harradine 1983, Clausager 2000), and it is constant over time (Fadat 1994). At a continental scale, one must consider that survival of woodcocks wintering in other countries might be higher. The woodcock is an important quarry species that needs large-scale management programmes. The influence of weather conditions found in this study highlights the necessity of careful management actions in countries such as France, Italy and Spain that host most of the eastern European population of woodcocks during winter. During the cold winter of 1984/85, the Office National de la Chasse et de la Faune Sauvage recommended the hunting activity to be temporarily suspended. However, the few recoveries during the period of suspension were largely compensated for by those collected two weeks later when the hunting activity was resumed (Fadat 1989). A more efficient management action during severe winters would be to shorten the hunting season, rather than temporarily suspend the hunting activity. Moreover, the monitoring of weather conditions and of woodcock recoveries during the first part of the hunting season, e.g. from 15 September to the end of November, could be used as a tool in an adaptive management of the wintering population (see for example Gibbs, Snell & Causton 1999). However, winter is not the only period in which the population is at risk. Summer hunting should also be carefully monitored. More specific studies should be carried out during the reproductive period, e.g. on fledging survival probability. Indeed, the low summer survival probability found in our study confirms that some selective pressures, other than those specific to reproductive success, might be acting in the breeding areas. Finally, in addition to the influence of severe winter conditions, a gradual habitat transformation might also contribute to a decrease in the demographic parameters. The progressive disappearance of pastures all over Europe might have reduced suitable nocturnal feeding areas. Lewis & Roberts (in Hagemeijer & Blair 1997) have suggested that the closure of the forest canopy in coniferous plantations was the main reason for the population decline in the United Kingdom.

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Appendix I

A simple matrix population model in which the number of woodcocks present in year i+1 can be related to the numbers presents in the previous year using age specific survival and reproductive parameters. In the model, age structure, survival probability and breeding success are assumed constant over time, and the model assumes full reproduction at one year.

$$\begin{bmatrix} Ny \\ Na \end{bmatrix}_{i+1} = \begin{bmatrix} p\times Sy_w\times S_x & p\times Sa_w\times S_x \\ Sy_w\times S_s & Sa_w\times S_s \end{bmatrix} * \begin{bmatrix} Ny \\ Na \end{bmatrix}_{i}$$

Ny = number of yearlings at the beginning of the winter
Na = number of adults at the beginning of the winter
p = number of fledged females per breeding female
S_x = post-fledging survival probability (from May to October)
Sy_w = survival from October to March of first-year birds
Sa_w = survival from October to March of adult birds
S_s = survival from the end of February to the end of September

Assuming a 1:1 sex-ratio at fledging, the number of females fledged per breeding female is between 0.9 and 1.6 (Hoodless & Coulson 1998). Given these values and the survival probabilities estimated in our study, post-fledging survival, S_x, should be between 0.58 and 1.00 (>97% of the adult survival for the same period) in order to maintain a constant population (population growth rate = 1.00).