Multi-annual spatial and numeric dynamics of the white-headed duck *Oxyura leucocephala* in southern Europe: seasonality, density dependence and climatic variability

PABLO ALMARAZ* and JUAN A. AMAT†

*Departamento de Biología Animal y Ecología, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain; and †Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas, Apartado 1056, E-41080 Sevilla, Spain

Summary

1. A statistical model is developed for the globally threatened white-headed duck during its regional expansion throughout Spain from 1980 to 2000; the model estimates the relative intrinsic, climatic and stochastic effects on population fluctuations and spatial expansion on several time-scales. Facing the current lack of knowledge on the nature and consequences of regulation for waterfowl populations, this type of study seems timely.

2. A measure of population density accounting for the spatial patchiness of the population was constructed for breeding and wintering counts. No relationship was found between spatial and numeric dynamics, which suggests different mechanisms for both dynamical patterns.

3. Although a lagged non-linear climatic effect during the period of chick rearing enhanced numeric brood recruitment through a cohort effect, in the short term brood production appeared to decrease with increasing population density, despite a long-term exponential numeric growth.

4. Both wintering population density and rainfall during post-nuptial moult exerted a positive effect on subsequent spatial expansion during breeding, which suggest a major role for social interactions during wintering and wetlands availability on spatial dynamics.

5. Altogether, the results suggest that seasonality, density-dependence and climatic forcing are all major processes in the spatio-temporal dynamics of the white-headed duck. Ignoring the relative biotic and abiotic effects and their temporal scale of interaction on population dynamics might thus yield misleading conclusions on the factors affecting the short- and long-term abundance of waterfowl populations.

Key-words: cohort effect, generalized least-squares, Mediterranean basin, spatio-temporal population dynamics modelling, waterfowl.

Introduction

The relative roles of intrinsic and extrinsic factors as determinants of population fluctuations in nature still remains an open question in ecology (May 1999), yet it is of paramount importance from ecological, evolutionary and applied standpoints. However, a wealth of empirical studies concerned with the mathematical and statistical analyses of ecological time-series is yielding

Correspondence: Pablo Almaraz, Departamento de Biología Animal y Ecología, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain. Fax: +34 958243 238; E-mail: almaraz@fedro.ugr.es

mounting evidence on the prevalence of joint intrinsic, extrinsic and stochastic effects on population fluctuations (e.g. Leirs *et al*. 1997; Lewellen & Vessey 1998; Dennis & Otten 2000; Barbraud & Weimerskirch 2003; see Bjørnstad & Grenfell 2001; Turchin 2003; Sæther, Sutherland & Engen, in press, for reviews). For example, facing current global climate change, a great deal of research is being focused on the role of climate fluctuations on animal population dynamics (Stenseth *et al*. 2002; Sæther *et al*., in press).

Although the issue of population dynamics and regulation is a fairly well-known subject in some vertebrate taxa (e.g. voles and ungulates; see Turchin 2003), the study of joint climatic and intrinsic effects on bird

populations is relatively new (Sæther *et al.*, in press). For instance, a recent survey (Newton 1998) found evidence of density-dependent and climatic effects across several waterfowl taxa. An early paper (Nudds 1983) suggested that density-dependence might be more common in diving waterfowl than in dabbling ducks due, among other things, to the higher habitat unpredictability of the former. Indeed, Vickery & Nudds (1984) found weak evidence for density-dependence among dabblers, and a general opposite pattern for diving ducks in a waterfowl guild inhabiting prairie wetlands of North America. Similarly, recent time-series analyses (Zeng *et al.* 1998; Pöysä & Pesonen 2003) failed to detect statistical density-dependence among several dabbling duck populations. On the other hand, it is clear that extrinsic, and especially climatic factors are of paramount importance in explaining waterfowl demography and population abundance, whether dabblers or divers (Hill 1984; Kaminski & Gluesing 1986; Bayliss 1989; Krivenko 1990; Johnson, Nichols & Schwartz 1992; Miller & Duncan 1999; Sjöberg *et al.* 2000; Blums, Clark & Mednis 2002). Therefore, although theory predicts strong density-dependence among diving and territorial waterfowl taxa, paradoxically most of the evidence of density-dependence in single waterfowl populations comes from dabbling ducks and /or harvested species (e.g. Hill 1984; Kaminski & Gluesing 1986; Bayliss 1989; Fox *et al.* 1989; Sjöberg *et al.* 2000; but see Vickery & Nudds 1984).

Given the lack of knowledge on the nature and consequences of regulation for duck populations, Runge (2003) recently highlighted several unresolved key issues in duck population dynamics. First, given the strong seasonality of most waterfowl habitats, multiple regulatory factors may act throughout the annual cycle (Johnson *et al.* 1992; Newton 1998). Secondly, these factors may operate non-linearly, non-additively and / or with time-lags (see, Zeng *et al.* 1998; Bjørnstad & Grenfell 2001; Beckerman *et al.* 2002; Stenseth *et al.* 2002; Turchin 2003). Thirdly, there may be spatial and/ or temporal heterogeneity in the regulatory process (Newton 1998; Zeng *et al.* 1998) and fourthly, the scale of the dynamical regulatory mechanisms can be very different from the scale of study (see Lewellen & Vessey 1998; Newton 1998, for implications).

The goal of the present paper is to provide a time-series analysis of the extrinsic and intrinsic factors affecting the short- and long-term abundance of a territorial diving duck, the globally threatened white-headed duck (*Oxyura leucocephala*) during its spatial expansion throughout southern Europe from 1980 to 2000. Specifically, this study will try to answer the following questions: (1) what are the relative dynamical roles of density-dependence, climatic variability, and stochasticity? (2) Are the same dynamic variables simultaneously affecting the spatial and numeric expansion of the population; in other words, is the spatial expansion coupled with the numeric expansion? (3) Is there any non-linearity and /or time-lag in the

dynamic effect of the intrinsic and extrinsic components? and (4) is there a seasonal structure in the importance of any of these factors? In order to answer these questions, a multidimensional statistical modelling approach is developed for the explicit implementation of the intrinsic, climatic and stochastic effects on the population dynamics of ducks; although the rationale of the method is similar to other approaches (e.g. Rothery *et al.* 1997; Dennis & Otten 2000; Sæther *et al.*, in press), no such method has been applied so far to waterfowl populations (but see Bayliss 1989). Moreover, to our knowledge no study has yet attempted to resolve these issues in a single waterfowl population, even though this would have essential implications in both pure and applied ecology (Runge 2003).

Materials and methods

The white-headed duck is a small diving stifftail of which a population of less than 20 000 birds (probably < 14 000) persist in shallow, brackish wetlands of Eastern Asia and the Western Palearctic (Green & Hughes 2001). Its spatial location seems to match closely that of its main food (chironomid larvae; Green *et al.* 1999; Sánchez, Green & Dolz 2000); thus, space can be regarded as a surrogate for food availability in this species (*sensu* Newton 1998). Females reach breeding maturity when 1 or 2 years old, mainly when aged 2 years (Green & Hughes 2001). Adult males are polygamous and defend several breeding territories within a breeding season, which usually expands from early April to late August, with peak brood emergence in June (Amat & Sánchez 1982; Green & Hughes 2001). Chicks are precocial, and fledgling period lasts from 8 to 10 weeks (Johnsgard & Carbonell 1996). Birds flock during winter (November–March, Amat & Sánchez 1982) and undergo two moults, one in late winter (pre-nuptial moult) and the other immediately after breeding (post-nuptial moult; Amat & Sánchez 1982; Green & Hughes 2001). The bill colour of males changes from dark grey to pale blue during the prebreeding period (December–March), and remains blue until post-breeding (August onwards; Amat & Sánchez 1982); this change in colour, and the increase in male aggressiveness associated with it, have been shown to exert a positive effect on spatial expansion of ducks (Amat & Sánchez 1982).

The study area covers all the distribution range of the white-headed duck in south-western Europe, limited to the Iberian Peninsula (see Torres & Moreno-Arroyo 2000; Green & Hughes 2001; see also Fig. 1). In 2000 this area accounted for almost 30% of the world population of the species (Green & Hughes 2001). The climate is temperate subtropical with dry, hot summers and cold, wet winters (Capel 2000); a remarkable feature of Mediterranean climate is the strong seasonality in the distribution of rainfall, with large differences
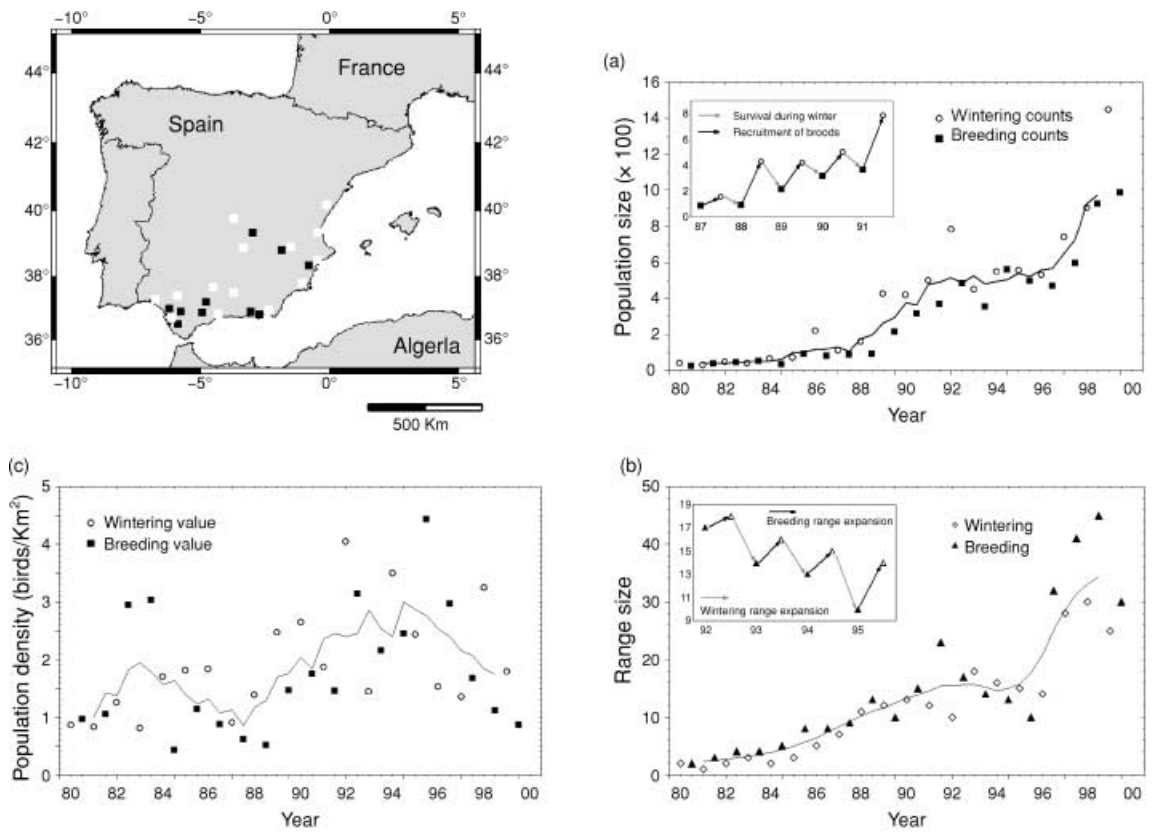
Fig. 1. Time-series of numeric and spatial dynamics of the white-headed duck in Spain from 1980 to 2000. The upper left panel shows the geographical location of the study area; black squares depict the 10 most important wetlands for the white-headed duck according to their long-term average population size, and white squares show the location of the 14 meteorological stations from which precipitation data were gathered. (a) Population size during wintering (open dots) and breeding (solid squares); the inner panel shows an example of short-term seasonal trajectories of wintering survival (grey arrows) and brood recruitment (black arrows) embedded within a long-term numeric increase. (b) Range size during wintering (open squares) and breeding (solid triangles); the inner panel shows an example of the short-term trajectories of wintering and breeding spatial expansion (grey and black arrows, respectively) within a long-term decrease in range size. (c) Population density (birds km^2) during wintering (open dots) and breeding (solid squares). In order to enhance the long-term behaviour of the data, population values in panels (a) to (c) were filtered with a 5-year running average, depicted as a solid black line within each graph.

between the dry and wet seasons (Fig. 2), and also a large spatio-temporal heterogeneity (Capel 2000). A total of 124 wetlands were included in this study.

The database comprises wintering (January) and breeding (June) field counts of the species throughout the study area, gathered from January 1980 to January 2000; during this period the population underwent a major spatial and numeric expansion (Fig. 1a,b). Data for the first 10 years (1980–1989) were gathered by one of the authors (J.A.A.), and the others were assembled by the Spanish White-headed Duck National Survey Team using the same methodology (see Torres & Moreno-Arroyo 2000 for further details). Because counts were carried out simultaneously throughout the species range, and given that the Iberian population is non-migratory (Green & Hughes 2001), it can thus be accepted that all the population was surveyed each time a census was carried out. Furthermore, hunting was banned at the beginning of the study period, so no harvest pressure underlies population counts. Two counts were not carried out (June 1990 and January 1991), so data for those years were imputed according to the Underhill & Prys-Jones (1994) index.
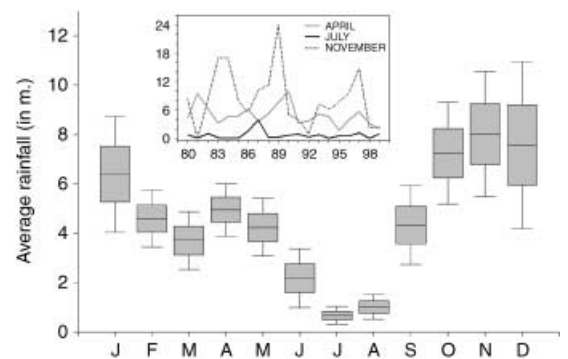

Fig. 2. Regional precipitation data gathered from the 14 meteorological stations spread throughout the study area. The main graph shows a box-plot of the long-term monthly average rainfall (horizontal lines within the boxes) and the 95% confidence intervals of each mean (whiskers). The inner panel depict the long-term behaviour of average rainfall during spring (April), summer (July) and winter (November).

Although population dynamic studies usually assume that the area surveyed is constant through time, we have valuable information on the spatial as well as the numeric expansion of the population. Thus, a

spatially implicit measure of regional population density at time t (d_t, birds km^2; Fig. 1c) was calculated as a weighted index of spatial crowding of birds:

$$d_t = \frac{\sum_{i=1}^{i=k} D_{it} \cdot f_{it}}{\sum_{i=1}^{i=k} f_{it}} \qquad \text{eqn 1}$$

where D_{it} denotes local population density (birds km^3) in site i at time t, and f_{it} is the total number of birds recorded at each site i during a given census t; k is range size (124 wetlands, see above). The choice of population density measures is a critical step in population dynamics studies (Mysterud, Coulson & Stenseth 2002); eqn 1 is a quite reliable algorithm because a single territorial male can hold breeding harems in several wetlands within a single breeding season, the study area thus conforming to a patchy population rather than to a network of local, partially isolated populations. Moreover, eqn 1 provides the advantage of taking into account in a weighted manner local gatherings, which occur regularly during the non-breeding period for the white-headed duck (Amat & Sánchez 1982; Torres & Moreno-Arroyo 2000; Green & Hughes 2001); that is, large population densities would suggest a spatially averaged pattern of strong social interactions among birds. On the other hand, a possible weakness of this method is that it measures realized density, in the sense that wetlands with no individuals at the time each census was carried out are not taken into account, and this possibly underestimates site availability; nevertheless, as the population has grown both in size and distribution range from the beginning of the study period, suitable wetlands for the settling of the species are very difficult to identify retrospectively. Overall, realized density provides a better measure of population density in this case (see Newton 1998 for problems in measuring density in birds).

Finally, data on monthly precipitation from 1975 to 2000 were assembled throughout the study area (see Fig. 2); a total of 14 meteorological stations were included in the database (see Fig. 1). Although some stations lack records for some years, most stations hold data from 1980 onwards. Raw data were grouped bimonthly from the Spanish National Meteorological Institute (INM-MMA), and include standardized absolute rainfall across stations; numeric and spatial dynamics (see below) were regressed against rainfall and population density (both with lags up to 2 years), using a distributed-lags analysis (StatSoft 2003); the lag yielding the largest partial regression coefficient for each variable was selected for the statistical modelling.

Let N_t denote population size (the number of birds summed across wetlands) at time t and let S_t stand for range size (the number of wetlands occupied) at time t; let $X_t = \ln d_t$ denote the weighted log$_e$-population density at time t (eqn 1). Let U_t be the abiotic component of growth rate (standardized rainfall at year t). Finally, let ε_t be the random component of growth rate. Making the assumption that density-dependence may arise in this species through competition for space and /or through a depletion of food resources at high population densities, and that population density can affect spatial expansion through territorial behaviour (see above; see also Newton 1998), the regional spatial and numeric dynamics of the population from time $t-1$ to t can be modelled as:

$$N_t = N_{t-1}[f(X_{t-1}, U_{t-1}, \varepsilon_{t-1})] \qquad \text{eqn 2a}$$

$$S_t = S_{t-1}[g(X_{t-1}, U_{t-1}, \varepsilon_{t-1})] \qquad \text{eqn 2b}$$

At this stage we define $\Delta N_t = N_t/N_{t-1}$ and $\Delta S_t = S_t/S_{t-1}$ as the numeric and spatial net growth rates between t and $t-1$, respectively (where the time unit is 1 year); thus, $f(X_{t-1}, U_{t-1}, \varepsilon_{t-1})$ and $g(X_{t-1}, U_{t-1}, \varepsilon_{t-1})$ are functions representing the effects of rainfall, population density and a stochastic component on numeric and spatial growth rates. Because population growth is a multiplicative process we will assume in eqn 2 that the functions $f(\cdot)$ and $g(\cdot)$ are exponential functions, $\exp(\cdot)$ (Royama 1992). Given that the age at first breeding in the white-headed duck is 2 years, delayed effects of density and/or rainfall may be important for population dynamics; furthermore, as the database consists of both breeding and wintering counts, eqn 2a, b can be rewritten as (see Stenseth *et al.* 2003 for a similar approache):

$$N_{gt} = \begin{cases} N_{gt-1}\exp[\alpha + \beta_i X_{t-\Delta t} + \omega_i U_{t-\Delta t} + \sigma\varepsilon_{t-\Delta t}], \\ \quad \text{if } g = \text{breeding} \\ N_{gt-1}\exp[\alpha + \beta_i X_{t-\Delta t} + \omega_i U_{t-\Delta t} + \sigma\varepsilon_{t-\Delta t}], \\ \quad \text{if } g = \text{wintering} \\ N_{ht}\exp[\alpha + \beta_i X_{t-\Delta t} + \omega_i U_{t-\Delta t} + \sigma\varepsilon_{t-\Delta t}], \\ \quad \text{if } g = \text{breeding}, h = \text{wintering} \\ N_{ht-1}\exp[\alpha + \beta_i X_{t-\Delta t} + \omega_i U_{t-\Delta t} + \sigma\varepsilon_{t-\Delta t}], \\ \quad \text{if } g = \text{wintering}, h = \text{breeding} \end{cases} \qquad \text{eqn 3a}$$

for numeric dynamics, and

$$S_{gt} = \begin{cases} S_{gt-1}\exp[\alpha + \beta_i X_{t-\Delta t} + \omega_i U_{t-\Delta t} + \sigma\varepsilon_{t-\Delta t}], \\ \quad \text{if } g = \text{breeding} \\ S_{gt-1}\exp[\alpha + \beta_i X_{t-\Delta t} + \omega_i U_{t-\Delta t} + \sigma\varepsilon_{t-\Delta t}], \\ \quad \text{if } g = \text{wintering} \\ S_{ht}\exp[\alpha + \beta_i X_{t-\Delta t} + \omega_i U_{t-\Delta t} + \sigma\varepsilon_{t-\Delta t}], \\ \quad \text{if } g = \text{breeding}, h = \text{wintering} \\ S_{ht-1}\exp[\alpha + \beta_i X_{t-\Delta t} + \omega_i U_{t-\Delta t} + \sigma\varepsilon_{t-\Delta t}], \\ \quad \text{if } g = \text{wintering}, h = \end{cases} \qquad \text{eqn 3b}$$

breeding for spatial dynamics.

In eqn 3, Δ is a time lag of a given length. Parameter α stands for the climate- and density-independent component of numeric and spatial growth rates, β_i represents direct (β_0) or delayed (β_1, β_2, ... β_n) statistical density-dependence, ω_i the direct or lagged abiotic (climatic) component of growth rate, and each ε_t is a set of IID (independent and identically distributed) random variables following a normal distribution with 0 mean and variance σ_e^2, $\sim N(0, \sigma_e^2)$. Note that it is assumed here that σ_e^2 is a constant term not depending on population size, so this term will account only for the effects of environmental stochasticity (Lande, Engen & Sæther 2003); as we dealt with small population sizes during some years (see Fig. 1a) demographic stochasticity might have also been important, so this is a possible caveat of our model. For this reason, separate models will be constructed with the variance σ_e^2 scaled to ($\sigma_e^2/\log_e N_t$) in eqn 3a in order to account for the stochastic effects of small population sizes (Lande *et al*. 2003); additionally, σ_e^2 will be scaled to ($\sigma_e^2 \cdot \log_e S_t$) in eqn 3b, in order to control for increasing sampling error with increasing spatial range size (P. Almaraz & J. A. Amat, unpublished work; see Discussion for caveats).

Parameter estimation is the key step in connecting a mathematical model with empirical data (Bollen 1989; Tong 1993; Dennis *et al*. 1995). Parameter values were found by specifying a generalized least-squares (GLS) loss function for each model (Bollen 1989; Draper & Smith 1998):

$$F_{\text{GLS}} = \frac{1}{2}\text{tr}(\{(S - \textstyle\sum) \times W^{-1}\}^2) \qquad \text{eqn 4}$$

where 'tr' is the matrix trace operator, and the term $(S - \sum)$ stands for the residual matrix of the difference between the empirical variance/covariance matrix of β_i, ω_i and $\Delta N_t/\Delta S_t$ (S) and the theoretical matrix implied by eqn 3 if our model was correct ($\sum$); these residuals are multiplied further by the inverse matrix generated by weighting the observations to correct for unequal variance and non-zero covariances of the error terms across the true observations (W^{-1}; see Bollen 1989; Draper & Smith 1998 for further technical details). A GLS loss function is suitable with small sample sizes and when the variances of the true observations are not equal and /or are correlated (Bollen 1989; Draper & Smith 1998), a characteristic feature of field population counts (Shenk, White & Burnham 1998). In addition, in contrast to maximum likelihood (ML) methods (Tong 1993; Dennis & Taper 1994; Dennis *et al*. 1995), least-squares loss functions are robust against non-Gaussian errors, as long as the stochastic component of the model ($\varepsilon_{t-\Delta t}$) has a stationary distribution (Tong 1993; Dennis *et al*. 1995). Nevertheless, as the residuals of all the models tested were roughly Gaussian [Lin–Mudholkar (LM) test for residual whiteness, Tong 1993: 324, $P > 0.2$ in all cases], and given that ML methods provide unbiased estimates of parameters in the presence of temporal autocorrelations in $\varepsilon_{t-\Delta t}$, iter-

ation of GLS was ended with a ML estimation. As an additional advantage, in contrast to GLS methods ML estimate W^{-1} as a function of $\sum$ and not S (Bollen 1989), so the weight matrix is updated at each iteration until convergence. Finally, uncertainty of point parameter estimates was assessed with the bias-corrected bootstrap method (Efron & Tibshirani 1993; Falck *et al*. 1995). With this technique, confidence intervals for parameters are constructed by adjusting the upper and lower percentiles of the bootstrapped distribution to the fraction of it that is more extreme than the original value (Efron & Tibshirani 1993). A total of 1000 bootstrapped samples were used, and a range of 90% around the point estimate was considered given the severity of this method when working with small and biased samples (Falck *et al*. 1995).

The most parsimonious model within each subset in eqn 3 was found by minimizing the small-sample corrected Akaike information criterion (AICc; Hurvich & Tsai 1989). Differences in AICc of 1 or more were considered suggestive of differing parsimony (Burnham & Anderson 1998). Residual diagnostic techniques were finally conducted for each model, as they are extremely useful in assessing the validity of a model as a descriptor of the pattern of variability in the data (Tong 1993; Dennis *et al*. 1995; Dennis & Otten 2000). At this stage, non-linearities in eqn 3 were tested by including quadratic terms for density ($X_{t-\Delta t}^2$) and rainfall ($U_{t-\Delta t}^2$), and selecting the model with those terms minimizing the AICc.

Altogether, taking into account the biology of the species and the conditions imposed in eqn 3, we will estimate the following biological processes with our models: (1) annual overwintering survival and expansion (when growth rate is measured from breeding to breeding, *sensu* Hill 1984); (2) annual overbreeding survival and expansion (from winter to winter); (3) numeric and spatial recruitment of broods (from breeding to wintering); because most of the numeric growth rates during this period were positive (Figs 1a and 3a), mortality is probably negligible from breeding to wintering relative to reproduction and survival; and (4) survival and expansion during prenuptial moult (from winter to breeding); numeric growth rates were mainly negative during this period (Figs 1a and 3b), so mortality is suggested to be the main demographic process from January to June (see Barbraud & Weimerskirch 2003; Stenseth *et al*. 2003; for similar examples).

Results

Figure 1a,b depicts population size and the number of wetlands occupied by the white-headed duck in Spain from 1980 to 2000, respectively. Across time, population size correlated highly with both the number of
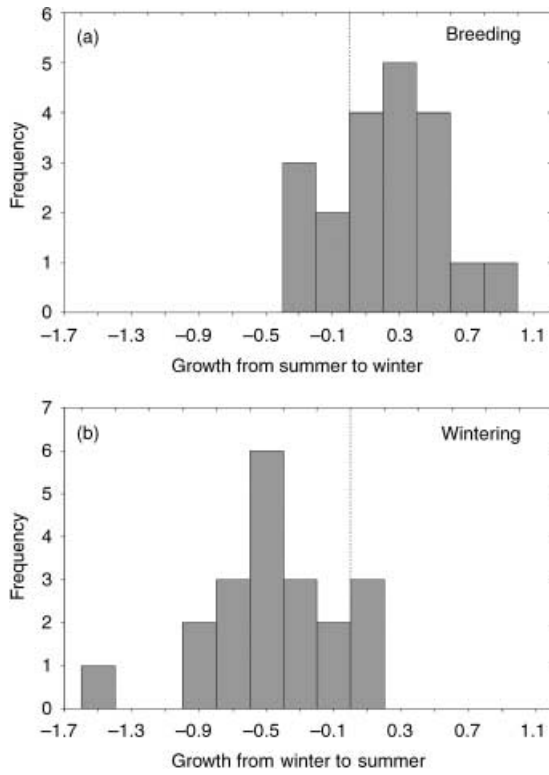
Fig. 3. Frequency distributions of net seasonal numeric growth rates during breeding (a), calculated as $\log_e N_{wt} - \log_e N_{bt-1}$; and wintering (b), estimated as $\log_e N_{bt} - \log_e N_{wt}$. Here, the subscripts w and b stands for wintering and breeding population counts, respectively.

wetlands used ($r = 0.87$, $P < 0.001$, $n = 40$; Pearson's product–moment correlation for January and June counts) and with the total surface of these wetlands ($r = 0.90$, $P < 0.001$, $n = 40$). Nevertheless, no relationship was found between spatial and numeric dynamics within any temporal subset ($P > 0.20$; Table 1). Additionally, population density (Fig. 1c) does not correlate with any of the variables shown in Table 1 ($P > 0.20$). Overall, this suggests that spatial dynamics are largely uncoupled from numeric dynamics, and validates further the construction of separate models for both variables.

According to the distributed-lags analysis, 1-year lagged rainfall during summer (July/August; see Fig. 2) was selected as the period with the largest relative effect on numeric dynamics for both the annual and seasonal models (Table 2). The modelling yielded large statistical direct density-dependence (β_1) and lagged rainfall (ω_2) parameter estimates for both the seasonal breeding (summer to winter) and overwintering (summer to summer) subsets, and the AICc further selected non-linear terms for rainfall variability in both of them (Table 2); nevertheless, the bootstrapped confidence interval for the climatic effect during numeric recruitment of broods was fairly large (asymptotic confidence intervals for this parameter do not include zero; see Table 3). On the other hand, density and rainfall in the prenuptial moult (winter to summer) and overbreeding (winter to winter) subsets did not capture adequately the growth of the species through time ($R^2 < 0.10$ in both cases). Additionally, note that a strong pattern was found in the residuals of the annual models (Table 2).

Overall, the numeric recruitment of broods subset yielded the largest estimate for both statistically direct density-dependence ($\beta_1 = -0.520$) and lagged non-linear climatic effect ($\omega_2 = 0.463$). Nevertheless, rainfall and density were correlated roughly during this period ($r = -0.41$, $P = 0.07$, $n = 20$), which slightly inflated the variance of individual parameter estimates when included together in the model [variance inflation factor (VIF) = 1.19]. Nevertheless, residual diagnostic techniques suggest that this model is a good descriptor of the stochastic variability in the time-series (LM = 0.403, $P = 0.655$) and an excellent one-step-ahead predictor of population sizes (Fig. 4a).

In contrast to the numeric dynamics subset, rainfall during post-nuptial moult (November/ December) exerted a large effect during the spatial expansion of the population from the next summer to winter and from

Table 1. 0-lag Pearson's product-moment correlations between spatial expansion (ΔS_t) and numeric expansion (ΔN_t) of the white-headed duck in Spain (1980–2000) measured during brood recruitment (Br, from June to January), overwintering survival (Ow, from June to June), prenuptial moult (Pm, from January to June), and wintering (Wi, from January to January); performing the analysis with lags of higher order yielded similar results. Significant correlations at $P < 0.05$ are shown in bold type

	ΔS_t Br	ΔS_t Ow	ΔS_t Pm	ΔS_t Wi	ΔN_t Br	ΔN_t Ow	ΔN_t Pm	ΔN_t Wi
ΔS_t Br	–	0·279	−0·006	−0·229	−0·198	0·015	−0·051	−0·209
ΔS_t Ow		–	0·299	**−0·538**	−0·139	−0·110	−0·218	−0·280
ΔS_t Pm			–	**0·644**	−0·039	−0·106	0·042	−0·003
ΔS_t Wi				–	0·077	−0·005	0·212	0·222
ΔN_t Br					–	**0·603**	−0·230	**0·699**
ΔN_t Ow						–	**−0·511**	0·148
ΔN_t Pm							–	**0·535**
ΔN_t Wi								–

Table 2. Statistical modelling of population density and climatic effects on numeric and spatial dynamics of the white-headed duck in Spain (1980–2000). Best results are shown for the four temporal subsets considered. The most parsimonious model selected within each temporal subset is shown along with the difference in the corrected Akaike information criterion (ΔAICc) between that model and the second most parsimonious. Coefficients are GLS-ML point estimates, and numbers in parentheses are 90% bias-corrected bootstrap confidence intervals (BCCI) constructed around the point estimates with 1000 bootstrapped samples; terms β_1 and ω_1 suggest that the effects take place prior to the period within which growth rate is measured; note that we consider for this table only that one time step stands for a season (6 months). ρ denotes the first-order serial autocorrelation of residuals, tested for significance with the Durbin–Watson test (Draper & Smith 1998)

| Model structure | ΔAICc | Density coefficients (90% BCCI) | | Climatic coefficients (90% BCCI) | | |
		β_0	β_1	ω_0	ω_1	ρ
Numeric dynamics, $N_{\Delta t}$						
Summer to summer	−1·16	−0·473 (−0·771, −0·134)	–	–	0·377 (−0·031, 0·682)†	−0·44*
Winter to winter	−0·74	−0·210 (−0·595, 0·090)	–	–	0·352 (−0·121, 0·702)	−0·39
Summer to winter	−3·37	−0·520 (−0·739, −0·184)	–	–	0·463 (−0·157, 0·803)†	−0·01
Winter to summer	−2·25	−0·227 (−0·476, 0·501)	–	–	−0·218 (−0·576, 0·131)	−0·30
Spatial dynamics, $S_{\Delta t}$						
Summer to summer	−3·51	–	−0·174 (−0·563, 0·193)	0·445 (0·106, 0·583)	–	−0·23
Winter to winter	−3·40	−0·447 (−0·826, −0·142)	–	0·150 (−0·529, 0·490)	–	−0·15
Summer to winter	−2·74	–	0·371 (0·001, 0·645)	0·361 (0·070, 0·572)	–	0·37
Winter to summer	−2·13	−0·129 (−0·456, 0·224)	–	–	−0·478 (−0·677, −0·163)	0·01

*Autocorrelations significant at $P < 0.05$. †Parameter estimates for non-linear climatic effects.

Table 3. Weighted least-squares (WLS) parameter estimates for the statistical modelling of the effects of density and weather on the spatio-temporal dynamics of the white-headed duck in Spain (see Table 1 for further details). With this method, the term σ_e^2 of eqn 3a is scaled to $(\sigma_e^2/\log_e N_t)$ in the numeric dynamics subset in order to account for demographic stochasticity (Lande *et al.* 2003). On the other hand, the term σ_e^2 of eqn 3b is scaled to $(\log_e S_t \cdot \sigma_e^2)$ in the spatial dynamics subset, in order to control for increasing sampling error with increasing spatial range size. Also shown is the difference in the corrected Akaike information criterion (ΔAICc) between the WLS model and the best GLS-ML model selected in Table 1 within each temporal subset; 90% asymptotic confidence intervals (90% ACI; StatSoft 2003) are shown in parenthesis

| Model structure | ΔAICc | Density coefficients (90% BCCI) | | Climatic coefficients (90% BCCI) | |
		β_0	β_1	ω_0	ω_1
Numeric dynamics, $N_{\Delta t}$					
Summer to summer	0·96	−0·470 (−0·798, −0·142)	–	–	0·376 (0·064, 0·689)
Winter to winter	1·08	−0·221 (−0·649, 0·207)	–	–	−0·011 (−0·474, 0·453)
Summer to winter	0·97	−0·415 (−0·705, −0·125)	–	–	0·473 (0·196, 0·749)
Winter to summer	0·07	−0·331 (−0·745, 0·084)	–	–	−0·178 (−0·582, 0·226)
Spatial dynamics, $S_{\Delta t}$					
Summer to summer	2·02	–	−0·139 (−0·512, 0·235)	0·446 (0·102, 0·790)	–
Winter to winter	1·39	0·070 (−0·287, 0·428)	–	−0·274 (−0·648, 0·100)	–
Summer to winter	2·08	–	0·340 (−0·097, 0·777)	0·124 (0·003, 0·244)	–
Winter to summer	1·62	−0·071 (−0·432, 0·290)	–	–	−0·373 (−0·771, 0·025)

summer to summer (Table 2). Additionally, population density during the past wintering season exerted a pos- itive effect on the spatial expansion from summer to winter; thus, a major seasonal effect of population density and rainfall is again suggested for the spatial expansion of the population, but in this case the AICc selected linear terms for rainfall variability.

Again, the spatial recruitment of broods subset yielded robust and positive parameter estimates for both the lagged statistical density-dependent ($\beta_2 = 0.371$) and direct climatic effects ($\omega_1 = 0.361$; Table 2). Nevertheless, note the weak pattern in the residuals of this model, in contrast to that of the others. In spite of this, residual diagnostic techniques suggest that this model is also a good descriptor of the stochastic variability in spatial dynamics ($LM = 0.078$, $P = 0.531$) and an excellent one-step-ahead predictor of range sizes (Fig. 4b).

Table 3 shows the weighted least-squares (WLS) parameter estimates for the models in eqn 3a, b. Although the estimates varied relative to GLS-ML methods for most of the models, the confidence intervals overlapped in all cases, and no evidence was found for a directional bias in the estimation of statistical density-dependence. Indeed, forcing the set of GLS-ML and WLS parameter estimates through a regression line of the form $Y = X$ (a 1–1 relationship) yielded high confidence ($R^2 = 0.678$, $P < 0.001$; $n = 16$ pairs of parameters) in the robustness of the results against demographic and sampling noise; however, note that there were large discrepancies in some cases. Yet, an interesting result was that the seasonal models for
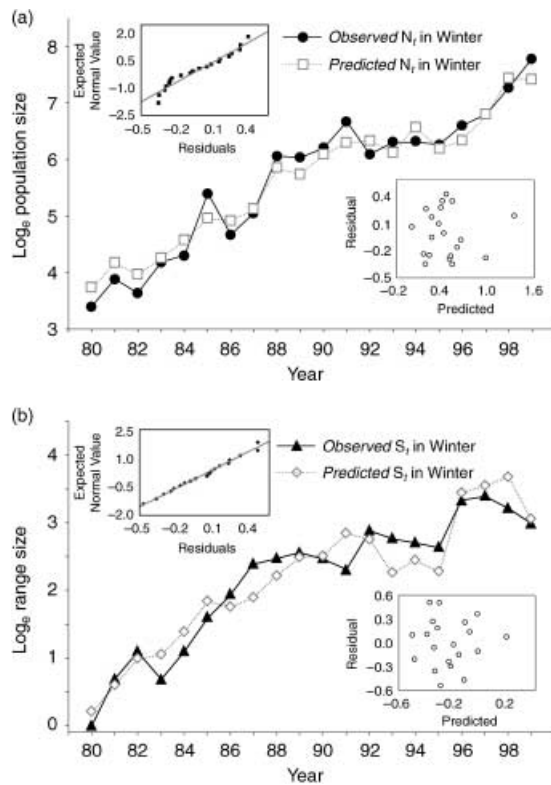
Fig. 4. One-step-ahead predictions and model residuals of the best models selected by the AICc for (a) numeric brood recruitment and (b) spatial brood recruitment. Main graphs shows the wintering population (a) and range size (b) predicted by breeding density and rainfall (open symbols), and the observed values (closed symbols) on a logarithmic scale. Within each graph, upper left panel shows the quantile–quantile plot of residuals and lower right panel shows the residual vs. predicted scatterplot; these figures allow for a qualitative probe on the adequacy of the statistical model in relation to the error variance structure (Tong 1993).

numeric and spatial brood recruitment where those for which the inclusion of demographic and sampling noise had the smallest effect (Table 3). Finally, the differences in the AICc between the models with and without the scaling terms of the error variance, suggested that the GLS-ML models were, in general, more parsimonious than the WLS models in describing the temporal dynamics of the population.

Discussion

Before discussing the results, some concerns regarding the method of scaling error variances in eqn 3a, b should be commented. Although sampling variability in population size estimates would have an effect on both the mean growth rate and its variance (e.g. Shenk *et al*. 1998; Lande *et al*. 2003), the modelling procedure used here ignores this. However, recent evidence (McNamara & Harding 2004) has shown that, besides a variance inflation effect, random sampling variability induces a negative autocorrelation (that is, a reduction in variance) in the population growth rate, and these

effects are exactly cancelled in large samples. Because the studied population has grown exponentially across time and space, it is reasonable to assume that the relative impact of demographic noise on the regional dynamics probably decreased in the same manner across the study period, with the magnitude of sampling variability increasing accordingly; this would result in a long-term stationary variance of the growth rate and hence in a similar effect to that observed by McNamara & Harding (2004). However, given its relevance, this is a subject deserving further study (P. Almaraz & J. A. Amat, unpublished work).

A common problem in studies on the demographic behaviour of increasing waterfowl populations (e.g. Cooch *et al*. 1989; Fox *et al*. 1989) is that the spatial distribution of bird numbers is largely ignored (Newton 1998). However, by using 20 years' seasonal data on the numeric and spatial expansion of a threatened bird, this problem has been largely circumvented here. Somewhat unexpectedly, this study has shown that the spatial and numeric dynamic patterns were largely uncoupled, even though a positive relationship was evident between range and population size through time. Thus, different biological mechanisms should produce the patterns observed. On one hand, the modelling revealed a direct statistical density-dependent signal on numeric recruitment of broods; because both density and frequency of territorial males peak from June to August in this population (Amat & Sánchez 1982), and given that adult male density correlates highly with total density ($r = 0.930$, $P < 0.0001$, $n = 40$), a reduction in brood recruitment through territorial behaviour (Johnson *et al*. 1992; Newton 1998) is the probable demographic mechanism behind the density-dependent signal (performing the analysis with adult male density instead of total density (not shown) yielded identical results). Whether this decline is due to a reduced overall brood production or to a higher brood mortality cannot be inferred directly from our data; nevertheless, the long-term average fledgling survival of the white-headed duck in the Iberian Peninsula during the last 20 years (0·67, $n = 870$ broods; P. Almaraz & J. A. Amat, unpublished work) is above the values reported for most waterfowl taxa (0·4–0·6; Johnson *et al*. 1992), so a reduction in overall brood production is probably the main cause of reduced brood recruitment. Thus, given the strong territorial behaviour of male white-headed ducks during breeding (Amat & Sánchez 1982; Green & Hughes 2001), an increase in the proportion of non-breeding birds with increasing density (Newton 1998) is the probable mechanism behind reduced overall brood production; this is consistent with the observation that most of the seasonal growth rates from breeding to wintering are positive (Fig. 3a), ruling out the possibility for a density-dependent mortality process to impact significantly on the dynamics. Additionally, these results are also consistent with both observational (Hill 1984; Kaminski & Gluesing 1986) and experimental evidence (Sjöberg

et al. 2000), suggesting that brood recruitment might be a density-dependent process in some waterfowl populations. On the other hand, wintering population density exerted a positive effect on subsequent spatial expansion during breeding. Social interactions during wintering (Amat & Sánchez 1982) are a possible explanation for this density-dependent signal on spatial dynamics. This kind of interaction seems to be important for waterfowl dispersal and population dynamics (Nichols 1996), but little empirical evidence currently exists on this topic (Nichols 1996; Newton 1998).

The non-linear effect of rainfall on numeric growth rate implies that precipitation during the annual drought period (the summer, July/August; Fig. 2) was a key determinant of breeding dynamics during the following year. As peak emergence of white-headed duck broods takes place from June to August in Spain (Green & Hughes 2001), summer climatic conditions seem to affect subsequent brood recruitment to the population in a lagged way. Summer rainfall is limited throughout the breeding range of the white-headed duck in the Iberian Peninsula (Casado & Montes 1995; Capel 2000; see also Fig. 2), so enhanced food availability and /or quality during wet summers may have a strong positive impact on chick development. We speculate that favourable abiotic conditions during this period can advance breeding maturity in this species, as observed in other taxa (Johnson *et al*. 1992); indeed, Green & Hughes (2001) suggest that the white-headed duck is able to breed during its first year, although the proportion of birds doing so in nature is unknown. Hence, this would be the signature of a cohort effect (Beckerman *et al*. 2002) operating through the early environment experienced by fledglings. In contrast, rainfall during the annual wet period (November/ December) had a direct and positive effect on spatial expansion from breeding to wintering. Most of the endorheic wetlands in southern Spain drop in water levels during late summer (Casado & Montes 1995), so habitat availability becomes limiting for the white-headed duck throughout this period. However, most of these wetlands become available again in the late fall and early winter (the Spanish rainy season); therefore, an increase in rainfall during this period should enhance the amount of potential wintering habitat for the species (see, e.g. Krivenko 1990).

The relationship between wetlands availability and population size is a general pattern in waterfowl (Kaminski & Gluesing 1986; Miller & Duncan 1999; see Newton 1998 for a review); habitat availability is indeed highly dependent on rainfall levels, and this has large effects on long-term population abundance across several waterbird taxa (e.g. Kaminski & Gluesing 1986; Bayliss 1989; Fox *et al*. 1989; Krivenko 1990; Newton 1998; Miller & Duncan 1999). Nevertheless, untangling the factors affecting the long-term dynamics of the numeric abundance is not trivial. In this sense, the present study has several important implications. First, although macroecological theory predicts

a relationship between spatial and numerical dynamics in species with expanding range boundaries (Gaston 2003) the present papers suggest that this need not be the case when complex regulation drives the dynamics of territorial species inhabiting patchy habitats. Secondly, a spatially implicit measure of population density detected a robust density-dependent signal in a non-stationary population. That is, although in the long term the white-headed duck expanded in a density-independent fashion (Turchin 2003), the seasonal modelling further uncovered complex short-term effects of population density and climate on the numeric dynamics; and thirdly, our data suggest that seasonality might be a key process during the multi-annual dynamics of waterfowl populations, as it is for rodents (Leirs *et al*. 1997; Lewellen & Vessey 1998; Stenseth *et al*. 2003; see also Barbraud & Weimerskirch 2003 for an example with a bird population). However, only long-term population and demographic data and new modelling approaches taking into account measurement error and process noise (Stenseth *et al*. 2003; Sæther *et al*., in press) may allow us to assess to what extent this conclusion applies to other populations.

Acknowledgements

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